Appendix M-2

Center for Biological Diversity References (Comment Letter O-9)

COMPREHENSIVE MULTI-SPECIES CONNECTIVITY ASSESSMENT AND PLANNING FOR THE HIGHWAY 67 REGION OF SAN DIEGO COUNTY, CALIFORNIA

SAN DIEGO STATE
UNIVERSITY

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LIST OF ACRONYMS AND ABBREVIATIONS

AWDT – Average Weekday Daily Traffic

BISON – Biodiversity Information Serving Our Nation

Caltrans – California Department of Transportation

CDFW – California Department of Fish and Wildlife

CEHC – California Essential Habitats Connectivity Plan

CFWO – Carlsbad Fish and Wildlife Office

CMSP – Connectivity Management Strategic Plan

CNLM – Center for Natural Lands Management

EHL – Endangered Habitats League

FLCP – Factorial Least Cost Path

GBIF – Global Biodiversity Information Facility

IEMM – Institute for Ecological Monitoring and Management

MCB – Marine Corps Base

MHCP – Multiple Habitats Conservation Plan

MOM – Master Occurrence Matrix Database

MSCP – Multiple Species Conservation Plan

MSPA – Management Strategic Plan Area

MSP – Management Strategic Plan

NCCP – Natural Community Conservation Plan

SANDAG – San Diego Association of Governments

SDMMP – San Diego Management and Monitoring Program

SDSU – San Diego State University

SR – State Route

TNC – The Nature Conservancy

USFWS – United States Fish and Wildlife Service

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EXECUTIVE SUMMARY

Through a comprehensive, multi-species connectivity analysis using robust analytical approaches, we created a connectivity plan, tools to facilitate the implementation of this plan, and a wildlife crossing infrastructure plan for key roadways in our study area. Through this data-driven approach, we:

- Assembled a multi-species connectivity analysis using a suite of data types and species complemented by a landscape-focused land facet analysis
- Analyzed a suite of data types using cutting-edge analytical techniques appropriate to each data type
- Leveraged survey and monitoring data from our study region, producing a data-informed connectivity plan without the collection of any new field data
- Identified and mapped 12 spatially-explicit focal species corridor segments and one land facet corridor to facilitate wildlife movement within the SR-67 region of San Diego's Multiple Species Conservation Plan area
- Assessed the potential functionality of those corridors for additional species including five federally listed species and 13 other species of interest
- Attributed those spatially-explicit corridors with data on land conservation status, biological variables, and threats and stressors to inform decision-making
- Created a decision support tool for scoring potential acquisitions, habitat restoration projects, or other land management and planning decisions
- Used our connectivity models, species data, site specific information, and previously collected data on crossing use and roadkill to inform wildlife crossing infrastructure recommendations for SR-67 as well as other roadways within our analysis area
- Worked with a variety of stakeholders throughout this process to gather information, feedback, and key input to generate a connectivity plan and conservation tool that could readily be implemented by the diverse range of land management and planning entities working in this region of San Diego County

INTRODUCTION

Importance of Connectivity

Habitat fragmentation and degradation are two of the greatest threats to habitat availability and quality, posing a direct risk to species' persistence and consequently, to biodiversity. As anthropogenic features such as roads and housing developments alter the landscape, landscape connectivity for wildlife may be reduced. Current land management plans throughout North America and Europe are designed to protect biodiversity by establishing a network of core habitat areas that are connected via corridors or linkages. The central tenet of this large-scale conservation planning is that viable populations and natural communities can be supported by a connected landscape network (Beier *et al.* 2006, Crooks and Sanjayan 2006, Boitani *et al.* 2007, Barrows *et al.* 2011), particularly as the landscape becomes altered by anthropogenic features. Landscape connectivity allows for movement among patches of suitable habitat, reduces the chance of extinction and the effects of environmental variability on small populations (Brown and Kodric-Brown 1977), and maintains gene flow between populations in patchy landscapes (Noss 1987). Connectivity also allows for more rapid recovery of populations after events such as fire and disease outbreaks. Over longer time scales, and in the face of changing abiotic conditions, connectivity may also prove critical for range shifts in response to landscape changes caused by a changing climate and altered disturbance regimes (Hannah *et al.* 2002, Heller and Zavaleta 2009).

Roadways in particular pose a significant challenge to landscape functioning (Laurence and Balmford 2013). Though roads can have many negative indirect effects on wildlife, two mechanisms directly impact habitat suitability and continuity (Fahrig and Rytwinski 2009): the *barrier effect* whereby the road blocks species' movement across the landscape, and *direct mortality* through wildlife-vehicle collisions (Bissonette 2002). The degree of impact of a road may depend on several factors such as the location of the road relative to open space and protected habitats, traffic volume and traffic speed (Fahrig *et al.* 1995), and the sensitivity of species affected by the road. Although many conservation network plans acknowledge the negative effects roads can have on connectivity, few have thoroughly assessed and developed approaches to mitigate barrier and mortality effects of roads that fall within ecological networks.

San Diego County Preserve Network and State Route 67

In southern California, the landscape-scale network approach has been adopted in response to the widespread habitat conversion and fragmentation that has resulted from development in the region (Riverside County 2003, County of San Diego 1998). Specifically, in San Diego County, there are a number of public and private conservations plans and ecological networks, including the San Diego Multiple Species Conservation Program (MSCP) and Multiple Habitats Conservation Program (MHCP), that were designed to create an interconnected preserve system. The overarching goal of these plans is to preserve the biological diversity of San Diego County through the conservation and management of functional habitats and linkages[1,2,3]. In January

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[1] Management Goals and Objectives (Section 1.51, p.49-50) under the Framework Management section of the San Diego MSCP Plan identify viability of ecosystem function and processes, long-term persistence of populations, functional habitats and linkages, as well as ability to adapt to changing circumstances as key goals of the plan.

[2] Poway Sub-Area Plan (SAP) p. 2-10 identifies two regional wildlife corridors through Poway and into adjoining jurisdictions, one of which is bisected by SR-67 study area.

2011, the Connectivity Monitoring Strategic Plan (CMSP) for the San Diego Preserve System was drafted. One of the primary objectives for connectivity management identified in the CMSP was to "inform adaptive management and other conservation actions by identifying important movement areas/chokepoints between cores for various species."[4] Based on the findings from previous research, as well as the initial studies conducted to meet the Priority Objectives in the CMSP, State Route (SR)-67 was named as one of the primary barriers to wildlife movement and connectivity in the MSCP and MHCP areas. The identification of SR-67 as a major threat/stressor was reiterated in the 2013 Management Strategic Plan (MSP)[5] for the MSCP area, which prioritized further connectivity research in the vicinity of SR-67 and the development of a wildlife crossing infrastructure plan as a management and mitigation goal[6]. This area has also been characterized as a priority area by the California Essential Habitat Connectivity Project (CEHC, Spencer *et al.* 2010) where local-scale analyses and road crossing improvement plans were recommended prior to the development of site-specific connectivity management and enhancement goals.

Further discussions about subregional connectivity in the area were prompted by a California Department of Transportation (Caltrans) proposal for a median barrier safety project as the major widening and highway improvement project that is expected to occur within the next 20 to 30 years. These projects may further challenge wildlife movement, but they also provide opportunities to make significant improvements to wildlife connectivity. Although the widening of SR-67 may not be initiated until 2040, a comprehensive, data-driven assessment is necessary to facilitate conservation planning in the interim. This planning will ensure acquisitions, habitat restoration, and management actions to establish a functionally connected landscape can progress towards a strategy that will support viable wildlife populations in perpetuity.

Multi-species Connectivity Planning for SR-67

In response to this need for data on wildlife movement along SR-67, The Institute for Ecological Monitoring and Management at San Diego State University (SDSU) has conducted a multi-faceted research project to examine connectivity across SR-67 and to preserve or improve existing crossings through identifying functioning crossing features along the highway. This assessment leverages previously collected telemetry, occurrence, camera, and road-kill data to conduct a multi-species comprehensive connectivity assessment for the SR-67 region. The goal of this project was to provide a data-driven analysis that would inform connectivity planning for the area. Our ultimate objective with this research was to improve functional connectivity of the SR-67 area and increase permeability of the roadway through installation of larger and appropriately-sited crossing structures. The analysis and data products produced during this project are intended to promote proactive conservation efforts within an area of the MSCP that has frequently been cited as a major threat to wildlife movement. One of the main objectives was to develop recommendations for improving connectivity across SR-67 and to preserve habitat and wildlife corridors adjacent to SR-67 prior to the initiation of any road development or improvement. This synthesis of data will facilitate the management of healthy wildlife

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[3] Poway SAP p. 3-2 highlights the needs to maintain functional connectivity within Poway as well as between Poway and adjoining jurisdictions.

[4] CMSP, p.5

[5] MSP, Volume 1, p. 2-2

[6] MSP, Volume 2, p. 4-31

populations within the MSPA by providing data-driven recommendations that can be used to take immediate action to improve landscape connectivity in the SR-67 area, and can serve as a template in other regions of San Diego's NCCP plans faced with limited connectivity caused by roadways.

Connectivity is often considered from two different perspectives, physical and functional connectivity. *Physical connectivity* indicates whether there is structure connecting two patches of habitat, whereas *functional connectivity* accounts for how wildlife respond to that structure and the implications of those considerations for the species of concern (Taylor *et al.* 1993, Tischendorf and Fahrig 2000a, 2000b). The distinction between physical connectivity and functional connectivity in fragmented landscapes is critical when implementing conservation and mitigation measures to prevent irreversible habitat fragmentation. There are a variety of factors that can affect this response, including but not limited to, life history traits of the affected species, habitat configuration, degree of habitat fragmentation, and type of fragmenting features (*e.g.*, roads, houses). Furthermore, this response will differ among species with some demonstrating a greater sensitivity to these factors than others. Quantifying or assessing landscape connectivity, however, is non-trivial (Fagan and Calabrese 2006) given the context-dependent nature of connectivity (Crooks and Sanjayan 2006) and the expense and effort of acquiring movement data for species of interest. Currently, one of the primary barriers to conducting data-driven connectivity analyses is the general lack of knowledge of how animals are currently using the landscape, and how landscape use changes in response to dynamic landscape processes over time. For this reason, one of the other main objectives of this research was to identify approaches for data synthesis that would allow us to leverage the existing data that had been collected during monitoring and management activities in San Diego's preserve network. We investigated a range of analytical techniques that would support a robust, comprehensive, data-driven study using cutting-edge methodologies to assess and map connectivity that were appropriate for the species-specific types of data that were available.

To fully assess connectivity throughout the portion of the preserve network surrounding SR-67 and provide clear, implementable actions to achieve the desired status of landscape connectivity, we carried out a two-phased project. Phase I focused on the collection, organization, and analysis of available data for a suite of focal species as well as comprehensive mapping of corridors. In Phase II, we utilized the data and resulting maps generated in Phase I to develop spatially-explicit corridors attributed with relevant management data that was linked to the Management Strategic Plan for the preserve network (Figure 1) as well as a wildlife infrastructure improvement plan for improving permeability of SR-67 and other roadways in the study area. This detailed infrastructure plan for the roadway identifies recommendations for improvements that can be made prior to the anticipated widening as well as the major wildlife infrastructure repairs and replacement that would take place during widening. Phase II products were developed in cooperation with land managers, conservation planners, Caltrans, and other stakeholders in the region.

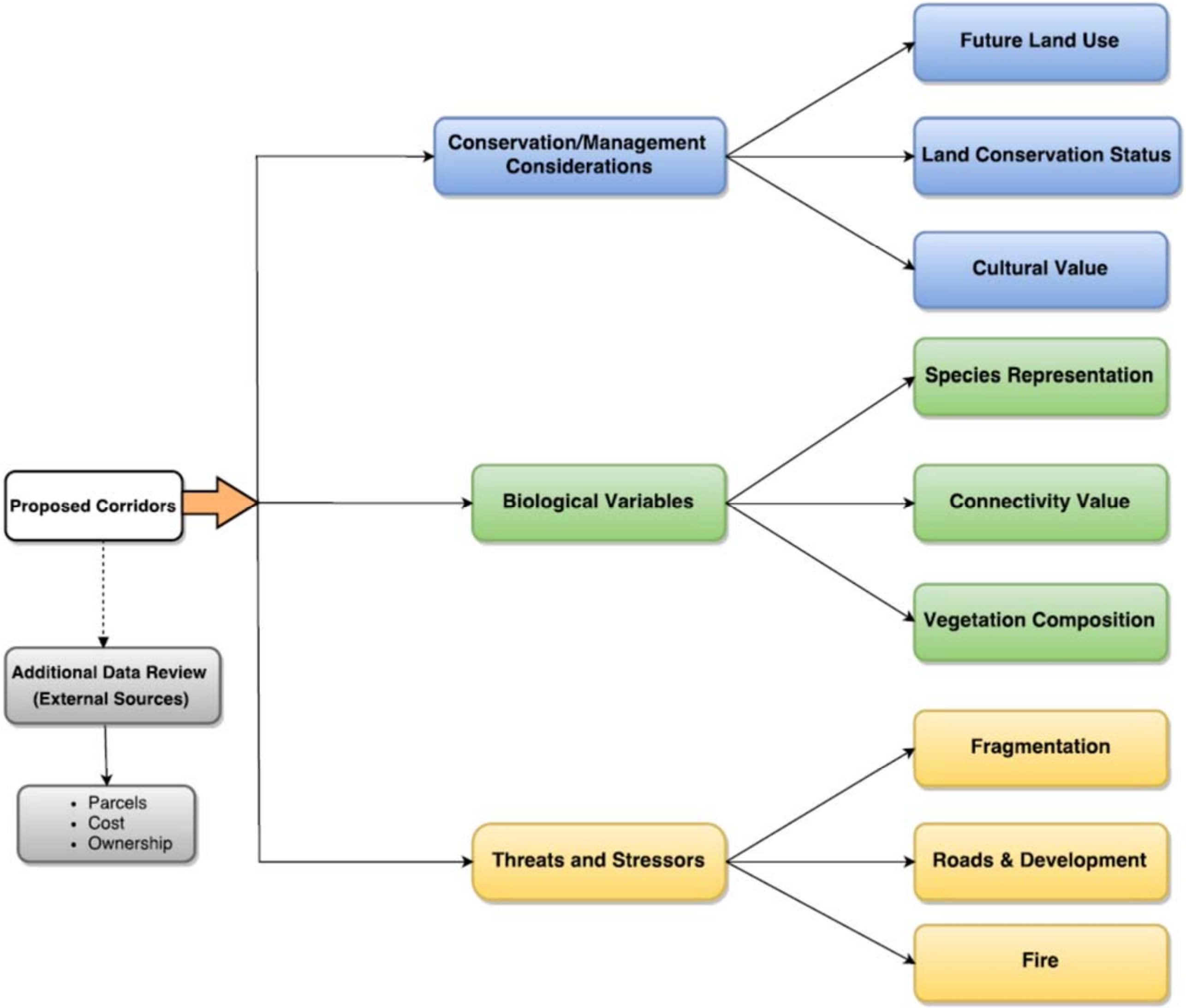


Figure 1. The corridor attribution guide developed for this project illustrates the three main categories of attributes as well as example data types for each.

The data integration, compilation, and analysis were used to inform the development of specific data products for this project:

Phase I – Data synthesis, analysis, and corridor mapping

- Habitat suitability surfaces for all focal species
- Probability of movement and landscape genetic surfaces for selected focal species
- Resistance surfaces for all focal species
- Connectivity flow for all focal species

Phase II – Identification and prioritization of management actions

- Spatially-explicit corridors and corridor attributes
- Decision support guide for using corridor criteria in decision making
- Infrastructure placement and design for wildlife road crossings

Stakeholder Coordination

A key component to the development of the geospatial and data products we produced for this project was stakeholder engagement. Since the inception of this project, we have coordinated with stakeholders to ensure we had as much information as possible on prior and current research that could inform our assessment. Based on this input, we have worked to identify any opportunities to leverage existing data and efforts of other projects. We also worked to share our findings during the course of this project with other researchers, planners, and land managers to facilitate wildlife and connectivity management in this region of San Diego County. Through these engagement sessions, we gathered information that allowed us to create actionable science and decision support tools that would allow end users to integrate the SR-67 connectivity implementation plan into ongoing efforts.

The process of stakeholder engagement began before this project started, in September 2014. That initial meeting, which served as a platform for information-sharing and coordination of research and planning activities involving SR-67, allowed us to fully form the research proposal for this project. Once we officially kicked off the SR-67 Multi-species Connectivity Planning Project in March 2016, we broadened our stakeholder outreach, eventually contacting 55 stakeholders from 19 organizations (Table F1). Our outreach and engagement sessions included three types of meeting formats: 1) full stakeholder meetings for all interested parties, 2) focused engagement sessions with small groups of experts in planning and management, and 3) one-on-one sessions with individual researchers or species experts. During the project period, we convened three stakeholder meetings of our full group, three focused engagement sessions with small groups, and numerous feedback sessions with experts at several stages of the project. Details on each of the engagement sessions as well as agendas, notes, and attendee lists from these meetings are included in Appendix F.

Through this engagement process, we have been able to hone and refine our analyses and data products in ways that will best serve the end users of our products. The requests and suggestions we received during our feedback sessions not only improved our data products and recommendations, but also have allowed our stakeholders to envision using these data products and influence their design and delivery.

METHODS

Study Area

The study was conducted within the San Diego Multiple Species Conservation Plan Area and a portion of the Draft North County Multiple Species Conservation Plan Area in southern California. This project was focused on areas surrounding SR-67 in central San Diego County between Mapleview Rd. in Lakeside and Etcheverry Street in Ramona, CA. The natural habitats and protected open space in the area are primarily publicly owned, and include Sycamore Canyon and Goodan Ranch Preserves, Boulder Oaks Preserve, San Vicente Highlands Preserve, Iron Mountain, Ramona Grasslands Preserve, San Dieguito River Park lands, and a portion of the Cleveland National Forest in the eastern portion of the study area. The analysis area included ~54,000 hectares (~133,500 acres) within the region identified as Management Unit 4 in the MSP area. Beyond the roadway, we evaluated connectivity based on previous data collected in MSCP core preserves 5, 6, 12, and 13 (Figure 2).

Elevation across the study site ranged from 58 meters (m) in the western section of the San Diego River and 1,110 m at the highest point of the study area, El Cajon Mountain. Vegetation types in the study area varied with elevation and proximity to the roadway. Habitat types in the study area varied with both elevation and distance from the coast, but was predominantly a shrubland ecosystem. Habitats across these areas included coastal sage scrub dominated by California sagebrush (*Artemesia californica*), chaparral habitat types generally dominated by scrub oak (*Quercus berberidifolia*), ceanothus (*Ceanothus* sp.), or chamise (*Adenostoma fasciculatum*), oak woodland with coast live oak (*Quercus agrifolia*), grasslands dominated by non-native annual grasses, riparian zones with an oak *(Quercus agrifolia*) or sycamore (*Platanus racemosa*) overstory and herbaceous understory, as well as urban and altered areas. Sections of the study area within the highway right-of-way and near industrial and urbanized areas near both Ramona and Lakeside were dominated by a mix of non-native plants (*e.g.*, *Bromus* spp., *Avena*, spp., *Centaurea melitensis*, and *Ricinus communis*), and barren or sparse areas, interspersed with coastal sage scrub and chaparral. The Mediterranean-climate of the study region is characterized by hot, dry summers and mild, wet winters with precipitation often less than 300 millimeters (mm).

State Route 67 is a highway that runs north and south for a distance of 24.38 miles from its southern terminus at Interstate 8 in El Cajon, CA to its northern end at the intersection of SR-78 in Ramona, CA. The highway is a four-lane divided freeway from El Cajon to Lakeside, CA, where it becomes an undivided highway ranging from two to four lanes. In 2008, traffic volumes on this section of highway ranged from 23,400 Average Weekday Daily Traffic (AWDT) to 26,600 AWDT. Expanding development in the backcountry of San Diego County has led to increasing traffic volumes on the road, which has in turn, added to traffic congestion. In addition, the speed at which vehicles are traveling on the highway has increased over the last decade, resulting in a number of severe and/or fatal collisions creating concerns for human. The convergence of a heavily traveled roadway bisecting the natural habitats along SR-67 has also led to a concurrent concern about safe road crossings for wildlife and wildlife-vehicle collisions, which we examined in this assessment.

Data Synthesis

To identify road crossings and assess landscape-level corridors across the study area, we (1) identified focal species and available data for those species, (2) ran spatially-explicit models to estimate habitat use and resistance to movement across the study area for each species, (3) modeled connectivity and road crossing locations for each species, and (4) combined results across species. San Diego County was the study area extent used to develop species habitat use, movement, and landscape genetic models. The connectivity and road crossing analyses were conducted in the SR-67 study area, described above and included a buffer to account for possible edge effects produced by the models (Figure 2). We used corridor attributes as the basis for a conservation decision-support tool and the road crossing attributes to prioritize crossing locations and provide wildlife-specific recommendations for the wildlife infrastructure plan. Methodological approaches are summarized below and detailed methods are provided in Appendix B.

Focal Species and Environmental Variables

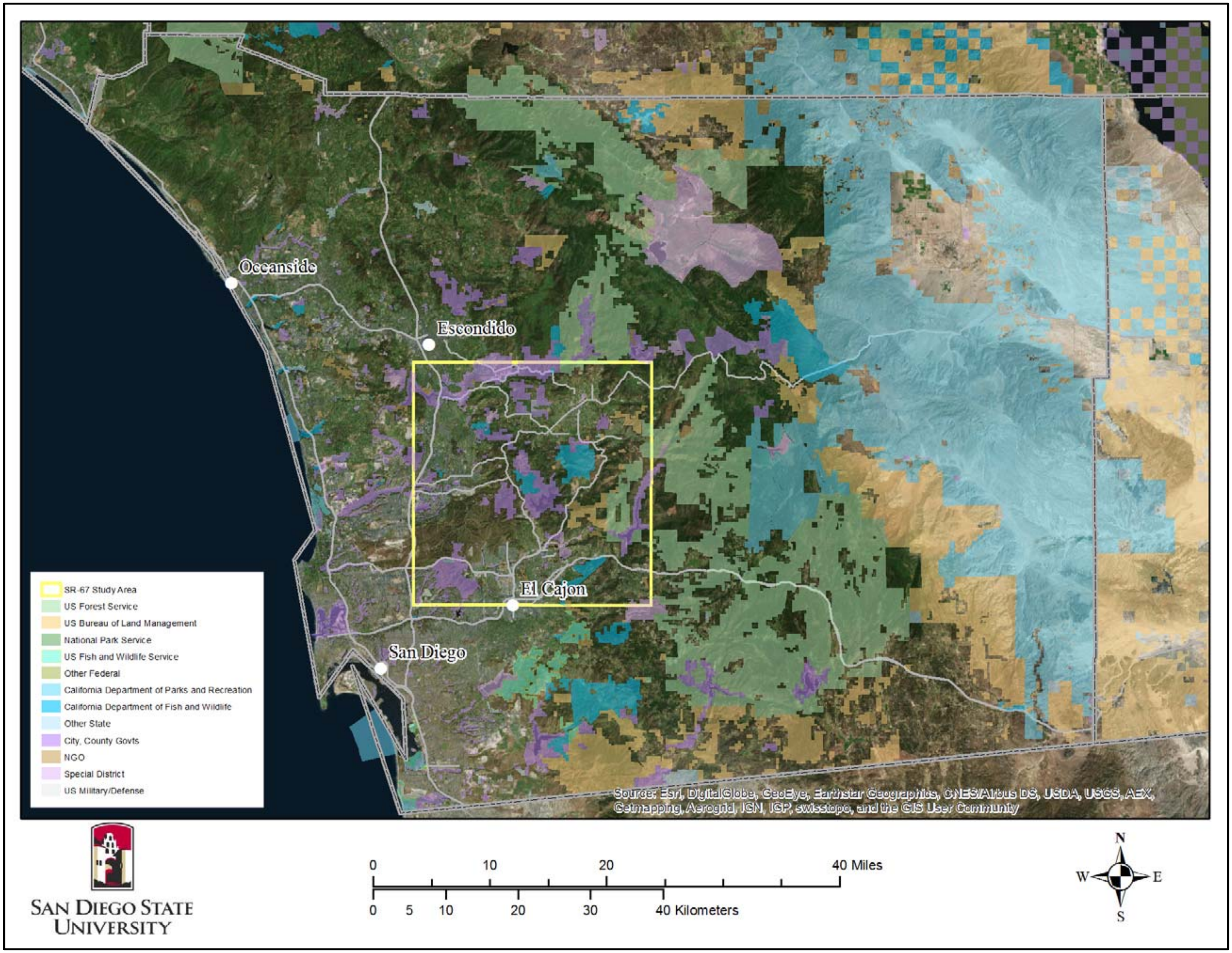
Through stakeholder input and discussions with local biologists, we identified a number of focal species for this analysis. This initial list was narrowed to nine species that had adequate data for analysis and represented a wide range of movement abilities and habitat requirements. Species and data sources are listed in Table 1.

We used environmental variables thought to affect habitat use and movement for the focal species. These included topographic, land cover, water, and human development variables (Table 2). These environmental variables were used for all species except for puma. The puma models were mostly developed during previous research in collaboration with Drs. Winston Vickers and Walter Boyce at the University of California – Davis, Karen C. Drayer Wildlife Health Center Southern California Mountain Lion Project.

Before running the models, we smoothed each environmental variable using various smoothing factors to capture the appropriate scale, or zone of influence for each variable for each species. We ran all our models for each variable at each scale and selected the scale for each variable that resulted in the best model performance for each species.

Habitat use and resistance modeling

For species with occurrence points, we combined occurrence points with the environmental variables to develop ensemble Species Distribution Models (SDMs, Araujo and New 2007, Grenouillet *et al.* 2011). These SDMs were used to predict habitat suitability across San Diego County. We assumed areas with a high habitat suitability would have a low resistance to movement and areas with a low habitat suitability would have a high resistance to movement. Therefore we used a non-linear inverse transformation to convert habitat suitability to resistance for each species.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2. Map of SR-67 study area, depicted in yellow box within the context of San Diego County's network of conserved lands.

Table 1. Focal species, available data types, data sources, and analytical models used in the analysis. Data sources are as follows: 1) San Diego Natural History Museum, *In Prep*; 2) County of San Diego 2016; 3) eBird 2016; 4) Jennings and Lewison 2013; 5) Marine Corps Base Camp Pendleton, *Unpublished Data*; 6) Center for Natural Lands Management, *Unpublished Data*; 7) San Diego Management and Monitoring Program 2016; 8) Mitelberg and Vandergast 2016; 9) Ernest *et al.* 2014 and Zeller *et al.* 2016; 10) Franklin *et al.* 2009.

Focal species ***(scientific name)***	**Data type(s)**	**Data source(s)**	**Analytical method(s)**
California mouse *(Peromyscus californicus)*	Occurrence points	SDNHM Mammal Atlas[1], SanBIOS[2]	Species Distribution Model
Big-eared woodrat *(Neotoma macrotis)*	Occurrence points	SDNHM Mammal Atlas[1], SanBIOS[2]	Species Distribution Model
Wrentit *(Chamaea fasciata)*	Occurrence points	eBIRD[3]	Species Distribution Model
Mule deer *(Odocoileus hemionus californicus)*	Occurrence points & Genetic data	SDNHM Mammal Atlas[1], SanBIOS[2], SDSU[4], MCB Camp Pendleton[5], CNLM[6], SDMMP MOM[7], USGS[8]	Species Distribution Model & Landscape genetics analysis
Bobcat *(Lynx rufus)*	GPS telemetry & genetic data	SDSU[4]	Resource and Movement Selection Functions & Landscape genetics analysis
Puma *(Puma concolor)*	GPS telemetry & genetic data	University of California, Davis[9]	Resource and Movement Selection Functions & Landscape genetics analysis
Coachwhip *(Coluber flagellum)*	Species Distribution Model	USGS[10]	Species Distribution Model
Western whiptail *(Aspidoscelis tigris)*	Species Distribution Model	USGS[10]	Species Distribution Model
Western toad *(Anaxyrus boreas)*	Species Distribution Model	USGS[10]	Species Distribution Model

For species with GPS telemetry data (puma and bobcat) we performed two analyses. First, we estimated resource use using a point selection function, which we used for estimating the relative probability of habitat use across San Diego County. Second, we estimated resource use during movement events with a path selection function (PathSF, Cushman *et al.* 2010, Zeller *et al.* 2016), which we used to estimate the relative probability of movement across San Diego County. We used the inverse of the probability of movement surfaces to estimate resistance for puma and bobcat.

For species with genetic data (puma, bobcat, and mule deer), we performed a landscape genetic analysis, which correlates the genetic distance between individuals across the landscape with the resistance distance between individuals across the landscape (Manel *et al.* 2013). This analysis estimates resistance directly so no transformation to resistance was needed. To develop the final resistance surface for species with genetic data, we multiplied the resistance surface derived from the SDM or PathSF analyses with that derived from the landscape genetic analysis and rescaled this surface from 1 – 100 (1 = low resistance and 100 = high resistance; Zeller *et al.* 2017).

Table 2. Environmental variables used in developing habitat use and resistance surfaces for each focal species.

	Variable	**Source/Derivation**	**Year**	**Citation**
Roads and Development	All Roads	Open Street Map	2014	Open Street Map 2014
	Primary roads	Open Street Map; Motorways	2014	
	Secondary roads	Open Street Map; primary road, secondary road, and trunk road	2014	
	Tertiary roads	Open Street Map; living street, residential, rest area, road, service, tertiary, and unclassified	2014	
	Unpaved roads/trails	Open Street Map; bridleway, cycleway, footway, path, and track,	2014	
	Percent Imperviousness	Derived from a hybrid of the National Land Cover Database percent impervious surface and updated data from the San Diego Association of Governments land use surface	2011/ 2012	NLCD 2011 SANDAG 2012
Topography	Elevation	National Elevation Dataset	2009	USGS 2009
	Percent Slope	Derived from National Elevation Dataset	-	-
	Terrain Ruggedness	Total curvature derived from National Elevation Dataset with DEM Surface Tools (Jenness 2013)	-	-
	Topographic Position Index	Derived from National Elevation Dataset	-	-
	Ridges	Derived from Topographic Position Index values >= 8		
	Canyons	Derived from Topographic Position Index values <=- 8		
	Steep Slope	Derived from Topographic Position Index values -8 – 8, slope >=6°		
	Gentle Slope	Derived from Topographic Position Index values -8 – 8, slope <=6°		
Water	Streams	National Hydrography Dataset streams layer	2011	USGS 2011
	Distance to Water	Derived from National Hydrography Dataset calculated as Euclidean distance to blue line streams		
Vegetation Type	Agriculture	Vegetation Data of San Diego County	2014	SANDAG 2014
	Chaparral	Vegetation Data of San Diego County	2014	SANDAG 2014
	Coastal Scrub	Vegetation Data of San Diego County	2014	SANDAG 2014
	Coniferous Forest	Vegetation Data of San Diego County	2014	SANDAG 2014
	Desert Scrub	Vegetation Data of San Diego County	2014	SANDAG 2014
	Hardwood Forest	Vegetation Data of San Diego County	2014	SANDAG 2014
	Herbaceous Grassland	Vegetation Data of San Diego County	2014	SANDAG 2014
	Riparian	Vegetation Data of San Diego County	2014	SANDAG 2014
	Sparse/Disturbed	Vegetation Data of San Diego County	2014	SANDAG 2014
	Water and Wetlands	Vegetation Data of San Diego County	2014	SANDAG 2014

A depiction of the data types and analytical methods used to estimate resistance for each species is provided in Figure 3.

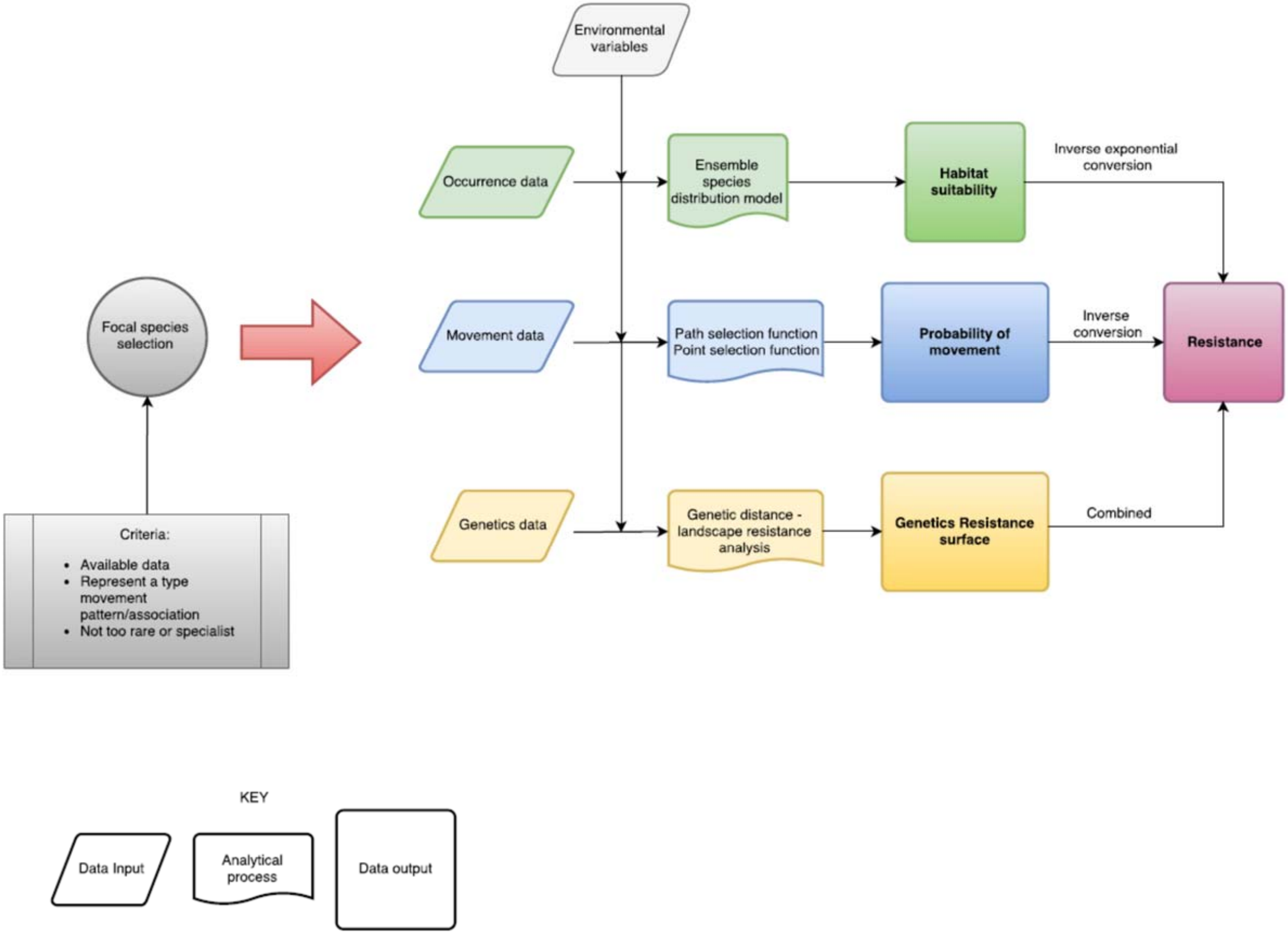


Figure 3. Analytical approaches used to develop resistance from each of the data types we had available for the multi-species connectivity planning project

We assessed the SDMs for coachwhip, western whiptail, and western toad that had been developed by Franklin *et al.* (2008) and provided by USGS. These SDMs were developed at a regional scale and at a coarse spatial resolution. Because of this, the predictive ability of these models was poor in the SR-67 study area. The input we obtained from the stakeholders confirmed that these layers were inadequate for connectivity modeling for this project. Therefore, we decided not to use these data or these species in the connectivity analysis. We did, however, use these data in the corridor attribution process.

Connectivity Modeling and Identification of Multi-species Corridors and Road Crossing Locations

Across the final resistance surface developed for each species, we identified landscape corridors using two connectivity modeling approaches; Resistant kernels (Compton *et al.* 2007) and OmniScape (McRae *et al.* 2016). Resistant kernels require the identification of source points in the study area from which connectivity is modeled. We identified 1,000 source points for each species. These points were distributed probabilistically on each habitat suitability surface so that areas with higher habitat suitability had more source points than areas with lower habitat suitability. OmniScape sources were identified as any pixel that had a resistance less than 20. To create a multi-species connectivity model, we averaged the connectivity surfaces derived from the resistant kernel analysis across all species. Discrete corridors were identified on this multi-species connectivity surface by clipping this surface to the top 30% of connectivity values (70-100% of connectivity values). These corridors were expanded slightly by including areas identified from the OmniScape analysis that enforced east-west and north-south connectivity across the study area. We divided the final corridor into 12 different sub-corridors based upon the location of protected areas and other important features on the landscape.

From this connectivity surface we also produced three additional layers that may be helpful in land management and planning; corridor isopleths, a normalized flow surface, and a corridor resiliency map. The corridor isopleths depict the top 10% of the multi-species connectivity surface (areas with the highest average connectivity across all six focal species), the top 10-20% of the connectivity surface, and the top 20-30% of the connectivity surface. The normalized flow surface shows the connectivity surface in terms of how concentrated or diffuse connectivity is across the study area. Areas of concentrated flow indicate naturally restricted flow, such as steep canyons, restricted flow due to human development, or a combination of these factors. Where flow is concentrated due to human development might be areas facing more imminent fragmentation threats. Normalized flow was derived by running the resistant kernel connectivity model across a uniform resistance surface (where there is no restriction of movement), and then dividing the multi-species connectivity surface by this unrestricted connectivity surface. The corridor resiliency map used a layer developed by The Nature Conservancy that depicts resiliency of areas to climate change. We multiplied this map by the multi-species connectivity surface to derive a map where high values indicate areas that are both good for connectivity and resilient to climate change.

We also conducted a Land Facet corridor analysis (Appendix E). Land Facets identify areas of similar topographic and climactic makeup. Corridors based on these land facets have been promoted as a way to ‘preserve nature’s stage’ in the face of climate change and allow for flow amongst similar topographic and climatic features (Anderson and Ferree 2010, Beier and Brost

2010). We identified 15 land facets across the study area, created resistance surfaces for each land facet, and derived corridors for each land facet using a least cost corridor analysis. Our multi-species corridor generally overlapped these land facet corridors, with the exception of one land facet composed of gentle slopes at mid-elevation with high solar insulation. This land facet encompassed grassland features across the study area, specifically, the Ramona grasslands. Because none of our focal species were associated with grasslands, we added this single land facet corridor to our final corridor layer so that grassland species were represented, bringing the total number of corridors to 13.

To identify road crossing locations, we ran Factorial Least Cost Paths (FLCPs) across our study area for each species (Cushman *et al.* 2014). FLCPs create pairwise least-cost paths between all source points on the landscape. Due to computational limitations, we reduced the number of source points to 300. We identified probable road crossing locations for each species at the intersection of FLCPs and major roadways in the study area (Cushman *et al.* 2014). These roads included SR-67 as well as SR-52, Interstate 8, Wildcat Canyon Road, Poway Road, and Scripps Poway Parkway. We conducted a point density analysis using the *Point Density Tool* in ArcGIS to determine a distance at which we could aggregate crossing locations into a single crossing zone. We determined that we had greater clustering at a distance of 300 m and created crossing zones around the largest clusters of FLCP points. We then reviewed the crossing zone locations, determined if the zone included an existing structure that could be retrofitted, and made slight placement adjustments to incorporate preexisting structures that had some level of functionality for wildlife movement.

A flow chart depicting the methodological approach for identifying corridors and road crossing locations is provided in Figure 4.

Development of Connectivity Decision Support Tool and Road Crossing Structure Recommendations

We attributed each of the 13 corridors with over 100 variables which we categorized into conservation and management variables, biological variables, and threats and stressors. Conservation and management variables included the conservation status of each corridor, future land use predictions, and cultural sites. Biological variables included attributes such as the multi-species connectivity value as well as connectivity values for each focal species, the presence of threatened and endangered species and other species of interest, and variables describing the composition and configuration of vegetation types. Threats and stressors included levels of development and fragmentation for each corridor, as well as the potential for fire.

We developed a Connectivity Decision Support Tool that incorporates parcel-level data as well as the corridor attributes described above to help managers and planners prioritize areas for acquisition and management. This tool requires planners and land managers to develop a scoring rubric that meets their mandates and can be applied consistently across decision points.

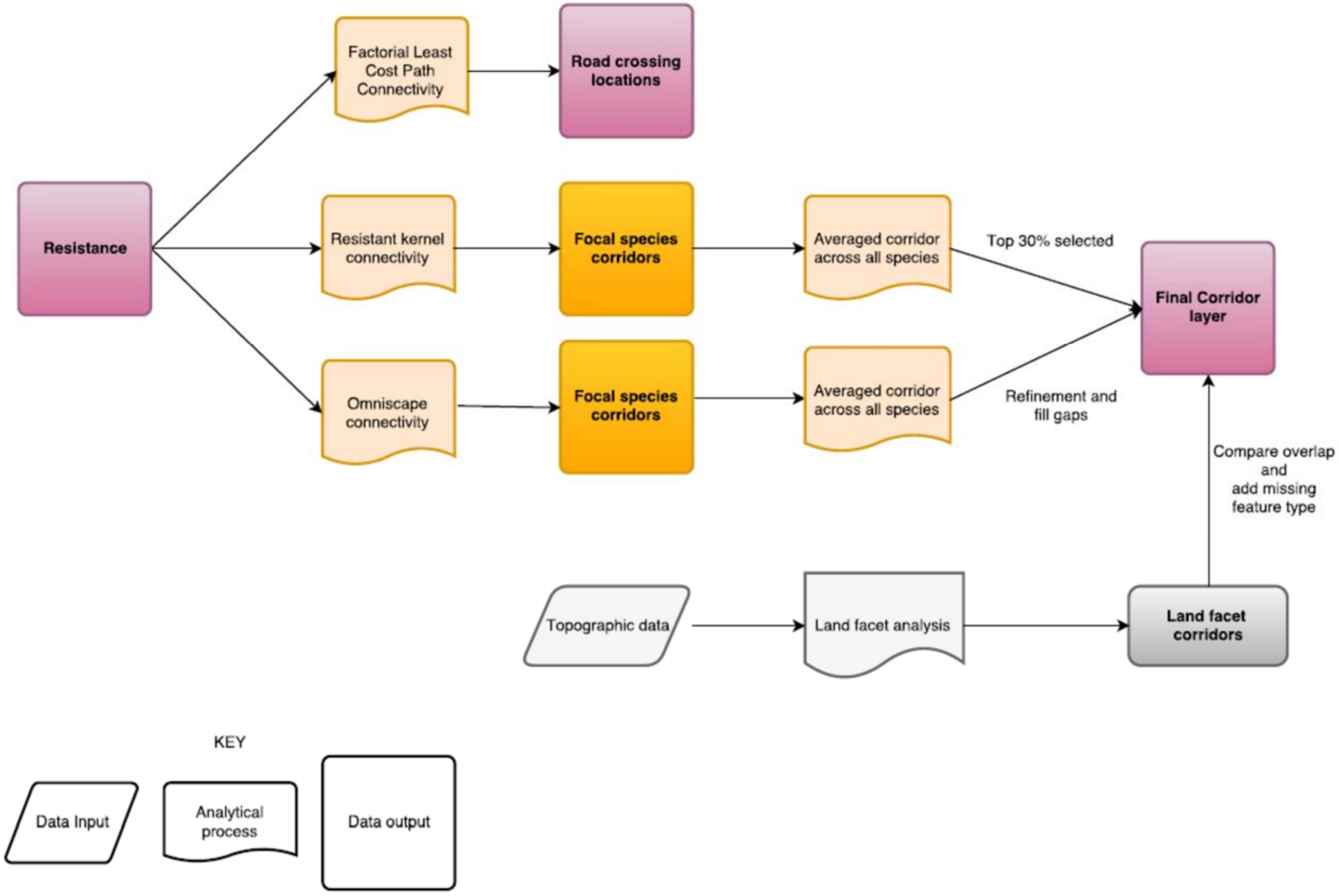


Figure 4. Flowchart of the methodological approach used to develop corridors and identify road crossing locations for the SR-67 area

Road Crossing Recommendation Process

The process we took for identifying road crossing locations and specifications was intended to generate recommendations that were optimal for supporting wildlife movement. This is the first step in the process for developing a fully scoped wildlife crossing infrastructure plan. The recommendations we present here are not cost-constrained and, although we did solicit feedback from Caltrans on our initial recommendations, further refinement will be necessary through collaboration and cooperation with a full team of Caltrans planners including engineers, hydrologists, and biologists. Once site-specific details and tradeoffs have been discussed, the final step will be to estimate costs and further refine the wildlife infrastructure plan based on the available budget.

To ensure our recommendations were appropriate and site-specific we reviewed site characteristics using terrain data, street-view in Google Earth, information from prior data collection, and location knowledge. During this process, we selected one site within each crossing zone (if there was no existing structure within the crossing zone), which we focused on for our design specifications. To identify the need for species-specific design specifications, we reviewed point location data for additional species of interest and identified which species we would want to accommodate at each structure to further inform our crossing structure design recommendations. We completed this by creating buffers around point data for our species of interest based on their dispersal abilities (Table 3). We categorized the size and type of species to be considered in the design of each structure and used a comprehensive literature review on wildlife crossing structure evaluations and guides (Appendix G) to make initial recommendations on crossing structure sizing and type. For each site, we provided recommendations on both the optimal design specifications as well as the minimum with respect to structure type and size. During our literature review, we also identified best management practices to complement the species-specific design recommendations for each crossing structure. We validated our structure recommendations with another site-specific review and added on species-specific design features to provide cover for smaller animals and to enhance connectivity for flying species. We then estimated the minimum length of fencing necessary based on the literature and site conditions to direct species towards structures and away from the roadway.

After completing a draft of these initial recommendations, we solicited input from biologists and a planner at Caltrans. Based on the input we received, we made further refinements and developed a prioritization criterion. To aid decision-making regarding wildlife crossing structure improvement, we added two prioritizations to our crossing structure recommendations. The first was focused on the importance of each site to the suite of wildlife we considered in our analyses. This includes not only the focal species we modeled, but the suite of species stakeholders requested we consider in our multi-species validation. The second prioritization was designed to allow transportation agencies to identify opportunities for near-term improvements based on whether existing crossings could be enhanced through minor alterations. These minor improvements include clearing of sediment and debris in existing crossing structures, enhancing line of sight through the structure, controlling invasive plants in areas surrounding the crossings, restoring native vegetation.

Table 3. Species considered for potential to use proposed road crossings and wildlife corridors. Data sources are as follows: 1) County of San Diego 2016; 2) San Diego Management and Monitoring Program 2016; 3) U.S. Fish and Wildlife Service 2017; 4) Marschalek; 5) BISON 2017 6) GBIF 2017; 7) San Diego Natural History Museum, *In Prep*

Species Common Name	Data source	Movement distance (m)	Movement distance reference
Quino checkerspot butterfly (*Euphydryas editha quino)*	SanBIOS[1], SDMMP[2], CFWO[3]	1,000	USFWS 2003
Arroyo toad (*Anaxyrus californicus)*	SanBIOS[1], SDMMP[2], CFWO[3]	1,082	Brehme and Fisher 2017
Cactus wren (*Campylorhynchus brunneicapillus)*	SanBIOS[1], SDMMP[2], CFWO[3]	1,590	Atwood 1997
California gnatcatcher (*Polioptila californica)*	SanBIOS[1], SDMMP[2], CFWO[3]	3,000	Mock 2004
Stephens' kangaroo rat (*Dipodomys stephensi)*	SanBIOS[1], SDMMP[2], CFWO[3]	400	Price *et al.* 1994
Hermes copper butterfly (*Lycaena hermes)*	SDSU[4], SDMMP[2]	100	Deutschman et al. 2010
Coachwhip (*Coluber flagellum)*	SanBIOS[1], BISON[5], GBIF[6]	1,618	Brehme et al., *Unpublished data*
Granite spiny lizard (*Sceloporus orcutti)*	BISON[5], GBIF[6]	91	Brehme et al., *Unpublished data*
Two-striped garter snake (*Thamnophis hammondii*)	SDMMP[2], BISON[5], GBIF[6]	239	Brehme et al., *Unpublished data*
Western toad (*Anaxyrus boreas)*	SanBIOS[1], BISON[5], GBIF[6]	1,552	Brehme et al., *Unpublished data*
Western whiptail (*Aspidoscelis tigris)*	BISON[5], GBIF[6]	300	Brehme et al., *Unpublished data*
Pallid bat (*Antrozous pallidus)*	SanBIOS[1], SDMMP[2]	2,000	Baker *et al.* 2008
Townsend's big eared bat (*Corynorhinus townsendii)*	SanBIOS[1], SDMMP[2]	10,500	Fellers and Pierson 2002
American badger (*Taxidea taxus)*	SDNHM[7]	1,450	Lindzey 2003
Ringtail (*Bassariscus astutus)*	SDNHM[7]	1,000	Lonsinger *et al.* 2015

RESULTS

Species-specific habitat suitability, resistance, and connectivity

Species-specific habitat suitability and movement models, resistance surfaces, and connectivity outputs are depicted for each of the six focal species in Appendix C. These data products and modeling outputs are available for individual species upon request.

Multi-species Connectivity and Corridor Products

The final corridor connects lands from east to west and north to south across the study area and has an area of 103,838 acres. Figure 5 displays the final multi-species connectivity surface across the study area and Figure 6 displays the final corridor product, which consists of 12 multi-species corridors and one land facet corridor. Currently 35% of the final corridor is comprised of protected lands, 9% is comprised of PAMA land, and 5% is comprised of draft PAMA lands from the Northern San Diego County MSCP. From a modeling study conducted by Butsic *et al.* (2017), we estimate that approximately 10% of the corridor is comprised of developable land (land that has not yet been developed, but has the potential to be developed in the future). Each of the 13 sub-corridors is described in detail in Appendix A.

To aid in the planning and management process, we provided additional spatial products derived from the multi-species connectivity surface: corridor isopleths (Figure 7), a normalized flow surface (Figure 8), and a corridor resiliency map (Figure 9). The normalized flow surface highlights areas of concentrated flow in the outer regions of the study area. In the northeastern part of the study area, this concentrated flow is due to natural features, however, in the northwest and the south, this concentrated flow is due to human development. Areas where flow is impeded mostly coincide with more heavily developed lands. The corridor resiliency map suggests that much of the center of the study area and corridors therein have high resilience to climate change, while corridors in the northeast and southeast of the study area have less resilience.

The conservation and management, biological, and threats and stressor attributes for each of the 13 corridors is provided in Table A1. We describe how each attribute was calculated along with the source of the data used and the minimum and maximum values across corridors. For cross-referencing purposes with the corridor GIS shape file product, we also provide the names of the shape file table that correspond with each attribute.

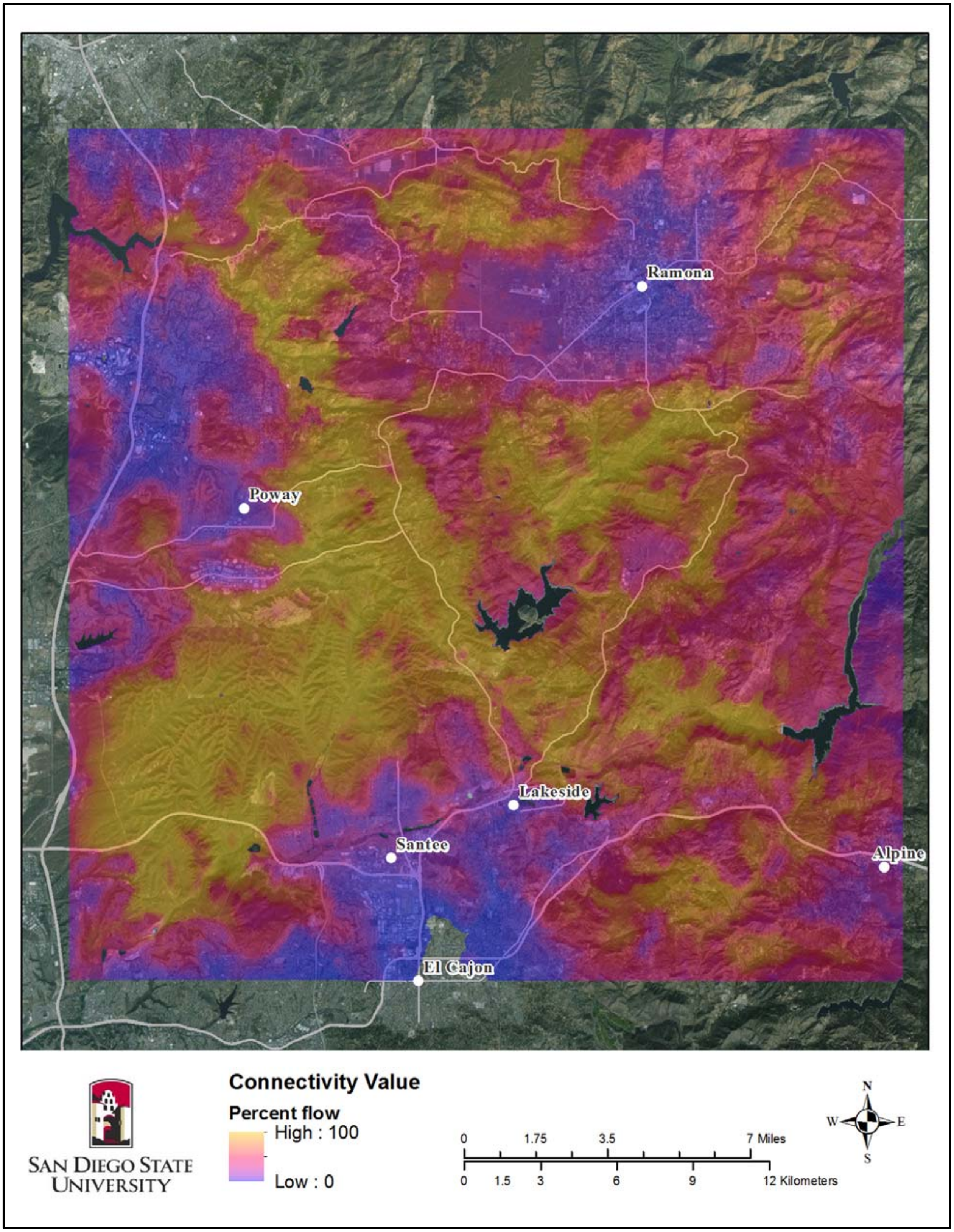


Figure 5. Multi-species connectivity value map depicts percent flow across the study area.

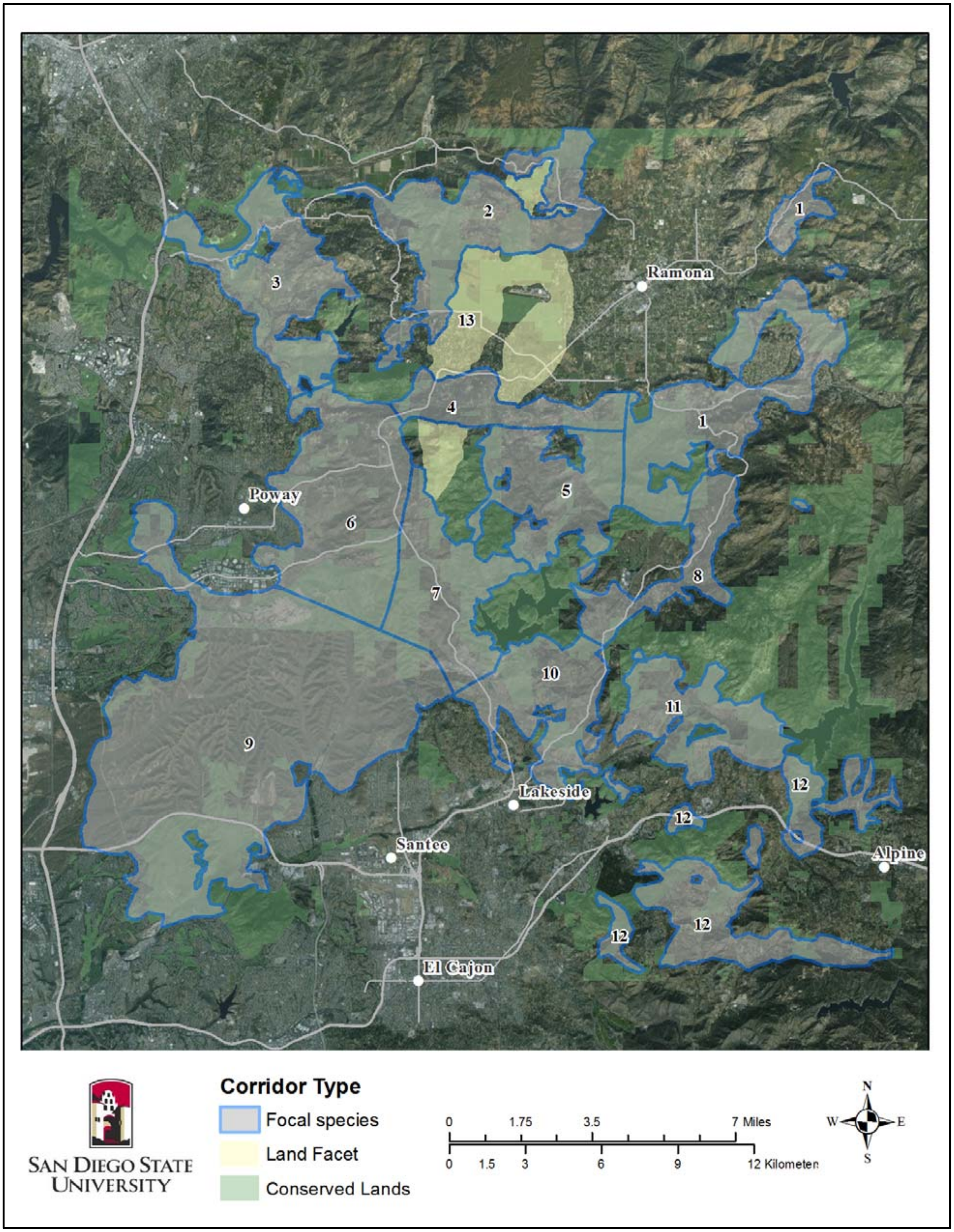


Figure 6. Final combined focal species and land facet corridor map with corridor segments labeled and conserved lands depicted.

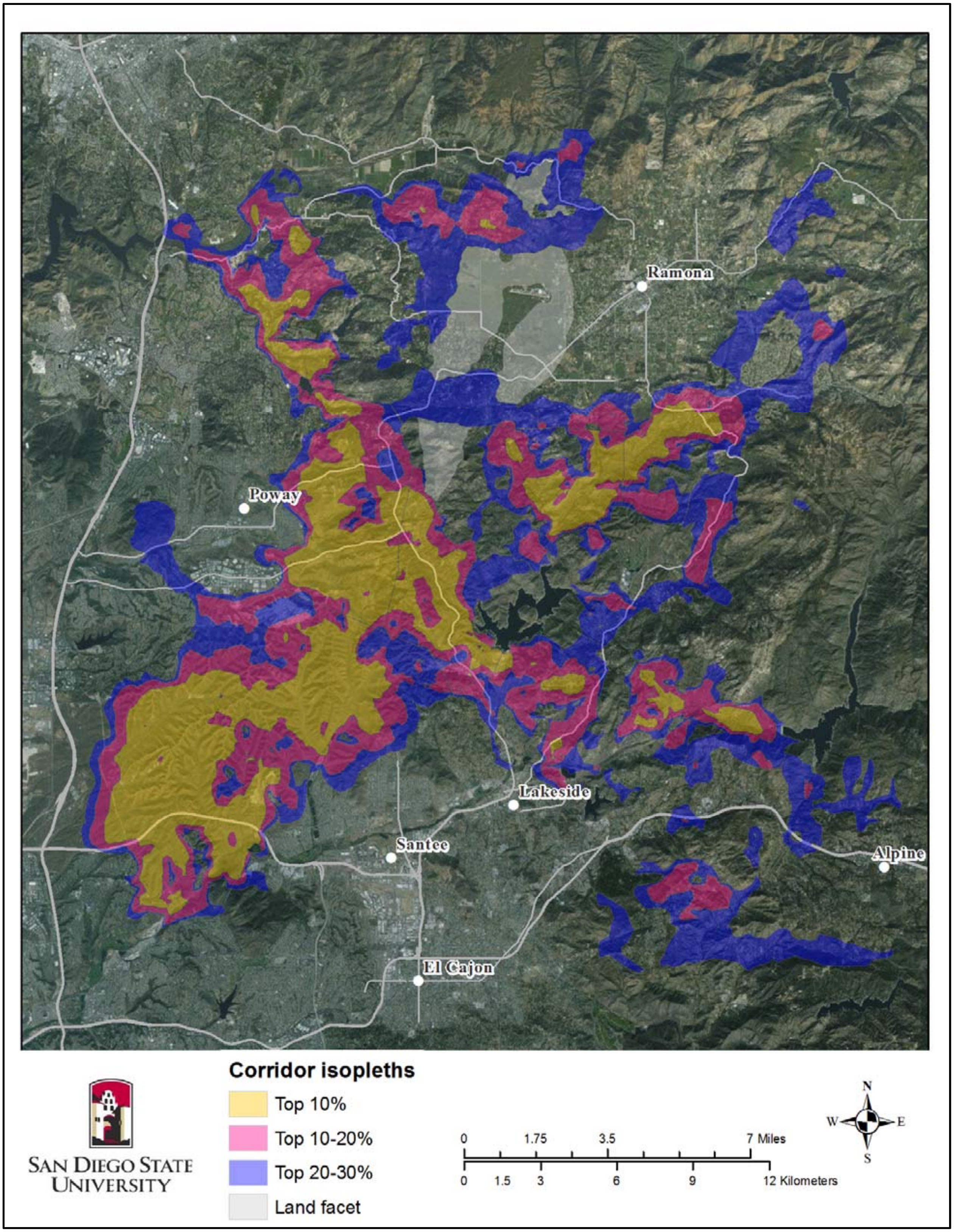


Figure 7. Map of corridor isopleths depicting each corridor broken down into the top 10%, top 10-20%, or top 20-30% of connectivity flow

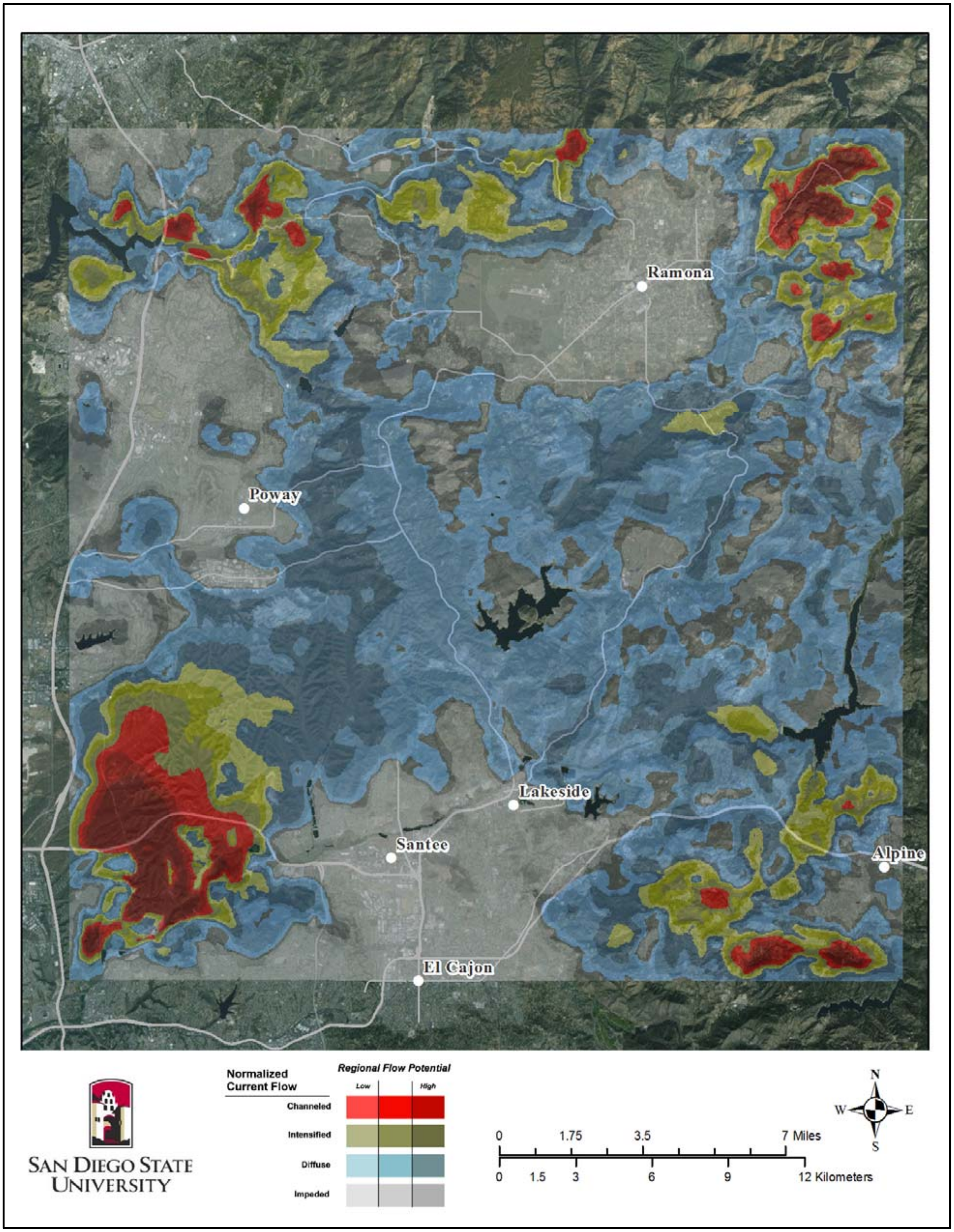


Figure 8. Normalized current flow map that depicts areas where connectivity flow is either channeled, intensified, diffuse, or impeded

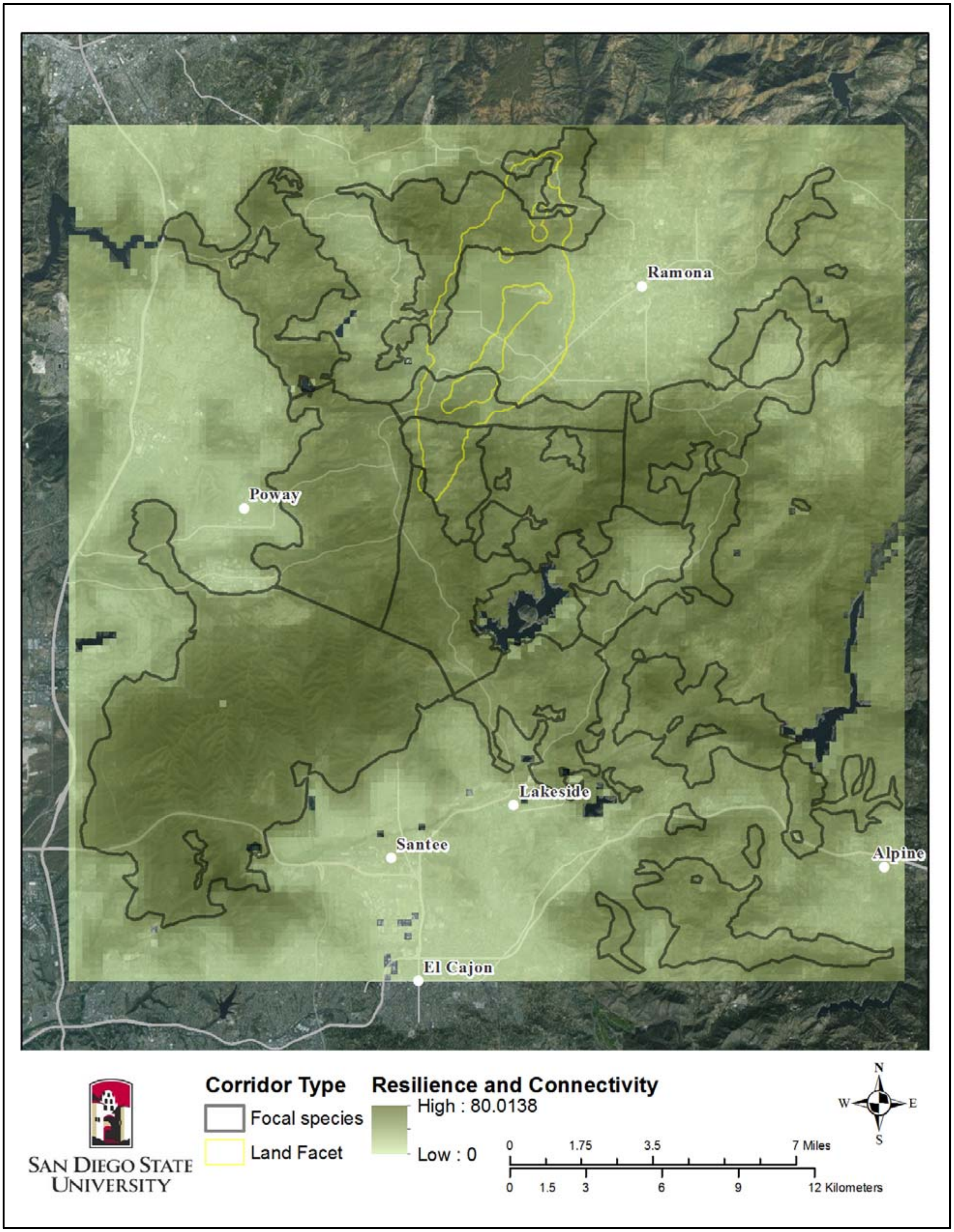


Figure 9. Map of the combined connectivity and resilience to climate change of the study area. Areas of darker green are both more resilient and provide for a greater degree of connectivity

Connectivity Decision Support Tool

The Connectivity Decision Support Tool was designed so that end users can apply a score to a parcel or management site of interest so that parcels and sites can be prioritized across a project. Figure 10 depicts decision points, assessment criteria, and where attributes of the parcel or site of interest might be assigned a score. We developed the support tool so that each land manager / planner could develop a unique scoring system that applies to their management objectives. We reiterate the importance of developing a single scoring rubric that is applied consistently across all decisions.

After identifying a parcel or site of interest, the first decision point is reached. If the site is within a corridor one may decide to move on in the scoring process. If the site is not within a corridor one may decide to examine another site. Then, one might assign a score to the site depending on which corridor isopleth that site falls within. Then, it might be helpful to look at site-specific data. For example, would acquisition be cost-prohibitive or not, what is the area of the parcel, does it fall within PAMA or draft PAMA lands, and by protecting that parcel, how much would that increase the proportion of conserved land in a corridor? Once assessing the parcel specific data, another decision point is reached and one must choose whether to proceed or not. Assuming the parcel still meets management criteria, corridor-specific scores can be applied to the conservation and management variables, biological variables, and threats and stressors of interest. The sum of all the scores results in a final compiled score for the site of interest, which can be compared with other sites for prioritization, acquisition, and management needs.

We have provided a brief example of a scoring rubric and will walk through the application of this rubric using two parcels selected in the study area (Table 4). Our example scoring criteria assigns a score from 1-5 for each variable assessed, with 5 being the best. Both example parcels are in a corridor area. Example parcel #1 is in Corridor 9 and is relatively small in size, whereas parcel #2 is in Corridor 10 and is relatively large. Following along with the Connectivity Decision Support Tool, once we deemed these parcels were in a corridor, we reached the first decision point and decided to move forward. We then noted that parcel #1 is in the middle isopleth (10-20% of the top connectivity values) while parcel #2 is in the top isopleth (the top 10% of connectivity values). We then applied scores to these parcels using our pre-determined scoring criteria. Then we assessed parcel-specific criteria and decided to move on to the corridor attributes. Once we reach this point in the Decision Support Tool, we pulled information directly from the corridor attributes table. We scored two conservation and management attributes, two Biological attributes, and two Threat and Stressors attributes. We then added up the scores for each parcel to obtain a final score. It is worth noting that there are dozens of attributes to select from in developing a scoring criteria and that this is a just a simplified example for illustrative purposes.

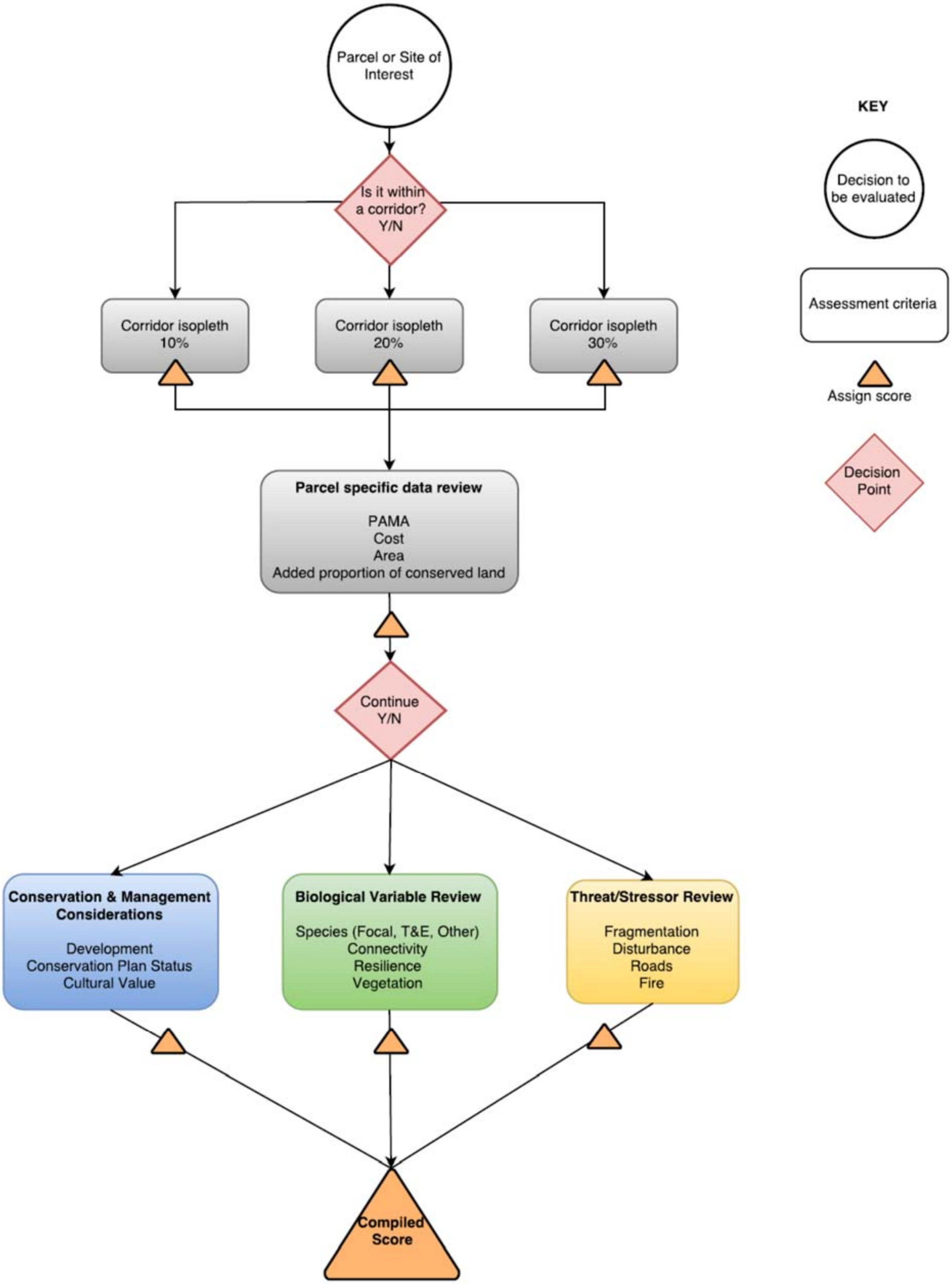


Figure 10. Diagram of the connectivity decision support tool created that depicts decision points, assessment criteria, and scoring guidance

Table 4. Example application of decision support tool to two parcels in the study area. The table provides a simplified version of how one would walk through the process of applying a scoring rubric to compare parcels. Our example scoring criteria assigns a score from 1-5 for each variable assessed, with 5 being the best.

Variable	Scoring criteria	Parcel #1 value	Parcel #1 score	Parcel #2 value	Parcel #2 score
Is it in a corridor?	Y / N	Y, Corridor 10	-	Y, Corridor 9	-
What isopleth is it in?	1 = 20 – 30 % 3 = 10 – 20% 5 = 1 – 10%	10 – 20%	3	1 – 10%	5
Parcel size	1 = small 3 = medium 5 = large	14 acres	3	240 acres	5
Proportion of corridor currently conserved	1 = 15 – 23% 2 = 23 – 31% 3 = 31 – 39% 4 = 39 – 47% 5 = 47 – 56%	30%	2	25%	2
Number of cultural sites	1 = 31 - 105 2 = 106 - 180 3 = 181 - 255 4 = 256 - 330 5 = 331 – 402	126	2	402	5
Whether Arroyo Toad has been detected in that corridor	0 = N 5 = Y	N	0	Y	5
Average multi-species connectivity value in corridor	1 = 68 - 72 2 = 73 – 77 3 = 77 – 81 4 = 81 - 85 5 = 86 – 90	86	5	81	4
Percent of corridor comprised of natural land cover types	1 = 80 - 83 2 = 83 - 86 3 = 86 - 89 4 = 89 - 92 5 = 92 – 96	80	1	89	3
Road density	1 = 6.3 - 5.5 2 = 5.5 - 4.7 3 = 4.7 – 4.0 4 = 4.0 - 3.3 5 = 3.3 - 2.6	6.29	1	5.4	2
Total Score			**17**		**31**

Wildlife Crossing Infrastructure Recommendations

Based on our initial FLCP corridors from our focal species analyses, we identified 176 potential crossing locations (Figure 11). After examining clusters of crossing points within a 300 m buffer distance, we narrowed those 176 locations down to 33 proposed road crossing zones. Of these 33 zones, 12 were along SR-67, three were on SR-52, four were on I-8, seven on Wildcat Canyon Road, one on San Vicente Road, two on Poway Road, and five on Scripps Poway Parkway. After determining whether there was already an existing structure at or near the crossing zones and attributing these with data on topography, vegetation composition, and our 17 validation species as well as our original six focal species, we performed a site-specific review and identified a proposed crossing site. If there was an existing structure at the site, we targeted it for a retrofit at the present site, otherwise we recommended new siting. At two of the locations on Scripps Poway Parkway, the topography and road cut was deemed to be prohibitive for placement of a wildlife crossing structure in the recommended zone or adjacent to it. We therefore eliminated those two locations from our final site recommendations bringing our site recommendations down to 31 locations. However, based on prior culvert monitoring data collected during an earlier study for Caltrans (Jennings and Lewison 2016), we noted that there were two existing culverts on SR-67 that were functioning for some species that were not incorporated into our initial 33 zones. We incorporated those two existing culvert locations into our proposed crossing site recommendations for a total of 33 sites (Figure 12).

On SR-67, the primary focus of our wildlife crossing infrastructure recommendations, we identified and prioritized 14 crossing sites (Table 5). All but one of these locations has an existing structure that could be retrofitted. Of those sites, six could be improved with minor effort whereas the remaining eight would require major redesign to facilitate wildlife movement. We identified four sites along the highway that were of extremely high importance to wildlife movement, six that were of high importance, and four that were of moderate importance. Sites targeted for minor improvements only fell within our high and moderate importance categories for wildlife movement. Site specific details for each of the recommendations for wildlife crossing structures on SR-67 as well as the recommendations on the other major roads in our study area can be found in Appendix B.

Based on a thorough review of the literature and input from Caltrans as well as our stakeholder group, we identified 25 best management practices to be incorporated into the wildlife infrastructure planning for SR-67 (Table 6). We classified these by the type of recommendation into seven categories related to conservation planning, design of structures, barriers, fencing, and material selection, and construction and maintenance considerations.

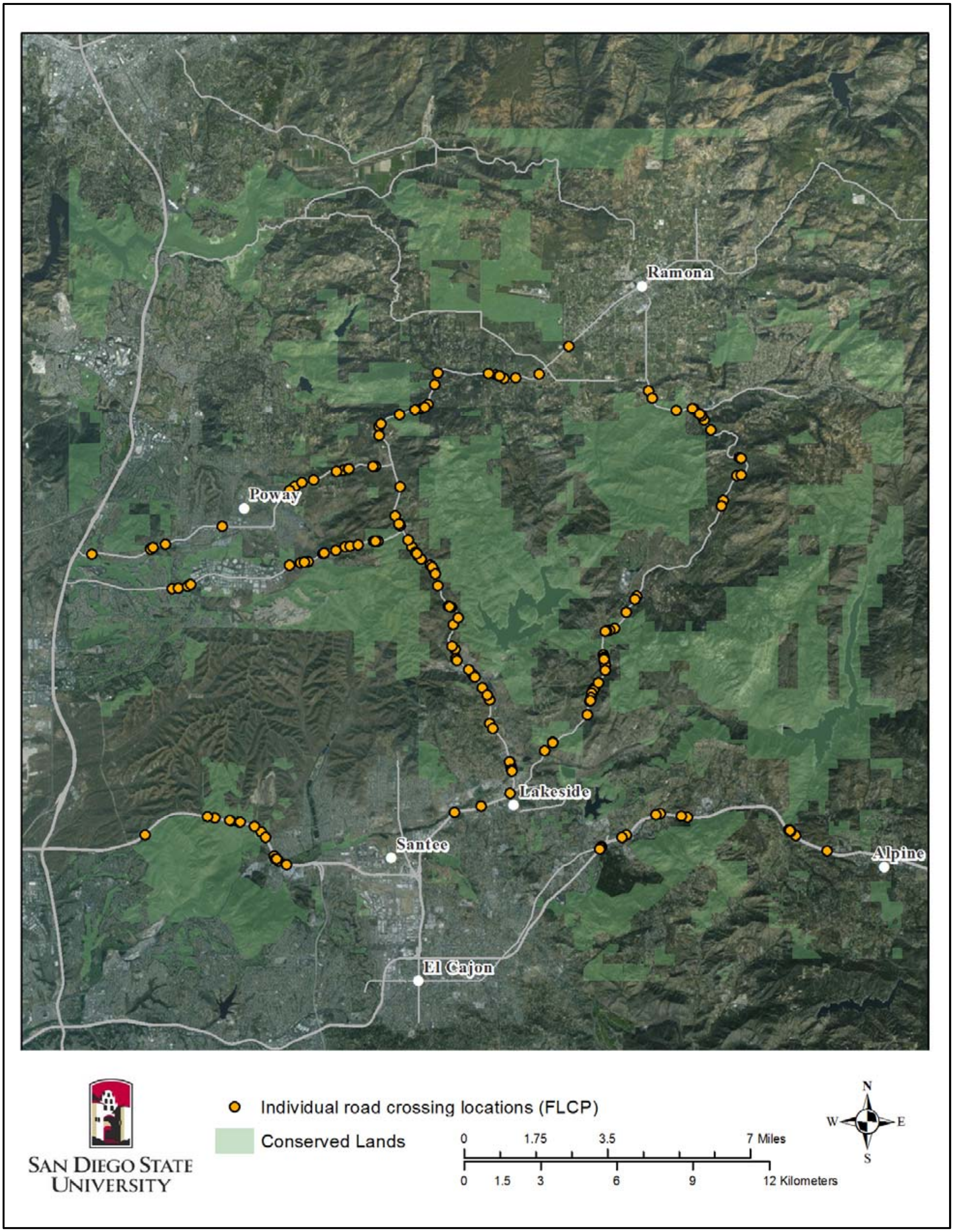


Figure 11. Map of potential road crossing locations identified from the factorial least cost path connectivity modeling (FLCP).

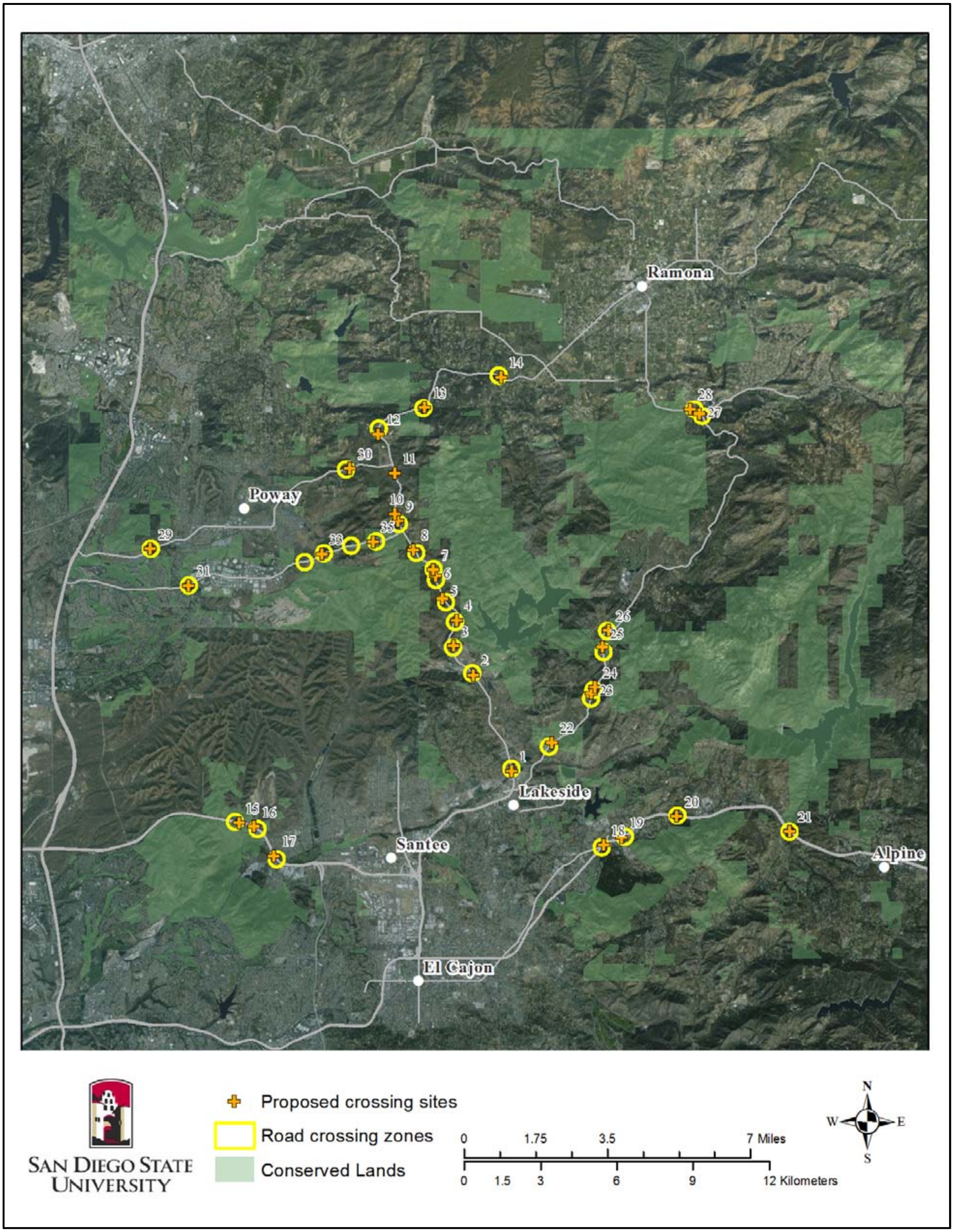


Figure 12. Map of potential road crossing locations identified from the factorial least cost path connectivity modeling (FLCP)

Table 5. Wildlife crossing infrastructure recommendations for SR-67

Site ID	Wild-life Priority	Improve-ment Type	Rd width (ft)	Right -of-way (ft)	Optimal Crossing Type	Minimum Crossing Type	New, Retro, or Exists	Optimal width (ft)	Optimal height (ft)	Min width (ft)	Min height (ft)	Existing diameter (ft)	Min fence length E or S (ft)	Min fence length N or W (ft)
1	2	Minor	45.9	164.0	Bridge		Exists	–	13.1	–	9.8	NA	–	–
2	3	Minor	114.8	141.1	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	7.0	–	7.0	590	656
3	1	Major	164.0	502.0	Arched or box culvert		Retrofit	26.2	14.8	19.7	13.1	4.0	1,312	1,476
4	2	Major	101.7	150.9	Arched or box culvert		Retrofit	16.4	9.8	13.1	6.6	1.5	1,640	2,460
5	3	Major	144.4	150.9	Pipe culvert		Retrofit	6.6	–	3.3	–	3.0	820	328
6	1	Major	131.2	150.9	Arched or box culvert		Retrofit	26.2	14.8	19.7	13.1	7.5	984	1,312
7	2	Minor	85.3	157.5	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	7.5	–	7.5	1,312	2,624
8	3	Minor	88.6	141.1	Arched or box culvert	Pipe culvert	Retrofit	13.1	6.6	6.6	–	3.0	771	1,082
9	1	Major	170.6	160.8	Arched or box culvert		Retrofit	26.2	14.8	16.4	9.8	5.5	1,148	820
10	2	Minor	55.8	150.9	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	7.0	–	7.0	1394.4	820.2
11	2	Minor	55.8	150.9	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	8.5	–	8.5	1378.0	2296.6
12	2	Major	82.0	150.9	Arched or box culvert	Pipe culvert	Retrofit	13.1	6.6	6.6		3.0	1804.5	1804.5
17.61	1	Major	114.8	311.7	Wildlife overpass		New	229.7		164.0				
20.17	3	Major	82.0	114.8	Arched or box culvert	Pipe culvert	Retrofit	13.1	6.6	6.6		3.0		

Table 6. Wildlife crossing infrastructure best management practices recommendations

Type	Best Management Practices Recommendations
Barriers	If median barriers are installed or the k-rails along the section of SR-67 just north of Vigilante Road remain, stagger placement and installing scuppers to allow wildlife to pass through if they become trapped in the roadway
Conservation	Work to acquire parcels on either side of the road at all crossing locations
Conservation	Work to acquire parcels to connect conserved lands on either side of crossing locations
Construction	Implement mitigation measures to protect wildlife from wildlife-vehicle collisions and impacts during construction
Construction	Implement a BACI study to monitor efficacy of structures beginning prior to construction
Crossings	Maintain small culvert structures for small animal use at intervals of ~90m (300 feet). Structures should have diameter of 0.5 - 1.5m
Crossings	Target an average of 1 crossing per 2 km (1.2 mi) of roadway for medium to large animals
Crossings	Ensure structures have a straight alignment with no bends or curves; there should be a continuous line of sight
Crossings	If hydrological issues preclude optimal structure design for wildlife, consider dual siting of structures for drainage and wildlife movement
Fencing	Bury fencing several inches to prevent digging underneath
Fencing	Construct fence lip to prevent climbing/jumping over
Fencing	Ensure fence ends are tied into existing barriers (topographic or anthropogenic) wherever possible. If none exist, consider adding boulders or a berm to block access and line of sight
Fencing	Construct longer fences for funneling wildlife to crossing structures where possible (especially for large mammals)
Fencing	Construct walls or fencing high enough to encourage flight up and over traffic to avoid bird-vehicle collisions, possibly with flagging added for visibility
Fencing	Install jump outs at regular intervals based on length of fencing segments
Fencing	Conduct roadkill monitoring after crossing construction to determine if extended fencing or jump outs are necessary
Fencing	Once final fencing lengths have been determined, identify locations for jump outs to allow wildlife to exit the roadway if they become trapped. Recommend jump outs at 1/2 mile spacing if there in uninterrupted fencing
Fencing	Consider working with home owners to install gates or cattle guards at driveways to improve the functionality of fencing
Fencing	If gates and cattle guards on driveways are not possible, consider fence turn arounds to redirect animals. Recommend revisiting literature for new driveway fencing guidelines prior to the finalizing fencing plan.
Fencing	Place fencing as close to roadway as possible (rather than at the ROW) to limit wildlife crossing fencing to reach attractive habitat on the other side
Maintenance	Maintain structures free of sediment and debris build up; remove invasive and native vegetation that block access or line of sight through structure
Material	Native surface bottoms when possible
Material	Use noise dampening structure materials
Material	Avoid zinc coating if crossing is to be made of metal
Material	Consider limiting the use of rip rap at structure entrances where possible to facilitate use by small animals

DISCUSSION

Through a comprehensive, multi-species connectivity analysis using robust analytical approaches, we created a connectivity plan, implementation guidance through a decision support tool, and a wildlife crossing infrastructure plan for key roadways in our study area. Through this data-driven approach, we:

- Assembled a multi-species connectivity analysis using a suite of data types and species complemented by a landscape-focused land facet analysis
- Analyzed a suite of data types using cutting-edge analytical techniques appropriate to each data type
- Leveraged survey and monitoring data from our study region, producing a data-informed connectivity plan without the collection of any new field data
- Identified and mapped 12 spatially-explicit focal species corridors and one land facet corridor to facilitate wildlife movement within the SR-67 region of San Diego's Multiple Species Conservation Plan area
- Assessed the potential functionality of those corridors for additional species including five federally listed species and 13 other species of interest
- Attributed those spatially-explicit corridors with data on land conservation status, biological variables, and threats and stressors to inform decision-making
- Created a decision support tool for scoring potential acquisitions, habitat restoration projects, or other land management and planning decisions
- Used our connectivity models, species data, site specific information, and past data collection on crossing use and roadkill to inform wildlife crossing infrastructure recommendations for SR-67 as well as other roadways within our analysis area
- Worked with a variety of stakeholders throughout this process to gather information, feedback, and key input to generate a connectivity plan and conservation tool that could readily be implemented by the diverse range of land management and planning entities working in this region of San Diego County

Application of the Connectivity Plan

The data products we developed during this project are intended to be used in planning for subregional connectivity between core complexes of the preserve network of the MSCP and the draft NCMSCP. This information can be applied to connectivity planning and implementation decision-making, particularly when considering connectivity as a key component of reserve design. The focal species approach as well as the species we selected was intended to identify corridors to provide connectivity for preserving biodiversity for the most species. By linking additional quantitative metrics to our corridors, we strived to facilitate acquisition decision-making, the identification of restoration targets to improve connectivity, and to aid in end-users in the evaluation of the potential impacts of development projects on wildlife connectivity in this region.

Although our focal species approach provides specific information about connectivity for the six species we used throughout our modeling process, the data we present here is not appropriate for use in single-species conservation planning or decision-making, particularly those species that are narrow habitat specialists such as those species reliant on native grasslands or vernal pools.

Our analyses and results are also not suitable for assessing connectivity for extreme dispersal-limited species that may move within a core, but not among core preserve areas. Finally, although we did model connectivity irrespective of the delineation of conserved lands, our final products are not appropriate for use in making determinations about core habitat, *e.g.*, habitats important for foraging or breeding, other than the importance of those areas to wildlife movement on a landscape scale.

Decision Support and Implementation

We have provided a suite of data products to support the use of this information in many different management and planning scenarios. By generating geospatial data on our corridor extents to represent the entire corridor area as well as isopleths of the top 10%, 20%, and 30% of connectivity flow for our focal species, we have considered the need for management options in different decision-making circumstances. To highlight the areas of greatest conservation need with the most channelized flow, we have generated a normalized flow surface to pinpoint locations where natural or anthropogenic features constrict connectivity. We have also provided options for end users to consider conserving resilience to climate change both through the land facet corridor analysis we performed, and by combining a resilience surface (The Nature Conservancy, San Francisco, CA, unpublished) with our multi-species connectivity surface.

Through our engagement with stakeholders, we identified an array of variables to facilitate use in planning and decision-making at many levels. We considered factors related to land conservation and management such as the conservation status within each corridor and targets under the NCCP plan. We also incorporated projections of future land use and development potential in our corridor attribution. To explore the potential co-benefits of the conservation of lands for connectivity and engage potential tribal stakeholders, we assessed a measure of cultural value by accounting for the number of archaeological sites, isolated artifacts, and historic structures within each corridor. To account for the range of biological variables relevant to our corridors, we calculated the modeled connectivity value of each segment for our focal species as well as the connectivity potential for five species listed under the Endangered Species Act and an additional 13 species of interest identified by the stakeholder group. We also evaluated the connectivity of different vegetation types within each corridor. Finally, we considered several threats and stressors in our corridor review. We accounted for fragmentation by calculating metrics such as the edge-to-interior ratio and intactness values as well as road density and the proportion of the corridor that had been developed. Metrics related to fire risk and increasing fire frequency were also incorporated into our corridor assessment.

In addition to providing relevant data for implementation of this connectivity plan, we also created a decision support tool to demonstrate how end users might apply the information provided about these corridors to their decision-making processes. Our worked example demonstrates how an organization might go about assigning their scoring criteria prior to decision making and continue through the process to determine whether land acquisition, habitat restoration, or conversely, development may or may not meet management goals and objectives related to connectivity. The example provided is not prescriptive, and we recommend that each organization carefully consider how to assign scoring prior to initiating use and then proceed to use that scoring process consistently. This type of decision support tool allows for transparency in the decision-making process and can lend quantitative backing to justify decisions that may require external support.

The wildlife crossing infrastructure plan we designed through this project is just the first phase in the process of designing a full infrastructure plan for SR-67 or other roadways in the study area. Implementation of a wildlife crossing plan will require further engagement with the full complement of Caltrans staff (including engineers, hydrologist, biologists, and planning) for review and planning. What we have established is a starting point informed by the data and our models that targets an optimal design for wildlife movement given the species, topography, and habitat. Although we did get initial feedback and guidance from Caltrans on our preliminary recommendations, the structure specifications we have provided are not cost-constrained and have not undergone full review by a transportation planning team. However, to facilitate that next step, we have added our two levels of prioritization, wildlife importance and improvement type, to the crossing structure recommendations we have made in this report. We believe these prioritizations should help guide discussions to improve the permeability of SR-67 for wildlife.

Future Applications

The science and statistical approaches for evaluating wildlife space-use, movement, and connectivity is constantly evolving and improving. Our ability to use a wider range of data to assess and plan for landscape connectivity has grown in recent years and now presents opportunities to expand on prior regional connectivity plans to address wildlife movement and barriers to that movement at different spatial and temporal scales. The products we have created for the SR-67 region illustrate how spatially-explicit corridors can be linked to the organization and guidance of management plans so they are directly connected with management actions and decision-making rather than standing out as a separate management task to be executed. Through this project, we have developed a model for utilizing commonly available biological data to design and implement a comprehensive multi-species connectivity plan. The analysis and implementation plan we have assembled here can readily be adapted to different regions, scenarios, species, and habitats to facilitate planning at many levels and should be applied more broadly to advance data-informed planning and management actions.

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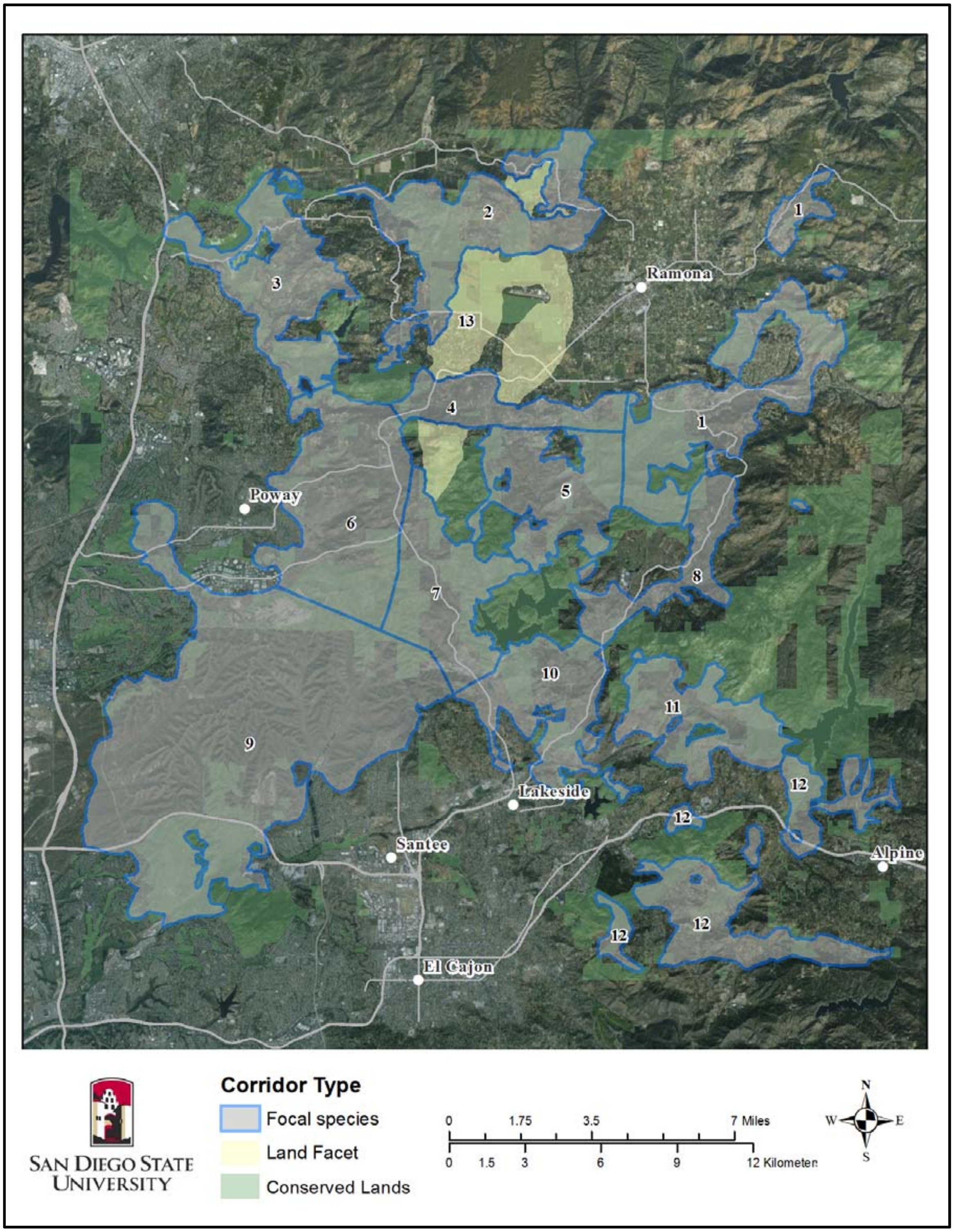
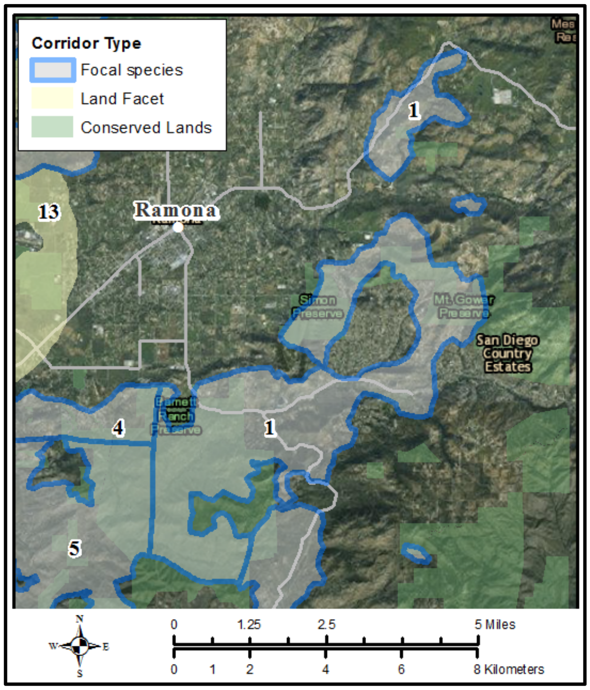
APPENDIX A. CORRIDOR SEGMENT MAPS AND DESCRIPTIONS AND CORRIDOR METADATA TABLE





Corridor 1

8,233 acres

46% conserved

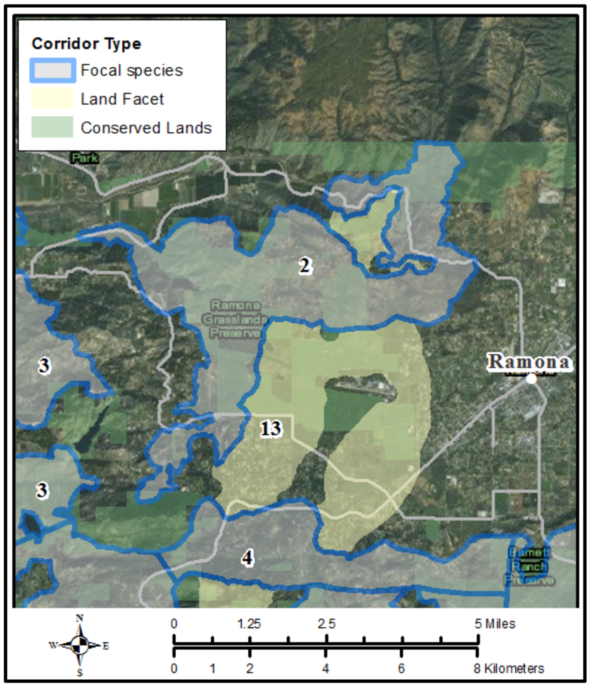
1% PAMA

32% Draft PAMA

Average connectivity value: 76

Corridor 1 is on the east side of the study area and runs just south of the developed lands of the city of Ramona. It provides connectivity from the Mesa Grande Reservation to the Barnett Ranch Preserve and is the only connection to the northeastern corner of the study area. This corridor also contains two important road crossing zones on Wildcat Canyon Road. The northernmost section of this corridor is in the outer isopleth (top 20-30% of connectivity values) and has highly channelized flow, indicating connectivity is restricted.

Eighty-five percent of this corridor is comprised of natural land cover types and two out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, hardwood forest and riparian. Developable parcels make up 10% of this corridor.



Corridor 2

7,579 acres

43% conserved

6% PAMA

13% Draft PAMA

Average connectivity value: 72

Corridor 2 is in the north-central part of the study area and encompasses much of the Ramona Grasslands preserve. It connects Cleveland National Forest lands in the northern part of the study area with Mt. Woodson in the south. Flow through this corridor is channelized in the very north, at its connection with the Cleveland National Forest, and then becomes more diffuse further south at Mt. Woodson. One of the critical connections of this corridor, from the Ramona Grassland Preserve to Mt. Woodson, is in the outer isopleth (top 20-30% of connectivity values).

Eighty-eight percent of this corridor is comprised of natural land cover types and four out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and riparian. Developable parcels make up 14% of this corridor.

Corridor 3

6,141 acres

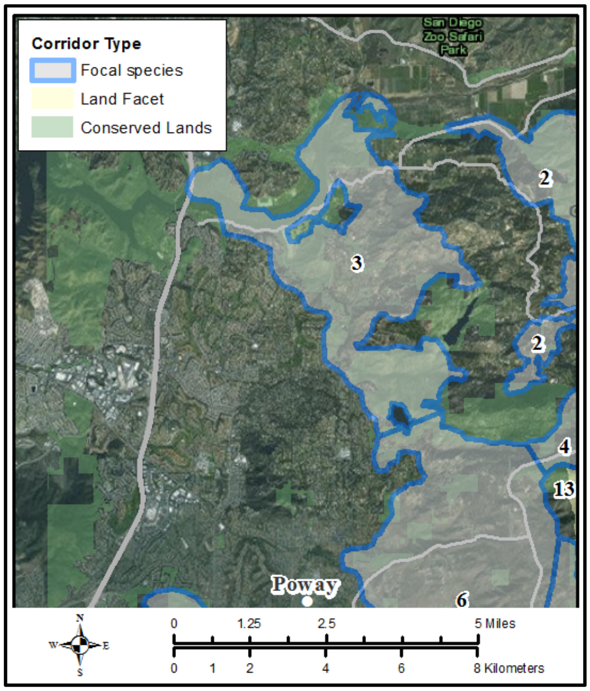
50% conserved

4% PAMA

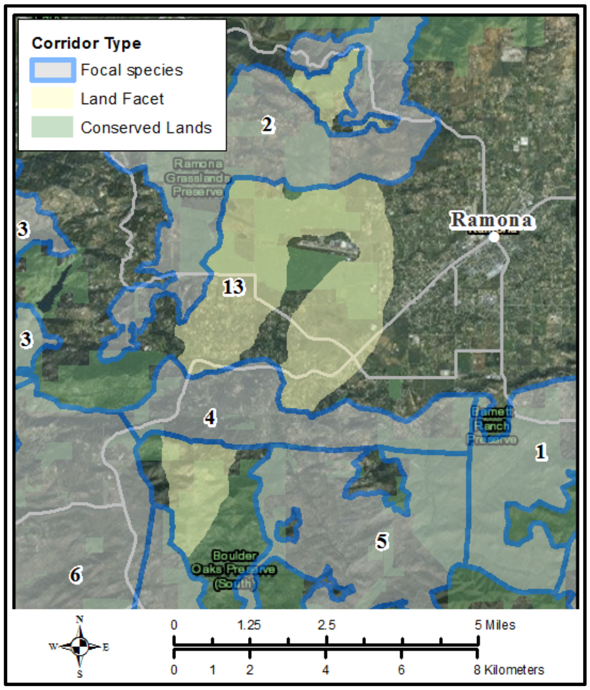
3% Draft PAMA

Average connectivity value: 84

Corridor 3 connects the San Dieguito River in the north with Lake Poway Recreation Area and the Blue Sky Ecological Reserve in the south. Though this corridor is mostly comprised of the inner two isopleths (top 1-20% of connectivity values), it has areas of highly channelized flow leading up to and along the San Dieguito River. Corridor 3 also has a narrow section (3,300 feet wide or less) south of the Maderas Golf Club along Old Coach Road that is vulnerable to fragmentation.



Eighty-three percent of this corridor is comprised of natural land cover types and three out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include coastal sage scrub and riparian. Developable parcels make up 19% of this corridor.



Corridor 4

3,205 acres

18% conserved

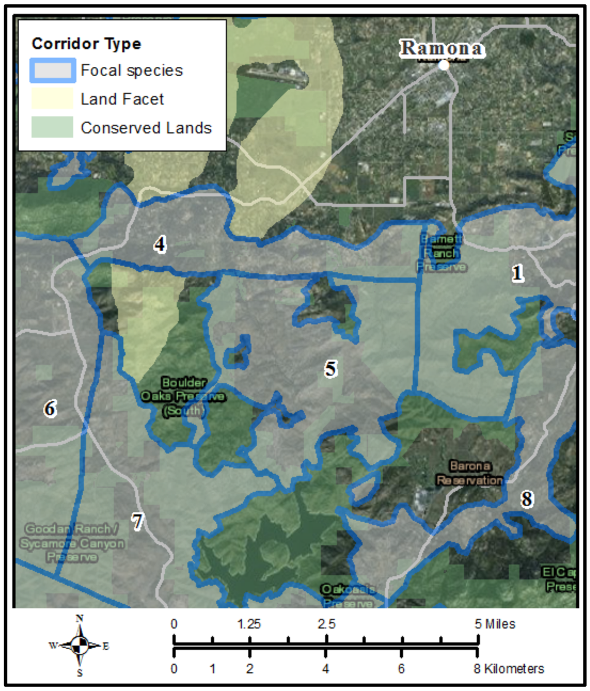
1% PAMA

5% Draft PAMA

Average connectivity value: 70

Corridor 4 provides east-west connectivity from Mt. Woodson, across SR-67 to the Barnett Ranch Preserve. This corridor is mostly comprised of the outer isopleth of connectivity values (top 20-30% of connectivity values). Corridor 4 contains two important wildlife road crossing zones along SR-67.

Eighty-four percent of this corridor is comprised of natural land cover types and one out of the five threatened and endangered species assessed is present here. Land cover types with good connectivity across this corridor include chaparral and hardwood forest. Developable parcels make up 39% of this corridor.



Corridor 5

5,518 acres

46% conserved

25% PAMA

Average connectivity value: 86

Corridor 5 is in the center of the study area between Boulder Oaks Preserve to the west and Barnett Ranch Preserve and Cañada de San Vicente to the east. Developable parcels make up 41% of this corridor. Corridor 5 is comprised of areas with diffuse flow, but has one pinchpoint between the north and south segments of the Boulder Oaks Preserve that measures only 750 feet across. This arm of the corridor is in the outer isopleth (top 20-30% of connectivity values).

Ninety-six percent of this corridor is comprised of natural land cover types and two out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, hardwood forest, and riparian.

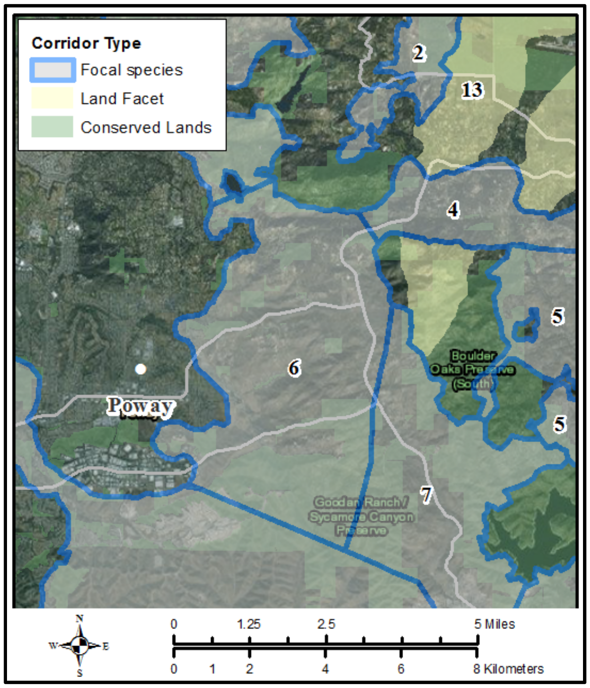
Corridor 6

9,422 acres

33% conserved

10% PAMA

Average connectivity value: 90



Corridor 6 is a fairly wide and intact north-south corridor connecting Mt. Woodson in the north with Sycamore Canyon. This corridor has diffuse flow and is mostly comprised of the top two connectivity isopleths (top 1-20% of connectivity values. Corridor 6 contains two important wildlife road crossing zones on SR-67, one on Poway Road, and three on Scripps-Poway Road.

Eighty-eight percent of this corridor is comprised of natural land cover types and one out of the five threatened and endangered species assessed is present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 41% of this corridor.

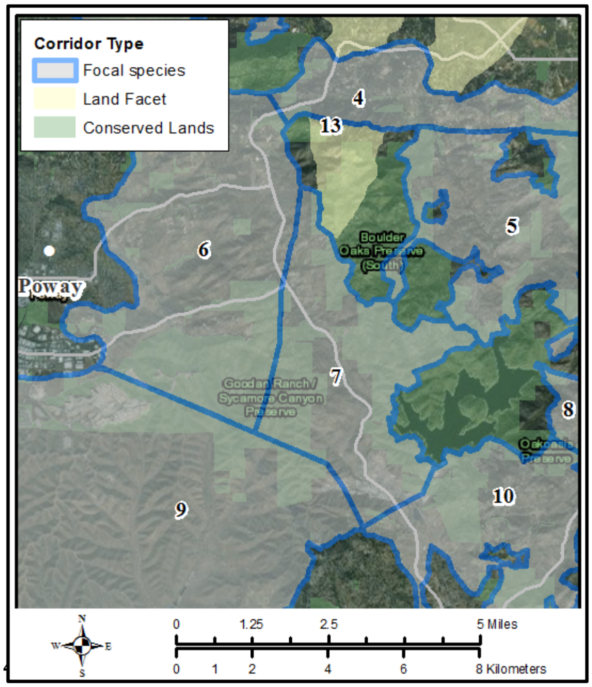
Corridor 7

5,599 acres

56% conserved

10% PAMA

Average connectivity value: 86



Corridor 7 provides connectivity from the San Vicente Highlands and Boulder Oaks preserves on the east side of SR-67 to Sycamore Canyon and Goodan Ranch Preserves on the west side. This corridor contains seven important wildlife road crossing locations on SR-67. Corridor 7 is mostly made up the top two corridor isopleths (top 1-20% of connectivity values), however there is one important arm of east-west connectivity north of the San Vicente Reservoir that is in the outer corridor isopleth (top 20-30% of connectivity values).

Ninety percent of this corridor is comprised of natural land cover types and two out of the five threatened and endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 34% of this corridor.

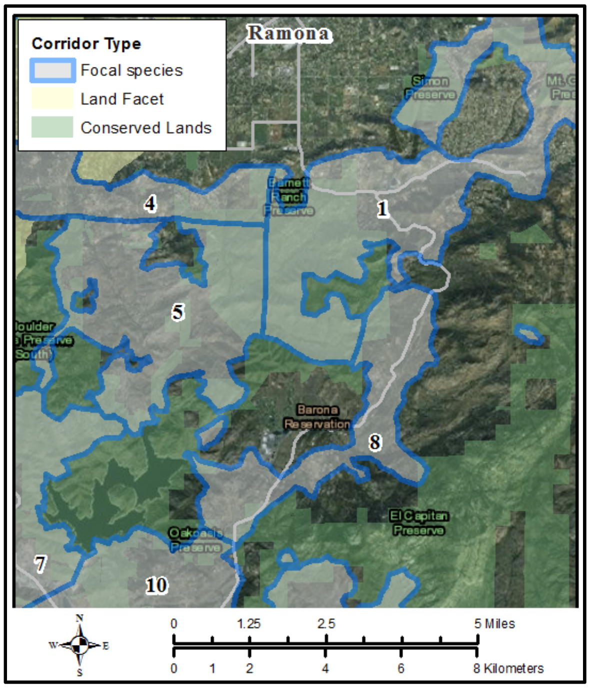
Corridor 8

3,143 acres

15% conserved

4% Draft PAMA

Average connectivity value: 78



Corridor 8 connects the Barona Reservation and Cañada de San Vicente Preserve in the northeast with the Oakoasis Preserve in the southwest. It is comprised of diffuse flow and the out two corridor isopleths (top 10-30% of connectivity values). Compared with other corridors in the study area corridor 8 is narrow and has a pinch point that measures only ~2,600 feet wide. Corridor 8 also contains one important wildlife road crossing location on Wildcat Canyon Road.

Ninety-four percent of this corridor is comprised of natural land cover types. None of the endangered species assessed are present in this corridor. Land cover types with good connectivity across this corridor include chaparral and hardwood forest. Developable parcels make up 8% of this corridor.

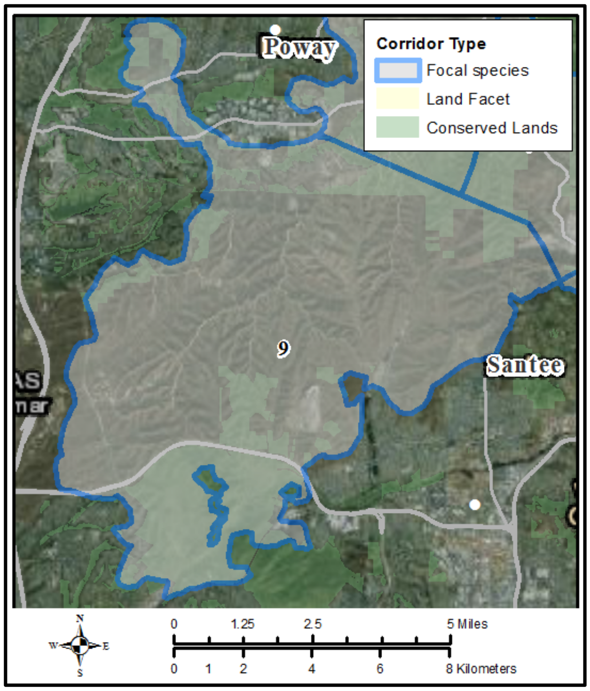
Corridor 9

27,849 acres

25% conserved

2% PAMA

Average connectivity value: 87



Corridor 9 is the largest corridor and connects Sycamore Canyon and Goodan Ranch Preserves in the north with Mission Trails Regional Park in the south. Marine Corps Air Station Miramar is a major land owner in this corridor. Corridor 9 contains diffuse flow in the north, but transitions to highly channelized flow in the south. It is mostly comprised of the top two corridor isopleths (top 1-20% of connectivity values). Corridor 9 has one important wildlife road crossing location on Poway Road, one on Scripps-Poway Parkway, and two on SR-52.

Eighty-nine percent of this corridor is comprised of natural land cover types and three of the five endangered species are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 9% of this corridor.

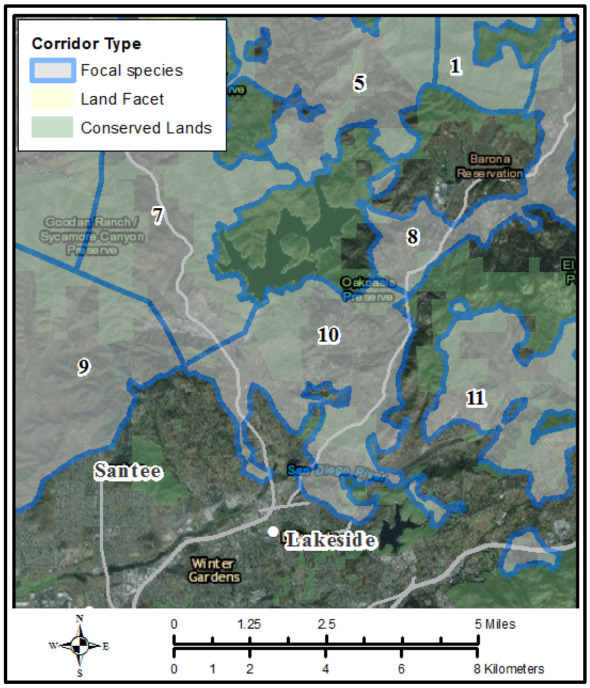
Corridor 10

5,211 acres

30% conserved

24% PAMA

Average connectivity value: 81



Corridor 10 connects the San Vicente Reservoir and the Oakoasis Reserve in the north with the San Diego River and Lake Jennings in the south. It contains diffuse flow and is comprised mostly of the outer two corridor isopleths (top 10-30% of connectivity values). It contains one important wildlife road crossing location on SR-67 and one on Wildcat Canyon Road.

Eighty percent of this corridor is comprised of natural land cover types, and two of the five endangered species assessed are present. Land cover types with good connectivity across Corridor 8 include chaparral, coastal sage scrub, and riparian. Developable parcels make up 37% of this corridor.

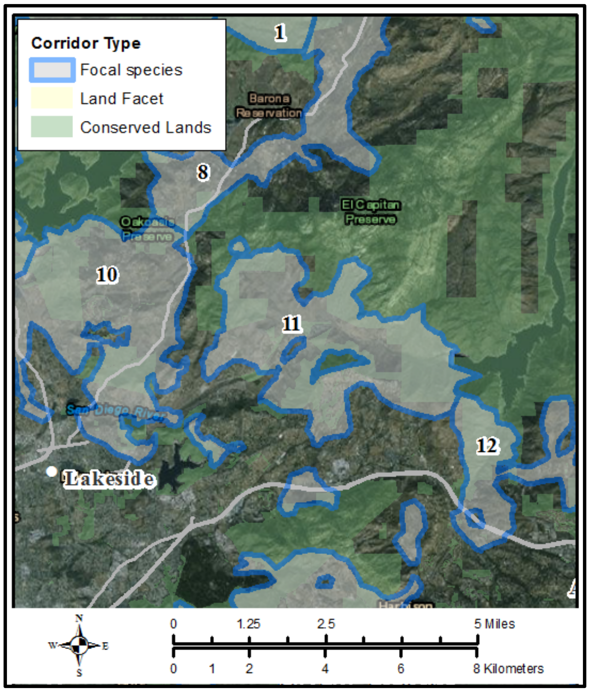
Corridor 11

4,648 acres

50% conserved

36% PAMA

Average connectivity value: 81



Corridor 11 is in the southeastern section of the study area and provides connections from the El Capitan Reservoir with El Capitan County Preserve and the Cleveland National Forest to the northwest. This corridor has mostly diffuse flow, though flow does begin to get more concentrated in the southeast near the reservoir.

Ninety-one percent of this corridor is comprised of natural land cover types and three of the five endangered species assessed are present here. Land cover types with good connectivity across Corridor 11 include chaparral, coastal sage scrub, and riparian. Developable parcels make up 21% of this corridor.

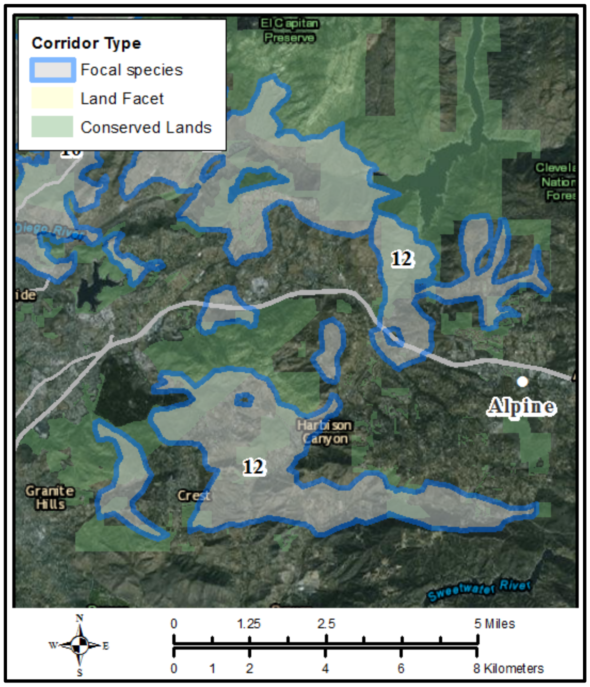
Corridor 12

7,332 acres

32% conserved

14% PAMA

Average connectivity value: 69



Corridor 12 is a collection of smaller connections in the very southeastern part of the study area. It contains and connects the Cleveland National Forest and El Capitan County Preserve to the north of Interstate 8 with Crestridge Ecological Reserve, Crest, and Crest-

Worley Preserves south of the interstate. Flow is restricted or highly channelized through most of this corridor and it is primarily comprised of the outer connectivity isopleth (top 20-30% of connectivity values). Corridor 12 has two important wildlife road crossing locations on I-8, one of which is the Chocolate Creek crossing.

Eighty-two percent of this corridor is comprised of natural land cover types and two of the five endangered species assessed are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and riparian. Developable parcels make up 4% of this corridor.

Corridor 13

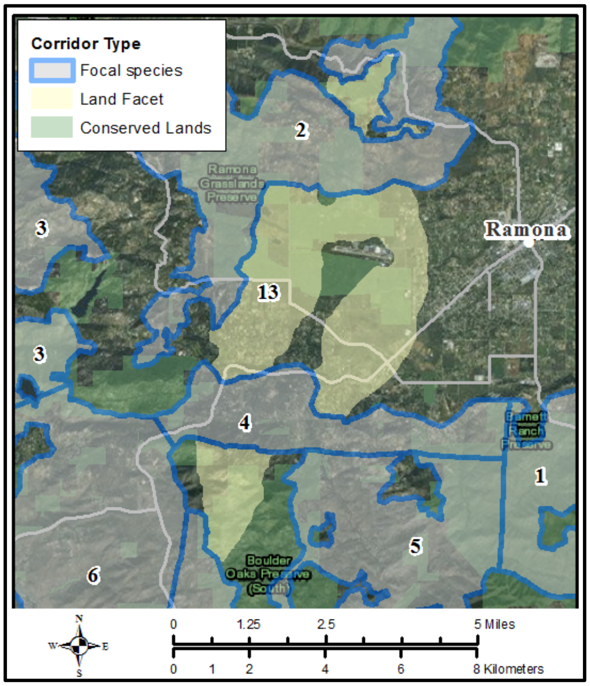
9,958 acres

34% conserved

3% PAMA

31% Draft PAMA

Average connectivity value: 42



Corridor 13, the land facet corridor, connects Cleveland National Forest lands in the north with Iron Mountain in the south through much of the Ramona Grasslands Preserve. This corridor contains one important wildlife road crossing on SR-67.

Seventy-five percent of this corridor is comprised of natural land cover types and three of the five endangered species are present here. Land cover types with good connectivity across this corridor include chaparral, coastal sage scrub, and grassland. Developable parcels make up 31% of this corridor.

Table A1. Corridor metadata table. This table displays the metric calculated for various attributes for each of the 13 corridors as well as the minimum and maximum value for each metric and the corresponding field abbreviation for the corridor shapefile product.

Category	Type	Variable / Metric	Shapefile field abbreviation	Min Value	Max Value
		Corridor ID number	Id	1	13
		Corridor Type, species–specific or land facet	C_Type		
		Corridor area in acres	Area_Ac	3,142	27,849
Conservation/Management	Conservation Status	Percent of corridor area with conserved status	Pct_Cnsvd	15	56
Conservation/Management	Conservation Status	Acres of corridor conserved	Ac_Cnsvd	479	6,874
Conservation/Management	Conservation Status	Acres of corridor unconserved	Ac_UNCnsvd	2,320	20,974
Conservation/Management	Conservation Status	Acres of corridor in PAMA	Ac_PAMA	0	1670
Conservation/Management	Conservation Status	Percent of corridor area in PAMA	Pct_PAMA	0	36
Conservation/Management	Conservation Status	Acres of corridor in with draft PAMA status	Ac_D_PAMA	0	2,597
Conservation/Management	Conservation Status	Percent of corridor area with draft PAMA status	Pct_DPAMA	0	32
Conservation/Management	Future Land Use	developable parcels	No_Dev_Pcl	10	330
Conservation/Management	Future Land Use	Number of parcels with developable land	Ac_Dev_Pcl	267	3,904
Conservation/Management	Future Land Use	Percent of corridor area with developable land	Pct_Dev_Pc	4	41
Conservation/Management	Future Land Use	Average probability of development	ProbDev_Av	0.001	0.043
Conservation/Management	Future Land Use	Minimum probability of development	ProbDev_Mn	0	0.002
Conservation/Management	Future Land Use	Maximum probability of development	ProbDev_Mx	0.004	0.327
Conservation/Management	Future Land Use	Area weighted mean average cost of developable land	priceAWM	$51,081	$984,126
Conservation/Management	Future Land Use	Area weighted sum of cost of developable land	priceAWS	$595,710	$113,979,498
Conservation/Management	Cultural	Number of recorded cultural sites in corridor	Csites	31	402
Biological Variables	Connectivity	Average value in corridor of the multi-species connectivity surface	All_spp_Val	68.6	89.9
Biological Variables	Resilience	Mean climate change resiliency value	Resilience	0.103	0.287
Biological Variables	Resilience	Proportion of corridor covered by Land Facet 1	Prop_LF1	0	71
Biological Variables	Resilience	Proportion of corridor covered by Land Facet 2	Prop_LF2	4	100
Biological Variables	Resilience	Proportion of corridor covered by Land Facet 3	Prop_LF3	0	91

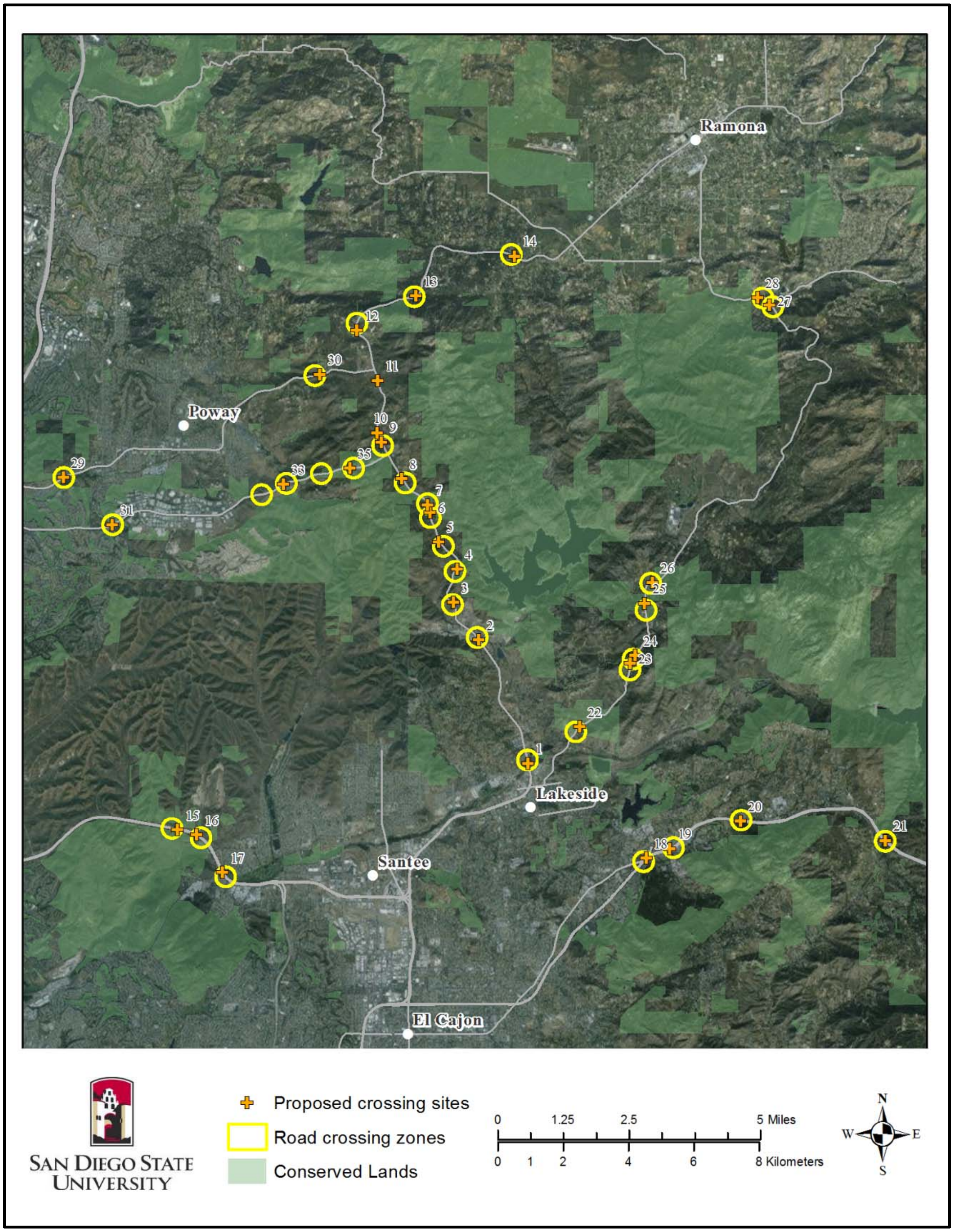
Category	Type	Variable / Metric	Shapefile field abbreviation	Min Value	Max Value
Biological Variables	Resilience	Proportion of corridor covered by Land Facet 4	Prop_LF4	0	95
Biological Variables	Focal Species Corridor	Proportion of the corridor covered by the puma-only corridor	Puma_Corr	2	100
Biological Variables	Focal Species Connectivity	Average value in corridor of the connectivity surface for puma	Puma_Val	33.4	95.3
Biological Variables	Focal Species Corridor	Proportion of the corridor covered by the bobcat-only corridor	Bcat_Corr	43	100
Biological Variables	Focal Species Connectivity	Average value in corridor of the connectivity surface for bobcat	Bobcat_Val	44.6	89.2
Biological Variables	Focal Species Corridor	Proportion of the corridor covered by the deer-only corridor	Deer_Corr	33	100
Biological Variables	Focal Species Connectivity	Average value in corridor of the connectivity surface for deer	Deer_Val	42	91.2
Biological Variables	Focal Species Corridor	Proportion of the corridor covered by the woodrat-only corridor	Wrat_Corr	73	97
Biological Variables	Focal Species Connectivity	Average value in corridor of the connectivity surface for woodrat	Wrat_Val	53.3	84.6
Biological Variables	Focal Species Corridor	Proportion of the corridor covered by the wrentit-only corridor	Wrtit_Corr	26	100
Biological Variables	Focal Species Connectivity	Average value in corridor of the connectivity surface for wrentit	Wrtit_Val	47.5	84
Biological Variables	Focal Species Corridor	Proportion of the corridor covered by the CA mouse-only corridor	Mouse_Corr	67	91
Biological Variables	Focal Species Connectivity	Average value in corridor of the connectivity surface for CA mouse	Mouse_Val	56.8	79.5
Biological Variables	T&E Species	Number of Arroyo toad occurrence points in corridor	ARTO_pts	0	149
Biological Variables	T&E Species	Proportion of Arroyo toad points in corridor out of total in study area	ARTOpropts	0	0.47
Biological Variables	T&E Species	Number of Cactus wren occurrence points in corridor	CACW_pts	0	7
Biological Variables	T&E Species	Proportion of cactus wren points in corridor out of total in study area	CACWpropts	0	0.048
Biological Variables	T&E Species	Mean habitat suitability value in corridor for Cactus wren	CACWMN	0.028	0.435
Biological Variables	T&E Species	Number of CA gnatcatcher occurrence points in corridor	CAGN_pts	0	181
Biological Variables	T&E Species	Proportion of California gnatcatcher points in corridor out of total in study area	CAGNpropts	0	0.17
Biological Variables	T&E Species	Mean habitat suitability value in corridor for California gnatcatcher	CAGNMN	0.017	0.463

Category	Type	Variable / Metric	Shapefile field abbreviation	Min Value	Max Value
Biological Variables	T&E Species	Number of Quino checkerspot butterfly occurrence points in corridor	QUCH_pts	0	6
Biological Variables	T&E Species	Proportion of Quino checkerspot butterfly points in corridor out of total in study area	QUCHpropts	0	0.286
Biological Variables	T&E Species	Mean habitat suitability value in corridor for Quino checkerspot butterfly	QUCHMN	0.088	0.362
Biological Variables	T&E Species	Number of Stephens' kangaroo rat occurrence points in corridor	SKR_pts	0	10
Biological Variables	T&E Species	Proportion of Stephens' kangaroo rat points in corridor out of total number	SKRpropts	0	0.059
Biological Variables	Species Representation	Number of Hermes copper butterfly occurrence points in corridor	HECO_pts	0	343
Biological Variables	Species Representation	Proportion of Hermes copper butterfly points in corridor out of total in study area	HECOpropts	0	0.762
Biological Variables	Species Representation	Number of coachwhip occurrence points in corridor	MAFL_pts	0	5
Biological Variables	Species Representation	Proportion of coachwhip points in corridor out of total in study area	MAFLpropts	0	0.091
Biological Variables	Species Representation	Number of granite spiny lizard occurrence points in corridor	SCOR_pts	0	10
Biological Variables	Species Representation	Proportion of granite spiny lizard points in corridor out of total number	SCORpropts	0	0.097
Biological Variables	Species Representation	Number of two-striped garter snake occurrence points in corridor	THHA_pts	0	6
Biological Variables	Species Representation	Proportion of two-striped garter snake points in corridor out of total	THHApropts	0	0.075
Biological Variables	Species Representation	Number of W. whiptail occurrence points in corridor	ASTI_pts	0	16
Biological Variables	Species Representation	Proportion of W. whiptail points in corridor out of total in study area	ASTIpropts	0	0.246
Biological Variables	Species Representation	Number of western toad occurrence points in corridor	ANBO_pts	0	151
Biological Variables	Species Representation	Proportion of western toad points in corridor out of total in study area	ANBOpropts	0	0.351
Biological Variables	Species Representation	Mean habitat suitability value in corridor for Bell's sparrow	SASPMN	0.61	0.738
Biological Variables	Species Representation	Mean habitat suitability value in corridor for California thrasher	CATHMN	0.425	0.631
Biological Variables	Species Representation	Mean habitat suitability value in corridor for Costa's hummingbird	COHUMN	0.471	0.688
Biological Variables	Species Representation	Number of pallid bat occurrence points in corridor	ANPA_pts	0	4

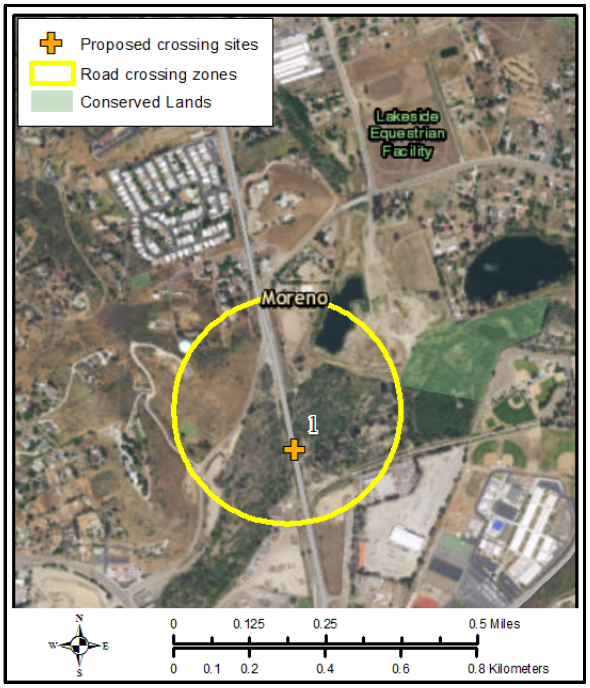
Category	Type	Variable / Metric	Shapefile field abbreviation	Min Value	Max Value
Biological Variables	Species Representation	Proportion of pallid bat points in corridor out of total in study area	ANPApropts	0.02	0.11
Biological Variables	Species Representation	Number of Townsend's big-eared bat occurrence points in corridor	COTO_pts	0	4
Biological Variables	Species Representation	Proportion of Townsend's big-eared bat points in corridor out of total	COTOpropts	0	0.308
Biological Variables	Species Representation	Number of American badger occurrence points in corridor	TATA_pts	0	2
Biological Variables	Species Representation	Proportion of American badger points in corridor out of total in study area	TATApropts	0	0.2
Biological Variables	Species Representation	Number of ringtail occurrence points in corridor	BAAS_pts	0	4
Biological Variables	Species Representation	Proportion of ringtail points in corridor out of total in study area	BAASpropts	0	0.364
Biological Variables	Vegetation	Vegetation types connected in corridor	Veg_connec	qualitative	
Biological Variables	Vegetation	Percent of corridor comprised of chaparral	PLAND_CHP	10.491	71.621
Biological Variables	Vegetation	Degree to which chaparral is aggregated in the corridor	CLUMPY_CHP	0.752	0.893
Biological Variables	Vegetation	Index of travel distance through chaparral in the corridor	GYRATE_CHP	322.921	2,850.39
Biological Variables	Vegetation	Percent of corridor comprised of coastal scrub	PLAND_CSC	1.694	49.27
Biological Variables	Vegetation	Degree to which coastal scrub is aggregated in the corridor	CLUMPY_CSC	0.717	0.89
Biological Variables	Vegetation	Index of travel distance through coastal scrub in the corridor	GYRATE_CSC	90.654	1,652.09
Biological Variables	Vegetation	Percent of corridor comprised of grassland	PLAND_GRS	1.052	7.803
Biological Variables	Vegetation	Degree to which grassland is aggregated in the corridor	CLUMPY_GRS	0.672	0.835
Biological Variables	Vegetation	Index of travel distance through grassland in the corridor	GYRATE_GRS	92.23	277.159
Biological Variables	Vegetation	Percent of corridor comprised of riparian	PLAND_RIP	0.648	7.223
Biological Variables	Vegetation	Degree to which riparian is aggregated in the corridor	CLUMPY_RIP	0.502	0.742
Biological Variables	Vegetation	Index of travel distance through riparian in the corridor	GYRATE_RIP	129.12	777.73
Biological Variables	Vegetation	Percent of corridor comprised of woodland	PLAND_WDL	0.754	16.61
Biological Variables	Vegetation	Degree to which woodland is aggregated in the corridor	CLUMPY_WDL	0.617	0.773
Biological Variables	Vegetation	Index of travel distance through woodland in the corridor	GYRATE_WDL	59.69	408.75
Threats and Stressors	Development	Percent of the corridor that has been developed	PCT_DEV	4.54	19.59

Category	Type	Variable / Metric	Shapefile field abbreviation	Min Value	Max Value
Threats and Stressors	Fragmentation	Mean intactness value in the corridor	Intactness	-0.277	0.408
Threats and Stressors	Fragmentation	Amount of corridor that is comprised of core area	EI_Ratio	18	73
Threats and Stressors	Roads	Average road density in the corridor	Road_Dens	2.597	6.285
Threats and Stressors	Fragmentation	Percent of corridor comprised of natural cover types	PLND_NAT	80	96
Threats and Stressors	Fragmentation	Degree to which natural areas are aggregated in the corridor	CLUMPY_NAT	0.5	0.77
Threats and Stressors	Fragmentation	Index of travel distance through natural areas in the corridor	GYRATE_NAT	1,572	4,046
Threats and Stressors	Disturbance	Percent of corridor comprised of sparse vegetation	PLAND_SPS	4.54	19.59
Threats and Stressors	Disturbance	Degree to which sparse vegetation is aggregated in the corridor	CLUMPY_SPS	0.712	0.828
Threats and Stressors	Disturbance	Index of travel distance through sparse vegetation in the corridor	GYRATE_SPS	127.38	1,013.83
Threats and Stressors	Fire	Frequency of departure from the mean fire return interval	FRIDMN	-54.94	-33.56
Threats and Stressors	Fire	Frequency of departure from the minimum fire return interval	FRIDMIN	-84.2	-67.1
Threats and Stressors	Fire	Frequency of departure from the maximum fire return interval	FRIDMAX	43.1	71.8
Threats and Stressors	Fire	Proportion of corridor in a low fire threat category	ThreatV0	0.021	0.209
Threats and Stressors	Fire	Proportion of corridor in a moderate fire threat category	ThreatV1	0.011	0.166
Threats and Stressors	Fire	Proportion of corridor in a high fire threat category	ThreatV2	0.012	0.537
Threats and Stressors	Fire	Proportion of corridor in a very high fire threat category	ThreatV3	0.096	0.879
Threats and Stressors	Fire	Proportion of corridor in an extreme fire threat category	ThreatV4		0.347

Appendix B: SR-67 Wildlife Crossing Structure Maps, Descriptions, and Infrastructure Recommendations



Crossing Site 1

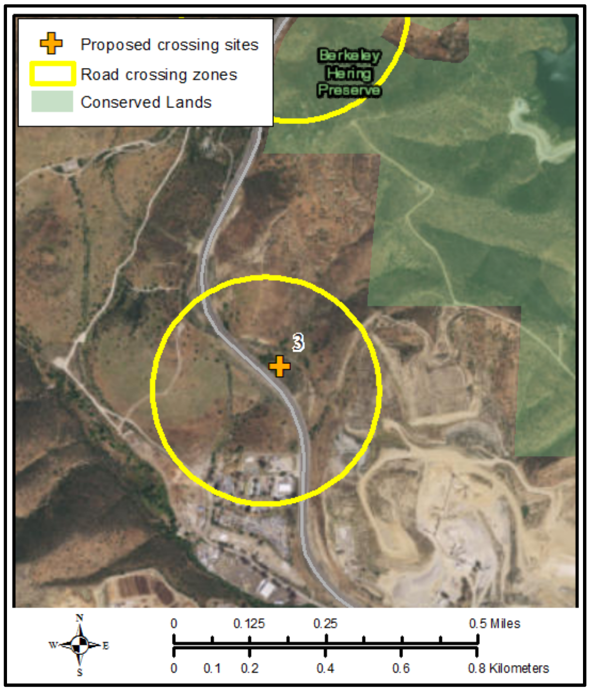


Crossing site 1 is located at the bridge over the San Diego River at Post Mile R5.95. The land on either side of the road in this location is in private ownership. The site is of high importance to wildlife and would only require minor improvements for enhancing wildlife movement. The overall size of the structure is appropriate but fencing is recommended on either side of the road running perpendicular to the bridge to prevent wildlife from accessing the industrial development in the surrounding area. Removal of the non-native vegetation in the San Diego River channel will also enhance wildlife movement through this structure.

Crossing Site 2

Crossing site 2 is located just south of Vigilante Road in Lakeside at Post Mile 9.05. It is of moderate importance to wildlife because there is limited suitable habitat for wildlife movement in the surrounding industrial development despite the proximity to conserved lands. The existing culvert is 7 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Removal of the non-native vegetation and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. Revegetation of the dirt span leading to the culvert on the east side of the road to connect to existing vegetation should also be prioritized. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 3

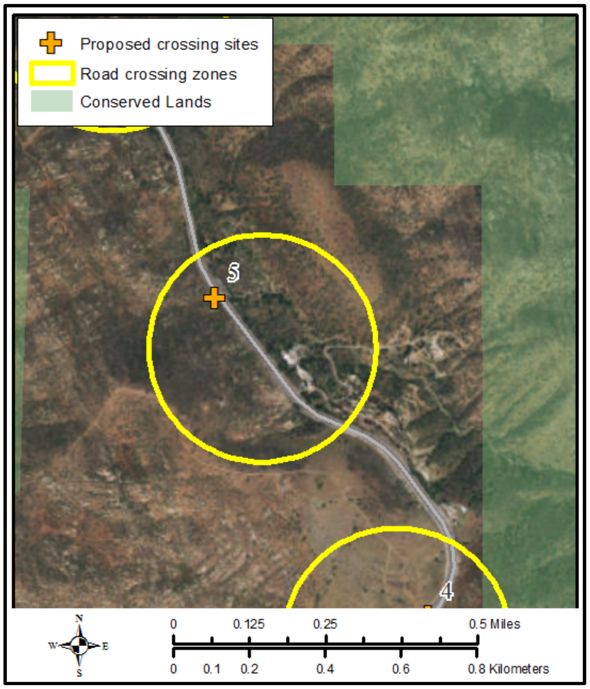


Crossing site 3 is located mid-slope on the grade leading out of Lakeside north of Vigilante Road at Post Mile 9.96. It is of extremely high importance to wildlife as it connects areas of suitable habitat and is adjacent to a large area of conserved land to the east. However, this section of road has experienced moderate levels of wildlife vehicle collisions. The existing culvert is long, narrow and set far back from the road, so will either need a major redesign or dual siting of a wildlife structure to accommodate wildlife movement. The optimal design for this site would be an arched or box culvert 26.2 feet wide by 14.8 feet high. However, the minimum recommendation for this site is 19.7 feet wide by 13.1 feet high. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 4

Crossing site 4 is near the top of the grade north of Lakeside at Post Mile 10.76. It is of high importance to wildlife to connect nearby preserved lands to the east. The existing culvert at this location is only 1.5 feet in diameter, so a major redesign is necessary to facilitate wildlife movement. The optimal design for this site would be an arched or box culvert 16.5 feet wide by 9.8 feet high. However, the minimum recommendation for this site is 13.1 feet wide by 6.6 feet high. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

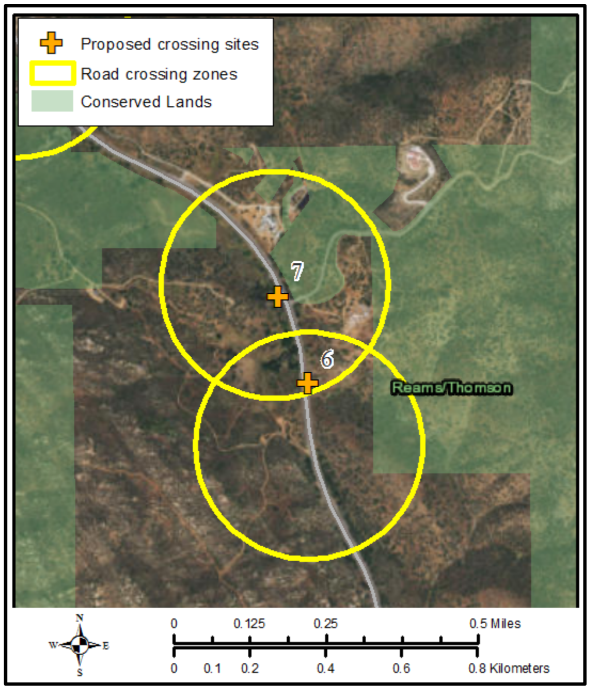
Crossing Site 5



Crossing site 5 is at the top of the grade north of Lakeside at Post Mile 11.46. It is of moderate importance to wildlife to connect nearby preserved lands. The existing culvert at this location is 3.0 feet in diameter, and will require a major redesign to facilitate wildlife movement. Because this crossing will primarily serve small animals, the optimal design is a pipe culvert 6.6 feet in diameter. However, the minimum recommendation for this site is a 3.3 foot diameter culvert. On both sides of the road, 3.5 foot high fencing with an impenetrable bottom should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 6

Crossing site 6 is located immediately south of Foster’s Truck Trail at Post Mile 12.05. It is of extremely high importance to wildlife as it connects areas of suitable habitat and is one of the few locations on the road where there are conserved lands on either side of the road. Although the existing culvert is large, with a diameter of 7.5 feet, it should be larger and more open to accommodate movement, particularly of larger species. The optimal design for this site would be an arched or box culvert 26.2 feet wide by 14.8 feet high. However, the minimum recommendation for this site is 19.7 feet wide by 13.1 feet high. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.



Crossing Site 7

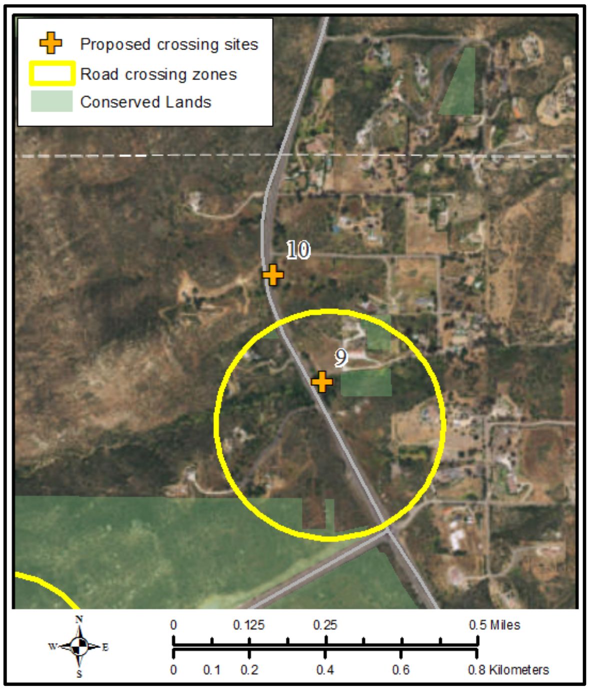
Crossing site 7 is located just north of Foster’s Truck Trail at Post Mile 12.25. It is of high importance to wildlife as it connects areas of suitable habitat and is one of the few locations on the road where there are conserved lands on either side of the road. However, the siting and approach to this culvert make it less attractive for wildlife movement than the site for Crossing 6. The existing culvert is 7.5 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Removal of the non-native vegetation and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 8

Crossing site 8 is located just north of Lazy Acres Drive at Post Mile 12.95. It is of moderate importance to wildlife as there is scattered housing through the area, which is dominated by non-native vegetation. There are adjacent conserved lands nearby, but they are not contiguous across the roadway. The existing culvert on site is 3.0 feet in diameter, and although the optimal crossing design would be an arched or box culvert 13.1 feet wide by 6.6 feet high, a pipe culvert 6.6 feet in diameter would still provide for adequate wildlife movement. Although this is a change in size from the current structure, we have identified it as a minor improvement because this retrofit could occur during normal culvert replacement. Removal of the non-native vegetation and addressing erosion and gullying leading to the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the structure.

Crossing Site 9

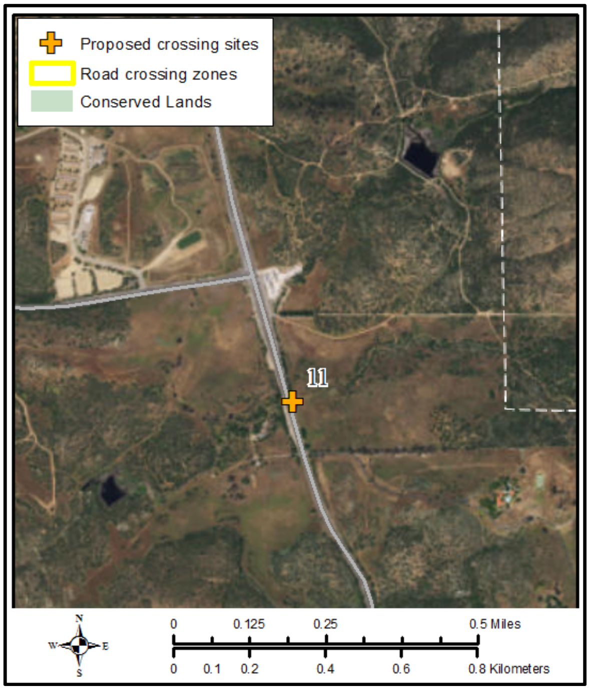
Crossing site 9 is located in the riparian zone that crosses SR-67 north of Scripps Poway Parkway at Post Mile 13.75. It is of extremely high importance to wildlife as it connects areas of suitable habitat and experiences moderate levels of wildlife vehicle collisions. The existing culvert is large at 5.5 feet in diameter, but major improvements are necessary to enhance wildlife movement across the road in this location. The optimal design for this site would be an arched or box culvert 26.2 feet wide by 14.8 feet high. However, the minimum recommendation for this site is 16.4 feet wide by 9.8 feet high. If hydrologic issues preclude optimal wildlife design, dual siting of structures for drainage and wildlife are recommended. On both sides of the road, 6-8 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.



Crossing Site 10

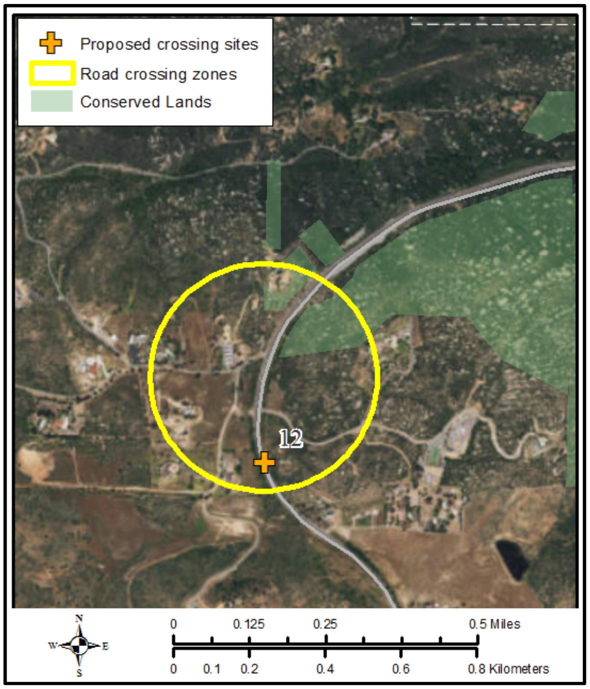
Crossing site 10 is located north of Scripps Poway Parkway at Post Mile 13.9. Although it was not identified by our modeling approach, it is of high importance to wildlife as it connects areas of suitable habitat and past monitoring has documented multiple species crossing the road at this location (Jennings and Lewison 2015). The existing culvert is 7.0 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Removal of the non-native vegetation and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 11



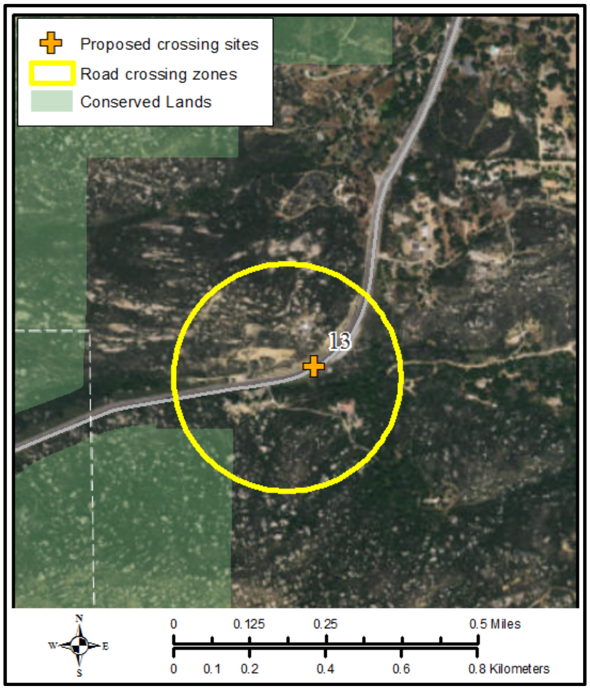
Crossing site 11 is located south of Poway Road at Post Mile 14.98. Although it was not identified by our modeling approach, it is of high importance to wildlife as it connects areas of suitable habitat and has been documented in past monitoring (Jennings and Lewison 2015) as accommodating multiple species crossing the road. The existing culvert is 8.5 feet in diameter and although the optimal design for wildlife would be an arched or box culvert 13.1 feet wide by 9.8 feet high, adequate wildlife movement could be achieved through minor improvements without increasing the size of the culvert. Enhancing native vegetation leading to the structure on the east side and clearing built up sediment that blocks the culvert would enhance wildlife movement through this structure. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 12



Crossing site 12 is south of Chaparral Way on a curve leading toward Mount Woodson at Post Mile 16.05. It is of high importance to wildlife as it connects areas of suitable habitat and is adjacent to conserved lands. The existing culvert at this location is only 3.0 feet in diameter, so a major redesign is necessary to facilitate wildlife movement. The limited grade relief at this site will require additional work to accommodate a larger structure. The optimal design for this site would be an arched or box culvert 13.1 feet wide by 6.6 feet high. However, the minimum recommendation for this site is a 6.6-foot diameter culvert. On both sides of the road, 6-8 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 13



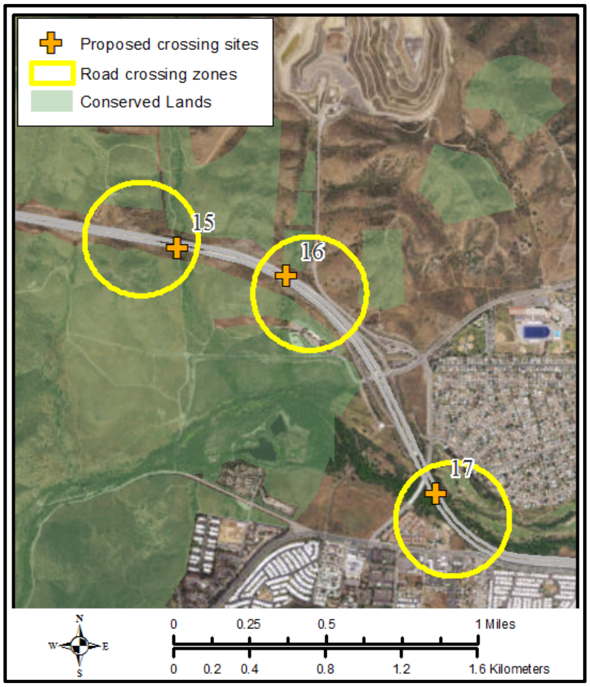
Crossing site 13 is located at the top of the Mount Woodson grade at Post Mile 17.61. It is of extremely high importance to wildlife as it connects areas of unique suitable habitat, conserved lands, and has experienced high levels of wildlife vehicle collisions. There is no existing structure providing for wildlife movement in this area, so it will require a major improvement to construct a suitable wildlife crossing structure. Based on topography and movement patterns of focal species for this crossing structure, a wildlife overpass is the optimal design for this site. The overpass should be between 164 and 230 feet wide and will need to connect in an area where wildlife will be likely to approach the overpass. The structure should also be appropriately vegetated to encourage wildlife to approach and use the structure for crossing the highway. On both sides of the road, 8-10 foot high fencing should also be used to reinforce wildlife movement through the existing culvert.

Crossing Site 14

Crossing site 14 is between Via Penasco and Rancho de Oro Drive at Post Mile 20.17. It is of moderate importance to wildlife as it connects areas of suitable habitat but there are no conserved lands in the vicinity. The existing culvert at this location is only 3.0 feet in diameter, so a major redesign is necessary to facilitate wildlife movement. The limited grade relief at this site will require additional work to accommodate a larger structure. The optimal design for this site would be an arched or box culvert 13.1 feet wide by 6.6 feet high. However, the minimum recommendation for this site is a 6.6-foot diameter culvert. Fencing should be considered for this site, but there are few places to anchor fence ends and there are a number of driveways in the area that could limit fence functionality.

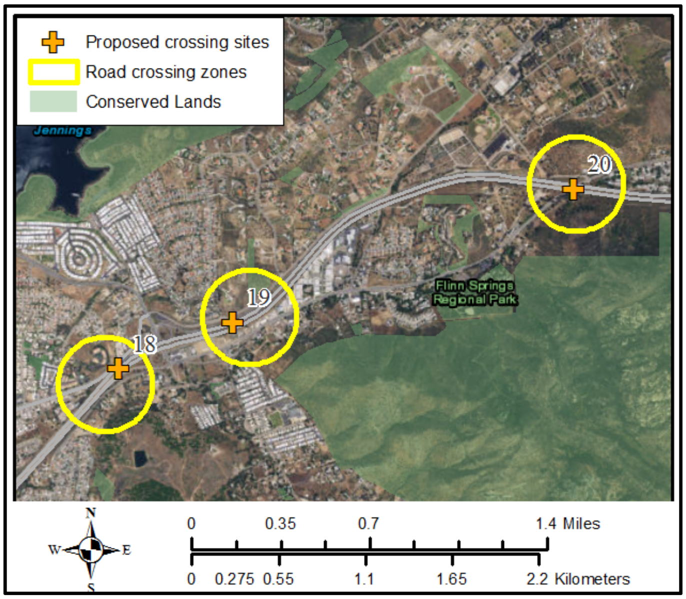
Additional Crossing Structures

SR-52 Crossings

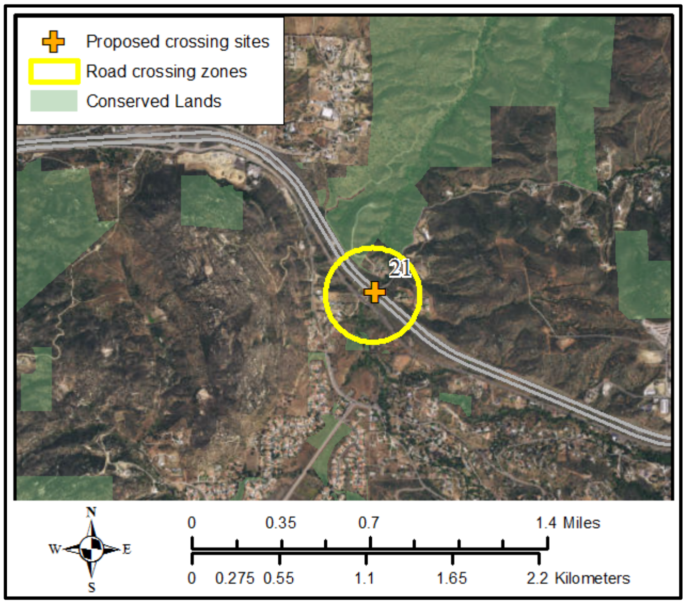


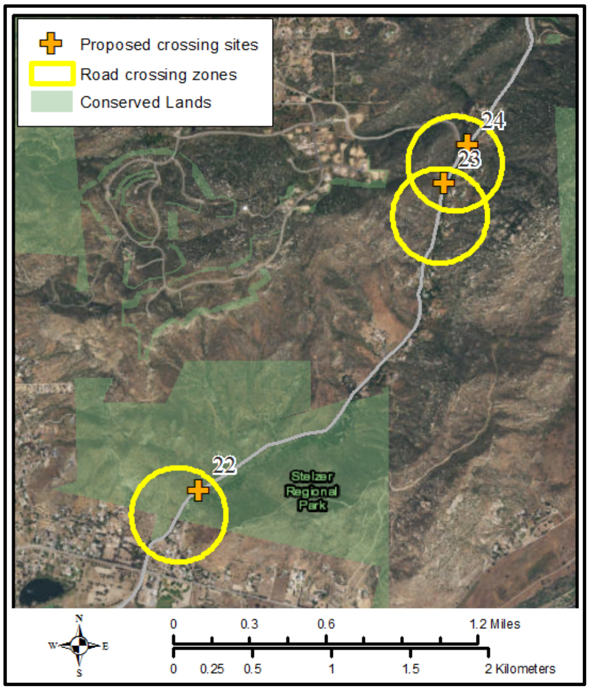
There are three sites along SR-52 that are important wildlife crossing areas: Post Miles 12.44, 12.64, and 13.72. This area is one of the primary connections for wildlife moving in and out of Mission Trails Regional Park. All three only require minor improvements as they likely facilitate wildlife movement in their current design. The installation of fencing to reinforce wildlife use of the structures, as well as some clearing of non-native vegetation under one of the bridges, is likely to improve the condition of the structures for wildlife movement.

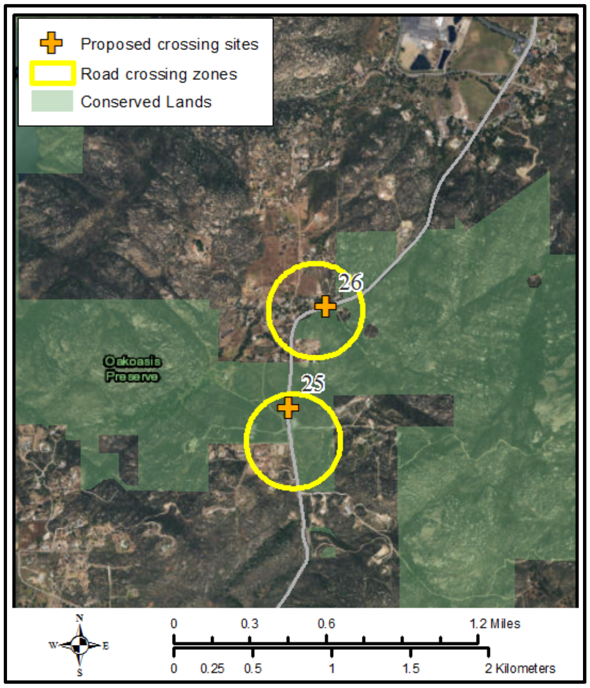
I-8 Crossings



There are four sites along I-8 that are important wildlife crossing areas: Post Miles 21.66, 22.13, 23.67, and 26.75. The first two are of moderate importance for wildlife movement, but the other two are of high and very high importance. As no structures exist at these sites that can accommodate wildlife movement, major improvements are necessary at all four sites. Once redesigned, the installation of fencing to reinforce wildlife use of the structures is likely to improve the condition of the structures for wildlife movement.

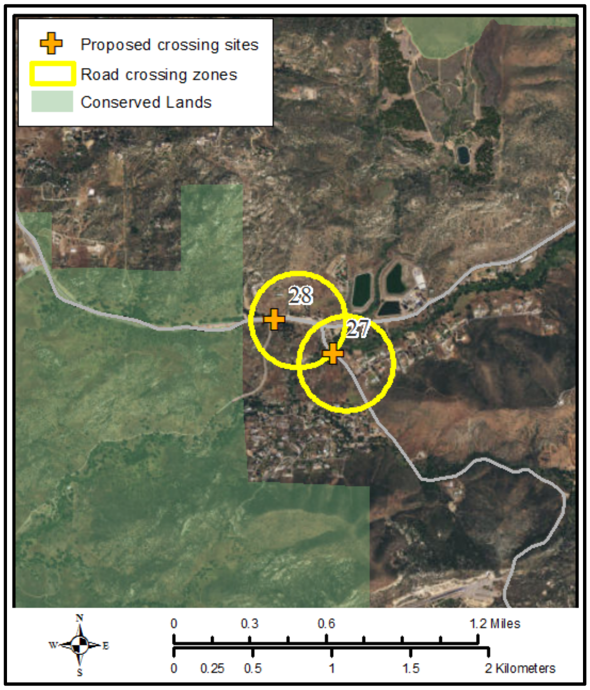


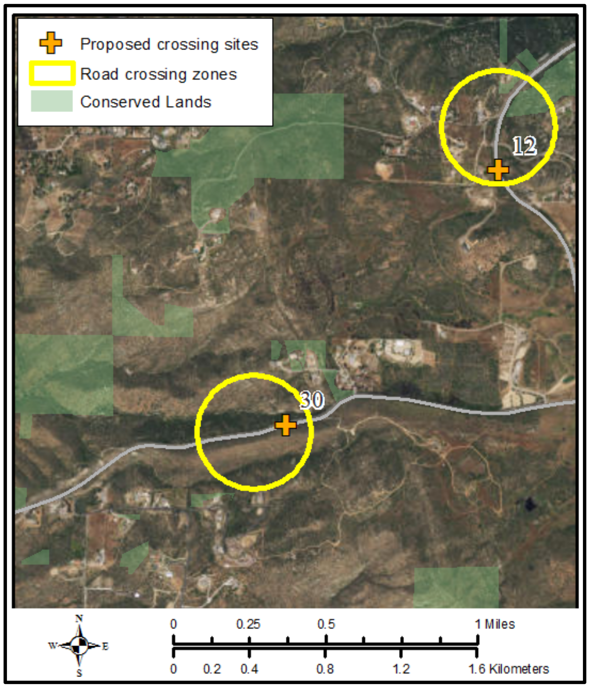




Wildcat Canyon Road Crossings

There are seven sites along Wildcat Canyon Road (with one of those being adjacent to Wildcat Canyon Road on San Vicente Road) that are important to wildlife movement. Most are of moderate or high importance to wildlife, but many require major improvements because there are not existing structures adequate to support wildlife movement. In total, four out of seven site will need major improvements. Only minor improvements are needed at the existing wildlife tunnel site. Some sediment flow and erosion control may be necessary here as well as revegetation with native species, but otherwise, this site appears functional. The installation of fencing to reinforce wildlife use of the structures, as well as some clearing of non-native vegetation under one of the bridges, is likely to improve the condition of the structures for wildlife movement.

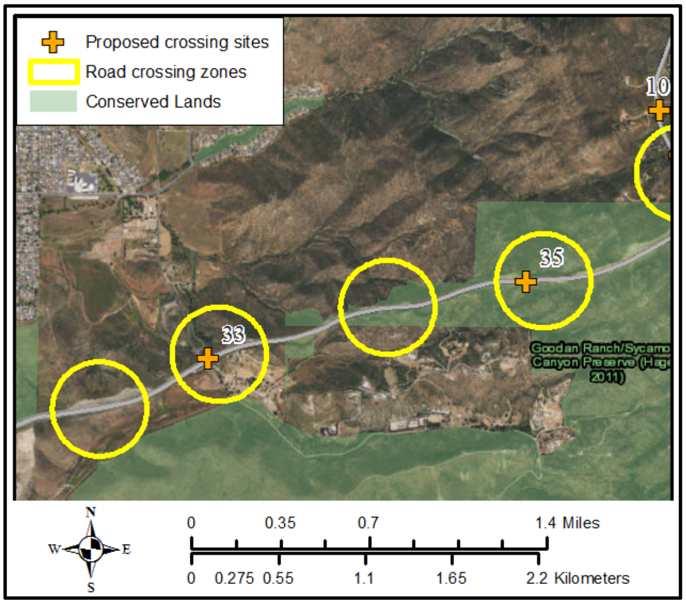




Poway Road Crossings

There were two sites identified as having a high importance to wildlife movement on Poway Road. At one site, there is no existing structure, and a major improvement is necessary. At the other, there is an existing culvert that can accommodate the movement by small animals at that location. The installation of fencing to reinforce wildlife use of the structures is also likely to improve the condition of the structures for wildlife movement.

Scripps Poway Parkway Crossings



Although there were originally five crossing zones identified along Scripps Poway Parkway through our modeling results, there are final recommendations for only three of those sites. The remaining two had few options for siting and placement given the topography, road cut, and proximity of other proposed wildlife crossings. Two of these three sites were of high importance for wildlife movement and require major improvements to accommodate an adequate degree of wildlife movement. The third site is the location of the Scripps Poway Parkway wildlife tunnel that is functional but could benefit from fence extension and improvement.

Table B1. Detailed wildlife crossing recommendations for SR-67

Id	Post Mile	Wildlife Priority	Improvement Type	Nearest Crossing (mi)	Rd width (ft)	Right-of-way (ft)	Optimal Crossing Type	Minimum Crossing Type	New, Retro, or Exists	Optimal width (ft)	Optimal height (ft)	Min width (ft)	Min height (ft)	Existing diameter (ft)	In corridor	Conserved	Min fence length E or S (ft)	Min fence length N or W (ft)
1	R5.95	2	Minor	1.209	45.9	164.0	Bridge		Exists	-	13.1	-	9.8	Unknown	Y	N	-	-
2	9.05	3	Minor	0.896	114.8	141.1	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	7.0	-	7.0	Y	N	590.6	656.2
3	9.96	1	Major	0.636	164.0	502.0	Arched or box culvert		Retrofit	26.2	14.8	19.7	13.1	4.0	Y	N	1312.3	1476.4
4	10.76	2	Major	0.629	101.7	150.9	Arched or box culvert		Retrofit	16.4	9.8	13.1	6.6	1.5	Y	N	1640.4	2460.6
5	11.46	3	Major	0.588	144.4	150.9	Pipe culvert		Retrofit	6.6	-	3.3	-	3.0	Y	N	820.2	328.1
6	12.05	1	Major	0.151	131.2	150.9	Arched or box culvert		Retrofit	26.2	14.8	19.7	13.1	7.5	Y	N	984.3	1312.3
7	12.25	2	Minor	0.151	85.3	157.5	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	7.5	-	7.5	Y	N	1312.3	2624.7
8	12.95	3	Minor	0.696	88.6	141.1	Arched or box culvert	Pipe culvert	Retrofit	13.1	6.6	6.6	-	3.0	Y	N	771.0	1082.7
9	13.75	1	Major	0.194	170.6	160.8	Arched or box culvert		Retrofit	26.2	14.8	16.4	9.8	5.5	Y	N	1148.3	820.2
10	13.9	2	Minor	0.194	55.8	150.9	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	7.0	-	7.0	Y	N	1394.4	820.2
11	14.98	2	Minor	0.996	55.8	150.9	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	8.5	-	8.5	Y	N	1378.0	2296.6
12	16.05	2	Major	1.034	82.0	150.9	Arched or box culvert	Pipe culvert	Retrofit	13.1	6.6	6.6	-	3.0	Y	N	1804.5	1804.5
13	17.61	1	Major	1.311	114.8	311.7	Wildlife overpass		New	229.7	-	164.0	-	-	Y	N	-	-
14	20.17	3	Major	2.016	82.0	114.8	Arched or box culvert	Pipe culvert	Retrofit	13.1	6.6	6.6		3.0	Y	N	-	-

Id	Post Mile	Fence specifics	Design features	Near-term Recommendation	Aerial connectivity considerations	Notes
1	R5.95	Site visit needed to determine if fencing to direct wildlife under bridge is necessary	Clear some vegetation to ensure clear path and line of sight. Remove invasives	Clear some vegetation to ensure clear path and line of sight. Remove invasives	Directional structure to encourage flight behavior higher than traffic	Fencing perpendicular to road may be possible within Caltrans right-of-way but would need adjacent land owners to agree
2	9.05	8-10 ft high, impenetrable bottom, fine mesh	Enhance vegetative strip on east side of road - expand to crossing structure. Improve water drainage in low area of crossing. Control erosion off of industrial development areas on the E side of highway	Clear sediment and debris in southern-most structure to increase height on east side (currently partially obstructed). Control invasives surrounding crossings, especially on west side. Restore native vegetation on both sides of highway	Directional structure to encourage flight behavior higher than traffic. Need to improve vegetative structure/height on east side to support aerial crossings	
3	9.96	8-10 ft high, impenetrable bottom, fine mesh	Lighting inside structure, contour entrance to structure on E side to enhance line of sight through structure. This should also happen on slope on W side	Install seasonal signage and flashing lights to increase awareness about this area as a wildlife-vehicle collision hot spot and slow traffic during fall evening rush hour	Directional structure to encourage flight behavior higher than traffic - topography and natural veg support aerial crossings just north of underpass location. Need additional vegetative structure on E and W slopes to support crossings	Lighting could come from skylight/tube in median, addition of reflective paint inside structure at either end, or a light powered via a wired solar panel outside the structure.
4	10.76	8-10 ft high, impenetrable bottom, fine mesh			Directional structure to encourage flight behavior higher than traffic; Could also plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides	
5	11.46	3.5 ft high, impenetrable bottom, fine mesh	Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species	Clear sediment and debris	Directional structure to encourage flight behavior higher than traffic; Could plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides	New structure will need to emerge at a higher elevation closer to road on east side than current structure
6	12.05	8-10 ft high, impenetrable bottom, fine mesh	Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species	Straighten structure to improve line of sight. Install minor lighting inside. Clear vegetation, especially on east side to allow easier access and line of sight	Directional structure to encourage flight behavior higher than traffic	Best existing structure for deer. Potential project in the future; flagged for future repair
7	12.25	8-10 ft high, impenetrable bottom, fine mesh		Clear some vegetation from W side to enhance visibility; remove some	Directional structure to encourage flight behavior higher than traffic; Could also	

Id	Post Mile	Fence specifics	Design features	Near-term Recommendation	Aerial connectivity considerations	Notes
				sediment to increase structure height; clean up debris on both sides to enhance habitat at structure; remove invasives (e.g., pepper tree)	plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides	
8	12.95	8-10 ft high, impenetrable bottom, fine mesh		Remove invasives near structure. Address erosion and gullying in drainage to structure	Directional structure to encourage flight behavior higher than traffic; Could also plant additional trees (e.g. sycamore or coast live oak) to match up canopy on E and W sides	
9	13.75	6-8 ft high; fine mesh and impenetrable bottom	Rocks and logs on inside and outside of structure for small-scale habitat			Only true riparian culvert on SR-67. Culvert in good condition and likely won't need replacement for drainage
10	13.9	8-10 ft high, impenetrable bottom, fine mesh				Metal pipe in poor shape; Caltrans will likely line
11	14.98	8-10 ft high, impenetrable bottom, fine mesh				Metal pipe in poor shape; Caltrans will likely line
12	16.05	6-8 ft high; fine mesh and impenetrable bottom	Restore native vegetation, control erosion/gullying in area		Topography may not support aerial connectivity here	
13	17.61	~800 ft on either side of roadway, 8-10 ft high			May be some connectivity for flying species if overpass is adequately vegetated	Recreational path on bridge should be physically and visually isolated from remainder of overpass
14	20.17	No good tie in. Any fencing should be fine mesh and have impenetrable bottom to funnel small animals	low cover on outside and inside of structure (rocks, logs)		Topography may not support aerial connectivity here	Location is a minor draw but topography is generally flat in this area

Table B2. Detailed wildlife crossing recommendations for other roads in the SR-67 regional study area

Id	**Road**	**Wildlife Priority**	**Improvement Type**	**Nearest Crossing (mi)**	**Rd width (ft)**	**Right-of-way (ft)**	**Optimal Crossing Type**	**Minimum Crossing Type**	**New, Retro, or Exists**	**Optimal width (ft)**	**Optimal height (ft)**	**Min width (ft)**	**Min height (ft)**	**In corridor**	**Conserved**	**Min fence length E or S (ft)**	**Min fence length N or W (ft)**
15	SR-52	1	Minor	0.371	820.2	508.5	Bridge		Exists		13.1		9.8	Y	Y		
16	SR-52	2	Major	0.371	180.4	511.8	Arched or box culvert	Pipe culvert	Exists	16.4	9.8	13.1	6.6	Y	Y	2460.6	984.3
17	SR-52	2	Minor	0.865	492.1	187.0	Bridge		Exists		13.1		9.8	N	N		
18	I-8	3	Major	0.487	426.5	475.7	Arched or box culvert		New	23.0	11.5	16.4	8.2	N	N	1148.3	721.8
19	I-8	3	Major	0.487	574.1	393.7	Arched or box culvert		New	23.0	11.5	16.4	8.2	N	N	2624.7	1443.6
20	I-8	2	Major	1.443	246.1	262.5	Bridge		Retrofit		13.1		9.8	Y	N		
21	I-8	1	Major	2.786	426.5	656.2	Bridge	Arched culvert	Retrofit or new addition	23.0	11.5	16.4	8.2	Y	N		
22	Wildcat Canyon	3	Major	1.209	65.6	62.3	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	6.6		Y	Y	1410.8	754.6
23	Wildcat Canyon	3	Major	0.176	65.6	62.3	Arched or box culvert	Pipe culvert	Retrofit	13.1	9.8	6.6		Y	N	820.2	246.1
24	Wildcat Canyon	2	Major	0.176	72.2	52.5	Arched or box culvert	Pipe culvert	New	13.1	9.8	6.6		Y	N	1017.1	754.6
25	Wildcat Canyon	2	Minor	0.426	78.7	59.1	Box culvert/tunnel		Exists	16.4	13.1	13.1	9.8	Y	Y		
26	Wildcat Canyon	2	Major	0.426	39.4	65.6	Arched or box culvert	Pipe culvert	New	13.1	9.8	6.6		Y	Y	1066.3	984.3
27	Wildcat Canyon	1	Minor	0.265	44.3	147.6	Bridge		Exists		13.1		9.8	Y	N		
28	San Vicente Rd	2	Minor	0.265	59.1	105.0	Multiple arched culvert		Exists	16.4	9.8	13.1	6.6	Y	N	1378.0	1640.4
29	Poway Rd	3	Major	1.293	105.0	105.0	Arched or box culvert	Pipe culvert	New	13.1	6.6	6.6		Y	N	459.3	1082.7
30	Poway Rd	3	Minor	1.090	39.4	131.2	Pipe culvert		Retrofit	6.6		3.3		Y	N		

Id	Road	Wildlife Priority	Improvement Type	Nearest Crossing (mi)	Rd width (ft)	Right-of-way (ft)	Optimal Crossing Type	Minimum Crossing Type	New, Retro, or Exists	Optimal width (ft)	Optimal height (ft)	Min width (ft)	Min height (ft)	In corridor	Conserved	Min fence length E or S (ft)	Min fence length N or W (ft)
31	Scripps Poway Pkwy	2	Major	1.293	121.4	108.3	Arched or box culvert	Pipe culvert	New and retrofit	13.1	6.6	6.6		Y	Y	918.6	820.2
33	Scripps Poway Pkwy	2	Major	1.292	105.0	124.7	Arched or box culvert	Pipe culvert	New	16.4	9.8	13.1	8.2	Y	N	1574.8	1066.3
35	Scripps Poway Pkwy	1	Minor	0.788	105.0	534.8	Box culvert/tunnel		Exists	16.4	13.1	13.1	9.8	Y	Y		

Id	Fence specifics	Design features	Near-term Recommendation	Aerial connectivity considerations	Notes
15				May be some connectivity for flying species under bridge	Check height and condition; May need invasive control or some native habitat restoration
16	8-10 ft high, impenetrable bottom, fine mesh	Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species; provide adequate native cover leading to either end of culvert		May be some connectivity for flying species	Major improvement needed because culvert outlets on south side and only extends north to median; must be extended full length of road to allow for wildlife crossings
17			Clear some vegetation to ensure clear path and line of sight. Remove invasives	May be some connectivity for flying species under bridge	Must cross both 52 and West Hills Parkway. Check height and condition under both
18	8-10 ft high, impenetrable bottom, fine mesh	Some vegetation restoration (as compatible with transmission line zone)		Ensure transmission lines have visual markers and low electrocution potential	At transmission line right-of-way
19	8-10 ft high, impenetrable bottom, fine mesh	Light tubes at intervals through median sections or install lighting in structure		Topography may not support aerial connectivity here	N side elevated above S side. May require deeper structure and site prep on N side or different structure type or angle
20	Increase fence height to 8-10 m. Current placement OK.			May be some connectivity for flying species under bridge	Crossing should be moved E to Flinn Springs bridge on Old Highway 80. Bridge length should be expanded and aprons moved back to allow for vegetated strip under bridge for wildlife movement parallel to traffic on either side. Good vegetative cover already
21	8-10 ft high, impenetrable bottom, fine mesh			May be some connectivity for flying species under bridge	Improve intersection of Peutz Valley Rd and Alpine Boulevard. Need N-S connection of canyon. On Peutz Valley Rd, native vegetation and slope parallel to road should be improved to allow for wildlife movement
22	8-10 ft high, impenetrable bottom,	low cover on outside and inside of structure (rocks, logs)		Topography and vegetation should support this naturally. May need directional structure to encourage	

Id	Fence specifics	Design features	Near-term Recommendation	Aerial connectivity considerations	Notes
	fine mesh			flight behavior higher than traffic.	
23	8-10 ft high, impenetrable bottom, fine mesh		Remove invasives	Directional structure to encourage flight behavior higher than traffic - topography and natural veg support aerial crossings here.	Perhaps a single structure just N of driveway for 12050 Wildcat Cyn Rd.
24	8-10 ft high, impenetrable bottom, fine mesh				Suggested placement - just north of Muth Valley Road
25		Potentially add internal structure elements (rocks, logs) to facilitate movement by smaller species. Consider creating a wildlife-only section of the crossing shielded from the human use area	Control erosion in surrounding area to enhance cover in vicinity of tunnel	May be some connectivity for flying species through tunnel	
26	8-10 ft high, impenetrable bottom, fine mesh	Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species		Directional structure to encourage flight behavior higher than traffic - topography and natural veg support aerial crossings here.	Suggested placement - just south of Cienga Road
27				May be some connectivity for flying species under bridge	Check height and condition; May need vegetation clearing to allow line of sight for crossings of species like deer
28	Need extended fencing, 8-10 ft high; fine mesh with impenetrable bottom		Ensure revegetation with some lower cover and native shrubs is part of restoration of site after widening of San Vicente Road	Topography may not support aerial connectivity here	Double arched culvert under San Vicente Road? Current dimensions may not be suitable for deer crossings
29	8-10 ft high, impenetrable bottom,		Install seasonal signage and flashing lights to increase awareness about this area as a		Area is a narrow pinchpoint but crossing is important for connecting open spaces to allow for movement into and out of Penasquitos Creek and

Id	Fence specifics	Design features	Near-term Recommendation	Aerial connectivity considerations	Notes
	fine mesh		wildlife-vehicle collision hot spot and slow traffic during fall evening rush hour		under I-15.
30			Ensure existing culverts in this stretch are cleared of debris and have adequate energy dissipators to avoid gullying and erosion	Topography will challenge aerial connectivity here	Difficult structure placement due to elevated S side of the road and canyon on N side of the road
31	8-10 ft high, impenetrable bottom, fine mesh	Need to restore native vegetation; need dry crossing in structure that runs NW-SE to cross both Pomerado and Scripps Poway Pkwy	Clear sediment and debris in existing crossing. Create dry crossing in existing culvert, restore native vegetation, and rocks, logs, and low veg near entrance and inside structure to provide low cover for small species		Area is a narrow pinchpoint but crossing is important for connecting open spaces to allow for movement to/from Sycamore Cyn, Beeler Cyn, and Penasquitos Cyn. Need to cross both Scripps Poway Pkwy and Pomerado here
33	6-8 ft high; fine mesh and impenetrable bottom	Rocks, logs, and low veg near entrance and inside structure to provide low cover for small species			Target crossing for east side of Sycamore Canyon Road
35	Possible need to extend fencing or increase fence height. Perhaps add wing top to fence to prevent climbing	Potentially add internal structure elements (rocks, logs) to facilitate movement by smaller species. Consider creating a wildlife-only section of the crossing shielded from the human use area		May be some connectivity for flying species through tunnel	Scripps Poway Parkway Wildlife Tunnel

Effects of Wildfire on Wildlife and Connectivity

Prepared by: Megan K. Jennings, Ph.D.

January 23, 2018

Introduction

In southern California, where human impacts from development are limiting habitat connectivity for wide-ranging vertebrate species, fire is a disturbance regime that may also fragment habitats, further impacting those species. Although fire is a natural process in the southwestern U.S., increasing human development near open spaces has led to unnatural fire regimes with increased fire starts and an increased potential for vegetation-type conversion as a result. In the biodiversity hotspot of southern California, many studies have focused on the effects of urbanization and landscape fragmentation on wildlife. However, there has been relatively little attention to how human-mediated landscape fragmentation may influence natural disturbance processes, like wildfire, and how these synergistic disturbances impact wildlife populations.

Both fire frequency and size are increasing in southern California and are correlated with increasing anthropogenic development and human population growth in the region (Syphard et al. 2007, 2009). These studies suggest that at high human population densities, fire is eliminated from the ecosystem when contiguous vegetation necessary to carry fire is broken up by asphalt, concrete, and buildings. However, at intermediate human densities, housing developments and roadways are a source of increased fire ignitions which then spread into wildlands (Syphard et al. 2007, 2009). Both scenarios (too little fire, too frequent fire) present potential threats for species and community dynamics in southern California as shifts in the natural fire regime, coupled with increasing habitat fragmentation, have the potential to impact wildlife populations, communities, and entire ecosystems. In the highly urbanized landscape of southern California, long-term impacts such as habitat fragmentation and loss and shifts in disturbance regimes like the natural fire cycles, have resulted in persistent landscape changes (Syphard et al. 2009).

This report focuses on the impacts to wildlife connectivity posed by the proposed Newland Sierra project in the context of wildfires and the need for corridor redundancy. The Newland Sierra project proposes to build more than 2,100 homes on the I-15 corridor in the unincorporated portion of San Diego County between Escondido and Temecula. The project would be located in the area proposed for the North County Multiple Species Conservation Program (NCMSCP) on a site that has been identified as pre-approved mitigation area (PAMA).

As described in my previous reports (Jennings 2017a, 2017b), this project poses risks to wildlife connectivity in the area and could compromise overall design objectives of the NCMSCP. The proposed Newland Sierra project will significantly affect high quality core habitat and wildlife movement for both more common and sensitive and protected species to a degree that is not mitigated by the project design. The proposed project will have long-term direct and indirect impacts on wildlife from roadways, increased human activity, edge effects, human activity, and increasing fire frequency on wildlife movement. Due to the risks of wildfire and the numerous cumulative projects proposed along the I-15 corridor in northern San Diego County and southern Riverside County, it is particularly important to account for corridor redundancy in considering the Newland Sierra project. Regional connectivity plans must provide corridor redundancy to serve the range of species that may need to move between patches of habitat (Pinto and Keitt

2009, McRae et al. 2012), and to buffer against landscape disturbances, such as wildfires (Mcrae et al. 2008, McRae et al. 2012, Cushman et al. 2013, Olson and Burnett 2013). The biological analysis in the project’s draft environmental impact report lacked sufficient consideration of these issues.

Impacts of Wildfires and Shifting Fire Frequencies on Wildlife

Disturbances that occur at large spatial scales, such as Santa Ana wind-driven fires in southern California, like the recent Lilac Fire in San Diego County, are most likely to change landscape configuration, or pattern, which can lead to change in resource availability, environmental features, and corresponding responses in the structure of populations and communities, all key metrics to landscape integrity (Sousa 1984, Pickett and White 1985, Fraterrigo and Rusak 2008, Turner 2010). Large-scale landscape changes, particularly fragmentation (Gardner et al. 1993), have been shown to alter biotic interactions, and lead to a loss of connectivity evidenced by a decline in dispersal, reduced survival rates (Riley et al. 2003), and limited gene flow (Riley et al. 2006). In southern California, the two disturbances that overlap and interact, fire and human development, are the predominant drivers of the landscape. In this region, empirical evidence suggests a shift is underway in the disturbance regime (Keeley and Fotheringham 2003, Safford and Van de Water 2014).

Shifts in fire regime typically involve changes to fire intensity, size, frequency, type, seasonality, and severity (Flannigan et al. 2000). Fire-return intervals, the average time between two fire events, in the shrubland habitats like the areas where the Lilac Fire occurred and the Newland-Sierra development is proposed were historically 30 to 100 years. In similar areas of the County, fires are 33% more frequent now than pre-settlement, due in large part to increased development and roadways (Figure 1; Keeley et al. 1999, Safford and Van de Water 2014). This shifting disturbance regime with shortened intervals between fires interrupts the successional cycle, reduces plant diversity, and results in vegetation and habitat type change to non-native and grass dominated landscapes (Keeley 2005), reducing habitat suitability and connectivity for species dependent on intact shrubland landscape. Shifting weather patterns resulting from climate change may also contribute to the alteration of fire regimes in southern California. Climate models predict that temperatures will increase and humidity will decrease (Miller and Schlegel 2006). Under these conditions, Santa Ana winds, the hot, dry winds from the deserts in the east, may occur more often and later in the season when fuels loads are highest (Miller and Schlegel 2006, Guzman-Morales et al. 2016). The concurrent disturbances of expanding human development and a shifting climate may alter how fire structures the landscape. Extensive development, particularly in exurban areas, results in increases in human-caused ignitions and fires of large spatial extents (Syphard and Keeley 2015), as well as an overall increase in fire threat (Figure 2), which can have long-lasting impacts on the landscape and wildlife habitat.

Many wildlife species that occur in the Mediterranean-type ecosystems of southern California have adapted to wildfires. Wildlife exhibit differential responses to wildfires depending on the availability of refugia and species’ mobility, which determine their susceptibility to impacts from the direct effects of the fire. Habitat and diet breadth, population size and growth rates, as well as landscape connectivity can affect post-fire colonization and overall resilience to these types of stochastic events. While some research efforts in southern California have taken advantage of the natural experiment presented by San Diego's 2003 and 2007 wildfires to gather information about bird (Mendelsohn et al. 2008), small mammal (Brehme et al. 2011, Diffendorfer et al. 2012), large mammal (Schuette et al. 2014), and herpetofauna (Rochester et al. 2010) responses to wildfire, there is much to learn about individual- and population-level responses, in particular as it relates to increasing fire frequency. Linking the effects of shifting fire regimes on wildlife where frequent fire may result in vegetation type conversion from shrublands to grass-dominated habitats (Keeley 2005, Keeley and Brennan 2012) is a significant challenge. There is evidence of the effect of increasing fire frequency on some species, such as the iconic coastal sage scrub species, the threatened California gnatcatcher (*Polioptila californica californica*). Already challenged by habitat loss and fragmentation in the coastal regions of southern California, frequent fires have degraded habitat for the gnatcatcher (Winchell and Doherty 2014) as California sagebrush (*Artemesia californica*), laurel sumac (*Malosma laurina*), and white sage (*Salvia apiana*), key habitat elements for the bird, have been replaced by non-native annual grasses in areas that have experienced repeated fires. Habitat specialists and small species are not the only ones subject to the impacts of increasing fire frequency. Despite the fact that mountain lions (*Puma concolor*) are highly mobile and able to move away from fires, the species is potentially at risk from vegetation-type conversion to non-native annual grasslands (Jennings et al. 2016). Although this species may tolerate grasslands when moving between habitats (Zeller et al. 2014), habitat fragmentation between San Diego County and the Santa Ana Mountains to the north has limited gene flow and resulted in inbreeding for the southern California population (Ernest et al. 2014), a situation which further habitat degradation, particularly as a result of increasing fire frequency, could worsen.

Wildfire and Connectivity

Habitat connectivity is essential to climate-smart landscape strategies (Heller and Zavaleta 2009) and strengthens ecosystem resilience to additional stressors such as habitat fragmentation (Beier and Gregory 2012), and other disturbances, e.g., fire and disease (Noss 1991, Hilty et al. 2006). Across much of southern California, the state's Natural Community Conservation Planning (NCCP) program and the federal Habitat Conservation Plan (HCP) have been used to establish conservation networks to protect natural communities and prevent further habitat fragmentation (Ogden Environmental and Energy Services 1996, Riverside County 2003). Although the direct effects of anthropogenic landscape alteration, namely habitat loss and fragmentation, are paramount in this region (Soulé 1991, Crooks 2002, Beier et al. 2006), the indirect effects of intense human development such as changing patterns of natural disturbance regimes, *e.g.* wildfire, may present an equally large risk to landscape integrity. As human populations in southern California have grown dramatically over the last century, particularly in coastal areas, short fire-return intervals paired with habitat fragmentation, may have synergistic and long-term impacts on landscape connectivity that present a formidable conservation challenge. Given that these disturbances exert measurable impacts individually (Lindenmayer et al. 2008, Turner 2010), it is likely that the synergistic effects of shifting disturbance regimes and fragmentation present a serious threat to landscape connectivity (Turner 2010).

Given the importance of landscape connectivity to ensuring population viability and persistence, accurate assessments of physical and functional connectivity are critical. Dynamic landscape processes, like wildfires, may impede movement for many species in the short-term, but an altered fire regime may permanently alter landscape linkages. In particular, shifting disturbance regimes, like the increase in fire frequency and size reported in southern California, may have synergistic impacts that erode landscape connectivity if efforts are not made to buffer the number or impacts of fire on landscape linkages. New approaches to identifying factors that impair physical and functional connectivity are needed to develop mitigation strategies to maintain landscape connectivity if urbanization is considered on fire-frequent landscapes, with a particular focus on the coastal areas that are most impacted by development, and foothills and valleys where the wildland-urban interface is most at risk for increases in fire frequencies and consequential type conversion.

Building resilience into these networks of conserved lands can be approached from two perspectives: 1) reducing ignitions in fire-prone areas, and 2) account for these altered disturbance dynamics in conservation planning efforts like the Draft NCMSCP. Robust measures to reduce ignitions should be employed. However, reducing ignitions alone is unlikely to protect San Diego County's open spaces from fire and must be paired with complementary approaches to provide for habitat and connectivity when fires do occur. This includes planning for redundancy in linkages connecting habitat patches (Pinto and Keitt 2009). Because a single path is unlikely to equally serve all individuals of a species, let alone all potential species that may need to move between patches of habitat, multiple corridors between landscape blocks are often necessary (Pinto and Keitt 2009, McRae et al. 2012). Furthermore, this redundancy can also buffer against uncertainty and dynamic processes, particularly disturbances, on the landscape (Mcrae et al. 2008, McRae et al. 2012, Cushman et al. 2013, Olson and Burnett 2013). As discussed in my previous comments on the Newland Sierra draft environmental impact report, the project's biological analysis is deficient in its consideration of corridor redundancy. Threats to wildlife connectivity from wildfire emphasize the need to consider corridor redundancy with respect to Newland Sierra and the NCMSCP.

Furthermore, the assessment of connectivity and redundancy to provide for wildlife movement under a variety of conditions must be conducted at a regional scale. For San Diego County, this means consideration of conservation planning efforts and acquisitions as well as development projects in Orange and Riverside Counties. In particular, the Santa Ana-Palomar landscape linkage that has been identified as a critical movement corridor for many species (South Coast Wildlands 2008), most notably the mountain lion (Vickers et al. 2015), spans both San Diego and Riverside Counties and could be affected by several development projects that could limit functional connectivity in northern San Diego County.

Together with the cumulative projects proposed in this region, Newland Sierra could restrict wildlife movement in northern San Diego County as well as any opportunities to build resilience into a regional connectivity plan by providing for corridor redundancy. The Merriam Mountains area is currently one of the few shrub-dominated open spaces in San Diego County that has not experienced overly frequent wildfires which lead to increased risk of vegetation-type conversion from shrublands to non-native annual grasslands (Figure 1). Preserving a relatively intact landscape, such as the Merriam Mountains, is critical to developing a functional preserve system for the NCMSCP. However, the proposed Newland-Sierra Project's new roadways, increased traffic, homes, and increased wildland-urban edge are all known sources of fire ignitions in southern California (Syphard and Keeley 2015) that will threaten to increase the fire frequency in this area, which is already at high risk of fire due to the site's vegetation and terrain features

(Figure 2), as well as the risk of vegetation-type conversion. These same project elements will also further restrict wildlife movement in an area where movement is already constrained. The synergistic effects of restricted movement and habitat degradation caused by increasing fire frequency could greatly reduce connectivity in this region and threaten the functionality of the proposed preserve network under the NCMSCP. Figure 1 illustrates that few linkages remain in San Diego County that are not challenged by crossing urban development or areas that have burned repeatedly and are at risk for weed incursion, habitat degradation, and vegetation-type conversion. When dynamic landscape processes are considered, effective planning for landscape connectivity will require consideration of all potential projects that may affect wildlife movement as well as the synergistic disturbances that also affect landscape connectivity. The NCMSCP provides an opportunity for this type of regional wildlife connectivity planning, but individual development proposals considered in isolation and without adequately accounting for regional corridor redundancy could threaten the overall effectiveness of the planning process.

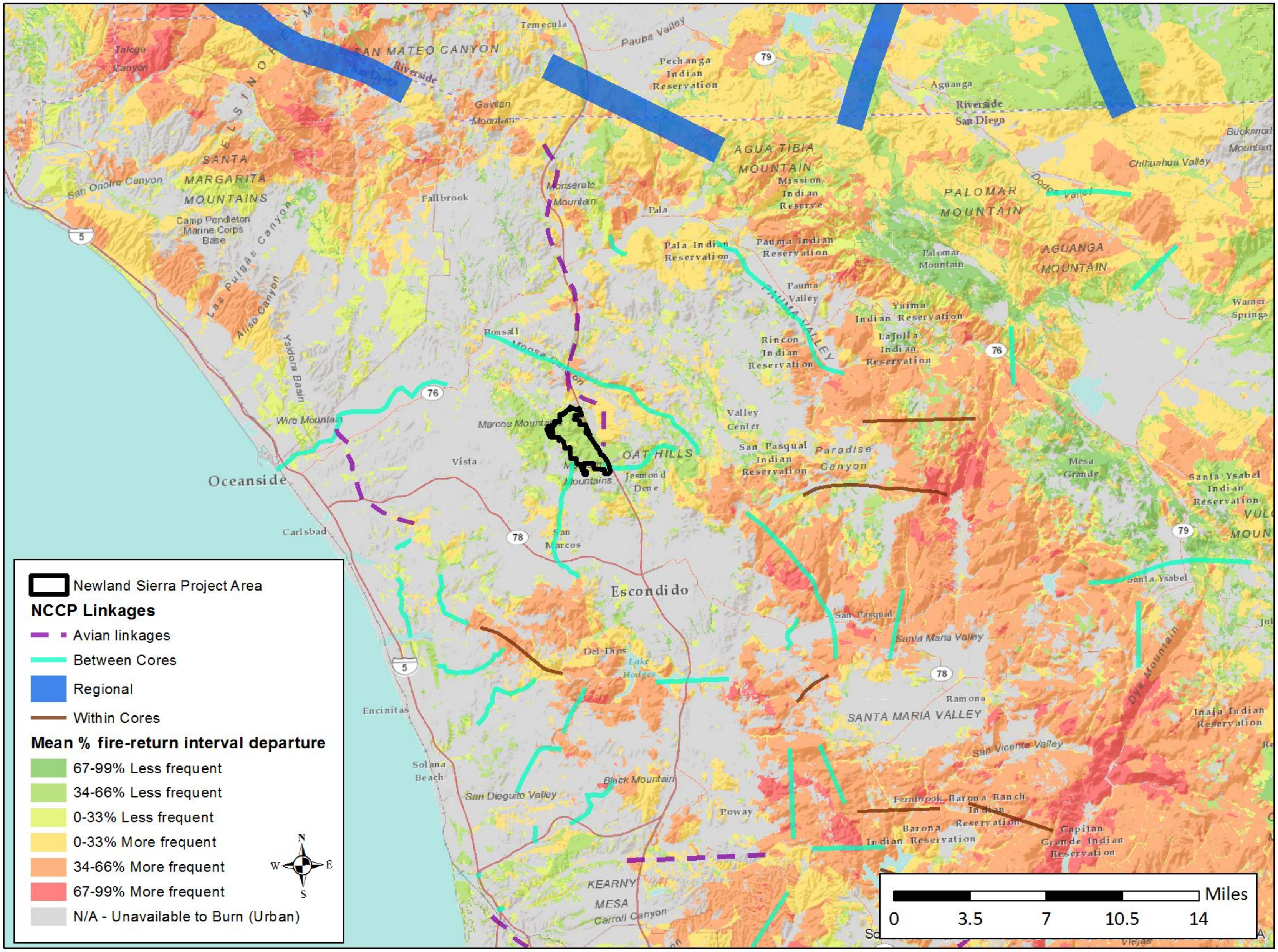


Figure 1. Map of fire-return interval departure (Safford and Van de Water 2014) for northern San Diego County and linkages identified in the Management Strategic Plan Connectivity documents for San Diego's NCCP areas.

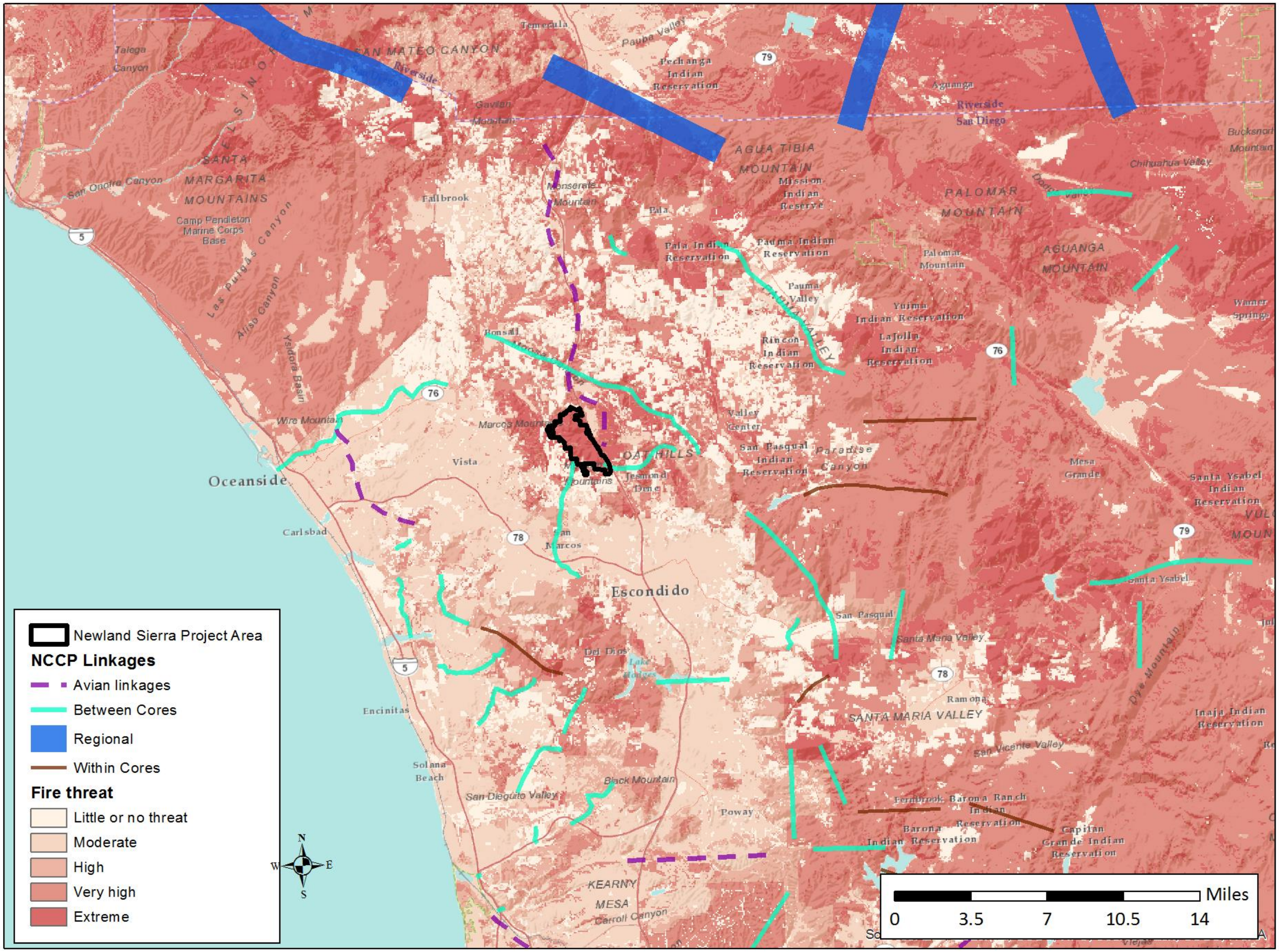


Figure 2. Map of fire threat for northern San Diego County as classified by California's Fire and Resource Assessment Program and linkages identified in the Management Strategic Plan Connectivity documents for San Diego's NCCP areas.

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Spatial risk assessment of eastern monarch butterfly road mortality during autumn migration within the southern corridor

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ABSTRACT

Road mortality may contribute to the population decline of eastern monarch butterflies (*Danaus plexippus* L.). We estimated autumn monarch roadkill rates within the primary Oklahoma to Mexico southern migration corridor (i.e., Central Funnel). Dead monarchs were surveyed along Texas roadsides during four weeks of autumn migration in 2016 and 2017. Roadkill averaged 3.4 monarchs per 100 m transect, reaching 66 per 100 m in a roadkill hotspot in southwestern Texas. Extrapolations of Central Funnel roadkill based on survey data and road types were 3.6 and 1.1 million in 2016 and 2017, respectively. Spatial distribution of roadkill across the Central Funnel was projected from Texas survey data using 30 m resolution MaxEnt niche models. Highest roadkill probability was linked to arid climate and low human population density. The latter variables may not be directly related to roadkill, but instead represent indirect correlates of increased densities of monarchs where the migration corridor narrows southwards. The higher roadkill projected in southwest Texas and Mexico by MaxEnt models agrees with previously reported monarch roadkill hotspots. MaxEnt-based 2016–2017 projections for annual roadkill rates throughout the Central Funnel averaged 2.1 million. This figure is similar to the result by simple extrapolation, and represents about 3% of the overwintering monarch population for these years. Mitigation at roadkill hotspots in the Central Funnel could reduce monarch roadkill mortality during migration and contribute towards conservation efforts for the monarch butterfly.

1. Introduction

Wildlife-vehicle collision is the most widely acknowledged impact of roads on wildlife, and can contribute to the decline of species of conservation concern (Tok et al., 2011; Visintin et al., 2016; Bennett, 2017), including globally declining pollinator insect species (Baxter-Gilbert et al., 2015). Roadkill can result in high mortality and lower abundance for species with large area requirements, pronounced migratory movements, small population sizes, and slow reproduction rates (Seiler and Helldin, 2006; Fahrig and Rytwinski, 2009). Wildlife-vehicle collisions are often spatially and temporally aggregated and substantial annual and inter-annual variation has been associated with environmental factors and traffic volume (Seiler and Helldin, 2006; Shilling and Waetjen, 2015). This tendency for high spatio-temporal variability in roadkill can be difficult to interpret based solely on the mapping of field survey data. Accordingly, there is a trend to use predictive spatial models to account for the variability in investigating the impacts of roads on wildlife mortality (Bennett, 2017). Typical roadkill niche models use a combination of environmental and anthropogenic variables and are often restricted to small areas (Visintin et al., 2016). Species distribution modeling has previously been used to project roadkill risk of mammals (Grilo et al., 2009; Roger and Ramp, 2009; Visintin et al., 2016, 2017) and owls (Gomes et al., 2009). Spatial models for insect roadkill have not yet been developed.

Only five out of 215 roadkill studies (2%) between 2011 and 2015 were specifically focused on invertebrates (Bennett, 2017). Despite this taxonomic bias in the literature, roadkill may be a substantial threat to certain insect populations. Baxter-Gilbert et al. (2015) projected that hundreds of billions of pollinating insects are lost annually to roadkill across North America. Although relatively few studies exist on butterfly road mortality, researchers have suggested that butterflies are one of the most common insect orders killed by vehicles (McKenna et al., 2001; Rao and Girish, 2007). Despite the high numbers of road-killed butterflies, the risk of Lepidopteran roadkill has been estimated as low to moderate (Baxter-Gilbert et al., 2015; Muñoz et al., 2015). Several studies have estimated butterfly roadkill numbers and examined

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contributing factors (Munguira and Thomas, 1992; McKenna et al., 2001; Ries et al., 2001; Rao and Girish, 2007; Skórka et al., 2013), but most of these studies concentrate on local, relatively sedentary butterfly populations and their utilization of roadside habitats rather than migratory butterflies. Migratory danaine butterflies (Nymphalidae: Danainae) may be especially susceptible to roadkill during migration (Her, 2008; Taiwan Environmental Protection Administration [EPA], 2010; Santhosh and Basavarajappa, 2014), including the monarch butterfly (*Danaus plexippus* L.) in the United States (McKenna et al., 2001) and Mexico (Correo Real, 2015).

Significant population decline of the eastern migratory monarch butterfly has been observed at the overwintering sites in Central Mexico during the past two decades (Vidal and Rendón-Salinas, 2014; Thogmartin et al., 2017). Consequently, the persistence of the migratory phenomenon of the eastern population may be endangered (Brower et al., 2012). The long-distance migration of monarchs is unique among butterflies. Mortality during the autumn migration (often referred to as fall migration) has been suggested as a contributing factor to the decline (Badgett and Davis, 2015; Ries et al., 2015a; Inamine et al., 2016; Agrawal and Inamine, 2018). Road mortality may significantly affect monarch survival during migration, especially where monarchs become highly concentrated as the migration narrows in Texas and northern Mexico (Badgett and Davis, 2015). Only McKenna et al. (2001) have previously evaluated monarch butterfly roadkill. They reported monarchs as the second-most killed butterfly species during six weeks of autumn in Illinois. They estimated that > 500,000 monarchs were killed statewide along interstate highways during one week in early September 1999 (McKenna et al., 2001). There are several unpublished citizen-science reports of locally high monarch roadkill occurrence in West Texas and northern Mexico during the autumn migration, with observed roadkill reaching 5.7 monarchs per meter near Monterrey, Mexico (Correo Real, 2015; Journey North, 2017). Incidences of high monarch road mortality in northern Mexico have led to the placement of road signs along portions of highways in to reduce speed in the presence of monarchs (Vangaurdia, 2016).

Monarch roadkill has yet to be quantified in relation to an overall population estimate. Seiler and Helldin (2006) point out that any sustained mortality factor, such as roadkill, can be especially damaging for species that are either approaching or are in an annual population decline, such as the monarch. The extent of monarch roadkill needs to be assessed to estimate its potential contribution to the population decline and support conservation planning. Our goal was to develop MaxEnt niche models for monarch road mortality during the autumn migration within the main migration pathway in Texas. The MaxEnt algorithm has been employed before to spatially investigate vehicle-animal collisions of birds and mammals (Ha and Shilling, 2017). The roadkill models were also projected throughout the Central Funnel, which is the identified main southern autumn migratory pathway within the Central Flyway for monarchs from Oklahoma to Mexico (Tracy, 2018; Tracy et al., 2018a). This study includes the first analysis of monarch roadkill data outside of Illinois, and the first development of a spatial roadkill model for an insect. Our specific objectives were to (1) conduct monarch roadkill field surveys within the Central Funnel in Texas, (2) develop MaxEnt niche models for roadkill within the Texas survey area, and project these models throughout the Central Funnel, (3) estimate monarch roadkill numbers within the survey area and the Central Funnel using both simple field survey-based and model-based extrapolation techniques, and (4) discuss the results in the context of monarch conservation and potential applications to other species of conservation concern.

2. Methods

2.1. Study species

The monarch autumn migration is uniquely accomplished by one generation. Adults begin migrating in late August to September from the summer breeding grounds, traveling to overwintering grounds in Central Mexico (Brower, 1995; Calvert and Wagner, 1999). Most migrants usually reach Oklahoma and North Texas in late September or early October (Calvert and Wagner, 1999; Monarch Watch, 2018a) and arrive at the overwintering grounds in November (Brower et al., 2006). There are two main migration routes, the Central Flyway and the Eastern or Coastal Flyway (Calvert and Wagner, 1999; Howard and Davis, 2009). The Central Flyway through the Great Plains is the most heavily traveled route (Howard and Davis, 2009), which narrows into the Central Funnel from Oklahoma southwards (Tracy, 2018; Tracy et al., 2018a).

Autumn migrants fly during the day and stop at night and during inclement weather to nectar and roost in trees and shrubs (Brower, 1996). These roosts may comprise a few individuals to several thousand individuals and may last one to several days (Davis and Garland, 2004; Howard and Davis, 2009). In the morning, roosting monarchs either resume migration or search for nectar. These behaviors are influenced by wind patterns or lipid levels (Brower, 1996; Davis and Garland, 2004). During unfavorable southerly winds, monarchs may roost for several days (Schmidt-Koenig, 1985). Migrating monarchs are observed to nectar in a variety of locations, including in right-of-ways (Brower et al., 2006), where they may be vulnerable to vehicle collisions. Brower et al. (2006) suggested that monarchs shift their behavior upon reaching Texas and spend more time nectaring to accumulate lipids for the winter and re-migration in the spring. Migrating monarchs regularly fly at high altitudes, around 300–500 m (Gibo and Pallett, 1979; Gibo, 1981, 1986), but may fly close to the ground, especially when facing headwinds or during overcast weather (Gibo, 1986; Brower, 1996), exposing them to road mortality. Citizen science observations also include reports of low flying fall migrating monarchs over roadways (Correo Real, 2015).

2.2. Monarch roadkill surveys and simple roadkill extrapolation

Monarch roadkill field surveys were conducted during the main autumn migration through the Central Funnel in Texas (Fig. 1). Four four-day surveys were conducted in each of the autumns of 2016 and 2017, between 10th October to 4th November and 3–27 October, respectively. The survey area was divided into four north to south sections, with surveys timed to generally occur after the dates of average peak migration (Journey North, 2017; Monarch Watch, 2018a) to allow time for the accumulation of road-killed monarchs. Observed monarch roadkill densities most likely represent accumulations of dead migrating monarchs over a period of one or two days to a few weeks during the main migration pulse through an area (Munguira and Thomas, 1992). Surveyed road types included (1) highways, (2) primary roads, and (3) secondary roads. Each survey location comprised at least a single 100 m by 1 m transect along the grassy edge of one side of the roadway. To assess if the side of the road surveyed influenced the number of dead monarchs, additional transects were surveyed across multiple edges of single and divided-lane highways at some sites. Transects were located using a handheld GPS device (accuracy up to ± 3 m). Roadkill transects were spaced according to travel and survey time constraints at about 30 to 100 km intervals along the primarily east to west pre-planned survey routes, with additional surveys in 2016 in the southwestern portion of the study area where high monarch roadkill was found (Fig. 1).

All dead monarchs or parts of monarchs were collected to estimate the total number and sex ratio of dead monarchs along transects. A similar spring monarch roadkill survey was conducted in Texas during April to May of 2017 (Fig. A.1; for details, see Appendix A, section 1.1). The boundary of the background evaluation extent for our roadkill study was defined by a 10 km buffer around a convex hull polygon formed using un-thinned 2016 to 2017 monarch roadkill survey data (Fig. 1). We extrapolated the mean roadkill counts for the three road

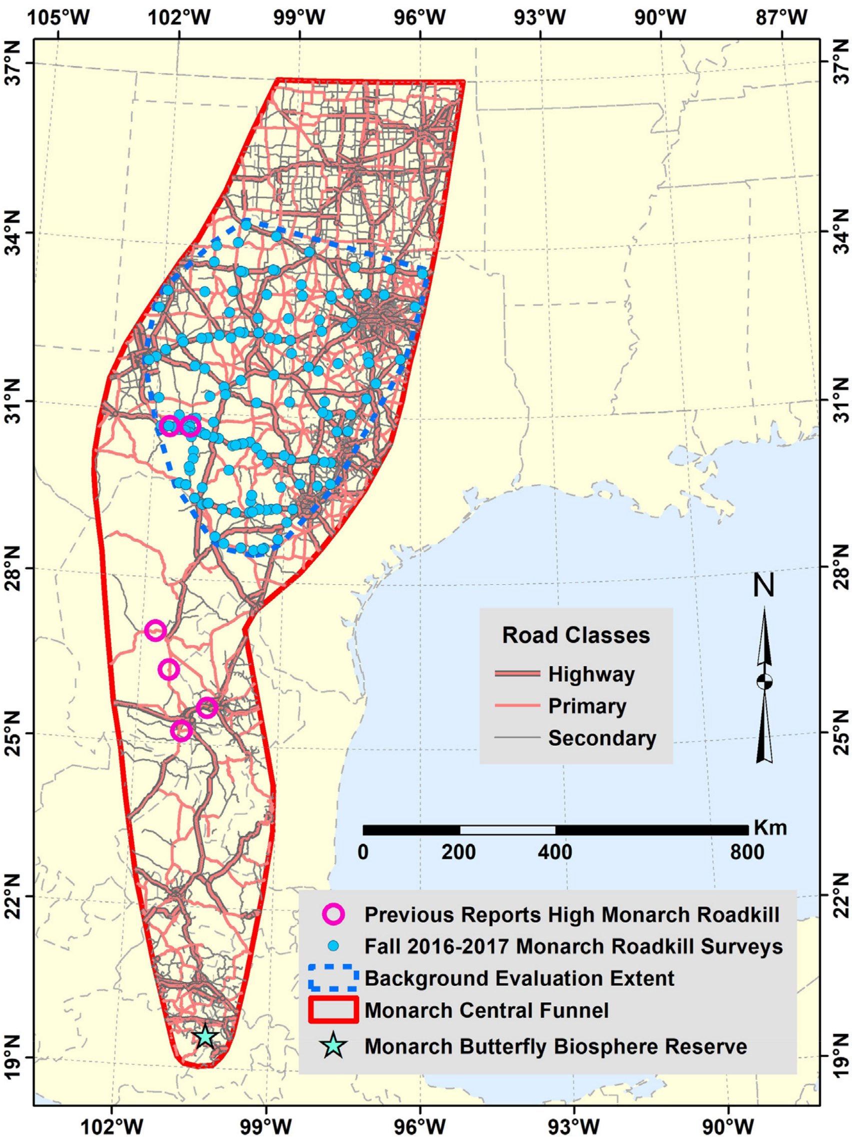

Fig. 1. Monarch roadkill survey 100 m transects for autumn 2016 and 2017 along three major road classes within the monarch Central Funnel in Texas.

types over the background evaluation extent and Central Funnel in a manner similar to that of McKenna et al. (2001). Roadkill rates in areas of locally high monarch roadkill (hotspots) can vary greatly between years and highly differ from other areas. Consequently, roadkill rates in hotspots can bias roadkill rates in larger areas if they are disproportionally represented in the sampling. Therefore, in some extrapolations, hotspot roadkill rates were considered separately for each year from non-hotspot locations. This separation allowed us to understand the importance of the roadkill hotspots within a year, and compare the hotspot differences between years. We also made roadkill extrapolations including hotspot roadkill rates with non-hotspot data and thinning the hotspot data in 2016 to be in proportion to the sample effort in non-hotpot locations (for details, see Appendix A, section 2.1).

2.3. Environmental variables

Thirty environmental variables were initially screened for use in the roadkill modeling (Table A.1, Fig. A.2). These variables were selected for their value in previous roadkill niche models and for their use in characterizing the environment of the study area. The variables consisted of nine topographic indices (including four stream indices), eight land cover indices, six road indices, three human population indices, and four climatic indices. All indices were either calculated at 30.8 m spatial resolution or resampled with bilinear interpolation to the 30.8 m resolution, to match the resolution of the base layer of 1 arc sec Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) data obtained from USGS Earth Explorer (https://earthexplorer.usgs.gov/). The high spatial resolution of 30.8 m facilitated modeling of roadkill along individual surveyed roadways over a broad area (see more details in Appendix A, section 7).

2.4. Monarch roadkill models

Preliminary MaxEnt model runs indicated that there was not enough data from 2017 to obtain good accuracy statistics for both single year models. Consequently, we combined 2016 and 2017 roadkill presence data, which were randomly spatially thinned to 2 km to reduce spatial autocorrelation. Ten thousand background points were randomly generated within the road mask evaluation area. We calculated background/presence versions of the area under the curve statistic (AUC_{bgp}) and true skill statistic (TSS_{bgp}) using R software (R Core Team, 2018) and the PresenceAbsence package (Freeman and Moisen, 2008). In the same manner, we calculated a presence/absence version of AUC (AUC_{pa}) and TSS (TSS_{pa}) using transects with no observed monarch roadkill as absence data, although we acknowledge roadkill may have occurred in these absence locations as well. We adjusted the MaxEnt beta regularization value to two and used only quadratic and hinge features to reduce model complexity and overfitting for improving model generalization (Jiménez-Valverde et al., 2008; Warren and Seifert, 2011; Tracy et al., 2018b).

Roadway rasters served as a mask for analysis of environmental variables. The original set of 30 environmental variables was decreased to 20 variables. We dropped nine variables exhibiting zero or negative testing gain of AUC_{bgp} from a MaxEnt threefold jackknife run (Table A.1, Fig. A.3). We also dropped traffic volume because data were not readily available for Mexico. Traffic volume was utilized in preliminary niche models for the Texas background evaluation extent. Preliminary runs indicated that no substantial gain in model performance was achieved with > 10 of the 20 variables, and that employing fewer variables (three) substantially increased undesired high spatial variability in roadkill among models. Consequently, final MaxEnt roadkill models were developed from ten random sets of ten of the 20 variables to represent model variability due to variable selection. The absolute Spearman rank correlation of variables within random variable sets was limited to < 0.7 using the multiple randomized sequential forward selection procedure within the random subset feature selection algorithm (RSFSA) of Tracy et al. (2018b). The final MaxEnt models were calibrated to binary presence/absence format using a threshold of maximum TSS_{pa} (Liu et al., 2013) and combined using frequency consensus to form a feature subset ensemble. We also created presence/absence niche models for monarch roadkill using linear and quadratic binomial logistic regression with the R Glmnet package (Friedman et al., 2010) for the same ten random sets of ten of 20 variables. These presence/absence models produced lower AUC_{bgp} values and similar AUC_{pa} values compared to MaxEnt models, and these models were not investigated further (results not shown).

3. Results

3.1. Monarch roadkill survey and simple roadkill extrapolation

We surveyed 16.1 km of roadsides (161,100 m transects), 8.8 km in 2016 and 7.3 km in 2017. We found 581 dead monarchs in 59 locations (102 absence locations) for an average of 3.4 monarchs per transect. We found 546 dead monarchs in 2016 and 35 in 2017 (for raw survey count data, see Appendix A, section 3.1). Of the 546 monarchs in 2016, 499 (91%) were located along or near IH-10 between Sonora and Sheffield (23 of 95 transects) (Fig. 2). This area was defined as a single large 2016 hotspot area extending 95 km along Interstate Highway (IH) 10 from Sonora to 24 km east of the Pecos River. This hotspot included a portion of Texas state highway (SH) 163 extending from 7.6 km south of Ozona to 5 km north of Ozona and a 2 km section of SH-137 extending west from the junction with SH-163. The hotspot was bounded along IH-10 in the west and east by counts of 15 and 10 roadkill per 100 m, and included counts of 21 and 6 roadkill per 100 m on SH-137 and SH-163, respectively. About 93% (466/499) of the dead monarchs in the 2016 hotspot occurred in 14 transects ranging from 10 to 66 per 100 m (Fig. A.4). A total of 257 monarchs were sexed in 2016–2017, of which ca. 38% were female (n = 98). The portion of females was 41% in 2016 (132 males, 91 females) and 21% in 2017 (27 males, 7 females). After the 2 km spatial thinning for spatial modeling, the field survey data consisted of 151 transects (53 presence and 98 absence) and 249 individual dead monarchs. Only two road-killed male monarchs were found among 54 transects in our spring 2017 roadkill survey (Fig. A.1).

Southern edges of roadsides contained 43.8% (± 36% SD, n = 13) of the roadkill found in the northernmost edge for both single and divided-lane roads. This relationship was used to estimate roadkill across all two to four edges per roadway when extrapolating roadkill per km per year (for details, see Appendix A, section 5). Estimated roadkill per km ranged from 6.15 to 645 monarchs per km depending on year, road type, and location in relation to the hotspot area (Table 1). In 2016, mean estimated roadkill per km along highways was significantly higher within the Sonora-Sheffield hotspot (645.38; SD = 446.92; n = 15) compared to outside the hotspot (12.64; SD = 22.30; n = 22) (P = 0.00008; Welch *t*-test). Between years, the estimated roadkill per km generally varied widely among road types, and there was no evidence of any hotspot in 2017 (Table 1). Estimates of roadkill within the hotspot area in 2016 and 2017 ranged from about 74,000 to 5000, representing about 10% and 1% of the entire mortality within the Texas background evaluation extent. Using the field survey data from the whole area, including the randomly thinned hotspot data, the estimated roadkill for the Central Funnel in 2016 rose to over 3.5 million monarch butterflies (Table 1). The estimate for 2017 was 1.1 million road-killed monarchs. Combining the data from both of the years yielded an annual estimate of 2.1 million road-killed monarchs. When the hotspot data were separated from the survey data, total estimated annual roadkill rates in 2016 and 2017 were about 1.6 million and 1.0 million monarchs, respectively. In 2016, about 47%–49% of the roadkill within the Central Funnel was projected to occur within the Texas background evaluation extent, of which 5% was projected to occur in the Sonora-Sheffield hotspot area. In 2017, only about 0.3% of the roadkill within the Central Funnel was projected within the hotspot area, and the percent roadkill in the background area ranged from 31% when hotspot data were analyzed separately to 48% when data from the hotspot area were included (Table 1, Appendix A, section 2).

3.2. Monarch roadkill model

The feature subset ensemble of ten MaxEnt roadkill niche models provided excellent discrimination of roadkill presence locations from background locations within the background evaluation extent, with AUC_{bgp} values ranging from 0.82 to 0.88 (0.86 ± 0.02, mean ± SD). The models provided marginally poor discrimination of roadkill presences from absences observed in the field, with AUC_{pa} values ranging from 0.60 to 0.67 (0.64 ± 0.02, mean ± SD). Among the top eight variables with the highest permutation importance in the MaxEnt models (Table 2) were three human population density indices and two climatic indices. Other top ranked variables included elevation (m), road density over a 3 km radius (km/~28 km^2), and percent cover of artificial surfaces within a 500 m radius. Traffic volume (annual average daily traffic, AADT) ranked third in permutation importance in preliminary models but was not available for Mexico, precluding its use in our final models.

The MaxEnt response curves for population density indices all indicated that lower human population densities had higher association with monarch roadkill (Fig. 3A, E). The climatic indices indicated that roadkill was associated with more arid climates (Fig. 3B, C). Lower road densities and lower percent cover of artificial surface were also associated with higher monarch roadkill (Fig. 4F, G). The response curve for traffic volume, which was not used in the final models, indicated that the highest roadkill was associated with lower traffic volume. The traffic volume response curve was very similar to that of percent cover of artificial surface (Fig. 3G, H), with which it was moderately correlated (r_s = 0.58).

The proportion of MaxEnt models projecting monarch roadkill generally increased from northeast to southwest within both the background evaluation extent and Central Funnel (Fig. 4; see Appendix Section 5 for embedded zipped shapefile of MaxEnt consensus model). The highest number of models projected roadkill within much of southwest Texas and Mexico in the Central Funnel. None of the MaxEnt models projected monarch roadkill over most of the northeastern Central Funnel, including the Dallas/Fort Worth metroplex and most of eastern Oklahoma.

Roadkill extrapolations for each of the ten individual MaxEnt models were made across each year and both years combined.

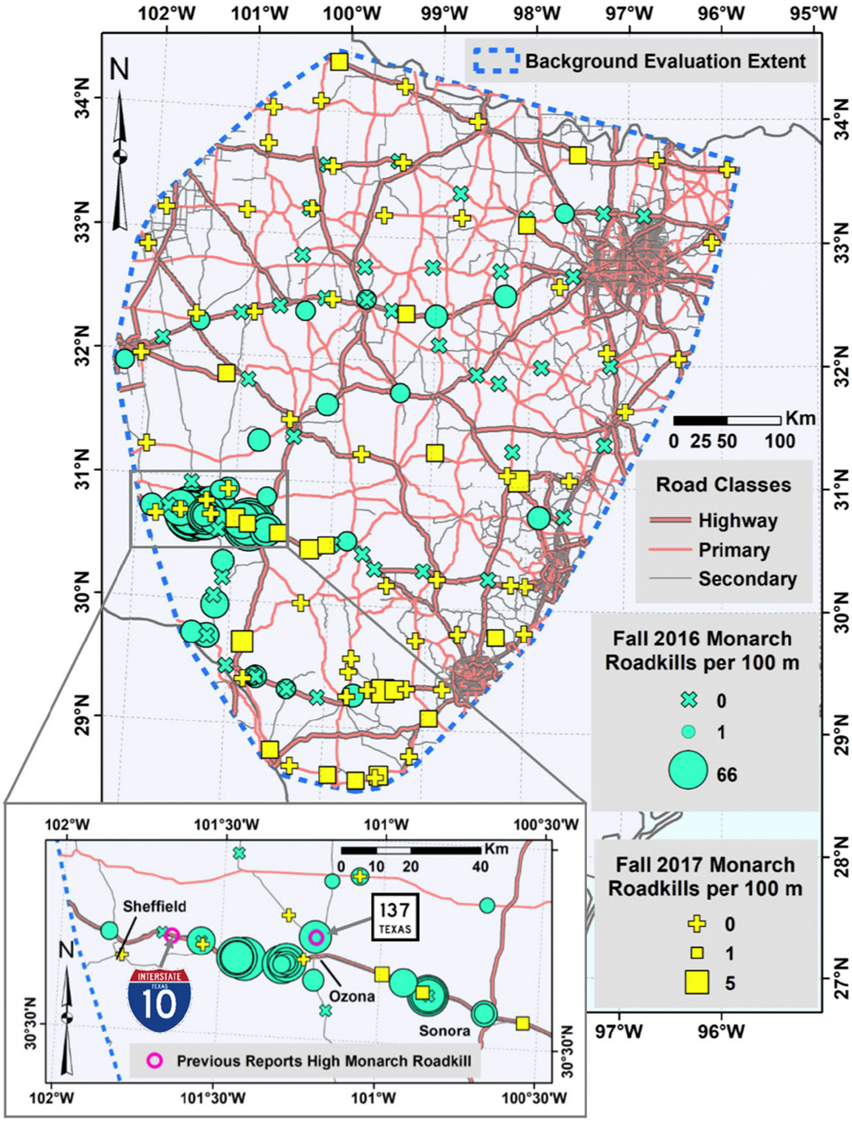

Fig. 2. Monarch roadkill autumn 2016 and 2017 survey results for 100 m transects along major road classes within the background evaluation extent in the monarch Central Funnel in Texas, including previously reported locations of high monarch roadkill.

Extrapolations were based upon roadkill rates per km for presence-only transects (no zero roadkill data) of each road type that were multiplied by the MaxEnt model predicted lengths of roadkill presence for the road type. Roadkill rate calculations for extrapolations included data from hotspot transects that were thinned for 2016 as done for simple extrapolations (for details, see Appendix A, sections 2.1, 5). Extrapolating roadkill rates across the Central Funnel, we estimated averages of 3.0 ± 0.7 and 1.1 ± 0.3 million (mean ± SD) road-killed monarchs for 2016 and 2017, respectively (Tables 1, A.2). Combining roadkill data across both years for the Central Funnel yielded annual roadkill rates of 2.1 ± 0.5 million. The mean projected percentage of road-killed monarchs in the Central Funnel that occurred within the Texas background evaluation extent ranged from 67% to 68% in 2016 and 2017 (Tables 1, A.4).

4. Discussion

4.1. Monarch roadkill survey

In our 2016 roadkill survey (but not 2017), we found a Sonora-Sheffield, Texas, monarch roadkill hotspot that corresponds to the only two previous citizen-science reports of monarch roadkill hotspots in the US (Fig. 2). It is unclear why hotspots have repeatedly occurred in this area. The hotspot location may be partly related to higher densities of migrating monarchs in more southern areas of the Central Funnel. In addition, local stochastic weather events probably influence the occurrence of roadkill hotspots, such as unfavorable winds that may induce lower monarch flight patterns or extended roosting and nectaring behavior close to the ground in the vicinity of roadways. More research is needed to evaluate how frequently roadkill hotspots occur in this region. It is possible that one or both years represent an outlier, and that hotspots may occur in additional areas.

The variation in roadkill rates observed between the two years of our survey was consistent with other roadkill studies (Seiler and Helldin, 2006). Our overall roadkill rates varied from 6 to 646 dead monarchs per km depending on year, road type, and location (Table 1). This range falls within previous reports for monarchs of from 1.3 to 11.9 butterflies per km per week in Illinois (McKenna et al., 2001) to a very high number of 115 road-killed monarchs within a 20 m stretch along toll highway 40D southwest of Monterrey, Mexico in October 2015 (Correo Real, 2015; see Appendix A, section 8 for data). Reported roadkill rates for other butterflies have ranged from 0.45 to 80 per km per day in North America, Asia, and Europe (Rao and Girish, 2007, De la Puente et al., 2008, Yamada et al., 2010, Skórka et al., 2013, Baxter-

Table 1
Monarch roadkill estimates per year for 2016 to 2017 over the Sonora-Sheffield roadkill hotspot, Texas background evaluation extent (BEE) and the Central Funnel (Figs. 1–2) from the field data by road type using simple extrapolation or MaxEnt model projections.

Year	Millions of monarch roadkill[a]						
	Simple extrapolation					MaxEnt model extrapolations $\bar{X} \pm$ SD (n = 10)[b]	
	Hotspot data separated			Hotspot data included		Hotspot data included	
	Sonora-Sheffield hotspot	Texas BEE	Central Funnel	Texas BEE	Central Funnel	Texas BEE	Central Funnel
2016							
Millions of dead	0.074	0.768	1.570	1.663	3.554	2.050 ± 0.760	3.041 ± 0.743
% Overwintering population[c]	0.09%	0.90%	1.82%	1.93%	4.03%	2.36 ± 0.86%	3.46 ± 0.82%
% Texas BEE mortality	9.58%						
% Central Funnel mortality	4.69%	48.95%		46.78%		66.48 ± 14.79%	
2017							
Millions of dead	0.005	0.492	1.042	0.533	1.131	0.738 ± 0.272	1.084 ± 0.258
% Overwintering population[c]	0.01%	0.79%	1.67%	0.86%	1.81%	1.19 ± 0.43%	1.73 ± 0.41%
% Texas BEE mortality	1.02%						
% Central Funnel mortality	0.32%	31.34%		47.16%		68.86 ± 14.18%	
2016–2017							
Millions of dead	0.058	0.561	1.138	0.995	2.118	1.460 ± 0.540	2.119 ± 0.510
% Overwintering population[c]	0.09%	0.91%	1.82%	1.59%	3.33%	1.96 ± 0.71%	2.82 ± 0.66%
% Texas BEE mortality	10.25%						
% Central Funnel mortality	3.66%	35.75%		27.99%		67.90 ± 15.08%	

[a] Mean roadkill rates (roadkill/km/year) (Table A.2) by road type for extrapolations are calculated from transects in the Texas BEE and incorporate estimates for all road edges. Roadkill rates are multiplied by length of road in various areas to obtain extrapolations (see Table A.3 for road lengths used in simple road type extrapolation) (for all calculations, see Appendix A, section 5).

[b] See Table A.4 for individual MaxEnt model estimates.

[c] Based on 84.61 (2016) and 61.4 (2017) million overwintering monarchs (Monarch Watch, 2018b). Estimated from 21 million monarchs per hectares overwintering (Thogmartin et al., 2017).

Gilbert et al., 2015).

The observed sex ratios of roadkill monarchs were also consistent with previous studies. About 38% of the dead monarchs in our autumn field surveys were females, ranging from 21% in 2017 to 41% in 2016. These figures generally match two separate citizen science observations on the percentage of female monarch roadkill in Mexico of 27% and 36% in October 2015 (Correo Real, 2015). They also are within the range reported from the other roadkill study (McKenna et al., 2001), as well as studies of sex ratios during migration (Borland et al., 2004) or on the overwintering grounds (Steffy, 2015). Davis and Rendón-Salinas (2010) found a decreasing trend (~10%) in percent female monarchs at the Mexican overwintering sites from 1976 to 2008, which they suggested could reflect female biased mortality due to the protozoan parasite *Ophryocystis elektroscirrha*.

While our estimates of monarch roadkill are likely conservative, carcass persistence is not likely to be a major source of bias. However, we did not evaluate persistence in our study, which could vary based on various factors, such as region, time of year, and weather conditions.

Munguira and Thomas (1992) placed butterfly specimens on roadsides and found that only one of their 50 specimens disappeared during

Table 2
MaxEnt model variable permutation importance for 19 variables used in ten random sets of ten of the 20 variables in monarch roadkill models.

Variable[a]	Abbreviation	Permutation importance[b], mean ± SD
Human population density per km^2 in 9 km radius (population/254.47 km^2)	*popden9kr*	44.2 ± 3.8 (3)
Autumn quarterly mean monthly actual evapotranspiration/potential evapotranspiration × 1000	*etrt_autq*	41.7 ± 23.3 (2)
Annual mean monthly rainfall (mm)	*prec_ann*	36.4 ± 15.6 (4)
Human population density per km^2 in 3 km radius (population/28.27 km^2)	*popden3kr*	30.1 ± 0.0 (1)
Elevation (m)	*elev*	27.9 ± 5.5 (4)
Distance to urban areas (areas with ≥ 300 humans per km^2) (km)	*urbdist*	27.1 ± 10.8 (4)
Road density, km road in 3 km radius (km/28.27 km^2)	*roadden3kr*	19.6 ± 2.4 (2)
Artificial surfaces % cover in 500 m radius	*artsur_500mr*	13.4 ± 3.2 (3)
Autumn quarterly mean monthly maximum temperature (°Celsius)	*tmax_autq*	10.5 ± 9.8 (3)
Distance to highways (m)	*hwydist*	10.4 ± 2.5 (7)
Latitude (decimal degrees)	*latitude*	6.4 ± 4.3 (3)
Grasslands % cover in 500 m radius	*grslnd_500mr*	5.6 ± 3.4 (9)
Autumn mean quarterly wind speed (m/s)	*wndsp_autq*	5.6 ± 5.4 (4)
Distance to secondary roads (m)	*secrddist*	5.1 ± 2.9 (8)
Shrublands % cover in 500 m radius	*shrub_500mr*	4.5 ± 3.4 (9)
Distance to primary roads (m)	*primrddist*	2.3 ± 3.0 (4)
Road density, km road in 500 m radius (km/0.79 km^2)	*roadden500mr*	2.2 ± 3.8 (5)
Distance to high flow accumulation areas ($> 60{,}000$ ~km^2 upslope grid cells) (m)	*strmhiflodist*	1.2 ± 1.0 (5)
Topographic Position Index (TPI), 3 km radius	*tpi3kr*	1.0 ± 0.2 (5)
Cultivated land % cover in 500 m radius[c]	*cult_500mr*	0.0 ± 0.0 (0)

[a] See Table S1 for sources of variables. Variables ordered from highest to lowest mean permutation importance.

[b] Permutation importance of the variable in the MaxEnt models, number of models in which the variable was used out of the 10 random models in parentheses.

[c] Cultivated land layer was initially included in all 10 random models, but it was not included by MaxEnt in calculating any of the models.

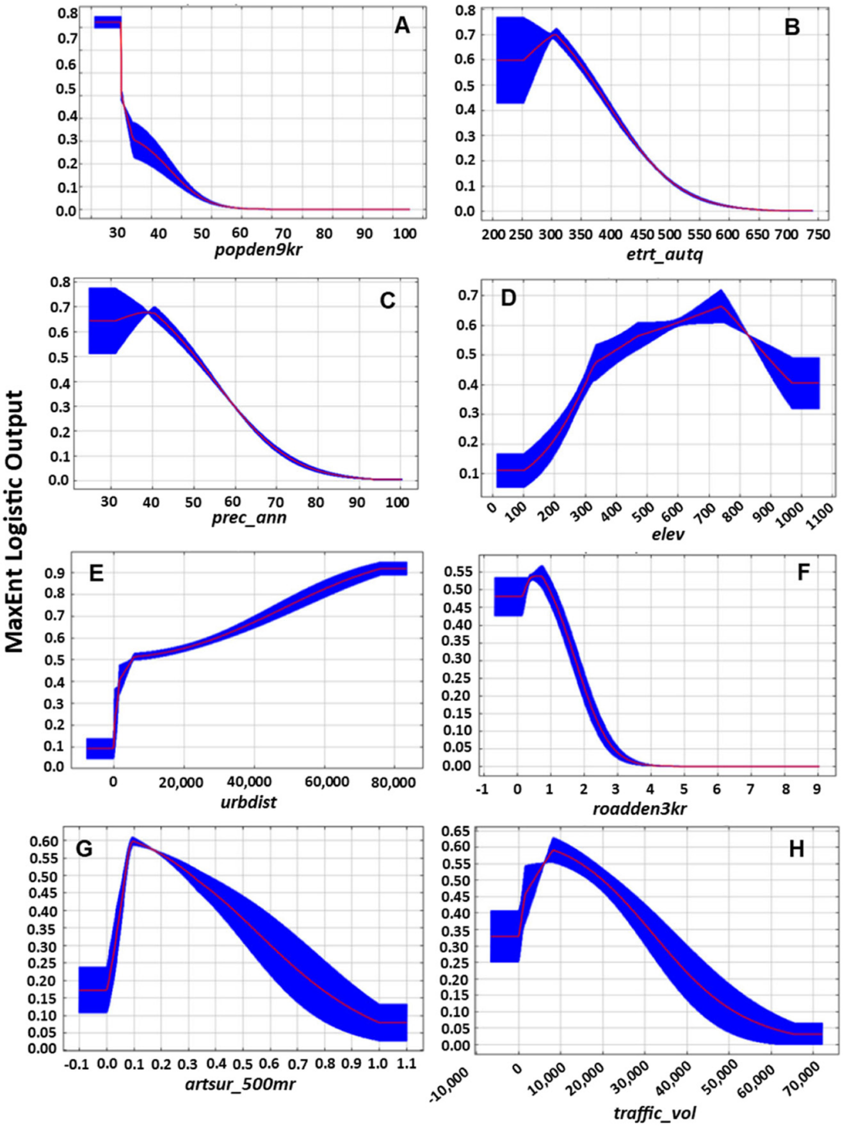

Fig. 3. MaxEnt variable response curves (logistic output probability of presence vs. variable) representative of the final ten models (A–G) and for a 30-variable model (H): (A) popden9kr, (B) etrt_autq, (C) prec_ann, (D) elev, (E) urbdist, (F) roadden3kr, (G) artsur_500mr, (H) traffic_vol (traffic volume for 2015) (see Table 2 for abbreviations and permutation importance).

two weeks (daily loss rate of 0.15%). Several factors contribute to the conservative nature of our estimates, including the difficulty in detection of dead monarchs, especially in taller vegetation, shredding of dead monarchs by roadside mowing, and a portion of the monarchs remaining attached to the colliding vehicles (McKenna et al., 2001; Seiler and Helldin, 2006). However, several studies indicate that road killed butterflies are mostly blown to the roadside edge, with individuals rarely trapped in car grills (Munguira and Thomas, 1992; Ries et al., 2001). The overall agreement of our roadkill results with previous studies in terms of the range of roadkill rate variability and sex ratios supports the reliability of the data for extrapolating monarch road mortality according to road types and spatial modeling.

4.2. Monarch roadkill models

4.2.1. Roadkill projections

Most of the MaxEnt models projected monarch roadkill from the southwestern portion of the Central Funnel from West Texas to Mexico (Fig. 4). Our MaxEnt consensus projection agrees with all seven of the previously known citizen science reports of monarch roadkill hotspots in North America (Fig. 4), including two hotspots in West Texas (Journey North, 2017) and five hotspots in northern Mexico (Correo Real, 2015; Rogelio Carrerra, Universidad Autonoma de Nuevo Leon, Nuevo Leon, Mexico, personal communication).

Our annual MaxEnt based roadkill estimates for monarch mortality throughout the Central Funnel was 3.0 to 1.1 million for 2016 and 2017, respectively. These MaxEnt roadkill estimates were similar to those based on simple roadkill extrapolation by road type when hotspot data were included (3.6 and 1.1 million, respectively). Most of the roadkill projected by MaxEnt models outside of the study area occurred in Mexico, indicating that more MaxEnt models are projecting roadkill along the sparser road network within the Central Funnel over northern and central Mexico than in the northern parts of the funnel (Fig. 4). As the autumn migration pathway narrows in the South, migrating monarchs become more concentrated in the Central Funnel. This higher concentration may contribute to higher roadkill densities in the southern parts of the Central Funnel in Mexico, where most previous reports of monarch roadkill hotspots originate (Fig. 4). Although our models project some increased southward mortality risk, additional data are needed to assess the extent of this risk in Mexico. The extrapolations including the hotspot data with other roadkill data and projecting higher annual roadkill of up to 3.6 million in the Central Funnel

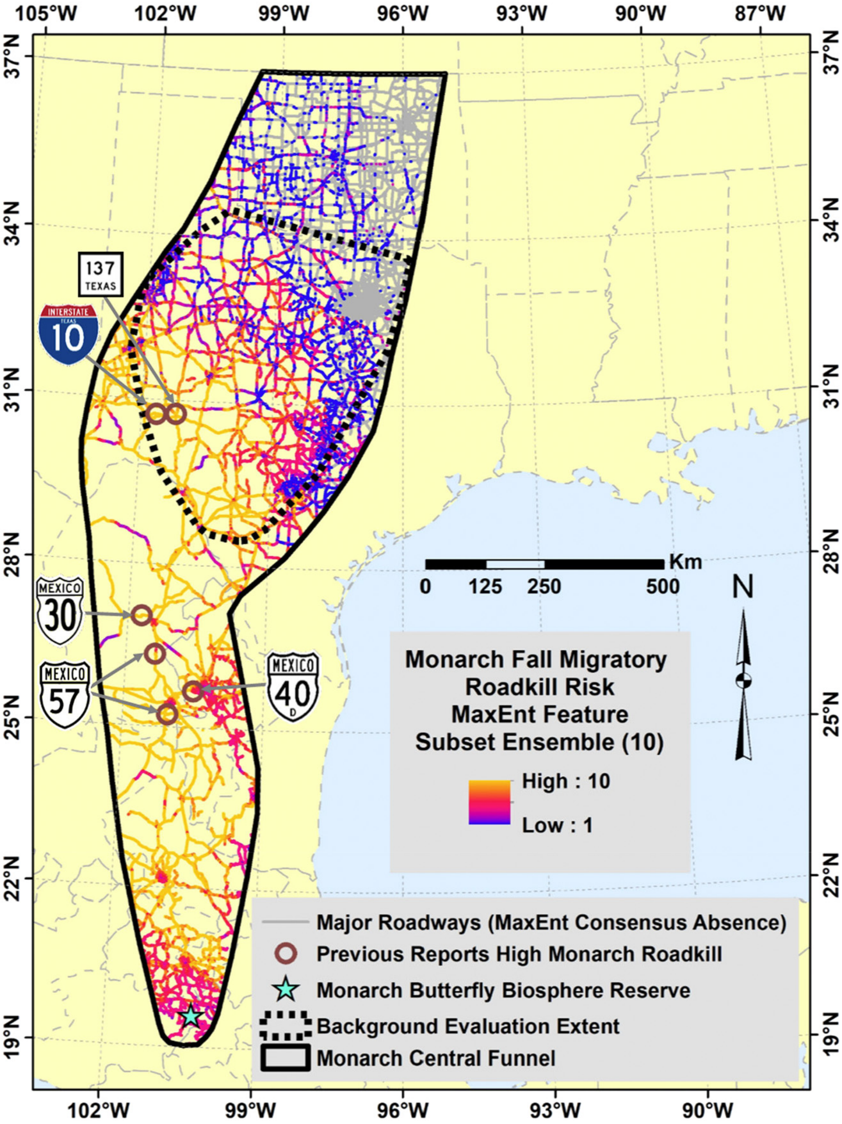

Fig. 4. MaxEnt frequency consensus for feature subset ensemble of ten models developed from random subsets of ten of 20 variables correlated < 0.7 (see Appendix Section 5 for embedded zipped shapefile of MaxEnt consensus model).

should be more realistic considering the occurrence of multiple roadkill hotspots in Mexico of higher density than seen in Texas. The MaxEnt models project little to no roadkill in the northeastern part of the funnel area, including the Dallas/Fort Worth area and eastern Oklahoma. However, some roadkill likely does occur in this area, but possibly at a lower rate than in the more southern areas of the Central Funnel. Further research and field surveys are needed to verify roadkill rates outside of our survey area in the southern and northern parts of the Central Funnel. Additional data may allow effective use of roadkill density models, rather than presence only MaxEnt models used in this study. Roadkill density models can better reveal regional roadkill patterns useful in refining projections, especially for northern Mexico where roadkill could be much higher than in Texas. Roadkill field surveys from other parts of the autumn migration pathways could improve estimates for the total impact of roadkill on the monarch population.

4.2.2. *Factors affecting roadkill*

MaxEnt projections of monarch roadkill within the Central Funnel were generally associated with more arid climate and less densely populated areas (Fig. 3). These conditions generally describe those for the seven previous monarch roadkill hotspots reported from Texas and Mexico, with the possible exception of the roadkill hotspot in the vicinity of Monterrey, Mexico (Fig. 4). This could be related to a variety of factors. For example, autumn migrating monarchs have been observed to spend additional time flying lower to the ground during the afternoon in desert areas, perhaps to seek shelter from the heat or find nectar (Journey North, 2018). Monarchs may need to spend more time searching for nectar in arid environments, although this has not been evaluated. Finally, the increased roadkill rates may simply reflect the increased number of monarchs in more southern areas of the Central Funnel. This southern locality factor cannot be associated with most of the predictors, with the exception of latitude, but it may have the highest influence. Local climate, weather patterns, and geography affect monarch movement and behavior, and they all are likely important contributors to road mortality. Wind patterns (direction, duration, and speed) may especially be more important than anthropogenic factors, but short-term weather events could not be incorporated in the models. Occurrence of these weather events is also highly variable and difficult to predict.

Traffic volume has been noted as one of the most important variables in previous roadkill studies (Bennett, 2017). Traffic volume ranked high in importance in our preliminary roadkill models, but we found that model accuracy (AUC) was not significantly affected by its removal. Other variables that were correlated with traffic volume likely compensated for its absence, including human population density, artificial surface cover, distance to urban areas (km to population ≥ 300/km^2), and road density. In our models including traffic volume, the highest roadkill was associated with fairly low AADT values, similar to the study by McKenna et al. (2001). In general, higher roadkill has been associated with higher traffic volume due to increased probability of vehicle collisions (Seiler and Helldin, 2006; Skórka et al., 2013). Samways (1994) suggested that roads with high traffic volume serve as corridors for high butterfly mortality. In our study, low traffic volume, along with related anthropogenic variables, is correlated with locations of monarch roadkill hotspots, but may not be directly related to the roadkill mortality. As the human population grows, traffic volume should increase, including in the lower traffic volume monarch roadkill hotspot areas, likely leading to higher roadkill rates (Bennett, 2017).

4.2.3. Spatial and temporal variation

Over 70,000 monarch roadkill were estimated in the Sonora to Sheffield, Texas hotspot in 2016, compared to about 5000 in 2017. This illustrates the high spatio-temporal variability of roadkill and the potential contribution of hotspots to the monarch road mortality. The timing of our field surveys relative to the peak migration in those years may have varied among transect locations and years, which could have influenced our results. If peak migration occurred after our field surveys in one or both years, we may have underestimated roadkill numbers. For example, the autumn migration in 2017 was later than usual due to unusually hot summer (Agrawal and Inamine, 2018). Few other studies have identified roadkill hotspots for butterflies (but see Samways, 1994, Her, 2008). Monarch roadkill hotspots may vary from year to year and may be difficult to locate or may not occur in some years.

We observed much higher monarch road mortality during autumn migration than in the spring (Fig. A.1), indicating that seasonality is a factor contributing to monarch roadkill rates. However, the monarch spring migration is more spatio-temporally dispersed making comparisons difficult. Temporal variability can occur between years, within the migration phase, or even within a day. For example, monarch behavior, such as flying low in the mornings (McKenna et al., 2001), probably affects the risk of roadkill at different times of day. Temporal patterns affecting monarch roadkill should be investigated further. Other sampling methods may be effective in detecting additional roadkill hotspots, such as adaptive cluster sampling, which was developed for inventorying scattered and clustered phenomena (Thompson, 1990). More frequent samples in a given location can also be critical for detecting roadkill hotspots (Santos et al., 2015).

4.3. Implications and impacts in relation to monarch conservation

4.3.1. Autumn migration mortality

Butterfly roadkill is a density independent mortality factor (Rodewald and Gehrt, 2014) with the incidence of roadkill being subject to high variability. Consequently, roadkill percentage of the migrating population is very unpredictable in any given year. We estimated a conservative annual percentage of migrating monarchs subject to road mortality in the Central Funnel by dividing a roadkill estimate by the sum of overwintering populations and roadkill estimate (overwintering cohort). The size of the overwintering populations is calculated by multiplying the hectares of roosting monarchs at the Mexican overwintering sites from Rendón-Salinas et al. (2018) by the value of 21.1 million monarchs per ha suggested by Thogmartin et al. (2017). Based on these amounts, the estimated annual roadkill rates from our combined years of 2016–2017 MaxEnt models in the Central Funnel represent an average of 2.8% (2.1 million) of the overwintering cohort. In 2016, roadkill within the Central Funnel may have represented about 4.0% of the overwintering cohort (Table 1). The corresponding roadkill for 2017 ranges from 1.5% to 1.8% of the overwintering cohort. In contrast, the projection of 500,000 road-killed monarchs by McKenna et al. (2001) in Illinois during one week in 1999 represents only 0.26% of the overwintering cohort that year (191 million, 9.05 ha), indicating potentially lower roadkill rates for areas north of the Central Funnel in some years.

The actual monarch population decline within a given year can be much higher than the differences in overwintering cohort sizes from year to year, since it includes the unknown quantities of butterflies recruited, or not recruited due to habitat loss, during spring and summer breeding. Mortality at the Mexican overwintering sites due to occasional winter storms can produce very high mortality, estimated at around 75% in 2002 (Brower et al., 2004) and > 40% in 2016 (Brower et al., 2017). Average monarch overwintering mortality is around 36% ± 21% (n = 7; range 4–55%) based on data from Ries et al. (2015b; see their Fig. 24.7). Lowered recruitment due to loss of milkweed habitat has been identified as the primary factor in monarch population declines (Pleasants, 2017; Thogmartin et al., 2017), with losses of milkweed resources in Iowa estimated at 76% from 1999 to 2014 (Pleasants et al., 2017). Other studies place more importance on mortality during the autumn migration in the decline of monarchs (Badgett and Davis, 2015; Inamine et al., 2016; Agrawal and Inamine, 2018). Consequently, it is complex to evaluate the relative importance of roadkill to other factors in the monarch population decline, but it is probably lower compared to the factors of milkweed habitat loss and overwintering mortality. Northward expansion of the monarch summer breeding range is anticipated with climate change (Batalden et al., 2007; Lemoine, 2015), making the southward autumn migration route even longer, increasing both exposure to traffic and associated road mortality (Badgett and Davis, 2015). Monarch roadkill during autumn migration should be further evaluated in the context of other mortality factors along the migration path (Baxter-Gilbert et al., 2015).

Brower et al. (2012) fitted an exponential decline curve to the estimated monarch overwintering populations (ha) in Mexico from 1995 (winter 1994–1995) to 2011 (P = 0.015, $R^2 = 0.336$). Inclusion of seven additional years of data through 2018 (Vidal and Rendón-Salinas, 2014; Monarch Watch, 2018b) strengthens fit of an exponential curve ($y = ae^{bx}$ Fig. 5) (P = 0.0009; adjusted $R^2 = 0.486$; ZunZun.com, 2018). A concave exponential curve represents the most serious form of species population decline, indicating constant proportional negative pressure on the population (Di Fonzo et al., 2013). A standard geometric population growth curve, fit to the modeled exponential curve,

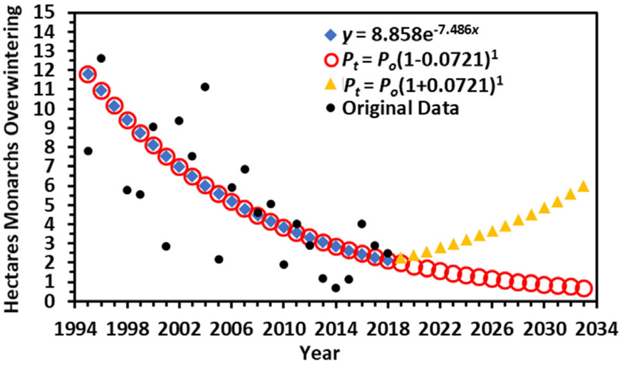

Fig. 5. Annual monarch population in hectares in Mexican overwintering sites from 1995 to 2018 (original data, black circles; Vidal and Rendón-Salinas, 2014; Monarch Watch, 2018b) with fitted exponential curve, $y = ae^{bx}$ (adjusted $R^2 = 0.49$; P = 0.00009; blue diamonds), and corresponding geometric population growth equation curve, $P_t = P_o(1 + r/n)^{nt}$, where P_t is the final hectares (2.11), P_o is the initial hectares (11.79), t is the number of years (23), n is the number of sub-periods (1), and r is the population growth (or declination) rate (derived population declination of 7.21% per year; open red circles). Fifteen years to restore 6 ha of overwintering monarchs based on totally reversing the current decline to 7.21% growth per year (gold triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reveals an average − 7.21% annual population decline over the last 23 years associated with an overall 82% population reduction (for details, see Appendix A, section 8). In comparison, a fitted exponential curve until 2011, as used by Brower et al. (2012), yielded a slightly lower annual decline rate of 6.46%. The updated results indicate that the decline rate may have increased or at least has not slowed down. Continuance of the 7.21% rate of decline would result in an average of 0.24 ha of overwintering monarchs occurring in 29 years (by 2046–2047), greatly increasing the chance of extirpation of eastern migrating monarchs by an extreme winter storm mortality event as the overwintering population crosses below the 0.25 ha quasi-extinction threshold (Semmens et al., 2016). A total reversal of the 7.21% annual monarch decline, coupled with an annual 7.21% population increase (net change 14.4%), would be needed to restore the size of the overwintering population to current conservations goal of six hectares (Thogmartin et al., 2017) over the next 15 years. A 0.5% annual reduction in migrating monarch mortality through roadkill mitigation could significantly contribute to a reversal in the long-term 7.2% annual exponential decline in monarch populations (Fig. 5).

4.3.2. Roadkill mitigation

While some major factors in the monarch decline are difficult to reduce, such as overwintering mortality, the opportunity for reducing road mortality is possible through roadkill mitigation (see Rytwinski et al. (2016) for a review on mammal roadkill mitigation). The potential ability to locate re-occurring monarch roadkill hotspots could facilitate more effective mitigation. Scattered and unpredictable monarch roadkill would be more difficult to mitigate. A variety of roadkill mitigation measures have been implemented for danaine migratory butterflies. In Taiwan, a four-meter high net was placed along a 400 m section of bridge on National Freeway 3 to successfully induce spring migrating purple crow butterflies (*Euploea* spp.) to fly over and above the traffic, reducing on site roadkill from around 2.5% to 0.5%. In addition, an outer traffic lane was closed when > 500 butterflies per minute were crossing (Her, 2008; Taiwan EPA, 2010). In response to heavy autumn migratory monarch roadkill observed in Coahuila state of Mexico, traffic signs were posted in 2015 limiting the maximum speed to 60 km per hour (37 mph) in the presence of monarchs (Miranda, 2015). Police have been observed slowing traffic in Nuevo Leon state in Mexico to reduce monarch mortality along a highway south of Monterrey (Dr. Orley R. Taylor, personal communication). Additional research is needed to test and assess the effectiveness of these types of butterfly roadkill mitigation strategies for monarch roadkill hotspots in west Texas and Mexico.

5. Conclusions

Our study represents a novel approach for projecting roadkill of a migratory insect through ecological niche modeling. Annual monarch roadkill rates during autumn migration varied substantially. We found close agreement between two methods of estimating monarch roadkill rates, simple extrapolation by road type and MaxEnt roadkill model projections. We project about 1.0 to 3.6 million road-killed monarchs per year during autumn migration over the Central Funnel, which could represent 2–4% of the Mexican monarch overwintering population. MaxEnt model roadkill projections also aligned with several previously known monarch roadkill hotspots, which suggests MaxEnt models could be used to identify additional monarch roadkill within the Central Funnel. Roadkill rates may differ throughout the Central Funnel compared to those observed in the Texas survey area, and should be further investigated. Monarch road mortality should also be investigated along the Coastal Funnel, especially from Texas to Mexico. We recommend more detailed investigation into the spatial and temporal variability in monarch road mortality in the Central Funnel, including how local and short-term weather events, especially related to wind, influence monarch roadkill hotspots. With the new information on monarch road mortality in the Central Funnel, conservation efforts could be implemented to mitigate mortality at monarch roadkill hotspots. Reducing roadkill rate over the Central Funnel for the eastern monarch population is as an important step towards reversing the continuing decline of this iconic butterfly.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.01.008.

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Reexamining Fire Suppression Impacts on Brushland Fire Regimes

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California shrubland wildfires are increasingly destructive, and it is widely held that the problem has been intensified by fire suppression, leading to larger, more intense wildfires. However, analysis of the California Statewide Fire History Database shows that, since 1910, fire frequency and area burned have not declined, and fire size has not increased. Fire rotation intervals have declined, and fire season has not changed, implying that fire intensity has not increased. Fire frequency and population density were correlated, and it is suggested that fire suppression plays a critical role in offsetting potential impacts of increased ignitions. Large fires were not dependent on old age classes of fuels, and it is thus unlikely that age class manipulation of fuels can prevent large fires. Expansion of the urban-wildland interface is a key factor in wildland fire destruction.

California shrublands frequently fuel massive high-intensity wildfires that are of increasing concern to resource managers and the public. Despite increased expenditures on fire suppression, each new decade experiences increased loss of property and lives from brushland wildfires (*1*). By the middle of this century, it was suggested that the problem stemmed in large part from the burgeoning population and poor zoning regulations attendant with urban sprawl into the foothills (*2*).

Accepting expanded urbanization as the source of the wildfire problem has profound economic and political implications. An alternative view to emerge in the early 1970s was that the primary problem was tied to the overly successful state and federal fire suppression programs. As a consequence of eliminating fires from the wildland ecosystem, it has been widely held that we have exacerbated the situation by allowing unnatural fuel accumulation (*3*). Thus, when the inevitable fire does come, it is larger and more destructive. A computer model relating fire size to chaparral fuel loading predicted that the prevailing management strategy of fire suppression in California brushlands leads to fewer, but larger and more intense fires (*4*).

A 9-year Landsat imagery record that showed that fires between 5000 and 10,000 ha were slightly more abundant in southern California than in adjacent Baja California (*5*) has been widely cited as support for a link between fire suppression and fire size. On the basis of this study, it has been hypothesized that large wildfires in California shrublands are a modern artifact, due to fire suppression, and that they can be prevented by creation of a mosaic landscape of patches of different ages (*6*). The model is predicated on assertions that, because of fire suppression, (i) the number of fires has declined over time, (ii) fires are substantially larger today than in the past, (iii) contemporary fires burn with greater intensity than in the past, (iv) large fires result from extensive stands of very old age classes, and (v) there has been a decline in area burned, as suggested by some (*3*), but not all (*5*), studies. None of these assertions have been documented.

To investigate historical changes in fire regimes, we used the recently available California Statewide Fire History Database, which includes all records from the California Department of Forestry and U.S. Forest Service and other county records (*7*). We limited our analysis to counties dominated by shrublands with a stand-replacing fire regime: from north to south, Monterey, San Luis Obispo, Santa Barbara, Ventura, Los Angeles, San Bernardino, Riverside, Orange, and San Diego. Records date from the late 19th century for some counties and from at least 1910 for others (*8*).

Collectively, since 1910, there has been a highly significant increase ($r^2 = 0.61$, $P < 0.01$, $n = 9$) in the number of fires per decade. This increase is due largely to southern California counties, which also had significant increases in area burned (Fig. 1) (*9*). In no county was there a significant decline in number of fires or area burned. All counties exhibited significant interdecadal differences in area burned [$P < 0.01$, one-way analysis of variance (ANOVA)]. For most counties, the 1920s and 1970s were high and the 1930s and 1960s low. Collectively, area burned was significantly correlated ($r^2 = 0.71$, $P < 0.01$, $n = 9$) with number of fires, which was also correlated ($r^2 = 0.51$, $P < 0.05$, $n = 9$) with population density (*10*).

All counties reported very large fires from the beginning of record keeping; indeed, one of the largest fires in Los Angeles County was a 24,076-ha fire in 1878 (Fig. 2). During the 20th century, there has been no increase in mean fire size for any county, but four exhibited significant declines (Fig. 2). One contributor to this decline could be a purported inclination by agencies early in the century to not record very small fires (*8*). However, if fires less than 100 ha in size are removed from the data set, there is still a slight downward trend in fire size this century (all counties combined, $r^2 = 0.02$, $P < 0.001$, $n = 2766$). Another factor that could explain a trend toward smaller mean fire size is the increase in human-caused (*11*) ignitions (Fig. 1), coupled with the fact that many are ignited under moderate weather conditions and along roadways, factors contributing to their suppression at a small size (*12*). If we focus just on large fires, greater than 1000 ha, the trend toward smaller fires disappears, but still no county had a significant increase in fire size (ranges: $r^2 = 0.00$ to 0.02, $P > 0.10$ to 0.99, $n = 82$ to 159). The assertion that large wildfires are an artifact of modern fire suppression is not supported.

Contrasting fires after 1950, when fire suppression impacts would be greatest (*13*), with those in and before 1950, we see no significant change in pattern of burning (Fig. 3A); a small percentage of fires account for the bulk of area burned, now and in the past [10% of the fires accounted for 75% (in and before 1950) to 79% (after 1950) of the area burned]. The primary change has been in the proliferation of fires between 10 and 100 ha (Fig. 3B), reflecting both increased ignitions under moderate conditions—that favor suppression—and increased reporting of small fires. In these brushland ecosystems, the frequency of small to medium size fires cannot be used to quantify the risk of large fires (*14*).

Contrasting fire regimes between the first and second halves of this century, we found that fire frequency increased in all but one county (Table 1). The majority of counties exhibited no significant change in mean or median fire size; however, three southern California counties had highly significant declines in mean fire size. Fire rotation intervals, the time required to burn the equivalent

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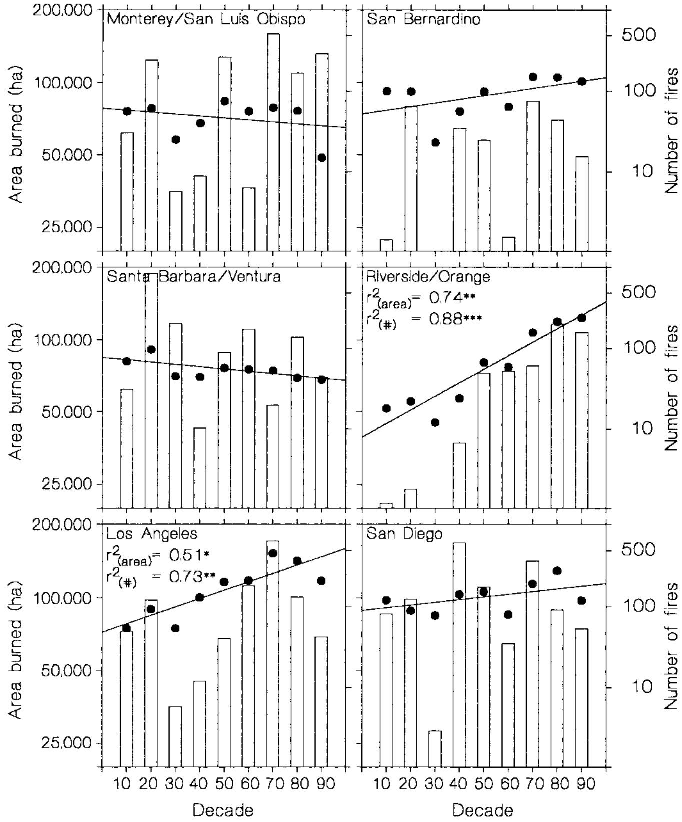

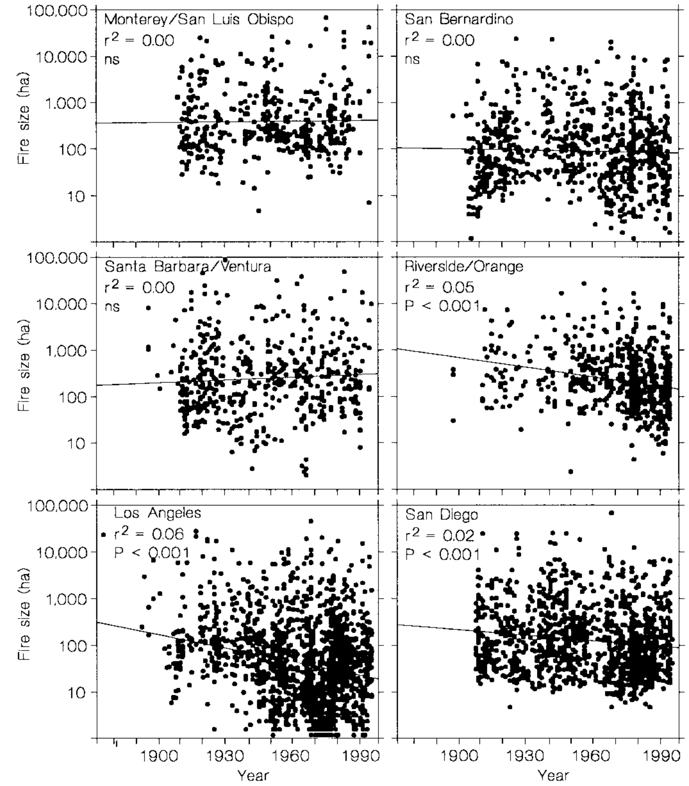

Fig. 1 (left). Area burned (bars) and fire frequency (circles) by decade (1910–1990) for brush-dominated counties in central-coastal and southern California. r^2 is included only when significant: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. **Fig. 2 (right).** Magnitude of individual fire size for all records for brush-dominated counties.

Table 1. Brush-covered area as of 1985 and fire statistics for 1910–1950 and 1951–1997 with estimated fire rotation interval (area of brush (*22*)/average area burned) for California counties. Trends with medians are the same for each county.

County	Brush (10^3 ha)	Number of fires		Mean fire size (ha)			Fire rotation interval (years)	
		Before 1951	After 1950	Before 1951	After 1950	*P*	Before 1951	After 1950
Monterey	358	102	129	1220	1998	>0.32	115	64
San Luis Obispo	250	93	119	1760	2068	>0.68	60	48
Santa Barbara	250	125	61	1622	2341	>0.45	47	81
Ventura	189	143	172	1568	1508	>0.93	121	34
Los Angeles	320	357	1392	827	360	<0.001	44	30
San Bernardino	209	311	544	609	480	>0.33	46	37
Riverside	290	57	613	871	565	<0.01	225	38
Orange	42	25	48	1721	1317	>0.68	36	29
San Diego	365	456	770	939	544	<0.001	35	41

of the total brush area in the county (Table 1), declined in all but two counties (*15*).

These fire rotation intervals do not support the assertion that large fires derive from ancient stands of brush. To investigate the true fire return interval, we used digitized fire maps for the Santa Monica Mountains in Los Angeles and Ventura counties (*16*). Fires in this brush-dominated range have included numerous large catastrophic and costly fires, such as the 1961 Bel Aire Fire or the recent 1993 Green Meadow Fire. Age classes of fuels consumed by all fires exceeding 5000 ha in the past 30 years demonstrate that large fires are not dependent on old classes (Fig. 4). Collectively, there was a significant ($P < 0.05$ with one-way ANOVA, $n = 8$) difference across age classes, with fuels 11 to 20 years old representing 38%, which was more than double the consumption of older age class fuels. Because of the proximity of this range to urban centers, the age classes consumed may not be representative of more remote sites; however, these data demonstrate that large catastrophic wildfires are not dependent on ancient stands of brush and contradict the assertion that young stands less than 20 years of age prevent fire spread (*5*, *6*).

Inferences that fires today are of greater intensity are based on the assertions that fire rotation intervals have increased and there has been a seasonal shift toward autumn burning (*6*). However, rotation intervals have generally declined (Table 1) and September has remained the peak month of burning throughout this century (Fig. 5).

Humans directly affect fire regimes in two ways: They ignite fires and they suppress fires. In brush-covered landscapes of southern and central-coastal California, there is no evidence that fire suppression has altered the natural stand-replacing fire regime in the manner suggested by others (*3*, *5*). This is

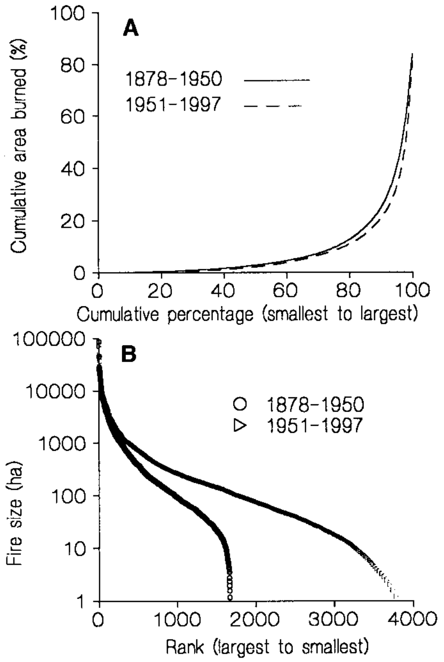

Fig. 3. (**A**) Cumulative area burned and (**B**) fire size distribution, for all counties before and including 1950 and after 1950.

in striking contrast to coniferous forests throughout much of the western United States, where the stand-thinning fire regime has proven amenable to near total fire exclusion, resulting in demonstrably hazardous fuel accumulation and increased potential for catastrophic wildfires (*17*). The primary hazard in brushland ecosystems is the marked increase in fire frequency during the latter half of this century that often results in type conversion to nonnative exotic grasslands (*18*), and fire suppression plays a crucial role in offsetting this impact.

Large catastrophic wildfires in brush-covered regions of California are often driven by high winds, and under these conditions even modern fire suppression techniques are ineffective (*19*). Today, people ignite most of these fires; however, in their absence, lightning storms that typically occur just weeks before the autumn foëhn winds (*11*) would have provided a natural source of ignition. Although fuel structure is an important determining factor in fire behavior, the role of structure diminishes markedly under foëhn winds that can blow at speeds exceeding 100 km/hour and are responsible for the majority of area burned in California brushlands (*19*). Under these conditions, fires readily burn through all age classes of fuels (Fig. 4), and thus, rotational burning programs that attempt to modify vast stretches of chaparral landscape through age class modification are not likely to be effective in stopping these catastrophic fires.

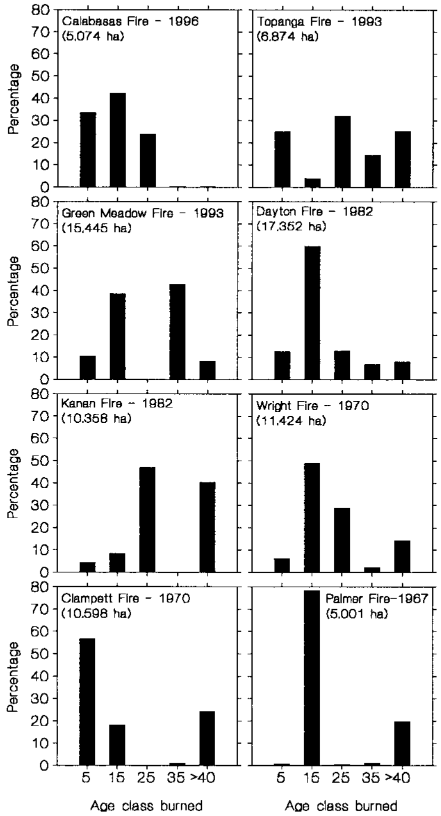

Fig. 4. Age classes burned by all fires over 5000 ha from 1967 to 1996 in the Santa Monica Mountains. Indicated on the abscissa are midpoints of age classes 1 to 10, 11 to 20, 21 to 30, 31 to 40, and over 40 years.

This may come as welcome news to resource managers because the combination of legal restrictions and financial constraints makes large-scale prescribed burning of brushland landscapes unobtainable. Our results support the conclusion that the most effective strategy (*20*) for reducing catastrophic losses from wildfires is to minimize the management effort spent on the bulk of the chaparral landscape and focus on strategic locations. The worst fires predictably follow landscape features, and these patterns can be used to select buffer zones at the urban-wildland interface for more intensive fuel management. However, the urban-wildland interface is so extensive now that even strategically focused intensive management could have enormous ecological impacts. Preference for a rural life-style and the skyrocketing cost of suburban housing in large metropolitan areas continue to expand the urban-wildland interface, and of particular concern is the prediction that rural population will soon exceed urban growth (*21*).

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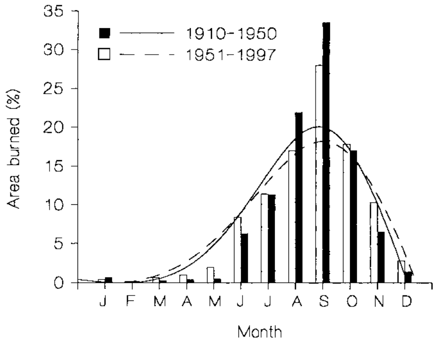

Fig. 5. Area burned by month for 1910–1950 and 1951–1997, for all counties except Riverside and San Bernardino, which were excluded because of incomplete data.

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7. California Department of Forestry, Fire and Resource Assessment Program (FRAP), Sacramento, CA. Small fires are not recorded; for example, the U.S. Forest Service records only fires over 16 ha. However, the threshold limit varies with the agency.
8. Fires recorded here burned predominantly in chaparral, which sometimes forms a mosaic with coastal sage scrub, grassland, oak woodland, and coniferous forests. Early in the century, there may be a deficit of small fires because of incomplete reporting, but total area burned is not likely to be affected because small fires are a minor portion and large fires are less likely to have been missed.
9. Adjacent counties were combined for presentation purposes; statistical tests discussed in the text were performed on counties both separate and combined. Data for the 1990 decade were standardized by dividing the average for the first 8 years by 0.8.
10. For population density statistics, see www.census.gov/population/cencounts/ca190090.txt
11. For these counties, natural lightning-ignited fires typically make up less than 5% of all fires [J. E. Keeley, *U.S. Forest Serv. Gen. Tech. Rep. PSW-58* (1982), pp. 431–437].
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Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests

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The incidence and importance of fire in the Amazon have increased substantially during the past decade, but the effects of this disturbance force are still poorly understood. The forest fire dynamics in two regions of the eastern Amazon were studied. Accidental fires have affected nearly 50 percent of the remaining forests and have caused more deforestation than has intentional clearing in recent years. Forest fires create positive feedbacks in future fire susceptibility, fuel loading, and fire intensity. Unless current land use and fire use practices are changed, fire has the potential to transform large areas of tropical forest into scrub or savanna.

Fire is recognized as a historic but infrequent element of the Amazonian disturbance regime (*1*, *2*). Currently, however, fires in Amazonian forests are frequent because of the accidental spread from nearby pastures and the increased susceptibility of partially logged or damaged forests (*3*–*6*). Here, positive feedbacks associated with accidental forest fires are reported; these constitute a threat to the integrity of a large part of the Amazonian forest.

Field studies were concentrated in the Tailândia region (Fig. 1). Ten 0.5-ha plots (eight fire-affected and two control), spread over 100 km^2, were established in 1996 to study fire impacts on forest structure, biomass, and species composition (*3*). These plots were recensused after the dry season of 1997, during which eight of the plots burned to varying degrees. Fire recurrence, tree mortality, and biomass combustion levels within forests of different burn histories were quantified. In addition, combustible fuel mass was assessed with the planar intersect method (*7*) as adapted by Uhl and Kauffman (*8*, *9*).

We also examined characteristics of fires while they were occurring in four forest types (previously unburned, once-burned, twice-burned, and more than two previous burns) in December 1997. Direct observations of fires were made at widely scattered locations within a 150-km^2 area south of Tailândia. For each observed fire, flame heights and depths (the width of the flaming front) were measured or estimated (*10*). The time the fireline took to move across a known distance was used to calculate the rate of spread and was combined with flame depth data to calculate the average range of flame residence times at a point. Flame height was used as a conservative estimate of total flame length for the calculation of fireline intensity (*11*) because wind and slope were minimal (*12*).

The first fire to enter a forest usually moves slowly along the ground (Table 1) and is similar to a prescribed burn ($<$50 kW m^{-1}) in intensity (*13*). These fires consume little besides the dry leaf litter, but because of the characteristically thin tree bark [7.3 ± 3.7 mm for $>$20 cm diameter at breast height (dbh) (*8*)] protecting the cambium tissues, they still kill roughly 95% of the contacted stems $>$1 cm dbh. Large, thicker barked trees survive. After the fire, a rain of combustible fuels of all sizes falls from the standing dead trees (Table 1) (*14*). Fire damage and windthrow in these thinned forests continue to cause mortality for at least 2 years after the fire (*4*, *15*). Fuel levels rise substantially and the open canopy (50 to 70% cover) allows greater solar heating and air movement to dry out the forest fuels. Previously burned forests thus become susceptible to fire during common dry season weather conditions (*3*).

Previously burned forests were much more likely to burn than were unburned forests in 1997 (Table 1). Burned forests are often adjacent to fire-maintained pasture and agricultural plots and are therefore frequently exposed to sources of ignition. Second fires are faster moving and much more intense. We estimate heat release (*12*) of $<$7500 kW m^{-2} in first burns but of 75,000 kW m^{-2} or more in subsequent burns. Because of the increased flame depth, the residence time increases despite faster rates of spread, resulting in greater tree mortality. Large trees have little survival advantage during these more intense fires. Fire-induced tree mortality can be modeled as a function of bark thickness and fire residence time (*16*). For the observed fire characteristics and bark thickness distribution (*8*), no more than 45% of trees over 20 cm dbh are susceptible to fire-induced mortality in the initial fires. However, in recurrent fires, up to 98% of the trees become susceptible to fire-induced mortality.

The impacts of recurrent fires are much worse than those of initial fires. Higher mortality results in a very open canopy (10 to 40% cover), large inputs of combustible fuels, and faster drying. During the 1997 fires, substantial amounts of carbon were released to the atmosphere, with combustion reducing onsite biomass by approximately 15, 90, and 140 Mg ha^{-1} in first, second, and recurrent burns, respectively. Invading grasses and weedy vines add highly combustible live fuels to the already

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Historic Fire Regime in Southern California Shrublands

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Abstract: *Historical variability in fire regime is a conservative indicator of ecosystem sustainability, and thus understanding the natural role of fire in chaparral ecosystems is necessary for proper fire management. It has been suggested that the "natural" fire regime was one of frequent small fires that fragmented the landscape into a fine-grained mixture of age classes that precluded large, catastrophic fires. Some researchers claim that this regime was lost because of highly effective fire suppression and conclude that if fire managers could "restore" a regime of frequent fires with widespread prescription burning, they could eliminate the hazard of catastrophic fires. The primary evidence in support of this model is a study that compared contemporary burning patterns in southern California, U.S.A., a region subject to fire suppression, with patterns in northern Baja California, Mexico, where there is less effective fire suppression. We found that differences in fire regime between these two regions are inconclusive and could not be ascribed conclusively to differences in fire suppression. Historical records suggest that the natural fire regime in southern California shrublands was rather coarse-grained and not substantively different from the contemporary regime. There is no evidence that fire-management policies have created the contemporary fire regime dominated by massive Santa Ana wind-driven fires. Increased expenditures on fire suppression and increased loss of property and lives are the result of human demographic patterns that place increasing demand on fire-suppression forces.*

Régimen Histórico de Incendios en Zonas Arbustivas del Sur de California

Resumen: *La variabilidad histórica del régimen de incendios es un indicador conservador de la sostenibilidad del ecosistema y por lo tanto se necesita conocer el papel natural del fuego en ecosistemas de chaparral para un manejo adecuado. Se ha sugerido que el régimen 'natural' de incendios estuvo compuesto por pequeños incendios que fragmentaron el paisaje en una mezcla de grano fino de clases de edades que previno incendios grandes catastróficos. Algunos investigadores aseguran que este régimen se perdió debido a la alta efectividad en la suspensión de incendios y concluyen que si los manejadores de incendios pudieran 'restaurar' un régimen de incendios frecuentes mediante la prescripción de quemas dispersas se podrían eliminar los peligros de los incendios catastróficos. La evidencia primaria en apoyo a este modelo es un estudio que comparó los patrones contemporáneos de incendios en el sur de California, USA (sujeto a supresión de incendios) con patrones del norte de Baja California, México (con menor supresión efectiva de incendios). Encontramos que las diferencias en el régimen de incendios entre estas dos regiones son inciertas y que estas diferencias no se pueden atribuir conclusivamente a las diferencias en supresión de incendios. Los registros históricos sugieren que el régimen natural de incendios en las zonas arbustivas del sur de California fue mas bien de un grano grueso y no fue sustancialmente diferente al régimen contemporáneo. No existe evidencia de que las políticas de manejo de incendios han creado el régimen contemporáneo de incendios dominado por fuegos masivos conducidos por vientos de Santa Ana. El incremento en gastos para la supresión de incendios y el incremento en la pérdida de propiedades y vidas son el resultado de patrones demográficos que colocan una demanda creciente en la supresión de incendios.*

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Introduction

The types of inferences drawn from observations differ among disciplines and often contribute to scientific disputes, such as the controversy over the natural fire regime in southern California and Baja California shrublands (Minnich 1983; Keeley et al. 1989; Moritz 1997; Conard & Weise 1998; Zedler & Oberbauer 1998; Minnich & Franco-Vizcaino 1999). We examined the evidence from past fire regimes, the inferences drawn from those observations, and the implications for contemporary fire management of southern California shrubland ecosystems.

Understanding the natural role of fire in any ecosystem has value beyond merely satisfying curiosity. Modern land managers are increasingly concerned with sustainable, ecosystem-level management, and the historical variability in fire regime is considered a conservative indicator of sustainability (Millar 1997). We know from empirical studies that diversity in chaparral is threatened by fire frequencies that are too high (Keeley 1995), and theoretical studies suggest that very low frequencies may also be a threat (Zedler 1995). Thus, an understanding of natural fire regimes may provide useful guidelines for future management.

Reconstructing the Natural Fire Regime in California Shrublands

Some ecosystems, such as the ponderosa pine–dominated forests in the western United States, have a well-documented fire history (Skinner 1997). Fire scarred trees indicate that low-intensity surface fires were common prior to European colonization, and fires have largely been suppressed during the twentieth century. In contrast, California shrublands burn in stand-replacing crown fires that kill all aboveground biomass; thus, we lack a precise historical record of fires. Consequently, conclusions about the historical role of fire in chaparral will always be more controversial than those for many other forested ecosystems.

One attempt to fill this void of historical information was a Landsat remote imagery study (Minnich 1983) comparing a 9-year record (1972–1980) of burning in chaparral and coastal sage shrublands between southern California and Baja California and demonstrating differences in burning patterns north and south of the U.S.–Mexico border (Fig. 1a). It was posited by Minnich (1983, 1989, 1995, 1998) that because fire suppression was not practiced in Mexico, the burning patterns observed south of the border reflected the "natural" condition for southern California. This regime was hypothesized to be one of frequent, small fires that fragmented the landscape into a fine-grained mixture of age classes that precluded large, catastrophic fires. Minnich claimed that the primary reason this natural regime had been lost in southern California was the practice of highly effective fire suppression. Further, he proposed that if fire managers could "restore" a natural fire regime of frequent, small fires through prescription burning, they could eliminate the hazard of catastrophic fires in southern California. This philosophy is currently reflected in fire-management plans for all southern California national forests (Conard & Weise 1998). Because of the social, economic, and political implications of these ideas, they deserve critical examination.

Evaluating the Baja California Model

Minnich's (1983) study, represented in Fig. 1a, has an inherent bias that has not been widely appreciated. Although the figure legend in the original paper purported to show only the difference in burning patterns as observed from Landsat remote imagery over a 9-year period (1972–1980) in both Baja and southern California, the figure was biased by the inclusion of two massive fires (1932 and 1970) in southern California that were outside the comparison period. These two fires were the largest in California's history and were mapped from U.S. Forest Service records not available for Baja California. With these two fires removed (Fig. 1b), the differences are far less striking and the conclusion that large fires are restricted to north of the border is called into question. Strauss et al. (1989) examined only the legitimate Landsat imagery comparison (Fig. 1b) and found no evidence of differences between the regions north and south of the border (cf. Chou et al. 1993).

Later studies (Freedman 1984; Minnich 1989, 1995, 1998; Minnich & Dezzani 1991) used historical aerial photographs of Baja California to compensate for the detailed records available north of the border. These studies concluded that, in contrast to the situation in southern California, large fires were absent from Baja California as far back as 1920.

Techniques used to achieve a long-term absence of large fires in Baja California make it difficult to embrace this finding. Studies by Minnich were based on three aerial photographic records, 1938, 1956, and 1972, representing a 16- to 18-year gap between photographs. Minnich contended he was able to detect all fire boundaries that had occurred during the gap between photographs; fire perimeters were even drawn back to 1920, despite a lack of photographs before 1938. The support for this procedure was the author's testimony that he could detect known fire perimeters many years after a fire. A more rigorous and acceptable scientific procedure is the use of a "blind control," in which an observer is asked to detect patterns without prior knowledge of fire perimeters. Although we do not doubt that localized fires known to the observer may remain detectable from aerial photographs for a decade or more, large fires not known to the observer, particularly ones with borders that extend beyond the scale of the photograph, may not be recogniz-

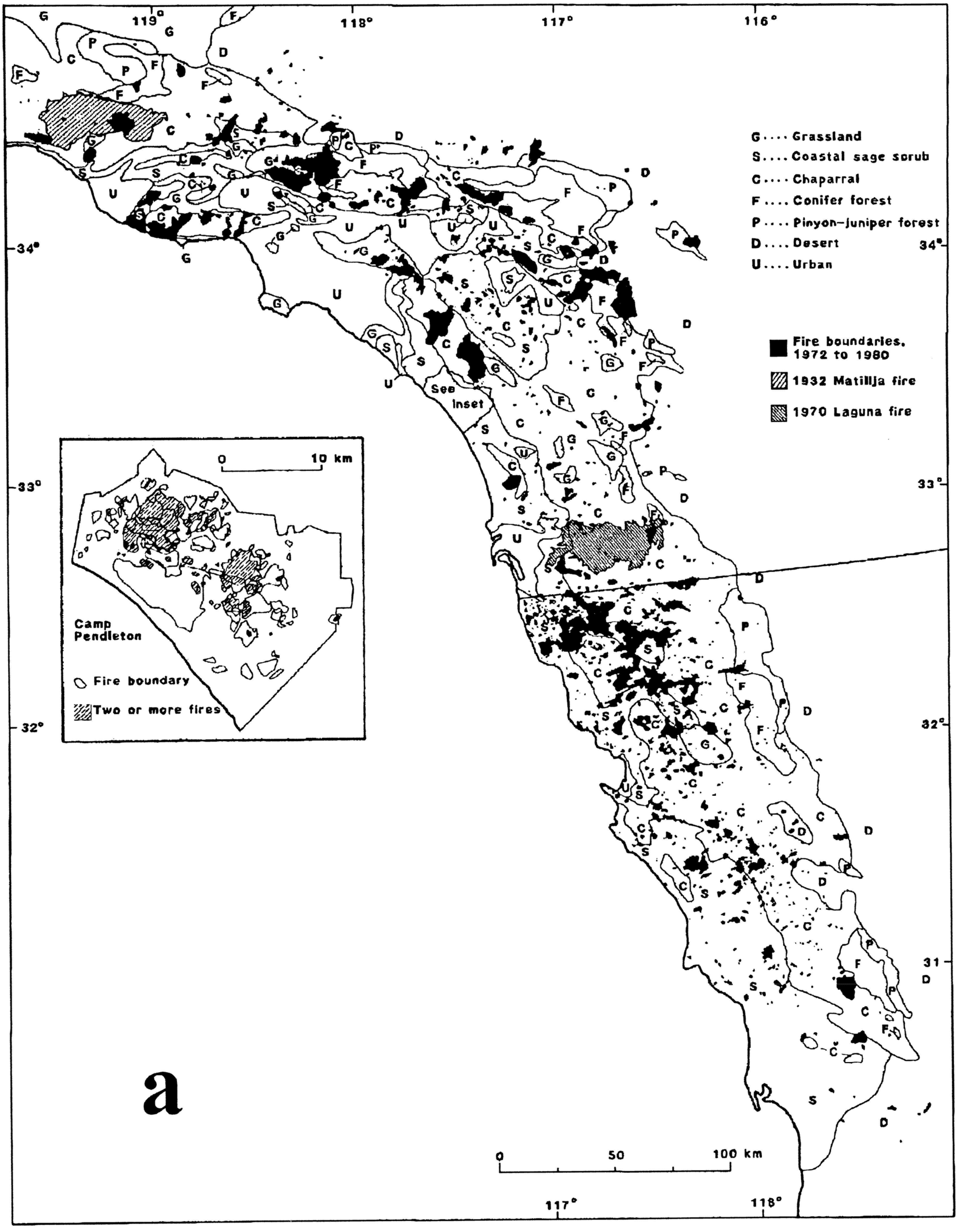

*Figure 1. Figure 1 from Minnich (1983) showing (a) "Wild-land fires in southern California and northern Baja California, 1972 to 1980. . .[D]ata were mapped from Landsat imagery." Although not stated in the original figure legend, (a) includes the two largest fires in California history, which occurred outside the Landsat imagery period. (b) Wildland fires in southern California, and northern Baja California, with large fires that fell outside the Landsat imagery study removed. We acknowledge permission of the American Association for the Advancement of Science to reprint Fig. 1 from Minnich (1983, Science **219:**1288).*

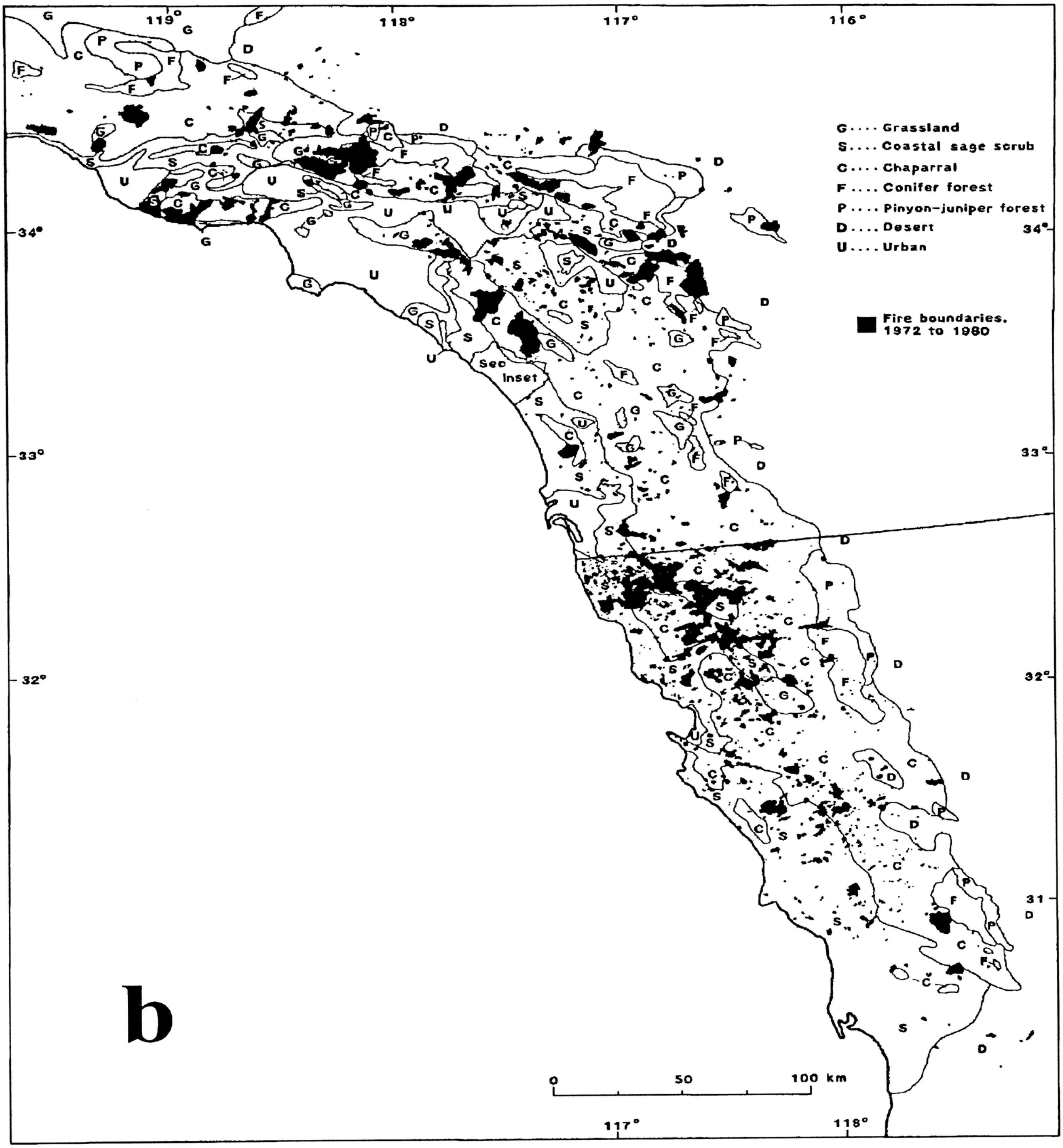

Figure 1. continued

able 16–18 years after a fire. At the very least, many researchers would require proof of such detective ability before drawing inferences about fire history. Such evidence is particularly important because several authors have reported large fires in northern Baja California (e.g., Henderson 1964; Haiman 1973; Amaya 1991).

In general, historical data for Baja California do not approach the quality of the written records available north of the border, so, beyond recent Landsat records, we know relatively little about the fire history of that region (Fig. 1b). Further, it is debatable whether or not the Landsat images demonstrate significant differences between southern California and northern Baja California (e.g., Strauss et al. 1989; c.f. Chou et al. 1993). But assuming, for the sake of argument, that one accepts the inference that differences exist, there is still much room for doubt as to the explanation for them. Minnich (1983, 1989, 1995, 1998) assumes that fire suppression policy is the only relevant difference between southern California and Baja California, but this contention has never been demonstrated rigorously. More important, this conclusion is unwarranted in the absence of consideration of potential differences in landscape, climate, and land use between southern California and Baja California.

Factors that need serious consideration before one can accept the contemporary Baja California burning regime as representative of the "natural" southern California fire regime include the following: (1) There is an extraordinary difference in fire frequency between regions north and south of the border. (2) Fire climates are not entirely comparable north and south of the border. (3) Climates and soils differ between the two regions in ways that could affect patterns of fuel production. (4) Landscape characteristics in Baja California may be less conducive to large fires such as those that occasionally occur north of the border. (5) There are many differences in land use between these regions, some of which could contribute to differences in patterns of burning.

Difference in Fire Frequency

Fire prevention is much less effective in Baja California and thus, due to human ignitions, fire frequency is up to five times greater there than in southern California (Minnich 1989, 1995; Minnich & Dezzani 1991; Henderson 1964; Haiman 1973; Keeley 1982; Freedman 1984). North of the border, the only place one sees a similar number of human-caused fires is on Camp Pendleton Marine Base, and these data were excluded from the earlier analysis of southern California because of "anomalously high ignition rates" (Minnich 1983). Higher ignition rates in Baja California are reflected in the marked differences observed in the amount of burning immediately north and south of the border (Fig. 1b).

Minnich et al. (1993) argue that in Baja California the larger number of human-caused ignitions is irrelevant in determining the mosaic pattern of burning because, even without this human subsidy, ignitions from lightning would be saturating. They reported approximately one lightning strike per 1000 ha per year in shrubland ecosystems of northern Baja California. No data were presented on the percentage of these strikes that ignite fires, and there was no direct evidence of saturation per se. Relative to other regions such as the southwestern United States (Reap 1986), northern Baja California experiences a low density of lightning strikes.

Saturation implies that additional ignitions will not affect fire frequency and burning patterns. Inconsistent with the notion of saturation is Haiman's (1973:174) report that in surveys of residents in the Sierra Juárez of northern Baja California, the major complaint was "directed towards the traditional ranchero activity of burning the montane ranges during the summer months." If lightning-ignited fires were "saturating," then the ranchero activities would not add to the fire regime and pose a risk to the local residents. It is implied by Minnich et al. (1993) that lightning saturates the environment north of the border as well, which would be evident if fire suppression did not extinguish these natural fires. But countless examples of humans subsidizing natural ignitions are noted to have occurred long before active fire suppression in southern California, beginning with the nineteenth-century settlement period (Barrett 1935; Brown & Show 1944; Lee & Bonnicksen 1978). Also, the assumption that lightning ignitions are saturating in the southern California environment is called into question by the fact that area burned is correlated with number of fires ($r^2 = 0.71$), which is correlated with population density (Keeley et al. 1999). Humans affect fire frequency, and this effect appears to be much greater south of the border. Even if lightning-ignited fires were saturating in Baja California, humans ignite fires far outside the natural fire season (Henderson 1964; Haiman 1973; Freedman 1984), and this alone could greatly alter natural burning patterns.

Comparability of Fire Climates

Massive fires in southern California are commonly driven by foëhn-type Santa Ana winds, but these winds diminish south of the border (Henderson 1964; Mitchell 1969; Markham 1972; Pyke 1972; Haiman 1973; Freedman 1984). Although these winds are controlled by regional synoptic patterns that include a Great Basin high-pressure cell and Pacific Coast trough of low pressure (Schroeder et al. 1964), their ultimate manifestation is a result of local topography (Fosberg et al. 1966; Schroeder & Buck 1970). For example, the steep eastern escarpment and lack of low passes precludes such foëhn winds on the western slopes of the southern Sierra Nevada. In Los Angeles County, these winds are funneled through passes in the east-west trending Transverse Ranges and thus are predominantly northern or northeastern winds (Edinger et al. 1964; Weide 1968). In San Diego County they are strictly eastern winds (Campbell 1906; Sommers 1978) because of the north-south orientation of the peninsular ranges. These ranges extend southward into Baja California, where the sharp eastern escarpment of the Sierra Juárez and the San Pedro Mártir, coupled with the Gulf of California to the east, limit the formation of foëhn winds (Henderson 1964).

Most fires in northern Baja California are driven by onshore northwestern breezes (Minnich 1983, 1989, 1998), and these have a different capacity for fire spread than fires driven by Santa Ana winds. Minnich contends that the absence of Santa Ana wind-driven fires south of the border is due to the lack of contiguous older stands of vegetation with fuel sufficient to carry fire. This conclusion is disputed by the fact that these winds diminish the further south of the border one goes, and the fact that in southern California Santa Ana winds will drive fire through nearly any age class of fuel (Keeley et al. 1999).

Factors Affecting Fuel Production

Annual precipitation is substantially different between the regions we compared. The "fire suppression zone" of southern California considered by Minnich (1983) extends northward to Santa Barbara and may have up to double the precipitation observed at comparable elevations in the "nonsuppression zone" of northern Baja California (Markham 1972; Pyke 1972; Haiman 1973) (Fig. 2). Haiman (1973) showed that winter cyclonic systems were more predictable in southern California than in Baja California, and that, for similar elevations and distance from the coast, only one out of six storms produced comparable precipitation at sites in northern Baja California. Also, half of the storms deposited more than 75% greater precipitation in San Diego County (Table 1). In addition, there is an earlier cut-off of late winter and early spring precipitation the further south of the border one goes (Pyke 1972). Although summer monsoon rains are more predictable south of the border, this input is of marginal importance because it comprises a small fraction of the annual precipitation. In addition, higher summer evaporative demand is thought to make much of it unavailable to shrubs (Minnich & Franco-Vizcaino 1999), as has been demonstrated for Arizona chaparral subject to similar summer monsoon rains (Vankat 1989).

Differences in precipitation between southern California and Baja California could have profound effects on primary productivity and rates of fuel production. Less fertile soils in Baja California chaparral (Franco-Vizcaíno & Sosa-Ramirez 1997) would further exacerbate differences in primary production. Although precise comparisons of primary production are not available, Freedman (1984) estimates that similar-aged chaparral stands have 40% less cover in Baja California than "comparable" sites north of the border. The positive correlation between precipitation and fire occurrence within the chaparral type north of the border in San Diego County is direct evidence that precipitation affects fire regime (Krausmann 1981). Slower fuel accumulation in Baja California could have profound effects on rates of fire spread and patterns of burning.

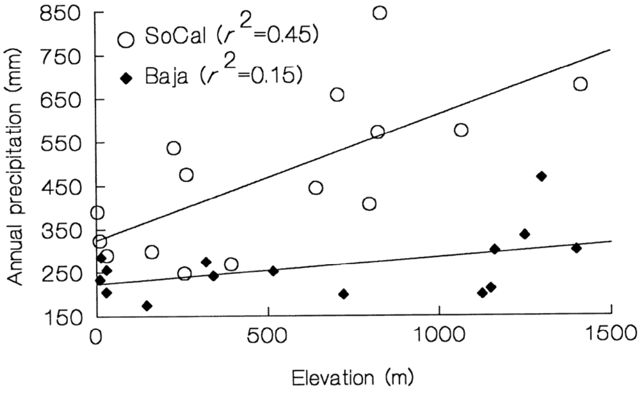

Figure 2. Precipitation for selected sites at different elevations in southern California (SoCal) and northern Baja California (Baja). Relationship between precipitation and elevation is significant ($p < 0.01$*) for southern California but not significant (*$p > 0.05$*) for Baja California (data from Henderson 1964; Haiman 1973; and National Oceanic and Atmospheric Administration, climatological data, annual summary).*

Landscape Features

Differences in landscape have not been considered. Immediately south of the interior border crossing at Tecate, the topography changes and much of the chaparral-dominated landscape is a plateau, which lacks the topographic heterogeneity present north of the border (Haiman 1973). This is important in terms of both direct and indirect effects on fire regime. Rugged topography directly affects rate of fire spread through heating of adjacent fuels as well as creation of wind turbulence. Indirectly, rugged terrain in semiarid regions may lead to greater primary production and thus greater fuel production. For example, a plateau receives three times greater solar insolation than north-facing slopes, and this difference is not offset by south-facing slopes, which at these latitudes differ from flat surfaces by only 12% (Frank & Lee 1966). Higher solar insolation in this region likely translates into greater evaporative loss and less production on the Sierra Juárez plateau than in the adjacent San Diego County. Also, vegetation on slopes commonly receive underground water subsidies from upslope drainage (Rowe et al. 1954). These differences could have profound effects on primary production, fuel accumulation, and ultimately on fire regimes.

Also, in Baja California chaparral comprises about one-third less area than it does north of the border (Minnich 1989), and it typically is bordered by less flammable pinyon communities on the east (Minnich & Franco-Vizcaíno 1998). In all of northern Baja California there are few if any areas of contiguous chaparral the size of the massive Santa Ana–driven Matilija or Laguna fires recorded in southern California (Fig. 1a).

Patterns of Land Use

Differences in land use may affect burning patterns. Working ranches north of the border are significantly larger than the legally mandated patchwork of small farms and ejidos south of the border (Henderson 1964), and on ejidos fire is used regularly to remove brush and expand grazing lands (Henderson 1964; Freedman 1984). In contrast, despite the thousands of permits issued by the State of California for brush burning since 1945, few ranch-

Table 1. Comparison of precipitation in six storms during the winter of 1970-1971 among southern California and comparable sites in northern Baja California (from Haiman 1973).

Location	*Distance to coast (km)*	*Elevation (m)*	*Precipitation (mm)*
California (lat. 32°35′-32°55′)			
San Diego	0	0	102
Barrett Dam	50	585	168
Cuyamaca	60	1305	201*
Baja California (lat. 31°50′-32°10′)			
Ensenada	0	0	86
Ojos Negros	30	700	77
San Juan Dios	62	1250	84

*n = 5.

ers in southern California have applied for such permits (California Division of Forestry 1978). In addition, in many parts of Baja California such as the Sierra Juárez, cattle graze over much of the chaparral lands (Henderson 1964), reducing fine fuels and physically trampling the shrubs (Freedman 1984), both of which affect fire spread.

Model of the Natural Fire Regime in Southern California Shrublands

Parameters of a fire regime include the mean and variance in fire frequency, fire intensity and severity, and fire season. In California chaparral and coastal sage scrub, the contemporary fire regime is reasonably well documented (Rogers 1942, Keeley 1982, 1992, 1998; Minnich 1983, 1989, 1998; Dunn 1989; Moritz 1997; Conard & Weise 1998; Keeley et al. 1999). Fire-rotation intervals, which are regional averages, are 30-40 years, and the range is illustrated by site-specific fire-return intervals, which vary from <5 to >100 years. They are always crown fires, and although the number of fires peaks in the summer, the bulk of the area is burned in autumn (Fig. 3). Fire intensity and severity are variable, depending upon fuels, weather, and topography. The majority of contemporary fires are small (10-10^3 ha), and only a tiny percentage become large (10^5-10^6 ha). These large fires are usually coincident with weather conditions generated by foëhn winds known as Santa Anas in southern California, Mono winds in central California, northeastern winds in northern California (Schroeder et al. 1964), or more localized "sundowner" winds in coastal Santa Barbara County (Ryan 1996).

It is questionable whether or not these parameters are representative of natural (pre-human influence) conditions because of the opposing anthropogenic impacts of fire suppression and increased fire ignitions. It is our intent to start with this contemporary regime and evaluate the extent to which the natural fire regime may have deviated from this pattern.

Based on the highly significant relationship between wildfire ignitions and increasing population density during the twentieth century (Fig. 4), it is apparent that the contemporary fire frequency is markedly higher than what would be experienced in the absence of human subsidy. This human influence is spatially variable, being most prominent in wildland areas adjacent to coastal population centers and decreasing in influence in the in-

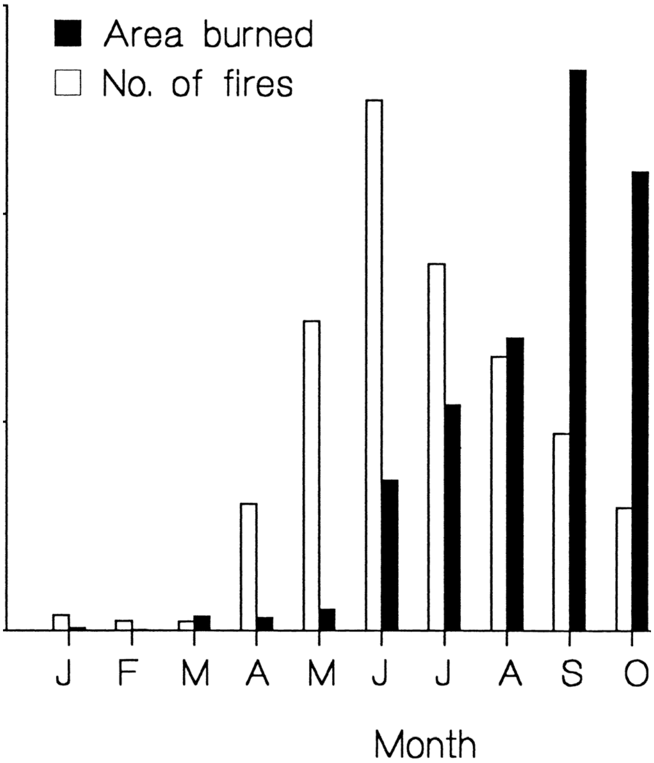

Figure 3. Monthly distribution of fire frequency and area burned (1910 -1999) for Los Angeles County (data from the California Fire History Database, California Division of Forestry and Fire Protection, Fire and Resource Assessment Program, Sacramento).

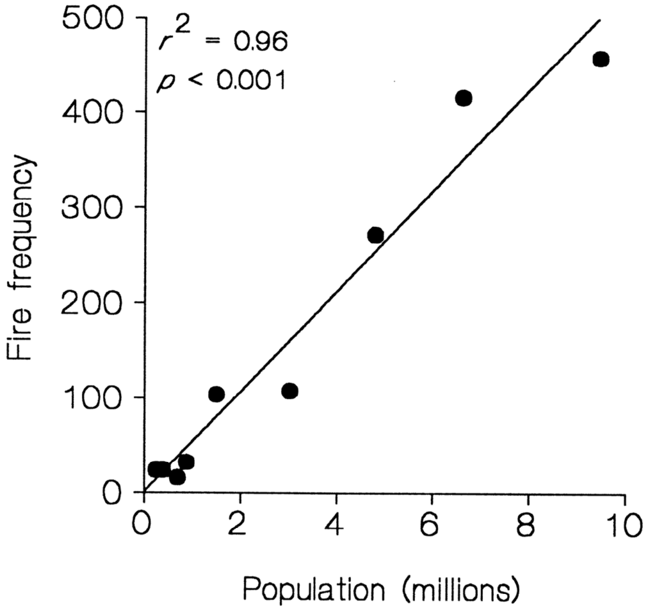

Figure 4. Fire frequency each decade since 1910 versus population density at the beginning of each decade for Riverside and Los Angeles counties in southern California (data from Forstall 1998; Keeley et al. 1999).

terior and at higher elevations (Keeley 1982; Keeley et al. 1999; Moritz 1999). This relationship between population density and number of fires has been noted since the early decades of the twentieth century (Brown 1945; Clar 1959).

Human fire subsidy began with the Native American occupation of California (Knowles 1953; Timbrook et al. 1982; Wickstrom 1987). Patterns of spatial variation were similar to those of contemporary anthropogenic effects, but, relative to contemporary California, were likely limited due to low population density and reduced mobility. Native Americans increased fire-return intervals in areas near coastal communities and surrounding slopes, but may have had limited effect on the broader landscape (Cooper 1922; Bolton 1927).

Under natural conditions, lightning is the only predictable source of ignition, but its importance varies spatially throughout the state in a pattern nearly opposite that of human-ignited fires (Keeley 1982). Thunderstorms are rare near the coast and most frequent at higher elevations in the interior. In the coast ranges east of Monterey, a 50-year record for the chaparral-dominated Pinnacles National Monument indicates only a single lighting-ignited fire (Greenlee & Moldenke 1982). In the coastal Santa Monica Mountains of southern California, no lightning-ignited fires have been recorded in the 60-year fire record (National Park Service fire records on file at the Santa Monica Mountains National Recreation Area Headquarters); lightning-ignited fires have been observed in this range (M. Morais, personal communication), but clearly they are not common.

In southern and central coastal California, lightning-ignited fires increase with distance from the coast and with elevation (Table 2). For example, the San Bernardino National Forest, the most interior forest with the highest elevation, has the highest density of lightning-ignited fires, most of which originate in coniferous forests. Even here, the density is not extraordinarily high, with an average of one lightning-ignited fire per year per 10,000 ha, which is more than an order of magnitude greater than the density in coastal foothills (Table 2).

Model of the Natural Fire Regime

Lightning-ignited fires are spawned by thunderstorms concentrated in interior mountains in July and August. Historical accounts of fire in the San Gabriel and San Bernardino mountains of southern California during the latter quarter of the nineteenth century (Minnich 1978, 1987) give some insight into fire behavior that was unabated by active fire suppression. Although these fires were not necessarily all natural lightning-ignited fires (e.g., Leiberg [1899*c*] was certain that miners were responsible for much of this burning), they nonetheless provide some insight into fire behavior in the absence of fire suppression.

Several conclusions can be drawn from this record: (1) Presuppression chaparral fires were always stand-replacing fires that burned with "irregular" behavior, sometimes creeping through brush and other times raging, so fire intensity and severity were variable. (2) Fires would commonly burn for months before being extinguished by rain or natural barriers, but despite this long period of activity they often covered a relatively modest area (e.g., the 1898 Mt. Lowe Fire burned for 3 months and consumed only 2300 ha). (3) Fires occasionally would "hold over" in logs, even during rainstorms, to be reignited at a later time.

The lightning-ignited fires that burned slowly for months or "held over" in logs would certainly have been a ready source of ignition when the predictable Santa Ana winds began in September. Although this juxtaposition may not have occurred frequently, when it did occur it likely would have resulted in a massive landscape-scale burn. Indeed, these Santa Ana winds of 100 km per hour, coupled with extremely low relative humidity, can generate fires that may cover 30,000 ha in a day (Phillips 1971), and often such fires will burn for days at a time (Chandler 1963; Schroeder et al. 1964; Countryman 1974). Thus, we hypothesize that the majority of fires were small in the pre-suppression landscape, but the bulk of the landscape burned in a few large fires that occurred at unpredictable intervals in association with autumn foëhn winds.

Site-specific fire-return intervals were almost certainly highly variable, with some montane lightning hotspots experiencing fires every few decades and coastal sites

Table 2. Total number of fires and hectares burned and percentage due to lightning during the 1970s for lower-elevation foothills (California Division of Forestry [CDF] jurisdiction) and higher-elevation interior mountains (U.S. Forest Service [USFS] national forests) in southern and central-coastal California (from Keeley 1982).

CDF ranger unit / USFS national forest	*Total no. of fires* (per 10^6 hectares per decade)	*Total area burned (ha)* (per 10^6 hectares per decade)	*No. due to lightning (%)*	*Area due to lightning (%)*
Foothills (CDF)				
Monterey/San Benito	3,140	53,570	2	<1
San Luis Obispo	3,310	44,130	2	<1
San Bernardino	9,680	12,240	4	11
Riverside	17,620	332,950	1	5
Orange	42,900	120,830	<1	<1
San Diego	9,450	20,930	3	6
Mountains (USFS)				
Los Padres	2,340	49,720	9	56*
Angeles	4,980	214,460	15	4
San Bernardino	4,400	41,030	24	6
Cleveland	4,870	121,370	11	<1

**Much of this is due to a single lightning-ignited fire (Marble Cone fire) in 1977.*

remaining fire-free for a century or more. Regional rotation intervals were likely longer than at present, perhaps 70 years or more for interior regions (Minnich 1989, 1998; Conard & Weise 1998) and presumably much longer near the coast. In short, the fire regime was one of localized fires, punctuated by periodic massive fires, a pattern predicted by modeling studies of the central coastal chaparral (Greenlee & Langenheim 1990).

Pros and Cons of the Fire Model

It could be argued that, despite the potential temporal juxtaposition of lightning-ignited fires prior to the severe autumn fire-weather conditions, frequent lightning fires that burned under moderate weather conditions would create a fine-grained mosaic of young age classes, capable of acting as a barrier to the spread of large Santa Ana–driven fires (Minnich 1989, 1995, 1998). Often cited in support of such a model are the nineteenth century forest-reserve surveys made by U.S. Geological Survey scientist John Leiberg in the San Gabriel, San Bernardino, and San Jacinto mountain ranges. These documents are extremely important because they represent some of the few descriptions of chaparral shrublands prior to fire control. One quote by Leiberg (1899*a*) is often cited in support of the age-mosaic model: “Recent fires—that is to say, within the last eight or ten years—have burned over about 14,000 or 15,000 acres [approximately 5920 ha] scattered throughout the reserve in small tracts.”

At a landscape scale, however, Leiberg’s comments do not describe a fine-grained age mosaic capable of preventing Santa Ana–driven fires. Indeed, Leiberg was reporting on the total burning observed across the 214,575 ha of brush on the San Jacinto Reserve (Leiberg 1899*a*, 1900*c*). Thus, according to his estimate, only about 2.8% had burned during the last decade of the nineteenth century (similar proportions appear to apply to the San Gabriel and San Bernardino reserves [Leiberg 1899*b*, 1900*a*, 1900*b*; Kinney 1887]). At this rate of burning it is estimated that, at any point in time, over 90% of the chaparral in the San Jacinto Reserve would have been three or more decades old, which surely describes a landscape capable of fueling a large, catastrophic Santa Ana–driven fire. Any lack of large fires at the turn of the century was not due to limited fuels but more likely to limited ignitions coincident with severe fire weather. Today, higher population density in the San Jacinto Range produces a greater number of ignitions, resulting in a rate of burning more than three times that observed by Leiberg (U.S. Forest Service, unpublished data).

It is hypothesized that, given sufficient time—half a century or more—most chaparral regions would have experienced the proper juxtaposition of lightning-ignited fires followed by severe fire-weather conditions to result in massive landscape-scale fires. On the time scale of centuries, fire-rotation intervals likely varied due to stochastic factors, although on longer time scales changes in climate might have altered return intervals as well (e.g., Swetnam 1993).

Illustrative of the natural pattern is the 72,400-ha Marble Cone fire ignited by lightning on the Los Padres National Forest in 1977 (Davis 1977). Some suggest that this fire resulted from unnatural fuel accumulation due to half a century of fire suppression. There was nothing unnatural about the Marble Cone Fire, however, because a similar-sized fire (60,700 ha) occurred in the same area in 1906, prior to active fire suppression (Greenlee & Moldenke 1982), and other large fires were recorded even earlier (Talley & Griffin 1980). Although the Marble Cone fire was not driven by foëhn-type winds, it did occur under severe fire-weather conditions. Another lightning-ignited fire on the Los Padres Forest in 1999 (the Kirk Complex Fire) illustrates that, under severe weather conditions, fires are not blocked by young stands of chaparral, because the Kirk Fire reburned much of the Marble Cone burn (M. Borchert, personal communication).

Other massive chaparral fires are also known from historical records prior to effective fire suppression. For example, one of the largest fires in Los Angeles County (24,000 ha) occurred in 1878 (Keeley et al. 1999). The largest fire in Orange County's history burned over a quarter million hectares in 1889 (Lee & Bonnicksen 1978); Kinney (1900), Barrett (1935), Brown and Show (1944), and Brown (1945) provide further examples of large chaparral fires prior to fire suppression. As is the case today, some of these historical fires were of sufficient intensity to severely denude slopes, resulting in catastrophic flooding, and this occurred often enough to be the primary impetus for the creation of California's first federal forest reserve—the San Gabriel Timberland Reserve—in 1892 (Lee & Bonnicksen 1978).

Paleoecological records reveal that these large fires driven by Santa Ana winds were a prominent feature of the landscape long before European settlement (Mensing et al. 1999). In the Santa Ynez Range of Santa Barbara County, massive Santa Ana–driven fires have occurred several times per century over the past 560 years, a frequency that did not change during the settlement period or following fire suppression.

The contemporary fire regime in southern California shrublands mirrors the natural fire regime far more closely than is generally credited (c.f., Bonnicksen & Lee 1979; Minnich 1983, 1995, 1998; Davis 1995; Pyne 1995). As is the case today, the natural fire regime was likely characterized by many small fires and a few large fires that consumed the bulk of the landscape. Fire intensity and severity were variable, as is the case today. The majority of fires occurred in summer, but in all likelihood the bulk of the landscape burned during autumn, when fuels were at their driest and weather conditions the most severe. This pattern has not changed today (Fig. 3). The primary change in the fire regime has been the marked increase in fire frequency in areas of high population density such as southern and central coastal California (Moritz 1997, 1999; Conard & Weise 1998; Keeley et al. 1999). One consequence of this shorter fire-return interval has been widespread conversion of shrublands to non-native annual grassland (Keeley 1990; Minnich & Dezzani 1998). Today, fire suppression is required just to maintain some semblance of the natural fire regime (Conard & Weise 1998).

Implications for Fire Management

Fire-management plans in southern California national forests have placed inordinate stock in the notion that fire suppression has been sufficiently effective to allow unnatural fuel accumulation, which has led to an unnatural fire regime that includes large, catastrophic wildfires. Fire suppression, however, has not effectively reduced the area burned (Conard & Weise 1998; Keeley et al. 1999; Moritz 1999). Also, large Santa Ana–driven fires are not dependent on an unnatural accumulation of fuel; rather, they appear to be a natural feature of this landscape (Mensing et al. 1999). The important implication of these findings is that we have not, through fire management policies, created the contemporary fire regime.

Nevertheless, nearly every decade in the twentieth century has been characterized by increased expenditure for fire suppression and greater losses of property and lives (California Department of Forestry and Fire Protection 1999). We propose that both increased fire-suppression costs and increased property loss are best explained by changes in human demography.

For much of this century, wildland fire frequency has been driven by population density (Fig. 4): more people on the landscape equals more fires. Because both state and federal fire-suppression funds are available on an as-needed basis (Mutch 1997), every decade requires more fire suppression just to maintain some semblance of status quo. In short, increased expenditure on fire suppression is a direct result of increased fire ignitions, coupled with increasingly sophisticated and expensive fire-fighting technology.

The determining factor in whether or not a fire becomes large is the coincidence of an ignition with severe fire weather. Indeed, nationwide, weather during fire is considered the most important determinant of the costs of suppression (Schuster et al. 1997). Fires ignited under severe weather conditions defy suppression, however, and thus fire managers have made limited progress in reducing the number of catastrophic fires. To their credit, though, the number of such fires has not greatly increased either. Indeed, fire suppression has become increasingly effective when measured as the area burned per number of fire starts (Keeley et al. 1999).

Why then does the loss of property and lives increase every decade? The primary culprit is the fact that growth in southern California cities has not come from changes in density but rather from expansion of boundaries, a pattern evident in cities in other parts of the United States and the world (Knight & Gappert 1989). Consequently, there has been an extraordinary expansion of the urban-wildland interface and a changing pattern of mixed urban and wildland patches (Davis 1989). During the twentieth century, changes in the fire regime have been dwarfed by changes in land-development patterns, which have made more people vulnerable to the natural forces long present on the landscape (Zivnuska & Arnold 1950; Davis 1965; Bradshaw 1987). Illustrative of this is the fact that in the 60-year period prior to 1980, 3802 structures were destroyed by wildfires in California; in the subsequent 14 years the number more than doubled (Coleman 1996). Further adding to the financial losses is the steady increase in property values attendant with economic inflation.

Management plans that call for widespread prescription burning to "recreate" a landscape mosaic of different age classes of vegetation will not stop large, catastrophic fires (Moritz 1997, 1999; Conard & Weise 1998; Keeley et al. 1999). We do not suggest that prescription burning is no longer an effective management tool. Under moderate weather conditions, young vegetation age classes may play a critical role in enhancing effective fire suppression, and fire suppression under moderate weather conditions will not lead to catastrophic fires if weather conditions change abruptly. In light of the many limitations to prescription burning in California shrublands (Conard & Weise 1998), increasing demands will be placed on the most cost-effective use of such fire-management practices and will require further study as to the most strategic placement of prescribed burns. Across the California shrubland landscape, however, fire suppression is still one of the most important tools in the fire manager's arsenal.

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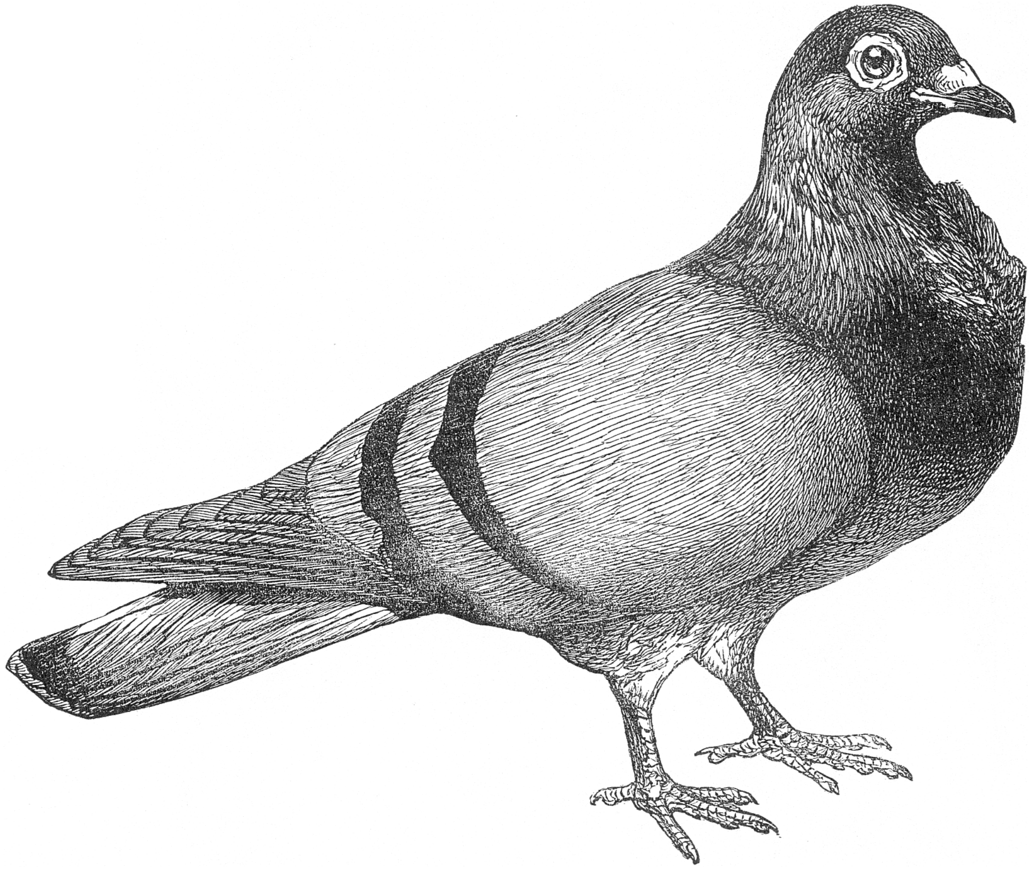


8. Impact of Past, Present, and Future Fire Regimes on North American Mediterranean Shrublands

Jon E. Keeley and C.J. Fotheringham

Mediterranean shrublands occur in five regions of the world, under a climate of mild wet winters and hot summer–fall droughts lasting six months or more. In California they dominate landscapes below 2000 m in the central and southern coastal ranges and foothills of the Sierra Nevada. One consequence of this distribution is that these shrublands, more than any other vegetation type, interface with urban areas (Fig. 8.1). These shrublands are subject to periodic massive wildfires (Fig. 8.2) that account for 40% of all wildland acreage burned in the United States (Lillard 1961), creating a particularly hazardous urban–wildland interface. Contributing to this fire hazard are the moderate temperatures during the rainy winter and spring, which prolong the growing season and generate broad bands of dense contiguous fuels. The long drought makes these fuels readily ignitable and the autumn foëhn winds that come each year at the end of the dry season produce the worst fire climate conditions in the country (Schroeder et al. 1964).

This chapter examines the past, present, and future fire regimes in California shrublands, particularly chaparral and coastal sage scrub. Although shrublands are recorded from nearly all counties in the state (Callaham 1985), this review will focus on those in the central and southern coastal ranges with the largest expanses of contiguous shrubland (Fig. 8.3). Of particular concern are the extent to which humans have altered this regime in the past and the extent to which future global change will affect fire regimes and vegetation patterns.

Humans directly influence fire regimes in two ways: they ignite fires and they suppress fires. Evaluating the net effect of these impacts is not simple because

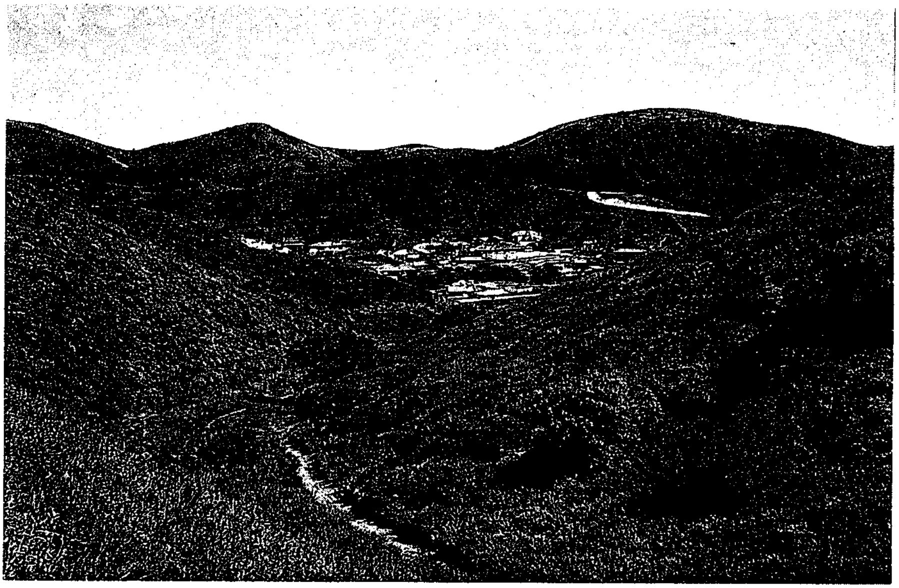


Figure 8.1. Interface between urban environments and evergreen chaparral (*right*) and semi-deciduous coastal sage scrub (*left*) in southern California (by J.E. Keeley).

their relative importance varies across the landscape. For example, in the montane coniferous forests of the Southwest, lightning-ignited fires are abundant and human ignitions are far less important than in lower-elevation shrublands of southern California where lightning is uncommon and humans cause the majority of fires (Fig. 8.4). Also fire suppression has been far more effective in western coniferous U.S. forests, often achieving nearly complete fire exclusion (Skinner and Chang 1996; Agee 1993), but this "fire-suppression = fire-exclusion" equation does not apply to shrublands of southern and central coastal California (Keeley and Fotheringham 2001b).

Determinants of Brushland Fire Regimes

Fire regimes are determined by the temporal and spatial pattern of ignitions, fuels, weather, and topography (Pyne, Andrews, and Laven 1996), and with regard to Californian shrublands there are two schools of thought on their relative importance. One is based on deductions from Rothermel's fire behavior model (Rothermel 1972) and argues that fire regime is a highly deterministic process driven by fuel load (Rothermel and Philpot 1973; Philpot 1974a,b, 1977). Under this model fire occurrence is unaffected by external drivers such as ignitions or weather, rather it is viewed as entirely dependent on community patterns of fuel accumulation (Minnich 1989, 1995,1998, 2001; Minnich and Cho 1997). The

Figure 8.2. Crown fire in chaparral (photo by USFS, Riverside Fire Lab).

alternative model argues that the fire regime is controlled by the coincidence of ignitions occurring under severe current and antecedent weather conditions that influence fuel flammability (Phillips 1971; Keeley et al. 1989; Davis and Michaelson 1995; Keeley and Fotheringham 2001a,b). Under this model any of these factors may be limiting, and the importance of each varies spatially and temporally with external drivers such as severe fire weather being of paramount importance in coastal California. These models have very different implications for fire management and affect our perception of anthropogenic impacts on fire regime and our ability to sort out future climatic signals.

Patterns of Ignition

In order to appreciate fully the role humans play in shrubland fire regimes, we need to first examine how ignitions, fuels, and weather interact to determine fire behavior. In California humans have been a source of ignitions for more than

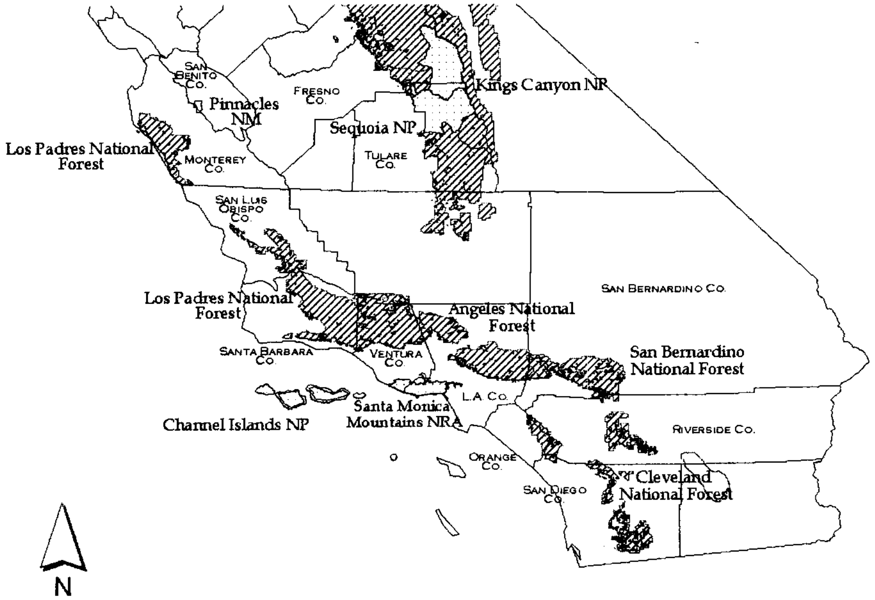


Figure 8.3. Central and southern California regions considered in this chapter. Central coastal California includes Monterey, San Luis Obispo, Santa Barbara, and Ventura counties, and southern California includes Los Angeles, San Bernardino, Riverside, Orange, and San Diego counties. Collectively these nine counties comprise nearly two million hectares of shrubland (Table 8.1).

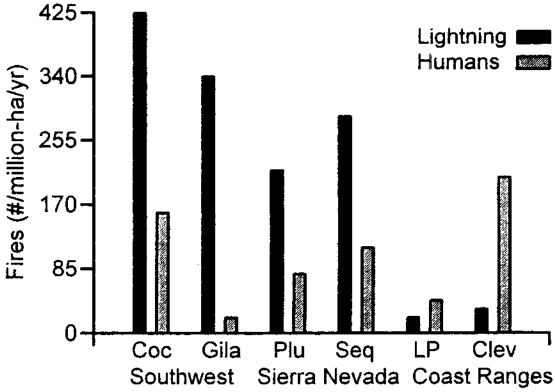


Figure 8.4. Regional comparison of lightning- and human-caused fires on USFS national forests. The Southwest includes the Coconino (Coc) in Arizona and Gilia in New Mexico. In California the Sierra Nevada forests are the Plumas (Plu) and Sequoia (Seq), and the California coastal ranges national forests are the Los Padres (LP) and Cleveland (Clev). Fire occurrence data from the published U.S. Forest Service, National Forest Fire Reports, 1970–1979, and forest area from (*http://www.fs.fed.us/land/*).

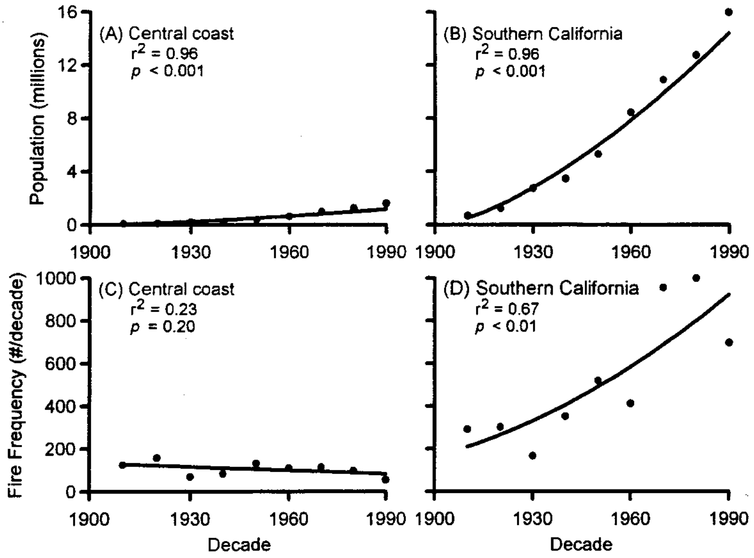


Figure 8.5. Decadal variation in population density (A–B) and fire frequency (C–D) for central coastal and southern California. Population data from the U.S. Department of Commerce, *http://www.census.gov/populations/cencounts/ca190090.txt*. (Fire data from the Statewide Fire History Data Base, California Department of Forestry, Fire and Resource Assessment Program (FRAP), Sacramento, CA, which includes historical fire records from the U.S. Forest Service national forests, California Division of Forestry ranger units and other protected areas, plus city and county records; minimum fire size recorded varied between 16 and 40 ha, depending on the agency).

10,000 years, but they likely have had a greater influence in the twentieth century due to the near exponential rise in population density and fire frequency in the southern part of the state (Fig. 8.5).

Under natural conditions lightning is a source of ignition but far less predictable than in other parts of the Southwest (Fig. 8.4). Within the state, lightning-ignited fires vary spatially because thunderstorms are rare near the coast and most frequent at higher elevations in the interior (Radtke, Atndt, and Wakimoto 1982; Keeley 1982; Greenlee and Moldenke 1982; Knipper 1998). Lightning is the dominant ignition source in the Sierra Nevada, but it is a far less common ignition source in the coastal ranges. Within the coastal ranges lightning varies with elevation; for example, in San Diego County lightning strikes are 10 times more abundant above 1800 m than below 500 m, and they vary temporally with 85% occurring between July and September (Wells and McKinsey 1994, 1995). Similar patterns are evident further south in Baja California (Minnich et al. 1993). The annual density of lightning discharges in this region is roughly 1 per 100 ha (Michael L. Wells, personal communication; Minnich et al. 1993). Based on the frequency of fires ignited by lightning in this region (Keeley 1982; Minnich et al. 1993), it would appear that only 2% to 5% of all lightning discharges ignite a wildfire. In other words, 95% of all lightning discharges strike inadequate fuels, or are extinguished by rain, before they reach a detectable size.

Lightning ignitions in coastal and southern California shrublands account for a highly variable amount of burning, ranging from less than 1% to more than 50% of the landscape per decade (Table 8.1). Both spatial and temporal factors are involved. Considering all of California, lightning ignitions account for an increasing fraction of burning from the coast to the interior and from south to north (Keeley 1982). Occasionally lightning may coincide with severe weather and fuel conditions and result in massive fires such as the Marble Cone Fire in 1977 on the Los Padres National Forest (Table 8.1). Longer-term data sets for the Los Padres show this to be an infrequent event (Davis and Michaelsen 1995), suggesting that lightning fires in these coastal ranges are capable of reaching extraordinary size but the temporal variance is high.

Lightning is more predictable in the higher interior Sierra Nevada Range (Fig. 8.4), and it varies inversely with elevation (van Wagtendonk 1992). In Sequoia National Park (located in the southern Sierra Nevada, Fig. 8.3) lightning-ignited fires reach a peak at elevations between 2000 and 3000 m and are considerably less frequent in the lower-elevation shrubland-dominated foothills (Parsons 1981; Vankat 1985). Within the park the lower-elevation shrublands experience fewer lightning-ignited fires than would be expected based on shrubland area ($p < 0.001$ with χ^2 test), and the opposite is true for higher-elevation mixed-coniferous forests. This pattern is repeated throughout the Sierra Nevada;

Table 8.1. Total number of fires and hectares burned and percentage due to lightning during the 1970s decade for lower-elevation foothills (California Division of Forestry Jurisdiction) and higher-elevation interior mountains (U.S. Forest Service national forests) in southern and central–coastal California

CDF Ranger Unit/USFS National Forest	Total fires (10^6 ha/ decade)	Total area burned (ha)	Fires due to lightning (%)	Area due to lightning (%)
Foothills (CDF)				
Monterey/San Benito	3,140	53,570	2	<1
San Luis Obispo	3,310	44,130	2	<1
San Bernardino	9,680	12,240	4	11
Riverside	17,620	332,950	1	5
Orange	42,900	120,830	<1	<1
San Diego	9,450	20,930	3	6
Mountains (USFS)				
Los Padres	2,340	49,720	9	56[a]
Angeles	4,980	214,460	15	4
San Bernardino	4,400	41,030	24	6
Cleveland	4,870	121,370	11	<1

Source: Keeley 1982.

Note: Sites are arranged from north to south, and national forest locations are shown in Figure 3. All of these ranger units or forests are dominated by chaparral, but they also include mixtures of grassland, sage scrub, woodlands, and forests.

[a] Much of this is due to a single lightning-ignited fire (Marble Cone Fire) in 1977.

foothill shrublands average about 10 lightning-ignited fires per year per million hectares and the higher-elevation montane forests experience 100 to 200 per year per million ha (Keeley 1982). Of course, making predictions about the elevational patterns of burning by lightning alone (i.e., in the absence of anthropogenic interference) is complicated by the likelihood that along this elevational gradient, conditions conducive to fire spread are inversely related to lightning fire frequency. Modeling is perhaps the only means of understanding the natural fire regimes in these ecosystems (e.g., Greenlee and Langenheim 1980; Davis and Burrows 1993; Davis and Michaelsen 1995; Zedler and Seiger 2000).

In general, rain or high humidity accompanies lightning fires, and there is often a time lag between ignition and changes in weather conducive to rapid fire spread. Thus, in forested ecosystems where lightning is the dominant ignition source (e.g., the Southwest, Fig. 8.4), fire suppression has been extraordinarily effective. Fire detection has become increasingly more reliable (Chandler 1960), and there is reason to believe that many suppressed lightning-ignited fires, in both forests and shrublands, would have burned out if never detected. This is supported by a greater number of reports of lightning-ignited wildfires in the latter half of the twentieth century (Keeley 1977, 1982; Greenlee and Moldenke 1982; Vankat 1985); however, it could reflect changes in fuel structure as well (Weatherspoon and Skinner 1996).

In the coniferous forests of the Sierra Nevada, lightning-ignited fires peak in the summer months of July and August and match closely the monthly distribution of human-ignited fires (Parsons 1981; Vankat 1985; van Wagtendonk 1992). Throughout the chaparral-dominated coastal ranges lightning-ignited fires are also concentrated in the summer months of July and August (Keeley 1982). However, humans are the dominant source of ignition (Fig. 8.4), and their impact on fire season varies from apparently very little effect in the central coast, as illustrated by a summer peak in burning to a much greater impact in the south, where anthropogenic fires result in a longer fire season and greater autumn burning (Fig. 8.6). Thus, in contrast to the situation in forests throughout the western United States where lightning is the dominant source of ignition and humans have successfully suppressed most fires, the vast majority of fires in chaparral and coastal sage scrub in the coastal ranges are ignited by humans (Keeley, Fotheringham, and Morais 1999; Keeley and Fotheringham 2001b). In short, fire suppression has not eliminated burning on this shrubland landscape. Human impact is most pronounced at lower elevations and in proximity to metropolitan areas. On shrubland landscapes under natural conditions, lightning is a predictable source of ignition but variably distributed in time and space.

Fuels and Weather

The spatial and temporal arrangement of fuels is a critical determinant of fire behavior, and fuel loading is determined largely by differences in site productivity and vegetation age. The extent to which fire will propagate across a landscape

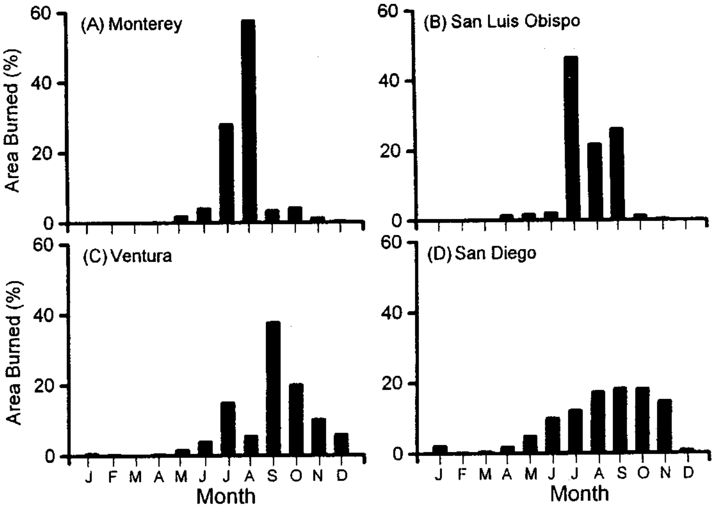


Figure 8.6. Seasonal distribution of burning reported for 1970 to 1999 for selected counties (data from the California Statewide Fire History Database; see Fig. 5).

is determined by the spatial arrangement of fuels and weather conditions prior to and during the fire. Fuel structure needs to be considered at different scales. In a stand of vegetation on a single slope face, the important fuel characteristics are the vertical and horizontal placement of fuels, fuel surface-area/volume ratio, and the moisture status of leaves and stems. At this scale shrubs are of uniform age and may be rather coarse grained in monotypic stands, becoming finer grained as the mixture of species increases. At the landscape level fuels are fine grained, and large expanses of homogeneous fuels are the exception. Barriers of reduced fuel loading, which could include rocks, rivers, alluvial fans, young age classes, or less flammable vegetation types, may inhibit fire spread. As seasonal drought progresses, different portions of the landscape are added as potential fuels, further contributing to inherent landscape heterogeneity of fuels. This interaction among landscape structure, fuels, and moisture limits the ability of models to predict fire spread, and the fine-grain nature of fuels leads to potentially large errors (Kessell and Cattelino 1978).

Fuel Structure and Fuel Moisture

In mature shrublands, surface fuels are insufficient to carry fire, and thus fires propagate through the canopy as crown fires. Recently burned sites have sufficient herbaceous growth to carry surface fires (Haidinger and Keeley 1993), and this may be exacerbated by artificial seeding of nonnative grasses (e.g., Zedler, Gautier, and McMaster 1983). However, sufficient herb biomass to carry surface fires is unlikely following dry winters or on highly infertile coarse-textured soils, such as occur in certain coastal sites (e.g., Lompoc, CA) or the interior ranges of Baja California (Franco-Vizcaino and J. Sosa-Ramirez 1997).

Normally, following a wet winter, high fuel moisture in chaparral shrubs makes them relatively resistant to fire in spring and early summer. However, as the amount of herbaceous matter in the stand increases, the seasonal window of burning increases. Dead herbaceous fuels dry rapidly and are capable of carrying fire within days of a rainfall event (Chandler 1963), and species composition plays a role as nonnative grasses typically die many weeks earlier than native herbs (Keeley, personal observations). As a result certain herbaceous fuels greatly extend the length of the fire season.

Shrublands that have been partially or fully type-converted to grasslands (e.g., Bentley 1967) have a greater probability of igniting but do not represent an extreme fire hazard as fire intensities are low and the fine herbaceous fuels fail to sustain embers or create the vortexes that carry the fire ahead of the moving front (Regelbrugge 2000). Even so, fires in a dense growth of non-native herbs, such as mustards (*Brassica nigra* and *Hirschfeldia incana*) on steep slopes, have been known to generate fire intensities sufficient to destroy homes (J. Keeley, personal observation).

For intact shrublands, two factors affect woody fuel moisture: the physiological activity (water potential) of live foliage and the quantity of dead fuels (Green 1981). Shrub species differ markedly in moisture status of foliage due in part to differences in rooting depth (Davis, Kolb, and Barton 1998)—shallow-rooted shrubs, such as chamise (*Adenostoma fasciculatum*) and *Ceanothus* spp., typically experience water potentials two to three times lower than more deeply rooted shrubs such as scrub oak (*Quercus berberidifolia*). Under prescription weather conditions fires may readily spread through *Adenostoma*-dominated chaparral but extinguish when they encounter patches of scrub oak (Chandler 1957; Green 1981). However, under extended drought, foliage moisture in scrub oak may drop to levels conducive to rapid-fire spread (Olsen 1960; Pirsko and Green 1967; Green 1981).

Dead fuels lack an internal water source and respond rapidly to changes in humidity; small diameter stems can dry completely within hours and larger fuels within days of experiencing low humidity (Chandler 1963; McCutchan 1977). Dead fuels not only combust readily, but as the proportion of dead/live material increases, there is an elevated potential for dead fuel combustion to cause drying of living foliage to a level sufficient for combustion. Because dead fuel carries fire and live fuel absorbs energy, the ratio of dead/live fuel is critical. This increase in combustibility of live fuels is enhanced by the common position of dead fuels beneath the living foliage. Topography plays a similar role. On steep terrain, head fires burning upslope enhance the combustion of fuels ahead of the front and may spread two to three times faster than on level ground—fire spread will roughly double for each 13 degree rise in slope (Green 1981).

Fuel Structure and Wind

At low wind speed, fuel structure and arrangement plays a critical role in fire spread. For example, fine-textured, low, compact fuels—particularly subshrubs with extremely high levels of volatiles, for example *Salvia* spp. (sage)—may readily combust and spread fire rapidly. However, under the same weather conditions, fire might naturally extinguish in a taller chaparral stand in which fuels are more widely scattered in the canopy, and there is little continuity with ground-level fuels (Green 1981). Under low to moderate wind conditions species-specific fuel characteristics in chaparral can promote fire spread. Many characteristics of *Adenostoma fasciculatum* (chamise) make it far more flammable than associated shrub species. About two-thirds of the plant is composed of twigs <25 mm diameter and thus has a stem surface area–volume ratio greater than that of other species (Conard and Regelbrugge 1994). Individual chamise leaves have a relatively low surface area/volume ratio, but they have an extremely high content of volatile compounds that vaporize and increase combustibility (Philpot 1969). On a whole plant basis, *Adenostoma* leaves have a very high surface area/volume ratio; they comprise 67% of surface area but only 16% of plant volume, reflecting the loose packing of foliage (Countryman and Philpot 1970; Barro and Conard 1991).

One of the key factors affecting flammability of *Adenostoma* is the fact that it does not self-prune dead twigs and branches; instead, they are held aloft in the canopy and increase canopy porosity (shrub canopy volume/leaf and stem volume), which often exceeds 99% (Rundel, Parsons, and Baker 1980). High canopy porosity increases flammability and extends the seasonal window of flammability. Also experimental studies demonstrate that this natural retention of dead branches substantially increases fire intensity over an artificial treatment of clipping and leaving as surface fuels (Schwilk 2000). Species with more densely packed fuels, and that self-prune dead branches and have thicker twigs and stems (e.g., scrub oak, *Quercus*, or chaparral holly *Heteromeles arbutifolia*), often will not burn under conditions suitable for fire spread in *Adenostoma*-dominated chaparral. It has been hypothesized that characteristics enhancing flammability have adaptive value (Mutch 1970) and shrubs with seedling recruitment restricted to postfire environments (*Adenostoma, Ceanothus, Arctostaphylos*) have significantly higher flammability than species that recruit independently of fire (*Prunus, Rhamnus, Quercus*) (Bond, unpublished data).

While high-canopy porosity increases flammability, it leads to lower bulk density (mass/volume) and fuel loading (mass/area), reducing the total energy available for combustion. Thus the *Adenostoma* fuel structure increases flammability under a wide range of conditions, whereas the *Quercus* fuel structure is limited in the range of conditions suitable for burning, but under the severest conditions *Quercus* fuels should be expected to generate the highest intensities.

Fuel structure appears to play a less deterministic role under windy conditions, but there is a complex interaction of wind, humidity, fuels, temperature, and topography. Cool moist marine air will extinguish fires (Coffin 1959), whereas warm dry air will lead to fire spread in fuels that otherwise would not burn. Wind accelerates oxygen supply and thus combustion (Green 1981) and is the primary mode of heat transfer. It carries heated air to adjacent fuels on the downwind side, raising the fuel temperature and driving off moisture. Wind also carries away water vapor as well as firebrands, which often occur when gusts are greater than 16km/hr (Green 1981). Topographic features frequently cause unstable and erratic changes in velocity and direction as winds adapt to the topography. On coastal-facing slopes onshore winds are channeled up-canyon and produce eddies at ridgelines that may become turbulent and erratic. The typical pattern is for local daytime up-canyon wind and nighttime down-canyon winds, and on coastal slopes in the central coastal region extraordinarily strong down-canyon winds known as Sundowners are occasionally experienced (Ryan 1996).

Overriding synoptic-scale winds can upset these local wind patterns, e.g., foëhn winds known as "north winds" or "mono winds" in central California (Greenlee and Langenheim 1980) and Santa Ana winds further south (Lessard 1988) (Fig. 8.7). These winds are controlled by regional synoptic patterns that include a Great Basin high-pressure cell and Pacific Coast trough of low pressure, but their ultimate manifestation is a result of local topography (Schroeder and Buck 1970; Fosberg et al. 1966). For example, in the southern Sierra Nevada, the steep eastern escarpment and lack of low passes keeps these winds aloft (Mitchell 1969), and thus foëhn winds are not experienced on the lower western slopes. In Ventura and Los Angeles counties these winds are funneled through passes in the east west trending Transverse Ranges and thus are predominantly northern or northeastern winds (Weide 1968; Schroeder et al. 1964). In San Diego County they are strictly eastern due to the north–south orientation of the Peninsular Ranges winds (Campbell 1906; Sommers 1978). These ranges extend southward into Baja California where their sharp eastern escarpment, coupled with the Gulf of California to the east, limit the formation of foëhn winds on the west slopes of the Sierra San Pedro Mártir (Keeley and Fotheringham 2001a,b).

In southern California these hot, dry Santa Ana winds often have less than 10% relative humidity and may exceed 100km per hour (Fosberg et al. 1966; Ryan 1969). Although referred to as "desert winds," the high temperatures and low humidity are the result of compression as air descends to form the "basin air mass" (Mitchell 1969), and on a local scale as it descends through coastal passes (Krick 1933). Santa Ana winds are most common in the autumn (Fig. 8.8). They have a mean life of about three days but may last two (Fosberg 1965) or three weeks (Campbell 1906), a critical factor since fire size is often determined by the duration of high wind conditions (McCutchan 1977). Under Santa Ana wind conditions fire spread is rapid. For example, the Kanan fire in the Santa Monica Mountains of southern California consumed 10,121 ha in 3 hours (Franklin 1987), and such fires may exceed 30,000ha in a single day (Phillips 1971). Such fires are unimpeded by many potential barriers, since firebrands may be carried as much as 8km beyond the front, igniting numerous new spot fires (Countryman

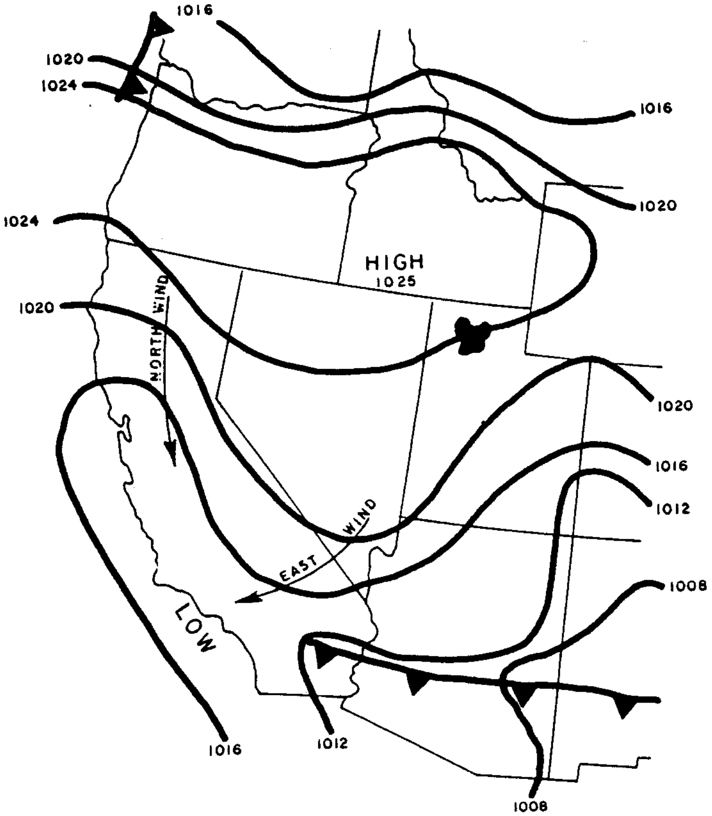


Figure 8.7. Surface weather map during the Great Basin high-pressure air mass that generates foëhn winds in central and southern California (from Phillips 1971).

1974). Under these conditions stands may burn regardless of stand age or species composition (Keeley, Fotheringham, and Morais 1999).

Fuel Mass and Stand Age

It has long been held that fuel mass increases with stand age (Philpot 1977), but this has been criticized as oversimplistic because it ignores tremendous species-specific variability in rates of biomass accumulation (Fig. 8.9). For example, some *Ceanothus* species may accumulate many times more biomass in less than 20 years than *Adenostoma fasciculatum* does in 60 years (Riggan et al. 1994; Regelbrugge 2000). Also at 10 years of age north-facing aspects may have greater biomass accumulation than drier south-facing slopes do at 80 years of age (Black 1987). This fact alone makes landscape-scale predictions of flammability based on stand age extremely difficult. Complicating the prediction of flammability with stand age is the increasing proportion of biomass in large diameter stems that

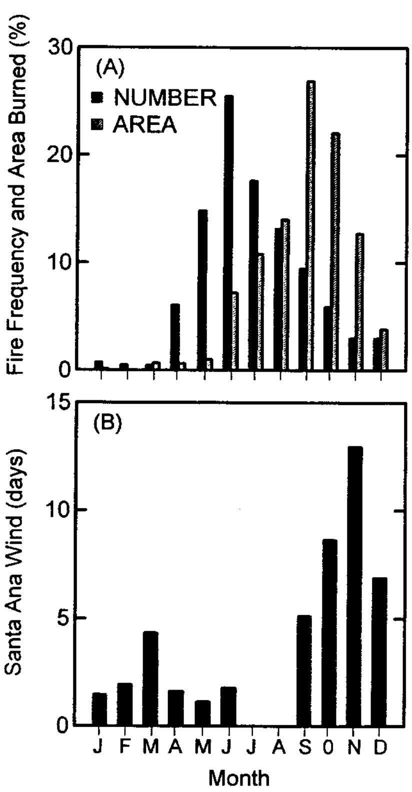


Figure 8.8. Seasonal distribution of fire occurrence and area burned during the twentieth century in Los Angeles County (data from Statewide Fire History Database; see Fig. 8.5) and seasonal distribution of Santa Ana winds (from Weide 1968).

combust only under the most extreme burning conditions. Also highly productive stands are often more mesic sites, and this, plus greater fuel density and higher fuel moisture, may reduce flammability. However, under extreme conditions, once ignited, productive sites sustain greater energy release than less productive stands (Riggan et al. 1988).

Successional changes in biomass (live and dead kg/ha) range from 1200 to 9000 in the first postfire year to 8000 to 13,000 after a decade, and 30,000 to 66,000

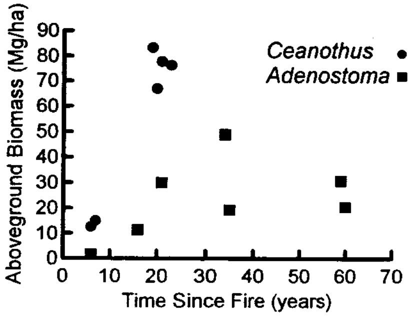
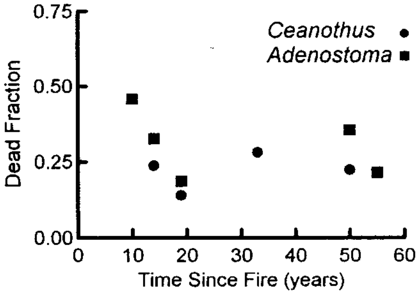


Figure 8.9. Live and dead aboveground biomass for chaparral shrubs at different times since fire based on several studies (data from Regelbrugge 2000).

Figure 8.10. Fraction of total biomass comprising dead material for chaparral shrubs at different times since fire based on several studies (data from Paysen and Cohen 1990; Regelbrugge 2000).



(sometimes 100,000) in mature stands (Specht 1969, 1981; Green 1970; Keeley and Keeley 1984). Specht (1969) reported that the proportion of dead biomass exceeded 50% in mature chamise chaparral, and Green (1970) found 66% dead in mature *Cercocarpus betuloides*. These early reports led to the generalization of 1% dead for each year after canopy closure (Green 1981). However, more extensive studies (Fig. 8.10) report 30% dead/live ratios across the span from 20 to 60 years and no significant relationship with age (Paysen and Cohen 1990; Conard and Regelbrugge 1994; Regelbrugge 2000). It is apparent that dead/live ratios are a complicated function of many aspects of site composition and history. For example, unusually severe soil droughts may dramatically increase mortality, particularly of shallow-rooted *Ceanothus* shrubs, and this can occur in young or old stands (Keeley 2000; Davis et al. 2002). Also prior fire history may play a role; for example, chaparral stands burned by light fires leave large volumes of standing dead biomass that can produce very high dead/live ratios in young successional stands where high volume of dead fuels is not expected (e.g., Fig. 8.10).

In general, chaparral less than 25 years old has less than 20% dead, and this is insufficient to carry fire under "prescribed fire weather conditions" (Green 1981). Under severe weather conditions stand age (and total biomass and proportion dead) is less important in determining fire spread (Dunn 1989; Keeley, Fotheringham, and Morais 1999; Zedler and Seiger 2000).

The conclusion that older stands of chaparral generate fires of greater intensity needs to be viewed with caution. Fire intensity, which is often measured as fireline intensity or energy released per meter of fire front (Borchert and Odion 1995), can vary greatly depending on the interaction between weather and fuels. Sometimes intensity is equated with fire severity, which is defined as the ecological impact of the fire, and is often measured by mortality or the amount of plant biomass consumed, or alteration of nutrient cycles. However, a fast-moving fire that consumes little fuel and a slow-moving fire that consumes more fuel can achieve the same fireline intensity, and thus intensity and severity can not always be equated. In general, fire intensity is important to understanding options for fire suppression (Countryman 1974), whereas fire severity is most relevant to postfire ecosystem recovery (Keeley 1998b). Lastly, large fires often are equated with fires of high intensity, but they need not be. Large fires or mass fires are often described as catastrophic fires, but this latter term best refers to the impact of fire upon property and lives.

Past and Present Shrubland Fire Regimes

Understanding the extent of human impact on chaparral ecosystems requires that we reconstruct historical fire regimes. Stand-replacing crown fires typical of shrublands (Fig. 8.2) are not conducive to the formation of a tree-ring record of fires, as with surface fire regimes in montane coniferous forests. Thus reconstructing historical burning patterns for chaparral requires alternative approaches such as interpretation of sedimentary charcoal records.

Charcoal deposits in varved sediment cores from the Santa Barbara Channel have generated estimates of prehistoric fire frequency. Byrne, Michaelsen, and Soutar (1977) calibrated this procedure by comparison of annual varves from modern cores with U.S. Forest Service fire records. They found a significant correlation between large charcoal deposition events and incidence of large fires (>20,000 ha) in the adjacent mountain range less than 50 km from the core site. Using a core for the period from AD 730 to 1505, they were able to detect significant charcoal deposition but less than in the modern period, suggesting a lack of frequent small fires, unlike the contemporary pattern (Moritz 1997). They did, however, find two major peaks approximately 100 years apart with smaller peaks at 20- to 60-year intervals, and suggested this period had few fires, widely spaced, which became large conflagrations capable of generating large pulses of charcoal. Mensing, Michaelsen, and Byrne (1999) analyzed similar cores at a finer resolution and concluded that large fires were a feature of this region long before modern fire suppression.

Native American Impacts

Tree-ring records of fire scars from the coastal ranges and the Sierra Nevada have been interpreted to suggest that during the few hundred years prior to Euro-American colonization fire frequencies exceeded the level expected from lightning alone (Reynolds 1959; Greenlee and Langenheim 1990). From historical records and ethnographic accounts there can be no doubt that California Indians regularly utilized fire to manage their environment (e.g., Lewis 1973; Timbrook, Johnson, and Earle 1982; Wickstrom 1987; Anderson and Moratto 1996). The extent to which this management practice altered landscapes is a matter of debate. Due to the naturally high fire frequency of lightning fires in the coniferous forests of the Sierra Nevada, Vale (1998) has argued that the additional burning by Indians did not alter landscapes except in localized areas (but cf. Anderson, Barbour, and Whitworth 1998). On the other hand, it has been hypothesized that direct use of fire by Native Americans greatly altered landscape patterns in the lower elevation coastal range foothills, primarily through type conversion of shrublands and woodlands to grasslands and other herbaceous associations (Cooper 1922; Wells 1962; Huenneke 1989; Keeley 1990, 2002; Hamilton 1997). This hypothesis is supported by the low lightning activity, high Indian populations, shrub-dominated landscapes, limited resources for Native Americans in undisturbed shrublands, and weak resilience of shrublands to high fire frequency (Keeley, in review).

Euro-American Settlement Impacts

Euro-American settlers further increased fire frequency during the nineteenth century, primarily for the purpose of expanding rangeland into chaparral and coastal sage scrub dominated landscapes. The economy of the Spanish and later Mexican period was primarily based on pastoralism, and most historical sources indicate extensive grasslands at the time of colonization and limited need for immediate rangeland expansion (Keeley, 2002). Nonetheless, there are historical reports of these early pastoralists using fire to open up shrublands and increase forage (Kinney 1887), and this is reflected in increases in grass pollen from sediment cores (Russell 1983).

By the middle of the nineteenth century there was increasing pressure for rangeland expansion, and this was felt most severely in the coastal ranges south of San Francisco where 80% of livestock production was confined (Ewing et al. 1988). Following the Gold Rush of 1849, with an influx of American settlers, brush burning for the improvement of grazing became extensive throughout California. Ranchers in the foothill regions regularly burned large areas of brushland, and it became the practice of itinerant sheepherders, after leaving a grazing area, to set fires (Brown 1945; Bauer 1974; Nichols, Adams, and Menke 1984). Burcham (1957) contends that all rangelands in the state were fully occupied by 1880. A similar perspective is that of Brown and Show (1944) who stated, "It is generally conceded that what is known as the 'pastoral era' of California ended in 1870. In that year, good pasture land, which was also agricultural in character, rose to a price of from 75 cents to $6.00 per acre." In the succeeding decades there was extensive pressure to utilize fire for the purpose of opening up shrublands and increasing forage (Lee and Bonnicksen 1978). The burning by these stockmen in mountain watersheds of southern California were thought to be responsible for damaging floods on both the coastal and interior sides of the San Gabriel Mountains, leading to its designation as the first forest reserve in California (Lockmann 1981).

One factor contributing to the use of fire in the opening up of shrublands was apparently the homestead laws that allowed acquisition of 65-ha parcels from public domain land (Lee and Bonnicksen 1978). Such parcel sizes were generally sufficient to maintain a homestead based on stock production, but this plan did not work in the rugged hills of southern California, where homesteads were centered in small valleys known as *potreros*, surrounded by impenetrable chaparral. "Since the potreros were too small to support an economically sound cattle operation, stockmen supplemented meadow grazing with forage produced by periodically burning the adjacent chaparral" (Lee and Bonnicksen 1978). Since brush burning was an essential resource use practice for stockmen, they burned extensive areas of chaparral (Barrett 1935; Brown and Show 1944; Brown 1945). For instance, in 1887 it was reported, that in the southern portion of San Diego County that "at least one third of the land covered with brush, grass and oak timber has been burnt off by settlers in the past eighteen months" (Lee and Bonnicksen 1978). As a consequence of early settler burning, fire control laws were enacted soon after statehood in 1850 (Clar 1959). Not surprisingly, in the early part of the twentieth century, ranchers were often the primary opponents to fire exclusion policies, which in southern California was prompted by the need for watershed protection in the coastal plain (Lee and Bonnicksen 1978).

In summary, it is apparent that during this settlement period the primary alteration in fire regime was to increase the frequency of fires on shrubland landscapes. This was an era of very limited fire suppression, and yet fires were much as they are today in that large crown fires covering tens of thousands of hectares were not uncommon (Kinney 1900; Barrett 1935; Brown and Show 1944; Brown 1945; Minnich 1987). For example, one of the largest fires in Los Angeles County (24,000 ha) occurred in 1878 (Keeley, Fotheringham, and Morais 1999), and the largest fire in Orange County's history was over a quarter million hectares and occurred in 1889 (Lee and Bonnicksen 1978).

Twentieth-Century Patterns of Burning

Burning patterns during the twentieth century are shown for the nine counties in central and southern coastal California (Fig. 8.11). Most counties exhibited little or no change in area burned except for Los Angeles and Riverside counties in southern California, which exhibited highly significant increases in area burned during the twentieth century. In contrast to the situation in western U.S. coniferous forests, fire suppression clearly has not excluded fire from these shrubland landscapes. Collectively the 1920s, 1940s, and 1970s were high decades, and the 1930s and 1960s were low. Possible explanations for these patterns are that they result from (1) decadal-scale variation in climate, (2) natural cycles resulting from fuel buildup, and/or (3) human demographic patterns.

Role of Climate/Weather

There are numerous suggestions in the literature of extended droughts contributing to extraordinarily severe fire seasons, but with a few notable exceptions, most lack statistical rigor. Minnich (1983) reported that there was a significant positive relationship between precipitation and area burned in coastal sage scrub of southern California and adjacent Baja California, but he presented no statistics to support this contention. He also inspected patterns of chaparral burning over this time period and concluded no such relationship existed with chaparral. However, others have reported a relationship between precipitation and burning

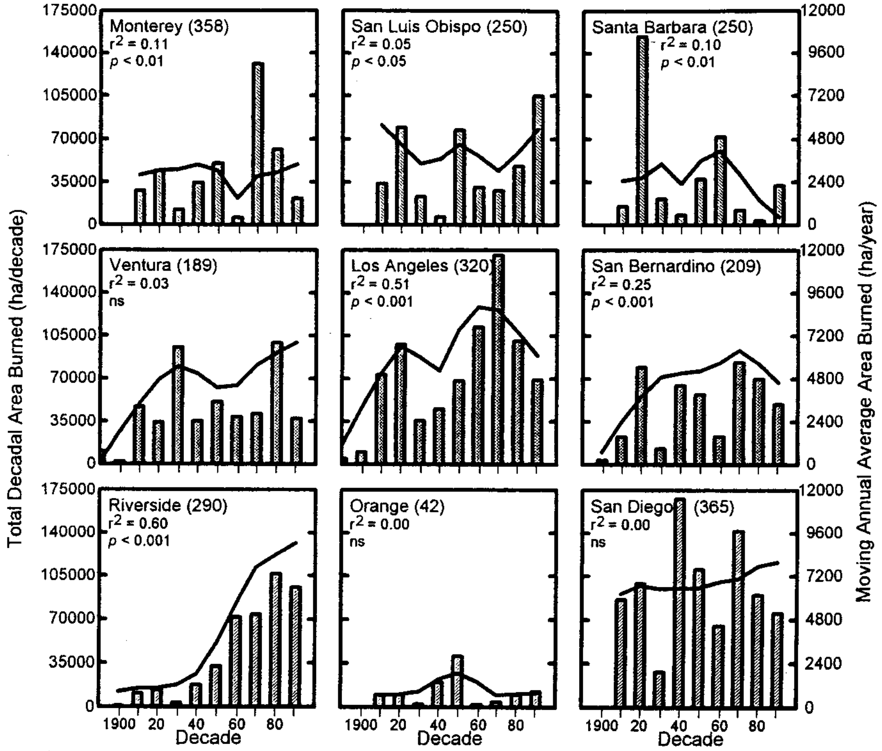


Figure 8.11. Area burned per decade and 10-year running annual average during the twentieth century for nine counties in central and southern California (data from the Statewide Fire History Database; see Fig. 8.5). Shrubland area in thousands of hectares shown in parentheses following the county name (from Callaham 1985).

in chaparral. One line of evidence is the spatial relationship between average precipitation and fire occurrence within the chaparral zone of San Diego County (Krausmann 1981). Another line of evidence is the demonstration that chaparral burning varies temporally with changes in precipitation; little area is burned following rainfall years where spring precipitation is >200 mm (Davis and Michaelsen 1995). These observations have been interpreted to mean that more rain translates into more biomass and thus greater fuels for burning in the subsequent fire season.

Using the FRAP data set (Fig. 8.11), we found few statistically significant correlations between patterns of rainfall and burning for chaparral and coastal sage shrublands combined. For each county separately, or all counties collectively, there was no significant relationship between total acreage burned per year and the nearest station with long-term records for:

1. total annual (January–December) precipitation,
2. growing season (November–June) precipitation,

3. spring (January–May) precipitation,
4. summer (June–August) precipitation, or
5. previous growing season's precipitation.

There was, however, a weak, but significant negative correlation ($p < 0.05$, $r^2 = 0.05$–0.06, $n \geq 88$) between October precipitation and area burned in each of the southern California counties, indicating that early autumn rains cut short the fire season at its peak.

Weather conditions affecting autumn foëhn wind-driven fires are most critical in determining area burned. Santa Ana wind conditions are largely responsible for fires becoming large and is reflected by the strong correlation between fire size and high temperatures. On the Los Padres National Forest fires generally ignite on days when the temperature is 3 to 5°C greater than the monthly average, and large fires never originate on days where temperatures are <25°C at the Santa Barbara airport (Davis and Michaelsen 1995; Moritz 1997). Moritz (1999) examined this relationship between severe fire weather (defined as days with maximum temperatures at the Santa Barbara airport ≥32°C) and extreme fire events in the central portion of the Los Padres National Forest. He found that large fires (>4000 ha) were strongly associated with severe fire weather. In this part of California severe fire weather is often, but not always, associated with foëhn winds (Schroeder et al. 1964; Dunn and Piierto 1987; Ryan 1996). However, farther south, for example, in the Santa Monica Mountains, all large fires appear to be driven by Santa Ana winds (NPS, Santa Monica Mountains National Recreation Area, unpublished data). In general, the largest wildfires in the central and southern coastal region are during severe fire weather conditions that include high temperatures, coupled with low humidity and high winds (Coffin 1959; Pirsko 1960; Schroeder et al. 1964; Weide 1968; Countryman, McCutchan, and Ryan 1969; Phillips 1971; Countryman 1974; Dunn and Piierto 1987; Gomes et al. 1993; Davis and Michaelson 1995; Minnich and Chou 1997).

Role of Fuel Cycles

Fuel accumulation was implicated in burning patterns in California shrublands by modeling studies published in the 1970s (Rothermel and Philpot 1973; Philpot 1974a,b). Based on untested assumptions about rates of fuel accumulation and effectiveness of fire suppression, it was concluded that large fires were increasingly more common because of an accumulation of older age classes of vegetation (Fig. 8.12). In support of this idea are many anecdotal references that fire fighters and fire researchers often relate about the tendency of fires to stop upon encountering young age classes of fuels (e.g., Philpot 1974a,b; Minnich 1998). An example of how these anecdotes are often used is the story about the 1970 Laguna Fire (one of the largest in California's history), in which it is claimed the fire died out when it encountered young age classes of vegetation (Rich Minnich, public communication, National Public Radio's "All Things Considered" radio broadcast, June 10, 1999). While that observation may be true, the deduction that

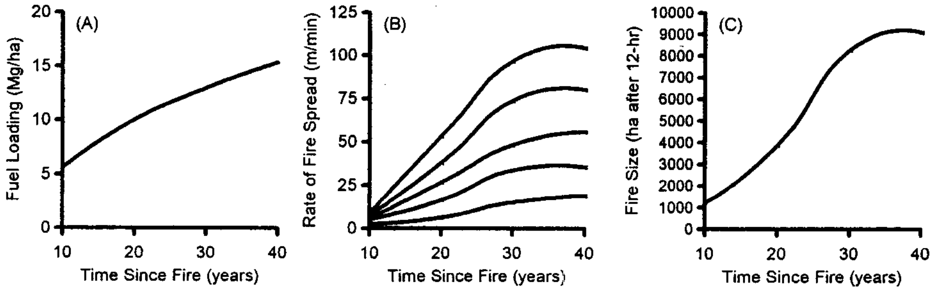


Figure 8.12. Modeling studies by Philpot (1974a, 1974b). (A) Assumed successional changes in fuel loads, (B) predicted rate of fire spread at increasing wind speeds from 10 to 50 kph, and (C) predicted fire size after 12 hours burning under sustained 50 kph wind speed. From these models it was concluded that as chaparral stands increase in age due to fire exclusion, there is a resultant increase in fuels, fire spread rate, and fire size. Following suggestions by Countryman (1974), these models were interpreted to support a fire management policy that relied heavily on prescription burning to produce a landscape comprising a mosaic of age classes.

there is a causal relationship is doubtful because the Laguna Fire burned over 10,000 ha of young vegetation (5–20 years) prior to its being extinguished (Dunn 1989), and the fire was contained only after a week of very severe Santa Ana winds subsided (Keeley, personal observations). In this fire, as well as other catastrophic fires, changes in fire behavior leading to containment often have had more to do with temporal changes in weather than spatial changes in fuels (Dunn and Piirto 1987). Although one can point to various fire perimeters that suggest fuel age is a barrier to fire spread (e.g., Philpot 1974), there are others that indicate it is not, such as half of the 5900 ha Romero Fire that burned above Santa Barbara in 1971 consumed seven-year old fuels from the 1964 Coyote Fire (Gomes et al. 1993). In short, there is no statistical evidence to support the notion that southern California landscapes supporting young vegetation are effective barriers to the spread of catastrophic fires. This of course is not meant to suggest that stand age has no effect on fire spread, only that its effectiveness is strongly controlled by weather (see the section below on Future Fire Management Strategies).

Fire history data also have been used to support the idea of fuel-driven fire behavior. Radtke, Arndt, and Wakimoto (1982) observed that peak decades of burning were followed by decades of very little burning in the Santa Monica Mountains of Ventura and Los Angeles counties. It was suggested that these decadal variations in burning represented a cyclical pattern driven by fuel loading. Their confidence in this model is illustrated by their future prediction that for the Santa Monica Mountains, the 1980s decade would be a peak and would be followed by a decline in burning during the 1990s. In retrospect we now know that, although the 1980s were high, the 1990s were even higher (Santa Monica Mountains Recreation Area, unpublished data). The primary weakness in explaining

Table 8.2. Shrubland area,[a] population density,[b] and estimated fire rotation intervals[c] for the shrub-dominated counties in California, arranged north to south

County	Brush (10^3ha)	People/ 10^6ha brush	Fire rotation interval (yr) pre-1951	Fire rotation interval (yr) post-1950
Monterey	358	0.99	115	64
San Luis Obispo	250	0.87	60	48
Santa Barbara	250	1.48	47	81
Ventura	189	3.54	121	34
Los Angeles	320	27.69	44	30
San Bernardino	209	6.79	46	37
Riverside	290	4.04	225	38
Orange	42	57.39	36	29
San Diego	365	6.84	35	41

[a] Area as of 1985, from Callaham 1985.

[b] Population density for 1990, from *http://www.census.gov/population/cencounts/ca190090.txt.*

[c] From Keeley et al. 1999.

decadal variations in burning by changes in fuel loads is the fact that the total burning during a decade comprises only a fraction of the fuels on the landscape and substantial fuel loads are available for burning every decade. For example, fire rotation intervals (Table 8.2) indicate that in most counties only 20% to 30% of the landscape burned in any given decade; thus decades of peak burning should not automatically be assumed to alter the future course of burning by leaving the landscape with limited fuels.

For southern and central coastal California, fire history data refute the contention made by Minnich (1989, 1998, 2001; Minnich and Cho 1997) that chaparral fire occurrence is constrained by the rate of fuel accumulation. Fire hazard estimates are either independent of age (Moritz 1999) or only weakly dependent up to 20 years of age (Schoenberg et al. 2001; Peng and Schoenberg 2001). In addition stand-age classes burned in the eight largest wildfires in the Santa Monica Mountains illustrate that these extreme events are not dependent on accumulations of older fuels (Keeley, Fotheringham, and Morais 1999). Indeed, in this range the greatest proportion of burned vegetation is in the younger aged stands, for both coastal sage scrub and chaparral (Fig. 8.13). Also vegetation type, which has a profound influence on fuel distribution (e.g., Fig. 8.9), has been shown to have little influence on fire history in the Los Padres National Forest (Moritz 1999).

Alterations in the landscape distribution of fuels have also been implicated in changes in fire size. It has been proposed that due to fire suppression, there has been an increase in the age and homogeneity of fuel distribution leading to larger and higher-intensity fires (e.g., Minnich 1989, 1995, 1998; Minnich and Cho 1997). The only data in support of this model are the high frequencies of small fires south of the U.S. border, which are interpreted as solely the result of natural burning cycles in the absence of fire suppression. However, north of the border

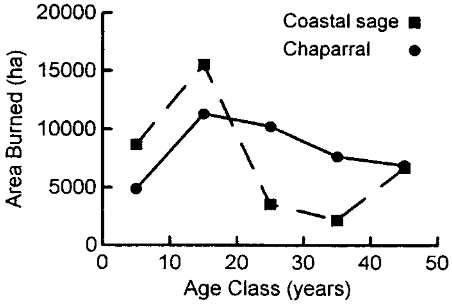


Figure 8.13. Age classes of chaparral and coastal sage scrub stands burned by all fires over 5000 ha from 1967 to 1996 in the Santa Monica Mountains (data from the U.S. National Park Service, Santa Monica Mountains National Recreation Area, Thousand Oaks, CA). Greater burning of young age classes of coastal sage scrub is likely due to more flammable fuels, longer fire season, and the concentration of this vegetation adjacent to urban centers, which are major sources of ignition.

fire suppression activities have not resulted in fire exclusion (Moritz 1997; Conard and Weise 1998; Keeley, Fotheringham, and Morais 1999; Weise et al., in press). Thus the patterns north and south of the border, while interesting, cannot be held up as an example of what happens to landscapes subjected to a fire suppression policy. Such fire management policies can not be held responsible for large destructive wildfires (Keeley and Fotheringham 2001a,b) as large fires have been a common feature of the southern California landscape throughout the ninteenth and twentieth centuries (Keeley, Fotheringham, and Morais 1999; Keeley and Fotheringham 2001a). Additionally sediment cores show the frequency of large fires has not changed during the past 450 years (Mensing, Michaelsen, and Byrne 1999), and colorful, but less authoritative, is the Digueño Indian legend of a large catastrophic fire sufficient to lead to migrations of tribes in San Diego County at about the time of Columbus (Odens 1971, p. 8). All of these observations suggest large fires are not a modern artifact of fire suppression as proposed elsewhere (Minnich 1989, 1995, 1998; Minnich and Dezzani 1991; Minnich and Chou 1997).

We now know that although the models developed by Philpot and others may be sound, their conclusions were flawed by incorrect assumptions. The assumption of a steady increase in fuels was inaccurate (Figs. 8.9 and 8.10), and the assumption that fire suppression was effectively excluding fire from shrubland landscapes was wrong (Fig. 8.11). In short, patterns of burning on shrubland landscapes cannot be explained solely by changes in accumulation of fuels (Moritz 1997, 1999; Conard and Weise 1998; Keeley, Fotheringham, and Morais 1999; Peng and Schoenberg 2001). Indeed, modeling studies that consider landscape patterns of fire spread conclude that stand age alone cannot constrain fire size (Zedler and Seiger 2000). If that were true, then just a single large Santa Ana wind-driven fire would reset the landscape to the same age class, which would forever be doomed to burn as a single large unit. Zedler and Seiger's model shows that even in the absence of Santa Ana fires, if stand age were the only controlling factor, over time, burn units would coalesce and become larger and larger with each fire cycle.

Role of Human Demography

Clearly, humans have perturbed shrubland fire regimes, but unlike the situation in many western U.S. forests, the primary impact has been through increased fire frequency (Table 8.1, Figs. 8.4 and 8.5c–d) and not through fire exclusion (Fig. 8.11). Collectively, across all counties considered in Figure 11, there was a significant correlation between fire frequency and population density and between fire frequency ($r^2 = 0.51$, $p < 0.05$, $n = 9$) and area burned ($r^2 = 0.71$, $p < 0.01$, $n = 9$). Southern California (defined in Fig. 8.3 legend), with the highest rate of population growth (Fig. 8.5b), also has had the greatest increase in wildfire ignitions (Fig. 8.5d). In contrast, the central coastal region has far fewer human ignitions (Figs. 8.4 and 8.5c), which is in line with the much lower population (Fig. 8.5a).

Indirectly the public infrastructure of roads contributes to patterns of burning. The central coastal region has substantial portions of its landscape lacking public roads, which is in stark contrast to the vast highway network connecting most parts of southern California. Fully one-third of all human-caused fires on Forest Service and CDF protected lands in southern California occur along roads (Gee 1974; Conard and Weise 1998). On shrubland landscapes near metropolitan areas, such as the Santa Monica Mountains, the vast majority of fires originate along roadways (Los Angeles County Fire Department, unpublished data).

In light of these considerations it seems probable that some portion of the decadal variation in burning during the twentieth century (Fig. 8.11) may have a human dimension. In the early part of the twentieth century populations in many parts of California were increasing rapidly (Fig. 8.5a–b). With this influx of people, came increased anthropogenic impact on the natural fire regime, driven largely by the increased mobility the automobile afforded; car registrations in California rose from 191,000 in 1915 to 1,500,000 in 1925 (Davis 1967). During the period 1908 to 1920, every county in southern California voted large bonds for road building (Davis 1967). Roads provided increased access to wildland areas. For example, a doubling in wildland use between 1916 and 1920 (Show and Kotok 1923) coincided with a marked increase in wildfire incidence in southern California (Fig. 8.5d). This rapid population growth and increased mobility strained the ability of fire protection in California during the early part of the twentieth century (Clar 1959). With the expanding population came an expansion of development at the urban–wildland interface, which then increased public susceptibility to wildfire impacts. As a consequence the decade of the 1920s witnessed some particularly destructive wildfires that increased public pressure for fire protection and prevention (Clar 1959).

In response, during the 1930s fire management agencies stepped up their attack on wildland fires by the introduction of lookout towers and aircraft for better reconnaissance, which decreased the size of some fires due to early detection (Clar 1969; Pyne 1982). During this period various innovations were introduced to suppress fires, although effective suppression was elusive due to the inaccessibility of remote wilderness areas (Brown and Show 1944; Pyne 1982). A system of fuel breaks was one early answer to this problem, and creation of 200 CCC (Civilian Conservation Corp) camps throughout the state during the Depression contributed significantly to this network. Increased fire suppression activities due to an excess of man power from federal relief programs (Clar 1969 described it as a "forced feed" of the California Division of Forestry), coupled with reduced "motor touring" (e.g., AAA memberships dropped 40% in the five years following 1929; Davis 1967) perhaps contributed to the drop in area burned during the Great Depression in many counties.

Diversion of resources to the "war effort" during the first half of the 1940s contributed to diminished fire suppression capacity (Brown 1945; Clar 1969) and may account for the peak burning that occurred in some counties during that decade (Fig. 8.11). San Diego County stands out because its worst decade for wildfires was the 1940s. Zahn (1944) suggests the extraordinary fires of this era were the result of the aircraft industry, which had concentrated a great deal of the war effort in San Diego County. He described the situation at the time as follows: "Bootleg fuel, high payrolls and a yen for the open spaces have resulted in hundreds of aircraft workers motoring to the hills—night or day—between work shifts. Most of these workers are newcomers to California, unfamiliar with the tinder-box potentialities of local brush."

The modern era of effective fire suppression was introduced in the 1950s with the development of air tankers for fire fighting (Pyne 1982), and this impact was evident in a 10-fold drop in burning across the country (Dombeck 2001). However, in California these techniques have not proved very successful in halting fires during extreme Santa Ana wind conditions (Countryman 1974).

In short, despite innovations, fire suppression has not diminished the wildland fire problem in California. Indeed, since the 1950s, there has been an increase in the allocation of funds to the California brushfire problem (Bonnicksen and Lee 1979; Kinney 1984), and an increase in the loss of property and lives (Rogers 1982; Martin and Sapsis 1995). Additionally, due to television, there has been increased public awareness of large-scale wildfires. Over this period there have been a number of workshops, conferences, and proceedings volumes published on this wildland fire problem—roughly one every 5 to 10 years since 1950—and these offer a diversity of opinions on the role of fire in the California landscape. Although not a popular view, it has been frequently suggested that the problem stemmed in large part to the burgeoning population and poor zoning regulations attendant with urban sprawl into the foothills. The problem was evident 50 years ago. For example, Zivnuska, Arnold, and Arment (1950) warned of this "potentially explosive situation," and noted "it is known that one of the significant trends in recent population changes has been the increase in number of residences in the flash-fuel types adjacent to primary watersheds." Under these conditions catastrophic fires are not necessarily the largest fires, as witnessed by the rather small

Oakland Hills Tunnel Fire in October 1991 (725 ha) that burned nearly 3000 structures and killed 25 people (Booker, Dietrich, and Collins 1995).

In summary, severe fire weather occurring each autumn coupled with human demographic patterns would seem to explain patterns of burning (Fig. 8.11) far better than changes in available fuels. During the twentieth century any changes in the fire regime have been dwarfed by the changes in land development patterns, which have increasingly placed more people at risk to the natural forces long present on the landscape (Davis 1965; Bradshaw 1987). This pattern continues—for example, in the 25 years prior to 1980, 2408 homes and other structures were destroyed by wildfires in California but in the subsequent 14 years the number tripled (*http://www.prefire.ucfpl.ucop.edu/wildfire.htm*). Preference for a rural lifestyle and the skyrocketing cost of suburban housing in large metropolitan areas has progressively increased the urban–wildland interface. Of particular concern is the prediction that rural population will exceed urban growth in the foreseeable future (Bradshaw 1987). For both economic and political reasons the notion that urban sprawl is responsible for natural wildfires becoming catastrophic fires is unpopular, in part, because it seems to defy the inherent belief that it is possible to engineer solutions to all environmental problems.

The Contemporary Versus Natural Fire Regime

There is reason to believe that the contemporary fire regime in these shrublands mirrors the natural crown fire regime far more than is generally accepted (cf. Bonnicksen and Lee 1979; Minnich 1983; Pyne 1982). Today in southern California, fire incidence peaks in the summer, but most area burned is from autumn fires (Fig. 8.8a). Likewise the natural fire regime was probably characterized by many small summer lightning-ignited fires and a few large autumn fires driven by Santa Ana or Mono winds that burned large areas (Keeley and Fotheringham 2001a). This model would seem to be contradicted by the fact that Santa Ana or Mono winds are northeast winds, whereas summer thunderstorms are associated with south winds, and the two do not commonly coincide (Coffin 1959). Consequently today it is rare for Santa Ana wind-driven fires to be other than anthropogenic in origin. However, under natural conditions the fact that lightning fires burned for months (Minnich 1987), coupled with the relatively close temporal juxtaposition of the July–August lightning fire season (Keeley 1982) with the September–November Santa Ana winds (Fig. 8.8b), makes it inevitable that lightning ignitions would occasionally have been spread by these foëhn winds (Keeley and Fotheringham 2001a). While such events could not have been frequent, we know from historical documents that summer lightning-ignited fires can burn for more than a month and consume on the order of 10^3 ha (Minnich 1987). This pales in comparison to the 10^4 ha that are often covered in a single day by a Santa Ana wind-driven fire (Phillips 1971).

Davis and Burrows (1993, 1994) modeled the long-term fire regime in chaparral by linking physical models based on fire spread equations to fuel models of stand senescence. Their simulations predicted a prehistoric fire regime of variable sized fires that produced a landscape mosaic of different age classes. With one ignition every 10 years (typical lightning-ignited fire frequency for coastal California; Keeley 1982) their model predicted that most fires would be large and over 80% of the landscape would burn at ages greater than 95 years. These conclusions are supported by other evidence that points to a natural fire regime of large fires and long fire return intervals for these coastal range landscapes (Greenlee and Langenheim 1990; Byrne, Michaelsen, and Soutar 1977; Mensing, Michaelsen, and Byrne 1999; Keeley and Fotheringham 2001a).

Alternatively, it has been argued that prior to the current fire suppression policy, landscapes were immune to Santa Ana wind-driven fires because lightning fires kept the shrublands in a fine-scale mosaic of young age classes (Minnich 1989, 1995, 1998). It is presumed that this mosaic was quickly erased by highly effective fire suppression during the first couple decades of the twentieth century (Minnich 1990). However, historical records do not support this notion. For example, 90% of the 214,000 ha of shrublands on the San Jacinto Forest Reserve were estimated to be 30 years or older when surveyed at the end of the nineteenth century, which represent far older age classes then present today (Keeley and Fotheringham 2001a). Clearly, this landscape was not a fine-scale mosaic immune to large fires. In addition the early history of forest protection does not support the idea that highly effective fire suppression was present in the opening decades of the twentieth century (Clar 1959; Lockmann 1981). Minnich and Chou's (1997) suggestion that fire suppression activities "culminated in extensive fire outbreaks as early as 1919" is contradicted by historical documentation that reports large fires in the region long before this date, and before any fire suppression activities (e.g., Kinney 1900; Barrett 1935; Brown and Show 1944; Brown 1945; Lee and Bonnicksen 1978; Radtke, Arndt, and Wakimoto 1982). Nationwide there is no evidence of substantive reductions in area burned due to fire suppression until midway through the twentieth century (Dombeck 2001).

Historically fire intensity was variable, and there is no credible evidence that it has increased during the era of fire suppression (Keeley, Fotheringham, and Morais 1999). The primary changes in the fire regime are that humans have replaced lightning as the primary source of ignition and fire frequency has increased, particularly in areas of high population density such as southern California (Figs. 8.4 and 8.5). Because fire prevention has been ineffective at eliminating human fires, presently and for the foreseeable future, fire suppression is required just to maintain some semblance of the natural fire regime.

Impacts on Vegetation

In contrast to the paradigm suggested for many western U.S. forests, ecosystem health of shrublands is threatened not by a lack of fire but by high fire frequencies that exceed the resilience of many species. Examples of high fire frequency induced extirpations are numerous (e.g., Gause 1966; Zedler et al. 1983;

Haidinger and Keeley 1993; Zedler 1995; Keeley 2000). Generally, the threat of high fire frequency is lessened on very low nutrient soils where postfire annual biomass is limited and less likely to carry a repeat fire. Where fires occur more than once in a decade, nonsprouting chaparral shrubs are entirely lost from the system. Commonly exotic grasses and forbs will take their place, and as these increase in importance, they appear to competitively displace the native annuals. A similar course is evident in coastal sage scrub under higher fire frequency. In both of these crown fire ecosystems, high fire frequency favors annuals over woody plants, and this advantage increases with increasing soil aridity (Wells 1962).

As fire frequency increases, fuel structure changes and subsequent fire behavior changes. With increasing exotic herbaceous cover, the seasonal window of flammability increases (Radtke, Arndt, and Wakimoto 1982), and fire behavior becomes a mixture of crown and surface fires. This has two very important consequences. Surface fires connect the woody fuels where otherwise they might be too widely spaced to carry a crown fire, and thus exotic herbs shorten the fire return interval. Another important consequence is that fire intensity is lower where surface fires occur and this contributes to increased survivorship of exotic annual seed banks (Fig. 8.14). With continued disturbance these nonnative invasives may replace the entire ecosystem (Keeley, 2001), and type conversions of shrublands to exotic grasslands are well documented (e.g., Cooper 1922; Bentley 1967; CDF 1978; Biswell 1989; Minnich and Dezzani 1998). As a consequence exotic grasslands tend to replace shrublands in the proximity to urban environments, where the higher ignition sources in the company of flashy fuels have the potential for even greater fire frequency. Evidence of this is seen in the substantially shorter fire return interval in grassland vegetation at the urban–wildland interface than observed for shrublands at the interface (J. Spero, California Division of Forestry, personal communication, 1999).

The extent of such type conversion is unknown because of past disturbances, which includes Indian burning throughout the Holocene and burning coupled with intensive livestock grazing in the past 200 years. In the coastal counties from Monterey southward (Fig. 8.3) exotic annual grasslands cover nearly two million hectares or 25% of the wildland landscape, and less than 1% has significant patches of native perennial bunchgrass (Huenneke 1989). Although it is often taken as a matter of faith that these landscapes have always been grassland (Heady 1977), there is evidence that many exotic grasslands were formerly dominated by woody associations (Cooper 1922; Wells 1962; Oberbauer 1978; Huenneke 1989; Keeley 1990, Hamilton 1997). Today these landscapes comprise a mosaic of vegetation patterns (Fig. 8.15) that appear to be disturbance induced (Wells 1962). Grasslands on this modern landscape comprise a new quasi-equilibrium of nonnative annuals that are somewhat resistant to recolonization by native shrubs. It is a dynamic process whereby as disturbances increase or wane, vegetation physiognomy shifts between exotic grassland and shrubland/woodland (Hobbs 1983; Freudenberger, Fish, and Keeley 1987; Callaway and Davis 1993).

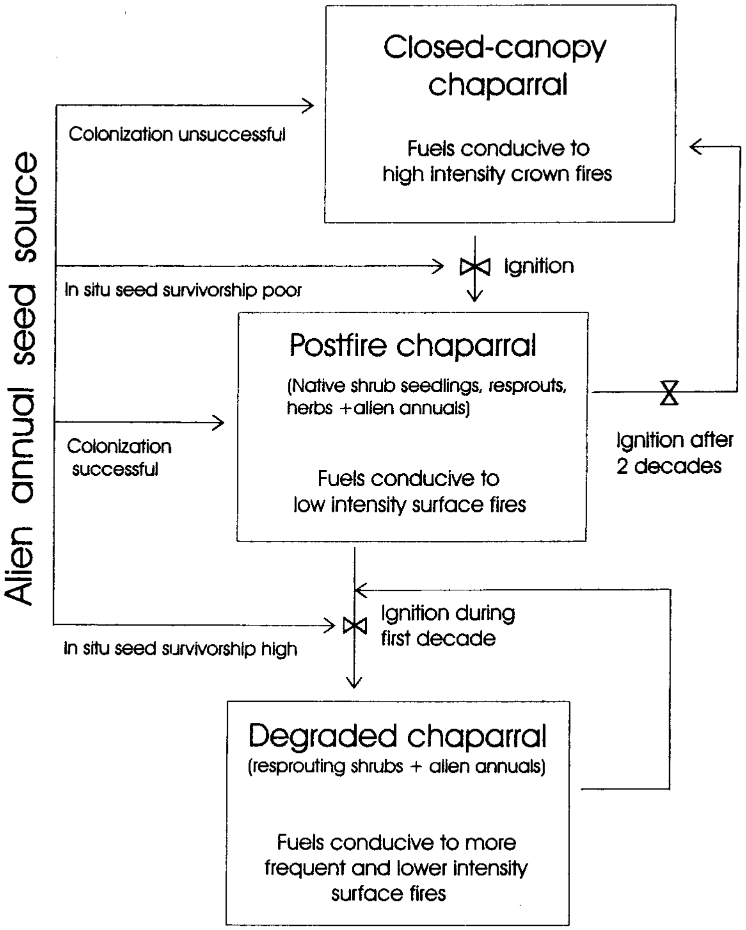


Figure 8.14. Schematic diagram of how rate of fire ignitions in chaparral affects alien plant invasion and how alien invasions affect fuel loads, which in turn alter fire frequencies, making sites more conducive to further invasion (from Keeley, 2001).

Future Fire Management Strategies

It has been suggested that "after nearly a century of suppression" there is a need for a reintroduction of fire into chaparral through prescribed burning (Minnich and Dezzani 1991; Minnich and Franco-Vizcaíno 1999). However, fire history data do not support this management strategy. On most shrubland landscapes there is an abundance of fire, and 60- to 70-year-old stands, considered to be the normal age for burning (Minnich 1989), are rare at the present time (Keeley 1992). Indeed, the current fire rotation interval of 30 to 40 years is shorter than

Figure 8.15. Vegetation mosaic of nonnative annual grassland and shrublands in the central coastal ranges of California (photo by J. Keeley).

that calculated for the early part of the twentieth century (Keeley, Fotheringham, and Morais 1999). In light of the expected trends in population growth in California, and the close association between population density and fire incidence (Fig. 8.5), increased fire prevention is far more important to protecting natural resources than prescription burning or other methods of "fire restoration."

Consequently there is a need to reevaluate prescribed burning strategies for California shrubland landscapes. There are two common motivations for prescription burning: (1) for the benefit of natural resources and (2) as a fuel manipulation technique, primarily to reduce fire hazard but also to reduce the threat of soil erosion or air quality hazards, which may be worse under wildfire conditions. In many western U.S. forests, prescription burning provides both resource benefits and a reduction in fire hazard However, the reality for some ecosystems is that prescriptions reducing fire hazard, may not always enhance resource values and sometimes may detract (Johnson and Miyanishi 1995; Keeley and Fotheringham 2001b).

Prescription Burning for Resource Benefit

There may be little justification for using fire for resource benefit, since vast portions of shrubland landscape currently experience a higher than normal fire frequency. Lack of fire does not appear to pose a risk because postfire studies demonstrate that both chaparral and coastal sage scrub regeneration are highly resilient to even the most extreme fire events occurring after a long hiatus of burning (Keeley 1998, 2000).

One proposed benefit of prescribed burns is that they are done under more moderate weather conditions than are typical for wildfires, leading to less intense fires and less severe impacts on plant and soil resources (Green 1981; Moreno and Oechel 1991; Riggan et al. 1994; Wohlgemuth, Beyers, and Conard 1999). However, some of the experimental work demonstrating fire intensity effects on seed banks and soils have been done on piles of cut fuels, which do not accurately represent the fuel structure under natural conditions and are likely to generate unnaturally high soil temperatures. More importantly, however, even the most extreme fire wildfire events today probably do not fall outside the natural range of variation for these ecosystems.

Other resource benefits from prescription burning include invasive plant control, but the primary invasive problems involve herbaceous species, which invade shrublands when fire frequency increases (Fig. 8.14). It is not likely that prescription burning would displace these invasive species, unless the target is vulnerable to a particular seasonal window of burning. In shrublands there are no such windows of opportunity that are not equally damaging to some native species. Nonnative legume shrubs known as brooms (*Cytisus scoparius* and *Genista monspesulanus*) are sometimes targeted for removal with prescription burning, but these are inevitably replaced by exotic grasses (D'Antonio 2000). However, prescription burning for restoration of shrubland communities may be useful if accompanied by vigorous revegetation with native shrubs and herbs.

In general, there are few places where fire-dependent shrublands are threatened by the lack of fire and few instances where prescription burning is needed for natural resource benefits. The primary justification for prescription burning is for fire hazard reduction. However, in these ecosystems any additional fire carries with it the potential for negative impacts on resources. Negative impacts may arise not just from burning but can be associated with other fuel manipulations. For example, fuel breaks are possible corridors for bringing nonnative invasive species into wildland areas (Keeley, 2001).

Prescription Burning for Fire Hazard Reduction

Prescription burning carries with it a risk of fires escaping, and escaped fires are quite hazardous in crown fire ecosystems, most particularly chaparral landscapes with a complex urban–wildland interface. In order to ensure successful containment of a prescribed burn, there are strict limitations on the acceptable wind speed, air temperature, relative humidity, and fuel moisture—typically wind speeds below 17 kph (10 mph), relative humidities above 30%, air temperature below 32°C (95°F), and fuel moisture above 75% (Fenner, Arnold, and Buck 1955; Green 1981). This, of course, varies with the fuel load and landscape, and various combinations will produce acceptable prescriptions (Paysen, Narog, and Cohen 1998). One approach to reducing the risk of escaped fires is to burn in the spring, assisted by pretreatment of mechanical crushing and drying. Thus the target fuels are surrounded by less flammable living vegetation (Wolfram 1962). This procedure is expensive, and it has the potential for producing resource damage. For example, unseasonable application of fire inhibits postfire vegetation recovery (Florence 1985; Rundel, Parsons, and Baker 1987; Parker 1990) and is correlated with increased soil erosion (Turner and Lampinen 1983).

Because prescriptions are designed for safety, they are often marginal for burning. Under prescription weather conditions, fire spread is markedly influenced by fuel structure, and fire spread is often inhibited in stands less than 20 years of age (Green 1981; Paysen and Cohen 1990; Conard and Regelbrugge 1994). This is largely due to the lack of sufficient dead fuels required to spread fire to live foliage, and to the lack of fuel continuity between the ground and the shrub canopy and between adjacent canopies, factors that are extremely critical to fire spread under low wind and high humidity. Controlled burning of younger stands requires either prescriptions with risky weather conditions or pretreatment with biodegradable herbicides (which increase the dead fuels) coupled with seeding of exotic grasses that increase flashy (readily ignitable) fuels and increase surface fire spread.

Evaluating the effectiveness of prescribed burning at reducing fire hazard is complicated by the fact that such fuel management practices are never going to be fully effective against all fires. Wildfires are often more readily contained when they encounter young stands of vegetation, largely because lower fire intensities allow for safer access by fire suppression forces (Countryman 1974). However, landscape age mosaics created by rotational burning will not pose a barrier to wildfires ignited under severe fire weather, since the high winds readily push fires through young age classes (e.g., Fig. 8.13). Under these conditions young vegetation is of minimal value in halting the forward spread, and also firebrands are capable of spreading the fire kilometers beyond the front. Containment of shrubland fires burning under severe weather conditions usually requires a change to more favorable weather (Rogers 1982; Dunn and Piirto 1987; Gomes et al. 1993).

Thus prescription burning presents a catch-22 situation. It can only be done safely under weather conditions that require mature chaparral, 20 years of age or more, but stands of vegetation this age and younger will not form effective barriers to fire spread under severe weather conditions. Modeling studies indicate that to be effective even under moderate weather conditions requires a substantial portion of the landscape be treated (Mark Finney, public communication, 2001). Thus, while landscapes managed by rotational burning may contribute to easier containment of fires burning under moderate weather conditions, they are of limited value during severe weather. However, these latter fires are the ones that become truly catastrophic and are responsible for the greatest losses. Consequently National Forest Service policy of landscape-scale rotational burning to produce a mosaic of age classes needs to be reconsidered (Conard and Weise

1998). This type of fuel management is extremely expensive, unlikely to prevent catastrophic wildfires, and has little resource benefit.

Future fire management policy needs to steer away from extensive landscape-scale prescription burning and focus on intensive and strategic use of fire hazard reduction techniques, both to minimize negative impacts of high fire frequency on natural resources and to maximize fire hazard reduction. The marked differences observed between the central coastal ranges and southern California (Fig. 8.5) suggests that regions may require different fire management strategies. Greater focus needs to be given to transportation corridors as roadways are primary sites of ignitions, and since roadways are required to connect developments, as the urban/wildland interface increases, these fire hazards increase. Roads could also play a role in minimizing the negative impacts of fire hazard reduction programs, since many of the negative impacts of fuel reduction techniques (e.g., aesthetic impacts, promoting invasive plants and animals) are also shared by roadways. Thus greater attention needs to be given to co-locating roads and fuel manipulations such as fuel breaks.

Considering the psychology of many who inhabit the urban–wildland interface, it is questionable whether or not education can play a substantive role in reducing future losses from wildfires (Gardiner, Cortner, and Widaman 1987). Regulations requiring fire "safe" construction have been implicated in reducing property losses in the past and will possibly reduce the degree of future losses (Cohen 2000). It seems inevitable that fire management policy will increasingly require involvement of city and county planners in order to solve the primary fire hazard problem of how to constrain the ever-expanding urban–wildland interface. Fire managers can play a key role in providing accurate analytical models of causal factors driving extreme fire events and educating planners on the limitations to fire hazard reduction (e.g., Sapsis 2001).

Global Change Impacts on Future Fire Regimes

Fire regime is an emergent property of landscapes arising from the interaction of vegetation, weather, topography, and land management (Davis and Michaelsen 1995). Fire regime is influenced directly by vegetation through flammability characteristics and the structural distribution of fuels. Weather affects fire regimes through timing of ignitions, and through frequency and severity of burning conditions as well as direct effects on vegetation distribution. Topography affects rates of natural lightning ignitions and wind patterns that ultimately control fire behavior. Land management affects the distribution of vegetation types and thus landscape patterns of fuels. Land management, in the broad sense, also controls the extent and pattern of the urban–wildland interface, which acts as a porous boundary where fires diffuse across in both directions. Wildland fires may diffuse out from the urban–wildland interface, but the most catastrophic fires result from wildfires burning into the urban environment. Global changes, including direct effects of increased atmospheric CO_2 levels, climate changes, and changing land use, all have the potential for changing fire regimes by altering vegetation, weather, and land management.

Future increases in atmospheric CO_2 levels may directly affect plant growth and potentially alter patterns of fuel distribution. In chaparral the effects are predicted to be variable and strongly dependent on levels of other resources (Oechel et al. 1995). Along gradients of increasing soil fertility we might expect increased biomass production, but the increased leaf area may place greater demands on the limited soil water resources in this semi-arid region, dampening potential increases in primary production. Further exacerbating this dampening effect is the expected increase in summer temperature. However, this could be offset by increased water use efficiency expected with elevated CO_2.

Climate change in California shrubland landscapes over the next half-century is predicted to increase winter and summer temperatures by 3°C and 1°C, respectively, and to increase winter precipitation by 25% (Field et al. 1999). Warmer and much wetter winter conditions will almost certainly contribute to higher primary production, although the magnitude is likely to decline with decreasing soil nutrients. It is assumed that this increased production will lead to higher fuel accumulation and more intense fires. However, these climate changes may also accelerate decomposition of dead fuels, which are critical to fire spread, and the importance of this dampening effect on fuel accumulation has not been evaluated. Expected increases in C:N ratios of dead fuels imply variations in rates of decomposition along soil fertility gradients, paralleling expected increases in primary production. Thus sites with the greatest increases in fuels may also experience the greatest increases in decomposition. Even if the net effect is an increase in rate of fuel accumulation, this should not automatically be assumed to lead to major changes in the fire regime. This is based on the fact that currently rates of fuel accumulation do not play a highly deterministic role in shrubland fire regimes (Moritz 1999; Schoenberg et al. 2001; Peng and Schoenberg 2001).

Expected changes in climate will affect vegetation structure through changes in energy balance as well as nutrient cycling, but this involves such complexity that presently one can only speculate what the future holds (Oechel et al. 1995). Attempts to understand how changes in precipitation and temperature will affect vegetation composition include documentation of contemporary climatic responses (Westman 1991) and growth simulations (Malanson and Westman 1991a, b; Westman and Malanson 1992; Malanson and O'Leary 1995). Realistic parameterization of these models is one limitation to their current usefulness, and thus the primary conclusion one can draw at this point is that changes in the relative abundance of species are to be expected. Another possibility is that changes in fire intensity due to greater fuel loads may affect changes in postfire recovery, although shrublands currently exhibit extraordinary resilience to a wide range of fire intensities (Keeley 1998). Ecotones are expected to be sites of greatest sensitivity to climate change (Peteet 2000), and the complex vegetation mosaic of California landscapes (e.g., Fig. 8.15) presents many opportunities for shifts in vegetation distribution. Considering the large role played by human interference, it seems likely that the greatest alteration in fire regimes will occur at the urban–wildland ecotone.

In general, GCM predictions for twenty-first-century climates in California are of limited value in understanding future fire regimes. Patterns of burning are driven by extreme events (Moritz 1997), and these are not well modeled (Field et al. 1999). One of the primary determinants of area burned is the coincidence of ignition with severe weather, and future changes in patterns of ignition might be expected to play a determining role in fire regimes. Climate-based models predict the California region will have a few percent increase in lightning fires (Price and Rind 1994), but this may not affect these shrubland landscapes where humans are the primary ignition source (Table 8.1, Figs. 8.4 and 8.5).

Future changes in land use are likely to have a more profound impact on shrubland fire regimes than other types of global change. Land use may also be the primary driver behind losses in biodiversity in California as well as in other Mediterranean-climate regions (Sala et al. 2000). Diversity loss is expected to result from increased population growth contributing to habitat loss, habitat fragmentation, and loss of corridors. Some of these factors will affect fire regimes, but, we expect that increased fire ignitions predicted from increased population growth will have a far more profound impact on these landscapes. As the fire return interval shortens, the native shrublands are degraded to mixtures of exotic grasses and forbs, and these invasives contribute to further decreases in fire return interval and loss of native plant diversity (Fig. 14). However, dampening this potential impact of shortened fire return intervals is the stepped-up rate of post-fire shrub recovery expected from predicted increases in winter temperature and precipitation. The impact of land-use changes on these landscapes makes it likely that it will far outweigh other global change impacts on fire regimes.

Conclusion

Throughout much of the shrubland landscape humans play a dominant role in promoting fires beyond what was likely the natural fire cycle. Future climate change is expected to have a minor role in altering fire regimes relative to other global changes such as population growth and habitat fragmentation. Future fire management needs to take a strategic approach to fuel manipulations and move beyond evaluating effectiveness strictly in terms of area treated. Fire management should consider designing strategies tailored to different regions as there are marked differences between the central coastal region and southern California in source of ignition (e.g., Table 8.1, Fig. 8.4), season of burning (Fig. 8.6), and historical patterns of population growth (Fig. 8.5a–b) and burning (Figs. 8.5c–d and 8.11). Presently we know relatively little about fire regimes in shrublands in the foothills of the Sierra Nevada and interior foothills of the northern coastal ranges, and thus it would be prudent to not transfer the conclusions drawn here too broadly until we have a clearer understanding of the extent of regional variation in shrubland fire regimes. One of the primary threats that all regions share is the increasing number of people being placed at risk to the natural wildfire threat because of the rapidly expanding urban–wildland interface. Fire management will need to play an increasingly active role in the planning process through critical analysis of causal factors driving fire regimes and the limitations to hazard reduction.

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Review

Fire Management Impacts on Invasive Plants in the Western United States

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Abstract: *Fire management practices affect alien plant invasions in diverse ways. I considered the impact of six fire management practices on alien invasions: fire suppression, forest fuel reduction, prescription burning in crown-fire ecosystems, fuel breaks, targeting of noxious aliens, and postfire rehabilitation. Most western United States forests have had fire successfully excluded for unnaturally long periods of time, and this appears to have favored the exclusion of alien plant species. Forest fuel reduction programs have the potential for greatly enhancing forest vulnerability to alien invasions. In part this is due to the focus on reestablishing pre-Euro-American fire regimes on a landscape that differs from pre-Euro-American landscapes in the abundance of aggressive non-native species. We may be forced to choose between restoring "natural" fire regimes or altering fire regimes to favor communities of native species. Intensive grazing in many western forests may exacerbate the alien problem after fire and temporally decoupling grazing and fire restoration may reduce the alien threat. Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural, high-intensity crown fire regime that is less amenable to forest restoration tactics. Historical use of prescribed fire for type conversion of shrublands to more useful grazing lands has played some role in the massive annual grass invasion that threatens these shrublands. Fuel breaks pose a special invasive plant risk because they promote alien invasion along corridors into wildland areas. Use of prescription burning to eliminate noxious aliens has had questionable success, particularly when applied to disturbance-dependent annuals, and success is most likely when coupled with ecosystem restoration that alters the competitive balance between aliens and natives. Artificial seeding of alien species as a form of postfire stabilization appears to cause more problems than it solves and may even enhance alien invasion.*

Key Words: exotic plants, fire suppression, fuel breaks, fuel reduction, non-native plants, postfire rehabilitation, prescription burning

Impactos de la Gestión de Fuego sobre Plantas Invasoras en el Oeste de Estados Unidos

Resumen: *Las prácticas de gestión de fuego afectan de diversas maneras a las invasiones de plantas. Consideré el impacto de seis prácticas de manejo de fuego sobre las invasiones: supresión de fuego, reducción de combustible forestal, quema prescrita en ecosistemas con fuego de dosel, guardarrayas, eliminación de invasoras dañinas y rehabilitación post fuego. En la mayoría de los bosques del oeste de Estados Unidos el fuego ha sido excluido exitosamente por largos períodos de tiempo no naturales y esto parece haber favorecido la exclusión de especies de plantas exóticas. Los programas de reducción de combustible forestal tienen el potencial para incrementar la vulnerabilidad de bosques a las invasiones de plantas exóticas. En parte, esto se debe al enfoque en el reestablecimiento de regímenes de fuego pre-Euroamericanos en un paisaje que difiere de paisajes pre-Euroamericanos en la abundancia de especies no nativas agresivas. Podremos ser forzados a elegir entre la restauración de regímenes de fuego "naturales" o la alteración de regímenes de fuego para favorecer a comunidades de especies nativas. El pastoreo intensivo en muchos bosques occidentales puede exacerbar el problema de invasoras después del fuego y la reducción temporal de pastoreo y gestión de incendios puede reducir la amenaza de las invasoras. Muchos ecosistemas con matorrales como la estepa de artemisa*

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West Intermountain o el chaparral California tienen un régimen natural de fuego de alta intensidad que es menos dócil a las tácticas de restauración de bosques. El uso histórico de quemas prescritas para la conversión de terrenos con matorrales a tierras de pastoreo más útiles ha jugado un papel en la invasión masiva anual de pastos que amenaza a estos terrenos con matorrales. Las guardarrayas constituyen un riesgo especial porque promueven la invasión de áreas silvestres a lo largo de corredores. El éxito del uso de quemas prescritas para eliminar invasoras dañinas es cuestionable, particularmente cuando se aplica a anuales dependientes de perturbación, y el éxito es más probable cuando se combinan con restauración de ecosistemas que altera el balance competitivo entre invasoras y nativas. La diseminación artificial de semillas de especies invasoras como una forma de estabilización posterior al fuego parece causar más problemas que los que resuelve e incluso puede favorecer la invasión de exóticas.

Palabras Clave: guardarrayas, plantas exóticas, plantas no nativas, quema prescrita reducción de combustible, rehabilitación post fuego, supresión de fuego

Introduction

U.S. federal policies incorporate alien plant concerns into management of public lands. For example, the U.S. National Park Service policy (U.S. Department of Interior 2001) mandates that "exotic species will not be allowed to displace native species if displacement can be prevented." The chief of the U.S. Department of Agriculture Forest Service (USFS) has identified invasive species as one of the four significant threats to U.S. forest and rangeland ecosystems (U.S. Department of Agriculture Forest Service 2004), and the USFS manual states that "determining the risk of noxious weed introduction or spread as part of the NEPA process for proposed actions, especially for ground-disturbing and canopy-altering activities" is the explicit responsibility of managers (U.S. Department of Agriculture Forest Service 1995). Here I explore how these policies may be complicated, and sometimes compromised, by fire management practices. I examined impacts from six fire management practices: (1) fire suppression, (2) fuel reduction in forests, (3) prescription burning in shrublands, (4) fuel breaks, (5) prescription burning to target noxious aliens, and (6) postfire rehabilitation.

Fire Suppression

Fire suppression policy over the past century has worked toward excluding fires from forests. For some forest types, such as Southwest ponderosa pine (*Pinus ponderosa* Laws.), the natural fire regime of frequent, low-intensity surface fires has been particularly amenable to fire suppression tactics. Consequently fires have been excluded over a significant portion of the landscape for much of the twentieth century (Allen et al. 2002). There is little debate about the critical nature of the fire hazard due to unnatural accumulation of understory fuels in these and many other western U.S. forest types. These fuels increase the probability of large, high-intensity wildfires and pose a threat to the long-term sustainability of these ecosystems (Graham et al. 2004).

Under this management policy of fire suppression, however, forests appear to have fared well in terms of minimal alien plant invasion (Pierson & Mack 1990*a*, 1990*b*; Weaver et al. 2001; Keeley et al. 2003). One of the major reasons for the resilience to invasion of undisturbed forests is that the closed forest canopy is highly inhibitory to aliens, most of which require high light levels (Rejmanek 1989; Pierson et al. 1990; Charbonneau & Fahrig 2004). Other factors that potentially play a role are the accumulation of surface litter, which diminishes sites for alien establishment, and reduced propagule sources (dense, closed canopy forests have little herbaceous growth to attract livestock).

Fuel Reduction in Forests

The National Fire Plan (U.S. Department of Agriculture Forest Service 2001) addresses the threat of catastrophic fires by reducing fuels with prescription burning or mechanical thinning. The Healthy Forests Restoration Act of 2003 (House Resolution 1904) increases the ability of resource managers to perform necessary fuel reduction projects and is called forest restoration because one of its goals is to return forests to their prefire-suppression-era structure and function. Fire lines and firefighting equipment associated with prescription burning directly favor alien species by creating soil disturbances and introducing alien propagules (Harrod & Reichard 2001; Backer et al. 2004), but the impact is potentially much broader. There is growing evidence that these fuel reduction projects alter ecosystem structure in ways that promote alien plant invasion.

Ponderosa pine forests in the Cedar Grove section of Kings Canyon National Park in the southern Sierra Nevada of California have been managed with prescription burning for more than two decades. The primary goal is to return a quasi-natural fire cycle for the resource benefit of these forests. In 1998, however, fire management voluntarily halted this program because of the recognition that associated with prescription burning was an explosion of cheatgrass (*Bromus tectorum* L.) in the burned forests (Caprio et al. 1999). Results of experiments on the interaction between cheatgrass and fire show that burning stimulates cheatgrass populations, regardless of whether it is late spring or early fall (T. McGinnis & J.E.K., unpublished data). Based on these studies, the only parameter with potential for inhibiting cheatgrass is accumulation of pine-needle litter, which suggests that lengthening the fire-return interval to significantly exceed the natural cycle may be one of the few options for controlling this alien invader.

Restoration includes restoring not only natural processes such as fire but also natural structure through mechanical thinning of forests, and these practices also may enhance alien invasion. Extensive forest restoration is currently under way in many western U.S. ponderosa pine forests. These treatments alone or in combination with burning of slash increase both the diversity and abundance of alien plant species (Griffis et al. 2001; Dodson 2004; Wienk et al. 2004). Longer-term studies are needed, however, to determine whether this is a short-lived invasion or whether such practices provide an opportunity for invasives to gain a foothold that will allow long-term persistence in these forests.

These examples suggest a potential conundrum. Forest restoration often has as one of its goals returning the system to historical fire regimes of high fire frequency (Covington & Moore 1994). These historical fires, however, occurred on a landscape that lacked a background of diverse alien species poised to take advantage of such disturbance regimes. This situation may force a choice between restoring "natural" fire regimes or altering those fire regimes to favor communities of native species. In reality, though, the question is not that simple because reducing the incidence of fire in these ecosystems has long-term impacts on forest structure, with potential cascading effects on alien species.

Many western U.S. forests have historically had rather complex fire regimes that included a mixture of surface fires and localized crown fires (Odion et al. 2004*b*). Low-intensity surface fires removed dead wood and thinned the sapling population, and localized patches of crown fire created gaps that were essential for reproduction (Keeley & Stephenson 2000). A century of fire suppression, coupled with other management activities such as grazing and logging, has added greatly to the amount and continuity of understory fuels such that now these perturbed forests face the reality that gaps created by high-intensity crown fire will be potentially orders of magnitude larger (Fig. 1). These canopy gaps are sinks for alien invasion (Keeley et al. 2003). Crawford et al. (2001) reported more than a dozen alien species in gaps produced by high-severity wildfires in northern Arizona ponderosa forests, and these aliens constituted more than a quarter of the understory cover. These invasive species change the fuel structure of forests (Brooks et al. 2004) and are capable of setting back both natural and artificial regeneration of the dominant forest trees.

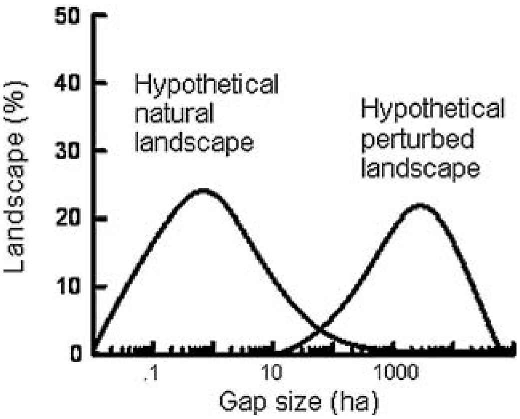

Figure 1. Hypothetical distribution of fire-generated gaps expected for natural fire regimes and future fire regimes in Sierra Nevada mixed conifer forests perturbed by a century of fire exclusion (from Keeley & Stephenson 2000).

There are perhaps ways to minimize effects of alien species in fuel reduction projects. For example, many of the aliens Crawford et al. (2001) recorded in their burned sites were weeds that are often transported by cattle (Arnold 1950; Wuerthner & Matteson 2002); thus, prescription burning or logging, when coupled with grazing, may be a dangerous combination, exacerbating the alien invasion problem. This is supported by the report that wildfires in ungrazed ponderosa forests of northern Arizona have relatively few alien species (Laughlin et al. 2004). If there is a connection, then it could be rather large because 70% of the western United States is grazed, including wilderness areas, national forests, and some national parks (Fleischner 1994). I suggest that rotating grazing areas so that livestock are removed for an extended period of time before prescription burning might be one means of reducing alien species' response to necessary fuel reduction treatments.

Manipulating fire severity during prescription burning can also affect the alien response because high-severity gaps are more vulnerable to invasion than low-severity gaps (Keeley et al. 2003). This, however, is complicated by the requirement of many dominant trees in high-severity gaps for successful seedling recruitment (Keeley & Stephenson 2000).

Manipulating treatment patch size may be another way of altering the invasive threat. For example, the size of burned patches affects postfire colonization by opportunistic species (Turner et al. 1997). Small patches have a greater perimeter-to-area ratio, making the burned area more vulnerable to invasion, whereas large burn patches have a smaller ratio, making the bulk of the burned area less susceptible to colonization from outside alien invaders. The landscape pattern of alien distribution, however, complicates drawing conclusions about community vulnerability to invasion. For example, forest patches adjacent to open habitat are much more susceptible to invasion than forests surrounded by more closed canopy forest (Charbonneau & Fahrig 2004). If aliens are sparsely distributed across the landscape, then small burn patches, despite their high perimeter-to-area ratio, are less likely to encounter alien populations, whereas large patches, with a greater absolute perimeter size, would have a higher probability of encountering alien populations.

In short, grazing history, alien distribution patterns, treatment size, and fire severity are all factors that might be manipulated to reduce the alien threat linked to necessary fuel-reduction projects. Roads and recreational use are other parameters that interact with fire and invasives (e.g., Gelbard & Belnap 2003) and could be manipulated in conjunction with fuel treatments to reduce alien invasion.

Figure 2. Alien-grass-dominated scar in chaparral shrublands 10 years after an out-of-season winter burn in chaparral at Pinnacles National Monument (central coastal California) (photo by J. Keeley). A similar effect was also reported for another cool-season chaparral prescription burn in northern California (Parker 1987).

Prescription Burning in Shrublands

Many shrubland ecosystems such as the Intermountain West sagebrush steppe or California chaparral have a natural fire regime of high-intensity crown fires. These ecosystems provide fewer options for fuel reduction because mechanical treatments are both expensive and unlikely to provide commercial profit. Prescription burning is one of the more economically feasible treatments but there are increasing constraints on its widespread use in shrubland ecosystems because of the hazards of high-intensity fires on populated landscapes. One of the realities of doing prescription burning in crown-fire ecosystems is the difficulty of defining controllable prescriptions (Keeley 2002*a*). This is particularly problematic for burns in the normal late summer through autumn fire season. One approach is to conduct burns outside the normal fire season, but such manipulations have the potential for extreme resource damage, as illustrated by the poor recovery of the native community and massive alien invasion following a winter burn in one California park (Fig. 2).

For shrublands as well as forests, prescription burning is justified if it provides either resource benefits to the ecosystem or reduces fire hazard for people. In California chaparral, prescription burning is primarily justified on the basis of fire-hazard reduction, whereas in the Intermountain West sagebrush, the primary justification is benefit to ecosystem resources. The most commonly cited resource benefits are improved rangeland for wildlife (Beardall & Sylvester 1976; Holechek 1981) or livestock (Pechanec 1944; Sapsis & Kaufmann 1991). Other justifications include returning these ecosystems to their historical structure, which is considered by some to have been a landscape of more open sagebrush steppe vegetation. Indeed, rangeland literature commonly refers to the unnaturally dense stands of sagebrush in need of prescription burning (Blaisdell et al. 1982; Miller et al. 1994). In light of the massive cheatgrass invasion across much of this landscape (Mack 1981), coupled with the potential for burning to favor cheatgrass expansion (Harnis & Murray 1973; Knapp 1997; Young & Allen 1997), there is need for a closer examination of prescription burning in these Intermountain West ecosystems.

Prescription burning in sagebrush ecosystems is a highly effective method of improving rangelands for livestock grazing. The dominant shrub, *Artemisia tridentata* Nutt., is immediately replaced by more palatable herbaceous plants and recovers slowly over a period of decades (Stewart & Young 1939; Pechanec 1944; Ralphs & Busby 1979). On the other hand, prescription burning for enhancement of wildlife habitat appears to be justifiable in very few cases, and generally the loss of sagebrush following burning represents important habitat loss (Miller & Eddleman 2001; Welch & Criddle 2003). Restoring historical fire regimes is perhaps the weakest justification for prescription burning because many lines of evidence suggest fire-rotation intervals are currently at the low end of the historical range of variability (Menakis et al. 2003). The natural fire regime in sagebrush ecosystems appears to have been one of infrequent fires at 60- to 110-year intervals (Whisenant 1990; Welch & Criddle 2003; W. Baker, personal communication), although at the mesic end of the gradient it may have been shorter (Winward 1984). Thus, except on rangelands where livestock production is the only goal, prescription burning may not be a desirable fire-management treatment because of the potential threat of exacerbating the cheatgrass invasion.

In California chaparral and sage scrub shrublands, a similar annual grass invasion has also occurred, although fire-management practices for rangeland improvement appear to have played a much bigger role. This began with burning by the Native Americans, largely to favor herbaceous vegetation over shrublands, which set much of the landscape in a quasi-disequilibrium vulnerable to rapid annual plant invasion upon the arrival of Europeans (Keeley 2002*b*). By the late nineteenth century rangelands were in short supply, widespread burning expanded the grazing lands, and the coastal analogues of cheatgrass, specifically *Bromus madritensis* L., *B. hordeaceous* L., and *B. diandrus* Roth., and forbs such as *Erodium cicutarium* (L.) L'Her., rapidly expanded to fill the void created by removing natural shrub dominants (Keeley 1990, 2001, 2004*b*). Initially these burning practices were unregulated, but in the mid-twentieth century organized efforts at rangeland expansion into shrublands was a state-sanctioned practice that resulted in substantial conversion to alien grasslands (Keeley & Fotheringham 2003).

Typically a repeat fire within the first postfire decade is sufficient to provide an initial foothold for aliens (Fig. 3). With the first entry of alien annuals into these shrubland ecosystems, there is a potential shift from a crown-fire regime to a mixture of surface and crown fires, where highly combustible grass fuels carry fire between shrub patches that have not yet attained a closed canopy capable of carrying crown fire under most weather conditions. As fire frequency increases there is a threshold beyond which the native shrub cover cannot recover (Zedler et al. 1983; Haidinger & Keeley 1993; Jacobson et al. 2004). Not only do alien grasses increase the probability of burning, but also the shift from crown fires to a mixture of surface and crown fires increases the probability of alien seedbank survivorship (Keeley et al. 2005) because grass fuels generate lower temperatures (Zschaechner 1985). In these shrublands and in other ecosystems, alien grasses alter fire regimes in ways that enhance their own success, in what has been described as a "grass/fire cycle" (D'Antonio & Vitousek 1992), "niche construction" (Keeley 2001), or "invasive engineering" (Cuddington & Hastings 2004).

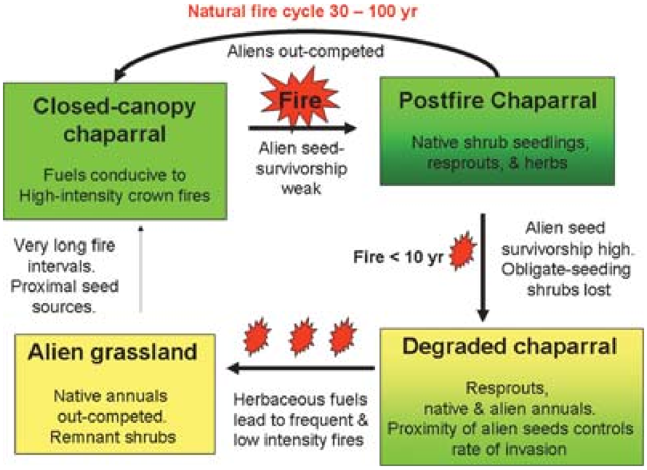

Figure 3. Model of fire and alien species interactions in California chaparral.

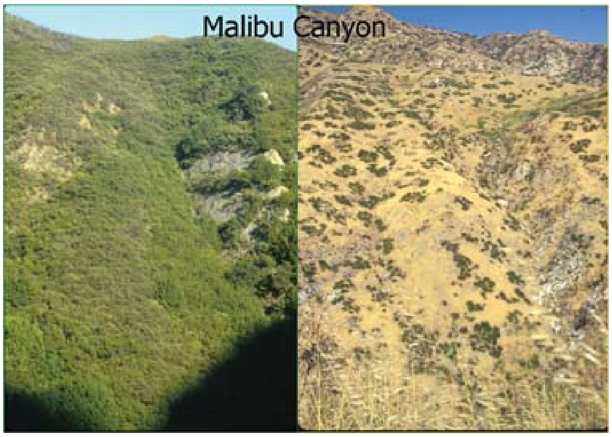

Figure 4. Type conversion recorded for Malibu Canyon, Santa Monica Mountains, California: left, natural chaparral landscape representative of chaparral in Malibu Canyon (photo by Anna Jacobsen); right, landscape dominated by alien annual grass after three fires in 12 years (based on Jacobson et al. 2004; photo by Steve Davis).

In recent years ineffective fire prevention has allowed an unnaturally high number of wildfires on chaparral landscapes, which has resulted in conversion to alien-dominated grasslands (Fig. 4). Such type conversions not only affect biodiversity, but replacing slopes dominated by natural shrublands with grasslands also makes these landscapes highly vulnerable to major changes in hydrological processes. For example, experimental type conversions performed for fire hazard reduction have resulted in soil slips and other major geomorphological changes (Keeley 2002*a*).

On shrubland landscapes where the excessive load of anthropogenic fires has stressed natural ecosystems to the point of collapse, fire managers need to be prudent about adding further fire in the form of prescription burning. Currently this applies to much of the Great Basin and all of the lower-elevation foothills in southern California, where type conversion to alien grasslands is happening at an alarming rate (J.K., personal observations). To be avoided are prescription burning at fire-return intervals of 5 years in southern California chaparral (Loomis et al. 2003; Gonzalez-Caban et al. 2006), which are likely to lead to type conversion to alien grassland and even exacerbate the sedimentation problems they are supposed to reduce (Keeley et al. 2004).

Fuel Breaks

Forests and shrublands, particularly in California, have had a long history of experimentation with different types of fuel breaks. They are constructed to create barriers to fire spread and to provide access and defensible space for fire-suppression crews during wildfires. These activities have the potential for creating suitable sites for alien plant invasion, and invasion is closely tied to the loss in overstory cover. In a recent study of 24 fuel breaks distributed throughout California, alien plants constituted as much as 70% of the plant cover and the proportion of aliens varied significantly with distance to roads, fuel break age, construction method, and maintenance frequency (Merriam et al. 2006). The association of alien species with fuel breaks raises two critical concerns. One is that the linear connectedness of these disturbance zones acts as corridors for alien invasion into wildland areas. Another is that these zones of reduced fuels produce lower temperatures and thus safe sites for alien propagules during wildfires, ensuring survivorship of seed banks (Keeley 2001, 2004*b*). Consequently, following fires these fuel breaks represent a major source area for alien invasion of adjacent wildlands (Fig. 5).

Prescription Burning to Target Noxious Aliens

Fire has diverse effects on alien species, and except for a small handful of cases, it generally promotes persistence of aliens (e.g., Grace et al. 2001; Harrod & Reichard 2001; Brooks et al. 2004). Invasive species in the western United States that seem to be controlled by fire include Mediterranean Basin macchi shrubs known collectively as "brooms." Some of these are vigorous resprouters after fire and thus are not readily controlled by burning. Others (e.g., Scot's broom [*Cytisus scoparius* (L.) Link]) are weak resprouters, and burning shows promise of control. All have dormant, fire-stimulated seed banks; thus several repeat fires appear to be required to extirpate brooms from a site (Tveten & Fonda 1999; Alexander & D'Antonio 2003; Odion & Haubensak 2004), not unlike what happens to native shrublands in the face of repeat fires (Figs. 3 & 4). Burning, however, typically replaces these noxious woody aliens with herbaceous alien species (Keeley 2001).

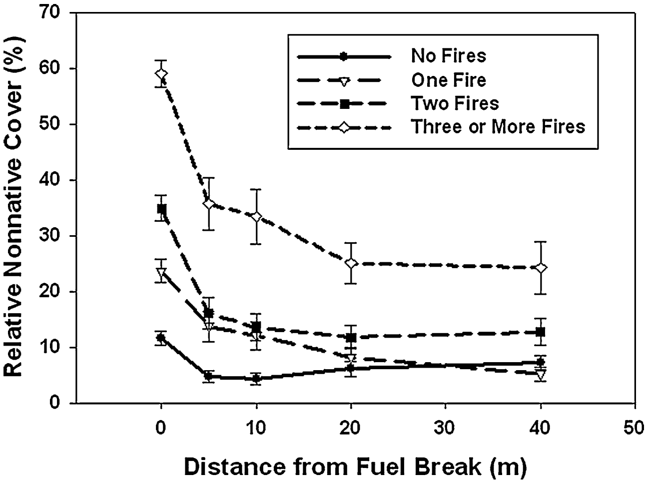

Figure 5. Interaction between number of fires and distance from the fuel break. Error bars represent + 1 SE (from Merriam et al. 2006).

Several lines of evidence point to precisely timed prescription burning as an effective treatment for eliminating certain noxious alien annuals with transient seed banks that are vulnerable to fire during spring seed dispersal. One example widely cited in recent alien plant review articles as a demonstration of such success is the application of spring burning in the control of yellow starthistle (*Centaurea solstitialis* L.). This European pest is distributed from Idaho to California and has been targeted as a particularly noxious alien because it alters range conditions and severely reduces soil water resources (Gerlach 2004). Confidence in prescribed burning treatment as a control for this species is based on the results of annual burning for 3 consecutive years in very dense stands that demonstrated 90–100% reduction in starthistle (DiTomaso et al. 1999; Odion et al. 2004*a*). Burn plans written by agencies undertaking prescribed burns in annual grasslands often use this as one of their primary goals (e.g., East Bay Regional Parks, http://www.ebparks.org/fire/rxfire). This species, however, like many aliens, has a relatively long-lived seed bank (Callihan et al. 1993), and longer-term study shows that this thistle rapidly reestablishes once burning is halted (Fig. 6). Clearly, prescribed burning provides only temporary reduction, does not effect sustainable control of this alien, and may exacerbate the alien situation.

Most alien herbs are opportunistic species that capitalize on disturbance. I offer the hypothesis that when it comes to eliminating such noxious aliens, control is most likely under conditions that limit the use of further disturbances such as fire (or grazing, mowing, or herbicides). In some cases prescribed fire may be appropriate if applied in a manner that affects the noxious target species more than potential native competitors and if coupled with active ecosystem restoration that alters the competitive balance between aliens and natives. Sustainable control of these aggressive weeds is most likely going to occur only when natural, intact ecosystems are restored. In the case of yellow starthistle, it invades annual grasslands that owe their origin to disturbance, either displacement of native perennial grassland or type conversion of shrublands and woodlands (Huenneke 1989; Keeley 1990; Hamilton 1997). In the absence of community restoration, prescription burning is likely to provide only temporary control of this, and other, noxious annual weeds, and not be cost-effective.

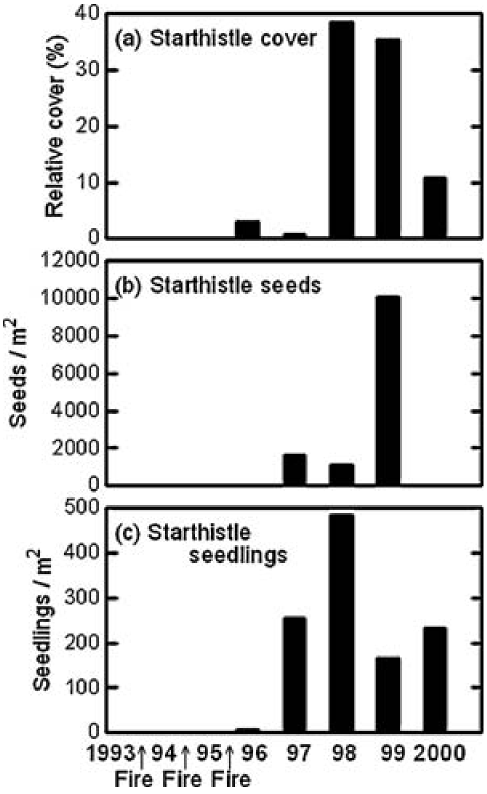

Figure 6. Yellow starthistle (a) cover, (b) seed, and (c) seedling production following three consecutive annual burns applied to extremely dense populations of this noxious alien weed. Immediate postfire results were promising (DiTomaso et al. 1999), but follow-up studies indicate that burning destabilized these grasslands and allowed subsequent reinvasion once burning was stopped (Kyser & DiTomaso 2002).

Postfire Rehabilitation

Propagule source is often the limiting step in the invasion process (D'Antonio et al. 2001) and thus postfire management practices such as site stabilization by seeding of non-natives must be considered a potential influence on alien plant invasion. These postfire rehabilitation projects illustrate well the Severide Principle, after the newscaster Eric Severide, who is quoted as saying, "Most problems begin as solutions."

Early efforts at such revegetation projects may have played a role in the spread of some noxious weeds. For example, postfire seeding in southern California chaparral in the 1940s aerially seeded black mustard (*Brassica nigra* [L.] Koch and possibly related taxa) on steep southern California watersheds (Gleason 1948). These aggressive weeds soon found their way into citrus orchards and other agricultural fields and were eventually abandoned by fire managers as a suitable slope stabilizer. These species, however, produce polymorphic seed banks with dormant fire-stimulated germination (Went et al. 1952), and decades later on many of the previously seeded slopes in the Los Angeles Basin this species still figures prominently in the postfire flora as a ghost of seedings past (Keeley et al. 2005). Eventually postfire seeding projects replaced mustard with various grass species (e.g., ryegrass [*Lolium multiflorum* Lam.], zorro fescue [*Vulpia myuros* (L.) C. Gmelin], crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.]) that appear to lack persistent seed banks. Although these grasses are not persistent on chaparral or forested slopes (Barclay et al. 2004; Beyers 2004), they are capable of invading adjacent grassland and savanna communities.

Because they lack an ability to invade communities, "sterile" or "nonpersistent" cereal grains have been considered a more desirable species for reseeding (Beyers 2004). Although seeding of these species may have achieved some of the intended goals of slowing soil erosion, they have introduced other problems. In one study in the Sierra Nevada the success of wheat seeding was so extraordinary (Fig. 7) that it resulted in the loss of substantial native plant diversity and pine reproduction (Keeley 2004*a*), a pattern common in many seeding projects (Beyers 2004). Seeding nonpersistent species also carries with it the problem that a marked loss of plant cover in the second postfire year will create an ecological vacuum, and aggressive alien invaders are well suited to exploit this situation.

Increasingly it is apparent that mechanical rehabilitation treatments, including straw mulch and hay bales, are more predictable means of reducing soil erosion and other postfire hydrological problems (Robichaud et al. 2000). Mulching treatments, however, are particularly hazardous in terms of introducing and promoting alien establishment (Kruse et al. 2004). In fact, accidental introduction of alien propagules is possible with any "burned

Figure 7. Postfire ponderosa pine forest reseeded with a nonpersistent variety of wheat after fire in the Giant Sequoia National Monument, Fresno County, California (photo by J. Keeley).

area emergency rehabilitation" project. For example, following the 2000 Cerro Grande Fire it is estimated that contamination of aerial seeding sources was responsible for inadvertently broadcasting more than 1 billion cheatgrass seeds on recently burned sites (Keeley et al. 2006).

Conclusions

Fire management practices could have widespread effects on invasions of alien species. This linkage is best understood when these problems are placed in a context of community ecology theory. Fire suppression and prefire fuel manipulations have ecological equivalents in that the former attempts to maintain ecosystem equilibrium by preventing disturbance and the latter introduces disequilibrium.

In western U.S. forests, a century of successful fire suppression policy has shifted the competitive balance in favor of long-lived trees that create ecosystem conditions unfavorable to alien invasion. Although greater ecosystem equilibrium appears to exclude alien plants, fire exclusion has set these forests on a trajectory of undesirable conditions for both forest sustainability and human fire hazard. Thus, forest thinning, fuel breaks, and prescribed burning are necessary and inevitable. But accompanying these management activities is a shift in ecosystem properties that favor early successional species, and when done in the context of a landscape with alien species it is likely to alter the balance of native and non-native species. The impact of these management practices may be altered by considering management practices that decouple grazing and burning practices and manipulate burning patterns in light of prefire alien presence.

In many western U.S. shrubland ecosystems, fire suppression policy—despite valiant efforts—has not kept up with an ever-increasing frequency of fires. These communities exhibit weak resilience to major deviations from the natural crown-fire regime and often the dominant life forms are lost, creating an ecological vacuum that is rapidly filled by alien weeds. In both the Intermountain West sagebrush and California chaparral (including sage scrub) this alien invasion has historically been exacerbated by fire management practices that included prescription burning for range improvement. Current infestations of annual grasses in both regions require enhanced efforts at fire prevention, fire suppression, and avoidance of prescribed burning under many situations.

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Historical patterns of wildfire ignition sources in California ecosystems

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Abstract. State and federal agencies have reported fire causes since the early 1900s, explicitly for the purpose of helping land managers design fire-prevention programs. We document fire-ignition patterns in five homogenous climate divisions in California over the past 98 years on state Cal Fire protected lands and 107 years on federal United States Forest Service lands. Throughout the state, fire frequency increased steadily until a peak *c.* 1980, followed by a marked drop to 2016. There was not a tight link between frequency of ignition sources and area burned by those sources and the relationships have changed over time. Natural lightning-ignited fires were consistently fewer from north to south and from high to low elevation. Throughout most of the state, human-caused fires dominated the record and were positively correlated with population density for the first two-thirds of the record, but this relationship reversed in recent decades. We propose a mechanistic multi-variate model of factors driving fire frequency, where the importance of different factors has changed over time. Although ignition sources have declined markedly in recent decades, one notable exception is powerline ignitions. One important avenue for future fire-hazard reduction will be consideration of solutions to reduce this source of dangerous fires.

Additional keywords: arson, debris burning, equipment, lightning, powerlines, smoking.

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Introduction

Increasing concern over wildfires has prompted a re-emphasis by the federal government to stop this trend (https://www.doi.gov/pressreleases/secretary-zinke-directs-interior-bureaus-take-aggressive-action-prevent-wildfires, accessed 1 April 2018; Bedard 2017). For many decades, the focus of fire management has been on fuel modification with success on certain landscapes (Kalies and Kent 2016) but limited improvement on others (Keeley and Safford 2016). Because humans are a dominant ignition source over the majority of North America (Balch *et al.* 2017; Syphard *et al.* 2017) there is reason to believe improvements in fire prevention may be a key to reducing fire impacts. Indeed, the United States Forest Service (USFS) has been reporting fire causes since it began collecting systematic data on fires in 1905, with the explicit purpose of helping land managers design fire prevention programs (Donoghue 1982*a*).

Effective fire-prevention requires a sound understanding of the patterns and causes of fire ignitions, which are closely aligned with both human and biophysical-landscape characteristics (Syphard *et al.* 2008). Prestemon *et al.* (2013) suggested a conceptual model that linked ignitions to changes in biophysical, societal, prevention and management variations that illustrates the complexities of ascertaining relationships between different sources and how they change over time.

An important characterisation of anthropogenic ignitions is that the most abundant ignition sources are not always associated with the greatest area burned (Syphard and Keeley 2016). Thus, a topic in need of further study is how to sort out those ignition sources that are most damaging, how those have changed over time, and in light of future needs, how climate change is likely to affect different ignition sources and losses. For example, it has been demonstrated for the state of Victoria, Australia, that some ignition sources, such as electrical distribution lines, may be limited in number but result in much more severe fire consequences (Miller *et al.* 2017). In addition, these fires are more likely during periods of elevated fire danger. If some ignition sources play a larger role in area burned, these might be targets for closer scrutiny and fire-management planning. This potential has been demonstrated for parts of southern California over recent decades, where powerlines have been shown to cause a substantial amount of area burned in both subregions in southern California (Syphard and Keeley 2015). Other important factors were arson in one subregion and equipment in another.

The goal of the present research is to expand that approach to include the entire written history of fires in the state. Our focus was on the spatial and temporal patterns of different ignition sources and the relationship between type of ignition and area burned. We took a long-term historical approach utilising data from 1910 to 2016 for USFS lands and from 1919 to 2016 for state protected Cal Fire lands. First, we examine the spatial and temporal patterns of natural lightning-ignited fires *v.* human fires in the state, and their contribution to area burned. Next, we investigated which anthropogenic causes are most frequent, their distribution within the state, their change over time and their contribution to area burned. Based on a study of state-protected lands in California, Syphard *et al.* (2007) found that fires increased from 1931 to the 1980s, but then decreased over the subsequent decades. A similar pattern for the whole state was also reported by Keeley and Syphard (2017) on both Cal Fire and USFS lands. Thus, the present study contrasts fire-ignition patterns within climatically homogenous sub-regions for the period before 1980 and for the period 1980–2016.We also investigated the extent to which seasonal climate parameters could explain patterns of ignitions and area burned for each type of ignition source.

Methods

Fire-history data for numbers of fires and area burned, by cause, were analysed separately for state-protected Cal Fire and federal USFS lands. Data for counties, forests and climate divisions were all normalised by the area protected each year and within each unit and expressed as number of fires, or hectares burned, per million hectares.

Cal Fire data included 51 of the state's 58 counties (see Fig S1, available as Supplementary material to this paper) as 7 counties had limited fire activity or records. Fire statistics were from direct protection areas (DPA), which are mostly state-responsibility lands with smaller amounts of federal lands, and included the years 1919–2016, summarised by county. The term DPA was first used in 1986 and the area included was equivalent to what was called State Zone (1972–1985), Zones I and II (1945–1971) and Zones 1, 2, 3 (1919–1944). Cal Fire data from 1919 to 1930 are unpublished and were only available as typed reports at the California State Archives in Sacramento. Data from 1931 to 2016 were available in annual reports variously named, Forest Fire Summary, Fire Statistics, Fire Activity Statistics, and Wildfire Activity Statistics, often referred to as the *Redbook* series, available from research libraries or directly from the agency. Only 30 counties had complete data (excluding 1927 for nearly all counties and a few additional years in other counties) beginning in 1919, and an additional 21 counties had continuous data beginning in 1945 (or slightly later in a few cases) (see Table S1 for years of records for each county). Area protected has changed through this period of record and thus data were normalised to the hectares protected for that year presented with the annual reports. There was a period from 1941 to 1952 area where protected-area data were not included in annual reports and, as best we can determine, those data are no longer available, so we used the areas protected in 1940. In all cases, the changes between 1940 and 1953, when such data were again available, were minor.

USFS fire data covered 17 national forests (Fig S2) and included the years 1910–2016 (see Table S2, two forests were created after 1910 carved out of area from adjoining forests). Area protected has changed through this period of record and thus data were normalised to the hectares protected for that year. Data for USFS lands through the 1980s were from annual fire statistics reports for Region 5, available in the Forestry Library (most of which was transferred to the Bioscience Library) at the University of California, Berkeley. More-recent data, 1970 to 2016, were from the National Wildfire Coordinating Group (see http://fam.nwcg.gov/fam-web/weatherfirecd/state_data.htm, accessed 1 June 2017).

Most investigators are unfamiliar with these historical fire records and are sometimes sceptical of their accuracy. For example, Stephens (2005) contended that USFS data before 1940 were inaccurate, but cited a source (Mitchell 1947) that provided no evidence of this. Likely, the idea comes from Donoghue's (1982*b*) comment '1940 marked the modern era of fire reporting'. However, that comment was in reference to the fact that 'the report issued at this time was the first designed for automated data processing and easy readability' and was not in reference to reliability.

Historians have generally been confidant in these early California fire records (Brown 1945; Show 1945; Clar 1969; Cermak 2005). The first author, J. E. Keeley, examined all of the California fire-related materials stored at the state and federal archives and believes collectively they show managers have always been conscientious about reporting accuracy and completeness. For example, beginning in 1905, USFS record-keeping required 15 items of information on the fire reporting Form 944, including the specific cause (Donoghue 1982*b*). On state-protected lands there was an incentive in that the 1911 *Federal Weeks Law* provided fiscal aid to states based on statistics of fire protection (see http://www.calfire.ca.gov/about/about_calfire_history2, accessed 23 May 2018). In 1919, the California state legislature appropriated money for fire prevention and suppression, and records in the state archive show that, by 1920, there were more than 400 fire wardens distributed throughout the state who were charged with fire-fighting and fire reporting. In 1920, there were 800 flights of the Army's 9th Aero Squadron fire patrol that covered 426 500 km during the 5-month California fire season (Cermak 1991).

One complication in studying ignition sources is that reported categories have changed over time. Certain causes have persisted over the entire period of record, including lightning, smoking and camping, but other categories have changed their names. For example, arson fires are a relatively new category as intentionally set fires have, in the past, been labelled as 'incendiary', and seem to have been more rural than contemporary urban arson fires (Kuhlken 1999) and in this paper they are all recorded as arson fires. Other changes include the term 'brush burning' being changed to 'debris burning', and the categorisation of brush burning has been folded into debris burning. Causes that were unknown or represented minor categories have been included as miscellaneous fires (Donoghue 1982*a*), but are not addressed here.

Cal Fire data were spatially explicit at the level of the county and USFS data at the level of the individual forest. However, for analysis, these were grouped into climatically homogenous areas as defined by the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center (NCDC) California Climate Divisions (Fig. 1), comprising the main fire-prone landscapes in the state (see http://www.ncdc.noaa.gov/temp-and-precip/time-series/index.php?parameter=pdsi&month=1&year=2008&filter=p12&state=4&div=5, accessed 15 June 2016). These include, from north to south, Division 1 (North Coast), 2 (North Interior), 5 (Sierra Nevada), 4 (Central Coast), and 6 (South Coast). Where boundaries did not match precisely, counties or forests were placed in the climate division comprising the majority of land area in that unit.

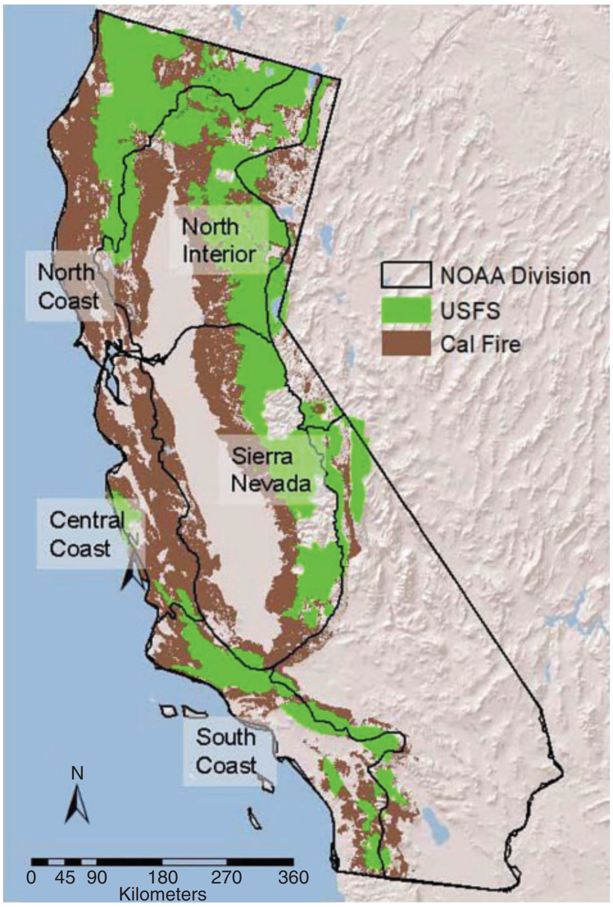

Fig. 1. NOAA climate divisions and Cal Fire protected and USFS protected lands in California for the five climate divisions with long-term fire history.

In 1919, Cal Fire-protected lands were 11.7×10^6 ha and increased to 12.5×10^6 ha in 2016. USFS lands comprised 9.8×10^6 ha in 1919 and decreased to 9.5×10^6 ha in 2016. Vegetation on state lands was dominated by grasslands and shrublands in the south and with significant woodlands and coniferous forests farther north (see Keeley and Syphard 2017 for more detailed vegetation data). USFS lands were dominated by coniferous forests, except in the southern part of the state where they were dominated by shrublands.

To evaluate climate impact on fire activity, we utilised PRISM climate for each county on Cal Fire-protected lands and each forest on USFS lands (Fig. 1). For every year in the analysis, we extracted 2.5 arc-minute PRISM data (PRISM Climate Group, Oregon State University, see http://prism.oregonstate.edu, accessed 15 February 2017) for areas within the boundaries of the Cal Fire and USFS lands. For each county and forest, we computed area-weighted averages of monthly mean precipitation and temperature, summarised by season – winter being December (prior year), January and February, spring being March, April and May, summer being June, July and August, and autumn being September, October and November.

Analysis was conducted with Systat software (ver. 11.0, Systat Software, Inc., San Jose, CA, http://www.systat.com/). For the climate analysis, we developed multiple regression models explaining area burned for USFS and Cal Fire based on seasonal temperature, precipitation and prior-season precipitation variables. To ensure multicollinearity would not be an issue, we calculated correlation coefficients among all potential explanatory variables and eliminated those that were strongly correlated ($P < 0.05$) with other variables in the model.

Results

Long-term averages show that on a per-unit-area basis fires were approximately twice as frequent or more on Cal Fire lands as on USFS lands in all five NOAA climate divisions (Table 1). However, the relationship between ignitions and area burned varied markedly between Cal Fire and USFS lands and between divisions. In the North Coast division, Cal Fire dealt with twice as many fires as the USFS but the average area burned was very similar. In contrast, in the interior from the Sierra Nevada northward, Cal Fire experienced approximately double the number of fires and nearly double the area burned. In the coastal

Table 1. Fire frequency and area burned on state and federal lands in California

NOAA division	Cal Fire (1919–2016) Fire frequency (n/year/10^6 ha)	Cal Fire (1919–2016) Area burned (ha/year/10^6 ha)	USFS (1910–2016) Fire frequency (n/year/10^6 ha)	USFS (1910–2016) Area burned (ha/year/10^6 ha)
North Coast	317	7780	150	7559
North Interior	421	9642	207	5914
Sierra Nevada	356	8436	169	4709
Central Coast	277	5496	66	18860
South Coast	656	15278	369	24442

Table 2. Cal Fire counties total fires, percentage due to human ignitions and regression coefficients for population density *v.* number of fires (per year per million ha) for years 1919–2016

Division	County	Total	Percentage human	<1980		≥1980	
				r	*P*	*r*	*P*
North Coast	Del Norte	330	97	0.39	0.007	0.07	0.667
	Humboldt	219	93	0.31	0.018	−0.62	0.000
	Lake	446	98	0.72	0.000	−0.66	0.000
	Marin	1155	100	0.10	0.526	−0.07	0.699
	Mendocino	255	94	0.46	0.000	−0.46	0.004
	Napa	493	99	0.79	0.000	−0.83	0.000
	Siskiyou	256	63	0.44	0.000	−0.07	0.681
	Sonoma	488	99	0.90	0.000	−0.71	0.000
	Trinity	229	75	0.05	0.709	−0.27	0.102
North Interior	Butte	929	95	0.89	0.000	−0.51	0.001
	Colusa	115	95	0.44	0.003	−0.60	0.000
	Glenn	87	93	0.28	0.069	−0.64	0.000
	Lassen	178	50	0.55	0.000	−0.39	0.017
	Modoc	113	51	0.42	0.020	0.04	0.811
	Nevada	936	97	0.72	0.000	−0.80	0.000
	Placer	1645	98	0.88	0.000	−0.89	0.000
	Plumas	489	74	0.67	0.000	0.08	0.654
	Shasta	469	90	0.77	0.000	−0.38	0.020
	Solano	406	99	0.55	0.000	−0.54	0.000
	Tehama	196	93	0.90	0.000	−0.48	0.000
	Yolo	226	97	0.61	0.000	−0.32	0.051
	Yuba	723	97	0.49	0.000	−0.26	0.118
Sierra Nevada	Amador	507	99	0.60	0.000	−0.47	0.003
	Calaveras	337	99	0.59	0.000	−0.57	0.000
	El Dorado	213	98	0.77	0.000	−0.26	0.123
	Fresno	100	96	0.84	0.000	−0.69	0.000
	Inyo-Mono	255	98	0.67	0.002	−0.63	0.000
	Kern	804	99	0.84	0.000	−0.51	0.002
	Kings	321	99	0.29	0.146	−0.32	0.107
	Madera	823	99	0.65	0.000	−0.48	0.003
	Mariposa	617	97	0.70	0.000	−0.45	0.005
	Merced	602	95	0.21	0.180	−0.42	0.010
	San Joaquin	850	97	0.05	0.789	−0.46	0.005
	Stanislaus	237	95	0.35	0.024	−0.20	0.244
	Tulare	180	93	0.77	0.000	−0.33	0.048
	Tuolumne	280	93	0.89	0.000	−0.23	0.174
Central Coast	Alameda	117	98	0.65	0.000	−0.68	0.000
	Contra Costa	447	93	0.59	0.000	−0.21	0.213
	Monterey	306	93	0.84	0.000	−0.83	0.000
	San Benito	151	93	0.62	0.000	−0.81	0.000
	San Luis Obi	322	99	0.77	0.000	−0.64	0.000
	San Mateo	158	97	0.74	0.000	−0.08	0.055
	Santa Clara	242	93	0.38	0.002	−0.63	0.000
	Santa Cruz	814	97	0.80	0.000	−0.57	0.000
South Coast	Los Angeles	778	98	0.41	0.007	−0.53	0.001
	Orange	1198	100	0.85	0.000	−0.62	0.000
	Riverside	790	98	0.82	0.000	−0.82	0.000
	San Bernardi	791	96	0.73	0.000	−0.81	0.000
	San Diego	576	97	0.63	0.000	−0.60	0.000
	Santa Barbar	347	99	0.70	0.000	−0.64	0.000
	Ventura	713	99	0.84	0.000	−0.42	0.010

areas from San Francisco to San Diego, there were substantially more fires on Cal Fire-protected lands but the area burned was substantially greater on USFS lands.

For Cal Fire-protected landscapes, the area-based average number of fires per year (1919 to 2016) varied from 1645 in Placer County to 87 in Glenn County (Table 2). Humans were

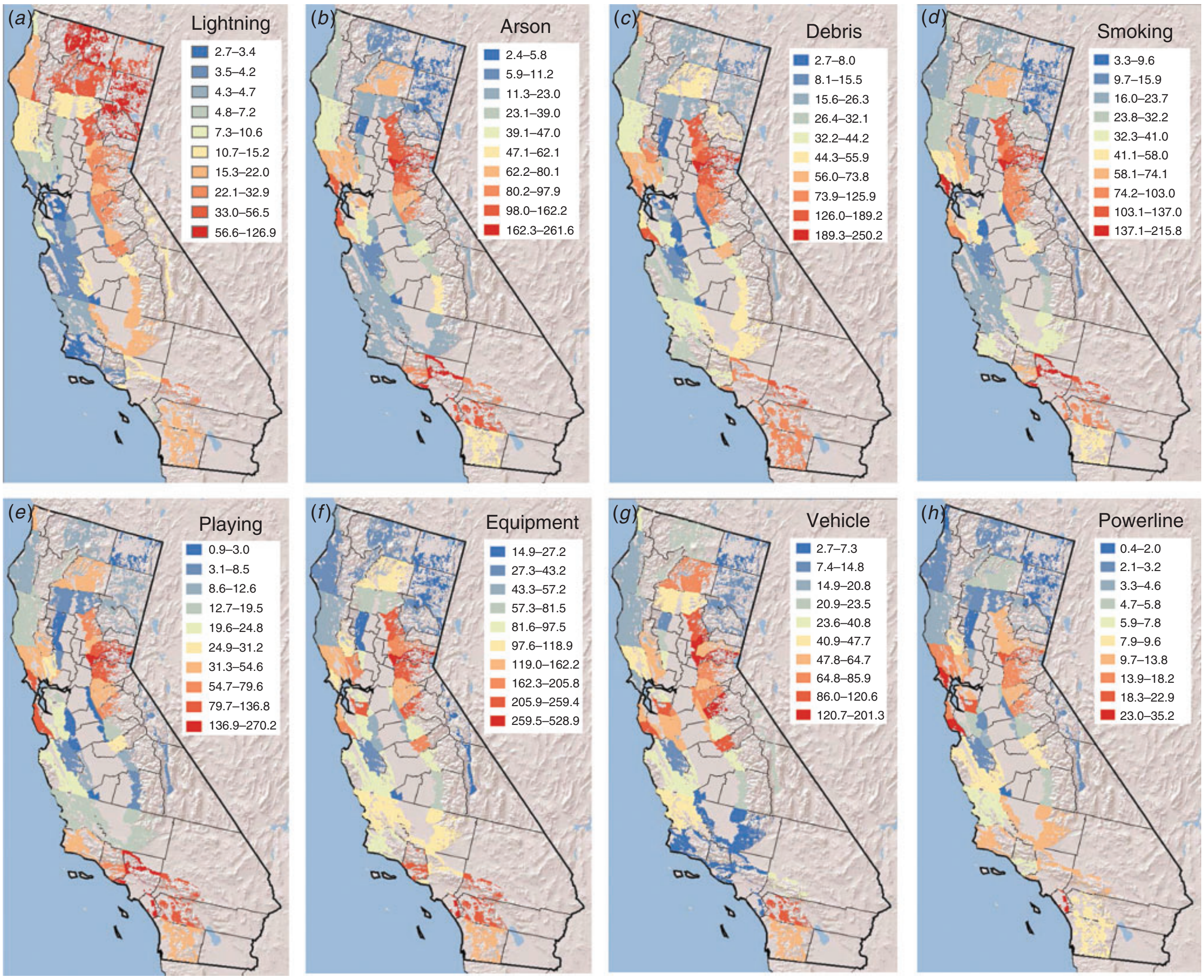

Fig. 2. Fire frequency for different ignition sources on Cal Fire protected lands in California for the years 1919–2016 (n/year/10^6 ha); note change in scales for each source.

responsible for most of fires, accounting for 95% or more of the ignitions in two-thirds of the counties. However, certain northern California counties stood out as notable exceptions, e.g. in Siskiyou, Trinity, Lassen, Modoc and Plumas counties lightning accounted for one-quarter to more than half of all ignitions, patterns illustrated in Fig. 2*a*. Regions with the lowest lightning-ignited fires extended through the coastal ranges from north of San Francisco to Santa Barbara. Area burned by lightning-ignited fires generally followed a similar pattern, although it was the source for significant burning in the San Bernardino County of southern California (Fig. 3*a*).

For USFS lands, the area-based average number of fires per year (1910 to 2016) varied from 478 in San Bernardino to 67 in Eldorado National Forest (Table 3). Humans accounted for far fewer fires than on Cal Fire lands. In the South Coast division, humans were responsible for 74–88%; however, in half of the other forests, humans accounted for less than 50% of the fires. As with Cal Fire landscapes, USFS lightning-ignited fires were most common in the north-east part of the state and declined markedly in coastal central and southern California (Fig. 4*a*). Area burned by lightning-ignited fires generally followed a similar pattern with the exception that parts of the North Coast and Central Coast, despite having few such ignitions, had substantial area burned by this source (Fig. 5*a*).

On both Cal Fire- and USFS-protected lands, humans played a substantial role in fire ignitions. During the first two-thirds of the 20th century there was a very strong positive relationship between population density and fire frequency in nearly 90% of the counties (Table 2) and more than 75% of the forests (Table 3). However, from 1980 to 2016, although population growth continued throughout the state, in most counties and forests, population density exhibited a highly negative relationship with fire frequency (Tables 2, 3).

On both Cal Fire- and USFS-protected lands, human-ignited fires derived from both intentional and accidental causes. The highest number of fires was from equipment, arson, debris

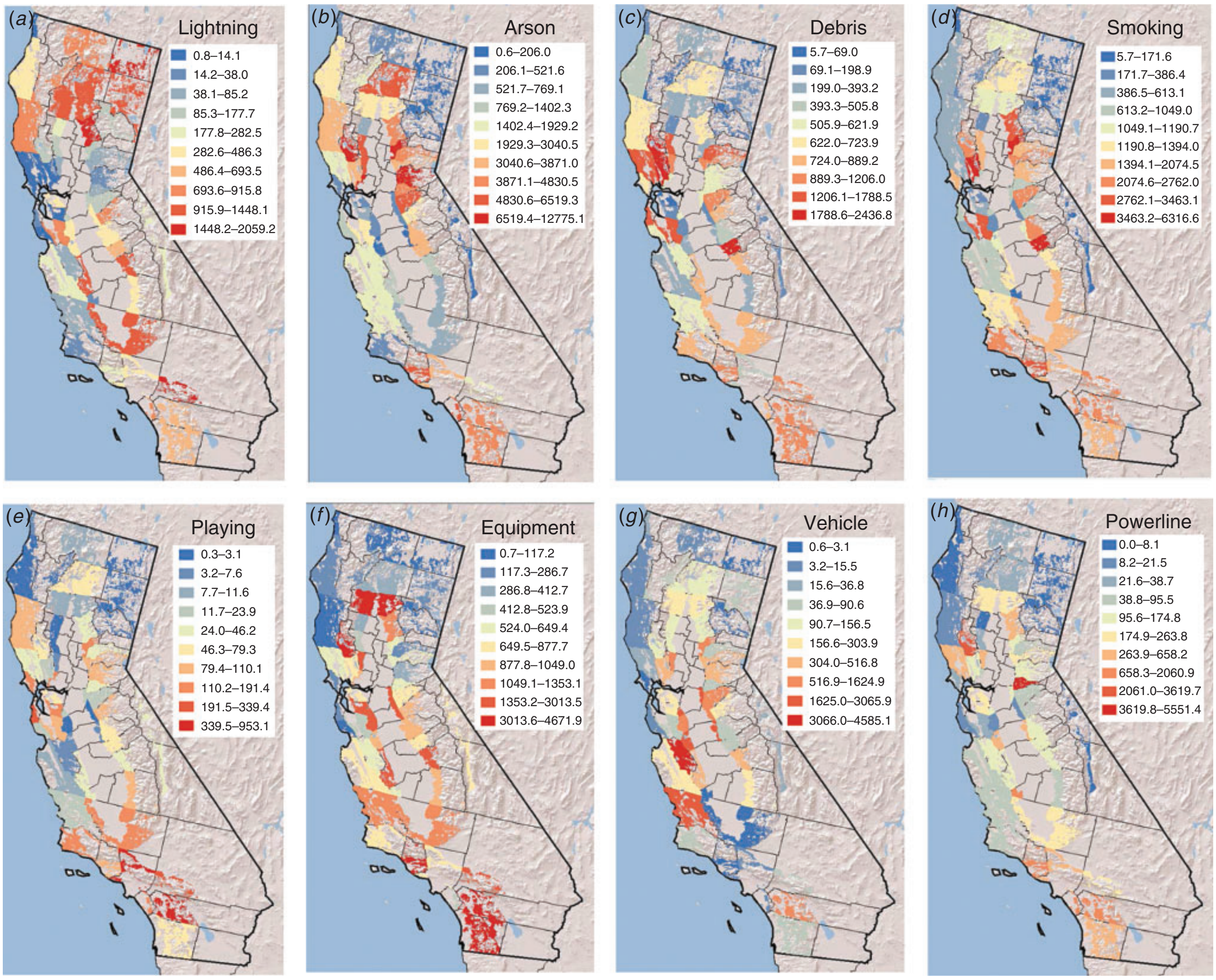

Fig. 3. Area burned by different ignition sources on Cal Fire protected lands in California for the years 1919–2016 (ha burned/year/10^6 ha); note change in scales for each source.

burning, children playing with fire, smoking, vehicles and powerlines (Tables S3–S6). Sources, such as railroads and lumber practices, did cause many fires in the early part of the record, but are of minor significance today (this change not shown).

These ignition sources exhibited marked geographical variation in their importance (Fig. 2–5). On lower elevation Cal Fire landscapes, arson was responsible for much of the area burned in the northern Sierra Nevada Mountains. (Fig. 3*b*), whereas debris burning was responsible for much of the area burned north and south of San Francisco (Fig. 3*c*), vehicles were the cause of much of the burning in the central coastal ranges (Fig. 3*g*) and equipment fires in southern California (Fig. 3*f*). Powerlines were responsible for significant number of fires in the north bay area of San Francisco and coastal communities from Santa Barbara south to the border (Fig. 3*h*).

In USFS forests, area burned in the South Coast was most heavily affected by arson and powerlines (Fig. 5*b*, *h*), but equipment and debris burning dominated in the Central Coast (Fig. 5*c*,*f*). Forests adjacent to high density metropolitan areas in Los Angeles and western San Bernardino counties had substantial burning due to smoking, children playing with fire, and powerlines (Fig. 5*d*, *e*, *h*).

Changing ignition patterns over time

The historical pattern of fire frequency on lower elevation Cal Fire-protected lands for 97 years and USFS lands for 107 years is illustrated in Fig. 6 for the five climate divisions. There was a common pattern across both Cal Fire and USFS lands and consistent within each of the five climate divisions – a highly significant increase in fire frequency from the beginning of records to 1979, and a switch to a highly significant decline in fires from 1980 to 2016 (Fig. 6), the single exception being the South Coast USFS lands (Fig. 6*r*). Despite a significant fit of these data to the linear regression models, there were some marked departures on Cal Fire lands during the early record. Plotting of linear regression residuals from 1919 to 1979 shows

Table 3. USFS forests total number of fires, percentage ignited by humans and regression coefficients for population density *v.* number of fires (per year per million ha) for years 1910–2016

Division	Forest	Total	Percentage human	<1980		≥1980	
				r	*P*	*r*	*P*
North Coast	Klamath	192	28	0.23	0.057	−0.33	0.045
	Mendocino	97	51	0.26	0.032	−0.36	0.030
	Six Rivers	137	65	0.46	0.007	0.11	0.528
North Interior	Lassen	271	38	0.66	0.000	−0.43	0.008
	Modoc	118	21	0.42	0.000	−0.06	0.730
	Plumas	280	46	0.36	0.002	−0.37	0.024
	Shast-Trinity	188	50	0.15	0.142	−0.41	0.012
	Tahoe	257	54	0.22	0.067	−0.44	0.007
Sierra Nevada	Eldorado	67	58	0.43	0.000	−0.25	0.129
	Inyo-Mono	237	40	0.85	0.000	−0.67	0.000
	Sequoia	79	39	0.75	0.000	−0.76	0.000
	Sierra	213	48	0.63	0.000	−0.68	0.000
	Stanislaus	201	49	0.50	0.000	−0.55	0.000
Central Coast	Los Padres	203	82	0.51	0.000	−0.50	0.002
South Coast	Angeles	367	87	0.58	0.000	0.49	0.002
	Cleveland	292	88	0.71	0.000	0.05	0.773
	Sbernardino	478	74	0.89	0.000	−0.50	0.002

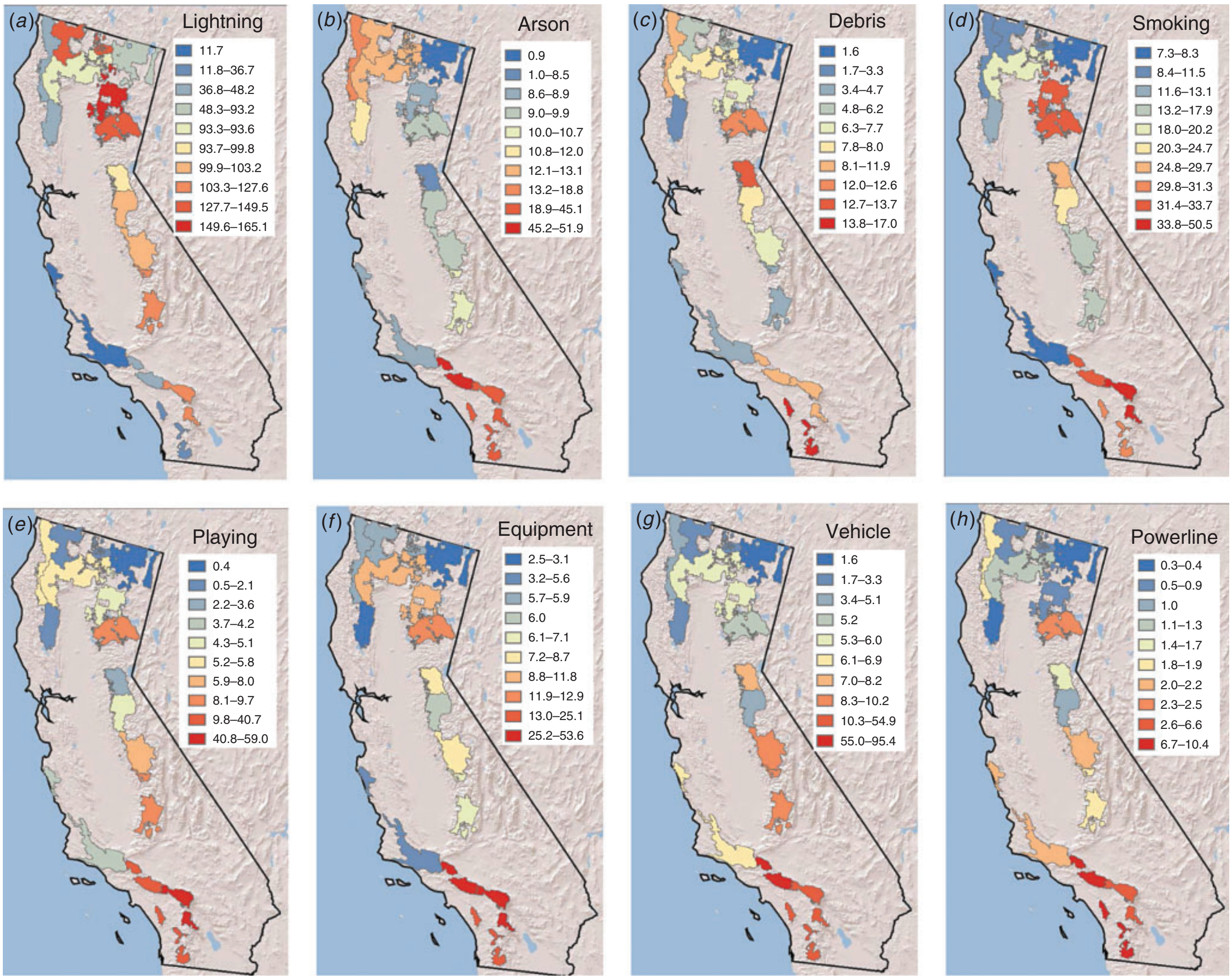

Fig. 4. Fire frequency for different ignition sources on USFS protected lands in California for the years 1910–2016 (*n*/year/10^6 ha); note change in scales for each source.

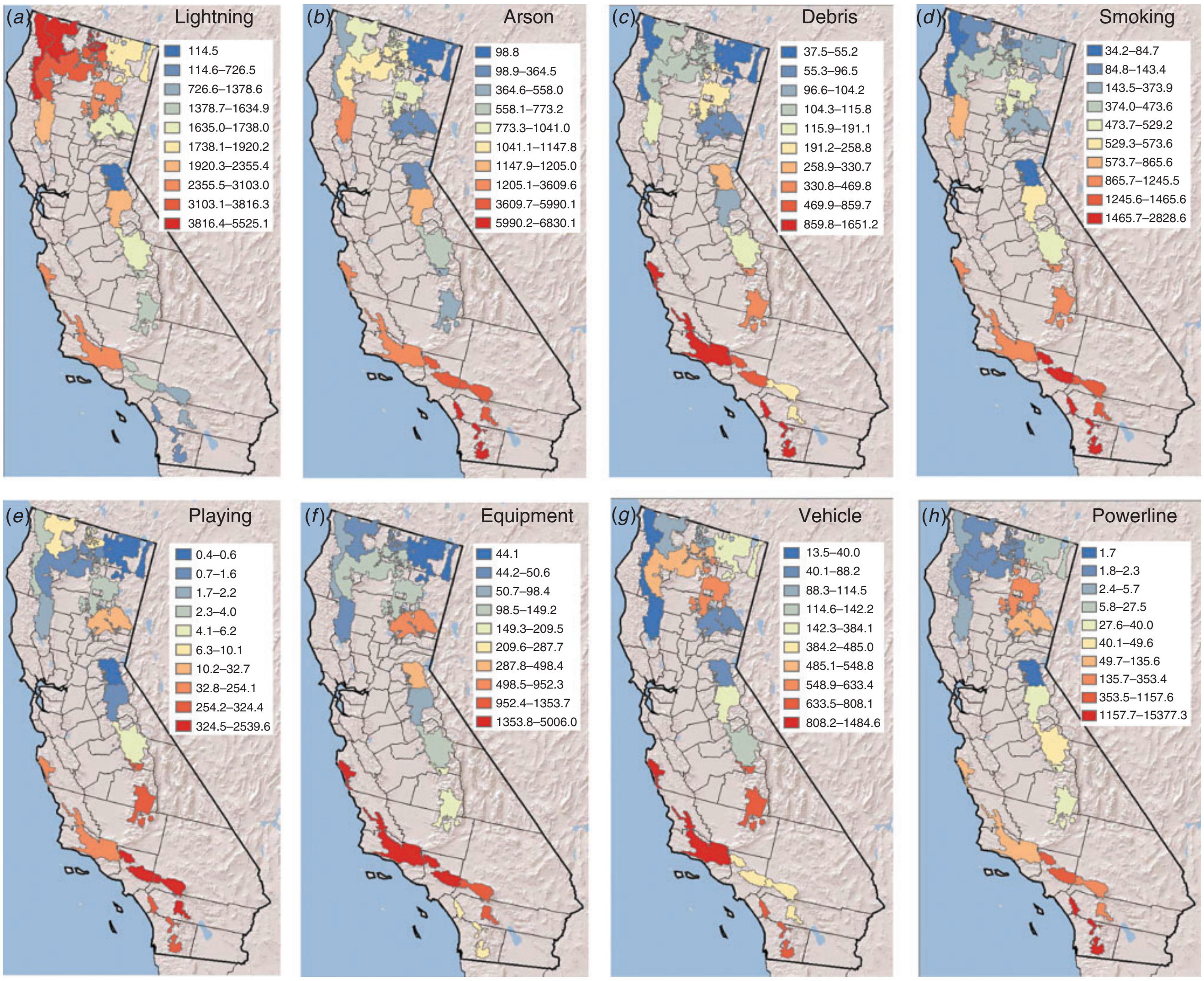

Fig. 5. Area burned by different ignition sources on USFS protected lands in California for the years 1910–2016 (ha burned/year/10^6 ha); note change in scales for each source.

marked and consistent diversions in most divisions (Fig. 7). Although the residuals early in the record are closely aligned with the regression line, during the 1920s and 1930s from the Sierra Nevada north there was a marked increase in ignitions. This pattern was less obvious in coastal central and southern California. In the 1950s and 1960s, there was a marked depression in ignitions in all climate divisions. It is worth noting that in the former period it was drier than the long-term average and in the latter period wetter (Fig. S3).

Changes in area burned did not closely follow changes in fire frequency (Fig. 6) – while fire frequency increased in the first three-quarters of the 20th century, area burned declined or stayed more or less constant. USFS forests in the northern part of the state showed a tendency for increased area burned in the last 4 decades (Fig. 6*d*, *l*) but in general there were no strong trends in area burned after 1980.

Of particular interest is how specific ignition sources have changed and, in order to simplify this presentation, we have consolidated climate divisions in the north (North Coast, North Interior and Sierra Nevada) and in the south (Central Coast and South Coast), which is justified by the marked similarities in ignition patterns within these two regions (see Fig. 2–5).

On Cal Fire-protected lands, it is noteworthy that changes in number of ignitions for lightning-ignited fires matched that of many human ignition sources, specifically increased ignitions during the first part of the record and decreased ignitions in recent decades (Fig. 8*a*, *e*). Numbers of lightning ignitions were more than double in the north than in the south, and substantially fewer than the leading anthropogenic causes. On USFS forests, lighting fire frequency (Fig. 9*a*, *e*) followed a temporal pattern similar to Cal Fire lands but were ~3 times more abundant than on Cal Fire landscapes and were one of the dominant ignition sources in forests. Despite changes in number of lightning-ignited fires, the area burned by this source did not exhibit consistent trends, although, in northern California forests, area burned by lightning-ignited fires has increased since 1980 (Fig. 8*i*, *m*, 9*i*, *m*).

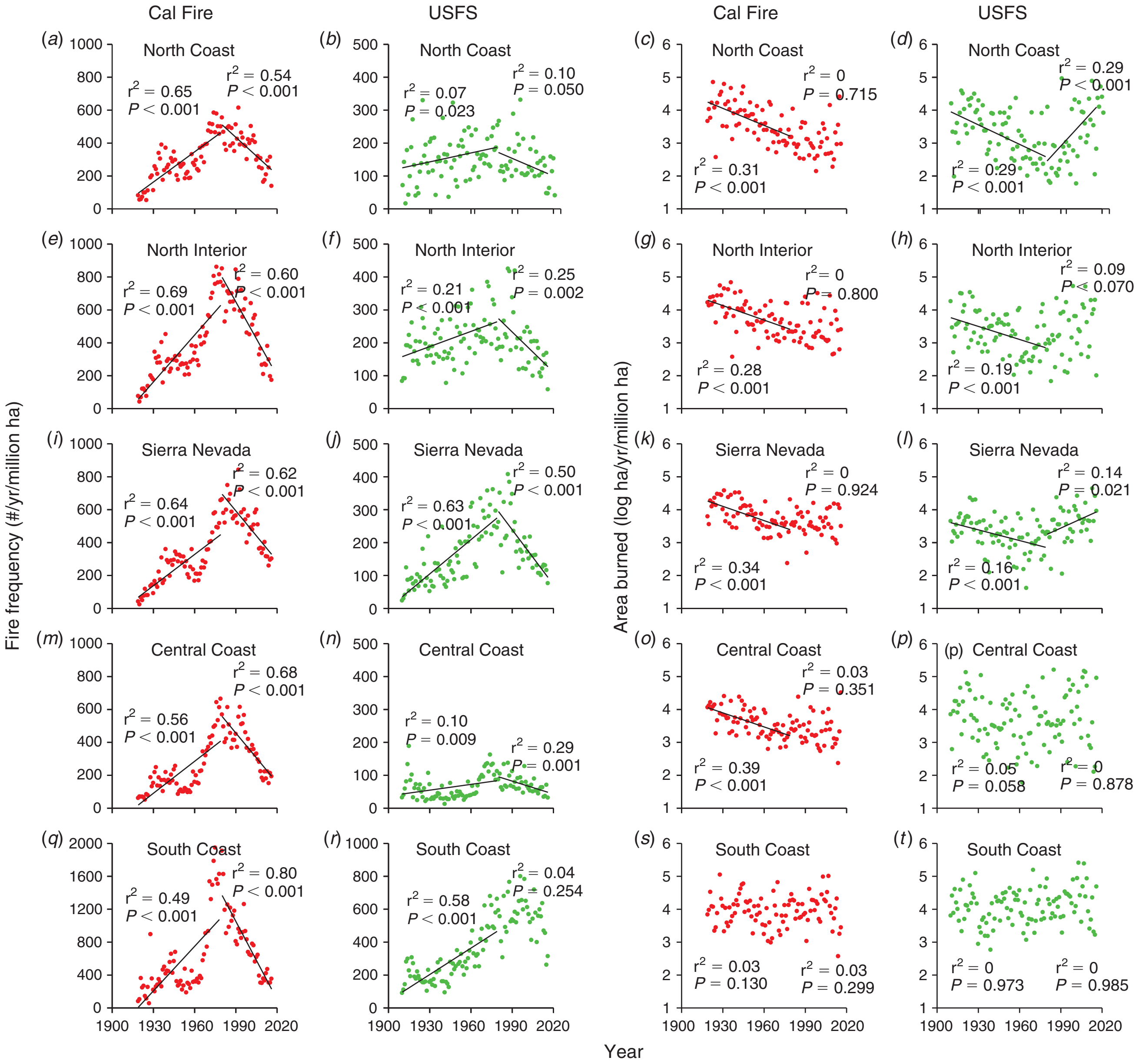

Fig. 6. Fire frequency for Cal Fire protected lands (*a*, *c*, *i*, *m*, *q*) and USFS lands (*b*, *f*, *j*, *n*, *r*) and area burned on Cal Fire (*c*, *g*, *k*, *o*, *s*) and USFS (*d*, *h*, *l*, *p*, *t*) lands. Note for frequency the change in scale between the South Coast and other divisions and between Cal Fire and USFS lands.

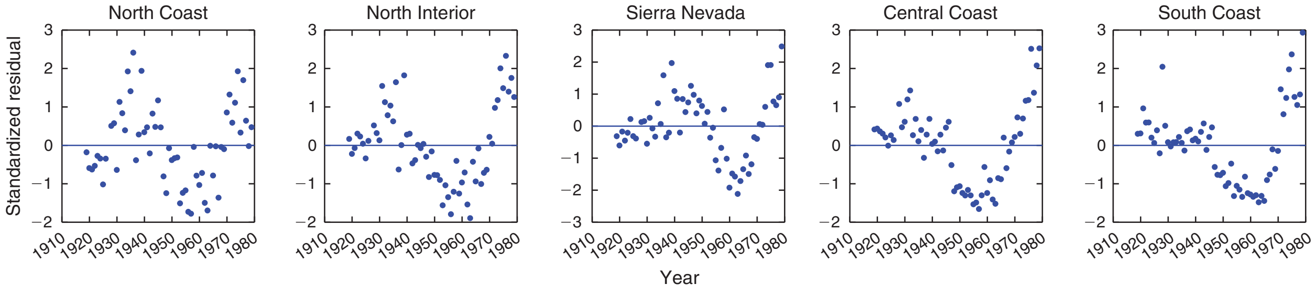

Fig. 7. Ignition sources recorded throughout the period 1919–2016 on Cal Fire protected lands by frequency (*a*–*h*) and area burned (*i*–*p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions from 1919 to 1979 and from 1980 to 2016; note the change in scale between lightning and anthropogenic sources for fire frequency.

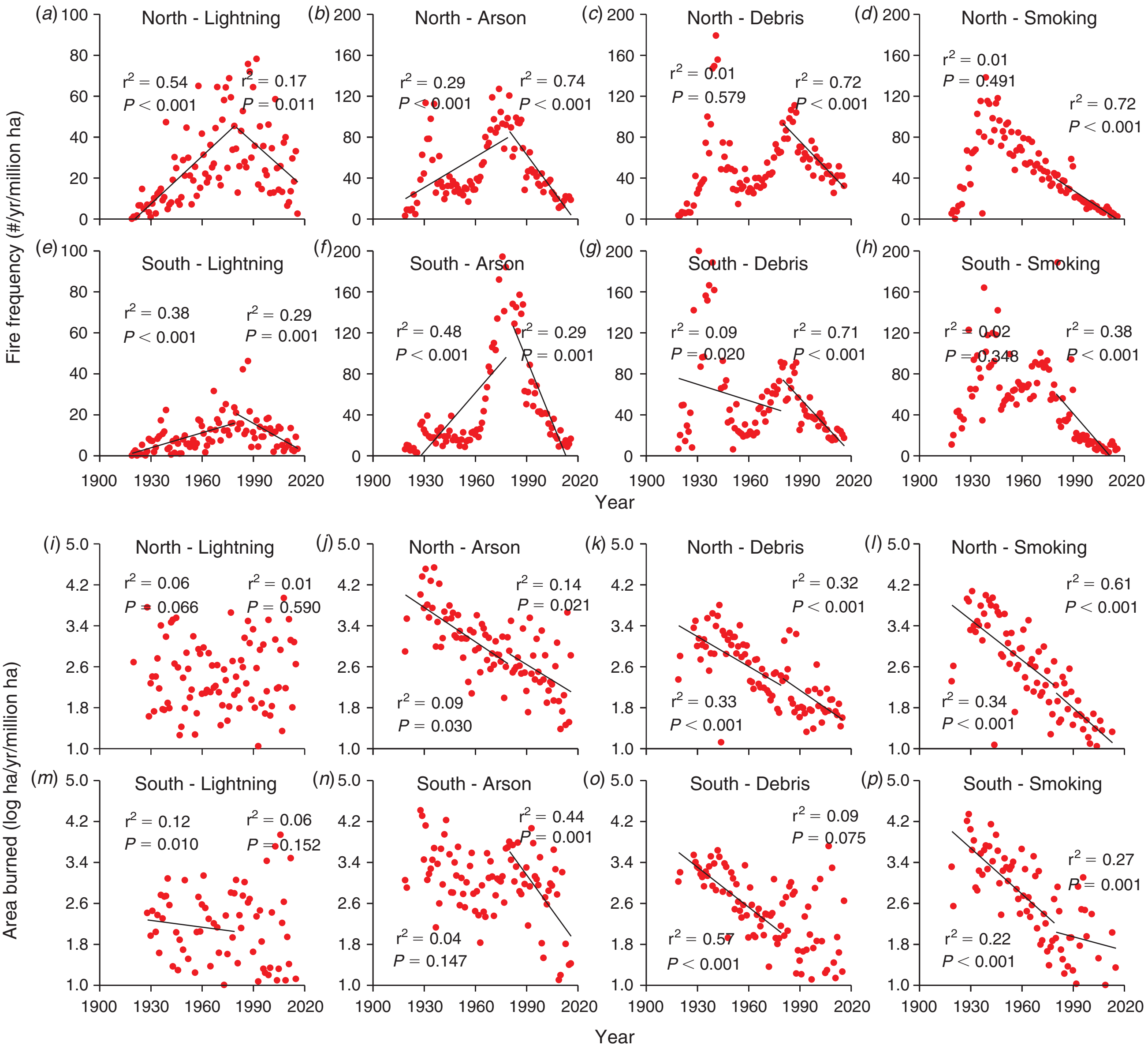

Fig. 8. Ignition sources not reported separately before 1960 on Cal Fire protected lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions before 1980 and 1980–2016; note the change in scale for fire frequency.

The main anthropogenic ignition sources on Cal Fire lands were arson, debris burning and smoking, and all showed a significant decrease in recent decades (Fig. 8*b–d*, *f–h*). Also, area burned by these ignition sources mostly showed a marked decrease in recent decades (Fig. 8*j–l*, *n–p*).

On USFS lands, arson and smoking were very important but camping was also a significant cause (Fig. 9). Arson fires exhibited remarkable similarity in the south of both jurisdictions with a marked decline in frequency and area burned since 1980 (Fig. 9*f*, *n*).

On both Cal Fire and USFS lands, some ignition sources, such as children playing with fire, equipment, vehicles and powerlines, were not specifically recorded during the early years (Fig. 10, 11). Children playing with fire declined significantly in both jurisdictions in the north and south (Fig. 10*a*, *b*, 11*b*, *f*) as did area burned by this source (Fig.10*i*, *m*, 11*j*, *n*). Equipment-ignited fires increased markedly between 1960 and 1979 on Cal Fire lands (Fig. 10*b*, *f*) but, during the same period, declined on USFS lands (Fig. 11*c*, *g*). Since 1980, this source of ignitions has declined sharply on Cal Fire lands in the north and south (Fig. 10*b*, *f*) but increased on USFS lands in the south (Fig. 11*g*). In contrast to all other ignition sources, powerline fires on Cal Fire and USFS lands in both the north and south have not declined in the last 4 decades (Fig. 10*d*, *h*, 11*d*, *h*) nor has area burned by this ignition source (Fig. 10*p*, 11*p*).

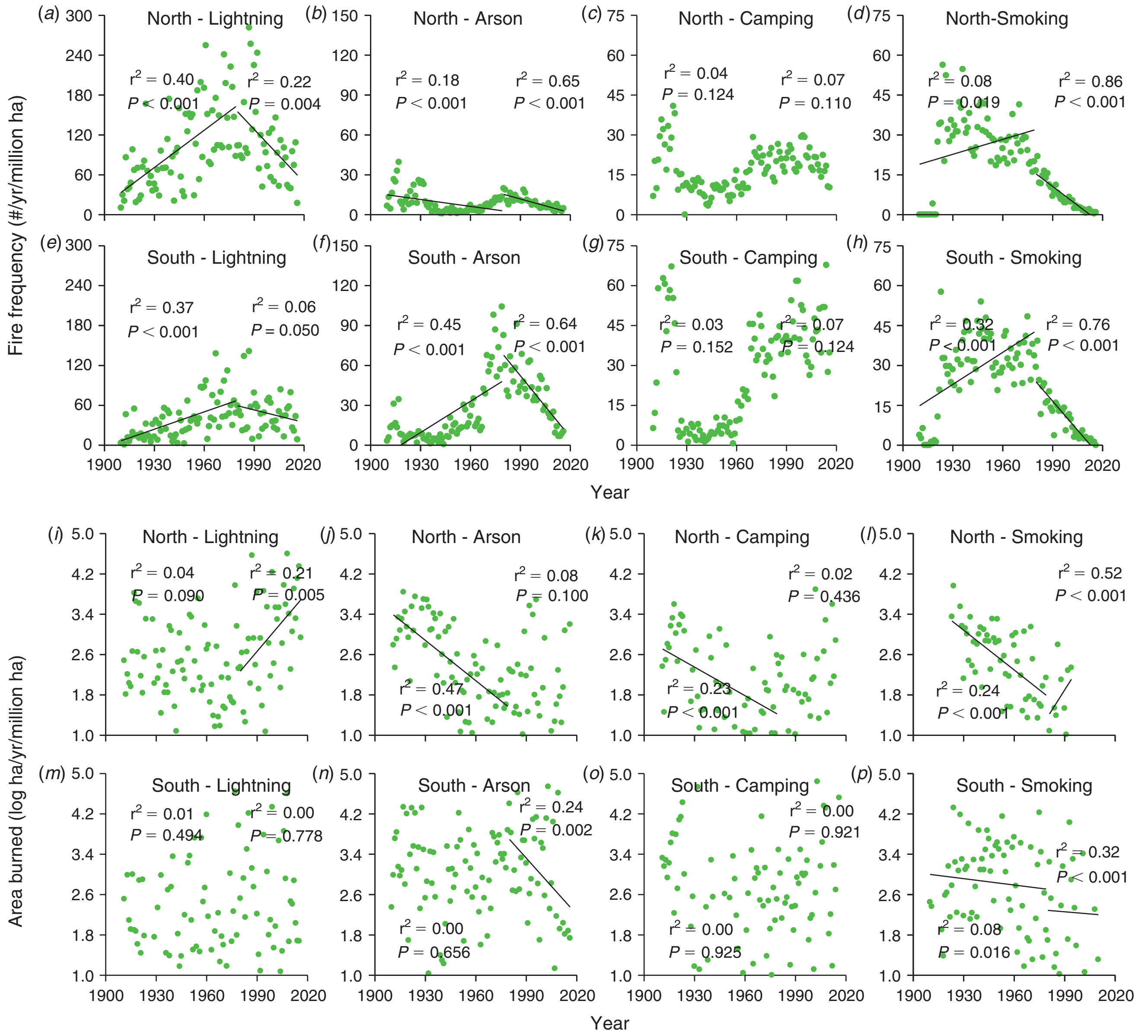

Fig. 9. Ignition sources recorded throughout the period 1910–2016 on USFS protected lands by frequency (*a*–*h*) and area burned (*i*–*p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions from 1910 to 1979 and from 1980 to 2016; note the change in scale between lightning and anthropogenic sources for fire frequency.

Climate relationships to ignitions

Based on the sharp change in ignition patterns through the period of record, it is critical to understand to what extent climate variation may have played a role. Considering the marked changes in climate over the period of this study (illustrated as decadal anomalies in seasonal temperature and precipitation in Fig S3), it is reasonable to expect climate variation has some explanatory value in understanding changes in ignition sources.

Multi-variate models used mean temperature and total precipitation for winter, spring, summer and autumn plus the prior-year winter–spring precipitation. Presented in Table 4 are those ignition sources with a significant $P < 0.05$ model. Not all ignition sources exhibited a significant climate mode and the models determining fire frequency were not the same as those for area burned. We note that, before 1980, the biggest driver of debris and railroad fires was prior-year precipitation. Since 1980, there was a negative relationship with summer temperature for debris burning, playing with fire, smoking and railroad fires. In the south, where lightning-ignited fires were uncommon (Fig. 2*a*), before 1980, they were strongly associated with high summer temperatures and autumn precipitation.

Total area burned on Cal Fire lands in the north before 1980 was significantly tied to low winter precipitation and high spring temperatures. In the south, area burned by both arson and powerlines was significantly tied to climate variation.

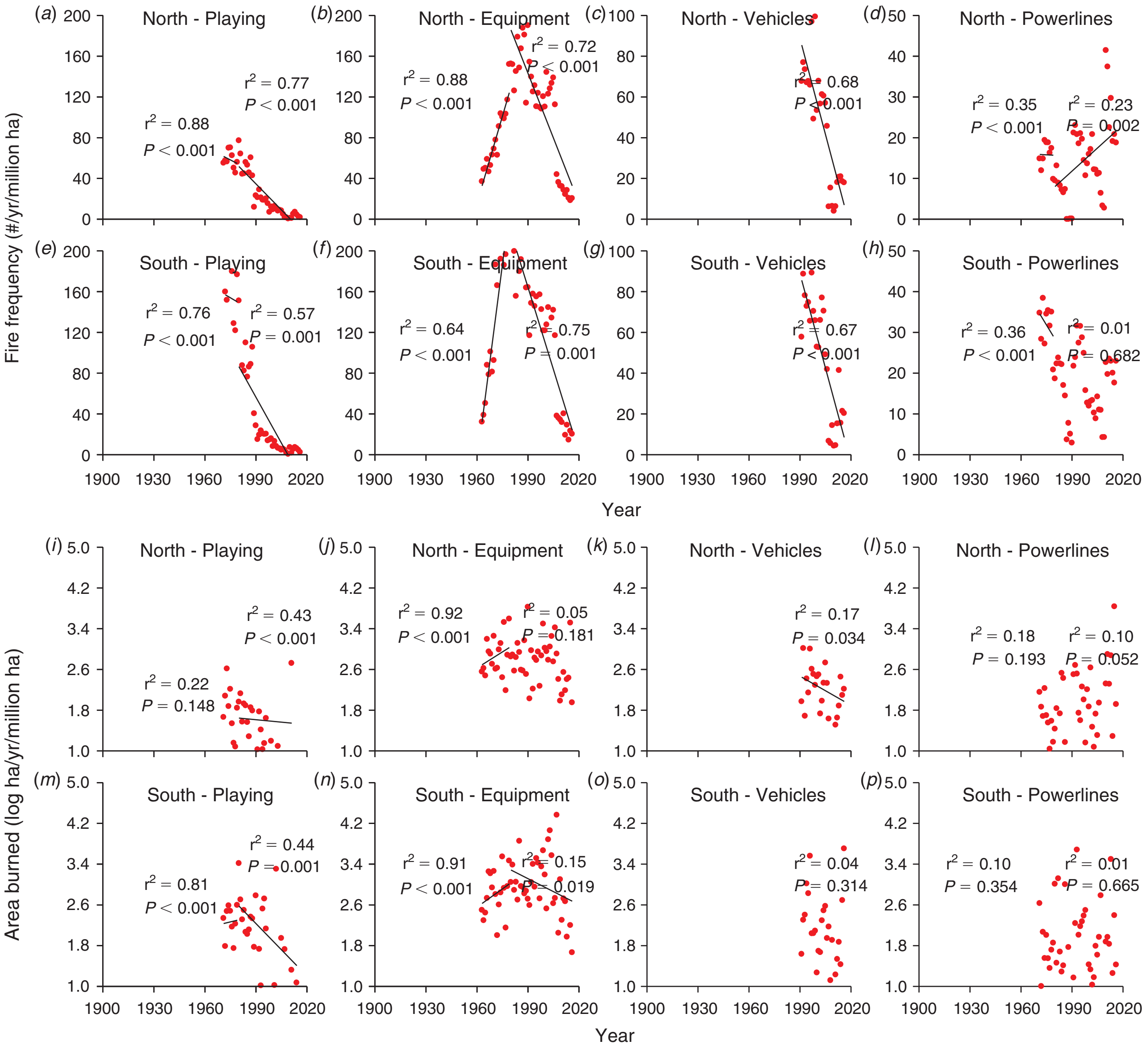

Fig. 10. Ignition sources variously recorded throughout the period 1910–2016 on USFS lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions before 1980 and 1980–2016; note the change in scale for fire frequency.

On USFS lands, total number of fires and area burned in both the north and south exhibited many significant climate models (Table 5). However, the patterns are complicated and not easily summarised as the specific climate models varied both spatially and temporally, as well as being different for different ignition sources.

For example, lightning fire frequency and area burned in both the north and south and before and after 1980 were significantly associated with climate variation, but, before 1980 in the north, the frequency of lightning fires was positively associated with summer precipitation, but the area burned was negatively associated with summer precipitation. After 1980 in the north, the model switched and there was a very strong effect of prior-year precipitation and summer temperature.

Since 1980, one of the strongest climate variables affecting both frequency and area burned was a positive relationship with prior-year precipitation. Although higher summer temperatures were associated with increased frequency of arson fires, it was noteworthy that lower summer temperatures were associated with an increased incidence of smoking, camping and children playing with fire in the north. Frequency of powerline fires were associated with elevated autumn temperatures and higher prior-year precipitation.

Cal Fire area-burned data were also presented by vegetation type and showed that in the north, forest and shrubland area

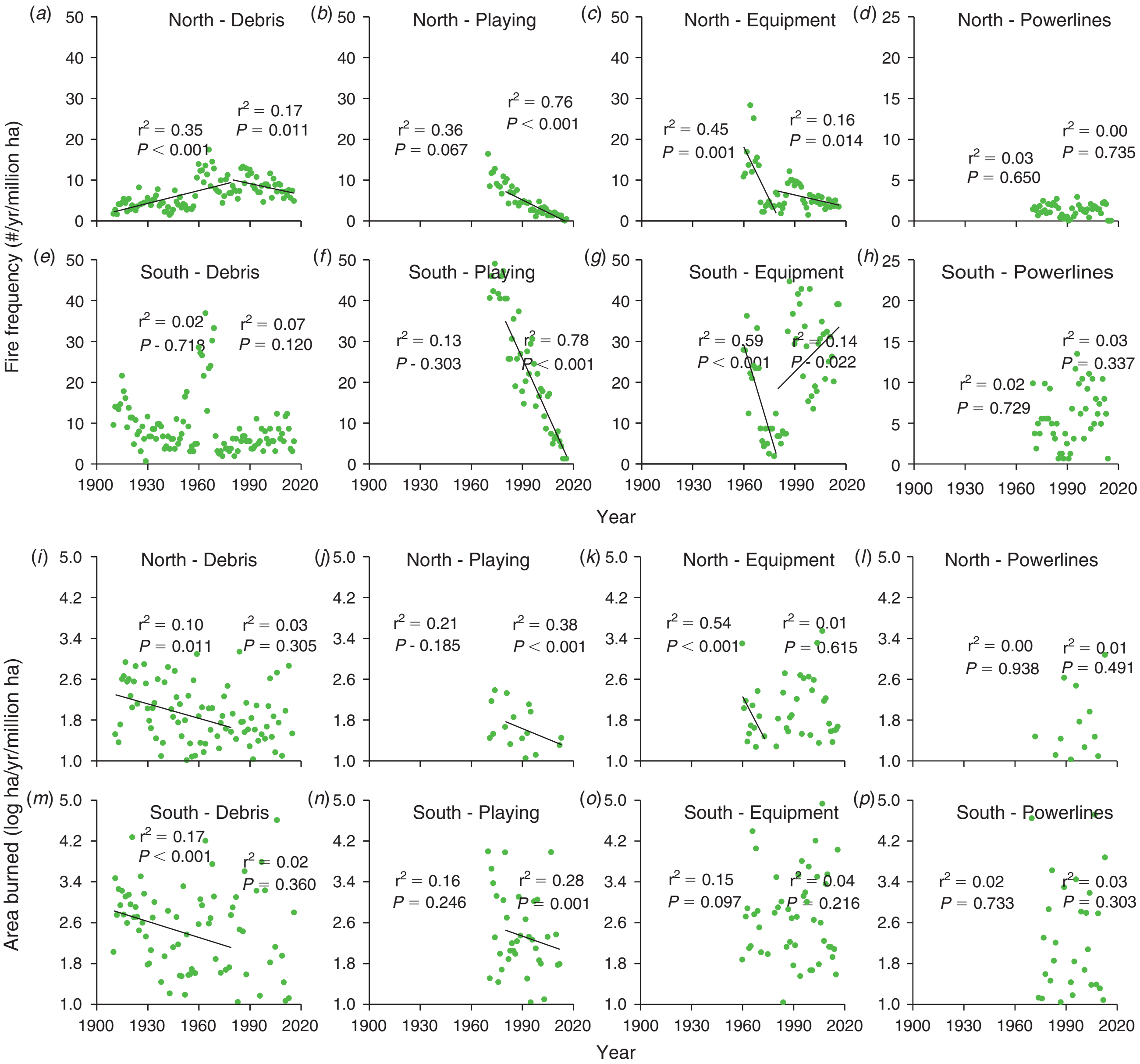

Fig. 11. Ignition sources variously recorded throughout the period 1910–2016 on USFS lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions prior to 1980 and 1980-2016; note the change in scale for fire frequency.

burned had significant relationships with climate variation before 1980 but not afterwards (Table 6). In the south, grasslands had a significant climate model after 1980.

Discussion

Particularly striking about California ignitions is the steady increase in number of fires since the early 1900s until a peak *c.* 1980, followed by a marked drop in fire frequency up to 2016. This happened on both lower-elevation Cal Fire-protected lands and higher-elevation USFS lands, and in most climate divisions (Fig. 6). Despite a significant increase in fires during the first three-quarters of the 20th century, there were marked departures from this linear model, with accelerated ignitions during the 1920s and 1930s and a marked drop in the 1950s and 1960s (Fig. 7). Climate may have had some role in these changes since the former decade was drier and the latter was wetter (Fig S3) and during this period total fires on USFS lands did have a significant climate model largely driven by high summer temperatures and low summer precipitation (Table 4). What is particularly striking is the disconnect between number of ignitions and area burned; during the first three-quarters of the 20th century, although ignitions were increasing, area burned was steadily decreasing through much of the state.

In contrast, since 1980, ignitions have steadily declined, yet area burned has either not changed or, in some northern parts of the state, has increased. In short, the number of ignitions does not directly explain area burned. However, as discussed below, this conclusion does not apply to individual ignition sources, and, in this respect, there may be particular sources worth targeting for fire management purposes.

Factors that may have played a role in these historical patterns of ignitions and area burned are changes in: population density, infrastructure development, fire-prevention success, fire-suppression effectiveness, vegetation-management practices, climate, and possibly record-keeping accuracy. The drivers behind changes in ignition patterns are quite possibly different for different sources, different parts of the state and at different times. First, we consider the patterns for natural lightning-ignited *v.* human-caused wildfires.

Lightning-ignited fires

In California, natural lightning-ignited fires decreased from north to south and from high (USFS) to low (Cal Fire) elevation (Fig. 2, 4). On USFS lands, Lassen and Plumas forests in the north-east averaged over 150 lightning-ignited fires per year per million hectares, whereas the coastal Los Padres Forest averaged one-tenth as many (Table S5). In northern California forests, such as the Klamath, Lassen, Modoc, Inyo-Mono and Sequoia, lightning accounted for the majority of fires, and on many others it is about equally important as human-ignited fires (Table 3). Notable exceptions are the coastal Los Padres and southern California Angeles, Cleveland and San Bernardino forests, where lightning accounted for less than one-quarter of all fires. In contrast, on lower-elevation Cal Fire-protected lands, lightning accounted for less than 10% of all fires in most counties, and in coastal areas from Sonoma County south, typically $<1\%$ of all ignitions (Table 2). These patterns closely follow the distribution of lightning strikes in the state (van Wagtendonk and Cayan 2008). In general, lightning-ignited fires in coastal California were substantially less than that observed over much of the USA (Prestemon *et al.* 2013). Thus, the report that extreme fire events driven by high winds are commonly due to human ignitions and not lightning (Abatzoglou *et al.* 2018) should not be too surprising in California because these extreme winds are largely restricted to coastal areas in southern California and the San Francisco Bay Area.

Area burned by lightning-ignited fires approximately paralleled these geographical patterns with a couple noteworthy exceptions. In the northern and central part of the state, more coastal USFS forests had low lightning-ignited fire frequency but these accounted for a substantial amount of area burned, although this was less evident on lower-elevation Cal Fire lands (Fig. 2–5). For interior forests where lightning is the dominant ignition source, fires have proven to be reasonably easy to extinguish, in large part because they typically occur in forests with a low-intensity surface-fire regime, and during lightning-storm weather conditions (van Wagtendonk and Cayan 2008), are conducive to rapid fire control. As a consequence, less than 1% of these forest lands burn each year and these landscapes have a fire-rotation interval of 100–200 years (Table 1), very different with what is believed to be the natural fire interval (Stephens 2005; Van de Water and Safford 2011; Safford and Van de Water 2014). In coastal central and southern California, lightning accounts for very little area burned, in large part because lightning strikes are very low, but also because human-ignited fires often occur under weather conditions more conducive to fire spread, contributing to a shorter fire-rotation interval, e.g. 40–50 years on southern California forest lands (Table 1).

Table 4. Significant climate models ($P < 0.05$) explaining frequency of ignitions and area burned for the period <1980 and ≥1980 for Cal Fire protected lands

Models tested mean temperature and total precipitation in winter, spring, summer and autumn, and prior year winter + spring precipitation (<1PptWinSpr)

Variable	Era	Adjusted R^2	P	Model
Frequency in North				
Debris	<1980	0.18	0.021	<1PptWinSpr
Debris	≥1980	0.24	0.050	- TempSum
Playing	≥1980	0.27	0.035	- TempSum + TempWin
Smoking	≥1980	0.32	0.016	- TempSum
Railroad	<1980	0.18	0.020	<1PptWinSpr + PptSpr
Railroad	≥1980	0.25	0.045	- TempSum + TempWin
Frequency in South				
Lightning	<1980	0.40	0.001	TempSum + PptAut
Debris	<1980	0.18	0.021	<1PptWinSpr – PptAut
Area in North:				
Total	<1980	0.23	0.007	- PptWin + TempSpr
Area in South:				
Arson	≥1980	0.25	0.045	- TempWin
Powerlines	<1980	0.99	0.046	- TempSum – PptSpr – PptAut
Powerlines	≥1980	0.24	0.050	- TempAut

Lightning fires have increased markedly over most of the 20th century on both Cal Fire and USFS lands, in the north and south (Fig. 8, 9). A possible explanation for this pattern is improvement in detection, as lightning-ignited fires often occur in remote areas and detection may have been less effective in the early part of the 20th century and improved in the latter part of the 20th century. However, there is there is reason to retain some level of scepticism that this pattern is an artefact of reporting (see the 'Methods' section), primarily because state and federal agencies have put in extraordinary effort at fire detection since the early 1900s (Clar 1969; Cermak 2005), including hundreds of thousands of kilometres of wilderness aircraft fire patrols beginning in 1919 (Cermak 1991).

Another reason for not simply dismissing historical patterns as an artefact of reporting is that there are physical factors that could account for such changes. For example, one potential factor for a 20th-century rise in lightning fires could be changes in forest fuel structure, which has been shown to affect lightning-ignited fire frequency on other landscapes (Krawchuk *et al.* 2006). In California, this would be expected based on the marked drop in area burned following the burning peak in the 1920s – for both Cal Fire and USFS lands, three times more area burned in that decade relative to the decadal average burned from 1950 to 1980 (Keeley and Syphard 2017). Thus, during the mid-20th century there was potentially an increase in fuels that

Table 5. Significant climate models ($P < 0.05$) explaining frequency of ignitions and area burned for the period <1980 and >1980 for USFS protected lands

Models tested mean temperature and total precipitation in winter, spring, summer and autumn, and prior year winter + spring precipitation (<1PptWinSpr)

Variable	Era	Adjusted R^2	P	Model
Frequency in North				
Total	<1980	0.27	0.001	TempSum – PptSum + PptAut
Lightning	<1980	0.21	0.005	TempSum + PptSum + PptAut
Arson	<1980	0.13	0.040	–PptAut – PptSpr
Arson	≥ 1980	0.28	0.030	TempSum
Smoking	≥ 1980	0.46	0.001	–TempSum – PptSum
Debris	≥ 1980	0.43	0.002	– PptWin – TempAut – PptSum
Camping	≥ 1980	0.26	0.039	–TempSum
Playing	≥ 1980	0.47	0.001	–TempSum – PptSum
Railroad	< 1980	0.28	0.007	PptAut
Railroad	≥ 1980	0.32	0.017	–PptWin + PptSpr
Equipment	≥ 1980	0.32	0.016	–TempSum – PptWin – PptSum
Powerlines	≥ 1980	0.35	0.010	<1PptWinSpr
Frequency in South				
Total	≥ 1980	0.29	0.026	Ppt–1WinSpr
Lightning	<1980	0.18	0.012	TempSum + PptAut
Powerlines	≥ 1980	0.28	0.029	TempAut + PptWin
Area in North:				
Total	<1980	0.35	<0.001	–PptWinSpr – PptSum
Total	≥ 1980	0.63	<0.001	<1PptWinSpr + TempSum – PptAut
Lighting	<1980	0.17	0.018	–PptSum
Lighting	≥ 1980	0.64	<0.001	<1PptWinSpr + TempSum
Arson	<1980	0.38	<0.001	–PptWin – PptAut – TempAut – TempWin
Debris	<1980	0.15	0.031	– PptWin –PptAut
Smoking	<1980	0.16	0.022	TempAut + TempSpr
Playing	≥ 1980	0.34	0.010	–TempSum –TempAut
Equipment	≥ 1980	0.28	0.030	<1PptWinSpr
Vehicles	≥ 1980	0.37	0.007	<1PptWinSpr
Powerlines	≥ 1980	0.47	0.001	–TempWin + <1PptWinSpr
Area in South				
Total	<1980	0.20	0.006	– PptAut – PptWin
Total	≥ 1980	0.24	0.048	TempSum – TempWin
Lighting	≥ 1980	0.25	0.043	–TempSpr – PptSpr

may have contributed to a greater chance of lightning strikes igniting fires.

Changes in reporting standards is also not likely to explain the pattern of decreased lightning-ignited fires from 1980 to 2016 (Fig. 8, 9). On Cal Fire and southern USFS lands, this did not produce any significant trend in area burned by this fire source, although northern California (including the Sierra Nevada) USFS lands showed an increase in area burned by this source, a pattern also seen in the northern Rocky Mountains (Stephens 2005). Climate is strongly implicated in this change (Table 5) as two-thirds of the annual variation in area burned by lightning-ignited fires is explained by a combination of prior-year precipitation and current-year summer temperature. Although the latter variable most likely affects fuel moisture at the time of fire, the former is thought to increase fires through its effect on herbaceous fuels in the following year (Littell *et al.* 2009; Crimmin and Comrie 2011; Keeley and Syphard 2016). A similar conclusion was drawn by Knapp (1995) for the climatic control of lightning-ignited fires in the Intermountain West.

The future projections are that lightning strikes will increase 50% over this century (Romps *et al.* 2014), but this is not easily translated into future lightning fire risks in California. Some landscapes, such as forests in the north-eastern part of the state, may already be saturated with lightning ignitions and coastal landscapes have very few strikes and thus a 50% increase may not significantly change lightning-ignited fire risk. In addition, changes in lightning-strike frequency will have very different impacts dependent on which season those changes occur in as well the state of future fuel conditions.

Human-ignition sources

The fact that in all climate divisions, the number of ignitions is not a monotonic function of time over the past 100 years suggests a complex model of how ignition sources affect burning activity. Prestemon *et al.* (2013) presented a conceptual model of biophysical, social, prevention and management drivers in controlling human ignition sources. These factors are not static, as illustrated by Guyette *et al.*'s (2002) dynamic anthropogenic fire regime model for the Ozark Mountains in Missouri. In their model, they found that the landscape changed over time from being ignition limited to fuel limited followed by stages dependent on fuel fragmentation and ultimately a culture-dependent stage. These temporal changes in drivers could explain a lot about the temporal changes observed in California ignitions.

It may be that the marked rise in ignitions during the first three-quarters of the 20th century in California is the result of increasing effectiveness of reporting, but this seems unlikely because the steepest rise in ignitions was in the latter part of the 20th century, i.e. 1960–1980 (Fig. 6). The 20th-century increase in ignitions was very strongly correlated with population growth (Tables 2, 3), but we believe that more is involved than just increasing population growth translates into more fires. This early–mid-20th-century growth spurt was correlated with road expansion throughout the state, which was bringing more people in contact with highly flammable fuels (Show 1945; Lockmann 1981; Keeley and Fotheringham 2003). In addition, because of migration patterns, growth included populations from less fire-prone parts of the US, and thus a population relatively naïve about the dangers of fire use in wildland areas (e.g. Zahn 1944; Show 1945). In addition, fire-prevention education was in its infancy and the population was slow to recognise their role in the fire problem. Included too is the widespread use of outdoor equipment that contributed to the sharpest rise in fires on Cal Fire landscapes between 1960 and 1980 (Fig. 10). On top of that, development of fire-response actions were far from perfect (Clar 1969). Also, during the period from 1940 to 1970 the State Resources Agency was actively involved in promoting burning of chaparral shrublands for the express purpose of type-converting native shrublands to exotic grasslands of greater economic value as rangelands (unpublished records in the State Archives). Indeed, the state was funding type conversion of private lands as this was perceived as a fire hazard reduction strategy, with an economic incentive of increasing rangeland.

Not directly related to changing demography is the significant decline in fires in the last several decades – while populations continued to grow after 1980, fire frequency was negatively related to population density (Tables 2, 3). This is consistent with the pattern of fire activity peaking under intermediate population density (Syphard *et al.* 2009). That is, the relationship between population density and ignition frequency is likely a function of finer-scale spatial processes regulating the degree of interspersion between development patterns and wildland vegetation. In other words, as both population and development expand into wildland areas, ignitions increase up to a point at which the area of development, or, impervious surface, far exceeds the area of wildland, and at that point, the relationship becomes negative. However, the timing of this switch varies with regions, e.g. south-east Australia continues to see a positive relationship in between population density and fire frequency (Collins *et al.* 2015).

Thus, these broad-scale patterns observed across the state may be reflecting macro-scale urbanisation trends over time. Massive areas of wildland vegetation have been developed and fragmented in California over the course of the 20th century (Hammer *et al.* 2007; Syphard *et al.* 2017), and the resulting extent and fragmentation of fuel surely has affected ignition trends and area burned. It may therefore be important to monitor areas that are becoming newly developed, as these may be the most fire-prone areas on the landscape, with sufficient people to start fires and wildland vegetation to carry fires (Radeloff *et al.* 2018).

Patterns such as these have been interpreted as indicating fires are not limited by human ignitions (Knorr *et al.* 2013; Moritz and Knowles 2016). This has prompted some to conclude that fire activity during the last several decades has been driven largely by climate change (Westerling *et al.* 2011). It is apparent that in mid–high-elevation forests in California seasonal climate variation has been an important factor in determining annual area burned (Table 5) and that global warming may exacerbate the fire situation on those landscapes (Keeley and Syphard 2016). However, in coastal California, climates are capable of generating large fire events most years (Keeley and Syphard 2017), with one exception being years with anomalous late spring rains (e.g. Dennison *et al.* 2008). In these coastal locations, big fire events occur during extreme wind events, however, these Santa Ana, Diablo or North Wind events occur predictably every year and yet big fires occur at unpredictable intervals, being determined by the coincidence of a human ignition with a wind event (Keeley and Zedler 2009).

During the first two-thirds of the 20th century more people translated into more fires, and greater fire activity. However, in recent decades the relationship between human population growth and fire activity has become more complex, nicely captured in Prestemon *et al.*'s (2013) model. In California in recent decades, increasing population density has increased the probability of ignitions under the worst weather conditions, either intentionally by arson for example or accidentally by powerline failures. This appears to be a widely seen situation throughout the USA where human-related ignitions are associated with conditions resulting in large wildfires (Nagy *et al.* 2018).

Decreasing ignitions over the last 4 decades is potentially reflective of increasing efficiency of fire prevention. However, it also likely reflects changes in human infrastructure; new roads in this era were tied to development projects that required demonstration of adequate fire response capabilities. In addition, an important factor behind declining ignitions is quite possibly the emergence of the California Fire Safe Council in the early 1990s (http://www.cafiresafecouncil.org/about-us/, accessed 11 August 2016), which made significant contributions to fire-safety education.

Arson has long been a major source of intentional human ignitions on both Cal Fire (Fig. 8) and USFS (Fig. 9) lands and on both jurisdictions arson ignitions increased during the first part of the 20th century and then dropped markedly in recent decades. Arson fires have always been one of the largest sources of area burned, although it was much higher in the early 20th century than in recent decades. This category comprises ignitions motivated for diverse reasons. Early in the 20th century, these were termed incendiary fires and were often motivated by goals of maintaining traditional burning practices (Coughlan 2016). As such practices became less socially (and legally) acceptable, the category was labelled arson fires. Arson fires exhibit interesting distribution patterns. On low-elevation Cal Fire lands they are a major ignition source in the northern Sierra Nevada (Fig. 2, 3) but on USFS lands they dominate in the southern part of the state (Fig. 4, 5), suggesting a need for more concentrated anti-arson prevention measures in those regions. This clustering of arson fires has been observed in parts of the Mediterranean basin and has prompted an early alert system (Gonzalez-Olabarria *et al.* 2012).

One of the real success stories illustrated by these data is the marked decline since 1980 in frequency and area burned by arson fires on both Cal Fire and USFS lands (Fig. 8, 9). This reduction in arson fires is a pattern observed for other parts of the country (Prestemon *et al.* 2013). In California, this may be attributed to better neighbourhood-watch programs, which include patrols during red-flag warnings, but broadcasted fire prevention messaging may also be a factor. Another factor may be increased penalties for arson; e.g. the person found guilty of starting the 2003 Old Fire in southern California was sentenced to death, as was the arson convicted of the 2006 Esperanza Fire (Gabbert 2012).

Another source of burning on both Cal Fire and USFS lands has been smoking. This was a significant cause in the earliest records, recording even ignitions from cigarettes thrown from open cockpit planes. Throughout the first half of the 20th century, smoking was a major cause of wildfires and was the focus of one of the earliest fire prevention campaigns. In 1942, over 100 000 'fag bags' were distributed to persons entering the Angeles National Forest, bright red bags designed to carry smoking materials and with a prominent fire-safety reminder stamped on them (Show 1945). The late 20th-century decline in smoking caused such fires to decline at a much faster rate (Fig. 8, 9) than due to simple reduction in smoking (Prestemon *et al.* 2013). Reductions in smoking-caused fires are due to a combination of less smoking, more fire-resistant cigarettes, and improved fire prevention (Butry *et al.* 2014).

Children playing with fire has been an important ignition source and it has exhibited a marked decline in frequency in recent decades on both Cal Fire (Fig. 10) and USFS (Fig. 11) lands. Increased fire-prevention effectiveness through better messaging and development of childproof lighters are potential factors. Perhaps stricter ordinances in power-tool usage in wildlands under red-flag warnings may be a factor as well as requirements for more effective spark arrestors.

Vehicles present another accidental fire source that has declined sharply on Cal Fire protected lands. Catalytic converters, which were first required in 1975, are thought to have been a significant ignition factor (Bertagna 1999; http://www.cbs8.com/story/35871110/how-a-cars-catalytic-converter-can-spark-a-massive-fire, accessed 1 June 2017) when they overheated, igniting roadside vegetation. However, modern vehicles have warning lights when they overheat, which has the potential for reducing vehicle fires and could be a factor in the decline of such fires. Another factor potentially reducing vehicle fires is improved vegetation treatment along roadside verges.

Electrical powerlines have been reported ignition sources since 1905 (Show 1945). In the present study, this source of ignition stands out in that, unlike many other human ignition sources, powerline fires and area burned by this ignition source have not declined in recent decades (Fig. 10, 11). Although powerlines do not account for many fires, they often account for substantial area burned, and some of substantial size (Keeley *et al.* 2009; Syphard and Keeley 2015). One reason that powerline fires are so dangerous is that they commonly occur during high winds and there are three effects of these winds: tree contact, line arcing, and metal fatigue resulting in lines down (Mitchell 2009). These winds create extremely dangerous fires capable of rapid spread over long distances. This is a serious problem in other regions such as southern Australia where it was found that electricity-caused wildfires are over-represented when fire danger is high (Miller *et al.* 2017) and similar conclusions were drawn by Ganteaume and Guerra (2018). Powerline distribution tends to follow roads and this may be part of the reason burning patterns are closely correlated with road distribution in southern California (Faivre *et al.* 2014). Also, they burn larger areas than fires ignited by most other causes and are associated with more significant impacts on lives and property (Collins *et al.* 2016).

Because these powerline failures typically occur in known extreme-wind corridors, it has been proposed that wiring these corridors with underground power could minimise the problem (Keeley *et al.* 2009). However, utility companies have shown a reluctance to accept this solution. One company in southern California, San Diego Gas & Electric, has opted for an alternative plan whereby they monitor weather throughout the county and use these data to shut down portions of the power grid when that area experiences high winds (https://www.cnbc.com/2017/12/13/southern-california-utilities-shut-off-power-to-prevent-wildfires.html, accessed 1 June 2017). In initial attempts to deal with fire hazards there have been significant complaints about the process of shutting down the power grid as it creates many unanticipated problems (https://www.nbcsandiego.com/news/local/Supervisor-Demands-State-Investigation-of-Power-Shut-offs-During-Lilac-Fire-467782743.html, accessed 1 June 2017). Other approaches have been to replace wooden poles with metal poles, however, this seems to be a distraction since wooden poles have not been blamed for starting fires (https://www.voiceofsandiego.org/topics/science-environment/sdge-environmentalists-are-at-opposite-poles-on-one-fire-prevention-method/, accessed 1 June 2017).

Climate change impacts on anthropogenic ignitions is rather difficult to parse out because climate affects both fire behaviour and human behaviour. For example, in forests, fire activity is enhanced by higher spring and summer temperatures through effects on fuel moisture (Westerling *et al.* 2006; Littell *et al.* 2009; Keeley and Syphard 2017). However, in the present study, fires started by camping, children playing with fire, and smoking were negatively correlated with summer temperatures, suggesting the possibility that cooler temperatures may have encouraged greater outdoor activity.

In general, climate variation exhibited a closer relationship with fire activity in the higher-elevation USFS lands in the northern part of the state, consistent with the flammability limited fire regimes in these regions (Keeley and Syphard 2017). Of particular significance is the importance of prior-year rainfall as this is well known to be due to increased fuel production in grass dominated ecosystems (Crimmins and Comrie 2004; Keeley and Syphard 2016). We found that this climate variable was strongly tied to powerline fires, suggesting perhaps that fine flashy fuels may be a marked hazard in association with powerlines and may be an additional management target.

Conclusions

Throughout California, fire frequency has increased steadily until a peak *c.* 1980, followed by a marked drop to the present. There was not a tight link between frequency of ignition sources and area burned by those sources and the relationships changed over time. Natural lightning-ignited fires decreased from north to south and from high to low elevation. Throughout most of the state human-caused fires dominated the record and were positively correlated with population density for the first two-thirds of the record, but this relationship reversed in recent decades. Most ignition sources have declined markedly in recent decades with one notable exception, powerline ignitions. One important avenue for future fire hazard reduction will be consideration of solutions to reduce this source of dangerous fires.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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EFFECT OF STAND WIDTH AND ADJACENT HABITAT ON BREEDING BIRD COMMUNITIES IN BOTTOMLAND HARDWOODS

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Abstract: Bottomland hardwood forests support an abundant and diverse avifauna, but area of this forest type has been reduced, and current projections indicate continued declines. We compared breeding bird abundance indices and species richness among bottomland hardwood stands ranging in width from <50 m to >1,000 m and enclosed by forested habitat. We also compared avian abundance indices and richness among stands enclosed by pine (*Pinus* spp.) forest and stands enclosed by field-scrub habitats. Total species richness and species richness of Neotropical migrants were associated positively ($P < 0.05$) with stand width in all years. Total bird counts differed among width classes in all years, with counts generally greatest in width classes <50 m and >1,000 m. Counts of Neotropical migrants differed ($P < 0.05$) among width classes in 1993 and 1995 and followed the same general trend as total bird count. Acadian flycatcher (*Empidonax virescens*), blue-gray gnatcatcher (*Polioptila caerulea*), and red-eyed vireo (*Vireo olivaceous*) were more abundant in smaller width classes ($P < 0.05$), whereas the opposite was true for white-eyed vireo (*Vireo griseus*) and northern parula (*Parula americana*). Probability of occurrence was associated positively ($P < 0.05$) with stand width for 12 species and negatively with stand width for 1 species. Total bird count and the counts of blue-gray gnatcatcher in 1995 and of northern cardinal (*Cardinalis cardinalis*) in both years were higher in field-enclosed stands (FES) than in pine-enclosed stands (PES). No species analyzed was more abundant in PES than in FES. We conclude that even narrow riparian zones can support an abundant and diverse avifauna, but that conservation of wide (≥500 m) riparian zones is necessary to maintain the complete avian community characteristic of bottomland hardwood forests in South Carolina.

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Key words: bottomland hardwoods, breeding birds, landscape management, minimum area requirement, South Carolina, species richness.

Bottomland hardwood forests (hereafter, bottomland hardwoods) are seasonally inundated floodplain forests dominated by oak (*Quercus* spp.), gum (*Nyssa* spp.), and cypress (*Taxodium* spp.), and they support an abundant and diverse avifauna (Dickson 1978, Hamel 1989) that includes approximately 70 breeding species (Pashley and Barrow 1993). Furthermore, up to 65% of the species at any given site may be Neotropical migrants (Pashley and Barrow 1993), including many forest interior species experiencing population declines (Askins et al. 1990, Peterjohn et al. 1995). However, the pre-Columbian (15th century) extent of bottomland hardwoods has undergone considerable reduction, largely because of agricultural conversion and construction of hydroelectric reservoirs (Harris and Gosselink 1990). Approximately 50% of the area existing in 1940 had been lost by 1985 (Harris and Gosselink 1990).

Currently, bottomland hardwoods are an important source of hardwood lumber, and demands on these forests likely will increase. Hardwood timber removals by the year 2030 are projected to have increased by 64% over 1984 levels (U.S. Forest Service 1988). During the same period, acreage of bottomland hardwoods in the Southeast is projected to decrease from about 5.5 million ha to about 4.7 million ha, a decline of 15% (U.S. Forest Service 1988). Much of the remaining bottomland hardwoods exist in narrow (<50 m) drainages and streamside management zones. Although narrow stands may contain substantial area because of their length, their utility to forest birds may be compromised because of a lack of interior habitat conditions.

Species richness and abundance of forest bird communities are associated positively with

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stand area (Galli et al. 1976, Whitcomb et al. 1981, Blake and Karr 1987). However, recent research attention has focused on width of riparian zones rather than area (Keller et al. 1993, Darveau et al. 1995, Dickson et al. 1995, Thurmond et al. 1995, Hodges and Krementz 1996) because of difficulties associated with defining area when riparian zones are interconnected. Further, species richness of some avian guilds is correlated positively with riparian zone width (Keller et al. 1993). However, most research on the effect of width on bird communities in Southeastern bottomland hardwoods has been restricted to narrow stands surrounded by young pine plantations. Although these studies are applicable in most forest management contexts, research addressing the range of stand widths encompassed in bottomland hardwood systems is necessary to assess the habitat requirements of area-sensitive species. We compared avian abundance indices and species richness among bottomland hardwood stands of various widths (<50 to >1,000 m) that were surrounded by closed-canopy pine (*Pinus taedu, P. palustris*) forest. We also compared abundance indices and species richness among stands enclosed by pine forest and stands enclosed by-field-scrub habitats.

STUDY AREA

The study was conducted on the U.S. Department of Energy's Savannah River Site, a 78,000-ha tract in Aiken, Bamwell, and Allendale counties, and on private property in Allendale County. This region lies in the Upper Coastal Plain of westcentral South Carolina and is bounded on the west by the Savannah River. Topography is characterized by gently rolling ridges, broad flat regions, and interspersed stream courses (Soil Survey Staff 1977). Elevation ranges from <25 m at the Savannah River to 80 m at first-order streams. Bottomland hardwoods are found along stream courses and may be flooded seasonally, usually during late winter-early spring. Dominant canopy species of bottomland hardwoods include sweetgum (*Liquidambar styraciflua*), swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), laurel oak (Q. *laurifolia*), overcup oak (*Q. lyrata*), and cherrybark oak (Q. *falcata* var. *paegodifolia*). The midstory is composed of American holly (*Ilex opaca*), sweet bay (*Magnolia virginiana*), and red bay (*Persea borbonia*). Switchcane (*Arundinaria gigantea*) and dog hobble (*Leucothoe axillaris*) dominate the shrub layer, and Christmas fern (*Polystichum acrostychoides*) and netted-chain fern (*Woodwardia areolata*) are the dominant ground cover (Workman and McLeod 1990).

METHODS

We used a completely randomized design with repeated measures across years. We selected 4 replicates of bottomland hardwood stands in each of 5 width classes: <50 m, 50–150 m, 150–300 m, 300–1,000 m, and >1,000 m. We used width classes rather than size classes because the forested watershed in which we worked was nearly continuous throughout the study area. Thus, first-order streams (narrow floodplains) were continuous with second- and third-order streams (wider floodplains), which made delineation of stand boundaries (and therefore determination of area) impossible. We believe that width was a good index to area because wider stands contained more area; hence, width was more useful in a forest management context. We used aerial photographs to locate sites from which we measured width of the entire floodplain, including both sides of a creek or drainage. The 2 largest sites were located on the Savannah River floodplain; width of these sites refers to 1 side only because the Savannah River constituted a significant break in the canopy (≥100 m) and likely served as an effective barrier to cross-stream movement of birds (Hodges and Krementz 1996). All sites were on different creeks, except those on the Savannah River, which were separated by >1 km to ensure independence of replicates. We selected sites characterized by Zone III, IV, and V vegetation types (Wharton et al. 1982) in an attempt to control for differences in vegetation among sites. Larger sites encompassed a greater diversity of habitat types, and a few plots slightly overlapped communities of baldcypress (*Taxodium distichum*)-water tupelo (*Nyssa aquatica*).

We measured habitat characteristics in 5 circular 0.04-ha plots (James and Shugart 1970) per stand in 1994. We measured canopy coverage with a densiometer and vegetation profile with a 3-m density board (Noon 1981); each measurement was from the cardinal points on the perimeter of each plot. We recorded species and size class of all trees in the plot (James and Shugart 1970). For analysis, we selected vegetation profile (PROFILE) as a measure of understory structure, basal area of hardwood pole timber (POLE), which we defined as hardwood stems 8-23 cm dbh and which provided a measure of midstory structure, canopy coverage (CANOPY), and basal area of hardwood sawtimber (SAW), which we defined as hardwood stems >23 cm diameter at breast height (dbh). This approach minimized the number of vegetation variables, yet provided measures of structure for 3 primary habitat layers and also included 2 variables commonly inventoried by forest managers. We subjected these data to principle components analysis (PCA; PROC PRINCOMP; SAS Institute 1990) to reduce the number of habitat variables included in the bird-habitat analyses (Hodges and Krementz 1996). We selected for inclusion in analyses of bird-habitat relations only those principal components (PC) that had eigenvectors ≥1.0. We used I-way analysis of variance (ANOVA; PROC GLM; SAS Institute 1990) to compare PC scores among width classes.

We used 5-min, fixed-radius (50 m) point counts (Hutto et al. 1986, Ralph et al. 1995, Smith et al. 1995) to sample the bird population for each stand. Within each stand, 2 points were spaced 200 m apart along a transect centered within each corridor and oriented parallel to the general bearing of the drainage. To aid in estimation of distance, we placed high-visibility flagging tape on trees at the perimeter of each plot in each of the cardinal directions. We visited each stand at approximately equal intervals 3 times per year between mid-May and late June 1993-95, once each during early, middle, and late morning. This design yielded 72 point counts in each width class during the study (4 stands X 2 points X 3 visits X 3 years). Smith et al. (1995) suggested 50 counts per factor level were sufficient to detect most biologically meaningful variation.

We conducted counts from sunrise to 3.5 hr after sunrise, except during periods of high wind or rain (Ralph et al. 1995). We only recorded birds once, if they were detectable from both points in a stand (Ralph et al. 1995). Birds flying over the stand were not recorded (Ralph et al. 1995). Species detected within the stand but beyond the 50-m radius or within ±3 min of the count period while en route to points were recorded for evaluation of species richness We took the high count for each species per point and averaged values from both points to obtain an index of relative abundance for each site (Blonde1 1981, Blake and Karr 1987). For stands with widths <100 m (i.e., too narrow for a plot of 50-m radius, $n = 4$), counts were adjusted by extrapolation based on the fraction of a 50-m-radius plot that each plot comprised. We assumed any bias in bird detection among points was minimal because vegetation characteristics did not differ among sites (see below), only 2 observers were used, weather conditions were standardized, and timing of counts within day and season was stratified.

We evaluated the effect of stand width (log-transformed), habitat variables (i.e., PC), and year on species richness via a generalized linear model (PROC GLM; SAS Institute 1990). We used the same procedure to evaluate the effect of corridor width on species richness of Neotropical migrants (forest interior and interior-edge species only; Whitcomb et al. 1981). We compared the slopes of our regressions of species richness by stand width to slopes from species-area relations of other studies to test the null hypothesis that the species-width slopes did not differ from species-area slopes. Because we were aware of no published species-area relations from bottomland hardwood habitats, we used slopes from studies in upland hardwood forests in South Carolina (Kilgo 1996) and Illinois (Blake and Karr 1987).

We tested the null hypotheses that total bird count, total Neotropical migrant count, and counts of each species did not differ among width classes. We analyzed only those species for which we recorded an average of ≥20 observations/year. We made comparisons among width classes with repeated-measures (3 yr) analysis of covariance (RM-ANCOVA; PROC GLM; SAS Institute 1990). The linear model included the following terms: width class, site (width class), year, year x width class, PC1, PC2, and PC3, where PC1-PC3 were PC scores. Before analysis, we converted covariates to deviations from the mean. We tested covariates and width class with the site-within-width class as the error term. When the year x width class interaction was significant ($P < 0.05$), we analyzed years separately. When covariate effects were nonsignificant, they were eliminated. When RM-ANCOVA revealed significance ($P < 0.05$), we separated covariate-adjusted means via the least significant difference, calculated with site-within-width class as the error term.

We used logistic regression (PROC LOGISTIC; SAS Institute 1990) to model the effect of year and width on the probability of occurrence for each species. We analyzed only species recorded in ≥5% of the 60 stand-years (20 stands sampled 3 yr). The year effect was nonsignificant for all species, so we pooled data among years. Significance of the model was assessed with the score statistic (SAS Institute 1990). When the linear model was not significant, we added a quadratic term, $B_2x_i^2$, (Robbins et al. 1989), and accepted the model with the greatest significance.

To examine the effect of adjacent habitat type, we added 4 stands in 1994 with field-scrub habitat adjacent on both sides: 2 in the width class of 50-150 m and 2 in the width class of 150-300 m. Vegetation was sampled in 1994, and birds were sampled in 1994–95. We compared data from these FES with those from the 8 PES in the same width classes. Habitat data from the 12 stands were subjected to PCA, and PC scores were compared between treatments with incomplete block design ANOVA, blocking on width class. We compared total species richness, species richness of Neotropical migrants, total bird count, Neotropical migrant count, and species counts between treatments (i.e., surrounding habitat type) with RM-ANCOVA as described above, but with the addition of the treatment term and associated interactions.

RESULTS

Each of the first 3 PC from the analysis of vegetation in the 20 PES had eigenvectors >1.0, and they accounted for 91% of the variation in vegetation measured among sites: PC1 = 35.3%, PC2 = 30.3%, and PC3 = 25.2%. High scores on PC1, which was correlated positively with PROFILE and SAW and negatively with POLE and CANOPY (Table 1), represented stands with an open midstory and canopy, dense understory, and high basal area of hardwood sawtimber. High scores on PC2, which was correlated positively with PROFILE and POLE and negatively with SAW (Table 1), represented stands with well-developed understories and midstories, but low basal area of hardwood sawtimber. Finally, high scores on PC3, which was correlated positively with SAW and CANOPY (Table 1), reflected stands with large trees and a closed canopy. The PC scores did not differ among width classes (P > 0.05).

Table 1. Eigenvectors for variables included in principal components (PC) analysis of 20 bottomland hardwood stands enclosed by pine forest in South Carolina, 1993–95. The PC1–PC3 (only components with eigenvalues >1.00) accounted for 91% of the variation in the variables measured among sites.

Variable	PC1	PC2	PC3
Vegetation profile	0.58	0.57	0.09
canopy coverage	-0.63	0.03	0.59
Basal area: hardwood pole timber[a]	-0.29	0.80	0.10
Basal area: hardwood sawtimber[b]	0.43	-0.18	0.80

[a] Defined as all hardwood stems 8–23 cm dbh

[b] Defined as all hardwood stems >23 cm dbh.

We detected 56 species of birds in the 20 PES of which 23 (41%) were forest-dwelling Neotropical migrants. No edge-scrub or field-edge Neotropical migrants (Whitcomb et al. 1981) were detected because we sampled at the centers of forested stands. We analyzed species richness data by year because both total and Neotropical migrant species richness differed among years ($P < 0.001$), with highest values ($P < 0.05$) in 1993. Total species richness and species richness of Neotropical migrants were associated positively ($P < 0.05$) with the natural log of stand width in all years (Fig. 1). The slope of the species-width relation did not differ in any year from that of species-area relations in upland hardwoods of South Carolina (slope = 3.5, Kilgo 1996; 1993: $F_{1,1}$ = 1.20, P = 0.471; 1994: $F_{1,1}$ = 1.79, P = 0.409; 1995: $F_{1,1}$ = 3.02, P = 0.332) and Illinois (slope = 5.2, Blake and Karr 1987; 1993: $F_{1,1}$ = 0.05, P = 0.862; 1994: $F_{1,1}$ = 0.24, P = 0.709; 1995: $F_{1,1}$ = 0.50, P = 0.609).

Total species richness was associated positively with PC2 in 1993 (P = 0.018), indicating that number of species increased with increasing understory and midstory development. Similarly, species richness of Neotropical migrants was associated positively with PC2 in 1993 (P = 0.021) and 1995 (P = 0.051) but was associated negatively with PC1 in 1993 (P = 0.032) and 1995 (P = 0.019), indicating a positive association with canopy coverage.

Because the year X width class interaction was significant for both total bird count ($F_{8,59}$ = 3.02, P = 0.014) and Neotropical migrant count ($F_{8,59}$ = 3.08, P = 0.012), we analyzed years separately. Total bird count was not associated with PC in any year ($P > 0.05$) but differed among width classes in each year (1993: $F_{4,19}$ = 26.18, $P < 0.001$; 1994: $F_{4,19}$ = 4.54, P = 0.013; 1995: $F_{4,15}$ = 3.62, P = 0.030; Fig. 2); counts generally were greatest in width classes <50 m and >1,000 m (Fig. 2). Neotropical migrant

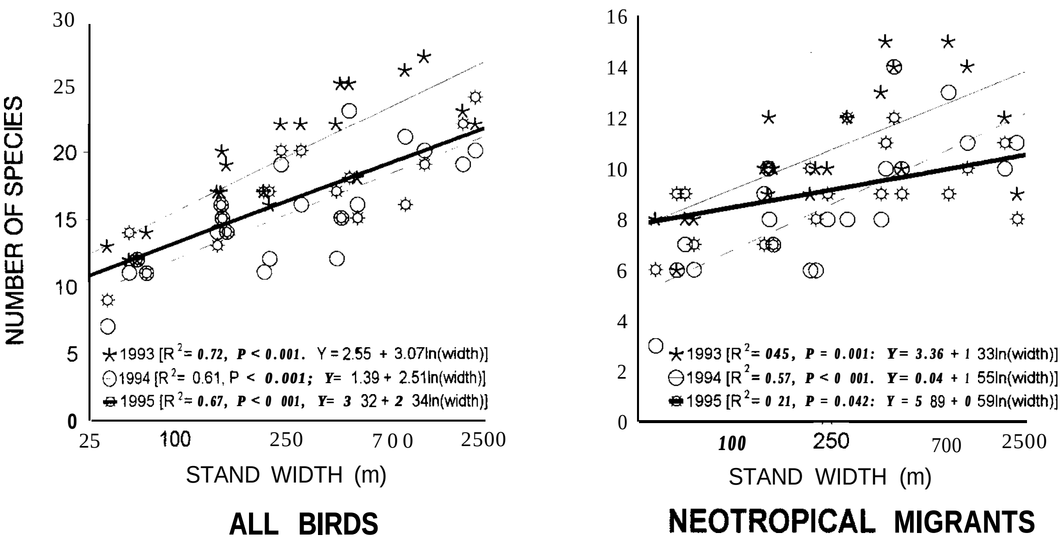

Fig. 1. Relation between breeding bird species richness and width of bottomland hardwood stands in South Carolina, 1993–95.

count differed among width classes in 1993 ($F_{4,19}$ = 28.41, $P < 0.001$) and 1995 ($F_{4,15}$ = 3.43, $P = 0.035$) and followed the same general trend as total bird count (Fig. 2). Neotropical migrant count also was associated negatively with PC3 in 1993 ($F_{1,12}$ = 6.91, $P = 0.022$).

Eight species had sufficient data for individual analysis: Acadian flycatcher, Carolina wren (*Thryothorus ludovicianus*), blue-gray gnatcatcher, white-eyed vireo, red-eyed vireo, northern parula, hooded warbler (*Wilsonia citrina*), and northern cardinal. Only blue-gray gnatcatcher count was associated with a habitat covariate (positively with PC3; $F_{1,12}$ = 7.20, $P = 0.020$). The year × width class interaction was significant for northern cardinal ($F_{8,59}$ = 3.21, $P = 0.009$), so years were analyzed separately; northern cardinal counts generally were greatest in width classes <50 m and >1,000 m (Fig. 2). Counts differed among width classes for the following species: Acadian flycatcher ($F_{4,15}$ = 9.53, $P = 0.001$), blue-gray gnatcatcher ($F_{4,12}$ = 10.51, $P = 0.001$), white-eyed vireo ($F_{4,15}$ = 5.54, $P = 0.006$), red-eyed vireo ($F_{4,15}$ = 11.99, $P < 0.001$), and northern parula ($F_{4,15}$ = 4.11, $P = 0.019$). Counts of Acadian flycatcher, blue-gray gnatcatcher, and red-eyed vireo were greatest in smaller width classes (Fig. 3), whereas counts of white-eyed vireo and northern parula were greatest in wider width classes (Fig. 3).

Probability of occurrence was associated positively with stand width for 12 species and negatively with stand width for 1 species (Table 2). The best model for 6 species contained a quadratic term, but only 3 of these models were significant ($P < 0.05$; Table 2). Acadian flycatcher was detected in every site in every year, and we failed to detect blue-gray gnatcatcher in only 1 site in 1 year.

The PC analysis of the vegetation characteristics in the 12 stands used to evaluate the effect of adjacent habitat type on the bird community revealed that PC1 and PC2 had eigenvectors >1.0 and together accounted for 70% of the variation among stands (PC1 = 40.4%, PC2 = 29.2%). High scores on PC1 represented stands with a closed canopy and high basal area of sawtimber but a poorly developed understory, and high scores on PC2 represented stands with a high basal area of sawtimber and a well-developed understory but poorly developed midstory (Table 3). We found no difference between width class or treatment scores along either PC1 or PC2 ($P > 0.05$).

The year × treatment interaction was significant for total species richness ($P < 0.001$); richness was greater in PES in 1994 and greater in FES in 1995 (Table 4). Total species richness was not related ($P > 0.05$) to habitat covariates in either year. Species richness of Neotropical migrants did not differ between treatments (Table 4) but was positively associated with PC1 ($F_{1,6}$ = 6.09, $P = 0.049$). Total bird count,

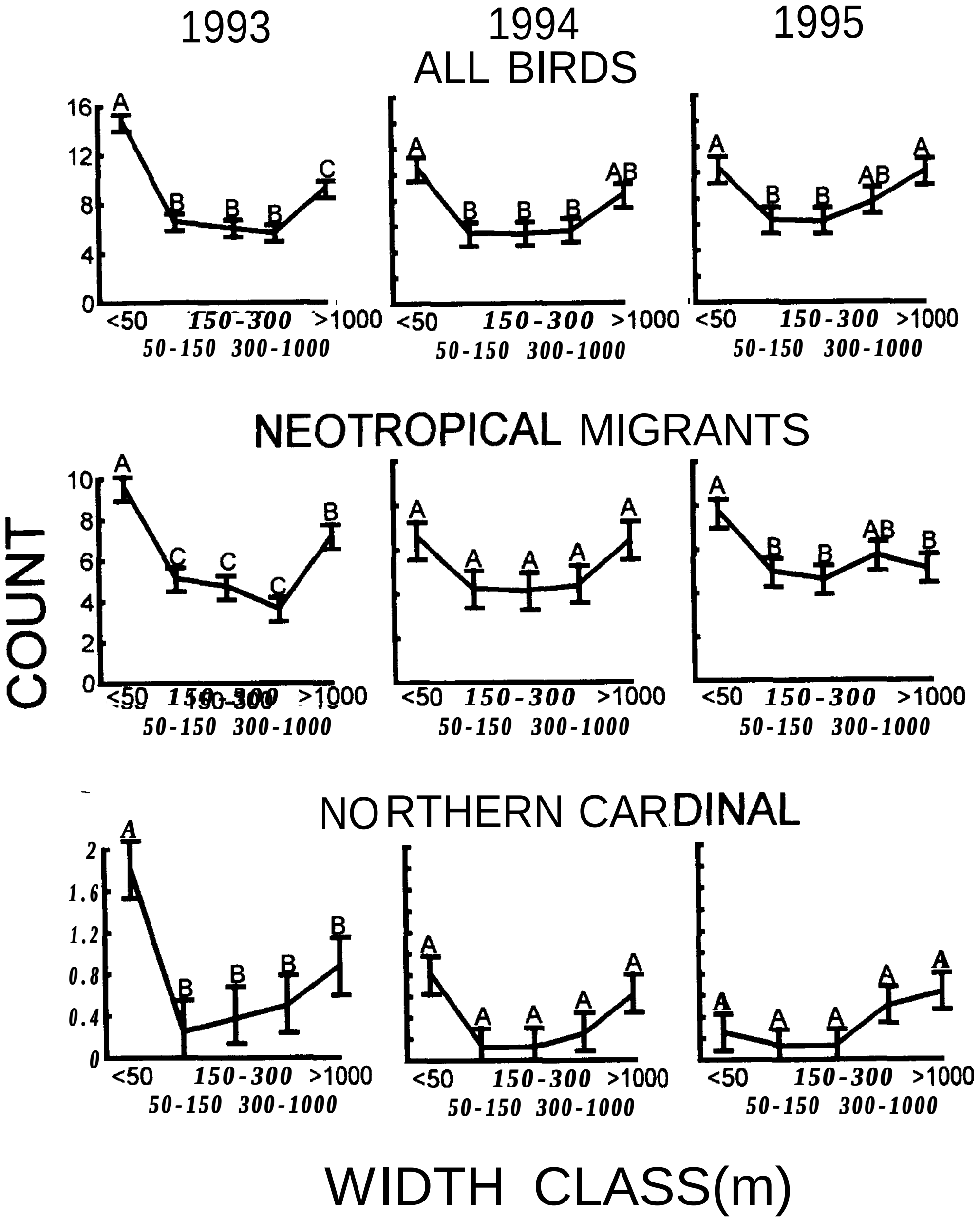

Fig. 2. Counts (mean ± SE) of breeding birds in 5 width classes of bottomland hardwood forests in South Carolina, 1993-95, analyzed by year because the year x width class interaction was significant ($P < 0.05$). Means with the same letter above them are not different ($P > 0.05$).

counts of blue-gray gnatcatcher in 1995, and counts of northern cardinal were greater in FES than in PES (Table 4). No species analyzed was significantly more abundant in PES than FES (Table 4), and no species' count was associated with PC1 or PC2 ($P > 0.05$).

DISCUSSION

Species richness exhibited a strong positive relation with bottomland forest width (Fig. 1). This relation existed although the adjacent habitat also was forested. Hence, there was a less abrupt ecotone in our study than in previous

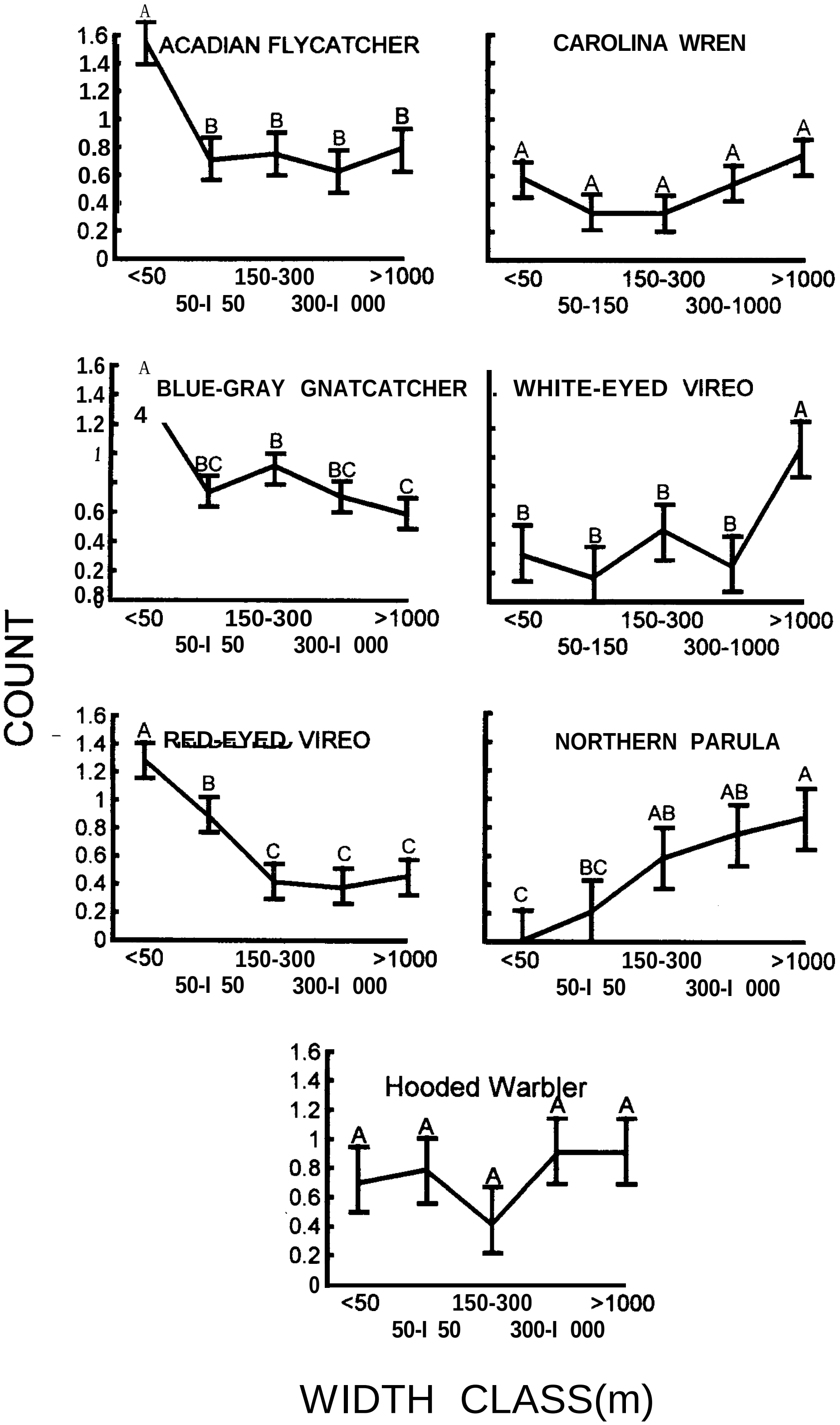
ACADIAN FLYCATCHER
CAROLINA WREN
BLUE-GRAY GNATCATCHER
WHITE-EYED VIREO
RED-EYED VIREO
NORTHERN PARULA
Hooded Warbler
A
B
BC
C
AB
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
<50
50-150
150-300
300-1000
>1000
COUNT
WIDTH CLASS(m)

Table 2. Probabilities of detecting species in bottomland hardwood forests of various widths, as estimated by logistic regression analysis of data from 20 stands measured from 1993 to 1995, in South Carolina. Species are ordered from those with the strongest positive relation with forest width to those with the most negative relation. Only species detected in ≥5% of the sites over all years are included.

Species[a]	Bottomland forest width (m) 25	50	100	200	500	1,000	2,500	Wald X^2	*P*
Swainson's warbler	0.05	0.05	0.06	0.07	0.14	0.36	0.95	23.86	0.000
American crow	0.13	0.14	0.15	0.19	0.30	0.56	0.97	17.08	0.000
Prothonotary warbler	0.13	0.14	0.15	0.18	0.28	0.51	0.95	16.02	0.000
Northern parula	0.07	0.12	0.28	0.78	1.00	1.00	1.00	13.60	0.000
Barred owl	0.05	0.06	0.06	0.07	0.11	0.22	0.76	13.38	0.000
Pileated woodpecker	0.40	0.41	0.43	0.47	0.60	0.78	0.98	7.40	0.01
Red-bellied woodpecker	0.32	0.36	0.44	0.60	0.92	1.00	1.00	6.33	0.01
White-eyed vireo	0.52	0.55	0.60	0.69	0.88	0.98	1.00	6.26	0.01
Summer tanager[b]	0.27	0.29	0.33	0.42	0.65	0.82	0.24	7.61	0.02
Kentucky warbler[b]	0.56	0.59	0.65	0.75	0.90	0.95	0.09	7.52	0.02
Yellow-billed cuckoo	0.54	0.55	0.57	0.61	0.73	0.86	0.99	4.97	0.03
Red-shouldered hawk	0.19	0.19	0.20	0.21	0.25	0.34	0.66	4.25	0.04
American redstart”	0.10	0.11	0.14	0.20	0.39	0.46	0.00	5.65	0.06
Downy woodpecker	0.28	0.29	0.29	0.31	0.36	0.45	0.73	3.39	0.07
Northern cardinal	0.71	0.72	0.75	0.79	0.89	0.97	1.00	3.22	0.07
Black-and-white warbler[b]	0.12	0.13	0.16	0.21	0.37	0.09	0.01	4.88	0.09
Hooded warbler	0.65	0.74	0.86	0.97	1.00	1.00	1.00	2.67	0.10
Yellow-throated vireo[b]	0.23	0.24	0.27	0.33	0.50	0.63	0.09	4.25	0.12
Tufted titmouse	0.86	0.90	0.95	0.99	1.00	1.00	1.00	1.00	0.32
Red-eyed vireo	0.83	0.95	1.00	1.00	1.00	1.00	1.00	0.57	0.45
Great-crested flycatcher	0.45	0.45	0.45	0.46	0.48	0.52	0.62	0.47	0.49
Carolina wren	0.83	0.95	1.00	1.00	1.00	1.00	1.00	0.40	0.53
Yellow-throated warbler	0.11	0.11	0.11	0.11	0.12	0.13	0.17	0.14	0.71
Ruby-throated hummingbird	0.04	0.04	0.04	0.05	0.07	0.10	0.35	0.07	0.78
Carolina chickadee	0.29	0.29	0.29	0.29	0.30	0.31	0.35	0.06	0.80
Common yellowthroat	0.14	0.14	0.15	0.15	0.15	0.16	0.17	0.03	0.87
Acadian flycatcher	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00
Blue-gray gnatcatcher[c]	0.98	0.98	0.98	0.98	0.98	0.98	0.98	N/A	N/A
Blue jay	0.23	0.23	0.22	0.21	0.18	0.13	0.05	1.00	0.32
Pine warbler	0.14	0.13	0.11	0.07	0.02	0.00	0.00	1.00	0.32
Mourning dove[b]	0.02	0.02	0.01	0.00	0.00	0.00	0.00	2.32	0.31
Louisiana waterthrush	0.44	0.43	0.42	0.39	0.31	0.21	0.05	3.36	0.07
wood thrush	0.70	0.70	0.69	0.67	0.60	0.49	0.19	4.75	0.03

[a] Scientific names of species not mentioned in text: American crow (Corvus *brachyrhynchos*); prothonotary warbler (*Protonotaria citrea*); barred owl (*Strix varia*); pileated woodpecker (*Dryocopus pileatus*); summer tanager (*Piranga rubra*); red-bellied woodpecker (*Melanerpes carolinus*); yellow-billed cuckoo (*Coccyzus americanus*); red-shouldered hawk (*Buteo lineatus*); American redstart (*Setophaga ruticilla*); downy woodpecker (*Picoides pubescens*); black-and-white warbler (*Mniotilta varia*); yellow-throated vireo (*Vireo flavifrons*); tufted titmouse (*Parus bicolor*); great-crested flycatcher (*Myiarchus crinitus*); yellow-throated warbler (*Dendroica dominica*); ruby-throated hummingbird (*Archilochus colubris*); Carolina chickadee (*Parus carolinensis*); common yellowthroat (*Geothlypis trichas*); blue jay (*Cyanocitta cristata*); pine warbler (*Dendroica pinus*); mourning dove (*Zenaida macroura*).

[b] The best-fit logistic regression equation included a quadratic term (width^2)

[c] Because we failed to detect blue-gray gnatcatcher in only 1 site in 1 year, convergence could not be attained in logistic regression analysis Therefore, the probability of detection reported is the proportion of all stands, by year, in which the species was detected. This represents the maximum-likelihood estimate appropriate when probability of detection is not related to width (Robbins et al. 1989).

studies relating species richness to area (Blake and Karr 1987, Robbins et al. 1989) or width (Keller et al. 1993). However, the slope of this relation did not differ from slopes of species-area relations, indicating that our wider stands did not exhibit a greater increase in species richness than was expected from simple species-area regressions. The general lack of associations between the bird community and habitat features is likely attributable to the general similarity of vegetation among the study sites; stands were selected because of their apparent similarity of vegetation. Thus, the observed relation of species richness to stand width is due

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Fig. 3. Counts (mean ± SE) of 7 breeding bird species in 5 width classes of bottomland hardwood stands in South Carolina, 1993-95. Means with the same letter are not different (P > 0.05).

Table 3. Eigenvectors for variables included in principal components (PC) analysis of 12 bottomland hardwood stands, 8 enclosed by pine forest and 4 enclosed by fields, in South Carolina, 1994-95. The PC1 and PC2 (only components with eigenvalues >1.00) accounted for 70% of the variation in the variables measured among sites.

Variable	PC1	PC2
Vegetation profile	-0.44	0.52
Canopy coverage	0.72	-0.12
Basal area: hardwood poletimber[a]	-0.04	-0.64
Basal area: hardwood sawtimber[b]	0.53	0.55

[a] Defined as all hardwood stems 8–23 cm dhh

[b] Defined as all hardwood stems >23 cm dhh.

either to a response to width per se or to unmeasured features of the habitat. Pashley and Barrow *(1993)* described several aspects of bottomland hardwood habitats important to birds. These included scour channels, Spanish moss (*Tilandsia usneoides*), canebrakes (i.e., switchcane thickets), vine tangles, and thickets of palmetto (*Sabal minor).* The wider a stand, the more likely it is to contain each of these features, yet all are difficult to quantify with the conventional techniques we used to sample avian habitat.

Both total and species-specific counts generally were greatest in the narrowest and widest width classes. This U-shaped pattern in total bird count was inconsistent with our expectation that fewer species in narrow stands would mean fewer birds. We suggest that the observed pattern might better be understood by examining the 2 segments of this relation separately (i.e., the portion of the abundance-width curve for which the relation is negative vs. that for which the curve is positive). Three factors may have contributed to the negative relation that characterized the narrow stands. First, the relation potentially resulted from the combined effects of species positively associated with width (e.g., nor-them parula, white-eyed vireo), and of species negatively associated with width (e.g., Acadian flycatcher, blue-gray gnatcatcher, red-eyed vireo). Second, a greater amount of edge habitat was censused in the narrow stands because census plots in these stands overlapped both stand edges. Consequently, edge species such as northern cardinal and Carolina wren were more abundant in the narrowest width classes than in the medium width classes (this trend was nonsignificant for Carolina wren). Finally, densities in our narrowest stands potentially were high simply because birds were confined within a smaller area, whereas territories were not as packed in medium width stands, because space was not limited. Previous studies reported that bird density decreased with increased width of the riparian zone, whereas species richness increased with width (Darveau et al 1995, Thurmond et al. 1995). Such a pattern is consistent with our results for the narrow width classes, which encompassed the widths

Table 4. Comparison of breeding birds in bottomland hardwood stands enclosed by pine forest (PES; $n = 8$) and enclosed by fields (FES; $n = 4$) in South Carolina, 1994-95.

Variable	PES		FES		P
	$\bar{x}$	SE	$\bar{x}$	SE	
Species richness					
All birds[a]					
1994	18.75	0.73	14.50	1.03	0.007
1995	14.63	0.82	19.00	1.16	0.012
Neotropical migrants[b]	8.42	0.54	8.02	0.76	0.530
Count					
All birds	5.88	0.45	9.03	0.63	0.015
Neotropical migrants	4.50	0.29	5.20	0.41	0.356
Acadian flycatcher	0.81	0.45	0.78	0.10	0.879
Carolina wren	0.34	0.07	0.59	0.10	0.301
Blue-gray gnatcatcher[a]					
1994	0.69	0.09	0.90	0.13	0.216
1995	0.56	0.07	1.15	0.10	0.001
White-eyed vireo	0.25	0.05	0.25	0.07	1.000
Red-eyed vireo	0.69	0.11	0.64	0.15	0.801
Northern parula	0.47	0.08	0.71	0.11	0.426
Hooded warbler	0.59	0.08	0.25	0.11	0.237
Northern cardinal	0.13	0.03	0.84	0.04	0.001

[a] Year × treatment interaction was significant ($P < 0$ 05). so years were analyzed separately.

[b] Species richness was positively correlated with PC1 ($P = 0.049$).

reported in these studies. For example, Thurmond et al. (1995) reported higher bird densities but fewer species in narrow (16-20 m) versus wide (53-58 m) streamside management zones in Georgia. Similarly, Darveau et al. (1995) reported that 20-m-wide riparian strips in Quebec contained greater bird densities but fewer species than 40- and 60-m-wide strips, although the wider strips supported a greater number of territories because they contained greater areas. Thus, the negative relation between count and width for narrow stands may be related to area and sampling effects, whereas counts from wider stands, for which no comparison from the literature is available, actually may reflect superior habitat conditions that support higher densities of birds.

Some species generally considered to be area sensitive (Robbins et al. 1989) exhibited unexpected patterns of occurrence and abundance. The probabilities of occurrence for wood thrush ***(Hylocichla mustelina)*** and Louisiana waterthrush (*Seiurus motacilla*) were negatively related to width. Capture rates of wood thrush in a concurrent mistnetting study (R. A. Sargent et al., unpublished data) also were negatively related to width. Keller et al. (1993) found these species positively associated with riparian zone width in the mid-Atlantic states. Counts of red-eyed vireo, also considered an area-sensitive species (Robbins et al. 1989, Keller et al. 1993), declined as width increased, although this species' probability of occurrence increased (nonsignificantly) with width. Similarly, Acadian flycatcher was detected even in our narrowest stands, and their counts declined in wider stands. Conversely, counts of white-eyed vireo, an edge species, were positively related to width. Our results for Acadian flycatcher and white-eyed vireo are corroborated by those of Hodges and Krementz (1996) from the Altamaha River basin, a tributary of the Savannah River. Reasons for lower densities in sites where a species is more likely to occur are unclear but may be related to the species' sociobiology. Density also is not necessarily an accurate reflection of habitat quality (Wiens 1989:306).

We failed to detect a consistent effect of adjacent habitat on species richness. We hypothesized that more species would be found in PES than in FES because the presence of an adjacent, closed canopy forest might serve as a buffer against negative edge effects (Harris 1984, Kilgo et al. In press), and thereby increase the functional width of the stand. Such an effect was evident in 1994, but the pattern was reversed in 1995. Similarly, we failed to detect an effect of adjacent habitat on the counts of area-sensitive species. The northern cardinal, an edge species, was more abundant in FES, but counts of the area-sensitive northern parula and white-eyed vireo (this study) were not affected negatively by the presence of field habitat adjacent to the stand. The expected pattern may have been evident had we sampled narrower FES (i.e., some species may be sensitive to external fragmentation below the range of widths we sampled).

MANAGEMENT IMPLICATIONS

We concur with the conclusion of Thurmond et al. (1995) that even retention of narrow streamside buffer zones can benefit local bird assemblages. Several area-sensitive species (e.g., Acadian flycatcher, wood thrush, red-eyed vireo, Louisiana waterthrush, Kentucky warbler [*Oporornis formosus*], hooded warbler) were common in our narrowest stands. However, because we sampled a broad range of widths, we detected several species that were highly area-sensitive and apparently would benefit only from conservation of very wide stands. For example, the narrowest stand in which we detected Swainson's warbler ***(Limnothlypis swainsonii)*** ***was 475*** m wide. Although we could not include them in our analysis, Mississippi kite ***(Ictinia mississippiensis)*** was recorded only in stands 21,000 m wide, and swallow-tailed kite (***Elanoides forficatus***) was recorded only in stands 21,900 m wide. Keller et al. (1993) and Hodges and Krementz (1996) recommended that a minimum forested buffer zone of ≥100 m be maintained adjacent to drainages to provide habitat for forest interior species. In our study, the width at which probability of occurrence was 50% of its maximum (i.e., a conservative estimate of the minimum amount of habitat required by a species for breeding; Robbins et al. 1989) exceeded 100 m for 8 species (pileated, red-bellied, and downy woodpeckers, yellow-throated vireo, northern parula, American redstart, black-and-white warbler, summer tanager) and exceeded 500 m for 6 additional species (barred owl, red-shouldered hawk, ruby-throated hummingbird, American crow, prothonotary warbler, Swainson's warbler). Thus, although narrow riparian stands are extremely valuable avian habitat, we feel that the complete avian community characteristic of bottomland hardwoods in South Carolina can be maintained only in the few remaining riparian zones that are extremely wide (>500 m).

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Effects of Road Networks on Bird Populations

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Review

Effects of Road Networks on Bird Populations

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Abstract: *One potential contributor to the worldwide decline of bird populations is the increasing prevalence of roads, which have several negative effects on birds and other vertebrates. We synthesized the results of studies and reviews that explore the effects of roads on birds with an emphasis on paved roads. The well-known direct effects of roads on birds include habitat loss and fragmentation, vehicle-caused mortality, pollution, and poisoning. Nevertheless, indirect effects may exert a greater influence on bird populations. These effects include noise, artificial light, barriers to movement, and edges associated with roads. Moreover, indirect and direct effects may act synergistically to cause decreases in population density and species richness. Of the many effects of roads, it appears that road mortality and traffic noise may have the most substantial effects on birds relative to other effects and taxonomic groups. Potential measures for mitigating the detrimental effects of roads include noise-reduction strategies and changes to roadway lighting and vegetation and traffic flow. Road networks and traffic volumes are projected to increase in many countries around the world. Increasing habitat loss and fragmentation and predicted species distribution shifts due to climate change are likely to compound the overall effects of roads on birds.*

Keywords: bird populations, roads, road mortality, roadway lighting, surface transportation, traffic noise

Efectos de las Redes de Caminos sobre Poblaciones de Aves

Resumen: *El incremento en la prevalencia de caminos, que han tenido varios efectos negativos sobre aves y otros vertebrados, es un potencial contribuyente a la declinación mundial de poblaciones de aves. Sintetizamos los resultados de estudios y revisiones que exploran los efectos de los caminos sobre las aves, con énfasis en caminos pavimentados. Los bien conocidos efectos directos de los caminos sobre las aves incluyen la pérdida y fragmentación de hábitat, mortalidad causada por vehículos y envenenamiento. Sin embargo, los efectos indirectos pueden ejercer una mayor influencia sobre poblaciones de aves. Estos efectos incluyen ruido, luz artificial, barreras al movimiento y bordes asociados con caminos. Más aun, los efectos indirectos y directos pueden actuar sinérgicamente para causar decrementos en la densidad poblacional y en la riqueza de especies. De los muchos efectos de los caminos, parece que la mortalidad y el ruido del tráfico tienen los efectos más significativos sobre las aves en relación con otros efectos y grupos taxonómicos. Las medidas potenciales para mitigar los efectos perjudiciales de los caminos incluyen estrategias de reducción de ruido y cambios en la iluminación y vegetación de los caminos y en el flujo de tráfico. Se proyecta que las redes de caminos y los volúmenes de tráfico incrementen en muchos países en el mundo. Es probable que el incremento en la pérdida y fragmentación de hábitat y los cambios pronosticados en la distribución de especies debidos al cambio climático compliquen los efectos de los caminos sobre las aves.*

Palabras Clave: caminos, iluminación en caminos, poblaciones de aves, mortalidad en caminos, ruido de tráfico, transportación terrestre

Introduction

Bird populations are declining around the world (BirdLife International 2008*a*). In North America the abundances of at least 20 species previously categorized as common have declined more than 50% in the last 40 years (Butcher & Niven 2007; BirdLife International 2008*b*). Additionally, abundances of over half the species of Neotropical

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migrants have declined substantially. The reasons for these declines are not fully understood (Butcher & Niven 2007; BirdLife International 2008*c*). One likely contributor is the expansion of paved roads, mostly in terms of widening (National Research Council 2005), and corresponding increases in the speed and volume of vehicles on those roads (Ritters & Wickham 2003). We synthesized these effects on birds to balance the much greater attention that has hitherto been paid to the effects of roads on mammals and to examine the potentially negative effects of roads on birds worldwide.

Reduced breeding success is correlated with proximity of birds to roads and road density for species ranging from passerines (Catchpole & Phillips 1992; Reijnen & Foppen 1994) to vultures (Donazar et al. 1993). In some cases, avian communities adjacent to roads differ from nearby avian communities (Glennon & Porter 2005), presumably because of some combination of the direct and indirect effects of roads on animals in general (Forman & Alexander 1998; Trombulak & Frissell 2000; Fahrig & Rytwinski 2009).

There is a little understanding of whether declines in persistence of birds are more affected by direct or indirect effects. If this could be determined in urban areas, it may be possible to increase bird abundance and species richness. It is also important to identify and mitigate any negative road effects in protected areas, which are assumed to buffer populations of wild animals from human activities.

Many of the negative effects of roads on other vertebrates (e.g., mortality, habitat fragmentation, and audiovisual disturbance, chemical pollution) also apply to birds (Forman et al. 2003; Jacobson 2005). There are a few ways roads can benefit birds. For example, roads retain heat that can reduce metabolic costs for birds that rest on road surfaces (Whitford 1985), associated road infrastructure (e.g., poles and bridges) can create nesting sites (Forman 2000), and verges increase availability of food sources (Lambertucci et al. 2009) and link patches of habitat (Meunier et al. 1999; Huijser & Clevenger 2006; Reijnen & Foppen 2006). We reviewed recent reports and peer-reviewed articles focused primarily on direct and indirect negative effects of roads on bird populations and identified some potential forms of mitigation. Much of the literature we reviewed concerns paved roads because they have been the subject of more study and because their ecological effects are assumed to be greater than gravel, dirt, or ice roads (Forman et al. 2003; National Research Council 2005).

Direct Threats Posed to Birds by Roads and Traffic

For bird populations the most visible direct negative effects of roads are habitat loss and mortality due to collisions with vehicles. Because the effects of habitat loss on birds have been comprehensively reviewed elsewhere (Andren 1994), we did not focus on this effect here. Nonetheless, roads have other effects that are related to habitat loss. For example, maintenance activities in the right-of-way can further reduce habitat quality and destroy nests, which may reduce population viability for rare species (e.g., Burrowing Owl [*Athene cunicularia*]) (Catlin & Rosenberg 2006). We focused on the negative effects associated with vehicular traffic.

Vehicle-Caused Mortality

For individual birds and other vertebrate groups, a direct threat of roads is death due to collisions with vehicles (Erritzoe et al. 2003). In the United States, vehicles are estimated to cause approximately 80 million bird fatalities each year (Erickson et al. 2005). Despite the high number of mortalities each year, vehicle-caused mortality has been assumed to have less of an effect on persistence than some indirect effects of roads (Forman & Alexander 1998; Reijnen & Foppen 2006). Only three bird species found in the United States appear to suffer population declines as a result of them: Florida Scrub-Jay (*Aphelocoma coerulescens*) (Mumme et al. 2000; IUCN 2008), Audubon's Crested Caracara (*Polyborus plancus audubonii*), and Hawaiian Goose (*Branta sandvicensis*) (Huijser et al. 2007; IUCN 2008). A greater understanding of what makes some species more susceptible to vehicle collision and population decline as a result of vehicle-caused mortality is needed, but some generalities emerge from the literature.

First, birds are more likely to collide with vehicles if they forage, roost, or nest near roads (Erritzoe et al. 2003; Huijser et al. 2007). Collision frequency can increase near watercourses (Erritzoe et al. 2003; Ascensao & Mira 2006) and houses (Ascensao & Mira 2006). Collisions are also more likely to occur at lower elevations (Clevenger et al. 2003) and in open areas than in forests (e.g., Clevenger et al. 2003; Ascensao & Mira 2006; Ramp et al. 2006).

Several other factors have less consistent effects on vehicle-induced bird mortality. For many species, vehicle-induced mortality increases during breeding and migration (Fulton et al. 2008; Gryz & Krause 2008), but for other species it increases during winter (Loos & Kerlinger 1993; Boves 2007). Collisions can increase (Jackson 2003) or decrease as roadside lighting increases (Hernandez 1988). Roadside trees, hedgerows, and other features that cause birds to fly higher across roads typically decrease collision frequency (Pons 2000; Bard et al. 2002; Clevenger et al. 2003; Erritzoe et al. 2003; Taylor & Goldingay 2004; Orlowski 2005), but they can also increase it (Ramp et al. 2006; Varga et al. 2006). Birds also vary in their responses to roads. Some individuals appear to learn to avoid vehicles (Mumme et al. 2000), whereas others do not (Loos & Kerlinger 1993; Jackson 2002).

It is difficult to measure the true extent of vehicle-induced mortality because estimates are typically far lower than the actual number of birds killed (Erickson et al. 2005). Estimation accuracy is reduced by variation in searcher efficiency, scavenger bias (Erickson et al. 2005; Boves 2007), and incorrect attribution of cause of death (Kerlinger & Lein 1988). Even long-term studies in which 100% of individuals are marked, researchers can fail to detect all instances of vehicle-caused mortality (Mumme et al. 2000). Vehicle collisions may also cause nonfatal injuries that increase the probability birds will die from other causes (Orlowski & Siembieda 2005). In addition, inaccurate estimates of vehicle-induced mortality can result if only carcasses are studied in the absence of data on species abundance (Hernandez 1988; Aebischer et al. 2005). Missing information about population size makes it difficult to compare rates of mortality in different areas, especially on different continents (Erritzoe et al. 2003).

Pollution and Poisoning

Deicing agents, petroleum-based organic compounds, nutrients, sediments, agricultural chemicals, and other substances regularly run off paved roads during construction, maintenance, and use (Buckler & Granato 1999). Road salt is a common deicing agent that attracts birds. Its ingestion can lead to death, which dispels the notion that road salt has a negative effect only because it attracts birds to the road surface, making them subject to collisions with vehicles (Mineau & Brownlee 2005). Dust on unpaved roads can change the composition of vegetation (Walker & Everett 1987), which can affect birds (Kalisz & Powell 2003). Gravel roads are frequently treated with dust suppressants, the environmental and toxicological effects of which are not well understood (Fay & Kociolek 2009). Despite the ubiquity of road contaminants from vehicles and maintenance activities, toxic effects of roads appear to be rare, even in areas with high traffic volumes (Buckler & Granato 1999), and pollution appears to have fewer effects on birds than other road-related effects (Reijnen & Foppen 2006).

Indirect Threats Posed to Birds by Roads and Traffic

Even in the absence of direct deleterious effects, many bird species appear to avoid roads purposely (e.g., Bollinger & Gavin 2004; Balbontin 2005; Gavashelishvili & McGrady 2006). Some species may be present near roads for a time, but they are more likely to abandon nests near roads (Gorog et al. 2005). For birds, road avoidance appears to be associated with the physical barrier to movement roads present, noise, artificial light, and edge effects.

Physical Barriers

Of the indirect threats of roads, the barriers to movement roads present may have the greatest effect on vertebrates (Forman & Alexander 1998). Several forest-dwelling bird species are unlikely to cross gaps in forest cover $\geq$50 m in areas dominated by agriculture (Desrochers & Hannon 1997), timber harvesting (Awade & Metzger 2008), and urban infrastructure (Tremblay & St. Clair 2009). Some species exhibit reluctance to cross dirt roads that are 10–30 m wide (Develey & Stouffer 2001). Nonetheless, the barriers caused by roads may be a simple function of the width of the gap they create in the surrounding habitat, unless the roads are also noisy (St. Clair 2003; Tremblay & St. Clair 2009) or are associated with tall features such as power lines (Pruett et al. 2009).

Noise

Traffic noise probably has the most widespread and greatest indirect effect on birds (Reijnen et al. 1995 (Table 1). Noise likely causes reductions in population densities that have been reported for several bird species that are present near roads (Reijnen & Foppen 2006; Patricelli & Blickley 2006). In grasslands the effects of noise appear to extend farther from roads than in forests (Forman et al. 2002), perhaps because grasslands have less vegetation to absorb sound. In addition to the effects of traffic volume and its associated noise, there may be synergistic effects of noise, habitat loss and fragmentation (Forman & Deblinger 2000), and edge effects (Habib et al. 2007).

Birds may be affected by anthropogenic noise because they rely extensively on acoustic communication (Table 1). Chronic industrial noise can reduce species richness, alter population age structure, and change avian predator–prey dynamics (Francis et al. 2009). Like industrial noise, chronic traffic noise appears to produce younger age structures and reduces population densities in several bird species (Reijnen & Foppen 2006). These effects may occur because anthropogenic noise masks the frequencies of calls used to attract mates (Rheindt 2003; Pohl et al. 2009), communicate with flock members (Lohr et al. 2003; Slabbekoorn & Ripmeester 2008) or offspring (Leonard & Horn 2005), defend territories (Habib et al. 2007; Mockford & Marshall 2009), and detect predators (Slabbekoorn & Ripmeester 2008; Francis et al. 2009) (Table 1). Effects of noise on both birds and anurans seem to depend on the frequencies and amplitudes of species-specific signals (Lengagne 2008; Slabbekoorn & Ripmeester 2008; Hu & Cardoso 2009). Some species seem unaffected by roads or traffic (Kaseloo 2005; Reijnen & Foppen 2006), and others may not come near roads when traffic volume is high (Bautista et al. 2004). Several urban-dwelling songbird species appear to counteract the masking effects of traffic noise (Table 1) by singing at a higher pitch (Slabbekoorn & Peet 2003), increasing song amplitude (Brumm 2004b), or singing

Table 1. The effects of anthropogenic noise on avian communities and communication.

Category	*Effect*	*References*
Community		
species richness	reduced as noise increases	Stone 2000
density & abundance (all species)	reduced as noise increases	Reijnen et al. 1995, 1996; Kuitunen et al. 1998; Bayne et al. 2008
	no overall reduction	Peris & Pescador 2004
densities & abundance (specific species)	reduced as noise increases	Reijnen & Foppen 1994; Reijnen et al. 1995, 1997
	dependent on species	Kuitunen et al. 1998; Peris & Pescador 2004
	higher abundance of birds with higher song pitch near roads	Rheindt 2003
age structure	younger at noisy sites	Reijnen & Foppen 1994; Habib et al. 2007
physiology	increased stress at higher noise levels	Campo et al. 2005
	no stress difference at higher noise levels	Byers et al., unpublished data
Breeding cycle		
pairing and mate retention	decreased time devoted to courtship behavior	Goudie & Jones 2004
	reduced pairing success	Habib et al. 2007
	reduced mate preference	Swaddle & Page 2007
territory and nest-site selection	farther from noise sources	Francis et al. 2009
nest success	increased as noise increases for some species	Francis et al. 2009
Foraging		
begging calls	reduced parental discrimination in noisy locations	Leonard & Horn 2005
prey location and probability of predation	predator reduction increases nest success in noisy locations	Francis et al. 2009
	potential alterations to interspecies interactions	Slabbekoorn & Halfwerk 2009
	increased vigilance as noise increases	Quinn et al. 2006
Communication		
temporal adjustment	sing more at night in noisy locations	Fuller et al. 2007
amplitude increase	sing louder as noise increases (Lombard effect)	Cynx et al. 1998; Brumm 2004a, 2004b; Brumm et al. 2009; Osmanski & Dooling 2009
	louder begging calls in noisy locations	Leonard & Horn 2005
pitch modification	increased pitch in noisy locations	Slabbekoorn & Peet 2003; Fernandez-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Parris & Schneider 2009; Kirschel et al. 2009; Nemeth & Brumm 2009
redundancy	no correlation between pitch and road noise	Skiba 2000
detection of con- and heterospecific vocal signals	more repetition in noisy locations	Brumm & Slater 2006
	reduced detection probability of signals in noisy locations	Langemann et al. 1998; Lohr et al. 2003
response to signals	strongest response to played-back signals when ambient noise levels are similar to local environment	Mockford & Marshall 2009
reviews	effects of noise and implications	Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Barber et al. 2010
Brain response		
gene activation	immediate early-gene ZENK expression in the neural pathway of the avian brain not modified by noise playback	Vignal et al. 2004

during periods of low traffic noise (Fuller et al. 2007). Other species may be unable to adapt their songs to accommodate chronic noise (Slabbekoorn & Ripmeester 2008; Barber et al. 2010), and pairing success of birds with relatively high amplitude songs is reduced when they are exposed to high levels of chronic noise (Habib et al. 2007).

Artificial Light

Light from roadways can have negative effects on many animals (Rich & Longcore 2006), including birds (Ogden 1996; Van De Laar 2007). Some lighting structures attract migrating bird species, which increases the probability they will be preyed on or collide with structures and often causes them to redirect flight paths and thus deplete energy stores (van de Laar 2007). Artificial lighting can also affect avian patterns of nestling development, singing, breeding, molting, and migration (De Molenaar et al. 2006). There is some evidence that roadway lighting may reduce habitat quality and change the timing of breeding for the Black-tailed Godwit (*Limosa limosa*), a species associated with grasslands in Africa, Europe, and Asia (De Molenaar et al. 2006). American Robins (*Turdus migratorius*) sing earlier in the morning in areas with more anthropogenic light (Miller 2006), but this response may be difficult to disentangle from the associated effect of road noise, which is more important than light for explaining nocturnal singing by European Robins (*Erithacus rubecula*; Fuller et al. 2007).

Edge Effects

Positive and negative effects of edges on breeding birds have been documented in many studies (Stephens et al. 2003). The edge effects of roads may be particularly acute when introduced species, such as rats (*Rattus rattus*), prey on ground-nesting birds (Delgado et al. 2001) or parasitic species, such as Brown-headed Cowbirds (*Molothrus ater*), target the nests of species of conservation concern (Chace et al. 2003). In some cases, these edge effects are contradictory (Bergin et al. 2000; Lariviere 2003).

Mitigation

Paved roads are a pervasive feature across much of North America, and existing roads are being widened, new roads are being built, and, and traffic volume is increasing (Forman et al. 2003; National Research Council 2005) throughout the world (Urban Land Institute 2007; Bhattacharya 2008). Efforts to mitigate road effects are most likely to increase probabilities of persistence of birds when applied across extensive areas (Stutchbury 2009).

New information about the ubiquity of the effects of noise on birds suggests reducing road noise may be cost-effective because it can benefit both birds and humans (Bluhm et al. 2007; Slabbekoorn & Ripmeester 2008; Barber et al. 2010). Promising measures to reduce road noise include temporal adjustments to traffic flow (Reijnen & Foppen 2006) and increased reliance on mass transit (Barber et al. 2010). The unvegetated area created by light-rail train tracks is more permeable to bird movement than roads of equivalent sizes, perhaps because they are quieter (Tremblay & St. Clair 2009). New tire designs (Carstens 2003) and noise-absorbing porous asphalt (Piepers 2001) can substantially reduce levels of highway noise (Elvik & Greibe 2003). Other noise-reducing strategies include the use of earth berms and vegetation that, unlike walls (Varga et al. 2006), do not create vertical barriers to animal movement, although this may depend on the animal. These features typically also increase quality of life and property values for human residents.

Changing roadway lighting may also benefit both birds and people through reductions in energy consumption and increases in safety (De Molenaar et al. 2006). Replacing red or white lights with green lights greatly reduces the negative effect of artificial lights on oil platforms on birds (van de Laar 2007). Such lighting could be used on highway (Poot et al. 2008).

Edge effects might be partially mitigated with vegetation management and restoration. Poisoning and nonpoint source pollution can be mitigated, in part, by policy aimed at encouraging use of nontoxic agents to maintain safe driving conditions. A practice that would reduce vehicle-induced bird mortality would be to refrain from planting along roadsides fruit-bearing vegetation that attracts birds.

Future Implications

In the United States road area is expected to increase by 27,900 km^2 by 2030, and lanes added to existing roadways to accommodate increased traffic volume is projected to increase road area by an additional 94,100 km^2 (Theobald 2010). Exponential increases in the road network and traffic volume are anticipated to occur in large, densely populated, countries such as China and India (Bhattacharya 2008). Among the factors studied to date, it appears that traffic noise has the greatest potential to reduce population abundance and species richness of birds (Reijnen & Foppen 2006; Barber et al. 2010). Although vehicle-caused mortality does not appear to affect persistence for most populations, it is a problem for some species (Huijser et al. 2007) and may exacerbate other anthropogenic threats to birds (Erickson et al. 2005). Given global traffic projections and in light of losses due to collisions, road-induced mortality of birds should be examined more systematically and comprehensively. Other road-related disturbances such as light and chemical pollution appear to have minor effects at the population level, but their spatial extent may still generate a large collective effect on birds. Finally, increasing habitat loss and fragmentation, in addition to predicted species distribution shifts due to climate change, are likely to compound the overall effect of roads (Heller & Zavaleta 2009).

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Los Angeles Times

Where SoCal Edison may shut off power in California

By **PRIYA KRISHNAKUMAR**, **BEN WELSH** AND **RYAN MURPHY**

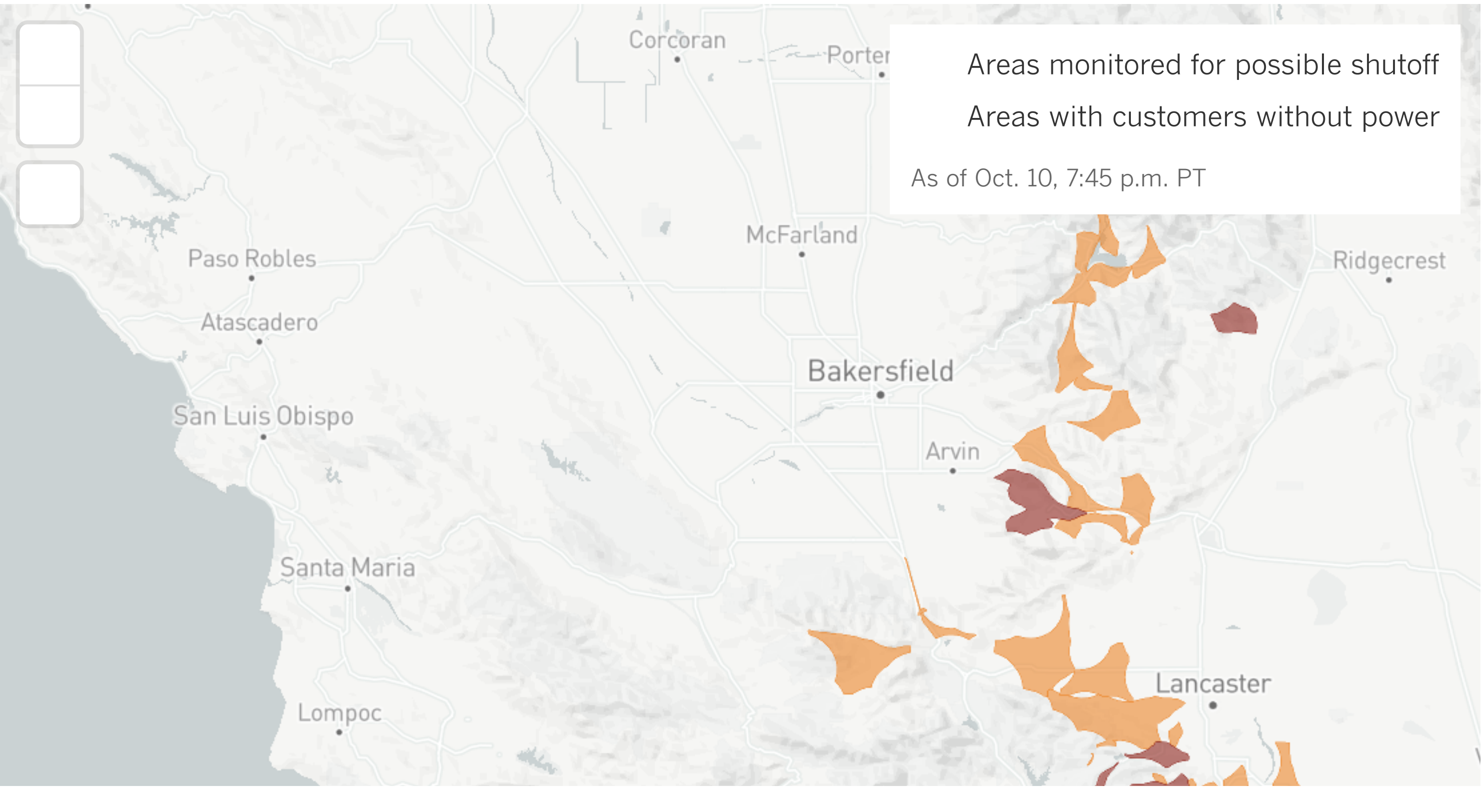
OCT. 9, 2019

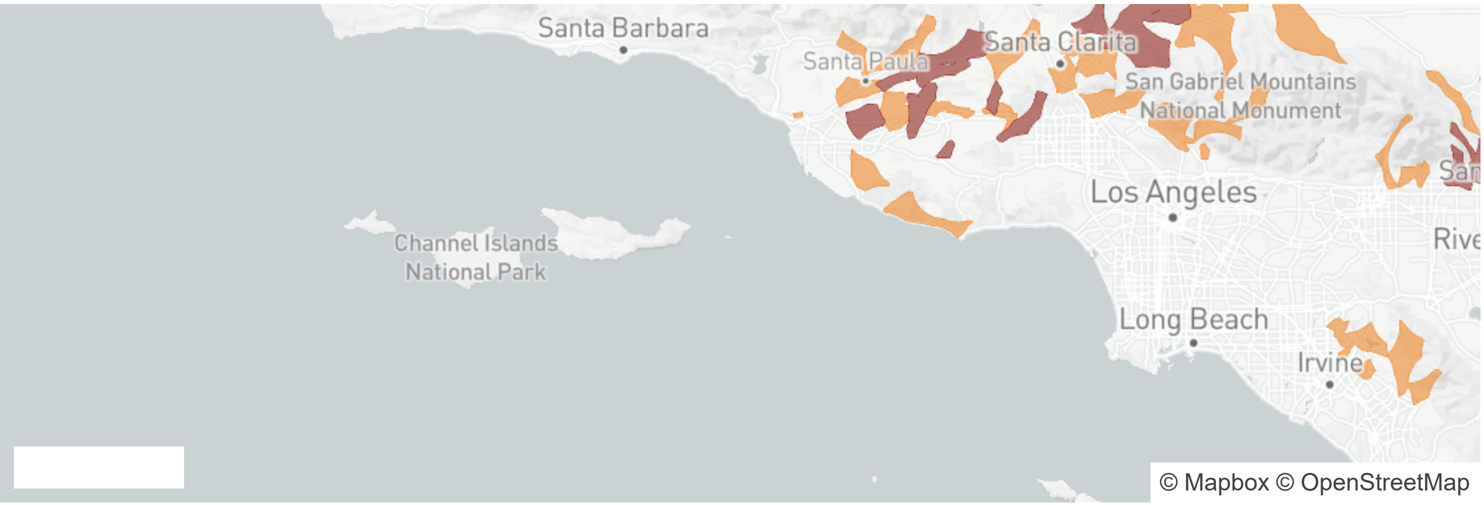
Southern California Edison has cut power to nearly 13,000 customers as firefighters battle several growing blazes fueled by strong Santa Ana winds. With forecasts for strong winds in the area, the utility said power could be cut off to more than 173,000 customers in parts of eight counties.

Edison's announcement follows a precautionary power outage in Northern California by Pacific Gas & Electric that began early Wednesday.

In the map below are the areas where Edison says the power has been and could potentially be turned off. Look up your address to see if you could be affected.

Search





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Edison outages may occur in the following areas:

Los Angeles County (about 49,439 customers)

- Lancaster
- Palmdale
- La Cañada Flintridge
- Malibu
- Pasadena
- Chatsworth
- San Fernando
- Santa Clarita
- Unincorporated areas including Acton, Agua Dulce, Boiling Point, White Heather, Sunland, Tujunga, La Crescenta, Montrose, Wildwood, Canyon Country, Newhall, Forest Park, Sleepy Valley, Del Valle, Leona Valley, Plum Canyon, Alpine, Merrie Dell, Indian Springs, Jumper Hills, Valencia, Stevenson Ranch, Mount Wilson, Valyermo, Paradise Springs, Humphreys, Placerita Canyon State Park, Little Rock, Pearblossom, Quartz Hill, Lake Hughes, Green Valley, Elizabeth Lake, Sylmar, Portal Ridge, Three Points, Upper Big Tujunga Canyon, and near Antelope Valley and unincorporated areas of Chatsworth and Sylmar

San Bernardino County (about 40,978 customers)

- Big Bear
- Calimesa
- Fontana
- Hesperia

- Rancho Cucamonga
- Rialto
- San Bernardino
- Yucaipa
- Yucca Valley
- Unincorporated areas, including the communities of Doble and Upper Holcomb Valley, Cajon Pass, Devore, Etiwanda, Lucerne Valley, Lytle Creek, Running Springs, Lake Arrowhead, Cedar Pines Park, Valley of Enchantment, Crestline, Valley View Park, Joshua Tree, Homestead Valley, Oak Hills, Muscoy, Green Valley Lake, Morongo Valley and unincorporated areas near Yucca Valley

Ventura County (about 23,139 customers)

- Fillmore
- Camarillo
- Simi Valley
- Santa Rosa Valley
- Ventura
- Unincorporated areas, including Sespe, Oak Village, north of Moorpark, Piru, Elkins Ranch Golf Course, Leesdale, north Fillmore, Santa Susana, Stauffer, Sycamore Canyon, Solromar, unincorporated areas near Piru and communities near Telegraph Road

Riverside County (about 21,366 customers)

- Banning
- Beaumont
- Calimesa
- Hemet
- San Jacinto
- Menifee
- Moreno Valley
- Perris
- Unincorporated Riverside County, including the communities of Whitewater and Bonnie Bell, Banning Pass, Cabazon, Owl, portions of Desert Hills Outlet Mall, North Palm Springs, Gilman Hot Springs, Lakeview, Nuevo, Mons, Mead Valley, Eden Hot Springs, Mountain Center, Good Hope and unincorporated areas near Beaumont and Banning

Orange County (about 7,250 customers)

- Rancho Santa Margarita
- Orange
- Unincorporated areas, including North Tustin

Kern County (about 19,313 customers)

- Tehachapi
- Unincorporated areas, including Frazier Park, Lake of the Woods, Pine Mountain Club, Bodfish, Kernville, Wofford Heights, Lake Isabella, Camp Owens, Lebec, Bear Valley Springs, Stallion Springs, Keene, Golden Hills, Sand Canyon, Alpine Forest, Manolith, Weldon, Bella Vista, Monolith, Onyx, Canebrake, and unincorporated areas of Walker Basin and Kernville

Mono County (about 13,963 customers)

- Mammoth Lakes
- Unincorporated areas near Bishop, including the community of Paradise and portion of Swall Meadows, Sunny Slopes, Mammoth Lakes (Trails, Core, North, Slopes), June Lake Village, Loop, Crestview, Mono Lake, Mono City, North Conway, Willow Springs, Bridgeport, Old Mammoth, Mammoth Lakes Basin, Lee Vining, Lee Vining Canyon, Falls Creek Tract and Bridgeport Valley to Twin Lakes Inyo County (about 131 customers)
- Unincorporated areas near Bishop, including Aspendell and Round Valley

Tulare County (about 108 customers)

- Unincorporated areas, including Fairview and Johnsondale

More fire coverage from the Los Angeles Times

L.A. County faces critical fire danger, possible power cuts as Santa Ana winds blow in

What makes the Santa Ana winds blow?

California's huge, humiliating power outages expose the vulnerabilities of PG&E's power grid

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Potential and current outage area data provided by Southern California Edison.

RESEARCH ARTICLE

Identifying riparian climate corridors to inform climate adaptation planning

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Abstract

Riparian habitats have been frequently identified as priority areas for conservation under climate change because they span climatic gradients and have cool, moist microclimates relative to surrounding areas. They are therefore expected to act as dispersal corridors for climate-induced species range shifts and to provide microclimatic refugia from warming. Despite recognition of these values, rigorous methods to identify which riparian areas are most likely to facilitate range shifts and provide refugia are currently lacking. We completed a novel analysis across the Pacific Northwest, USA, that identifies potential riparian corridors featuring characteristics expected to enhance their ability to facilitate range shifts and provide refugia. These features include large temperature gradients, high canopy cover, large relative width, low exposure to solar radiation, and low levels of human modification. These variables were used to calculate a riparian climate-corridor index using a multi-scale approach that incorporates results ranging in scale from local watersheds to the entire Pacific Northwest. Resulting index values for potential riparian corridors in the Pacific Northwest were highest within mountainous areas and lowest within relatively flat, lowland regions. We also calculated index values within ecoregions, to better identify high-value riparian climate corridors within the relatively flat, degraded areas where they may most contribute to climate adaptation. We found that high-value riparian climate-corridors are least protected in flat, lowland areas, suggesting that such corridors should be high priorities for future conservation effort. Our analysis provides critical information on valuable riparian climate-corridors to guide climate adaptation efforts (and riparian management and restoration efforts) in the Pacific Northwest, while offering a novel approach that may be applied to similar efforts in other geographies.

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Introduction

As climate change progresses and concern grows over the ability of species and ecosystems to adapt [1–2], considerable effort has been devoted to identifying areas on the landscape expected to promote biological resilience to change [3–5]. Riparian areas have been frequently

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identified as important features to conserve for climate adaptation [6–9], because they span the climatic gradients species are likely to follow as they track shifting areas of climatic suitability [10–12] and contain microclimates that are significantly cooler and more humid than immediately surrounding areas [13]. For these reasons, they are expected to provide dispersal corridors for species undergoing climate-induced range shifts [7,9] and microclimatic refugia from warming for species with limited movement capacities [14,5–6]. Riparian areas may also offer especially effective conservation umbrellas under climate change, because they disproportionately contribute to regional species richness [15–16], provide habitat for many upland species as well as riparian specialists [15–16], and directly contribute to the climate resilience of adjacent freshwater aquatic habitats [17–18]. Despite this recognition, few methods have been proposed for identifying priority riparian areas for climate adaptation.

Riparian areas are frequently prioritized in conservation planning efforts (e.g., [19–20]), but there are few examples of approaches aimed at identifying those that are most likely to promote climate adaptation. Available approaches for identifying riparian corridors to promote climate-induced range shifts include a conservation planning analysis for South Africa that included riparian corridors constructed by applying a fixed buffer around rivers connecting coastal to inland habitats to promote elevational species range shifts [21]. Similarly, riparian areas associated with 2nd order streams linking the Pacific Ocean to high elevations were prioritized in a climate adaptation analysis for California, USA [22]. In another analysis, a land facet corridor analysis aimed at promoting species range shifts in Arizona, USA, connected large blocks of natural habitat using riparian corridors identified by applying a fixed buffer around expert-identified streams and riparian habitats [23]. Most of these analyses used rivers as coarse proxies for riparian habitat, and none rigorously accounted for variability in riparian area quality, which we argue strongly influences the degree to which riparian areas may facilitate range shifts and provide refugia.

To address the need for a rigorous approach to identify priority riparian areas for climate adaptation, we completed a novel analysis that identifies potential riparian corridors expected to promote the ability of biodiversity to respond to climate change. Specifically, we developed a riparian climate-corridor index to quantify the degree to which riparian areas may promote range shifts and provide refugia, identifying those riparian areas that: 1) span large temperature gradients, 2) have high levels of canopy cover, 3) are relatively wide, 4) have low solar insolation, and 5) exhibit low levels of human modification. These variables were derived from the theoretical and empirical literature on species' responses to observed and projected climatic change. For example, riparian corridors that span large climatic gradients may help promote climate-induced range shifts from warmer to cooler areas [11–12]; riparian areas are already used as movement corridors for both riparian and upland species [24–26], and those spanning climatic gradients may offer particularly effective conduits for range migration, particularly across flat, degraded landscapes [27]. The effectiveness of such corridors would be further enhanced by high levels of canopy cover and greater riparian area width, features that have been shown to increase wildlife use of riparian areas as movement corridors [25], and to help moderate temperatures within riparian areas and promote the resilience of neighboring aquatic systems [17, 28]. Riparian corridors with lower exposure to solar insolation may also feature cooler temperatures and greater moisture [13, 29], increasing their value as microclimatic refugia [30–32]. Finally, riparian corridors with lower levels of human modification are likely to be more permeable to wildlife movement [33], while also being less vulnerable to exotic species invasion and other stressors that may inhibit species movements and reduce refugia quality [34].

Because these characteristics are likely to vary by the scale of analysis, and because scales of climate-induced range shifts and microclimatic refugia are likely to vary among species and over time [35,14], we developed a multi-scale approach to calculating riparian climate-corridor index values that incorporates results ranging in scale from local watersheds to the entire Pacific Northwest, USA. We also evaluated the protected status of riparian climate-corridors to help inform potential conservation action for maintaining riparian climate-corridor networks. Our analysis may thus provide critical information for guiding riparian management and climate adaptation efforts in the Pacific Northwest, while offering a novel approach that may be applied to similar efforts in other geographies.

Materials and methods

Study area

We completed our analysis for the Pacific Northwest, USA (USGS Water Resource Region 17; Fig 1). The Pacific Northwest includes a relatively cooler, moister region between the Pacific Coast and Cascade Range that is dominated by evergreen temperate forest; and a relatively drier region between the Cascade Range and Rocky Mountains that experiences more pronounced seasonality in temperature and features more diversity in vegetation types, from mixed forest at higher elevations to sagebrush-steppe in more arid lowlands.

Fig 1. Analysis extent. We completed our analysis for the Pacific Northwest hydrologic region (Water Resource Region 17, in dark gray).

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Analysis inputs

To identify high value riparian climate-corridors, we used a map of potential riparian areas identified by Theobald et al. [36], rather than a map of riparian vegetation. The potential riparian area map identifies the physical template where the dynamics of riparian vegetation are expected to occur, based on hydrological (stream discharge) and geomorphological (valley bottom shape) information rather than the (current) presence of riparian vegetation [36]. This 30 m data layer thus provides a comprehensive and consistent estimate of potential riparian area while avoiding many of the data gaps and inconsistencies [37] associated with existing maps of riparian vegetation derived from land cover (e.g., US LANDFIRE, US Fish & Wildlife Service National Wetland Inventory), which often have difficulty distinguishing riparian from non-riparian vegetation at 30 m resolution [37]. The potential riparian area dataset also provides key additional data layers (e.g., flow direction; see below) required by our analysis.

Our analysis aimed to identify the extent to which riparian corridors span large temperature gradients, have high levels of canopy cover, are relatively wide, have low exposure to solar radiation, and exhibit low levels of human modification. Our analysis thus included the following five variables (Table 1): mean annual temperature, canopy cover, riparian area width, potential relative radiation, and landscape condition.

We calculated mean annual temperature (T) as the 30-year mean of mean annual temperatures from 1961–1990, using a 90 m digital elevation model and the ClimateWNA tool [38], which extracts and downscales PRISM [39] monthly data and calculates climate variables for specific locations based on latitude, longitude, and elevation. For canopy cover (C), we used the percent tree canopy cover dataset for 2011 from the National Land Cover Dataset [40, 41]. We calculated potential riparian area (A), a measure of the width of potential riparian areas, directly from the 30 m potential riparian area data layer from Theobald et al. [36]. We used the 30 m National Elevation Dataset [42] to calculate potential relative radiation (R), a unitless measure of solar radiation that takes into account temporal changes in solar orientation as well as topographic shading from adjacent landforms [43]; such shading has been shown to contribute to lower temperatures in complex terrain [13–14]. We used the landscape condition (L) model [44] as a measure of the degree to which potential riparian areas have been affected by human activities. Although a more recent and higher-resolution dataset on human modification was available [45], we used L to be consistent with the Western Association of Fish and Wildlife Agencies Crucial Habitat Assessment Tool [46].

Table 1. Analysis variables and source data.

Analysis Variable	Base Layer	Base Layer Resolution	Year Represented by Base Layer	Base Layer Sources
Mean Annual Temperature (T)	PRISM Mean Annual Temperature (downscaled using Climate WNA)	90 m	1961–1990 (mean historical temperature)	Daly et al. [39] (http://prism.oregonstate.edu/), Wang et al. [38] (http://climatewna.com/)
Canopy Cover (C)	NLCD Percent Canopy Cover	30 m (resampled to 90 m using bilinear interpolation)	2011	National Land Cover Dataset [40]
Riparian Area (A)	Potential Riparian Area	90 m	2009 (digital elevation model)	Theobald et al. [36]
Potential Relative Radiation (R)	Potential Relative Radiation (calculated using digital elevation model)	30 m (resampled to 90 m using bilinear interpolation)	2009 (digital elevation model)	This study, following methods of Pierce et al. [43], and using a digital elevation model from the National Elevation Dataset (http://ned.usgs.gov/).
Landscape Condition (L)	Landscape Condition	270 m (resampled to 90 m using bilinear interpolation)	2010 (roads); 2006 (development); 2001 and 2006 (landcover)	Western Association of Fish and Wildlife Agencies Crucial Habitat Assessment Tool [46], based on the NatureServe Landscape Condition Model [44]

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Calculating a riparian climate-corridor index

We calculated an index of riparian climate-corridor quality for individual, ecologically-relevant spatial units that we call "potential riparian corridors," which we define as the potential riparian area that runs longitudinally along a stream/river from the stream outlet (or mouth) up through the hydrologic network of a watershed, ending at the stream initiation point (or headwater). For each potential riparian corridor, we calculated a riparian climate-corridor index using three main steps.

First, we accumulated the values of four variables (*C*, *A*, *R*, *L*) from locations (cells) within potential riparian areas laterally (i.e., orthogonal to the neighboring stream) to the nearest cell along the central flow path that follows the mid-line of streams/rivers (Fig 2a).

Second, we accumulated the values longitudinally along the central flow path within the stream/river, from its outlet to its headwater (Fig 2b). We accumulated values upstream rather than downstream to simulate the process of upward range movement along riparian corridors, from watershed outlets toward higher-elevation headwaters. Accumulating upstream also allowed us to calculate index values for individual riparian corridors adjacent to a stream/river reach running between its headwater and watershed outlet, because accumulating downstream would result in a single accumulated index value for an entire watershed. Third, we used these accumulated variable values to calculate an index of climate adaptation quality for the riparian climate-corridor from the outlet to headwater. Representing potential riparian corridors using a raster representation (rather than stream line vectors) allowed us to account for subtle gradients and variations within potential riparian areas—vital information lacking in previous

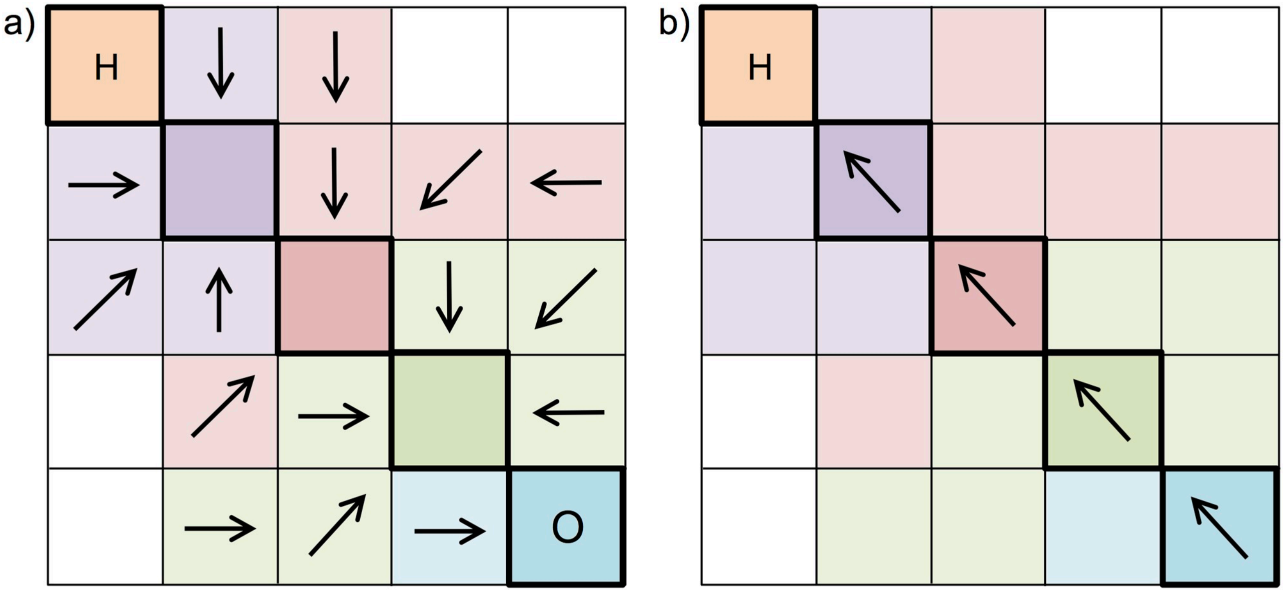

Fig 2. Using Flow Direction, Flow Accumulation, Flow Length tools to calculate the riparian climate-corridor index for a potential riparian corridor. a) For all potential riparian cells draining into a given cell in the streamline (outlined in bold, with it and all cells draining into it shown in the same color), we calculate, for each variable (*C*, *R*, *L*), the average value across the cells that contribute (accumulate) to the stream flow cell, and attribute this average value to the streamline cell (or the midline cell, for larger water bodies) using the Flow Direction and Flow Accumulation tools in ArcGIS. We calculate *A* as the number of potential riparian cells draining into the streamline cell. b) We then calculate, for each variable (*C*, *R*, *L*, *A*), the average value across all streamline cells from the outlet (O) to the headwater (H), and attribute this average value to the headwater using the Flow Length tool in ArcGIS. We also attribute a value for *T*, calculated as the absolute difference in temperature between the outlet and headwater cells. We then standardize (0–1) the average value for each variable (for equal weighting) and calculate the index, attributing this index value to the headwater cell. This is repeated for each downstream outlet until reaching the ocean, each time attributing the index value to the headwater cell. Each streamline cell is then given the average index value attributed to its upstream headwaters.

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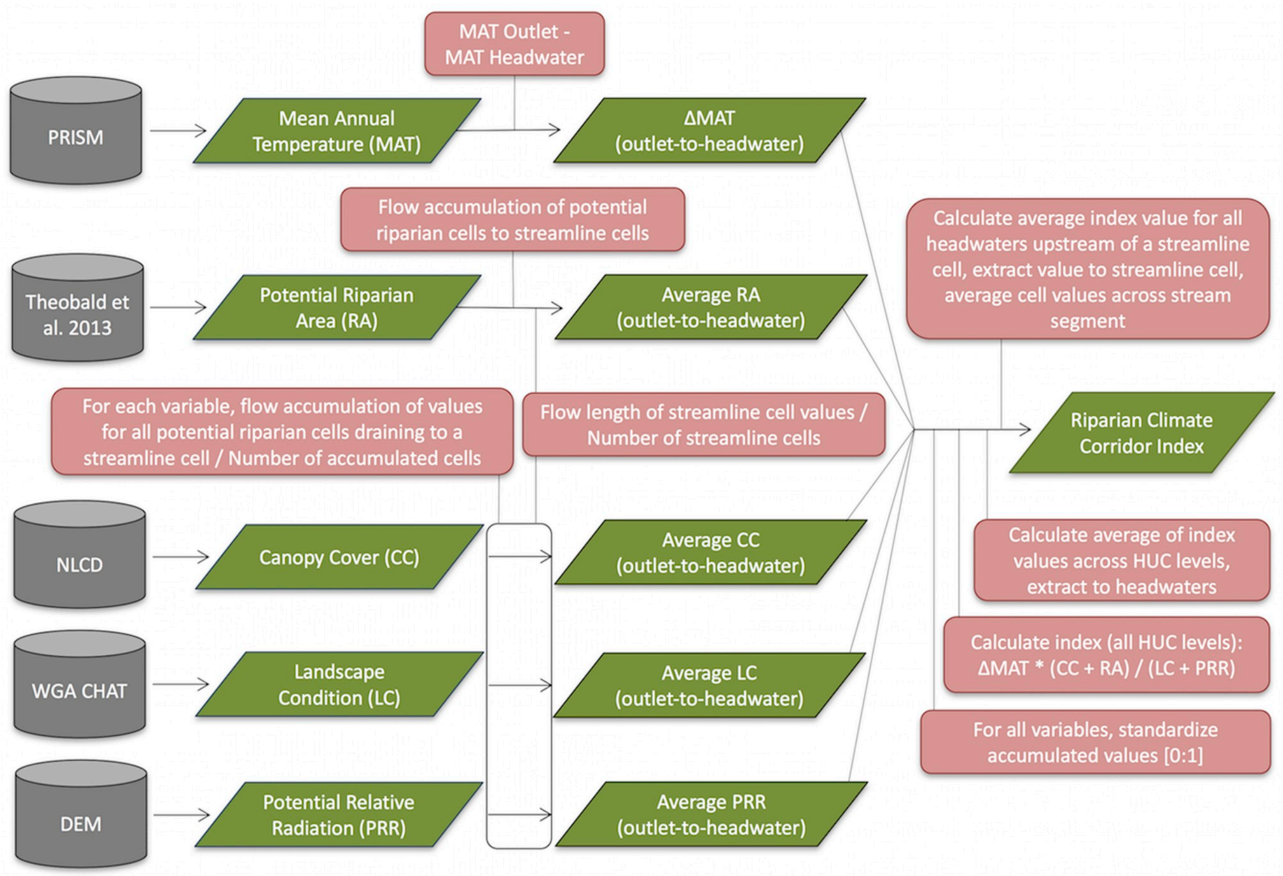

Fig 3. Summary of modeling approach, including key inputs, outputs, and analysis steps. Data sources are shown in gray, processing steps in pink, and inputs and outputs in green.

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studies. For rivers wider than 90 m, we excluded water cells when calculating variable values. Note that we represented spatial features, such as elevation and land cover, at 30 m resolution, but accumulated the up-scaled data at 90 m for computational purposes. A more detailed description of our analysis is provided below, and summarized in Fig 3.

1. Accumulate values within potential riparian corridors laterally to the stream line. We clipped the *C*, *R*, and *L* rasters to the extent of the potential riparian area. We then accumulated C, R, and L values along flow paths for all potential riparian cells draining into a given cell that represents the center of the stream line (i.e. the central flow path). That is, each cell located along the central flow path was attributed with the sum of the values for that variable for all the potential riparian cells that drain into it, using hydrologic tools in ArcGIS v10 software [47]. We then divided the accumulated value for each variable by the number of accumulated cells, so that, for each variable, each central flow path cell in the adjacent stream/river was ultimately attributed with the average variable value for its contributing potential riparian cells. The flow-accumulated area for the potential riparian area (*A*) was calculated in a similar manner, by accumulating the number of potential riparian cells draining into each central flow path cell in the adjacent stream/river. In cases where no potential riparian area cells drained into a central flow path cell, values for each variable were measured for only the central flow path cell itself, which was given an *A* value of 1.

2. Accumulate values for each variable longitudinally from stream/river outlet to headwater. We accumulated values along individual streamlines running from the watershed outlet to a stream's headwater, for each of the four variables (C, A, R, L). These accumulated values were then extracted to the central flow path cell at the stream/river's headwater, and divided by the number of contributing central flow path cells, to provide an average value for each variable for the associated potential riparian corridor. Mean annual temperature (T) was also extracted at each watershed outlet (or sink, in the case of closed basins) and for each headwater, and the difference between the two calculated and extracted to each stream/river's headwater. The average value for each variable was then divided by the largest value for that variable within the full study region, to standardize values to the range 0:1.

3. Calculate riparian climate-corridor index for each watershed-scale riparian corridor. We used the averaged, standardized values for each variable to calculate a Riparian Climate-Corridor Index for each watershed-scale riparian corridor, using the following formula:

$$Riparian\ Climate - Corridor\ Index = \Delta T \times [(C + A)/(R + L)]$$

Index values will thus be highest for those riparian corridors with the largest change in temperature (T) from outlet to headwater, highest percent canopy cover (C), greatest width (A), lowest exposure to solar radiation (R), and lowest level of human modification (L). Where ΔT was negative (indicating a higher temperature at the headwater than at the outlet), the index value was set to 0, to maintain higher index values for corridors leading from warmer to cooler areas across scales (see description of multi-scale approach, below). Our analysis is thus similar to other climate-gradient corridor approaches [11–12] in that it prioritizes corridors connecting warm areas to cool (in this case, headwater and outlets) using pathways that follow monotonic gradients (i.e., moving along gradients in only one direction, from warm to cool). All index values were extracted to the headwater associated with each potential riparian corridor.

4. Account for scale effects. We calculated a multi-scale, riparian climate-corridor index using the above procedure for riparian corridors within 6th, 5th, 4th, 3rd, 2nd, and 1st field HUCs (i.e., nested watersheds, from smallest to largest, respectively). HUCs are hierarchical hydrologic unit codes (HUC) assigned to all watersheds in the US [48]; the watershed cataloguing system nests watersheds into progressively larger units, similar to Pfafstetter codes that are also used globally. Our method should thus be applicable to any similar watershed cataloguing system in other countries. This procedure resulted in up to six index values being extracted to each headwater, corresponding to the index values of progressively longer downstream potential riparian corridors adjacent to each stream/river from its headwater to its outlet for progressively larger watersheds, eventually terminating at the ocean (or sink, in the case of closed basins). We scaled each of these nested index values to the range (0:1) and averaged them (equally-weighted), so that the final index value extracted to each headwater would reflect the climate adaptation value of all of its downstream riparian corridors. Finally, we calculated, for each individual central flow path cell within streams/rivers, the average of the index values attributed to all of its upstream headwaters. The final index values for each flow path cell within streams/rivers thus reflect the degree to which its adjacent potential riparian area cells are expected to help facilitate range shifts and provide refugia, from local to regional scales.

We also calculated a measure of riparian climate-corridor quality for entire watersheds by calculating the average of index values for all riparian climate-corridors within a given HUC. To account for differences in index values among ecoregions, and to more easily identify the highest quality riparian climate-corridors within each ecoregion, we binned all index values into 5 equal-area quintiles within each Level III ecoregion [49].

GAP analysis and sensitivity testing

We evaluated the degree to which high-value riparian climate-corridors identified by our analysis fall within currently designated protected areas by measuring the GAP status of riparian climate-corridors within 1) the top quintile of index scores, 2) the top two quintiles, and 3) all quintiles, for both the entire Pacific Northwest and within ecoregions. GAP status codes are provided by the US Geological Survey's Gap Analysis Program (GAP), and measure the degree to which lands in the US are managed for conservation [50]. Code 1 and 2 denote the highest degree of management for conservation (and meet the IUCN definition of protected), while Code 3 is given to lands that support multiple uses, including resource extraction. Code 4 lands are unprotected or have unknown management intent.

We also tested the sensitivity of the riparian climate-corridor index to the inclusion of individual input variables by removing individual variables one at a time, re-calculating the index, and measuring resulting differences across the study area. We also calculated correlation coefficients among these index values, as well as correlation coefficients among individual variables, to aid in interpretation of results.

Results

Riparian climate-corridor index values

We found that the climate adaptation potential of riparian corridors varies considerably, both across the Pacific Northwest (Fig 4) and within individual watersheds (Fig 5). Index values ranged from 0 to 0.83 (Fig 6), with the highest index values found in mountainous areas (e.g., the Cascade Range), and the lowest index values found in relatively flat, lowland regions such as the Columbia Plateau. Mountainous areas exhibited higher ΔT scores, on average, as well as higher canopy cover (C), solar insolation (R), and landscape condition (S1–S4 Figs). These effects were amplified by positive correlations among all input variables but riparian area (S5 Fig): relatively flat areas with low ΔT tended to also have lower canopy cover (C), were in poorer landscape condition (L), and had higher solar insolation (R). Indeed, removing ΔT from the index calculation resulted in a spatial pattern similar to that seen when the calculation included ΔT (Fig 7); including ΔT generally reinforced the pattern of lower values in areas with gentler topographic relief (often near outlets) and higher values in mountains (often near headwaters).

Most potential riparian corridors had relatively low index values (Fig 6). The relatively high number of potential riparian corridors with index values equal to 0 is due in large part to the relatively cool temperatures of the Pacific Northwest coast; many interior headwaters have warmer mean annual temperatures than their streams' coastal outlets. Because negative ΔT values were converted to zero and ΔT is multiplied by the rest of the index, such potential riparian corridors receive a zero value, though they may otherwise be of high quality (Fig 7). For example, the low index scores received by otherwise high-quality riparian areas in the western Olympic Peninsula were due to negative or relatively low ΔT between coastal stream outlets and headwaters (Fig 7, S1 Fig).

Areas with no headwaters (and thus no index scores) were seen in regions lacking surface water due to high aridity and/or high soil permeability (Fig 4).

GAP analysis and sensitivity testing

We found that riparian climate-corridors varied regionally in their level of protection (Fig 8). For riparian climate-corridors with the highest 20% of index scores, 35.5% were fully protected (GAP status 1–2) and 50.4% were partially protected (GAP status 3) across the Pacific

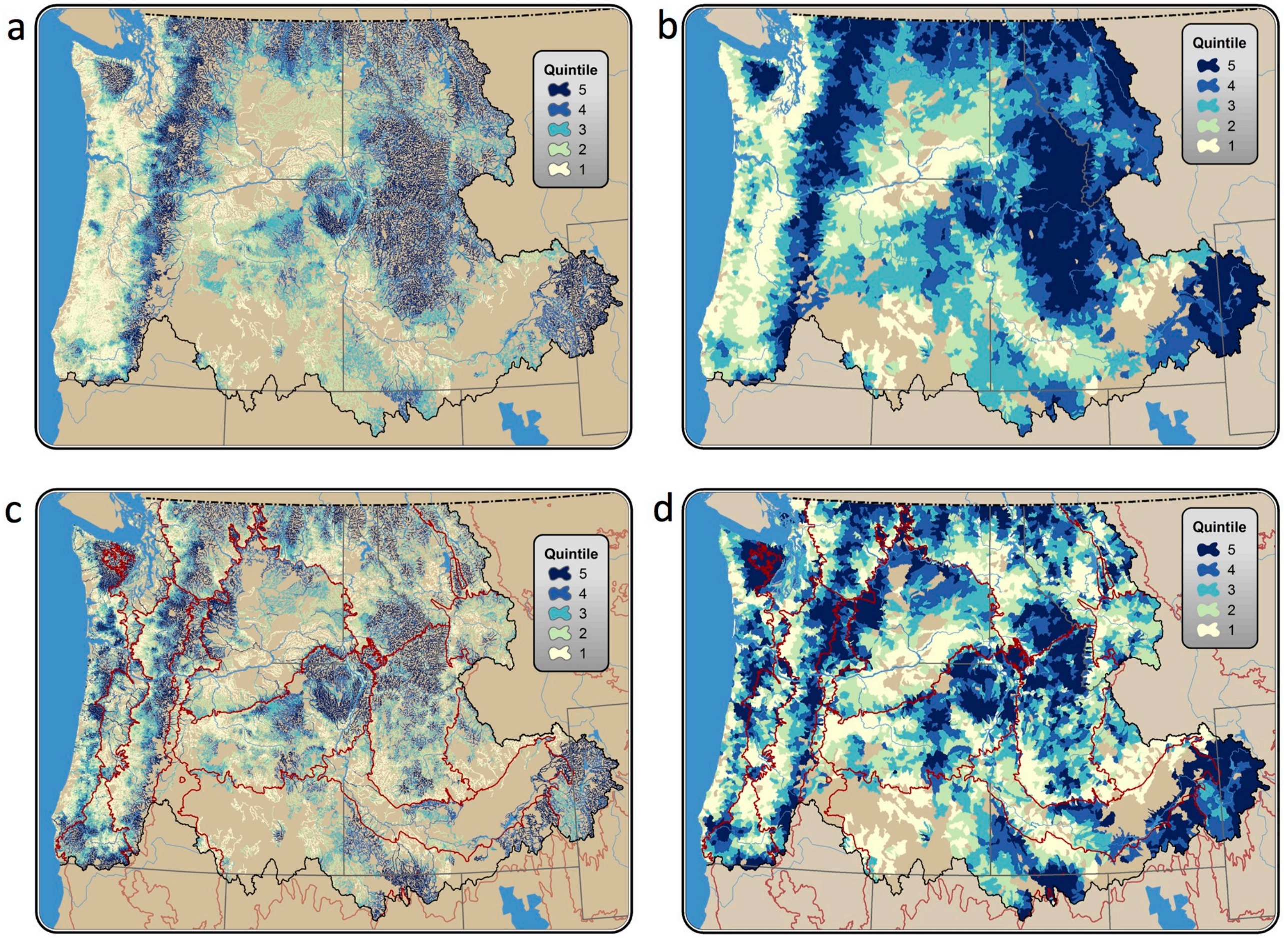

Fig 4. Riparian climate-corridor index values for the Pacific Northwest. Values are averaged across nested watershed scales (6th to 1st field HUCs), attributed to streamlines associated with potential riparian corridors. Values are shown by quintile for the Pacific Northwest, USA (panels a and b), and within ecoregions (panels c and d); and for both individual riparian corridors (panels a and c) and averaged across 6th field HUCs (panels b and d).

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Northwest. Within ecoregions, GAP status of riparian climate-corridors with the highest 20% of index scores varied from 83.8% fully protected and 14.6% partially protected in the North Cascades, to 1.3% fully protected and 18.8% partially protected in the Columbia Plateau.

We found that riparian climate-corridor index values were relatively insensitive to individual input variables (Fig 7). Removal of individual variables from the index calculation resulted in little change to index scores across the study area, resulting in an average change in index values of -0.0126 for removal of mean annual temperature (ΔT), +0.0051 for landscape condition (L), -0.0168 for canopy cover (C), -0.0607 for riparian area (A), and -0.1154 for potential relative radiation (R). Given the strong correlations among index variable values and elevation (i.e., that relatively flat areas with low ΔT also have lower canopy cover (C) and landscape condition (L), and higher solar insolation (R)), variable exclusion generally resulted in decreased values in mountainous areas and increased values in lower-elevation areas. Exclusion of R had a slightly stronger effect on index values in mountainous areas (lowering index values), and exclusion of T, C, and L had a slightly stronger effect on lower-elevation coastal areas (increasing values).

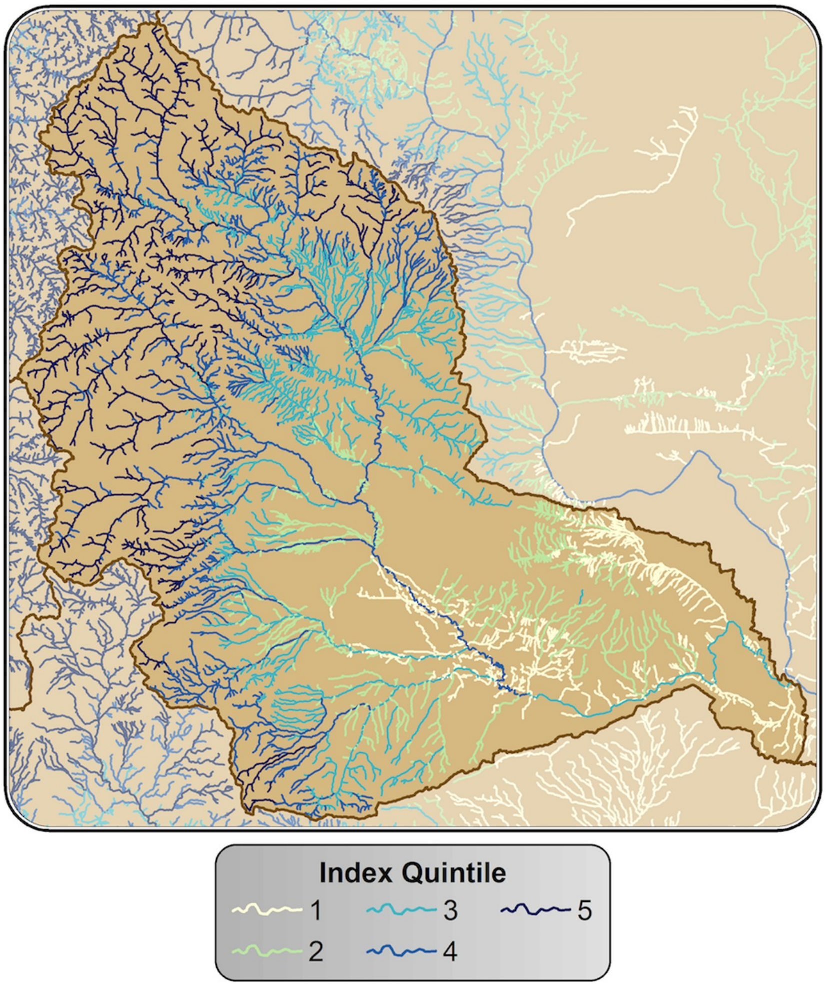

Fig 5. Riparian climate-corridor index values shown for an individual watershed. Values are shown by quintile and attributed to streamlines associated with potential riparian corridors.

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Discussion

Our analysis identified potential riparian corridors that span climatic gradients, have high canopy cover, low levels of solar exposure, low levels of human modification, and are relatively wide—characteristics expected to facilitate climate-induced range shifts and provide micro-climatic refugia. Not surprisingly, we found that potential riparian corridors in mountainous regions—which tend to be steep, forested, topographically shaded, and have low levels of human modification—had the highest riparian climate-corridor index values. We also found that potential riparian corridors in lowland areas—which tend to be flat and have low canopy cover, less topographic shading, and high levels of human modification—had the lowest values (Fig 4a and 4b). Because of the correlations of temperature with other variables, change in temperature—which we had expected to be a key variable for identifying riparian corridors with strong climatic gradients—in fact had a relatively modest impact on index scores (Fig 7), generally reinforcing the pattern of lower index values in areas with gentler topographic relief and higher values in mountains. The index is thus robust to our coarse approach to measuring temperature gradients along riparian corridors.

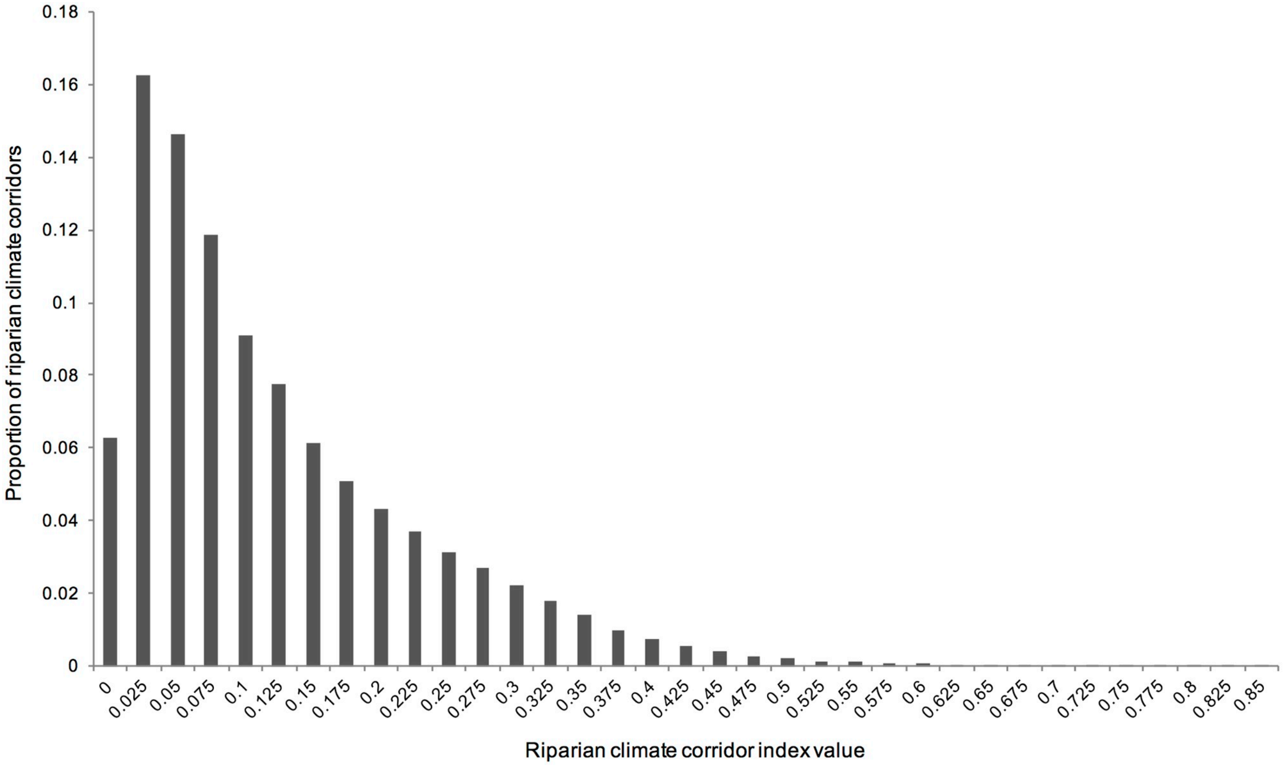

Fig 6. Distribution of riparian climate-corridor index values. Shown for all watershed-scale riparian corridors in the Pacific Northwest.

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We also found that relatively flat and highly modified ecoregions (e.g., the Columbia Plateau and Puget Lowlands ecoregions; Fig 4c and 4d) had the least protected high-scoring riparian climate-corridors among Pacific Northwest ecoregions (Fig 8). High-scoring riparian climate-corridors in these areas thus suggest immediate priorities for conservation action (e.g., protection or restoration), as they may provide some of the best adaptation opportunities in flat, highly modified landscapes that may limit species range movements and persistence in microclimatic refugia. We also found that a large number of otherwise high-quality potential riparian corridors along the coast received low index scores, because their interior headwaters have warmer mean annual temperatures than their streams' cooler, coastal outlets. These results emphasize that our index is designed to identify riparian climate-corridors expected to promote species range shifts from warmer to cooler areas, which may in some cases result in low scores for corridors that have high conservation value under static or current climates.

Index values for riparian climate-corridors along large rivers (e.g., the Columbia River) often had higher values than corridors within nearby lower-order streams (e.g., headwater streams). This is because higher-order streams frequently have tributaries at higher elevations; riparian climate-corridors associated with these higher-elevation tributaries tend to have relatively high index values, and the index values of riparian climate corridors along higher-order streams incorporate these upstream values. The high index values of riparian climate-corridors along higher order streams thus reflect their connectivity to high-scoring upstream corridors, and thus their capacity to promote range shifts and provide access to climatic refugia at a regional scale. Indeed, shorter riparian corridors, such as those that would be found along headwater streams, have been shown to be more effective at promoting species movements [51]. Thus, the trade-off of this multi-scale approach—designed to accommodate diverse

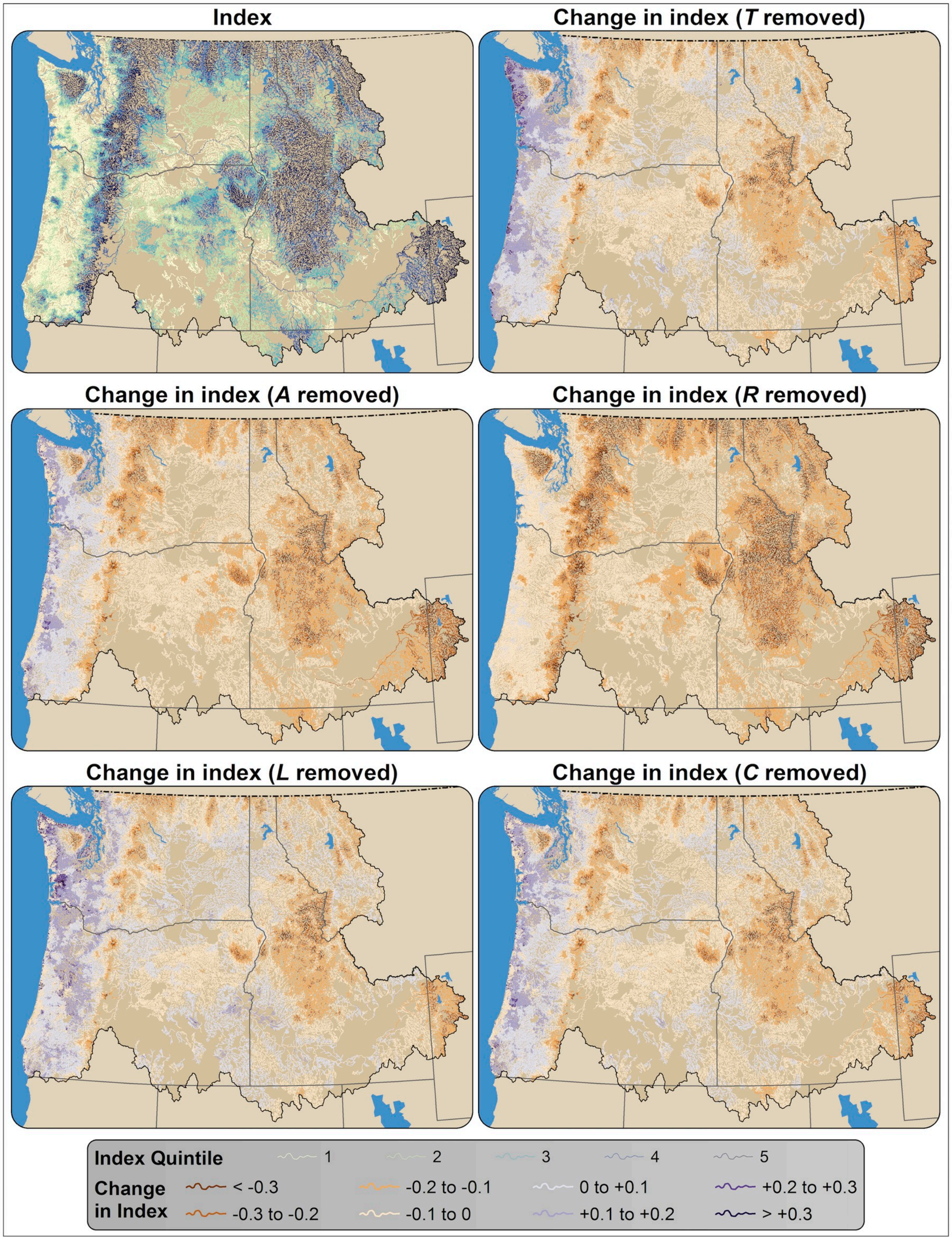

Fig 7. Sensitivity of riparian climate-corridor index values to individual analysis variables. Panels show the index with all variables included (top left), and the index with change in mean annual temperature (*T*) removed, with riparian area (*A*) removed, with potential relative radiation (*R*) removed, with landscape condition (*L*) removed, and with canopy cover (*C*) removed.

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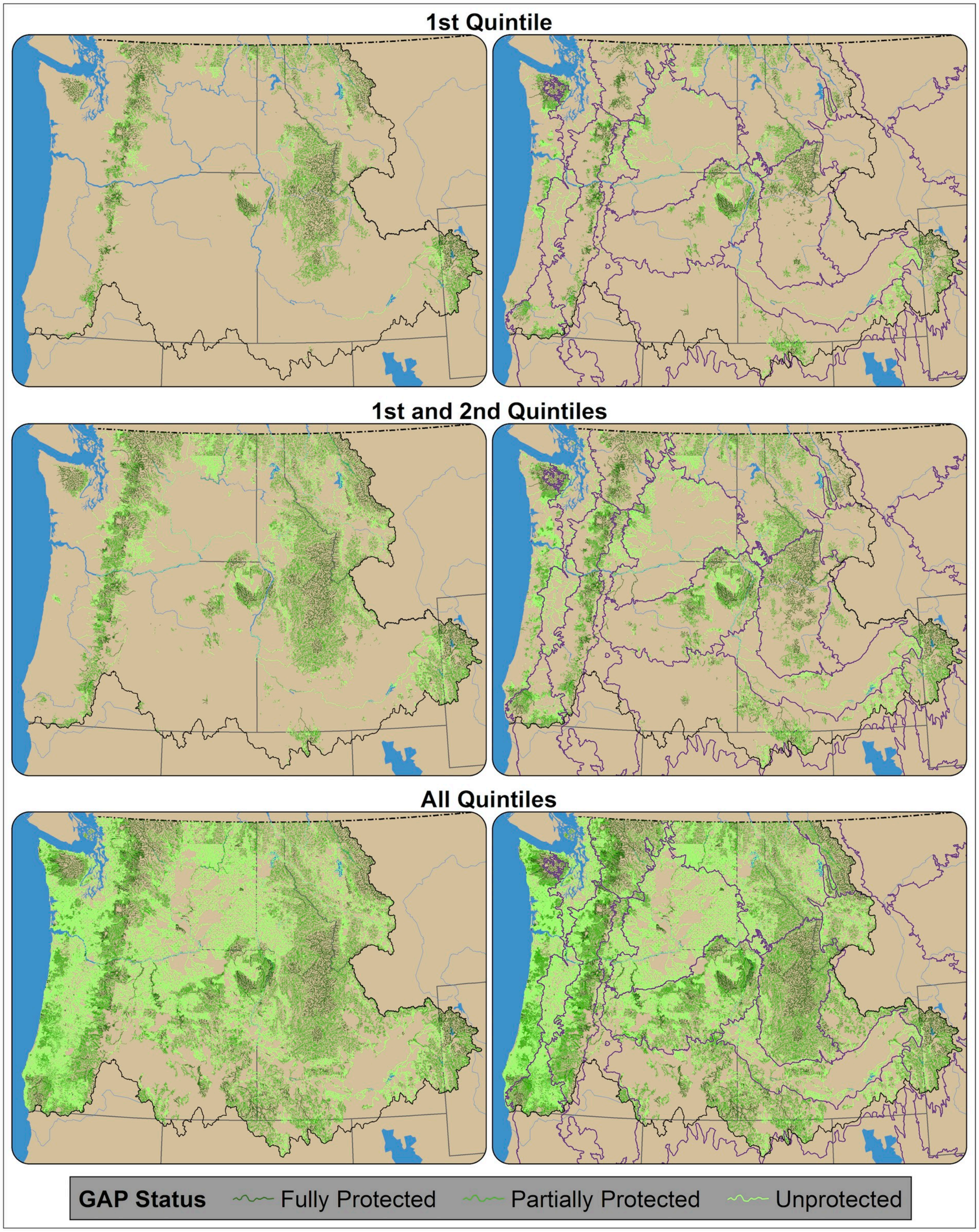

Fig 8. GAP status of riparian climate-corridors. GAP status is shown for riparian corridors within the top quintile of riparian climate-corridor index values (top row), top two quintiles (middle row), and all quintiles (bottom row); by both the entire Pacific Northwest (left column) and within ecoregions (right column). GAP status is shown for fully protected (GAP status 1 and 2; forest green), partially protected (GAP status 3; kelly green), and unprotected (GAP status 4; lime green) riparian climate-corridors.

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species with needs for movement and refugia at a range of scales—is its potential to overlook riparian climate-corridors that may be valuable at a more local scale, but do not meaningfully contribute to broader-scale, regional adaptation. Identifying riparian climate-corridors with high index values within ecoregions (Fig 4c and 4d) or local watersheds (S6–S10 Figs) may help address needs for more local-scale prioritization.

We recommend considering several caveats when applying the riparian climate-corridor index. First, this approach only indirectly accounts for connectivity along riparian corridors; while index values will decrease with increasing human modification along a corridor, the effect of local but severe movement barriers (e.g., towns, cliffs) on index values could be muted if human modification is low elsewhere along the corridor, particularly at broader scales. The analysis could thus be improved by incorporating explicit connectivity measures that sufficiently penalize high-resistance, local barriers that could sever connectivity; a range of connectivity modeling approaches could be adapted for this purpose (e.g., [52]). The analysis could also be improved by further validating analysis inputs and assumptions, such as empirically measuring canopy cover and solar insolation across riparian areas and testing their influence on temperature, and, ultimately, range shifts and refugia. Future comparison of our index to other indices of riparian quality (e.g., [53]) would also aid in interpretation of results. Thus, we recommend using this analysis as a means of identifying priority riparian areas for additional evaluation (e.g., field validation, comparison with other data sets, integration with other conservation values) before making decisions regarding conservation action.

We also recognize the scaling challenges in mapping riparian vegetation and modeling potential riparian areas. Our analysis provides estimates of potential riparian climate-corridors at (>90 m) due to data resolution and computation limitations. Future work can apply our approach using high resolution data that have (or will likely) become available. An additional caveat is the risk of unintended negative consequences (e.g., spread of invasive species or disease) by protecting or restoring riparian climate corridors to promote species movements. Our analysis reduces this risk by prioritizing those riparian areas that are in good condition, and therefore expected to be less vulnerable to invasion. Further, previous research has shown that the benefits of corridors outweigh potential negative effects [54], including potential risks related to climate-induced range shifts [55]. Indeed, the synergistic threats of habitat loss, fragmentation and climate change present an urgent need to restore landscape features such as riparian corridors that have historically provided natural conduits for species movement.

Although riparian areas are expected to provide critical movement corridors and refugia under climate change [6–7,9], they are also among the most threatened habitats in many regions [56]. Our analysis offers a first step toward identifying, for large regions, those riparian areas most likely to promote species' ability to respond to climate change, as well as those that may be most vulnerable to climate change and in need of restoration measures. Such information may offer valuable guidance for future investments in riparian protection and restoration as part of climate adaptation efforts.

Supporting information

S1 Fig. Mean annual temperature (*T*), based on the 30-year mean of mean annual temperatures from 1961–1990, using a 90 m digital elevation model and the ClimateWNA tool [34], which extracts and downscales PRISM [35] monthly data and calculates climate variables for specific locations based on latitude, longitude, and elevation.
(TIFF)

S2 Fig. Canopy cover (*C*), based on the percent tree canopy cover dataset from the National Land Cover Dataset [36].
(TIFF)

S3 Fig. Potential relative radiation (*R*), a unit-less measure of solar radiation that takes into account temporal changes in solar orientation as well as shading effects from neighboring topography [38], based on a 30 m digital elevation model from the National Elevation Dataset [36].
(TIFF)

S4 Fig. Landscape condition (*L*), provided by the Western Governors' Association's Crucial Habitat Assessment Tool (WGA 2013) as a measure of the degree to which potential riparian areas have been affected by human activities using the landscape condition model [39], where higher values correspond to lower landscape intactness.
(TIFF)

S5 Fig. Riparian area (*A*), based on the potential riparian area data layer from Theobald et al [32].
(TIFF)

S6 Fig. Riparian climate-corridor index values averaged across individual watersheds (6th field HUCs).
(TIFF)

S7 Fig. Riparian climate-corridor index values averaged across individual watersheds (5th field HUCs).
(TIFF)

S8 Fig. Riparian climate-corridor index values averaged across individual watersheds (4th field HUCs).
(TIFF)

S9 Fig. Riparian climate-corridor index values averaged across individual watersheds (3th field HUCs).
(TIFF)

S10 Fig. Riparian climate-corridor index values averaged across individual watersheds (2nd field HUCs).
(TIFF)

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Writing – review & editing: Meade Krosby, David M. Theobald, Robert Norheim, Brad H. McRae.

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Health Effects of the 2003 Southern California Wildfires on Children

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Rationale: **In late October 2003, Southern California wildfires burned more than 3,000 km^2. The wildfires produced heavy smoke that affected several communities participating in the University of Southern California Children's Health Study (CHS).**

Objectives: **To study the acute effects of fire smoke on the health of CHS participants.**

Methods: **A questionnaire was used to assess smoke exposure and occurrence of symptoms among CHS high-school students (n = 873; age, 17–18 yr) and elementary-school children (n = 5,551; age, 6–7 yr), in a total of 16 communities. Estimates of particulate matter (PM_{10}) concentrations during the 5 d with the highest fire activity were used to characterize community smoke level.**

Main Results: **All symptoms (nose, eyes, and throat irritations; cough; bronchitis; cold; wheezing; asthma attacks), medication usage, and physician visits were associated with individually reported exposure differences within communities. Risks increased monotonically with the number of reported smoky days. For most outcomes, reporting rates between communities were also associated with the fire-related PM_{10} levels. Associations tended to be strongest among those without asthma. Individuals with asthma were more likely to take preventive action, such as wearing masks or staying indoors during the fire.**

Conclusions: **Exposure to wildfire smoke was associated with increased eye and respiratory symptoms, medication use, and physician visits.**

Keywords: air pollution; asthma; sore throat; wheezing

AT A GLANCE COMMENTARY

Scientific Knowledge on the Subject

Adverse effects of fire smoke are known, but results in children are inconsistent due to a lack of large population-based studies.

What This Study Adds to the Field

The study quantifies effects of fire smoke on eye, upper, and lower respiratory symptoms. It gives first evidence of benefits of preventive actions.

In October 2003, a series of devastating wildfires burned in Southern California. The hot and dry Santa Ana winds encouraged the spread of fires across several locations to the north, east, and south of the Los Angeles metropolitan area, and dense plumes of smoke dominated much of the area for several days. Local air-quality monitors recorded hourly particulate matter concentrations approaching 1,000 $\mu g/m^3$ particles of aerodynamic diameter up to 10 μm (PM_{10}); these levels were 10 to 20 times the typically observed ambient levels (1, 2). The fires occurred over a wide geographic area, over a 480-km swath affecting six Southern California counties (Ventura, Los Angeles, San Bernardino, Riverside, Orange, and San Diego). The fires consumed more than 3,100 km^2 (750,000 acres) and destroyed 3,640 homes, 33 commercial properties, and 1,141 other structures (including several regional air-monitoring stations).

Most wildfire investigations focus on short-term changes in hospital admissions or on segments of the population believed to be especially sensitive to respiratory stress, such as patients with chronic obstructive lung disease (COPD) or asthma, or on those individuals especially prone to exposure, such as firefighters (3, 4). Medical surveillance data from San Diego County revealed significant increases in hospital emergency room visits for asthma, respiratory problems, and eye irritation during the 2003 fire period (5). Population-based investigations of the acute respiratory health effects of fire smoke on children's health have been limited and based on small samples. The lack of data may be contributed, in part, to the logistical challenge of implementing population-based studies during fire emergencies. Australian researchers investigated the health effects of bush fires and reported increased evening wet cough among a panel of 32 children with asthma but nonsignificant results for wheeze and β-agonist use (6). PM_{10} peaks were much lower (130 $\mu g/m^3$) than in the 2003 California fires. Associations of fire smoke and evening peak flow were also not conclusive (7). In Asia, the large 1997 fires resulted in an increased use of health services (4) and higher mortality rates both among infants and adults (8).

The Southern California fires offered a unique opportunity to conduct a population-based, large-scale investigation of the health consequences of the smoke from wildfires on children's health. The region affected by the wildfires included several communities participating in a long-term ongoing health study of California schoolchildren, the University of Southern California Children's Health Study (CHS) (9, 10). The goal of the CHS is to understand the contribution of long-term or lifetime exposure to ambient air pollution to children's respiratory health (9–11). Initial cohorts of children were recruited (1993 and 1996) from 12 communities across six Southern California counties. In 2002, an additional cohort of kindergarten and first-grade children

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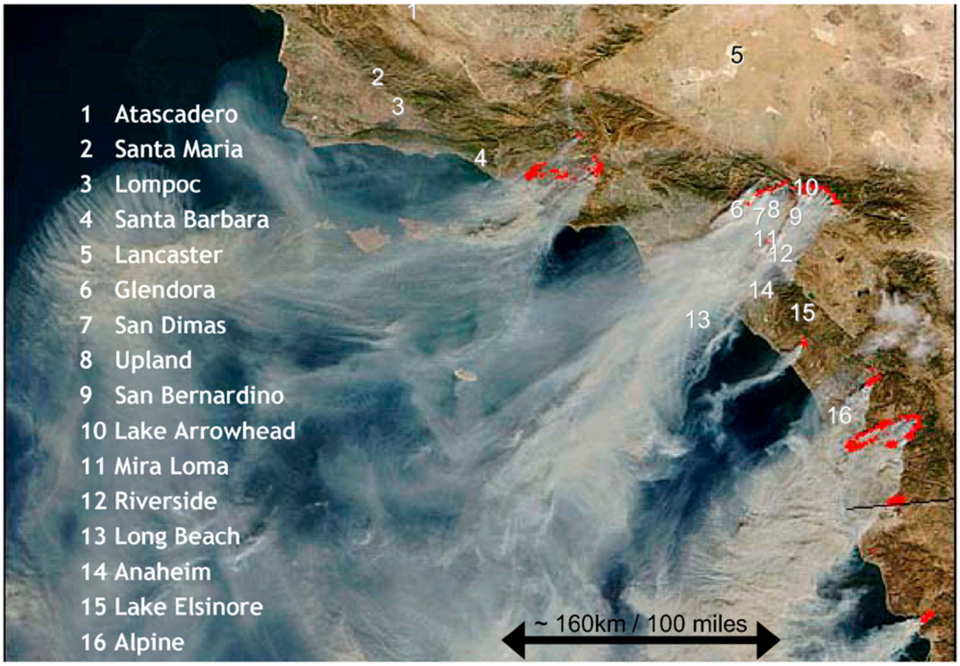

Figure 1. Satellite image of Southern California taken on October 24, 2003, showing the smoke plumes from numerous fires. Locations of the 16 Children's Health Study communities participating in the fire study are *highlighted*. Image courtesy of MODIS Rapid Response Project at NASA/GSFC.

(aged 5 to 6 yr) were enrolled from 13 partly overlapping communities (10). At least 12 of the 16 cohort communities were either directly affected by the fire (i.e., the community was the site of fire damage and human evacuation) or indirectly affected (by dense smoke covering the community). Figure 1 presents the cohort study towns in a satellite image of the wildfire areas taken in late October 2003.

To assess the effects of the wildfires, we implemented a questionnaire-based investigation of fire smoke exposure and symptoms for two of the existing and accessible study cohorts (12th-grade high-school students, and first- and second-grade elementary-school children). The availability of extensive sociodemographic and health data among this large sample of children offered a unique opportunity to efficiently investigate and quantify the health consequences of fire smoke exposure in both children with asthma and nonasthmatic children. Some of the results of this study have been previously reported in the form of an abstract (12).

METHODS

The CHS methods have been published elsewhere. Details about the fire study are provided online. In brief, the CHS consists of repeated annual health assessments to monitor the course of respiratory health. The fire questionnaire study focused on participants of two ongoing CHS cohorts, including one cohort of high-school students (17 to 18 yr old during the fire), originally enrolled in 1996, and a cohort of elementary-school children (aged 6 to 7 yr), recruited in 2002. The older student cohort included high schools from the 12 (9, 10) original CHS communities and the elementary-school cohort involved 13 communities (nine of which were the same) (10). The study protocol was approved by the institutional review board for human studies at the University of Southern California, and written, informed consent was provided by participating students and a parent or legal guardian of minors.

The 2003 Southern California fires peaked between October 20 and November 2. During November–December 2003, the high-school students and the parents of the elementary-school children received the fire questionnaire by mail (*see* online supplement) and/or during the first 6 mo in 2004 as an annex activity of the ongoing CHS. The reporting period referred to the "two weeks of the October 2003 fire period." Although the first page of the fire questionnaire asked about health-related problems, the second page referred to exposure to fire smoke and personal measures taken to modify this exposure (including evacuation, wearing of masks, reduction in time spent outdoors, and changes in physical activity). To quantify exposure duration, questionnaire response categories included the following: "not at all," "1–2 d," "3–5 d," "6–10 d," or "all days" (i.e., up to 2 wk).

Objective smoke measurements (i.e., PM_{10} [U.S. Environmental Protection Agency–approved Federal Reference Methods to quantify PM_{10}]) were available only on the community rather than on an individual level. PM_{10} was the strongest marker of fire smoke pollution (1, 2). High concentration periods lasted approximately 5 d; thus, we used the 5-d mean PM_{10} level to characterize fire smoke. Missing air-quality data required estimation procedures of the 5-d average PM_{10}. Five-day average PM_{10} concentrations were estimated for 5 of the 16 communities. San Dimas, Glendora, and Anaheim had all 5 d (October 24–28) estimated, and San Bernardino had 4 d (October 25–28) estimated. Because Alpine was directly affected by the fires from October 26 to 28, PM_{10} concentrations at Alpine were averaged over the 3 fire days with 2 d estimated (October 27–28). For more details, *see* text and Table E1 in the online supplement and Reference 1.

Statistical Analyses

To investigate the association between fire smoke exposure and symptoms, we chose multilevel approaches to distinguish within-community differences in exposure from the contrasts between communities. We used the reported "smell of fire smoke indoors" as the primary measure of exposure. We created two components of reported exposure response. The first was a between-community measure, derived from the community-specific mean response. The second was a within-community response, created by subtracting the community mean from the individual response, using a mixed-effects model with a logistic link. As described in the online supplement, the five exposure categories were combined into three levels, providing comparison across the following groups of "fire smoke smelled": no fire smoke, fire smoke smelled 1 to 5 d, and fire smoke smelled 6 d or more.

The first set of analyses was based on the reported levels of fire smoke smelled at home indoors, reflecting the change in symptoms due to an increase in the duration of (perceived) fire smell. In a second set of models, we replaced the reported community mean fire smoke response with the ambient 5-d mean PM_{10}. Thus, these between-community estimates reflected the change in symptoms for a change in ambient PM_{10} during the 5 most extreme days of fire smoke.

TABLE 1. HIGH-SCHOOL STUDENTS AND PARENTS (ELEMENTARY-SCHOOL CHILDREN) RESPONDING TO THE FIRE QUESTIONNAIRE WITHIN 8 WEEKS OF THE FIRE (EARLY RESPONSE, NOVEMBER/DECEMBER 2003) AND TOTAL RESPONSE (INCLUDING JANUARY TO JUNE 2004 DURING CHILDREN'S HEALTH STUDY HEALTH VISITS)

	High-School Students (17–18 yr old)			Elementary-School Children (6–7 yr old)		
Community	Baseline Population	Early Response (2003), n (%)	Total Response (2003/04), n (%)	Baseline Population	Early Response (2003), n (%)	Total Response (2003/04), n(%)
Alpine	75	35 (46.4)	70 (93.3)	397	165 (41.5)	299 (75.3)
Anaheim	—	—	—	419	90 (21.4)	251 (59.9)
Atascadero	74	68 (91.8)	70 (94.5)	—	—	—
Glendora	—	—	—	466	228 (48.9)	374 (80.2)
Lake Arrowhead	70	28 (40.5)	67 (95.7)	401	163 (40.6)	301 (75.0)
Lake Elsinore	66	23 (35.3)	62 (93.9)	386	254 (65.8)	254 (65.8)
Lancaster	64	27 (41.5)	61 (95.3)	—	—	—
Lompoc	80	32 (40.0)	78 (97.5)	—	—	—
Long Beach	85	35 (41.6)	79 (92.9)	366	87 (23.7)	239 (65.3)
Mira Loma	64	51 (78.4)	62 (96.8)	510	280 (54.9)	286 (56.0)
Riverside	69	53 (76.8)	67 (97.1)	439	150 (34.1)	285 (64.9)
San Bernardino	—	—	—	410	94 (22.9)	255 (62.1)
San Dimas	74	39 (52.7)	74 (100)	393	169 (43.0)	213 (54.1)
Santa Barbara	—	—	—	468	166 (35.4)	360 (76.9)
Santa Maria	66	25 (39.0)	62 (93.9)	470	125 (26.5)	311 (66.1)
Upland	86	39 (46.4)	82 (95.3)	426	198 (46.4)	347 (81.4)
Total	873 (100)	455 (52.4)	834 (95.5)	5,551 (100)	2,169 (39.0)	3,775 (68.0)

The final models included those covariates that were independent predictors and/or confounders in the models of at least one symptom, namely sex, ethnicity, educational level of parents, asthma status before the fire (physician-diagnosed asthma), and cohort (high-school vs. elementary-school cohort). A p value of 0.05 or less was considered statistically significant. In addition, all analyses were stratified by asthma status. All analyses were conducted with the statistical software SAS/STAT, version 9 (2002; SAS Institute, Cary, NC).

RESULTS

Table 1 summarizes the study populations and participation. High-school students' participation rates during the first 8 wk (2003) reached 52.4%, whereas only 39.0% of the parents (younger cohort) returned the mail-in questionnaire. The extended distribution of the fire questionnaire during 2004 strongly improved response rates, ultimately reaching 95.5% in the older and 68.0% in the younger cohort.

Table 2 summarizes the distribution of reported fire exposure and the ambient levels of measured or estimated PM_{10} (*see* METHODS). Both the subjective and objective measures of fire smoke showed that communities not directly affected by local fires suffered substantial smoke exposure (e.g., Mira Loma, Riverside, and Anaheim).

Table 3 summarizes the prevalence of the reported outcomes, by cohort and asthma status. As expected, prevalence rates were much higher among individuals with asthma. Dry cough, medication, and physician visits were more frequently reported by parents of elementary-school children, whereas high-school students were more likely to report eye symptoms. Home loss due to fire was reported by 35 (0.75%) study participants. In Alpine and

TABLE 2. PREVALENCE OF REPORTED SMELL (%) OF FIRE SMOKE INDOORS (BY COHORT), 5-DAY MEAN PM_{10} DURING THE FIRE PERIOD,* AND LONG-TERM AMBIENT PM_{10} IN THE 16 COMMUNITIES

	High-School Students (*n = 834*)				Elementary-School Children (*n = 3,775*)				PM_{10} in $\mu g/m^3$	
Town	Not at All	1–2 d	3–5 d	⩾ 6 d	Not at All	1–2 d	3–5 d	⩾ 6 d	5-d Mean (fire period)	1992–2003, Mean
Alpine	27.1	21.4	20.0	31.4	21.1	23.8	19.1	33.6	201	25.3
Anaheim	—	—	—	—	64.4	10.2	6.4	13.6	132	36.9
Atascadero	97.1	1.4	0	0	—	—	—	—	52	21.3
Glendora	—	—	—	—	54.4	20.9	8.4	13.9	158	32.5
Lake Arrowhead	63.6	14.6	12.1	10.6	57.7	20.1	10.4	9.4	172	19.8
Lake Elsinor	64.5	17.7	3.2	9.7	59.0	16.1	10.8	11.7	104	35.6
Lancaster	45.9	29.5	11.5	9.8	—	—	—	—	45	29.0
Lompoc	88.5	2.6	1.3	5.1	—	—	—	—	32	14.4
Long Beach	63.3	17.7	11.4	5.1	62.2	15.9	5.2	11.6	135	36.8
Mira Loma	54.1	16.4	13.1	16.4	47.1	13.2	13.2	23.2	250	66.3
Riverside	52.2	13.4	14.9	16.4	47.1	16.4	12.9	16.4	172	42.3
San Bernardino	—	—	—	—	24.2	15.3	13.3	41.1	199	51.0
San Dimas	55.6	19.4	11.1	12.5	45.5	15.8	18.7	16.8	191	36.7
Santa Barbara	—	—	—	—	80.3	9.7	2.9	2.6	30	28.2
Santa Maria	90.3	6.5	0	1.6	90.8	2.6	0.3	1.6	51	22.0
Upland	26.6	7.6	24.1	39.3	20.1	18.6	20.4	39.0	252	40.7

* Rows do not add up to 100% due to rounding and a few "don't know" answers.

TABLE 3. PREVALENCE (%) OF SYMPTOMS REPORTED FOR THE FIRE PERIOD, BY STUDY COHORT AND BY ASTHMA STATUS (BASED ON THE LAST CHILDREN'S HEALTH STUDY QUESTIONNAIRE AVAILABLE PRIOR TO THE FIRE)

	High-School Students (*n* = *834*)			Elementary-School Children (*n* = *3,775*)			Both Cohorts (*n* = *4,609*)		
Symptom	No Asthma (*n* = *616*)	Asthma (*n* = *218*)	All	No Asthma (*n* = *3,287*)	Asthma (*n* = *488*)	All	No Asthma (*n* = *3,903*)	Asthma (*n* = *706*)	All
Itchy/watery eyes	41.1	47.7	42.8	29.9	51.6	32.8	31.7	50.4	34.6
Irritated eyes	41.6	50.9	44.0	30.9	51.8	33.6	32.6	51.5	35.5
Sneezing/blocked nose	38.6	49.3	41.4	37.6	65.8	41.3	37.7	60.7	41.3
Cold	26.0	27.5	26.4	24.4	33.9	25.7	24.7	31.9	25.8
Sore throat	32.3	41.3	34.6	30.8	42.5	32.3	31.0	42.1	32.7
Dry cough at night	14.3	22.5	16.4	24.1	49.3	27.4	22.6	41.0	25.4
Dry cough first in morning	13.0	19.3	14.6	20.7	43.5	23.7	19.5	36.0	22.0
Dry cough other times	17.5	28.4	20.3	19.3	43.8	22.4	19.0	39.0	22.0
Wet cough	13.7	16.2	14.5	12.9	24.0	14.3	13.0	21.6	14.3
Wheeze/general	7.3	18.9	10.4	6.8	39.9	11.0	6.8	33.3	10.9
Wheeze/disturbed sleep	2.3	7.0	3.5	3.5	21.9	5.8	3.3	17.3	5.4
Wheeze/ limited speech	1.0	1.9	1.2	0.9	4.3	1.3	0.9	3.5	1.3
Asthma attack	1.0	11.0	3.6	1.3	17.4	3.3	1.2	15.4	3.4
Bronchitis	3.3	2.8	3.1	3.7	9.9	4.5	3.6	7.7	4.2
Medication*	12.9	23.6	15.7	23.7	50.6	27.2	22.0	42.3	25.1
Visit a doctor*	5.6	9.7	6.7	9.8	22.0	11.4	9.2	18.2	10.6
Missed school*	9.8	14.7	11.1	11.8	24.8	13.5	11.5	21.7	13.1

* For above problems.

Lake Arrowhead, more than 3% of study participants lost their homes (n = 15 and 10, respectively).

The main results are summarized in Table 4. Six or more days of fire smell indoors was significantly associated with all outcomes, and the smaller risk estimates for 1 to 5 d of exposure reached statistical significance in all but two outcomes (asthma attacks and bronchitis). Having fire smoke smell indoors for more than 6 d was associated with more than fourfold higher rates of eye symptoms, approximately threefold increased rates of dry cough and sneezing, and more than twofold higher rates of cold, sore throat, wet cough, medication use, physician visits, and missed school due to symptoms. The three types of wheezing (general, sleep-disturbing, and speech-limiting) occurred 3.5, 4.9, and 5.5 times more often, respectively, among those with 6 or more days of fire smell indoors. Asthma attacks increased 63%. The trend across the different levels of fire smell duration was highly significant for all outcomes except for asthma attacks (p = 0. 12).

The between-community comparisons were analyzed with two different metrics, namely PM_{10} and the community mean

TABLE 4. MAIN EFFECT OF FIRE SMOKE ON ALL OUTCOMES (ODDS RATIOS AND 95% CONFIDENCE INTERVALS)

	Within-Community (reported)				Between-Community (PM_{10})	
Symptom	OR 1–5 d	95% CI	OR ⩾ 6 d	95% CI	OR 210	95% CI
Itchy/watery eyes	**2.26**	1.90–2.68	**4.11**	3.36–5.02	**2.97**	2.00–4.40
Irritated eyes	**2.38**	2.01–2.82	**4.42**	3.61–5.41	**3.13**	2.15–4.55
Sneezing; runny/blocked nose	**1.98**	1.68–2.33	**2.79**	2.30–3.39	**1.94**	1.44–2.61
Cold	**1.50**	1.25–1.81	**2.13**	1.73–2.63	0.92	0.67–1.25
Sore throat	**1.81**	1.53–2.14	**2.50**	2.05–3.05	**1.79**	1.45–2.20
Dry cough at night	**2.25**	1.87–2.71	**3.35**	2.71–4.15	**1.92**	1.38–2.67
Dry cough first thing morning	**2.24**	1.85–2.72	**2.91**	2.33–3.63	**1.93**	1.36–2.73
Dry cough other times	**2.67**	2.20–3.24	**3.27**	2.61–4.09	**2.49**	1.86–3.33
Wet cough	**1.42**	1.13–1.79	**2.15**	1.67–2.77	1.01	0.72–1.41
Wheezing or whistling	**2.15**	1.63–2.83	**3.53**	2.62–4.75	1.37	0.86–2.20
Wheeze/disturbed sleep	**2.29**	1.56–3.37	**4.94**	3.33–7.33	0.89	0.56–1.42
Wheeze/limited speech	**2.23**	1.03–4.83	**5.49**	2.63–11.48	0.78	0.29–2.10
Asthma attack	1.32	0.84–2.07	**1.63**	1.00–2.67	1.03	0.58–1.80
Bronchitis	1.33	0.87–2.02	**2.23**	1.45–3.43	0.79	0.39–1.59
Medication for above problems	**1.82**	1.51–2.19	**2.33**	1.89–2.88	**1.38**	1.03–1.84
Visit a doctor for above problems	**1.33**	1.02–1.74	**2.03**	1.53–2.71	0.81	0.59–1.12
Missed school for above problems	**1.59**	1.25–2.02	**2.24**	1.72–2.91	0.96	0.72–1.27

Definition of abbreviations: CI = confidence interval; OR = odds ratio.

Within-community ORs are based on individually reported smell of fire smoke indoors (no fire smell = reference, OR = 1.0; not shown; 1-5 d; and ⩾ 6 d of fire smell). Between-community ORs show the associations scaled to the contrast in PM_{10} between the communities with the highest and lowest levels, respectively (~ 210 vs. 30 $\mu g/m^3$). Models are adjusted for baseline asthma, ethnicity, parental education, and study cohort. Statistically significant estimates ($p \leqslant 0.05$) are in bold type.

response to the fire smell question. Results are presented for the former only (Table 4) as they were similar for both metrics. The community mean of the reported level of fire smoke indoors and the estimates of the 5-d mean PM_{10} were highly correlated ($r = 0.81$) in both high-school and elementary-school students. Comparing highest with lowest community exposures, the between-community results were statistically significant and similar for both metrics in case of dry cough, eye, nose, and throat symptoms, as well as for medication. Eye symptoms were approximately three times as frequent in the communities most affected by fires as compared with lesser-affected communities. The between-community estimate for wheezing was significant only with the mean reported smoke (odds ratio [OR], 1.37 per unit change) but not with PM_{10} (Table 4). The other outcomes were not significantly associated with either community-level metric.

The model presented in Table 4 also adjusted for asthma status before the 2003 fire period ("physician-diagnosed asthma"). Therefore, the model also estimates the contribution of physician-diagnosed asthma to symptom frequency in the end of October 2003, independent of the fire smoke. We present these effects (ORs) in Table E3 to highlight the much higher symptom rates among children with asthma (*see also* Table 3). Children with asthma were two to three times more likely to report symptoms than nonasthmatic children. Thus, the effect of having asthma was similar to the effects of fire smoke. In the case of wheezing, asthma status was more strongly related to the symptom (OR = 7.4; *see* Table E3.) than fire smoke (OR = 3.5; *see* Table 4).

The effect of fire smoke was, however, not restricted to children with asthma. Results of Table 4, stratified by asthma status, are presented in the online supplement (Tables E4 and E5). In fact, among nonasthmatic children, coefficients were either very similar or stronger (wheezing) than in children with asthma (n = 706) in whom point estimates tended to be smaller and not statistically significant for speech-limiting wheezing, asthma attacks, bronchitis, cold, wet cough, physician visits, and missed school. The between-community estimates followed a similar pattern as in nonasthmatic children, with significant associations among nine questionnaire items.

To evaluate the joint effects of fire and asthma status on reported symptoms, we examined five indicator variables for the combinations of fire smell (none, 1–5 d, ⩾ 6 d) and asthma status (yes/no) using nonasthmatic children without fire exposure as the reference group. Figure 2 presents the effects of fire smoke among children with and without asthma.

Preventive Action and Fire-related Health Outcomes

We distinguished those who took action such as wearing masks, spending less time outdoors, or using air conditioners for at least 1 to 2 d from those not reporting preventive strategies. Those taking action also reported higher rates in almost all outcomes, and in many cases, these differences were statistically significant. For example, those reporting "wearing a mask" had symptom rates more than twice as high as those not using masks, whereas those reporting the use of air conditioners or spending "less time outdoors" during the fire had 1.2- to 1.6-fold rates in symptoms. Of particular interest is the interaction between preventive actions and reported duration of fire smell indoors (*see* Table 5). As a general pattern, we observed larger risk gradients related to fire smoke among those who did not take preventive action as compared with those who did. The interaction term reached statistical significance in several models (*see* Table 5). Compared with those who reported no fire smell, subjects with 1 to 5 d of smoke smell indoors who did not wear a mask were twice as likely to report sneezing (OR = 2.02 [1.7–2.4]). For those who did wear a mask (and reported 1–5 d of smoke), sneezing rates were only 25% higher. In the most exposed subgroup (> 6 d of smoke), those without masks had an OR of 2.8 [2.3–3.5], whereas the OR among those with a mask was only 1.67.

DISCUSSION

To our knowledge, this is the largest investigation of acute effects of wildfire smoke on children's health. We confirmed very substantial effects of wildfire smoke exposure on eyes as well as upper and lower respiratory symptoms, in both children with asthma and nonasthmatic children. The study was population based; thus, findings may be generalized more broadly to other comparable populations. Our findings are consistent with other studies conducted after wildfire outbreaks and occupational studies among firefighters, which suggest that wildfire smoke leads to acute exacerbations of respiratory and eye symptoms and increased demand for health services (13). Like ambient urban air pollution, wildfire smoke contains numerous primary and secondary pollutants, including particles, polycyclic aromatic hydrocarbons, carbon monoxide, aldehydes, organic acids, organic compounds, gases, free radicals, and inorganic materials with diverse toxicologic properties (14), which may explain the wide range of acute symptoms observed in our survey (15).

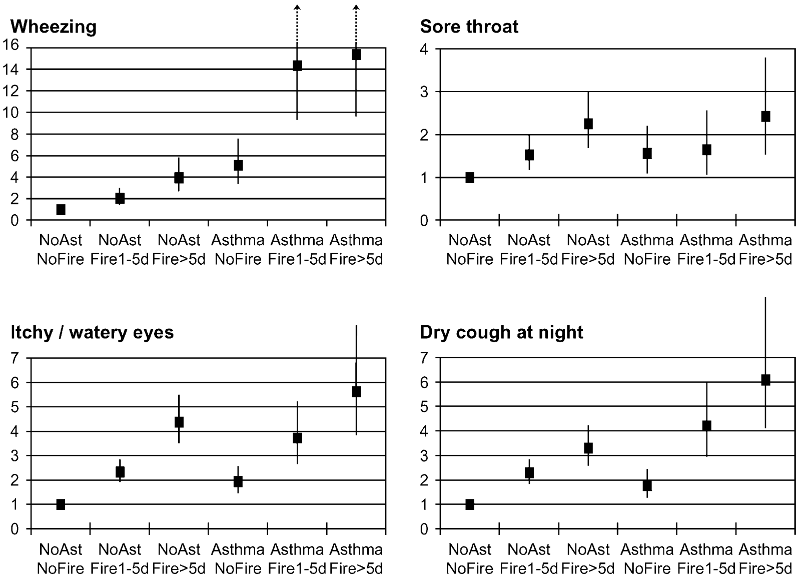

Figure 2. Effect of reported smell of fire smoke indoors (during 1–5, > 5 d, respectively) for four symptoms among children with and without asthma. Odds ratios and 95% confidence intervals from models with interaction terms for asthma and fire, adjusted for sex, ethnicity, educational level of parents, and cohort. No asthma (No Ast), no fire = reference.

TABLE 5. ODDS RATIOS FOR SYMPTOMS AMONG THOSE WITH AND WITHOUT PREVENTIVE ACTIONS AND WITH NO REPORTED SMOKE EXPOSURE (REFERENT GROUP), 1–5, OR ⩾ 6 DAYS OF FIRE SMOKE SMELL INDOORS

	Use of Mask		Air Conditioner Use		Less Outdoors	
Symptom Exposure Level	No OR (*95% CI*)	Yes OR (*95% CI*)	No OR (*95% CI*)	Yes OR (*95% CI*)	No OR (*95% CI*)	Yes OR (*95% CI*)
Sneezing or runny/blocked nose, n	3,673	396	3,158	911	1,371	2,698
No fire smell (referent)	1.00	1.00	1.00	1.00	1.00	1.00
1–5 d fire smell	2.01 (1.70−2.39)	1.58 (0.86–2.91)	2.14 (1.77–2.59)	1.75 (1.26–2.43)	1.84 (1.25–2.73)	1.76 (1.46–2.11)
6 or more days fire smell	2.81 (2.27−3.47)	2.30 (1.22–4.31)	3.05 (2.42–3.85)	2.23 (1.52–3.25)	2.54 (1.60–4.01)	2.47 (1.98–3.09)
Wheezing, n	3,630	387	3,111	906	1,357	2,660
No fire smell (referent)	1.00	1.00	1.00	1.00	1.00	1.00
1–5 d fire smell	2.05 (1.51−2.79)	1.50 (0.68–3.31)	2.29 (1.64–3.18)	1.79 (1.79–3.07)	4.80 (2.51–9.20)	1.76 (1.28–2.42)
6 or more days fire smell	3.47 (2.49−4.85)	2.23 (1.52–3.25)	3.46 (2.41–4.98)	3.00 (1.71–5.27)	7.65 (3.74–15.63)	2.91 (2.06–4.09)

For definition of abbreviations, *see* Table 4.

Total n varies between 4,017 and 4,069 due to varying number of "don't know" answers). The interactions of fire smell and preventive actions were statistically significant (likelihood ratio test, $p < 0.05$) for mask and air conditioner use in case of sneezing/blocked nose, and for "less outdoors" in case of wheezing. Note that in each exposure category, those taking preventive action had higher symptom rates than those not taking action (*see* text).

Biases require particular attention in the interpretation of these findings. Because many parents and students completed the fire questionnaire several months after the fire (from 1 to 7 mo later), and because both exposure and outcome are reported by participants, the study may be subject to interrelated reporting, recall, and selection biases. Due to the lack of individual-level PM_{10} data, we were able to compare effects of objective (PM_{10}) and subjective (reported) markers of exposure in the between-community comparison only. We used the community mean of reported fire smoke as the subjective aggregate exposure.

For reported fire smoke, the estimates for individual and community mean were similar for most outcomes. However, between-community estimates using the mean reported fire smell were not entirely consistent with those based on PM_{10}. The latter showed no clear association with cold, cough, asthma symptoms, physician visits, and missing school. There are several possible reasons for these inconsistencies.

First, the exposure metrics are inherently different and measure different domains of exposure. PM_{10} estimates the average concentration during the 5 most extreme days. In contrast, the questionnaire-based approach relates to the duration (i.e., number of days of observed smoke) rather than the level of the smoke in the community. Duration may characterize the true contrasts in exposure better than the 5-d average PM_{10} because some communities experienced fire smoke for longer or shorter periods.

Second, PM_{10} levels had to be estimated for five fire communities (*see* METHODS and online supplement). The unknown errors in these estimates may lead to under- or overestimation in the between-community effects. Thus, the results based on "objective" measures of community-level exposure are not necessarily unbiased.

Third, PM_{10} community levels are not sensitive to spatial differences in smoke densities that may have occurred within communities. Therefore, PM_{10} concentrations at the monitor may not represent the mean of the true, but unknown, home outdoor PM_{10} levels. We have no objective data to validate the reported diversity on the individual level. Wu and colleagues estimated PM_{10} distributions all across the Southern California area during the wildfire period, using PM measurements, light extinction, meteorologic data, and smoke information from satellite images (1) (*see* Figure E1). We used these results to investigate the range of daily mean PM_{10} concentrations for small areas representing size and location of several CHS communities. For example, the PM_{10} concentration estimates for a 1 × 1–km grid within a 10-km buffer around San Dimas indicated substantial temporal differences during the fire period, with daily means ranging from 115 $\mu g/m^3$ (October 28) to 220 $\mu g/m^3$ (October 26) as well as large spatial gradients across the grid points. For example, on October 25, the point estimates ranged from 54 to 250 $\mu g/m^3$, and from 90 to 337 $\mu g/m^3$ the next day, with spatial standard deviations up to 50% of the daily means (*see* Figure E1). Although these PM_{10} estimates may be associated with significant uncertainties at the neighborhood scale, they demonstrated substantial spatial heterogeneity, which corroborates the notion that smoke concentrations may vary substantially within communities. The distribution of reported smoke—and thus the community mean of the reported conditions—may reflect these distinct spatial gradients that are influenced by topography and wind patterns (1, 2).

Fourth, the community-level PM_{10} does not take into account PM_{10} levels in locations to which the children might have been evacuated, nor does it account for other individual preventive action taken during the fire period. Thus, the monitor PM_{10} value may again be offset from the true, but unknown, mean PM_{10} across children.

Fifth, the reported fire smell related to the indoor environment where most of the time was spent, whereas outdoor PM_{10} levels are not sensitive to differences among children's indoor environments.

The community mean of the reported fire smell was highly correlated with measured PM_{10}. However, others have shown that community mean reported annoyance of ambient air pollution correlates highly with objective measurements, whereas individual scores may poorly correlate with the home outdoor NO_2 measurements (16). Reporting was associated with health status and sex. A recent review also concluded that reported exposure to traffic was poorly associated with objective data (17). It is not clear whether findings for reported ambient air pollution also apply to fire smoke perception. Reporting of fire smoke may be less affected by personal attitudes than reported ambient air pollution, given the strong smell of fire smoke, the visibility of the problem, and the exceptional situation of the fire period. Reporting was also associated with sex. Eye symptoms, cold, medication, and physician visits were significantly more often reported among girls, whereas boys were more likely to report wheezing (data not shown). However, sex did not confound nor modify the main effects of fire smoke.

In conclusion, although it is neither possible to dismiss the possibility of biases nor to quantify their effects on our results, we believe that the arguments outlined above support the questionnaire-based results.

Effect of Fire Smoke on Children with Asthma

With the exception of bronchitis, we consistently observed larger coefficients of reported fire smoke among the nonasthmatic children, a general pattern also true for the between-community comparison. However, the smaller effect sizes in children with asthma must be seen in light of the much higher baseline rates for all symptoms among these children (*see* Tables 3 and 4). Therefore, a small increase in the relative risk may constitute a much larger effect in the children with asthma than in the nonasthmatic children. This is apparent in Figure 2. Symptom rates among children with asthma with no fire smoke were generally as high as those among nonasthmatic children with 1 to 5 d of fire smoke.

Children with asthma were usually treated and may have had better access to medical treatment. A Centers for Disease Control and Prevention surveillance reported increased over-the-counter sales of medication after this 2003 fire period (13). The fire questionnaire did not ask about specific treatments such as steroids.

We also have evidence that children with asthma were more likely to change their behavior (data not shown). For example, 15% of children with asthma reported to have worn a mask for at least some days, whereas only 2% of nonasthmatic children reported taking this personal protective measure. More children with asthma reported reduction in time spent outdoors, outdoor sports, and indoor physical activity due to the fire than did nonasthmatic children. This is in line with results from a previous California fire study indicating that those with preexisting conditions were more likely to follow public advisories to prevent smoke exposure (18). The use of air cleaners in that study was twice as high among those with preexisting health problems.

During a 1987 fire period in California, emergency room visits due to asthma and a range of upper and lower respiratory problems increased significantly beyond the expected rates (19). This was also observed in San Diego County during this 2003 wildfire (5). Large fires in Lithuania also affected crude rates of asthma exacerbation (20). Australian scientists found inconclusive results in their investigation of bushfire effects among a panel of 32 children with asthma. Only evening wet cough was associated with fire smoke (21). Interaction with medication use was not assessed (7), but statistical power may have been a major limitation.

We conclude that the much higher background rates of symptoms was the major reason for the weaker effect estimates observed among children with asthma, and that limitations in the assessment of asthma activity, severity, and medication added further random error to the assessment of effects in children with asthma.

We did investigate effects of fire on boys and girls separately (data not shown). Although baseline frequencies differed by sex for some symptoms, sex did not confound nor did it modify the effects of fire smoke.

Long-term Ambient Air Pollution and Fire Smoke

Some of the CHS communities with high long-term ambient pollution were heavily affected by fire; thus, we investigated confounding by long-term exposure to air pollution (data not shown). Communities with high long-term pollution had significantly higher reporting of "bronchitis" and "missed school." However, the long-term mean ambient PM did not confound the association between fire smoke and fire-related outcomes. Regular exposure to wood smoke has been reported to be a risk factor for chronic respiratory diseases (22). Tan and colleagues (23) and van Eeden and colleagues (24) have shown that acute exposure to wildfire smoke was associated with the stimulation of the bone marrow to release polymorphonuclear leukocytes in men, which reflects a systemic response that may be relevant to subsequent lung injury. However, the long-term relevance of a single wildfire exposure is not clear. Follow-up of the CHS fire study participants may allow an investigation of the long-term consequences of this unusual episode.

We stratified the analyses by cohort to investigate age-related differences in the effect of fire smoke. Results among the (larger) cohort of elementary-school children were more often statistically significant than in the cohort of high-school students. Coefficients tended to be larger in the latter, however, in particular for the between-community estimates (data not shown). It is difficult to assign these differences to age, given the differences in the study methods, with parents reporting for their young children and high-school students self-reporting symptoms.

Participation rates immediately after the fires in 2003 were low in some cities, so the presence of possible selection bias based on exposure and/or symptoms might have been an issue. However, survey administration efforts during 2004 resulted in increased response rates. We evaluated the effect of time elapsed since the fire on reported symptom prevalence. For some symptoms, the likelihood of reporting steadily decreased as time elapsed between the fire and answering the questionnaire (results not shown). Reporting of eye-related symptoms increased with elapsed time. This analysis demonstrates the importance of obtaining symptom-related information from study subjects in as timely a manner as possible after an unexpected natural event or emergency. Attempts to maximize early responses are important strategies for future studies. Inclusion of some control outcome not believed to be affected by fire smoke (e.g., stomach or digestive complaints) could have enhanced the assessment of reporting biases.

Our study suggests there was a beneficial effect of wearing masks, spending less time outdoors, and/or using air conditioning—actions that were recommended during the fire by public health agencies and the media. As recently shown in a fire smoke intervention study conducted in Colorado, ventilation patterns including the use of air filters can have substantial effects on the indoor levels of fire-related PM (25); thus, our results are plausible. However, because our assessment of exposure, symptoms, and preventive action were cross-sectional and self-reported, caution is appropriate in the interpretation of these results.

In summary, this investigation indicates substantial effects of fire smoke on children's health. The study provides suggestive evidence for protective health benefits of simple strategies, such as staying indoors, wearing a mask, or the use of air conditioners during wildfire smoke periods.

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Gene flow and pathogen transmission among bobcats (*Lynx rufus*) in a fragmented urban landscape

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Abstract

Urbanization can result in the fragmentation of once contiguous natural landscapes into a patchy habitat interspersed within a growing urban matrix. Animals living in fragmented landscapes often have reduced movement among habitat patches because of avoidance of intervening human development, which potentially leads to both reduced gene flow and pathogen transmission between patches. Mammalian carnivores with large home ranges, such as bobcats (*Lynx rufus*), may be particularly sensitive to habitat fragmentation. We performed genetic analyses on bobcats and their directly transmitted viral pathogen, feline immunodeficiency virus (FIV), to investigate the effects of urbanization on bobcat movement. We predicted that urban development, including major freeways, would limit bobcat movement and result in genetically structured host and pathogen populations. We analysed molecular markers from 106 bobcats and 19 FIV isolates from seropositive animals in urban southern California. Our findings indicate that reduced gene flow between two primary habitat patches has resulted in genetically distinct bobcat subpopulations separated by urban development including a major highway. However, the distribution of genetic diversity among FIV isolates determined through phylogenetic analyses indicates that pathogen genotypes are less spatially structured—exhibiting a more even distribution between habitat fragments. We conclude that the types of movement and contact sufficient for disease transmission occur with enough frequency to preclude structuring among the viral population, but that the bobcat population is structured owing to low levels of effective bobcat migration resulting in gene flow. We illustrate the utility in using multiple molecular markers that differentially detect movement and gene flow between subpopulations when assessing connectivity.

Keywords: carnivores, disease ecology, gene flow, habitat fragmentation, microsatellites, viral phylogenetics

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Introduction

Habitat loss and degradation are the leading causes of species declines around the world (http://www.iucnredlist.org/). Urbanization, an extreme form of habitat degradation, results in immediate displacement of wildlife from developed areas, followed by the increasing isolation of groups of animals confined to shrinking natural areas (McKinney 2002; McDonald *et al.* 2008). A common effect of urbanization is the fragmentation of once contiguous landscapes into smaller patches of noncontiguous habitat.

Maintaining functional connectivity, the extent to which organisms and genetic material move between

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habitat patches, can be essential for population persistence in fragmented landscapes (Crooks & Sanjayan 2006). Reduced functional connectivity between habitat patches can result in physically and genetically isolated subpopulations prone to inbreeding and to the loss of genetic diversity through genetic drift (Frankham 2006). However, measuring functional connectivity can be difficult, especially for cryptic solitary species such as large carnivores (Crooks 2002). One commonly used method of evaluating functional connectivity involves characterizing patterns of gene flow using molecular markers to evaluate the distribution of genetic diversity within and among groups of individuals (Frankham 2006; Balkenhol & Waits 2009; Ruell *et al.* in press). Populations with high connectivity should exhibit homogenous distributions of genetic diversity. Populations with low connectivity will be genetically structured, exhibiting localized variations in genetic diversity as a consequence of reduced gene flow among isolated groups of individuals.

Microsatellites are neutral heritable molecular markers commonly used to evaluate genetic structure, and hence connectivity, among natural populations (Avise 2004; Hedrick 2005a). These polymorphic, codominant markers provide a powerful means for assessing gene flow. However, microsatellite markers only reflect individual movement within structured populations if a migrant is sampled or if a migrant successfully reproduces and at least one offspring is sampled. Transient movements between subpopulations, or migrants that do not reproduce, may not be detected by analysing microsatellites (Riley *et al.* 2006). Therefore, while powerful, host genetic markers may not accurately characterize connectivity when individual movements do not result in gene flow.

Because directly transmitted obligate pathogens are inextricably linked to their hosts, pathogens can serve as alternative or additional markers for studies of wildlife population dynamics (Nieberding & Olivieri 2007; Liu *et al.* 2008). Feline immunodeficiency virus (FIV), a retrovirus that naturally infects many felid species (Troyer *et al.* 2005; Vandewoude & Apetrei 2006), has many characteristics that render it potentially useful as a marker of population dynamics in wild cats. First, the mutation rate of FIV is significantly faster than that of host genetic markers (approximately $\mu = 1–3\%$ every 10 years in mountain lions) (Biek *et al.* 2003). Also, infection with FIV is life-long because an obligatory step in viral replication involves the permanent insertion of a copy of the viral genome into the host's chromosomal DNA. Therefore, FIV genotypes have the capacity to serve as life-long molecular markers for each infected individual. Furthermore, the virus cannot be transmitted by insect vectors, nor is it stable in the environment, and thus, transmission events are indicators of direct contact between individuals.

Finally, the strains of FIV, which infect domestic cats, are genetically distinct from the strains isolated from wild felids. The domestic cat strains have never been documented to infect nondomestic felids in the wild, and therefore, the genetic diversity of FIV among nondomestic felids is only influenced by the distribution, movement and contact rates among conspecifics across the landscape.

Indeed, previous studies have demonstrated that patterns of FIV relatedness closely reflect the geographical distribution of bobcats, mountain lions and African lions at various geographical scales (Biek *et al.* 2006; Franklin *et al.* 2007a; Antunes *et al.* 2008). Specifically, Franklin *et al.* (2007a) demonstrated that the FIV isolates infecting bobcats north and south of Los Angeles, CA are genetically distinct, having diverged since the isolation of the two host populations. Because of these characteristics, viral genetic analyses may provide novel and powerful techniques for assessing connectivity and population structure with improved resolution, supplementing that which is currently possible using host genetic markers.

Bobcats (*Lynx rufus*), with large home ranges and high resource requirements, are susceptible to the effects of habitat loss and fragmentation in urbanizing systems (Crooks 2002; Riley *et al.* 2003, 2006, 2010). We investigated patterns of genetic diversity among bobcats and FIV isolates from a fragmented landscape in southern California to evaluate how urbanization affects connectivity among bobcats in this region. We specifically evaluated the extent to which several large freeways, and the developed areas surrounding them, are barriers to gene flow and pathogen transmission between habitat patches. We predicted that decreases in connectivity would lead to significant genetic structure among both host and pathogen populations. We performed standard population genetics analyses using 16 unlinked microsatellite loci from 106 bobcats. We also constructed phylogenetic trees to assess patterns of relatedness among FIV isolates from 19 of these individuals infected by the virus.

Our findings, presented below, demonstrate that two spatially structured, genetically distinct bobcat subpopulations exist. However, the pathogen phylogeny revealed no association between FIV relatedness and bobcat population structure, suggesting movements, contacts and disease transmission between subpopulations continue despite very low levels of host gene flow. This finding was inconsistent with our hypothesis that decreased gene flow among bobcats would lead to similar genetic structure among the virus population. However, these results are consistent with other studies that have found major roads and urban development to be more permeable to transient bobcat movements than to effective migration, allowing for the potential movement of pathogens in the absence of gene flow (Riley *et al.* 2006; Ruell *et al.* in press). We illustrate the utility in using multiple molecular markers, each with different determinants of movement throughout populations, to assess complex questions of connectivity.

Methods

Location and field sampling

This study was located south and west of Los Angeles, CA and included four habitat patches divided by three large freeways—Interstate-5 (I-5), the Riverside Freeway (SR-91) and the San Joaquin Hills Transportation Corridor (SR-73) (Fig. 1). I-5 through this region was constructed from 1944 to 1958 and has an average annual daily traffic volume (AADT) of ~262 000 cars per day (California DOT 2009). SR-91 was originally completed in 1971 and underwent a major expansion in 1995. The AADT of this freeway is ~264 000 cars per day (California DOT 2009). SR-73 was constructed in 1996 and has an AADT of ~73 000 cars per day (California DOT 2009). Aside from these roads and adjacent urban development, the only potential natural barrier to bobcat movement is the Santa Ana River, which flows about 100 m to the north of SR-91. No other natural barriers to gene flow (i.e. major mountain ranges) exist between these habitat patches, which are primarily characterized by chaparral, coastal scrub and grassland vegetative communities.

A total of 106 bobcats were included in this study. The majority of bobcats ($n = 75$) were live-captured between December 2002 and March 2009 using wire cage traps baited with visual and odour attractants (Lyren *et al.* 2006, 2008a,b). Animals were anesthetized, and blood samples were collected. Animals were captured, sampled and released with permission of cooperating agencies after approval by all appropriate animal care and use committees. The remaining individuals ($n = 31$) were opportunistically sampled postmortem; when possible, heart blood clots, thoracic fluid, ear punch and hair samples were collected from these bobcats. Blood and tissues were stored at USGS facilities in Irvine, CA, and aliquots were sent to Colorado State University for analysis as described below.

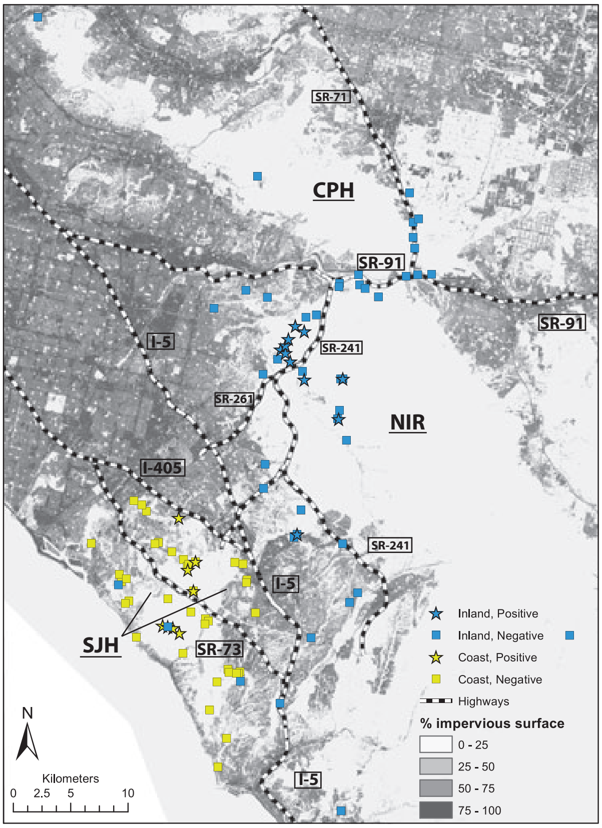

Fig. 1 Map of study locations southeast of Los Angeles, California. GPS capture locations of 105 bobcats indicated by squares [feline immunodeficiency virus (FIV) negative] or stars (FIV positive). Blue or yellow fill of each symbol represents the genetic assignment of an individual to an inland (east of I-5) or coastal (west of I-5) subpopulation, respectively (see Fig. 2). The a priori assignment of individuals to putative subpopulations (SJH-W: San Joaquin Hills West; SJH-E: San Joaquin Hills East; NIR: North Irvine Ranch; CPH: Chino Puente Hills) was based on the capture location of bobcats relative to the focal roads SR-73, I-5 and SR-91, which were investigated as potential barriers to gene flow. Degree of urban development (% impervious surface) is represented by grey shading.

Putative subpopulation assignments

Bobcats were assigned to one of four putative subpopulations based on the GPS coordinates of the capture or road kill location relative to freeways I-5, SR-91 and SR-73 (Fig. 1). These three freeways were the focus of our investigation because they completely traverse the study area (i.e. animals cannot move between habitat fragments without crossing one of these freeways), and these roads represent a gradient of permeability to bobcat movements based on previous studies [see discussion and also Lyren *et al.* (2008a,b)]. The San Joaquin Hills west subpopulation [SJH-west ($n = 29$)] was located between the coast and SR-73, which merges with I-405 to the north and I-5 to the south. The San Joaquin Hills east subpopulation [SJH-east ($n = 20$)] included individuals sampled between SR-73 and I-5. The North Irvine Ranch [NIR ($n = 44$)] subpopulation comprised individuals captured east of I-5 and south of SR-91, whereas the Chino Puente Hills [CPH ($n = 12$)] subpopulation consisted of individuals captured east of

I-5 and north of SR-91. One individual did not have a recorded capture location, and thus, it was not included in analyses that required the above subpopulation assignments. The following population genetics analyses were, except where noted, performed using this a priori assignment of individuals to putative subpopulations and the multilocus microsatellite genotype data for each individual.

Genotyping microsatellites

Bobcat genomic DNA was extracted from whole blood, peripheral blood mononuclear cells (PBMCs) or tissue using QIAamp® DNeasy blood and tissue kit (Qiagen Inc., Valencia, CA, USA). Seventeen microsatellite loci (Table 1) were amplified using primer pairs for polymerase chain reaction (PCR) developed by Menotti-Raymond *et al.* (1999): FCA008, FCA023, FCA026, FCA031, FCA043, FCA045, FCA077, FCA090, FCA096, FCA132, FCA149, FCA559; Menotti-Raymond *et al.* (2005): FCA740, FCA742; and Faircloth *et al.* (2005): BCE5T, BCD8T, BCG8T. Primers BCE5T and BCG8T were modified to contain the M-13 sequence instead of the CAG sequence as published. We selected these primer pairs from the above publications based on the following criteria: longer repeat units, efficiency of amplification and maximal heterozygosity. The 5′ end of the forward primer of each primer pair was modified with a 16-bp tail comprising the M-13 sequence (5′–GTA AAA CGA CGG CCA G–3′). Reverse primers were not modified. All microsatellite PCR products were fluorescently labelled using a second forward primer consisting of the above M-13 sequence with 6-FAM on the 5′ end.

PCR methodologies were adapted from Boutin-Ganache *et al.* (2001) and Riley *et al.* (2006). PCR reaction conditions included 94 °C for 3 min followed by 22 cycles of (94 °C for 30 seconds; 59 °C for 30 seconds; and 72 °C for 45 seconds), followed by 10 cycles of (94 °C for 30 seconds; 53 °C for 30 seconds; and 72 °C for 45 seconds), and a final cycle of 72 °C for 10 min. Randomly selected PCR products as well as the negative control for each reaction were visualized under UV light using gel electrophoresis with ethidium bromide in 2% agarose gel to confirm the presence of amplicons of appropriate length. Precise PCR product fragment lengths were determined using an ABI 3730xl DNA Analyzer and Peak Scanner 1.0 software (Applied Biosystems, Foster City, CA, USA). PCR and genotyping were repeated in ten per cent of randomly chosen bobcat samples for each microsatellite locus to confirm genotypes and prevent scoring errors. All duplicated genotypes were consistent with the primary analysis, demonstrating a high degree of assay reproducibility and reducing the likelihood of genotyping errors owing to false alleles or allelic dropout.

Table 1 Characterization of 17 microsatellite loci in 106 bobcats

Locus	Size range	No. of alleles	Repeat	Chromosome	H_O	H_E	PIC	References
FCA008	140–156	8	di	A1	0.71	0.77	0.73	1
FCA023	144–158	6	di	B1	0.67	0.72	0.67	1
FCA026*	138–166	13	di	D3	0.79	0.83	0.81	1
FCA031	237–255	8	di	E3	0.78	0.80	0.77	1
FCA043†	131–139	5	di	C2	0.78	0.73	0.68	1
FCA045*	147–173	7	di	A1	0.63	0.83	0.81	1
FCA077†	130–140	6	di	C2	0.77	0.74	0.70	1
FCA090*	108–126	7	di	A1	0.41	0.52	0.48	1
FCA096	189–209	8	di	A2	0.80	0.77	0.75	1
FCA132*	182–194	7	di	D3	0.66	0.78	0.74	1
FCA149	133–149	9	di	B1	0.76	0.78	0.75	1
FCA559	115–135	6	tetra	B1	0.64	0.67	0.60	1
FCA740	333–353	6	tetra	C1	0.84	0.79	0.76	2
FCA742	104–134	7	tetra	D4	0.65	0.67	0.61	2
BCD8T	156–180	5	tetra	Unknown	0.21	0.21	0.20	3
BCE5T	256–280	7	tetra	Unknown	0.70	0.75	0.71	3
BCG8T	275–299	11	di	Unknown	0.73	0.78	0.74	3

H_O, observed heterozygosity; H_E, expected heterozygosity; PIC, polymorphic information content.
*Null alleles may exist in one subpopulation.
†FCA077 and FCA 043 were found to be in linkage disequilibrium; FCA043 was not used in population genetics analyses.
References: (1) Menotti-Raymond *et al.* (1999); (2) Menotti-Raymond *et al.* (2005); and (3) Faircloth *et al.* (2005).

Validating and characterizing microsatellite data

Microsatellite data were screened for genotyping errors because of stuttering, null alleles and large allele dropout at all loci in MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004). There was no evidence of errors because of stuttering or large allele dropout at any loci. The following three loci showed evidence of null alleles when testing across all individuals with no subpopulation information: FCA045, FCA090 and FCA132. The null alleles at these loci correspond to NIR (FCA045 and FCA090) and SJH-west (FCA132) when the same analysis was run with a priori subpopulation assignments.

Tests for linkage disequilibrium among loci were performed in GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). The results for linkage disequilibrium varied greatly between subpopulations with seven significant tests in SJH-west (120 total tests; $\alpha = 0.009313$), four significant tests in SJH-east (120 total tests; $\alpha = 0.009313$), two significant tests in NIR (136 total tests; $\alpha = 0.009102$) and one significant test in CPH (104 total tests; $\alpha = 0.009567$). Loci FCA077 and FCA043 were in linkage disequilibrium in all four putative subpopulations, and therefore, FCA043 was eliminated from further analyses.

Hardy–Weinberg equilibrium probabilities were calculated using GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). Three of four subpopulations significantly deviated from Hardy–Weinberg equilibrium at one unique locus: FCA023 in SJH-west (15 tests; $\alpha = 0.015068$), FCA045 in NIR (16 tests; $\alpha = 0.014790$) and BCE5T in CPH (16 tests; $\alpha = 0.014790$). The remaining loci in each subpopulation did not deviate from HW equilibrium, and therefore, all subpopulations were assumed to be in HW equilibrium. Observed and expected heterozygosity and the polymorphic information content (PIC) for each locus were determined using the program CERVUS 3.0 (Table 1) (Kalinowski *et al.* 2007).

Assessment of population structure

Population differentiation based on allele frequencies was calculated for each pair of putative subpopulations using GENEPOP 4.0 (96 tests; $\alpha = 0.0097$) (Raymond & Rousset 1995; Rousset 2008). Allelic richness, estimated using rarefaction to avoid bias caused by differences in sample size (Leberg 2002), was calculated for each putative subpopulation using FSTAT 2.9.3.2 (Goudet 1995). Allelic richness results were confirmed to be normally distributed using a Ryan Joiner Test in Minitab Student Version 14.11.1 (Ryan Joiner test; $P > 0.1$). Analysis of variance (ANOVA) was used to determine whether allelic richness differed significantly between subpopulations ($\alpha = 0.05$). Estimates of subpopulation differentiation (D_{est}) were calculated using the online program Software for Measurement of Genetic Diversity (Jost 2008; Crawford 2010). Fst values were calculated in FSTAT (Goudet 1995). The use of F_{ST} values as measures of population differentiation has recently been criticized (Hedrick 2005b; Jost 2008). Therefore, we include them here as supplemental information only to allow a general comparison among similar, previously published studies (Table S1, Supporting information).

Bayesian clustering in program STRUCTURE 2.3.3 was used to infer the number of genetically distinct subpopulations (K) and to assign each individual to the subpopulation with which they share the highest genetic similarity. Parameters were set to include 50 000 burn-in and 500 000 Markov Chain Monte Carlo iterations (Pritchard *et al.* 2000). Data were first analysed without a priori source population information for individuals. Independent allele frequencies among subpopulations and genetic admixture were included as parameters so as not to introduce an upward bias in the estimation of K (Pritchard *et al.* 2000). This analysis was repeated five times for each K to verify the consistency of likelihood values between runs. K was varied from $K = 1$ to 5, representing a range of greater than expected K values to ensure our analysis included all ecologically plausible values of K.

This was followed by additional analyses with the data set divided into two groups: coastal animals (SJH-west and SJH-east) and inland animals (NIR and CPH) to more closely evaluate possible substructure within each of these two groups (Pritchard *et al.* 2010). The parameters of this model were the same as above, with each analysis repeated five times for each K from $K = 1$ to 3 for each group. For all of the above analyses, posterior probability values were computed for each K according to Pritchard *et al.* (2010). Additionally, ΔK values, which have been shown to accurately reflect the actual number of genetic clusters, were calculated according to Evanno *et al.* (2005).

Structure was also used to identify individuals that were captured in one subpopulation but genetically assigned to another and thus represent migrants. The parameters for this analysis were the same as described above except subpopulation assignments were included in the analysis with the migration prior set to 0.05. Individuals with a probability of assignment to their source population ≤0.01 were considered migrants. Individuals with ambiguous assignment probabilities were considered hybrids.

An individual pairwise relatedness test was performed after correction for null alleles using the program Maximum-likelihood (ML)-Relate (Kalinowski *et al.* 2006; Wagner *et al.* 2006; Carlsson 2008). The average pairwise relatedness of each subpopulation was compared using a *t*-test.

Detection of FIV infection

All bobcats for which serum samples were available (n = 91) were screened for antibodies to FIV by Western blot as previously described (Franklin *et al.* 2007b). Of these, 24 (26.4%) were scored as 'weak positive' or 'positive' for FIV antibodies. PCR was used to confirm FIV infection in these samples (two to four PCR attempts per seropositive individual) using DNA extracted from whole blood or PBMCs. We used a set of degenerate nested primers, which was previously shown to amplify a region of the *RT-pol* gene from a diverse set of FIV isolates (Troyer *et al.* 2005). All bobcats that were not screened by Western blot (n = 15) were screened for FIV infection by the PCR method only. In total, 19 individual bobcat FIV isolates were amplified by PCR and included in the FIV genetic analyses.

FIV pol and env PCR amplification and sequencing

Two gene regions were analysed to evaluate viral phylogeny using both a highly conserved region (*RT-pol*, encoding the essential viral polymerase) and a region that is less evolutionarily constrained (*env*, encoding the surface envelope protein) (Pecon-Slattery *et al.* 2008). PCR amplification of a region of the *RT-pol* gene was performed using degenerate primers as previously described (Troyer *et al.* 2005). Primers to amplify a region of the *env* gene were designed by first performing an alignment of two previously published FIV sequences: PLV-14 [GeneBank (accession no. U03982)] isolated from a Florida panther (*Puma concolor coryi*) and PLV-1695 [GenBank (accession no. DQ192583)] isolated from a puma (*Puma concolor cougar*) in British Columbia. Degenerate nested primer pairs were designed from regions of homology including first-round primers mJLenvF1 (5′–GTG CAI GTC ATI AGA TGT AGA G–3′) and mPLVenvR7 (5′–GGG GTG TCA TTA TAA IIA GTA AAA TT–3′), amplifying a fragment of ~700 bp, and second-round primers mPLVenvF8 (5′–GGG TGC ATT IGT IAA AGA ICC ATT TTT AG–3′) and mPLVenvR6 (5′–GGT GCI TTG AAI GGA CAC ATT CC–3′), which amplified a 570-bp product. Underlined bases indicate 5′ tail sequences added to the primers to lengthen primers and increase strength of primer binding to the template DNA.

Fifty microlitre PCR reaction mixtures contained 25 μL iQSuperMix (Qiagen), 400 nM of each primer and 10 μL DNA. DNA concentrations varied among samples resulting in a range of ~100–500 ng template per reaction. PCR reaction conditions for both rounds included a hot start at 94 °C followed by 20 cycles of melting at 94 °C for 30 seconds, touchdown annealing temperatures ranging from 55 to 46 °C decreasing by 1 °C every 2 cycles for 30 seconds, extension at 72 °C for 30 seconds, followed by 25 cycles of melting at 94 °C for 30 seconds, annealing at 52 °C for 30 seconds and extension at 72 °C for 30 seconds with a final extension at 72 °C for 3 min. This protocol successfully amplified proviral *env* fragments from three FIV-positive bobcats.

The resulting sequences were aligned, and the regions of highest homology were used to develop the following nested primer pairs that successfully amplified *env* fragments from all remaining bobcats with amplified *pol* sequences (n = 16). First-round primers were envfw201 (5′–TTT CTC ATG TTC CTT GAA TGG TAC–3′) and envrv202 (5′–CAC ATT CCA CTT AAT TGG TAT TG–3′), resulting in approximately a 450-bp amplicon. Second-round primers were envfw202 (5′–TGG TAC ATT CTG GGT GTT TAA ATC–3′) and envrv201 (5′–CTA TTT TGG TCA CTC TCT GAT GC–3′), resulting in approximately a 400-bp product. PCR reagents and reaction conditions were the same as above with the exception that touchdown annealing temperatures ranged from 58 to 49 °C and the annealing temperature for the last 25 cycles was 54 °C. PCR products were visualized under UV light using gel electrophoresis with ethidium bromide in 2% agarose gel to confirm the presence of product bands.

PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc.) prior to sequencing. Forward and reverse sequences were aligned using BLAST (National Center for Biotechnological Information, Bethesda, MD, USA), and a single consensus FIV sequence was produced for each infected bobcat. All sequences were verified manually. All sequences are available in the NCBI GenBank under accession numbers JN383436–JN383465.

Genetic alignments and phylogenetic analyses

Sequences were trimmed at the 5′ and 3′ ends resulting in all sequences having the same length (*pol* = 427 bp, *env* = 347 bp). Trimmed consensus sequences for each gene fragment (n = 19 *pol* & *env*) were converted to coding frame using an online DNA translator tool (Swiss Institute of Bioinformatics; http://www.isb-sib.ch/), prior to alignment in Clustal X2 (Larkin *et al.* 2007). Alignments were input into jModeltest (Posada 2008) to estimate the best-fit model of nucleotide substitution, which was the TPM2uf model with among-site rate variation for both gene segments (Kimura 1981). The estimated model parameters used for *pol* were [Lset base = (0.4030 0.1312 0.1592) nst = 6 rmat = (7.3755

50.7381 7.3755 1.0000 50.7381) rates = gamma shape = 0.2280 ncat = 4 pinvar = 0]. The model parameters for *env* included [Lset base = (0.3707 0.1869 0.1840) nst = 6 rmat = (4.2249 11.3706 4.2249 1.0000 11.3706) rates = gamma shape = 0.2250 ncat = 4 pinvar = 0].

Maximum-likelihood phylogenetic analyses were conducted in Phylogenetic Analysis Using Parsimony (PAUP) (Sinauer Associates, Sunderland, MA, USA) (Swofford 2003). The corresponding *pol* and *env* gene regions from an FIV isolate sequenced from a Florida panther in 1994 were included to provide a root for each tree (Langley *et al.* 1994). ML trees were constructed using an NJ starting tree, followed by a heuristic search using the tree-bisection-reconnection branch-swapping algorithm. The *pol* and *env* trees were found to be congruent, and therefore, a single *pol-env* concatenated sequence was used to construct the final phylogenetic tree for analysis. Bootstrap analyses were performed with 100 iterations for all trees. Viral isolates were divided into four 'FIV Groups' based on clusters of related isolates arising from a basal node supported with an ML bootstrap value of 70 or greater.

We estimated the number of FIV migration events between coastal and inland bobcat subpopulations by calculating the *s* statistic for the observed ML phylogenetic tree in Mesquite 2.75 (Maddison & Maddison 2011). The *s* statistic reflects the minimum number of parsimony steps that explain the discord between subpopulations as monophyletic groups on the tree (Slatkin & Maddison 1989).

To estimate the timeline of past virus transmissions within and between subpopulations, the concatenated viral sequence data were analysed in the coalescent framework as implemented by the program BEAST 1.6.2 (Drummond & Rambaut 2007). The SDR06 substitution model was used with a relaxed uncorrelated lognormal molecular clock (Drummond *et al.* 2006). The tree model included a piece-wise linear Bayesian Skyline prior with five groups and a randomly generated starting tree (Drummond *et al.* 2005). An initial run of 10 000 000 Markov chain Monte Carlo (MCMC) iterations, sampled every 1000 runs, was performed to estimate model parameter values. The first 10% of logged values were discarded as burn-in. From this analysis, the following model parameter priors were changed from default settings: (i) the relative rate parameters were set to vary from 0 to 10; (ii) the Bayesian Skyline population size was set to vary from 0 to 500; and (iii) the mean rate for the uncorrelated relaxed molecular clock was set to vary from 0 to 10.

The final analysis included the above settings with 50 000 000 MCMC iterations sampled every 1000 runs. The first ten per cent of logged values were again discarded as burn-in. The estimated values and associated effective sample size (ESS) for each model parameter were viewed in TRACER 1.5 (Rambaut & Drummond 2007). ESS values for all parameters were >500. The maximum clade credibility tree was produced in TREEANNOTATOR 1.6.2 (Rambaut & Drummond 2002). The resulting tree was viewed in FIGTREE 1.3.1 (Rambaut 2006), and the mean posterior probability heights with 95% highest posterior density (HPD) intervals were labelled on internal nodes.

Results

Bobcat population structure

Distribution of alleles. An analysis of population differentiation performed in GENEPOP indicated that the distribution of alleles among bobcats from the two coastal subpopulations, SJH-west and SJH-east, differed significantly ($P = 0.0064$) at only the FCA008 microsatellite locus. Therefore, the coastal bobcats, regardless of whether they were captured east or west of SR-73, had a similar distribution of alleles at 15 of the 16 microsatellite loci examined. Similarly, the two inland subpopulations, NIR and CPH, significantly differed in allelic distribution at only FCA026 ($P = 0.0025$) and FCA077 ($P = 0.0048$). This finding demonstrates that bobcats captured north and south of SR-91 had a similar distribution of alleles at 14 of the 16 microsatellite loci we analysed. However, the distribution of alleles differed greatly between the coastal and inland subpopulations. SJH-west bobcats significantly differed from NIR and CPH bobcats at 13 and 10 microsatellite loci, respectively, and SJH-east bobcats differed from both NIR and CPH bobcats at 13 loci ($P < 0.01$ all significant pairwise tests). These results indicate a high degree of genetic differentiation exists between bobcats separated by I-5 and its associated urban development.

Genetic diversity. No pairwise difference existed in allelic richness (Table S2, Supporting information) when comparing the two coastal subpopulations ($F_{1,29} = 2.59$, $P = 0.118$) or the two inland subpopulations ($P = 0.982$, $F_{1,30} = 0.00$). However, the coastal bobcats (combined SJH-W and SJH-E) had significantly lower allelic richness than the inland bobcats (combined NIR and CPH) ($P < 0.001$, $F_{1,62} = 12.62$). This further suggests that coastal and inland bobcats are genetically distinct and indicates that coastal bobcats have lower genetic diversity than inland bobcats. Interestingly, the BCD8T locus appears to have drifted to fixation in coastal bobcats as only one allele was sampled at this locus from all 49 coastal bobcats. Although the frequency of this allele was also high in NIR (0.82) and CPH (0.67), four and five alleles, respectively, were present at this locus in these subpopulations.

Departures from random mating. The overall estimate of genetic differentiation among the four putative subpopulations, $D_{est} = 0.11$, indicates a moderate amount of genetic structure exists within this population. Pairwise D_{est} values were lowest when comparing the two coastal subpopulations ($D_{est} = 0.008$, SJH-west:SJH-east) or the two inland subpopulations ($D_{est} = 0.014$, NIR:CPH) and highest between the coastal and inland subpopulations ($D_{est} = 0.11$, SJH-west:NIR; $D_{est} = 0.13$, SJH-west:CPH; $D_{est} = 0.14$, SJH-east:NIR; $D_{est} = 0.19$, SJH-east:CPH). The estimated differentiation between the coastal bobcats (combined SJH-W and SJH-E) and the inland bobcats (combined NIR and CPH) was $D_{est} = 0.14$. Locus-specific D_{est} values are reported in Table S2 (Supporting information).

We found no evidence of inbreeding within the overall population ($F_{IS} = 0.013$; 95% CI: −0.29–0.065), nor in any of the putative subpopulations [F_{IS} = (0.011, SJH-W; −0.045, SJH-E; 0.029, NIR; 0.034, CPH)].

Individual assignment tests. Bayesian clustering indicated the assumption of two genetically distinct subpopulations ($K = 2$) best explained the variation in our microsatellite data (Fig. S1, Supporting information). This result was the same regardless of whether or not source population information was used as a prior in the analysis. All bobcats caught east of I-5 (NIR and CPH bobcats $n = 56$) were assigned to one 'inland' subpopulation, while 46 of 49 bobcats caught west of I-5 (SJH-west and SJH-east bobcats) were assigned to a 'coastal' subpopulation (Fig. 2). Three individuals captured west of I-5 were genetically assigned to the inland subpopulation and thus represent possible migrants. However, no bobcats captured east of I-5 were genetically assigned to the coastal subpopulation. If any additional human development and/or freeways in this region (i.e. SR-91, SR-73, SR-241, SR-261) were causing genetic structure, a population model with $K > 2$ should have had the highest support. Therefore, the I-5 corridor is the only human development in this region implicated as a cause of genetic structure among bobcats during our period of sample collection.

Three individuals were identified as first-generation migrants as they were captured in the coastal area but had assignment probabilities of 1.00 to the inland population when capture locations were included in the Structure analysis (denoted by * in Fig. 2b). Three other bobcats captured in the coastal area had the genetic profile of hybrids with partial assignment to both subpopulations (denoted by # in Fig. 2b). No individuals sampled from the inland area were identified as migrants or hybrids from the coastal area.

Relatedness of individuals. The average relatedness of bobcats in the coastal population ($R = 0.096$; SE = 0.0037)

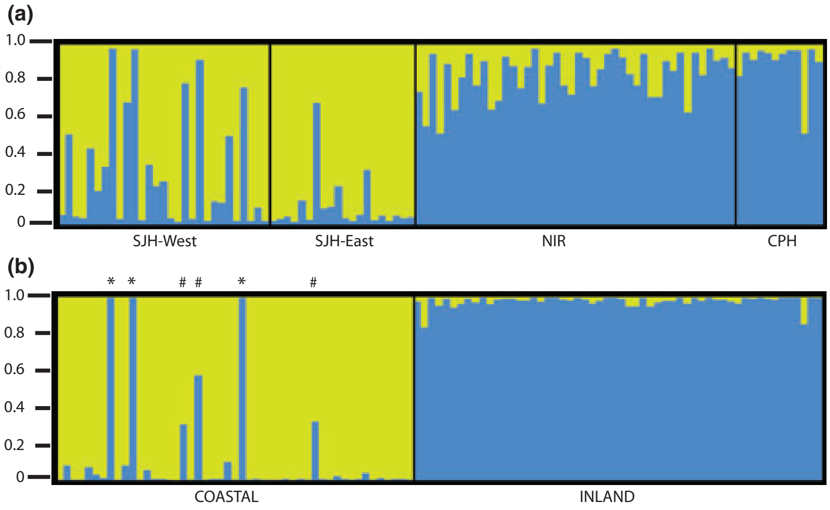

Fig. 2 Individual bobcat genetic assignments to each of two distinct subpopulations. Each vertical bar represents one individual. Values on the y-axis are the probability of assignment of each individual to one of the two genetic groups identified (Fig. S1). The shading of each bar corresponds to the probability of genetic assignment to either the coastal group (yellow) or the inland group (blue) of bobcats. (a) Results for simulation of $K = 2$ without including a priori capture locations. The majority of individuals captured west of I-5 had strong assignment to one subpopulation (coastal—yellow), while all of the individuals captured east of I-5 had a high probability of assignment to a second subpopulation (inland—blue). (b) Three migrants (*) and three hybrids (#) were identified in Structure using a priori assignments to coast or inland subpopulations based on capture locations. All gene flow was detected from the inland to the coastal subpopulation.

was significantly higher ($t_{5634} = 7.23$; $P < 0.001$) than in the inland population ($R = 0.064$; SE = 0.0026).

FIV phylogenetic analyses

We amplified a 427-bp region of *pol* and 347-bp region of *env* by PCR from 19 bobcats (four in SJH-west, four in SJH-east and 11 in NIR) bobcats. These included 17 of the 24 (70.8%) bobcats putatively seropositive by Western blot, one bobcat that was negative by Western blot and one bobcat that was screened by PCR only. The inability to amplify FIV sequences from a subset of putatively seropositive bobcats is similar to the findings of previous studies (Troyer *et al.* 2005; Franklin *et al.* 2007b). This is probably the result of a difference in the sensitivity and specificity of these two assays and/or a relatively low FIV proviral load present in a subset of infected animals.

The demographic information for 18 of the 19 FIV-positive bobcats was known: 13 were adult males, one was a yearling male, two were adult females and two were yearling females. The age-specific prevalence of FIV was 14.2% (3/21) for yearlings and 23.8% (15/63) among adults.

The ML phylogenetic tree built from *pol-env* concatenated gene sequences (Fig. 3) shows no evidence of association between capture location (coastal vs. inland) and FIV relatedness (see also Fig. 4). The basal nodes have low bootstrap support, suggesting little overall genetic structuring within the virus population. The number of parsimony steps (*s* statistic) that best explains the discord of FIV relatedness between subpopulations indicates a minimum of three FIV transmission events have occurred between the coastal and inland subpopulations (Slatkin & Maddison 1989).

We estimated the past timeline of virus movement within and between bobcat subpopulations using a coalescent Bayesian model (Drummond *et al.* 2005; Drummond & Rambaut 2007). Figure 5 illustrates the maximum clade credibility tree with labels representing the estimated year of coalescence (mean posterior node ages) for each internal node. The age of the basal nodes is difficult to interpret because of large 95% HPD intervals (analogous to 95% confidence intervals). Therefore, it is impossible to reconstruct a precise timeline of ancestral divergence into the observed FIV groups. However, the more terminal nodes are insightful as they depict the estimated year of recent FIV coalescent events. FIV Group 4, the largest supported group of isolates, comprises six isolates from inland bobcats (x23, x24, x27, x31, x37 and x55) and two isolates from coastal bobcats (x240 and x46). The two coastal isolates in this group share a common ancestor with two of the inland isolates (x23 and x27) in *c.* 1990 (Fig. 5; 95% HPD: 1967–2003). Similarly, FIV Group 2, with 99% bootstrap support, contains nearly identical sequences from three inland bobcats (x22, x34 and x35) and two coastal bobcats (x39 and x44), which share a common ancestor in approximately the year 2000 (Fig. 5; 95% HPD: 1995–2003).

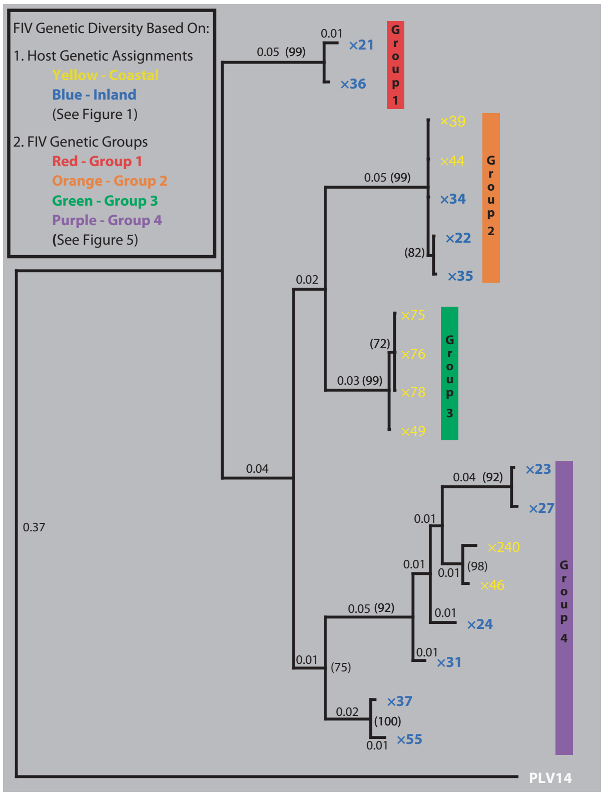

Fig. 3 Maximum-likelihood phylogenetic tree of feline immunodeficiency virus (FIV) concatenated *pol-env* sequences from 19 infected bobcats. The tree was constructed using a single 774-bp sequence (427 bp from *pol*, 347 bp from *env*) of proviral DNA from each individual. All sequences are in coding frame. Bootstrap values >70 are indicated in parentheses. Branch lengths ≥0.01 are also indicated. Individuals have been coloured to represent their genetic assignment based on the results of the *Structure* analysis (see Figs 1 and 2). Because no migrants were infected with FIV, the colour of an individual also represents whether an individual was captured west (yellow) or east (blue) of I-5. FIV isolates were assigned to groups based on the four most basal supported nodes to illustrate the distribution of FIV genetic diversity across the landscape (See Fig. 4). The tree is rooted with PLV-14, a viral sequence from the same FIV clade, which was sequenced from a Florida panther in 1994.

Feline immunodeficiency virus Group 3 contains four closely related viral isolates (Fig. 3; x75, x76, x78 and x49) from related coastal bobcats ($r > 0.25$). To our knowledge, this is the first evidence of FIV familial transmission among bobcats. Familial transmission of

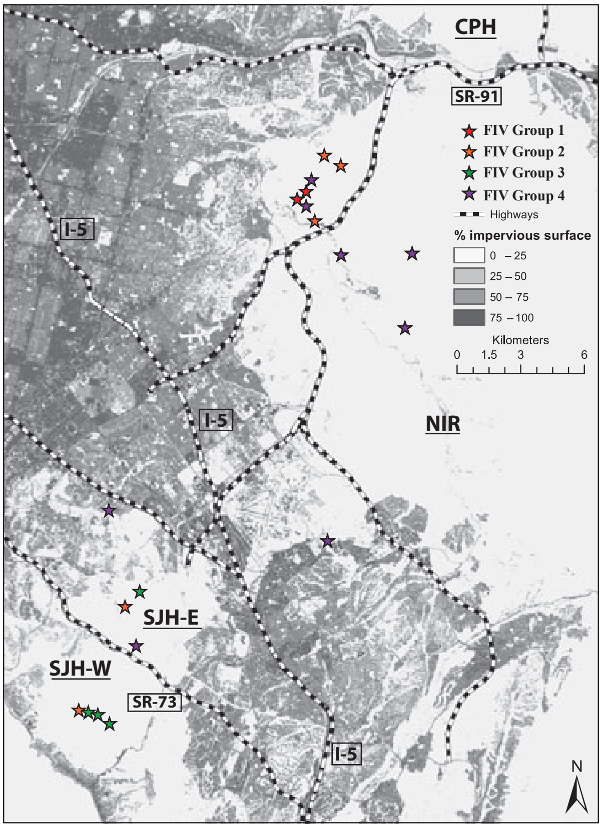

Fig. 4 Geographical distribution of feline immunodeficiency virus (FIV) genetic diversity among inland and coastal bobcats. Each star indicates the capture location of one FIV-positive bobcat. The stars are coloured corresponding to which of the four groups of related FIV isolates was sampled from each bobcat (See Fig. 3). FIV Groups 1 (red) and 3 (green) contain isolates sampled only from inland or coastal bobcats, respectively. FIV Groups 2 (orange) and 4 (purple), containing both inland and coastal bobcats, resulted from the movement of FIV across Interstate-5. Degree of urban development (% impervious surface) is represented by grey shading.

FIV has been previously documented in mountain lions (Poss *et al.* 2008).

Discussion

Bobcat population structure

Understanding the degree of connectivity among populations in heterogeneous landscapes is an important goal of ecology, population genetics and conservation biology (Taylor *et al.* 1993; Crooks & Sanjayan 2006; Fischer & Lindenmayer 2007). We evaluated host and pathogen genetic markers to investigate connectivity among bobcats throughout a fragmented urban landscape in southern California. Our results indicate that two genetically distinct groups of bobcats existed in our study area, defined as coastal and inland subpopulations, separated by urban development including Interstate-5 (Figs 1 and 3). This finding is in agreement with other analyses performed previously with a small subset of these bobcats and four of the 16 microsatellite loci utilized in this report (Ruell *et al.* in press).

Our results indicate that the coastal and inland bobcat subpopulations had a different distribution of alleles at most of the microsatellite loci examined and a low, unidirectional pattern of migration from the inland to the coastal area. We also observed reduced genetic diversity and increased relatedness among individuals in the coastal population. These findings suggest the observed genetic differentiation is because of decreased migration through the urban matrix between the inland and coastal habitat patches. We therefore conclude that urban development, including I-5, has been a physical barrier that has reduced bobcat movement and gene flow between isolated groups of individuals.

We did not detect substructure among bobcats separated by the two other freeways that we specifically evaluated, SR-91 and SR-73 and nor did we find evidence of genetic structure because of any other freeways (i.e. SR-241, SR-261) or human development in the region. The maintenance of gene flow across SR-91 and SR-73 is probably explained by the fact that these roadways are perforated by more functional wildlife underpasses and are bordered by more natural habitat than I-5. Therefore, the distance between habitat patches is shorter across SR-91 and SR-73 than across I-5, a factor that has been shown to be an important determinant in carnivore movement among habitat fragments in this region (Crooks 2002). It is possible that because SR-91 and SR-73 are newer roads, any isolation these may be causing has not yet resulted in detectable genetic structure.

Our findings, revealed by analyses of empirical genetic data, are supported by observations from remotely triggered cameras placed near underpasses of all three focal roadways. Cameras placed near the only potential wildlife corridor under I-5 that directly links SJH-E to NIR did not document any movement of bobcats between these habitat patches during 204 consecutive days of observation (Lyren *et al.* 2008a). Cameras, however, did not monitor another potential path across I-5 connecting NIR to SJH-W to the south; road kill carcasses and models of connectivity both suggest this path may be utilized by bobcats (Lyren *et al.* 2008a). In contrast to the lack of remote camera observations of bobcat movement across I-5, a similar duration of camera monitoring of potential wildlife corridors under SR-91 documented many successful movements between NIR and CPH (E. E. Boydston, unpublished data). Likewise, multiple bobcat movements between

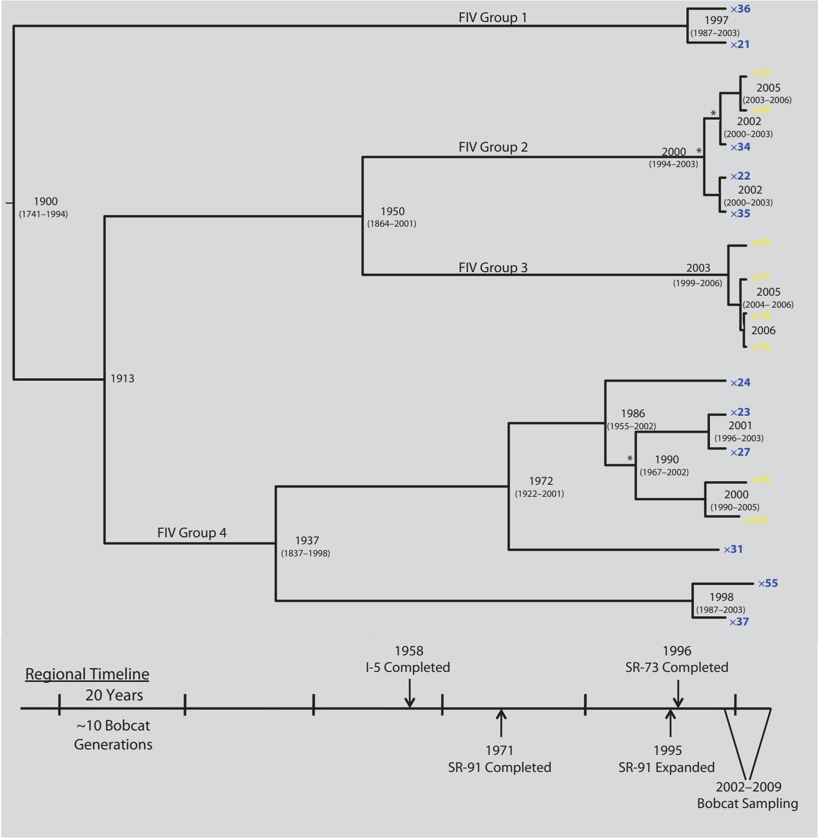

Fig. 5 The estimated timeline of viral coalescent events. Maximum clade credibility Bayesian phylogenetic tree of *pol-env* concatenated sequences constructed using dated tips. Internal node labels correspond to the highest mean posterior probability estimate [with 95% highest posterior density (HPD) interval] for the year of coalescence. The estimated dates on basal nodes lack precision; therefore, it is impossible to accurately reconstruct the timeline of ancestral diversification into the current four-group structure of feline immunodeficiency virus (FIV). Estimates of recent coalescent events are more precise and depict contemporary FIV transmission within and between bobcat subpopulations. *Indicates common ancestor to contemporary isolates sequenced from both inland and coastal bobcat isolates. Viral movement across I-5 has probably occurred since the estimated date of these coalescent events, resulting in the presence of related viral strains sampled in both subpopulations (See Fig. 4).

SJH-W and SJH-E were also recorded during 358 days of camera observations near SR-73 (Lyren *et al.* 2008b).

Interstate-5 and the surrounding urban matrix have greatly increased in size over time since the original construction was completed in 1958. While it is difficult to know when I-5 became a 'barrier' to bobcat movement, Crooks (2002) estimated that the coastal San Joaquin Hills might have become effectively isolated from inland natural areas around 1980. Given the generation time of bobcats (*c.* 2 years) (Knick *et al.* 1985), between 12 (*c.* 1980) and 25 (*c.* 1958) generations have passed because the inland and coastal bobcat subpopulations became physically isolated.

FIV phylogenetic analyses

Directly transmitted pathogens are inextricably linked to their hosts, and therefore, the geographical distribution of pathogens reflects the movement and contacts of their hosts throughout the landscape. We analysed two gene sequences from FIV, a retroviral pathogen of bobcats, to evaluate whether the gene flow (transmission) of the virus revealed information about bobcat movement not discernable from traditional host genetic analyses. We hypothesized that urban development, which limits bobcat gene flow, would also limit viral transmission between bobcat subpopulations. Given that only one in five bobcats are infected with FIV, the expected virus migration rate is five times lower than the host migration rate. Thus, we expected each of the two bobcat subpopulations would be infected with a genetically distinct viral strain, divergent from one another owing to years of isolation, low viral migration rates and the high mutation rate of FIV.

This prediction is consistent with previous literature demonstrating that geographical or social barriers, which prevent mixing between neighbouring host subpopulations, result in genetically structured retrovirus populations (Franklin *et al.* 2007a; Liu *et al.* 2008; see also Fig. S2, Supporting information—demonstrating clear divergence between FIVs isolated from bobcats north or south of Los Angeles). However, the phylogenetic trees constructed in this study from FIV gene segments demonstrated a pattern that differs from these previously published findings. The relatedness of FIV isolates is mixed among coastal and inland bobcat subpopulations, indicating that there is no association between FIV relatedness and the geographical/genetic structure of its host (Figs 3 and 4). While this finding differs from our prediction based on the ecology of FIV, it is consistent with previous studies of urban bobcats in southern California, which have found that individual movements (and thus opportunities for disease transmission) between fragmented habitat patches occur more frequently than predicted by observed levels of gene flow (Riley *et al.* 2006; Ruell *et al.* in press).

The topology of the ML phylogenetic tree (Fig. 3) illustrates that neither the coastal nor the inland bobcats are infected with a monophyletic cluster of viruses. Instead, we identified four groups of related FIV isolates but found no evidence to suggest these groups developed because of the population structure of bobcats. While two of the four groups contained only coastal or inland isolates (FIV Groups 1 and 3), these were the smallest groups sampled and the other two FIV groups did not follow this pattern. Instead, FIV Groups 2 and 4 contained closely related viruses arising from both bobcat subpopulations. The coastal isolates within each of these two groups shared recent common ancestry with inland viruses (Fig. 5), and thus, we conclude that FIV-infected bobcat migration events across I-5 are responsible for the observed mixing of isolates. Half of the viruses infecting coastal individuals (4/8) recently originated from, or were transmitted to, inland bobcats. The former is likely to have occurred in FIV Group 2 as suggested by the presence of multiple inland isolates basal to the two coastal isolates and evidence of a long Group 2 residence time within the inland subpopulation.

Utilizing host and pathogen genetics

The presence of related FIV strains on both sides of I-5 suggests that the intervening urban development is somewhat permeable to bobcat movement and disease transmission, despite the presence of distinct genetic structure among the host population. There may be several explanations for the discrepancy between the population structure of FIV and its host. One hypothesis is that a recent increase in bobcat migration across I-5 has led to the observed mixing of viral genotypes, but not enough time has passed for this recent increase in migration to counteract previously established genetic structure among the bobcats. While possible, we consider this unlikely as human development along the I-5 corridor has increased over time, and no notable changes have been made in the area (e.g. underpasses, culverts) that would account for a recent increase in connectivity between the two subpopulations.

An alternative hypothesis is that FIV exchange between the two subpopulations is not necessarily linked to bobcat gene flow. Transient movements of individuals across a semi-permeable barrier such as I-5 may not result in the exchange of genetic material, but may involve sufficient contact between individuals to allow for disease transmission. Under this hypothesis, the contrasting patterns of population structure may reflect differences in the underlying ecology of the two molecular markers.

Microsatellite markers are useful for detecting host gene flow, the specific process involving animal movement which results in the exchange of genetic material from one group of individuals to another (Endler 1977). According to this definition, gene flow is dependent upon successful mating after migration. FIV transmission, however, can occur both vertically *and* horizontally, allowing FIV isolates to move between individuals and subpopulations in the absence of gene flow. For example, Biek *et al.* (2003) reported that for one population of mountain lions, horizontal transmission among adults resulted in the majority of new FIV infections and accounted for the observed increasing prevalence of FIV with age. Vertical transmission, resulting in a cohort of young individuals infected prior to adolescence, was equally important in explaining the dynamics of FIV in the population.

Given that bobcats and mountain lions share many life history characteristics, it is probably that similar FIV transmission dynamics occur in bobcats. Indeed, the relative prevalence of FIV in yearlings (14%) vs. adults (24%) in this study is similar to the age–prevalence relationship described in Biek *et al.* (2003). Young infected individuals may therefore play an important role in the maintenance and spread of FIV in this population. At adolescence, juvenile (usually male) bobcats often make transient movements during dispersal from their natal range while attempting to establish a new home range (Kitchings & Story 1984; Knick 1990; Hansen 2007). Young bobcats infected prior to dispersal therefore represent a potentially important mode of virus movement within and between subpopulations.

In fragmented landscapes such as southern California, where urban development and freeways act as boundaries limiting animal movement, bobcat home ranges may shrink, and the amount of overlap between neighbouring home ranges may increase (Riley 2006; Riley *et al.* 2006). This pattern of 'home-range pile-up' has been described in other bobcat populations in California (Riley *et al.* 2006). This phenomenon decreases the probability that juveniles dispersing to a neighbouring subpopulation will successfully mate. Under these conditions, the actual rate of bobcat movements, contacts and opportunities for disease transmission between subpopulations would be higher than expected based on migration rates estimated from gene flow.

The low level of gene flow we detected across I-5 occurred in a unidirectional pattern from the inland area towards the coast. The coastal population, while reduced in overall genetic diversity, contains both migrants and hybrids from the inland population. This suggests that, while rare, inland bobcats can successfully migrate to and breed in the coastal population, while the reverse was not seen. However, inland FIV isolates do not form a monophyletic group; two of the three FIV groups infecting coastal bobcats also infect inland bobcats. There are two possible explanations to this pattern. One is that movement of FIV has occurred repeatedly one-way from the inland subpopulation to the coast, causing the diversity among coastal isolates to closely mirror that observed inland. This hypothesis is consistent with the one-way pattern of bobcat movement we detected from the microsatellite analysis.

The other possibility is that a coastal virus population diverged from inland viruses after the two groups were isolated by urban development and has since been transmitted back into the inland subpopulation multiple times via transient movements and contacts resulting in disease transmission but not gene flow. Tracking the movements of individual bobcats, evaluating FIV diversity in other neighbouring bobcat populations and utilizing spatially explicit phylogeographic analyses may help to distinguish between these alternatives.

In conclusion, our findings indicate that bobcats inhabiting this fragmented landscape in southern California are physically isolated and genetically structured. This pattern is consistent with decreased connectivity across urban development, resulting in low levels of migration and/or a low probability that migrants establish a home range and successfully mate. However, movements are apparently made, allowing for disease transmission between these habitat fragments. This conclusion carries with it conservation implications as populations with these characteristics are susceptible to decline as a result of a continued loss of genetic diversity from genetic drift and decreased individual fitness because of inbreeding depression (Frankham 2006). In addition, both subpopulations should be managed as a unit when considering treatment and prevention interventions during future disease outbreaks. Habitat conservation and restoration as well as connectivity enhancements such as functional underpasses to better facilitate movement of bobcats under roadways may help safeguard their persistence in the face of substantial ongoing threats posed by humans in this region.

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The authors are interested in research involving ecology, conservation, and/or infectious diseases of carnivores. They share particular interest for topics relating to the effects of human activities on carnivores.

Data accessibility

DNA sequences—GenBank accession numbers JN383436–JN383465. Microsatellite data—DRYAD entry doi:10.5061/dryad.mm317th7.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 F_{ST} values calculated from 16 bobcat microsatellite loci.

Table S2 Measures of genetic structure among bobcats calculated from 16 microsatellite loci.

Fig. S1 Estimating the number of genetic subpopulations (*K*) of bobcats.

Fig. S2 Maximum-likelihood phylogenetic tree built from *pol* sequences using the same model parameters as those described to produce the Maximum-likelihood tree in Fig. 4 (see Methods).

COMMENTARY ENVIRONMENT MY TURN

My turn: Here's how rooftop solar can combat wildfires

BY GUEST COMMENTARY

PUBLISHED: FEBRUARY 13, 2019

Workers installing solar panels on a residential homes roof.

By Audrey Lee, Special to CALmatters

U.S. District Court Judge William Alsup recently issued an unprecedented directive to Pacific Gas & Electric: Inspect its entire electric grid in the coming months and turn off power during fire-prone weather if its equipment has not been deemed safe for those conditions.

After the terrible losses caused by wildfires in recent years, this dramatic turn of events portends greater challenges to utilities in the face of a changing climate.

The Fourth National Climate Assessment reports that climate change and extreme weather events are going to make power disruptions and related wildfires even more common.

Californians deserve real solutions to reduce fire risk while meeting their energy needs. PG&E, other utilities, and the rooftop solar industry should partner to design wildfire mitigation plans that truly protect communities and address the concerns identified by state residents, policymakers, advocates, and the courts.

Local solar power paired with batteries can provide reliable energy and keep electricity running for communities in need, particularly at times when a power line needs to be turned off for safety reasons. This technology might also reduce the chances of electric sparks on overhead lines, which could result in dangerous wildfires.

Electrical lines can only safely carry a certain amount of power without getting too hot. When an electric line heats up with too much energy running through it, the line can sag and drop closer to potential hazards.

Currently, utilities can manage higher power flows for a short time to carry out limited repairs without transmission and distribution lines reaching extreme temperatures, but it may not be enough to handle increased wildfires.

If communities were to deploy more local solar and batteries, we could reduce the amount of power flowing through electricity lines, and coordinate with utilities in real time, leading to an improved scenario for utilities to carry out maintenance, reroute power in case of problems, and ensure overall safety of fire-prone communities.

I have been working to promote energy innovation for decades, first with the U.S. Department of Energy, then at the California Public Utilities Commission, and now as the head of Energy Services at Sunrun.

Let me paint a picture of how this could work.

Consider a community of 500 homes, each using about 5 kilowatts of power, which is roughly the profile of a significant number of homes in fire-prone areas in California.

All these homes are currently connected to the wider network by a single electricity line. For a small community such as this, as few as five to 10 houses with rooftop solar and batteries could

at the required level for safe conditions during times of high demand.

Even in the case that this community were to require more energy and the electricity line supporting it reaches 100 percent capacity, this community would only need 50 to 100 homes with rooftop solar and storage to return to safe conditions.

Naturally, local solar and batteries are more useful as more homes have them. But the minimum threshold to be valuable to engineers can be as low as a handful of customers, depending on how the electricity system in that area has been designed and built, as well as the needs of the supported community.

Home solar and batteries can provide for more resilient energy solutions in high-risk fire areas serviced by electric lines. More importantly, they can help reduce or even prevent power outages for homes, businesses, and other critical facilities.

We have a short period of time until the next fire season hits us. Californians are demanding better solutions from their utilities, now.

Sustainable business models and partnerships with solar leaders looking to protect fire-prone communities are a start. Let's use this opportunity to come together—state leaders, regulators, local policymakers, the rooftop solar industry and utilities—to swiftly bring more solar and batteries to the communities that need them when it matters most.

Audrey Lee is vice president for energy services, Sunrun, based in San Francisco, with services in 23 states plus Washington, D.C., and Puerto Rico. audrey.lee@sunrun.com. She wrote this commentary for CALmatters.

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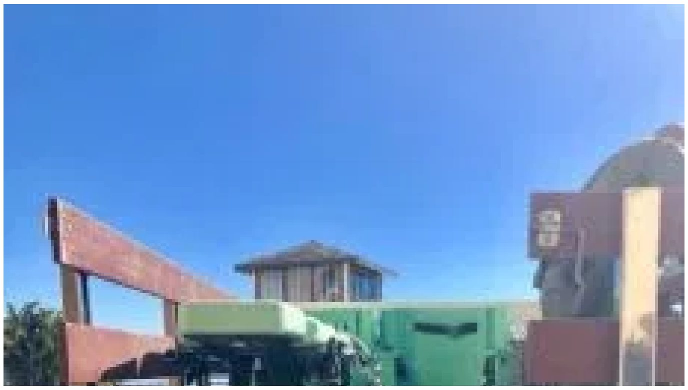

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A systematic review of the physical health impacts from non-occupational exposure to wildfire smoke

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Abstract

Background—Climate change is likely to increase threat of wildfires, and little is known about how wildfires affect health in exposed communities. A better understanding of the impacts of the resulting air pollution has important public health implications for the present day and the future.

Method—We performed a systematic search to identify peer-reviewed scientific studies published since 1986 regarding impacts of wildfire smoke on health in exposed communities. We reviewed and synthesized the state of science of this issue including methods to estimate exposure, and identified limitations in current research.

Results—We identified 61 epidemiological studies linking wildfire and human health in communities. The U.S. and Australia were the most frequently studied countries (18 studies on the U.S., 15 on Australia). Geographic scales ranged from a single small city (population about 55,000) to the entire globe. Most studies focused on areas close to fire events. Exposure was most commonly assessed with stationary air pollutant monitors (35 of 61 studies). Other methods included using satellite remote sensing and measurements from air samples collected during fires. Most studies compared risk of health outcomes between 1) periods with no fire events and periods during or after fire events, or 2) regions affected by wildfire smoke and unaffected regions. Daily pollution levels during or after wildfire in most studies exceeded U.S. EPA regulations. Levels of PM_{10}, the most frequently studied pollutant, were 1.2 to 10 times higher due to wildfire smoke compared to non-fire periods and/or locations. Respiratory disease was the most frequently studied health condition, and had the most consistent results. Over 90% of these 45 studies reported that wildfire smoke was significantly associated with risk of respiratory morbidity.

Conclusion—Exposure measurement is a key challenge in current literature on wildfire and human health. A limitation is the difficulty of estimating pollution specific to wildfires. New

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methods are needed to separate air pollution levels of wildfires from those from ambient sources, such as transportation. The majority of studies found that wildfire smoke was associated with increased risk of respiratory and cardiovascular diseases. Children, the elderly and those with underlying chronic diseases appear to be susceptible. More studies on mortality and cardiovascular morbidity are needed. Further exploration with new methods could help ascertain the public health impacts of wildfires under climate change and guide mitigation policies.

Keywords

Wildfire; Air pollution; Health; Smoke; Forest Fire

1. Introduction

Much remains unknown regarding the public health impacts of forest fire smoke, but interest in the topic is growing as forest fire incidence rises in many parts of the world (Dimopoulou and Giannikos 2004). There is broad consensus that climate change is increasing the threat of forest fires (Albertson *et al.*, 2010; Balling *et al.*, 1992; Flannigan and Vanwagner 1991; Keeton *et al.*, 2007; Malevsky-Malevich *et al.*, 2008; Spracklen *et al.*, 2009), with fires that burn more intensely, occur more frequently, and can spread faster (Fried *et al.*, 2008; Fried *et al.*, 2004; Parry *et al.*, 2007; Westerling and Bryant 2008). The U.S. Forest Service noted that forest fires have already become more intense and that the forest fire season has expanded (U.S. Forest Service 2009). While an increasing frequency of forest fires has often been attributed to many factors including changes in land use, higher spring and summer temperatures may be more relevant (Westerling *et al.*, 2006). The Intergovernmental Panel on Climate Change (IPCC) anticipates that climate change will lengthen the window of high summertime forest fire risk in North America by 10–30%, and result in increased frequency of forest fires in many other parts of the world (Parry *et al.*, 2007). As a result, exposure to air pollution from forest fires is anticipated to increase in coming decades (Interagency Working Group on Climate Change and Health 2010).

The U.S. Forest Service recognizes forest fire smoke as a hazard to human health and identifies airborne particulate matter (PM) as the component of greatest concern for the public (U.S. Forest Service 2010). Numerous studies have demonstrated links between airborne particles and health outcomes including mortality and hospital admissions (Lepeule *et al.*, 2012; Medina-Ramon *et al.*, 2006; Peng *et al.*, 2008; Pope and Dockery 2006). However, not all particles appear to be equally toxic as research indicates that the size and chemical composition of airborne particles affect its impact on health (Ebisu and Bell 2012; Franck *et al.*, 2011; Zanobetti *et al.*, 2009). In general, effects are stronger for smaller particles, which can deposit deeper in the respiratory tract (Valavanidis *et al.*, 2008). The specific mechanistic pathways to adverse health outcomes remain unclear, but chemical composition, particle size, number, and shape have been identified as of putative importance. As the chemical composition of forest fire smoke is likely to differ from those of other sources (e.g., vehicles) (Mao *et al.*, 2011; Pio *et al.*, 2008; Robinson *et al.*, 2011), the observed health associations for more commonly studied air pollutants and sources, such as particulate matter in urban settings, may not be generalizable to pollution from forest fires. Thus, scientific evidence is needed on the health burden from forest fire smoke specifically.

Understanding how forest fire smoke affects public health has the potential to inform intervention-focused policies to protect public health in the present day, climate change mitigation policies, research on health impacts from a changing climate, and economic estimates of the health costs of forest fires. We reviewed and summarized the published literature regarding the public health impacts of forest fire smoke with the goals of synthesizing existing information and identifying gaps in scientific knowledge.

2. Methods

Eligibility criteria

We reviewed peer-reviewed journal articles on the topic of forest fire/wildfire smoke and health, published between 1 Jan 1986 and 30 May 2014. We included studies written in English or Portuguese (with English abstract), and excluded papers written in other languages. We considered all papers relevant to non-occupational exposure to wildfire smoke and physical health impact. We excluded experimental/chamber studies because it is not clear how relevant the exposure level/composition is to those experienced by the community. We excluded conference abstracts, unpublished studies, and non-research publications, such as commentaries. Natural fires were included and controlled prescribed burns were excluded. We did not exclude studies based on type or diversity of vegetation, such as trees peat bog or savannah. All fires are referred to as ‘wildfire’ hereon. We excluded studies of indoor and outdoor wood burning for heating or cooking purposes. Studies that investigated occupational exposures were excluded, as the focus of this review was impacts on communities or broader populations. Therefore, we excluded studies of fire fighters. Since mental health issues are not direct physical health consequences from exposure to wildfire smoke, we excluded studies that investigated only mental health outcomes. As this review focussed on wildfire smoke we also excluded studies that investigated non-smoke related morbidities, such as burns and accidents. Thus, we focused on wildfire smoke and its physical health impacts on the general population.

Information sources

We considered papers indexed in PubMed, a database of biomedical literature and life science journals, managed by the U.S. National Library of Medicine (NIH 2011) and Scopus, a comprehensive database of research literature (Elsevier 2013). References of the resulting papers were examined to better ensure a complete assessment of the literature.

Search terms

Detailed information on the search terms is provided in the supplemental material. Briefly, key words included “wildfire”, “forest fire”, or “bushfire” with any of the following: “health”, “hospital*”, “respir*”, “pulmon*”, “asthma*”, “cardiac”, “cardiovascular”, or “mortality”, where “*” stands for any combination of letters (*e.g.*, hospital* can represent hospitalizations or hospital) (Appendix A).

Summary measures

We summarized the papers with respect to study setting, study design, exposure and outcome assessment, participant vulnerability, key findings, and estimates of association (*e.g*., odds ratios) when provided.

Study assessment

As exposure assessment is a critical challenge in the study of health impacts from wildfire smoke, we described the approaches used by identified studies to estimate exposures. We assessed the overall state of scientific evidence on associations between wildfire smoke and health outcomes for respiratory morbidity, cardiovascular morbidity, mortality, and other outcomes. The approaches to assess health outcomes are diverse, and we summarized the sources of health data for each study. We grouped the studies by health outcomes and summarized the results on health effects. We described factors that might have influenced the summary of evidence based on the studies reviewed. Finally, we highlighted the limitations of these studies and identified needs for future research.

3. Results

The database searches identified 926 papers. We then excluded 277 duplicates (i.e., papers identified by more than one search). We eliminated papers that did not meet the inclusion criteria, by first screening the titles and abstracts (526 papers excluded) and then by a review of the full articles (62 papers excluded). We also excluded studies for which wildfire smoke exposure was not a dominant component relative to other ambient sources (e.g. Sarnat *et al*., 2008). The final review included 61 studies of human health impacts of wildfires in community populations (Table 1).

Study setting

More studies were identified for more recent years, with 4 studies published before 2000 and 35 studies published in the last 5 years. Most studies focused on the Brazilian Amazon, Southeast Asia and the Pacific, the North American West, and the Mediterranean, where wildfires are common. The U.S. and Australia were the most frequently studied countries (18 U.S. studies, 15 Australian studies). Southeast Asia was also frequently studied (9 studies). No studies were set in Africa. Geographic scales ranged from a single small city (population about 55,000) (Huttunen *et al*., 2012) to the entire globe (Johnston *et al*., 2012). Most studies focused on cities or regions close to fire events.

Study design

The majority of studies were based on either spatially or temporally aggregated populations, such as ecological studies (37 of 61 studies). There were relatively fewer cohort or panel studies (14 of 61 studies). Most of the studies compared the risk of health outcomes between 1) periods with no fire events and periods during or after the fire events, or 2) regions not affected by wildfire smoke and regions affected by wildfire smoke. The selection of model adjustment variables was not universal, but can be classified as 1) meteorological; 2) air pollutants other than the pollutants of interest; 3) community-level socio-demographics; and 4) temporal effects (seasonal or secular trend). Of these, meteorological factors were the most prevalent adjustment variables. Some studies controlled for individual variables, such as age group and sex, by stratification (Analitis *et al.*, 2012; Castro *et al.*, 2009; Delfino *et al.*, 2009; Frankenberg *et al.*, 2005; Henderson *et al.*, 2011; Mott *et al.*, 2005; Nunes *et al.*, 2013; Prass *et al.*, 2012; Rappold *et al.*, 2011; Sarnat *et al.*, 2008)

Health outcomes investigated and outcome assessment

Respiratory disease was the most frequently studied outcome (45 studies (74% of 61 studies)) (Supplementary Table A.4). The outcomes included contacts with emergency departments (ED), hospitals or other primary care providers (33 studies (54%)), respiratory symptoms or lung function measurements (9 studies (15%)), and dispensation or consumption of medication (three studies (5%)). Relatively few studies examined cardiovascular morbidity (14 studies) or mortality (13 studies) (Table 2).

Other outcomes investigated were diarrhea due to power outage after wildfire events (identified from surveillance records), birth weight (obtained from hospital birth records), blood biomarkers for systemic inflammation and bone marrow content. The studies of lung-function, blood biomarker concentration and bone marrow content were all cohort studies measuring subjects' lung function or blood samples both before and after fire events.

The most common source of information for health outcomes was the use of datasets maintained by governmental agencies or statistical bureaus (32 studies), followed by hospital admission records or billing records (19 studies), interviews or surveys (10 studies), and subject tests such as lung function or blood samples (seven studies). Some studies used multiple methods to assess health outcomes. All mortality data came from governmental agencies or bureaus. Use of individual surveys (*e.g.*, "smell of wildfire smoke indoors" (Kunzli *et al.*, 2006)) was the most employed method in assessing personal exposure and self-reported symptoms for short-term studies.

Exposure assessment

The most commonly used method for either designating a fire period or area, or assessing exposure for previously designated fire and non-fire periods or areas, was use of measurements from land-based air pollutant monitors (35 studies), followed by satellite-based imagery or models (11 studies), air quality modelling (six studies) and personal exposure from individual surveys, personal reports, or personal photometers (three studies) (Supplementary Table A.3). Of the 61 studies, seven studies used other methods to assess exposure, such as air sample analysers. Satellite-based methods became popular in studies from recent years.

Pollutant data from air monitors were usually obtained by governmental agencies or research institutions and were used as the exposure variable in statistical models. The monitoring data usually covered pre-, during- and post-fire periods. Most of the studies determined "exposed period" based on the start/end dates of fire events but did not specify how the start/end days were identified. Some studies used thresholds of air monitoring data to categorize days, for example, high PM days with aerodynamic diameter $<2.5\mu m$ ($PM_{2.5}$) $>40\mu g/m^3$, low PM days with $PM_{2.5}<10\mu g/m^3$ (*e.g.*, Johnston *et al.*, 2002). Personal surveys and reports generally asked questions such as “did you smell any smoke?” or “did you have any health symptoms?” plus the respondents’ personal characteristics, such as age and education. Personal photometers were used to measure personal exposure to $PM_{2.5}$ (Huttunen *et al.*, 2012).

Satellite-based imagery or models are increasingly common in the recent studies to aid exposure assessment. Some satellite-based studies used satellite images to detect “hotspots”, which were used as indicators of fire events (*e.g.*, Castro *et al.*, 2009; de Mendonca *et al.*, 2006)). Some studies determined “exposed region” based on either satellite images or proximity to fire events (*e.g.*, Kunii *et al.*, 2002). The majority of the studies using satellite-based methods measured exposure for at least 5 years. In contrast, studies using individual photometers or reports usually investigated individual-specific exposure among subjects of a prospective cohort for a shorter period of a few days to a few months (Frankenberg *et al.*, 2005; Kunii *et al.*, 2002; Kunzli *et al.*, 2006).

The length of exposure measurement varies from a few days to over a dozen years. Huttunen *et al.* assessed daily average exposure of $PM_{2.5}$ and PM with aerodynamic diameter < 10μm (PM_{10}) during a 12-day fire that occurred in Kotka, Finland from Apr. 25 to May 6, 2006 (2012). Many studies compared longer-term exposure across months or seasons (Hanigan *et al.*, 2008; Johnston *et al.*, 2007; Smith *et al.*, 1996). Elliott *et al.* (2013) measured exposure during fire seasons (Apr. 1 to Sep. 30) in each year (2003–2010) and compared the health risk during fire seasons with non-fire seasons. Evaluation of long-term exposure was more common in regions with distinct fire seasons, such as Australia (*e.g.*, Hanigan *et al.*, 2008; Johnston *et al.*, 2011; Morgan *et al.*, 2010; Smith *et al.*, 1996) and Canada (Elliott *et al.*, 2013). Johnston *et al.* (2011) investigated long-term mortality effect by measuring PM_{10} exposure attributed to wildfires over 13.5 years, from 1994 to 2007 in Sydney, Australia.

Other studies compared exposure and health during the period when forests were burning to the periods before and/or after the fire (Supplementary Table A.3). Of these studies, Duclos *et al.* (1990), Frankenberg *et al.* (2005), and Moore *et al.* (2006) compared exposure and health during the fire events or seasons with control periods in preceding and/or subsequent years. Many studies estimated short-term (*e.g.*, a few days to one or two weeks) exposure under a certain fire event and compared the health risk during the fire event with that during short pre- or post-fire periods (*e.g.*, Schranz *et al.*, 2010; Sutherland *et al.*, 2005; Vora *et al.*, 2011). This exposure timeframe was common in studies based on local populations and a single fire event. Many studies compared longer-term exposure across months or seasons (*e.g.*, Hanigan *et al.*, 2008; Johnston *et al.*, 2007; Smith *et al.*, 1996).

Almost all studies mentioned that air pollutant levels, especially particulate matter levels, increase dramatically during wildfire events. Figure 1 shows estimated air pollutant levels during fire periods compared with levels in control periods. $PM_{2.5}$ levels in most studies exceeded the U.S. EPA National Ambient Air Quality Standard for 24-hour $PM_{2.5}$ (35μg/m^3). Some studies indicated particulate levels during fire periods over 100 μg/m^3 for $PM_{2.5}$ and over 500 μg/m^3 for PM_{10} (*e.g.* Hänninen *et al.*, 2009; Holstius *et al.*, 2012; Kolbe and Gilchrist 2009; Kunii *et al.*, 2002)

3.1 Association between wildfire smoke and health outcomes

3.1.1 Respiratory morbidity—Of the health outcomes examined, respiratory morbidity had the strongest evidence of an association with wildfire smoke, with a statistically significant adverse association reported for 43 of the 45 respiratory studies (Supplementary Table A.4). Analysis of respiratory-related contacts with primary care providers constituted 31 studies that reported associations and 2 studies that did not detect an adverse association. ED contacts for asthma in Darwin, Australia were 2.4 (95% confidence interval 1.5–3.9) times greater on a fire day (PM_{10}>40μg/m^3) than on a non-fire day (PM_{10}<10 μg/m^3) (Johnston *et al.*, 2002). Two other Australian studies reported greater risk of hospital admission for elevated exposure two days before the hospital admission day (Morgan *et al.*, 2010) and five days before the admission day (Chen *et al.*, 2006). Associations for longer lags (greater than five days) between exposure and hospitalization were not directly investigated in any study. From cross-sectional studies there were increases in primary care contacts for a 12-week period of exposure to wildfire smoke in California (Lee *et al.*, 2009) and a five-week exposure period in Canada (Moore *et al.*, 2006) compared to the same period in previous years when there were no fires. However, it remains unclear as to whether admissions increased due to high acute exposures over short periods (days) and/or lower levels accumulated over a longer period (months). Associations were consistently reported between wildfire related exposure and respiratory symptoms or dispensation/use of medication (all 12 studies). Adverse associations were observed for cough, wheeze and eye irritation (Supplementary Table A.4).

A statistically significant association between exposure to wildfire smoke and hospital or emergency room admissions for respiratory diseases was not reported in two of the 45 studies (Azevedo *et al.*, 2011; Smith *et al.*, 1996). A study of Sydney compared ED records in seven hospitals during a two-week fire period with that during the same period in the previous year. The researchers found no difference in asthma ED visits during the two periods (Smith *et al.*, 1996). The Northern Portugal study reported that high ozone level (greater than 100μg/m^3) during the three-month fire period was not associated with respiratory disease admissions.

3.1.2 Cardiovascular morbidity—Of the 14 studies that assessed the relationship between wildfires and cardiovascular morbidity, six reported a statistically significant increase in risk of cardiovascular outcomes with exposure to wildfire smoke. Some authors reported change in risk per unit (such as per 100 μg/m^3) increase in daily measurement of certain wildfire-promoted pollutants, such as ozone, PM_{10} or $PM_{2.5}$ (Azevedo *et al.*, 2011; Lee *et al.*, 2009; Rappold *et al.*, 2012). Others reported changes in risks comparing regions or time periods of wildfires with non-wildfire regions or times (Delfino *et al.*, 2009; Rappold *et al.*, 2011). PM_{10} was the most commonly studied pollutant for cardiovascular diseases and most of the PM_{10}-CVD studies (eight out of nine) did not find any significant association. Other air pollutants from wildfires were less studied and their impact on cardiovascular illness remains unclear. Study findings varied geographically, with no report of a statistically significant cardiovascular impact of wildfire smoke in any study from Australia and Canada (seven out of 14) (Crabbe 2012; Hanigan *et al.*, 2008; Henderson *et al.*, 2011; Johnston *et al.*, 2007; Martin *et al.*, 2013; Moore *et al.*, 2006; Morgan *et al.*, 2010). Contrastingly, five out of six U.S. studies reported that exposure to wildfire smoke was associated with hospital admissions for cardiovascular diseases, such as cardiac arrests, or symptoms such as chest pain (Delfino *et al.*, 2009; Lee *et al.*, 2009; Rappold *et al.*, 2012; Rappold *et al.*, 2011). All studies assessed cardiovascular disease by hospital admissions or emergency room visits. A U.S. study found that a 100μg/m^3 increase in wildfire smoke-related $PM_{2.5}$ was associated with a significant 42% (95%CI: 5%–93%) increase in emergency room visits for congestive heart failure (CHF) (Rappold *et al.*, 2012). However, there were too few studies on specific cardiovascular endpoints, such as ischemic heart disease (*e.g.*, Azevedo *et al.*, 2011; Crabbe 2012; Moore *et al.*, 2006) to establish consistency of associations.

3.1.3 Mortality—Mortality was associated with wildfire smoke for nine of 13 studies. Only three of these studies assessed non-accidental mortality (Analitis *et al.*, 2012; Johnston *et al.*, 2011; Vedal and Dutton 2006). Two investigated cause-specific mortality for respiratory and COPD (Castro *et al.*, 2009; Nunes *et al.*, 2013). Other studies examined total all-cause mortality. The increase in mortality under exposure to wildfire smoke, compared with periods of no fires, ranged from 1.2% for children during the fire event (Jayachandran 2009) to 92.0% for respiratory mortality during days with large fires (Analitis *et al.*, 2012). Large fires (>3000 hectares burned) had larger estimated associations with mortality than smaller fires (Analitis *et al.*, 2012). As wildfire events occur more often in summer, Shaposhnikov *et al.*, (2014) examined the interaction between heat and wildfire smoke. They found that temperature and PM_{10} (largely due to wildfires) collectively contributed to over 2000 deaths. One of the three studies that investigated shorter-term exposure and did not report a statistically significant association did not provide numeric results (Vedal and Dutton 2006) while the effect estimates reported in the other two studies were in the positive direction, i.e., adverse mortality effects (Hänninen *et al.* (2009) and Morgan *et al.* (2010)).

3.1.4 Other health outcomes—Eleven studies investigated other health outcomes in relation to wildfire smoke. These included studies on birth weight (Holstius *et al.*, 2012; Prass *et al.*, 2012), bone marrow content (Tan *et al.*, 2000), systematic inflammation (Huttunen *et al.*, 2012), physical strength and overall health (Frankenberg *et al.*, 2005), diarrhea (Viswanathan *et al.*, 2006), diabetes (Lee *et al.*, 2009), and injuries (Cameron *et al.*, 2009; Cleland *et al.*, 2011). For the two studies that investigated birth weight, results were inconsistent (Holstius *et al.*, 2012; Prass *et al.*, 2012). All three cohort studies reported significant adverse associations between wildfires and health: systemic inflammation (Huttunen *et al.*, 2012), bone marrow content (Tan *et al.*, 2000), and physical strength and overall health (Frankenberg *et al.*, 2005). Diarrhea and diabetes were mentioned as health outcomes of interest in multiple studies (Aditama 2000; Jalaludin *et al.*, 2000; Lee *et al.*, 2009; Viswanathan *et al.*, 2006), but only two reported the results (Lee *et al.*, 2009; Viswanathan *et al.*, 2006). Exposure to wildfire smoke did not show discernible effects on either diarrhea or diabetes.

Vulnerable sub-populations: A limited number of studies assessed whether some populations face higher health risk from exposure to wildfire smoke than others, examining population characteristics such as age categories. The age cut-offs for age categories varied by study. Larger positive associations between wildfire smoke and cardiorespiratory morbidities were observed for middle-aged adults (Henderson *et al.*, 2011) and older adults compared to other age groups (Analitis *et al.*, 2012; Castro *et al.*, 2009; Delfino *et al.*, 2009; Frankenberg *et al.*, 2005; Morgan *et al.*, 2010; Nunes *et al.*, 2013; Shaposhnikov *et al.*, 2014). Elevated levels of wildfire smoke had larger risk estimates for asthma hospitalizations among adults aged 40–64 years (Mott *et al.*, 2005), 15–64 years (Morgan *et al.*, 2010), and 19–64 years (Rappold *et al.*, 2011) compared to other age groups. Risk of respiratory-related hospital contacts associated with wildfire smoke was higher for children (<5 years) compared with other age groups (Ignotti *et al.*, 2010).

Men and women may have different health risks when exposed to wildfire smoke. Risks for asthma-related symptoms or visits in relation to wildfire smoke were greater for women than men (Lee *et al.*, 2009; Rappold *et al.*, 2011). However, Henderson *et al.* (2011) and Prass *et al.* (2012) did not find differences in wildfire effect estimates between men and women in respiratory and cardiovascular physician visits, and birth weight, respectively.

Three studies reported effect modification by socio-economic status (SES), race, or co-morbidities. Larger risk estimates between wildfire smoke and risk of asthma and congestive heart failure were observed among counties of lower SES compared to higher SES counties (Rappold *et al.*, 2012). Aboriginal Australians had higher risk of respiratory admissions and emergency admissions than other races when exposed to PM_{10} (Hanigan *et al.*, 2008; Johnston *et al.*, 2007). Johnston *et al.*, (2007) did not detect an association between PM_{10} and cardiovascular admissions for the general population, but restriction of analyses to the Aboriginal population with ischemic heart disease resulted in findings of the greatest risk of respiratory-related hospital admissions three days after exposure (Johnston *et al.*, 2007). It is plausible that associations at longer lags might have only been observable for such high-risk sub-populations, most susceptible to wildfire. Lee *et al.* (2009) and Mirabelli *et al.*, (2009) reported that adults with pre-existing respiratory conditions or weakness (i.e. small airway size) were more likely to seek care or have additional symptoms after wildfire exposure than persons without those conditions. However, Künzli *et al.* (2002) reported opposite results, as children without pre-existing asthmatic conditions had greater increase in respiratory symptoms under exposure than did other children. The authors suggested that children with pre-existing asthmatic conditions tended to be on medication and have better access to care, hence their smaller increase in symptoms when exposed to wildfire smoke. In an Australian study, no adverse association was observed between wildfire related PM_{10} and lung function (peak expiratory flow) except when analysis was restricted to children with no bronchial hyper-reactivity (Jalaludin *et al.*, 2000).

4. Discussion

Overall, wildfire smoke exposures, as measured by proxies such as criteria air pollutants, were consistently associated with mortality and respiratory morbidities. Respiratory-related effects of wildfire smoke included increases in risk of hospitalization, use of respiratory medication, cough, wheeze and eye irritation. In one study, risk of emergency department contact for asthma could be more than two times greater after exposure to wildfire smoke (Johnston *et al.*, 2002). As most mortality studies investigated all-cause mortality, further research is needed to better identify the specific causes of mortality most strongly associated with wildfire smoke exposures. The magnitude of the effects on mortality varied by study. Respiratory mortality almost doubled from exposure to a wildfire in Greece (Analitis *et al.*, 2012), but some wildfires were not associated with changes in the mortality rate (Morgan *et al.*, 2010). The only global study posited that 339,000 deaths per year were attributable to wildfires, with Sub-Saharan Africa and Southeast Asia the most affected regions (Johnston *et al.*, 2012). However, this review highlighted disproportionately fewer studies in Southeast Asia and no other studies conducted in Sub-Saharan Africa. Some parts of the world such as Sub-Saharan Africa are affected by wildfire events but have not been studied. Those places, usually the less-developed regions, may contribute the most to the global burden of many diseases. It is also unlikely that these parts of the world can respond to such risk as well as more developed nations. Therefore, more studies are needed in these less studied countries.

Although our review of studies on forest fires and health is the most extensive to date, past reviews on related topics have also contributed substantially towards knowledge on the health effects of wildfire smoke. An early review by Naeher *et al.* (2007) focused on the toxicity of wood smoke, thereby establishing biological plausibility of the association, and called for further studies on the topic. Two later reviews investigated effects on respiratory outcomes of bushfire smoke (Dennekamp and Abrahmson 2011) and on respiratory outcomes for forest fires (Henderson and Johnston 2012). Dennekamp and Abramson (2011) identified that elevated PM concentrations from bushfire smoke explained associations with increased respiratory morbidity. Henderson and Johnston (2012) confirmed consistency of associations with acute respiratory outcomes and identified the need for studies in equatorial regions with rainforest depletion. Finlay et al. (2012) included non-respiratory outcomes and focused on demonstrating the current stage of investigation on this issue in the U.K. and identified literature gaps for the U.K. Finlay et al. identified the potential burden on cardiovascular and ophthalmic outcomes. Our review confirms that there still remain too few studies on these endpoints to establish consistency. The findings of our comprehensive review add to those of the previous reviews that focused on specific types of wildfire, health outcomes, or countries. Our review also quantified the substantial increase in exposure levels from wildfires and how these increases differed across studies. This was the first review to identify the dearth of studies from sub-Saharan Africa and paucity of studies in Southeast Asia, which are regions that experience a large health burden and are less able to respond to the increasing frequency and intensity of wildfires that accompany climate change. Our review also identified the shift in exposure assessment from the dominant use of measurements from ground-based air monitors to use of satellite imagery and chemical transport models.

In our review we found that results were most consistent among cohort studies, as almost all cohort studies found significant impact of wildfire smoke on health in at least one of the health outcomes and part of the population studied. Studies involving direct physiological measurements on recruited patients, such as bone marrow (Tan *et al.*, 2000) and Peak Expiratory Flow Rates PFFR (e.g. Jalaludin *et al.*, 2000), also tend to discern significant impacts. Ecological studies generally had inconsistent results. However, it is difficult to draw conclusions as to how study design and methods affected the reported associations because of heterogeneity in these and other design factors across studies, significant difference between pollutant levels during wildfire and non-wildfire periods, and how this difference varied across studies.

Studies consistently reported substantially higher levels of air pollution during fire periods and locations compared to non-fire periods and areas. Daily average PM_{10} levels in an exposed city (Jambi, Indonesia) exceeded 1800μg/m^3 during fire events (Kunii *et al.*, 2002), which was 12 times the WHO interim target-1 standard (150μg/m^3 24-hour) and 36 times the WHO air quality guideline (50μg/m^3 24-hour). Daily average $PM_{2.5}$ levels during wildfires exceeded 150μg/m^3, more than 6 times greater than the WHO air quality guideline (25μg/m^3 24-hour) (Moore *et al.*, 2006). Levels of carbon monoxide can increase 30–40% during wildfire periods compared with periods with no fires (Sutherland *et al.*, 2005; Tan *et al.*, 2000). These results indicate that wildfire events can result in severe levels of exposures. In addition to high levels, the chemical composition of wildfire smoke is distinctive. Wildfire smoke is accompanied by elevated levels of black carbon (Crabbe 2012), and polycyclic aromatic hydrocarbons can be 15 times higher than background levels (Aditama 2000).

4.1 Methods used to assess exposure to wildfire smoke

This review identified assessment of exposure as a key challenge in health studies of wildfires, with a range of methods applied. It is difficult to identify a direct marker that can represent air pollutants only from wildfires. Studies used indicators such as criteria air pollutants, aerosol optical depth or area burnt as indirect proxies. Although use of indirect proxies can be a useful approach, it is difficult to ascertain the fraction of health morbidity due to wildfire smoke excluding health morbidities due to those proxies in non-wildfire periods and from other sources during wildfire periods. The most commonly used marker for wildfire smoke used in the reviewed studies was particulate matter (PM) (Phuleria *et al.*, 2005). Although the fine fraction of particulate matter ($PM_{2.5}$) has been more consistently associated with adverse health effects than larger particles in studies of particulate matter more generally (Pope and Dockery 2006), fewer studies investigated the health effects of wildfire smoke-related $PM_{2.5}$. Notably, in all countries, the measurement of $PM_{2.5}$ began more recently than PM_{10}. A further exposure-related limitation of many of the reviewed studies was the coarse spatial resolution of exposure, due primarily to the use of ground-based ambient air monitors and the available monitoring network. An exception to this was studies that used remotely sensed satellite-derived imagery of area burnt (de Mendonca *et al.*, 2006). However, it is unclear as to whether area burnt is a suitable proxy for wildfire smoke exposure because it must be interpreted relative to population's distance to the wildfire, wind speed and direction, and atmospheric mixing depth (Naeher *et al.*, 2007; Ward 1990). Wildfire smoke also varies with vegetation type as, for example, wood from eucalypt forest has more oil content and releases higher concentrations of PM_{10} than pine, acacia or cork oak (Goncalves *et al.*, 2010).

Exposure assessment is an ongoing challenge in epidemiological studies of wildfire smoke. Ground-based monitors do not measure the complicated mixture of pollution from the source of wildfires specifically. Monitors measure the level of a specific pollutant, such as

$PM_{2.5}$, and cannot measure the pollution solely from fires as opposed to other sources. Therefore, it is difficult to separate the health effect of wildfire-emitted pollutants from that of pollutants from other sources. Moreover, ground-based air pollution monitors are not located in all places or time periods with affected populations. Exposure estimates based on satellite data provide more comprehensive spatial coverage (Kloog *et al.*, 2011; Lee *et al.*, 2011), but do not address the issue of specificity of the exposure estimates for wildfire smoke. It is critical to better understand the levels of wildfire smoke-specific pollutants (e.g., particulate matter from wildfires), as the range of health responses to the chemical signature specific to wildfire smoke is currently unclear (Wegesser *et al.*, 2009). Recent developments in chemical transport models may help address this limitation in future work. Chemical transport models, such as GEOS-Chem models, can estimate air pollutants specifically from wildfires (e.g. Singh *et al.*, 2010). Johnston et al (2012) employed this method to estimate the global exposure to wildfire-emitted $PM_{2.5}$. They found that 339,000 deaths could be attributed to wildfires annually. One limitation of using chemical transport models is that the wildfire-specific pollutant estimates may be difficult to validate. Modeled data could also be computationally expensive and requires collaboration efforts of atmospheric scientists (Kleeman *et al.*, 2009).

4.2 Health outcomes affected by wildfire smoke

The health endpoints investigated by the reviewed studies mainly focused on mortality and respiratory morbidity. Over 90% of the studies on respiratory morbidity and about 70% of the studies on mortality found significant association with wildfire smoke. There was insufficient evidence to conclude a consistent association between wildfire smoke and cardiovascular morbidities due to the relatively fewer number of studies. Despite the inconsistent association for cardiovascular morbidities globally, the association was mostly consistent in North America (five out of six studies found significant impact), where prevalence of cardiovascular diseases are higher than many other study areas. Causal links have been established between PM_{10} more generally and a range of cardiovascular endpoints (Brook *et al.*, 2010). Other potential health endpoints that have been studied in the context of air pollution are hypertensive disorders (*e.g.* van den Hooven *et al.*, 2011), ophthalmic outcomes (*e.g.* Versura *et al.*, 1999), adverse pregnancy outcomes (*e.g.* Ritz *et al.*, 2002), and non-respiratory atopic disease (Morgenstern *et al.*, 2008). Future studies on the health impacts from wildfires may investigate these outcomes.

4.3 Susceptibility/Vulnerability

Among other factors, variation in the magnitude and statistical significance of observed effect estimates across the reviewed studies was likely attributable, in part, to differences in the underlying characteristics of the study population, including biological susceptibility, sociodemographic vulnerability, or other factors. Air pollution research more broadly has acknowledged population characteristics that can lead to greater biological susceptibility or sociodemographic vulnerability (Gouveia and Fletcher 2000). However, for wildfire smoke exposure, our review identified a paucity of studies on potentially vulnerable/susceptible subpopulations. There was some indication of elevated vulnerability to adverse health-effects of wildfire smoke among certain sub-populations: young children, older adults, and individuals of lower socioeconomic status. It is plausible that individuals with pre-existing respiratory morbidities are more susceptible to the respiratory effects of wildfire smoke possibly due to elevated sensitivity to environmental hazards by weaker immune systems. Pre-existing morbidities, such as asthma, that may not be fully controlled by medication might lead to greater susceptibility to adverse health effects of wildfire smoke. Although not specific to wildfire smoke, PM_{10} has been associated with poorly controlled asthma among adults (Jacquemin *et al.*, 2012) and the effect of air pollutants on respiratory exacerbation among asthmatic children appears to be greater for those not on anti-inflammatory medication (Delfino *et al.*, 2002).

In the identified studies, five of six U.S. studies reported associations between wildfire smoke and cardiovascular hospital admissions, whereas associations were not observed in studies for other locations, including Australia and Canada. Cardiovascular diseases are more prevalent in U.S. adults (more than 1 in 3 adult Americans have cardiovascular diseases) (Lloyd-Jones *et al.*, 2010) than in Australia (about 1 in 6) (The Heart Foundation 2011). The mortality rates due to cardiovascular diseases are also higher in the U.S. than in Canada or Australia (Lloyd-Jones *et al.*, 2010). The different findings by region may result from higher risk for cardiovascular responses from wildfire smoke for population with high CVD prevalence.

4.4 Recommendations for future research

More studies in wildfire-affected but less-developed regions, such as Africa and Southeast Asia are needed. These regions face the highest health risk to wildfire smoke because they lack well-developed health care infrastructure and resources (Watson *et al.*, 2007). They are also less able to adapt to climate change compared to the developed world (Matthes 2008), leading to even higher risk to wildfires in the future. The populations are particularly vulnerable because behavioral interventions are complex (e.g., remaining indoors might increase exposure due to use of solid fuels, and chronic exposure to indoor solid fuels can lead to higher susceptibility to respiratory diseases (Po *et al.*, 2011)) (Smith *et al.*, 2004).

More large-scale studies are needed to obtain more reliable results on health impact of wildfires. Most of the identified studies were based on single-episode fire events, with fewer long-term studies. Studies based on multiple-episode fire events might be useful to identify consistency of an association over time or change in vulnerability or behavioral adaptation (*e.g*., remaining indoors) to wildfire smoke exposure. Similarly, most studies focused on local regions, with few studies at national or other large geographic scales. Investigating larger geographies will introduce greater sociodemographic variation that might reveal communities at the greatest risk of wildfire smoke-related health responses. Large-scale studies can also help policy-makers by identifying the most vulnerable communities and populations for policy reference.

In addition, future studies could also adapt more new technologies to advance exposure assessment. Chemical transport models, dispersion models and satellite-based models could help address the limitations of assessing wildfire smoke exposure using air monitors. Moreover, as wildfire potential has been projected to increase in the future (Liu *et al.*, 2010), studies that estimate future wildfire-related health impact are needed. In our review, no identified studies projected the future health risk from wildfires under climate change, or identified high-risk regions or populations under future conditions. Studies projecting future health impact of wildfires can raise awareness of the health impact of wildfires in communities, promote preventive public health programs in high-risk communities, and aid in our understanding of the health consequences of a changing climate.

5. Conclusion

Our review indicates that wildfire events have potential to induce a substantial health burden. As wildfires are likely to occur more frequently and intensely under the impact of climate change, this health burden may increase in the future. Air pollution from wildfires was consistently associated with respiratory outcomes, and more studies are needed to investigate cardiovascular morbidity and mortality in community populations. Most of the current studies were based on single episodes and local populations. Conducting multiple episode and larger scale studies may reveal effects of wildfire smoke and help elucidate changes in wildfire frequency and possible adaptation. It was not possible to separate completely the health effect of wildfires from that of other ambient sources for the reviewed studies. Key challenges in current research include the assessment of exposure of wildfire-specific pollutants and the health risk modelling for source-specific air pollutant estimates. More research is needed to investigate the health effects of fine particulate matter from wildfires in Africa and Southeast Asia, the susceptible/vulnerable populations under exposure to wildfire smoke, and future health burden from wildfires under climate change.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- Wildfire smoke dramatically increased ambient air pollutant levels
- Wildfire smoke consistently associated with increased risk of respiratory disease
- Suggestive evidence wildfire smoke linked with cardiovascular diseases & mortality
- Key challenge of exposure assessment: estimating fire-specific pollutants

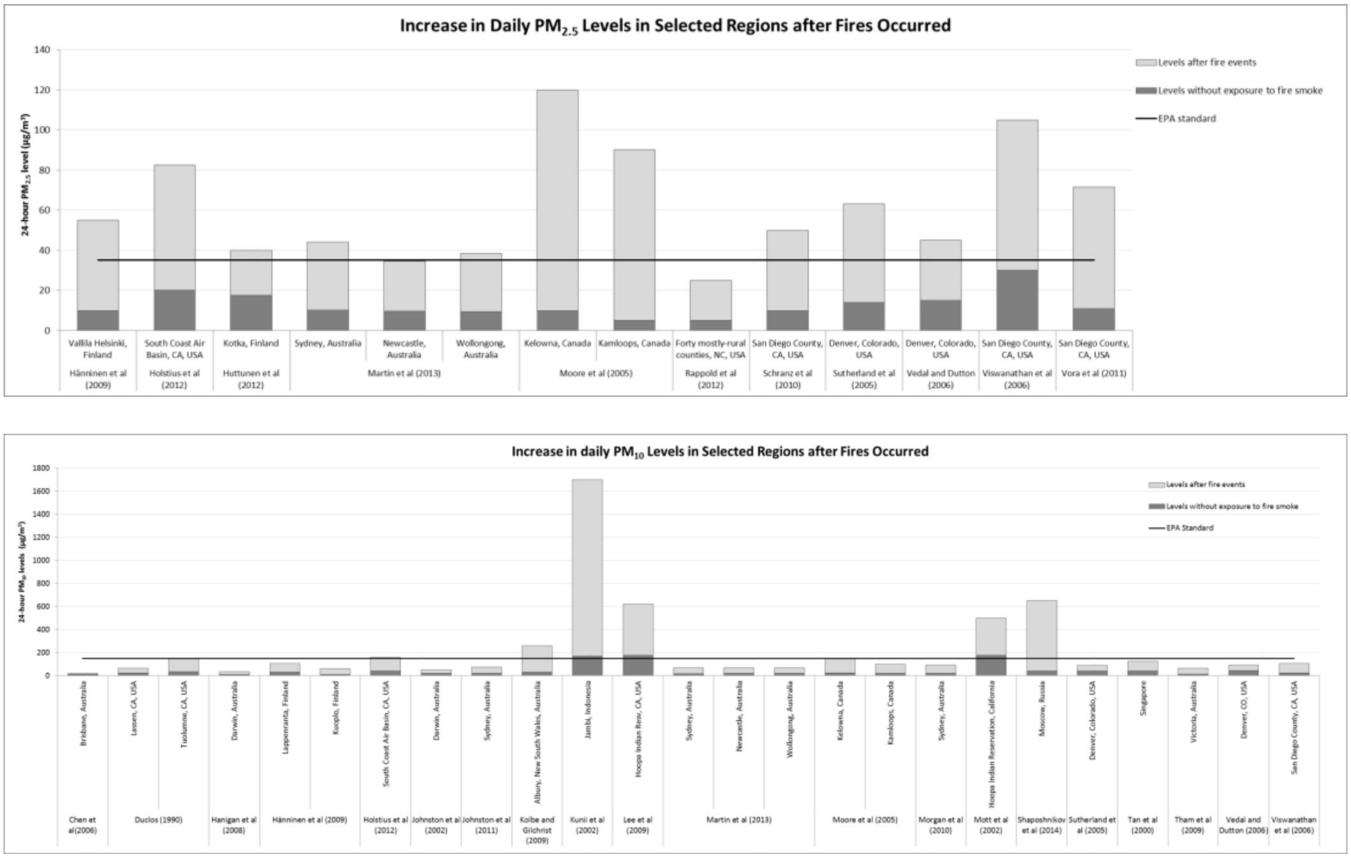

Figure 1.

$PM_{2.5}$ (top) and PM_{10} levels (bottom) during wildfire events and non-fire periods

Table 1

Summary of studies on wildfire smoke and population health

Study	**Location**	**Background population or cohort size**	**Time of fire**	**Major health outcome**	**Exposure metric**
Aditama (2000)	Multiple provinces in Indonesia	12,360,000 residents exposed to smoke	major fire: July–Oct. 1997	Respiratory symptoms	CO, SO_2, PM_{10}, TSP, NOx, O_3, organic compounds
Analitis *et al.*, (2012)	Athens, Greece	More than 3 million residents	1994–2004	Mortality	Sizes of area burned
Azevedo *et al.*, (2011)	Northern coast of Portugal	Elderly among Porto (total population 1.4 million)	June to Aug. 2005	Cardiovascular (CVD), respiratory admissions	O_3
Caamano-Isorna et al., (2011)	Galicia, Spain	About 2 million inhabitants	Summer 2006	Respiratory medicine usage	Exposure classified into three categories based on number of fires
Cameron *et al.*, (2009)	Victoria, Australia	5.2 million residents	Feb. 2009	Injuries	Not specified
do Carmo *et al.*, (2010)	Alta Floresta municipality, Mato Grasso, Brazil	51,136 residents in Alta Floresta, Mato Grosso (9% children <5y, 5% elderly >64y)	Jan. 2004 – Dec. 2005	Respiratory admissions	$PM_{2.5}$
Castro *et al.*, (2009)	State of Rondônia, western Brazil	1.6 million residents	1998–2005	Mortality	Number of fire “hotspots”
Centers for Disease Control and Prevention (CDC) (1999)	Central Florida	Not specified	Jun.– Jul. 1998	Respiratory and cardiovascular Emergency Room (ER) visits	Wildfire v. non-wildfire periods
Centers for Disease Control and Prevention (CDC) (2007)	Panhandle region and 9 other counties, Texas, U.S.	Not specified	March 12–20, 2006	Mortality	Presence of wildfire smoke
Centers for Disease Control and Prevention (CDC) (2008)	San Diego Co., California, U.S.	Not specified	Oct. 22–26, 2007	Respiratory ER visits	Wildfire v. non-wildfire periods
Chen *et al.*, (2006)	Brisbane, Australia	Not specified	Fire seasons 1997–2000	Respiratory admissions	PM_{10}
Cleland *et al.*, (2011)	Melbourne, Australia	Not specified	Feb. 2007	Injuries	Not specified
Crabbe (2012)	Darwin, Australia	110,000 residents	1993–1998	Respiratory, CVD ER visits	PM_{10}, black carbon
Delfino *et al.*, (2009)	Southern California, U.S.	20.5 million residents	Oct. 21–30, 2003	CVD, respiratory admissions	$PM_{2.5}$
Dohrenwend *et al.*, (2013)	San Diego Co., California, U.S.	Not specified	Oct 21–Nov 6, 2007	Respiratory ER visits	Wildfire v. non-wildfire periods
Duclos *et al.*, (1990)	6 counties in California, U.S.	Residents in 6 counties (population size not specified)	Aug. 30–Sep. 3, 1987	Respiratory ER visits	PM_{10}, TSP

Study	Location	Background population or cohort size	Time of fire	Major health outcome	Exposure metric
Elliott *et al.*, (2013)	British Columbia (BC), Canada	Residents from 29 local health areas (LHA) in BC; population ranges 7,024–352,783 people	Fire seasons 2003–2010	Respiratory medicine usage	$PM_{2.5}$, PM_{10}
Emmanuel (2000)	Singapore	> 3 million residents	End of Aug. to early Nov. 1997	Respiratory admissions; all-cause mortality	PM_{10}, SO_2, NO_2, O_3, CO, total hydrocarbon
Frankenberg *et al.*, (2005)	Kalimantan and Sumatra, Indonesia	10,869 subjects > 30y	July–Oct., 1997	Respiratory illness/symptoms; physical strength, overall health	Aerosol
Hanigan *et al.*, (2008)	Darwin, Australia	110,000 residents	Dry seasons (Apr. – Nov.) of 1996–2005	Respiratory, CVD admissions	PM_{10}
Hänninen *et al.*, (2009)	11 provinces in southern Finland	3.4 million residents	Aug. 26–Sep. 8, 2002	Mortality	$PM_{2.5}$, PM_{10}
Henderson *et al.*, (2011)	Southeastern corner of BC, Canada	281,711 subjects	Summer 2003	CVD, Respiratory admissions	PM_{10}
Holstius *et al.*, (2012)	South Coast Air Basin, California, U.S.	886,034 infants in exposed group; 747,590 infants in control group	Oct. 2003	Birth weight	Exposed or unexposed to fire during pregnancy
Huttunen *et al.*, (2012)	Kotka, Finland	52 elderly people (>50 y) with ischemic heart disease	Apr. 25–May 6, 2006	Blood concentration of inflammatory markers	$PM_{2.5}$
Ignotti *et al.*, (2010)	Microregions in northern states of Brazilian Amazon, with Mato Grosso and Maranhão	24 million inhabitants affected; subpopulations: Children (<5 y), elderly (>64), and an intermediate age group (5–64 y)	2004–2005	Respiratory admissions	$PM_{2.5}$
Jalaludin *et al.*, (2000)	Sydney, Australia	32 children	Jan. 1994	Peak expiratory flow rates (PEFR)	PM_{10}, NO_2, O_3
Jayachandran (2009)	Indonesia	~1.3 million children (<3 y), infants or fetuses	Aug.–Oct. 1997	Mortality	Aerosols
Johnston *et al.*, (2002)	Darwin, Australia	115,000 residents	Apr. 1–Oct. 31, 2000	Asthma ER visits	PM_{10}
Johnston *et al.*, (2006)	Darwin, Australia	251 asthmatic adults and children, about half < 18y	7 months in 2004	Asthmatic symptoms	$PM_{2.5}$, PM_{10}
Johnston *et al.*, (2007)	Darwin, Australia	110,000 residents	Fire seasons of 2000, 2004, 2005	Respiratory, CVD admissions	PM_{10}
Johnston *et al.*, (2011)	Sydney, Australia	~ 4 million residents	1994–2007	Mortality	PM_{10}, O_3
Johnston *et al.*, (2012)	Global	Not specified	1997–2006	Mortality	$PM_{2.5}$
Kolbe and Gilchrist (2009)	Albury, New South Wales, Australia	389 interviewees	Jan–Feb, 2002	Respiratory symptoms	PM_{10}
Kunii *et al.*, (2002)	Jambi, Sumatra (affected) and Jakarta, Java (control), Indonesia	543 subjects in Jambi	July–Oct. 1997	Respiratory symptoms	CO, CO_2, SO_2, NO_2, O_3, PM_{10}, inorganic ions, PAHs

Study	**Location**	**Background population or cohort size**	**Time of fire**	**Major health outcome**	**Exposure metric**
Kunzli *et al.*, (2006)	16 communities in Southern California, U.S.	873 high school students, 5551 elementary school students	Oct. 2003	Respiratory symptoms	PM_{10}
Lee *et al.*, (2009)	Hoopa Indian Reservation, California, U.S.	2,633 residents	Late summer and fall 1999	Respiratory, CVD, diabetes admissions	PM_{10}
Martin *et al.*, (2013)	Sydney, Newcastle and Wollongong, Australia	About 4.5 million residents	Fire seasons 1994–2007	All non-trauma admissions	PM_{10}, $PM_{2.5}$
Mascarenhas *et al.*, (2008)	Rio Branco, Brazil	19,581 ER visits	Sep. 1–30, 2005	Respiratory ER visits	$PM_{2.5}$
de Mendonca *et al.*, (2006)	261 districts in Brazilian Amazon	Residents in Amazon regions (population size not specified)	Fire seasons 1996–2000	Respiratory admissions	hot pixels from satellite data
Mirabelli *et al.*, (2009)	12 counties in California, U.S.	465 non-asthmatic students (16–19 y) in the Children’s Health Study	Oct. – Nov. 2003	Respiratory symptoms	Number of days subjects smelled smoke
Moore *et al.*, (2006)	Kelowna and Kamloops regions in British Columbia, Canada	146,199 residents in Kaelowna; 100,548 residents in Kamloops	Aug. 2003	Respiratory, CVD	PM_{10}, $PM_{2.5}$
Morgan *et al.*, (2010)	Sydney, Australia	~ 3.48 million residents	Jan. 1994–June 2002	Respiratory admissions; Mortality	PM_{10}
Mott *et al.*, (2002)	Hoopa Reservation, California	289 residents in Humboldt Co. interviewed (26% of population)	Aug. 23–Nov. 3, 1999	Respiratory admissions	PM_{10}
Mott *et al.*, (2005)	Kuching, Malaysia	~400,000 residents affected	Aug. 1–Dec. 31, 1997	Respiratory symptoms	PM_{10}
Nunes *et al.*, (2013)	107 micro areas in Brazilian Amazon	Not specified	Dry season 2005	Mortality due to circulatory diseases	Annual % hours with $PM_{2.5}$ greater than $25 \mu g/m^3$
Prass *et al.*, (2012)	Porto Velho, Amazon region	22,012 live births	2001–2006	Birth weight	Number of fires
Rappold *et al.*, (2011)	42 contiguous counties in eastern North Carolina, U.S.	Not specified	June 2008	Respiratory, CVD ER visits	Aerosol optical depth (AOD)
Rappold *et al.*, (2012)	40 mostly rural counties, North Carolina, U.S.	Not specified	June to July, 2008	Asthma, CVD ER visits	$PM_{2.5}$
Sastry (2002)	Kuala Lumpur and Kuching, Malaysia	Not specified	July–Dec. 1997	Mortality	PM_{10}
Schranz *et al.*, (2010)	San Diego Co., California, U.S.	Not specified	Oct. 21–24. 2007	Respiratory ER visits	$PM_{2.5}$
Shaposhnikov *et al.*, (2014)	Moscow, Russia	11.5 million residents	Jul–Aug 2010	Mortality	PM_{10}, O_3
Shusterman *et al.*, (1993)	Alameda Co., California, U.S.	Not specified	Oct. 20–21, 1991	Respiratory, injury ER visits	Not specified
Smith *et al.*, (1996)	Western Sydney, Australia	907,450 residents	Jan. 5–12,1994	Respiratory, asthma ER visits	PM_{10}, NO_2

Study	**Location**	**Background population or cohort size**	**Time of fire**	**Major health outcome**	**Exposure metric**
Sutherland *et al.*, (2005)	Denver, Colorado, U.S.	21 residents who are >40 y, smoke, and with pre-existing COPD	June 8 to July 18, 2002	Respiratory symptoms	$PM_{2.5}$, PM_{10}, CO
Tan *et al.*, (2000)	Singapore	30 male volunteers	Sep.–Oct. 1997	Bone marrow content	SO_2, PM_{10}, NO_2, O_3; CO
Tham *et al.*, (2009)	Northeastern and Alpine district, Victoria, Australia	Not specified	Jan.–March, 2003	Respiratory ER visits	PM_{10}
Thelen *et al.*, (2013)	San Diego Co., California, U.S.	Not specified	Oct. 2007	Respiratory ER visits	$PM_{2.5}$, PM_{10}
Vedal and Dutton (2006)	Denver, Colorado, U.S.	~ 2 million residents	June 9–18, 2002	Mortality	$PM_{2.5}$, PM_{10}
Viswanathan *et al.*, (2006)	San Diego Co., California, U.S.	2.8 million residents	Oct. 2003	Respiratory, CVD, diarrhea admissions	$PM_{2.5}$, PM_{10}, O_3, NO_2, SO_2, CO
Vora *et al.*, (2011)	San Diego Co., California, U.S.	8 subjects in downtown San Diego with asthma	Oct. 2007	Respiratory function, rescue medication use	$PM_{2.5}$
(Wiwatanadate and Liwsrisakun (2011))	Chiang Mai, Northern Thailand	1.7 million residents	Aug. 2005 – June 2006	PEFR, asthma symptoms	CO, O_3, NO_2, SO_2, $PM_{2.5}$, PM_{10}

Table 2

Summary of studies based on health outcome and observed associations

	Total number of studies	**Statistically significant associations observed**	**No statistically significant associations observed**	**Studies that found significant association**
Blood biomarker concentration	1	1	0	Huttunen *et al*. (2012)
Asthma	5	4	1	Johnston *et al.* (2006); Martin et al (2013); Rappold *et al.* (2012); Johnston *et al.* (2002)
Birth weight	2	1	1	Holstius *et al*. (2012)
Bone marrow content	1	1	0	Tan *et al*. (2000)
Cardiovascular	14	6	8	Azevedo *et al*. (2011); CDC (1999); Delfino *et al.* (2009); Lee *et al.* (2009); Martin et al (2013); Rappold *et al*. (2011); Rappold *et al.* (2012)
Diabetes	1	0	1	
Diarrhea	1	0	1	
Injuries	3	3	0	Cleland *et al.* (2011); Cameron *et al.* (2009); Shusterman *et al.* (1993)
Mortality	13	9	4	Analitis *et al.* (2012); CDC (2007); de Castro, *et al.* (2009); Jayachandran (2009); Johnston *et al.* (2011); Johnston *et al.* (2012); Nunes et al, (2013); Sastry (2002); Shaposhnikov *et al.* (2014)
Opthalmic symptoms	5	5	0	Aditama (2000); Hänninen et al, (2009); Kunzli *et al.*,(2006); Mirabelli et al (2009); Viswanathan et al (2006)
PEFR	2	2	0	Jalaludin *et al.* (2010); Wiwatanadate and Liwsrisakun (2011)
Physical strength and overall health	1	1	0	Frankenberg *et al.* (2005)
Rescue medication use	3	3	0	Vora *et al.* (2011); Elliott *et al.* (2013); Caamano-Isorna (2011)
Other Respiratory diseases	37	35	2	Aditama (2000); Cardoso de Mendonça (2006); CDC (2008); Chen *et al.* (2006); Delfino *et al.* (2009); do Carmo *et al.* (2010); CDC (1999); Dohrenwend *et al*, (2013); Duclos, (1990); Emmanuel, (2000); Hanigan *et al.* (2008); Henderson *et al*. (2011); Ignotti *et al.* (2010); Kolbe and Gilchrist (2009); Kunii *et al.* (2002); Künzli *et al*. (2006); Lee *et al.* (2009); Martin *et al* (2013); Mirabelli *et al.* (2009); Moore *et al.* (2005); Morgan et al. (2010); Mott *et al.* (2002); Mott *et al.* (2005); Schranz *et al.* (2010); Sutherland *et al.* (2005); Viswanathan *et al.* (2006); Crabbe (2012); Frankenberg *et al.* (2005); Johnston *et al.* (2007); Mascarenhas *et al.* (2008); Shusterman et al. (1993); Tham *et al.* (2009); Thelen *et al* (2013); Rappold *et al.* (2011); Vora *et al.* (2011)

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FORECASTING RELATIVE IMPACTS OF LAND USE ON ANADROMOUS FISH HABITAT TO GUIDE CONSERVATION PLANNING

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Abstract. Land use change can adversely affect water quality and freshwater ecosystems, yet our ability to predict how systems will respond to different land uses, particularly rural-residential development, is limited by data availability and our understanding of biophysical thresholds. In this study, we use spatially explicit parcel-level data to examine the influence of land use (including urban, rural-residential, and vineyard) on salmon spawning substrate quality in tributaries of the Russian River in California. We develop a land use change model to forecast the probability of losses in high-quality spawning habitat and recommend priority areas for incentive-based land conservation efforts. Ordinal logistic regression results indicate that all three land use types were negatively associated with spawning substrate quality, with urban development having the largest marginal impact. For two reasons, however, forecasted rural-residential and vineyard development have much larger influences on decreasing spawning substrate quality relative to urban development. First, the land use change model estimates 10 times greater land use conversion to both rural-residential and vineyard compared to urban. Second, forecasted urban development is concentrated in the most developed watersheds, which already have poor spawning substrate quality, such that the marginal response to future urban development is less significant. To meet the goals of protecting salmonid spawning habitat and optimizing investments in salmon recovery, we suggest investing in watersheds where future rural-residential development and vineyards threaten high-quality fish habitat, rather than the most developed watersheds, where land values are higher.

Key words: conservation targeting; ecological thresholds; exurban development; forecasting land use change; Oncorhynchus *spp.; Russian River, California; salmonid spawning habitat; urban sprawl; watershed risks.*

INTRODUCTION

Land use change is a primary driver of habitat loss and ecosystem degradation at local-to-global scales (Foley et al. 2005), yet our ability to forecast the influence of landscape attributes and future impacts on ecosystems has lagged behind other advances in environmental sciences (Harte 2001). To reduce future losses of biodiversity and ecosystem function, resource managers, decision-makers, and conservation organizations are increasingly requesting information and tools to identify where species and ecosystems are most vulnerable to future land use conversion (Newburn et al. 2005, 2006, Armsworth et al. 2006). Developing spatially explicit projections of land use changes and their consequences has thus emerged as one of the eight grand challenges in environmental science (Clark et al. 2001, National Research Council 2001). In this study, we explore nonlinear thresholds beyond which land use change will result in the degradation of aquatic ecosystems, and then forecast future land use change and its effects on these systems.

Aquatic ecosystems are particularly sensitive to land use activities within their watersheds (e.g., Roth et al. 1996, Harding et al. 1998), and rapid land use changes have contributed to disproportionately high numbers of endangered aquatic species and the decline of economically valuable fisheries, such as anadromous salmonids (Richter et al. 1997, Ricciardi and Rasmussen 1999). The mechanisms by which land use activities affect aquatic ecosystems include elevated production and delivery of fine sediment to streams, which diminish water quality, alter channel morphology, and degrade habitat conditions for organisms ranging from invertebrates to fish (ASCE Task Committee on Sediment Transport and Aquatic Habitats 1992, Soulsby et al. 2001, Greig et al. 2005). The scale of influence and relative contribution of land use activities remain debated (e.g., Strayer et al. 2003), but recent work from Pacific temperate to mediterranean climate watersheds points to watershed-scale rather than local influences driving changes in sedimentation (Pess et al. 2002, Opperman et al. 2005).

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While many factors can limit salmonid spawning and rearing habitat, embeddedness, the extent to which grains of fine sediment (particle size <2 mm) surround spawning-sized substrate, is a key attribute of spawning gravel quality (see Kondolf 2000 for review) that can be affected by watershed-scale land use patterns (e.g., Opperman et al. 2005). Successful incubation requires spawning gravels that have low concentrations of fine sediment, which can fill a redd's interstitial framework and thereby reduce exchange rates of oxygen and metabolic wastes and impede fry emergence (Phillips et al. 1975, Everest et al. 1987, Groot and Margolis 1991). Kondolf (2000) concluded from his review of the literature that salmonid survival and emergence are reduced by 50% when fines exceed 30%. Thus, research elucidating the relative impacts of different land uses on levels of fine sediment in streams can inform management of salmonid populations, and forecasts of future land use changes can be invaluable for species recovery programs. Moreover, forecasts can provide ecological support for rural land use planning (Theobald et al. 2005) and guide conservation programs and planning (Van Sickle et al. 2004, Chan et al. 2006, Newburn et al. 2006).

Forecasting the environmental consequences of land use change requires addressing several challenges, including limited data availability and resolution (Clark et al. 2001, Nilsson et al. 2003, Rindfuss et al. 2004). For example, natural scientists often rely on land-cover classifications derived from remotely sensed imagery, such as Landsat TM, to classify urban development (<1 acre per house; 1 acre = 0.405 ha) and intensive agriculture; however, this imagery cannot distinguish rural-residential development (>1 acre per house; see Plate 1) from more extensive land covers such as forest (Sutton et al. 2006). The omission of low-density development in previous studies may therefore have led to biased parameters in statistical models overestimating the effects of urban development and agriculture as the effects from rural-residential land use were incorrectly attributed to adjacent urban development and agriculture.

Assessing the specific impacts of rural-residential development is particularly important because rural-residential development is the fastest growing land use type in the United States (Heimlich and Anderson 2001, Theobald 2003, Brown et al. 2005; see Plate 1) and is expanding in Canada and Europe (Dubost 1998, Azimer and Stone 2003). Using nighttime satellite imagery, Sutton, Cova, and Elvidge (2006) found that exurban development occupies 14% of U.S. land area, whereas the urban footprint was only 1.7%. Further studies are needed evaluating the impact of rural-residential development given recent documented impacts of exurban development on wildlife abundance, including carnivores (Odell and Knight 2001) and bird communities (Merenlender et al. 1998, Odell et al. 2003, Parsons et al. 2003). More importantly, rural-residential development has recently been shown to be a fundamentally different type of growth than urban development (Newburn and Berck 2006). Specifically, urban development requires sewer and water infrastructure before higher-density development (<1 acre per house) can be built. Conversely, rural-residential development (1–40 acres per house) is almost invariably serviced by private wells and septic systems and thus not bound to existing or planned sewer and water service areas (SWSA). These differences between urban and rural-residential development extend the possible range and associated environmental impacts of rural-residential development, such as sedimentation, but also temperature and nutrient loading from septic systems, well beyond the urban fringe (Hansen et al. 2005, Newburn and Berck 2006). These findings together suggest that biophysical models must explicitly determine the relative effects of rural-residential vs. urban development, and land use change models must distinguish between these different residential densities to forecast land use development patterns.

Finally, projection of the environmental consequences of land use change requires an understanding of biophysical thresholds, the amount of disturbance that an ecosystem can withstand without changing the processes and variables that control its structure (Gunderson and Holling 2002). A growing body of theoretical and empirical research suggests that ecosystems often display nonlinear responses to stressors (Scheffer et al. 2001, Carpenter 2003, Folke et al. 2004), necessitating the use of nonlinear models and extensive data on the response variables (e.g., Yuan and Norton 2004, Donohoe et al. 2006). Understanding how responses vary with initial land use conditions is also important to minimize the marginal losses to ecological systems from expected future land use conversion.

Here we assess the impacts of existing and projected future land use on spawning-substrate quality in tributaries of the Russian River in Sonoma County, California, and discuss the implications of future land use conversions on salmonid spawning habitat. Specifically, we analyze the relative impacts of three different land uses (urban, rural-residential, and vineyard) on the levels of fine sediment in streams. In Sonoma County, almost all intensive agriculture is vineyard for premium wine production. Urban development consists mainly of single-family residences (<1 acre per house) and here also includes paved roads, commercial, and industrial uses. Rural-residential development is defined as parcels with 1–40 acres per house. We hypothesized that low-density rural-residential development is a significant predictor of elevated levels of fine sediment in streams and differs in its severity of impact on stream conditions compared to higher-density urban development.

Our analysis integrated several modeling improvements for the first time. First, we developed an ordinal logistic response model to estimate the relative impact of each land use type on the probability distribution of levels of fine sediment in these watersheds. Ordinal logistic regression is designed to detect nonlinear threshold responses (Neter et al. 1996): in this case, the

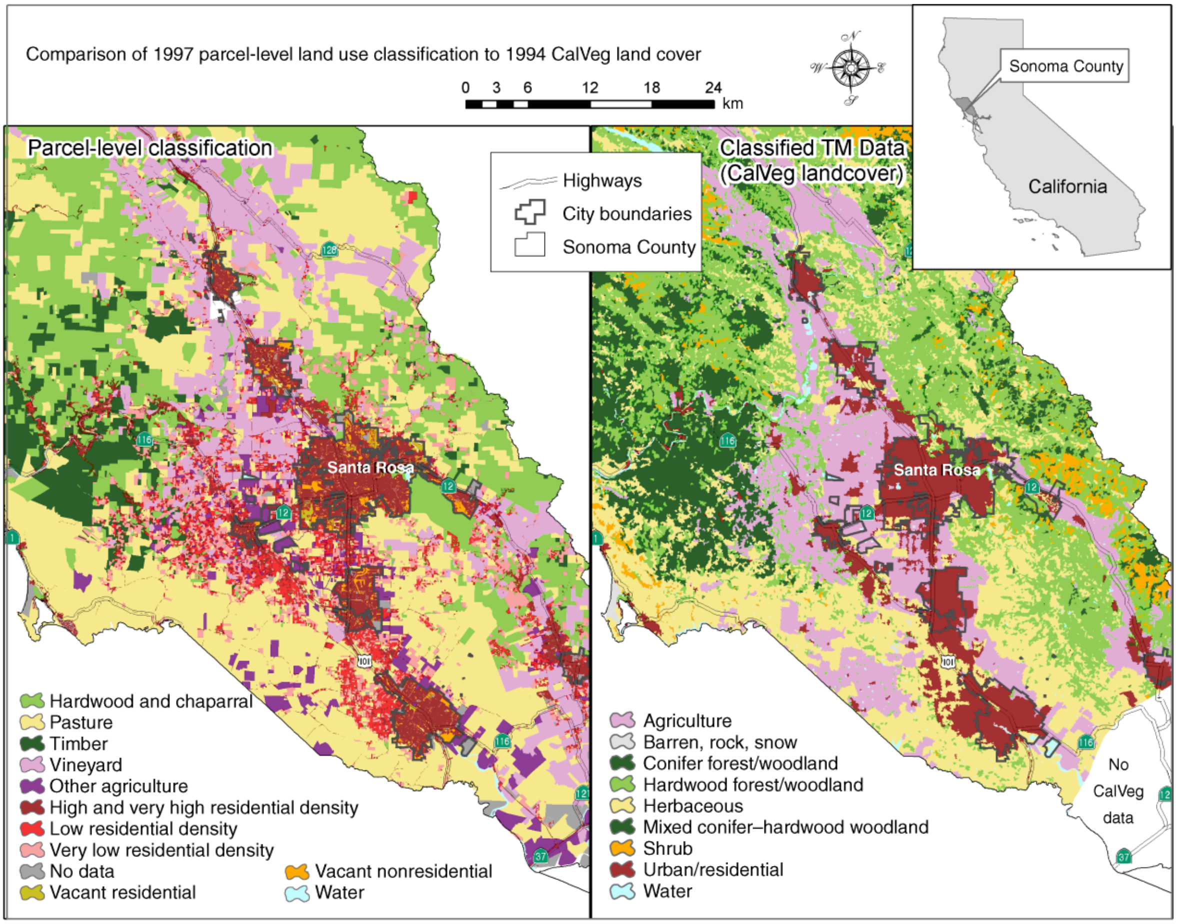

FIG. 1. Comparison of parcel-level and LANDSAT TM imagery land use (based on CalVeg classification) in the study region in Sonoma County, California. Parcel-based land use classification for 1997 shows rural-residential development (1–40 acres per structure; 1 acre ≈ 0.4 ha) and urban development (<1 acre per structure). Residential densities were based on parcel records obtained from the Sonoma County tax assessment office. Vineyard land use was digitized from aerial photographs in 1997.

probability of a spawning site within a given reach declining in spawning-substrate quality with increases in different land uses. Second, we develop a spatially explicit land use change (LUC) model using individual owner land use conversion decisions (including rural-residential, urban, and vineyard development) as a function of the parcel-level characteristics. The LUC model was used to calculate the expected probability of future conversion for each land use type on all remaining developable parcels, which was then integrated with the biophysical model to forecast the expected loss in substrate quality in each watershed. We performed the last critical step of forecasting land use change and its impacts on future levels of fine sediment to aid planners and other decision-makers in preventing further damage to salmonid spawning sites in the Russian River Basin. After combining our forecasts on the expected impacts to spawning habitat with hedonic models for estimating land costs, we conclude with recommendations of priority areas for land conservation efforts and for future development.

METHODS

Study basin

The Russian River basin is 3850 km^2, and is located in Sonoma and Mendocino Counties in northern California. The basin is underlain primarily by the Jurassic-Cretaceous age Franciscan Formation and experiences a mediterranean climate, with cool, wet winters and hot, dry summers; mean annual rainfall ranges from 69 to 216 cm. Natural vegetation consists mostly of mixed-hardwood forests, oak savannas, and grassland, with conifer-dominated forests occurring near the coast and on north-facing slopes throughout the basin. Primary land uses include vineyards, orchards, and other agriculture, sheep and cattle grazing, timber harvest, and urban and residential development.

We focused our studies on tributaries of the Russian River in Sonoma County that (1) support anadromous salmonid spawning habitat, and (2) where stream habitat and digital parcel-level land use data were available (Fig. 1). Focal tributaries included Green

Valley, Mill, Willow, Mark West, Dutch Bill, Maacama, Atascadero, Ward, and Austin Creeks. In the Russian River, three species of anadromous salmonids, including the Central California Coast steelhead (*Oncorhynchus mykiss*), Central California Coast coho (*Oncorhynchus kisutch*), and California Coastal chinook (*Oncorhynchus tshawytscha*), have been listed as threatened under the Federal Endangered Species Act.

Indicator of spawning gravel quality

We used a database from the California Department of Fish and Game (CDFG) for spawning streams in the Russian River Basin to characterize the levels of fine sediment in salmonid spawning habitat. Field crews working for CDFG evaluated the degree of embeddedness of spawning habitat in surveys conducted from 1994 to 2002. Embeddedness was defined as the extent to which fine sediment (particle size <2 mm) surrounded spawning-sized substrate (i.e., gravel and cobbles). Each potential spawning site in a stream reach was ranked for the level of fine sediment surrounding the appropriate spawning substrate, using a four-level ordinal system. Rank 1 indicates low levels of fine sediment (0–25%) surrounding spawning-sized substrate, and Rank 4 indicates very high levels of fine sediment (75–100%) surrounding the substrate. We estimated the distribution of substrate quality for each reach surveyed from 1994 to 1997, and used the rank level of each spawning site as our dependent variable. We employed a geographic information system (GIS) to segment these data by stream reach (Byrne 1996, Radko 1997). We restricted our analyses to depositional reaches (gradient <0.03) most likely to be impacted by sediment. This data set included 93 stream reaches with an average of 54 spawning sites per reach.

To examine the relationship between land use and embeddedness as a measure of spawning habitat quality, we used a 10-m Digital Elevation Model (DEM) and the ArcView extension FlowZones (ESRI 2002) to delineate watersheds above the downstream end of each surveyed reach that had a minimum of five spawning sites. Ten spawning sites per reach, representing the actual distribution of rankings observed at each reach, were used in model development to avoid overrepresentation of sites in particularly long reaches. For example, if a reach had 100 spawning sites and 70, 20, 10, and 0% of the spawning sites were Rank 1, 2, 3, and 4, respectively, then we represented this distribution in the model as 7, 2, 1, and 0 spawning sites (10 total) with Rank 1, 2, 3, and 4, respectively, for that given reach. No more than five reaches nested in the same drainage area were used to reduce overrepresentation of any given watershed and to minimize spatial autocorrelation. Watersheds ranged in size from 500 to 18 165 ha. Finally, we excluded those few watersheds in the study area that currently or historically supported extensive timber harvesting to avoid problems associated with the land use legacies (Harding et al. 1998). Other extensive uses such as historic livestock grazing, orchards, and other agriculture were treated as baseline land uses. In total, 93 watersheds were used for model development; 58 reaches were excluded to reduce overrepresentation of different watersheds and/or land use legacies, resulting in a model based on 922 spawning sites.

Parcel-based land use classification

For land use classifications, we used tax assessment parcel-level data linked to a digital parcel map within a GIS to provide information on residential development density classes. This approach provides more accurate residential classification than LANDSAT TM imagery, which was used in our previous work in the Russian River basin (Opperman et al. 2005), because tax assessment parcel data provide information on residential density. Specifically, the Sonoma County tax assessment data contain information on the number of housing units and lot size for each landowner, and therefore they can be used to determine housing density. By comparison, LANDSAT data do not indicate residential density; they only classify areas as either urban, or extensive uses such as agriculture or hardwood forest. We note to planners and managers that LANDSAT still has better spatial resolution and accuracy for vegetation cover than parcel level data.

For this study, residential development was categorized into four density classes: very high density (<0.25 acres per structure), high density (0.25–1 acres per structure), low density (1–5 acres per structure), and very low density (5–40 acres per structure). These four residential density classes were used in the land use change model described below. For the biophysical model, however, very low and low classes were later combined into the rural-residential class for the ordinal logistic regression in order to reduce multicollinearity, because these two classes were highly correlated within watersheds ($r^2 = 0.68$). Similarly, very high and high-density classes were combined into urban development. The urban classification also included paved roads, parking lots, and commercial uses (industrial uses were relatively uncommon within the CDFG-surveyed watersheds). The specific distinction between urban (<1 acre per structure) and rural-residential (1–40 acres per structure) was made at 1 acre per structure because this density is the typical limit on residential development serviced by septic systems (Newburn and Berck 2006). To obtain the amount of vineyard land use in each watershed, we digitized vineyard boundaries from 1997 aerial photographs. Vineyard parcels were classified as vineyard if the parcel had $\geq 10\%$ vineyard or ≥ 5 ha of vineyard, based on the intersection of the parcel and aerial photo vineyard classification. A comparison of land use classification by parcel-level data and LANDSAT TM imagery is provided in Fig. 1.

Model development

We developed ordinal logistic response models (cumulative proportional odds) using the rank level of substrate quality at each spawning site as our response variable (Hosmer and Lemeshow 2000). Explanatory variables included existing areal percentages of vineyard, urban, and rural-residential land use in 1997 within each watershed and biophysical watershed variables as controls (Hosmer and Lemeshow 2000). These watershed variables included continuous variables such as stream-power index (product of stream gradient and watershed size), road density, soil particle size, a hillslope stability index from a shallow landslide model, SHALSTAB (Dietrich et al. 2001) (*available online*)[5] as well as categorical variables including channel type, dominant geology type (Franciscan mélange, volcanic, and sedimentary), and bank substrate material (bedrock, boulder, silt/clay, cobble). Other extensive land uses including historic livestock grazing, orchards, and other agriculture were thus treated as baseline uses in our model; the impact of an additional 1% of specified land use (e.g., vineyard, urban, rural-residential) is the amount of impact above the baseline impact of extensive uses.

Given the response variable y taking on ordinal values from 1 to J and the $1 \times K$ vector of explanatory variables X^i for watershed i, the proportional odds model is expressed as

$$\log(P_j^i/1 - P_j^i) = \alpha_j + \beta X^i, \quad j = 1, 2, \ldots, (J - 1)$$

where $\beta X^i = \beta_1 X_1^i + \beta_2 X_2^i \cdots \beta_k X_k^i$ and P_j^i denotes the probability that a spawning site in watershed i falls into rank category j or lower. The cumulative proportion odds specification indicates a nonlinear relationship between the probability of each rank level and the explanatory variables. Furthermore, α_j provides the threshold parameters between the rank categories j and $j + 1$. The models were constructed such that Rank 1 corresponded to the highest substrate quality and Rank 4 corresponded to the lowest. Therefore, a negative sign in the parameter estimates indicates reduced substrate quality, because in this case, a marginal change in the variable would lower the probability of observing a high-quality spawning site with Rank 1.

Log-likelihood (LL) ratio tests were used to test the difference between a given model and any nested model and decide which variables to drop from or add to the model. Chi-square is the difference in log-likelihood ratios (−2LL) for the two models. If the computed chi-square was equal to or greater than the critical value of chi-square for the given degree of freedom, then the models were significantly different and the dropped variable in the nested model was considered significant in predicting the dependent. For category variables (dominant geology and bank substrate quality), we assessed the significance of these variables by comparing the chi-square difference of the full model and a model with all the variables in a dummy set dropped (e.g., bedrock, boulder, cobble/gravel, and silt/clay). Thus we treated the dummy variables associated with the categorical variable as a block (Hosmer and Lemeshow 2000).

We evaluated the goodness of fit and performance of the biophysical model on an additional data set of watersheds not used previously for model building. First, we refitted the model including the additional data set. Second, the full model, which included all variables, was compared with a partial model that excluded rural residential development. The partial and full models were used to predict substrate quality based on additional streams surveyed from 1998 to 2002 ($n = 45$ reaches) and updated 2002 parcel-level data and aerial photos of vineyard. We evaluated the capability of both the partial and full model to predict the values observed in the validation set of watersheds using the mean square prediction error (sum of squared errors/number of watersheds in the validation set) (Neter et al. 1996).

Land use change model

A parcel-level LUC model was constructed for the period 1994–2002, using the tax assessment data to determine residential development and aerial photos to determine vineyard development. The data were initially compiled to determine the set of developable parcels in 1994, and then used to assess whether the developable parcels were converted to either vineyard or one of several housing densities from 1994 to 2002. A parcel was considered developable if there was no vineyard use in 1994 and the existing housing density in 1994 was less than one structure per 40 acres. Hence, the set of developable parcels excluded those parcels protected in parks and reserves and already converted to vineyard or residential development before 1994. Residential development was categorized into the four density classes described above. Land use conversion was defined as transitions from developable parcels into vineyard development or one of the four residential density classes during the period 1994–2002.

A multinomial logit model was developed to explain land use transitions as a function of parcel-site characteristics, including average slope, growing degree-days (microclimate), 100-year floodplain, accessibility to major employment centers, designated sewer and water services, and minimum lot size zoning. The 1989 General Plan was used because it was in effect as the planning document during 1994–2002 and therefore guided new development location and type. An indicator variable was used to specify whether a given parcel is located outside the existing 1989 sewer and water service area. Urban development is expected to be less likely in places without access to public water and sewer service. However, it should be noted that rural-residential homes built in the unincorporated areas are often privately serviced by groundwater wells and septic systems, and thus are still likely to occur outside the sewer service area. Zoned minimum lot size is included as another

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[5] ⟨http://socrates.berkeley.edu/geomorph/⟩

proxy for potential residential development, represented in natural log form.

Average percentage slope and elevation in meters were calculated for each parcel. Growing degree-days, summed over the April to October vineyard growing season, served as a proxy for microclimate. A dummy variable was used to represent whether a given parcel was situated within the 100-year floodplain. An optimal routing algorithm within the GIS was used to calculate the minimum travel time in minutes between each parcel and San Francisco along the road network, utilizing weighted travel speeds of 55 mph (88 km/h) on major highways and 25 mph (40 km/h) on county roads. The distance in kilometers from each parcel centroid to the nearest major highway was calculated. This variable represents access to local employment centers within Sonoma County, because all incorporated cities are located along these transportation corridors.

We used the estimated coefficients from the multinomial logistic regression to predict the site-specific conversion probabilities for each land use type on each developable parcel remaining in 2002, given that the site characteristics were already known for all parcels within the GIS. Zoning variables and sewer water service area boundaries were updated to the 2001 General Plan. We note that although the county had a relatively high population growth rate, 2–3% annually, the zoning and sewer and water service area boundaries changed by a very small amount from 1989 to 2001. We then used the LUC model to simulate the expected amount and location of development for each land use type within each watershed. According to the site-specific conversion probabilities, each parcel may remain developable or become converted to one of the five developed land use types in a given simulation. We repeated the simulations 1000 times to obtain average expected watershed area converted to each land use type. The amount of future development from the LUC model spanned an eight-year period, 2002–2010, because the LUC model was calibrated over an eight-year development period, 1994–2002. Over this short planning horizon period, we assumed no additional changes in urban zoning and boundaries. Hence, the forecasted amounts of land use change from 2002 to 2010 represent a "business-as-usual" scenario. The two rural residential classes were then grouped, and two urban classes were also grouped, to simplify the ordinal logistic model on spawning-substrate quality. We then calculated the percentages of the three land uses in each watershed (percentage of total watershed area) for 2002–2010. To obtain the forecasted land use in 1997–2010, the amount of forecasted change in 2002–2010 was added to the actual extent of land use change measured from aerial photos and tax assessment data.

Hedonic price model for estimating land values

We used a hedonic price model to determine the market value for developable land as a function of the site-specific characteristics. Specifically, recent property transactions of developable parcels were used to estimate the actual sales price as a function of the parcel land characteristics. The Sonoma County Tax Assessor's database provides the necessary information on individual parcels for the land value, current land use, and other property characteristics. Using the GIS, we used a similar set of explanatory variables for each parcel, including characteristics for land quality (slope, elevation, microclimate, 100-year floodplain), accessibility (travel times to urban centers, sewer and water service), neighboring land use externalities (percentage of protected open space and urban), and zoning (land use designations, minimum lot size).

Coefficients in the hedonic equation are interpreted as the marginal implicit value of a unit change in the explanatory variable. For example, the hedonic coefficient on travel time to San Francisco estimates the gradient in land values as one travels away from the urban center. We are then able to estimate the value of developable land for each developable parcel, since key site characteristics are known within the GIS. The predicted value of developable land was observed to range over several orders of magnitude. The large degree of variation in land prices highlights why priority setting should include the spatial heterogeneity in land values. See Newburn et al. (2006: Table 2) for more details on the hedonic model used here to estimate the land value of developable parcels in Sonoma County.

Forecasting environmental consequences of land use change

We forecasted the probability distribution of spawning-substrate quality based on the expected percentages of each land use type in 2010 and the estimated parameters in the ordinal logistic model. To estimate the relative impact of each land use type in 2010, we calculated the change in the probability distribution of substrate quality in response to each land use type in 2010, conditional on holding the other two land use types at the existing amount in 1997. Furthermore, in order to demonstrate how nonlinear responses to future land use development is sensitive to the initial levels of land use in each watershed, we categorized watersheds into quartiles (most developed, moderate, less, least developed) based on the summed percentages of all three types of existing development in 1997 (87 watersheds with forecasts).

A targeting rule was used to identify priority areas for protection based on the expected loss of high-quality spawning substrate from future land use conversion and the average land costs in each watershed. Hence, we maximized conservation goals based on the objective of minimizing the expected loss in environmental benefit per unit cost (Newburn et al. 2006). Applying this targeting rule to our results, we identified priority areas by summing the relative probabilities of loss of Ranks 1

TABLE 1. Average existing development (1997) and forecasted changes in land use (1997–2010) in the least to most developed watersheds (as a percentage of the watershed) and across all watersheds ($n = 87$ watersheds).

		Land use in watershed (%)				
Variable	Land use	Least	Less	Moderate	Most	All watersheds
Existing development, 1997	urban	0.06	0.48	0.64	5.05	1.56
	rural-residential	0.10	1.74	6.43	22.59	7.71
	vineyard	0.36	1.07	4.29	2.41	2.03
	total	0.52	3.28	11.36	30.05	11.30
Change 1997–2010	urban	0.10	0.05	0.10	0.21	0.11
	rural-residential	1.66	1.71	1.14	1.64	1.54
	vineyard	1.58	1.98	2.85	2.82	2.31
	total	3.35	3.73	4.08	4.67	3.96

and 2 and dividing by the average cost per acre for that watershed.

RESULTS

The parcel-level land use classification in Sonoma County revealed that urban (<1 acre per structure) and vineyard land use represented only 1.56% and 2.03% of the land area in 1997 within the CDFG-surveyed watersheds, respectively, while rural-residential development (1–40 acres per structure) represented 7.71% (Table 1). Indeed, rural-residential development constituted $>80\%$ of the total land area developed for residential use, although it only represented $<20\%$ of the total population in the area. The spatial distribution of these land uses was extremely variable among the study watersheds (Fig. 1). On average, the most-developed watersheds had an order of magnitude more development than the least-developed watersheds (Table 1).

Ordinal logistic regression models (cumulative proportional odds) were used to estimate the probabilities for observing each of the four spawning-site quality levels within a given reach as a function of the percentages of watershed-scale land uses in 1997 and biophysical variables. Thus, each reach had a unique set of four probabilities, corresponding to the watershed characteristics for the specific reach. The best ordinal logistic regression model on spawning-substrate quality included land use variables for the percentages of urban, rural-residential, and vineyard use within each watershed and biophysical watershed variables for stream power index, geology, and bank substrate material (Table 2). The model results showed that all three land use variables were negatively and significantly associated with spawning-substrate quality. Partial likelihood ratio tests excluding rural-residential indicated that this land use type significantly improved the model fit ($G = 16.55$, $P < 0.0001$), supporting the hypothesis that increased rural-residential development is a significant predictor of elevated levels of fine sediment in streams. An index of stream power, the product of watershed size and stream gradient, and stream bank substrate material were the only significant biophysical watershed variables. Strict adherence to conventional levels of statistical significance would have dictated that we consider a smaller model deleting dominant geology. However, due to the fact that geology is an important control variable on

TABLE 2. Final model for projection of spawning habitat quality under land use change.

Term	Estimate	SE	Lower 95% confidence limit	Upper 95% confidence limit	Chi-square	P*
Intercept [1]†	−0.859	0.313			7.53	0.0061
Intercept [2]†	1.268	0.314			16.27	<0.0001
Intercept [3]†	2.524	0.323			61.19	<0.0001
Stream power index	−1.764	0.617	−2.925	−0.608	8.18	**0.0042**
Urban 1997 (%)	−0.120	0.033	−0.189	−0.059	12.96	**0.0003**
Rural-residential 1997 (%)	−0.034	0.008	−0.051	−0.018	17.01	**<0.0001**
Vineyard 1997 (%)	−0.055	0.022	−0.099	−0.013	6.38	**0.0115**
Substrate [bedrock]	−0.173	0.231	−0.651	0.296	0.56	0.4541
Substrate [boulder]	1.169	0.431	0.278	2.124	7.36	**0.0067**
Substrate [cobble/gravel]	−0.226	0.210	−0.668	0.206	1.16	0.2819
Geology [Franciscan]	0.398	0.260	−0.058	0.935	2.34	0.1260
Geology [sedimentary]	−0.167	0.271	−0.647	0.384	0.38	0.5381
Geology [volcanic]	0.381	0.265	−0.084	0.923	2.07	0.1501

Notes: Estimated ordinal logistic regression terms, coefficients and standard errors (SE), and confidence limits are reported. Chi-square is the likelihood-ratio chi-square test for the hypothesis that all regression parameters are zero, and P value is the probability of obtaining a greater chi-square value by chance alone if the specified model fits no better than the model that includes only intercepts. $N = 922$ pools; −2 log-likelihood = 199.9.

* The values in boldface type indicate significance at the $P < 0.05$ level.

† The ordinal logistic model fits a different intercept, but the same slope, for each of $r - 1$ cumulative logistic comparisons, where r is the number of response levels. There are three intercept parameters because there are four response categories.

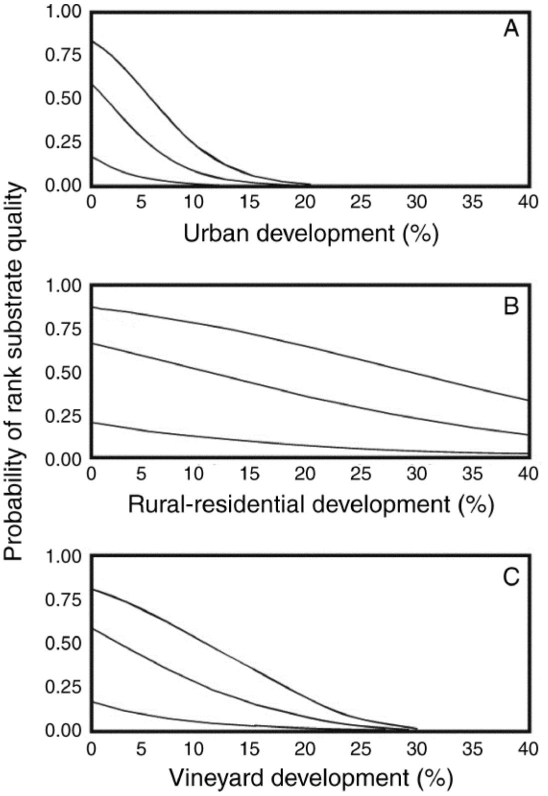

FIG. 2. Ordinal response regression models for (A) the percentage of urban development, (B) the percentage of rural-residential development, and (C) the percentage of vineyard development in the watershed.

sediment production and delivery, dominant geology was retained to control for this factor across watersheds (Hosmer and Lemeshow 2000). Significance of stream bank substrate material indicated more local-scale influences on spawning gravel quality.

The probability of observing low levels of fine sediment in spawning gravels decreased as the percentage of different types of development increased in the watershed (Fig. 2). The marginal effects of urban development (i.e., the change in the probability of substrate quality with 1% increase in urban development) were larger than either vineyard or rural-residential development in lesser-developed watersheds (Fig. 2). However, the marginal effect of urban land use decreased when there was already a high percentage of existing development. In the least-developed watersheds, >65% of spawning sites were high quality (Ranks 1 and 2), whereas >70% of the sites in the most-developed watersheds were highly embedded with sediment (Ranks 3 and 4) (Fig. 3). Thus, prior development had already impacted the majority of spawning sites in the most-developed watersheds.

Estimating the model with all the data (1994–2002) did not significantly alter the coefficient estimates in the final model indicating goodness of fit. Results from projecting the effects of land use change from 1997 to 2002 on stream conditions on the test set of watersheds ($n = 45$) showed that the mean prediction error only decreased 7% with the full model compared to the partial model. Biased parameter estimates for urban and vineyard could help to explain why there were only minor differences in the mean squared prediction errors between the models; the partial model overestimated the effects from urban and vineyard because it had mistakenly attributed the effect from the omitted exurban variable to urban and vineyard.

Forecasting land use change

The estimation results from the LUC model indicated that urban and rural-residential development responded very differently to land use regulations. Designation of sewer and water service area boundaries was the most important determinant of urban development (Table 3). Calculating the odds ratios for the two urban classes showed that very high and high-density development were respectively 44.5 and 4.5 times less likely to occur outside of sewer and water service area boundaries compared to areas with existing and planned sewer service. In contrast, designation of sewer and water service areas did not affect rural-residential development, as development at this density only requires the installation of private groundwater wells and septic systems. The odds ratios for the two rural-residential classes show that very low and low-density development are actually 5.9 and 2.7 times more likely outside of sewer and water service area boundaries. Hence, because of these different responses to land use controls, the LUC model showed that rural-residential development actually leapfrogged into less-developed areas well beyond sewer and water service area boundaries. Furthermore, urban development at high and very high densities was less likely on steeper slopes, within the 100-

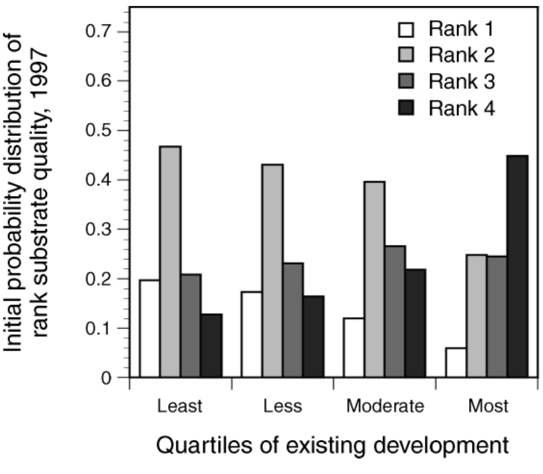

FIG. 3. Estimated probability distribution of quality levels of spawning habitat within stream reaches, grouped according to the quartiles of existing land use development in 1997 (least, less, moderate, and most developed).

Table 3. Estimated coefficients of multinomial logit model for land use conversion (to very high, high, low, and very low housing density, or vineyard) during 1994–2002 on undeveloped parcels in Sonoma County, California.

	Housing density classes				
Variable	Very high	High	Low	Very low	Vineyard
Outside sewer service areas	−3.797**	−1.510**	1.006**	1.781**	2.469**
	(0.199)	(0.153)	(0.176)	(0.372)	(0.324)
Travel time to San Francisco	−0.015**	0.008*	−0.022**	−0.0294**	0.011**
	(0.003)	(0.003)	(0.004)	(0.006)	(0.003)
Distance to nearest highway	−0.304**	−0.146**	−0.041	0.004	−0.112**
	(0.055)	(0.047)	(0.031)	(0.030)	(0.018)
Slope	−0.053**	−0.052**	−0.036**	0.001	−0.049**
	(0.006)	(0.005)	(0.005)	(0.005)	(0.004)
Growing degree-days	0.198	−0.059	−0.154	0.696**	1.796**
	(0.144)	(0.152)	(0.156)	(0.198)	(0.115)
Floodplain	−1.111**	−1.811**	−1.116**	−1.066	−0.500*
	(0.252)	(0.416)	(0.345)	(0.589)	(0.199)
Elevation	−0.008**	0.0026**	0.002**	0.002**	−0.001
	(0.002)	(0.001)	(0.001)	(0.001)	(0.001)
ln(zoned minimum lot size)	0.089**	−0.177**	−0.112**	0.085	0.539**
	(0.029)	(0.0379)	(0.038)	(0.049)	(0.034)
Constant	−0.603	−2.092**	−2.672**	−7.282**	−11.669**
	(0.494)	(0.552)	(0.568)	(0.755)	(0.506)

Notes: "Remain undeveloped" is the baseline alternative. Standard errors are in parentheses. For the ordinal logistic model in Table 2, the very high and high-density classes were combined into urban development, while the very low and low-density classes were combined into rural residential development. $N = 20\,487$ parcels; log likelihood $= -8732.04$.

* $P < 0.05$; ** $P < 0.01$.

year floodplain, and farther from major highways. (See Newburn and Berck [2006] for more details on differences between urban and rural-residential development.) Finally, vineyard development was more likely on areas with lower slope and higher growing degree-days (warmer microclimate).

We used the LUC model to forecast development for the period 1997–2010. Although urban development resulted in the largest marginal change in probability in substrate quality per unit increase in development (Fig. 2), the amount of future urban development was relatively small, largely due to no changes in urban zoning and boundaries. For the forecast period 1997–2010, the area developed as urban in CDFG watersheds was estimated to increase only 0.11%, whereas rural-residential and vineyard development were estimated to increase by 1.54% and 2.31%, respectively (Table 1).

Forecasting land use impacts on spawning-substrate quality

Future vineyard and rural-residential development had larger relative impacts on spawning-substrate quality than future urban development across all watersheds (Fig. 4). Initial conditions of the watersheds largely determined which watersheds had the most to lose with respect to good-quality spawning substrate (Ranks 1 and 2) (Fig. 5). The amount and type of expected land use change also factored into which watersheds were expected to lose good spawning habitat (decreases in Ranks 1 and 2) and to be impaired by sedimentation (increases in Ranks 3 vs. 4) (See Fig. 6, but also the Appendix for forecasts for all watersheds.) The interplay between these two factors, initial conditions and expected land use change, was observed across the watersheds in Sonoma County. Specifically, watersheds near Cloverdale, farthest from the San Francisco Bay area, were less disturbed and generally responded to expected land use change with declines in the probability of observing high-quality spawning sites (declines in Rank 1; Fig. 6a). In watersheds near Healdsburg, particularly to the east near Napa County, high amounts of projected vineyard development and, to a lesser extent, rural-residential development, led to large expected losses of Rank 1 and Rank 2 sites and large increases in Rank 4 sites (Fig. 6b). Whereas the southern most-developed watersheds near Santa Rosa showed little change in the probable loss in Rank 1 spawning sites because spawning-substrate quality was already low, watersheds showed large probable gains in Rank 4 sites from expected losses of Ranks 2 and 3 sites (Fig. 6c).

The average land cost per acre varied widely across watersheds in the study area and generally decreased from south to north (Fig. 5). Based upon land costs and the likelihood of future development, watersheds in the northern and central part of the study area (shaded in red and orange, Fig. 6) had the highest probability of loss of good substrate quality per unit land cost. Watersheds colored red represent the highest benefit-cost option for conserving habitat. In contrast, watersheds in the south (yellow watersheds, Fig. 6) had relatively low probable loss of good substrate quality per unit land cost.

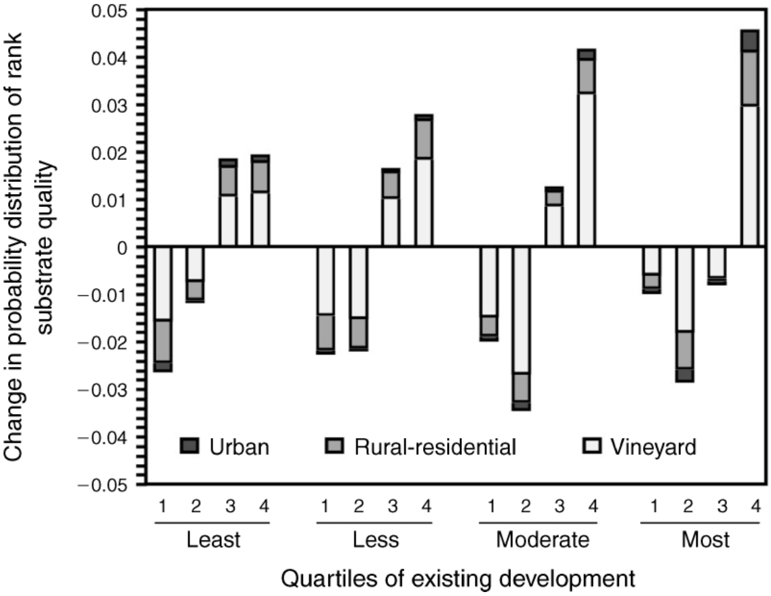

FIG. 4. Average change in the probability distribution of spawning site quality (Rank 1–4) in least to most developed watersheds. Shading in bars indicates the relative impacts of forecasted rural-residential, urban, and vineyard development on the change in spawning site quality.

DISCUSSION

We quantified nonlinear relationships between land use (including low-density residential development) and relative levels of fine sediment in streams and then forecasted the expected impacts of land use change on spawning habitat for endangered salmon. Elevated inputs of fine sediment from land use conversion can negatively impact salmonid populations through the degradation of both spawning and rearing habitat (Reiser and White 1988, O'Connor and Andrew 1998, Kondolf 2000, Suttle et al. 2004), aggradation of pools (McIntosh et al. 2000), simplification of habitat (McIntosh et al. 2000), and suppression of invertebrate prey base for juvenile fish (Osmundson et al. 2002, Suttle et al. 2004). Taken together, results presented here and the linkages between fine sediment and salmonid population decline suggest that steelhead trout and coho salmon, already listed as threatened, are vulnerable to future increases in fine sediment loads due to expected land use conversions.

In this study, urban and vineyard land use were significant predictors of in-stream levels of fine sediment, consistent with our previous work (Opperman et al. 2005) and other studies (Wang et al. 2001, Pess et al. 2002, Morse et al. 2003, Donohoe et al. 2006). Unlike previous studies, however, we were able to distinguish and evaluate the effects of rural-residential development based on a spatially explicit, parcel-level land use change model. We found that the proportion of high-quality spawning sites decreased significantly with the percentage of rural-residential development in the watershed (see Plate 1). Findings suggest that previous studies relying on Landsat TM for land-cover data likely have omitted an important type of development that adversely impacts aquatic ecosystems (Fig. 1). As the amounts of urban and rural-residential development were more likely to occur within the same watershed (correlation coefficient = 0.52 in our watersheds), omission of the rural-residential variable in the regression model would have mistakenly attributed much of its effect to urban development. As a result, decision-makers might adopt policies to curb or redirect urban development, such as urban-growth boundaries (UGB) on sewer infrastructure expansion, while allowing rural-residential development to continue unabated (Newburn and Berck 2006). While our findings point to the previously omitted impacts of rural-residential development, the use of parcels as the spatial reporting unit likely overestimated the percentage of the watershed impacted by this type of land use because the entire parcel may not be impacted by the developed area. More research is needed to quantify the actual area of development associated with low-density residential development. We have begun to use pixel-based and object-based remote sensing to calculate the development footprint around existing rural residences, and have found that these methods effectively delineate the developed areas as long as tree cover does not hide structures and roads. Beyond the actual developed area, indirect impacts associated with the presence and use of roads for rural-residential development remain poorly characterized and likely extend the disturbance footprint of rural-residential development (Havlick 2002, Forman et al. 2003). Research in this area is underway to calculate the development areas for a large number of parcels, as

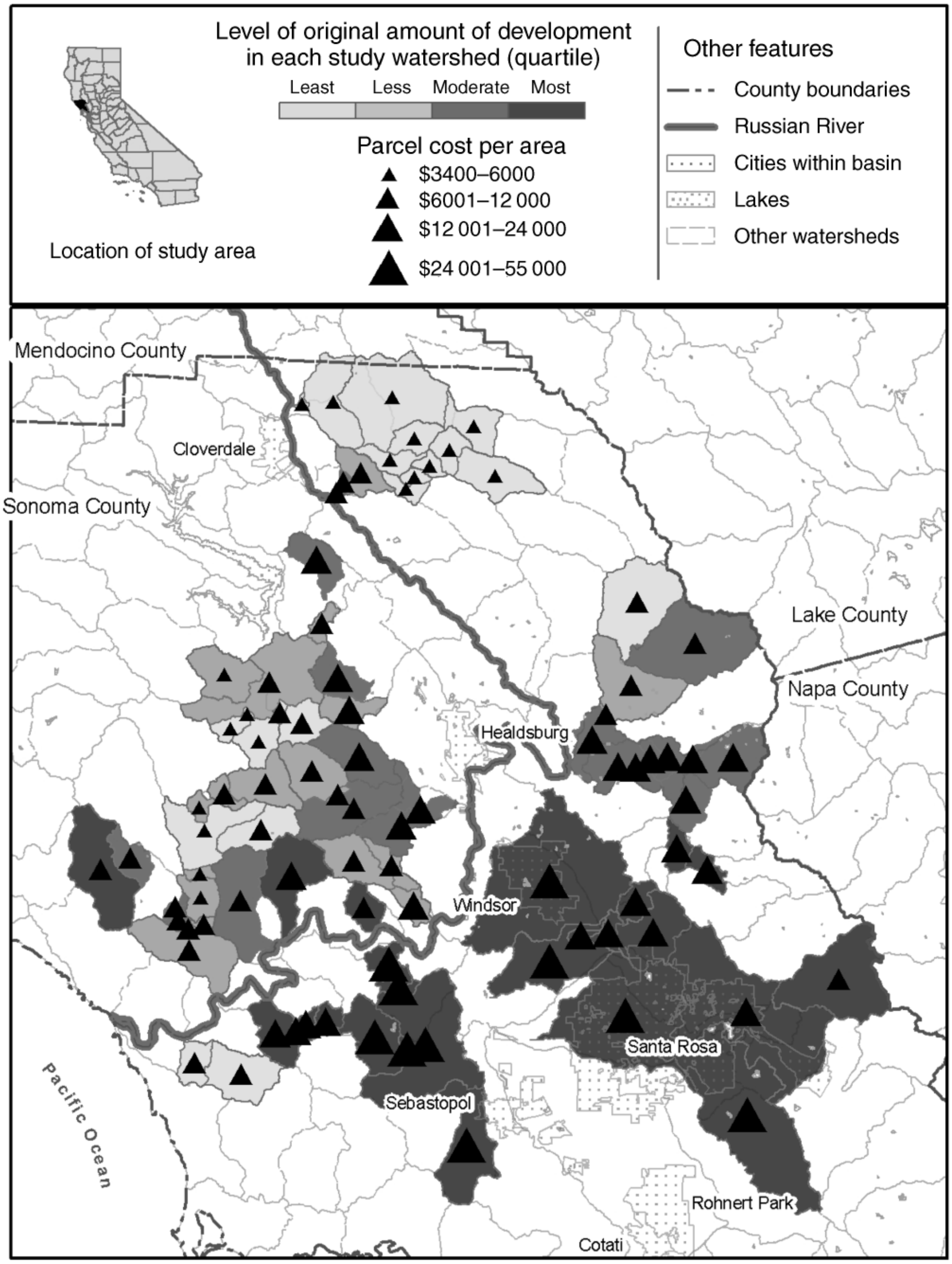

FIG. 5. Initial conditions of land use development in the study watersheds and cost per parcel area (see *Methods: Hedonic price model* for description of estimating land values from tax assessor's database on parcels).

there appears to be a high level of variability that can in part be explained by parcel size.

Our results also indicate that urban, rural-residential, and vineyard development differed in their severity of impact on streams. While urban development had the largest marginal effects (greatest response per unit of land use change), our data suggest that future rural-residential may have a greater overall impact than urban development on spawning-substrate quality. We expect this greater impact because the LUC model predicts 10 times as much land to be converted to rural-residential compared to urban development. In addition, the model projects rural-residential development to occur in watersheds ranging from the least to the most developed, and thus will affect reaches that currently have suitable habitat to support salmon reproduction. In contrast, the LUC model predicts future urban development to be more likely in areas that already have high levels of urban land use and low-quality spawning habitat (Fig. 6c). Finally, our results indicate that future

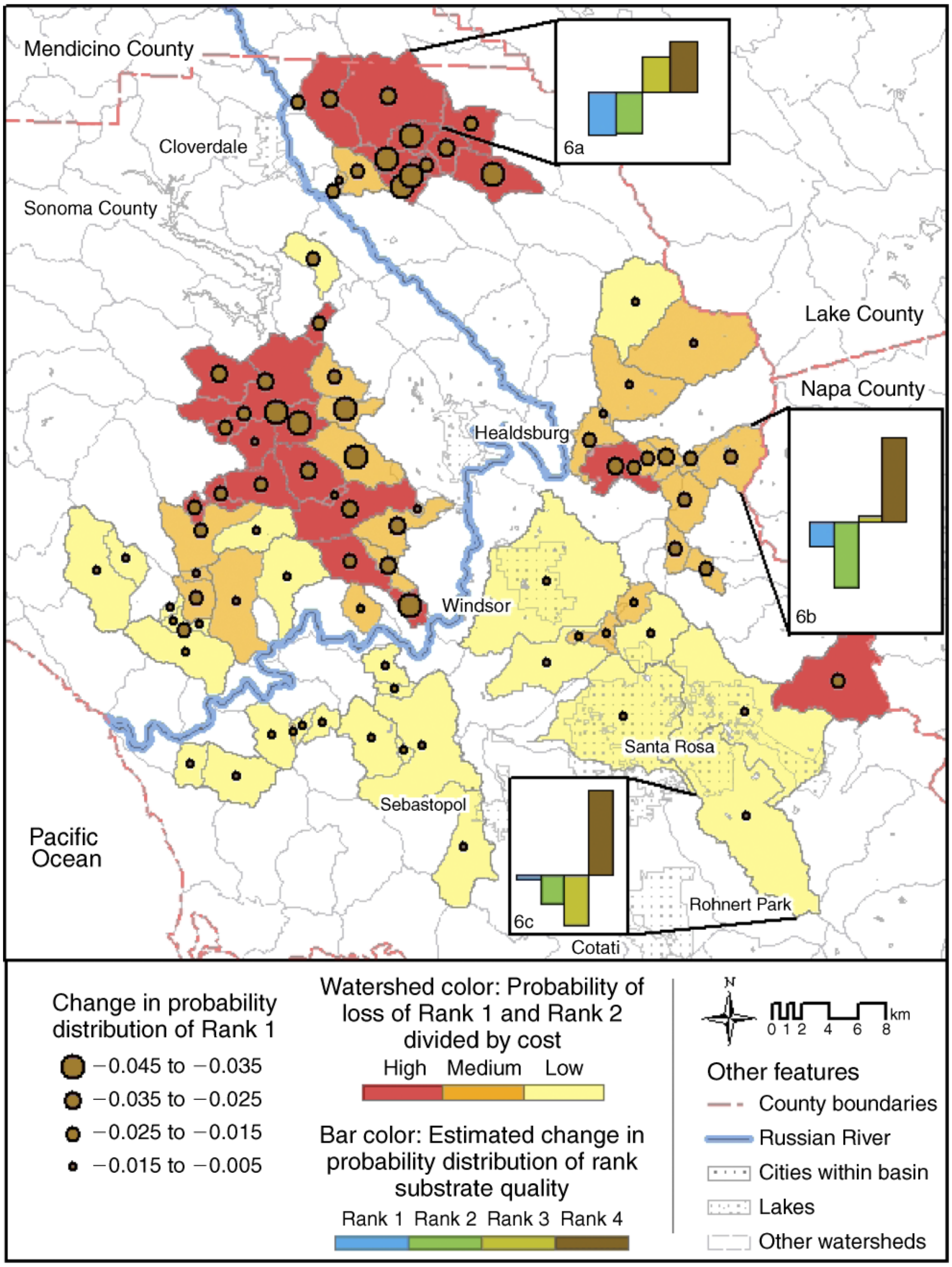

FIG. 6. Change in probability distribution of high-quality spawning sites (Rank 1) with forecasted land use change (key with circles) and probability of loss of high-quality substrate ÷ land cost in least to most developed watersheds in the Russian River Basin (watershed color). The watersheds colored red represent the lowest cost option for conserving high-quality spawning habitat. Inset bar color graphs show examples of estimated change in probability distribution of substrate quality within that rank for (6a) least, (6b) moderate, and (6c) most developed watersheds.

vineyard conversion could lead to high levels of sedimentation, and hence have a larger relative impact than urban development. Together, our findings suggest that fundamentally different land use types should not be aggregated in risk-assessment models.

Due to the nonlinearity of the responses, watersheds that differed in their level of initial development conditions had varying vulnerability to degradation of spawning habitats from future development. Based on the forecasting model, watersheds with lower percentages of existing development showed relatively large declines in the probability of high-quality spawning habitat (Ranks 1 and 2) (Fig. 6a). This sensitivity declined within the most-developed watersheds largely because these reaches initially had a small proportion of high-quality spawning habitat (Fig. 6c). Watersheds with large amounts of expected land use change (particularly agriculture) also showed large gains in the

Plate 1. Example of rural-residential development in Sonoma County, California, USA. Photo credit: A. M. Merelender.

highest sediment levels (Fig. 6b). High sensitivity to development emphasizes the need to protect salmon habitat very early in the development process (or trajectory), often before many regulations designed to protect water from land use activities are triggered.

In this study, we forecasted changes over a short planning horizon (only about a decade) because the LUC model was calibrated over an eight-year development period, 1994–2002. Over longer planning horizons, market forces and urban service boundaries may change, making land use change projections more uncertain and assumptions underlying the models invalid. In a detailed study of exurban and urban development scenarios, Newburn and Berck (2006) showed that the probability of urban development increased 10-fold if they extended a sewer and water service area boundary, but rural-residential development did not change. We expect that the impacts of urban development in our model results would have been larger if sewer and water service areas were extended. Nonetheless, the impacts would still have been felt mostly in watersheds of already low-quality habitat. Thus, altered urban boundaries would not have likely changed the priority of conservation targets. Over a longer time frame (25–50 years), we expect the projected losses of habitat quality would be much larger due to urban expansion but also to rural-residential development in lesser-developed watersheds. Again, we expect conservation priorities would be similar to our short-term forecasts because priorities are based on relative rankings, in this case, the relative probabilities of loss of good spawning substrate divided by the average cost per acre for that watershed. Longer range forecasts are a topic of ongoing research.

The nonlinear relationships between various land uses and fine sediment described here can provide decision-makers with information on vulnerability of high-quality spawning habitat to different development pressures. Because resources for land conservation are limited, this forecasting approach can be used to prioritize areas for conservation efforts intended to reduce sediment loading to streams, such as purchasing conservation easements, reconnecting streams to floodplains, and reducing the sediment production from road networks. Funding for land conservation will likely be more fiscally efficient if areas with low-to-moderate threat to land use conversion are targeted rather than land at the urban fringe with the highest threat. Land costs at the urban fringe are several orders of magnitude higher than low-threat areas, making compensation to landowners for forgoing development far more costly (Fig. 5) (Newburn et al. 2005, 2006). Such a process will also identify locations where existing land use development may overwhelm the future efficacy or marginal benefit of conservation programs.

Through local zoning and other land use policies, decision-makers can work to influence the density and location of future residential development. Transfer of development rights (TDR) programs, for example, can be used to create a market between properties with existing rural-residential development rights located in environmentally sensitive areas (sending areas) and regions that are already serviced for denser urban development (receiving areas). For instance, local planners in Montgomery County, Maryland downzoned properties with 5-acre minimum lot sizes and credited the landowners with the development rights. These development rights were then sold to developers who wanted to build urban housing at high densities within areas that already had SWSAs (Johnston and Madison 1997). In the context of our study, we recommend that a TDR program be implemented to curtail lower-density rural-residential development within moderate- and less-developed watersheds (sending areas in red and orange, Fig. 6), while encouraging higher-density infill urban development to take place in areas already highly disturbed (receiving areas in yellow watersheds, Fig. 6) (Johnston and Madison 1997, Nilsson et al. 2003, Merenlender et al. 2004).

In concert with these more transformative planning tools, effective runoff and construction control techniques can be employed when development does occur in sensitive watersheds. Best management practices for road construction and maintenance include guides for environmentally sensitive maintenance of dirt and gravel roads, as well as basic road design elements (Roads, Highways, Bridges–NPS categories) (*available online*).[6] Other low-impact development (LID) strategies for storm water management are also available to use at a local scale (Low-Impact Development) (*available online*).[7] The next research steps in spatial targeting include spatial prioritization within targeted watersheds that will begin to meet the needs of conservation groups who require finer scale spatial information on the relative value of individual parcels. On this research front, Newburn et al. (2006) have taken the first step toward parcel-level targeting within these watersheds, but had the simplicity of a linear benefit function in their model. Our future research will work toward integration of a dynamic optimization of the economic and land use change model with our biophysical model encompassing cumulative and nonlinear threshold effects.

While we effectively assessed the nonlinear response of spawning habitat to land use change, we still need a better understanding of hysteresis, as the conditions under which spawning sites shift to higher fine-sediment levels may differ from those that will shift the system back to lower levels. Reductions in fine sediment may occur through punctuated changes in stream flow or shifts in stream geomorphology. In general, a better understanding of the mechanism of sediment transport in these watersheds is desirable; we need to address questions about how water extraction and channel incision and other changes to stream geomorphology associated with development influence sediment dynamics. This increased understanding would inform management efforts to improve the quality of stream habitat where existing conditions fall below desired thresholds.

CONCLUSIONS

It is well recognized that urban development and intensive agriculture can increase sediment production and delivery to downstream stream reaches, rendering them unsuitable for successful fish spawning. In this study, we were also able to examine the impacts of exurban land use and found that increases in the percentage of total exurban development in a watershed significantly reduced the probability of observing high-quality stream habitat. In fact, results from this study suggest that exurban development may have a greater relative impact than urban development on stream conditions in the next decade because 10 times as much land is expected to be developed in exurban than urban areas, and exurban development has the ability to leapfrog into less-developed watersheds, which contain high-quality habitat, compared to urban development, which is typically constrained by urban growth boundaries. As exurban development now takes up 15 times the area of higher-density development (Brown et al. 2005) and is the fastest-growing type of land use in the United States (Theobald 2001), these findings raise concern for other areas where low-density residential development is on the rise.

Results from our study also demonstrate that urban and rural residential development are fundamentally different and thus require different land use policies to reduce their impacts on stream ecosystems and upland areas. Future urban development will tend to be clustered in areas that already have high levels of urban development and little high-quality spawning habitat. In contrast, exurban development is more likely to leapfrog into remote areas well beyond sewer water service areas and impact watersheds with good habitat quality. Hence, limits on the sewer service extension, a key objective of an urban growth boundary, will likely be effective in curbing urban expansion. However, it would have little or no influence on rural residential development. The application of our findings demonstrates the need to target conservation efforts in watersheds with the lowest cost option for protecting high-quality habitat. This approach directs resources away from those watersheds with the greatest threat of future development, which tend to have the highest land costs, and toward watersheds with low to moderate threat of future development. These watersheds contain high-quality habitat and have significantly lower land costs and are still at risk of low-density development in the near future. We recommend that local governments implement purchase and transfer of development rights programs as a primary strategy for influencing patterns of rural-residential development. In addition, we need to inform planners about the potential impacts of this type of land use and its consequence for environmental degradation because few existing policies, regulations, and incentive-based conservation programs are in place to adequately address the problem.

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[6] ⟨http://www.epa.gov/owow/nps/roadshwys.html⟩

[7] ⟨www.EPA.gov/owow/nps/lid/⟩

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APPENDIX

A figure showing the change in probability distribution of spawning site quality with forecasted land-use change in the study watersheds (*Ecological Archives* A018-013-A1).

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Review

Estimation of Bird-Vehicle Collision Mortality on U.S. Roads

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ABSTRACT Roads have numerous direct and indirect ecological impacts on wildlife. Vehicle collisions are a top impact of roads on birds, with tens of millions of birds thought to be killed each year in the United States. However, currently available mortality estimates are extrapolated from a single study. We reviewed the literature and used 20 mortality rates extracted from 13 studies to systematically quantify data-driven estimates of annual U.S. mortality from bird-vehicle collisions. We generated 4 separate estimates along with uncertainty using different subsets of data deemed to be rigorous enough to contribute relatively little bias to estimates. All of our estimates of vehicle mortality are higher than previous U.S. figures. When averaging across model iterations, we estimated that between 89 and 340 million birds die annually from vehicle collisions on U.S. roads. Sensitivity analyses indicated that uncertainty about survey-related biases (scavenger removal and searcher detection of carcasses) contributes the greatest amount of uncertainty to our mortality estimates. Future studies should account for these biases to provide more accurate local estimates of mortality rates and to inform more precise national mortality estimates. We found relatively little information available to quantify regional, seasonal, and taxonomic patterns of vehicle collision risk, and substantial uncertainty remains about whether collisions contribute to large-scale impacts on bird populations. Nonetheless, the large magnitude of bird mortality caused by vehicle collisions combined with evidence that collisions can contribute to local population declines for some species highlights the need for implementation of conservation and management actions to reduce this mortality. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS anthropogenic mortality, automobiles, birds, detection probability, roadkill, roads, scavenger removal, systematic review, United States, vehicles.

The global proliferation of road networks has led to a multitude of ecological impacts that affect biological diversity. In the United States, the greater than 6.5 million kilometers of roads (U.S. Department of Transportation 2012) ecologically affect at least 22% of the nation's land area (Forman 2000), causing loss and fragmentation of habitat; pollution with chemicals, light, and noise; alteration of animal movement and behavior; and direct mortality of wildlife from vehicle collisions (Forman and Alexander 1998, Trombulak and Frissell 2000, Forman et al. 2003, Coffin 2007). For birds, vehicle collisions are one of the greatest threats posed by roads (Kociolek et al. 2011), with as many as 80 million birds thought to be killed annually in the United States (Erickson et al. 2005) and roughly 13 million birds estimated to be killed annually in Canada (Bishop and Brogan 2013). Moreover, roadkills have the potential to constitute the vast majority of total mortality for some bird species—most notably, barn owls (*Tyto alba*) (Moore and Mangel 1996, Newton et al. 1997). Roadkill mortality can also result in the creation of population sinks (Mumme et al. 2000, Boves and Belthoff 2012, Grilo et al. 2012) and may be an additive source of mortality that contributes to population declines (Bujoczek et al. 2011).

A large body of literature has identified numerous factors that influence bird-vehicle collision rates. Mortality rates have been found to increase with increasing traffic speed and volume (Case 1978) and rates are generally highest during spring and summer. Mortality rates are also greater for juvenile birds, in areas with favorable bird habitat in close proximity to the road, and where bird populations are abundant (Loos and Kerlinger 1993, reviewed by Erritzoe et al. 2003, Gunson et al. 2010, Boves and Belthoff 2012). In some cases, mortality rates have been found to increase with increasing width of the road corridor (Oxley et al. 1974) or to be greater along road segments that are elevated above the surrounding land (Baudvin 1997, Lodé 2000). Often, 2 or

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more of the above factors are strongly correlated—i.e., wider roads usually have a higher traffic volume than narrow roads—making it difficult to dis-entangle the relative impact of each factor. Furthermore, exceptions to the above relationships occur and are illustrative of how mortality rate correlates are often region-, taxa-, and habitat-specific. For example, several studies have found no link between traffic volume and mortality rates (Massemin et al. 1998, Lodé 2000, Coelho et al. 2008, Kambourova-Ivanova et al. 2012).

Current estimates of annual U.S. bird mortality from vehicle collisions—ranging from 60 to 80 million—are highly speculative, based on extrapolation of mortality rates from a single British study (Hodson and Snow 1965) to the entire U.S. road network (Banks 1979, Erickson et al. 2005). Comprehensive meta-analyses of studies that quantify bird populations have concluded that roads are consistently associated with reductions in bird abundance (Fahrig and Rytwinski 2009, Benitez-Lopez et al. 2010), but no clear evidence exists that vehicle collision mortality is a significant driver of these road-related declines. In addition, no such comprehensive analyses have been completed to assess bird-vehicle collision mortality in the United States. When compared to speculative or extrapolative estimates based on small samples of data, such systematic and quantitative reviews provide a more rigorous approach to estimating mortality, an improved understanding of the sources of uncertainty associated with estimates (Loss et al. 2012, 2013*a*, 2014; Machtans et al. 2013), and a more valid evidence base on which to prioritize policy and management strategies and to identify major research needs (Calvert et al. 2013, Machtans and Thogmartin 2014).

We reviewed the North American and European bird-vehicle collision literature and defined inclusion criteria to screen and remove studies likely to bias our estimates substantially. Based on data extracted from the remaining studies, we 1) systematically quantified the magnitude of bird mortality (along with uncertainty) caused by collisions with vehicles on U.S. roads by combining probability distributions of mortality rates, the length of U.S. roads, and biases associated with surveys for dead birds; 2) used sensitivity analyses to quantitatively investigate factors contributing to estimate uncertainty and to identify major research needs; and 3) summarized the available species-specific data on bird-vehicle collisions in the United States.

METHODS

Literature Search and Inclusion Criteria

We used Google Scholar and the Web of Science database to search for publications about bird-vehicle collisions on roads. The search terms we used were "bird-vehicle collision," "bird-vehicle roadkill," the previous terms with "bird" replaced by "avian" and "vehicle" replaced by "automobile," "car," and "truck." We checked reference lists to locate additional sources, and we also referenced an annotated bibliography that included approximately 670 sources covering the impacts of roads on wildlife (Nietvelt 2002). For 5 North American studies (Nero and Copland 1981, Decker 1987, Smith et al. 1994, Sutton 1996, Potvin and Bishop 2010), we were unable to access full-text articles and instead extracted the data as summarized in a review of bird-vehicle collisions in Canada (Bishop and Brogan 2013). Because of the large quantity of international studies—many that are published in languages other than English or inaccessible online or through North American libraries—we could not exhaustively review this literature. However, our review of the North American literature was comprehensive, and we likely located all studies that included a systematic sampling component. We may have overlooked some North American publications containing descriptions of incidentally found roadkill victims; however, these studies would have been excluded from analyses based on our inclusion criteria described below.

We defined several criteria for studies to be included in our estimation models. We designed inclusion criteria to remove studies that were not useful for generating mortality rate estimates or that were likely to substantially bias estimates. We excluded studies prior to in-depth review if they included no original data; were conducted in a region other than the United States, Canada, or Europe; or were published in a language other than English. In addition, because we sought to generate mortality estimates that were relevant to relatively modern road types and traffic patterns, we arbitrarily selected 1970 as the earliest date for which publications could be included in analyses (see also Bishop and Brogan 2013). Following in-depth review of the remaining 53 studies, we also excluded studies that 1) were retrospective, based on assessment of opportunistically collected data sets or recoveries of banded or radio-tagged birds, 2) focused on particular bird species or groups without sampling or presenting data for all species and groups, 3) included an experimental component without presenting control and treatment data separately, 4) were prospective but also included incidentally collected data without presenting it separately, 5) did not provide information about the proportion of the year covered by sampling, 6) did not present the length of road corridor sampled or a per kilometer mortality rate, 7) were based on a single survey or a series of surveys that covered less than 1 month, and 8) did not separately report fatalities from vehicle collisions and other collision sources (e.g., roadside fences). After implementing the above inclusion criteria, 16 of the 53 reviewed studies remained (9 U.S. and 7 European studies; Table 1; see Table S1 for excluded studies).

For the summary of species representation of mortality, we included data from U.S. studies meeting criteria 1–4 and 7–8 above. We considered criteria 5 and 6 unnecessary for producing unbiased species summaries. We used 7 of the 9 U.S. studies meeting inclusion criteria for the mortality estimate for the species analysis. The 2 excluded studies did not provide data at the species level (Oxley et al. 1974, Gerow et al. 2010).

Data Extraction

From most studies meeting the above inclusion criteria, we extracted a single mortality rate. However, for studies that

Table 1. Meta-data and mortality rates for studies meeting inclusion criteria for 1) estimation of annual bird-vehicle collision mortality on U.S. roads and/or 2) species mortality summary.

Location	Sampling coverage	Used?		Road type	Mortality per km[c]	Study
		Total[a]	Species[b]			
United States						
Southern Idaho	Yr-round	Yes	Yes	4-lane paved	2.01	Boves and Belthoff (2012)
Bow River Valley, AB	Apr–Nov	Yes	Yes	2-lane paved	0.38	Clevenger et al. (2003)—Bow Valley Parkway
Bow River Valley, AB	Apr–Nov	Yes	Yes	4-lane paved	0.37	Clevenger et al. (2003)—Trans-Canada Highway
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	6.54	Glista et al. (2008)—South River Road
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	5.69	Glista et al. (2008)—State Road 26
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	4.85	Glista et al. (2008)—U.S. Highway 231
Central California	25 May–26 Nov	Yes	Yes	4-lane paved	1.20	Moore and Mangel (1996)
Athens County, Ohio	Yr-round	Yes	Yes	4-lane paved	6.56	Seibert and Conover (1991)
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	Unpaved	0.23	Oxley et al. (1974)—Gravel unpaved road 1
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	Unpaved	2.11	Oxley et al. (1974)—Gravel unpaved road 2
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	2-lane paved	2.96	Oxley et al. (1974)—2-lane paved highway
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	4-lane paved	3.22	Oxley et al. (1974)—4-lane paved highway
Long Point, ON	Apr–Oct	No[d]	Yes	2-lane paved	91.43	Ashley and Robinson (1996)
Tippecanoe County, IN	Yr-round	No[d]	Yes	2-lane paved	24.44	Glista et al. (2008)—Lindberg Road
Alachua County, FL	Yr-round	No[d]	Yes	4-lane paved	43.44	Smith and Dodd (2003)
Saguaro Nat. Park, AZ	Yr-round	No[e]	No	?	NA	Gerow et al. (2010)—Rincon Mountain
Saguaro Nat. Park, AZ	Yr-round	No[e]	No	?	NA	Gerow et al. (2010)—Tucson Mountain
Europe						
Northeast France	Yr-round	Yes	No	2-lane paved	1.54	Baudvin (1996)
Northeast Poland	Yr-round	Yes	No	2-lane paved	11.55	Gryz and Krauze (2008)
Galanta, Slovakia	Yr-round	Yes	No	?	17.09	Hell et al. (2005)
Belovo, Bulgaria	Mar–Oct	Yes	No	?	3.00	Kambourova-Ivanova et al. (2012)—1st-class road
Belovo, Bulgaria	Mar–Oct	Yes	No	?	8.09	Kambourova-Ivanova et al. (2012)—Trakia highway
Western France	Apr–Nov	Yes	No	?	8.80	Lodé (2000)
Wroclaw, Poland	Mid-Mar–Oct	Yes	No	?	5.89	Orlowski (2005)
Spain and France	Yr-round	Yes	No	?	0.65	Pons (2000)

[a] Whether we used the mortality rate to estimate bird-vehicle collision mortality on U.S. roads.

[b] Whether we used the source to calculate average proportional representation for individual species (excluded U.S. studies focused on particular bird group(s) without including all species; we excluded all international studies).

[c] We calculated mortality rates using raw data (i.e., we did not directly extract reported rates from studies because calculation approaches varied among studies and were not always calculated transparently). We first divided the total number of fatalities reported for a road segment by the length of road corridor covered by that segment. For rates representing >1 year of sampling, we then divided by the number of years sampled; we applied a partial-year sampling correction in the mortality estimation model (see Methods section in main text for details).

[d] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is a statistical outlier among studies meeting criteria.

[e] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is adjusted for biases associated with carcass surveys (detection probability and scavenger removal); these biases were separately accounted for in our mortality estimation model.

sampled along more than 1 road type (e.g., paved and unpaved roads and/or roads with different numbers of lanes) or used different sampling methods (e.g., different sampling intervals or survey types) for different portions of the study area, we extracted separate mortality rates. This resulted in extraction of 25 mortality rates (17 U.S. and 8 European rates; Table 1) from the 16 included studies. We calculated all rates as the number of dead birds found per kilometer of road corridor sampled. This approach is different than that of some studies that calculate mortality rates using the total length of lanes sampled (e.g., for a 2-lane road, lane-length is twice the length of the road corridor). Some studies did not provide enough information to clarify how they calculated mortality rates. Therefore, rather than directly extracting the reported rates, we recalculated rates based on the number of fatalities reported for a road segment divided by the length of road corridor covered by that segment. Because we recalculated rates using this raw data, the mortality rate we calculated was sometimes different than that presented in the original study.

We then used one of several approaches to convert multi-year mortality rates to annual rates. For multi-year studies that sampled across the entire calendar year in every year of the study, we divided mortality rates by the number of years to generate the annual rate (Table 1). We also took this approach for multi-year studies that only sampled a portion of each year; we accounted for partial-year sampling coverage separately (see following subsection). For 4 studies that sampled at least 1 entire calendar year as well as an additional partial year (Seibert and Conover 1991, Baudvin 1997, Hell et al. 2005, Glista et al. 2008), we treated the partial year as a full year when calculating the annual rate. This approach led to conservative rate estimates because mortality was spread across a longer time period than it actually occurred in.

We excluded 3 mortality rates from the above data set for being statistical outliers and 2 for being adjusted for various sampling biases that we accounted for separately in the mortality estimation model (see Supplementary Methods, available online at www.onlinelibrary.wiley.com). The final data set used for estimation of mortality therefore included 20 mortality rates (12 U.S. and 8 international rates) extracted from 13 studies (6 U.S. and 7 European studies; Table 1).

Quantification of Annual Bird Mortality

To increase the comparability of mortality estimates from different studies, mortality rates should ideally be standardized to account for varying proportions of the year being covered by sampling (Loss et al. 2012). Potential standardization approaches include 1) using mortality rates from year-round studies to proportionally correct partial-year studies (Longcore et al. 2012, Loss et al. 2013*a*), 2) including a correction factor in the mortality estimation model that accounts for partial-year sampling (Loss et al. 2014), or 3) using only full-year mortality rates to generate mortality estimates. We were unable to implement the first approach because year-round vehicle collision studies either do not present data separately for different portions of the year or only provide seasonal data for single bird species or taxa other than birds. Because the second and third approaches were both possible, we repeated mortality estimation using each approach. We expected the estimate generated using approach 2 would represent a maximum value because this approach assumed that mortality rates observed during the sampled portion of the year—typically the peak periods of vehicle collision mortality in spring, summer, and/or autumn—also applied to the un-sampled portion of the year (see Supplementary Methods).

Our approach for estimating mortality was to combine a mortality rate probability distribution with a probability distribution for the length of U.S. roads susceptible to that range of mortality rates. We defined the maximum susceptible road length to be the entire U.S. road network and the minimum susceptible length to be only the length of roads in rural areas (see Supplementary Methods). This approach assumes that mortality rates in urban areas are likely lower than in rural areas, but does not entirely discount mortality in urban areas. We also incorporated correction factors to account for sampling coverage of less than the entire calendar year (for estimates that included partial-year morality rates) and for biases associated with carcass surveys (all estimates), including removal of carcasses by scavengers and imperfect detection of carcasses by surveyors (Loss et al. 2013*a*, 2014). Because a preliminary analysis found little support for differences in mortality rates between 2-lane, 4-lane, and gravel roads, and because the sample of mortality rates was too small to generate separate probability distributions for different road types, we applied the same range of mortality rates across all U.S. road types. This simplified approach contributes uncertainty to our mortality estimate; however, we did not have enough available data to allow separate mortality estimates for different road types. In addition to repeating mortality estimation with and without inclusion of partial-year studies, we also estimated mortality with and without inclusion of European mortality rates. Thus, we generated 4 separate estimates of annual mortality using different subsets of data: U.S. year-round mortality rates, U.S. year-round and partial-year rates, U.S. and Europe year-round rates, and U.S. and Europe year-round and partial-year rates.

For the estimates based only on year-round mortality rates, we used the model:

$$\text{Mortality}_{\text{year-round studies}} = R \times K_{\text{year-round studies}} \times B \tag{1}$$

where R is the length of U.S. roads susceptible to the range of mortality rates in the mortality rate probability distribution (K), K is the is the range of collision mortality rates per km of road corridor, and B is a bias correction factor to account for removal of carcasses by scavengers prior to surveys and imperfect detection of carcasses remaining at the time of surveys.

For the estimates based on year-round and partial-year rates, we used the model:

$$\begin{aligned}&\text{Mortality}_{\text{year-round and partial-year}}\\&\quad = R \times K_{\text{year-round and partial-year}} \times Y \times B\end{aligned} \tag{2}$$

where Y is a correction factor that accounts for the average proportion of the calendar year not covered by sampling in the studies used to develop the mortality rate distribution (Loss et al. 2014). The partial-year sampling correction factor was a fixed value; however, we defined all other parameters as uniform probability distributions (specific distributions shown in Table 2; rationale for distributions in Supplementary Methods). For all estimates, we used the runif function in Program R (R Version 3.0.1., <http://www.r-project.org/>. Accessed 14 Apr 2014) to draw random values from each probability distribution, and we calculated mortality using the above formulas. We repeated this calculation 10,000 times for each of the 4 estimation approaches to generate ranges of uncertainty for mortality estimates.

Sensitivity Analyses

We used sensitivity analyses to quantitatively investigate the factors contributing to uncertainty in our mortality estimates.

Table 2. Probability distributions used for estimation of annual bird-vehicle collision mortality on U.S. roads.

Parameter	Distribution type	Distribution parameters	Source
Total length of road corridors in the United States[a]	Uniform	Min. = 3.76 M; max. = 4.33 M	U.S. Department of Transportation (2012)
Morality rates (per km)			
U.S. studies (yr-round)[b]	Uniform	Min. = 3.48; max. = 6.78	95% CI across 5 rates meeting inclusion criteria
U.S. studies (all)[c]	Uniform	Min. = 2.78; max. = 6.73	95% CI across 12 rates meeting inclusion criteria
U.S. + Europe studies (yr-round)[b]	Uniform	Min. = 2.85; max. = 9.70	95% CI across 9 rates meeting inclusion criteria
U.S. + Europe studies (all)[c]	Uniform	Min. = 4.24, max. = 8.58	95% CI across 20 rates meeting inclusion criteria
Partial-yr sampling correction			
U.S. studies (all)[c]	NA[d]	Estimate = 1.49	1/average proportion of yr covered by mortality rates
U.S. + Europe studies (all)[c]	NA[d]	Estimate = 1.37	1/average proportion of yr covered by mortality rates
Bias correction factor	Uniform	Min. = 3.26; max. = 11.46	Bruun-Schmidt (1994), Gerow et al. (2010), Santos et al. (2011), Boves and Belthoff (2012), Texeira et al. (2013)

[a] Includes length in millions (M) of kilometers of all public roads in all states excluding Alaska and Hawaii.

[b] Estimate is based only on mortality rates from studies with year-round sampling coverage.

[c] Estimate is based on mortality rates from all studies meeting inclusion criteria.

[d] Parameter is a point estimate, not a probability distribution.

We defined univariate regression models with the 10,000 replicated mortality estimates as the dependent variable and randomly drawn values of model parameters as the independent variable. We repeated this analysis 4 times, once for each of the 4 mortality estimate models. We used the adjusted R^2 values for each independent variable (averaged across the 4 sensitivity analysis iterations) to interpret the percentage of estimate uncertainty attributable to each model parameter (Blancher 2013, Loss et al. 2013*a*).

Vehicle Collision Mortality by Species

In addition to estimating total annual mortality for all U.S. birds, we also calculated the average proportional representation of each bird species (Longcore et al. 2013, Loss et al. 2013*a*). We used this calculation rather than estimating species-specific mortality because the data from studies meeting inclusion criteria only represented 100 bird species. This value is likely much lower than the actual number of species killed along U.S. roadways each year. Estimates of species-specific mortality would therefore be biased high for observed species and biased low for species killed but not reported in the literature. Therefore, we would be unable to draw unbiased conclusions about species-specific collision risk. Nonetheless, to provide a rough summary of the findings to date, we estimated average proportional representation of species by 1) calculating the proportion of each study's total count represented by each species (i.e., multiple proportions calculated for each species, 1 from each study), and 2) averaging each species' individual-study proportions across all studies. For averaging, we only included zero-values of proportions (i.e., species was not found in study) when a species could have been found, as determined by overlap of breeding, migration, and/or wintering ranges with study sites (Sibley 2000).

RESULTS

We found considerable variation (41.8%) among median mortality estimates produced using the 4 models (Table 3). The model using only year-round mortality rates from the United States produced the lowest annual estimate (median = 145.7 million; 95% CI = 61.9–274.6 million), and the model including both year-round and partial-year mortality rates and rates from both the United States and Europe produced the highest estimate and the estimate with the greatest range of uncertainty (median = 250.5 million; 95% CI = 103.8–476.8 million). Averaging across all 4 models (i.e., averaging the 4 estimates produced in each model iteration and then averaging these values across 10,000 iterations) resulted in a median annual mortality estimate of 199.6 million birds (95% CI = 88.7–339.8 million). Regardless of the model used, sensitivity analyses indicated that the bias correction factor for scavenger removal and searcher detection contributed the greatest uncertainty to estimates (average variance explained = 63.2%), followed by the mortality rate (32.5%) and the road corridor length over which the mortality rate applies (1.3%).

Among the species documented in studies meeting inclusion criteria, the barn owl had the highest average proportional representation across studies, averaging 32.4% of total counts (all species proportions in Table S2). Four other species, including 3 in the Corvidae family, had average proportional representation of at least 5%: common raven (*Corvus corax*; 6.3%), gray jay (*Perisoreus canadensis*; 6.0%), black-billed magpie (*Pica hudsonia*; 5.0%), and European starling (*Sturnus vulgarus*; 5.0%). Several species were found in 3 or fewer studies, and these species' proportions were more likely to be biased by abnormally high or low counts documented in single studies. Given the small sample of

Table 3. Estimates of annual bird-vehicle collision mortality on U.S. roads.

Mortality data used	Total mortality (millions)		Mortality per km	
	Median	95% CI	Median	95% CI
United States	145.7[a]	61.9–274.6[a]	36.0[a]	15.3–68.0[a]
	197.1[b]	78.2–397.9[b]	48.8[b]	19.4–98.5[b]
United States + Europe	171.0[a]	59.6–381.5[a]	42.3[a]	14.8–94.4[a]
	250.5[b]	103.8–476.8[b]	62.0[b]	25.7–118.0[b]
Average across models	199.6	88.7–339.8	49.4	22.0–84.1

[a] Estimate based only on mortality data from studies with year-round sampling coverage.
[b] Estimate based on data from all studies meeting inclusion criteria.

studies included in the species summaries (7 studies including 3,246 total fatality records), caution should be used when interpreting these results.

DISCUSSION

Annual Bird-Vehicle Collision Mortality on U.S. Roads

All of our estimates of annual bird-vehicle collision mortality exceed the previous estimates of between 60 and 80 million birds, which were produced by extrapolating the results of 1 British study (Hodson and Snow 1965) across the entire U.S. road network (Banks 1979, Erickson et al. 2005). We improved upon these earlier estimates by systematically incorporating 20 mortality rates from 13 studies that used a prospective sampling design and reported results for all potentially killed bird species. Even when considering the lowest estimate range (between 62 and 275 million birds), our results suggest that bird-vehicle collisions outrank many other sources of direct anthropogenic mortality. Among threats with estimates that are data-driven and systematically derived, only predation by free-ranging domestic cats (Loss et al. 2013*a*) and collisions with buildings and their windows (Loss et al. 2014) are estimated to cause greater annual bird mortality in the United States. Estimates of total numbers of birds killed by anthropogenic threats are useful for prioritizing conservation and management efforts. However, increased attention should also be given to documenting which species and regions are most vulnerable to vehicle collisions and other mortality sources (Longcore et al. 2013; Loss et al. 2013*b*, 2014).

As expected, estimates that incorporated both year-round and partial-year mortality rates were higher than those that used only year-round rates. This likely occurred because the partial-year correction factor was calculated under the assumption that mortality rates were constant across all seasons. Among the studies we used, sampling periods typically covered spring, summer, and/or autumn, seasons characterized by relatively high mortality rates for most species (Loos and Kerlinger 1993, Smith and Dodd 2003, Orlowski 2005, Gryz and Krauze 2008). Extrapolating mortality rates from these peak seasons to un-sampled seasons that are generally characterized by lower mortality rates may have inflated our estimates. Estimates from models including partial-year rates should therefore be viewed as maximum values. Additional year-round studies that present results separately by month and/or season are needed to clarify intra-annual variation in vehicle collision mortality rates.

Estimates that included European mortality rates were higher than those that used only U.S. rates. This may have occurred due to the inclusion of 2 European rates that were not statistical outliers but were higher than all U.S. rates meeting inclusion criteria (11.6 and 17.0 birds/km/yr; Hell et al. 2005, Gryz and Krauze 2008). Although exceptionally high annual mortality rates of up to 91 birds/km (Ashley and Robinson 1996) have been documented locally in the United States, such rates likely do not apply across most roads. Roadkill fatalities are often clustered in hotspots (e.g., Gunson et al. 2010), and these areas are often the focus of mortality studies. This tendency to focus on areas already known to experience bird mortality may have contributed positive bias to individual estimates of mortality rates and to our national mortality estimates. Nonetheless, we sought to minimize this source of bias by removing mortality rates that were identified as statistical outliers.

We were unable to assess regional variation in bird-vehicle collision mortality rates and to produce regional mortality estimates. Only 6 U.S. studies met our inclusion criteria; this sample was insufficient to allow for quantification of regional variation. Filling this data gap will require rigorous and prospective studies across a broad cross-section of the United States within numerous ecosystems, states, and regions. Individual studies that randomly sample roadkill mortality across a large spatial scale (e.g., entire states or regions) will also provide increased understanding of regional variation.

Research Needs and Estimate Limitations

The relatively small sample of data meeting inclusion criteria resulted in substantial uncertainty in our mortality estimates. When assessing specific uncertainty contributions of individual model components, sensitivity analyses indicate that the model parameter contributing the greatest uncertainty to our estimates is the bias correction factor, which accounts for both scavenger removal and imperfect detection of carcasses. Further research on these biases may decrease the uncertainty associated with this correction factor and allow for increased precision of future mortality estimates. However, the magnitude of these biases depends on a suite of factors, including the local scavenger community, habitat type, traffic volume, and weather conditions (Santos et al. 2011, Boves and Belthoff 2012, Guinard et al. 2012, Texeira et al. 2013). Development of a narrow distribution of bias correction factors that apply across a national scale may therefore not be possible. An alternative approach is for future studies to estimate scavenger removal and searcher detection rates to calculate adjusted mortality rate estimates. A large sample of locally adjusted mortality rates would obviate the need for post hoc correction factors (Loss et al. 2013*b*). Recent studies outline considerations for scavenger removal and detection trials (Santos et al. 2011, Texeira et al. 2013). Of particular promise are approaches that allow for estimation of both biases using a single experimental trial incorporated into standard fatality monitoring (Smallwood 2013) or using only the dead birds found during fatality monitoring, thus removing the need for separate experimental trials (Etterson 2013).

Mortality rate probability distributions also contributed substantial uncertainty to our estimates. The relatively small sample of studies meeting inclusion criteria along with the inherently variable nature of collision rates likely contributed to this uncertainty. To increase the number of mortality rates that can be used to estimate national mortality, future studies should seek to meet the level of rigor captured by our inclusion criteria. In particular, more studies are needed that sample and present data for all bird species. When summarizing average proportional representation of collision mortality, we found that a few species (particularly barn owls and several corvids) comprise a relatively large percentage of all fatalities that have been identified to species. However, sample sizes of usable studies and available data were small, and results of the species summary were likely biased by high detection probabilities for large species and by geographical biases in sampling. Taking a more species-inclusive approach to studying bird-vehicle collisions will improve understanding of species- and taxa-specific vulnerabilities to vehicle collisions. Because of the above limitations, species proportions should not be used to draw conclusions about national-scale vulnerabilities of bird species to vehicle collisions. Nonetheless, they provide a descriptive summary of the bird species that have been documented as roadkill victims along U.S. roads.

In addition to estimate bias caused by scavenger removal and imperfect detection of carcasses, an unknown number of birds that collide with vehicles fly out of detection range (i.e., crippling bias; Slater 2002, Texeira et al. 2013) or are destroyed or carried away by vehicles (Stewart 1973, Mumme et al. 2000). Because these biases have never been formally quantified in the context of vehicle collisions, substantial uncertainty remains about to what degree they contribute to under-estimation of roadkill mortality rates. Future research of these bias sources is necessary for fully understanding the magnitude of bird mortality caused by vehicle collisions.

Numerous biotic and abiotic factors influence bird collision mortality rates along roads. These correlates collectively result in bird fatalities being clustered along particular road segments (Clevenger et al. 2003, Smith and Dodd 2003, Glista et al. 2008, Gunson et al. 2010). Further research is needed to clarify the combination of factors that lead to carcass clustering (e.g., habitat, characteristics of the road and its cleared corridor, and community composition and population abundance of birds) and to assess how these correlates vary seasonally and regionally. When possible, studies should employ sampling designs that allow for separation of often-confounded mortality correlates (e.g., road width, traffic volume, and traffic speed).

The negative bias contributed to mortality rate estimates by scavenger removal is amplified with increasing time intervals between surveys. This occurs because—with all other factors held constant—more collisions occur between surveys, and a greater proportion of carcasses are removed by scavengers. Because carcass removal adjustment factors are less accurate across long search intervals (Smallwood 2013) and because carcass removal rates appear to be especially high along roadways (Bruun-Schmidt 1994, Antworth et al. 2005, Santos et al. 2011, Texeira et al. 2013), optimal search intervals for documenting roadkill mortality are very short (e.g., sampling on alternate days for large birds and daily for small birds; Santos et al. 2011). Because the search intervals in the studies we used were between 2 and 15 days, mortality rates in individual studies could have been substantially under-estimated. This under-estimation could have contributed negative bias to our mortality estimates.

In addition to using long search intervals for carcass surveys, the studies we used conducted surveys using various transportation methods, including foot, bicycle, and automobile. Because of the relatively high speed at which sampling is conducted, automobile surveys usually detect only a small fraction of carcasses (Slater 2002, Gerow et al. 2010, Guinard et al. 2012, Texeira et al. 2013). In the sample of mortality rates extracted from studies meeting our inclusion criteria, the majority of rates (15 of 20) were based on automobile surveys, and estimated mortality rates for automobile surveys averaged 2.3 times lower than for other survey types. Therefore, the use of automobile surveys may have contributed additional under-estimation bias to our mortality estimates. The use of automobile surveys may have also influenced our species summary, with surveys likely over-representing large-bodied species (e.g., raptors and corvids) that are relatively easy to detect from a fast-moving automobile.

MANAGEMENT IMPLICATIONS

The large magnitude of mortality caused by vehicle collisions combined with the potential for impacts at the population level highlights the need for conservation and management attention to mitigate this threat. Mitigation efforts may be most relevant at areas known to experience exceptionally high rates of collision mortality (e.g., clear examples include the studies that were identified as statistical outliers for our mortality estimate). Following identification of mortality hotspots, potential options to reduce bird collision mortality along roads include (see also Boves and Belthoff 2012, Bishop and Brogan 2013) placing flight deflectors along roadsides to force birds to fly above vehicle height (Bard et al. 2001, Ramsden 2003, Gomes et al. 2009), locally reducing speed limits and erecting signage to alert drivers, reducing or removing the amount of favorable bird habitat along roadsides, and using visual or auditory deterrents. All of these approaches have rarely been implemented and remain largely untested. Research is therefore needed to determine which combinations of the above approaches are most effective at reducing mortality and to clarify how responses vary by bird species, region, habitat, season, and road type. Identification and implementation of effective conservation measures is especially crucial given the increasing length of U.S. roadways, increasing traffic volume, and an increasing number of direct and indirect anthropogenic threats to bird populations.

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SUPPORTING INFORMATION

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Recent ecological responses to climate change support predictions of high extinction risk

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Predicted effects of climate change include high extinction risk for many species, but confidence in these predictions is undermined by a perceived lack of empirical support. Many studies have now documented ecological responses to recent climate change, providing the opportunity to test whether the magnitude and nature of recent responses match predictions. Here, we perform a global and multitaxon metaanalysis to show that empirical evidence for the realized effects of climate change supports predictions of future extinction risk. We use International Union for Conservation of Nature (IUCN) Red List criteria as a common scale to estimate extinction risks from a wide range of climate impacts, ecological responses, and methods of analysis, and we compare predictions with observations. Mean extinction probability across studies making predictions of the future effects of climate change was 7% by 2100 compared with 15% based on observed responses. After taking account of possible bias in the type of climate change impact analyzed and the parts of the world and taxa studied, there was less discrepancy between the two approaches: predictions suggested a mean extinction probability of 10% across taxa and regions, whereas empirical evidence gave a mean probability of 14%. As well as mean overall extinction probability, observations also supported predictions in terms of variability in extinction risk and the relative risk associated with broad taxonomic groups and geographic regions. These results suggest that predictions are robust to methodological assumptions and provide strong empirical support for the assertion that anthropogenic climate change is now a major threat to global biodiversity.

anthropogenic warming | elevated temperature | extinction crisis | climate warming

Many scientists argue that we are entering the sixth great mass extinction and that anthropogenic climate change is one of the major threats to global biodiversity (1–3). Comprehensive, multitaxon reviews suggest that 10–70% of plant and animal species assessed so far could be at increased risk of extinction from climate change (4) or that by 2050, climate-induced changes in habitat will commit 15–37% of species to extinction (1). Both these estimates are based on approaches that can be sensitive to ecological and methodological assumptions (5–8), and the latter study considers only geographical range shifts resulting from changes in temperature and rainfall (1). Many species are also expected to be adversely affected by changes in sea-level and ocean chemistry (9), and the impacts of climate change may include breakdowns in biological interactions as species respond individualistically to climate change (10), loss of habitat because of sea-level rise (11), and higher mortality because of increased ocean acidity (12). The spectrum of approaches used to predict ecological responses to climate change has also broadened in recent years, enabling more robust estimates of future changes to be made (13). Here, we use International Union for Conservation of Nature (IUCN) Red List Criteria (14) to derive estimates of extinction risk from a wide range of climate impacts, ecological responses, and methods of analysis. Importantly, the broad evidence base that now exists for realized ecological responses to recent climate change allows us to validate future predictions by comparison with responses that have already been observed.

We identified 130 observed and 188 predicted ecological responses to climate change using a robust review of 10 leading scientific journals from 2005 to 2009 (*Methods*). The responses included documented changes to extinction risk, population size, and geographic range size for 305 taxa from all major groups of organisms, covering a high proportion of the global terrestrial and marine surface (Table S1). All 318 climate change responses were expressed in terms of extinction risk using IUCN Red List criteria, which is possible, because the threshold values used to assign IUCN categories on the basis of population decline are linearly related to the logit transform of threshold extinction risk values (Fig. S1). Estimates of the mean extinction risk for taxa and the proportion subject to varying degrees of extinction risk were derived with an intercept-only generalized linear model with an inflated β-error distribution and logit link function (*Methods*).

A range of factors relating to the selection of study systems (climate impact type, taxon, and region) and the publication of results could influence whether the sampled climate change responses gave unbiased estimates of mean extinction risk. To determine whether there was publication bias, we investigated whether extinction risk was related to the journal in which the study was published and also, created a funnel plot of extinction risk against sample size (Fig. S2). The presence of asymmetry in a funnel plot signifies bias to the publication of significant results (15). To account for biases in the type of impact studied, we incorporated impact type as a factor into models and compared the results of averaging across impact types with those results obtained by averaging across studies. To account for possible phylogenetic nonindependence of extinction risk, we constructed a phylogenetic tree and added the residual of each tip relative to its branch to the mean across all tips in instances where branches were significant. Research carried out in regions where taxa are disproportionately threatened by climate change could also bias overall estimates of threat, and therefore, we controlled for spatial patterns in extinction risk by spatially averaging our results (*Methods*).

To examine whether there were consistent ecoregional and taxonomic patterns across studies making predictions and studies reporting empirical data, we subdivided our data into three major taxonomic groups (plants, invertebrates, and vertebrates) and four major ecoregions: (*i*) polar and boreal, (*ii*) temperate, (*iii*) tropical and subtropical, and (*iv*) marine; we compared observations with predictions.

Results and Discussion

Across all studies, the mean extinction risk over 90 y (i.e., to 2100) was 11.2%. Separating projections of extinction risk based on predicted and observed responses yielded a mean extinction

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risk of 6.7% based on predictions but 14.7% based on observations (Table 1).

The proportion of taxa qualifying as threatened by 2100 using IUCN criteria would be 7.6% based on predictions and 31.7% based on observations. The proportion of taxa more likely to go extinct than not was 1.9% based on predictions but 12.0% based on observations (Table 1). The degree of variability in extinction risk across observations and predictions is similar (Fig. 1), with the majority of taxa (>80%) at low risk (<5%) of extinction; this finding suggests that predictions are not invalidated by methodological assumptions. The symmetry of the funnel plots of extinction risk against sample size (Fig. S2) suggests very little evidence of publication bias. However, extinction risk for both observations and predictions was affected by climate impact type. More studies reported threats from changes in temperature and rainfall, but the few studies on the effects of reductions in sea ice and changes in ocean circulation patterns showed higher predicted extinction risk (Table S2). More studies on effects such as changes in oceanic circulation patterns and acidity on marine organisms would improve estimates of extinction risk. Nevertheless, models that controlled for climate impact type did not lead to marked changes in mean extinction risk, either for empirical observations or predictions (Fig. 1 and Table 1).

There was evidence of phylogenetic nonindependence of extinction risk, with both observations and predictions suggesting high levels of threat to vertebrates and lower levels of threat to plants and invertebrates. This finding was also supported by comparisons of extinction risk within each of these three major taxonomic groups (Fig. 2). There was a high degree of consistency between observations and predictions, with most taxa observed to be at high risk also predicted to be highly threatened in the future. After accounting for phylogeny, estimated extinction risks from observations decreased to 14%, whereas those risks from predictions did not change (Table 1). Thus, observed responses may be slightly exaggerated by work on more threatened taxa. Spatial averaging of results did not alter estimates of

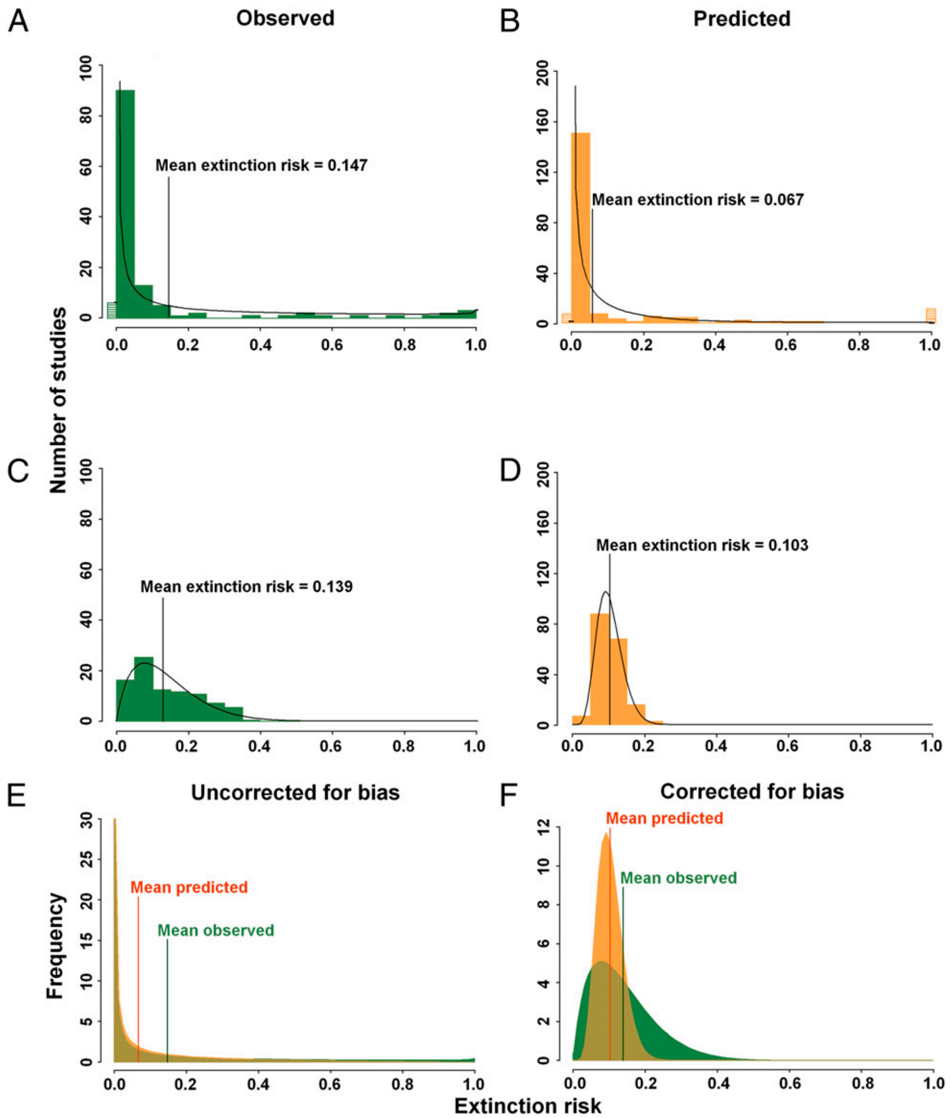

Fig. 1. Proportion of taxa subject to varying degrees of extinction risk by 2100. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The horizontal hatched bars (actual) and horizontal black lines (modeled) represent the number of studies with an extinction risk of zero or one. (*A* and *B*) Uncorrected estimates derived from observed (*A*) and predicted (*B*) data. (*C* and *D*) Estimates accounting for biases (*Methods*) derived from observed (*C*) and predicted (*D*) data. (*E* and *F*) Modeled probability density functions (green, observed; orange, predicted) overlaid to show that, when uncorrected (*E*), the variance in extinction risk derived from observed and predicted data is similar, and when corrected (*F*), the means are similar.

Table 1. Projected extinction risk by 2100 based on observations and predictions

	Expected extinction risk			>50% probability of extinction			Threatened with extinction		
Method	All	Observed	Predicted	All	Observed	Predicted	All	Observed	Predicted
Estimate derived from values given in each study	0.112	0.147	0.067	0.069	0.120	0.019	0.291	0.318	0.076
Estimate obtained by averaging across impact types	0.116	0.158	0.061	0.073	0.132	0.035	0.298	0.333	0.204
Estimate obtained by averaging across taxa	0.104	0.140	0.061	0.051	0.104	0.049	0.296	0.329	0.375
Estimate obtained by spatially averaging across the globe	0.118	0.139	0.103	0.000	0.002	0.000	0.620	0.648	0.600

Expected extinction risk is based on the β-distribution of observed or predicted extinction risks ($n_{\text{predicted}}$ = 188; n_{observed} = 130). Taxa categorized as threatened were those taxa exceeding a modeled extinction risk by 2100 of 0.09. IUCN categories: CR, critically endangered; EN, endangered; VU, vulnerable.

observed extinction risk (13.9%), whereas predicted risk increased (10.3%), implying that models of future effects of climate change may, to some extent, have neglected regions subject to higher levels of threat (Table 1). Comparisons of extinction risk in broad ecoregions suggest that marine taxa are particularly threatened and that taxa in the terrestrial tropics and subtropics are less threatened than those taxa in terrestrial temperate and high latitude areas, and the relative threat predicted for different regions was quite well-supported by empirical observations (Fig. 3). However, for both observations and predictions, there were few studies from the terrestrial tropics: the larger number of predictions from the subtropical and tropical category is mostly of tree responses in Mexico (16). In the marine environment, there is a bias to research on corals, which may be disproportionately affected by climate change. More research from tropical areas, where most species occur and are expected to have climates for which no current analog exists (17) and on a greater variety of marine taxa, would improve estimates of the realized threat to biodiversity from climate change.

Our approach, using IUCN criteria to translate between population or range changes and extinction risk, has allowed us to include more examples than simply population viability studies, which estimate extinction risk directly. We, thus, reduce possible bias in threat levels that could result, because particular methodologies might focus on endangered species. However, we make the assumption that the threshold values for criteria relating to decline and extinction risk are comparable (*SI Methods*). Although the rules used to assign taxa to IUCN categories represent inter-

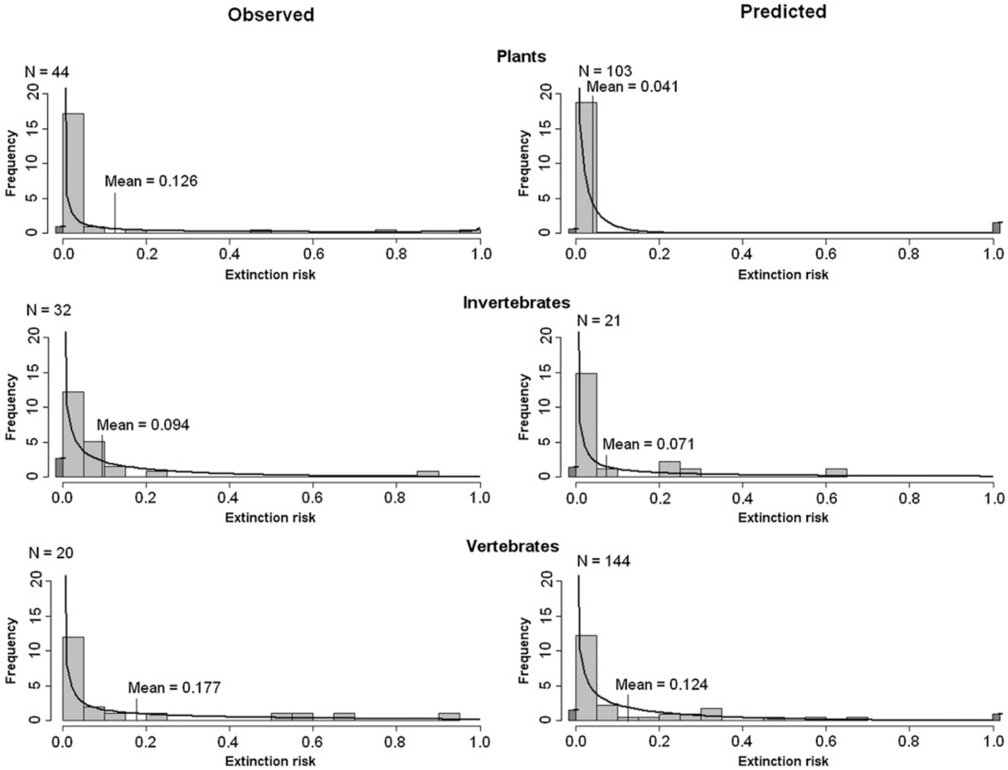

Fig. 2. Frequency distribution of extinction risk by 2100 in (*Left*) observed and (*Right*) predicted studies of taxa: (*Top Left* and *Top Right*) plants, (*Middle Left* and *Middle Right*) invertebrates, and (*Bottom Left* and *Bottom Right*) vertebrates. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The dark bars (actual) and horizontal black lines (modeled) represent the frequency of studies with an extinction risk of zero or one. Data are scaled such that the total area of histogram bars and under the modeled extinction risk line is equal to one. *N* is the number of samples in each category.

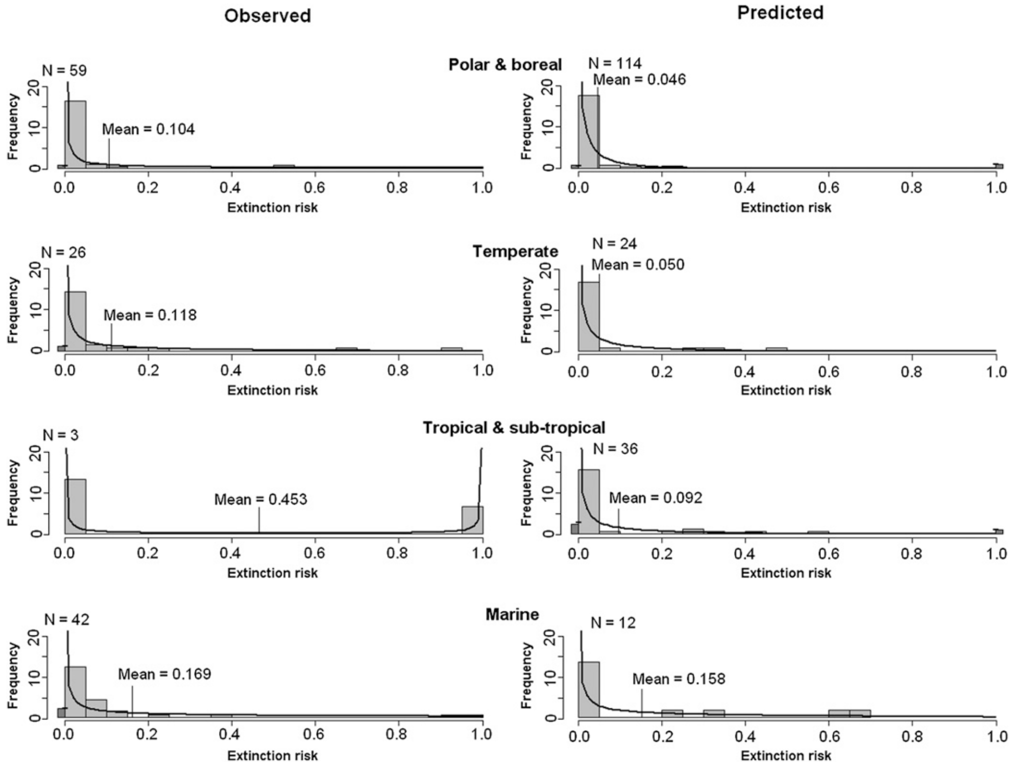

Fig. 3. Frequency distribution of extinction risk by 2100 in (*Left*) observed and (*Right*) predicted studies of ecoregions: (row 1) polar and boreal, (row 2) temperate, (row 3) tropical and subtropical, and (row 4) marine. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The dark bars (actual) and horizontal black lines (modeled) represent the frequency of studies with an extinction risk of zero or one. Data are scaled such that the total area of histogram bars and under the modeled extinction risk line is equal to one. *N* is the number of samples in each category.

nationally accepted decision tools in conservation biology (14, 18) and broad consistency between criteria was sought during their development (19), variation among species makes it difficult to validate the equivalence of thresholds for different criteria (20). Moreover, phylogenetic nonindependence of extinction risk could also reflect difficulties in assessments for poorly known taxa, with generally fewer experts and less data available (14). For example, the apparent low threat to invertebrates may partly reflect the lack of detailed understanding of climate threats facing most insects, with the majority of studies being on Lepidoptera (21). Direct predictions of extinction, as determined, for example, by population viability analyses, yielded higher estimates of extinction risk than estimates provided by changes in population and range size (Fig. S3). However, we suspect that this finding is primarily caused by these studies focusing on particularly endangered species. Our results were not unduly sensitive to the assumed relationship between range change, population change, and extinction risk (Table S3), suggesting that our overall estimates of extinction risk are relatively robust to any lack of equivalency among IUCN criteria. Furthermore, interactions between taxonomic group and method did not significantly affect estimates of extinction risk, suggesting that variation in the degree of difficulty in estimating extinction risk across categories is unlikely to invalidate our cross-taxonomic findings.

Estimated extinction risk was not related to the journal of publication or the time period over which observations were carried out or predictions were made. The sample size in each study could still influence the reliability of results, but we did not use formal metaregression techniques for two reasons. First, it was our intention to report means and variances in extinction risk across taxa rather than provide a single measure. Each estimate is derived from different taxa and could stem from any one of a number of different responses. Consequently, the effect being measured is not common across studies, and there is no reason to attribute a higher weighting to studies with larger sample sizes. Second, many studies do not report complete or comparable measures of uncertainty. Therefore, the use of metaregression to calculate the uncertainty in extinction risk across all studies would not be valid. Consequently, we attached the same weighting to all studies, irrespective of sample size. This weighting is unlikely to cause major bias in estimates of extinction risk, because there was no evidence of a consistent relationship of reported extinction risks with either sample size or the number of species studied (*SI Methods* and Fig. S3).

There are many unknowns when projecting declines in biodiversity, and the values here should be interpreted with caution. Nevertheless, our results were robust to publication, taxonomic, geographical, and impact-type biases, and assumed theoretical relationships between extinction risk, population decline, and range change. Furthermore, the degree of variance is also similar across observations and predictions, suggesting that predictions are not invalidated by methodological assumptions. Given that climate change is expected to accelerate and hence, exacerbate impacts, empirical evidence suggests that many predictions of extinction risk may be somewhat conservative. However, in terms of consistent phylogenetic and ecoregional patterns, the results suggest that realized ecological responses to climate change support predictions of future change. Our estimates of extinction risk are lower than previous estimates of the proportion of species committed to extinction by 2050 (1), but they are within the same order of magnitude. Moreover, commitment to extinction is not the same as extinction risk, because decades may elapse between habitat loss or climate change and the resultant species-level extinctions (22). Consequently, one would expect estimated extinction risk over a specified period to be lower.

Our results lend support to the contention, based on entirely different data and methods (1), that anthropogenic climate warming at least ranks alongside other recognized threats to global biodiversity. Based on published results, we endeavor to distinguish between responses to climate and other drivers of change, although in many cases, the mechanisms behind species responses to climate change are not known. Several studies suggest that changes to biotic interactions have led to increased extinction risk for at least one interacting species (10, 23). Habitat degradation (24), invasive species (25), and overexploitation (26) play additional roles, and interactions among these threats and climate change will increasingly threaten populations of species. In addition, rapid climate change has the potential to overwhelm the capacity for adaptation in many populations, reducing the ability to resist and recover from other environmental stressors (27). Our metaanalysis showing high predicted levels of extinction, backed up by consistent data for changes that have already occurred, shows the need to give climate change high priority in conservation planning and to communicate its potentially wide-ranging consequences to policy makers and the wider public.

Methods

Details of the studies and methods are provided in *SI Methods* and Table S1.

Selection of Studies. We reviewed 1,120 papers published from 2005 on in 10 leading journals focused on general science, ecology, or conservation. We searched all papers with climate change in the title, abstract, or keywords in *Biological Conservation*, *Conservation Biology*, *Ecological Applications*, *Ecology Letters*, *Journal of Applied Ecology*, *Nature*, *Proceedings of the Royal Society of London Series B Biological Sciences*, and *Science*, and all papers with climate change and biodiversity in *Global Change Biology* and PNAS. Those papers in which extinction probabilities, IUCN Red List categories, or a change in population size or range were reported were shortlisted for metaanalysis. We extracted data only from those articles in which changes could primarily be attributed to climate change or where climate was distinguished from other effects. From each paper, we recorded the taxon and number of species, the start and end of the study period, the type of climate change impact (changes in temperature and/or rainfall, ocean circulation patterns, ocean acidity, or sea ice, or responses to habitat change such as loss of habitat because of sea-level rise), and the number of spatial and temporal replicates. We also specified whether the response was observed or predicted. In all, we extracted data from 74 studies (32 observations and 42 predictions), providing 318 (130 observations and 188 predictions) taxon-specific climate change response estimates (*SI Methods* and Table S1).

Estimating Extinction Risk. We used IUCN Red List criteria to derive estimates of extinction risk from changes in population or range size, with a change in range size measured as the change in the area occupied. We assumed that a change in range is directly equivalent to a change in population size, an approach that is likely to give conservative estimates of population decline (28). Extinction risks can be standardized over any given period using multiple event probability theories (Eq. **1**):

$$E_s = 1-(1-E_t)^{\frac{s}{t}}, \qquad [1]$$

where E_s is the extinction probability of the desired time period s and E_t is the extinction probability over time period t. When extinction probabilities associated with each of the three IUCN Red List categories are standardized to 55.628 y and logit transforms are applied to ensure a continuous range of values, there is a perfectly linear relationship with the equivalent population size reductions over 10 y in each of the categories (Fig. S1). It is, thus, possible to infer extinction risk for any given change in population size, including increases. We also included studies where species had been assigned to IUCN Red List categories by assuming conservatively that their extinction risk corresponded to the threshold value for the category in which they had been placed. We assessed extinction risk over a 90-y period to give estimates for 2100. Full details of the method used to infer extinction risk from each study are given in Table S1. Because extinction estimates are constrained to values between zero and one and were zero- and one-inflated, estimates of the mean extinction risk for taxa and the proportion subject to varying degrees of extinction risk were derived by fitting a zero- and one-inflated β-error distribution to the data with a logit link function using the R (29) package GAMLSS (30).

To test for publication bias to studies that reported a high extinction risk, we examined the relationship between extinction risk and sample size. To test for researcher bias to species particularly threatened by climate change, we applied the same method using the number of species studied instead of sample size. There was no evidence of either researcher or publication bias (*SI Methods* and Fig. S2).

The potential effects of mean time of study, journal, and impact type on extinction estimates were assessed using a generalized linear model in R (29). All combinations of variables, including the null model, were tried, and the final model was selected using Akaike's Information Criterion (31). For both observed and predicted data, models in which impact type was included yielded the lowest Akaike's Information Criterion. We, thus, averaged across impact types to give a revised estimate.

To examine whether there were consistent taxonomic patterns across studies making predictions and empirical data, we subdivided our data into three major taxonomic groups: plants, invertebrates, and vertebrates. Bacteria, fungi, and taxa such as algae that were resolved to insufficient taxonomic detail were excluded from these analyses. To examine whether there were consistent ecoregional patterns across studies, we subdivided our data into four major ecoregions: (*i*) polar and boreal (ice sheets, tundra, and taiga), including studies of high altitude taxa at mid-latitudes, (*ii*) temperate (forest and steppe), (*iii*) tropical and subtropical, including xeric and Mediterranean habitats, and (*iv*) marine (all latitudes). Freshwater wetland taxa were assigned to the ecoregion in which the wetland was located. Studies spanning more than one ecoregion were excluded from these analyses.

Phylogenetic Relationships. A composite phylogeny of all study taxa was constructed using information contained in ref. 32, with branch lengths scaled to be approximately equal to time since divergence. Often, extinction estimates were for groups of species only, and in such instances, a dummy species was created that branched from the node encompassing all species within the group. Using the standardized normal residuals from the Generalized Linear Model (GLM) modeling, the mean residual value across all descendant terminal taxa was then calculated for each branch using the analysis of traits function in Phylocom 4.1 (33). The significances of branch values relative to the mean value across all terminal taxa were calculated by randomizing values for each taxon across all tips. To control for the extent to which particular taxa differed in terms of their extinction risk when calculating global estimates, the residual of the tip relative to the branch was added to the mean across all tips in instances where branches were significant. To test the robustness of our results to uncertainties associated with divergence time estimation, we also ran our analyses on the same tree but with branch lengths set to one. This change did not affect observed estimates of extinction risk, but predicted estimates increased from 6.1% to 6.5%.

Spatial Relationships. The geographical boundaries of all study sites from which extinction estimates were derived were mapped as polygons in ArcGIS 9.2 using a Cylindrical Equal Area projection (ESRI). The centroids of all study areas were then calculated, and spatial kriging with a spherical semivariogram model was performed using the Spatial Analyst tool in ArcGIS. Because it is not possible to define a projection that preserves true distances between all points on the globe, a North Pole Azimuthal Equidistant projection was used to perform spatial kriging in the northern hemisphere, and a South Pole Azimuthal Equidistant projection was used to perform spatial kriging in the southern hemisphere. The two hemispheres were then joined and converted back to a cylindrical equal area projection with a 1-km^2 resolution. The individual pixel values were then exported as an ASCII file, and a zero- and one-inflated β-error distribution with a logit link function was fitted to these data to estimate the mean extinction risk and the proportion of taxa subject to varying degrees of extinction risk.

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Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation
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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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USING CIRCUIT THEORY TO MODEL CONNECTIVITY IN ECOLOGY, EVOLUTION, AND CONSERVATION

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Abstract. Connectivity among populations and habitats is important for a wide range of ecological processes. Understanding, preserving, and restoring connectivity in complex landscapes requires connectivity models and metrics that are reliable, efficient, and process based. We introduce a new class of ecological connectivity models based in electrical circuit theory. Although they have been applied in other disciplines, circuit-theoretic connectivity models are new to ecology. They offer distinct advantages over common analytic connectivity models, including a theoretical basis in random walk theory and an ability to evaluate contributions of multiple dispersal pathways. Resistance, current, and voltage calculated across graphs or raster grids can be related to ecological processes (such as individual movement and gene flow) that occur across large population networks or landscapes. Efficient algorithms can quickly solve networks with millions of nodes, or landscapes with millions of raster cells. Here we review basic circuit theory, discuss relationships between circuit and random walk theories, and describe applications in ecology, evolution, and conservation. We provide examples of how circuit models can be used to predict movement patterns and fates of random walkers in complex landscapes and to identify important habitat patches and movement corridors for conservation planning.

Key words: circuit theory; dispersal; effective distance; gene flow; graph theory; habitat fragmentation; isolation; landscape connectivity; metapopulation theory; reserve design.

INTRODUCTION

Connectivity among habitats and populations is considered a critical factor determining a wide range of ecological phenomena, including gene flow, metapopulation dynamics, demographic rescue, seed dispersal, infectious disease spread, range expansion, exotic invasion, population persistence, and maintenance of biodiversity (Kareiva and Wennergren 1995, Ricketts 2001, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Moilanen et al. 2005, Crooks and Sanjayan 2006, Damschen et al. 2006, Fagan and Calabrese 2006). Preserving and restoring connectivity has become a major conservation priority, and conservation organizations are investing considerable resources to achieve these goals (Beier et al. 2006, Kareiva 2006).

Understanding broad-scale ecological processes that depend on connectivity, and making effective conservation planning decisions to conserve them, requires quantifying how connectivity is affected by landscape features. Thus, there is a need for efficient and reliable tools that relate landscape composition and pattern to connectivity for ecological processes. Many ways of predicting connectivity using landscape data have been developed (reviewed by Tischendorf and Fahrig 2000*a*, *b*, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Fagan and Calabrese 2006). Common approaches include the derivation of landscape pattern indices (e.g., Schumaker 1996), individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005), and analytic measures of network connectivity, such as graph theory and least-cost path models (Keitt et al. 1997, Urban and Keitt 2001, Adriaensen et al. 2003, Minor and Urban 2007). The latter have gained increasing attention in recent years and are widely

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applied in connectivity modeling and in conservation planning.

We propose that connectivity models from electrical circuit theory can make a useful addition to the approaches available to ecologists and conservation planners. Circuit theory has been applied to connectivity analyses in chemical, neural, economic, and social networks, and has recently been used to model gene flow in heterogeneous landscapes (McRae 2006, McRae and Beier 2007). The same properties that make circuit theory useful in these fields hold promise for ecology and conservation as well. Because connectivity increases with multiple pathways in circuit networks, distance metrics based on electrical connectivity are applicable to processes that respond positively to increasing connections and redundancy. Additionally, previous work has shown that current, voltage, and resistance in electrical circuits all have precise relationships with random walks (Doyle and Snell 1984, Chandra et al. 1997). These relationships mean that circuit theory can be related to movement ecology via random-walk theory, providing concrete ecological interpretations of circuit-theoretic parameters and predictions. Finally, because algorithms to implement circuit models are well developed, they can be applied to large networks and raster grids.

Here we present several ways in which circuit theory can be used to model connectivity in ecology and conservation. We describe ecological applications of previously developed theory relating resistance, current, and voltage in electronic circuits to random walks on analogous graphs (Doyle and Snell 1984, Klein and Randic 1993, Chandra et al. 1997). This theory can be applied to predict movement patterns and probabilities of successful dispersal or mortality of random walkers moving across complex landscapes, to generate measures of connectivity or isolation of habitat patches, populations, or protected areas, and to identify important connective elements (e.g., corridors) for conservation planning. Our approach does not require new ways of representing landscape data; rather, it takes advantage of graph-theoretic data structures, which are already familiar to many ecologists, and can be applied in traditional graph-theoretic or raster GIS frameworks. Coupled with applications of circuit theory to predict equilibrium patterns of gene flow (McRae 2006, McRae and Beier 2007), these new applications comprise a modeling framework that integrates spatial aspects of ecology, evolution, and conservation.

BASIC CONCEPTS

Graph data structures and terminology

Connectivity models from circuit theory are applied to *graphs* (Harary 1969), so we will use the terminology of graph theory here (see Urban and Keitt 2001 for a review). Briefly, graphs are networks comprised of sets of *nodes* (connection points which represent, e.g., habitat patches, populations, or cells in a raster landscape) connected by *edges* (Fig. 1). Edges reflect functional connections, such as dispersal, between nodes. The *weight* of each edge typically corresponds to the strength of the connection (e.g., the ease of movement or number of dispersers exchanged) between the nodes it connects.

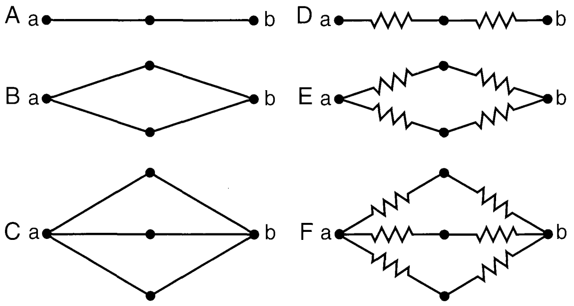

FIG. 1. Three graphs at left (A, B, C), with edge weights of 1. Traditional shortest path or geodesic distance, *d*, between nodes a and b is identical ($d = 2$) all three cases. At right (D, E, F), edges have been replaced with unit resistors to create analogous circuits. Effective resistance, $\hat{R}$, measured between nodes a and b decreases from top to bottom ($\hat{R} = 2$, 1, and 2/3, respectively), reflecting additional contributions from multiple pathways (figure modified from Klein and Randic [1993]).

Circuit theory

In this paper, circuits are defined as networks of nodes connected by *resistors* (electrical components that conduct current) and are used to represent and analyze graphs (Fig. 1). The basic concepts of resistance, conductance, current, and voltage all apply, and their definitions and ecological interpretations are summarized in Table 1. Recall Ohm's law, which states that when a voltage V is applied across a resistor, the amount of current I that flows through the resistor depends on (1) the voltage applied and (2) the resistance R, such that $I = V/R$. The lower the resistance (or the higher the conductance, G, which is simply the reciprocal of resistance), the greater the current flow per unit voltage. Similarly, when a voltage is applied across two nodes in a resistive circuit (e.g., between nodes a and b in the circuits shown in Fig. 1), the total amount of current that flows across the circuit is determined by (1) the voltage applied and (2) the configuration and the resistances of the resistors the circuit contains. The *effective resistance* ($\hat{R}$) between the nodes is the resistance of a single resistor that would conduct the same amount of current per unit voltage applied between the nodes as would the circuit itself, i.e., $\hat{R} = V/I$.

In simple circuits, such as those shown in Fig. 1, effective resistance can be calculated using some basic rules. First, two resistors connected in series may be replaced by a single resistor with a resistance is that the sum of the two resistances. Thus, the effective resistance in the top circuit in Fig. 1D would be $\hat{R} = R_1 + R_2 = 2$ ohms. Conversely, connecting resistors in parallel decreases their effective resistance, such that they may be replaced by a single resistor whose conductance is

TABLE 1. Electrical terms and their ecological interpretations.

Electrical term (symbol, unit)	Ecological interpretation
Resistance (R, ohm), the opposition that a resistor offers to the flow of electrical current.	Opposition of a habitat type to movement of organisms, similar to ecological concepts of landscape resistance or friction. Graph edges or grid cells allowing less movement are assigned higher resistance.
Conductance (G, siemens), inverse of resistance and a measure of a resistor's ability to carry electrical current.	Analogous to habitat permeability. In random-walk applications, it is directly related to the likelihood of a walker choosing to move through a cell or along a graph edge relative to others available to it. In population genetic applications (see McRae 2006), it is a measure of migrants exchanged between neighboring populations.
Effective resistance ($\hat{R}$, ohm), the resistance to current flow between two nodes separated by a network of resistors.	Also known as the *resistance distance*, a measure of isolation between pairs of nodes on a graph or cells on a raster grid. Similar to ecological concept of effective distance, but it incorporates multiple pathways (Fig. 1D–F). It scales linearly with equilibrium genetic differentiation in population genetic applications.
Effective conductance ($\hat{G}$, siemens), inverse of effective resistance, a measure of a network's ability to carry current between two nodes.	A measure of connectivity between pairs of nodes on a graph or cells on a raster grid. It increases with additional available pathways and scales linearly with effective migration in population genetic applications.
Current (I, ampere), flow of charge through a node or resistor in a circuit.	Current through nodes or resistors can be used to predict expected net movement probabilities for random walkers moving through corresponding graph nodes or edges (Fig. 2).
Voltage (V, volt), the potential difference in electrical charge between two nodes in an electrical circuit. Related to current and resistance by $V = IR$.	Voltages can be used to predict the probability that random walkers leaving any point on a graph will reach a given destination (representing, e.g., successful dispersal) before another (representing, e.g., mortality; Fig. 3).

given by the sum of the conductances of the two resistors, that is, $\hat{G} = G_1 + G_2$. (In terms of resistance, these quantities are given by: $\hat{R} = R_1R_2/[R_1 + R_2]$.) Applying these equations to the circuits shown in Fig. 1, the effective resistance declines from the top to the bottom circuit.

Applying circuit theory to graphs involves preserving the same graph structure with interconnected nodes, but replacing graph edges with resistors, as in Fig. 1. The conductance of each resistor is typically a function of the corresponding edge weight or probability of movement between the pair of nodes it connects. The resistance of a resistor is the reciprocal of its conductance and can be thought of as representing isolation or movement cost between nodes.

INTERPRETATION OF RESISTANCE, CURRENT, AND VOLTAGE

Resistance and conductance

The simplest connectivity measure from circuit theory is the *resistance distance* (Klein and Randic 1993), a distance metric defined as the effective resistance between a pair of nodes when all graph edges are replaced by analogous resistors (as in Fig. 1D–F). A convenient property of the resistance distance is that it incorporates multiple pathways connecting nodes, with resistance distances measured between node pairs decreasing as more connections are added. Hence, the resistance distance does not reflect the distance traveled or movement cost accrued by a single individual. Rather, it incorporates both the minimum movement distance or cost and the availability of alternative pathways. As additional links are added, individuals do not necessarily travel shorter paths, but have more pathways available to them. For example, in the three graphs in Fig. 1A–C, the minimum distance required to travel from node a to b (called geodesic distance in graph theory) is the same. However, the resistance distance decreases as more connections are added, reflecting increased flow capacities and levels of redundancy. In short, the resistance distance is small when two nodes are connected by many paths with low resistance (high conductance) edges and large when there are few paths with high resistance. Resistance distances can be calculated across irregular networks or with continuous landscape data, which are typically represented as discretized lattices or grids. On continuous surfaces, the resistance distance increases linearly with Euclidean distance in homogeneous one-dimensional habitats and with its log transformation in two-dimensional habitats, a property important for modeling gene flow (McRae 2006).

Resistance distances can also be related to random-walk times between nodes. For the theory and examples that follow, we assume that conductances are chosen so that the probability of moving from a node along any given edge is equal to the conductance assigned to the edge divided by the sum of the conductances of all edges connected to the node. For an organism moving through a habitat network (the main focus of this paper), this would correspond to a scenario where the individual chooses to move along an edge in proportion to the edge's conductance, a surrogate for habitat quality or (inverse) perceived risk, relative to the quality of all other choices of direction; this choice is then repeated at each subsequent step. For genes moving across a network of populations over many generations, this would correspond to a scenario where edge conductances correspond to per-generation migration rates (McRae 2006).

Chandra et al. (1997) showed that, when resistors are parameterized in this way, the resistance distance between a pair of nodes is precisely related to the *commute time* between the nodes, i.e., the expected time for a random walker to move from one node to the other and back again. The commute time between any pair of nodes u and v can be calculated using the following formula:

$$\text{Commute time} = \hat{R}_{uv}\sum_{x=1}^{n}\sum_{y=1}^{n}(1/R_{xy}) \qquad (1)$$

where R_{xy} is the resistance of the resistor connecting nodes x and y and n is the number of nodes in the network. Note that Eq. 1 accommodates resistors connecting a node to itself, which would reflect a nonzero probability of staying at the node for any time step. Chandra et al. (1997) also provided formulas to calculate a commute *cost*, if there is a cost imposed for each step that is independent of the resistance (and thus independent of the behavior of a random walker). An interesting result of Eq. 1 is that if the goal is to minimize commute times between a pair of nodes, there is a penalty for adding connections which is offset by the degree to which the new connections help to lower effective resistance between the two nodes. Within a fixed network, commute times between different pairs of nodes will be directly proportional to the effective resistances measured between them. Another potentially useful way to apply resistance calculations across graphs is to compute upper and lower bounds for the *cover time*, or the expected number of steps of a random walk visiting all nodes in the graph (Chandra et al. 1997).

"Functional" or "effective" distance.—Used as an ecological distance metric, the resistance distance provides a conceptual complement to commonly used least-cost distances in two important ways. First, it integrates all possible pathways into distance calculations, whereas least-cost distances are measured along a single optimal pathway. Second, it offers a measure of isolation assuming a random walk, whereas least-cost distances presumably reflect the route of choice if a disperser has complete knowledge of the landscape it is traversing.

The resistance distance also provides a quantitative complement to least-cost distances. If only a single pathway between two nodes is available (e.g., in Fig. 1A or in any graph that is a tree), the resistance distance will equal the least-cost distance. On the other hand, when two identical and independent pathways connect a pair of nodes in parallel, the resistance distance will be half the least-cost distance. This suggests an interpretation of the resistance distance as an indicator of redundancy in connections relative to the least-cost distance:

$$\text{Redundancy} = (\text{least-cost distance})/(\hat{R}).$$

Thus, the two measures can be compared directly, their ratio providing a rough measure of parallel pathways available to dispersers.

The relationship between resistance distances and commute times is one way to link circuit and ecological theories and is the basis of using resistance distances to predict patterns of gene flow and genetic structuring in heterogeneous landscapes (McRae 2006). Calculating commute times directly may provide valuable additional information because commute times take into account how efficiently a given landscape configuration will channel dispersal between source and destination nodes. Additional pathways that primarily result in increased wandering behavior rather than directed movement may reduce resistance distances but will increase commute times. Low commute times and low resistance distances between pairs of nodes indicate that dispersers will be efficiently directed between them.

Current

Currents in circuits can also be interpreted in terms of random walks on corresponding graphs. Consider again a graph in which the probability that a random walker will move from a node along any graph edge is proportional to its conductance. Doyle and Snell (1984) showed that when 1 A (ampere) of current is injected into one node (node a in Fig. 2A) and a second node (node e) is tied to ground, the current i_{xy} flowing through the resistor connecting any pair of nodes x and y is equivalent to the expected net number of times that a random walker, starting at a and walking until it reaches e, will move along that branch. Because we are tallying net passages through the branch, movements from x to y are counted as positive, whereas movements from y back to x are counted as negative.

Corridor identification and dispersal predictions.—By predicting net movement probabilities along branches or through nodes, current density can be used to identify landscape corridors or "pinch points," i.e., features through which dispersers have a high likelihood (or necessity) of passing. High current through a node or branch indicates that removing or converting it will have a high impact on connectivity. In Fig. 2, all the current passes through node b; removing that node (or the link between nodes a and b) would completely disconnect nodes a and e, whereas removing node c, through which only half the current passes, would reduce redundancy but would still leave nodes a and e connected via the lower branch. In graph terminology, node b is a *cutnode*, and the resistor connected nodes a and b is a *cutlink*.

Voltage

Doyle and Snell (1984) also showed that voltage can be related to random walk probabilities. Consider a graph in which a voltage source set to 1 V is connected to one node (or to a set of nodes), and another node (or set of nodes) is connected to ground (Fig. 3). The voltage measured at any remaining node on the graph will equal the probability that a random walker, starting at that

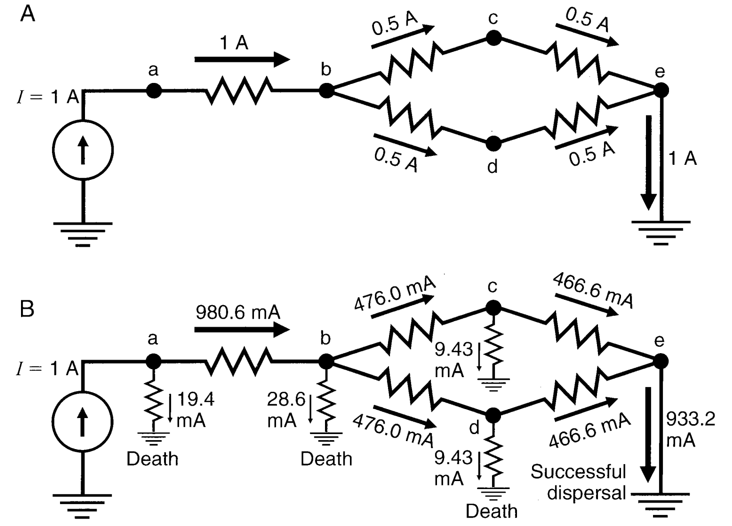

FIG. 2. (A) A simple circuit, with a 1-A (ampere) current source (I) placed at node a, and with node e tied to ground. Branch currents that would be observed with unit resistors are shown and reflect the net number of times that a random walker, starting at node a, is expected to pass along each branch before reaching node e. All random walkers must pass across the first branch, but half would be expected to take the upper pathway, and half the lower. Resistances connecting nodes were set to 1 ohm for this simple example; the methods we describe here can accommodate heterogeneous resistances with values from 0 to infinity. (B) The same circuit as in (A), but with ground resistors added to reflect a 1% probability of mortality as the random walker passes through each node. To achieve this, resistances to ground for nodes a–d were set to 99, 33, 49.5, and 49.5 ohms, respectively. Currents show the expected number of net movements along each branch, as well as the expected number of deaths at each node. For example, the proportion of dispersers leaving node a expected to successfully reach node e is 0.9332 (933.2 mA equivalent). Deaths at each node exceed 1% because nodes are visited multiple times by random walkers, with the highest numbers of deaths observed in nodes with the highest numbers of visits. Only one possible dispersal destination was included here, but the method can accommodate as many dispersal destinations as desired. Although we tied the destination node directly to ground, resistors could be added between destination nodes and ground, with their conductances set to reflect a finite probability that a walker would settle rather than continue walking once reaching a node.

node, will reach any of the nodes set to 1 V before reaching any node connected to ground. The most obvious application of this property is to predict the probability of successful dispersal via a random walk from any node on a graph. Suitable destination patches for dispersal can be set to 1 V, whereas mortality can be represented by resistors connected to ground, with their conductances reflecting probabilities of mortality (Fig. 3).

APPLYING CIRCUIT ANALYSES TO RASTER GRIDS

Predicting connectivity using circuit theory requires translating spatial data sets into a graph structure, but that doesn't mean that primary landscape data must be in a patch-based or network-style format. In fact, we envision most landscape applications operating on raster data, with a graph extracted from these data as is done for least-cost path analyses (Adriaensen et al. 2003). Since well-developed computer algorithms allow millions of cells to be processed, large raster landscapes can be accommodated.

Analyzing a raster grid involves first assigning resistances to different habitat types in the grid. Fig. 4 shows a simple example with three different habitat types: assigned unit, infinite, and zero resistance. The last is useful when practitioners wish to measure connectivity or identify important connective elements between areas (representing, for example, habitat patches or reserves), rather than points on a landscape. To represent a grid as a circuit, cells with finite resistances are converted to nodes (gray), whereas cells with infinite resistance (i.e., those representing complete barriers, black) are dropped. Adjacent nodes are connected by resistors, with resistances reflecting a function (typically the mean) of the resistances of the cells they connect. Adjacent cells with zero resistance (open) are consolidated into a single node that is then connected by resistors to all nodes adjacent to the zero-resistance patch. Following this procedure, the 16-cell

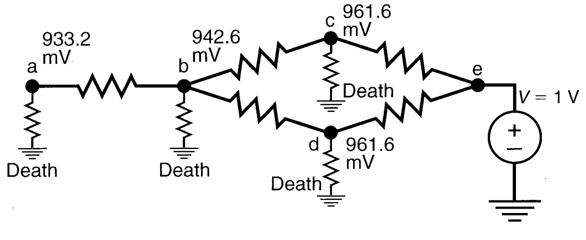

FIG. 3. The same circuit shown in Fig. 2B, but with a voltage source (V) of one volt at node e instead of a current source at node a. Node voltages reflect the probability that a random walker, starting at each node, will successfully reach node e. Consistent with the result from Fig. 2B, the probability of successful dispersal from node a to node e is 0.9332.

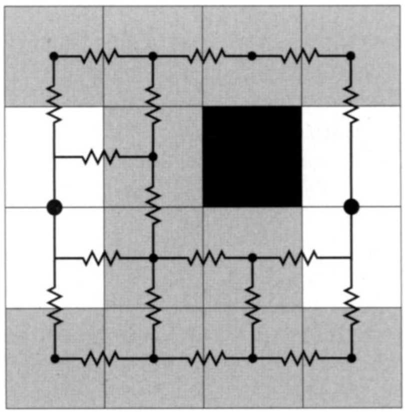

FIG. 4. A simple landscape represented as both a grid and a circuit. The landscape contains two contiguous patches of 0-resistance cells (open), dispersal habitat of finite resistance (gray), and one "barrier" cell with infinite resistance (black). Cells with finite resistance are replaced with nodes (small dots), and adjacent nodes are connected by resistors. Patches of cells with 0 resistance are each consolidated into a single node (large dots). Connections between diagonal neighbors and nonadjacent cells can also be incorporated, the latter representing "hops" over intervening cells. Current sources, voltage sources, and ground connections can be added as in Figs. 2 and 3.

grid in Fig. 4 is now represented as a circuit with 13 nodes and 18 resistors.

COMPUTATION

Although simple circuits can be solved by hand, *nodal analysis* is typically used to analyze larger circuits, such as those derived from raster grids (McRae 2006). Given a circuit with current or voltage sources, nodal analysis uses Kirchoff's and Ohm's laws in matrix form to solve for a vector, specifying voltages at each node; once these are known, Ohm's law can be used to calculate currents passing through individual resistors or nodes. Effective resistance between a pair of nodes is given by the voltage between them when one is connected to a 1-A current source and the other is connected to ground (e.g., Fig. 2A). The method is described in standard circuit theory textbooks (e.g., Dorf and Svoboda 2003); an example of its use to calculate effective resistances is provided by McRae (2006).

Computer languages used for scientific computing such as Java, C, MATLAB, and Python include linear solver routines that can solve for effective resistances on graphs. Fast graph operations can be used to define connected components in a landscape and discard from a graph any components that are completely isolated. Very large graphs can be processed relatively easily and efficiently; we have solved for effective resistances, voltages, and current on landscapes containing over 1 million cells using Java (Sun Microsystems, Mountain View, California, USA), and up to 48 million cells using a parallel version of MATLAB (MathWorks, Natick, Massachusetts, USA) implemented using Star-P (Interactive Supercomputing, Waltham, Massachusetts, USA). Solving 1 million cells on a notebook computer with a 2-GHz processor and 2 GB of RAM took us 16 minutes using Java and only 20 seconds using MATLAB. This calculation must be repeated for each configuration of current sources and grounds, but typical connectivity applications will require a small number of calculations (e.g., for each pair of populations or reserves between which connectivity is to be modeled). Calculations between multiple pairs can be sped up considerably using matrix preconditioning and/or parallel processing. Software implementing many of the algorithms in this manuscript is available (B. H. McRae, *unpublished data*).

EXAMPLE APPLICATIONS TO HETEROGENEOUS LANDSCAPES

Here we provide examples of the applications described above to predict connectivity and movement of random walkers across large raster grids. For the example analyses described next, we solved for effective resistances and node currents using code written in MATLAB R2007b. The example landscapes (i.e., resistance surfaces) were all created using ArcView GIS 3.2 (ESRI, Redlands, California, USA) and exported as ASCII raster grids, with cell values corresponding to resistances ranging from 0 to infinity (Fig. 5). For circuit analyses, cells with finite resistances were converted to nodes, whereas those with infinite resistances were dropped. Cells were connected to their eight neighbors such that the resistance between a pair of first-order neighbors was set to the mean of the two cells' resistances, and the resistance between a pair of second-order (diagonal) neighbors was set to the mean resistance multiplied by the square root of 2 to reflect the

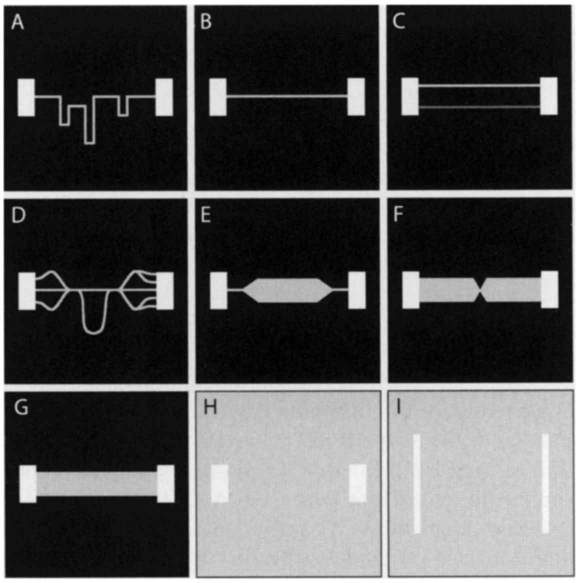

FIG. 5. Nine simple raster landscapes (A–I), consisting of 1000 × 1000 cells. Habitat patches (shown in white and assigned 0 resistance, or infinite conductance) are connected by different configurations of dispersal habitat (light gray, 10 ohms/cell; dark gray [lower corridor in panel C], 20 ohms/cell; black = infinite resistance or 0 conductance).

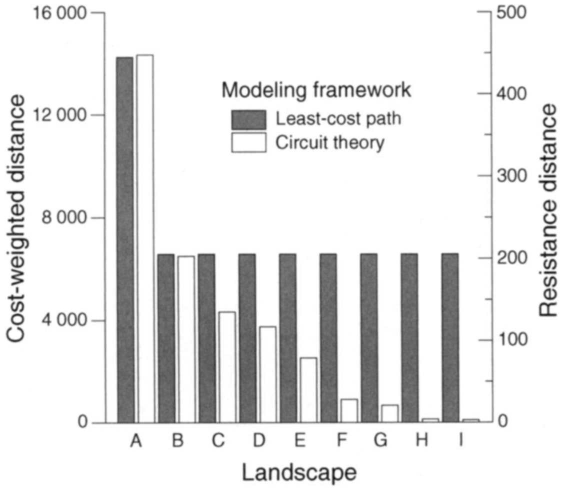

FIG. 6. Least-cost distances and resistance distances between habitat patches for the nine simple landscapes shown in Fig. 5. Least-cost distances decrease from (A) to (B) but are equivalent for all remaining maps. Effective resistances decrease not only from (A) to (B), but also from (B) to (I), reflecting the availability of more and wider pathways. Redundancy, defined here as the ratio of least-cost distance to effective resistance, would be roughly equal for cases (A) and (B) but would increase from (B) to (I). Cost-weighted distance (measured in cost units) were calculated using PATHMATRIX software. Resistance distances (measured in ohms) were calculated using Circuitscape software.

greater distance between cell centers. We converted individual cells to single nodes, except for cells in areas of zero resistance, i.e., open source/target patches; as in the simple landscape in Fig. 4, these cells were considered collectively and consolidated into a single node for the analyses. For all examples, we used the same resistance surfaces to calculate least-cost distances and map least-cost corridors using PATHMATRIX software (Ray 2005).

We started with nine simple landscapes (Fig. 5) meant to illustrate different properties of circuit models. The landscapes consisted of 1000 × 1000 cells each and contained two primary habitat patches, which were always the same distance from one another and always occupied the same total area. Least-cost and resistance distances calculated between habitat patches in the nine simple landscapes illustrate some advantages of the resistance distance (Fig. 6). Although least-cost distances correctly identify decreased isolation between habitat patches in landscape B relative to A, they were identical in landscapes B through I. Resistance distances show a similar decrease from landscape A to B, but they also decrease from B to I, reflecting the availability of additional, or wider, pathways. Note that between landscapes H and I, only the shape of the primary habitat patches has changed, and not their area or the distance separating them. Yet the resistance distance differs because the greater surface area of each habitat patch in landscape *I* acts as a "drift fence" to better intercept or release dispersers.

Commute times ranged from 1.2 million steps (landscapes B, C, and G) to 6.2 million steps (landscape A). They were intermediate for landscapes D, E, F, H, and I, which had commute times of 2.6, 3.0, 1.6, 2.7, and 2.0 million steps, respectively. Lower commute times reflect configurations in which dispersers are efficiently channeled between habitat patch pairs, minimizing wandering time.

These same simple landscapes also demonstrate how current maps (Fig. 7) can highlight connective elements in raster frameworks. As the availability of multiple pathways increases, current density—indicating cells through which dispersers are likely to pass moving from one patch to the other—decreases. Pinch points are highlighted in landscapes D–F, and the "drift fence" effect resulting from the more linear shape of the habitat patches in landscape I is evident as well. Fig. 7J shows a least-cost path map for the "braided stream" corridor configuration. The technique identifies the route with the lowest cumulative cost, but gives no information about the contribution of alternative pathways. By contrast, the current map (Fig. 7D) clearly indicates the importance of different corridor segments, with current densities at their highest in the two critical linkages and at their lowest in segments that are most redundant.

We can now illustrate how these models can be used to analyze connectivity in more realistic landscapes. Fig. 8A shows a complex landscape, with patches of high-quality habitat, lower quality "matrix" habitat, corridors, and complete barriers. Fig. 8B shows cumulative travel cost mapped between two high-quality patches using standard least-cost path techniques. The map highlights the most efficient pathway between the two patches, as well as low-cost detours that do not actually contribute to connectivity, e.g., into habitat cul-de-sacs or along "corridors to nowhere." By contrast, the current map between the same two habitat patches (Fig. 8C) highlights critical pinch points between the two patches. Habitat cul-de-sacs and corridors that do not contribute to connectivity have minimal current flow. The current map also indicates two broad routes linking the habitat patches, whereas only one is highlighted in the least-cost map. The current map thus gives important insight into the redundancy that would be lost if the second route were to be blocked.

Often it will be useful to summarize connectivity between many habitat patches or protected areas in a single map. Fig. 9A shows the result of adding 10 pairwise current maps calculated among all pairs of five habitat patches. These maps show which landscape elements are most important for overall connectivity among the five habitat patches, indicating the net number of times random walkers are expected to move through raster cells if one random walker moves from each patch to each other patch.

We could also extend the analyses of our raster maps in much the same way as the analyses in Fig. 2A were extended in Figs. 2B and 3. Ground resistors could be added to incorporate mortality or finite probabilities of

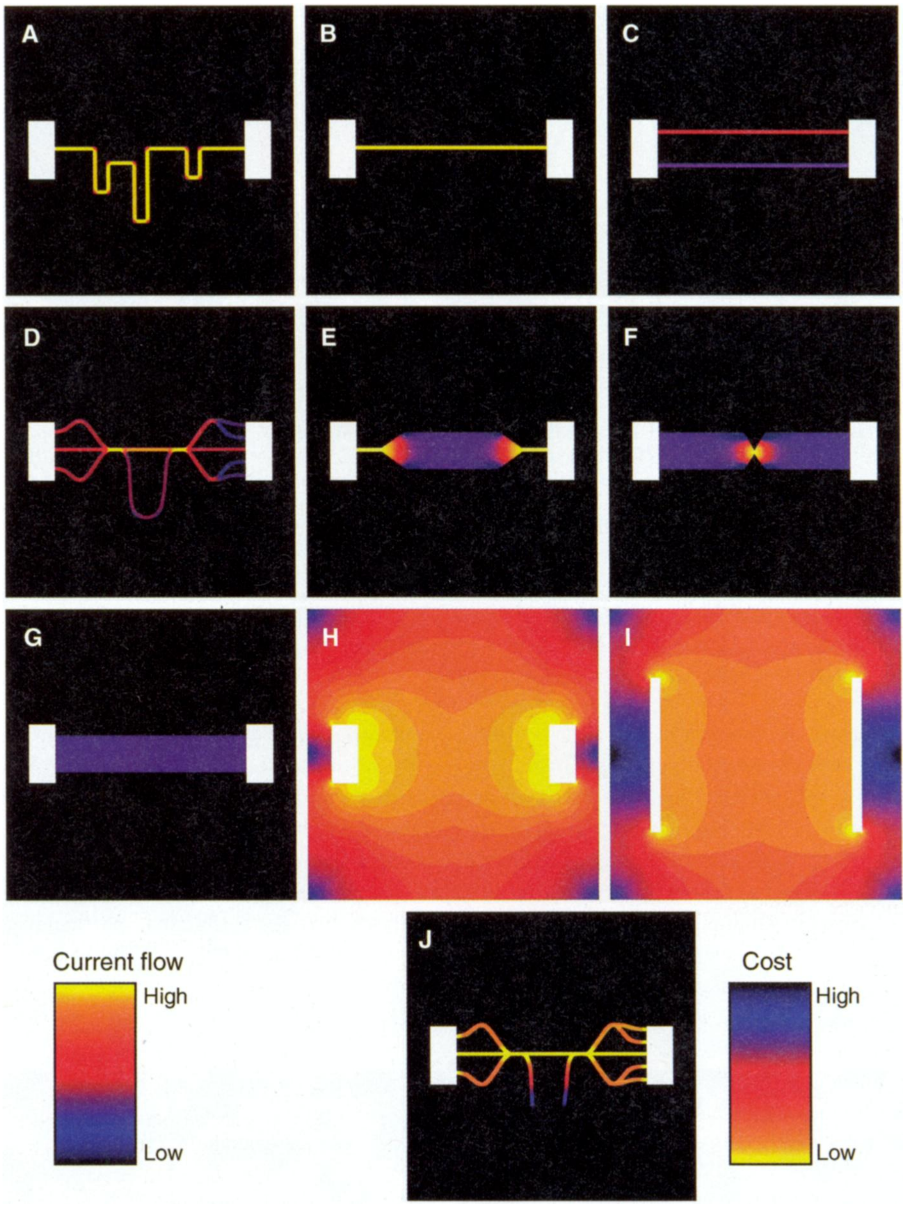

FIG. 7. Current flow through landscapes shown in Fig. 5 when 1 A (ampere) of current is injected into one habitat patch and the other is connected to ground. Current maps were log-transformed to facilitate display. Among the nine panels, three different quantitative scales are applied to the color schemes in order to most clearly illustrate differences in current densities. The three schemes are applied in panels (A)–(D), (E)–(G), and (H)–(I). Highest maximum current densities (indicating the greatest impact of habitat cell removal or conversion) are observed in (A), (B), and (D)–(E), where connectivity depends on single, narrow corridor segments. The lowest maximum current densities are observed in landscape (I), which provides the most redundancy and lowest effective resistance. This landscape also exhibits a drift-fence effect, in which the linear shapes of the habitat patches act to intercept dispersing individuals. (J) The least-cost path solution of the "braided stream" landscape shown in Fig. 5D. Whereas this technique highlights the most efficient travel path, it gives no indication of pinch points or effects of multiple parallel corridors.

settling once a disperser reaches a habitat patch or protected area. With multiple destination patches, a matrix of asymmetrical dispersal rates between all patch pairs could be generated. Or, target patches could be set to 1 V and probabilities of successful dispersal (or dispersal to one patch vs. others) from any point on the landscape could be mapped. Finally, additive maps (such as the one shown in Fig. 9A) could be adjusted to give greater weight to important source or destination patches, with more current released or absorbed by larger or higher quality habitat patches.

Model sensitivity to landscape scale

Representing a landscape as a raster grid always involves choosing an appropriate scale of analysis (cell size and map extent). Because different species respond

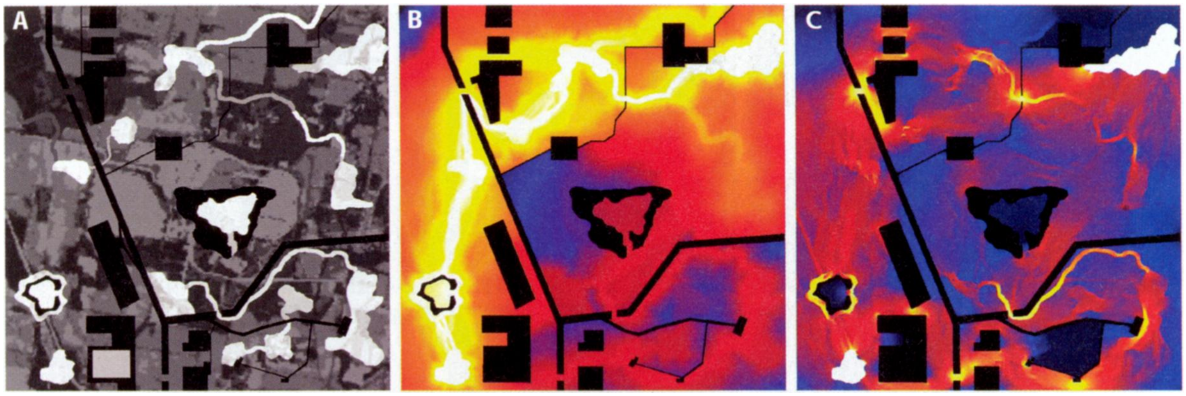

FIG. 8. Connective elements identified using least-cost path and circuit models in a complex landscape. (A) Map of the landscape, with resistances and costs for circuit and least-cost path analyses ranging from 1 (light gray) to 100 (dark gray) to infinite (black). (B) Results from least-cost modeling between habitat patches in lower left and upper right corners of the map. The value assigned to each cell indicates the cost accumulated moving along the most efficient possible route that passes through the cell from one habitat patch to the other; brighter areas indicate cells along the route of lowest cumulative cost. Some habitat cul-de-sacs are highlighted because the most efficient path connecting one patch to the other via the cul-de-sac has a low cost relative to most other features in the landscape. For the same reason, some "corridors to nowhere" are highlighted, such as the one leading off of the top of the map. (C) Current map between the same two habitat patches. Higher current densities indicate cells with higher net passage probabilities for random walkers moving from one patch to the other. The map highlights "pinch points," or critical habitat connections, between the two patches. Habitat cul-de-sacs have minimal current flow because they do not contribute new, independent pathways between habitat patches.

to landscape structure at different scales (Wiens 1985, Wiens and Milne 1989; Beier et al., *in press*), there will be no single correct approach to this. The extent of an analysis will obviously have important consequences, since map edges will constrain potential movement routes. Cell size is also important, but our analyses indicate that as long as it remains fine enough to capture relevant landscape elements, such as narrow corridors and barriers, there is considerable robustness in the technique to changes in cell size. Fig. 9B shows the same landscape as in Fig. 9A, but analyzed using cell sizes that are an order of magnitude larger. Notably, current densities and resistance distances calculated among habitat patches are highly correlated between the two scales, a consistent result in our analyses in a wide range of natural and artificial landscapes. However, these analyses also show that it is particularly important to capture absolute barriers to movement that may not easily be detected at coarser cell sizes. Such barriers (such as the narrow roads in Fig. 9A) were automatically

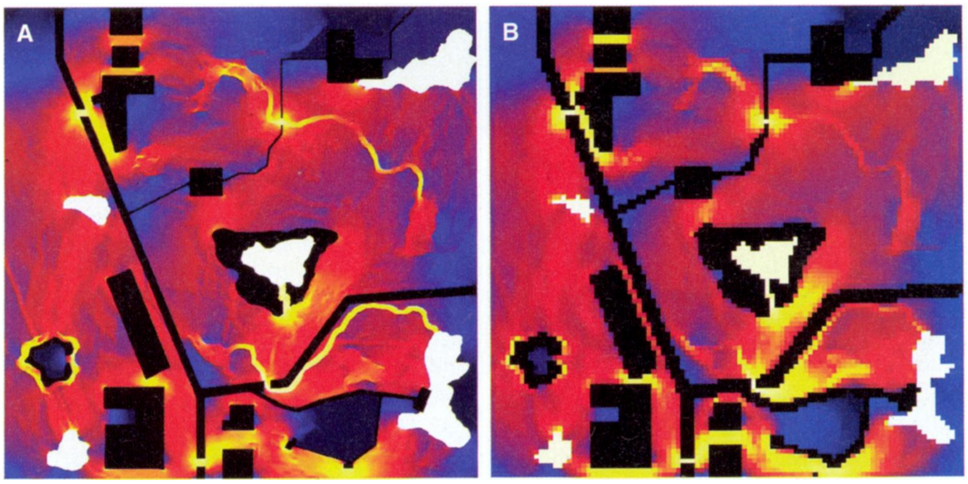

FIG. 9. Summed current from all pairwise current maps between five habitat patches, each shown in white. Calculations were performed (A) at the original 1000 × 1000 cell resolution and (B) at a reduced 100 × 100 cell resolution. To produce the coarser resolution habitat map, blocks of 10 × 10 cells were converted to single cells, with the resistance of each new cell set equal to the mean resistance of the 100 cells it contained. The current maps at the two resolutions identify the same pinch points and important corridors, and pairwise effective resistances measured between all habitat patch pairs at the two scales are highly correlated ($R^2 = 0.963$), illustrating the method's robustness to scale.

Plate 1. Puma mother and kitten in Caspers Wilderness Park, Orange County, California. Cirtuit theory is being applied to inform efforts to conserve connectivity for pumas in the region. Photo credit: Donna Krucki.

incorporated into our analyses in Fig. 9B because we averaged resistances among consolidated cells, with infinite resistances "trumping" all others.

Discussion

Although a wide variety of methods exists for predicting connectivity across landscapes, circuit-theoretic models provide some distinct advantages. First, the precise relationships between circuit theory and random walks lend theoretical justification to these models and mean that the metrics they generate can genuinely be considered to be process based. Second, these relationships also mean that circuit models will often be more straightforward to parameterize than other connectivity models because conductances and resistances assigned to edges or raster cells have clear interpretations in terms of movement probabilities. Third, unlike commonly applied least-cost path approaches, circuit methods incorporate multiple pathways, not only in generating metrics of connectivity and isolation, but also in identifying corridors and other important landscape elements connecting habitat patches or protected areas. An advantage of this property is that when dispersal pathways are lost, the predicted importance of remaining pathways increases. Finally, circuit models have an intuitive appeal in that the idea of using resistance and current to model connectivity across landscapes is readily understood by both practitioners and nonscientists. In effect, we find that the method objectively identifies important connective elements similar to those identified by the human eye, replicating expert opinion but removing potential sources of bias once relative resistance values and scales of analysis have been defined.

Niches for circuit models

We envision several roles for circuit theory in evolution, ecology, and conservation. Circuit theory has already been shown to be useful for predicting patterns of gene flow in heterogeneous landscapes, particularly when data on absolute population sizes and migration rates are lacking, but relative population densities or permeabilities to movement are hypothesized for different landscape features (McRae 2006, McRae and Beier 2007). As discussed in the section below, the theory underlying gene flow modeling is similar to that described here, but relates resistance distances to random walks of genes over multiple generations rather than to random walks of individuals within single lifetimes.

In ecology, circuit models can be used as simple movement models, e.g., when data or time required for simulations are lacking or when the comparison of simple and complex model predictions is desirable. An example application would be to predict dispersal rates between populations based on simple landscape data in order to parameterize metapopulation models. Additionally, just as it can be used to predict gene flow, circuit theory may be useful in modeling other emergent processes that depend on dispersal. Some ecological phenomena, e.g., community similarity and diversity, may respond to dispersal not of one species, but of several species with only somewhat similar dispersal abilities or habitat requirements. Here, simulations may be prohibitive or inappropriate because of the large number of species involved. However, analytic approaches like ours may be able to adequately capture these processes without imposing prohibitive data or computational requirements.

Measurements of resistance distances, commute times, and current densities have clear applications in conservation planning, such as corridor design or predicting the effects of different land use practices on connectivity. Circuit theory should provide an especially powerful tool for designing robust reserve networks, i.e., those that still provide for connectivity in the face of uncertainty in species distribution data and/or future habitat loss (Moilanen et al. 2006*a*, O'Hanley et al. 2007; Pinto and Keitt, *in press*). Importantly, circuit methods can be applied to the same resistance surfaces that are commonly employed in least-cost path analyses, and with little added computational expense.

In this paper, we limited our examples of circuit-based analyses to accessible interpretations of resistance, voltage, and current. However, there should be a large number of tools that could be derived from these basic properties. For example, metrics that combine predictions of efficient travel paths, pinch points, and mortality risks could allow practitioners to map landscape features that most effectively contribute to connectivity while minimizing mortality rates. Or, metrics derived from shortest path or least-cost distances, such as the Harary index (Ricotta et al. 2000, Jordán et al. 2003) or the integral index of connectivity (Pascual-Hortal and Saura 2006) could be modified by substituting resistance distances for least-cost distances in their calculation. Additionally, algorithms like edge and node thinning, used to evaluate impacts to connectivity of habitat loss in graph theory (Urban and Keitt 2001), can also be applied using circuit-based measures.

A note about ecological vs. evolutionary applications

It is important to be aware of subtle differences in assumptions behind applications of circuit theory to different processes. So far we have identified two distinct frameworks, one which models gene flow across population networks and the other focused on individual movement across habitat networks. The former assumes nodes (or cells) represent subpopulations (or occupied habitat for continuously distributed populations), with resistors representing numbers of migrants exchanged between adjacent nodes per generation (McRae 2006). By contrast, applications focused on individual movement will typically be implemented at finer temporal and spatial scales, with nodes (cells) mapped at the scale at which individual movement decisions are made. Thus, the two will often be applied at different scales and with (at least somewhat) different habitat models. Similarly, predictions from the two frameworks must also be interpreted differently. For example, in applications where nodes or cells represent occupied habitat exchanging migrants, a decrease in the resistance distance between two nodes corresponds to a proportional increase in gene flow predicted between them; however, when nodes represent dispersal habitat rather than subpopulations, a decrease in the resistance distance corresponds only to an increase in available dispersal pathways, and not necessarily a commensurate increase in individual movement rates or gene flow. It does, however, indicate that there will be more pathways available to dispersers, and presumably greater robustness of the network to future habitat loss. Conservation applications may be implemented using either framework, but it is important to specify the process being modeled.

Model parameterization

A critical and challenging step in applying circuit models to landscape data will be assigning relative movement, mortality, and/or settlement probabilities to different land cover classes. Many of the same strategies for parameterizing least-cost path models using expert opinion, literature review or data on species occurrences, animal movement paths, or interpatch movement rates (reviewed by Beier et al., *in press*) will be useful in circuit modeling, particularly when viewed in light of the concrete interpretations of resistances in terms of random walk probabilities outlined here. Practitioners should also consider approaches taken to parameterize other models that consider habitat heterogeneity, such as diffusion and simulation models (e.g., Dunning et al. 1995, Schumaker 1996, Ovaskainen 2004; Arellano et al., *in press*; Ovaskainen et al., *in press*).

Connections between resistance distances and gene flow (McRae 2006, McRae and Beier 2007) should facilitate the use of genetic data to estimate relative resistances of different habitats. Still, because assumptions differ between evolutionary and ecological applications of circuit theory (as discussed here), using data from one to parameterize the other must be done with care.

Regardless of the method used to assign them, there will always be uncertainty in resistance values. We encourage uncertainty analyses to address how decisions at each modeling step affect results; Beier et al. (*in press*) reviewed strategies for conducting uncertainty analysis in least-cost path modeling, and these should be equally applicable to circuit theory. Additionally, for corridor and reserve designs, uncertainty in landscape resistances could be incorporated in much the same way as proposed by Moilanen et al. (2006*b*), with penalties that reflect modeled error incorporated into landscape resistance input maps.

Limitations and alternatives

As with other methods for describing connectivity in complex landscapes, there are limitations to our approach that should be considered when deciding if it is appropriate for a given problem. First, because resistors are isotropic, i.e., their resistance to current flow is the same in both directions, the methods described here cannot accommodate movement that is biased in one direction (as in directed graphs). This will limit applications in some systems, e.g., marine environments, where directional currents play a large role in determining dispersal rates. Second, circuit models are restricted to Markovian random walks, i.e., random walks in which each step is independent of previous moves. Random walkers thus have no "memory," and our framework cannot incorporate correlated random walks, changes in movement behavior with time, or mortality rates that increase with an organism's age. Even when the assumption of constant mortality with time is reasonable, incorporating mortality into circuit models must be done with care. Because they have no memory or long distance perception, random walkers can retrace their steps over and over, inflating mortality rates because travel time and exposure to mortality risks are increased (Fig. 2B).

Several other connectivity modeling frameworks provide complements to ours. The conceptually and computationally simplest are based on Euclidean distances, and can be quickly calculated on grids with millions of cells (e.g., Moilanen et al. 2005, Moilanen and Wintle 2007). Least-cost path models have been applied for over a decade in connectivity analyses and have proven useful in conservation planning efforts (e.g., Beier et al. 2006, Rouget et al. 2006). Although they do not have the theoretical foundation in random walk theory that circuit models do, their intuitive appeal and ability to identify efficient movement pathways make them useful counterparts to the applications we have described here. Recently, variants on these approaches have been developed that identify and rank the importance of multiple pathways across landscapes (Theobald 2006; Pinto and Keitt, *in press*).

More sophisticated analytical and simulation models can be used to derive results similar to those produced by circuit theory, with some advantages. Markov chain models use the same data structures as those described here, but can accommodate directionality in movement along edges, providing more flexibility for modeling, e.g., effects of directed dispersal, prevailing winds, or ocean currents. Still, although Markov chain models have been available for decades, ecologists and conservationists have been slow to adopt them, whereas simpler, more intuitive least-cost path models have been widely employed. Spatially structured diffusion models (Ovaskainen 2004) are promising because they also integrate over all movement paths and can approximate correlated random walks in their long-term behavior, but their mathematical formulation can be quite challenging. Of course, individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005) offer much more flexibility than analytic models, can incorporate subtle effects of dispersal behavior and other aspects of life history, and can simulate transient effects of landscape characteristics that evolve over time. However, the data and computational requirements of such models will likely continue to limit their use in many applications (Minor and Urban 2007). Our hope is that circuit models will fill a niche between simpler Euclidean or least-cost path analyses and more powerful analytic and simulation approaches.

Future prospects

Our focus has been on measuring connectivity in heterogeneous landscapes using models from circuit theory. Even in this context, there remain many exciting applications to explore. Nonequilibrium circuit analyses may be applicable to ecological problems (McRae and Beier 2007), and nonlinear circuit elements show promise as well (for example, diodes would allow incorporation of movement probabilities with directional bias). Additionally, analytical techniques developed to minimize effective resistances across networks (Ghosh et al. 2006) may be useful in designing optimal networks for connectivity conservation. More broadly, circuit theory will likely benefit other areas of ecology that deal with networks, such as the analysis of community interactions, food web structure, exotic invasion, or disease transmission. In the meantime, circuit models are being actively applied to conservation planning for species of concern in rapidly developing landscapes, including pumas (*Puma concolor*; see Plate 1) in southern California.

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Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits

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Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits

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Abstract

Landscape connectivity is crucial for many ecological processes, including dispersal, gene flow, demographic rescue, and movement in response to climate change. As a result, governmental and non-governmental organizations are focusing efforts to map and conserve areas that facilitate movement to maintain population connectivity and promote climate adaptation. In contrast, little focus has been placed on identifying barriers—landscape features which impede movement between ecologically important areas—where restoration could most improve connectivity. Yet knowing where barriers most strongly reduce connectivity can complement traditional analyses aimed at mapping best movement routes. We introduce a novel method to detect important barriers and provide example applications. Our method uses GIS neighborhood analyses in conjunction with effective distance analyses to detect barriers that, if removed, would significantly improve connectivity. Applicable in least-cost, circuit-theoretic, and simulation modeling frameworks, the method detects both complete (impermeable) barriers and those that impede but do not completely block movement. Barrier mapping complements corridor mapping by broadening the range of connectivity conservation alternatives available to practitioners. The method can help practitioners move beyond maintaining currently important areas to restoring and enhancing connectivity through active barrier removal. It can inform decisions on trade-offs between restoration and protection; for example, purchasing an intact corridor may be substantially more costly than restoring a barrier that blocks an alternative corridor. And it extends the concept of centrality to barriers, highlighting areas that most diminish connectivity across broad networks. Identifying which modeled barriers have the greatest impact can also help prioritize error checking of land cover data and collection of field data to improve connectivity maps. Barrier detection provides a different way to view the landscape, broadening thinking about connectivity and fragmentation while increasing conservation options.

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Introduction

Landscape connectivity, or "the degree to which the landscape facilitates or impedes movement among resource patches" [1], is crucial for many ecological and evolutionary processes, including dispersal, gene flow, demographic rescue, and movement in response to climate change [2–7]. Many research and conservation planning efforts have focused on mapping areas important for connectivity using GIS models (e.g., [8–12]). The results of these analyses are guiding investments by governmental and non-governmental organizations to promote ecological connectivity across large areas. In the USA and Canada, for example, numerous broad-scale conservation efforts such as the U.S. Department of Interior Landscape Conservation Cooperatives, the Western Governors' Association's Initiative on Wildlife Corridors and Crucial Habitat, and the Yellowstone to Yukon Conservation Initiative are working to integrate and coordinate connectivity conservation actions spanning millions of acres and crossing many political and ecoregional boundaries.

Conservation practitioners employ two primary strategies to promote connectivity. The first focuses on conserving areas that *facilitate* movement; the second focuses on restoring connectivity across areas that *impede* movement (e.g., by removing a fence or building a wildlife-friendly highway underpass). Most connectivity analyses have focused on the former strategy by modeling and mapping areas important for movement under present landscape conditions. A wide array of tools have been developed for this purpose: least-cost corridor modeling [8,13,14], circuit theory [15], individual-based movement models (e.g., [16–18]), graph theory [19,20], and centrality analyses (e.g., [21,22]) have all been used to identify areas important for movement of plants and animals. Outputs from such models are now being used as inputs to reserve selection algorithms (e.g., [23]) to optimize actions to conserve connectivity.

In contrast, there has been little effort by conservation scientists towards identifying candidate areas for the second strategy: that is detecting restoration opportunities by mapping barriers that strongly reduce movement potential. We define a barrier as a landscape feature that impedes movement between ecologically important areas, the removal of which would increase the potential for movements between those areas. Here we are concerned with movements important for access to resources, demographic rescue, gene flow, range shifts, and other ecological and evolutionary processes. In this context, barriers are distinguished from features that are impermeable but not situated such that they block biologically relevant movement routes. Barriers are thus the inverse of corridors, which delineate pathways facilitating movement. Barriers can either be complete (impermeable) or partial (e.g., land cover types that hinder movement relative to ideal conditions, but may still provide some connectivity value). Barriers may be human-made (e.g., roads, fences, or urban areas) or natural (rivers or canyons); they may be linear (e.g., highways) or span large areas (agricultural fields). As with traditional connectivity concepts [1,24], what constitutes a barrier, the impact it has, and whether it reduces connectivity through behavioral inhibition, increased mortality, or other means will differ among species.

Detecting barriers to movement would complement traditional connectivity analyses in several important ways. First, some barriers may be restorable. Knowing where barriers have the greatest impact would help practitioners decide where and how to invest scarce conservation resources to conserve and enhance connectivity. For example, it may be cheaper to restore a barrier that blocks a movement corridor through public land than to establish permanent protection of a functioning corridor that runs through private land [25]. Quantifying such trade-offs would be necessary to integrate connectivity restoration into systematic conservation planning analyses aimed at optimizing conservation investments [26–28], but tools to incorporate connectivity conservation and/or restoration into such efforts remain rare [29–31]. Second, consider that corridor modeling often produces corridors that may not be good enough to realistically support movement [32]. Barrier detection analysis could reveal such cases, allowing practitioners to 'triage' a landscape, focusing efforts on more viable movement routes. Finally, surprising results in a barrier analysis could alert analysts to situations in which poor land cover data or incorrect model parameterization may be causing spurious results.

In this paper, we introduce a new method to identify barriers and rank them by their impact on connectivity. Our method complements existing connectivity modeling approaches, is applicable in least-cost and other connectivity modeling frameworks, and can be extended to centrality analyses. The method can be readily applied across large landscapes, efficiently analyzing barriers among many locations and at different scales corresponding to different sizes of barriers and types of restoration activities. It also quantifies the extent to which restoration can be expected to improve connectivity. We provide example applications of the method, showing that the potential for connectivity conservation is not constrained to narrow corridors, but includes options spanning much more of the landscape when restoration options are considered. We also discuss how our approach can facilitate sensitivity analyses, data quality screening, and prioritization of areas for error checking of GIS base data.

Method for Detecting Barriers and Restoration Opportunities

Our method identifies areas that most reduce connectivity between two locations on a landscape. Making these areas permeable to movement would therefore most increase connectivity between the locations. Thus, these are areas that practitioners should consider when implementing restoration to promote connectivity.

To illustrate the method, we use a least-cost corridor modeling framework [13,14,32], which is commonly used to map and prioritize areas important for connectivity conservation (e.g., [8–12]). However, our approach could also be used with other modeling frameworks capable of producing measures of effective distance, such as circuit theory and individual-based movement models (see Discussion).

As with least-cost corridor models, input data include locations to be connected (hereafter, "patches") and a raster resistance surface (Figure 1A). The former may consist of points or polygons, and typically represent natural landscape blocks, protected areas, or core habitat for a particular species or species guild [33]. The resistance surface represents the difficulty, energetic cost, or mortality risk associated with movement through each pixel (see [34] for a review of resistance surface development).

Least-cost methods calculate the cost-weighted distance (*CWD*) of all pixels to a source location, creating a raster of *CWD* values (Figures 1B and 1C). Adding together *CWD* rasters from two locations produces a corridor (Figure 1D), showing the pathways with the lowest cumulative movement cost between the locations [14]. The minimum value of the corridor raster is the least-cost distance (*LCD*); this represents the cumulative resistance encountered moving along the optimal path from one location to the other, and is a common measure of isolation in spatial ecology (e.g., [35,36]), landscape genetics (e.g., [37,38]), and related fields.

Our method is based on this simple assumption: if a certain area (the size is defined by the user) is restored such that the resistance across it is reduced, then the *LCD* of the best route connecting the patches through the restoration area will also be reduced. Systematically quantifying the potential reduction across a landscape will allow us to detect those areas where restoration would lead to the greatest reduction in least-cost distance.

The method begins with *CWD* calculations from two patches (Figures 1B and 1C). However, rather than adding the two *CWD* surfaces together to produce a corridor, we instead calculate the minimum value of each *CWD* surface within a localized area around each pixel location (e.g., within a 500 m radius). We then add the minimum values from both *CWD* surfaces to calculate the cumulative resistance that would be incurred moving between the patches and through the focal pixel assuming the area within the search window is restored:

$$LCD' = CWD1_{MIN} + CWD2_{MIN} + (L \, * \, R'), \qquad (1)$$

where LCD' is the least-cost distance of the best path between the patches passing through the focal pixel after barrier removal, $CWDX_{MIN}$ is the minimum *CWD* value from patch *X* within the search window, *L* is the length of the longest axis of the search window, and R' is the resistance value of the feature replacing (or cutting through) the barrier. We use a circular moving window to illustrate the method (Figure 2), but consider alternative search window shapes in the Discussion. Note that the longest axis of a circle is its diameter.

For each pixel, this formula yields the cost of the best corridor that would pass through that pixel if the resistance of a strip of land crossing the search window were changed to R'. Including R' and the search window length accounts for the cost of moving across the search window, assuming restoration or removal of the intervening barrier.

If LCD' is less than *LCD*, then restoration across the moving window (e.g., the circle in Figure 2) would reduce effective distance and increase connectivity between the two patches. When this is

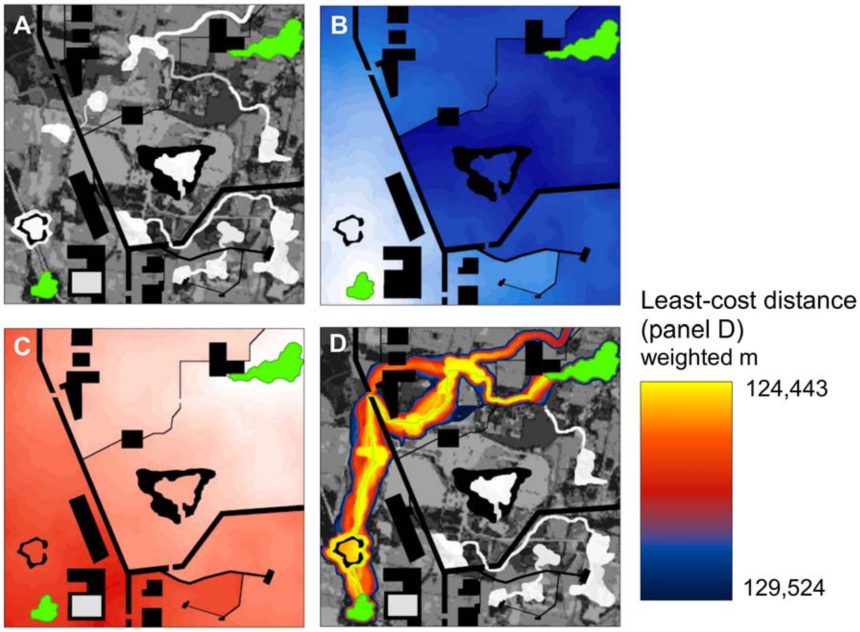

Figure 1. Cost-weighted distance modeling. (A) Example 3 km×3 km landscape with a pixel size of 3 m (from [15]). Two habitat patches (green) are embedded in a matrix of land cover types with differing resistance to movement. Resistances range from 1 (white) to 100 (dark grey); complete barriers with infinite resistance (e.g., linear features representing roads and highways) are shown in black. (B) Cost-weighted distance (*CWD*) from leftmost patch, with darker shades representing higher cumulative resistance from the patch. (C) *CWD* from rightmost patch, with darker shades representing higher cumulative resistance from the patch. (D) Modeled least-cost corridor produced by adding *CWD* surfaces shown in panels B and C (best 20% of study area shown). The least-costly path (traced in green) has a cumulative least-cost distance (*LCD*) of 124,443 weighted meters.
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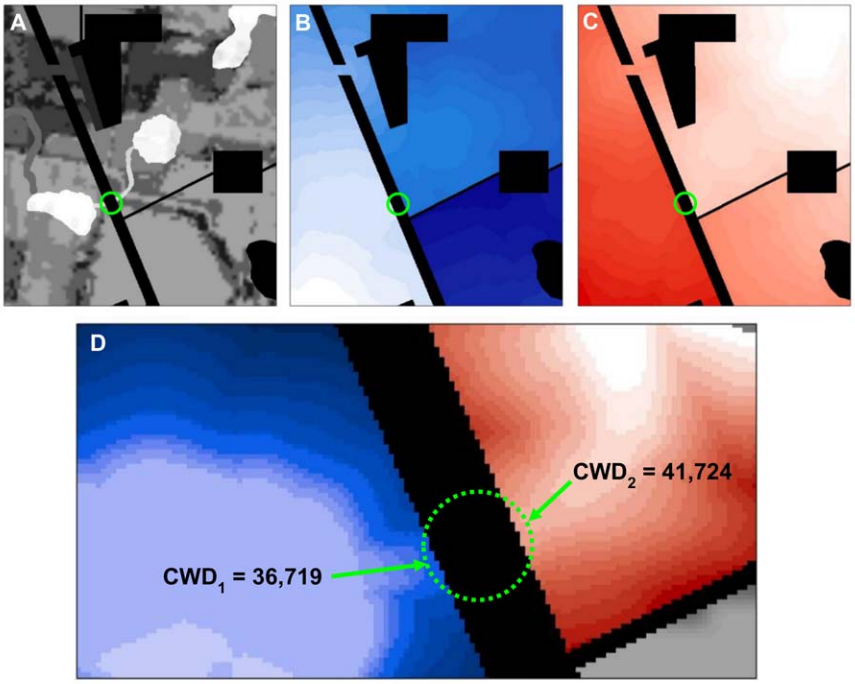

Figure 2. Detail of resistance and *CWD* surfaces with circular moving window. For a window with a diameter of 60 m (20 pixels) centered on the barrier, the arrows show the pixels in the window that have the lowest *CWD* to each patch (values shown are in weighted meters). Because the lowest *CWD* values from each patch will always be found on the edge of a moving window, only pixels on the perimeter need to be examined, increasing processing efficiency.
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the case, a simple metric of connectivity improvement that would result from restoration across the moving window is:

$$\Delta LCD = LCD - LCD' \qquad (2)$$

Dividing ΔLCD by the search diameter gives the connectivity benefit per unit distance restored; dividing ΔLCD by LCD gives the proportional improvement relative to unrestored effective distance.

To illustrate the method, we first apply it to the relatively simple landscape described in Figure 1 using a search window with a diameter of 60 m (20 pixels at 3 m resolution; Figure 2). The search window size is chosen to match the size of the barrier that one is interested in detecting: a diameter of 20 pixels will fully incorporate effects of barriers up to 20 pixels across. We assign a resistance of 1 to optimal movement habitat, so that the cumulative cost of movement is identical to the Euclidean distance traversed when no barriers are encountered. For the circular window centered on the highway in Figure 2, the lowest *CWD* values from the left and right patches are 36,719 and 41,724 weighted meters, respectively. Summing these values and adding 60 (the cost of crossing the circle if it were restored to optimal movement habitat with a resistance of 1), gives the least-cost distance of the path crossing through the restored area (36,719+41,724+60 = 78,503 weighted meters). Since this is considerably lower than the least-cost distance between the patches without restoration (124,443 weighted meters), this location is a potent barrier, and the center pixel is assigned an improvement value of 45,940 weighted meters. This is repeated for every pixel on the landscape using standard GIS neighborhood analyses, resulting in a raster surface of improvement scores (Figure 3A).

The removal of the barrier where the improvement score is maximal – for example, by constructing a wildlife crossing structure – would re-route the best movement path (Figure 3B) and lower the effective distance between the two patches by 37% (45,940/124,443). Once that improvement is carried out, a second barrier analysis with the altered landscape conditions suggests that additional restorations along the highway will not further reduce the *LCD* at this point (Figure 3C). The next priority would be a road crossing in the upper right of the panel (dark orange in Figure 3C), connecting the rightmost patch to high-quality movement habitat above the road. The method is computationally efficient enough that different restoration scenarios can be tested iteratively: a barrier analysis with a 20- pixel search diameter across a landscape with 1 million pixels takes less than 2 seconds using a 2.7 GHz notebook computer.

Identifying barriers across scales and across large landscapes with multiple patches

The method described above can be extended across scales and across networks of patches, and we explore a few approaches to accomplish this here. By modifying the search diameter, the method can detect barriers of different sizes (Figure 4). Windows the width of a highway will best highlight where highways act as barriers, as in Figures 2 and 3. Larger windows will best detect barriers like agricultural fields, or cases in which narrow barriers run parallel to one another. Summary maps showing barrier effects across search window sizes may be created by first dividing improvement scores by the window size to produce maps of barrier strength per unit width, and then taking the maximum pixel score across scales (Figure 4B). This puts results from different analysis scales in the same units, allowing them to be summarized in a single map. Alternative summary metrics are possible, and we address some of them in the Discussion.

To summarize across multiple sets of patch pairs, we have implemented a similar approach in which the maximum or sum of improvement scores across all patch pairs is assigned to a pixel. Taking the maximum of improvement scores shows the features that have the greatest effect for any patch pair (Figure 4C). Summing improvement scores highlights those barriers that isolate multiple pairs of patches from one another, extending the method to quantify barrier centrality (Figure 4D).

The methods described in this paper have been implemented in Barrier Mapper software [39], freely available as a new addition to the Linkage Mapper Toolkit for ArcGIS [40].

Example application in a landscape undergoing active conservation planning

The Washington Wildlife Habitat Connectivity Working Group, a collaboration of land and resource management agencies, non-governmental organizations (NGOs), universities, and Washington treaty tribes, recently completed a connectivity analysis across the Columbia Plateau Ecoregion in Washington, Oregon, and Idaho, USA [41]. The Working Group focused on the Columbia Plateau because the ecoregion is home to a large portion of Washington's sensitive plant and animal species but is also highly fragmented by agriculture and other anthropogenic activities. The Group modeled corridors to connect habitat for 11 focal species and also to connect natural landscape blocks scoring highly on an index of landscape integrity (i.e., large areas with relatively low levels human modification). Products from the analysis are being used to inform conservation planning efforts by several state and federal agencies and NGOs. Many of the corridors identified by the analysis pass through human-dominated landscapes, where roads, agricultural fields, and other human uses likely still act as barriers to movement.

We reanalyzed results for a corridor connecting two natural landscape blocks identified by the Working Group in Douglas County, Washington (Figure 5). We chose these blocks because they have been identified as important for many species of concern; for example, the blocks contain important habitat or corridors for 8 of 11 focal species analyzed by the Working Group. Moreover, both are occupied by greater sage-grouse (*Centrocercus urophasianus*, categorized as a Species of Greatest Conservation Need in Washington and a candidate for listing under the US Endangered Species Act), and both fall within a recovery area designated for the species by Washington State [42]. In addition, this landscape contains a complex mix of native systems and agricultural lands – the latter including both annual cropland and perennial vegetation cover – and includes roads, transmission lines, and other human-made features affecting animal movement [41].

To represent species with differing degrees of sensitivity to human modification, the Working Group used different resistance surfaces for landscape integrity analyses [41]. These surfaces all contained resistance values that increased with the degrees of human modification, differing only in the range of resistances assigned. Resistance scores of 1–100, 1–1000, and 1–10,000 were used for minimum, medium, and maximum sensitivity surfaces respectively (see [41] for details). We present results from a barrier analysis using the medium sensitivity resistance surface.

The modeled least-cost corridor connecting the patches dips south from the western patch, runs east to Banks Lake, and then north along a narrow strip of native vegetation and cliffs sitting between the lake and cropland (Figure 6A). A secondary and much longer corridor follows broad swaths of native vegetation through

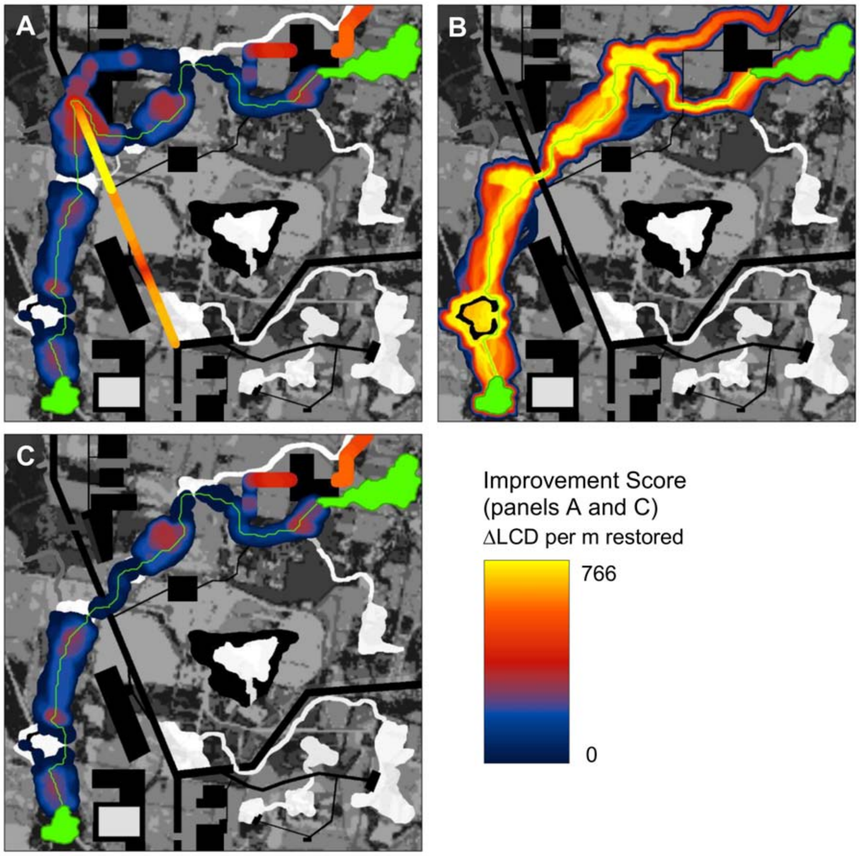

Figure 3. Barrier analysis of landscape. (A) Improvement scores (*ΔLCD*) for a 60 m search diameter using an enhanced version of Linkage Mapper software ([40]). Only positive values (indicating barriers whose removal would reduce isolation) are shown. To facilitate visualization of the barriers, scores were mapped so that they filled the search window (i.e. the maximum *ΔLCD* value within the search radius of each pixel is displayed). The greatest improvement potential was detected crossing the highway. Note that a natural corridor is bisected by the highway at the point with the highest improvement potential (see detail in Figure 2). (B) Creating a new gap in the barrier where restoration potential is highest re-routes the modeled least-cost corridor and greatly reduces resistance between the patches (*LCD* = 78,503 weighted meters compared with an *LCD* of 124,443 pre-restoration). Best 20% of study area shown. (C) Barrier detection at 60 m search diameter after restoration.
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Moses Coulee and Beezley Hills to the south. A barrier analysis indicates numerous opportunities for improving the least-cost corridor, particularly within its east-west segment (Figure 6B). There are also opportunities outside of the main corridor, occurring along the longer route to the south and to the north as well (Figure 6B). Restoring any of these latter areas would re-route the modeled least-cost corridor, causing it to occur in a different location than it did in the unrestored landscape.

Restoration of any of several barriers identified to the south would improve connectivity as measured by *LCD* (Figure 6B); however, this would result in a much longer least-cost corridor. Restoration to the north has the potential to both improve *LCD* and shorten the distance traversed by the corridor. We simulated a restoration by changing a 1 km^2 (500 m×2 km) swath of agricultural land (indicated by the arrow in Figure 6B) to a resistance of 1. We chose 2 km because the greatest improvement was detected at the 2 km scale, and we assumed 500 m was wide enough to accommodate movement. A second corridor analysis following the simulated restoration shows the new corridor to the north (Figure 6C). The corridor has 9.4% less cumulative resistance than the original (1348 weighted km *vs.* 1489 weighted km), and its least-cost path is 44% shorter in un-weighted length. A post-restoration barrier analysis indicates that the highest improvement scores now fall along the new corridor (Figure 6D); restoring a second 1 km^2 swath in this new corridor at the point indicated by the arrow would further reduce *LCD* by 50%.

Discussion

Connectivity models have provided valuable guidance to conservation planning efforts, as well as predictions of movement, gene flow, and isolation important to landscape genetics and other fields concerned with movement ecology. Yet they have almost exclusively emphasized identifying features that facilitate, rather than impede, movement; this emphasis gives an incomplete picture of how landscape features affect connectivity, what connectivity management strategies might be appropriate, and the uncertainty underlying model predictions. We see considerable potential for barrier detection analyses to help practitioners overcome these limitations. In particular, the ability to identify restoration opportunities can provide valuable alternatives to traditional conservation efforts focused on existing movement corridors.

Our reanalysis of the Columbia Plateau data (Figure 6) illustrates these points, showing how detecting barriers can increase conservation options available to practitioners, improve understanding of analysis products, and result in more robust conservation plans. Without a barrier analysis, conservation

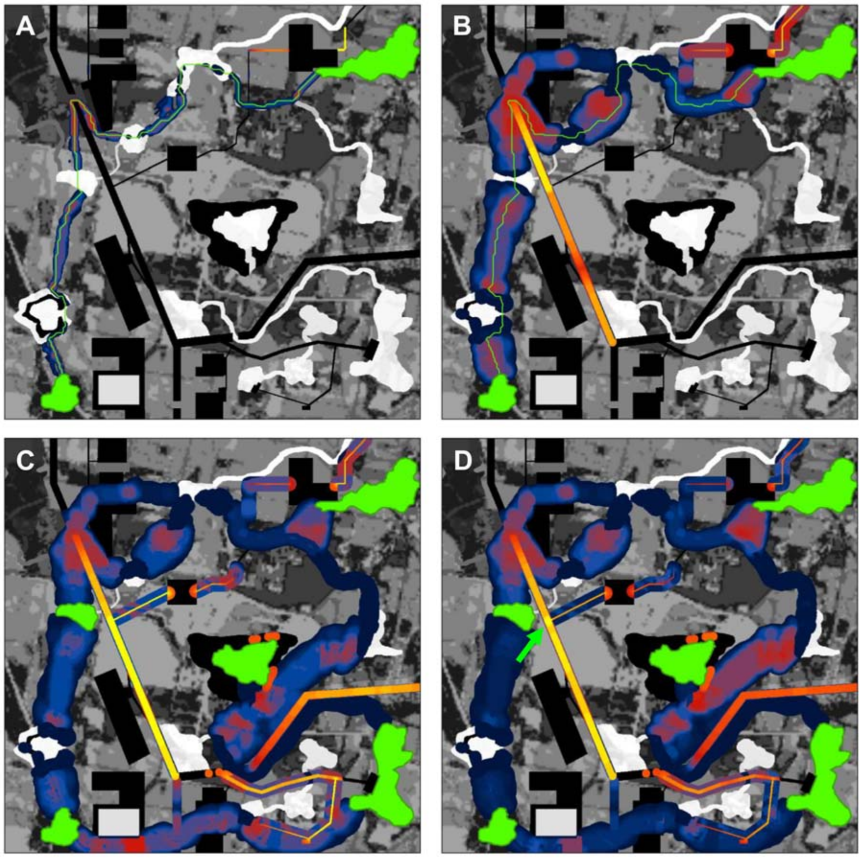

Figure 4. Barrier analyses integrating across multiple scales and patch pairs. (A) Results of barrier analysis with original patch pair at 12 m search diameter, which detects restoration opportunities equal to or less than 12 m across (e.g., local roads). (B) Maximum per-meter improvement value across 10 search window sizes (from 6 m to 60 m, with 6 m steps between search diameters). The map highlights where actions at different scales would have highest impact per meter restored. (C) Maximum per-meter improvement value across same window sizes and 5 patches, showing where greatest improvement could be achieved for any single pair of patches. (D) Sum of improvement scores among 5 patches (green). As in Panels A–C, the maximum per-meter improvement score was calculated for each patch pair at each scale. These were then summed across patch pairs to incorporate cumulative benefit for multiple patch pairs across multiple scales. The area scoring highest (bright yellow) had high improvement scores for multiple patch pairs; we interpret this area as having high 'barrier centrality,' i.e. being an important restoration opportunity for keeping the overall network connected. Note that the area occurs at a road intersection; if practical, placing a wildlife crossing structure here would re-route four corridors connecting the two leftmost patches to both the central and upper-right patch.
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planners would likely have focused on conserving land in or adjacent to the original least-cost corridor. Our analysis revealed numerous opportunities to improve this corridor, but also that restoration of a 1 km^2 swath of cropland would create a new corridor with several desirable characteristics. Specifically, the new corridor has a lower least-cost distance, is shorter in length, and appears to have fewer pinch-points (narrow sections) than the original corridor—all desirable characteristics for corridor design [15,32]. Moreover, if the two original corridors remain in place, the new, northern corridor adds redundancy to connections between the natural landscape blocks. This is important because organisms seldom follow a single optimal path [43], and because redundant connections help to ensure continued connectivity in the face of unpredictable environmental changes [15].

The analysis showed that connectivity conservation options need not be limited to a small portion of the landscape, opening up much more area for actions that could conserve or enhance connectivity and illustrating tradeoffs between different conservation strategies and target locations. Beyond the corridor quality differences cited above, we note that the original corridor runs along a narrow stretch of land bordering Banks Lake, sometimes traversing cliffs. The cliffs were assigned low resistance because the landscape integrity model used by the Working Group only quantified the degree to which pixels have been converted to human land uses. Practitioners, however, may consider cliffs to be impermeable for some species of conservation concern. The barrier analysis allows the user to quickly focus a more critical examination of corridor characteristics on areas influencing the results, and to identify options for alternative corridors that may better fit specific planning needs.

Similarly, the analysis underscored the potential sensitivity of corridor mapping to errors in GIS base data: our results show how the misclassification of a single agricultural field could have entirely altered the location of the original least-cost corridor shown in Figure 6A. The sensitivity of connectivity analysis results to landscape features at key locations has consequences for disciplines that depend on corridor maps (like conservation planning) and for disciplines that depend on connectivity measures (like landscape genetics). We discuss applicability of barrier detection methods to sensitivity analysis and error checking below.

Following the first barrier analysis and simulated restoration, a subsequent barrier analysis indicated that the restoration would

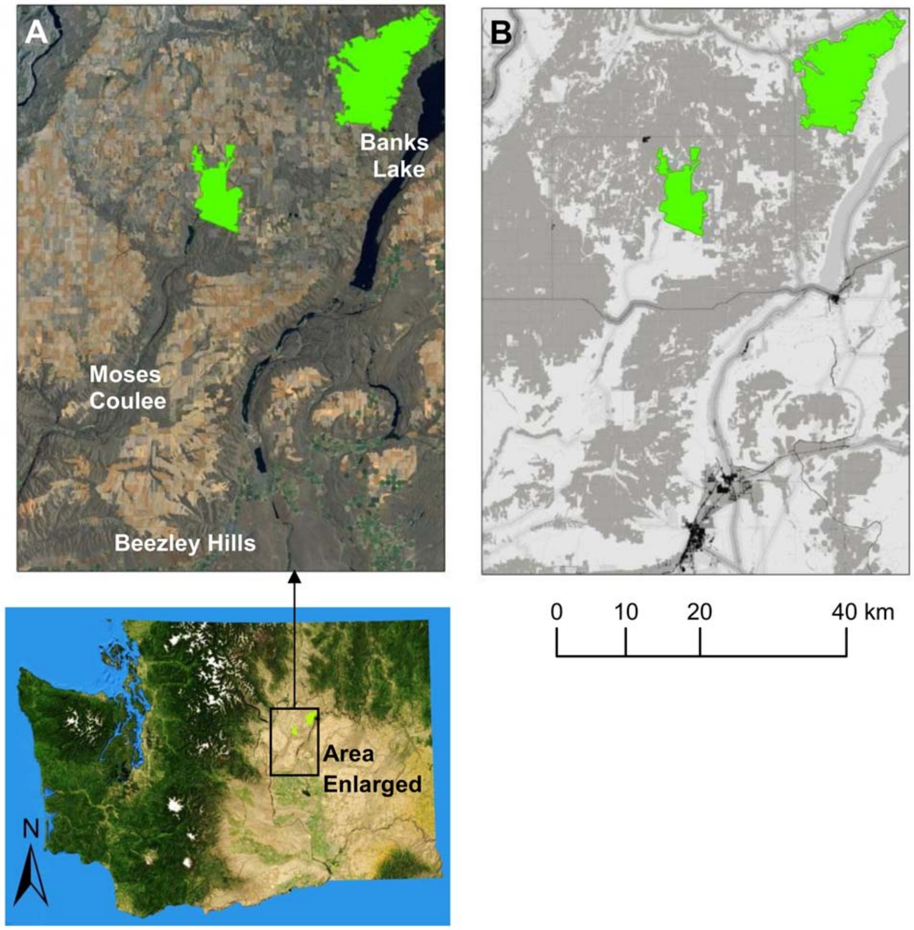

Figure 5. Corridor analysis in a landscape undergoing active conservation planning. (A) 60 km by 80 km study area in eastern Washington, USA, containing two natural landscape blocks to be connected (green). (B) Resistance map used to model corridors in a recent multi-partner connectivity analysis across the Columbia Plateau Ecoregion [41]; values range from 1 (white) to 1000 (black). Low resistance areas include native grassland and shrub-steppe, whereas high resistance areas include roads, developed areas, and agriculture.
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open up further restoration opportunities of considerable value, one of which would cut *LCD* values by half. Thus, simulating restorations and re-running corridor and barrier analyses will likely improve final conservation and restoration plans.

Although we are aware of no other efforts to automate identification of terrestrial connectivity restoration opportunities, least-cost corridor analyses have been used to guide placement of crossing structures across roads to restore connectivity for wildlife. For example, Beier et al. [44] assigned a single, finite resistance value to all segments of a highway between two protected areas, regardless of whether a segment contained wildlife crossing structures. The least-cost corridor between the areas crossed the highway at the location where a crossing structure would result in the lowest ecological cost of travel. If highway crossing structures were not located in this corridor, Beier et al. [44] recommended specific structures at particular locations. This approach is useful, but does not quantify the improvement compared to existing conditions, does not identify restoration opportunities outside of least-cost corridors, and cannot be readily applied to barriers more complex than roads.

In addition to overcoming these limitations, our method is also amenable to highlighting barriers that affect multiple corridors, introducing the concept of barrier centrality. As shown in Figure 4, barriers can be mapped across all patch pairs, and the results summed. This identifies barriers with high network centrality, similar to analyses that identify corridors or pathways with high centrality [21,22,45,46].

Applications for error checking and sensitivity analyses

GIS land cover data used to develop resistance layers for connectivity analyses are typically based on satellite or aerial imagery and often suffer from high levels of classification error [34,47]. Although our method relies on these same base data, it can help to prioritize error checking of the data by highlighting mapped features that strongly influence corridor locations. If a permeable feature is misclassified as impermeable and identified as a barrier, the misclassification could entirely alter a corridor's location. We recommend examining detected barriers, either by manually checking aerial imagery or conducting field surveys. Similarly, impermeable features misclassified as permeable that occur along least-cost paths can change corridor locations as well. Examining features along least-cost paths in tandem with barriers could thus further reduce the effects of classification error in connectivity analysis products.

Barrier detection can also be applied to parameter sensitivity analyses, important because resistances are often assigned based on expert opinion, which can be unreliable [34,47,48]. For example, if a given land cover type fell along a corridor's least-cost

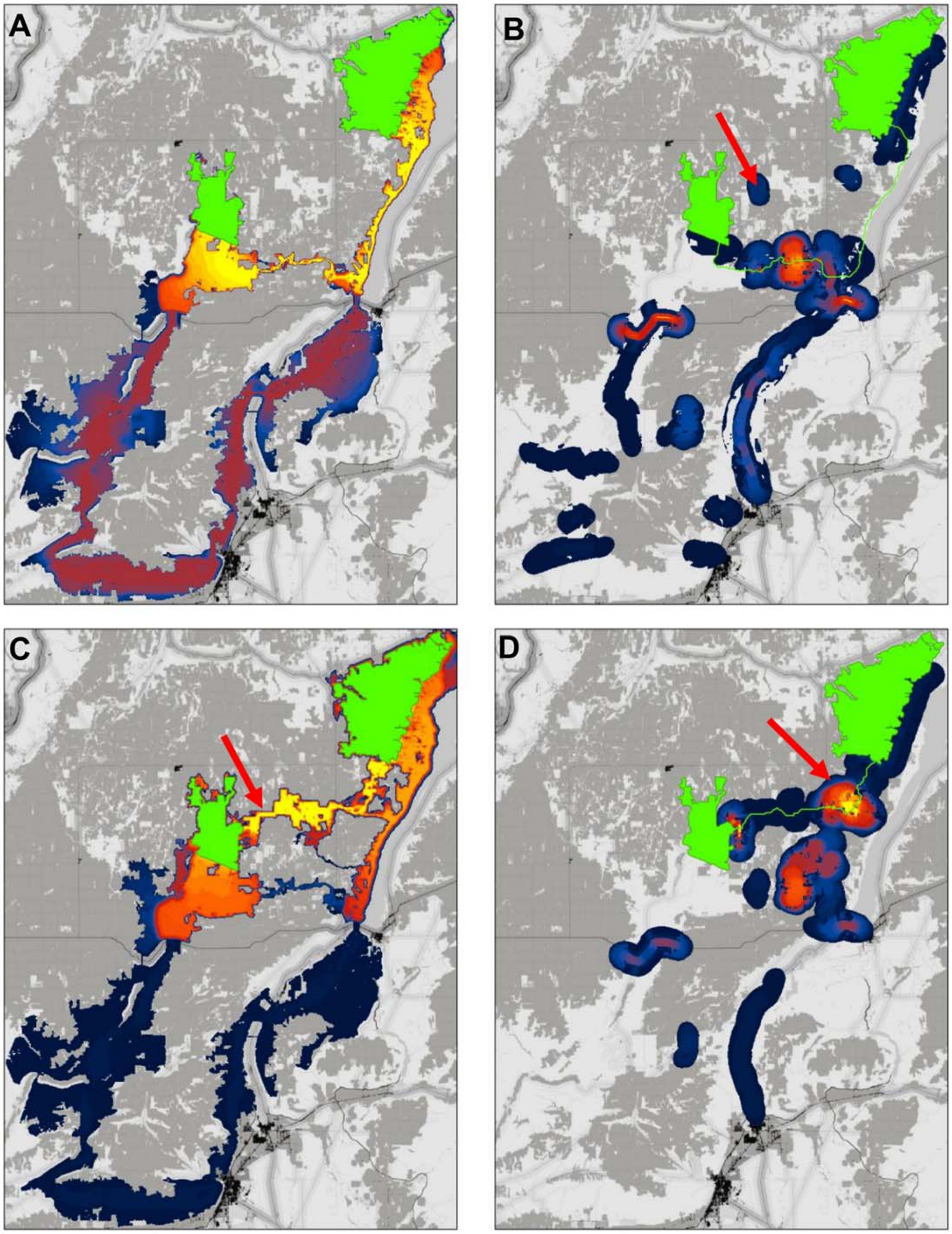

Figure 6. Reanalysis of connectivity modeling results using barrier detection algorithm. (A) Corridor connecting natural landscape blocks, showing least-cost movement routes. Best 20% of study area shown. (B) Barriers detected at diameters from 200 m to 2 km, with original least-cost path shown in green for reference. Mitigating barriers along the least-cost path (i.e., intersecting the green line) would improve the existing corridor without changing its location; mitigating barriers away from the path would re-route the best modeled corridor. (C) Restoring a 1 km^2 (500 m×2 km) swath spanning the barrier indicated by the arrow establishes a new least-cost corridor to the North. (D) A barrier analysis incorporating the simulated restoration indicates opportunities to substantially improve the new corridor with additional restorations.
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path or encompassed an influential barrier outside of the corridor, the resistance assigned to that land cover type would be known to influence the corridor's location. The sensitivity of the corridor's location to the resistance value assigned the land cover type could then be analyzed using alternative parameterization methods as described by Beier et al. [47]. As with connectivity models, our method will depend on the grain size of the resistance raster; to adequately resolve features that potentially impede movement, we recommend pixels no larger than ½ the width of barriers one is interested in detecting.

Potential enhancements

Directionality of barrier effects. Our methods could be improved to more precisely pinpoint barriers. For example, elongated moving windows (search polygons) could perform better than circles to identify the best path for an improved corridor design. Measuring *ΔLCD* along elongate polygons placed at different angles, although more computationally complex than measuring across circles, would allow the attribution of directionality to barrier effects as well as adjustment of improvement scores at large search distances to reflect improvement achievable at smaller (nested) distances. New procedures to select the best orientation and width of such polygons could obviate the need to subjectively orient restoration polygons, like the 500 m×2 km polygon in our simulated restoration (Figure 6).

Restoration cost. We measured barrier strength by conservation improvement per meter restored because it was the simplest way to illustrate our approach. An alternative metric would be conservation improvement per restoration dollar; this would reflect, for example, that the cost per meter of a 10 m road crossing structure exceeds the cost per meter of a 50 m crossing structure, which in turn exceeds the cost per meter of restoring agricultural land. This enhancement would facilitate incorporation of connectivity restoration into return-on-investment analyses [49,50], helping managers to balance improvement potential, corridor importance, costs, and risk of conversion or degradation when deciding which parts of a landscape should be conserved or restored. The disadvantage, or course, is that this metric would require more data to calculate.

Restoration efficacy. Different R' resistance values could be applied to different land cover types to reflect the fact that some barriers would be more permeable to movement following restoration than others. For example, a highway underpass installed to allow animal movement may still have considerable resistance, whereas a restored forest stand may have resistance similar to undisturbed forest.

Other enhancements. Just as areas that cannot be conserved can be removed from reserve selection algorithms [51], unremovable barriers, such as urban areas, could be excluded from barrier analyses. The metrics described in equation (2) could be modified to incorporate restoration costs that vary by feature type, or land prices mapped using parcel data. Metrics of corridor importance (e.g., link centrality) could be integrated by multiplying improvement scores by such metrics, which would highlight opportunities to restore the most potent barriers in the most important corridors. Or, rather than focusing on pairs of patches, the method could be altered to focus on the connectedness of each patch by summing barriers detected between each patch and all others. Lastly, improvement scores may be expressed in terms of absolute improvement or percent improvement relative to unrestored corridor resistance. An advantage of the latter approach is that it would favor restoration in corridors in which *LCD* values are already low, presumably meaning they are more viable.

Which of these enhancements are most valuable will depend on the objectives of individual users and projects.

Application in other connectivity modeling frameworks

Although least-cost corridor models are by far the most commonly applied connectivity planning tool, they rely on simple assumptions about animal movement and other processes [43,48,52,53]. However, our approach can be applied in any connectivity modeling framework that produces measures of effective distance. For example, circuit-based connectivity analyses can model the relative proximity of each pixel to two patches by setting the voltage of one patch to 1 and the other to ground (see [15] for details on applying circuit modeling to landscapes). The resulting voltage surface gives the probability that a random walker will reach one patch before reaching the other [15,54]. Strong gradients in voltage indicate barriers that separate areas relatively accessible to one patch from areas relatively accessible to the other. If removed, such barriers would reduce effective resistance between the patches, an analog to *LCD* that takes into account the availability of multiple, parallel connections. A similar approach is widely used in microchip design: simulated voltage levels reveal areas with strong voltage gradients (known as IR drops) where electrical connectivity must be enhanced [55]. Thus barrier analysis using circuit theory can identify opportunities to provide valuable redundant connections even when *LCD* would not be reduced. In contrast, barrier analysis using least-cost methods will not identify these opportunities.

Individual-based movement models provide a more complex but also more powerful framework for modeling connectivity, capable of incorporating more biological realism and behavioral information than least-cost or circuit analyses [56]. As long as an individual-based model can produce maps of effective distance (e.g., based on the probability of, or energetic expenditure associated with, reaching different locations from a source patch), the approach described here could be applied to the model. Models such as PATH [16] and HexSim [17] can be used to derive such measures.

Potential for integration with systematic conservation planning

Our method is not a substitute for algorithms like Marxan [57] or Zonation [51], which are designed to optimize selection of reserves or sets of conservation actions. Although our method identifies and ranks candidate areas for restoration actions, it does not select optimal *sets* or portfolios of conservation actions to achieve given conservation goals while minimizing cost. The same can be said for algorithms designed to map areas that most facilitate movement and connectivity (e.g., [22,40,46,58–60]); rather than incorporating optimization routines, such algorithms instead produce maps that must be interpreted by practitioners, who then make conservation decisions in light of costs, benefits, and other management objectives.

Although it has long been recognized as important to reserve network design [61], incorporating connectivity directly into optimization algorithms has proven difficult. Most such efforts can be characterized as minimizing local fragmentation by either considering the geographic proximity of candidate areas to other areas (e.g., [62–64]) or maximizing the compactness and contiguity of reserves by favoring selection of adjacent cells or using boundary quality or length penalties (e.g., [29,57,65,66]). Because these algorithms favor conserving or restoring contiguous natural areas, they may neglect areas that, although fragmented, contribute to connectivity between natural areas. Thus, relying solely on maximizing the proximity or contiguity of protected areas could lead to elimination of movement routes that cross human-dominated landscapes.

Progress toward synthesizing connectivity and optimization algorithms has likely been hampered by the ‘network’ nature of connectivity planning: conservation in one area can affect the function and value of distant areas, contingent upon the conservation status and characteristics of the intervening landscape. Incorporating this complexity into optimization algorithms becomes computationally prohibitive with large numbers of planning units [67]. Still, practitioners are beginning to use outputs of multi-species connectivity models as inputs to optimization algorithms like Zonation [23,68]. Such examples are promising, and should be equally applicable with restoration-oriented algorithms such as ours.

An alternative to our approach that would seek to develop a near-optimal set of conservation actions would be to employ a routine similar to that used by Zonation software, which begins with an intact landscape and iteratively removes grid cells with low conservation value [51,69]. Starting with a landscape in which all restorable barriers have been removed, different sets of barriers could be added back in and connectivity metrics recalculated at each iteration. As with traditional connectivity models, however, this would be computationally prohibitive with large numbers of patches or restoration sites because of the computational time required for recalculating connectivity metrics. A promising hybrid approach could be to use the method described in this paper to identify sets of pre-screened restoration opportunities, which could then be removed from a resistance surface and added back in using an algorithm like Zonation's.

Practical considerations for improving conservation and restoration decisions

Managing for connectivity to facilitate gene flow, climate adaptation, and other processes is challenging without reliable maps to guide practitioners [33]. Connectivity analyses have provided valuable implementation guidance in the past; barrier mapping can increase the rigor of such analyses and the range of conservation options they reveal. It can help practitioners a) decide if connectivity conservation is a worthy investment in a landscape; b) identify opportunities to restore vs. conserve different areas; c) reduce uncertainty due to errors in GIS base data; and d) balance potential improvement against costs so that investments can be prioritized.

The goals of managers and planners can be used to guide applications of barrier detection methods. For example, if a transportation agency is interested in determining which highway segments are likely to have the greatest impact on wildlife movement, the search window should correspond to the width of highways, with outputs clipped to highways and the R' value determined based on the estimated resistance of the kind of crossing structure (or alternative structures) being considered. If a land management agency is prioritizing restoration of degraded native vegetation, the search window should relate to the size of appropriate restoration projects, and outputs should be clipped to the eligible land base (e.g., limited to the type of vegetation the restoration would target). If an NGO is identifying landowners interested in obtaining voluntary incentive payments for wildlife-friendly management, the window should reflect the scale of such management. Summarizing barrier analyses across multiple scales will be desirable for collaborations among organizations with differing goals and mandates. As noted above, iterative application of the model with simulated restorations will likely provide the most informative results and most robust conservation plans.

Similarly, the method may have potential to help adapt results from coarse-filter connectivity assessments, such as landscape integrity/human modification-based connectivity maps, to more fine-filter objectives (see [70] for a review of coarse- and fine-filter conservation planning). Alternative corridors revealed by the method could be assessed for their suitability under different planning constraints (e.g., corridors for species that must avoid cliffs, as in the Columbia Plateau example). While not a replacement for species-specific connectivity analyses, such an approach could help land managers evaluate alternatives if a mapped corridor is deemed unsuitable for their particular needs.

Connectivity maps do not always identify functioning routes that need to be maintained and protected; rather, they frequently map routes that may not be currently viable, but appear to provide the best opportunities for future work toward enhancing connectivity. In this sense connectivity maps often represent visions and goals for desired future conditions [71]. Barrier detection can add insight into the practicality of these goals, and identify specific options for achieving them. It can also help practitioners to 'triage' a connectivity plan, identifying corridors that traverse numerous barriers – and therefore would require significant investment to fully restore – so that efforts may be focused on more viable movement routes.

Perhaps most importantly, the ability to detect options to re-route corridors also opens up a broader suite of potential actions to improve connectivity. It can help managers identify new corridors that add additional movement pathways in areas important to the overall connectivity of a landscape (i.e. linkages with high centrality). Combined with spatially explicit land cost data, the method could help to improve conservation efficacy while reducing costs.

We hope barrier analyses will expand conservation options available to managers, and broaden conversations about restoration of connectivity more generally. By identifying new ways to improve connectivity in a particular area, the method can allow managers to consider different suites of strategies, or engage with new sets of stakeholders with interests in different areas. Both from the perspective of entities mandated to carry out conservation actions, and from the perspective of stakeholders with interests in the lands that are the focus of such actions, broadening the suite of alternatives and tools can only increase the opportunities for finding common ground in pursuit of multiple objectives.

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Author Contributions

Conceived and designed the experiments: BHM. Performed the experiments: BHM. Analyzed the data: BHM. Contributed reagents/materials/analysis tools: BHM. Wrote the paper: BHM SAH PB DMT. Suggested refinements to methods and analyses: SAH, PB, DMT.

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Improving the Success of Wetland Creation and Restoration with Know-How, Time, and Self-Design
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IMPROVING THE SUCCESS OF WETLAND CREATION AND RESTORATION WITH KNOW-HOW, TIME, AND SELF-DESIGN[1,2]

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Abstract. The creation and restoration of new wetlands for mitigation of lost wetland habitat is a newly developing science/technology that is still seeking to define and achieve success of these wetlands. Fundamental requirements for achieving success of wetland creation and restoration projects are: understanding wetland function; giving the system time; and allowing for the self-designing capacity of nature. Mitigation projects involving freshwater marshes should require enough time, closer to 15–20 yr than 5 yr, to judge the success or lack thereof. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. Ecosystem-level research and ecosystem modelling development may provide guidance on when created and restored wetlands can be expected to comply with criteria that measure their success. Full-scale experimentation is now beginning to increase our understanding of wetland function at the larger spatial scales and longer time scales than those of most ecological experiments. Predictive ecological modelling may enable ecologists to estimate how long it will take the mitigation wetland to achieve steady state.

Key words: achieving successful wetland mitigation; creating wetlands; ecological engineering; ecological modelling; freshwater marshes; functional analysis of wetlands; mitigation of wetland loss; Olentangy River Wetland Research Park, Ohio; wetland succession.

INTRODUCTION

The way in which we measure "success" of created or restored wetlands and our ability to achieve success are two issues that have come under increased discussion in recent years by wetland scientists and managers. Success in the general sense here means the establishment of a biologically viable and sustainable wetland ecosystem. Some call a wetland a success when it replaces the functions lost in a wetland that is being replaced; others would gauge success of a created or restored wetland against natural reference wetlands in the region. Unfortunately, there has been little formal published follow-up of the poorly named (see Renner 1994) "mitigation wetlands" that are constructed to replace wetlands that are unavoidably lost and there are few satisfactory methods for assessing replacement of the functions lost with the original wetland (Mitsch and Gosselink 1993). Regulators and consultants have chosen to use simple indicators of "success" to expedite the process and to keep monitoring costs low. Normally 3–5 yr of simple once- or twice-per-year monitoring is required, with easily measured parameters such as plant lists, animals witnessed, and percentage vegetation cover as the overall indicators. Assessing success is then based on comparing these easily measured parameters with a relatively simple set of criteria that were stipulated in the original permit for the project; these criteria may or may not accurately reflect wetland function.

After reviewing pertinent literature, we discuss three fundamental requirements for achieving success of wetland creation and restoration projects: understanding wetland function, giving the system time, and appreciating the idea of self-design. Our hypothesis is that most attempts to measure and achieve success of created and restored wetlands—caused by a lack of application of good wetland science to the problem and compounded by the existing construction-schedule-driven process—are flawed because of misunderstanding or misapplication of these factors. We then argue that ecosystem-level research and ecosystem modelling may provide better guidance on when created and restored wetlands can be expected to comply with criteria that measure their success.

STUDIES ON WETLAND MITIGATION SUCCESS

Most studies suggest that there is much room for improvement in the building of wetlands. Maguire (1985) used area, vegetative cover, and implementation of permit conditions to estimate mitigation success in Virginia and found that only 50% of 23 mitigation wetlands were "successful." In most unsuccessful cases, the mitigation project had not been implemented. An additional study by Reimold and Cobler (1985) conducted for the U.S. Environmental Protection Agency (EPA) gave similar results. Glubiak et al. (1986) and Quammen (1986) both suggested the need for better management of mitigation wetlands. Additionally Glubiak et al. (1986) predicted that while the protection

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[1] Manuscript received 10 June 1994; revised 3 April 1995; accepted 12 April 1995.

[2] For reprints of this group of papers on wetland mitigation, see footnote 2, page 33.

of wetlands through a permit process—Section 404 of the Clean Water Act enacted by the U.S. Congress in 1972—was somewhat effective, it would not prevent wetland area losses as effectively as it should.

In the mid-1980s some scientists involved in wetland restoration and mitigation believed that mitigation was working (Harvey and Josselyn 1986), while others suggested that more research needed to be done and that, if not properly conducted, a wetlands mitigation project could easily fail (Race 1986). Kusler and Groman (1986) raised concerns about the granting of Section 404 permits to contractors when alternative sites are available. Many questions and issues were raised by Kusler and Groman (1986) and Golet (1986) regarding permitting processes and the actual success of wetland mitigation projects. Their major issues were: When should destruction/damage and subsequent creation/restoration be permitted? How is the damage to the original system measured and how is the creation/restoration deemed sufficient? Golet (1986) suggested that under no circumstances should damage to a wetland be allowed unless there is absolutely no alternative.

While there are many factors that could be used to monitor progress of mitigation wetlands, observing vegetation has often been the easiest and probably the most common method (see, e.g., Wentworth et al. 1988, Jarman et al. 1991, Atkinson et al. 1993). This concept has already been codified in several parts of the country. For example, in Massachusetts, vegetation cover of $\geq 75\%$ is the major success criterion, even if vegetation composition is very different from that of the original wetland (Jarman et al. 1991). Reinartz and Warne (1993) argue that while vegetation cover may be an easy measure of success, it is a poor indicator of function.

Recent investigations of wetland mitigation projects, as a greater number of mitigation sites have become available for scrutiny, generally reinforce the early concerns. For example, Erwin (1991) found that, of 40 mitigation projects in south Florida involving wetland creation and restoration, only about half of the required 430 ha of wetlands had been constructed and that 24 of the 40 projects (60%) were judged to be incomplete or failures. The most significant problems identified with created wetlands were improper water levels and hydroperiod. Sifneos et al. (1992) collected information from permits on Louisiana, Alabama, and Mississippi wetland mitigation projects and found that in Louisiana (their primary area of interest) only 8% of areas impacted by dredge-and-fill activity was compensated for, and $>50\%$ of the areas receiving permits covered <0.4 ha. Additionally, only 10% of the mitigation wetlands were monitored by at least one site visit. The lack of standardized record-keeping from state to state made the study difficult. The study suggests that follow-up monitoring and information on wetland functions be required in future permit decisions. Kentula et al. (1992) investigated several mitigation wetlands in Oregon and Washington and found a net loss in wetland area of 43% for Oregon and 26% for Washington. Data were either incomplete or of poor quality and up-to-date standardized databases were recommended. In a similar study, but without field checks, Holland and Kentula (1992) examined >300 Section 404 permits issued in California from 1971 to 1987 and found that while 1260 ha of compensatory mitigation (wetland creation, restoration, or preservation) had been required for impacts to 1180 ha of wetlands over that period, there was little follow-up of the permits and fewer than one-third (31.5%) required any field monitoring. Confer and Niering (1992) found that when comparing five created freshwater marshes with five nearby natural ones, the created marshes generally had greater water depth and thus more open water. They state that most of their created wetlands were highly dependent on highway runoff as a water source. Roberts (1993), quoting several ecologists, summarizes the skepticism by calling wetland trading "a loser's game."

IMPROVING THE ODDS OF WETLAND SUCCESS

We propose three general concepts that will need attention of those involved in wetland mitigation if we are truly going to address the issue of creating and restoring viable wetland ecosystems: (1) Understand wetland function; (2) Give the system time; and (3) Allow for the self-designing capacity of nature. These points are discussed in detail below.

Understand wetland function

Mitsch and Cronk (1992) proposed that the "know-how" of building and restoring wetlands is based on an empiricism with little scientific backing, and is learned and relearned every time a new wetland is built. Wetland restoration and creation are relatively new fields and few engineers are trained in ecology and few ecologists have any experience in engineering methods. Engineers, consultants, scientists, and landscape architects can, and frequently do, claim to be experts with little experience or little knowledge of wetland ecology; without any certification standards for individuals involved in wetland creation and restoration, projects are often carried out by organizations and individuals not well versed in wetland ecology. A relatively high number of "failures" of mitigation wetlands can be attributed to a general lack of understanding of first principles of wetland science.

For example, an understanding of wetland hydrology as the fundamental forcing function of wetlands is well understood conceptually (Mitsch and Gosselink 1993) yet not always put into practice by many of those involved in wetland mitigation. The importance of hydrology is discussed in detail in a companion paper by Bedford (1996). Erwin (1991) pointed out that a number of Florida wetlands were considered failures in his Florida study because they lacked suitable hydrology. In so-called "on-site mitigation," wetlands are devel-

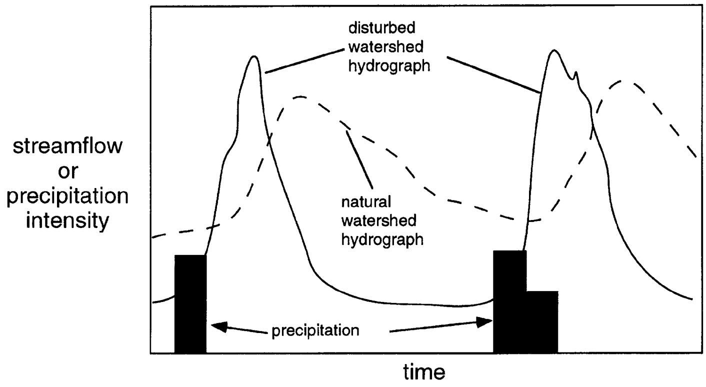

FIG. 1. Comparison of a hypothetical stream hydrograph in a natural watershed vs. one from a highly disturbed urban or suburban watershed. Placing the wetland in either of these two watersheds would probably lead to significantly different wetland structure and function.

oped in watersheds near the wetlands being drained or lost; their success is often problematic because of the usual proximity of the mitigation project to a human-altered landscape and the accompanying changes in hydrologic conditions. In these settings, created and restored wetlands can be subjected to "flashy" streams and human-regulated hydrologic conditions. In urban and suburban settings, floods are often greater and occur more quickly after precipitation; low-flow conditions are drier than in a "natural" hydrology (Dunne and Leopold 1978). Both of these conditions lead to generally greater water level fluctuations compared to those in more natural settings (Fig. 1). Unpredictable and rapidly fluctuating hydrology can lead to washouts, scouring, planting failure, and animal and macroinvertebrate emigration, leading to decreased biodiversity and even loss of water quality function.

Give the system time

A flaw in the measurement of mitigation wetland success is the limited amount of time that regulators and the land development process allow for newly created wetlands to develop before passing judgment. The legal and economic necessities seem to dictate the ecological patterns of nature, encouraging "quick-fix" wetlands while not allowing for the stochasticity of nature. Engineers have long recognized the probabilistic nature of hydrologic events (e.g., precipitation and streamflow) yet relatively deterministic indicators such as wetland plant viability, open water area, endangered species, and waterfowl are expected to develop in a relatively short time span, usually 5 yr. The very best that we can have after 5 yr of monitoring a mitigation wetland is a general idea of the wetland's ecological trajectory and even less understanding of its function.

In one of the longest-running documentations of a constructed wetland in this country, an 8-ha freshwater tidal marsh (Windmill Point), was constructed in 1974–1975 within dikes in the James River in eastern Virginia, USA. Early indications, from 1978 to 1982, considered the wetland a success as it supported a diversity of herbaceous vegetation typical of tidal freshwater marshes (Newling and Landin 1985). At that time the monitoring was referred to as "long-term." But the dikes were breached in 1986 due to flooding on the James River, eliminating the vegetation and submersing the wetland in the river (Landin 1994, *personal communication*). Sixteen years after construction the project could be termed by some as a hydrologic and ecologic failure if long-term survival of the wetland was one if its goals.

Because of the stochastic nature of hydrologic events and the slow development of ecosystems, sometimes in spurts, sometimes in the slow process of recruitment and growth, the 5-yr time horizon can be viewed as arbitrary and probably much too short. As ecological models show (see e.g., Jørgensen 1994), the further initial conditions are from steady-state, the longer it will take for that system to reach or approach steady state (Fig. 2). Short monitoring times favor measuring success with transplanted vegetation and pioneer organisms; long-term success is less dependent on these initial conditions.

Allow self-design

There are two general approaches for introducing vegetation (and other organisms) in wetland creation and restoration projects. One is the "designer" approach of introducing species and expecting their survival in Gleasonian zones, akin to gardening or landscape architecture. The other emphasizes the "self-design" or "self organization" capacity of Nature to both recruit species on its own and to make choices from those species introduced by humans (Odum 1989, Mitsch 1993). In self-design the emphasis is on the introduction of as many species as possible, knowing that natural forces will help in the ultimate design by choosing the most appropriate species. Self-design also recognizes the importance of natural colonization of species in wetlands.

In one of the few studies to make a preliminary comparison of these two general approaches, Reinartz and Warne (1993) compared 11 created wetlands in southeastern Wisconsin that were naturally colonized with 5 wetlands in the same region where 22 species were

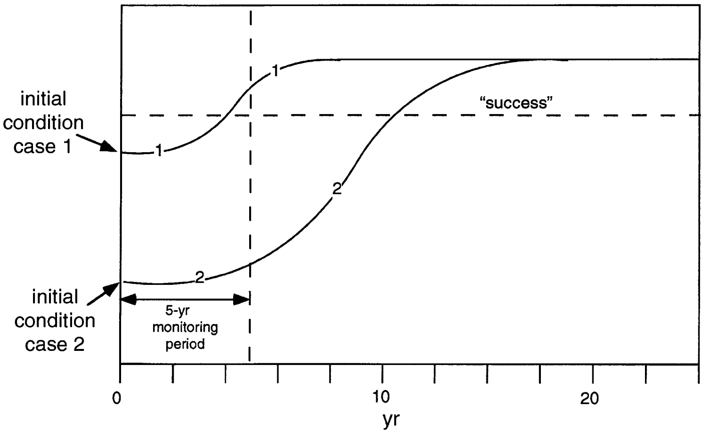

FIG. 2. Hypothetical comparison of the pattern of one wetland criterion for "success," e.g., percentage vegetation cover, for two different initial conditions at the same hypothetical wetland site. In Case 1 the wetland would be considered a "success" after 5 yr, while in Case 2 the wetland would be considered a "failure." Each wetland case could end up eventually at the same level, but well after 5 yr. In reality, a multiplicity of criteria would be used in this comparison.

introduced by seeding. The diversity and richness of plants in the colonized wetlands increased with age, size, and proximity to the nearest wetland source even though *Typha* spp. comprised 15% of the vegetation for 1-yr-old wetlands, and 55% for 3-yr-old wetlands. Seeded wetlands had a high species diversity and richness after 2 yr and *Typha* cover in the seeded sites was lower than in the naturally colonized sites after a 2-yr period.

Many studies to date (e.g., Confer and Niering 1992, McKnight 1992), especially those on restoration of non-coastal wetlands, have probably over-predicted—because of short time horizons and small spatial scales—the survivability of transplanted species in "designer" wetlands. (An exception to this short time horizon is the long-term observation of Frenkel and Boss [1988], through aerial photography, of the spread of *Spartina patens* in areas along Oregon's coastal wetlands.) With enough time and space, introduced species may be less successful than we initially believed. A better idea is to give the wetland system many possibilities through multiple-seeding, multiple-transplanting, and establishment of hydrologically open systems; this allows nature to participate in the wetland design.

PROVIDING THE NEEDED RESEARCH TOOLS

In addition to the above suggestions for wetland managers and ecological engineers who are attempting to design and monitor wetlands, there are some important approaches that wetland scientists can use to reduce the uncertainty of wetland mitigation.

Select the proper experimental scale

The limited ability of science as we generally practice it to both understand and solve our dilemmas in natural resource conservation was argued by Ludwig et al. (1993) and debated in the pages of *Ecological Applications* (Levin 1993). Taking the cue from Holling (1993) and Costanza (1993) in that discussion, we question whether reductionistic experimental science, with its short time scales (often the time required for a Ph.D. dissertation) and its small spatial scales (often in laboratories or small field plots) can correctly prescribe how to build large wetlands. A holistic systems approach, with the appropriate time and space scales, should at least have equal emphasis.

As one example, a number of studies of wetland function were carried out with four full-scale constructed wetlands at the Des Plaines River Wetland Demonstration Project in northeastern Illinois (Sanville and Mitsch 1994). Hydrologic conditions were varied for high- and low-flow conditions for entire wetlands (average size: 2.4 ha), not just experimental plots; the studies were carried out over 3 yr. Researchers had important findings in estimating detention and mixing (Kadlec 1994), water quality function (Hey et al. 1994, Phipps and Crumpton 1994), sedimentation (Brueske and Barrett 1994, Fennessy et al. 1994*a*), vegetation development (Fennessy et al. 1994*b*), aquatic metabolism (Cronk and Mitsch 1994*a, b*), and avian success (Hickman 1994) in created wetlands, most as a function of hydrology.

In a comparison of two natural tidal marshes with a 0.65-ha constructed marsh in coastal Virginia 5 yr after construction, Havens et al. (1995) found seasonal differences in fish and shellfish abundances between natural and constructed marshes, with lower numbers in the latter. They attribute the differences to relative lack of organic carbon and less morphometric heterogeneity (e.g., stream rivulets, microtopography) in the created marsh.

We recently initiated a full-scale comparison of "self-design" and "designer" approaches to wetlands at the Olentangy River Wetland Research Park at The Ohio State University (Fig. 3; Mitsch and Wu 1995, Mitsch 1995). In one newly constructed wetland basin (1 ha), we planted, in approximately the stratification that we would find in nature, ≈2500 individuals representing 14 species of wetland plants. In an identical constructed wetland basin nearby, we planted nothing. Hydrologic conditions are being maintained as similar as possible in the two basins and there is no predeter-

FIG. 3. The Olentangy River Wetland Research Park at The Ohio State University in Columbus, Ohio, USA, is a whole-ecosystem long-term experiment begun on 14 May 1994 with the planting of one of the deep-water marshes shown in foreground (right basin) with ≈2500 plants representing 15 wetland species. The second deep-water marsh (left basin) remains unplanted. Each basin is 1 ha in size and water is supplied by pumps in the lower right-hand corner of the site to create a similar hydrology for each basin. The Olentangy River, shown flowing from bottom right to the top of the picture (with the university ≈0.5 km downstream of the site on the horizon of the picture), is the source of the water, which is pumped in proportion to the river flow in the same patterns for each wetland basin. The photo was taken in November 1993 prior to the introduction of water to the wetlands (photo by Mark Myers, Apex, Columbus, Ohio).

mined completion date to our experiment. We believe that our "experiment" is closer to the scale necessary for documenting the forces, e.g., plant recruitment, geese and muskrat invasions, etc., that influence ecosystem development. Working at this full scale precludes extensive replication because of land and construction costs, yet our understanding of ecosystem development and other wetland functions will come only from studying spatial scales and longer time scales to supplement traditional ecological experiments.

Develop predictive modelling

Little attention has been paid to ecological modelling—the one tool that can expand the time horizon—in predicting success of created and restored wetlands. While this approach must be used with caution and proper qualifications, it enables ecologists to project into the future and estimate how long it will take the mitigation wetland to achieve some type of steady state. A few publications (Costanza and Sklar 1985, Mitsch et al. 1988, Mitsch 1994) have reported on the state of the art of simulation modelling in wetland ecology, but this powerful "systems" tool has rarely been used to predict mitigation success. Stochastic inputs, adaptive model structure (Jørgensen 1994), higher-order modelling languages (e.g., STELLA) and spatially dynamic models are useful advances in ecological modelling, but simple-structure models that aggregate components into overall variables such as "vegetation" or "nutrients" can be just as effective (Mitsch et al. 1995). In an application of modelling for a mitigation project in central Ohio, Niswander and Mitsch (1995) used simulation models both to "fill in" information to make calculations about ecosystem function (phosphorus retention) of a created freshwater marsh and to "enhance the time horizon" by predicting one structural aspect of this project well into the future—the survival of planted wetland trees over the next 50 yr. Modelling, of course, will not provide an exact prediction of conditions well into the future but, when used with good wetland ecology and sufficient field monitoring, it can provide another tool for those interested in predicting the future of created and restored wetlands.

CONCLUSIONS

There is optimism that wetlands can be created and restored and that wetland function can be replaced, despite a recent spotty record in the United States with the mitigation of wetland loss. The spotty record is due, in our opinion, to little understanding of wetland function by those constructing the wetlands, insufficient time for the wetlands to develop, and a lack of recognition or underestimation of the self-design capacity of nature. Understanding wetlands enough to be able to create and restore them requires a substantial training in plants, soils, wildlife, hydrology, water quality, and engineering. We should give mitigation projects involving freshwater marshes enough time, closer to 15–20 yr rather than 5 yr, before judging their success. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. For example, the restoration of certain coastal salt marshes has been suggested to require at least 50 yr (Frenkel and Morlan 1991). Finally, we should recognize that Nature remains the chief agent of both self-design and ecosystem development; humans are not the only participants in the design process.

Science will need to make significant contributions to the process of reducing our uncertainty about predicting wetland success. Wetland mitigation needs to become part of an applied ecological science, not a technique that is relearned each time without theoretical underpinnings. Scientists need to make the connections between structural measures (e.g., vegetation density, diversity, productivity) and functions such as wildlife use, organic sediment accretion, or nutrient retention in quantitative and carefully designed experiments. Simply having a list of plant species is inadequate for regulators or managers to estimate ecosystem function. Simulation models and experimentation at the proper spatial and temporal scales should be able to help us predict the behavior of these wetlands and estimate proper designs.

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Rapid decline of California’s native inland fishes: A status assessment

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ABSTRACT

A quantitative protocol was developed to determine conservation status of all 129 freshwater fishes native to California. Seven (5%) were extinct; 33 (26%) were found to be in danger of extinction in the near future (endangered); 33 (26%) were rated as sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable); 34 (26%) were rated as declining species but not in immediate danger of extinction. Only 22 (17%) species were found to be of least concern. Of 31 species officially listed under federal and state endangered species acts (ESAs), 17 (55%) were rated as endangered by our criteria, while 12 (39%) were rated vulnerable. Conversely, of the 33 species that received our endangered rating, only 17 (51%) were officially listed under the ESAs. Among the seven metrics used to assess extinction threat, climate change, area occupied and anthropogenic threats had the largest negative impacts on status. Of 15 categories of causes of decline, those most likely to diminish status were alien species, agriculture, and dams. Overall, 83% of California’s freshwater fishes are extinct or at risk of becoming so, a 16% increase since 1995 and a 21% increase since 1989. The rapid decline of California’s inland fishes is probably typical of declines in other regions that are less well documented, indicating a strong need for improved conservation of freshwater ecosystems.

1. Introduction

Extinction in freshwater environments is a world-wide crisis (Moyle and Williams, 1990; Saunders et al., 2002; Dudgeon et al., 2006) which is poorly documented (Strayer and Dudgeon, 2010; Vörösmarty et al., 2010). Loss of biodiversity seems to be occurring more rapidly from fresh water than from any other broad habitat type (Jenkins, 2003; Dudgeon et al., 2006). Driven by recent global assessments of mollusks (Bogan, 2008), crabs (Cumberlidge et al., 2009), amphibians (Stuart et al., 2004), and dragonflies (Clausnitzer et al., 2009), the number of freshwater species listed on International Union for the Conservation of Nature (IUCN) Red Lists has more than tripled since 2003 (Darwall et al., 2008). Nevertheless, the best-studied indicators of the problem remain freshwater fishes (Magurran, 2009) which account for about one-third of all described vertebrates, with roughly 13,000 species (Helfman, 2007; Lèvêque et al., 2008). In 1992, 20% of the world’s freshwater fish fauna was estimated to be extinct or in serious decline (Moyle and Leidy, 1992). Less than 20 years later, 37% of the 3481 freshwater fish species evaluated globally by IUCN were regarded as extinct or imperiled (declining towards, or threatened, with extinction, Vié et al., 2009), although the IUCN database is likely biased towards including declining species. At the continental scale, 46% of 1187 described freshwater and diadromous fish species native to North America are extinct, imperiled, or have one subspecies or distinct population that is imperiled (Jelks et al., 2008) with the rate of extinction steadily increasing (Ricciardi and Rasmussen, 1999). Not surprisingly, the number of imperiled fish species is highly correlated with human population and economic growth (Limburg et al., 2011).

While large-scale assessments spotlight the global extent of the crisis, severity and causes are best understood through intensive studies of regional fish faunas because status can be repeatedly, systematically, and quantitatively documented over relatively short time periods. In this paper, we analyze the status of California’s 129 native freshwater fishes. This regional fauna is reasonably well documented, occupies a wide variety of habitats, and exhibits a wide range of life history patterns including anadromy (Moyle, 2002; Moyle et al., 2008, 2010). Their status was previously analyzed in 1989 (Moyle and Williams, 1990) and 1995 (Moyle et al., 1995). Here, we use a new quantitative protocol to determine conservation status of each species. This protocol allows us to make status determinations independent of official agency designations and to find species needing protection that have been overlooked so far by state and federal agencies. Comparisons with official status designations also serve as a check on the usefulness of our protocol. In this paper, we answer the following questions:

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1. What is the status of California's inland fish fauna?
2. Are the fishes continuing to decline?
3. What factors are most strongly associated with declining status?
4. How do our results fit with official status designations?

1.1. The inland fishes of California

California's large size (411,000 km^2), length (1400 km and 10° latitude) and complex topography result in diverse habitats, including 50 isolated watersheds in which fish have evolved independently (Moyle, 2002, Moyle and Marchetti, 2006). For most of the state, the climate is Mediterranean; most precipitation falls in winter and spring, followed by long dry summers. This results in rivers that have high annual and seasonal variability in flows (Mount, 1995) and native fishes adapted to hydrologic extremes. There are 129 native inland fishes (defined as those breeding in fresh water) currently recognized (Appendix 1, which includes scientific names of fishes mentioned). Of these, 63% are endemic to the state and an additional 19% are also found in one adjacent state. Thus California's fishes fall within political and zoogeographic boundaries that largely coincide, important for a bioregional assessment (Moyle, 2002).

Conditions in California have produced an unusual number of anadromous fishes (24%) as well as fishes that thrive in isolated environments such as desert springs, intermittent streams, and alkaline lakes. Most fishes live in rivers of the Central Valley and North Coast, areas having the most water and most diverse aquatic habitats. Recent genetic and taxonomic studies have underscored the distinctiveness of California fishes and increased the number of taxa from 113 in 1989 (Moyle and Williams, 1990) to 129 in the present study.

Most California rivers have been dammed and diverted to move water from places of abundance to places of scarcity, where most Californians live (Hundley, 2001). Not surprisingly, native fishes have been in steady decline since the mid-19th century, although the first formal evaluation of their status was not conducted until 1989. At that time, 7 species (5%) were extinct, 15 (13%) were formally listed as Threatened or Endangered under the state or federal ESAs, and 51 (43%) were designated as Species of Special Concern by the State of California, indicating they were in decline or had small, vulnerable populations but were not yet threatened with immediate extinction (Moyle and Williams, 1990). The number of declining species has steadily increased so that in 1995, there were 18 (16%) listed and 51 (44%) in decline (Moyle et al., 1995). Today, the numbers are 30 (23%) listed and 70 (54%) in decline, meaning that 83% of California's native fishes have the potential to go extinct in coming decades or are already extinct (Appendix 1) (Fig. 1).

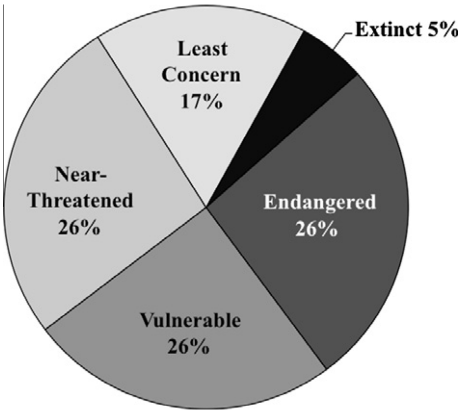

Fig. 1. Status of fishes ($N = 129$) native to inland waters of California in 2010. All threat categories are approximately equivalent to IUCN threat levels of the same name. Extinct = globally extinct or extirpated in the inland waters of California. Endangered = highly vulnerable to extinction in its native range, approximately equivalent to IUCN threat level of *endangered* or *critically endangered*. Vulnerable = could easily become threatened or endangered if current trends continue. Near threatened = populations in decline or highly fragmented. Least concern = no extinction threat for California populations.

2. Methods

2.1. Sources of information

Taxa used were those that qualified as species under the federal Endangered Species Act of 1973, so include species, subspecies, Evolutionarily Significant Units, and Distinct Population Segments recognized by one or more agencies. The biology and status of each species was determined from information in Moyle (2002), Moyle et al. (1995, 2008, 2010), additional reports and papers from intensive literature searches, and by personal communications with biologists working with each taxon. The information was summarized in standardized species accounts which included evaluation of status. All accounts were reviewed by experts on each species. In a few cases, information was updated by field investigations by the authors. The status of each species is as of December 31, 2010.

2.2. Quantitative evaluation of status

Species status was determined using seven metrics scored on a 1–5 scale (Table 1) where 1 was a low score indicating major negative impact on status and 5 was a high score, indicating either no or a positive impact on status. Scores were assigned according to a rubric which was standardized to each threat category (Table 2). Metrics were designed to capture all significant risk factors faced by freshwater fishes while keeping redundancy among metrics to a minimum. Principal component analysis revealed relatively equal weighting of all seven metrics on the final status scores (eigenvectors for principal component one: area occupied, 0.322; adult population, 0.398; intervention dependence, 0.405: tolerance 0.341: genetic risk 0.406; climate change 0.381: anthropogenic threats 0.382). For each species, the seven criteria were averaged to produce a single score for which the threat of near-term extinc-

Table 1
Metrics for determining the status of California fishes, with Sacramento splittail as example. Each metric is scored on a 1–5 scale where 1 is a major negative factor contributing to status, 5 is a factor with no or positive effects on status, and 2–4 are intermediate values. Scoring is described in Table 2.

Metric	Score	Justification
Area occupied	2	Two distinct populations in San Francisco Estuary, using different rivers for spawning
Estimated adult abundance	4	Large in upper estuary, likely small in lower
Intervention dependence	3	Floodplain areas need special management for spawning during droughts
Tolerance	5	One of the most physiologically tolerant native fishes
Genetic risk	3	Two populations; genetically fairly diverse
Climate change	1	Extremely vulnerable to droughts and sea level rise reducing habitat
Anthropogenic causes of decline	2	Multiple, see Table 3
Average	2.9	20/7
Certainty (1–4)	3	Well studied

tion increased as the score decreased. The scores were placed in categories following the IUCN categories for imperiled species (Vié et al., 2009). Fishes with scores between 1.0 and 1.9 were rated *endangered* and regarded as being in serious danger of extinction, while those scoring 4.0–5.0 were regarded as *least concern*. Species with scores of 2.0–2.9 were rated *vulnerable* and regarded as likely to become threatened or endangered in the near future, while those scoring between 3.0 and 3.9 were in decline but not yet in immediate danger of extinction and so were rated *near-threatened*. In order to simplify discussion, all species scoring between 1.0 and 3.9, were collectively referred to as ‘‘imperiled’’ because they either had declining populations or had small, isolated populations that increased their risk of extinction. The scores only apply within California, so rare species with wide distributions and high abundance outside the state (e.g., chum and pink salmon) might receive low scores within the state even if there is no danger of extinction as species.

2.3. Metrics used to score taxon status

2.3.1. Area occupied

We assumed that extinction threat was lower for species spread over many watersheds than for those with limited distributions. Inland fishes were scored by number and interconnectedness of large watersheds occupied. Anadromous fishes were scored on number of watersheds occupied (i.e., Functionally Independent Populations, Lindley et al., 2004, 2006).

2.3.2. Estimated adult abundance

In general, the more adult individuals in a population, the more likely it is to persist through time. However, quantitative population estimates are rare, especially for non-game fishes (Jelks et al., 2008). We therefore used order-of-magnitude estimates of average annual numbers of mature individuals at the time of the study as a proxy for population size (Table 2). While we recognized

Table 2

Scoring rubric for seven metrics used to evaluate status of native freshwater fishes of California. Final status score is the average score of all seven metrics.

1A. Area occupied: resident fish

1. 1 watershed/stream system in California only based on watershed designations in Moyle and Marchetti (2006)
2. 2–3 watersheds/stream systems without fluvial connections to each other
3. 3–5 watersheds/stream systems with or without fluvial connections
4. 6–10 watersheds/stream systems
5. More than 10 watersheds/stream systems

1B. Area occupied: anadromous fish

1. 0–1 apparent self-sustaining populations
2. 2–4 apparent self-sustaining populations
3. 5–7 apparent self-sustaining populations
4. 8–10 apparent self-sustaining populations
5. More than 10 apparent self-sustaining populations

2. Estimated adult abundance

1. ⩽500
2. 501–5000
3. 5001–50,000
4. 50,001–500,000
5. 500,000+

3. Dependence on human intervention for persistence

1. Captive broodstock program or similar extreme measures required to prevent extinction
2. Continuous active management of habitats (e.g., water addition to streams, establishment of refuge populations, or similar measures) required
3. Frequent (usually annual) management actions needed (e.g., management of barriers, special flows, removal of alien species)
4. Long-term habitat protection or improvements (e.g., habitat restoration) needed but no immediate threats need to be dealt with
5. Species has self-sustaining populations that require minimal intervention

4. Environmental tolerance under natural conditions

1. Extremely narrow physiological tolerance in all habitats
2. Narrow physiological tolerance to conditions in all existing habitats or broad physiological limits but species may exist at extreme edge of tolerances
3. Moderate physiological tolerance in all existing habitats
4. Broad physiological tolerance under most conditions likely to be encountered
5. Physiological tolerance rarely an issue for persistence

5. Genetic risks/problems

1. Genetic viability reduced by fragmentation, genetic drift, and isolation by distance, owing to very low levels of migration, and/or frequent hybridization with related fish
2. As above, but limited gene flow among populations, although hybridization can be a threat
3. Moderately diverse genetically, some gene flow among populations; hybridization risks low but present
4. Genetically diverse but limited gene flow to other populations, often due to recent reductions in connectivity
5. Genetically diverse with gene flow to other populations (good metapopulation structure)

6. Vulnerability to climate change

1. Vulnerable to extinction in all watersheds inhabited
2. Vulnerable in most watersheds inhabited (possible refuges present)
3. Vulnerable in portions of watersheds inhabited (e.g., headwaters, lowermost reaches of coastal streams)
4. Low vulnerability due to location, cold water sources and/or active management
5. Not vulnerable, most habitats will remain within tolerance ranges

7. Anthropogenic causes of decline

1. 1 or more causes rated critical or 3 or more threats rated high–indicating species could be pushed to extinction by one or more threats in the immediate future (within 10–25 years)
2. 1 or 2 causes rated high; species could be pushed to extinction in the foreseeable future (within 50 years)
3. No causes rated high but 5 or more threats rated medium; no single threat likely to cause extinction but all threats in aggregate could push species to extinction in the next century
4. 1–4 causes rated medium; no immediate extinction risk but taken in aggregate causes reduce population viability
5. 1 medium, all others low; known causes do not imperil the species

that the effect of adult population size upon persistence differs for large, long-lived species in contrast to small, short lived species (Flather et al., 2011), we rarely found this to be an issue for California fishes.

2.3.3. Dependence on human intervention for persistence

This metric scored how dependent a species was on direct human intervention for its continued survival. Thus, Eagle Lake rainbow trout received a score of '1' because it is completely dependent on artificial propagation for its persistence, while rough sculpin (a state listed species) scored a '4', because it needs only continued protection of its spring-fed streams (managed for trout fisheries) to maintain abundance.

2.3.4. Environmental tolerance under natural conditions

This metric measures overall physiological tolerance in relation to existing conditions in a species' range. Where possible this was based on results of laboratory or field studies of responses to ranges of temperature, salinity, dissolved oxygen and similar variables. However, if a species had fairly broad physiological tolerances in the laboratory but lived in waters (e.g., streams in southern California) where habitat conditions naturally approached the species limits of tolerance to temperature and other factors, its environmental tolerance was scored lower than that of a species likely to rarely encounter such conditions.

2.3.5. Genetic risks

This metric incorporates two concepts, hybridization and genetic bottlenecks. Hybridization with a related species, especially an introduced species, can result in sterility, reduced fitness and swamping of native genomes (Perry et al., 2002). Similarly, interbreeding between artificially propagated (hatchery) and wild individuals can reduce fitness of offspring (Araki et al., 2009).

In order to avoid over-weighting the impact of small population size on status, genetic impacts of small population size were not considered here. However, low genetic variation from hatchery management and/or other past reductions of effective population size may increase extinction threat (e.g., reduce the ability of species to adapt to environmental change) irrespective of current population size and so was included under this metric.

2.3.6. Vulnerability to climate change

Climate change is already having effects, as reflected in rising water temperatures and more variable stream flow; such effects are only likely to increase (Hayhoe et al., 2004; Anderson et al., 2008; Cayan et al., 2009). Vulnerability to future climate change was determined by examining geographic range of each species, its isolation (potential for finding refuges), and the types of habitat it inhabits. Species considered to have low vulnerability included those with broad thermal tolerances and those living in aquatic environments shielded (at least for now) from climate-driven change, such as spring-fed systems with constant sources of water (e.g., bigeye marbled sculpin and Saratoga Springs pupfish).

2.3.7. Anthropogenic causes of decline

We rated fifteen major categories of landscape-level factors likely to increase extinction risk as having no, low, medium, high or critical effect on species status, based on available information for each species summarized in Moyle (2002), and Moyle et al. (2008) (Table 3). A cause rated "critical" could push the species to extinction in three generations or 10 years which ever is less. A cause rated "high" could push the species to extinction in 10 generations or 11–50 years which ever is less. A cause rated "medium" was unlikely to drive a species to extinction by itself but contributed to increased extinction risk over the next century. A cause rated "low" could reduce populations but extinction was considered unlikely as a result. A cause rated "no" (no effect) has no known negative impact to the taxon under consideration.

For some species, a single threat was considered grave enough to cause extinction (e.g., hybridization for California golden trout), but for most species, number as well as severity of potential causes contributed to our final score (Table 2). We judged any species with even one critical rating as being in danger of extinction in the near future. The 15 causes of decline are summarized below.

2.4. Anthropogenic causes of decline

2.4.1. Large dams

Dams and their reservoirs had high impacts on status if they blocked access to much of the species range, caused major changes to physical habitat, or changed water quality and quantity. We regarded dams as having a low impact if they were present within the range of the species but their effects were small or beneficial.

2.4.2. Agriculture

Effects of agriculture were rated high if agricultural effluent polluted waterways of major importance to the species, if diversions severely reduced flow, if large amounts of silt flowed into streams from farmland, if pesticides had significant effects, and if other agricultural factors directly affected waters in which a species lives. We regarded agriculture as having a low impact if it was not pervasive in the species' range or was not known to be causing significant changes to a species' habitats.

Table 3
Ratings of major anthropogenic factors causing declines of freshwater fishes of California, using Sacramento splittail as an example. See text for definitions of ratings of causes.

Status metric	Rating	Explanation
Major dams	High	All waters have flows regulated by dams and diversions; frequency of flooding of spawning areas reduced
Agriculture	Medium	Pollution, channel modification, entrainment in major diversions
Grazing	Low	Little known impact but occurs in spawning areas
Rural residential	Low	Residences on the edges of rearing marshes
Urbanization	Medium	Most habitat is on urban fringes; sewage; water diversion and entrainment
Instream mining	Low	Some gravel mining in floodplain areas
Mining	Low	Legacy effects of gold mining, e.g. mercury
Transportation	Medium	Migratory corridors lined with roads and railroads,
Logging	No	No known impact
Fire	Low	Indirect impacts from marsh/floodplain fires possible
Estuarine alteration	High	Major habitat areas highly altered
Recreation	Low	Recreational boating etc. may affect habitat
Harvest	Medium	Some harvest for bait and of migrating adults for food
Hatcheries	No	No known impact
Alien species	Medium	Effects of new invaders unpredictable; predation and competition possible

2.4.3. Grazing

We separated livestock grazing from other agriculture because its effects are widespread on range and forest lands throughout California. Impacts were rated high where stream banks were trampled and riparian vegetation was removed, resulting in incised streams, drying of adjacent wetlands, and lowering of water tables. Removal of vegetation can also result in increased siltation, higher water temperatures, and decreased summer flows. Impacts were rated low where grazing was present but had minimal negative effects.

2.4.4. Rural residential

As California's human population grows, people spread across the landscape, often settling in diffuse patterns along or near streams. Rural development results in water removal, streambed alteration (to protect houses, create swimming holes, construct road crossings, etc.), and pollution (especially from septic systems). We rated such housing as having high effect on fishes where it was abundant and unregulated and caused major changes to streams. Where such housing was present but scattered, the effects were usually rated as low.

2.4.5. Urbanization

Streams that flow mostly through cities are generally highly altered to reduce flooding and remove water, while pollution is pervasive, from sewage, runoff, and storm drain discharges. Generally, the more the important waters for a species were encompassed by urban development, the higher we rated the effects of urbanization on the species.

2.4.6. Instream mining

The most severe instream mining in California took place during the 19th and early 20th centuries when miners buried (through hydraulic mining), excavated, and dredged riverbeds for gold. We often gave the legacy effects on fishes of mining medium or high ratings. Similar scores were given to species affected by legacy effects of instream gravel mining, which creates large pits in streambeds and alters stream banks. Such mining is largely banned (in favor of mining off-channel areas) today. Impacts of contemporary recreational and professional suction dredge mining resulted in some intermediate ratings.

2.4.7. Mining

The effects of hard-rock mining (mostly for gold and mercury) were rated according to how much of a species' habitat was affected by tailings and acidic mine drainage. We gave high ratings where major mines, even if abandoned, had toxic tailings poised on edges of waterways (e.g., Iron Mountain Mine near Redding, on the Sacramento River). Our low threat scores usually came from situations where old mines were present but effects on biota of nearby streams were not evident.

2.4.8. Transportation

Many rivers and creeks have roads and railroads running along one or both sides, confining stream channels and causing pollution from siltation, vehicle emissions, waste disposal, and accidents. In addition, culverts and other hydrologic modifications associated with transportation often restrict fish movements. Our ratings here were based on how much a species depended on streams altered by roads and railways and how severe the alterations were.

2.4.9. Logging

Timber harvest is a major use of forested California watersheds which support many native fishes, including anadromous salmonids. Logging was relatively unregulated until mid-20th century, resulting in major alteration and degradation of stream habitats. Although better regulated today, logging is still a pervasive activity resulting in siltation of streams and reduced habitat complexity. We gave high threat ratings to species dependent on streams degraded by either legacy or contemporary effects of logging. Low threat ratings were given where such effects are of small significance.

2.4.10. Fire

Wildfires are part of California's natural landscape but human activities have increased their intensity and frequency. High ratings were given where fish habitat was, or has the potential to be, seriously degraded by catastrophic wildfire, via post-fire erosion, loss of riparian canopy, increased temperature and spilled fire-fighting chemicals. We assigned low ratings to fishes that live in areas where wildfires occur but for various reasons, such as low fuel load, have minimal impact on streams.

2.4.11. Estuary alteration

Many California fishes depend on estuaries for at least part of their life cycle. All California estuaries are highly altered by human activity, including siltation, pollution, diking and draining, bridge construction, and removal of sandbars between the estuary and ocean. Thus, the more estuarine-dependent a fish species is, the more likely we were to assign a high rating to estuary alteration as a cause of decline.

2.4.12. Recreation

Recreational use of streams has greatly increased with the human population. We found recreational effects usually to be low, although they were often concentrated when stream flows were low. We rated recreation effects as high when a taxon depended on streams that are heavily disturbed (e.g., by off-road vehicles) or contains enough boaters and swimmers to disturb spawning or holding (e.g., salmon and steelhead).

2.4.13. Harvest

We rated harvest effects as high for fishes known to be subject to overharvest, especially large species (e.g., sturgeons) or species that become isolated and are therefore vulnerable to poaching (e.g., summer steelhead). We rated both legal and illegal harvest, although for most native resident fishes, legal fishing was rarely an issue.

2.4.14. Hatcheries

Most fishes are not supported by fish hatcheries but for those that are, hatchery fish often have negative effects on wild populations through competition for habitat and food, direct predation, and interbreeding which results in loss of genetic diversity (Moyle, 2002). We rated severity of these effects based in part on hatchery dependence and/or known interbreeding between wild and hatchery populations. We regarded conservation hatcheries that focus on rare species as having relatively low impacts because of their efforts to reduce negative hatchery effects as much as possible.

2.4.15. Alien species

Non-native species are present in every California watershed and their impacts on native species through hybridization, predation, competition, and disease are often severe (Moyle and Marchetti, 2006). We rated this category as high for a species if there were major direct or indirect impacts of alien invaders. We rated it as low if contact with alien species was infrequent or not known to be negative.

2.5. Certainty index

Because quality, amount and reliability of information varied among species, we developed a certainty index for our scores, on a 1–4 scale, where we scored status evaluations as follows:

1. Based on expert opinion (including our own) with little hard data.
2. Based on expert opinion supplemented with limited data and reports.
3. Based on extensive information found mainly in agency reports.
4. Based on reports from multiple sources including peer-reviewed literature.

This index lets managers know the risks involved in basing management decisions on our results.

3. Results

Of 129 freshwater fishes native to California, four are globally extinct (3%) and three (2%) are extirpated from the state (scores of 0). Another 33 (26%) are in danger of extinction in the near future if present trends continue (endangered, scores of 1.0–1.9) while 33 (26%) are sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable, scores of 2.0–2.9). Thirty-four (26%) are in long-term decline or have small isolated populations but do not face extinction in the foreseeable future, unless conditions change (near-threatened, scores of 3.0–3.9). The remaining 22 species (17%) are of least concern (4.0–5.0) (Fig. 1). The average status score of all extant taxa was 2.7. The certainty ratings of our status evaluations averaged 2.7 out of 4.0 (SD 1.2), with 66% of accounts based on extensive literature (4.0) and only 5% based mainly on our professional judgment (1.0).

Of the 31 species currently listed as Endangered or Threatened under federal and/or state endangered species acts, 17 had status scores of 1.0–1.9 and 12 had scores of 2.0–2.9 by our rating system (Appendix Table 1). Listed species made up half of the 33 species to which we gave status scores of 1.0–1.9 and 44% of extant species with scores <2.9. The number of listed species increased from 14 in 1989 to 18 in 1990 to 31 in 2010, a listing rate of about 0.8 species per year (Fig. 2). The total number of imperiled species increased from 55 to 100 in this same period (2.1 species per year) (Fig. 2). While the increase was partly the result of 14 taxa being added to the fauna, most of the increase reflects real declines in species status. Previous status determinations (Moyle and Williams, 1990; Moyle et al., 1995) were made without benefit of our systematic approach and were constrained by prior agency designations. However, because the senior author was in charge of all three assessments, the evaluations are fairly consistent.

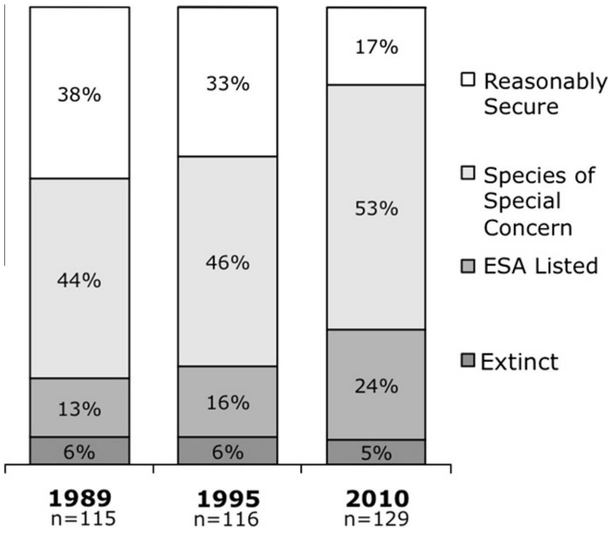

Fig. 2. Status of the native fishes of California from three surveys over 21 years, as shown by percentages of known species in conservation categories used by the state of California. Listed species are those listed under the state and federal endangered species acts as either Threatened or Endangered. Special Concern species are those in decline or in small isolated populations that are likely to be eligible for listing in the near future. For 2010, some Special Concern status determinations have not yet been officially recognized.

Table 4
Percentages of 122 extant California freshwater fishes assigned ratings of severity for 15 causes of fish declines. A cause rated 'critical' had the most severely negative effect on a species. See text for descriptions of causes and for definitions of critical, high, medium, and low rating levels.

Cause	Critical	High	Medium	Low	No effect
Percent of fish taxa with rating					
Major dams	3	21	32	27	17
Agriculture	1	17	50	25	7
Grazing	0	9	48	41	2
Rural residential	2	1	28	65	5
Urbanization	0	9	30	39	22
Instream mining	0	3	28	44	5
Mining	0	3	8	84	6
Transportation	0	4	46	48	3
Logging	2	4	27	55	12
Fire	0	4	42	50	4
Estuary alteration	2	10	22	7	61
Recreation	0	2	16	77	6
Harvest	1	8	13	29	49
Hatcheries	3	11	7	14	66
Alien species	11	23	35	30	1

In this status review, the metrics contributing most often to overall status scores of 1.0–2.9 were climate change (62% of species with such scores), anthropogenic threats (56%) and area occupied (55%). In contrast, fishes with scores of 4.0 and above had large populations, wide distributions, and high tolerance of environmental change. The anthropogenic threats that led to the most species with "critical" or "high" ratings were alien species (34%), dams (24%) and agriculture (18%) (Table 4). Twenty-five species (19%) had at least one "critical" rating, indicating high likelihood of extinction in the near future, while 63 species (49%) received at least one "high" rating. The largest number of "high" ratings awarded to a single species was six. All species had different combinations of causes of decline by kind and severity.

4. Discussion

4.1. What is the status of California's freshwater fish fauna?

In 1989, only 14 species were formally ESA listed as Threatened or Endangered (Moyle and Williams, 1990). Today, 31 species are formally listed and about one additional species is being listed every two years, despite a general slow-down in the listing process (Greenwald et al., 2006). In addition, seven species have gone extinct in the past 50 years. Clearly, the native fish fauna of California is in serious decline by official standards. However, our analysis indicates that the decline is more severe than recognized, with 107 (83%) of the native fishes prone to extinction. The major cause of decline is a growing human population that enjoys living in a mild Mediterranean climate where water is in short supply, especially in the dry summer season or during periods of drought. This shortage results in most waterways being dammed, diverted, polluted, or otherwise altered, with the additional threat of frequent invasions of alien fishes (Moyle, 2002; Moyle and Marchetti, 2006). The highly endemic fishes of the region are vulnerable to change because many are confined to limited geographic areas or to habitats where conditions are naturally stressful. However, even many wide-ranging species (e.g., all salmon species and steelhead rainbow trout) are imperiled (Moyle, 2002; Moyle et al., 2008). Native species that have managed to thrive under altered conditions are those that have naturally large ranges, broad habitat requirements, high tolerance of adverse conditions, and an ability to become part of new fish assemblages that include alien species (e.g., Tahoe sucker, Sacramento pikeminnow).

4.2. Are the fishes continuing to decline?

Today, 83% of California's freshwater fishes are imperiled or extinct, a 16% increase since the last assessment in 1995 and a 21% increase since 1989. The increase is partly the result of improved information, but declines of most species are also real, as illustrated below by coho salmon, Central Valley fall Chinook salmon, delta smelt, Clear Lake hitch, and Sacramento perch.

Coho salmon (Salmonidae) are native to hundreds of coastal streams from Monterey Bay north to the Oregon border and once supported sport and commercial fisheries (Moyle, 2002). In the 1940s, estimated numbers of adults spawning in California streams were 200,000–400,000 (Moyle et al., 2008). They were regarded by Moyle and Williams (1990) as being in sharp decline but still common. Subsequent studies documented their rapid disappearance from their native streams throughout the state and by 1996 the two Evolutionary Significant Units (ESUs) of coho salmon present in California had been listed as federal Threatened or Endangered species. Our analysis scored status of the Central Coast ESU as 1.1 and the Southern Oregon Northern California Coast ESU as 1.7. The 2010 federal ESA recovery plan for California coho salmon is consequently regarded as more an extinction prevention plan than a real plan for recovery (NMFS, 2010).

Central Valley fall Chinook salmon ESU once historically made up the largest run of salmon in the Sacramento and San Joaquin River basins, with runs once estimated to be around a million fish annually; adult populations through most of the 20th century were 200,000–400,000 fish. Moyle and Williams (1990) considered it to be abundant and perhaps even increasing in abundance. However, its status score here is 2.0, because of a recent precipitous population crash (Moyle et al., 2008) which is apparently the indirect result of the population being almost entirely composed of fish of hatchery origin (Barnett-Johnson et al., 2007).

Delta smelt (Osmeridae) are endemic to the San Francisco Estuary and require fresh water for spawning (Moyle, 2002). In the 1970s, they were still one of the most abundant fish in the upper estuary but declined rapidly so that Moyle and Williams (1990) indicated they merited listing as a threatened species. They were listed as Threatened by both state and federal governments in 1993. Nevertheless, their decline has continued as the result of major environmental changes to the upper estuary related to increasing water exports and other factors (Bennett, 2005), despite major efforts to curtail mortalities in recent years. With a 1-year life cycle, they may be on verge of extinction and accordingly were given a score of 1.4.

Clear Lake hitch (Cyprinidae) is endemic to Clear Lake, a large natural lake in the Coast Range of California (Moyle, 2002). Although the lake has been highly altered for human use and has been heavily invaded by alien species, hitch are one of the few native species that have persisted; Moyle and Williams (1990) found them to be abundant but possibly declining. However, dramatic reduction in numbers of individuals in spawning streams, presumably related to the expanding population of piscivorous Florida largemouth bass (*Micropterus floridae*) in the lake as well as continued environmental degradation, resulted in a status score of 1.9.

Sacramento perch (Centrarchidae) were once one of the most abundant fish in the Central Valley and subject to commercial fisheries in the 19th century (Moyle, 2002). Today they are extirpated from their native range largely from competition and predation by introduced centrarchids (Crain and Moyle, 2011). They have persisted only because they have been introduced into scattered reservoirs and lakes in other parts of California and the western USA. However, many introduced populations are now gone and most others are located in waters that are not secure (Crain and Moyle, 2011). Moyle and Williams (1990) indicated concern about its decline but thought it did not merit listing as a threatened species. Because so many populations have disappeared or declined since then, it scored 1.6 in our evaluation.

4.3. What factors are most strongly associated with conservation status?

The causes of the declines have their roots in the 19th and early 20th centuries when unrestricted mining, logging, and wetland conversion, combined with wide-scale dam building, severely altered most rivers, lakes, and estuaries. In addition, approximately 50 species of alien fishes were successfully introduced, many of them better suited to altered environments than native species (Moyle and Marchetti, 2006). Nevertheless, each native species has its own idiosyncratic response to this changing environment, as a result of its natural characteristics interacting with changes occurring in its particular habitats. Our analyses showed that each imperiled species has its own combination of causes of decline but most common were factors reflecting large-scale landscape changes (dams, agriculture, logging, urbanization, Table 4). An issue common to all species is climate change, which was often an important factor affecting our final status score for each species. Increases in water temperatures and variability in stream flows are becoming an increasingly important limiting factor for most species, but especially those relying on streams with perennial flows of cool (<20–22 °C) water. Thus a systematic conservation approach has to deal both with broad issues and those particular to each species.

4.4. How do our results fit with official status designations?

Of the 31 California fish species listed under the ESA, 94% fell into our two most at-risk status categories, indicating that our scoring system approximates the criteria used in official ESA listing determinations. However, only 51% of 33 species that we rated as endangered (scores <2.0) were officially listed under the ESA, indicating that official protection is not keeping pace with the rapid decline of California's inland fishes. That ESA designations are not concordant with current status is also born out by the fact that 12 (36%) of the 33 species we rated as vulnerable (scores of 2.0–2.9) and two (6%) of the species we rated as near-threatened (scores of 3.0–3.9) were listed as threatened or endangered under the ESA. The reasons for the discrepancies between our ratings and official status are complex but largely stem from better information being available now than at the time of listing. For example, the rough sculpin (score of 3.4) was one of the first fishes listed under state law, when little was known about its distribution and biology. Subsequent studies have indicated it is fairly widespread in spring streams of the Pit River watershed and is even expanding its range in reservoirs (Moyle, 2002). However, recent genetic studies suggest rough sculpin is actually two disjunct populations (A. Kinziger, pers. comm. 2010), perhaps species, which might qualify for listing if treated independently.

Rating the quality (certainty) of the information on which each species status score was based enables managers to determine which species need more study. Most of our species status determinations are based on strong published evidence. However, species with low certainty scores should be re-evaluated for status frequently.

5. Conclusions

The native inland fish fauna of California is in rapid decline and many species are likely to disappear from the state within the next century if present trends continue. Unfortunately, global climate change and human population growth are likely to increase fish extinction rates as competition with humans for increasingly scarce water intensifies, stream flows become more variable, and water quality, especially temperature, changes. For coldwater fishes, thermal refuges may disappear from streams in many areas, leaving no place to escape unfavorable conditions. The patterns of decline we see in California have been documented in freshwater fishes in other arid climates (Moyle and Leidy, 1992; Aparicio et al., 2000; Maceda-Veiga et al., 2010). However, the decline of California's inland fishes is likely characteristic of freshwater fishes and their ecosystems worldwide. As better information and similar systematic approaches are employed in other regions, we predict more imminent extinctions will be detected than are presently appreciated. Given trends of rapid decline that we have documented it is likely that many species will be lost before effective conservation plans can be implemented. There is, therefore, no time to be lost in designing and implementing conservation efforts for freshwater species in California and worldwide.

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Appendix

Table 1. List of all native fishes known to breed in the inland waters of California, ranked by level of extinction threat. Asterisks denotes taxon listed by federal or state Endangered Species Acts. Extinct= globally extinct or extirpated from the inland waters of California. Status scores of 1.0-1.9 are roughly equivalent to IUCN threat level of *endangered* or *critically endangered*; 2.0-2.9, IUCN threat level of *vulnerable*; 3.0-3.9, IUCN threat level of *Near Threatened;* 4.0-5.0, IUCN threat level of *Least Concern*.

Species	Status Score
Thicktail chub, Siphatales crassicauda	Extinct
High Rock Springs tui chub, *S. b. subsp.*	Extinct
Bonytail, *Gila elegans*	Extinct
Clear Lake splittail, *P. ciscoides*	Extinct
Colorado pikeminnow, *P. lucius*	Extinct
Bull trout, *Salvelinus confluentus*	Extinct
Tecopa pupfish, *C. n. calidae*	Extinct
Long Valley speckled dace, *R. o. subsp.*	1.0
Central coast coho salmon, *O. kisutch*	1.1*
Shoshone pupfish, *C. n. shoshone*	1.1
Razorback sucker, *Xyrauchen texanus*	1.3*
Pink salmon, *O. gorbuscha*	1.3
Shay Creek stickleback, *G. a. subsp.*	1.3
Owens tui chub, *S. b. snyderi*	1.4*
Mojave tui chub, *S. mohavensis*	1.4*
Delta smelt, *Hypomesus pacificus*	1.4*
Owens pupfish, *C. radiosus*	1.4*
Southern green sturgeon, *A. medirostris*	1.6*
Amargosa Canyon speckled dace, *R. o. nevadensis*	1.6
Santa Ana speckled dace, *R. o. subsp.*	1.6
Modoc sucker, *Catostomus microps*	1.6*
Flannelmouth sucker, *C. latipinnis*	1.6
Eulachon, *Thaleichthys pacificus*	1.6*
Upper Klamath-Trinity spring Chinook salmon, *O. tshawytscha*	1.6
Southern Oregon Northern California coast coho salmon, *O. kisutch*	1.6*
Chum salmon, *O. keta*	1.6
Sacramento perch, *Archoplites interruptus*	1.6
Lost River sucker, *C. luxatus*	1.7*
Santa Ana sucker, *C. santaanae*	1.7*
Central Valley late fall Chinook salmon, *O. tshawytscha*	1.7
Klamath Mountains Province summer steelhead, *O. mykiss*	1.7
Southern California steelhead, *O. mykiss*	1.7*
Paiute cutthroat trout, *O. c. seleneris*	1.7*
Clear Lake hitch, *L. e. chi*	1.9
Owens speckled dace, *R. o. subsp.*	1.9
Northern California coast summer steelhead, *O. mykiss*	1.9*
McCloud River redband trout, *O. m. stonei*	1.9
Kern River rainbow trout, *O. m. gilberti*	1.9
Desert pupfish, *Cyprinodon macularius*	1.9*
Unarmored threespine stickleback, *G. a. williamsoni*	1.9*
Kern brook lamprey, *L. hubbsi*	2.0
White sturgeon, *A. transmontanus*	2.0
Red Hills roach, *L. s. subsp.*	2.0
Klamath largescale sucker, *C. snyderi*	2.0
Shortnose sucker, *Chasmistes brevirostris*	2.0*
Longfin smelt, *Spirinchus thaleichthys*	2.0*
Central Valley winter Chinook salmon, *O. tshawytscha*	2.0*
Central Valley spring Chinook salmon, *O. tshawytscha*	2.0*
Central Valley fall Chinook salmon, *O. tshawytscha*	2.0
California golden trout, *O. m. aguabonita*	2.0
Little Kern golden trout, *O. m. whitei*	2.0*
Eagle Lake rainbow trout, *O. m. aquilarum*	2.1
Lahontan cutthroat trout, *O. c. henshawi*	2.1*
Cow Head tui chub, *S. t. vaccaceps*	2.1
Goose Lake sucker, *C. o. lacusanserinus*	2.1
Saratoga Springs pupfish, *C. n. nevadensis*	2.1
Arroyo chub, *Gila orcutti*	2.3
Amargosa River pupfish, *C. n. amargosae*	2.3
Lahontan Lake tui chub, *S. b. pectinifer*	2.4

(*continued on next page*)

Appendix (*continued*)

Species	Status Score
Cottonball Marsh pupfish, *C. s. milleri*	2.4*
Northern green sturgeon, *Acipenser medirostris*	2.4
Upper Klamath-Trinity fall Chinook salmon, *O. tshawytscha*	2.4
California Coast fall Chinook salmon, *O. tshawytscha*	2.4*
Central Valley steelhead, *O. mykiss*	2.4*
South Central California coast steelhead, *O. mykiss*	2.4*
Salt Creek pupfish, *C. s. salinus*	2.6
Goose Lake lamprey, *Entosphenus sp.*	2.6
Monterey hitch, *L. e. harengeus*	2.7
Central California coast winter steelhead, *O. mykiss*	2.7*
Bigeye marbled sculpin, *C. klamathensis macrops*	2.7
Sacramento splittail, *Pogonichthys macrolepidotus*	2.9
Tidewater goby, *Eucyclogobius newberryi*	2.9*
Northern Roach, *L. mitrulus*	2.9
Russian River roach, *L. s. subsp*	3.0
Navarro Roach, *L. s. navarroensis*	3.0
Gualala roach, *L. parvipinnus*	3.0
Tomales Roach, *L. s. subspecies*	3.0
Upper Klamath marbled sculpin, *C. k. klamathensis*	3.0
Clear Lake tule perch, *H. t. lagunae*	3.0
Western brook lamprey, *L. richardsoni*	3.1
Clear Lake roach, *L s. subsp.*	3.1
Clear Lake prickly sculpin, *C. a. subsp.*	3.1
Russian River tule perch, *H. t. pomo*	3.1
Eagle Lake tui chub, *S. b. subsp.*	3.3
Sacramento hitch, *Lavinia e. exilicauda*	3.3
Monterey roach, *L. s. subditus*	3.3
Mountain sucker, *C. platyrhynchus*	3.3
Northern California coast winter steelhead, *O. mykiss*	3.3
Goose Lake redband trout, *O. m. subsp.*	3.3
Lower Klamath marbled sculpin, *C.k. polyporus*	3.3
Blue chub, Gila coerulea	3.4
Central California roach, *L. s. symmetricus*	3.4
Pacific lamprey, *Entosphenus tridentata*	3.4
Goose Lake tui chub, *S. t. thalassinus*	3.4
Hardhead, *Mylopharodon conocephalus*	3.4
Coastal cutthroat trout, *O. clarki clarki*	3.4
Rough sculpin, *Cottus asperrimus*	3.4*
Riffle sculpin, *C. gulosus*	3.4
Sacramento tule perch, *Hysterocarpus t. traski*	3.4
River lamprey, *Lampetra ayersi*	3.6
Pit-Klamath brook lamprey, *L. lethophaga*	3.6
Southern Oregon Northern California coast fall Chinook salmon, *O. tshawytscha*	3.7
Klamath River lamprey, *E. similis*	3.9
Reticulate sculpin, *C. perplexus*	3.9
Owens sucker, *C. fumeiventris*	3.9
Mountain whitefish, *Prosopium williamsoni*	3.9
Klamath Mountains Province winter steelhead, *O. mykiss*	3.9
Pit River tui chub, *S. thalassinus subsp.*	4.0
Klamath tui chub, *S. b. bicolor*	4.1
Sacramento speckled dace, *Rhinichthys osculus subp.*	4.1
Monterey sucker, *C. o. mnioltiltus*	4.1
Klamath smallscale sucker, *C. rimiculus*	4.1
California killifish, *Fundulus parvipinnis*	4.1
Inland threespine stickleback, *G. a. microcephalus*	4.1
Humboldt sucker, *C. o. humboldtianus*	4.3
Pit sculpin, *C. pitensis*	4.3
Coastrange sculpin, *C. aleuticus*	4.4
Sacramento blackfish, *Orthodon microlepidotus*	4.4
Paiute sculpin, *C. beldingi*	4.4
Coastal threespine stickleback, *Gasterosteus a. aculeatus*	4.6
Lahontan stream tui chub, *S. b. obesus*	4.7
Sacramento pikeminow, *Ptychocheilus grandis*	4.7
Coastal rainbow trout, *O. m. irideus*	4.7
Coastal Prickly sculpin, *C. asper subsp.*	4.7
Lahontan redside, *Richardsonius egregius*	4.8
Lahontan speckled dace, *R. o. robustus*	4.8
Klamath speckled dace, *R. o. klamathensis*	4.8
Tahoe sucker, *Catostomus tahoensis*	5.0
Sacramento sucker, *C. o. occidentalis*	5.0

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Geometry of Forest Landscape Connectivity: Pathways for Persistence

Deanna H. Olson and Kelly M. Burnett

Abstract

Streamside areas may be dispersal funnels or runways for a variety of species. For over-ridge dispersal, headwaters offer the shortest distance links among riparian zones in adjacent drainages. We summarize landscape designs for connectivity of habitats using headwater riparian linkage areas as the foundation for a web of landscape-scale links. We developed management considerations for placement of headwater linkage areas including: 1) providing connections between larger basins; 2) maintaining habitat connectivity in the face of climate change; 3) incorporating place-based disturbance regimes such as headwater debris-flow-prone areas; 4) targeting connectivity areas to address sensitive species conservation strongholds; and 5) accounting for geometry at the forest-stand scale of a single project or proposed timber sale, including managing habitats to connect lands on adjacent federal ownerships, by means of connecting corners of checkerboard landscape blocks along diagonals. Although our proposed linkage areas are designed to target headwater species, the resulting web of connections across the landscape is expected to benefit many forest-dependent species.

Keywords: watersheds, forest, headwaters, biodiversity, linkage areas, dispersal.

Introduction

Biodiversity retention and restoration is an emerging priority for global ecosystems. Astounding losses within major taxonomic groups have been reported nationally and internationally (41 percent of amphibians, 25 percent of mammals, 15 percent of bony fishes, 13 percent of birds: Hoffmann et al. 2010; 50–60 percent of turtles: Kiester and Olson 2011). In particular, protection and restoration of forests and forest biodiversity has become a paramount concern worldwide (e.g., Convention on Biological Diversity: *www.cbd.int/forest/*). A toolbox of management approaches has been developed to conserve forest biodiversity, largely through a mixture of fine- and coarse-grained habitat protections (e.g., United States Northwest Forest Plan: USDA and USDI 1993, 1994; Cissel et al. 1998; Lindenmayer and Franklin 2002; Raphael and Molina 2007; Lindenmayer et al. 2007) and site-specific designs to maintain or restore forest structural heterogeneity (McComb 2001; Lindenmayer and Franklin 2002; Brockerhoff et al. 2008).

Development of landscape designs to manage habitat connectivity for multiple species is an especially active research topic in forest biodiversity conservation, due to continuing trends of forest fragmentation and to an upswing

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in world reforestation efforts. Managing forested landscapes for connectivity functions benefiting biodiversity requires incorporating several fundamental conservation concepts. These basic conservation tenets include identifying the critical habitats used throughout species' life histories (breeding, foraging, overwintering, and dispersal habitats), and commensurate habitat protections to ensure that these biotic functions are retained. If an organism uses different habitats through its life cycle, then maintaining connectivity among these habitats is essential to ensure its persistence. Of particular relevance is the characterization and retention or restoration of dispersal habitat. This includes the home ranges of individuals and the broader dispersal of offspring or individuals that tie sub-populations and populations together over larger areas. This broader-scale dispersal function maintains genetic variation within natural populations, which may foster resiliency needed to adapt to changing environmental conditions. The future of species may rely on our careful attention to managing for connectivity now.

Defining the adequacy of dispersal habitat in forests is a complex topic (Noss et al. 1997) and may address a variety of elements, including habitat condition, corridor sizes (length, width), and corridor redundancy (Pinto and Keitt 2008). Redundancy is especially relevant because multiple connectivity pathways can assist dispersal across landscapes by organisms in different locations and increase the probability of movement in the face of many interacting site-specific factors (microsite features, disturbances). Redundancy of habitat connectivity hedges against catastrophe, uncertainty, and stochastic processes that can affect individuals and sub-populations that vary in their movement propensities, possibly related to patch size, habitat quality, and population demography.

Low-mobility species may merit special attention devoted to the placement and redundancy of connectivity corridors, because barriers to dispersal may arise as a result of their basic biology and ecology (Raphael and Molina 2007). These species may move slowly and require refugia along corridors because it may take them years to move between optimum habitat patches. Due to a potentially longer residency time within connectivity corridors, low-mobility species may be particularly vulnerable to sub-optimal corridor conditions and stochastic processes. Hence, redundancy of connections may be critically important to increase their likelihood of successful movement across landscapes for such low-mobility species. Patches of higher-quality habitat within dispersal corridors may be used as stepping stones for such species and may be an essential aspect of their long-term persistence (e.g., Grant et al. 2010). Such stepping stones may function as habitat refugia or "stopover reserves" (Dobson et al. 1999), which promote survival of individual organisms as they move through the environment. Stepping stones may have more suitable physical habitat conditions than the surrounding area, or may allow individuals to forage to replenish energy reserves or survive harsh seasons (summer, winter) in localized refugia, from which they may disperse again later.

Herein, we synthesize our ongoing studies of the utility of headwater riparian areas as proposed connectivity corridors, or linkage areas, for dispersal of riparian-associated and low-mobility species in Pacific Northwest forests. Once designed, such headwater linkage areas may benefit many taxa. Our studies also conceptually integrate aquatic network and upland-forest habitats, functions, and processes. The combination of protections for aquatic and upland systems is providing new insights into forest ecosystem management approaches. We summarize the key considerations for the geometric orientation of connectivity pathways to assist migration of species across watersheds and across webs of connections, to maintain linked aquatic-terrestrial populations at landscape scales. Our goal here is to provide a summary of these conceptual designs, while research continues to address these issues and advance design effectiveness.

Utility of Watersheds as Redundant Landscape-scale Linkage Units

Watersheds are widely accepted units for monitoring and evaluating the effects of land use on aquatic resources (Omernik and Bailey 1997). Where their boundaries can be clearly mapped, watersheds are increasingly common units for forest management planning and conservation designs. For example, in the U.S., the Aquatic Conservation Objectives of the federal Northwest Forest Plan (USDA and USDI 1994: p. B-11), address connectivity among watersheds:

> *"Maintain and restore spatial and temporal connectivity within and between watersheds. Lateral, longitudinal, and drainage network connections include floodplains, wetlands, upslope areas, headwater tributaries, and intact refugia. These network connections must provide chemically and physically unobstructed routes to areas critical for fulfilling life history requirements of aquatic and riparian-dependent species."*

Hydrologic units (HUs), delineated by the U.S. Geological Survey (Seaber et al. 1987), are also a convenient and widely used basis for forest assessment and planning (e.g., Maxwell et al. 1995; Suring et al. 2011). The HU coding describes a hierarchical system of units nested by drainage area; larger code numbers designate smaller drainage areas. Watersheds or segments of watersheds comprise HUs. Even though the majority of HUs at each level of the hierarchy are not true topographic watersheds, such a perspective can aid biodiversity conservation designs, especially as smaller headwater basins are delineated and used for replicating protected areas (e.g., 6t^{h}-code HUs: Suzuki et al. 2008) and creation of redundant connections across landscapes (via 6th- and 7th-code HUs: Olson and Burnett 2009).

The value of using headwater basins as the premise for establishing connectivity corridors across forested landscapes is due to their habitat conditions, potential use by a variety of organisms, frequency of occurrence on the landscape, and minimization of dispersal distances (fig. 1). Olson et al. (2007) summarized some of the merits of headwater riparian habitats for species in the northwest, including providing cool, moist microclimates for interior-forest dependent organisms and aquatic-riparian associated species such as amphibians. Some taxa may use these areas due to their habitat suitability; others may respond to streams as movement barriers, and then move along banks parallel to such barriers. Streamside areas may be dispersal funnels or runways for a variety of species. For example, we have seen terrestrial salamanders (species that do not use stream or pond habitats for breeding or other life-history functions) moving predominantly through near-stream areas (D. Olson and M. Kluber, unpubl. data). Additional taxa that use riparian corridors in northwestern forests include a variety of lichens, bryophytes, fungi, vascular plants, mollusks, mammals (e.g., ground-dwelling mammals: Wilk et al. 2010), birds, and general forest-obligates that may occur in legacy forest attributes such as wolf trees along riparian buffer zones. As a minimum estimate across taxonomic groups, over 100 species were identified as likely to benefit by habitat protections of combined intermittent and perennial streams provided by riparian reserves in federal forest lands in the range of the Northern Spotted Owl (*Strix occidentalis caurina*) (table 1) (USDA and USDI 1997). Species with restricted dispersal abilities were identified for special consideration relative to utility of riparian reserves during watershed analyses under the Northwest Forest Plan (USDA and USDI 1997).

Furthermore, the high density of small streams in upland northwest forests has been widely recognized over the last 20 years, as our basic

Table 1—Species benefitting from interim riparian reserves developed for the federal Northwest Forest Plan (from table B1 in USDA and USDI 1997). Riparian reserve protection includes a one site-potential tree-height or 30.5 m (100 ft) buffer, whichever is greater, as an interim measure along all intermittent streams, and a two site-potential tree-height buffer as an interim measure along perennial streams (see USDA and USDI 1993, page III-9).

Taxonomic group	**Species**
Bryophytes	*Antitrichia curtipendula, Douinia ovata, Kurzia makinoana, Scouleria marginata, Tritomaria exectiformis*
Fungi	
Rare chanterelles	*Polyozellous multiplex*
Rare gilled mushrooms	*Clitocybesubditopoda, C. senilis, Neolentinus adherens, Rhodocybe nitida, Rhodocybe speciosa, Tricholomposis fulvenscens*
Rare cup fungi	*Helvella compressa, H. crassitunicata, H. elastica, H. maculata*
Jelly mushroom	*Phlogiotis helvelloides*
Moss-dwelling mushrooms	*Cyphellostereum leave, Galerina atkinsoniana, G. cerina, G. hetrocysis, G. sphagnicola, G. vittaeformis, Rickenella setipes*
Lichens	
Riparian lichens	*Certelia cetrarioides, Collema nigrescens, Leptogium burnetiae var. hirsutum, L. cyanescens, L. saturninum, L. teretiusculum, Platismatia lacunose, Ramalina thrausta, Usnea longissima*
Aquatic lichens	*Dermatocarpon luridum, Hydrothyria venosa, Leptogium rivale*
Vascular plants	*Bensoniella oregano, Botrychium minganense, B. montanum, Coptis trifolia*
Mollusks	*Ancotrema voyanum, Crypotmastix devia, C. henersoni, Monadenia fidelis salmonensis, Verspericola depressa, V. sierranus, Fluminicola* spp. nov. 1-20*, F. seminalis, Helisoma newberryi newberryi, Juga (C.) acutifilosa, J. (C.) occata, J (O.)* spp. nov. 2-3, *J. (Oreobasis) orickensis, Lanx alta, Lyogyrus* sp. nov. 1, 3, *Pyrgulopsis intermedia, Vorticifex klamathensis sintsini, V.* sp. nov. 1
Amphibians	
Riparian	*Aneides flavipunctatus, Rhyacotriton cascadae, R. kezeri, R. variegatus, Dicamptodon copei, Plethodon vandykei, Ascaphus truei*
Fish	Coho Salmon (*Oncorhynchus kisutch*), fall and spring Chinook Salmon (*O. tshawytscha*), resident and sea-run Cutthroat Trout (*O. clarkii clarkii*), resident Rainbow Trout (*O. mykiss*), summer and winter Steelhead (anadromous *O. mykiss*)
Birds	Common Merganser (*Mergus merganser*) [Marbled Murrelet, *Brachyramphus marmoratus*; Northern Spotted Owl, *Strix occidentalis caurina*]
Bats	Fringed, Long-eared, and Long-legged Myotis (*Myotis thysanodes, M. evotis, M. volans*), Hoary Bat (*Lasiurus cinereus*), Pallid Bat (*Antrozous pallidus*), Silver-haired Bat (*Lasionycteris noctivagans*)
Other mammals	Fisher (*Martes pennanti*), Marten (*Martes americana*), Red Tree Vole (*Arborimus longicaudus*)

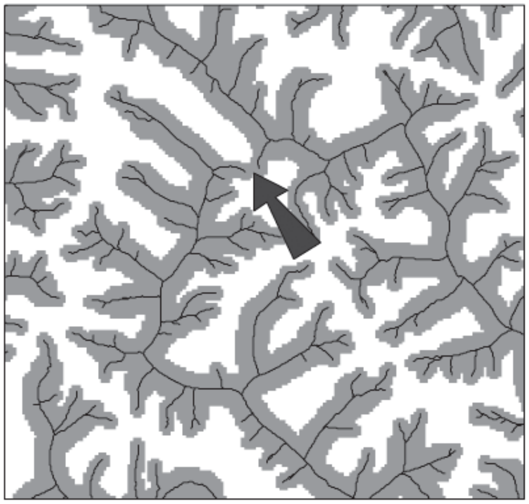

Figure 1—Example interim riparian reserve network from the US federal Northwest Forest Plan implemented in the Pacific Northwest, showing frequency of headwater streams on the landscape and the resulting one and two site-potential tree-height buffers along streams (upper left quadrant). Arrow indicates example over-ridge area where the distance between headwater riparian reserves in different watersheds is small and over-ridge connectivity may be more easily achieved. These headwater riparian areas can be used to facilitate landscape linkage area designs for organism dispersal and aquatic-terrestrial habitat connectivity functions.

knowledge of stream and forest ecology has expanded. In some areas, headwaters comprise 80 percent of a stream network (Gomi et al. 2002). This realization intersected with forest management practices when mapping of Northwest Forest Plan scenarios revealed that large percentages of watersheds were being incorporated into interim riparian reserves due to the high density of headwater stream networks (fig. 1). An additional value of using headwater drainages to plan landscape connectivity designs is that the distance from headwater streams to ridgelines is the shortest within a watershed, hence reducing travel distances for overland dispersal to neighboring stream-riparian areas or forest reserve blocks. Distance analysis tools, such as for "least-cost path" in landscape modeling (e.g., ArcGIS, Environmental Systems Research Institute, Inc., Redlands, CA), have been developed to assess distances between habitat patches. These tools would be useful for designing least-distance headwater linkage areas. Least "cost" path is a relevant term applied to the economics of animal movements, to minimize the distance moved—especially for mobility-restricted organisms. This term may also apply to the economics of forest management if identification of a dispersal corridor results in a financial cost for on-the-ground implementation or affects revenue from resource extraction in a managed forest context.

Northwest Forest Plan riparian reserves were intended as major contributors to the maintenance and restoration of aquatic conservation objectives, including aquatic network connectivity (USDA and USDI 1994). The importance of linking headwater stream functions and processes to those of downstream stream networks has been a focus of much work in the last two decades. Welsh (2011) captured many elements of the developing history of stream network theory and the role of aquatic connectivity in summarizing the conceptual frameworks of geomorphic channel processes (transfer and depositional zones), nutrient cycling (upstream marine influence via salmonid migration, downstream nutrient spiraling via down wood movements), aquatic-riparian linkages via reciprocal subsidies, and the intersection of herpetofaunal distributions with the classic stream continuum concept of taxonomic patterns that vary with stream order. As we look up the aquatic network into headwater streams and beyond, we summarize how extending riparian buffers up drainages and connecting them over ridgelines can both maintain terrestrial connectivity and functionally link aquatic-terrestrial systems.

Several conceptual designs of riparian buffer widths and patch reserves have been proposed to assist over-ridge migration of organisms within forests (fig. 2; Olson et al. 2007). Over-ridge connectivity considerations were further developed by Olson and Burnett (2009), and modeled for the Oregon Coastal Province. This model of connectivity linked every 6th- and 7th-code HU to each neighboring HU. Focusing on the Siuslaw River basin, a 4th-code HU within that area, the linkage design illustrated where one over-ridge link could connect each adjacent HU (fig. 3). At the 7th-code HU scale, one link between each adjacent 7th-code watershed resulted in roughly 15 percent of headwater streams being extended and connected For the Oregon Coastal Province, this resulted in over 5,000 links, with about one link per 4.6 km^2. This is an example of redundant connectivity, essentially creating a web of connections across the landscape. Using the 6th-code HU scale, the amount of connectivity created is approximately halved, with one link per 9.3 km^2 for the Oregon Coastal Province.

There are no defined guidelines for how many links or how much habitat connectivity is necessary to maintain populations. The amount of dispersal habitat that might be needed to sustain even highly researched species, such as

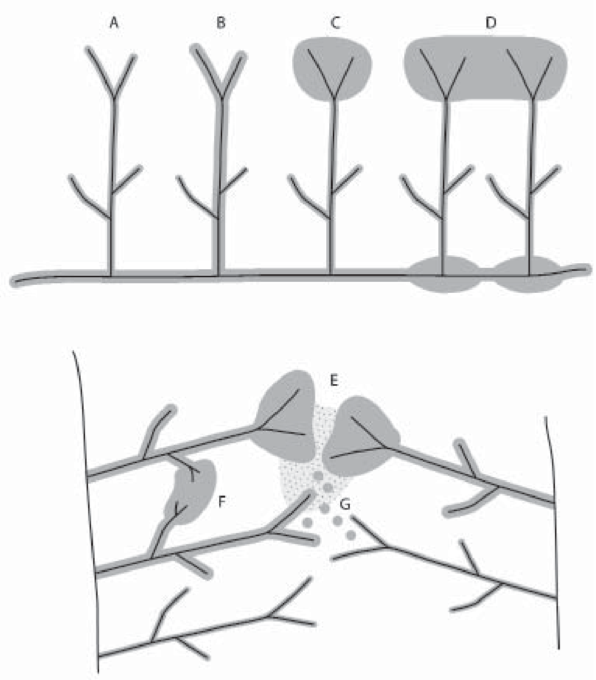

Figure 2—Headwater management considerations to retain aquatic-riparian biodiversity by stream buffers of different widths (A, B) and provide linkage areas between adjacent basins (C-G) using alternative forest management practices including uncut blocks (C, D, F), thinning (E), and leave islands (E, G) (from Olson et al. 2007).

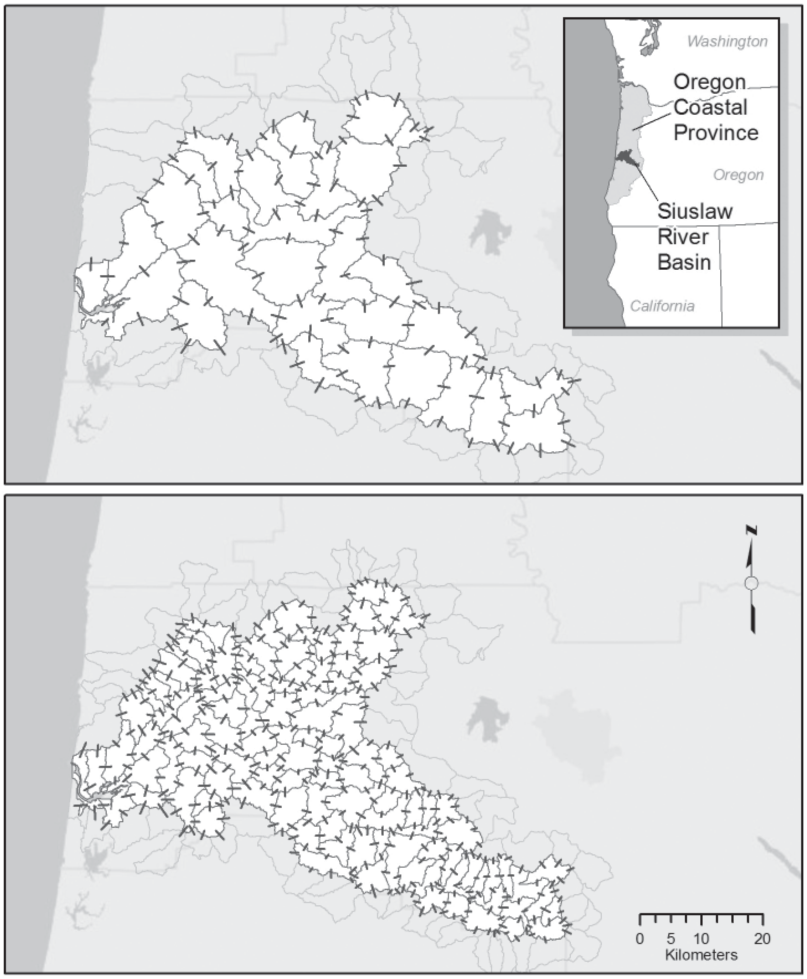

Figure 3—Linkage areas between watersheds can provide connectivity of headwater habitats across landscapes. In the Oregon Coast Range Province, the Siuslaw River basin, a 4th-code Hydrologic Unit (HU), is used to illustrate: A) a single connection between adjacent 6th-code HUs; and B) a single connection between adjacent 7th-code HUs, which results in 376 connections across the basin and if expanded to the entire province, about 5000 links within 23 000 km^2 (from Olson and Burnett 2009).

the northern spotted owl, is unknown; a "more is better" attitude prevails in the face of this uncertainty. Nevertheless, research is accruing about how much dispersal may be needed to maintain genetic diversity within and among populations. The "one migrant per generation" rule has been offered as a minimum level to reduce genetic isolation, inbreeding, and bottlenecks (e.g., Mills and Allendorf 1996). However, such a rule has many underlying assumptions that may not be supported when the complexities of natural systems are considered (e.g., Wang 2004).

Furthermore, relating effective migration rates to habitat protections in managed systems is not a straightforward exercise: if we build corridors, will they be used? Ongoing mark-recapture, radio tracking, and genetic studies are helping us to answer this question. For example, genetic connectivity analyses of stream-associated Rocky Mountain Tailed Frogs (*Ascaphus montanus*) in Idaho supported this species' affiliation with intact forested habitats: their path of connectivity followed riparian corridors in managed forests (Spear and Storfer 2010). This pattern supports the "riparian corridors as funnels" concept, but it contrasted with Coastal Tailed Frog (*A. truei*) genetic connectivity pathways in the Olympic Peninsula, Washington, which were primarily overland in areas that had timber harvest activities (Spear and Storfer 2008). Precipitation and population differences between these areas were hypothesized as accounting for these differences, as the more mesic conditions that prevail in northwestern Washington may facilitate the upland dispersal of moisture-reliant tailed frogs. Other studies (Wahbe et al. 2004; Johnston and Frid 2002; Dupuis and Steventon 1999; Nauman and Olson 2004) also found differences in riparian-corridor associations of various amphibian species in response to climate and forest conditions, generally supporting their ability to respond to microsite gradients with an apparent affiliation to cool, moist local conditions (e.g., riparian "funnels") (Olson et al. 2007). Furthermore, Spear et al. (2012) reported that Coastal Tailed Frogs track remnant tree patches in their migration pathways after the volcanic blast at Mount St. Helens, Washington. So, if we build it, will they come? The early answer is "yes, but…" —meaning that a variety of organisms appear to be occurring in or moving along pathways of retained habitats, but with geographic, taxonomic, and population-specific contexts being important considerations. A similar conclusion has recently been supported for hedgerows as corridors between woodland fragments (Davies and Pullin 2007). More research on the design of effective linkage areas will be needed. In the interim, conceptual priorities for landscape connectivity designs can be identified, and these relate directly to emerging research priorities.

Priority Areas for Habitat Connectivity

Prioritizing linkage area placement may be important to address connectivity objectives under economic constraints, and to advance research into the effective design of linkage areas. Because linking all adjoining watersheds at small HU scales may be difficult for land managers to plan and implement in the face of myriad conflicting resource objectives, priorities may guide the first steps in connecting habitats. Olson and Burnett (2009) itemized linkage area considerations at two spatial scales, landscape and drainage area (table 2). Here, we further develop five of these priority considerations:

1. "Triads," where three large basins, with limited or no aquatic connectivity, converge at their headwaters;
2. Climate change considerations including north-south, east-west, and altitudinal linkages;
3. Landslide-prone areas;
4. Species conservation strongholds; and
5. Diagonal considerations.

Table 2—Design considerations for placement of headwater linkage areas to assist migration of forest-dependent species in the Pacific Northwest (Olson and Burnett 2009). **Bold-face type** indicates new concepts discussed further in text.

Linkage Area Design Considerations	Priorities
Landscape scale	
1. Connections across large basins	**"Triads"** – headwater locations that link three adjoining basins having no aquatic connectivity.
2. Climate change migration corridors	North-south (latitudinal) dispersal routes. Altitudinal dispersal routes. Migration across ecoregion boundaries. **East-west dispersal routes.**
3. Linking landscape fragments	Connecting remnant late-successional and old-growth (LSOG) forest patches to other patches or restored habitats may aid dispersal of LSOG-associated species, especially those with dispersal limitations such as lichens, bryophytes, and mollusks; creation of connected archipelagos of patches.
4. Disturbance frequency	Correlating frequency of connections with rates of landscape-scale disturbances, natural or anthropogenic; i.e., more linkage areas in more-disturbed places.
5. **Redundancy**	Planning for multiple paths across landscapes will improve dispersal probabilities.
Drainage-basin scale	
6. Known sites for target species	Low-mobility species. LSOG-associated species. Species with status of concern. **Biodiversity hotspots** – communities. **Species "strongholds"** – priority species management areas such as key watersheds
7. Existing protections	Co-location of linkages on current set-asides (e.g., federal late-successional reserves, owl "cores", Survey and Manage species sites, botanical set asides, landslide-prone areas included in riparian reserves)
8. Short connections	For economy of space, with economic and ecological benefits, shorter connectivity corridors are preferred; ecologically, shorter distances for dispersal may reduce energetic costs for individual movements and time needed for propagules to disperse.
9. Paths of least resistance	Easier dispersal routes may be lower-gradient or lower-elevation "saddles" across ridgelines. Wind-dispersers may have least resistance in paths that follow wind directions during seasons of dispersal.
10. Risk of disturbance	Use hazard models for disturbances such as landslides, debris flows, ice/wind damage, and fire in placement of linkage areas, or in decisions about the need for redundant linkages. For example, debris-flow-prone areas may be headwater set-asides during riparian reserve delineation, and such areas may be co-located with dispersal corridors; redundant links may be considered in fire-prone areas. Mapped overlays of roads, recreation areas, human development, and mining might be avoided during linkage area delineation, when alternative locations exist.
11. Land ownership patterns	Co-location of links on federal and state lands, where possible. **Diagonal linkage areas across checkerboard ownerships.**

Each of these five considerations results in a geometric view of how connectivity webs may be arranged across landscapes.

These five considerations are not mutually exclusive; how they may interact during prioritization exercises also is developed briefly here. Although they were derived for northwest forest landscapes, these concepts may have broader utility worldwide.

1. "Triads"

In the Oregon Coastal Province, Olson and Burnett (2009) highlighted the potential importance of linking larger river basins, which have no freshwater connectivity, through existing riparian buffer networks. Over-ridge forest habitat linkages may be absent unless reserves are placed in the area. Streams in such basins may flow directly to the Pacific Ocean or into a much larger river without a forested riparian area, and so have headwaters that are functionally disconnected. Here, we examined 4th-code HUs for the Oregon Coastal province, the scale of the Siuslaw River basin highlighted above. We then looked for locations where three of these 4th-code HUs joined at their headwaters: we call this a "triad" location. For example, headwaters of the Siuslaw River, Yaquina River, and Marys River converge at Marys Peak (between Corvallis, Newport, and Waldport, OR), which would be one such triad. Only 18 of these headwater triads exist for the Oregon Coastal Province (fig. 4). We suggest that such triads be considered priorities for habitat linkage areas because these would be spatially economical for land managers to implement and potentially ecologically efficient as connections across three watershed boundaries simultaneously.

A current research priority is to empirically assess the proposed linkage-area function of landscape locations such as headwater triads. Using a genetic approach, we have sampled northwestern amphibians from headwater streams of adjacent drainages that are potentially connected across ridgelines in the Oregon Coast Range, including three adjoining headwaters in triads (such as Marys Peak). Preliminary genetic analyses of the Coastal Giant Salamander, *Dicamptodon tenebrosus*, generally support our contention of over-ridge connectivity among drainages (L. Knowles and M.R. Marchán-Rivadeneira, Univ. Michigan, unpubl. data). Previous studies have supported overland connectivity of stream-breeding amphibians (e.g., Spear and Storfer 2008, 2010), and such animals have been found up to 400 m from streams (Olson et al. 2007), but no previous published study has designed

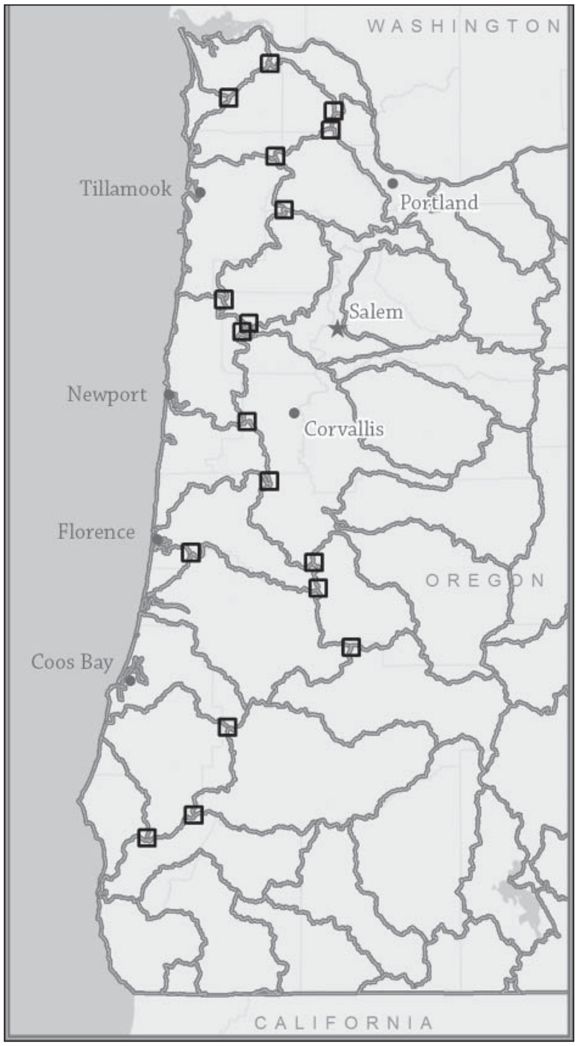

Figure 4—"Triads" are indicated (squares) where three 4th-code Hydrologic Units in the Oregon Coast Range Province meet at their headwaters. Triads are priority locations for linkage area or 'species stronghold' placement to effectively manage for species dispersal simultaneously across three distinct watershed boundaries.

sampling to specifically address headwater over-ridge connectivity among discrete drainages. This remains an information gap that could be addressed for all forest taxonomic groups, and would aid the adaptive management of the triad connectivity concept.

2. Climate Change

A second priority consideration for northwest forest connectivity is assisting migration in the face of climate change (Olson and Burnett 2009). Predicted climate change effects on northwest forest habitats include drought, insect, and fire effects on forest stands, with large conifers and high-elevation trees being vulnerable to losses (Spies et al. 2010). Aquatic habitat changes in forested landscapes are anticipated in cold-water mountain streams (Spies et al. 2010) and in headwaters (Olson and Burnett 2009). Increasing stream temperatures, with negative implications for cold-water fauna, are already apparent across the northwest (Isaak et al. 2011). Given uncertainty in the geographic specificity of climate change trajectories due to complex El Niño and Pacific Decadal Oscillation cycles, "dynamic and adaptive thinking" (Spies et al. 2010) is needed. A prudent course for linkage area placement may be to consider connected routes in north-south, east-west, and altitudinal directions within and among watersheds (fig. 5). Such consideration may allow multiple potential pathways of movement for species facing changing conditions. Pockets of suitable microhabitats for species persistence may be related to local conditions, and may occur as "stepping stones" along these linear trajectories, like beads along a string. Providing connectivity paths adjoining both riparian areas and north-facing slopes is one such example, with both near-stream areas and hill shading resulting from topographic relief providing cool, moist conditions for target species such as some late-successional and old-growth (LSOG)-associated salamanders (e.g., Suzuki et al. 2008). Landscape-scale monitoring of forest conditions and species distributions may inform adaptive management of likely climate change refugia for different taxa.

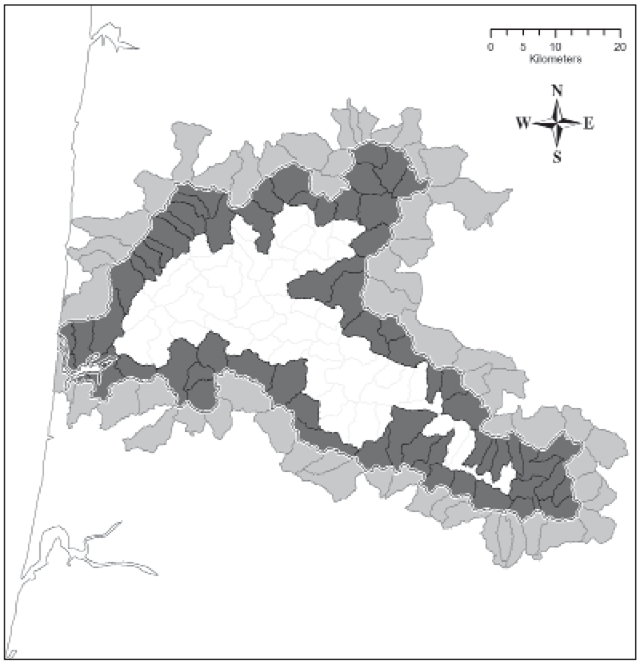

Figure 5—Designs for assisted migration of species in the face of climate change might include prioritizing headwater linkage area placement across north-south and east-west watershed boundaries. The Siuslaw River basin, a 4th-code Hydrologic Unit in the Oregon Coast Range Province, is shown highlighting perimeter sub-drainages (dark grey) where linkage areas could be made to discrete drainages to the north, south, and east.

3. Managing Disturbances: Landslide-Prone Areas

A third priority consideration for the design of linkage areas is to integrate their placement with local disturbance regimes. Landslides and debris flows can be dominant disturbance processes affecting headwater streams in forested, mountainous regions (e.g., Benda 1990; Iverson et al. 1997). The Northwest Forest Plan directs that riparian reserves incorporate landslide-prone areas to reduce the probability that activities associated with timber harvest will alter wood and sediment inputs to streams by changing the rate, magnitude, composition, or timing of debris flows. Co-locating linkage areas with existing riparian reserves, where these include steep areas prone to landsliding, can provide economic efficiency and conservation synergy for land and resource managers. Burnett and Miller (2007) modeled differences among hill slopes and headwater channels in probabilities of initiating and transporting debris flows that deliver to fish-bearing channels for the Oregon Coastal Province (fig. 6). Those headwaters with the highest likelihood of affecting downstream areas important for fish might be high priorities for extending riparian reserves over ridgelines. Because debris flows can be important sources of large wood (May and Gresswell 2003; Hassan et al. 2005), a fundamental component of stream habitat complexity (Bilby and Bisson 1998; Gregory et al. 2003), managing these expanded riparian reserve areas to accelerate tree growth could be an additional consideration. Redundancy of connections would be important when planning ground-disturbing activities for linkage areas with a high probability of landsliding. To aid identification and adaptive management of landslide-prone areas, these areas have been mapped for many northwest forests by the NetMap interactive web-tool developed by Earth Systems Institute (*http://netmaptools.org/*).

4. Species Strongholds

"Species strongholds" are areas where biodiversity conservation is a priority, and where thriving populations can occur to anchor species persistence in the region. Retaining connectivity among species strongholds enhances the likelihood of persistence under the uncertainty of stochastic events (catastrophic fire, disease outbreaks) or emerging patterns of disturbance (climate change) that may affect any particular stronghold. Managing stronghold-to-stronghold connectivity is a fourth priority to consider in developing linkage area designs across forest landscapes. Species strongholds may be created for communities of diverse taxa at larger spatial scales by land-use allocations such as

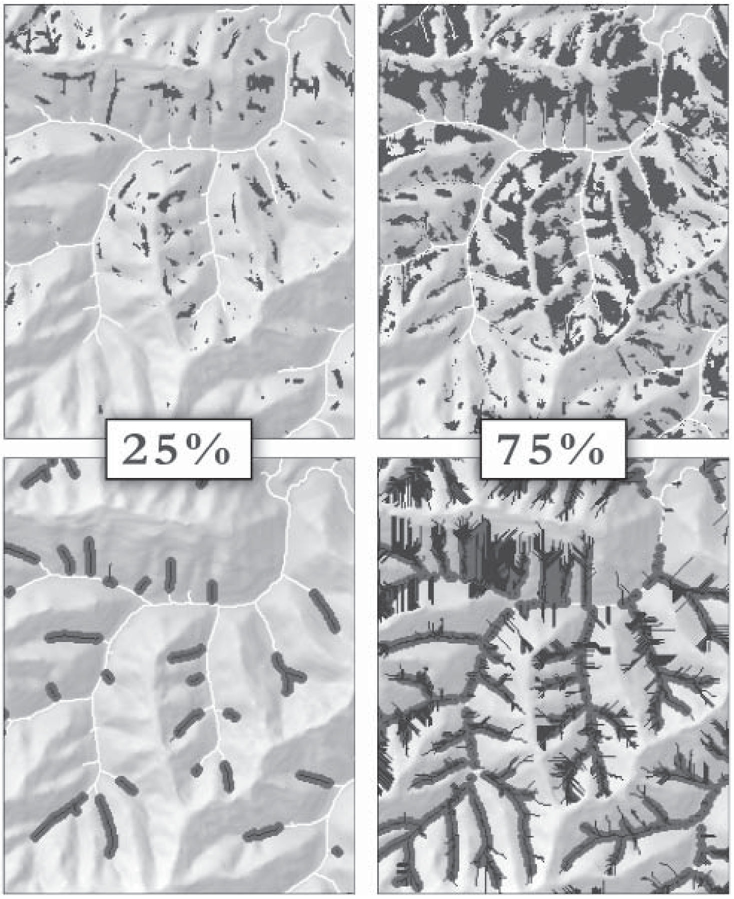

Figure 6—Placement of between-drainage links might consider other landscape-scale provisions such as management scenarios to retain the natural disturbance regime, including landslide-prone areas managed to deliver wood and sediment to streams. Top figures show models of 25 percent and 75 percent of the landslide-prone hillslopes in an example forest landscape, and bottom figures show their likely traversal paths to streams (Burnett and Miller 2007). Headwater riparian buffers of these areas provide long-term wood and sediment inputs for stream biota. From Olson and Burnett 2009.

Congressionally reserved lands (wilderness areas, national parks), or the Northwest Forest Plan late-successional reserves or key watersheds (USDA and USDI 1993, 1994). At smaller spatial scales, strongholds for a targeted species of concern may be critical habitat areas, such as caves, ponds, meadows, botanical set-asides, or areas managed for Survey and Manage species under the federal Northwest Forest Plan (USDA and USDI 1993, 1994). Riparian buffers themselves might be considered as strongholds, but here, we expand that perspective to other areas.

Developing new species strongholds is particularly important when considering connectivity issues. Three examples follow. First, areas with high "intrinsic potential," the capacity to support high-quality habitats for salmon (Burnett et al. 2007), may serve as nuclei for designing linkage areas. Intrinsic potential models have been developed and broadly applied for salmonids in the Pacific Northwest and elsewhere (e.g., Mollot and Bilby 2008; Sheer et al. 2009; Busch et al. 2011; Barnett and Spence 2011). Streams with high intrinsic potential can be identified and then targeted, as appropriate, for salmon conservation across a landscape. Such areas of high intrinsic potential are essentially "species strongholds" from which aquatic-terrestrial linkage areas can originate. Areas of high intrinsic potential for some salmonid species may occur in larger streams, but tools exist to easily identify headwater streams that feed into these both laterally and from upstream (Clarke et al. 2008).

Second, criteria for Priority Amphibian and Reptile Conservation Areas (PARCAs) are under development for nationwide application (Riley et al. 2011). PARCAs are being discussed for integration into the landscape planning processes of other entities, such as the U.S. Department of Interior Landscape Conservation Cooperatives (*http://www.doi.gov/lcc/index.cfm*), which is a partnership network to sustain America's land, water, wildlife, and cultural resources. Once established, PARCAs would function as species strongholds. Similarly, the International Union for the Conservation of Nature (IUCN) is developing criteria to identify sites of global significance for biodiversity conservation, called Key Biodiversity Areas. Such areas are synonymous with the concept of species strongholds. The additional element that we suggest is to provide connectivity among such areas.

Third, triads, as we previously described, could be ideal locations for species strongholds, as these occur at the ridgeline junction of three large basins. However, we note that triads are not established biodiversity hotspots, and are proposed here as a conceptual design.

Development of landscape-scale linkage webs from either new or existing species strongholds is needed to reduce isolation of those areas, and as possible to allow them to function as potential "source" habitats with optimal conditions that can anchor species over time and also connect to adjoining areas, in a metapopulation context. Linking dispersal pathways from strongholds up and over ridgelines to adjacent watersheds and neighboring strongholds is a direct approach that may offer a least-cost path. Relevant to our proposed headwater linkage areas concept, connecting such species strongholds to headwaters which then extend and connect over ridgelines is another consideration. Additionally, strongholds may be linked to protected riparian areas along larger streams that are subsequently extended upstream into headwaters and connected over ridgelines. Multiple connectivity pathways may be conceived. As a web of connections is considered relative to species stronghold connectivity, the previous priorities discussed above and outlined in table 2 can be overlain, including large basins and triads, linear trajectories to address for climate change gradients, and occurrence of landslide-prone areas.

Adaptive management of strongholds may need to be addressed over the long term as future conditions unfold. As applied here, the concept of a stronghold evokes less of an immovable fortress than an anchor. A species stronghold intended to anchor habitat may need to function as do real anchors on occasion, and be repositioned or "drag" across landscapes in response to changing conditions or management priorities (Olson et al. 2007). The temporal scale of strongholds can be addressed at the time of their development, and interact with the spatial scale of stronghold designs and the frequency of strongholds. For example, habitat anchors designed to drag across landscapes may be implemented more easily if they are smaller and more numerous. Olson et al. (2007) suggested considering 6th-code watersheds (HUs) as a spatial scale for amphibian habitat anchors. The anchor concept warrants testing, with a sufficient timeframe to weigh success at the landscape scale, in addition to replication. It may have greater success if it were to be implemented in areas with more resilient ecosystems.

5. Thinking Diagonally: Funnels and Chains

The geometry and land-management context of land-use and land-ownership parcels on the landscape is a final set of priority considerations for linkage-area placements that we will develop briefly here. The northwest forest landscape is a patchwork of land ownerships and land-use allocations, each with differing management priorities, which creates a complex challenge for biodiversity conservation (Suzuki and Olson 2007). During planning for large blocks of forest land, and during planning of individual projects at smaller spatial scales, managing for connectivity within and among ownership areas can be difficult due to differing priorities across boundaries. To diminish the dilemma of achieving effective biodiversity conservation in such a multi-ownership landscape, it may help to think of streams as dispersal "funnels" that serve to channel organisms along protected riparian areas, and connectivity corridors or linkage areas as "chains" functionally moving animals up and over ridgelines (Olson and Kluber, unpubl. data). Overlaying many of the previously discussed priorities can provide an integrated perspective for addressing the challenges of land-ownership/allocation geometries.

Diagonal linkage areas are of specific relevance in a landscape with a checkerboard ownership pattern (fig. 7), and in other landscape geometries that abut at corners or other edge types (Olson and Kluber, unpubl. data). Species dispersal along such diagonals might be promoted by forest management actions that retain habitat elements toward the corners of such lands. For example, weighted green-tree retention, leave islands, and directional felling of down wood (recruitment of large logs, in particular) from corners may assist migration of species along the diagonal by providing chains or stepping stones of suitable microhabitats for species refugia. Linking chains of habitat elements from corners to stream- and riparian-protected areas, especially headwaters (fig. 7B), may functionally extend and connect riparian buffers. Organisms that are funneled along riparian areas may venture through corners via these habitat chains. A chain of habitat need not extend from headwaters, but could extend from any part of a riparian buffer, or from a species stronghold, as discussed above.

It may be neither feasible nor desirable to address habitat connectivity at all corners of adjacent lands within an ownership. Similarly, when land parcels are in close proximity but do not adjoin, it may not be possible to consider linkage areas along their entire boundaries. Several additional design concepts arise and interface with ideas presented above.

First, linkage areas among land parcels might be "stream-lined" if streams align through corners (fig. 8), or connect nearby land blocks. When streams follow diagonals in a checkerboard landscape, riparian protection may more effectively promote multi-species diagonal dispersal: funnels without the added chains linking across diagonals. Streams that loosely follow diagonals, not intersecting exactly at corners, could be quite functional to assist species

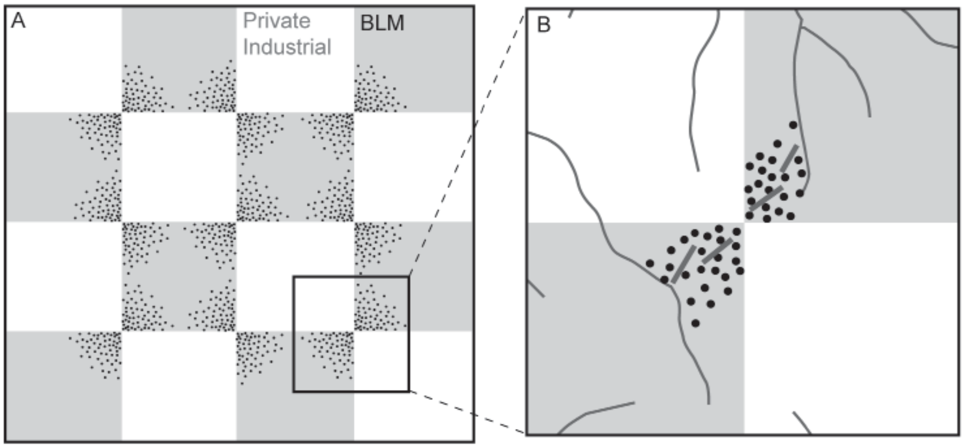

Figure 7—In a checkerboard ownership pattern, such as that created by the Oregon and California Lands Act (1937) where US Bureau of Land Management (BLM) and private industrial forestlands are intermixed, management for connectivity along diagonals may improve likelihood of species dispersal within ownerships. A: Corners are shaded to show linkage area considerations. However, routes along selected diagonals to species strongholds, reserves, or triads might be used to prioritize which corners are chosen for connectivity emphasis. B: Forest management options to facilitate species dispersal from stream corridors (which may serve to funnel species movements) to corners might include chains of habitat structures provided by green tree retention, directional log placement from corners to streams, or both. Concepts could be applied to other ownership geometries with corners or edges in proximity.

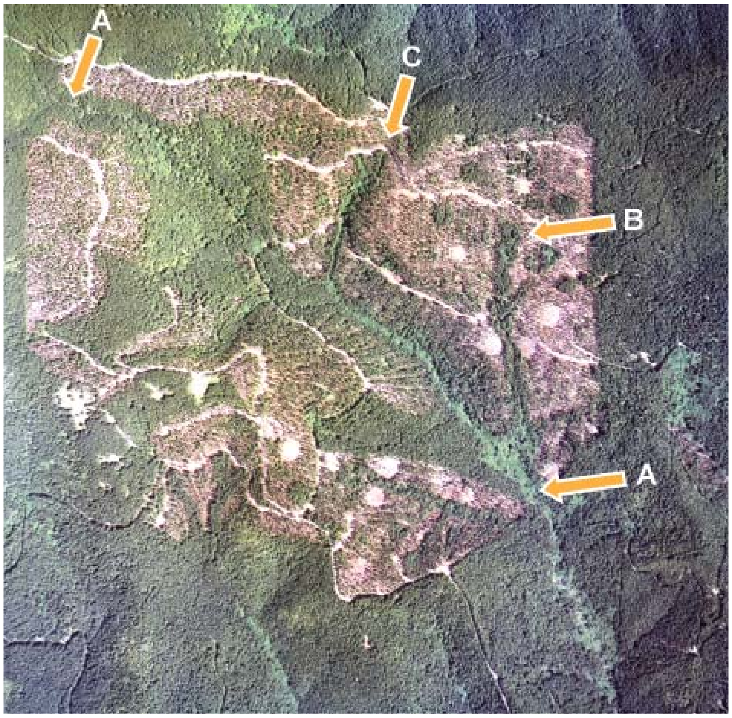

Figure 8—Connectivity designs to aid species dispersal among ownership blocks may overlay on streamside riparian management zones. This US Bureau of Land Management study site for the Density Management and Riparian Buffer Study of western Oregon (Cissel et al. 2006) shows riparian buffers extending along the full diagonal (A) as well as laterally toward an opposing corner (B), with leave islands and dispersed tree retention aiding habitat connectivity, and to a neighboring private land block (C). "Stream-lined" connectivity (A) may aid within-watershed dispersal, but overland connectivity designs (B and C) may warrant consideration to link or "chain" habitats overland between watersheds. Photo provided by Oregon Bureau of Land Management.

migration, in this regard. Streams that link disconnected parcels may similarly function to funnel organisms' movements. The context of the adjoining lands may need to be assessed, however. Managing such a stream-line to promote its potential connectivity function is a consideration, but such stream-lined connectivity does not address overland dispersal. Chains from streams to ridgelines are needed to fully integrate aquatic and terrestrial landscape connectivity functions. Collaborative management of such stream-lines and overland chains among ownerships and across land-use allocations within ownerships, remains a challenge.

Second, in multi-ownership landscapes, road densities may be higher than in single owner landscapes. An assessment of the effects of roads on species connectivity designs may be particularly important in these landscapes. In particular, paved roads or high-use unpaved roads may be barriers to low-mobility species. As roads intersect streams, aquatic organism passage may be affected, with consequences for overland connectivity. Site-specific designs can include these considerations.

Third, as hazard models of disturbances are developed for a landscape, it may be helpful to ask how hazards align with land-ownership boundaries, land-use allocations, and existing connectivity webs. For example, how are landslide-prone areas arranged relative to the geometry of lands by ownership and land-use allocation? As discussed above, can priority linkage areas be designed to overlay on landslide-prone areas that are already set-asides for riparian reserve management, and now also serve "to chain" habitats to adjoin land-ownership blocks?

Fourth, in a larger landscape context, it may be useful to know how larger basins, climate change projections, and species strongholds are arranged and whether these be used to prioritize connectivity area pathways. Can dispersal routes be conceived from streams and then through land-ownership diagonals or between ownership blocks to foster connections relative to these issues?

Multiple overlapping considerations are emerging, and a stepwise process may be needed to integrate them. Limitations may emerge due to topography, geometry of land configurations at local scales, or pre-existing conditions. For example, a dispersal barrier such as a road may need to be considered first. The existence of under-road culverts may create spatially explicit bottlenecks for connectivity planning. Routing linkage area pathways to those stream corridors and culverts may be needed to increase the odds of dispersal across the road. Culverts that act as dispersal nodes in this way could be prioritized for enhancement to provide passage for non-aquatic species. Similarly, triads and species strongholds, as discussed above, are essentially dispersal nodes. Routing dispersal routes via headwater linkage area pathways to triads and strongholds could increase the overall effectiveness of these conservation measures.

Conclusions

Forest biodiversity conservation is an ecosystem service that will continue to be addressed at local-to-landscape scales in the coming century. Retaining organisms across managed forest landscapes requires a toolbox of approaches including fine- and coarse-scale habitat protections and restoration practices, retaining or creating structural elements that are critical habitats for species, and development and management of connectivity pathways to allow gene flow. Renewed efforts to address communities of organisms as well as species of concern are called for as emerging stressors need evaluation, new knowledge is accrued, and adaptive management of existing forest plans are needed.

We review the numerous benefits of forest connectivity designs that rely on headwater linkage areas, and emphasize priorities for their placement at landscape scales. The benefits of headwater linkage areas include their likely functional role in integrating aquatic and terrestrial systems, their potential use by multiple taxonomic groups, their utility for creating webs of connections across forested lands to increase their effectiveness for biodiversity conservation, and their efficiency in minimizing both the distances that animals must move overland and the financial burdens of forest manager.

Placement of headwater linkage areas may include consideration of a variety of factors (table 2). Prioritizing linkage areas can provide a starting point for managing connectivity among critical habitat areas, suggest directional routes for dispersal among areas, or identify dispersal nodes as anchors for connectivity webs. The five priority considerations that we developed include triads that effectively link three larger basins, north-south and east-west directional routes to address climate change scenarios, linkages overlaid on management of disturbances such as landslide-prone areas, links among species strongholds, and diagonal links that route dispersal across management boundaries. These five concepts can be integrated into an overall geometry of landscape connectivity designs. Our conceptualization of headwater linkage area utility and these priority considerations are posed as hypotheses warranting further study and development. We offer these ideas with the caveat that they will not benefit all taxa in forested landscapes. Extremely rare or patchily distributed organisms with low mobility may need a finer-grained, site-by-site conservation approach (Raphael and Molina 2007).

Acknowledgments

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Species' traits influenced their response to recent climate change

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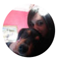

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LETTERS

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Species' traits influenced their response to recent climate change

Michela Pacifici[1]*, Piero Visconti[2,3], Stuart H. M. Butchart[4,5], James E. M. Watson[6,7], Francesca M. Cassola[1] and Carlo Rondinini[1]

Although it is widely accepted that future climatic change—if unabated—is likely to have major impacts on biodiversity[1,2], few studies have attempted to quantify the number of species whose populations have already been impacted by climate change[3,4]. Using a systematic review of published literature, we identified mammals and birds for which there is evidence that they have already been impacted by climate change. We modelled the relationships between observed responses and intrinsic (for example, body mass) and spatial traits (for example, temperature seasonality within the geographic range). Using this model, we estimated that 47% of terrestrial non-volant threatened mammals (out of 873 species) and 23.4% of threatened birds (out of 1,272 species) may have already been negatively impacted by climate change in at least part of their distribution. Our results suggest that populations of large numbers of threatened species are likely to be already affected by climate change, and that conservation managers, planners and policy makers must take this into account in efforts to safeguard the future of biodiversity.

The rate of warming over the past 50 years (0.13 °C ± 0.03 °C per decade) is nearly twice that for the previous 50 years[5], and the global temperature by 2100 is likely to be 5–12 standard deviations above the Holocene mean[6]. The effects of climate change on some species are already being witnessed, with changes documented in spatial distribution, abundance, demography, phenology and morphology[7,8]. However, to date, no quantification of the number of species for which at least one population has been currently impacted by climate change, and the extent of these impacts, has been conducted, even for the better-studied taxa such as birds and mammals. The predominant focus of climate change assessments for species has been that of bioclimatic niche modelling, which focuses on correlative analyses between species' geographic ranges and bioclimatic variables[9,10], but these studies ignore observed changes in distribution, phenology and abundance of species in response to contemporary climate change[10]. Species' life-history traits, such as dispersal and generation length, have been hypothesized to be important in determining species' sensitivity to climate change and their capacity to adapt to it[11], but only a limited number of studies[12,13] have so far provided evidence that animal species with certain traits are more likely than others to be adversely affected by changes in climate[12–15].

In this study we first aimed at performing a meta-analysis to identify the life-history traits that confer vulnerability to climate change in birds and mammals (Supplementary Table 1). From a literature search, we identified 70 studies covering 120 mammal species and 66 studies relating to 569 bird species whose populations had (or sought evidence for) a response to climate change in recent decades. We divided this response into four categories: negative, if >50% of the populations experienced reductions in one or more of the following parameters: population size, geographic range size, reproductive rate, survival rate, body mass; positive, if the species experienced increases in one or more of the parameters and/or adaptability to new climatic conditions; unchanged, if no response was observed despite the recorded change in climate; and mixed, if the species showed opposite responses of one or more of the parameters across its geographic range (Supplementary Table 2; see Methods). For all mammals and birds covered by the studies, we compiled data on selected intrinsic traits and spatial traits to assess quantitatively which of these are associated with negative responses to climate change. To control for the magnitude of climate change experienced, we also computed the mean difference in temperature between the present and the recent past within the geographic range of each species, treating breeding and non-breeding ranges separately for migratory birds.

By using information on the impacts of climate change in the study areas and life-history traits, we were able to identify the species whose populations are more likely to have experienced negative impacts in the regions affected by climatic changes as those described in the analysed papers. We estimated the likelihood of a species' population to have exhibited any of the four categories of responses to climate change with a multinomial regression model. This allowed us to test our hypotheses about the relationship between intrinsic and spatial traits and the responses of mammals and birds to climate change. Since we believe that these factors mediate the response to climate change similarly worldwide, although future studies will be crucial to test this assumption, we then predicted the likely past responses of all birds and terrestrial non-volant mammals listed as threatened in the IUCN Red List of Threatened species[16]. By making predictions on the species for which the levels of climatic hazard experienced are known, we provide the first quantification of the number of taxa that may have already been impacted, although further data need to be collected to say with certainty that there has been an effect on the whole species' persistence. We focused on threatened species because the vast majority are known or inferred to have declined; therefore, if they are at risk from climate change there is a real chance that it

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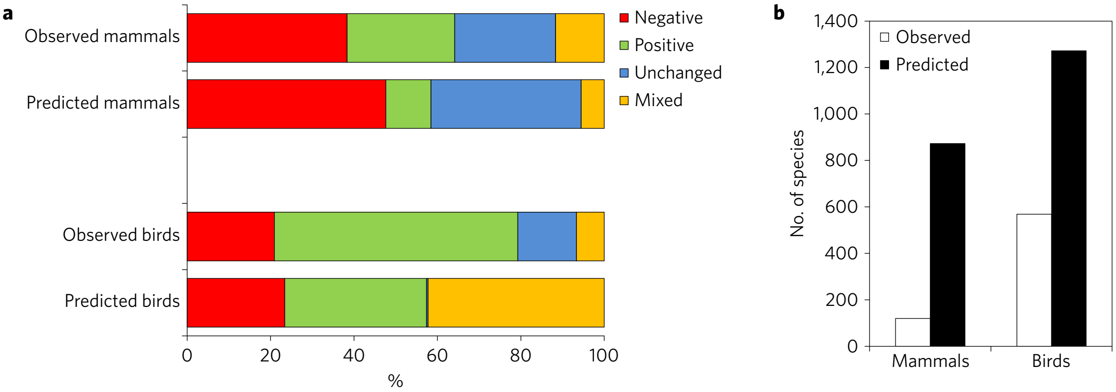

Figure 1 | Observed and predicted response of mammals and birds to climate change. a, Red bars show the percentage of species whose populations were documented to have had, or are predicted to have had, a negative response to climate change in the study period (studies spanned from 1858 to 2010); green bars represent the percentage of species with a positive response; blue bars indicate the percentage of species with no response; yellow bars show the percentage of species with mixed responses. **b**, Bars with the number of species whose populations had an observed response to climate change are coloured in white, whereas those used for predictions are shown in black.

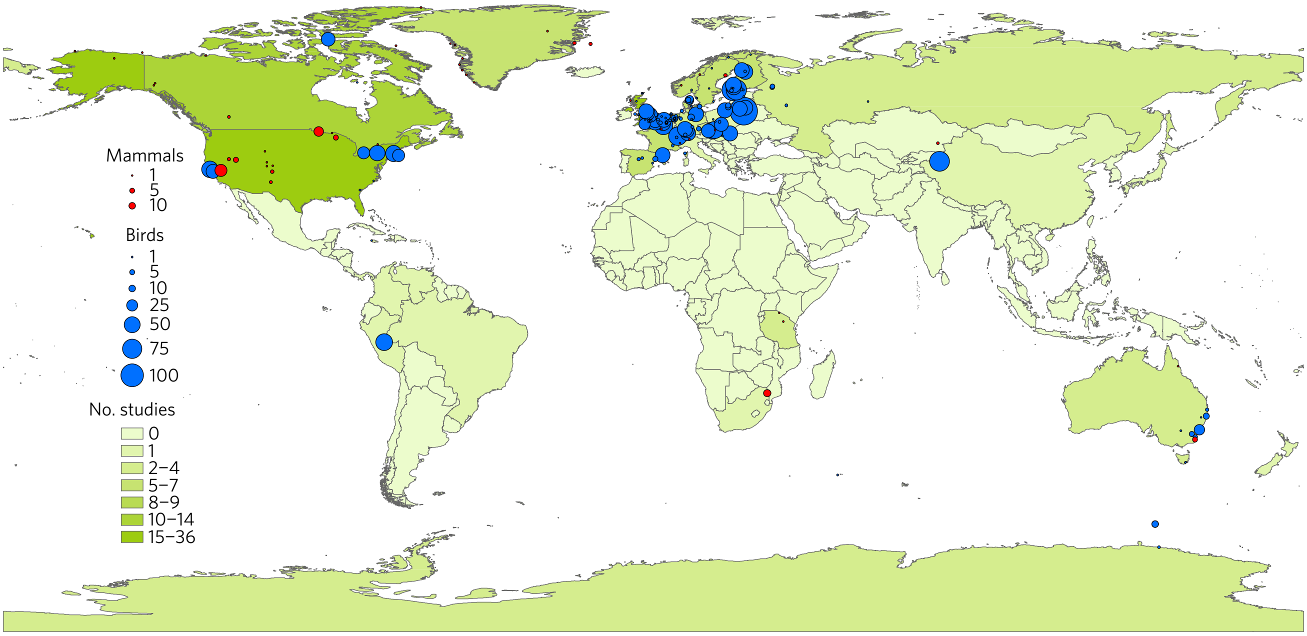

Figure 2 | Map of the study sites. Circle size represents the number of bird (blue) and mammal (red) species studied in each site. Colour of countries (shade of green) represents the number of studies per country.

has played a role in these declines, even if it was not recorded in the assessments.

For the first time we identified a relationship between a set of several variables, both intrinsic and spatial, and the response of mammals and birds to climate change, whereas previous studies mostly focused on a few biological traits and their relation with the type of impact[3,4,17,18]. In addition, we were able to provide insights into the estimation of climate change threat for poorly studied species.

Characteristics of impacted species

The observed response to recent climate change was negative for 38.3% of mammals and 20.9% of birds in our data set (Fig. 1a). Birds and mammals in Europe and North America were the subjects of considerably more studies (54% and 38%, respectively) than were taxa in South America (4%) and Oceania (2%), and less than 1% of species in our data set were in Africa, Asia and Antarctica (Fig. 2). This spatial bias implies that, for species with particular traits living in less studied continents, our findings might be less generalizable.

Mammals most at risk from climate change are those not fossorial, that experienced large changes in temperature in the past 60 years and have low precipitation seasonality within their distributional ranges (Supplementary Table 3). In areas with reduced precipitation and/or temperature seasonality, it is likely that plant species may have narrower climatic tolerances, and therefore that these areas may have already experienced vegetation changes with consequential loss of habitat for animals living there[19]. A more specialized diet was also associated with greater probability of negative responses in mammals. Our findings are in agreement with previous studies on the predictors of general extinction risk[20], in which species with narrower diet breadths were associated with lower ability to exploit resources and adapt to new environmental conditions and selective pressures.

For birds, negative responses in both breeding and non-breeding areas were generally observed in species that experienced large changes in temperatures in the past 60 years, live at high altitudes, and have low temperature seasonality within their distributions. Negative impacts were also associated with relatively high maximum temperature recorded within breeding areas, and low dispersal distances, longer generation lengths, reduced precipitation seasonality and restricted altitudinal ranges in non-breeding distributions (Supplementary Tables 4 and 5). Populations of species living at high altitudes and in colder places have fewer opportunities to move towards cooler areas or upslope to avoid increasing temperatures, and hence may have increased extinction risk. Modest shifts to higher or lower altitudes are associated with large changes in ambient temperature[21], thus facilitating potential adaptive flexibility. In addition, temperature is an important determinant of laying dates of birds because higher temperatures may induce earlier laying[22], and so for animals living in these environments the effects of temperature changes may have been exacerbated, potentially leading to disruption in synchronization between the timing of chick-feeding and peak food availability[23]. Interestingly, we found that birds with longer generation times have responded less to warming. In long-lived species, the effects of climate change have probably been less evident because adaptation and range shifts occur over a longer time span[24]; therefore, we would need to monitor the populations of these species for an extended period to observe any changes.

On average, it is likely that at least one population of 414 threatened mammals out of 873 species (47%), and 298 threatened birds out of 1,272 (23.4%) has responded negatively to climate change (Fig. 1 and Supplementary Tables 6 and 7), because they have the same combinations of traits as those species documented to have declined owing to climate change. This implies that, in the presence of adverse environmental conditions, populations of these species had a high probability of being negatively impacted by recent climatic changes.

Mammals had only 2 orders out of 11 (that is, rodents and insectivores) that mostly benefited from recent climatic changes. Both of these orders are generally characterized by fast reproductive rates and low habitat specialization[25]. Moreover, most of the species in these orders are fossorial, and they may be less exposed to climate change owing to buffering of temperatures in burrows. Primates, Proboscidea and marsupials are the mammals with the highest percentage of threatened species predicted to have been negatively impacted by climate change (Table 1), and for which we are more confident about our predictions (Supplementary Table 10). Primates and marsupials are mostly concentrated in tropical areas[26], most of which have had climatically stable environments during the Holocene. Therefore, many of these taxa have evolved to live within restricted environmental tolerances and are likely to be most affected by rapid changes and extreme events[27]. In addition, primates and elephants are characterized by very slow reproductive rates that reduce their ability to adapt to rapid changes in environmental conditions[15].

Birds showed the opposite trend, with only 3 orders out of 19 (that is, Anseriformes, Charadriiformes and Cuculiformes) having more species with a predicted negative impact than not (Table 1). Most of the species included in the first two orders inhabit aquatic environments, which are considered among the most vulnerable to temperature increase due to habitat loss, fragmentation[28] and harmful algal bloom expansions[29]. In addition, changes in climate in tropical and subtropical forest areas, already exacerbated by habitat degradation[2], may threaten forest-dependent species (for example, Cuculiformes).

Conclusions

The vast majority of assessments of species' risk from climate change have focused on future projections (for example, refs 30,31), while analyses of observed impacts to date have focused on detecting a signal of climate change rather than quantifying the number of species whose populations are likely to have been impacted. By undertaking a systematic review, we found evidence of observed responses to recent changes in climate for almost 700 species of mammals and birds. We note that only 7% of mammals and 4% of birds for which we found evidence of a negative response are coded on the IUCN Red List of Threatened Species as threatened by 'climate change and severe weather' under the 'threats classification scheme' (Supplementary Tables 8 and 9). Although this can partly be explained by the fact that species classified as 'Least Concern' on the Red List generally have few or no threats coded, the figures we found were 11% and 31%, respectively for threatened mammals and birds. This apparent mismatch is probably due to the severity of decline driven by climate change being uncertain for most species. Reasons for this include: information from other parts of their distribution is not available; other threats (for example, habitat loss from agricultural expansion, overexploitation and so on.) may have had a greater impact, thus masking the effects of climate; and/or data on climatic trends at a local scale are difficult to obtain, making it difficult to make inferences about the threat severity. Furthermore, threats to several species remain poorly understood because the majority of threatened species live in tropical areas which are generally poorly studied and monitored[32].

Table 1 | Predicted responses of threatened species in different taxonomic orders to climate change.

Taxonomic order	Negative	Positive
Mammals		
Carnivora	18 (29.51%)	35 (57.38%)
Cetartiodactyla	56 (59.57%)	2 (2.13%)
Dasyuromorphia	12 (100%)	0
Didelphimorphia	0	9 (100%)
Diprotodontia	44 (100%)	0
Eulipotyphla	0	4 (4.82%)
Lagomorpha	10 (55.56%)	0
Perissodactyla	8 (61.54%)	0
Primates	199 (100%)	0
Proboscidea	2 (100%)	0
Rodentia	65 (19.23%)	44 (13.02%)
Birds		
Accipitriformes	8 (16%)	34 (68%)
Anseriformes	10 (40%)	8 (32%)
Bucerotiformes	0	0
Caprimulgiformes	8 (13.11%)	21 (34.43%)
Charadriiformes	26 (57.78%)	3 (6.67%)
Ciconiiformes	3 (50%)	3 (50%)
Columbiformes	16 (25%)	47 (73.44%)
Coraciiformes	0	17 (89.47%)
Cuculiformes	6 (66.67%)	2 (22.22%)
Falconiformes	2 (33.33%)	0
Galliformes	22 (29.33%)	3 (4%)
Gruiformes	13 (29.55%)	29 (65.91%)
Passeriformes	171 (30%)	112 (19.65%)
Pelecaniformes	6 (31.58%)	8 (42.11%)
Piciformes	5 (14.71%)	17 (50%)
Podicipediformes	1 (25%)	1 (25%)
Procellariiformes	0	8 (13.56%)
Psittaciformes	0	103 (99.04%)
Sphenisciformes	1 (10%)	0
Strigiformes	0	6 (13.95%)
Suliformes	0	10 (100%)

Positive responses were assigned to species that benefited from recent climatic changes. Percentages indicate the proportion of threatened species for each type of response.

Although our predictions for individual species may be subject to varying degrees of uncertainty, depending on the taxonomic order and the spatial or intrinsic trait considered, the confidence intervals around the number of species whose populations may have been negatively impacted suggest that our extrapolation is robust, especially for mammals. Improved monitoring of the abundance and distribution of those taxa identified as most vulnerable (Supplementary Figs 1–6), and targeting such monitoring in areas where the effects of climate change are likely to occur soonest—particularly in the tropics—are crucial to increase empirical knowledge about climate change impacts on species, and to validate and improve projections of future impacts.

Despite these uncertainties, our results suggest that the impact of climate change on mammals and birds in the recent past is currently greatly underappreciated: large numbers of threatened species have already been impacted in at least part of their range. Given that scientific efforts in this field have largely focused on predicting the impact of future climate change on species and ecosystems[33], we recommend that research and conservation efforts give greater attention to the 'here and now' of climate change impacts on life on Earth. This also has significant implications for intergovernmental policy fora such as the Convention on Biological Diversity and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, and the revision of the strategic plan of the United Nation Framework Convention on Climate Change.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

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Author contributions

M.P., P.V., C.R. and J.E.M.W. designed the framework for the meta-analysis. M.P. conducted the analyses and collected the data for mammals. P.V. contributed to the analyses. S.H.M.B. provided data and examined the results for birds. F.M.C. collected data for birds. All authors contributed to the writing, discussed the results and commented on the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.P.

Competing financial interests

The authors declare no competing financial interests.

Methods

Using ISI Web of Knowledge we conducted a systematic literature search of all relevant articles—published between 1990 and 2015—that reported an observed change in climate in the study area; indicated that birds and/or mammals have undergone a change (for example, in distribution, population size, phenology, behaviour, genotype, phenotype) attributable to climate in the past 100 years; and/or suggested that populations of a species were not affected by recent climate change. For each study and each species considered (70 studies and 120 species for mammals, 66 studies and 569 species for birds), we identified the type of impact experienced.

A negative response was assigned to a species if all (at least one) or >50% of its populations (if the species had both negative and no responses in different portions of its range) were reported to have undergone declines in population size, geographic range size, survival or reproductive rate, and body mass, thus reducing the risk of false attributions. These responses were confidently attributable to recent climate change by the authors of the studies, for instance due to the fact that the most significant change in environmental and biotic conditions reported in the area in which the population of the species was impacted was related to climatic variables. Although we acknowledge that some of the studies may have been more rigorous than others, with such variation in the methods used and the effect size themselves it would have been difficult to adjudicate the level of confidence around the claimed relationship, although we believe that evaluating the strength of attribution is a priority for future work.

A positive response was assigned if the majority of the populations of a species experienced geographic range expansions, increase in population size, survival rate and/or reproductive rate, body mass, and/or changes in phenology. An unchanged response was attributed if no response was observed despite the recorded change in climate. Finally, species that exhibited a combination of the negative and positive (not necessarily in the same proportion) responses in different parts of their range were classified as mixed.

Statistical analysis. To identify the relationships between the observed response of mammals and birds to climate change and a set of intrinsic and spatial variables (see Supplementary Methods for description of these predictors and a priori hypotheses), we performed a multinomial logistic regression using the 'nnet' package in *R*. This model uses maximum likelihood estimation to evaluate the probability of the different possible outcomes of a categorical dependent variable with more than two classes. To reduce the overdispersion in models and avoid collinearity, we performed Spearman's correlation tests between the predictors and removed those that were highly correlated ($R^2 > 0.75$) and led to the minimum loss in model performance.

We included taxonomic order as fixed variable of our models, for a total of 11 orders of mammals and 22 of birds. By including taxonomy as a fixed effect, we aimed to control for the non-independence of observed responses across species, and for the latent variables that may affect the responses to climate change that are phylogenetically conserved. We did not include taxonomic family or genus because it resulted in strong underdispersion, as observed data on the response to climate change (which we used as a base for our predictions on threatened species) were often available only for the populations of one species per family/genus. Since we are not aware of frequentist methods to implement phylogenetically corrected models with a multinomial distribution, and concerned that phylogenetic non-independence in the species in our data set could nevertheless be important, we tested for the existence of phylogenetic signal in the residuals of our models. We used phylogenetic trees for mammals and birds[34,35] to estimate Pagel's lambda, assuming a star-shaped phylogeny and the actual phylogeny (Brownian motion models). We tested whether the value of lambda differed significantly from 0 (no phylogenetic signal) and 1 (trait distribution matches a Brownian model of evolution), by computing the likelihood ratio, and then comparing it to a Chi-squared distribution with one degree of freedom. If the test is significant there is phylogenetic signal in the residuals. However, we found lambda values of 6.73e-05, 5.56e-04 and 2.68e-04, and *p*-values of 0.51, 0.47 and 0.62 for mammals, birds in breeding ranges and birds in non-breeding ranges, respectively. Therefore we conclude that there is no phylogenetic signal in the residuals of the models and a phylogenetically informed model is not justified.

We performed a model selection using the Akaike Information Criterion (AIC) to find the set of predictors to include in the final model that minimize the Kullback–Leibler distance between the model and the observed values. We applied logarithmic and quadratic transformations to the predictors and included variable interactions in the models, but most of them did not lead to a decrease in AIC or increase in model performance calculated by using the Area Under the Curve (AUC). Finally, to test our models for overdispersion, we calculated the sum of squared Pearson residuals and compared it to the residual degrees of freedom by using a Chi-squared test. *P*-values close to 1 indicate that the probability of the model being overdispersed approaches 0 (Supplementary Table 13).

On the basis of the relationship between the observed response of species and our independent variables found with the best multinomial models, we predicted the probabilities of the four classes of response to climate change by using the function predict in *R*. For predictions we considered all threatened birds (1,272 species, as listed on the 2014 IUCN Red List) and terrestrial non-volant mammals (873 species) with available data. We excluded sea mammals from our analysis because the environmental variables that influence the persistence of marine and terrestrial species are different, and most of the variables important for marine species (for example, sea temperature, salinity) were not available for the study period. Chiroptera could not be considered in this study because of the paucity of data available on their life history.

Our model is at the species level, but our data (observed responses to climate change) is at the population level. Because the spatial extent of the study area was not available for the vast majority of studies, we were forced to average the annual temperature change experienced by the species across all of its range. However, the average climatic change might not be representative of the change experienced by the populations we used to train the model, especially with species with large range size. By resampling the response category assigned to each species from the multinomial distribution 100 times and deriving coefficient intervals and mean values of the richness of species with negative responses, we tried to reduce the uncertainty around our predictions. In addition, to identify the taxonomic orders for which our predictions were most reliable, we used a Kolmogorov–Smirnov nonparametric test which quantifies the distance between the empirical continuous distribution functions of two samples, and the null hypothesis is that the samples are drawn from the same distribution. By comparing the distribution of the same numeric trait in both the observed and the predicted sample, if the *p*-value of the test is above the α threshold, that is, 0.05, we can assume that threatened species in the considered taxonomic order are well represented in the sample of observed data. This means that, for this order, our predictions are more robust.

Data availability. The authors declare that (the/all other) data supporting the findings of this study are available within the article and its Supplementary Information files.

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A globally coherent fingerprint of climate change impacts across natural systems

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Causal attribution of recent biological trends to climate change is complicated because non-climatic influences dominate local, short-term biological changes. Any underlying signal from climate change is likely to be revealed by analyses that seek systematic trends across diverse species and geographic regions; however, debates within the Intergovernmental Panel on Climate Change (IPCC) reveal several definitions of a 'systematic trend'. Here, we explore these differences, apply diverse analyses to more than 1,700 species, and show that recent biological trends match climate change predictions. Global meta-analyses documented significant range shifts averaging 6.1 km per decade towards the poles (or metres per decade upward), and significant mean advancement of spring events by 2.3 days per decade. We define a diagnostic fingerprint of temporal and spatial 'sign-switching' responses uniquely predicted by twentieth century climate trends. Among appropriate long-term/large-scale/multi-species data sets, this diagnostic fingerprint was found for 279 species. This suite of analyses generates 'very high confidence' (as laid down by the IPCC) that climate change is already affecting living systems.

The Intergovernmental Panel on Climate Change[1] (IPCC) assessed the extent to which recent observed changes in natural biological systems have been caused by climate change. This was a difficult task despite documented statistical correlations between changes in climate and biological changes[2–5]. With hindsight, the difficulties encountered by the IPCC can be attributed to the differences in approach between biologists and other disciplines, particularly economists. Studies in this area are, of necessity, correlational rather than experimental, and as a result, assignment of causation is inferential. This inference often comes from experimental studies of the effects of temperature and precipitation on the target species or on a related species with similar habitats. Confidence in this inferential process is subjective, and differs among disciplines, thus resulting in the first divergence of opinion within the IPCC.

The second impasse came from differences in perspective on what constitutes an 'important' factor. Anyone would consider a currently strong driver to be important, but biologists also attach importance to forces that are currently weak but are likely to persist. In contrast, economic approaches tend to discount events that will occur in the future, assigning little weight to weak but persistent forces. Differences of opinion among disciplines can therefore stem naturally from whether the principal motivation is to assess the magnitude of immediate impacts or of long-term trajectories. Most field biologists are convinced that they are already seeing important biological impacts of climate change[1–4,6–9]; however, they have encountered difficulty in convincing other academic disciplines, policy-makers and the general public. Here, we seek to improve communication, provide common ground for discussion, and give a comprehensive summary of the evidence.

How should a 'climate fingerprint' be defined? A straightforward view typical of an economist would be to conclude that climate change was important if it were principally responsible for a high proportion of current biotic changes. By this criterion a climate fingerprint appears weak. Most short-term local changes are not caused by climate change but by land-use change and by natural fluctuations in the abundance and distribution of species. This fact has been used by non-biologists to argue that climate change is of little importance to wild systems[10]. This approach, however, effectively ignores small, systematic trends that may become important in the longer term. Such underlying trends would be confounded (and often swamped) by strong forces such as habitat loss. Biologists have tended to concentrate on studies that minimize confounding factors, searching for trends in relatively undisturbed systems and then testing for significant associations with climate change. Economists have viewed this as biased (nonrandom exclusion of data) whereas biologists view this as reducing non-climatic noise. Thus, economists focus on total direct evidence and apply heavy time discounting; biologists apply a 'quality control' filter to available data, accept indirect (inferential) evidence and don't apply time discounting.

The test for a globally coherent climate fingerprint does not require that any single species show a climate change impact with 100% certitude. Rather, it seeks some defined level of confidence in a climate change signal on a global scale. Adopting the IPCC 'levels of confidence'[11] and applying the economists' view of a fingerprint, we would have "very high confidence" in a fingerprint if we estimated that more than 95% of observed changes were principally caused by climate change, "high confidence" between 95% and 67%, "medium confidence" between 33% and 67%, and "low confidence" below 33%. In contrast, the biologists' confidence level comes from the statistical probability that global biotic trends would match climate change predictions purely by chance, coupled with supporting experimental results showing causal relationships between climate and particular biological traits.

Here, we present quantitative estimates of the global biological impacts of climate change. We search for a climate fingerprint in the overall patterns, rather than critiquing each study individually. Using the biologists' approach, we synthesize a suite of correlational studies on diverse taxa over many regions to ask whether natural systems, in general, have responded to recent climate change. Furthermore, we attempt a cross-fertilization by applying an economists' measure—the estimated proportion of observed changes for which climate trends are the principal drivers—to data sets chosen using biologists' criteria. We call this a 'global coherence' approach to the detection of climate change impacts.

First, we explore a biologists' confidence assessment with two types of analyses of observed change: statistical meta-analyses of effect size in restricted data sets and more comprehensive categorical analyses of the full literature. Second, we present a probabilistic model that considers three variables: proportion of observations matching climate change predictions, numbers of competing explanations for each of those observations, and confidence in causal attribution of each observation to climate change. These three variables feature equally in a model that explores an economists' 'confidence' assessment. Finally, we explore diagnostic 'sign-switching' patterns that are predicted uniquely by climate change.

The evidence

A few studies indicate evolutionary responses of particular species to climate change[12–14], but the generality of evolutionary response remains unknown. Here, we focus on phenological (timing) shifts, range boundary shifts, and community studies on species abundances (Table 1).

Meta-analyses

We developed databases suitable for meta-analysis[15] on two phenomena: range-boundary changes and phenological shifts. To control for positive publishing bias, we used only multi-species studies that reported neutral and negative results as well as positive (see Methods).

For range boundaries, suitable data spanned 99 species of birds[16], butterflies[17] and alpine herbs[18,19] (see Methods). The meta-analysis showed that the range limits of species have moved on average 6.1 ($\pm$2.4) km per decade northward or m per decade upward, significantly in the direction predicted by climate change (bootstrapped 95% confidence interval of the mean ($\mathrm{CI_{mean}} = 1.3$–$10.9\,\mathrm{km\,m^{-1}}$ per decade; one-sample t-test, degrees of freedom (d.f.) $= 98$, $t = 2.52$, $P = 0.013$; Table 2).

For phenologies, suitable data were reported for herbs[20–23], shrubs[20–25], trees[20,23–25], birds[20,21], butterflies[26] and amphibians[27,28], a total of 172 species (see Methods). There was a mean shift towards earlier spring timing of 2.3 days per decade, with a bootstrapped 95% CI of 1.7–3.2 days advancement per decade (significant at $P < 0.05$).

Categorical analyses

The remaining studies were not included in the meta-analyses, either because they were on single species or because they did not present data in the raw form of x unit change per y time units per species. These less-detailed data were simplified into four categories: changed in accord with or opposite to climate change predictions, changed in some other fashion or stable (see Methods).

As with previous studies[17], analyses ignore species classified as 'stable'. This category does not represent a single result, as apparent stability could arise from a diversity of situations[17] such as: 1) the phenology, abundance or distribution of the species is not driven by climatic factors; 2) the species is actually changing, but poor data resolution could not detect small changes; and 3) the phenology, abundance or distribution of the species is driven by climatic factors, but fails to respond to current climate change. Such failure could stem from anthropogenic barriers to dispersal (habitat fragmentation) or from a lag in response time. Lags are expected when limited dispersal capabilities retard poleward/upward colonization[29], or when a necessary resource has slower response time than the focal species[17].

Phenological shifts. We quantitatively assessed 677 species reported in the literature (Table 1). Over a time period range of 16–132 years (median 45 yrs), 27% showed no trends in phenologies, 9% showed trends towards delayed spring events, whereas the remaining 62% showed trends towards spring advancement. Observed trends include earlier frog breeding[27,28], bird nesting[30–32], first flowering[20–25], tree budburst[23–25], and arrival of migrant birds and butterflies[20,21,26,33] (Table 1). Shifts in phenologies that have occurred are overwhelmingly (87%) in the direction expected from climate change ($P < 0.1 \times 10^{-12}$; Table 2).

Distribution/abundance shifts. In a quantitative assessment covering >1,046 species, we were able to categorize 893 species, functional

Table 1 **Summary of data studying phenological and distributional changes of wild species**

Taxon	Ref. number	Total no. of species (or species groups)	Spatial scale L	Spatial scale R	Spatial scale C	Time scale (range years)	Change in direction predicted (*n*)	Change opposite to prediction (*n*)	Stable (*n*)	No prediction (*n*)
Phenological changes										
Woody plants	20,23,24*,25*	*n* = 38 sp		2	1	35–132	30	1	7	–
Herbaceous plants	20,21*	*n* = 38 sp	1	1		63–132	12	–	26	–
Mixed plants	22*	*n* = 385 sp	1			46	279	46	60	–
Birds	20,21*,30,31,32,33	*n* = 168 sp	2	3	1	21–132	78	14	76	–
Insects	26	*n* = 35 sp		1		23	13	–	22	–
Amphibians	27,28	*n* = 12 sp	2			16–99	9	–	3	–
Fish	20	*n* = 2 sp		1		132	2	–	–	–
Distribution/abundance changes										
Tree lines	54,55,56*	*n* = 4 sp + 5 grps	2	1		70–1,000	3 sp + 5 grps	–	1	–
Herbs and shrubs	18,19,41*,42*	*n* > 66 sp, 15 detailed		3		28–80	13	2	–	–
Lichens	36	4 biogeographic grps (*n* = 329 sp)	1			22	43	9	113	164
Birds	8*	*n* = 3 sp		1		50	3	–	–	–
	16,57*	N sp (*n* = 46 sp)		2		20–36	13	15	18	
		S sp (*n* = 73 sp)		2		20–36	36	16	21	6
	43*	Low elevation (>91 sp)	1			20	71	11	9	–
		High elevation (>96 sp)	1			20	37	27	32	–
Mammals	37	*n* = 2 sp		1		52	2	–	–	–
Insects	17,49*	*n* = 36 sp		1	1	98–137	23	2	10	1
	17	N boundaries (*n* = 52 sp)		1		98	34	1	17	–
		S boundaries (*n* = 40 sp)		1		98	10	2	28	–
Reptiles and amphibians	43*	*n* = 7 sp	1			17	6	–	1	–
Fish	39	*4* biogeographic grps (*n* = 83 sp)	1			–	2 grps	–	1 grp	1 grp
	40*	N sp (*n* > 1 sp)		1		70	>1	–	–	–
		S sp (*n* > 1 sp)		1		70	>1	–	–	–
Marine invertebrates	34*,40*	N sp (*n* > 21)	1	1		66–70	>19	2	–	>1 sp not classified
		S sp (*n* > 21)	1	1		66–70	>20	1	–	
		Cosmopolitan sp (*n* = 28 sp)	1			66	–	–	–	28
Marine zooplankton	40*	Cold water (*n* > 10 sp)		1		70	>10	–	–	>8 sp not classified
		Warm water (*n* > 14 sp)		1		70	>14	–	–	
	35	6 biogeographic grps (*n* ≥ 36 sp)			1	39	6 grps	–	–	–

N, species with generally northerly distributions (boreal/arctic); S, species with generally southerly distributions (temperate); L, local; R, regional (a substantial part of a species distribution; usually along a single range edge); C, continental (most or the whole of a species distribution). No prediction indicates that a change may have been detected, but the change was orthogonal to global warming predictions, was confounded by non-climatic factors, or there is insufficient theoretical basis for predicting how species or system would change with climate change.

*Study partially controlled for non-climatic human influences (for example, land-use change). Studies that were highly confounded with non-climatic factors were excluded. (See Supplementary Information for details of species classification.)

groups or biogeographic groups (Table 1). Less than one-third (27%) of these have exhibited stable distributions during the twentieth century. Others (24%) show changes that are impossible to relate to climate change predictions. These two types of result neither support nor refute a climate change signal, although it will be important for predictive biological models to eventually determine what proportion of these are truly stable systems.

Some range shifts have been measured directly at range boundaries, whereas others have been inferred from abundance changes within local communities. Over all of the range and abundance shift data, 434 species were categorized as changing over time periods of 17–1,000 years (median 66 years) (Table 1). Of these, 80% have shifted in accord with climate change predictions (see Methods) ($P < 0.1 \times 10^{-12}$; Table 2). New species have colonized previously 'cool' regions, including sea anemones in Monterey Bay[34] and lichens and butterflies in Europe[17,36], whereas some Arctic species have contracted in range size[35,37]. Over the past 40 years, maximum range shifts vary from 200 km (butterflies[17]) to 1,000 km (marine copepods[34]).

Probabilistic coherence

How strong is the climate change signal in the light of confounding factors and lack of experimentation? We investigate this argument in a probabilistic context. We formulated a probabilistic model to ask whether a climate change fingerprint exists in a disparate set of n observed biological changes. Let n'/n indicate the proportion of observations counter to climate change predictions and p indicate the probability that climate change is the only possible causal agent of the observed biological change in any of the $n - n'$ species that do conform to climate change predictions. In practice, this can be estimated across a set of species by assigning each species a 0 or a 1, depending on whether or not competing explanations exist; p then is the proportion of species that have no competing explanations.

Competing (non-climatic) explanations can, therefore, be expected in $\{(1 - p)(n - n')\}$ of the reported analyses. Finally, for any of the $n - n'$ climate-conforming species, let π indicate the probability, determined from previous empirical study, that climate change is the principal causal agent of a particular biological change (independent of p).

These three variables, each varying from 0 to 1, are inputs to a binomial probability model whose output estimates the proportion of all species that are, in truth, being impacted by climate change. In practice, confounding factors can never be eliminated completely from observational studies; therefore, p would normally have a low value. Here, we consider only the conservative case where $p = 0$; that is, we assume that non-climatic alternative explanations exist for every species. In the Supplementary Information, we present modelling schemes where p varies from 0 to 1.0.

The importance of non-climatic explanations should decrease with increasing scale. Most local changes are idiosyncratic and consist of noise when scaled up; however, atmospheric carbon dioxide levels have risen nearly uniformly across the globe. Increased CO_2 can directly cause earlier flowering[38], as does increased temperature, making these effects difficult to separate. However, these two effects can be viewed as different aspects of global warming, legitimizing discussion of their joint impacts.

The variable π reflects the extent to which previous study and experimentation provides clear mechanistic understanding of the links between climate variables and a species' behaviour and ecology. To understand the importance of π, consider the case of the silver-spotted skipper butterfly (*Hesperia comma*) that has expanded its distribution close to its northern boundary in England over the past 20 years. Possible ecological explanations for this expansion are regional warming and changes in land use. Comparing the magnitudes and directions of these two factors suggests that climate change is more likely than land-use change to be the cause of expansion[29]. Deeper support was provided by previous empirical studies documenting strong thermal limitation. At the northern boundary, development of offspring was restricted to the hottest microclimates (south-facing chalk slopes). Range expansion coincided with colonization of non-southern slopes. Simulation models based solely on previously measured thermal tolerances (that is, without land-use change) closely matched the observed expansion of 16.4 km (model prediction 14.4 km)[12]. Thus, mechanistic understanding of the system generates a high estimate for π.

Figure 1 shows relationships between the n'/n proportions and the minimum value of π that would be required to sustain different degrees of confidence for $p = 0$. For example, the medium confidence region shows minimum values of π that would be required across the displayed range of n'/n proportions to guarantee that about half of the observed species impacts were in truth being driven principally by climate change. Claiming a climate fingerprint with high confidence would require high minimum values for π (>0.67) regardless of n'/n.

Applying the probabilistic model

Using all of the data from Table 2 to parameterize the model, $n' = 147$ and $n = 770$, making $n'/n = 0.16$ (16% of species changing opposite to climate change predictions). We now consider π. The extent to which climate change can be isolated as the predominant driving force is extremely variable among species and systems. Such attribution results from a subjective synthesis of experimental and observational research, often conducted well before and independently of any study of long-term trends. The species for which π is high are those with a history of basic biological research, especially where research has been conducted along several axes (controlled laboratory/greenhouse experiments, field manipulations and observations).

Table 2 **Summary statistics and synthetic analyses derived from Table 1**

Type of change	Changed as predicted	Changed opposite to prediction	*P*-value
Phenological ($N = 484/(678)$)	87% ($n = 423$)	13% ($n = 61$)	$<0.1 \times 10^{-12}$
Distributional changes			
At poleward/upper range boundaries	81%	19%	–
At equatorial/lower range boundaries	75%	25%	–
Community (abundance) changes			
Cold-adapted species	74%	26%	–
Warm-adapted species	91%	9%	–
$N = 460/(920)$	81% ($n = 372$)	19% ($n = 88$)	$<0.1 \times 10^{-12}$
Meta-analyses			
Range-boundaries ($N = 99$)	6.1 km m^{-1} per decade northward/upward shift*		0.013
Phenologies ($N = 172$)	2.3 days per decade advancement*		<0.05

Data points represent species, functional groups or biogeographic groups. *N*, number of statistically or biologically significant changes/(total number species with data reported for boundary, timing, or abundance processes). The no prediction category is not included here.

*Bootstrap 95% confidence limits for mean range boundary change are 1.26, 10.87; for mean phenological shift the limits are −1.74, −3.23.

This sort of biological detail reveals that climate and extreme weather events are mechanistically linked to body size, individual fitness and population dynamics for diverse species[3–9] (but not for all). Species for which confidence in climate as the primary driving mechanism is low are those for which long-term observational records exist, but not detailed empirical research on target species or on ecologically similar species. The black line in Fig. 1 suggests that medium confidence can be claimed for $n'/n = 0.16$ if $0.35 < \pi < 0.7$. Other contingencies, such as complications from a positive publishing bias or non-independence among confounding factors, can be considered through variations of the model (see Supplementary Information).

Differentiating diagnostic patterns

Predictions of the impacts of climate change are not unidirectional, but may show opposite trends within communities and across long time spans or large spatial scales. Alternative causal agents would therefore have to be able to switch the sign of their impacts within a study if they were to form credible competing explanations. Such differentiating patterns greatly reduce the likelihood of hidden, non-climate competing explanations, thereby increasing P and decreasing the value of π necessary to achieve a given confidence level (see Supplementary Information). High confidence could be obtained under this scheme with existing patterns ($n'/n \leq 0.33$) and poor mechanistic understanding (low π). Sufficient data to quantify the differential impacts on species' distributions or phenologies across time periods or geographic regions were available for 334 species, among which 84% showed a sign-switching diagnostic of climate change response ($P < 0.1 \times 10^{-12}$; Table 3).

Community representation sign switching

Community studies in regions of overlapping 'polar' and 'temperate' species base their climate change attribution on differential responses of these two categories. Among marine fish and intertidal invertebrates (for example, snails, barnacles, anemones, copepods and limpets) off the Californian coast[34,39] and in the North Atlantic[35,40], lichens in the Netherlands[36], foxes in Canada[37] and birds in Great Britain[16], polar species have tended to be stable or decline in abundance, whereas temperate species at the same site have increased in abundance and/or expanded their distributions. Analogous shifts are occurring even within the Arctic and Antarctic among penguins[8], woody plants[41] and vascular plants[42]. Similar patterns exist for lowland compared with highland birds in the tropics[43]. Most of these studies are local, with high variability of individual species' population dynamics. Even so, 80% of changes in community representation are in accord with climate change predictions (Tables 2 and 3).

Temporal sign switching

Long-term studies encompass periods of climate cooling as well as warming. If the distributions of species are truly driven by climate trends, these species should show opposite responses to cooling and warming periods. Such sign switching has been documented in the United Kingdom for marine fish, limpets, barnacles and zooplankton[40], in the United Kingdom and Estonia for birds[20,31,44,45], and in the United Kingdom, Finland and Sweden for butterflies[17,46–48] (see also Table 3 legend). A typical pattern includes northward range shifts during the two twentieth-century warming periods (1930–45 and 1975–99), and southward shifts during the intervening cooling period (1950–70). No species showed opposing temporal trends (Table 3).

Spatial sign switching

Whole-range, continental-scale studies, by encompassing the extremes of a species' distribution, allow testing for differential spatial impacts. In North America and Europe, detailed temporal data spanning the twentieth century were compiled for 36 butterfly species at both northern and southern range extremes[17,49]. Eight species (22%) exhibited a diagnostic pattern of northward expansion (new colonizations) and southern contraction (population extinctions). No species showed opposing range shift trends (northward contraction and southward expansion) (Table 3).

Discussion

The logic of a global focus on biological change is analogous to that for climate change itself. With climate change, attribution of recent warming trends to changes in atmospheric gases comes from analysis of global patterns, not from detailed data from individual meteorological stations. Similarly, when assessing biological

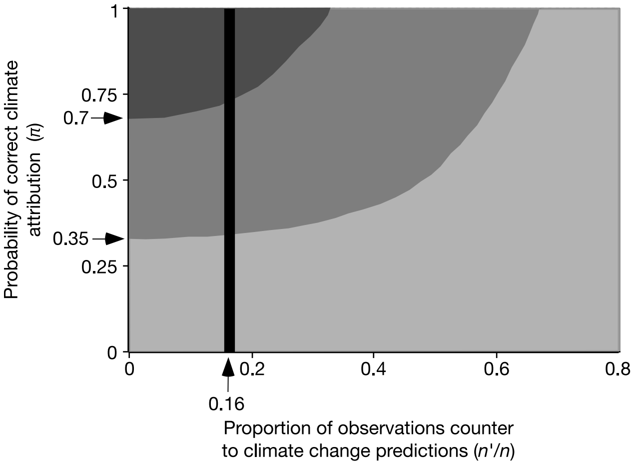

Figure 1 Probabilistic model based on parameter estimates from a review of the literature. Levels of confidence in the linkage of biological changes to global climate change are: high (dark grey), medium (mid-grey) and low (light grey). Confidence regions assume $p = 0$ (competing explanations exist for all studies). The black line indicates the region of confidence possible using the probabilistic model on the basis of the parameter estimate of n'/n from the literature review, and allowing π to vary freely.

Table 3 **Biological fingerprint of climate change impacts**

Sign-switching pattern	Percentage of species showing diagnostic pattern
Community Abundance changes have gone in opposite directions for cold-adapted compared with warm-adapted species. Usually local, but many species in each category. Diverse taxa, $n = 282$*.	80%
Temporal Advancement of timing of northward expansion in warm decades (1930s/40s and 1980s/90s); delay of timing or southward contraction in cool decades (1950s/60s), 30–132 years per species. Diverse taxa, $n = 44$*.	100%
Spatial Species exhibit different responses at extremes of range boundary during a particular climate phase. Data are from substantial parts of both northern and southern range boundaries for each species. All species are northern hemisphere butterflies, $n = 8$*.	100%

Differential sign-switching patterns diagnostic of climate change as the underlying driver.
*Numbers of species represent minimum estimates, as not all species were described in sufficient detail in each study to classify. A few species showed two types of sign switching, and so are included in more than one cell. Data are from references in text and from raw data provided by L. Kaila, J. Kullberg, J. J. Lennon, N. Ryrholm, C. D. Thomas, J. A. Thomas and M. Warren.

impacts, the global pattern of change is far more important than any individual study.

The approach of biologists selects study systems to minimize confounding factors and deduces a strong climate signal both from systematic trends across studies and from empirically derived links between climate and biological systems. This deduction is made even if climate explains only a small part of the observed biological change. The meta-analyses of 334 species and the global analyses of 1,570 species (or functional/biogeographic groups) show highly significant, nonrandom patterns of change in accord with observed climate warming in the twentieth century, indicating a very high confidence ($>95\%$) in a global climate change fingerprint (Table 2).

The approach of economists takes a broader view. In its purest form, applied to all existing data and incorporating time discounting, this approach would conclude that climate change has little total impact on wild species. We argue that this approach misses biologically important phenomena. Here we hybridize the two approaches by applying an economists' model to data that biologists would consider reasonable, and forego time discounting. A total of 74–91% of species that have changed have done so in accord with climate change predictions (Table 2) giving an estimate of $n'/n = 0.16$ for the hybrid model. Assessment of π, the probability of correct attribution to climate, is subjective and relies on the level of confidence in inferential evidence. Such evidence comes from empirical analyses and experimental manipulations, which have documented the importance of climatic variables to the dynamics, distributions and behaviour of species[3,5,8,9]. From these studies, biologists infer that expected values of π are often high. We show that moderate values of π (0.35–0.70) are consistent with medium confidence in a global climate change fingerprint.

The different approaches raise two distinct questions of the data and result in different levels of confidence in a climate change fingerprint. The questions are: (1) whether climate change can be shown to be an over-riding factor currently driving natural systems; and (2) whether there is sufficient evidence to implicate climate change as a common force impacting natural systems on a global scale. In an absolute sense, land-use change has probably been a stronger driver of twentieth century changes in wild plants and animals than has climate change (question 1). From a biological view, however, finding any significant climate signal amidst noisy biological data is unexpected in the absence of real climate drivers (question 2). Such small, persistent forces are inherently important in that they can alter species interactions, de-stabilize communities and drive major biome shifts.

A review of the literature reveals that the patterns that are being documented in natural systems are surprisingly simple, despite the real and potential complexity of biotic change. Change in any individual species, taxon or geographic region may have a number of possible explanations, but the overall effects of most confounding factors decline with increasing numbers of species/systems studied. Similarly, uncertainty in climate attribution for any particular study does not prevent the development of a global conclusion on the basis of a cumulative synthesis. In particular, a clear pattern emerges of temporal and spatial sign switches in biotic trends uniquely predicted as responses to climate change. With 279 species (84%) showing predicted sign switches, this diagnostic indicator increases confidence in a climate change fingerprint from either viewpoint.

The published IPCC conclusion stated high confidence ($P > 0.67$) in a climate signal across observed biotic and abiotic changes. Analyses presented here support that conclusion. Furthermore, a driver of small magnitude but consistent impact is important in that it systematically affects century-scale biological trajectories and ultimately the persistence of species. The climate fingerprint found here implicates climate change as an important driving force on natural systems. ☐

Methods

Climate change predictions

Expected phenological shifts for regions experiencing warming trends are for earlier spring events (for example, migrant arrival times, peak flight date, budburst, nesting, egg-laying, and flowering) and for later autumn events (for example, leaf fall, migrant departure times, and hibernation)[50,51]. Response to climate warming predicts a preponderance of polward/upward shifts[50,51]. Dynamics at the range boundaries are expected to be more influenced by climate than are dynamics within the interior of a species range. Thus, community level studies of abundance changes are used best to infer range shifts when they are located at ecotones involving species having fundamentally different geographic ranges: higher compared with lower latitudes, or upper compared with lower altitudes. Response to climate warming predicts that southerly species should outperform northerly species at the same site[50,51].

Selection of studies for review

This was not an exhaustive review. The studies listed in Table 1 comprise the bulk of wild species studied with respect to climate change hypotheses. Selection of papers was aimed at those with one or more of the following attributes: long temporal span (>20 years), data covering a large geographic region, and/or data gathered in an unbiased manner for a multi-species assemblage (typically species abundance data of locally well-documented communities). We excluded several high-quality studies of single species performed at local scale or highly confounded by non-climatic global change factors. The stable category represents species for which any observed changes are indistinguishable from year to year fluctuations, either from a statistical test for trend using very long time series data or from comparing net long-term movement to expected yearly variation on the basis of basic biological knowledge of dispersal/colonization abilities.

Meta-analyses

To create databases, studies were combined that made similar types of measurements and that reported quantitative estimates of change over a specified time period. All species were used; that is, even species that are categorized as stable in Table 1 were included in the meta-analysis. We treated phenological and distributional changes separately. To minimize positive publishing bias, only multi-species studies were included.

We considered each species as an independent data point, rather than each study. Only data reported in terms of change per individual species were included. This precluded use of studies that only report mean change across a set of species.

We used only distributional studies at range boundaries. We excluded equatorial and lower elevational boundaries because of a paucity of data combined with theoretical reasons for treating these boundaries separately from poleward/upper elevational boundaries[52]. Three studies met the criteria for data detail, covering 9 alpine herbs[18,19], 59 birds[16] and 31 butterflies[17]. The geographic locations of these boundaries were non-overlapping, reducing the likelihood of correlated confounding variables. Altitude was converted to latitudinal equivalent (for temperature clines, 1 km northward = 1 m upward). The United Kingdom bird data compared mean northern boundary in 1999 to that in 1972 using the ten northernmost occupied grid cells (on 10 km^2 grids) from published atlases. The Swedish butterfly data compared mean northern boundary in the period 1971–97 to mean northern boundary in 1900–20 using the five northernmost records per year. The Swiss herb data showed changes in species assemblages over the twentieth century in fixed plots up altitudinal gradients on 26 mountains.

The effect size per species was the absolute magnitude of range boundary shift, standardized across species to be in units of km m^{-1} per decade, with northward/upslope shifts positive and southward/downslope shifts negative. Data were not skewed, and *n* was large. Therefore, a one-sample *t*-test was used to evaluate the null hypothesis of no overall trends (that is, H_o: mean boundary change across all species is zero). Variances were not available for all species, so we used an unweighted analysis. We performed an additional bootstrap analysis of 95% confidence limits on the mean boundary shift (10,000 iterations)[53].

The phenological meta-analysis was on spring timing events—there were insufficient studies on autumn phenology to warrant analysis. Nine studies published magnitudes of shift over a given time period (17–61 years). They included 11 trees[20,23–25], 6 shrubs[20,21,23–25], 85 herbs[20–23], 35 butterflies[26], 21 birds[21], 12 amphibians[27,28] and 2 fish[20]. This data set was inappropriate for the *t*-test owing to skew, but bootstrapped confidence limits provided an estimate of the probability that the true mean shift includes zero.

For both analyses, geography and taxa are confounded. For the range boundary analysis, all bird data are from the United Kingdom, all butterfly data from Sweden, and all herb data from Switzerland. For the phenological analysis, most shrub and bird data are from the United States, butterfly data from Great Britain, and trees from Europe. Therefore, it is not meaningful to split the analyses further.

Categorical analyses

Reported data from all studies listed in Tables 1 and 3 were included in the categorical analyses. The predicted direction is a change predicted by global warming scenarios[50,51]. All studies were conducted in temperate Northern Hemisphere, except for 194 species in Costa Rica[43] and 5 species in Antarctica[8,42]. Two categories showing changes either predicted by or opposite to predictions of climate change theory were tested against the random expectation of an equal probability of observing changes in either direction. Analyses were by binomial test with H_o: $P = 0.5$.

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Ecological and Evolutionary Responses to Recent Climate Change

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aquatic, global warming, phenology, range shift, terrestrial, trophic asynchrony

Abstract

Ecological changes in the phenology and distribution of plants and animals are occurring in all well-studied marine, freshwater, and terrestrial groups. These observed changes are heavily biased in the directions predicted from global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research. Range-restricted species, particularly polar and mountaintop species, show severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change. Tropical coral reefs and amphibians have been most negatively affected. Predator-prey and plant-insect interactions have been disrupted when interacting species have responded differently to warming. Evolutionary adaptations to warmer conditions have occurred in the interiors of species' ranges, and resource use and dispersal have evolved rapidly at expanding range margins. Observed genetic shifts modulate local effects of climate change, but there is little evidence that they will mitigate negative effects at the species level.

INTRODUCTION

Historical Perspective

Climate change is not a new topic in biology. The study of biological impacts of climate change has a rich history in the scientific literature, since long before there were political ramifications. Grinnell (1917) first elucidated the role of climatic thresholds in constraining the geographic boundaries of many species, followed by major works by Andrewartha & Birch (1954) and MacArthur (1972). Observations of range shifts in parallel with climate change have been particularly rich in northern European countries, where observational records for many birds, butterflies, herbs, and trees date back to the mid-1700s. Since the early part of the twentieth century, researchers have documented the sensitivity of insects to spring and summer temperatures (Bale et al. 2002, Dennis 1993, Uvarov 1931). Ford (1945) described northward range shifts of several butterflies in England, attributing these shifts to a summer warming trend that began around 1915 in Britain. Ford noted that one of these species, *Limenitis camilla*, expanded to occupy an area where attempted introductions prior to the warming had failed. Kaisila (1962) independently documented range shifts of Lepidoptera (primarily moths) in Finland, using historical data on range boundaries dating back to 1760. He showed repeated instances of southward contractions during decades of "harsh" climatic conditions (cold wet summers), followed by northward range expansion during decades with climate "amelioration" (warm summers and lack of extreme cold in winter). Further corroboration came from the strong correlations between summer temperatures and the northern range boundaries for many butterflies (Dennis 1993).

Similar databases exist for northern European birds. A burst of papers documented changed abundances and northerly range shifts of birds in Iceland, Finland, and Britain associated with the 1930s–1940s warming period (Gudmundsson 1951; Harris 1964; Kalela 1949, 1952; Salomonsen 1948). A second wave of papers in the 1970s described the subsequent retreats of many of these temperate bird and butterfly species following the cool, wet period of the 1950s–1960s (Burton 1975, Heath 1974, Severnty 1977, Williamson 1975).

Complementing this rich observational database is more than 100 years of basic research on the processes by which climate and extreme weather events affect plants and animals. As early as the 1890s, Bumpus (1899) noted the differential effects of an extreme winter storm on the introduced house sparrow (*Parus domesticus)*, resulting in stabilizing selection for intermediate body size in females and directional selection for large body size in males (Johnston et al. 1972). The first extensive studies of climate variability as a powerful driver of population evolution date back to the 1940s, when Dobzhansky (1943, 1947) discovered repeated cycles of seasonal evolution of temperature-associated chromosomal inversions within *Drosophila pseudoobscura* populations in response to temperature changes from spring through summer.

In summary, the history of biological research is rich in both mechanistic and observational studies of the impacts of extreme weather and climate change on wild species: Research encompasses impacts of single extreme weather events; experimental studies of physiological tolerances; snapshot correlations between climatic variables and species' distributions; and correlations through time between climatic trends and changes in distributions, phenologies, genetics, and behaviors of wild plants and animals.

Anthropogenic Climate Change

In spite of this wealth of literature on the fundamental importance of climate to wild biota, biologists have been reluctant to believe that modern (greenhouse gas-driven) climate change is a cause of concern for biodiversity. In his introduction to the 1992 *Annual Review of Ecology, Evolution, and Systematics* volume on "Global Environmental Change," Vitousek wrote, "ultimately, climate change probably has the greatest potential to alter the functioning of the Earth system . . . . nevertheless, the major effects of climate change are mostly in the future while most of the others are already with us." Individual authors in that volume tended to agree—papers were predominantly concerned with other global change factors: land use change, nitrogen fertilization, and the direct effects of increased atmospheric CO_2 on plant ecophysiology.

Just 14 years later, the direct impacts of anthropogenic climate change have been documented on every continent, in every ocean, and in most major taxonomic groups (reviewed in Badeck et al. 2004; Hoegh-Guldberg 1999, 2005b; Hughes 2000; IPCC 2001a; Parmesan 2005b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Sparks & Menzel 2002; Thomas 2005; Walther et al. 2002, 2005). The issue of whether observed biological changes can be conclusively linked to anthropogenic climate change has been analyzed and discussed at length in a plethora of syntheses, including those listed above. Similarly, complexity surrounding methodological issues of detection (correctly detecting a real trend) and attribution (assigning causation) has been explored in depth (Ahmad et al. 2001; Dose & Menzel 2004; Parmesan 2002, 2005a,b; Parmesan & Yohe 2003; Parmesan et al. 2000; Root et al. 2003, Root & Hughes 2005, Schwartz 1998, 1999; Shoo et al. 2006). The consensus is that, with proper attention to sampling and other statistical issues and through the use of scientific inference, studies of observed biological changes can provide rigorous tests of climate-change hypotheses. In particular, independent syntheses of studies worldwide have provided a clear, globally coherent conclusion: Twentieth-century anthropogenic global warming has already affected Earth's biota.

Detection: ability to discern long-term trends above yearly variability and real changes from apparent changes brought about by changes in sampling methodology and/or sampling intensity

Attribution: teasing out climate change as the causal driver of an observed biological change amid a backdrop of potential confounding factors

Globally coherent: a common term in economics, a process or event is globally coherent when it has similar effect across multiple systems spread across different locations throughout the world

Scope of This Review

This review concentrates on studies of particularly long time series and/or particularly good mechanistic understanding of causes of observed changes. It deals exclusively with observed responses of wild biological species and systems to recent, anthropogenic climate change. In particular, agricultural impacts, human health, and ecosystem-level responses (e.g., carbon cycling) are not discussed. Because they have been extensively dealt with in previous publications, this review does not repeat discussions of detection and attribution, nor of the conservation implications of climate change. Rather, some of the best-understood cases are presented to illustrate the complex ways in which various facets of climatic change impact wild biota. The choice of studies for illustration attempts to draw attention to the taxonomic and geographic breadth of climate-change impacts and to the most-recent literature not already represented in prior reviews.

Researchers have frequently associated biological processes with indices of ocean-atmosphere dynamics, such as the El Niño Southern Oscillation and the North Atlantic Oscillation (Blenckner & Hillebrand 2002, Holmgren et al. 2001, Ottersen et al. 2001). However, the nature of the relationship between atmospheric dynamics, ocean circulation, and temperature is changing (Alley et al. 2003, IPCC 2001b, Karl & Trenberth 2003, Meehl et al. 2000). Therefore, there is large uncertainty as to how past relationships between biological systems and ocean indices reflect responses to ongoing anthropogenic climate change. Although I use individual examples where appropriate, this complex topic is not fully reviewed here.

OVERVIEW OF IMPACTS LITERATURE

An extensive, but not exhaustive, literature search revealed 866 peer-reviewed papers that documented changes through time in species or systems that could, in whole or in part, be attributed to climate change. Some interesting broad patterns are revealed. Notably, the publication rate of climate-change responses increases sharply each year. The number of publications between 1899 and January 2003 (the date of two major syntheses) was 528. Therefore, approximately 40% of the 866 papers compiled for this review were published in the past three years (January 2003 to January 2006).

The studies are spread broadly across taxonomic groups. Whereas distributional studies concentrated on animals rather than plants, the reverse is true of phenological time series. This may simply be because historical data on species range boundaries have higher resolution for animals than for plants. Conversely, local records of spring events are much more numerous for plants (e.g., flowering and leaf out) than for animals (e.g., nesting).

Although there is still a terrestrial bias, studies in marine and freshwater environments are increasing in proportional representation. The largest gaps are geographic rather than taxonomic. In absolute numbers, most biological impact studies are from North America, northern Europe and Russia. Few biological studies have come from South America, and there are large holes in Africa and Asia, with most of the studies from these two continents coming from just two countries: South Africa and Japan. In past decades, Australia's impact studies have stemmed predominantly from the coral reef community, but in recent years scientists have dug deep to find historical data, and terrestrial impact studies are now emerging. Similarly, the Mediterranean/North African region (Spain, France, Italy, and Israel) has recently spawned a spate of studies. Antarctica stands out as a region where impacts (or lack of impacts) on most species and systems have been documented, even though data often have large geographic or temporal gaps.

Few studies have been conducted at a scale that encompasses an entire species' range (i.e., a continental scale), with only a moderate number at the regional scale (e.g., the United Kingdom or Germany). Most have been conducted at local scales, typically at a research station or preserve. Continental-scale studies usually cover most or all of a species' range in terrestrial systems (Both et al. 2004, Burton 1998a,b, Dunn & Winkler 1999, Menzel & Fabian 1999, Parmesan 1996, Parmesan et al. 1999). However, even a continental scale cannot encompass the entire ranges of many oceanic species (Ainley & Divoky 1998, Ainley et al. 2003, Beaugrand et al. 2002, Croxall et al. 2002, Hoegh-Gulberg 1999, McGowan et al. 1998, Reid et al. 1998, Spear & Ainley 1999). Terrestrial endemics, in contrast, can have such small ranges that regional, or even local, studies may represent impacts on entire species (Pounds et al. 1999, 2006).

Meta-analysis: set of statistical techniques designed to synthesize quantitative results from similar and independent experiments

Meta-Analyses and Syntheses: Globally Coherent Signals of Climate-Change Impacts

A handful of studies have conducted statistical meta-analyses of species' responses or have synthesized independent studies to reveal emergent patterns. The clear conclusion across global syntheses is that twentieth-century anthropogenic global warming has already affected the Earth's biota (IPCC 2001a; Parmesan 2005a,b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Thomas 2005; Walther et al. 2002, 2005).

One study estimated that more than half (59%) of 1598 species exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years (Parmesan & Yohe 2003). Analyses restricted to species that exhibited change documented that these changes were not random: They were systematically and predominantly in the direction expected from regional changes in the climate (Parmesan & Yohe 2003, Root et al. 2003). Responding species are spread across diverse ecosystems (from temperate grasslands to marine intertidal zones and tropical cloud forests) and come from a wide variety of taxonomic and functional groups, including birds, butterflies, alpine flowers, and coral reefs.

A meta-analysis of range boundary changes in the Northern Hemisphere estimated that northern and upper elevational boundaries had moved, on average, 6.1 km per decade northward or 6.1 m per decade upward ($P < 0.02$) (Parmesan & Yohe 2003). Quantitative analyses of phenological responses gave estimates of advancement of 2.3 days per decade across all species (Parmesan & Yohe 2003) and 5.1 days per decade for the subset of species showing substantive change (>1 day per decade) (Root et al. 2003).

A surprising result is the high proportion of species responding to recent, relatively mild climate change (global average warming of 0.6°C). The proportion of wild species impacted by climate change was estimated at 41% of all species (655 of 1598) (Parmesan & Yohe 2003). This estimate was derived by focusing on multispecies studies that reported stable as well as responding species. Because responders and stable species were often sympatric, variation of response is not merely a consequence of differential magnitudes of climate change experienced.

PHENOLOGICAL CHANGES

By far, most observations of climate-change responses have involved alterations of species' phenologies. This is partly a result of the tight links between the seasons and agriculture: Planting and harvest dates (and associated climatic events such as day of last frost) have been well recorded, dating back hundreds of years for some crops. But the plethora of records also stems from the strong sociological significance of the change of the seasons, particularly in high-latitude countries. Peoples of Great Britain, the Netherlands, Sweden, and Finland have been keen on (some might say even obsessed with) recording the first signs of spring—the first leaf on an oak, the first peacock butterfly seen flying, the first crocus in bloom—as a mark that the long, dark winter is finally over. Fall has not captured as much enthusiasm as spring, but some good records exist, for example, for the turning of leaf color for trees.

The longest records of direct phenological observations are for flowering of cherry trees *Prunus jamasakura* and for grape harvests. Menzel & Dose (2005) show that timing of cherry blossom in Japan was highly variable among years, but no clear trends were discerned from 1400 to 1900. A statistically significant change point is first seen in the early 1900s, with steady advancement since 1952. Recent advancement exceeds observed variation of the previous 600 years. Menzel (2005) analyzed grape-harvest dates across Europe, for which April-August temperatures explain 84% of the variation. She found that the 2003 European heat wave stands out as an extreme early harvest (i.e., the warmest summer) going back 500 years. Although such lengthy observational records are extremely rare, these two unrelated plants on opposite sides of the world add an important historical perspective to results from shorter time series.

Several lines of evidence indicate a lengthening of vegetative growing season in the Northern Hemisphere, particularly at higher latitudes where temperature rise has been greatest. Summer photosynthetic activity (normalized difference vegetation index estimates from satellite data) increased from 1981–1991 (Myneni et al. 1997), concurrent with an advance and increase in amplitude of the annual CO_2 cycle (Keeling et al. 1996). White et al. (1999) modeled meteorological and satellite data to estimate actual growing season length each year from 1900–1987 in the United States. Growing season was unusually long during the warm period of the 1940s at all 12 sites. However, patterns have recently diverged. Since 1966, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° latitude), not in the three warmest zones (32°–37° latitude). Across the European Phenological Gardens (experimental clones of 16 species of shrubs and trees at sites across Europe), a lengthening of the growing season by 10.8 days occurred from 1959–1993 (Menzel 2000, Menzel & Fabian 1999). Analysis of climatological variables (e.g., last frost date of spring and first frost date of fall) mirrors this finding, with an estimated lengthening of the growing season of 1.1–4.9 days per decade since 1951 (Menzel et al. 2003).

Bradley et al. (1999) built on Aldo Leopold's observations from the 1930s and 1940s on the timing of spring events on a Wisconsin farm. Of 55 species resurveyed in the 1980s and 1990s, 18 (35%) showed advancement of spring events, whereas the rest showed no change in timing (with the exception of cowbirds arriving later). On average, spring events occurred 7.3 days earlier by the 1990s compared with 61 years before, coinciding with March temperatures being 2.8°C warmer.

Another long-term (100-year) study by Gibbs & Breisch (2001) compared recent records (1990–1999) of the calling phenology of six frog species in Ithaca, New York, with a turn-of-the-century study (1900–1912). They showed a 10–13-day advance associated with a 1.0–2.3°C rise in temperature during critical months. Amphibian breeding has also advanced in England, by 1–3 weeks per decade (Beebee 1995). Ecophysiological studies in frogs have shown that reproduction is closely linked to both nighttime and daytime temperatures (Beebee 1995).

In the United Kingdom, Crick et al. (1997), analyzing more than 74,000 nest records from 65 bird species between 1971 and 1995, found that the mean laying dates of first clutches for 20 species had advanced by an average 8.8 days. Brown et al. (1999) found a similar result for the Mexican jay (*Aphelocoma ultramarina*) in the mountains of southern Arizona. In the North Sea, migrant birds have advanced their passage dates by 0.5–2.8 days per decade since 1960, with no significant difference between short- and long-distance migrants (Hüppop & Hüppop 2003). In contrast, Gordo et al. (2005) found that three of six long-distance migrant birds had significantly delayed arrival to breeding grounds in Spain, with arrival date highly correlated with climatic conditions in their overwintering grounds in the southern Sahara.

Butterflies frequently show a high correlation between dates of first appearance and spring temperatures, so it is not surprising that their first appearance has advanced for 26 of 35 species in the United Kingdom (Roy & Sparks 2000) and for all 17 species analyzed in Spain (Stefanescu et al. 2003). Seventy percent of 23 species of butterfly in central California have advanced their first flight date over 31 years, by an average of 24 days (Forister & Shapiro 2003). Climate variables explained 85% of variation in flight date in the California study, with warmer, drier winters driving early flight.

There are only two continental-scale studies of bird phenology. Dunn & Winkler (1999) analyzed changes in breeding for tree swallows (*Tachycineta bicolor*) from 1959 to 1991 over the entire breeding range in the contiguous United States and Canada. Laying date was significantly correlated with mean May temperature and had advanced by an average of nine days over the 32-year period. In a complementary study, Both et al. (2004) analyzed the pied flycatcher (*Ficedula hypoleuca*) at 23 sites across Europe and found a significant advance in laying date for nine of the populations, which also tended to be those with the strongest warming trends. Continental-scale studies of both lilac (*Syringa vulgaris*) and honeysuckle (*Lonicera tatarica* and *L. korolkowii*) in the western United States have shown an advance in mean flowering dates of 2 and 3.8 days per decade, respectively (Cayan et al. 2001).

Aquatic systems exhibit similar trends to those of terrestrial systems. In a lake in the northwestern United States, phytoplankton bloom has advanced by 19 days from

1962 to 2002, whereas zooplankton peak is more varied, with some species showing advance and others remaining stable (Winder & Schindler 2004). The Arctic seabird Brunnich's guillemot, *Uria lomvia*, has advanced its egg-laying date at its southern boundary (Hudson Bay) with no change at its northern boundary (Prince Leopold Island); both trends are closely correlated with changes in sea-ice cover (Gaston et al. 2005).

Roetzer et al. (2000) explicitly quantified the additional impacts of urban warming by comparing phenological trends between urban and rural sites from 1951 to 1995. Urban sites showed significantly stronger shifts toward earlier spring timing than nearby rural sites, by 2–4 days. An analysis of greening across the United States via satellite imagery also concluded that urban areas have experienced an earlier onset of spring compared with rural areas (White et al. 2002).

Researchers generally report phenological changes as a separate category from changes in species' distributions, but these two phenomena interplay with each other and with other factors, such as photoperiod, to ultimately determine how climate change affects each species (Bale et al. 2002, Chuine & Beaubien 2001).

INTERACTIONS ACROSS TROPHIC LEVELS: MATCHES AND MISMATCHES

Species differ in their physiological tolerances, life-history strategies, probabilities of population extinctions and colonizations, and dispersal abilities. These individualistic traits likely underlie the high variability in strength of climate response across wild species, even among those subjected to similar climatic trends (Parmesan & Yohe 2003). For many species, the primary impact of climate change may be mediated through effects on synchrony with that species' food and habitat resources. More crucial than any absolute change in timing of a single species is the potential disruption of coordination in timing between the life cycles of predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects, and insect pollinators with flowering plants (Harrington et al. 1999, Visser & Both 2005). In Britain, the butterfly *Anthocharis cardamines* has accurately tracked phenological shifts of its host plant, even when bud formation came two to three weeks early (Sparks & Yates 1997). However, this may be the exception rather than the rule.

Visser & Both (2005) reviewed the literature and found only 11 species' interactions in which sufficient information existed to address the question of altered synchrony. Nine of these were predator-prey interactions, and two were insect–host plant interactions. In spite of small sample size, an important trend emerged from this review: In the majority of cases (7 of 11), interacting species responded differently enough to climate warming that they are more out of synchrony now than at the start of the studies. In many cases, evidence for negative fitness consequences of the increasing asynchrony has been either observed directly or predicted from associated studies (Visser & Both 2005).

In one example, Inouye et al. (2000) reported results of monitoring between 1975 and 1999 at Rocky Mountain Biological Laboratory in Colorado, where there has been a 1.4°C rise in local temperature. The annual date of snowmelt and plant flowering did not change during the study period, but yellow-bellied marmots (*Marmota flaviventris*) advanced their emergence from hibernation by 23 days, changing the relative phenology of marmots and their food plants. In a similar vein, Winder & Schindler (2004) documented a growing asynchrony between peak phytoplankton bloom and peak zooplankton abundances in a freshwater lake.

More complex phenomena resulting from trophic mismatches have also been documented. For example, phenological asynchrony has been linked to a range shift in the butterfly *Euphydryas editha*. Warm and/or dry years alter insect emergence time relative to both the senescence times of annual hosts and the time of blooming of nectar sources (Singer 1972, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996, Weiss et al. 1988). Field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions. Long-term censuses revealed that population extinctions occurred during extreme droughts and low snowpack years (Ehrlich et al. 1980, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996), and these extinctions have been highly skewed with respect to both latitude and elevation, shifting mean location of extant populations northward and upward (Parmesan 1996, 2003, 2005a).

Van Nouhuys & Lei (2004) showed that host-parasitoid synchrony was influenced signficantly by early spring temperatures. Warmer springs favored the parasitoid wasp *Cotesia melitaearum* by bringing it more in synchrony with its host, the butterfly *Melitaea cinxia*. Furthermore, they argue that because most butterfly populations are protandrous (i.e., males pupating earlier than females), temperature-driven shifts in synchrony with parasitoids may affect butterfly sex ratios.

Intergovernmental Panel on Climate Change: a scientific panel formed under the auspices of the United Nations and the World Meteorological Organization for the purpose of synthesizing literature and forming scientific consensus on climate change and its impacts

OBSERVED RANGE SHIFTS AND TRENDS IN LOCAL ABUNDANCE

Expected distributional shifts in warming regions are poleward and upward range shifts. Studies on these shifts fall mainly into two types: (*a*) those that infer large-scale range shifts from small-scale observations across sections of a range boundary (with the total study area often determined by a political boundary such as state, province, or country lines) and (*b*) those that infer range shifts from changes in species' composition (abundances) in a local community. Studies encompassing the entire range of a species, or at least the northern and southern (or lower and upper) extremes, are few and have been concentrated on amphibians (Pounds et al. 1999, 2006), a mammal (Beever et al. 2003), and butterflies (Parmesan 1996, Parmesan et al. 1999). The paucity of whole-range studies likely stems from the difficulties of gathering data on the scale of a species' range—often covering much of a continent.

Shifts at Polar Latitudes

Broad impacts of climate change in polar regions—from range shifts to community restructuring and ecosystem functioning—have been reviewed by the Intergovernmental Panel on Climate Change (Anisimov et al. 2001), the Arctic Climate Impact Assessment (2004) and the Millenium Ecosystem Assessment (Chapin et al. 2006).

SST: sea surface temperature

Antarctic. Plant, bird, and marine life of Antarctica have exhibited pronounced responses to anthropogenic climate change. These responses have been largely attributed to extensive changes (mostly declines) in sea-ice extent, which in turn appears to have stimulated a trophic cascade effect in biological systems. Declines in sea-ice extent and duration since 1976 have apparently reduced abundances of ice algae, in turn leading to declines in krill (from 38%–75% per decade) in a large region where they have been historically concentrated, the southwest Atlantic (Atkinson et al. 2004). Krill (*Euphausia superba*) is a primary food resource for many fish, seabirds, and marine mammals. Interestingly, McMurdo Dry Valleys, which actually cooled between 1990 and 2000, also showed declines in lake phytoplankton abundances and in soil invertebrate abundances (Doran et al. 2002).

Penguins and other seabirds in Antarctica have shown dramatic responses to changes in sea-ice extent over the past century (Ainley et al. 2003, Croxall et al. 2002, Smith et al. 1999). The sea-ice dependent Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*, respectively) have nearly disappeared from their northernmost sites around Antarctica since 1970. Emperors have declined from 300 breeding pairs down to just 9 in the western Antarctic Peninsula (Gross 2005), with less severe declines at Terre Adélie (66° S), where they are now at 50% of pre-1970s abundances (Barbraud & Weimerskirch 2001). Adélies have declined by 70% on Anvers Island (64°–65° S along the Antarctic peninsula (Emslie et al. 1998, Fraser et al. 1992), whereas they are thriving at the more-southerly Ross Island at 77° S (Wilson et al. 2001)—effectively shifting this species poleward. In the long-term, sea-ice-dependent birds will suffer a general reduction of habitat as ice shelves contract [e.g., as has already occured in the Ross Sea (IPCC 2001b)] or collapse [e.g., as did the Larsen Ice Shelves along the Antarctic Peninsula in 2002 (Alley et al. 2005)].

In contrast, open-ocean feeding penguins—the chinstrap and gentoo—invaded southward along the Antarctic Peninsula between 20 and 50 years ago, with paleological evidence that gentoo had been absent from the Palmer region for 800 years previously (Emslie et al. 1998, Fraser et al. 1992). Plants have also benefited from warming conditions. Two Antarctic vascular plants (a grass, *Deschampsia antarctica*, and a cushion plant, *Colobanthus quitensis*) have increased in abundance and begun to colonize novel areas over a 27-year period (Smith 1994).

Arctic. Nearly every Arctic ecosystem shows marked shifts. Diatom and invertebrate assemblages in Arctic lakes have shown huge species' turnover, shifting away from benthic species toward more planktonic and warm-water-associated communities (Smol et al. 2005). Across northern Alaska, Canada, and parts of Russia, shrubs have been expanding into the tundra (Sturm et al. 2005). Field studies, experimentation, and modeling link this major community shift to warming air temperatures, increased snow cover, and increased soil microbial activity (Chapin et al. 1995; Sturm et al. 2001, 2005). Populations of a pole-pole migrant, the sooty shearwater (*Puffinus griseus*), have shifted their migration routes by hundreds of kilometers in concert with altered sea surface temperature (SST) in the Pacific (Spear & Ainley 1999).

Sea-ice decline in the Arctic has been more evenly distributed than in the Antarctic. Because of differing geology, with an ocean at the pole rather than land, Arctic species that are sea-ice dependent are effectively losing habitat at all range boundaries. Polar bears have suffered significant population declines at opposite geographic boundaries. At their southern range boundary (Hudson Bay), polar bears are declining both in numbers and in mean body weight (Stirling et al. 1999). Climate change has caused a lengthening of ice-free periods on Hudson Bay, periods during which the bears starve and live on their reserves because an ice shelf is necessary for feeding. Furthermore, researchers have also linked warming trends to reductions of the bears' main food, the ringed seal (Derocher et al. 2004, Ferguson et al. 2005). At the bears' northern range boundaries off Norway and Alaska, sea ice has also been reduced, but poorer records make it is less clear whether observed declines in body size and the number of cubs per female are linked to climate trends or to more basic density-dependent processes (Derocher 2005, Stirling 2002).

Shifts in Northern-Hemisphere Temperate Species

On a regional scale, a study of the 59 breeding bird species in Great Britain showed both expansions and contractions of northern range boundaries, but the average boundary change for 12 species that had not experienced overall changes in density was a mean northward shift of 18.9 km over a 20-year period (Thomas & Lennon 1999). For a few well-documented bird species, their northern U.K. boundaries have tracked winter temperatures for over 130 years (Williamson 1975). Physiological studies indicate that the northern boundaries of North American songbirds may generally be limited by winter nighttime temperatures (Burger 1998, Root 1988).

Analogous studies exist for Lepidoptera (butterflies and moths), which have undergone an expansion of northern boundaries situated in Finland (Marttila et al. 1990, Mikkola 1997), Great Britain (Hill et al. 2002, Pollard 1979, Pollard & Eversham 1995, Warren 1992), and across Europe (Parmesan et al. 1999). Depending on the study, some 30% to 75% of northern boundary sections had expanded north; a smaller portion (<20%) had contracted southward; and the remainder were classified as stable. In a study of 57 nonmigratory European butterflies, data were obtained from both northern and southern range boundaries for 35 species (Parmesan et al. 1999). Nearly two thirds (63%) had shifted their ranges to the north by 35–240 km, and only two species had shifted to the south (Parmesan et al. 1999). In the most-extreme cases, the southern edge contracted concurrent with northern edge expansion. For example, the sooty copper (*Heodes tityrus*) was common in the Montseny region of central Catalonia in the 1920s, but modern sightings are only from the Pyrenees, 50 km to the north. Symmetrically, *H. tityrus* entered Estonia for the first time in 1998, by 1999 had established several successful breeding populations, and by 2006 had reached the Baltic Sea (Parmesan et al. 1999; T. Tammaru, personal communication).

Another charismatic insect group with good historical records is Odonata (dragonflies and damselflies). In a study of all 37 species of resident odonates in the United Kingdom, Hickling et al. (2005) documented that 23 of the 24 temperate species had expanded their northern range limit between 1960–1995, with mean northward shift of 88 km.

Nondiapausing (i.e., active year-round) butterfly species are also moving northward with warmer winters. The northern boundary of the sachem skipper butterfly has expanded from California to Washington State (420 miles) in just 35 years (Crozier 2003, 2004). During a single year—the warmest on record (1998)—it moved 75 miles northward. Laboratory and field manipulations showed that individuals are killed by a single, short exposure to extreme low temperatures (–10°C) or repeated exposures to –4°C, indicating winter cold extremes dictate the northern range limit (Crozier 2003, 2004). The desert orange tip (*Colotis evagore*), which historically was confined to northern Africa, has established resident populations in Spain while maintaining the same ecological niche. Detailed ecological and physiological studies confirm that *C. evagore* has remained a specialist of hot microclimates, needing more than 164 days at greater than 12°C to mature. It has not undergone a host switch in its new habitat, and it has not evolved a diapause stage (Jordano et al. 1991).

In the Netherlands between 1979 and 2001, 77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community (van Herk et al. 2002). Combined numbers of terrestrial and epiphytic lichen species increased from an average of 7.5 per site to 18.9 per site. An alternate approach to documenting colonizations is to document extinction patterns. Comparing recent censuses across North America (1993–1996) with historical records (1860–1986), Parmesan (1996) documented that high proportions of population extinctions along the southern range boundary of Edith's checkerspot butterfly (*E. editha*) had shifted the mean location of living populations 92 km farther north (Parmesan 1996, 2003, 2005a).

Shifts of Tropical Species Ranges

Warming trends at lower latitudes are associated with movements of tropical species into more-temperate areas. The rufous hummingbird has undergone a dramatic shift in its winter range (Hill et al. 1998). Thirty years ago it wintered mainly in Mexico, and between 1900 and 1990, there were never more than 30 winter sightings per year along the Gulf Coast of the United States. In the early 1990s, sightings increased to more than 100 per year in the southern United States. The number of sightings has increased steadily since then—up to 1,643 by 1996, with evidence that, by 1998, resident populations had colonized 400 km inland (Howell 2002). Over this same period, winter temperatures rose by approximately 1°C (IPCC 2001b). In Florida, five new species of tropical dragonfly established themselves in 2000, an apparently natural invasion from Cuba and the Bahamas (Paulson 2001).

Similarly, North African species are moving into Spain and France, and Mediterranean species are moving up into the continental interior. The African plain tiger butterfly (*Danaus chrysippus*) established its first population in southern Spain in 1980 and by the 1990s had established multiple, large metapopulations (Haeger 1999).

Elevational Shifts

Montane studies have generally been scarcer and less well documented (lower sampling resolution), but a few good data sets show a general movement of species upward in elevation. By comparing species compositions in fixed plots along an elevational gradient in Monteverde National Park, Costa Rica, Pounds et al. (1999, 2005) documented that lowland birds have begun breeding in montane cloud-forest habitat over the past 20 years. A similar study across 26 mountains in Switzerland documented that alpine flora have expanded toward the summits since the plots were first censused in the 1940s (Grabherr et al. 1994, Pauli et al. 1996). Upward movement of treelines has been observed in Siberia (Moiseev & Shiyatov 2003) and in the Canadian Rocky Mountains, where temperatures have risen by 1.5°C (Luckman & Kavanagh 2000).

The few studies of lower elevational limits show concurrent contractions upward of these warm range boundaries. Because warm boundaries generally have data gaps through time, these studies have conducted recensuses of historically recorded (sedentary) populations and looked for nonrandom patterns of long-term population extinctions.

A 1993–1996 recensus of Edith's checkerspot butterfly (*E. editha*) populations recorded 1860–1986 throughout its range (Mexico to Canada) documented that more than 40% of populations from 0–2400 m were extinct (in spite of having suitable habitat), whereas less than 15% were extinct at the highest elevations (2400–3500 m) (Parmesan 1996). Over the past 50–100 years, snowpack below 2400 m has become lighter by 14% and melts 7 days earlier, whereas higher elevations (2400–3500 m) have 8% heavier snowpack and no change in melt date (Johnson et al. 1999). In concert with altered snow dynamics, the mean location of *E. editha* populations has shifted upward by 105 m (Parmesan 1996, 2003, 2005a).

In southern France, metapopulations of the cool-adapted Apollo butterfly (*Parnassius apollo*) have gone extinct over the past 40 years on plateaus less than 850 m high but have remained healthy where plateaus were greater than 900 m high (Descimon et al. 2006). The data suggest that dispersal limitation was important, and this strong flyer can persist when nearby higher elevation habitats exist to colonize. In Spain, the lower elevational limits of 16 species of butterfly have risen an average of 212 m in 30 years, concurrent with a 1.3°C rise in mean annual temperatures (Wilson et al. 2005).

In the Great Basin of the western United States, 7 out of 25 recensused populations of the pika (*Ochotona princeps*, Lagomorpha) were extinct since being recorded in the 1930s (Beever et al. 2003). Human disturbance is minimal because pika habitat is high-elevation talus (scree) slopes, which are not suitable for ranching or recreational activities. Extinct populations were at significantly lower elevations than those still present (Parmesan & Galbraith 2004). Field observations by Smith (1974) documented that adult pika stopped foraging in the midday heat in August at low elevation sites. Subsequent experiments showed that adults were killed within a half hour at more than 31°C (Smith 1974).

Marine Community Shifts

Decades of ecological and physiological research document that climatic variables are primary drivers of distributions and dynamics of marine plankton and fish (Hays et al. 2005, Roessig et al. 2004). Globally distributed planktonic records show strong shifts of phytoplankton and zooplankton communities in concert with regional oceanic climate regime shifts, as well as expected poleward range shifts and changes in timing of peak biomass (Beaugrand et al. 2002, deYoung et al. 2004, Hays et al. 2005, Richardson & Schoeman 2004). Some copepod communities have shifted as much as 1000 km northward (Beaugrand et al. 2002). Shifts in marine fish and invertebrate communities have been been particularly well documented off the coasts of western North America and the United Kingdom. These two systems make an interesting contrast (see below) because the west coast of North America has experienced a 60-year period of significant warming in nearshore sea temperatures, whereas much of the U.K. coast experienced substantial cooling in the 1950s and 1960s, with warming only beginning in the 1970s (Holbrook et al. 1997, Sagarin et al. 1999, Southward et al. 2005).

Sagarin et al. (1999) related a 2°C rise of SST in Monterey Bay, California, between 1931 and 1996 to a significant increase in southern-ranged species and decrease of northern-ranged species. Holbrook et al. (1997) found similar shifts over the past 25 years in fish communities in kelp habitat off California.

Much of the data from the North Atlantic, North Sea, and coastal United Kingdom have exceptionally high resolution and long time series, so they provide detailed information on annual variability, as well as long-term trends. Over 90 years, the timing of animal migration (e.g., veined squid, *Loligo forbesi*, and flounder *Platichthys flesus*) followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years (Southward et al. 2005).

In the English Channel, cold-adapted fish (e.g., herring *Clupea harengus*) declined during both warming periods (1924 to the 1940s, and post-1979), whereas warm-adapted fish did the opposite (Southward et al. 1995, 2005). For example, pilchard *Sardina pilchardus* increased egg abundances by two to three orders of magnitude during recent warming. In the North Sea, warm-adapted species (e.g., anchovy *Engraulis encrasicolus* and pilchard) have increased in abundances since 1925 (Beare et al. 2004), and seven out of eight have shifted their ranges northward (e.g., bib, *Trisopterus luscus*) by as much as 100 km per decade (Perry et al. 2005). Records dating back to 1934 for intertidal invertebrates show equivalent shifts between warm- and cold-adapted species (e.g., the barnacles *Semibalanus balanoides* and *Chthamalus* spp., respectively), mirroring decadal shifts in coastal temperatures (Southward et al. 1995, 2005).

Pest and Disease Shifts

Pest species are also moving poleward and upward. Over the past 32 years, the pine processionary moth (*Thaumetopoea pityocampa*) has expanded 87 km at its northern range boundary in France and 110–230 m at its upper altitudinal boundary in Italy (Battisti et al. 2005). Laboratory and field experiments have linked the feeding behavior and survival of this moth to minimum nighttime temperatures, and its expansion has been associated with warmer winters. In the Rocky Mountain range of the United States, mountain pine beetle (*Dendroctonus ponderosae*) has responded to warmer temperatures by altering its life cycle. It now only takes one year per generation rather than its previous two years, allowing large increases in population abundances, which, in turn, have increased incidences of a fungus they transmit (pine blister rust, *Cronartium ribicola*) (Logan et al. 2003). Increased abundance of a nemotode parasite has also occurred as its life cycle shortened in response to warming trends. This has had associated negative impacts on its wild musk oxen host, causing decreased survival and fecundity (Kutz et al. 2005).

In a single year (1991), the oyster parasite *Perkinsus marinus* extended its range northward from Chesapeake Bay to Maine—a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford 1996). A kidney disease has been implicated in low-elevation trout declines in Switzerland. High mortality from infection occurs above 15°–16°C, and water temperatures have risen in recent decades. High infection rates (27% of fish at 73% of sites) at sites below 400 m have been associated with a 67% decline in catch; mid-elevation sites had lower disease incidence and only moderate declines in catch; and the highest sites (800–3029 m) had no disease present and relatively stable catch rates (Hari et al. 2006).

Changes in the wild also affect human disease incidence and transmission through alterations in disease ecology and in distributions of their wild vectors (Parmesan & Martens 2006). For example, in Sweden, researchers have documented marked increases in abundances of the disease-transmitting tick *Ixodes ricinus* along its northernmost range limit (Lindgren & Gustafson 2001). Between the early 1980s and 1994, numbers of ticks found on domestic cats and dogs increased by 22%–44% along the tick's northern range boundary across central Sweden. In the same time period, this region had a marked decrease in the number of extremely cold days ($<-12°C$) in winter and a marked increase in warm days ($>10°C$) during the spring, summer, and fall. Previous studies on temperature developmental and activity thresholds indicated the observed warmer temperatures cause decreased tick mortality and longer growing seasons (Lindgren & Gustafson 2001).

Trees and Treelines: Complex Responses

A complex of interacting factors determines treeline, often causing difficulties in interpretation of twentieth-century trends. Some species are "well behaved" in that they show similar patterns of increased growth at treeline during the early warming in the 1930s and 1940s as during the recent warming of the past 20 years. In recent decades, treelines have shifted northward in Sweden (Kullman 2001) and eastern Canada (Lescop-Sinclair & Payette 1995), and upward in Russia (Meshinev et al. 2000, Moiseev & Shiyatov 2003) and New Zealand (Wardle & Coleman 1992).

However, in other studies, researchers saw a strong response to warming in the late 1930s and 1940s but a weaker (or absent) response in recent warm decades (Innes 1991, Jacoby & D'Arrigo 1995, Lescop-Sinclair & Payette 1995, Briffa et al. 1998a,b), possibly resulting from differences in rainfall between the two warm periods. In Alaska, recent decades have been relatively dry, which may have prevented trees from responding to current warming as they did before (Barber et al. 2000, Briffa et al. 1998b). In contrast, treelines in the arid southwest United States, which has had increased rainfall, have shown unprecedented increased tree-ring growth at high elevations (Swetnam & Betancourt 1998).

An impressive study across all of northern Russia from 1953–2002 showed a shift in tree allometries. In areas where summer temperatures and precipitation have both increased, a general increase in biomass (up 9%) is primarily a result of increased greenery (33% more carbon in leaves and needles), rather than woody parts (roots and stem). In areas that have experienced warming and drying trends, greenery has decreased, and both roots and stems have increased (Lapenis et al. 2005).

EXTINCTIONS

Amphibians

Documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species. Many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds et al. 1999, 2005). Among harlequin frogs in Central and South American tropics, an astounding 67% have disappeared over the past 20–30 years. Pounds et al. (2006) hypothesised that recent trends toward warmer nights and increased daytime cloud cover have shifted mid-elevation sites (1000–2400 m), where the preponderance of extinctions have occurred, into thermally optimum conditions for the chytrid fungus, *Batrachochytrium dendrobatidis*.

Tropical Coral Reefs

Elevated sea temperatures as small as 1°C above long-term summer averages lead to bleaching (loss of coral algal symbiont), and global SST has risen an average of 0.1°–0.2°C since 1976 (Hoegh-Guldberg 1999, IPCC 2001b). A more acute problem for coral reefs is the increase in extreme temperature events. El Niño events have been increasing in frequency and severity since records began in the early 1900s, and researchers expect this trend to continue over coming decades (Easterling et al. 2000, IPCC 2001b, Meehl et al. 2000). A particularly strong El Niño in 1997–1998 caused bleaching in every ocean (up to 95% of corals bleached in the Indian Ocean), ultimately resulting in 16% of corals rendered extinct globally (Hoegh-Guldberg 1999, 2005b; Wilkinson 2000).

Recent evidence for genetic variation among the obligate algal symbiont in temperature thresholds suggests that some evolutionary response to higher water temperatures may be possible (Baker 2001, Rowan 2004). Changes in genotype frequencies toward increased frequency of high-temperature-tolerant symbiont appear to have occurred within some coral populations between the mass bleaching events of 1997–1998 and 2000–2001 (Baker et al. 2004). However, other studies indicate that many entire reefs are already at their thermal tolerance limits (Hoegh-Guldberg 1999). Coupled with poor dispersal of symbiont between reefs, this has led several researchers to conclude that local evolutionary responses are unlikely to mitigate the negative impacts of future temperature rises (Donner et al. 2005, Hoegh-Guldberg et al. 2002).

One optimistic result suggests that corals, to some extent, may be able to mirror terrestrial range shifts. Two particularly cold-sensitive species (staghorn coral, *Acropora ceervicornis*, and elkhorn coral, *Acropora palmata*) have recently expanded their ranges into the northern Gulf of Mexico (first observation in 1998), concurrent with rising SST (Precht & Aronson 2004). Although continued poleward shift will be limited by light availability at some point (Hoegh-Guldberg 1999), small range shifts may aid in developing new refugia against extreme SST events in future.

Although impacts have not yet been observed, the fate of coral reefs may be as, or more, affected in coming decades by the direct effects of CO_2 rather than temperature rise. Increased atmospheric CO_2 since industrialization has significantly lowered ocean pH by 0.1. The more dire projections (a doubling to tripling of current CO_2 levels) suggest that, by 2050, oceans may be too acidic for corals to calcify (Caldeira & Wickett 2003, Hoegh-Guldberg 2005a, Orr et al. 2005).

Population Extinctions Leading to Range Contractions

Many species have suffered reduced habitable area due to recent climate change. For those species that have already been driven extinct at their equatorial or lower range boundaries, some have either failed to expand poleward or are unable to expand due to geographic barriers. Such species have suffered absolute reductions in range size, putting them at greater risk of extinction in the near future.

This is particularly evident in polar species, as these are already pushed against a geographical limit. Researchers have seen large reductions in population abundances and general health along the extreme southern populations of Arctic polar bears (Derocher 2005, Derocher et al. 2004, Stirling et al. 1999) and the extreme northern populations of Antarctic Adélie and emperor penguins (Ainley et al. 2003, Croxall et al. 2002, Emslie et al. 1998, Fraser et al. 1992, Smith et al. 1999, Taylor & Wilson 1990, Wilson et al. 2001). In the United Kingdom, four boreal odonates have contracted northward by an average of 44 km over 40 years (Hickling et al. 2005).

Similarly, high numbers of population extinctions have occurred along the lower elevational boundaries of mountaintop species, such as pikas in the western United States (Beever et al. 2003) and the Apollo butterfly in France (Descimon et al. 2006). For 16 mountain-restricted butterflies in Spain, warming has already reduced their habitat by one third in just 30 years (Wilson et al. 2005). Warming and drying trends on Mt. Kiliminjaro have increased fire impacts, which have caused a 400-m downward contraction of closed (cloud) forest, now replaced by an open, dry alpine system (Hemp 2005). Temperate low-elevation species are not immune: Twenty-five percent of temperate butterflies in Europe contracted northward by 35–50 km over a 30–70-year period. For one of these, its northern range boundary had not expanded, so it suffered an overall contraction of range size (Parmesan et al. 1999).

EVOLUTION AND PLASTICITY

Species ranges are dynamic. Historically, ecologists have viewed species' niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers).

There is no doubt that climate plays a major role in limiting terrestrial species' ranges (Andrewartha & Birch 1954; Bale et al. 2002; Parmesan et al. 2000, 2005; Precht et al. 1973; Webb & Bartlein 1992; Weiser 1973; Woodward 1987). Recent physiological and biogeographic studies in marine systems also implicate temperature as a primary driver of species' ranges (Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg & Pearse 1995).

However, evolutionary processes clearly can substantially influence the patterns and rates of response to climate change. Theoretically, evolution can also drive range shifts in the absence of environmental change (Holt 2003). A prime example of this is the hybridization of two species of Australian fruit fly that led to novel adaptations, allowing range expansion with no concomitant environmental change (Lewontin & Birch 1966).

The problem of estimating the relative roles of evolution and plasticity is tractable with extensive, long-term ecological and genetic data. For example, genetic analysis of a population of red squirrels in the Arctic indicated that 62% of the change in breeding dates occurring over a 10-year period was a result of phenotypic plasticity, and 13% was a result of genetic change in the population (Berteaux et al. 2004, Réale et al. 2003).

Geneticists in the 1940s noticed that certain chromosomal inversions in fruit flies (*Drosophila*) were associated with heat tolerance (Dobzhansky 1943, 1947). These "hot" genotypes were more frequent in southern than in northern populations and increased within a population during each season, as temperatures rose from early spring through late summer. Increases in the frequencies of warm-adapted genotypes have occurred in wild populations of *Drosophila ssp* in Spain between 1976 and 1991 (Rodríguez-Trelles & Rodriguez 1998, Rodríguez-Trelles et al. 1996, 1998), as well as in the United States between 1946 and 2002 (Levitan 2003). The change in the United States was so great that populations in New York in 2002 were converging on genotype frequencies found in Missouri in 1946.

In contrast, red deer in Norway show completely plastic responses. Their body size responds rapidly to yearly variability of winter temperatures. Warmer winters cause developing males to become larger while females become smaller (Post et al. 1999). In consequence, the end result of a gradual winter warming trend has been an increase in sexual dimorphism.

A surprising twist is that species whose phenology is under photoperiodic control have also responded to temperature-driven selection for spring advancement or fall delay. Bradshaw & Holzapfel (2001) showed that the pitcher plant mosquito, *Wyeomyia smithii*, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

The Role of Evolution in Shaping Species' Impacts

Increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating negative impacts of future climate change (Baker 2001, Baker et al. 2004, Davis & Shaw 2001, Rowan 2004). However, in spite of a plethora of data indicating local adaptation to climate change at specific sites, the fossil record shows little evidence for the evolution of novel phenotypes across a species as a whole. Pleistocene glaciations represent shifts 5–10 times the magnitude of twentieth-century global warming. These did not result in major evolution at the species level (i.e., appearance of new forms outside the bounds of known variation for that species), nor in major extinction or speciation events. Existing species appeared to shift their geographical distributions as though tracking the changing climate, rather than remaining stationary and evolving new forms (Coope 1994, Davis & Zabinski 1992, Huntley 1991).

Most of the empirical evidence for rapid adaptation to climate change comes from examples of evolution in the interiors of species' ranges toward higher frequencies of already existing heat-tolerant genotypes. In studies that focus on dynamics at the edge of a species' range or across an entire range, a different picture emerges. Several studies suggest that the effects of both genetic constraints and asymmetrical gene flow are intensified close to species' borders (Antonovics 1976, Garcia-Ramos & Kirkpatrick 1997, Hoffmann & Blows 1994). It is expected that a warming climate strengthens climate stress at equatorial range boundaries and reduces it at poleward boundaries. Equatorial boundary populations are often under natural selection for increased tolerance to extreme climate in the absence of climate change, but may be unable to respond due to lack of necessary genetic variance. Furthermore, gene flow from interior populations may stifle response to selection at the range limits, even when sufficient genetic variation exists (Kirkpatrick & Barton 1997).

Because of strong trade-offs between climate tolerance and resource/habitat preferences, a relaxation of selection on climate tolerance at northern boundaries may cause rapid evolution of these correlated traits. This process has been investigated in the European butterfly *Aricia agestis*, in which populations near the northern range boundary had previously adapted to cool conditions by specializing on the host genus, *Helianthemum*, which grows in hot microclimates and hence supports fast larval growth. Climate warming did not initially cause range expansion because *Helianthemum* was absent to the immediate north of the range limit. However, warming did permit rapid evolution of a broader diet at the range limit, to a host used in more southern populations, *Geranium*, which grows in cooler microclimates. Once this local diet evolution occurred, the boundary expanded northward across the band from which *Helianthemum* was absent but *Geranium* was present (Thomas et al. 2001).

This example shows how a complex interplay may occur between evolutionary processes and ecological responses to extreme climates and climate change. However, these evolutionary events did not constitute alternatives to ecological responses to climate change; they modulated those changes. Adaptive evolution of host preference occurred at the northern range boundary in response to temperature rise, but genetic variation for host use already existed within the *A. agestis* butterfly. In this case, evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. This is not likely to be an isolated example because populations of other species near poleward boundaries are known to specialize on resources that mitigate the effects of cool climate. Such resources either support rapid growth or occur in the hottest available microclimates (Nylin 1988, Scriber & Lederhouse 1992, Thomas et al. 2001).

In addition to resource choice, dispersal tendency evolves at range margins in response to climate change. In nonmigratory species, the simplest explanation of northward range expansions is that individuals have always crossed the species' boundary, and with climate warming, some of these emigrants are successful at founding new populations outside the former range. When dispersal tendency is heritable, these new populations contain dispersive individuals and higher rates of dispersal will soon evolve at the expanding boundary.

Evolution toward greater dispersal has indeed been documented in several species of insect. Two species of wing-dimorphic bush crickets in the United Kingdom have evolved longer wings at their northern range boundary, as mostly long-winged forms participated in the range expansion and short-winged forms were left behind (Thomas et al. 2001). Adults of newly colonized populations of the speckled wood butterfly (*Pararge aegeria*) in the United Kingdom have larger thoraces and greater flight capability than historical populations just to the south (Hill et al. 1999). Variation in dispersal abilities can be cryptic. Newly founded populations of the butterfly *M. cinxia* contained females that were genetically superior dispersers due to increased production of ATP (Hanski et al. 2004).

Overall, empirical evidence suggests that evolution can complement, rather than supplant, projected ecological changes. However, there is little theoretical or experimental support to suggest that climate warming will cause absolute climatic tolerances of a species to evolve sufficiently to allow it to conserve its geographic distribution in the face of climate change and thereby inhabit previously unsuitable climatic regimes (Donner et al. 2005; Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg et al. 2002; Jump & Peñuelas 2005).

CONCLUDING THOUGHTS ON EVOLUTION AND CLIMATE CHANGE

For species-level evolution to occur, either appropriate novel mutations or novel genetic architecture (new gene complexes) would have to emerge to allow a response to selection. Lynch & Lande (1993) used a genetic model to infer rates of environmental change that would allow populations to respond adaptively. However, Travis & Futuyma (1993)—discussing the same question from broad paleontological, population, genetic, and ecological perspectives—highlighted the complexity of predicting future responses from currently known processes. Fifteen years later, answers still lie very much in empirical observations. These observations indicate that, although local evolutionary responses to climate change have occurred with high frequency, there is no evidence for change in the absolute climate tolerances of a species. This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming, resulting in contraction of species' ranges at these warm boundaries, as well as by extinctions of many species.

SUMMARY POINTS

1. The advance of spring events (bud burst, flowering, breaking hibernation, migrating, breeding) has been documented on all but one continent and in all major oceans for all well-studied marine, freshwater, and terrestrial groups.
2. Variation in phenological response between interacting species has already resulted in increasing asynchrony in predator-prey and insect-plant systems, with mostly negative consequences.
3. Poleward range shifts have been documented for individual species, as have expansions of warm-adapted communities, on all continents and in most of the major oceans for all well-studied plant and animal groups.
4. These observed changes have been mechanistically linked to local or regional climate change through long-term correlations between climate and biological variation, experimental manipulations in the field and laboratory, and basic physiological research.
5. Shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics.
6. Range-restricted species, particularly polar and mountaintop species, show more-severe range contractions than other groups and have been the first groups in which whole species have gone extinct due to recent climate change. Tropical coral reefs and amphibians are the taxonomic groups most negatively impacted.
7. Although evolutionary responses have been documented (mainly in insects), there is little evidence that observed genetic shifts are of the type or magnitude to prevent predicted species extinctions.

FUTURE ISSUES

1. Ocean-atmosphere processes are dynamically changing in response to anthropogenic forcings. Indices such as the El Niño Southern Oscillation and the North Atlantic Oscillation may be a poor basis for projecting future biological impacts.
2. Projections of impacts will be aided by a better mechanistic understanding of ecological, behavioral, and evolutionary responses to complex patterns of climate change, and in particular to impacts of extreme weather and climate events.

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Air quality impacts of the October 2003 Southern California wildfires

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[1] In Southern California, dry summers followed by hot and dry westerly wind conditions contribute to the region's autumn fire season. In late October 2003, 13 large Southern California wildfires burned more than 750,000 acres of land, destroyed over 3500 structures, and displaced approximately 100,000 people. The fire episode was declared the deadliest and most devastating in more than a decade, and local media advised individuals to stay indoors to avoid exposure to excessive levels of PM, CO, VOCs, and ozone caused by the wildfires. This study examines the actual impact of these wildfires on air quality in urban Los Angeles (LA) using "opportunistic" data from other air pollution studies being conducted at the time of the fires. Measurements of pollutant gases (CO, NO_x, and ozone), particulate matter (PM), particle number (PN) concentrations, and particle size distributions at several sampling locations in the LA basin before, during, and after the fire episode are presented. In general, the wildfires caused the greatest increases in PM_{10} levels (a factor of 3–4) and lesser increases in CO, NO, and PN (a factor of up to 2). NO_2 levels remained essentially unchanged, and ozone concentrations dropped during the fire episode. Particle size distributions of air sampled downwind of the fires showed number modes at diameters between 100 and 200 nm, significantly larger than that of typical urban air. The particles in this size range were shown to effectively penetrate indoors, raising questions about the effectiveness of staying indoors to avoid exposure to wildfire emissions.

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1. Introduction

[2] Wildfires can produce substantial increases in the concentration of gaseous pollutants such as carbon monoxide (CO), nitrogen oxides (NO_x), ozone (O_3), and volatile organic compounds (VOCs) [*Cheng et al.*, 1998; *Crutzen and Andreae*, 1990] as well as particulate matter (PM) [*Dennis et al.*, 2002; *Lighty et al.*, 2000]. In recent years, there has been much interest in studying the impact of wildfires in elevating the concentrations of pollutants in the atmosphere. For instance, high CO concentrations that occurred episodically in the southeastern United States during the summer of 1995 have been attributed to large forest fires in Canada [*Wotawa and Trainer*, 2000]. In addition to regional and local impacts [*Bravo et al.*, 2002] wildfires contribute significantly to global emissions of atmospheric trace gases including NO_x, CO, and CO_2 [*Crutzen et al.*, 1979]. Concerns arising from PM emissions from wildfires include acute health effects, direct and indirect climate forcing, and regional visibility [*Bravo et al.*, 2002; *LeCanut et al.*, 1996].

[3] Emission inventories by the U.S. Environmental Protection Agency (U.S. EPA) estimate that, for the calendar year 2001, wildfires in the U.S. emitted 7.1 million tons of CO, 0.98 million tons of VOCs, 0.60 million tons of $PM_{2.5}$, and 0.66 million tons of PM_{10} to the atmosphere (National Emissions Inventory-Air Pollutant Emissions Trends, Current Emission Trends Summaries, August 2003, U.S. EPA), http://www.epa.gov/ttn/chief/trends/index.html). These amounts are significant, contributing 6%, 5%, 8% and 3% of the total CO, VOC, $PM_{2.5}$, and PM_{10} emissions to the atmosphere in the United States in 2001, respectively. These figures obviously vary from year-to-year with the degree of wildfire activity, and in the severe fire season of 2000, 18% of the total $PM_{2.5}$ emissions in the U.S. were estimated to originate from wildfires. Other emission inventories in specific areas have calculated significant NO_x emissions from wildfires as well [*Dennis et al.*, 2002]. Some systematic studies and source testing have been carried out for prescribed burns and controlled fires in North America [*Einfeld et al.*, 1991; *Radke et al.*, 1991;

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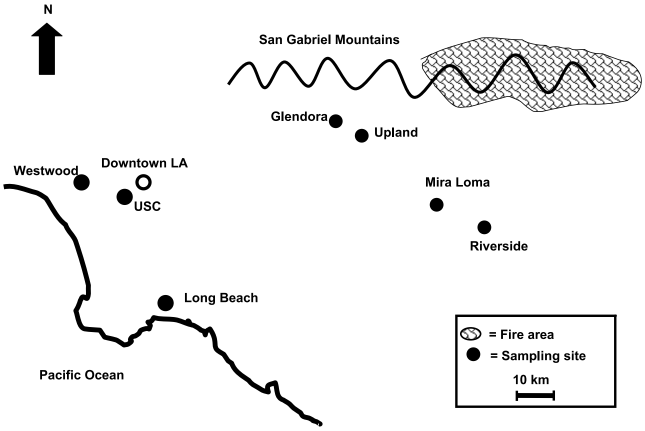

Figure 1. Map showing the fire area and the sampling sites in the Los Angeles basin.

Woods et al., 1991]. Other studies on wildfire emissions have taken advantage of existing pollution monitoring networks and other focused air pollution studies which happen to be sampling when a wildfire event occurs [*Bravo et al.*, 2002; *Brunke et al.*, 2001; *Cheng et al.*, 1998; *Goode et al.*, 2000; *Nance et al.*, 1993]. Such "opportunistic" studies can provide valuable information on wildfire pollutant emission rates and the impacts on air quality levels.

[4] Dry summers, followed by conditions of hot and dry westerly winds (known as Santa Ana winds) contribute to Southern California's fire season in the autumn months. While the fire season usually starts around the middle of May, the exact date varies from year to year based on weather patterns and the moisture content, distribution, and amount of wild vegetation present. The fire season usually ends when cooler weather and precipitation conditions prevail. This usually occurs toward the end of October, but the fire season is occasionally extended well into January in some Southern California areas (California Department of Forestry and Fire Protection, Fire Statistics, http://www.fire.ca.gov/MiscDocuments/FAQs.asp#13). The presence of thick and dry foliage and bushy chaparral adds to the fire danger in the fire season in Southern California. In general, pollution levels are observed to be high during fire events [*Bravo et al.*, 2002]. The Los Angeles basin is surrounded by high mountains on three sides, opening to the Pacific Ocean to the west and southwest. The topography and frequent temperature inversions lead to the accumulation of airborne pollutants, particularly in the eastern portion of the basin, due to the prevailing westerly sea breeze [*Lu and Turco*, 1996].

[5] In late October 2003, 13 large Southern California wildfires, ranging from Simi Valley in the North to San Diego 150 miles to the south, burned more than 750,000 acres of land, destroyed over 3,500 structures, including 2,700 homes, and displaced 100,000 people. Twenty human deaths were attributed to the wildfires. The cost of the damage has been estimated to be $2 billion. The fires having the greatest effect on the air quality of the Los Angeles (LA) Basin included the Grand Prix and Old fires in San Bernardino County and the adjacent Padua fire in Los Angeles County. These fires were located to the northeast of central Los Angeles, with Santa Ana wind conditions, blowing toward the southwest, transporting emissions to the western portions of the Basin. The fuel was predominantly mixed chaparral, California sagebrush, annual grass and canyon live oak. Pine, perennial grass and other urban vegetation were also burned. The fires started around 23 October and had significant impacts on the air quality of the LA basin until 29 October, when the winds reversed direction and resumed their normal onshore pattern (National Interagency Coordination Centre, 2003, Statistics and Summary, http://www.nifc.gov/news/2003_statssumm/intro_summary.pdf). This fire episode was declared the deadliest and most devastating in more than a decade, and there was a significant level of worldwide press coverage. Local media advised individuals to stay indoors to avoid exposure to excessive levels of PM, CO, VOCs, and ozone caused by the wildfires. This motivated the following analysis that examines the actual impact of these wildfires on air quality and measured pollutant concentrations in urban Los Angeles. This paper presents measurements of pollutant gases (CO, NO_x, and ozone) as well as PM concentrations and characteristics at different sampling locations in the LA basin before, during, and after the October 2003 fire episode. In addition, the effect of fire on indoor particle concentrations and size distributions was also investigated. Since the fire episode could not be predicted, the current study took advantage of several preexisting air pollution studies that were being conducted at the time of the wildfires. Given the "opportunistic" nature of these samples, the measurement techniques were not necessarily targeted for fire emissions, and not all of the data is complete in all sampling sites.

2. Methods

[6] As part of the routine sampling of an ongoing study associated with the University of Southern California (USC) Children's Health Study (CHS), supported by the South Coast Air Quality Management District and the California Air Resources Board, concentrations of carbon monoxide (CO), ozone (O_3), nitrogen oxide (NO), nitrogen dioxide ($NO_{2,}$), particulate matter with aerodynamic diameters less than 10 μm (PM_{10}) and particle number (PN) are continuously measured in several locations in Southern California. Continuous data were collected concurrently throughout the calendar year 2003, and five sites within the LA Basin impacted by the wildfires were examined in this study: Long Beach, Glendora, Mira Loma, Upland and Riverside (see Figure 1). The choice of these sampling sites was based on their location within the Los Angeles Basin, the availability of the data for the desired period, and the observed impacts of the Grand Prix, Old and Padua fires. Generally, these urban sites are the most polluted among the monitoring sites of the CHS.

[7] Located near a busy surface street, the Long Beach station is about 1 km northeast of a major freeway. The Glendora station is located in a residential area nestled in the foothills of the San Gabriel Mountains. It is at least 1 km away from major roadways and 3 km from the nearest freeway. The Upland site is also located in a residential area about 6 km downwind of the Glendora site, but is located within 1 km of the I-210 freeway. The Mira Loma site is located in a building on the Jurupa Valley High School

campus. It is directly east of a major freeway interchange, is surrounded by several major warehouse facilities, and is located about 80 km east of downtown Los Angeles. The sampling location at Riverside is within the Citrus Research Center and Agricultural Experiment Station (CRCAES), a part of the University of California, Riverside. It is about 10 km southeast of the Mira Loma site and is situated upwind of surrounding freeways and major roads.

[8] The concentrations of CO were measured near-continuously by means of a Thermo Environmental Inc. Model 48C trace level CO monitor. Concentrations of NO and NO_2 were measured with a Continuous Chemiluminescence Analyzer (Monitor Labs Model 8840), and O_3 concentrations were monitored using a UV photometer (Dasibi Model 1003 AH). Total particle number concentrations (greater than about 10 nm in diameter) were measured continuously by a Condensation Particle Counter (CPC, Model 3022/A, TSI Incorporated, St. Paul, MN) set at a flow rate of 1.5 L min^{-1}. At the Upland site, the CPC was connected to a Scanning Mobility Particle Sizer (SMPS, Model 3936, TSI Incorporated, St. Paul, MN), to measure the size distribution of submicrometer aerosols (15–750 nm) using an electrical mobility detection technique. In this configuration, the CPC flow rate was maintained at 0.3 L min^{-1} (with the sheath flow of the SMPS set at 3 L min^{-1}), and particle number counts were calculated from the SMPS size distributions. Unfortunately, due to a brief power outage and limited site access resulting from the nearby fires, SMPS data were lost from the morning of 24 October to noon of the 29 October (the peak of the fire impact). However, the other monitors at this site continued to function properly in this time window. Continuous particle number and gaseous copollutant concentrations were averaged to form 1-hour and 24-hour average values for the subsequent analysis.

[9] Hourly PM_{10} mass concentrations in each site were measured by a low temperature Differential Tapered Element Oscillating Microbalance monitor (low temperature TEOM 1400A, R&P Inc., Albany, NY). The design and performance evaluation of this monitor is described in greater detail by *Jaques et al.* [2004]. Briefly, the system consists of a size-selective PM_{10} inlet, followed by a Nafion® dryer that reduces the relative humidity of the sample aerosol to 50% or less. Downstream from the Nafion dryer and ahead of the TEOM sensor is an electrostatic precipitator (ESP) allowing for the removal of particles from the sample stream. The ESP is alternately switched on and off, for equal time periods of about 10 min. This dual sampling channel design makes it possible to account for effects such as volatilization of labile species, adsorption of organic vapors and changes in relative humidity and temperature, all of which affect the TEOM signal. The study by *Jaques et al.* [2004] showed that the time averaged TEOM PM_{10} mass concentrations agreed within ±10% with those of collocated Federal Reference Methods (FRM).

[10] In addition to the data collected at the CHS sites, semicontinuous $PM_{2.5}$ (fine) and ultrafine PM mass concentrations were measured at the Southern California Supersite located near downtown Los Angeles at the University of Southern California (USC). Two-hour PM mass concentration data were collected with a Beta Attenuation Monitor (BAM, Model 1020, Met One instruments, Inc., OR) [*Chung et al.*, 2001]. The BAM consisted of a size-selective inlet (2.5 μm for fine and 0.15 μm for ultrafine) [*Chakrabarti et al.*, 2004], a filter tape, a beta radiation source, and a beta radiation detector. The difference in the transmission of beta radiation through the filter tape before and after a particulate sample has been collected, is measured and used to determine the mass of collected particulate matter. Continuous operation is achieved by automatic advancement of the filter tape between sampling periods.

[11] Finally, in a concurrent but unrelated study, particle size distributions were measured indoors and outdoors of a two-bedroom apartment in the Westwood Village area near the University of California, Los Angeles. The residence is located about 100 m mostly downwind (east) of the I-405 freeway, a very busy traffic source. A Scanning Mobility Particle Sizer (SMPS 3936, TSI Inc., St. Paul., MN) was set up in a bedroom and sampled alternating indoor and outdoor size distributions on a 24-hour basis. The aerosol sampling flow rate of the SMPS was set to 1.5 L min^{-1} in order to measure particles as low as 6 nm as well as to minimize the diffusion losses of ultrafine particles during sampling. The maximum size detectable at these settings was 220 nm, and a scan time of 180 s was used. The sampling lines were kept the same length and as short as possible (1.5 m) for both indoor and outdoors samples. Measurements were made through a switching manifold that alternately sampled indoor and outdoor air, each for 9-min periods, in which three size distributions were taken in sequence. There were no known major indoor sources of aerosols in the residence for the period from 1000 to 1900 LT, when the residents were at work and from 2300 to 0700 LT when the residents were asleep in the other bedroom. The door of the sampling bedroom was always kept closed to minimize the influence of any other possible indoor activity. The residence was under natural ventilation with windows closed at all times during the sampling period. This study provided a unique opportunity to monitor infiltration of PM of outdoor origin into the indoor environment, and to estimate indoor exposures to PM from the wildfires.

3. Results and Discussion

[12] Figures 2a–2e present the 24-hour average concentrations of CO, NO, NO_2, O_3, PM_{10} and particle number (PN) before, during and after the October fire period in Southern California at the five CHS sampling sites examined in this study. A summary of the average concentrations of the pollutants before, during and after the fire is given in Table 1. As surmised from the news reports and the data, the period of fire influence was from 23–29 October. Figure 2 clearly shows that the concentrations of all the pollutants drastically decreased on 30 October and then increased back to more typical levels by 4 or 5 November. The rapid decline is associated with the wind reversal on the afternoon of 29 October when an onshore wind pattern replaced the Santa Ana conditions, followed by rainfall on 30 and 31 October. Figure 3a displays a satellite photo from NASA Earth Observatory on 28 October 2003 showing the extent of the fires and the prevailing wind direction during the peak of the fire episode. On 29 October, the winds shifted to an onshore pattern (Figure 3b) blowing fresh fire emissions

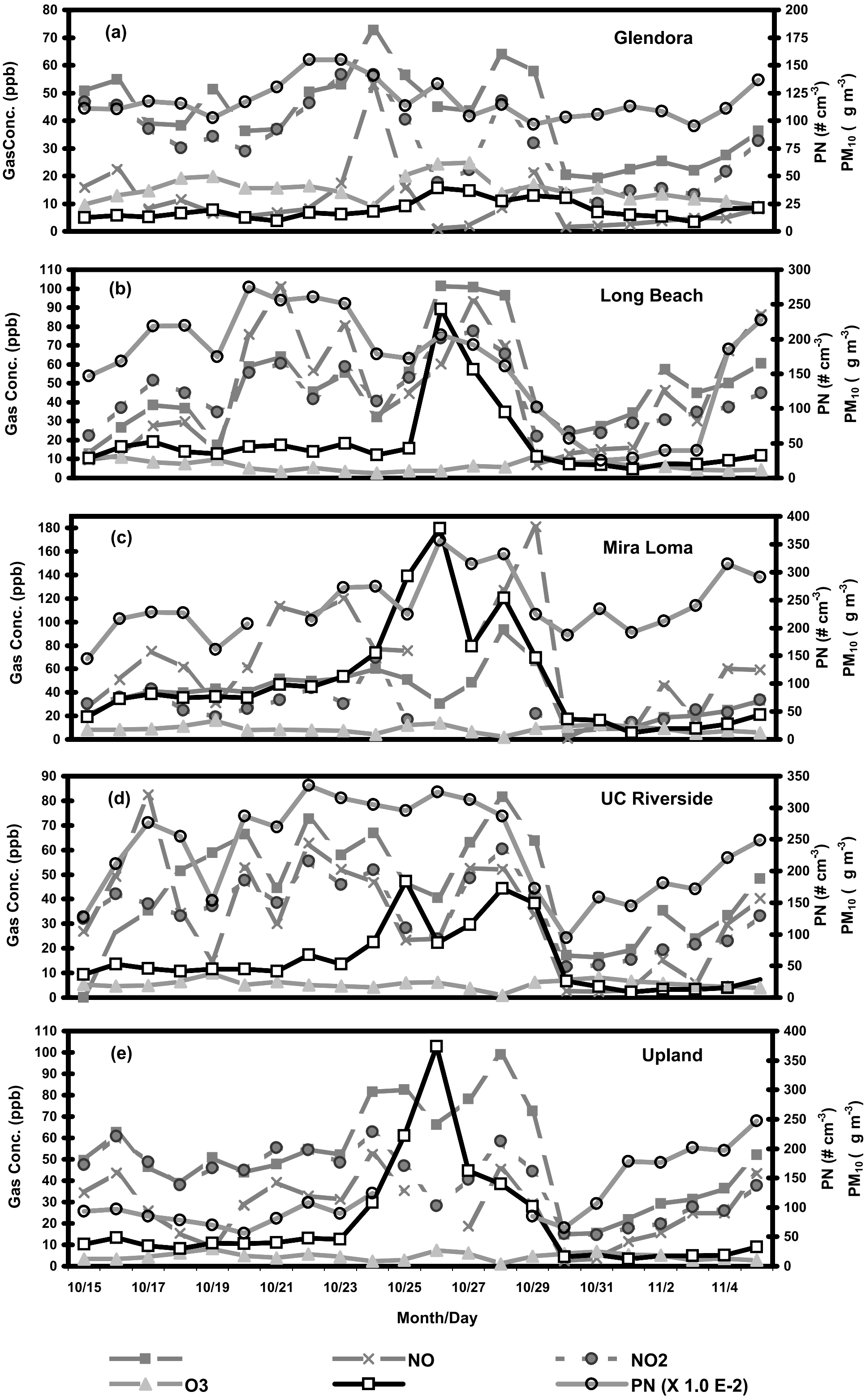

Figure 2. The 24-hour averaged PM and gaseous pollutant concentrations during the study at (a) Glendora, (b) Long Beach, (c) Mira Loma, (d) UC Riverside and (e) Upland. For comparison purposes, CO concentrations (in ppb) have been divided by 20, and PN concentrations (in cm^{-3}) have been divided by 100, as indicated in the legend.

Table 1. Average Hourly Concentrations of Pollutants With the Standard Deviation at the Five CHS Sites Before, During, and After the Fire[a]

			Average Concentration, ± SD			
	CO, ppm	NO, ppb	NO_2, ppb	O_3, ppb	PM_{10}, $\mu g\ m^{-3}$	PN, particles cm^{-3}
			Prefire			
Glendora	9 ± 3	11 ± 16	37 ± 16	37 ± 21	12 ± 14	10,400 ± 5500
Long Beach	6 ± 6	23 ± 49	47 ± 19	29 ± 18	33 ± 16	19,300 ± 12,400
Mira Loma	6 ± 4	45 ± 54	29 ± 14	25 ± 26	61 ± 35	16,200 ± 8200
UC Riverside	8 ± 6	40 ± 29	33 ± 19	29 ± 29	47 ± 23	16,200 ± 12,100
Upland	10 ± 4	24 ± 28	44 ± 16	21 ± 23	39 ± 18	9000 ± 3700
			During Fire			
Glendora	11 ± 5	**25 ± 30**	39 ± 28	44 ± 23	**27 ± 25**	12,200 ± 6200
Long Beach	**14 ± 9**	**55 ± 68**	56 ± 24	**15 ± 16**	**93 ± 92**	18,000 ± 8500
Mira Loma	**12 ± 8**	**105 ± 85**	39 ± 26	**17 ± 18**	**215 ± 171**	**28,500 ± 14,600**
UC Riverside	**12 ± 7**	**46 ± 36**	42 ± 22	**18 ± 21**	**121 ± 112**	**28,800 ± 16,100**
Upland	**15 ± 7**	**43 ± 34**	47 ± 24	**15 ± 16**	**165 ± 138**	data not available
			Postfire			
Glendora	5 ± 2	5 ± 5	17 ± 11	31 ± 11	18 ± 29	11,000 ± 6300
Long Beach	8 ± 6	39 ± 49	32 ± 11	16 ± 12	21 ± 10	8600 ± 9700
Mira Loma	4 ± 3	57 ± 45	20 ± 11	19 ± 15	28 ± 16	23,900 ± 10,700
UC Riverside	6 ± 4	14 ± 25	20 ± 10	23 ± 15	18 ± 10	1,7400 ± 11,000
Upland	6 ± 4	21 ± 25	23 ± 12	17 ± 13	19 ± 10	16,700 ± 8600

[a] Data in bold indicate statistically significant differences between the prefire and during-fire concentrations at $p = 0.05$.

toward the east away from the LA Basin. The fires continued to burn for many days after, but the cooler and wetter weather helped the firefighting effort and the fires were under control within another week.

[13] The data summary in Table 1 indicates that with the exceptions of NO_2 and O_3, the concentrations of CO, NO, PM_{10} and PN during the fire event were significantly higher (at the $p = 0.05$ level) than their respective values preceding the fire event. Statistical comparisons between during and postfire concentrations was not conducted, because, as evident from the data in Table 1 and Figure 2, the unstable and wet weather conditions during the week of 30 October to 5 November resulted in lower than average air pollutant concentrations. It is of particular note, however, that the most dramatic increase in the concentrations of any pollutant during the fire events was observed for the PM_{10} concentrations, which, with the exception of one site (Glendora), rose by almost three to four-fold in all sites during this period. While typical PM_{10} concentrations in Los Angeles are on the order of 50 $\mu g\ m^{-3}$ or less [*Christoforou et al.*, 2000], levels rose to near or above 200 $\mu g\ m^{-3}$ at some sites during the fires. PM_{10} levels at Glendora did not rise to the same degree, possibly due to the site's location at the base of a canyon in the San Gabriel Mountains. The Santa Ana winds tend to blow down the mountain canyons, and there was little or no fire activity in or upwind of this particular canyon. Upland, on the other hand, was within 2–3 km and directly downwind of extreme wildfire activity. The other three sites were all further downwind from the wildfires, but all sites experienced atypical PM_{10} levels. It is possible that the higher wind speeds during Santa Ana conditions increased re-suspended dust emissions that contributed to the elevated PM_{10} levels. This effect, if dominant, should be observed at all sites. However, the fact that Glendora PM_{10} levels remained within the "typical" range indicates that the impact of fire smoke plumes is the main cause of the elevated PM_{10} levels. Previously reported data during Santa Ana events without fires also demonstrate that such high levels of PM_{10} are not typically observed on a 24-hour basis [*Geller et al.*, 2004].

[14] By contrast, the total particle number concentrations, also shown in Figure 2, did not exhibit the same extreme concentration increases during the fires. PN levels increased significantly only in Mira Loma and perhaps Riverside, and only by an approximate factor of two. Even these higher levels of PN have been observed on occasion under typical, nonfire influenced, conditions in the LA Basin [*Kim et al.*, 2002]. No significant increase in PN was observed at Long Beach, and Glendora, the latter being minimally affected by the fires as discussed above. Owing to the aforementioned power outage, PN data were not available at the closest site to the fires, Upland, during the wildfire period. Emissions testing of foliar fuels demonstrate that high particle number levels are emitted from these sources. However, given the observed high PM mass levels, and thus the increased PM surface area in the fire smoke plumes, it is conceivable that emitted smaller particles are scavenged by coagulation with larger particles in the smoke plume [*Formenti et al.*, 2003]. This process may occur over the few hours that it takes for the fire particles to reach our sampling sites. Many of the smaller particles, which make up the majority of particle number concentrations, may no longer exist as individual particles. Thus PM mass levels remain high while PN levels are diminished. This hypothesis may explain why the largest PN increase was seen at Mira Loma and Riverside, both of which are much closer to the fire areas than the sites further downwind such as Long Beach.

[15] Similar to particle number, CO concentrations at these sites were only modestly affected by the fires. With the exception of Glendora, the observed increases were statistically significant at the $p = 0.05$ level, but the degree of increase was much less than that observed for PM_{10}. Mira Loma, Upland and Long Beach experienced CO around twice normal levels during the fire. As in the case of PN, CO concentrations in the area of Glendora appear to be

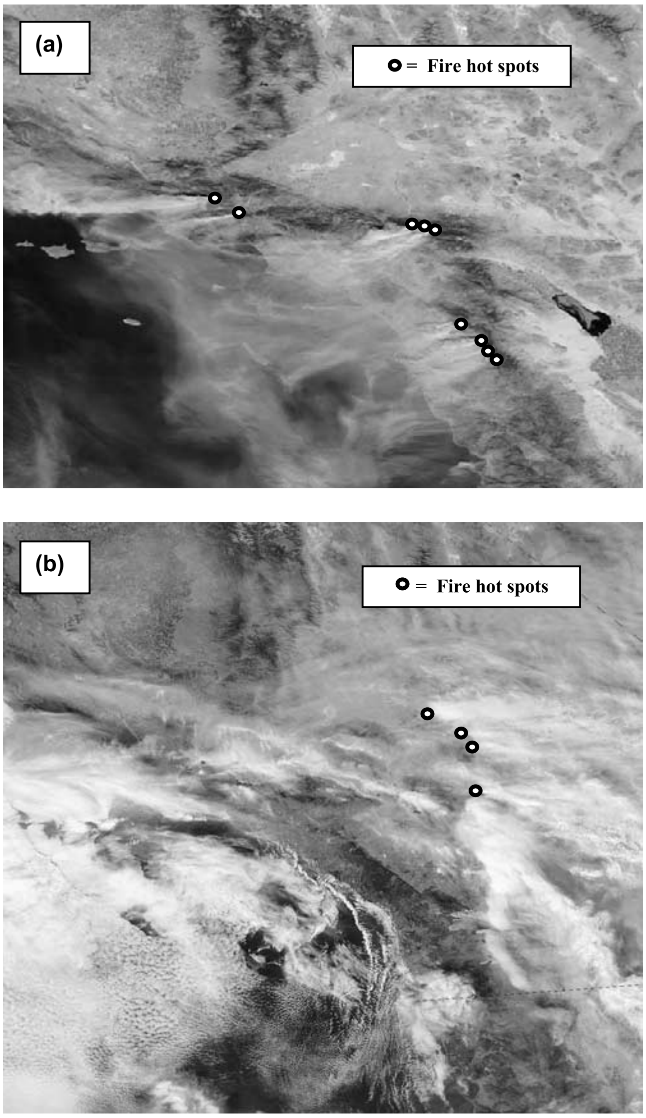

Figure 3. Satellite images from NASA earth observatory showing (a) Southern California during the peak of the fire episode on 28 October 2003, with the smoke plumes blowing west, and (b) the same area after the wind reversal with a visible marine layer and blowing the smoke plumes toward the northeast on the afternoon of 29 October 2003.

unaffected by the fire events. The relatively low increase in CO due to the fires can be explained by other, more significant sources of CO in Los Angeles. Emission factors from the U.S. EPA (AP-42, Fifth Edition, Volume I-Chapter 13.1: Wildfires and Prescribed Burning, U.S. EPA, October 1996) and other studies [*Barbosa et al.*, 1999; *Pereira et al.*, 1999; *Scholes et al.*, 1996] show that the ratio of CO mass to PM_{10} mass in wildfire emissions lies typically between 8 and 16. The same ratio for various motor vehicles under varying driving conditions is much higher, ranging from about 200 to over 2000 [*Cadle et al.*, 2001; *Chase et al.*, 2000]. In urban areas dominated by vehicular sources, wildfires will thus affect ambient levels of CO to a lesser degree than the ambient levels of PM_{10}. A review of historical pollutant data during Santa Ana conditions without fire activity (9 February 2002 and 6 January 2003) shows that CO levels can diminish due to fewer CO sources upwind and increased basin ventilation. However, this effect is inconsistent, and varies greatly with sampling site and from event to event. Thus no true "Santa Ana baseline" can be established for comparison purposes. For this reason, comparisons are limited to the "typical" conditions before the fire episode.

[16] NO concentrations follow similar trends with those for CO and PN (i.e., they increase significantly in every location during the fire) but this increase is on the order of two-fold or less, hence smaller than the increase observed for PM_{10}. While the increase in NO concentrations during the fire event seems to be minor at the Riverside location, the nearby Mira Loma site shows more than double the NO levels relative to levels before the fire events. It is possible that Mira Loma may have been more directly downwind of fire areas than Riverside, which would explain this discrepancy. This is supported by the observed PM_{10} levels at these two sites, which also increased more dramatically in Mira Loma than in Riverside. Relative to NO, PN, and PM_{10}, the effect of fires was negligible for NO_2 as the concentrations did not change significantly in any of the five sampling sites during the fire events. While some NO_2 is emitted directly from combustion processes, most of the NO_2 in urban air is formed in the atmosphere by the reaction of NO with ozone. Under normal conditions in Los Angeles, NO, and thus NO_2 levels are dominated by diesel vehicle emissions [*Fujita et al.*, 2003]. However, the NO increases observed during the fires were not accompanied by corresponding increases in NO_2 concentrations. Although no conclusive explanation can be determined from the current data, it is possible that the PM in the fire smoke blanketing the LA basin blocked incoming solar radiation and thus reduced photochemical activity in the atmosphere. This would result in lower ozone levels and thus lower observed levels of NO_2. Increased concentrations of organic gases (VOCs) emitted by the fires may also play a role in the complex atmospheric chemistry of NO, NO_2, and ozone [*Cheng et al.*, 1998]. Interestingly, with the exception of Glendora, which experienced marginally (but not significant) increased O_3 concentrations during the fire episode, the concentrations of O_3 decreased by about 25–50% at all the other sites during the fire period. As mentioned above, the fire smoke covering the basin and the corresponding reduction in photochemical activity may be a possible explanation for this decrease in concentration.

[17] The effect of the wind direction change can also be seen in the hourly concentrations of the measured pollutants in Upland as shown in Figures 4a and 4b. The high concentrations of PM_{10} at Upland can be clearly seen during the entire fire period, with the highest hourly concentration measured at 769 $\mu g\ m^{-3}$. On 29 October, at 12:00 P.M., the PM_{10} level was 153 $\mu g\ m^{-3}$ and within one hour it dropped to 65 $\mu g\ m^{-3}$. Within four hours, PM_{10} concentrations dropped to below 20 $\mu g\ m^{-3}$. This marks the time of the wind reversal mentioned above. Unfortunately, hourly data of particle number concentrations in this time frame are not available due to the power outage. Similar to the 24-hour data, the hourly gaseous pollutant levels did not increase as much as the PM_{10} levels during the period of wildfire influence. However, with the exception of ozone, concentrations of all the gaseous pollutants dropped precipitously when the wind reversal occurred.

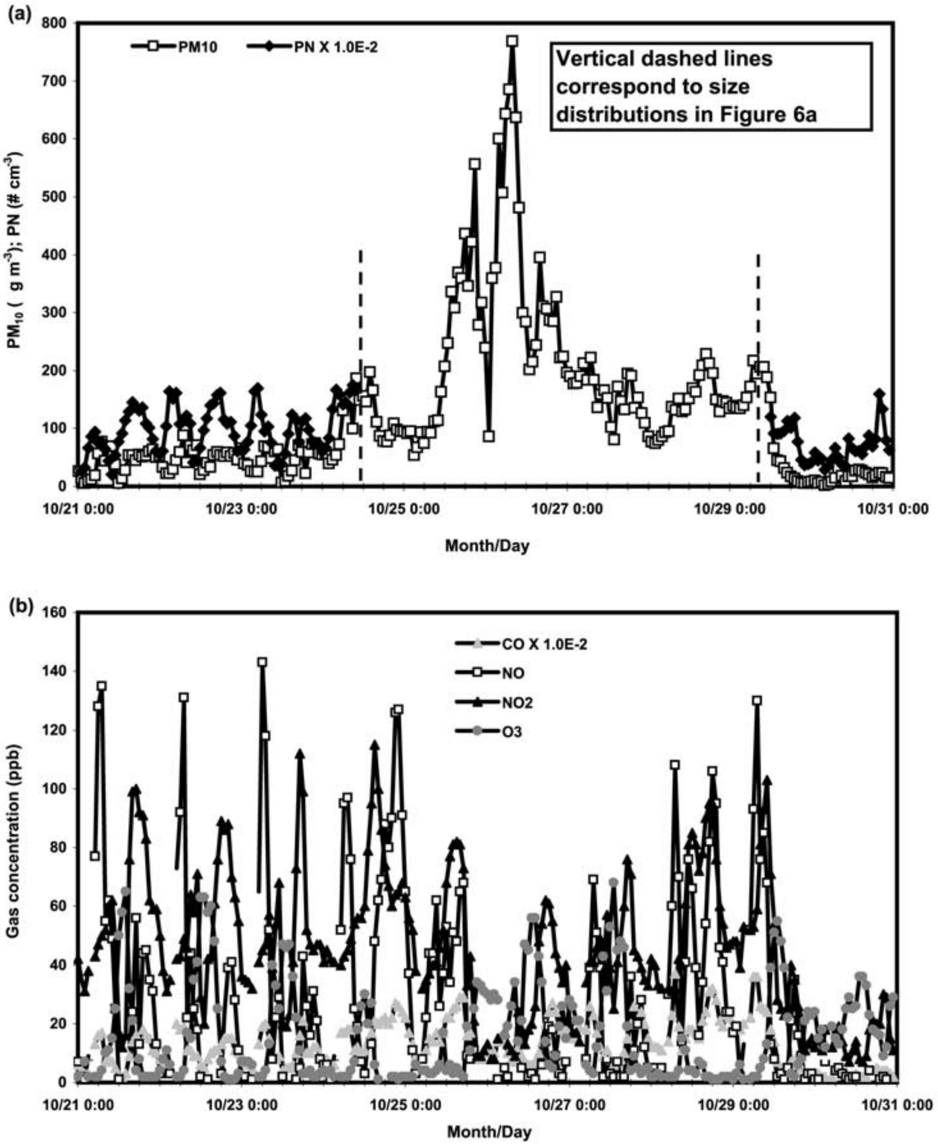

Figure 4. Hourly (a) PM and (b) gaseous pollutant concentrations at Upland.

[18] Semicontinuous ultrafine and fine ($PM_{2.5}$) particle mass concentration data support the argument that the atmospheric concentrations of smaller particles (measured above as PN), increased to a lesser extent than the larger particles. Figure 5 displays the 2-hour ultrafine and fine PM mass obtained from the BAM measurements at the USC site. The average ultrafine particle mass concentrations increased from an average value of 5.4 (±2.3) to 6.9 (±2.7) $\mu g\ m^{-3}$. While this increase is statistically significant ($p < 0.01$), it is still less dramatic than the obvious increase in $PM_{2.5}$ during the fire events. The average concentration of $PM_{2.5}$ more than doubled, from 19.1 (±5.2) to 51.3 (±26.1) $\mu g\ m^{-3}$. The highest fine particle mass measured during the fire episode at USC was 115 $\mu g\ m^{-3}$. The wind reversal was marked by a steep reduction in fine particle mass midday on 29 October when the fine PM dropped from 105 $\mu g\ m^{-3}$ in the morning to 25 $\mu g\ m^{-3}$ by 2:00 P.M.

[19] Figures 6a and 6b show the one-hour averaged particle size distribution at Upland corresponding to the times marked by vertical lines in Figure 4a. Because of the loss of SMPS data for almost entire fire period, we have selected times just before (Figure 6a) and just after (Figure 6b) the power outage. The particle size distribution at a given hour (1000 and 1200 LT) was averaged for different days before and after the fire, and compared to the same hour during the influence of the fires. It can be seen that the size distribution corresponding to the periods of fire influence significantly differs from those without the fire influence. The mode in the number-based particle size distribution spans from 100 to 300 nm and is indicative of the wildfire smoke. Previous emissions testing have shown similarly large number modes in the particle size distributions from the burning of foliar fuels [*Hays et al.*, 2002]. Such large diameter number modes are not normally seen in urban locations [*Kim et al.*, 2002] where particle number concentrations are dominated either by primary vehicular emissions or by nucleation processes [*Woo et al.*, 2001]. Since particle volume is proportional to the cube of the

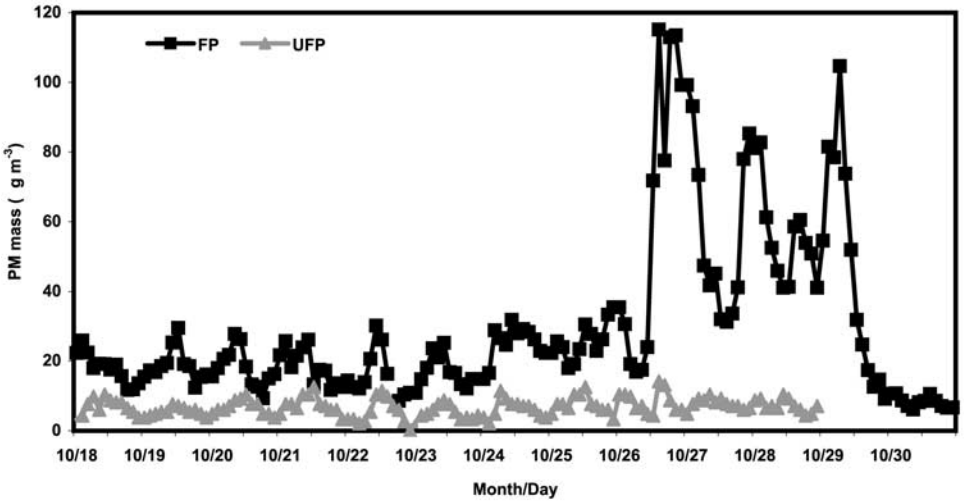

Figure 5. Two-hour averaged fine (FP) and ultrafine (UFP) particle mass concentrations at USC.

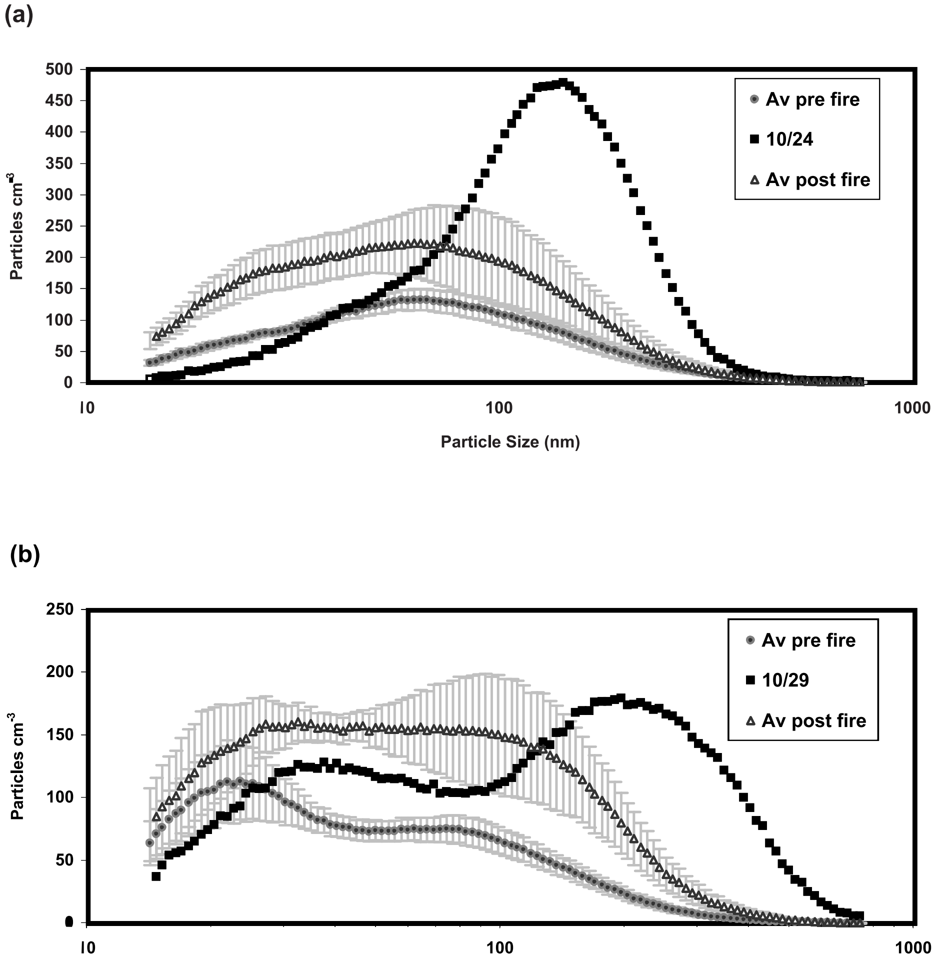

Figure 6. Particle size distributions at Upland (a) at 1000 LT before (24 October 2003) and after the fires and b) at 1200 LT before (29 October 2003) and after the fires.

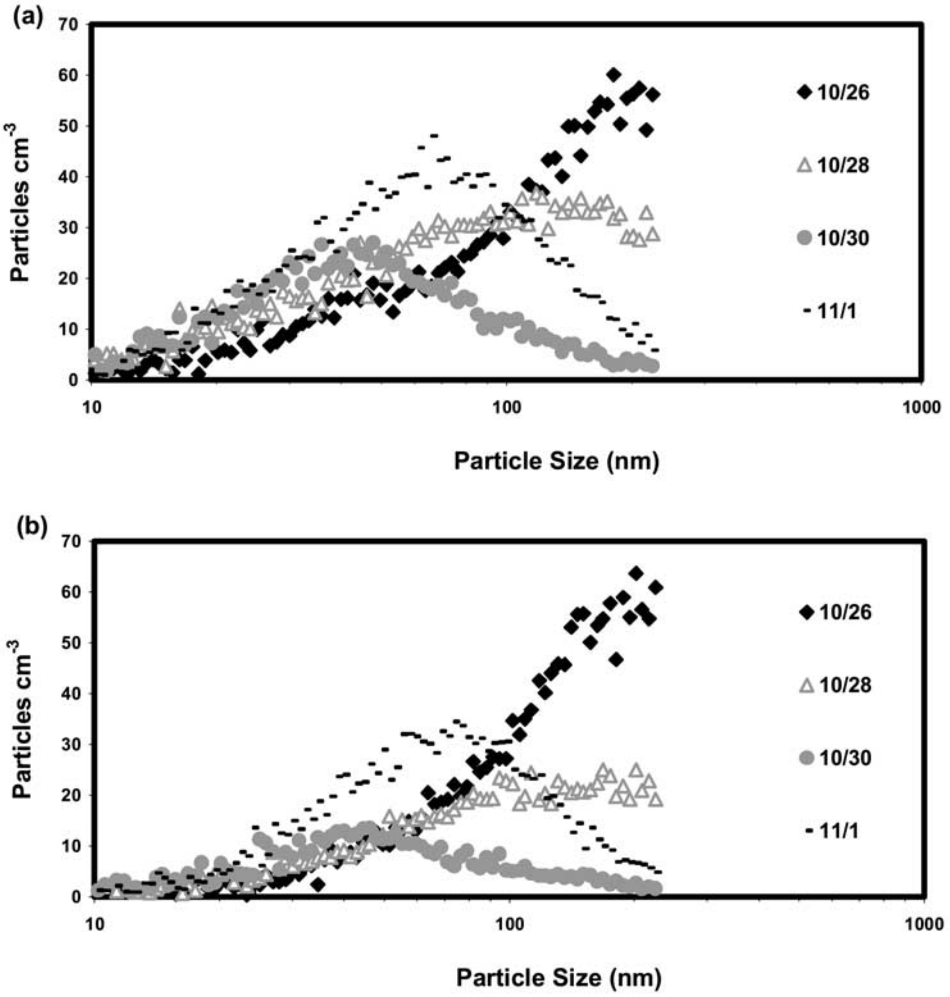

Figure 7. Particle size distributions on different days at 2300 LT in Westwood Village: (a) outdoor and (b) indoor.

diameter, a modest increase in particle number concentrations in these larger size modes is sufficient to account for the larger increases observed for PM mass.

[20] Indoor and outdoor particle number size distributions were also available from a concurrent study near UCLA in the western portion of the Los Angeles Basin. Figures 7a and 7b display ambient and corresponding indoor particle size distributions from 2300 to 2400 LT for different days during and after the fire events. This period was selected to minimize the influence of any possible indoor sources (i.e., cooking, cleaning) and outdoor traffic from the nearby freeway. The effect of the fires on indoor concentration is evident, with an aerosol mode diameter at about 200 nm on 26 and 28 October, and then a shift to a lower size range (between 50 to 70 nm) on 30 October and 1 November, respectively. Number concentrations both indoors and outdoors also decrease as we move away from the fire period. It is of interest to note that on 26 October (i.e., in the middle of the wildfire period), the indoor and outdoor size distributions are virtually identical in both number concentration and mode, which suggests that the majority of the outdoor aerosol infiltrated indoors with a penetration value close to 1. This is not a surprising result, considering that based on our measurements, the majority of the particles emitted from the fire are in the 100–300 nm range. This is also the range of maximum indoor penetration of outdoor aerosols and minimum indoor deposition rate [*Allen et al.*, 2003; *Long et al.*, 2001]. As the mode in aerosol size distributions shifts to smaller sizes, the indoor concentrations are approximately 50–75% lower than outdoors, which is also consistent with the penetration values determined by *Long et al.* [2001] and *Wallace and Howard-Reed* [2002] for the particles in the 40–80 nm range.

[21] To put the above results in perspective, Figures 8a and 8b show the measured indoor and outdoor particle size distributions during the morning traffic commute period, from 0600 to 0700 LT, while the wildfires were still active (27 October) and after the fire event (4 November). The outdoor size distribution on 27 October is characterized by one dominant mode at about 25 nm, which is associated with vehicular emissions [*Zhu et al.*, 2002a, 2002b], followed by a second mode at about 200 nm, which reflects the influence of the wildfires. The indoor size distribution for that date (Figure 8a) shows that the super-100 nm particles are virtually at identical concentrations with their corresponding outdoor levels, whereas the concentrations

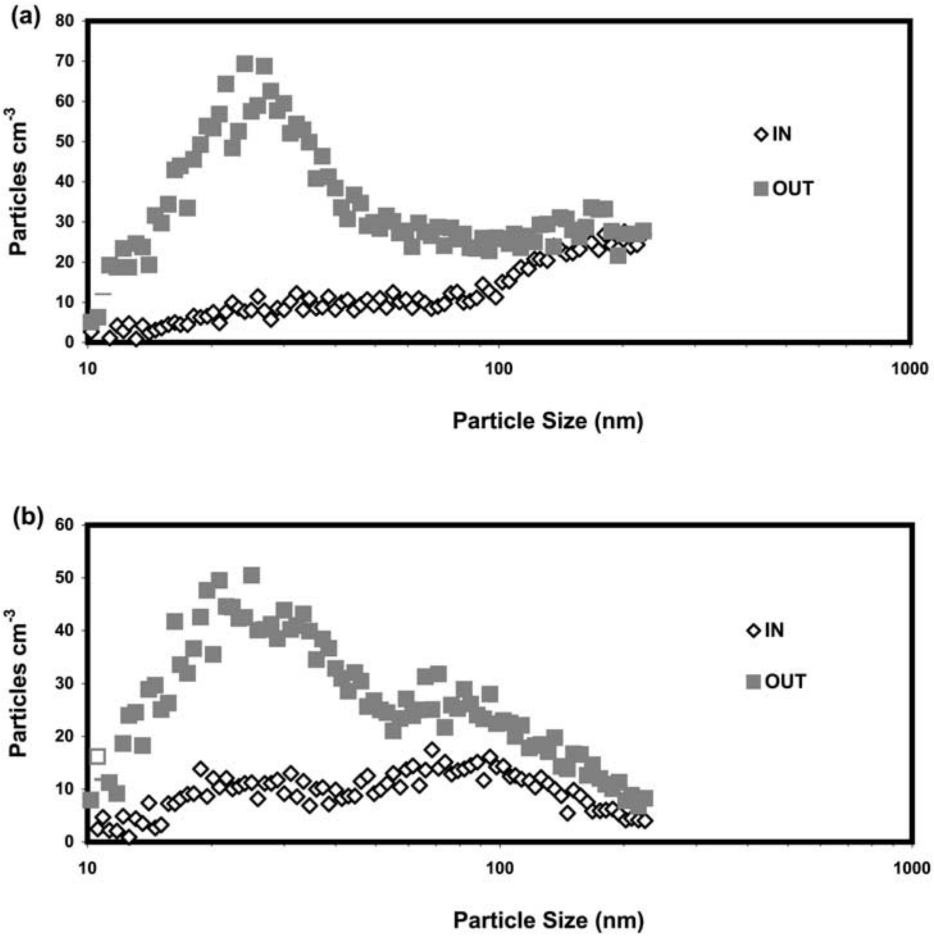

Figure 8. Indoor/outdoor particle size distributions at 0600 LT in Westwood Village on (a) 27 October 2003 and (b) 4 November 2003.

of smaller particles indoors are substantially lower than those outdoors. Similar trends are also shown in Figure 8b, with the exception that the second mode in the 200 nm range observed during the fire period no longer exists in either the indoor or outdoor environment.

[22] The data plotted in Figures 8a and 8b indicate an average outdoor-to-indoor penetration ratio of about 0.15 to 0.20 for particles in the 20–50 nm range, which, as stated above, originate from nearby traffic sources. This value is somewhat lower than the indoor penetration ratios reported by *Long et al.* [2001] and *Wallace and Howard-Reed* [2002] for that size range, which normally range between 0.3–0.7, depending on home characteristics and air exchange rates. One possible explanation for the lower values observed in our study may be that, as shown in recent reports in the literature [*Sakurai et al.*, 2003; *Tobias et al.*, 2001], sub-50 nm particles from vehicular emissions consist of semivolatile material, compared to the mostly nonvolatile particles in the 50–100 nm range. Thus, after penetrating indoors, they may have completely evaporated or shrunk to sizes below about 6 nm, the lower size detection limit of the SMPS. It is unknown what source, size or composition of ambient PM is responsible for the observed health effects. However, our results show that the prevailing advice during the fire episode for people to stay indoors may not be effective in reducing exposure to most of the particles emitted from wildfires.

4. Summary and Conclusions

[23] Coincidental air pollution sampling campaigns proved valuable in determining the impacts of the October 2003 wildfire episode on pollutant levels in the Los Angeles Basin. The greatest impact was observed on PM_{10} concentrations which increased by factors of three or four depending on location. CO and NO levels increased to a lesser extent (a factor of approximately two), most likely due to the different relative emission rates of these pollutants from wildfires compared to typical urban sources such as traffic. Particle number concentrations and NO_2 were essentially unchanged, except at the sites nearest the fires where PN levels almost doubled. Ozone levels during the fires were observed to be lower during the fires at some sites, a possible result of light scattering by the smoke plume reducing photochemical activity levels. Particle number distributions downwind of the fires displayed number modes with diameters between 100 and 200 nm, larger than typical urban aerosol and explaining the larger increases in PM_{10} and $PM_{2.5}$ mass concentrations than that for ultrafine particle mass and particle number. These particles were also

shown to penetrate effectively indoors, calling into question the prevailing advice to the public to remain inside to avoid exposure to harmful wildfire emissions.

[24] **Acknowledgments.** This work was supported by the California Air Resources Board and the South Coast Air Quality Management District through grants 53-4507-7822 and 53-4507-7823 to USC. Additional funding was provided by the Southern California Particle Center and Supersite (SCPCS), funded by the U.S. EPA (STAR award R82735201). This manuscript has not been subjected to the EPA and ARB's peer and policy review, and therefore does not necessarily reflect the views of the Agencies. No official endorsement should be inferred.

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Beyond the least-cost path: Evaluating corridor redundancy using a graph-theoretic approach

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RESEARCH ARTICLE

Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach

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Abstract The impact of the landscape matrix on patterns of animal movement and population dynamics has been widely recognized by ecologists. However, few tools are available to model the matrix's influence on the length, relative quality, and redundancy of dispersal routes connecting habitat patches. Many GIS software packages can use land use/land cover maps to identify the route of least resistance between two points—the least-cost path. The limitation of this type of analysis is that only a single path is identified, even though alternative paths with comparable costs might exist. In this paper, we implemented two graph theory methods that extend the least-cost path approach: the Conditional Minimum Transit Cost (CMTC) tool and the Multiple Shortest Paths (MSPs) tool. Both methods enable the visualization of multiple dispersal routes that, together, are assumed to form a corridor. We show that corridors containing alternative dispersal routes emerge when favorable habitat is randomly distributed in space. As clusters of favorable habitat start forming, corridors become less redundant and dispersal bottlenecks become visible. Our approach is illustrated using data from a real landscape in the Brazilian Atlantic forest. We explored the effect of small, localized disturbance on dispersal routes linking conservation units. Simulated habitat destruction caused the appearance of alternative dispersal routes, or caused existing corridors to become narrower. These changes were observed even in the absence of significant differences in the length or cost of least-cost paths. Last, we discuss applications to animal movement studies and conservation initiatives.

Keywords Agroecosystems · Atlantic forest · Brazil · Functional connectivity · Corridors · Cost distance · Dispersal · Fragmentation · Graph theory · Matrix · Migration · Shortest path

Introduction

Animal movement can occur at a range of temporal scales, influencing foraging, migration, and gene flow (Crooks and Sanjayan 2006). The dispersal routes associated with these processes can be strongly constrained by the landscape matrix. Thus models specifying the effect of matrix heterogeneity on movement rates can more successfully predict patch occupancy (Ricketts 2001; Verbeylen et al. 2003), metapopulation dynamics (Vandermeer and Carvajal

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2001), genetic structure (Stevens et al. 2006), and persistence in fragmented landscapes (Laurance et al. 2002). The role of behavior and natural history in shaping species' responses to the matrix has recently motivated the concept of functional connectivity (Calabrese and Fagan 2004). While many connectivity studies have described the influence of different land cover types in channeling or repelling movement of particular species (e.g., Burel 1996; Lees and Peres 2008), few tools are available to integrate data on matrix heterogeneity and species' habitat preferences to model dispersal routes.

A challenge in modeling animal dispersal routes is that individuals rarely use a single optimum route (e.g., Driezen et al. 2007), and connectivity measures focusing on optimum routes fail to incorporate variation in individual behavior (Belisle 2005). In this paper, we model the location of multiple dispersal routes across a heterogeneous matrix. We employ a movement model that assumes successfully dispersing organisms are more likely to use the route of least resistance when moving between two points, or the least-cost path. Despite its simplifying assumptions, the least-cost path has been successfully used to predict patch occupancy (Chardon et al. 2003; Verbeylen et al. 2003) and inter-patch movement rates (Sutcliffe et al. 2003). The least-cost path is identified using a graph theory algorithm, Dijkstra's breadth-first search (Cormen et al. 2001). Many GIS software packages have functions to locate the least-cost path between two points. Although only one path is obtained, Dijkstra's algorithm can be easily modified to output multiple paths with similar costs. We describe this modification and its two outputs, the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs).

We propose that corridors are heterogeneous structures that may contain multiple dispersal routes. However, we do not advocate a method for designing corridors (including few or many dispersal routes), neither do we attempt to quantify corridors' role in conserving biodiversity. Rather, our goal is to integrate information on species' habitat preferences into regional-scale depictions of habitat connectivity. This paper has three parts. First, we applied our method to artificial landscapes in order to illustrate the effect of matrix heterogeneity on the cost and spatial distribution of dispersal routes. Second, we studied the effect of small, localized disturbance on large-scale dispersal routes. This was performed using data from the highly fragmented Brazilian Atlantic forest (Morellato and Haddad 2000). Last, we discussed how the approach proposed here can be refined and incorporated in animal movement studies and conservation initiatives.

Methods

The landscape graph

In this section, we describe the approach routinely employed to perform any type of distance calculations on grids. Most GIS software packages use graphs (Urban and Keitt 2001) to represent grid maps. Graphs are composed of vertices (V) placed on cell centers, and edges (E) that connect each vertex to its eight nearest neighbors (Fig. 1). Using this representation, we define two cost grids:

(a) Relative cost grid (Figs. 2a, 3a), also referred to as a friction layer (Verbeylen et al. 2003). Each vertex contains the relative cost to cross it in any direction.

(b) Cumulative cost grid (Figs. 2b, 3b). Consider a source (S) composed of one or more vertices. Each vertex in the cumulative cost grid contains the minimum cumulative cost to reach S. This is calculated in two steps: first, the cost to move between pairs of vertices is stored as edge weights. The weight W for an edge connecting vertices V1 and V2 is calculated as:

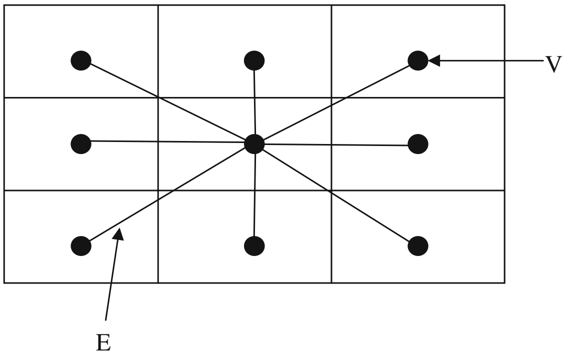

Fig. 1 The landscape graph. In most software packages, grid maps are internally represented as a graph. Vertices (V) are located in cell centers. Each vertex is connected to its eight nearest neighbors by an edge (E). Edge weights (not shown) hold information on the cost to move between pairs of vertices

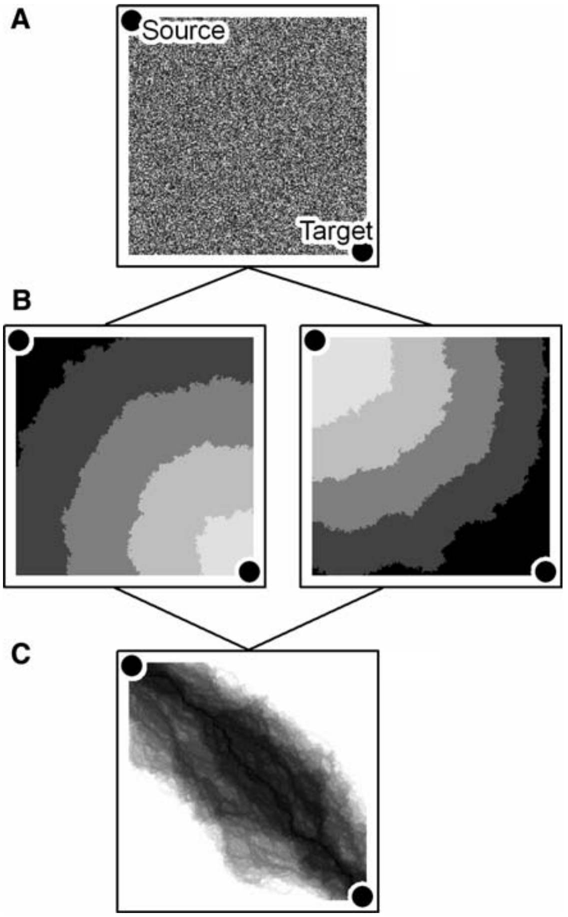

Fig. 2 Illustration of the procedure for calculating the CMTC. **a** Relative cost grid. **b** The cumulative cost grid for the target (*left*) and the source (*right*). Lighter shades indicate lower cumulative cost. **c** The two grids from (**b**) are added to produce the CMTC grid

$$W = [\text{Relative Cost}\,(\text{V1}) + \text{Relative Cost}\,(\text{V2})]/2 \tag{1}$$

For diagonal edges, edge weights W' are calculated as:

$$W\prime = W \times \sqrt{2} \tag{2}$$

Second, Dijkstra's breadth-first search algorithm (Cormen et al. 2001) is used to calculate the least-cost path between S and each vertex in the graph. The minimum cumulative cost between S and a given vertex (V) is the sum of all edge weights in the least-cost path connecting S and V. To calculate the least-cost path between two habitat patches P1 and P2 we define all vertices in P1 as sources and all vertices in P2 as targets. The least-cost path between patches P1 and P2 will most likely link the two patches' most external vertices.

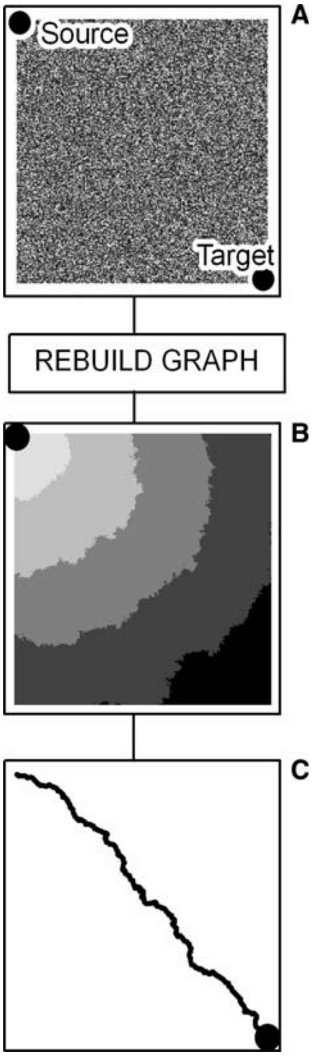

Fig. 3 Illustration of the procedure for locating MSPs. **a** Relative cost grid, **b** cumulative cost grid for the source. *Lighter shades* indicate lower cumulative cost. This was calculated after rebuilding the graph that represents the landscape, **c** with the cumulative cost grid, we trace the least-cost path between source and target, **b** and **c** are repeated 100 times to produce 100 least-cost paths

In the next two sections, we build on the above representation and describe two methods that extend Dijkstra's breadth-first search algorithm.

Conditional minimum transit cost (CMTC)

Consider a vertex (V) located between groups of source vertices (S) and target vertices (T). The Conditional Minimum Transit Cost (CMTC) for V is the cost-weighted distance to move from S to T, conditional on the route forming the shortest passage between S and T while passing through V. It is calculated as (Fig. 2):

$$\begin{aligned}\mathrm{CMTC}(\mathrm{V},\mathrm{S},\mathrm{T}) = {} & \mathrm{Cumulative\,cost}(\mathrm{V},\mathrm{S}) \\ & + \mathrm{Cumulative\,cost}(\mathrm{V},\mathrm{T})\end{aligned} \tag{3}$$

The final CMTC grid was obtained by masking out all cells with CMTC values larger than the minimum CMTC value plus 10% (Fig. 2c). The remaining values were then divided by the grid's maximum CMTC. According to Forman (1995), a corridor is "a narrow strip of land that differs from the matrix on either side". We assume that areas within the 10% threshold form corridors, but emphasize that our choice of corridor width was arbitrary.

Our analysis generates corridors that are highly heterogeneous. Visually inspecting the CMTC grid (Fig. 2c) enables identification of contiguous cells with low CMTC value. We refer to these cell groups as "dispersal routes", while recognizing that distinction between routes that are close together is arbitrary. The least-cost path is invariably located within one dispersal route.

In practice, obtaining a CMTC grid is straightforward with modules such as spatial analyst within ArcGIS (Esri, California). Some conservation biologists strongly advocate the CMTC approach for designing wildlife corridors (Majka et al. 2007). But to our knowledge, the relationship between matrix heterogeneity and the distribution of dispersal routes as predicted by the CMTC has not yet been explored.

Multiple shortest paths (MSPs)

We developed a stochastic version of Dijkstra's algorithm (Fig. 3) that outputs multiple realizations of the least-cost path, or Multiple Shortest Paths (MSPs). As described above, the least-cost path is obtained from a relative cost grid. Dijkstra's breadth-first search algorithm (Cormen et al. 2001) proceeds by iteratively marking vertices in the order of their cumulative distance from the source. At each step, the algorithm must identify the set of neighbors associated with the marked vertices. Standard algorithms use a static definition of the neighborhood, typically the nearest eight cells on a rectangular grid (Fig. 1). Our approach is to redefine the neighborhood as a stochastic function such that adjacency is non-deterministic and is instead determined randomly in proportion to edge weights. The algorithm proceeds as follows (Fig. 3):

1. Draw a number (U) between 0 and 1 from a random uniform distribution.
2. Delete edges in the graph. An edge with weight W connecting two adjacent vertices V1 and V2 is deleted if $W > U$. That is, connections with lower costs are more likely to be maintained.

A program implementing Dijktra's algorithm (with the above modification) was run 100 times in order to produce 100 MSPs for each study case (Fig. 3c shows one path). The cumulative cost associated with each path is a measure of effective distance and is calculated by adding the weights of all edges in the path. The programs used to obtain both CMTCs and MSPs were written in the Java programing language.

Applications to artificial landscapes

We generated artificial landscapes with different degrees of spatial autocorrelation using the method of wavelet synthesis (Keitt 2000). We started with a grid containing values between 0 and 1, drawn from a random uniform distribution. Using this grid, each landscape was created in four steps: (a) apply the discrete Haar wavelet transform; (b) obtain wavelet coefficients; (c) multiply coefficients by 2 ^ ($L \times \beta$), where L is the coefficient level (higher levels representing low-frequency variation); (d) apply the inverse Haar wavelet transform on the modified coefficients; (e) map results to a random uniform distribution (min = 0; max = 1). The last step is taken to ensure that the distribution of quality values is consistent across all landscapes. The values of the parameter β were 0, 0.25, 0.50, 0.75, and 1. A β value of zero generates a white noise landscape with no spatial autocorrelation. Increasing β produces autocorrelated landscapes, where clusters of favorable habitat can be identified. Each artificial landscape represents one relative cost grid that served as input in calculations of CMTC and MSPs (Fig. 4a). We used ANOVA to test for differences among landscapes, in terms of

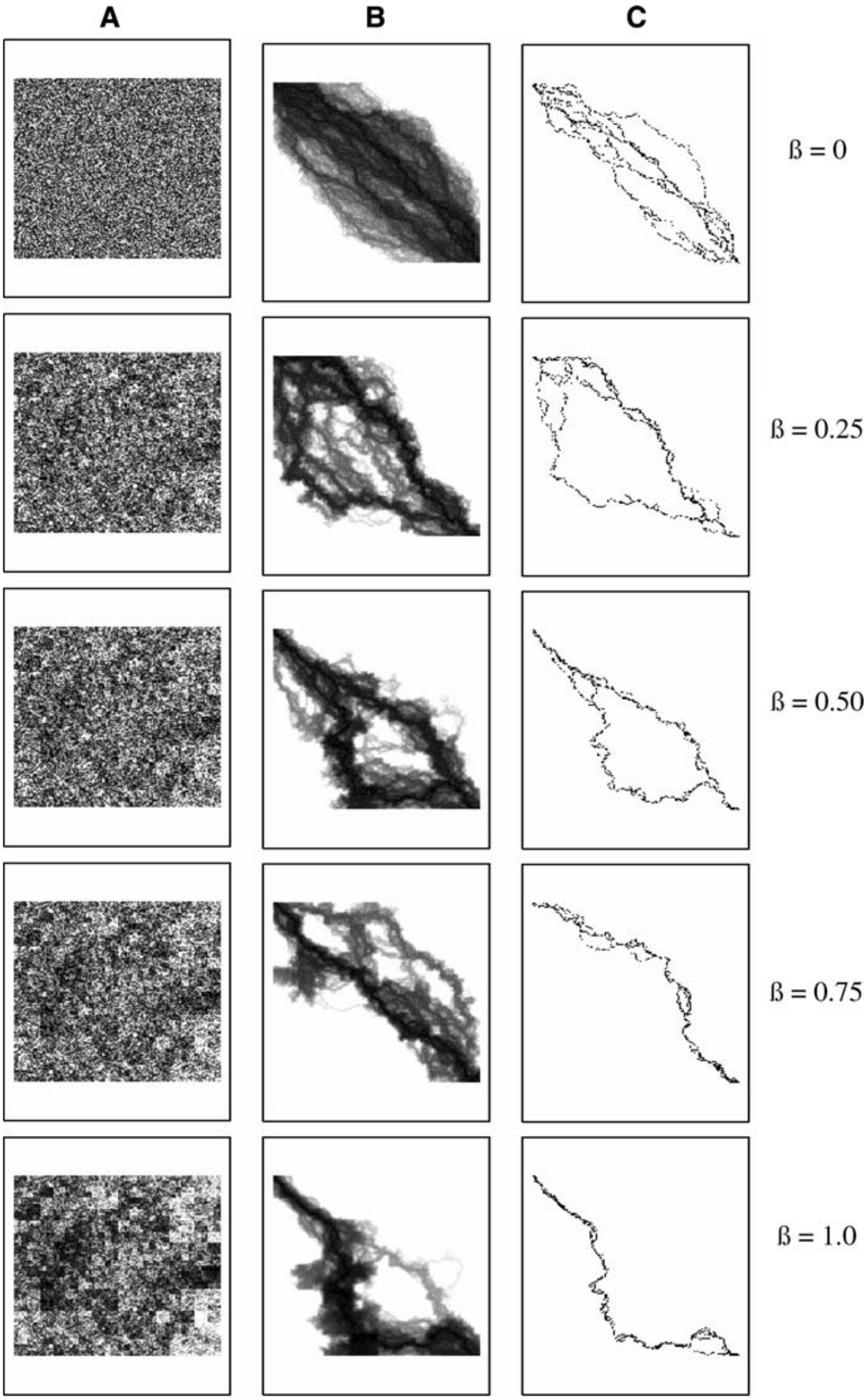

Fig. 4 Relative cost grids generated with the use of wavelet transforms (**a**), and the values of CMTC (**b**) and location of MSPs (**c**) for each landscape. A β value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as β values increase

cumulative costs associated with MSPs and mean CMTC. The generation of artificial landscapes and ANOVA tests were performed using the R programing language (R Core Development Team 2008).

Applications to real landscapes

We studied a real landscape (Fig. 5) that covers 111 km^2 of the Brazilian state of São Paulo (upper

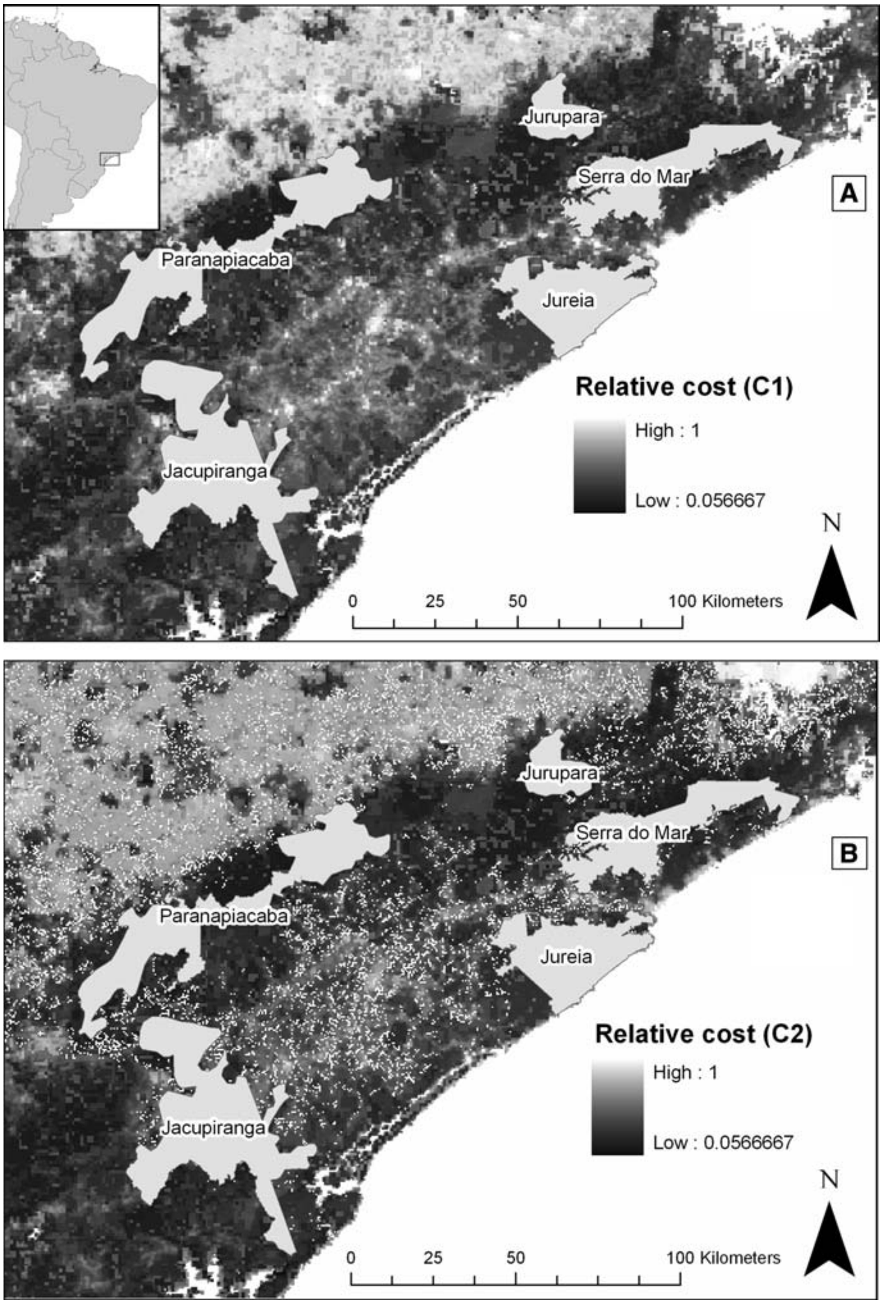

Fig. 5 Study site in the Brazilian Atlantic forest, showing conservation units in Sao Paulo State. **a** Relative cost values for scenario C1. **b** Relative cost values for scenario C2 (after deletion of small forest fragments)

left coordinates: 23.60S, 49.00W; lower right coordinates: 25.40S, 46.20W). Remaining forests are part of the Atlantic forest biome (for a description, see Oliveira-Filho and Fontes 2000). Despite its location in highly industrialized São Paulo state, the study area still contains large forest tracts and rural properties. A recent vegetation map (Eva et al. 2002) estimates that 11.1% of the study area is devoted to intensive agriculture, 7% contains a mix of agriculture and degraded vegetation, 23% is a mix of agriculture and degraded forest, and 46% is covered with forest. Excluding São Paulo's metropolitan area, human populations per municipality range in size from 3,403 to 412,243 (mean = 60,410; IBGE 1991). Five conservation units are considered here: Pedro de Toledo Nucleus within Serra do Mar State Park (868 km^2), Juréia-Itatins Ecological Reserve (801 km^2), Jurupara State Park (259 km^2), Jacupiranga State Park (1,552 km^2), and the contiguous units Intervales State Park, Carlos Botelho State Park, Ecological Station Xitué, and Alto do Ribeira Touristic State Park (1,282 km^2), referred together here as "Paranapiacaba" due to their location along the Paranapiacaba Valley.

Our analyses consisted of modeling dispersal routes between all pairs of conservation units. We have built a relative cost map in an attempt to capture the habitat preferences of species that move in forested areas and suffer higher mortality when crossing disturbed habitat. In the discussion, we describe how more detailed models can be built and refined to reflect the habitat preferences of a particular species. Three land use/land cover maps were the main input for our analyses (Table 1).

1. The Modis continous fields, (Hansen et al. 2003) contains estimates of percent tree cover. Values were manipulated (Table 1) in order to obtain a grid with values ranging between 0 (=100% tree cover) and 1 (=no tree cover).
2. The human footprint map (Sanderson et al. 2002) is a global dataset with estimates of anthropogenic impact ranging from 0 (pristine land) to 100 (most disturbed land), normalized per ecosystem. These estimates were based on patterns of human population density, land use, and transportation networks. We divided original values by 100 (Table 1) to obtain a grid with values ranging from 0 (=pristine land) to 1 (=most disturbed land).
3. The South American vegetation map (SAVM; Eva et al. 2002) contains information on forest distribution, degree of forest disturbance, and mixture with agricultural lands. We assigned each class in the SAVM grid (Table 1) a relative cost value ranging from 0 (=closed or dense forest) to 1 (intensive land use or non-forested ecosystems).

The Footprint and SAVM grids were rescaled so as to bring their spatial resolution to 500 m. The first relative cost map (C1; Fig. 5a) was obtained by averaging the values in the three grids described above (Table 1). As a result, we obtained a grid where cell values ranged from 0.057 (minimum relative cost to cross) to 1 (maximum relative cost to cross).

The second cost map (C2; Fig. 5b) simulated the removal of small forest fragments from C1, which could result from clear cutting, selective logging, or road construction. Results do not necessarily reflect actual land cover changes taking place in the Atlantic forest, but they enable us to explore the effect of small, localized disturbance on regional connectivity patterns. The C2 map was built in three steps. First, we produced a binary map with areas classified as "forest" or "non-forest" based on the SAVM map. This binary map was eroded and dilated (Serra 1982) by 0.5 pixel, resulting on the deletion of fragments with area <5 ha and linear elements (such as riparian corridors) <500 m wide. Last, C2 was obtained by assigning the maximum relative cost (1) to the deleted cells. All other cells contained the same values as C1, and the range of relative cost values for the entire grid remained unchanged (0.057–1). It was assumed that individuals could not move through water, thus a cost value of positive infinity was assigned to cells representing water bodies in both C1 and C2 scenarios. Finally, we calculated the CMTC and MSPs for both C1 and C2 scenarios. All GIS layers were processed using programs written in Java

Table 1 Grids used to construct the relative cost maps used in the present study, their original spatial resolution (pixel size), period of data collection, and operations performed on original grid values

Layer	Resolution (m)	Years	Operations performed on the original raster values
South America vegetation map	1,000	1995–2000	0 = closed, dense, transitional forest 0.25 = open forest 0.5 = mosaic agriculture/degraded forest 0.75 = shrubland, savannah, grassland 1 = intensive agriculture, mosaic agriculture/degraded vegetation, desert, urban
Human footprint	1,000	1960–2001	Final value = (original value)/100
Modis continuous fields, % tree	500	2000–2001	Final value = (100 − original value)/100

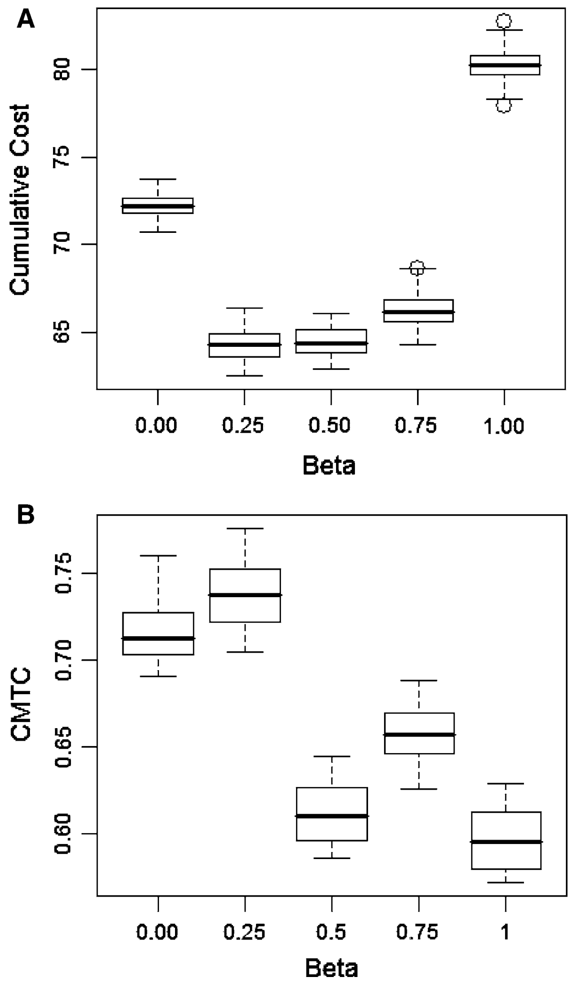

Fig. 6 The distribution of values of **a** Multiple Shortest Paths **b** and Conditional Minimum Transit Costs. A β value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as β values increase

programing language, and illustrations were produced in ArcMap (Esri, California).

Results

Artificial landscapes

The two graph theory approaches proposed here outlined the influence of matrix heterogeneity on dispersal routes. We detected a significant difference in mean cumulative costs associated with Multiple Shortest Paths (MSPs) among the five artificial landscapes (ANOVA, $F = 6{,}934.5$; $P < 0.001$). MSPs with lowest costs were observed when landscapes had intermediate patchiness (Fig. 6a; Tukey multiple comparisons of means, 95% family-wise confidence level, $P < 0.001$). We also observed significant differences in mean Conditional Minimum Transit Cost (CMTC) values (ANOVA, $F = 474{,}104$; $P < 0.001$). The most autocorrelated landscapes produced the lowest CMTC values (Fig. 6b; Tukey multiple comparisons of means, 95% family-wise confidence level; $P < 0.001$). In addition, we observed differences in the spatial distribution of dispersal routes. Landscapes with little autocorrelation in relative habitat quality produced redundant corridors with more alternative dispersal routes (Fig. 4; β closer to 0). As clusters of favorable habitat started to form, corridors became restricted to fewer routes (Fig. 4; β closer to 1). This was evidenced in the outputs of both the CMTC and MSPs calculations.

Real landscapes

We tested the influence of small, localized disturbance on corridors connecting five conservation units in the Brazilian Atlantic forest (Fig. 5). There were no significant differences in mean cumulative path costs calculated from MSPs, or in mean CMTC values (t-test, $P > 0.05$) between scenarios C1 and C2. But in most cases, simulated fragment removal influenced the spatial distribution of dispersal routes. Since small fragments were not homogeneously distributed in the study area, corridors obtained under scenario C1 were differentially affected by simulated fragment removal in scenario C2 (Table 2).

Table 2 Conservation units included in the present study

	Jacupiranga	Jurupará	Serra do Mar	Paranapiacaba
Juréia	72.321	35.391	6.905	3.993
	5	3.6	10.4	5.5
Jacupiranga		115.502	104.800	7.868
		4.0	5.0	21.0
Jurupará			7.263	43.739
			2.0	1.2
Serra do Mar				51.183
				2.3

Each unit in a pair can serve as a source or a target for dispersing organisms. The first line contains the straight-line distance between units (in kilometers), and the second line shows the percentage of 500-m^2 cells deleted from the corridor as a result of simulating fragment removal

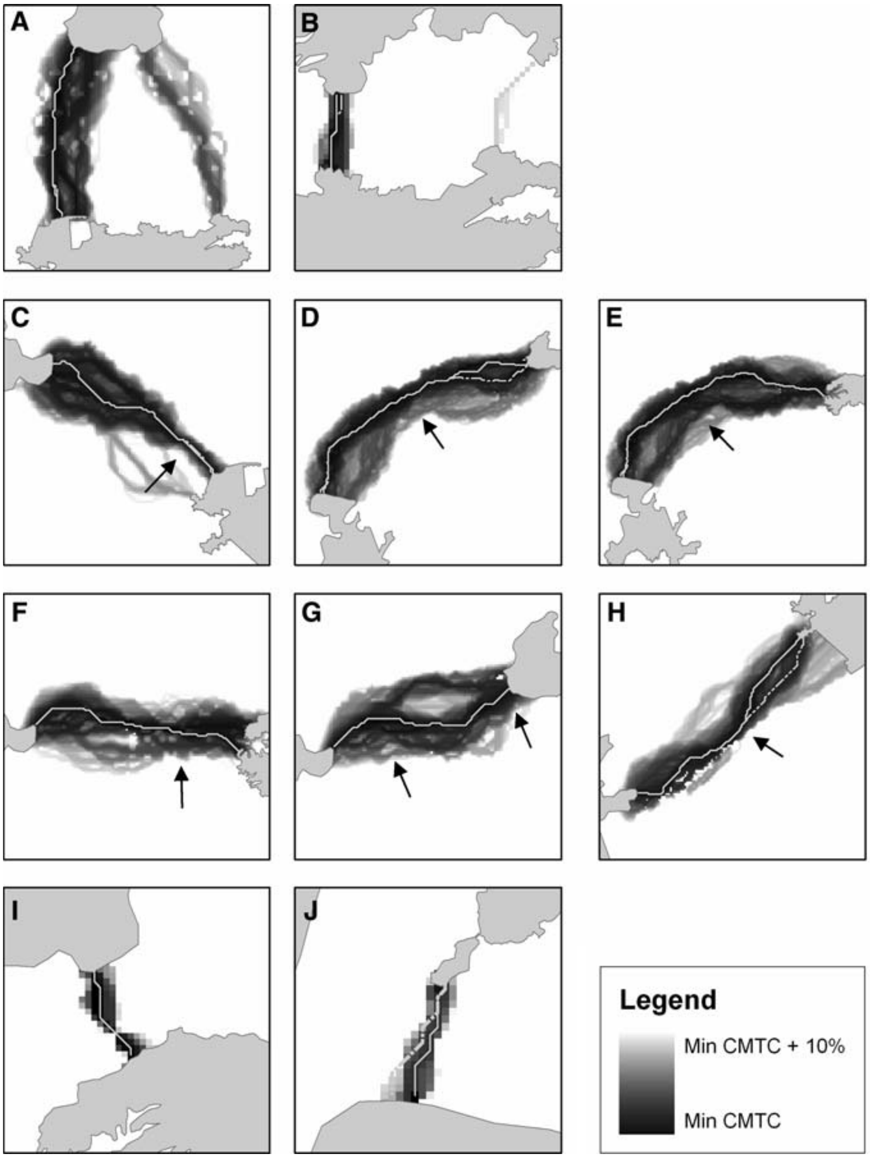

Fig. 7 CMTC grids for the corridor connecting conservation units in São Paulo, Brazil. The pairs are: **a** Juruparа́–Juréia, **b** Juréia–Serra do Mar, **c** Juréia–Paranapiacaba, **d** Jacupiranga–Jurupará, **e** Jacupiranga–Serra do Mar, **f** Paranapiacaba–Serra do Mar, **g** Paranapiacaba–Jurupará, **h** Juréia–Jacupiranga, **i** Serra do Mar–Jurupará, **j** Paranapiacaba–Jacupiranga. *Gray lines* show the least-cost path. *Solid lines* represent least-cost paths obtained for scenarios C1 and C2, whereas *interrupted lines* represent sections of the least-cost path obtained for scenario C2 only. *Arrows* indicate potential dispersal bottlenecks

In most cases, the CMTC grid displayed more than one alternative route between conservation units, one of them being the least-cost path (Fig. 7a–h). When conservation units were close, the distance between them was small with respect to the variation in their shape. In this case, the CMTC grid produced narrow corridors, coinciding with the links representing the shortest Euclidian distance (Fig. 7b, i, j). When corridors contained alternative routes, these were rarely disjoint (Fig. 7a, b). The constriction zones where dispersal routes merged represented potential dispersal bottlenecks (Fig. 7c–h). In most cases, the location of the least-cost path did not change substantially as a result of small fragment removal (Fig. 7a–c; e–g; i, j). But in two cases, the least-cost path for scenario C2 was displaced to an alternative route located a few kilometers away from the least-cost path for scenario C1 (Fig. 7d, h).

We also identified the MSPs between pairs of conservation units. Compared to the CMTC calculation, this tool provided a better assessment of the impact of fragment removal on corridor redundancy. Examining the MSPs produced for the scenarios C1 and C2, we observed two trends. In some cases,

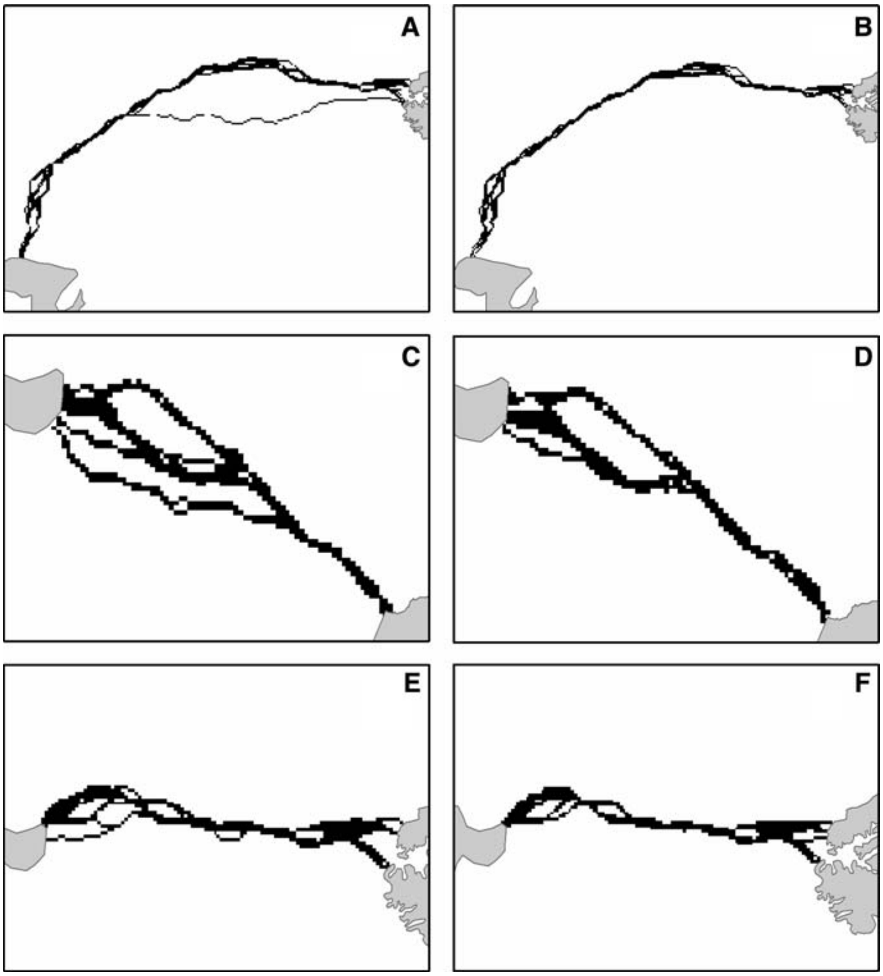

Fig. 8 Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Jacupiranga–Serra do Mar, scenario C1; **b** Jacupiranga–Serra do Mar, scenario C2; **c** Juréia–Paranapiacaba, scenario C1; **d** Juréia–Paranapiacaba, scenario C2; **e** Serra do Mar–Paranapiacaba, scenario C1; **f** Serra do Mar–Paranapiacaba, scenario C2

fragment removal led to the disappearance of external dispersal routes; corridors became narrower and less redundant (Fig. 8). In other cases, new, more external routes emerged after fragment removal (Fig. 9).

Discussion

Analyses of artificial landscapes show the influence of matrix heterogeneity on landscape connectivity. Redundant corridors with multiple alternative dispersal routes emerged in white noise landscapes, where favorable habitat is randomly distributed (Fig. 4, β closer to 0). As patches of favorable habitat started forming, corridors became narrower and less redundant (Fig. 4, β closer to 1). The cumulative cost of MSPs was on average lower in landscapes with intermediate degree of autocorrelation (Fig. 6a). This is because paths in white noise landscapes will often cross areas of high cost, whereas the presence of contiguous habitat patches in autocorrelated landscapes can lead to longer, more tortuous paths (Fig. 4c). The CMTC was on average lower in autocorrelated landscapes (Fig. 6b). This follows from our choice of CMTC value used to delimit corridors—under a 10% threshold, white noise landscapes produced wider corridors with higher CMTC values.

In addition to studying artificial landscapes, we illustrated our methods using data from a real landscape in the Brazilian Atlantic forest. In this region, a complex landscape matrix produced dispersal routes that were not apparent in land use/land cover maps (Fig. 7a–f, h–j), with the exception of the pair Paranapiacaba–Jurupará that is separated by an artificial dam (Fig. 7g). CMTC maps revealed highly heterogeneous corridors displaying bottlenecks to animal movement (indicated by arrows in Fig. 7c–h). Removing small fragments did not produce a significant increase in the mean cumulative cost of MSPs but led to changes in their spatial distribution (Figs. 8, 9). Our work illustrates two possible large-scale effects of small, localized disturbance on the landscape matrix. Narrower corridors were produced (Fig. 8), and the importance of external dispersal routes increased (Fig. 9). The latter case included the two pairs of conservation units with the largest amount of deleted habitat in the scenario C2 (Table 2; Fig. 9c–f).

Results of least-cost path analyses are strongly dependent on the selection of relative cost grids (Adriaensen et al. 2003; Rae et al. 2007). Our choice of relative cost grids (Table 1) was made as an attempt to approximate the habitat preferences of a forest specialist. Relative cost grids can be further refined and validated for a particular species using patch occupancy data (Verbeylen et al. 2003) or from ecological niche modeling and tools such as the Mahalonobis distance (Farber and Kadmon 2003). In addition to habitat preference estimates, an important issue is the time scale over which individuals are expected to disperse. Here, we were not concerned with the time interval or number of generations that individuals (or populations) took to move between source and target fragments (conservation units). More realistic models can be obtained by adjusting the maximum Euclidian distance allowed between source and target fragments so as to match the maximum distance that can be crossed by a species given a particular time interval (Keitt et al. 1997). The issue of time scale is related to the question of whether corridors should function as habitat or as

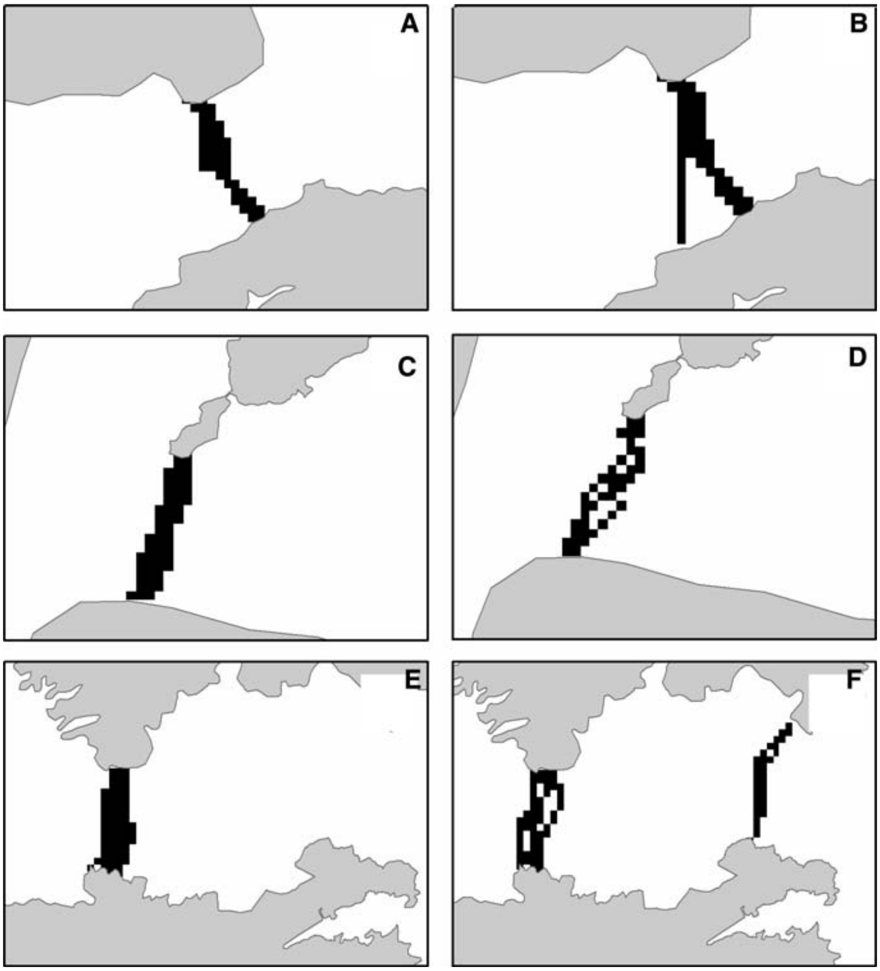

Fig. 9 Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Serra do Mar–Jurupara, scenario C1; **b** Serra do Mar–Jurupará, scenario C2; **c** Paranapiacaba–Jacupiranga, scenario C1; **d** Paranapiacaba–Jacupiranga, scenario C2; **e** Juréia–Serra do Mar, scenario C1; **f** Juréia–Serra do Mar, scenario C2

conduits (Hess and Fischer 2001)—i.e., individuals are expected to spend more time in habitat corridors. Corridor width can be adjusted by increasing the CMTC threshold to ensure that corridors contain minimum habitat requirements.

The ability to identify multiple dispersal routes can be desirable in conservation studies, for three main reasons. First, least-cost paths have been employed in the design of linked reserve systems (Hoctor et al. 2000; Schadt et al. 2002; Larkin et al. 2004). This approach, however, can lead to very narrow linkages (Alagador and Cerdeira 2007) that might not be located in land tracts available for purchase. Second, dispersal routes that appear similar may differ in terms of their conservation value. For example, field studies in Canada (Clevenger et al. 2001) show that drainage culverts can act as habitat linkages for several mammal species, but culverts near roads with higher traffic volume and noise levels are less commonly used. Third, the approach shown here enable the visualization of functionally unique landscape structures (Manning et al. 2006): narrow corridors or dispersal bottlenecks within corridors (e.g., Fig. 7).

Considerable attention has been given to quantifying the role played by agroecosystems in conservation (i.e., Bestelmeyer and Wiens 1996; Reitsma et al. 2001; Mas and Dietsch 2003). Agricultural lands can help support wild populations by providing critical habitat (Moguel and Toledo 1999) and influencing neighboring fragments, in which case potential outcomes depend on the spatial configuration and degree of mixture with pristine habitat (Perfecto and Vandermeer 2002; Perfecto et al. 2003; Tscharntke et al. 2005). Our study of the Brazilian Atlantic forest shows that private lands can collectively influence ecological processes occurring at large spatial scales and supports the assertion that small fragments can potentially shape regional patterns of gene flow (Bodin et al. 2005). This raises the necessity to view agricultural lands' contribution to biodiversity in a larger context.

Movement behavior is a key aspect in functional connectivity studies, but detailed data on animal movement remains hard to collect, especially for large spatial scales. In fact, the ability to produce accurate movement models has long been recognized as one of the main challenges of population biology studies (Turchin 1998). There is no consensus on the amount of biological detail that should be used in functional connectivity studies. It has been suggested that movement models ought to increase in complexity in order to capture the behavior of particular species (Goodwin 2003). At the same time, conservation biologists have raised the need for rigorous methods that predict the location of dispersal routes for many species (Boitani et al. 2007). Clearly a compromise is needed, which requires determining how much simplification can be made before losing predictive power (Baguette and Van Dyck 2007). Least-cost path predictions can be derived for many species, given the ever growing maps of habitat quality produced by ecological niche modeling. Also, rigorous protocols already exist to compare least-cost predictions with field data (Driezen et al. 2007).

Conclusions

In the present paper, we extended the graph theory algorithm that serves as the basis for least-cost path calculations. The two outputs are the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs). Our goal was to integrate information on habitat preferences to model dispersal patterns across a heterogeneous matrix. In addition to the path of least resistance between two points, the methods presented here outlined additional paths with similar length and relative cost. Results from artificial landscapes show that the location and relative cost of dispersal routes are strongly influenced by the spatial distribution of favorable habitat in the matrix. In addition, study of a real landscape shows that small, localized disturbance such as removal of small fragments can affect large-scale dispersal routes. Models producing multiple dispersal routes present a practical advantage over models assuming optimum behavior. Although the choice of number of dispersal routes or their location is application specific (and beyond the scope of this paper), our results suggest that the least-cost path is a flexible approach with a wide range of applications.

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Rapid growth of the US wildland-urban interface raises wildfire risk

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The wildland-urban interface (WUI) is the area where houses and wildland vegetation meet or intermingle, and where wildfire problems are most pronounced. Here we report that the WUI in the United States grew rapidly from 1990 to 2010 in terms of both number of new houses (from 30.8 to 43.4 million; 41% growth) and land area (from 581,000 to 770,000 km^2; 33% growth), making it the fastest-growing land use type in the conterminous United States. The vast majority of new WUI areas were the result of new housing (97%), not related to an increase in wildland vegetation. Within the perimeter of recent wildfires (1990–2015), there were 286,000 houses in 2010, compared with 177,000 in 1990. Furthermore, WUI growth often results in more wildfire ignitions, putting more lives and houses at risk. Wildfire problems will not abate if recent housing growth trends continue.

wildfires | housing growth | sprawl | development | fragmentation

The wildland-urban interface (WUI), defined as the area where houses are in or near wildland vegetation, is the area where wildfires pose the greatest risk to people due to the proximity of flammable vegetation (1). Wildfires frequently burn houses in the WUI (2, 3), and are most difficult to fight there. Furthermore, the WUI is where people often ignite wildfires (4), and the vast majority of fires are human-caused (5). While fires are an integral part of many ecosystems and the Earth system as a whole (6), humans have changed fire regimes globally (7) and throughout the United States (5), and climate change will increase fire frequency in the future, including in the WUI (8).

The close proximity of houses and wildland vegetation does more than increase fire risk (9). As houses are built in the WUI, native vegetation is lost and fragmented (10); landscaping introduces nonnative species and soils are disturbed, causing nonnatives to spread (11); pets kill large quantities of wildlife (12); and zoonotic disease, such as Lyme disease, are transmitted (13). Thus, understanding WUI patterns and WUI growth is important with respect to wildfires and many other environmental problems.

The WUI is widespread in the United States (1, 14) and in many other parts of the world (15, 16), including Argentina (17), Australia (18), France (19), and South Africa (20). Furthermore, both the annual area burned (8, 21, 22) and fire suppression costs (23) have rapidly increased in the United States. The area burned annually nearly doubled, from an average of 18,000 km^2/y in 1985–94 to 33,000 km^2 in 2005–14 (22). Concomitantly, federal wildfire suppression expenditures tripled from \$0.4 billion/y to \$1.4 billion/y (23), and exceeded \$2 billion in 2017.

While there is ample evidence that houses in the WUI pose problems, it is not clear how fast the WUI is growing. Overall, the US population grew by 60 million people and 29.2 million homes from 1990 to 2010, but how much of that growth occurred in the WUI is uncertain. Previous assessments of WUI growth (24, 25) analyzed only housing data up to 2000, and did not account for changes in wildland vegetation. Post-2000 housing data are important, because the United States entered a recession after 2008, accompanied by a strong downturn in the housing market. Similarly, without data on vegetation change, the major cause of WUI growth is unclear. Areas where forests are regrowing on abandoned farmland, such as in the New England states (26), could see WUI growth without any additional houses. Fundamentally, two processes can create new WUI: construction of new homes in or near existing wildland vegetation, and an increase in wildland vegetation within and near previously developed areas. The prevalence of each process is unclear.

Knowing how the WUI is growing, and why, is essential when evaluating management and policy responses (3, 8). In the United States, federal wildfire management policy prioritizes fuel treatments and the promotion of fire-adapted communities in the WUI. Local jurisdictions use a variety of land use planning tools to limit the environmental impacts of housing growth in the WUI. The importance of the WUI for the environment and for national policy, accompanied by the lack of information about WUI growth in the most recent decade, highlight the need to both assess WUI growth and identify its causes. Thus, we addressed three major questions: (*i*) how much has the WUI in the conterminous United States grown from 1990 to 2010; (*ii*) whether WUI growth is caused mainly by housing growth or by vegetation growth; and (*iii*) how much WUI growth has occurred within recent wildfire perimeters.

The lack of consistent, fine-resolution longitudinal housing data has been the biggest impediment to a nationwide assessment

Significance

When houses are built close to forests or other types of natural vegetation, they pose two problems related to wildfires. First, there will be more wildfires due to human ignitions. Second, wildfires that occur will pose a greater risk to lives and homes, they will be hard to fight, and letting natural fires burn becomes impossible. We examined the number of houses that have been built since 1990 in the United States in or near natural vegetation, in an area known as the wildland-urban interface (WUI), and found that a large number of houses have been built there. Approximately one in three houses and one in ten hectares are now in the WUI. These WUI growth trends will exacerbate wildfire problems in the future.

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The authors declare no conflict of interest.

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of WUI growth. The decennial US Census provides fine-resolution housing data for 1990, 2000, and 2010, but the boundaries of the smallest units for which housing units are reported (i.e., census blocks) often shift between decades, precluding direct change analyses (27). We have developed algorithms to convert the decennial Census data at census block resolution into a consistent dataset on housing growth across the conterminous United States (*Methods*), which we combined with 1992, 2001, and 2011 National Land Cover Data (NLCD) on wildland vegetation: forests (classes 41–43), shrublands (classes 51 and 52), grasslands (class 71), and woody wetlands (class 90). We mapped decadal WUI change from 1990 to 2010 within 2010 census block boundaries, based on the WUI definitions in the *Federal Register* and our previously developed WUI mapping algorithms (1, 14), and conducted several robustness checks of our new dataset (*Supporting Information*). Because of concerns about housing growth and wildfire management, we calculated housing growth for 1990–2010 within WUI burned areas identified in Landsat imagery between 1990 and 2015 (22).

We found that the WUI was widespread in 2010, covering 9.5% of the conterminous United States (Fig. 1), and that the WUI grew rapidly from 1990 to 2010 in all its aspects (Fig. 2).

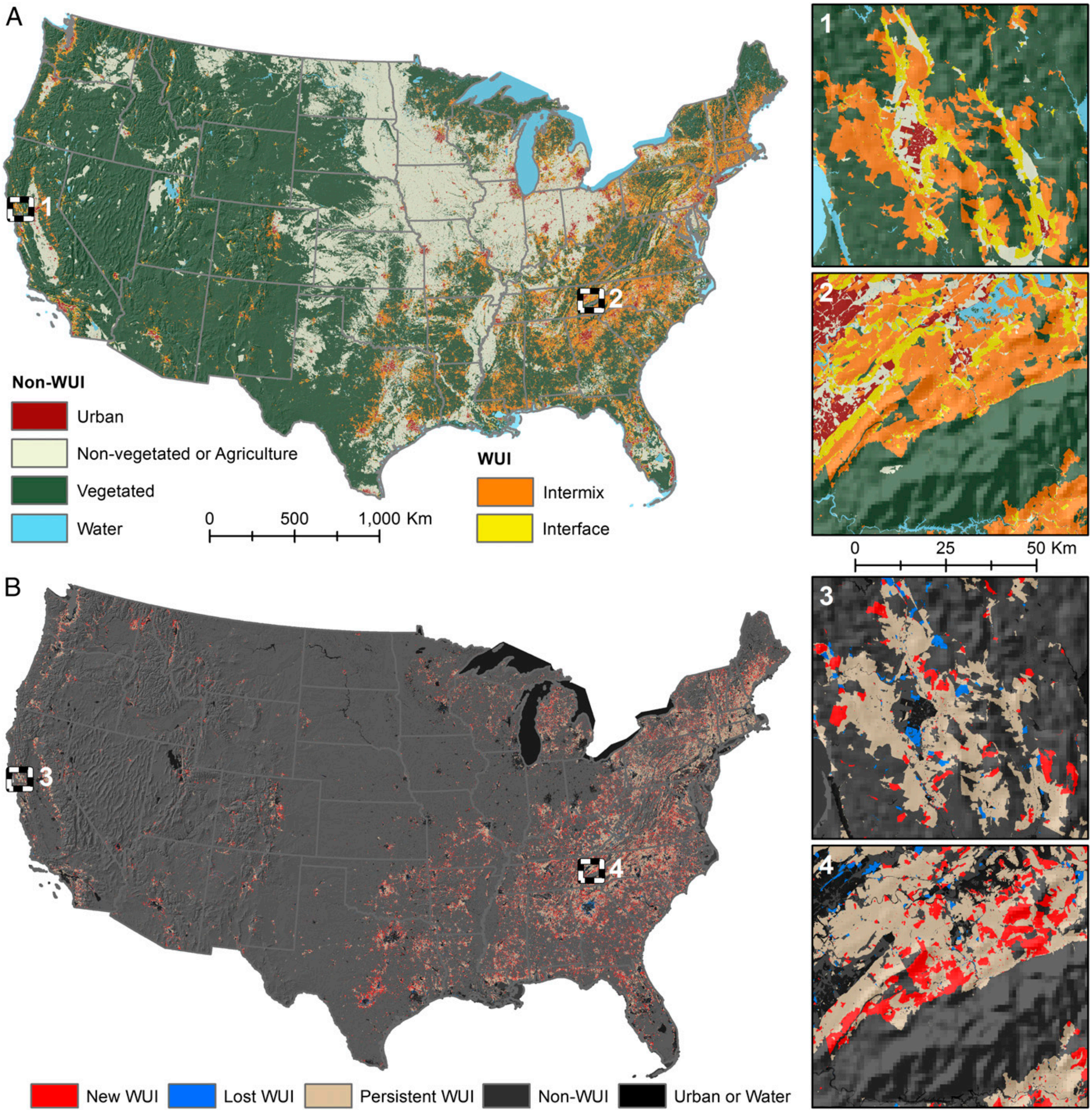

Fig. 1. The WUI in the United States was widespread in 2010 (*A*), as were changes in WUI area (*B*), for example, in and around Santa Rosa, California (1, 3), and Gatlinburg, Tennessee (2, 4), areas where wildfires destroyed many homes in 2017 and 2016, respectively.

The number of housing units ("houses" hereinafter) in the WUI grew fastest, followed by the number of people in the WUI and then WUI area (Fig. 2*B* and Table S1). New WUI area totaled 189,000 km^2, an area larger than Washington State. At 33%, WUI area growth is faster than that of any of the level I land cover categories included in the NLCD (28). Increases in houses and people were also strong, with 12.7 million more houses and 25 million more people in the WUI in 2010 compared with 1990. The overall combination of more WUI area (7.2% of the conterminous United States in 1990 vs. 9.5% in 2010; Fig. 2*C*) and higher growth rates for both houses and people in the WUI, compared with the nationwide averages (Table S1), increased the percentage of houses (from 30.3% to 33.2%) and people (from 29.4% to 31.9%) in the WUI from 1990 to 2010 (Fig. 2*C*). Even though the WUI occupies less than one tenth of the land area of the conterminous United States, 43% of all new houses were built there, and 61% of all new WUI homes were built in areas that were already in the WUI in 1990 (and remained in the WUI in 2010) (Tables S1 and S2).

There are two main types of WUI: intermix WUI, the area where houses and wildland vegetation directly intermingle, and interface WUI, where settled areas abut wildland vegetation (1). We found that intermix WUI was both more extensive and expanded much more rapidly in area (from 5.6% to 7.5% of the conterminous United States from 1990 to 2010) than interface WUI (from 1.6% to 2.0%). However, interface WUI had higher housing growth rates (43% from 1990 to 2010) than intermix WUI (38%) and non-WUI areas (23%; Table S1). In absolute numbers, there were 4.7 million more houses in the intermix WUI and 8.0 million more in the interface WUI in 2010 than in 1990.

Regional differences in WUI growth were striking (Fig. 3). The highest absolute gains in WUI area occurred in the East, whereas high gains in houses and people in the WUI were most common in the South and Southwest. Absolute gains are most relevant for management agencies, because they indicate how much area and how many people and houses may require management actions; however, rapid growth often garners the most attention. Across the United States there is an interesting dichotomy in that states in the East had large absolute gains, but relatively low WUI growth rates, largely because WUI was already so widespread in 1990. In contrast, states in the northern Rockies saw much smaller absolute gains in WUI area and houses, but rapid WUI growth rates.

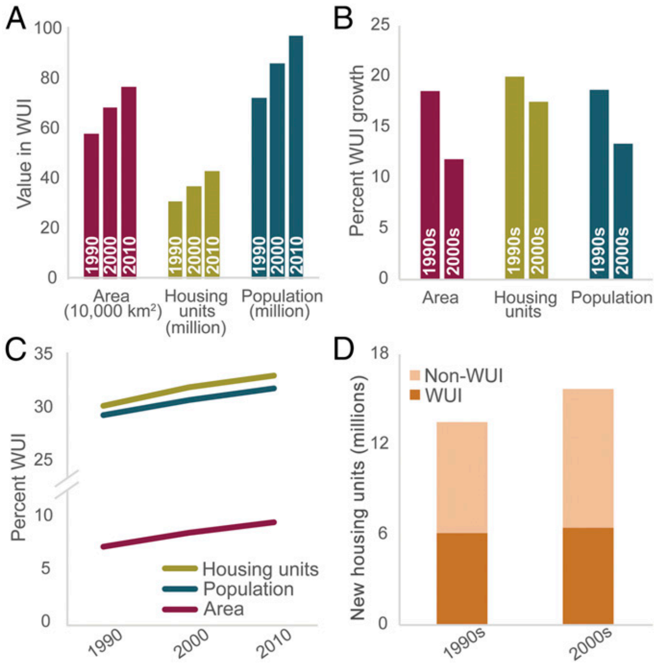

Fig. 2. WUI growth was rapid in terms of the absolute numbers of the area, houses, and people in the WUI in 1990, 2000, and 2010 (*A*); WUI growth rates during the 1990s and the 2000s (*B*); the proportion of all houses and people, as well as the land area in the WUI in 1990, 2000, and 2010 (*C*); and the absolute number of all new housing units within and outside the WUI during the 1990s and 2000s (*D*).

New WUI areas arise either when new houses are built in or near wildland vegetation or when wildland vegetation regrows in or near settled areas. Between these two possible causes, housing growth was unambiguously the main cause for new WUI areas, with increases in vegetation contributing minimally. Of all new WUI areas, 97% were caused by housing growth in sparsely settled areas, pushing these areas over the threshold of 1 house per 40 acres (6.17 homes/km^2). Only 2% of new WUI area was due to vegetation growth alone, and 1% was due to the combination of both housing and vegetation growth (Table S2). Similarly, new houses were the cause of >80% of WUI growth in all states except Delaware, the District of Columbia, Maryland, and New Jersey (Fig. S1).

Among areas that were WUI in 1990, the vast majority were still WUI in 2010, and both homes and population increased in those areas over that time (Table S2). A small proportion (6%) of the 1990 WUI areas dropped out of the WUI by 2010. Among all WUI changes (i.e., gains and losses combined), 13% of the changes in WUI area and 23% of the changes in WUI houses from 1990 to 2010 were losses. In terms of the causes of WUI area loss, reduced housing density was the most important (65.0%), whereas the loss of vegetation accounted for 32.6%. Housing density may have declined due to actual removal of housing units, or possibly due to enumeration errors in the Census data. Loss of vegetation was the dominant driver of loss of homes from the WUI (65.0%), which occurred largely in densely settled areas where additional housing development, deforestation, or fuel management may have removed wildland vegetation.

The number of houses within burned areas in the different decades is a strong indication of how much WUI growth can exacerbate wildfire problems. In 1990, there were 177,000 houses within the perimeters of the fires that occurred in the subsequent 25 y. By 2010, there were 286,000 housing units in the same fire perimeters, i.e., 109,000 more, which corresponds to 62% growth (far outpacing the average US housing growth rate of 29%). Of these new houses, those built before the wildfires occurred complicated firefighting because more houses had to be protected and more residents had to be evacuated. Similarly, houses built after fires occurred are of concern because new development in areas that burned recently, and thus are known to have a high fire risk, suggests that there is little adaptation to fire risk (2).

Our results provide compelling evidence that the WUI in the United States has grown rapidly, despite the risks that wildfires pose to homes and lives (3) and despite the other environmental problems caused by housing development in or near wildland vegetation (9). Our findings are generally in alignment with previous studies that found rapid previous WUI growth (24) and widespread potential for future WUI growth (25, 29), even though absolute numbers are not comparable because of differences in WUI definitions, datasets, and time periods (30). Furthermore, the WUI is not unique to the United States, but is widespread in many other countries as well (15, 16, 18–20). Rampant WUI growth demonstrates that the social and economic factors that together propel WUI growth are strong. WUI areas are attractive places to live because of affordability and ready access to natural settings and recreation (31). As WUI areas attract new residents, the number of houses per capita often increases as well, due to increasing rates of seasonal homeownership and declining family size (32). Indeed, despite the economic downturn after 2008, the absolute number of

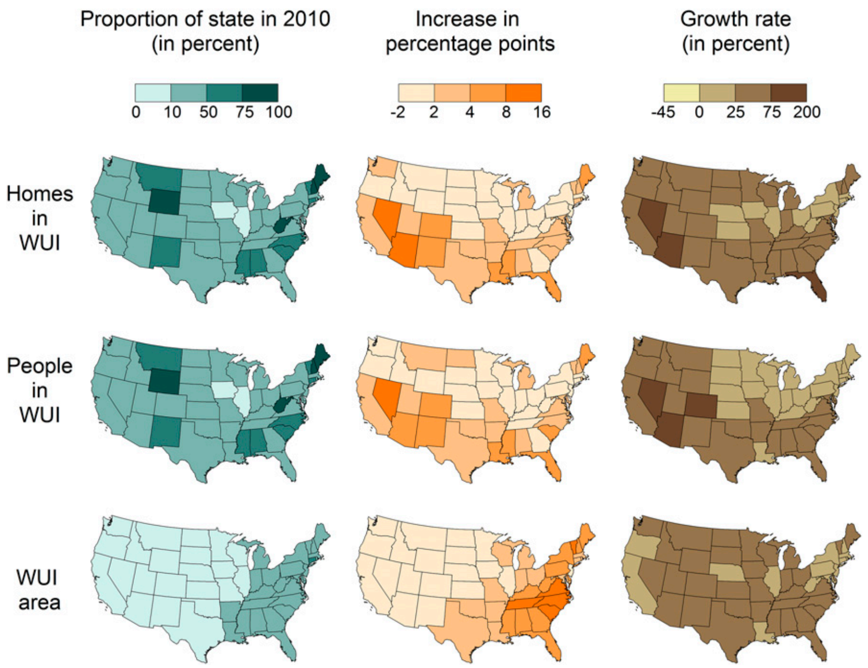

Fig. 3. WUI growth differed greatly among states, especially in the Southwest versus the Southeast, in terms of houses in the WUI, people in the WUI, and WUI area, calculated as the percentage of the state total in 2010, change in the WUI percentage from 1990 to 2010, and the growth rate (in percent) of the WUI from 1990 to 2010. Only the District of Columbia had negative absolute growth in the WUI (homes, people, and area). Fig. S2 summarizes these metrics at the county level.

houses built in the WUI, and in the United States as a whole, was higher between 2000 and 2010 than between 1990 and 2000 (Table S1). Demographic trends do not suggest slower future WUI growth. Furthermore, climate change projections indicate that conditions favorable for wildfires will occur more frequently in the future (8). Thus, increased wildfire ignition rates due to WUI expansion will initiate more wildfires in vegetation that is more susceptible to fire spread, leading to more widespread fires and possibly more severe fire behavior (33). This suggests that WUI growth and climate change together will compound the existing problems with wildfires in the WUI.

As WUI growth continues, there are many management options and policy tools to consider for addressing both wildfire and other environmental problems. Just as WUI-related problems involve actors (e.g., homeowners, community leaders) at many levels, so too must their solutions involve actors at multiple levels (i.e., local, regional, state, and national) (3, 8). Homeowners can reduce their individual fire risk by removing vegetation directly adjacent to their house (i.e., the home ignition zone; refs. 3 and 34), changing roofing and building materials, and following additional Firewise recommendations (35). To limit some of the other environmental problems associated with living in the WUI, homeowners can keep cats inside and dogs on a leash, limit fertilizer and pesticide use, and landscape with native plants (9). To reduce wildfire impacts, communities can coordinate fuel reduction efforts, educate homeowners, train firefighters, and establish wildfire management plans. Insurance companies can offer reduced premiums for communities taking mitigation action to incentivize community-level efforts to reduce wildfire losses. Communities and local jurisdictions could anticipate wildfires and environmental impacts more explicitly when planning future land use to avoid housing expansion in high-risk wildfire areas and other environmentally sensitive areas (36). State and federal agencies typically do not regulate development directly, but can allocate resources to areas experiencing rapid WUI growth, support local and regional planning efforts, and provide important research data and information to help communities adapt to fire-prone environments. Agencies managing public lands could consider targeted purchases of private inholdings to limit future housing growth within the administrative boundaries of public lands, which has been particularly rapid (37). In summary, there are many concrete management actions and policy responses that can limit the negative effects of WUI growth on wildfire risk and other environmental problems, but changes will require efforts at all levels by homeowners and community leaders, local and county governments, and state and federal agencies.

Housing development in the WUI greatly exacerbates wildfire problems and other environmental issues in the United States (1, 5, 8), and globally (16, 18–20). Our results highlight the magnitude and rapid rates of WUI growth in the US, underscoring the urgency of identifying what can be done to address WUI growth and its associated wildfire challenges (3). Past federal fire policy has focused largely on fighting and preventing wildfires and on fuel reduction, public outreach campaigns, and other actions (38). Although laudable, such efforts are unlikely to be successful by themselves, because housing growth is clearly the dominant cause of WUI growth, as well as a major factor contributing to wildfire occurrence and cost. As long as WUI growth is unchecked, wildfire problems will likely worsen. On a more hopeful note, to the extent that WUI growth reflects an affinity for nature, the evident consequences and costs of growth could prompt discussions on how to sustain those highly valued ecosystems in which so many people have chosen to live.

Materials and Methods

Our WUI definition is based on the definition published by the US government in the *Federal Register* (39) and that has been widely used for WUI assessments in the past (1, 14, 40). It specifies two types of WUI, intermix and interface. Intermix WUI is where houses and wildland vegetation intermingle, with both a housing density of >1 house per 40 acres (6.17 houses/km^2) and >50% of the area in wildland vegetation. Interface WUI represents settled areas that have <50% vegetation, but lie within

1.5 miles (2.4 km) of a densely vegetated area (at least 75% wildland vegetation) that is at least 5 km^2 in size (so that settlements near small urban parks are not included in the WUI).

Our WUI assessment was based on two main datasets: US Census data, which provided housing data (TIGER shape files for block boundaries, plus Census summary files for attribute data), and the US Geologic Survey's NLCD, which provided information on wildland vegetation. We derived housing data from the US Decennial Censuses for 1990, 2000, and 2010 at its finest resolution, the census block level. However, a major obstacle to conducting change analyses is that census block boundaries frequently change from one decade to the next, preventing direct change analyses (27). Indeed, 62% of all blocks changed their boundaries from 1990 to 2000, and 56% changed from 2000 to 2010, invalidating any housing density change analysis that does not account for these boundary changes. We used additional information available from the US Census Bureau as relationship files that details for each decade which blocks of the starting date were at least partly contained by which block in the second decade, and vice versa, to calculate the number of 1990 and 2000 housing units for the boundaries for each 2010 census block.

Based on the Census Bureau relationship files, we first allocated 1990 housing units to 2000 block boundaries by identifying the type of relationship for each 1990 block to 2000 block(s), classifying the relationship as one-to-one, one-to-many, many-to-one, or many-to-many. For one-to-one and many-to-one relationships, 1990 housing units were allocated directly to corresponding 2000 blocks. For one-to-many relationships, 1990 housing units were allocated proportionally based on the number of housing units in the 2000 blocks. For many-to-many relationships, we identified the least common denominator of polygons that fully contained groups of both 1990 and 2000 blocks. For each least common denominator polygon, we then summed the 1990 housing units and allocated them based on the proportion of the 2000 housing units. To minimize instances of many-to-many relationships and maximize direct relationships, we removed blocks that were classified as water in 1990 and as vacant in 2000, as well as all 1990 and 2000 blocks that intersected by <1% of their area. Once 1990 housing units were allocated to 2000 census block geometry, we repeated the process using the 2000–2010 relationship files to allocate 2000 housing units to 2010 block boundaries. We then joined the 1990 housing units allocated to 2000 block boundaries with the 2000–2010 relationship files, and repeated the process to allocate 1990 housing units to 2010 block boundaries. The end result of our algorithms are 1990 and 2000 housing units allocated to the 2010 block geometry across the conterminous United States, i.e., a dataset that permits valid analyses of housing growth across the United States at fine spatial resolution and that minimizes erroneous changes due to changing census block boundaries.

We further refined census block boundaries by integrating them with information on the boundaries of protected areas. The boundaries of protected areas were provided by the Protected Area Database, version 2. Where protected areas intersected census block boundaries, we assumed that the houses in that block were located in nonprotected areas only. However, where census blocks with houses were entirely within a protected area, we made no changes, and assumed a uniform housing density throughout the block.

The 30-m resolution NLCD provided us with data on wildland vegetation. We analyzed both the 1992/93–2001 and the 2001–2011 land cover change products and calculated the percentage of each NLCD land cover class within each census block after refinement by the protected area boundaries. We included forest and grass/shrub land cover classes as wildland vegetation and excluded open water, urban, barren, wetlands, and ice/snow.

For each decade, we mapped the WUI separately, by combining 1990 Census data with 1992/93 data from the 1992/93–2001 land cover change product, and 2000 and 2010 Census data with 2001 and 2011 data from the 2001–2011 land cover change product. We first identified all intermix WUI areas based on the housing and vegetation thresholds. We then identified contiguous vegetation areas that were at least 5 km^2 in size and had >75% wildland vegetation, selecting areas within 2.4 km that were above the housing threshold (but below the 50% vegetation threshold), and labeling these as interface WUI. When census blocks were only partly within this distance, we split them.

The NLCD change products are not fully consistent, in that the 2001 land cover in the 1992/93–2001 change product differs from the 2001 land cover in the 2001–2011 change product. Thus, we conducted a sensitivity analysis and mapped the 2001 WUI twice, based on the two representations, and then compared the resulting WUI maps. The differences between the two WUI maps were very minor.

To calculate the number of homes within fire perimeters over time, we analyzed all fire perimeters of fires that burned between 1990 and 2015 according to the Monitoring Trends in Burn Severity (MTBS) dataset, which includes all fires >404 ha (1,000 ac) in the West and 202 ha (500 ac) in the East. We then assessed which census blocks were at least partially within these fire perimeters and calculated an area-weighted estimate of the number of housing units within the fire perimeters in 1990 (177,000), 2000 (210,000), and 2010 (286,000). We note that this is a conservative estimate of the number of houses affected by wildfires because the MTBS dataset does not include small fires.

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ENVIRONMENTAL HEALTH

RESEARCH **Open Access**

Cardio-respiratory outcomes associated with exposure to wildfire smoke are modified by measures of community health

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Abstract

Background: Characterizing factors which determine susceptibility to air pollution is an important step in understanding the distribution of risk in a population and is critical for setting appropriate policies. We evaluate general and specific measures of community health as modifiers of risk for asthma and congestive heart failure following an episode of acute exposure to wildfire smoke.

Methods: A population-based study of emergency department visits and daily concentrations of fine particulate matter during a wildfire in North Carolina was performed. Determinants of community health defined by County Health Rankings were evaluated as modifiers of the relative risk. A total of 40 mostly rural counties were included in the study. These rankings measure factors influencing health: health behaviors, access and quality of clinical care, social and economic factors, and physical environment, as well as, the outcomes of health: premature mortality and morbidity. Pollutant concentrations were obtained from a mathematically modeled smoke forecasting system. Estimates of relative risk for emergency department visits were based on Poisson mixed effects regression models applied to daily visit counts.

Results: For asthma, the strongest association was observed at lag day 0 with excess relative risk of 66%(28,117). For congestive heart failure the excess relative risk was 42%(5,93). The largest difference in risk was observed after stratifying on the basis of Socio-Economic Factors. Difference in risk between bottom and top ranked counties by Socio-Economic Factors was 85% and 124% for asthma and congestive heart failure respectively.

Conclusions: The results indicate that Socio-Economic Factors should be considered as modifying risk factors in air pollution studies and be evaluated in the assessment of air pollution impacts.

Keywords: Disparities and susceptibility, Air pollution, Climate change, Asthma, Congestive heart failure, Wildfires

Background

Numerous studies have shown associations between air quality and cardio-respiratory morbidity and mortality. Particulate matter, particularly fine fraction ($PM_{2.5}$), can aggravate asthma and has been linked to irregular heartbeats, heart attacks, and premature death. However, it is clear that not all communities are affected equally. In particular, communities with lower socio-economic status (SES) typically measured by income, education, and racial composition, have consistently been shown to be at increased risk from air pollutants [1-4] but other health factors associated with low SES such as limited access to clinical care or an unhealthy diet may also play an important role in determining a community's health outcome to poor air quality [5-8]. Characterizing the relative importance of these health factors is an important step to understanding differences in community level risk and is critical to setting appropriate policy.

The most common difficulty encountered in evaluating community risk to air pollutants is that many health factors associated with poor health outcomes occur in

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communities where exposure to air pollutants is high. Several studies have shown that compared with those of higher SES, individuals in communities with low SES are more likely to be exposed to poorer air quality in ambient, residential and occupational environments [1,2]. Community risk studies are further complicated by the need to identify reliable health metrics that can be tracked consistently across communities [9]. Here, we sought to overcome these two obstacles and characterize community health factors indicative of acute health outcome risk by taking advantage of a natural phenomenon. We evaluated health responses following brief but acute wildfire smoke exposure in a region with low background pollution and utilized County Health Rankings (CHR) [10], based on a well established model of population health that characterize factors which determine community health. Concentrations of fine particulate matter ($PM_{2.5}$) from smoke forecasting models averaged to the county are taken as the exposure matrix.

In 2008, burning deposits of peat during a wildfire in the Pocosin Lakes National Wildlife refuge in North Carolina produced smoke and haze intermittently for a number of weeks. Previously, we evaluated health effects that occurred during a three day episode in which the smoke plume moved inland and dispersed hazardous concentrations of air pollutants over the eastern and central part of the state [11]. In contrast to the current analysis the episode of exposure was determined using satellite measured aerosol optical density rather than $PM_{2.5}$ concentrations. We found significant increases in emergency department (ED) visits for congestive heart failure (CHF), asthma, chronic obstructive pulmonary disease, pneumonia, and acute bronchitis in those counties which were most impacted by the wildfire. We hypothesized that the strong associations observed in the analysis may have been observed, in part, because the affected population was on average economically disadvantaged, rural, and with high prevalence of hypertension, diabetes, obesity, high blood pressure and other health conditions in comparison to the remainder of the state.

The use of 2010 County Health Rankings permits us to examine the modifying effect of health factors on ED visits for CHF and asthma at the community level. These rankings measure: health behaviors such as tobacco use, diet and exercise; access and quality of clinical care; social and economic factors such as education and income; and the physical environment. In addition, they provide a measure of the general health of the community by measuring two types of health outcomes (mortality, morbidity) at the county level. We focus on two clinical outcomes, CHF and asthma, that have distinct pathology but that have both been associated with susceptibility to the health effects of air pollution exposures [7,12,13]. We examine these indicators as modifiers of risk of adverse health outcomes following smoke exposure and show that the most important are socio-economic factors and measures of the overall health of counties.

Methods

Emergency department visits

Daily counts of ED visits were obtained from the NC Disease Event Tracking and Epidemiologic Collection Tool [14], a statewide, public health surveillance system. NCDETECT records daily ED visits from 111 of 114 civilian NC EDs with county of residence, gender, age, and discharge ICD-9-CM codes. In the study presented here we considered visits for two clinical outcomes: for asthma in patients over 18 years old (ICD-9-CM code 493); and for CHF patients over 44 years old (ICD-9-CM code 428). The study period was defined between the onset of the wildfire by lightening (June 1, 2008) and July 14th when the first rainfall, increased humidity, and controlled flooding contained the fire. During this period, average daily temperatures ranged from 69 to 86° F and no heat events were observed. More details are reported in [11]. The Human Subjects Institutional Review Board of the University of North Carolina at Chapel Hill, East Carolina University, and the Environmental Protection Agency approved the study.

Exposure estimates

Concentrations of fine particulate matter dispersed from the Pocosin Lakes National Wildlife Refuge wildfire were obtained from the National Oceanic and Atmospheric Administration Smoke Forecasting System [15]. These estimates are based on smoke dispersion simulations from the Hybrid Single Particle Lagrangian Integrated Trajectory Model (HYSPLIT). The HYSPLIT model relies on satellite information of the wildfire location, U.S. Forest Service estimates for wildfire smoke emissions, and meteorological inputs from the North American Mesoscale mode. These are used as inputs to resolve vertical column integrated average concentrations hourly, at 0.15° latitude and longitude grid (~13.5 km). The estimated concentrations for the lowest 100 m surface layer were used and averaged over a 24 h period starting with midnight EST. We were unable to obtain a valid HYSPLIT simulation for June 4th GMT, the first day when the fire became an open flame wildfire, underestimating concentrations on June 4th and the night of June 3rd. Daily averages at the county level were subsequently calculated by averaging the 24 h period over the county boundaries using Monte Carlo approximation. Daily concentrations were obtained for the duration of the study period June 1st – July 14th 2008.

Effect modifiers

We used the 2010 County Health Rankings for North Carolina to characterize community health factors that could potentially influence health outcomes [10]. These were developed by the Robert Wood Johnson Foundation and the University of Wisconsin Population Health Institute. CHR groups determinants of community health into four types of Health Factors: Health Behaviors, factors measuring access and quality to Clinical Care, Socio-Economic Factors, and the Physical Environment. In addition to these factors, two types of health outcomes (mortality and morbidity) are used. These measure how long people live (mortality) and how healthy people feel while alive (morbidity) and are general indicators of community health. Health Factors and Health Outcomes thus measure two distinct aspects, determinants vs outcomes, of county health. The County Health Rankings use data from variety of national data sources including Behavioral Risk Factor Surveillance System survey data (BRFSS) of Centers for Disease Control and Prevention, American Community Survey, as well as Dartmouth Atlas of Healthcare.

Health Factors, Outcomes, and individual measures along with their relative weights are listed in Table 1. Among the counties of eastern North Carolina, Mortality and Morbidity Outcome Rankings and Socioeconomic Factor rankings are strongly inter-correlated and mildly correlated with Health Behavior Factors (Additional file 1). The remaining factors, Clinical Care and Physical Environment Factors, are only weakly correlated among themselves and with all other factors. We classified 40 counties into “top” and “bottom” ranked groups relative to the median rank of each outcome and factor. Top ranking by all measures is a more desired outcome, indicating communities with better health ranking.

Statistical approach

The goal of the analysis was to consider the modifying effect of community level determinants of health on the risk for CHF and asthma visits relative to the concentrations of $PM_{2.5}$. We applied a generalized linear mixed effects model with county specific intercept for Poisson count data to daily counts of ED visits (R version 2.11.1, lme4 package). Among the predictors, in the analysis we also included an indicator of daily concentration of $PM_{2.5}$ above the common detection limit (0.1 $\mu g/m^3$) to control for 0 inflated measurements arising from county-days without smoke. Log-transformed county population size estimates were used as the offset term in the analysis. A separate analysis was performed for two clinical outcomes by individual CHR outcome and factor. Relative risk of ED visits was examined with respect to the exposure concentrations on the day of the visit (lag 0), a day prior to the visit (lag 1), and the average of the two (average over lags 0 and 1) and compared with AIC/BIC criterions. In the case of asthma, exposure on the day of the visit was chosen as the best fitting model while in the case of CHF, the day prior to the visit was the main exposure variable. Results for health outcomes are summarized by excess relative risk or percent change ((RR-1)*100%) per 100 $\mu g/m^3$ increase in daily concentration of $PM_{2.5}$.

Table 1 Health Ranking Weights for the 2010 County Health Rankings (source www.countyhealthrankings.org accessed July 2010)

	Cumulative Weight	Measure	Weight
Health Outcomes			
Mortality	50%	Years of potential life lost before age 75	50%
Morbidity	50%	Quality of life	50%
Health Factors			
Health Behavior	30%	Tobacco use	10%
		Diet and exercise	10%
		Alcohol us	5%
		Unsafe sex	5%
Clinical Care	20%	Access to care	10%
		Quality of care	10%
Socioeconomic Factors	40%	Education	10%
		Employment	10%
		Income	10%
		Family and social support	5%
		Community safety	5%
Physical Environment	10%	Environmental quality	5%
		Built environment	5%

Results

Counties experienced varying concentrations of smoke and length of time in the plume during the study period (Figure 1). Maximum daily smoke related $PM_{2.5}$ concentration ranged from 4 to 129 $\mu g/m^3$ (Figure 2). On average, during the study period, counties had 18 days of daily average concentrations above the detectable level and 3 days with average concentration higher than 20 $\mu g/m^3$. Average daily concentrations and average concentrations over the study period were comparable between top and bottom grouped counties for most rankings. The exception was found for Mortality Outcome and the Clinical Care Factor rankings. Worse ranked counties by Mortality had significantly lower particle concentrations than their better ranked counterparts. Opposite was true for Clinical Care Factor, where

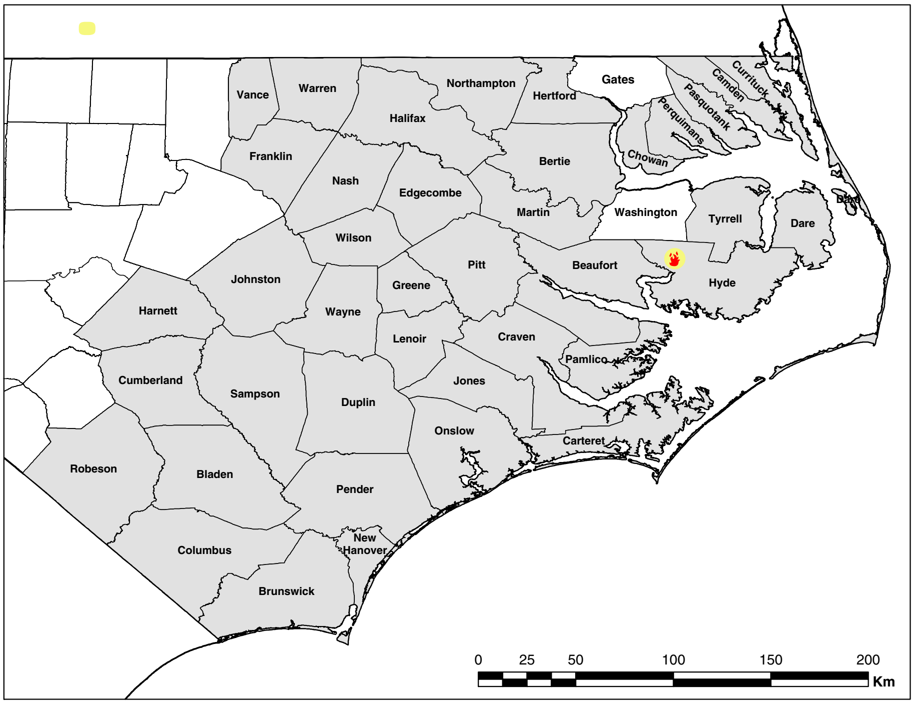

Figure 1 An a real map of counties affected by the smoke. Residents of two eastern counties, Washington and Gates, were excluded from the study; ED in Washington County did not participate in the surveillance program and Gates County was impacted by another fire.

worse ranked counties had significantly higher concentration of particles.

For asthma, the strongest association was observed on the day of the exposure (lag day 0) with 66 (28, 117)% increase in the rate of visits (per 100 μg/m3) while strongest association for CHF was observed with the day after the exposure (lag day 1) with 42 (5, 93)% increase in the rate of visits. The results for asthma are consistent with associations previously reported in the literature. The most common associations between exacerbations

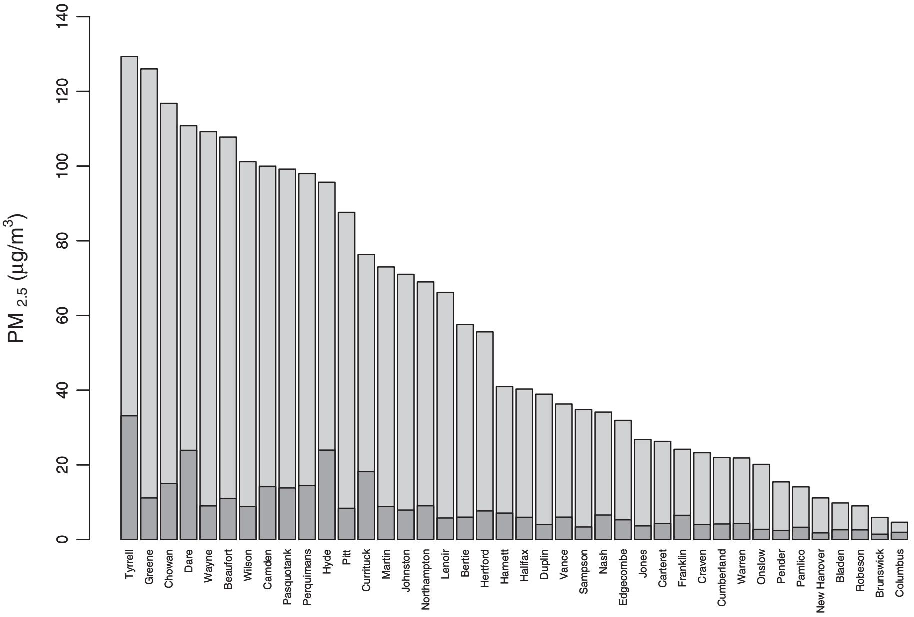

Figure 2 Distribution of maximum daily concentrations (grey) and mean concentrations over the exposed (concentration > 1μg/m^3) days.

of asthma and wildfire smoke have been reported at lag days 0 and 1 and the average of the two [16-18]. Studies of wildfire smoke report more mixed associations with cardio-vascular effects. However, urban air pollution studies consistently show effects at lag day 0 and 1 following exposure. The lag structure in respiratory and particularly, cardiovascular outcomes, is likely determined not only by the time course of the physiological and biological health effect but cultural, social and environmental conditions that determine one's use of the health care system.

Relative Risk (RR) in asthma, associated with the day of exposure (lag 0), was highly elevated or statistically significant in 'top' and 'bottom' ranked groups of counties across all factors and outcomes (Figure 3A). The largest difference however, between bottom and top ranked counties among the individual factors and outcomes was observed for Socio-Economic Factors and Mortality Outcomes. Bottom ranked counties had 85% and 67% percent points higher risk than top ranked counties for these two measures respectively. Stratification by the aggregate measures, Health Factors and Health Outcomes, similarly showed sizeable differences in risk of 76% and 45% respectively. For all other measures, RR was comparable in magnitude between counties when similarly dichotomized.

We observed significantly increased risk in the counties ranked at the bottom by Socio-Economic Factors, Physical Environment Factors and both outcome measures, one day following the exposures (lag 1) (Figure 3B). By contrast, no changes were observed for the top ranked counties at this time. Difference in relative risk between top and bottom ranked counties by these two measures were 65% and 51% respectively. Stratification by both aggregate measures, Health Factors and Health Outcomes, similarly showed sizeable differences in risk of 68% and 92% respectively. Additionally, differences between top and bottom grouped counties were statistically significant when counties were stratified by Mortality and by Health Outcomes. No changes in RR were observed for either group of county as defined by Health Behaviors and Clinical Care Factors. We did not observe any changes in RR at lag day 0 for congestive heart failure (Figure 4A).

However, associated with the day following the exposure (lag day 1), we observed significantly increased RR in bottom ranked counties by Socioeconomic Factors and Physical Environment, both outcome measures, as well as combined Health Factors and Health Outcomes (Figure 4B). In comparison, no changes in RR were observed for top ranked counties. Additionally, a statistically significant modifying effect was observed for counties grouped by Socio-Economic Factors, Health Behavior Factors and combined Health Factors.

The largest difference in risk between bottom and top ranked counties was again observed for Socio-Economic Factors with a difference of 124%. Mortality and Morbidity produced differences of 59% and 61% respectively. An opposite pattern was found for Health Behavior Factors where top ranked counties showed statistically significant risks while bottom ranked counties had no change.

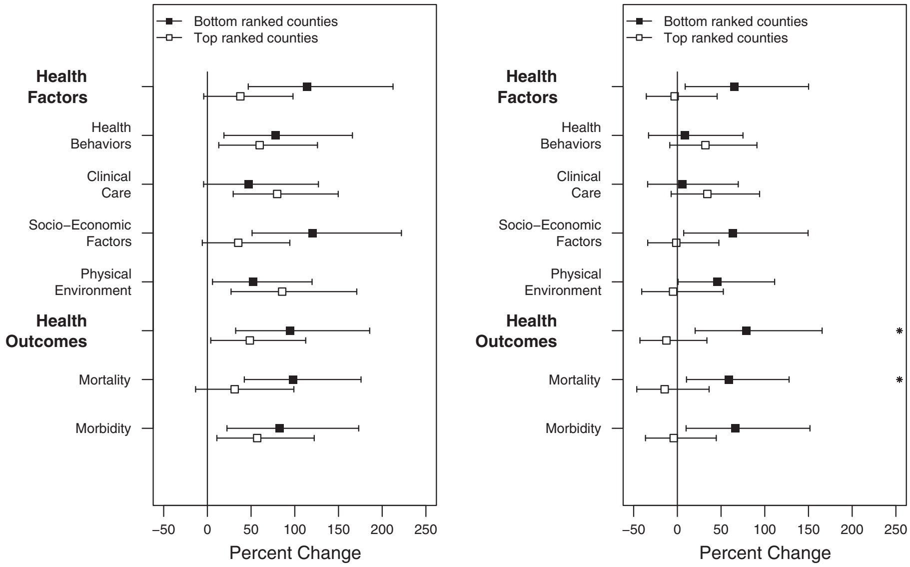

Figure 3 Excess relative risk of emergency department visits for Asthma a) on the day of the exposure (at lag 0) and b) on the day following the exposure (lag 1). Stars denote statistically significant difference in risk between two groups of counties. Estimates are reported per 100 μg/m^3 of PM$_{2.5.}$

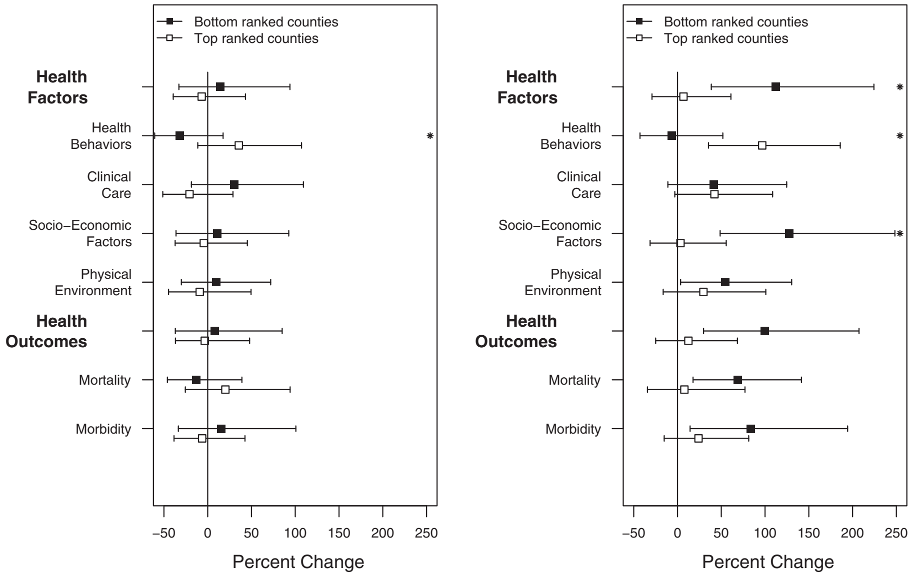

Figure 4 Excess relative risk of emergency department visits for congestive heart failure a) on the day of the exposure (at lag 0), b) on the day following the exposure (lag1). Stars denote statistically significant difference in risk between two groups of counties. Estimates are reported per 100 μg/m^3 of PM$_{2.5.}$

Among the individual measures of Socio-Economic Factor, 'Employment', 'Family and Social Support', and 'Community Safety' showed consistent differences between top and bottom ranked counties for both asthma and CHF. The most pronounced difference in RR for asthma was observed for 'Poverty' measured by children below poverty where bottom ranked counties had 2 times higher relative risk than top ranked counties (2.68 vs. 1.38) at lag 0, and 53% higher at lag 1. In the case of CHF, the largest differences were observed for 'income inequality' where 223% higher risk was observed in bottom ranked counties.

Discussion

The results presented here support the hypothesis that general and specific determinants of community health may be used as indicators of susceptibility to adverse health effects following environmental exposures. Numerous studies have shown evidence of association between particulate matter and cardio-respiratory morbidity and many have addressed the biological and genetic factors that influence the association. However, relevant social factors are less well understood. With a nearly complete record of ED visits and detailed daily maps of smoke related PM$_{2.5}$ concentrations, we examined the impact of health factors on the risk of CHF and asthma in relation to the acute emissions of this pollutant. We demonstrate that among the different factors assessed, the strongest difference in relative risk for ED visits in both clinical outcomes was observed when counties were stratified on the basis of Socio-Economic Factors followed by indicators of community health Mortality and Morbidity Outcomes.

The category of Socio-Economic Factors measures 'Employment', 'Community Safety', 'Income', 'Education', and 'Family and Social Support'. Of these, 'Income' was the best indicator of risk. Although different strategies have been used to quantify income and financial resources of the community, CHR uses poverty and income inequality as basic indicators of the community's ability to meet the need for food, clothing, and shelter [10]. For asthma, poverty was the most important predictor while for CHF it was income inequality. Why these measures are better indicators than other factors more directly associated with clinical outcomes such as access to care or diet is unclear. There is a considerable literature on the detrimental health effects of poverty. A recent study [19], showed that poverty imposed the greatest burden of disease in the United States and is at least as important as smoking. Psychological and physical stress, highly present at conditions of severe poverty [20], and perceived inequalities by individuals have also been shown as important determinants of population health [21] explaining health inequalities at all social levels [22]. Stress impacts allostatic load in individuals, thus increasing the susceptibility to diseases. Populations with low SES share larger health burden as they have higher prevalence of chronic and under-treated medical conditions leading to an increased likelihood of adverse health effect in response to the exposures. Long-term exposure to psychological and social stress experienced in communities of low SES can also modify endocrine function and induce epigenetic changes transferable to the children [23-25]. In addition to biological mechanisms, poverty impacts many of the other factors measured by the CHR through the ability to pay for medical care, access to healthy foods, community safety and social support; all factors we show are associated with risk from $PM_{2.5}$ exposure. The role of income inequality in defining health disparities has been long hypothesized and discussed area of research in social epidemiology. A traditional criticism has been the inability to separate individual and aggregate effects of income inequality in the society. However, more recent studies using multilevel data and multilevel statistical techniques suggest that evidence in support of association particularly at the aggregate levels such as counties and states [26].

The results for other Health Factors and specific measures were more complex. In particular, for asthma we observed an unexpected association between access to health care and ED visits on the day of the exposure. Those counties that ranked well in this category had higher rate of ED visits for asthma than the poorly ranked ones. Similarly, on the day following the exposure counties with higher primary care provider rate had increased risk of ED visits for CHF while poorly ranked counties did not. Access to health care is measured by the percentage of adults with no health insurance and the population per primary care provider in CHR. A possible explanation is that in the affected region, counties with a lower percentage of uninsured adults appear to have lower average income level and reflect communities comprised of many of the working poor. More specifically, using data from Census 2000 we have estimated a 1% (p value = 0.0063) increase in percent of uninsured adults for every $10 K increase in median household income at the county level. This is likely due to the large number of adults under the age of 65 that qualify for federal and state assistance and subsidized health plans in this region. While access and the quality of care may be important determinant of susceptibility at the individual level [8], at the community level we did not observe it to be a determinant of susceptibility.

A limitation of present study is in the ecological nature of the data on both exposures and effect modifiers, which are known only at the county level. For exposures, we have assumed that exposure to ambient air pollution are ubiquitous among the general population, that the mean personal exposures in a county are proportional to the county-wide concentration, and that personal exposures will be subject mainly to Berkson errors. Our analysis of HYSPLIT predictions against the satellite and monitoring data suggests that mis-specification of the magnitude of exposure as more likely source of error then mis-classification of day to day exposure status. For effect modifiers, the relationships at the county level examined in our study may not truly reflect relationships at the individual level due to an ecological bias. Our analysis shows that counties with higher poverty have stronger health associations with ambient smoke concentrations, suggestive that poor individuals may be more sensitive or vulnerable. However, an alternative explanation might be that all individuals in an impoverished county are equally sensitive regardless of individual level socioeconomic status, or even that wealthy individuals in impoverished counties are especially sensitive. Without individual level socioeconomic data on both cases and the referent population, one cannot distinguish between sensitivity or vulnerability conferred by individual or ecologic characteristics.

Environmental exposures often fall disproportionately on economically disadvantaged populations and minorities [3]. However, recent air pollution studies indicate that even after accounting for differences in exposure, the health risks are not equally distributed among populations. For example, urban studies where exposure to traffic pollution is positively associated with socioeconomic disparities [8,27] and those where negative association is observed [6], both report consistent results indicating enhanced health burden among socioeconomically disadvantaged communities. The results from the presented study suggest that, following an acute exposure, the same results may be transferable to the populations that experience generally low levels of background pollution and are unlikely to be due to levels or longevity of the exposure alone. This suggests that SES increase the susceptibility to health outcomes independently of the vulnerability to exposures.

Conclusions

In the work presented here we evaluate general and specific measures of community health as indicators of susceptibility to adverse events following air pollution exposures. The results suggest that, among various measures of health, Socio-Economic Factors played the most important role in defining susceptibility at the community level. These factors are not commonly considered as modifiers of risk in pollution studies because they can be confounded with number of other susceptibility enhancing factors. For example, SES is typically confounded with short and long term exposures as well as the prevalence of existing medical conditions. Here, we use a wildfire episode during which smoke blanketed the region irrespective of the community health characteristics to evaluate differences in risk. The results, suggesting that SES characteristics should be considered as risk modifiers to the impacts of air pollution exposures, are important steps to understanding differences in community risk and for setting appropriate policies.

Additional file

Additional file 1: Table S1. Spearman Rank Correlation coefficient between Community Health Ranking indices over 40 counties. Table S2. County Ranking Summaries for counties of eastern North Carolina and the remaining counties in the state.

Abbreviations

$PM_{2.5}$, Particulate matter with and average aerodynamic diameter of less then 10 μm, fine particulate matter; CHF, Congestive heart failure; RR, Relative risk; SEF, Socio-economic factors; SES, Socio-economic status; CHR, County health ranking; ED, Emergency department; NC, North Carolina; NCDETECT, North Carolina disease event tracking and epidemiologic collection tool; ICD-9-CM, International classification of diseases, ninth revision, clinical modification; HYSPLIT, Hybrid single particle Lagrangian integrated trajectory model.

Competing interests

Authors have no competing interests to declare.

Authors' contributions

AGR has contributed substantially to the concept, design, analysis, interpretation of results and writing of the manuscript, WEC has contributed substantially to the concept and interpretation of results, VJK has contributed substantially to data collection and writing of the manuscript, SLS has contributed substantially to data collection and writing of the manuscript, LMN has contributed substantially to the concept, interpretation of results and writing of the manuscript, RBD has contributed substantially to the concept, interpretation of results and writing of the manuscript, DD-S has contributed substantially to the concept, interpretation of results and writing of the manuscript. All authors read and approved the final manuscript.

Disclaimer

The research described in this article has been reviewed by the National Health and Environmental Effects Research Laboratory, U.S. EPA, and approved for publication. The contents of this article should not be construed to represent Agency policy nor does mention of trade names or commercial products constitute endorsement or recommendation for use. The NC DETECT Data Oversight Committee does not take responsibility for the scientific validity or accuracy of methodology, results, statistical analyses, or conclusions presented.

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Critical Review of Health Impacts of Wildfire Smoke Exposure

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Background: Wildfire activity is predicted to increase in many parts of the world due to changes in temperature and precipitation patterns from global climate change. Wildfire smoke contains numerous hazardous air pollutants and many studies have documented population health effects from this exposure.

Objectives: We aimed to assess the evidence of health effects from exposure to wildfire smoke and to identify susceptible populations.

Methods: We reviewed the scientific literature for studies of wildfire smoke exposure on mortality and on respiratory, cardiovascular, mental, and perinatal health. Within those reviewed papers deemed to have minimal risk of bias, we assessed the coherence and consistency of findings.

Discussion: Consistent evidence documents associations between wildfire smoke exposure and general respiratory health effects, specifically exacerbations of asthma and chronic obstructive pulmonary disease. Growing evidence suggests associations with increased risk of respiratory infections and all-cause mortality. Evidence for cardiovascular effects is mixed, but a few recent studies have reported associations for specific cardiovascular end points. Insufficient research exists to identify specific population subgroups that are more susceptible to wildfire smoke exposure.

Conclusions: Consistent evidence from a large number of studies indicates that wildfire smoke exposure is associated with respiratory morbidity with growing evidence supporting an association with all-cause mortality. More research is needed to clarify which causes of mortality may be associated with wildfire smoke, whether cardiovascular outcomes are associated with wildfire smoke, and if certain populations are more susceptible.

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Introduction

Wildfires are a global occurrence. Changes in temperature and precipitation patterns from climate change are increasing wildfire prevalence and severity (Westerling et al. 2006; Settele et al. 2014) resulting in longer fire seasons (Flannigan et al. 2013; Westerling et al. 2006) and larger geographic area burned (Gillett et al. 2004). Wildfire smoke contains many air pollutants of concern for public health, such as carbon monoxide (CO), nitrogen dioxide, ozone, particulate matter (PM), polycyclic aromatic hydrocarbons (PAHs), and volatile organic compounds (Naeher et al. 2007). Current estimated annual global premature mortality attributed to wildfire smoke is 339,000 (interquartile range of sensitivity analyses: 260,000–600,000) (Johnston et al. 2012), but the overall impact on public health in terms of respiratory, cardiovascular, and other morbidity effects is unknown. A better synthesis of current knowledge on the health effects of wildfire smoke is needed to guide public health responses.

Wildfire smoke epidemiology is an active area of research (Henderson and Johnston 2012) with new methods uncovering associations that were previously undetectable. Studies of health outcomes associated with wildfire smoke exposure tend to be retrospective and researchers have to rely on administrative health outcome data such as mortality or hospitalization records. Achieving adequate statistical power has been challenging because such severe outcomes are less common, fires tend to be episodic and short in duration, and exposed populations from individual events are often small. Many recent studies have increased statistical power by investigating very high exposure events that last for longer periods, large populations over many years in regions with frequent fires, more common health outcomes such as medication dispensations, or a combination of these methods.

Previous reviews of wildfire health impacts have either not included the full range of health end points associated with community exposure to wildfire smoke (Dennekamp and Abramson 2011; Henderson and Johnston 2012) or have summarized the literature without critical analysis of specific studies (Finlay et al. 2011; Liu et al. 2015; Youssouf et al. 2014). Our review follows a modified version of the systematic review methodology outlined in Woodruff and Sutton (2014) to analyze studies critically and to only evaluate the strongest evidence.

Methods

We searched PubMed, Web of Science, and PsychInfo to identify scientific papers related to wildfire smoke exposure and relevant health outcomes. We conceptualized wildfires as those within the definition of landscape fires defined in Johnston et al. (2012). Our search strategy (Figure 1) yielded 778 journal articles in PubMed and 1,248 journal articles in Web of Science in November 2013. We then selected studies that potentially focused on human health effects related to wildfire smoke based on title and yielded 248 journal articles from PubMed and 217 from Web of Science. After discarding duplicates, 350 articles remained. PsychInfo did not yield any new peer-reviewed journal articles.

After reading abstracts, we removed articles if they assessed only exposure and not associated health effects, reported health surveillance outcomes without analysis of associations with exposure, did not analyze primary or secondary health data, did not adequately describe the exposure assessment or it was not clearly related to wildfire smoke, or were not published fully in English. This

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yielded 103 studies that we reviewed. We continually searched for new papers and subsequently added 12 more by August 2015. These papers included human experimental studies of woodsmoke, studies of effects on wildland firefighters, and studies whose outcomes were self-reported respiratory symptoms associated with wildfire smoke, but these are not included in this paper.

From the remaining epidemiological studies (*N* = 53), we extracted information and made an expert judgment on the risk of bias for each study based on their sample size, exposure assessment methods, control for potential confounding factors, and use of objective outcome measures (see Table S1). We deemed studies to have a lower risk of bias if there were no concerns in any of these categories, moderate risk if there were minor concerns in one or more categories, and higher risk if either there were multiple concerns about bias or if one concern was sufficiently large based on our collective judgment.

All evaluation of results from these studies is based on the authors' interpretation of the reported findings in each paper. In this review "significant" means a 95% confidence interval (CI) that does not include the null, "suggestive" means a 95% CI that does include the null but would not with a slightly relaxed criterion such as a 90% CI, and "no association" means that the 95% CI includes the null with no indication of a relationship. We assumed that exposure to smoke from all types of landscape fires were comparable. We use the term wildfire to refer to all types of landscape fires.

Assessing human exposure to wildfire smoke is challenging for many reasons. Wildfires tend to occur in rural areas in which air pollution monitoring networks might be absent or less comprehensive than in cities. The studies we reviewed used various exposure assignment methods such as self-report, assignment to the nearest regulatory air pollution monitor, comparison of fire periods to non-fire periods, and use of satellite data or air quality modeling output. Heterogeneity of exposure assessment methods across studies (Table 1; see also Table S1) made a quantitative meta-analysis of effect estimates inappropriate. While publication bias could be present in this literature, we could not assess its extent due to the scarcity of studies for each health outcome.

Results

Our review covers the following health outcomes: mortality, respiratory morbidity, cardiovascular morbidity, birth outcomes, and mental health. We further discuss the evidence from toxicological studies and for susceptible population subgroups. Table S1 provides more details on reviewed studies.

After review of 53 epidemiological papers, we evaluated 27 as having lower potential for bias, 17 as moderate potential for bias and 10 as higher potential for bias. Of the 10 deemed to have higher risk of bias, 4 did not adequately adjust for important covariates (Azevedo et al. 2011; Cooper et al. 1994; Prass et al. 2012; Resnick et al. 2015), 2 were likely underpowered due to small sample size (Cooper et al. 1994; Vedal and Dutton 2006), 3 used retrospective self-report for exposure assessment with high potential for bias (Ho et al. 2014; McDermott et al. 2005; Marshall et al. 2007), and the exposure assessment in 2 other studies was not clearly related to smoke from wildfires (Analitis et al. 2012, Caamano-Isorna et al. 2011). The remaining 43 studies deemed to have low to moderate risk of bias are discussed below. More detail

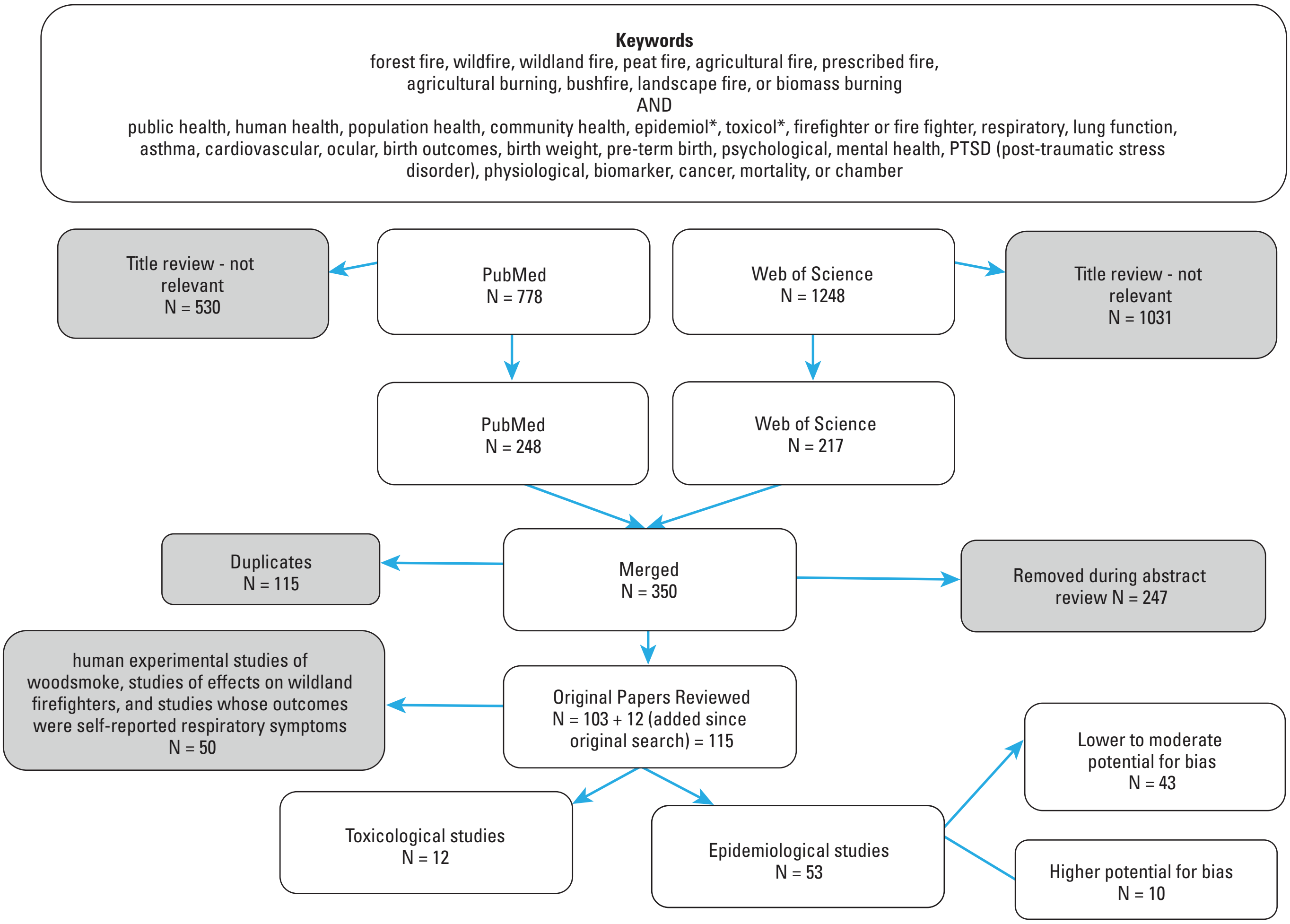

Figure 1. Review of studies flow chart.

on the findings from each study is provided in Table S2.

Mortality

Growing evidence from the more recent, adequately statistically powered studies demonstrates associations between wildfire smoke exposure and all-cause mortality, but more studies are needed to determine whether specific causes of mortality are most affected.

A study of the 1997 southeast Asian wildfire found an increase in mortality in Malaysia associated with a measure of visibility and measured PM_{10} ($PM \leq 10$ μm in aerodynamic diameter) both linearly and with various discrete levels of PM_{10} (Sastry 2002). A study of the 2010 heat wave and wildfires in Moscow reported findings of an interaction between high temperatures and high PM_{10} on deaths and that smoke exposure was responsible for about 29% of the 10,859 excess deaths during the 44-day heat wave (Shaposhnikov et al. 2014). A cross-sectional analysis of cardiovascular mortality among people older than 65 years in the Brazilian Amazon, where the predominant source of air pollution is from wildfires, found a significant association between the percentage of hours of $PM_{2.5}$ over 25 $\mu g/m^3$ and cardiovascular mortality (Nunes et al. 2013).

The most recent studies of wildfire smoke and mortality take advantage of long time series data and provide growing evidence of significant increases in mortality. A study of 13.5 years of data including 48 days affected by wildfire smoke in Sydney, Australia, demonstrated a significant increase in mortality associated with smoke-affected days (Johnston et al. 2011). An earlier study of mortality in Sydney, using 8 years of data, found a suggestive increase in mortality associated with wildfire-related PM_{10} (Morgan et al. 2010). A meta-analysis of data from 2003 to 2010 in 10 cities in southern Europe found increases in cardiovascular mortality associated with PM_{10} that were stronger on smoke-affected days than on non-affected days, but smoke was not significantly associated with respiratory mortality (Faustini et al. 2015). In Madrid, mortality, but not specifically respiratory or cardiovascular mortality, was associated with PM_{10} on days with advection events associated with biomass burning (Linares et al. 2015). Further multi-year studies in regions regularly affected by wildfire smoke could help clarify if specific causes of mortality are associated with wildfire smoke exposure.

Respiratory Morbidity

Epidemiological studies have demonstrated significant associations between wildfire smoke exposure and declines in lung function among non-asthmatic children (Jacobson et al. 2012, 2014), and increases in physician

Table 1. Findings from epidemiological research studies (*N* = 43) ordered by health outcome.

Outcome	Article	Exposure assessment type	Direction of association
Mortality			
All	Sastry 2002	Monitored PM	↑↑
	Morgan et al. 2010	Monitored PM	↑↑
	Johnston et al. 2011	Smoky versus non-smoky days	↑↑
	Faustini et al. 2015	Smoky versus non-smoky days	↑↑
	Linares et al. 2015	Monitored PM	↑↑
	Shaposhnikov et al. 2014	Monitored PM	↑↑
Respiratory	Johnston et al. 2011	Smoky versus non-smoky days	↔
	Morgan et al. 2010	Monitored PM	↔
	Faustini et al. 2015	Smoky versus non-smoky days	↔
	Linares et al. 2015	Monitored PM	↔
Cardiovascular	Nunes et al. 2013	Modeled PM and satellite data	↑↑
	Faustini et al. 2015	Smoky versus non-smoky days	↑↑
	Johnston et al. 2011	Smoky versus non-smoky days	↑
	Morgan et al. 2010	Monitored PM	↔
	Linares et al. 2015	Monitored PM	↔
Respiratory morbidity			
Lung function in people without asthma or bronchial hyperreactivity	Jacobson et al. 2012	Monitored PM	↓↓
	Jacobson et al. 2014	Monitored PM	↓↓
	Jalaludin et al. 2000	Monitored PM	↓↓
Physician visits	Lee et al. 2009	Monitored PM	↑↑
	Henderson et al. 2011	Monitored PM	↑↑
		Modeled PM	↑
		Binary satellite indicator of smoke	↑
	Moore et al. 2006	Temporal comparison	↑↑
	Mott et al. 2002	Temporal comparison	↑↑
	Lee et al. 2009	Monitored PM	↑↑
ED visits	Rappold et al. 2011	Temporal and spatial comparisons	↑↑
	Tham et al. 2009	Monitored PM	↑↑
	Thelen et al. 2013	Modeled PM	↑↑
	Johnston et al. 2014	Smoky versus non-smoky days	↑↑
Hospitalizations	Morgan et al. 2010	Monitored PM	↑↑
	Henderson et al. 2011	Monitored PM	↑↑
		Modeled PM	↑
		Binary satellite indicator of smoke	↑
	Johnston et al. 2007	Monitored PM	↑
	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↑↑
	Martin et al. 2013	Smoky versus non-smoky days	↑↑
	Chen et al. 2006	PM monitoring for categorical exposures	↑↑
	Cançado et al. 2006	PM monitoring	↑↑
	Mott et al. 2005	Temporal comparison	↑↑
	Ignotti et al. 2010	% annual hours > 80 $\mu g/m^3$	↑↑
	Tham et al. 2009	Monitored PM	↔
Asthma			
Lung function among people with asthma	Jacobson et al. 2012	Monitored PM	↔
	Jalaludin et al. 2000	Monitored PM	↔
	Vora et al. 2011	Temporal comparison	↔
	Wiwatanadate and Liwsrisakun 2011	Monitored PM	↔
Medications	Elliott et al. 2013	PM monitoring, statistical modeling, and satellite information	↑↑
	Yao et al. 2016	Modeled PM	↑↑
	Tse et al. 2015	Temporal and spatial comparisons	↑↑
	Vora et al. 2011	Temporal comparison	↑↑
	Johnston et al. 2006	Monitored PM	↑↑
	Arbex et al. 2000	Measurement of PM	↑
Physician visits	Henderson et al. 2011	Monitored PM	↑↑
		Modeled PM	↑↑
		Binary satellite indicator	↑
	Yao et al. 2014 2016	Monitored PM	↑↑
		Modeled PM	↑↑
ED visits	Johnston et al. 2002	Monitored PM	↑↑
	Rappold et al. 2011	Temporal and spatial comparisons	↑↑
	Duclos et al. 1990	Temporal comparison	↑↑
	Johnston et al. 2014	Smoky versus non-smoky days	↑↑
	Smith et al. 1996	Temporal comparison	↑
	Tse et al. 2015	Temporal and spatial comparisons	↔

Table continued

visits for respiratory problems (Henderson et al. 2011; Lee et al. 2009; Moore et al. 2006; Mott et al. 2002), respiratory emergency department (ED) visits (Johnston et al. 2014; Rappold et al. 2011; Tham et al. 2009; Thelen et al. 2013) and respiratory hospitalizations (Cançado et al. 2006; Chen et al. 2006; Delfino et al. 2009; Henderson et al. 2011; Ignotti et al. 2010; Martin et al. 2013; Morgan et al. 2010; Mott et al. 2005). Findings for specific respiratory end points are reviewed below.

Asthma. Evidence from multiple epidemiological studies demonstrates that wildfire smoke exposure contributes to exacerbations of asthma. Studies have documented increased physician visits (Henderson et al. 2011; Yao et al. 2016), ED visits (Duclos et al. 1990; Johnston et al. 2002, 2014; Rappold et al. 2011) and hospitalizations (Arbex et al. 2007; Delfino et al. 2009; Martin et al. 2013; Morgan et al. 2010; Mott et al. 2005) for asthma associated with wildfire smoke exposure. Some studies found suggestive increases in asthma ED visits (Smith et al. 1996) and asthma hospital admissions (Johnston et al. 2007); these studies may have lacked statistical power due to short time periods (Smith et al. 1996) or small affected populations (Johnston et al. 2007). Another study did not find a significant increase in ED visits or hospitalizations among a cohort of asthmatic children in the year after large wildfires in San Diego, California, compared to the year prior to those fires (Tse et al. 2015).

Four studies demonstrated no significant acute changes in lung function among people with asthma related to PM from wildfires (Jacobson et al. 2012; Jalaludin et al. 2000; Vora et al. 2011; Wiwatanadate and Liwsrisakun 2011), although significant declines in lung function were found among those without asthma (Jacobson et al. 2012) and children without bronchial hyperreactivity (Jalaludin et al. 2000). One possible explanation for these counter-intuitive findings is increased use of rescue medication in response to elevated levels of smoke among those diagnosed with asthma as was found in one (Vora et al. 2011) of two studies (Vora et al. 2011; Jacobson et al. 2012) that investigated this mechanism.

Other studies documented associations between medication usage for obstructive lung disease and wildfire smoke exposure. Both usage of reliever medication and initiation of oral steroid use were associated with wildfire smoke in a panel study of adults and children in Australia (Johnston et al. 2006). People with asthma reported elevated levels of rescue medication usage during a wildfire in Southern California (Vora et al. 2011). Dispensations of reliever medications were related to metrics of wildfire smoke exposure

Table 1. *Continued.*

Outcome	Article	Exposure assessment type	Direction of association
Hospitalizations	Morgan et al. 2010	Monitored PM	↑↑
	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↑↑
	Arbex et al. 2007	PM monitoring	↑↑
	Martin et al. 2013	Smoky versus non-smoky days	↑↑
	Johnston et al. 2007	Monitored PM	↑
	Tse et al. 2015	Temporal and spatial comparisons	↔
COPD			
Physician visits	Yao et al. 2016	Monitored PM	↑↑
		Modeled PM	↑↑
ED visits	Rappold et al. 2011	Temporal and spatial comparisons	↑↑
	Duclos et al. 1990	Temporal comparison	↑↑
	Johnston et al. 2014	Smoky versus non-smoky days	↑↑
Hospitalizations	Morgan et al. 2010	Monitored PM	↑↑
	Johnston et al. 2007	Monitored PM	↑↑
	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↑↑
	Martin et al. 2013	Smoky versus non-smoky days	↑↑
	Mott et al. 2005	Temporal comparison[a]	↑↑
Respiratory infections			
Physician visits	Yao et al. 2016	Monitored PM[b]	↑↑
		Modeled PM[b]	↔
		Monitored PM[c]	↑↑
		Modeled PM[c]	↑↑
	Henderson et al. 2011	Monitored PM[d]	↔
ED visits	Duclos et al. 1990	Temporal comparison[b]	↑↑
	Rappold et al. 2011	Temporal and spatial comparisons[b]	↑
Hospitalizations	Johnston et al. 2007	Monitored PM	↔
Pneumonia and bronchitis			
ED visits	Rappold et al. 2011	Temporal and spatial comparisons	↑↑
	Johnston et al. 2014	Smoky versus non-smoky days	↔
Hospitalizations	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↑↑
	Morgan et al. 2010	Monitored PM	↑↑
	Martin et al. 2013	Smoky versus non-smoky days	↑
	Duclos et al. 1990	Temporal comparison[e]	↑↑
Cardiovascular morbidity			
Physician visits	Henderson et al. 2011	Monitored PM	↔
		Modeled PM	↔
		Binary satellite indicator	↔
	Moore et al. 2006	Temporal comparison	↔
	Lee et al. 2009	Monitored PM	↔
	Yao et al. 2016	Monitored PM	↓↓
		Modeled PM	↔
ED visits	Rappold et al. 2011	Temporal and spatial comparisons	↔
	Johnston et al. 2014	Smoky versus non-smoky days	↔
Hospitalizations	Morgan et al. 2010	Monitored PM	↔
	Hanigan et al. 2008	PM estimated from visibility data	↔
	Henderson et al. 2011	Monitored PM	↔
		Modeled PM	↔
		Binary satellite indicator	↔
	Johnston et al. 2007	Monitored PM	↔
	Martin et al. 2013	Smoky versus non-smoky days	↔
CHF			
ED visits	Rappold et al. 2011	Temporal and spatial comparisons	↑↑
Hospitalizations	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↑
	Morgan et al. 2010	Monitored PM	↔
	Martin et al. 2013	Smoky versus non-smoky days	↔
Cardiac arrest			
Out-of-hospital	Dennekamp et al. 2015	PM monitoring	↑↑
	Haikerwal et al. 2015	Modeled PM	↑↑
ED visits	Johnston et al. 2014	Smoky versus non-smoky days	↔
Acute MI			
ED visits	Haikerwal et al. 2015	Modeled PM	↔
Hospitalizations	Haikerwal et al. 2015	Modeled PM	↑↑

Table continued

in British Columbia (Elliott et al. 2013; Yao et al. 2016). Researchers found increases in physician-dispensed short-acting beta-agonists but not physician-prescribed oral corticosteroids for children with asthma in years after two catastrophic wildfires in southern California compared to the year prior to each wildfire (Tse et al. 2015). An association between visits to hospitals for inhalation therapy and daily mass of air particle sediment collected in four nearby water containers was found during one sugarcane-burning season in Brazil (Arbex et al. 2000).

All previously mentioned studies examined exacerbations of asthma, whereas only one study investigated incident asthma related to wildfire smoke. Methodological concerns in that portion of the study suggest a high potential for bias as new diagnoses occurring after, but not during, two large wildfire episodes were included (Tse et al. 2015).

Chronic obstructive pulmonary disease (COPD). Epidemiological evidence of associations between wildfire smoke exposure and exacerbation of COPD is mounting. Elevated rates of hospitalizations (Delfino et al. 2009; Johnston et al. 2007; Martin et al. 2013; Morgan et al. 2010; Mott et al. 2005), ED visits (Duclos et al. 1990; Johnston et al. 2014; Rappold et al. 2011), and physician visits for COPD (Yao et al. 2016) have been associated with wildfire smoke exposure. Additionally, the findings of increased reliever medication dispensing during wildfire smoke exposure in British Columbia may indicate increases in COPD or asthma exacerbations (Elliott et al. 2013; Yao et al. 2016).

Respiratory infections. The evidence for associations between wildfire smoke exposure and respiratory infections is inconsistent. Duclos et al. (1990) found a higher rate of ED visits for respiratory infections during major wildfires in California compared to a reference period. Rappold et al. (2011) found a suggestive increase in ED visits for upper respiratory infections in smoke-affected counties in North Carolina during peat fires compared to a reference period and this temporal increase was not found in non-smoke-affected counties. Henderson et al. (2011) and Yao et al. (2016), however, found no association between wildfire smoke exposure and physician visits for upper respiratory infections in British Columbia. Johnston et al. (2007) reported no association between PM predominantly from wildfires and hospitalizations for respiratory infections in Australia.

The evidence does suggest an association between wildfire smoke and acute bronchitis and pneumonia, however. Although Johnston et al. (2014) did not find an association between ED visits for pneumonia and bronchitis associated with wildfire smoke in Australia, most other studies did. Yao et al. (2016) found significant increases in physician visits for lower respiratory infections associated with $PM_{2.5}$ over 10 fire seasons in British Columbia. Rappold et al. (2011) documented increased ED visits for pneumonia and acute bronchitis associated with exposure to smoke from a peat fire. Duclos et al. (1990) found higher rates of hospitalization for bronchitis during a wildfire compared to a reference period. Moreover, Martin et al. (2013) reported associations between days with high levels of bushfire smoke and hospitalizations for pneumonia and acute bronchitis in Newcastle, Australia, although this association was not found in the larger city of Sydney; the authors attribute this to lack of precision in estimates of specific respiratory outcomes. Two studies have documented similar associations between wildfire smoke and background PM with bronchitis and pneumonia (Delfino et al. 2009; Morgan et al. 2010), suggesting that effects of wildfire and urban PM on these outcomes are similar.

Cardiovascular Morbidity

Results from studies of associations between cardiovascular outcomes and wildfire smoke exposure are inconsistent. Many studies of wildfire smoke exposure have found no associations with grouped cardiovascular disease outcomes (Hanigan et al. 2008; Henderson et al. 2011; Johnston et al. 2007, 2014; Lee et al. 2009; Martin et al. 2013; Moore et al. 2006; Morgan et al. 2010; Rappold et al. 2011; Yao et al. 2016), although a few have documented evidence for specific end points. Rates of out-of-hospital cardiac arrests were associated with wildfire-related $PM_{2.5}$ in Australia (Dennekamp et al. 2015; Haikerwal et al. 2015). Hospitalizations but not ED visits for acute myocardial infarctions (MI) were associated with wildfire-related $PM_{2.5}$ during the same fires (Haikerwal

Table 1. *Continued.*

Outcome	Article	Exposure assessment type	Direction of association
IHD			
Physician visits	Lee et al. 2009	Monitored PM	↑↑
ED visits	Johnston et al. 2014	Smoky versus non-smoky days	↑
	Haikerwal et al. 2015	Modeled PM	↑
Hospitalizations	Mott et al. 2005	Temporal comparison	↑
	Haikerwal et al. 2015	Modeled PM	↑
	Morgan et al. 2010	Monitored PM	↔
	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↔
	Johnston et al. 2007	Monitored PM	↓↓ and ↑↑[f]
	Martin et al. 2013	Smoky versus non-smoky days	↔
Hypertension			
Physician visits	Henderson et al. 2011	Monitored PM	↔
Hospitalizations	Arbex et al. 2010	PM monitoring	↑↑
Cardiac dysrhythmias/arrhythmias			
ED visits	Johnston et al. 2014	Smoky versus non-smoky days	↔
Hospitalizations	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↔
	Martin et al. 2013	Smoky versus non-smoky days	↔
Cerebrovascular disease			
ED visits	Johnston et al. 2014	Smoky versus non-smoky days	↔
Hospitalizations	Delfino et al. 2009	PM monitoring, statistical modeling, and satellite information	↑
	Morgan et al. 2010	Monitored PM	↔
Angina			
Dispensations of fast-acting nitroglycerin	Yao et al. 2016	Monitored PM	↑↑
ED visits	Haikerwal et al. 2015	Modeled PM	↑
Hospitalizations	Haikerwal et al. 2015	Modeled PM	↔
Birth outcomes			
Birth weight	Holstius et al. 2012	Temporal comparison	↓↓
Proportion of cohort surviving	Jayachandran 2009	Satellite data	↓↓
Low birth weight	Cândido da Silva et al. 2014	Monitored PM	↑↑
Mental health			
Physician visits	Moore et al. 2006	Temporal comparison	↔
Hospitalizations	Duclos et al. 1990	Temporal comparison	↔

[a] Asthma and COPD combined.
[b] Upper respiratory infections.
[c] Lower respiratory infections.
[d] Upper respiratory infections and acute bronchitis combined.
[e] Bronchitis alone.
[f] Significantly elevated for indigenous population, but significantly lower risk for whole population.
↔ No association. ↑ Suggestive increase. ↑↑ Significant increase. ↓↓ Significant decrease.

et al. 2015). ED visits for congestive heart failure (CHF) were associated with wildfire smoke exposure from a peat fire in North Carolina (Rappold et al. 2011), but only a suggestive association was found for CHF hospitalizations and $PM_{2.5}$ during a wildfire in southern California (Delfino et al. 2009). Johnston et al. (2014) did not find any association between wildfire smoke and ED cardiac failure. Other studies have found no associations between wildfire smoke exposure and CHF (Martin et al. 2013; Morgan et al. 2010) or cardiac dysrhythmias (Delfino et al. 2009; Johnston et al. 2014; Martin et al. 2013). And no associations were found in the one study that investigated angina in relation to wildfire $PM_{2.5}$ (Haikerwal et al. 2015).

Study results are also mixed for ischemic heart disease (IHD). Higher counts of hospitalizations for IHD than expected based on historical data were found in Sarawak, Malaysia, during the prolonged very high PM levels of the 1997 Southeast Asian wildfires (Mott et al. 2005). ED visits for IHD were higher on smoke-affected days in Sydney, Australia (Johnston et al. 2014), but two other studies in Australia (Martin et al. 2013; Morgan et al. 2010) and one in California (Delfino et al. 2009) reported no associations for IHD hospital admissions. A study in Darwin, Australia, found increased risk of IHD hospitalizations only among the indigenous population, whereas the results suggested an inverse association among the whole population (Johnston et al. 2007). Researchers also found a positive association between PM_{10} during a wildfire and clinic visits for IHD in a Native American reservation in California (Lee et al. 2009).

Very few studies have investigated other cardiovascular outcomes, making definitive conclusions difficult. Arbex et al. (2010) found increases in hospitalizations for hypertension associated with exposure to total suspended particles over 2 years within a community seasonally exposed to smoke from burning sugarcane, but there was no clear difference in this finding between burning and non-burning periods, which implies that the relationship may not be due to the source of the particles. Henderson et al. (2011) did not find any relationship between PM_{10} during a wildfire and physician visits for hypertension. One (Delfino et al. 2009) of three (Delfino et al. 2009; Morgan et al. 2010; Johnston et al. 2014) studies to investigate cerebrovascular disease or stroke found a suggestive association with wildfire smoke exposure.

Too few studies and too many inconsistencies in findings exist to determine whether wildfire smoke exposure is associated with specific cardiovascular outcomes, despite evidence that exposure to ambient PM is associated with increased risk of cardiovascular morbidity (Brook et al. 2010).

Birth Outcomes

Corroborative evidence suggests that wildfire smoke exposure effects on birth outcomes are plausible. For example, a growing literature exists on associations between adverse birth outcomes and exposure to ambient air pollution (Woodruff et al. 2010), to wood smoke from household cooking and heating in developing countries (e.g., Lakshmi et al. 2013) and to household heating in developed countries (Gehring et al. 2014). While these exposures are chronic compared to the more acute nature of exposure to smoke from some wildfires, some studies have demonstrated links between wildfire smoke exposure and birth outcomes. Holstius et al. (2012) found lower birth weights, overall and for the second and third trimesters specifically, for babies that gestated during the 2003 southern California wildfires compared to babies from the same region born before or more than 9 months after the fires. Jayachandran (2009) found that prenatal smoke exposure from the 1997 Southeast Asian wildfire in the third trimester was the most important predictor of ‘missing’ children from the Indonesian 2000 Census, the only way to estimate early life deaths from the scant data in Indonesia. Pregnant women exposed to very high levels of $PM_{2.5}$ from agricultural burning in the Brazilian Amazon had higher rates of low birthweight babies compared to those exposed to lower levels (Cândido da Silva et al. 2014).

Mental Health Outcomes

Although many studies have documented evidence of psychological impairment related to wildfires (e.g. Papanikolaou et al. 2011), few have investigated smoke exposure as a cause. We found six studies that investigated the association between objective mental health impacts and wildfire smoke exposure; however, four of those were deemed to have higher potential for bias (Ho et al. 2014; McDermott et al. 2005; Marshall et al. 2007; Caamano-Isorna et al. 2011). In the two studies that remain, one found no increase in physician visits for mental illness associated with PM during the 2003 wildfire season in British Columbia (Moore et al. 2006) and the other found no increase in mental health hospitalizations during the 1987 California fires compared to a reference period (Duclos et al. 1990).

Toxicological Studies

A major pathway by which PM causes respiratory effects is through pulmonary oxidative stress and inflammation (Nakayama Wong et al. 2011). Systemic responses are the main pathways through which PM is thought to influence cardiovascular health. These are hypothesized to be induced either directly by the movement of pro-inflammatory, procoagulation, and pro-oxidant components of PM to the circulation, indirectly as a consequence of the pulmonary changes induced by PM, or through PM-mediated changes in the autonomic nervous system (Brook et al. 2010; Delfino et al. 2010).

In vivo animal studies of wildfire-derived PM exposure compared to controls have demonstrated increased oxidative stress and cell death in mice (Williams et al. 2013), and lower counts of lung macrophages, higher levels of inflammatory cells and cytokines, and greater antioxidant depletion in a study of smoke from a California wildfire in a mouse model (Wegesser et al. 2009, 2010). Similarly, increased respiratory inflammation and reduced lung mechanics compared with controls was documented from a mouse study of biomass smoke from burning sugarcane in Brazil (Mazzoli-Rocha et al. 2008). *In vivo* studies in humans have also demonstrated increased inflammatory responses, specifically elevated band neutrophil counts in peripheral blood (Tan et al. 2000) and elevated cytokines (van Eeden et al. 2001) associated with air pollution levels during the 1997 Southeast Asian wildfires.

In vitro studies have documented increased inflammation in rat alveolar macrophages exposed to $PM_{2.5}$ from prescribed fires (Myatt et al. 2011) and in human bronchial epithelial cells exposed to wildfire-derived $PM_{2.5}$ compared to cells exposed to ambient PM (Nakayama Wong et al. 2011). After exposure to wildfire-derived PM, human lung epithelial cells showed declines in glutathione, an important antioxidant (Pavagadhi et al. 2013); mouse peritoneal monocytes showed increased hydrogen peroxide production and oxygen radical generation (Leonard et al. 2007); and mouse macrophages (Franzi et al. 2011), rat macrophages (Myatt et al. 2011), and human lung epithelial cells (Pavagadhi et al. 2013) had increased cell death.

Oxidative stress can also lead to DNA damage. All size fractions of PM extracted from wildfire smoke caused DNA damage in mouse peritoneal monocytes (Leonard et al. 2007). Studies in regions near sugarcane burning in the Brazilian Amazon observed higher numbers of micronucleated cells, a measure of genotoxicity, in buccal cells from children in highly smoke-affected areas compared to children in a control community (Sisenando et al. 2012); however, it is unclear if the higher pollution in the study communities was solely due to agricultural burning because two factories are located in the exposed but not in the control region. Another study found more micronucleated buccal cells in sugarcane workers compared to nearby hospital administrative workers (Silveira et al. 2013), but the authors do not mention any control for other differences in these two populations that could explain this finding.

A recent study demonstrated the potential for early life exposure to wildfire smoke to confer immune effects, measured as reduced cytokine synthesis in peripheral blood cells, lasting into adolescence in Rhesus macaque monkeys (Miller et al. 2013). Short-term inhalation of wood smoke in general and not specifically from a wildfire can compromise lung immune responses, which may be one reason for the observed increased likelihood of lung infections in children exposed to wood smoke (Zelikoff et al. 2002). There is therefore growing evidence to support the theory that incidence of respiratory infections can be increased by exposure to wildfire smoke.

In summary, existing toxicological evidence supports potential respiratory and cardiovascular health effects of wildfire smoke exposure. The body of evidence, however, is relatively small compared to toxicological studies of general PM.

Vulnerable Populations

Few epidemiological studies have investigated whether specific populations are more susceptible to wildfire smoke exposure than the general population. Susceptibility factors investigated include those related to lifestage, pre-existing disease, socioeconomic status (SES), and ethnicity. Unless otherwise stated, all subgroup differences are based on observed changes in the magnitudes of point estimates, not on significance tests.

The findings for differential effects by age are inconclusive. A study of PM_{10} exposure in Malaysia from the 1997 Southeast Asian wildfires found higher rates of mortality among people 65–74 years old compared to others; a smaller suggestive effect was found among those ≥ 75 years old (Sastry 2002). People ≥ 65 years old had higher rates of respiratory hospitalizations compared to younger adults exposed to biomass burning in the Brazilian Amazon (Ignotti et al. 2010) and wildfire smoke in Australia (Morgan et al. 2010). Such older adults were also found to have higher rates of hospitalization for asthma than their younger counterparts during California wildfires (Delfino et al. 2009), and higher rates of out-of-hospital cardiac arrests and hospitalizations for IHD in Victoria, Australia (Haikerwal et al. 2015).

Other studies, however, have found higher effects for younger adults than for older adults. Wildfire PM-related respiratory admissions during Indonesian wildfires exceeded predictions for 40- to 64-year-olds but not for those ≥ 65 years (Mott et al. 2005). Similarly, ED visits for COPD, and pneumonia and acute bronchitis were more strongly associated with peat fire smoke among people < 65 years old compared to people ≥ 65 in North Carolina (Rappold et al. 2011). Although respiratory physician visits were associated with PM_{10} among people 60–70 years old and among those ≥ 80 in a British Columbia wildfire, younger adults exhibited stronger associations (Henderson et al. 2011). No differences were found in either of the two studies that investigated differential effects by age for cardiovascular outcomes (Morgan et al. 2010, Henderson et al. 2011).

Children with asthma did not experience increased respiratory symptoms or medication use during Australian wildfires, whereas adults did (Johnston et al. 2006). Similarly, the highest PM-related increase in physician visits for asthma during a wildfire in British Columbia was found for adults (Henderson et al. 2011), as was true for ED visits for asthma on smoke-affected days in Australia (Johnston et al. 2014). Asthma hospitalizations among children ages 0–5 years were more strongly associated with wildfire $PM_{2.5}$ exposure than were asthma hospitalizations for both older children and adults < 65 years old during a California wildfire; but the greatest association was found for people ≥ 65 years (Delfino et al. 2009).

Some studies have used previous health care utilization as a measure of pre-existing health conditions. One study found no effect modification by number of physician visits in the previous year (Henderson et al. 2011). In contrast, people ≥ 65 years old who were hospitalized for any cardiorespiratory outcome in the first half of the year were at increased risk of being hospitalized during the 1997 Southeast Asian fires compared with similar temporal comparisons in previous years without fires (Mott et al. 2005). Pre-existing cardiac or respiratory conditions may plausibly increase vulnerability to wildfire smoke exposure; however, the available evidence is currently inconclusive.

A recent study found that body mass index modified the association of wildfire smoke exposure on exacerbations of asthma, as measured by prevalence of physician-dispensed short-acting beta-agonists for children with asthma in southern California (Tse et al. 2015).

Few studies have investigated how socioeconomic status (SES) influences responses to wildfire smoke exposure. Henderson et al. (2011) noted findings of no effect modification by neighborhood SES on associations between wildfire smoke exposure and physician visits in British Columbia, Canada, but detailed results were not presented. In contrast, during a North Carolina peat fire, North Carolina counties with lower SES had higher rates of ED visits for asthma and CHF compared to counties with higher SES (Rappold et al. 2012). Similarly, in Indonesia, districts with lower food consumption demonstrated larger adverse associations between smoke exposure and survival of birth cohorts than those with higher household food consumption (Jayachandran 2009).

To our knowledge only one ethnic subgroup has been studied in relation to differential health outcomes associated with wildfire smoke exposure. Indigenous people in Australia experienced higher rates of hospitalization for respiratory infections (Hanigan et al. 2008), and IHD (Johnston et al. 2007) associated with exposure to bushfire smoke than non-indigenous people. This effect may be explained by underlying health status, access to medical services, or other social characteristics in this group (Martin et al. 2013).

Discussion

Our critical review demonstrated consistent evidence of associations between wildfire smoke exposure with general respiratory morbidity and with exacerbations of asthma and COPD (Table 1). Mounting epidemiological evidence and plausible toxicological mechanisms suggest an association between wildfire smoke exposure and respiratory infections, but inconsistencies remain. Increasing evidence suggests an association between wildfire smoke exposure and all-cause mortality, especially from more recent, higher-powered studies (e.g., Johnston et al. 2011; Morgan et al. 2010; Faustini et al. 2015). The current evidence for cardiovascular morbidity from wildfire smoke exposure remains mixed; many studies are inconclusive or negative, but some have demonstrated significant increases for specific cardiovascular outcomes, such as cardiac arrests. Toxicological findings are consistent with cardiac effects through evidence of systemic inflammation and increased coagulability. Most of the other end points of interest, including birth outcomes, mental health, and cancer have not been sufficiently studied.

Our review highlights the lack of information about which populations are most susceptible to wildfire smoke exposure. People already diagnosed with asthma or COPD are more susceptible. We found inconsistent evidence of differential effects by age or SES. Two studies have suggested differential effects by Australian indigenous status with no investigation of other ethnic groups.

Many gaps exist in understanding the public health implications of exposure to wildfire smoke. Larger studies with greater statistical power and more spatially refined exposure assessments are needed to better characterize impacts on mortality, cardiovascular disease, birth outcomes, and mental health effects. Currently, evidence exists of exacerbation, but not incidence, of asthma and COPD from wildfire smoke exposure. In temperate parts of the world, where wildfire smoke exposure is episodic, it is unlikely that changes in asthma incidence would be observed. Studies have not been conducted in populations more chronically exposed to wildfire smoke. Additionally, other health outcomes associated with wildfire smoke exposure have not yet been sufficiently studied, such as otitis media, which has been associated with exposure to secondhand tobacco smoke (Kong and Coates 2009), air pollution from woodsmoke (MacIntyre et al. 2011) and recently wildfire smoke (Yao et al. 2016). Human experimental studies of exposures to wildfire smoke could help clarify biological mechanisms. Very little information exists on health effects associated with measures of pollutants in wildfire smoke other than PM, such as ozone or PAHs. Although this review combined results from studies of various types of fires, it is possible that smoke originating from peat fires, forest fires, grassland fires, and agricultural burning could lead to differential health effects due to different constituents in the smoke. To our knowledge, no studies have yet investigated chronic exposure to wildfire smoke, but many populations in Southeast Asia, Africa, and Latin America are exposed regularly for extended periods (Johnston et al. 2012).

Characterization of the exposure–response function is critical for setting smoke levels for public health warnings or interventions, and it is not yet known whether current levels based on undifferentiated PM sufficiently characterize the effects of wildfire smoke. Four studies (Arbex et al. 2010; Chen et al. 2006; Johnston et al. 2002; Sastry 2002) have attempted to identify effects at different exposure levels, but these studies are hard to compare because of differences in exposure assessment methods, health outcomes, types of fires, and population susceptibilities.

Conclusions

We found consistent evidence of associations between wildfire smoke exposure and respiratory morbidity in general, and specifically for exacerbations of asthma and COPD. Growing evidence suggests associations with respiratory infections and all-cause mortality. More research is needed to determine whether wildfire smoke exposure is consistently associated with cardiovascular effects, specific causes of mortality, birth outcomes, and mental health outcomes. Research into which populations are most susceptible to health effects from wildfire smoke exposure is also needed to inform public health planning for future wildfires.

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FAST-TRACK

A southern California freeway is a physical and social barrier to gene flow in carnivores

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Abstract

Roads present formidable barriers to dispersal. We examine movements of two highly mobile carnivores across the Ventura Freeway near Los Angeles, one of the busiest highways in the United States. The two species, bobcats and coyotes, can disappear from habitats isolated and fragmented by roads, and their ability to disperse across the Ventura Freeway tests the limits of vertebrates to overcome anthropogenic obstacles. We combine radio-telemetry data and genetically based assignments to identify individuals that have crossed the freeway. Although the freeway is a significant barrier to dispersal, we find that carnivores can cross the freeway and that 5–32% of sampled carnivores crossed over a 7-year period. However, despite moderate levels of migration, populations on either side of the freeway are genetically differentiated, and coalescent modelling shows their genetic isolation is consistent with a migration fraction less than 0.5% per generation. These results imply that individuals that cross the freeway rarely reproduce. Highways and development impose artificial home range boundaries on territorial and reproductive individuals and hence decrease genetically effective migration. Further, territory pile-up at freeway boundaries may decrease reproductive opportunities for dispersing individuals that do manage to cross. Consequently, freeways are filters favouring dispersing individuals that add to the migration rate but little to gene flow. Our results demonstrate that freeways can restrict gene flow even in wide-ranging species and suggest that for territorial animals, migration levels across anthropogenic barriers need to be an order of magnitude larger than commonly assumed to counteract genetic differentiation.

Keywords: carnivores, conservation genetics, gene flow, habitat fragmentation, road and anthropogenic barriers, territoriality

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Introduction

Roads are the primary threat to dispersal between habitat patches in urban landscapes (Forman & Alexander 1998) and, without dispersal, isolated populations may be doomed to extinction (Brown & Kodric-Brown 1977; Hanski *et al*. 1996). Roads can also isolate populations previously in genetic communication, and the resulting genetic erosion may contribute to population decline (Saccheri *et al*. 1998; Westemeier *et al*. 1998). Empirical data on the frequency of dispersal across roads and its effect on genetic variation and population persistence are few and limited to small and relatively abundant species with low vagility (e.g. frogs, Reh & Seiz 1990; voles, Gerlach & Musolf 2000; beetles, Keller & Largiadér 2003). In contrast, the ability of large carnivores to disperse long distances could mitigate the effects of genetic isolation. However, for carnivores, population densities are low and home range

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sizes and dispersal distances are large (Sunquist & Sunquist 2001), so their persistence should be strongly influenced by the isolating effects of roads and development. Additionally, carnivores are susceptible to the deleterious genetic effects of inbreeding in small populations (O'Brien *et al.* 1985; Roelke *et al.* 1993; Vila *et al.* 2003; Liberg *et al.* 2005). Although conservation biologists have focused on the importance of connectivity for carnivores, actual demonstrations of the genetic consequences of roads for such long-lived and mobile species have been lacking.

We studied dispersal and genetic differentiation in coyote (*Canis latrans*) and bobcat (*Lynx rufus*) populations separated by a wide and heavily travelled freeway in the highly urbanized landscape of southern California. To obtain a direct estimate of dispersal, we radio-tracked animals on both sides of the freeway over seven years, from 1996 to 2003. To obtain a genetic estimate of dispersal, we genotyped individuals using highly variable microsatellite loci and then used genetic assignment tests based on the composite genotypes to assign animals genetically to each side of the freeway. We then assessed levels of genetic differentiation between populations on the same and different sides of the freeway to measure the effect of the road on gene flow (genetically effective migration). Finally, we determined whether levels of observed migration were consistent with levels of gene flow estimated by a coalescent model based on the number of generations since the freeway was established. The use of both radio-tracking information and genetic data to monitor migration and gene flow allows an assessment of the long-term genetic consequences of roads and other anthropogenic barriers on genetic diversity and can lead to the development of plans to mitigate their effects.

Materials and methods

We studied coyote and bobcat populations separated by the Ventura Freeway (US101), a congested 10–12 lane road in the San Fernando Valley 40 km from downtown Los Angeles. More than 150 000 vehicles use the road daily and the presence of a meridian fence largely restricts dispersal to underpasses and culverts (Fig. 1A) (Ng *et al.* 2004). The freeway was established in 1949 from a relatively undeveloped secondary road with minimal traffic (B. Marquez, personal communication), and there are no other natural barriers such as rivers or topographic features following the freeway that would have historically restricted gene flow. The study area consisted of 358 km^2 of chaparral, grassland, and oak woodland habitat (Table S1, Supplementary material) interspersed with secondary roads and housing developments. The 28.4-km length of the freeway connects the towns of Agoura Hills and Thousand Oaks that have a combined population of 200 000. The area is considered a critical habitat corridor connecting the Santa Monica Mountains with extensive natural habitat to the north (Penrod *et al.* 2001).

Animal capture and radiotelemetry

Bobcats and coyotes were captured with padded foot-hold traps in 1996–1998 and with box traps (bobcats) and neck snares (coyotes) in 2000–2003. We also genotyped a population of bobcats from northern California where bobcats were captured with box traps from 1992 to 1995 (Riley *et al.* 2004). Captured animals were aged, sexed, weighed, measured, ear-tagged, radio-collared, and released at the capture site. Blood, hair, scat, and in some cases tissue samples were taken for genetic analyses.

Animals were radio-located by triangulation using three consecutive or two simultaneous compass directions obtained with a peak directional antenna. Locations were obtained throughout the 24-h daily cycle. We computed 95% minimum convex polygon home ranges for animals with at least 20 locations. Home range overlap was computed for animals that were radio-tracked concurrently. We computed overlap as the total percentage of the home range that intersected with any other animals of the same sex.

Genetic sampling

All bobcat and coyote DNA samples were extracted from blood or tissue (ear punch) samples taken at time of capture. Standard phenol–chloroform extraction methods were utilized. Seven dinucleotide microsatellite loci developed for the domestic cat (Menotti-Raymond *et al.* 1999) and validated for polymorphism in the bobcat (Ernest *et al.* 2000) were used to genotype all bobcat specimens (FCA026, FCA043, FCA045, FCA077, FCA090, FCA096, and FCA132). Seven tetranucleotide microsatellite loci developed for the domestic dog (Breen *et al.* 2001) and validated as polymorphic for the coyote by the authors were used to type all coyote specimens (FH2001, FH2137, FH2422, FH2062, FH2226, FH2293, and PEZ19). Polymerase chain reactions (PCR) utilized either (i) a fluorescent dye-labelled forward primer, or (ii) a hybrid combination of forward primers consisting of the published forward primer with the M13F (–20) sequence (16 bp) added to the 5′ end and a fluorescent dye labelled M13F (–20) primer. The unlabelled reverse primer was used in both cases. We used the PCR conditions for the hybrid combination primer (a two-step cycle) (Boutin-Ganache *et al.* 2001). Primer dye labelling utilized BeckmanCoulter dye D4 and PCR products were sized on the BeckmanCoulter CEQ2000XL DNA Analysis System.

Genetic analysis

Observed and expected heterozygosities, allelic diversity, and deviation from Hardy–Weinberg equilibrium were assessed with GENEPOP (Raymond & Rousset 1995; Table S2, Supplementary material). Bonferroni corrections to significance levels were applied to account for multiple

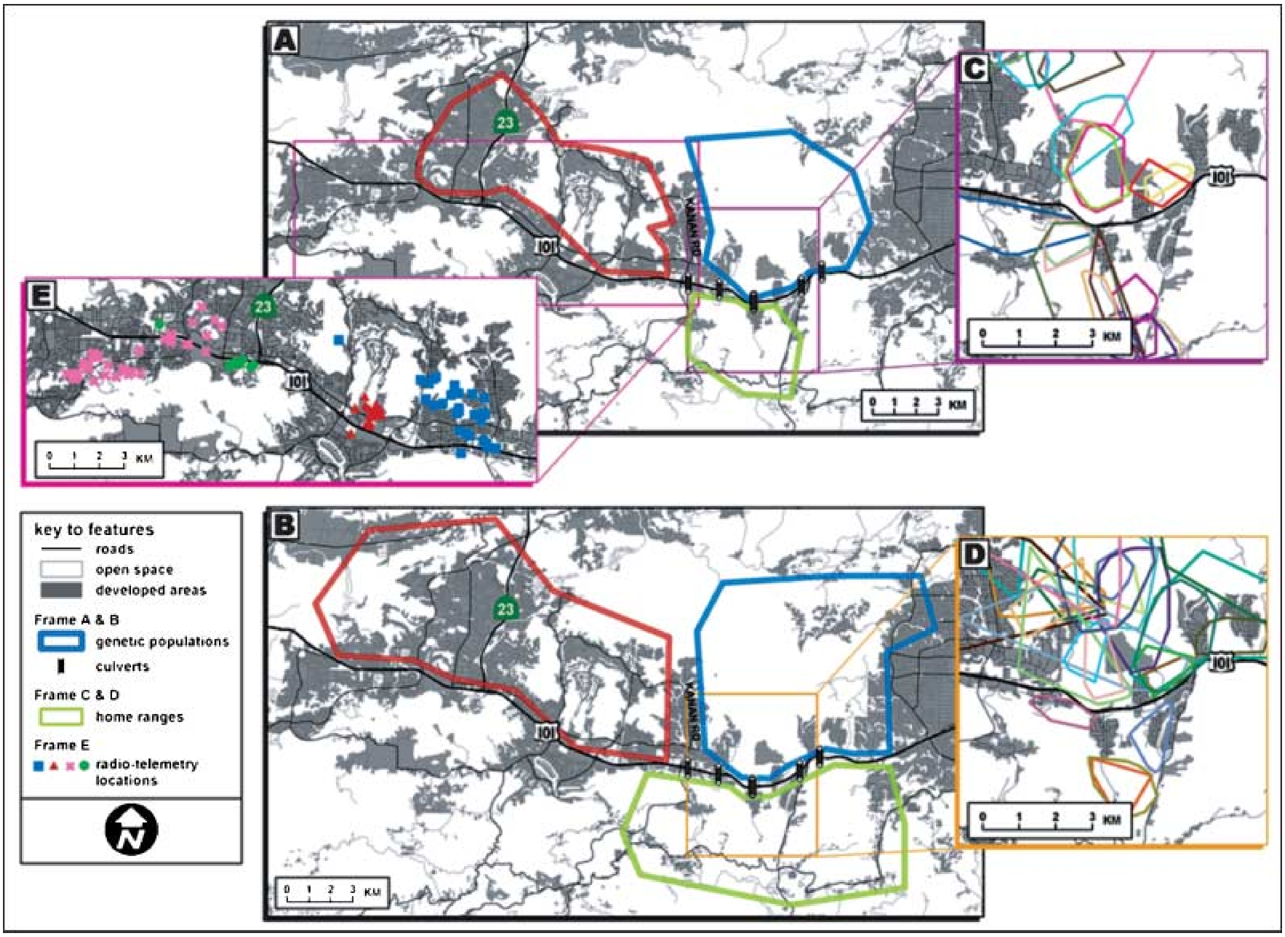

Fig. 1 Study populations, home ranges and radio-locations of bobcats and coyotes near the Ventura Freeway in southern California. Bobcat (A) and coyote (B) study populations are located north and south of the Ventura Freeway. The north side populations are further divided by Kanan road into northeast and northwest populations. 95% minimum convex polygon (MCP) home ranges are shown for all radio-tracked bobcats (C) and coyotes (D) near the freeway between the south and northeast populations. In (E), radio-telemetry locations are shown for four bobcats with locations north and south of the freeway that were captured north of the freeway but assigned genetically to the population south of it (see Fig. 2).

tests in the determination of heterozygote deficiency/excess (Rice 1989). Coyote samples were grouped into two populations north and south of the freeway, whereas bobcats were divided into three populations, two north and one south of the freeway according to STRUCTURE results (see Results and discussion).

To obtain a genetic estimate of dispersal, we used assignment tests based on the composite microsatellite genotypes. Assignment tests identify the population of origin for each individual, and thus individuals assigned to a population other than the one in which they were caught can be considered migrants (Berry *et al*. 2004). We used the program STRUCTURE (Pritchard *et al*. 2000) to assign individuals to populations. STRUCTURE is a Bayesian clustering algorithm that uses multilocus genotypes to infer population structure and assign individuals to populations. All individuals were combined into one data set for analysis, without any a priori population assignments. We utilized a burn-in of 50 000 iterations, followed by 500 000 iterations of the Gibbs sampler. Admixture was allowed. We evaluated *K* values, the number of assumed populations, from 1 to 6. Each value of *K* was run a minimum of three times to evaluate stability. For the highest likelihood *K* value, we then evaluated the cluster assignment results for each individual with respect to its capture location.

For potential migrants identified in the initial STRUCTURE analysis, we modified the STRUCTURE input data file to reassign them to their putative population of genetic origin based on the cluster assignment results. We then calculated the posterior probability of correct population assignment with this revised data set in STRUCTURE using the ancestry model with admixture, incorporating population information with the migration parameter set to $v = 0.1$ (Table S5, Supplementary material).

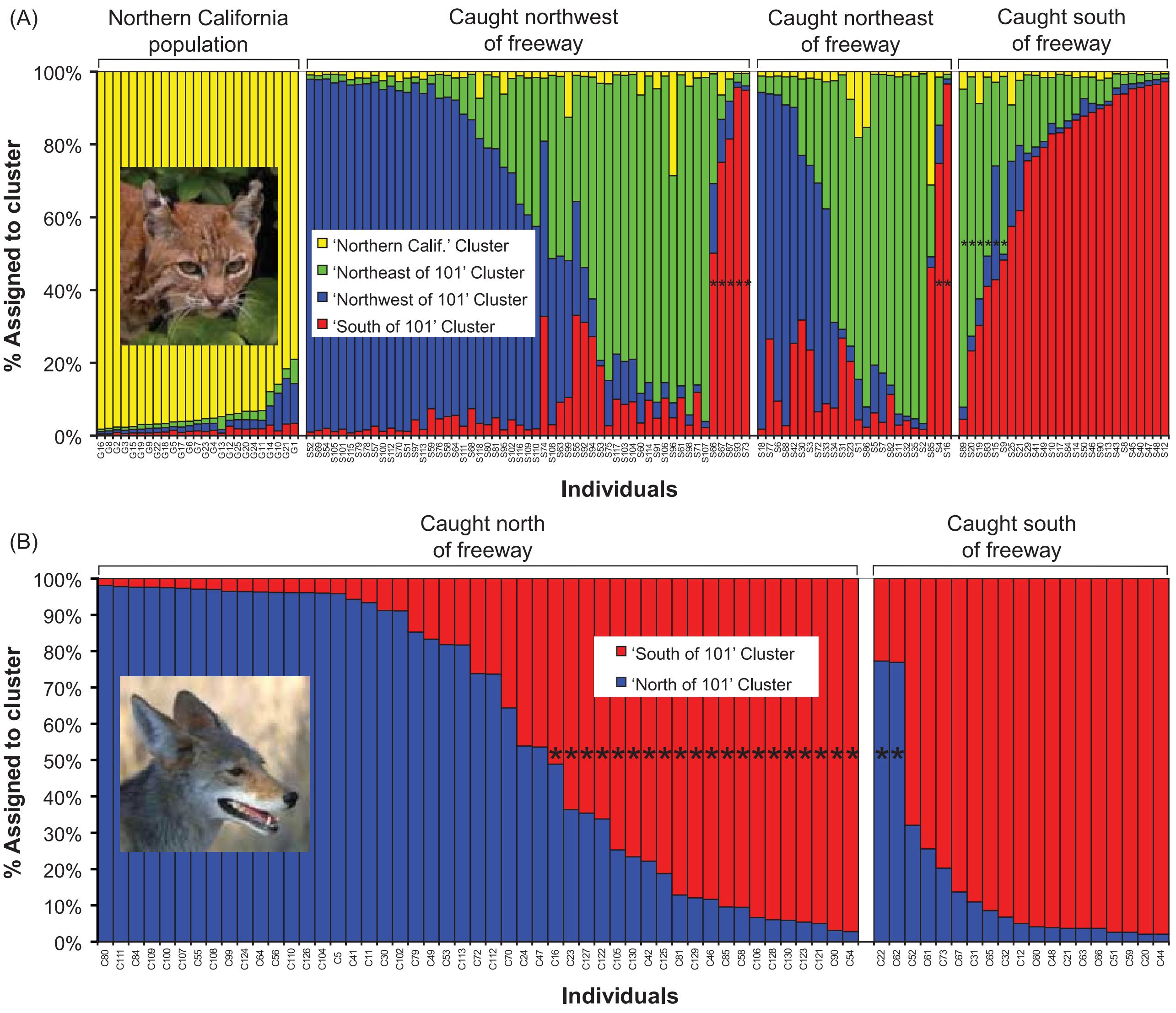

Fig. 2 Genetic assignment results from the program STRUCTURE for bobcat (top) and coyote (bottom) populations. Individuals are grouped according to capture location. Genetic population clusters are coded with different colours and the fraction of colour for each individual represents the probability of assignment to the cluster with that colour. Four clusters were found in bobcats, corresponding to a northern California group (yellow), two groups on the north side of the freeway (blue and green) and one group on the south side of the freeway (red). In coyotes, two clusters are supported by STRUCTURE, corresponding to a north (blue) and south (red) cluster. Asterisks denote misassigned individuals (individuals with greater than 50% assignment to a cluster different from the capture location) that are potential migrants.

We measured population differentiation by calculating population pairwise F_{ST} values and significance (g-test) using the program FSTAT (Goudet 2002). We estimated gene flow as the number of genetic migrants (Nm) between populations from F_{ST} values [$F_{ST} \approx 1/(1 + 4Nm)$; Wright 1921]. Population membership was based on the capture location north or south of the Ventura Freeway. The northern population was additionally split into northwest and northeast populations to measure differentiation between populations on the same side of the freeway. Computing F_{ST} between these two populations north of the freeway allows us to compare the amount of genetic differentiation across the freeway with that over the same or greater distance without the barrier. The east and west populations were divided by Kanan Road, a secondary road, and surrounding development (Fig. 1A,B).

We also computed the pairwise relatedness coefficient, R between individuals, (Queller & Goodnight 1989) using the program KINSHIP (Goodnight 2005). We identified pairs of individuals significantly related ($\alpha = 0.05$) at the $R \geq 0.25$ level by first performing a simulation in KINSHIP using the complete population data set at $R = 0.25$, followed by log-likelihood calculations for all possible pairs. Based on the three defined populations, two north and one south of the freeway, for both bobcats and coyotes, we then determined the percentage of number of close relatives ($R \geq 0.25$) across the freeway, across a similar distance on the same side of the freeway, and within each population (Fig. S1, Supplementary material).

We used coalescent simulation to generate predicted levels of genetic differentiation based on a population isolation event with the program SIMCOAL (version 1.0) (Excoffier 2004). SIMCOAL is a computer program for the simulation of molecular genetic diversity in an arbitrary number of diploid populations based on a retrospective coalescent approach. SIMCOAL was utilized to estimate expected population pairwise F_{ST} values for both bobcat and coyote microsatellite results, based on the time since the freeway was built. A sensitivity analysis was performed on the parameter space of inference for the simulations by varying population effective sizes, sample sizes, migration rates, number of generations since a historical event (population separation), and microsatellite mutation rate. The microsatellite mutation rate was varied from 10^{-3} to 10^{-2} based on observed mutation rates for dinucleotide and tetranucleotide microsatellites for the domestic dog (Francisco *et al*. 1996). Effective population sizes (N_e) were estimated as the number of territorial adults in the study area based on telemetry observations. This calculation assumes that all territorial individuals reproduce equivalently; however, sensitivity analysis showed that results were not sensitive to small changes in N_e or sample size. One thousand analysis iterations were performed for each combination of input parameters. SIMCOAL output results were then analysed using ARLEQUIN (Schneider *et al*. 2000) for pairwise population F_{ST} estimation. F_{ST} values were determined by averaging the F_{ST} values of all 1000 iterations. Because sensitivity analysis showed that population effective size and sample size had minimal effect on F_{ST} within the range of our study values, they were held constant at 200/50 (population effective size/sample size) for bobcats and 75/25 for coyotes. The number of generations since separation was varied from 25 to 100, and migration rate was varied from 0 to 10% of source population. We assume a 2-year generation time for coyotes and bobcats (Knick *et al*. 1985; Bekoff & Wells 1986).

Results and discussion

We captured bobcats and coyotes on the north and south sides of the freeway and placed radio-telemetry collars on 110 (92 north side, 18 south side) coyotes and 87 (64 north side, 23 south side) bobcats. Using radio-telemetry, from 1996 to 2003 five (4.5%) radio-collared coyotes and 10 (11.5%) radio-collared bobcats were observed to cross the freeway, whereas 58 (52%) coyotes and 40 (45%) bobcats crossed major secondary roads. Because a principal study objective was to understand the effects of roads, and in particular the freeway, on carnivore movement, all radio-collared animals were captured within dispersal distance, and many within an average home range diameter, of both the freeway and secondary roads. However, only 213 (2.3%) of 9311 bobcat locations and 19 (0.4%) of 4565 coyote locations were on the opposite side of the freeway from the capture location of the individual.

Home range perimeters followed but did not cross roads such as the freeway, implying that they functioned as artificial territorial boundaries (Fig. 1C, D). For both male and female bobcats, home ranges that bordered on hard boundaries such as the freeway or development were significantly smaller than those that did not (males: $t = -1.919$, one-sided $P = 0.033$; females: $t = -2.186$, one-sided $P = 0.018$). Also, for adult female bobcats, the age class most important for reproduction, home range overlap was three times higher among individuals with home ranges adjacent to development and the freeway than in those with nonadjacent home ranges (38.8% vs. 12.4% overlap; $t = -1.77$, one-sided $P = 0.045$). For coyotes, we did not radio-track a sufficient proportion of territorial individuals throughout the study area to reliably measure territory overlap. Overall, the freeway was a significant barrier to movement as only about 5–10% of individuals crossed in the 7 years of observation, and home range boundaries, overlap, and size were affected by its proximity.

We genotyped 68 (49 north side, 19 south side) coyotes and 108 (82 north side, 26 south side) bobcats for variation in seven microsatellite loci. Microsatellite loci were highly polymorphic for both species (Table S2, Supplementary material). We also typed a population of 25 bobcats from Golden Gate National Recreation Area in the San Francisco Bay Area, a geographically remote and genetically distinct population (Riley *et al*. 2004). For bobcats, the STRUCTURE assignment test results determined that four populations best fit the data (Table S3, Supplementary material), with the northern California population clearly separated from those in southern California and two populations located north and one south of the freeway (Fig. 2A). All bobcats from northern California were assigned correctly to that population. However, seven bobcats caught north of the freeway, five to the west and two to the east, were assigned genetically to the south side population with assignment probabilities and posterior probabilities of greater than 50% (Fig. 2A; Table S5, Supplementary material). We had radio-telemetry observations on six of these seven bobcats, and four of the six were located south of the freeway at least once (Fig. 1E), corroborating their status as migrants. Six bobcats assigned north of the freeway were captured to the south (Fig. 2A). None of these bobcats were found north of the freeway based on radio-telemetry observations, although three were located within 500 m of it, and two within 100 m. Therefore, based on genetic assignment and in part supported by telemetry observations, 9% (7 of 80) of the bobcats sampled from the north side of the freeway and 23% (6 of 26) of the bobcats sampled from the south side are putative migrants (see Fig. 2A). Considering the limited sampling of activity provided by radio-telemetry, the genetically derived estimate of migration (13 of 106 individuals or 12.3%) and that based on telemetry (10 of 87 individuals or 11.5%) are remarkably similar and suggest that about 12% of the sampled bobcat population crossed the freeway over the 7-year study period, or 3.4% per generation.

For coyotes, the assignment test determined that two populations best fit the observed data, one north and one south of the freeway (Fig. 2B; Table S3, Supplementary material). Two of 19 individuals (11%) captured south of the freeway were assigned to the north side population with assignment probabilities and posterior probabilities of greater than 50% (Fig. 2B; Table S5). Radio-telemetry observations were available for one of these two coyotes, and none of the 107 locations were north of the freeway, although six of the first seven locations were within 1.5 km of it, indicating that this coyote may have dispersed from the north. Twenty of the 49 coyotes (41%) captured on the north side of the freeway were assigned to the south side. We had radio-telemetry observation on 18 of these coyotes, and none showed evidence of crossing the freeway, although 11 of 18 were observed within 1 km of it. Consequently, the genetic results suggest that 10% of the South side population and as much as 41% of the north side population may be migrants. This implied migration fraction of 32% (22 of 68 individuals) or 9.1% per generation is much larger than the value of 4.5% or 1.3% per generation based on telemetry observations. Considering higher assignment thresholds of 80% and 90%, 21% (14 of 68) or 5.9% per generation and 10% (7 of 68) or 2.9% per generation, respectively, are still misassigned and likely to be migrants. The discrepancy between genetic- and telemetry-based estimates may reflect the unlikely probability of observing dispersal with limited radio-telemetry observations or the difficulty of classifying migrants in genetically similar populations. The use of assignment tests to measure dispersal requires a modest degree of genetic differentiation between populations, otherwise historical gene flow will confound the assessment of recent dispersal events (Berry *et al*. 2004). However, two observations argue for a higher dispersal rate than suggested by telemetry observations. First, coyotes generally disperse farther than bobcats (Van Vuren 1998), which had higher observed and implied rates of migration (see above). Second, of the 22 coyotes that were genetically misclassified, 14, or 64%, were juveniles or yearlings, the ages when coyotes typically disperse (Gese *et al*. 1989). This compares to 39% juveniles or yearlings in the population of coyotes that were not misclassified.

Although the freeway is a barrier to movement, rates of migration of 3.4% per generation for bobcats and from 1.3% to 9.1% per generation for coyotes as suggested by telemetry or genetic data imply high rates of gene flow sufficient to counteract drift (Mills & Allendorf 1996; Vucetich & Waite 2000). To assess levels of differentiation, we measured F_{ST}, the fixation index, for the seven microsatellite loci. For both species, we found that F_{ST} values between populations on different sides of the freeway were two to nine times larger (and *Nm* 2–9 times smaller) than those between populations on the same side, although the latter populations were separated by greater distances (Figs 1A, B and 3). Additionally, 39.2% of alleles for coyotes and 23.6% of alleles for bobcats were unique to one side of the freeway (Table S4, Supplementary material). For coyotes, both pairwise F_{ST} values across the freeway ($F_{ST} = 0.030$ northwest-south, $F_{ST} = 0.037$ northeast-south) were significantly different from zero ($P < 0.003$), whereas the F_{ST} values between the two subpopulations on the same side of the freeway (0.004, northwest-northeast) was not ($P = 0.134$). For bobcats all three pairwise F_{ST} values were significantly different from zero ($F_{ST} = 0.064$ northwest-south, $F_{ST} = 0.039$ northeast-south, $F_{ST} = 0.018$ northwest-northeast) ($P < 0.003$), suggesting that Kanan Road, a busy secondary road, and the wide development corridor flanking it, may also be a significant barrier to gene flow for bobcats

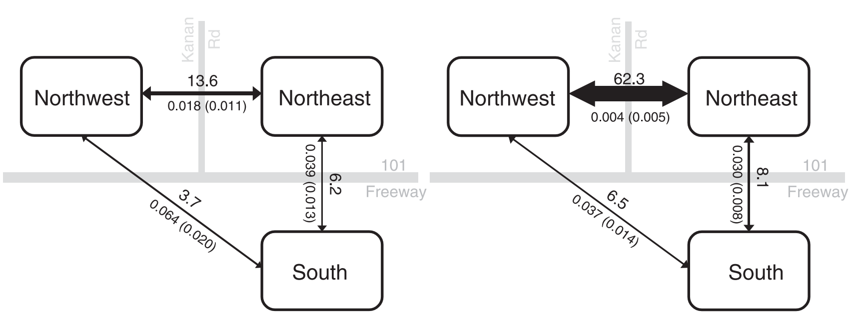

Fig. 3 The number of genetic migrants (*Nm*, above line) and levels of genetic differentiation (F_{ST}, below line, standard error in parentheses) between populations across the freeway (northwest vs. south and northeast vs. south) and on the same side of the freeway (northeast vs. northwest) for bobcats and coyotes. Arrow widths are proportional to *Nm* values.

(Fig. 3). Relatedness values also indicated substantially more closely related pairs of animals ($R \geq 0.25$) between populations on the same side of the freeway (northeast vs. northwest) than across it (northeast vs. south) (Fig. S1, Supplementary material). Overall, these results clearly show that the Ventura Freeway is an imposing barrier to gene flow for both species.

To assess if these levels of genetic differentiation were consistent with population history and the observed and implied migration rates, we used coalescent simulation modelling to estimate north side–south side pairwise F_{ST} indices resulting from the division of a single population by the creation of the freeway in 1949. The simulation results (Fig. 4) showed that a genetically effective migration rate of approximately 0.5% per generation or less is required to explain the observed level of population differentiation for both carnivore species. Consequently, given that our observations span a period of about three generations (Knick *et al.* 1985; Bekoff & Wells 1986), the genetically effective migration rates estimated by the coalescent simulation are approximately 3–18 times lower than migration rates between populations separated by the freeway based on direct observation or genetic population assignment.

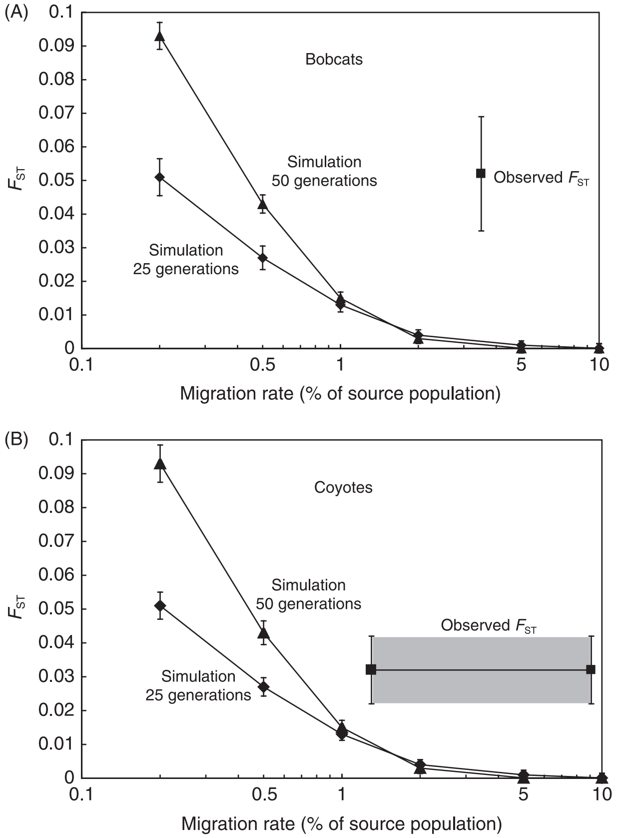

Fig. 4 Comparison of predicted genetic divergence (F_{ST}) using coalescence simulations (*Y*-axis) with observed F_{ST} values as a function of migration rate (*X*-axis) between bobcat (A) and coyote (B) populations north and south of the freeway. Migration rates for observed F_{ST} values are based on radio-tracking observations and genetic assignment tests (see text). Error bars for F_{ST} values represent one standard error. Observed genetic differentiation is consistent with a migration rate of 0.5% or less for both species given 25 or 50 generations since isolation.

The disparity between observed migration rates and inferred gene flow likely reflects the lack of reproductive success of migrants. For example, 6 of the 10 bobcats that were found on both sides of the freeway were located across it less than four times, and of the four that stayed across, the two females were known not to have produced kittens the following spring. Of the five coyotes radio-tracked across the freeway, four did not reproduce since they were located six or fewer times across the road and over only a short period of time outside the reproductive season. Further, of the potential migrants observed by telemetry and implied by genetic results, 54% were classified as less than 2 years old. In undisturbed populations, young dispersers enter a matrix of occupied and unoccupied territories, reflecting natural mortality of territorial adults. However, in our study area, home ranges follow the freeway boundary (Fig. 1C, D) and consequently, territorial and reproductive individuals contribute genes to the population on one side of the freeway only. Additionally, in our urban study area, mortality from hunting and trapping is low or nonexistent, and carnivore survival rates were high (Riley *et al.* 2003). High survival rates, small home ranges, high home range overlap, and the barrier effect of roads and development all resulted in territory packing along hard boundaries such as the freeway. This territory pile-up likely produced a formidable social and behavioural barrier to genetically effective dispersal because dispersers are unlikely to obtain and hold territories near the freeway. This unique genetic-isolating effect of roads and other artificial boundaries likely applies to other territorial species.

Conceivably, genetic differences may also correspond to changes in habitat composition across the freeway. For example, continent-wide climate and habitat changes have been associated with genetic structure in grey wolves (*Canis lupus*; Geffen *et al.* 2004), and regional-scale biome changes, e.g. between mountainous regions and flat valley expanses, were associated with genetic structure in coyotes (Sacks *et al.* 2004). However, both the geographic scale and diversity in habitats sampled by these studies far exceed the habitat differences observed throughout the area that we studied. Both sides of the freeway consist of a similar mix of the three dominant types of vegetation in the Santa Monica Mountains and Simi Hills including mixed scrub (64–85%), grassland (8–26%) and riparian and oak woodland (2–11%; Table S1, Supplementary material). There is variation in the amounts of specific types of scrub communities (e.g. coastal sage scrub, dominated by *Salvia* spp. and *Artemisia californica*, and chaparral, dominated by *Adenostoma fasciculatum* or *Ceanothus* spp.) across the entire study area, but coyotes and bobcats on both sides of the freeway used both of these scrub communities, indicating a lack of ecological specialization. Coyotes and bobcats are generalist carnivores, and we feel such small-scale ecological differences are an unlikely explanation of our results. Unfortunately, there are too few historical specimens from our study area in museum collections to directly assess genetic differentiation prior to the construction of the freeway.

Roads are a primary threat to the persistence of animal populations in urban landscapes. This threat is caused directly through vehicle mortality or indirectly by increasing the probability that isolated populations will become extinct through random demographic processes (Forman 2003). Our results show that the genetic effects of roads can also be substantial even for large, highly mobile species. Levels of differentiation between coyote and bobcat populations isolated for about 50 years are as large as those between coyote populations separated by several hundred kilometres (Roy *et al*. 1994). These levels of differentiation were found even between high-density populations of bobcats and coyotes. The isolating effects of roads would likely be even more severe for very small populations and rare species (Spielman *et al*. 2004). An additional insidious factor is the effect of roads in decreasing gene flow well below that expected from migration rates or existing between similarly spaced populations on the same side of the freeway. We suggest this decrease may be caused by: (i) roads acting as home range boundaries for terrestrial and reproductive individuals, and thus decreasing the migration rate of genes, and (ii) home range pile-up near roads that make it less likely that dispersing individuals can find territories. To counteract such genetic isolation, corridors across freeways could conceivably include more natural habitat so that home ranges could extend across the freeway and rates of genetic exchange might be increased. Five of the six potential crossing points in our study (Fig. 1A, B) were unvegetated culverts or paved underpasses. Finally, our results imply that observed migration rates across anthropogenic barriers may be poor surrogates for gene flow, and that molecular genetic studies of even recently isolated populations may provide new insights for conservation.

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Supplementary material

The supplementary material is available from http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC2907/MEC2907sm.htm

Table S1 Percentage of different habitat types in the sampled areas, determined by overlaying the polygons for each population (Fig. 1) on a vegetation map of the Santa Monica Mountains and Simi Hills (Franklin 1997). Chaparral consists of scrub habitat dominated by chamise (*Adenostoma fasciculatum*) and ceanothus (*Ceanothus* spp.); coastal sage scrub consists of scrub habitat dominated by sage (*Salvia* spp.) and California sagebrush (*Artemisia tridentata*); grassland is mostly introduced annual grasses; woodland consists of oak and riparian woodlands and some walnut woodlands.

Table S2 Observed and expected heterozygosities, allelic diversity and deviations from Hardy–Weinberg equilibrium (significant deviations indicated by ±).

Table S3 Likelihood values for inferred number of genetic clusters (*K*) from STRUCTURE (3 iterations per value of *K*).

Table S4 Private alleles as percentage of total alleles per locus in each population.

Table S5 Cluster assignment and posterior probability of correct genetic population assignment of potential migrants.

Fig. S1 Comparison of the percentage bobcat and coyote pairs that were closely related genetically, as defined by having an *R* value of 0.25 or greater between populations across the freeway (south vs. northwest and northeast) and on the same side of the freeway (across Kanan road, northwest vs. northeast). Bar widths are proportional to percentage values.

Fig. S2 Sensitivity of the SIMCOAL simulation algorithm for F_{ST} as a function of microsatellite mutation rate (μ), migration rate, and number of generations since population separation (since construction of the freeway).

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Report

Individual Behaviors Dominate the Dynamics of an Urban Mountain Lion Population Isolated by Roads

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Summary

Large carnivores can be particularly sensitive to the effects of habitat fragmentation on genetic diversity [1, 2]. The Santa Monica Mountains (SMMs), a large natural area within Greater Los Angeles, is completely isolated by urban development and the 101 freeway to the north. Yet the SMMs support a population of mountain lions (*Puma concolor*), a very rare example of a large carnivore persisting within the boundaries of a megacity. GPS locations of radio-collared lions indicate that freeways are a near-absolute barrier to movement. We genotyped 42 lions using 54 microsatellite loci and found that genetic diversity in SMM lions, prior to 2009, was lower than that for any population in North America except in southern Florida, where inbreeding depression led to reproductive failure [3–5]. We document multiple instances of father-daughter inbreeding and high levels of intraspecific strife, including the unexpected behavior of a male killing two of his offspring and a mate and his son killing two of his brothers. Overall, no individuals from the SMMs have successfully dispersed. Gene flow is critical for this population, and we show that a single male immigrated in 2009, successfully mated, and substantially enhanced genetic diversity. Our results imply that individual behaviors, most likely caused by limited area and reduced opportunities to disperse, may dominate the fate of small, isolated populations of large carnivores. Consequently, comprehensive behavioral monitoring can suggest novel solutions for the persistence of small populations, such as the transfer of individuals across dispersal barriers.

Results

Movements, Mortality, and Dispersal in an Urban Landscape

We captured, genotyped, and radio-tracked 26 mountain lions in the Santa Monica Mountains (SMMs; n = 21) and Santa Susana Mountains (including the Simi Hills; n = 5) from July 2002 through July 2012 (Figure 1). We also genotyped 17 other mountain lions from opportunistically collected samples, including from Angeles National Forest and the Verdugo Hills. Large freeways, including the 101 freeway (Figure 2A), the 5 freeway (Figure 2B), and the 405 freeway (Figure 2A), were significant barriers to movement (i.e., were almost never crossed by mountain lions) and often acted as home-range boundaries. One smaller freeway, the 118 freeway between the Simi Hills and the Santa Susana Mountains (Figure 1), was crossed at least 23 times by two radio-collared mountain lions in an area with a large tunnel and natural habitat on both sides [6]. In February 2009, subadult male P12 crossed the 101 freeway into the SMMs, the only time that a radio-collared mountain lion crossed 101, which separates the SMMs from all areas to the north.

Fourteen radio-collared lions died during the study period: six from intraspecific strife, two from vehicles, two of anticoagulant toxicosis from ingesting rodenticides, one from poaching, one from starvation as a young kitten, and two from unknown causes. Overall, 50% of mortalities of known cause were from intraspecific strife. An uncollared young male was also killed by another lion, for a total of seven instances of intraspecific killing. In five of these cases we were able to identify the surviving individual, and in all five we found that an adult male killed his offspring, his brother, or a previous mate (Table S1 available online).

We tracked the fate of young mountain lions, especially males, to assess dispersal. In the SMMs, we radio-tracked ten subadult male mountain lions and sampled five others that originated there (Table S1). Not one of these 15 young males was known to disperse from the SMMs to a home range with mating opportunities. Of the 12 young males from the SMMs whose ultimate fates are known, 11 died before or during dispersal from intraspecific strife (n = 5), vehicle strikes (n = 4), control action by police (n = 1), and unknown causes (n = 1). The only young male to successfully disperse from the SMMs, P22, settled in Griffith Park, requiring the crossing of two freeways (405 and 101; Figure 1). For more than 2 years, this male inhabited a home range of 26 km^2, as compared to 500 km^2 for adult male P1 (Figure 1). P22's home range was entirely bounded by freeways and urbanization, and he was its sole occupant.

North of 101, we radio-tracked three subadult males and sampled three others that were killed on roads (Table S1). All three collared animals successfully crossed roads and established home ranges as adults. P3 moved regularly between the Simi Hills and the Santa Susana Mountains across the 118 freeway. P12 crossed 101 and subsequently established himself as a dominant male in the SMMs. Perhaps most instructive, young male P16, who shared the eastern Santa Susana Mountains with his father, P21, dispersed north across highway 126 and established a home range (Figure 1). Among radio-collared animals of known fate, the least biased sample for mortality and dispersal, none of the seven subadult males from the SMMs successfully dispersed and established viable home ranges, while all three from the Santa Susana Mountains did.

Population Genetics of a Small, Isolated Population

We found very low genetic diversity compared to large, contiguous populations in California and in other parts of the west

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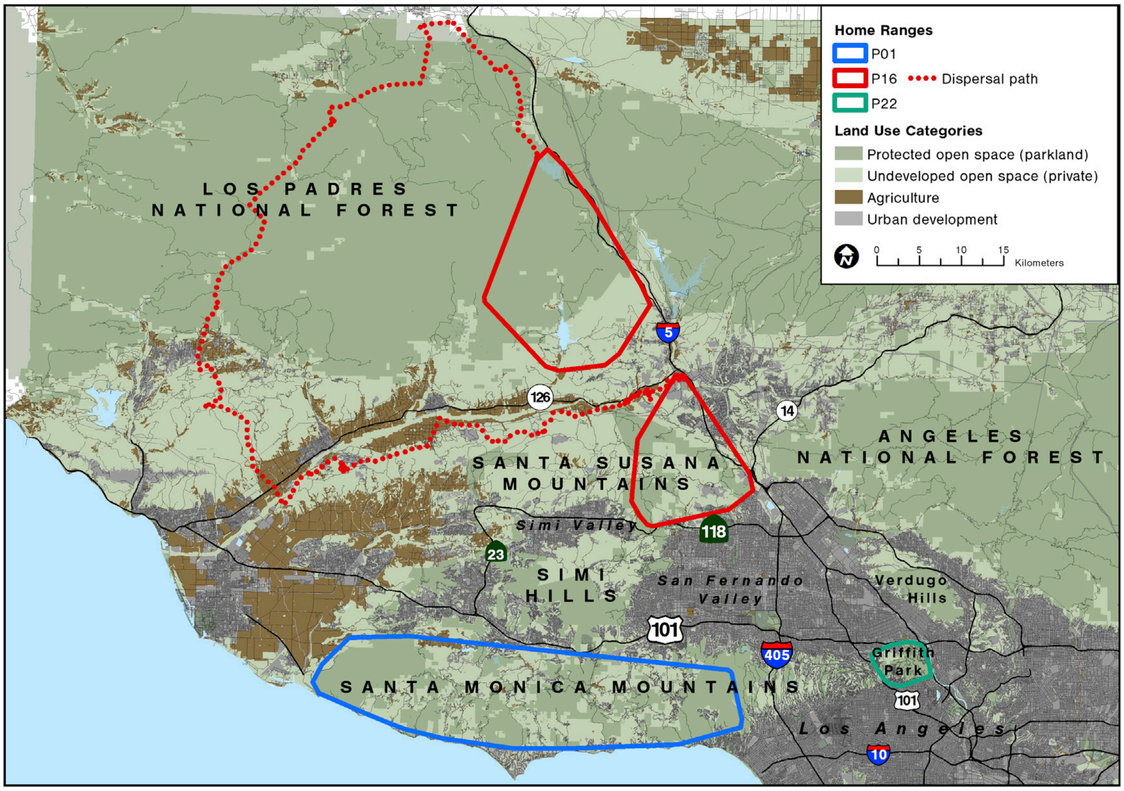

Figure 1. Study Area for Mountain Lion Movements and Population Genetics in and around Santa Monica Mountains National Recreation Area Northwest of Los Angeles

Large natural areas and major freeways are labeled. Home ranges are 100% minimum convex polygons for male P22 in Griffith Park, male P01 in the SMMs, and male P16 that dispersed from the eastern Santa Susana Mountains, across highway 126 to Los Padres National Forest. See also Table S1.

(Tables 1 and S2). Genetic diversity was particularly low in the SMMs south of the 101 freeway, which is the largest and busiest road to the north (175,000 vehicles/day versus 115,000 for the 118 freeway and 22,000 for highway 126; [7]). This population is also farthest away from the putative source populations in Los Padres and Angeles National Forests. The expected heterozygosity (H_E), total number of alleles (N_A), and number of effective alleles (N_E) were all significantly lower in the SMMs than north of the 101 freeway (Table 1). For private alleles (defined here as those present only in one study population), 67 of 172 discovered alleles were absent from the SMM population, and 78% of loci (42 of 54) had at least one private allele north of 101.

Genetic differences between local populations were also apparent from Bayesian cluster analyses (Figure 3A). Despite the small sample sizes, the program STRUCTURE [8] indicated strong clustering into three groups (K = 3 by the Evanno ΔK method [9]; Figure S1). The F_{ST} value between populations north and south of the 101 freeway was 0.12 ($p < 0.05$), three times larger than that previously found for other carnivores in the area [10]. The SMM mountain lion population showed evidence of having experienced a genetic bottleneck based both on significant heterozygote excess (program Bottleneck [11]; single-step mutation probabilities of 90%, p = 0.00044 and 78%, p = 0.00004) and Garza and Williamson's M ratio test ([12]; average M = 0.75; for single-step mutation proportion, 90%, $p < 0.0001$). The current effective population size, N_E, for mountain lions south of 101 was just six individuals.

The Influence of Specific Behavioral Events on Population Demography and Genetics

Our analysis of a genetically based pedigree showed that specific behavioral events greatly affected population dynamics and genetic composition (Figure 3B). For example, the migration into the SMMs of P12, who was genetically assigned to the population north of 101 (Figure 3A, blue cluster) and had private northern alleles at 33% of microsatellite loci, demonstrated that the 101 freeway can be traversed. Critically, P12 then survived in the SMMs and bred with resident females, including female P13 twice and his daughter, P19 (Figure 3B). This was the second instance of father-daughter mating, as P13 was the result of male P01 mating with his daughter, female P06 (Figure 3B) [13].

The immigration and subsequent matings of male P12 increased the genetic diversity and decreased the internal relatedness (IR) of the SMM population (Table 1) and thus is an example of a genetic rescue. P12 possessed 20 private alleles from north of the freeway, 19 of which he passed on to his offspring, such that private alleles absent from the SMMs decreased from 67 to 47, loci with private alleles to the north decreased from 42 to 32, and monomorphic loci in the SMMs decreased from 13 to 9. Bayesian clustering analysis also clearly showed the impact of P12's immigration (Figure 3A). Ninety-seven percent of P12's genome was assigned to the Santa Susanna Mountain population, and he fathered eight offspring based on our pedigree (Figure 3B). Six of these, including the five with P13 (99% assigned to the SMMs) exhibited a near equal mix of the

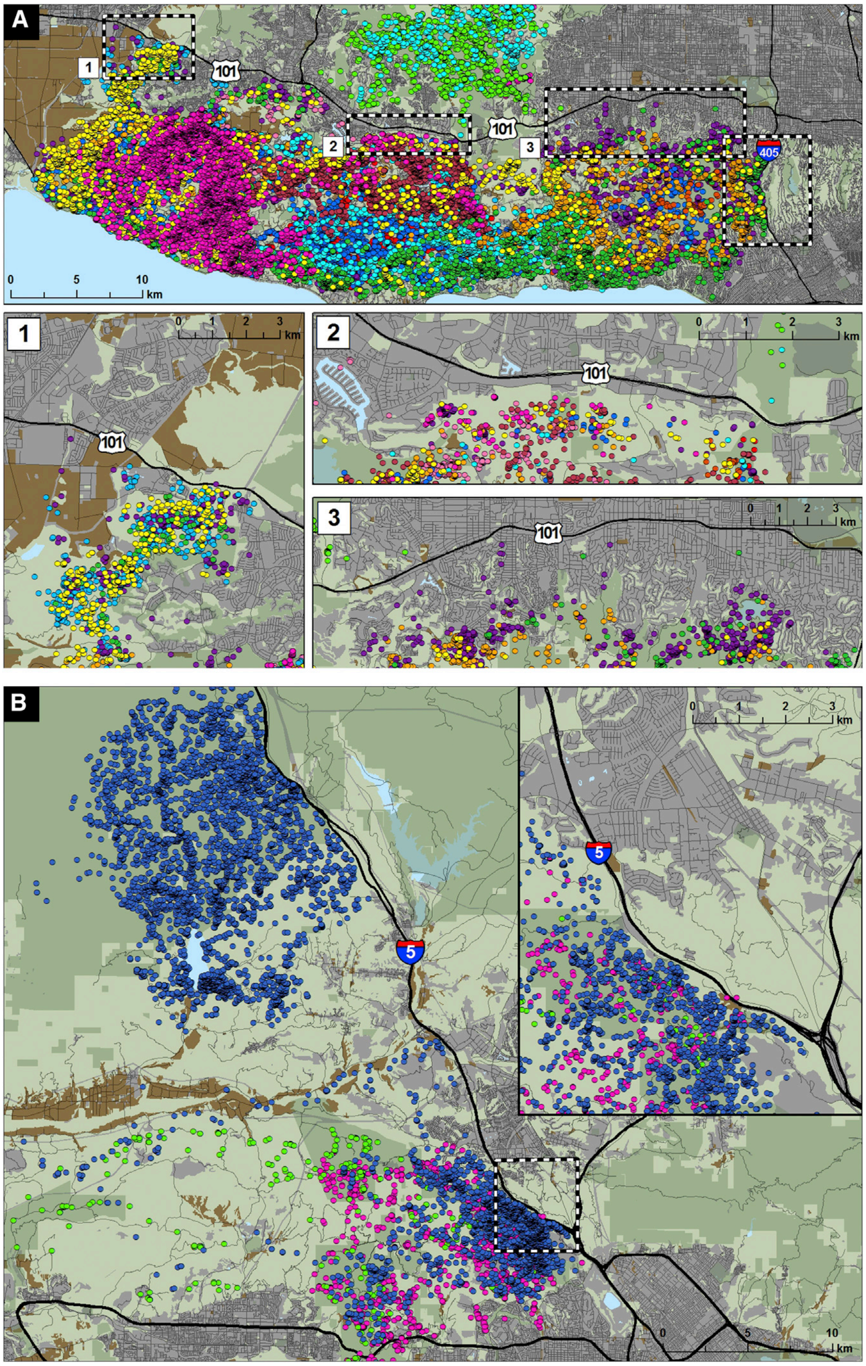

Figure 2. Locations of Mountain Lions along Freeways in Southern California from GPS Radio Collars, 2002–2012

(A) Locations near the 101 freeway, which runs east-west north of the Santa Monica Mountains. Because there is urban development along most of this freeway, in many areas (insets 2 and 3) animals do not approach the freeway. Toward the east end of the SMMs, the 405 freeway passes north-south through the mountains. This freeway is also a major barrier to mountain lion movement.

(B) Locations north of 101 in the Santa Susana Mountains and Los Padres National Forest near the 5 freeway, which runs north-south through the region.

SMM (green) and Santa Susanna Mountain (blue) clusters (Figure 3A). Interestingly, P23 and P24, the offspring of P12 and his daughter, P19, each had about three-quarter assignment to the Santa Susana Mountains, as expected (Figures 3A and 3B).

The effects of individual mating events on population genetic measures were also evident as quantified with our pedigree by gene-drop analysis (program PMx [14]) applied for the first time to a wild population. Both the mean inbreeding coefficient (F) and mean kinship increased in 2007 after male P1 bred with his daughter, decreased in 2010 after migrant P12 began to produce offspring in the SMMs, and then rose again in 2013 after P12 bred with his daughter. Similarly, gene diversity showed the opposite pattern, decreasing after the first close inbreeding event, rising in 2010 after P12 bred, and then decreasing with the second inbreeding event (Table S3). The dramatic shifting values of these coefficients over short time periods demonstrate how important individual matings are to the levels of inbreeding and relatedness in the population (Figure S2).

Finally, the IR, a measure that has the potential to provide novel insight about inbreeding and genetic health [15], reflected both the initial bottleneck and the effects of the inbreeding and genetic rescue events. The mean IR for SMM animals dropped from 0.09 (SE = 0.014) to 0.03 (SE = 0.036) when P12 and his offspring were included, as IR values for the initial offspring of the genetic rescue event were low and averaged −0.16 (range −0.10 to −0.35). For P23 and P24, the incestuous offspring of P12 and his daughter, IR values rose again to 0.10 and 0.09, indicating that one close inbreeding event may have reversed much of the value of the genetic rescue.

Our results from this small, isolated population also indicate how individual male mountain lions can monopolize breeding opportunities and genetically dominate future generations. Two males, first P01 and later P12, had very high reproductive success based on the pedigree (Figure 3B). Specifically, P01 fathered ≥15 offspring, P12 fathered ≥8 offspring, and no individual in the SMM population was fathered by any other male. The pedigree and PMx analyses indicated that P01 had 22 descendants, including six of the seven animals known in the population in 2013, and that P12 had eight descendants, including four of the seven current animals; 33.9% of the copies of the genome in the current population are derived from P01 and 35.7% from P12 (see Table S4).

Table 1. Genetic Diversity Based on 54 Microsatellite Loci for Mountain Lions in and around the Santa Monica Mountains, California, 2002–2012

Population	N_A	N_E	Poly (%)	H_E	H_O	IR
Santa Monica Mountains only, south of the 101 freeway before P12 crossing (n = 17)	1.9 ± 0.2	1.6 ± 0.1	76%	0.31 ± 0.03	0.38 ± 0.04	0.09 ± 0.04
North and east of the Santa Monica Mountains, north of the 101 freeway (n = 15)	3.1 ± 0.1	2.1 ± 0.1	100%	0.48 ± 0.02	0.42 ± 0.02	0.17 ± 0.05
Santa Monica Mountains only, south of the 101 freeway after P12 crossing (n = 26)	2.3 ± 0.1	1.8 ± 0.1	83%	0.36 ± 0.03	0.36 ± 0.03	0.03 ± 0.04

Populations are from the SMMs before the genetic rescue event (the dispersal of subadult male P12 from north to south), from north of 101 in the Santa Susana Mountains and San Gabriel Mountains, and from in the SMMs after the genetic rescue event. N_A is the total number of alleles, N_E is the number of effective alleles, poly (%) is the percentage of loci that are polymorphic, H_E is expected heterzygosity, H_O is observed heterozygosity, and IR is individual heterozygosity or internal relatedness (see the Supplemental Experimental Procedures for details). N_A, N_E, and H_E are significantly lower (nonoverlapping 95% confidence intervals) for the SMMs before P12 crossed than for north of the 101 freeway. Mean ± SE is shown. See also Table S2.

Discussion

Individual Effects on Population Dynamics and Genetic Diversity

Urban environments are generally inhospitable for large carnivores. Therefore, it is remarkable that a population of a large carnivore extends into the metropolitan area of Los Angeles, one of 30 world megacities (metropolitan areas of >10,000,000 people). However, the challenges for the long-term persistence of this population are substantial. Freeways in the area are almost complete barriers to mountain lion movement (Figure 2). This severe isolation most likely caused a striking assignment of lions to a single genetic cluster in the SMMs (Figure 3A). SMM lions were also clearly differentiated from those east of the 5 freeway (red cluster in Figure 3A), which separates the Angeles National Forest from the Santa Susana Mountains and Los Padres National Forest (Figure 1). The F_{ST} value of 0.12 across the 101 freeway is high given its relatively recent age (1949) and given that other studies of *Puma concolor* microsatellite loci have found $F_{ST} < 0.10$ among 15 subpopulations across the state of Idaho (distances of $\geq$500 km; [16]) and an average F_{ST} of 0.041 among 20 subpopulations from four southwestern states (700 by 700 km; [17]).

Genetic diversity in SMM mountain lions also is very low relative to populations north of the 101 freeway and elsewhere in California and the western US (Table S2). A measure that is less affected by sample size, the expected heterozygosity, is 0.31 for the SMMs before the immigration event, a value that is the lowest ever reported for western mountain lions, with the exception of another isolated population in the Santa Ana Mountains of Southern California that has comparable variability (H.B.E., unpublished data). The average number of alleles per locus (N_A) was also lower in the SMMs than north of 101 and was one-half to two-thirds of the average value from other populations across the western range (Table S2). The sole population with lower genetic diversity than the SMM population across all of these measures is the Florida panther, *Puma concolor coryi*, a federally endangered subspecies that suffered from substantial inbreeding depression and had been isolated for more than a century before lions from Texas were introduced to alleviate inbreeding depression (Table S2) [4, 5].

In the small, isolated SMM population, individual behavioral events can have a significant impact on population dynamics and genetics. We documented only one movement across the 101 freeway, by subadult male P12. But after his establishment as a dominant breeding male, new alleles entered the population, and, particularly for his mixed offspring, genetic diversity increased and measures of inbreeding decreased. However, first-order inbreeding events (father-daughter matings) by males P1 and P12 had the opposite effect, increasing inbreeding and reducing diversity. This kind of close inbreeding has only rarely been documented in mountain lions, specifically in the small and isolated southern Florida population [3, 4].

We also found significant effects of individual behavior on two other critical aspects of population dynamics, dispersal and mortality. Although typically every young male and half of young females disperse out of their natal range [18], not a single subadult mountain lion has successfully dispersed out of the SMMs. Instead, young males have died, principally from intraspecific strife and vehicles. In the one dramatic case, male P22 dispersed from the SMMs into the Hollywood Hills and has lived for 2 years in a home range of 26 km^2, the smallest annual range ever reported for an adult male. In this range, P22 was surrounded by roads and development (Figure 1) and had no opportunity to mate. Male mountain lion home ranges are typically an order of magnitude larger, at 300–400 km^2 or more [18, 19], and overlap with those of multiple females. By contrast, all three of the young males that we radio-tracked in the Santa Susanna Mountains successfully dispersed and established home ranges.

Intraspecific strife, the most common cause of mortality, can also be important in other populations, particularly those that are not hunted [20, 21]. However, in the SMMs, we documented repeated cases of males killing their offspring, their brothers, and previous mates. Little has been reported about paternity or kin recognition in mountain lions [18, 22], but clearly this is rarely a sound evolutionary strategy as the survivorship of offspring or siblings is traded against the probability of future reproduction [23]. It is particularly hard to imagine an advantage from killing potential mates or female offspring (Table S1). In fact, in the Santa Susanna Mountains, we observed the opposite pattern. Male P21 was the father of subadult males P12 and P16 (Figure 3B), both of which successfully emigrated and established long-term home ranges: P12 south into the SMMs and P16 north across highway 126 (Figure 1). None of the young males originating in the SMMs, dominated by adult males P1 and P12, have lived beyond age 2, so with respect to male mountain lions, the SMMs are a population sink. In other aspects of ecology and behavior, including home-range size (males, 300–500 km^2; females, 100–200 km^2), diet ($\geq$90% deer), annual adult survival ($\geq$75%), and litter size (two to four) [6], the SMM lion population is similar to those throughout the southwest [20].

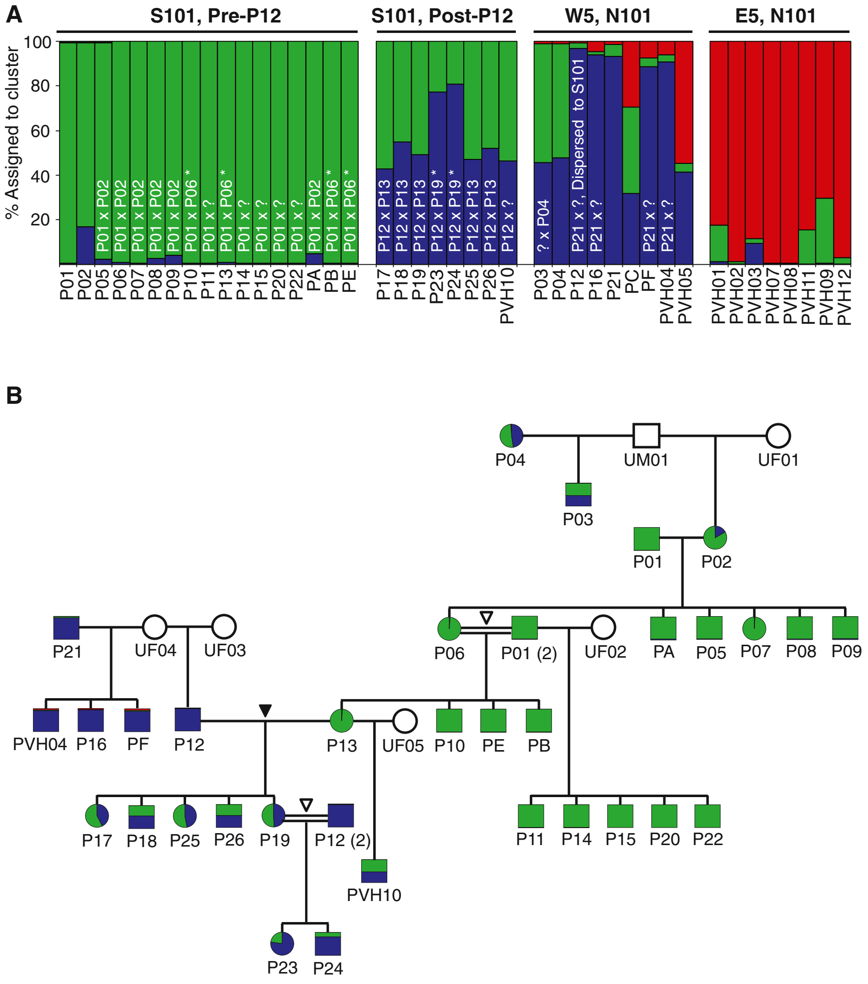

Figure 3. Genetic-Based Cluster Assignments and Recreated Pedigree Based on 54 Microsatellite Loci

(A) Results of program STRUCTURE for 42 mountain lions in the SMM region in Southern California, 2002–2012. The “S101, pre-P12” group is mountain lions from the SMMs, south of the 101 freeway (see Figure 1), before male P12 crossed the 101 freeway from the Simi Hills to the SMMs. The “S101, post-P12” group includes animals sampled in the SMMs that are the offspring of male P12 after he crossed the 101 freeway. “W5, N101” includes animals from the Simi Hills and Santa Susana Mountains, north of the 101 freeway. “E5, N101” includes mountain lions east of the 5 freeway in the San Gabriel Mountains and Verdugo Hills. White lettering for the first three groups indicates the known parentage based on the recreated pedigree. See also Figure S1.

(B) Pedigree for mountain lions in and around the SMMs, 2002–2012. The pedigree was constructed using the programs CERVUS and Colony (see the Supplemental Experimental Procedures). Colors for individual animals correspond to the genetic cluster assignments determined using STRUCTURE: green is the SMM cluster, and blue is the “W5, N101” or Santa Susana Mountains cluster. Symbols with two colors indicate animals with assignment to both clusters. Animals that were not sampled but whose presence is presumed are labeled “UF” for unknown females or “UM” for unknown males. Double lines and open triangles between animals indicate close inbreeding events, specifically father-daughter mating. The black triangle indicates the outbreeding event when P12, from north of the 101 freeway, bred with P13, from the SMMs. See also Figure S2 and Tables S3 and S4.

Very small populations are subject to Allee effects in which low growth rates result from low density, often caused by social disruption as individuals are too sparse to form social groups or find mates [24]. In the SMMs, the inverse has occurred as a small mountain lion population is at high density but lives in a spatially constrained area, resulting in social disruption through negative interactions between close relatives that normally would be rare or nonexistent. The result is reduced population health as indicated by low genetic diversity and increased inbreeding. Such “inverse Allee effects” leading to social disruption could be an important but largely unrecognized problem in isolated and densely packed urban environments.

Implications for Management and Conservation of Large Carnivores in Urban Landscapes

The importance of specific behavioral events such as dispersal, inbreeding, and killing of close relatives in this small, isolated mountain lion population has implications for conservation in fragmented landscapes. First, detailed behavioral and genetic monitoring may be critical for understanding the factors that threaten population persistence. Only through the collection of extensive demographic and behavioral data on most of the population were we able to identify the most important behaviors affecting population dynamics and genetic diversity.

Second, the maintenance and restoration of habitat connectivity is vital for small populations of large carnivores. Migration events between populations may not have to be frequent to maintain genetic diversity [25], and we have observed that one successful migrant can have a significant impact, especially in mountain lions, where individual males can have high reproductive success. However, the skewed reproduction in small mountain lion populations [26] can result in dominance of the gene pool by individual males, especially when close inbreeding is also occurring, which may be detrimental to population persistence. In the wolves at Isle Royale National Park, although a single male wolf immigrated into the population and increased genetic diversity, the effects were reversed by reproductive dominance of this individual and associated inbreeding [27, 28]. Connectivity is also important because stochastic effects, such as the loss of one dominant male through a vehicle collision, are more extreme and can result in extinction. Previous research on mountain lions in the Santa Ana Mountains suggested that an area of less than 1,100 km^2 was unlikely to support mountain lions without some immigration [29], and the SMMs are only about 660 km^2. In highly developed areas, the conservation of natural habitat on both sides of freeways and effective corridors across them [30] or translocations may be necessary if large carnivores are to persist in proximity to the megacities of the future.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.07.029.

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Effects of urbanization on cougar foraging ecology along the wildland–urban gradient of western Washington

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Abstract. Humans have dramatically altered ecosystem structure through landscape manipulation, often leaving refuge patches of suitable habitat for wildlife amidst inhospitable terrain. Large carnivores are especially vulnerable to such habitat modification because they tend to have low population densities and wide-ranging movements necessitated by their food requirements. Cougars (*Puma concolor*), unlike many other large carnivores, have demonstrated an ability to exploit resources in fragmented and managed landscapes. The influence of increasing landscape development on cougar foraging behavior, however, has yet to be fully elucidated. Accordingly, we investigated variation in cougar use of three prey types (synanthropes, ungulates, and rodents) along a wildland–urban gradient in western Washington to determine how urbanization affects the foraging ecology of this apex predator. We predicted that cougar diets would comprise more synanthropic prey (e.g., prolific urban species) and fewer deer as a function of increasing residential development. Generalized linear mixed model results showed that the odds of cougar predation on synanthropic prey did increase with urbanization. The odds of ungulate predation, however, remained relatively consistent across the wildland–urban gradient despite cougar use of black-tailed deer (*Odocoileus hemionus columbianus*) and elk (*Cervus canadensis*) increasing over time. These results suggest that cougar–ungulate predator–prey systems can persist in landscapes with substantial human presence. The odds of forest-associated rodent (*Castor* sp., *Aplodontia* sp.) predation decreased with increasing development, suggesting that urbanization may coincide with more intensive beaver management near residences and thereby reduce beaver and mountain beaver presence in exurban landscapes in western Washington. Most cougars exhibited similar diets, but certain individuals deviated significantly from the population averages characterizing use of all three major prey categories. This variation suggests that cougar population responses to urbanization are unlikely to be uniform and that cases of human–cougar conflict may be linked to individual cats, rather than the population as a whole.

Key words: building density; development; exurban; *Odocoileus hemionus; Puma concolor;* rodents; specialization; synanthropes.

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INTRODUCTION

Since the onset of plant and animal domestication ~12,000 yr ago (Diamond 2002, Price and Bar-Yosef 2011), humans have been reshaping ecosystems through landscape modification (Ellis et al. 2010, Moss et al. 2016*a*). Today, landscape development in the form of agriculture and urbanization are among the greatest drivers of species extinction and biodiversity decline worldwide (Pimm and Raven 2000, Maxwell et al. 2016). Urbanization, and the development of wild landscapes specifically, often happens in the form of residential sprawl, which creates a gradient of human disturbance at the interface of built and natural ecosystems (Radeloff et al. 2005, Conedera et al. 2015). Recent studies have shown that human activities can alter patterns of disturbance and resource availability along such gradients and that these effects may extend well into rural and even wildland areas (Palkovacs et al. 2012, McDonnell and Hahs 2015, Alberti et al. 2017). There remains a need, however, for a better understanding of how species and ecological communities respond to the varying amounts of development that characterize wildland–urban gradients.

Community assemblages along wildland–urban gradients are often shaped by differences in species' capacity to exploit anthropogenic resource subsidies and their tolerance for human proximity and disturbed landscapes (Markovchick-Nicholls et al. 2008, Ordeñana et al. 2010, Newsome et al. 2015*b*). In northeastern Illinois, USA, for example, urbanization has translated into changes to mesopredator community structure, as certain species, like raccoons (*Procyon lotor*), continue to increase in abundance, limiting resources for Virginia opossums (*Didelphis virginiana*) and striped skunks (*Mephitis mephitis*; Prange and Gehrt 2004). Large mammalian carnivores are especially vulnerable to human development as these species tend to have low reproductive rates, must roam widely in search of prey, and often come into conflict with humans over livestock depredation and personal safety (Cardillo et al. 2005, Ripple et al. 2014). Consequently, many large carnivores have experienced substantial population declines and range contractions in the face of ongoing anthropogenic landscape development (Laliberte and Ripple 2004, Newsome et al. 2016). Some carnivores, however, have shown the ability to adapt to living in human-dominated environments (Tigas et al. 2002, Newsome et al. 2015*a*). In Luxembourg, for example, the socio-spatial organization of stone marten (*Martes foina*) populations is largely unaffected by urbanization (Herr et al. 2009). In urban Chicago, USA, Newsome et al. (2015*a*) showed that individual variation in movement and diet facilitated the successful establishment of coyotes (*Canis latrans*) throughout the Chicago metropolitan area. Additional studies exploring carnivore use of human-modified landscapes could help to build a general framework for predicting which species are likely (and not likely) to exhibit population-level resilience to ecosystem disturbances (Weaver et al. 1996) and potentially aid wildlife managers in mitigating conflicts between humans and wildlife (Lowry et al. 2013, Moss et al. 2016*a*).

Cougars (*Puma concolor*) are solitary, far-ranging felids that are capable of occupying a broad range of habitat types in both temperate and tropical environments (Sunquist and Sunquist 2002). Historically, cougars were associated with wildland environments, but recent studies have revealed that cougars are capable of utilizing areas with an extensive human presence (Beier et al. 2010, Kertson et al. 2013, Wilmers et al. 2013). Though some studies across the western United States and southern Canada have indicated that cougar presence decreases as urbanization intensifies (Kertson et al. 2011*b*, Lewis et al. 2015*a*, Gray et al. 2016), cougars in urban environments have also demonstrated the capacity to adapt by changing their foraging behavior and temporal activity patterns (Knopff et al. 2014, Wang et al. 2015, Blecha et al. 2018). Cougars in urbanized ecosystems have also been found to increase their consumption of non-ungulate prey, which is presumably a by-product of increased availability due to landscape development (Smith et al. 2015, Moss et al. 2016*a*, *b*). As urbanization intensifies, overlap between cougar and human populations will increase, especially in areas where residential development extends into cougar activity spaces and wild landscapes. Thus far, however, only two studies from the same ecosystem in northern Colorado have addressed changes in cougar foraging behavior over time along a wildland–urban gradient (Moss et al. 2016*a*, *b*). No study has yet considered changes in the probability of particular prey species being killed by cougars as they exploit increasingly urbanized portions of the landscape. Additional longitudinal studies of this nature are crucial to broadening our understanding of how the intensity of urbanization functionally changes cougar ecology and for predicting how cougar populations will fare as urbanization continues to increase. Accordingly, we examined changes to cougar foraging behavior over time along an urbanizing wildland–urban gradient in western Washington.

In the state of Washington, many cougar populations overlap with exurban and suburban environments, making them ideal for long-term research on predator responses to anthropogenic disturbance. In western Washington at the foothills of the Cascade Mountains, cougars occur throughout a well-defined wildland–urban gradient (0–>10 residences/ha; Robinson et al. 2005, Kertson et al. 2013). Examination of cougar space use along this gradient revealed that resident cougars exhibited similar movement patterns in wildland and residential environments (Kertson et al. 2011*b*) but varied markedly in their space use. By inference, cougars in this system have been able to find suitable habitats and resources within a matrix of residential development while keeping interaction rates with humans low (1.6 interactions/1000 radio days; Kertson et al. 2013). Moreover, Kertson et al. (2011*a*) documented differential prey use across the gradient, suggesting that urbanization and corresponding residential development have shaped cougar diets in western Washington. The spatiotemporal relationship between building density and cougar diets in this system has not been investigated, however. Accordingly, we evaluated changes to cougar diets spatially across a wildland–urban gradient using kill site data collected during two study periods, the years 2004–2008 (termed hereafter as "study period 1") and 2013–2016 (termed "study period 2" hereafter), in a region where we were also able to quantify building density (per ha). Under the hypothesis that cougars adjust their foraging behavior to take advantage of widely available prey (Kertson et al. 2011*a*, Moss et al. 2016*a*), we predicted that increasing building density would be associated with an elevated presence of synanthropic species (e.g., prolific urban species; McKinney 2006, Moss et al. 2016, Alberti et al. 2017) in cougar diets, and a commensurate decrease in forest-associated ungulates and rodents that are generally taken in wildland portions of the study area (Kertson et al. 2011*a*). We also included a study period variable in our analysis to determine if any temporal changes to cougar diets occurred between the two data collection phases. Lastly, we hypothesized that while cougars would forage opportunistically, individuals would be likely to vary in their foraging responses to urbanization, mirroring the individual variation exhibited in their space use (Kertson et al. 2013).

METHODS

Study site

We examined cougar kill site locations in a 4450-km^2 study site encompassing portions of King, Snohomish, and Pierce counties in Washington, USA (590,000 E, 5,260,000 N; Fig. 1). Landownership within the study site was an amalgamation of state, federal, municipal, and private property. Major landowners included the Washington Department of Natural Resources, the United States Forest Service, City of Seattle, King County, Campbell Global, Hancock Forest Management, and Fruit Growers Supply Incorporated (King County GIS Center, 2016). Major cities and towns within the study area include Bellevue (population 139,820), Redmond (60,598), Issaquah (36,081), Snoqualmie (13,169), Duvall (7674), and North Bend (6679; US Census Bureau 2015).

The study site is topographically complex and characterized by a gradual east–west gradient spanning wildland, exurban (<2.5 residences/ha), suburban (2.5–10 residences/ha), and urban (>10 residences/ha) environments (Robinson et al. 2005, Kertson et al. 2011*b*). Private timberland, Washington Department of Natural Resources forest, and United States Forest Service holdings comprise the majority of the eastern portion of the study site. The majority of wildland spaces within the study area consist of temperate coniferous forests typical of the North Cascades ecoregion (Franklin and Dyrness 1973). The topographic, physiographic, and developmental characteristics of the study site are described at greater length in Kertson et al. (2011*b*, 2013).

Radio-tagging and GPS cluster analysis

We used trained dogs and cage traps to capture and radio-tag cougars throughout the study site from 2004 to 2008, and again from 2013 to 2016. Once captured, cougars were immobilized, given a physical examination, and outfitted with

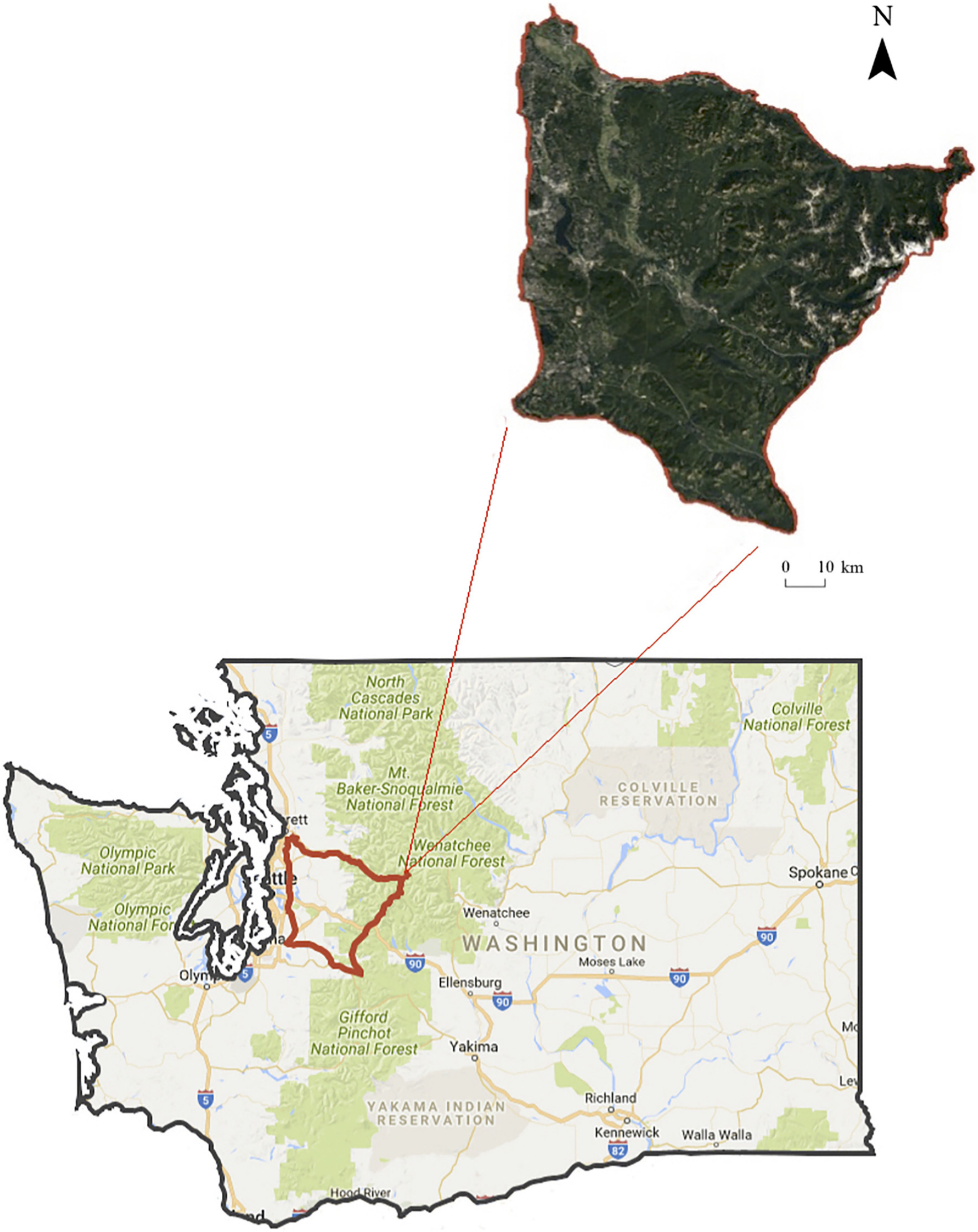

Fig. 1. Location of the 4450-km^2 cougar (*Puma concolor*) study site encompassing portions of King County, Snohomish County, and a small section of wildland in Pierce County (<75 km^2). The study site used by Washington's

(Fig. 1. *Continued*)
Department of Fish and Wildlife during period 1 was smaller (3500 km^2), although King County portions of the study site were identical. Residential and suburban development was concentrated in the western third of the study area with development densities generally decreasing from west to east.

a global positioning system (GPS) radio collar equipped with Vhf/Uhf download or Globalstar satellite uplinks (Models GPS-Simplex; Televilt, Lindesberg, Sweden, and GPS Plus-2; Vectronic Aerospace, Berlin, Germany). All captured cougars were anesthetized using a 10:1 mixture of ketamine hydrochloride and xylazine hydrochloride (Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) at a dosage of 8.8 mg/kg ketamine and 0.88 mg/kg xylazine and handled in accordance with University of Washington Institutional Animal Care and Use Committee (IACUC) protocol No. 3077-07. All capture methods have been vetted previously and described in detail elsewhere (Kertson and Marzluff 2010, Kertson et al. 2011*a*, *b*, 2013).

We programmed GPS radio collars to attempt a satellite fix for 180 s every four hours at 2:00, 6:00, 10:00, 14:00, 18:00, and 22:00 hours. The 4-h fix interval was chosen to maximize data acquisition and battery life (Cain et al. 2005, Kertson et al. 2011*b*). We identified potential kill site locations during study period 2 in accordance with the methodology used by Kertson et al. (2011*a*) during study period 1. Namely, we first plotted cougar relocations in ArcMap 10.3 and 10.4 (Environmental Systems Research Institute 2016) and Google Earth (Google, Mountain View, California, USA) and then defined location clusters as ≥3 GPS fixes occurring within an area ≤100 m^2 (methods by Anderson and Lindzey 2003 adapted to account for small prey items). We used a handheld GPS receiver (Model Etrex 20; Garmin, Schaffhausen, Switzerland) to navigate to the geometric center of the cluster, and we searched in concentric circles varying between 5 and 10 m apart (depending on visibility) out to the extent of the cluster radius (up to 100 m) or until prey remains were discovered. We recorded a GPS location at the kill site if prey remains were found that closely matched the dates during which the cluster was created and if we also found definitive evidence of cougar feeding behavior (e.g., carcass caching behavior, drag marks, hemorrhaging, skeletal remains, and cougar scat; Knopff et al. 2009, Kertson et al. 2011*a*, Wilckens et al. 2016).

Kill site assessment

Kill site assessment followed the same methodology during study period 2 as in study period 1. Namely, after confirming each kill site location, we adjusted kill site coordinates on-site to correspond to the location of the rumen. Cougars may cache a carcass 0–80 m from the initial kill location during subsequent feeding bouts (Beier et al. 1995), so designating the position of the rumen as the kill location allowed for more consistent assessment of kill site features. Whenever possible, we documented prey species, sex, age, condition, and relative carcass consumption (Kertson et al. 2011*a*). We determined prey sex in ungulates based on antler presence or absence, and prey age using dentition and patterns of tooth wear and replacement (Severinghaus 1949).

Statistical analysis

We used generalized linear mixed models (GLMMs) to test whether building density, a proxy for urbanization intensity (Theobald 2005, 2010), had an effect on the occurrence of certain prey items at cougar kill sites across the wildland–urban gradient. To create a building density predictor variable, we quantified urbanization within the study site using ArcMap 10.4 (Silverman 1986) and GIS parcel data from King and Snohomish counties, Washington, USA. We acquired parcel data for years 2007 and 2015 (King County) and 2004 and 2016 (Snohomish County) through the University of Washington Libraries media archive, along with the associated assessor's tables containing parcel attribute data, and created landscape categories based on Robinson et al. (2005) and Alberti et al. (2007), and urbanization was quantified as the density of built structures per hectare. We used the 2004 and 2007 shapefiles to approximate the extent of landscape development at kill site locations in both Snohomish and King counties during study period 1, whereas the 2015 and 2016 shapefiles were used to approximate landscape development at kill sites during study period 2. Parcels with forms of development such as parking lots, residences, office spaces, shopping centers, major roads, schools, hospitals, and government institutions were used to generate building density raster layers. In other words, the measure of urbanization in this study can be considered the density of actual physical obstructions to cougar movement across the landscape. Regression models used by Alberti et al. (2007) indicated that land-use and housing density data along Washington's wildland–urban gradient are good predictors of land cover composition and configuration.

To quantify building density at each cougar kill location throughout the study site, we determined the year in which each kill was made and then calculated building density at that location from the most temporally relevant parcel layer (e.g., the King County 2004 parcel layer was used to measure building density at a kill in King County from 2005). Once all kills had a temporally appropriate representation of building density, we extracted raster cell values for all kill site locations. The resulting values represented a continuous building density variable per hectare. Average building density at kill site locations was 0.05 structures/ha. All kills that occurred in the Pierce County portion of the study area occurred in wildland areas, obviating the need to quantify building density for Pierce County kill sites. To address the hypothesis that building density would affect the occurrence of different prey species in cougar diets, we modeled the type of species killed using logistic regressions with building density, cougar sex, and study period as independent variables, and cougar ID included as a random effect. To achieve sample sizes necessary for modeling of cougar diets, we grouped prey species into three ecologically relevant categories: ungulates, synanthropes, and rodents. These prey categories closely mirror those used by Moss et al. (2016*b*), who grouped prey into meaningful categories based on isotopic signatures. The ungulate group in this study consisted of species heavily preyed upon by cougars in western Washington: namely, black-tailed deer (*Odocoileus hemionus columbianus*), elk (*Cervus canadensis*), and mountain goat (*Oreamnos americanus*). Rodents (i.e., beaver, *Castor canadensis*; mountain beaver, *Aplodontia rufa*) are largely wildland obligates in our system. Synanthropic species included coyotes, raccoons, opossums, and domestic species. Whereas coyotes are capable of occupying all land cover types in the study area, coyote predation by cougars often occurred along the urban fringe in western Washington, supporting the inclusion of this species in the synanthrope group. Null models contained only a single fixed intercept. We considered all possible interaction effects among fixed predictor variables in candidate models for each response.

We built candidate model sets (i.e., various predictor variable combinations) for each of the three prey categories, with a binary response of either 1 for the prey type of interest (e.g., synanthropes) or 0 for the other two prey categories combined (e.g., ungulates, rodents). We then ranked candidate models based on differences in the Akaike information criterion (AIC) in accordance with Burnham and Anderson (2002). Differences in AIC (ΔAIC) were calculated relative to the best model, and we only considered models with ΔAIC ≤2 relative to the best model to be competitive (Burnham and Anderson 2002). We considered fixed and random effects significant if 95% confidence intervals (CIs) for their respective coefficient estimates did not overlap 0. Profile CIs were used to evaluate the standard deviation of the cougar ID random effect in each top model, and standard Wald CIs were used to quantify the uncertainty of fixed effect estimates. Odds ratios and their associated 95% CIs were used to evaluate the effect magnitude of the fixed and random effects in each of the top models and were considered significant if they did not overlap 1.0. We built all models using the glmer and glm functions in the lme4 package (Bates et al. 2016) in the R statistical package (R Core Team 2016).

Results

Cougar foraging behavior

We evaluated diets from 20 individual cougars to determine whether cougar diets varied spatially (i.e., across the urban gradient), and whether cougar diets changed over time (i.e., between study periods). Overall, cougar diets included 15 different prey species (Fig. 2), with black-tailed deer (*n* = 407 kills) and American beaver (*n* = 70 kills) accounting for the majority of cougar kills based on investigation of GPS clusters (Table 1). Spatially, synanthropic species tended to occur in areas with greater building density than areas associated with rodent and ungulate kills (Appendix S1: Fig. S1). The study period fixed effect was only included in the ungulate and rodent top models (Table 2), indicating little temporal change in cougar predation on synanthropes. The distributions of kill site locations from study period 1 and study period 2 were roughly equivalent across the wildland–urban gradient, minimizing the likelihood that differences in cougar diets between study periods were a function of differences in sampling effort in residential areas (Fig. 3; Appendix S1: Table S1). Despite synanthropic species occurring in areas with greater building density, building density changed little among prey groups across time, and the average residential density at which kill site locations occurred did not vary markedly across all years of the investigation (Fig. 4).

The occurrence of synanthropic species in cougar diets was strongly tied to individual cougar identity, as well as the extent of urbanization (Fig. 5). Namely, the top synanthrope model included building density as the sole fixed effect (Table 2) and indicated that there was a multiplicative increase of 4.92 (95% CI: 1.09, 22.23) in the odds of cougar predation on synanthropic species with each additional building per hectare. The cougar random effect in this model accounted for a considerable amount of variability in synanthrope usage, where the estimated standard deviation of the random effects was $\hat{\sigma} = 1.26$ (95% CI: 0.68, 2.26). Predicted probabilities of synanthrope kills calculated at average building density were similar across the majority of cougars in this study (Fig. 6). Three individuals (F30, M324, and F325), however, differed significantly from the study average in their predicted probability of predation on synanthropic prey.

There was a high probability of ungulate predation across the wildland–urban gradient (Fig. 5), and individual cougar identity was also the dominant driver of cougar predation on ungulates. Specifically, the top ungulate model included fixed effects for sex and study period and the random cougar effect with no interaction

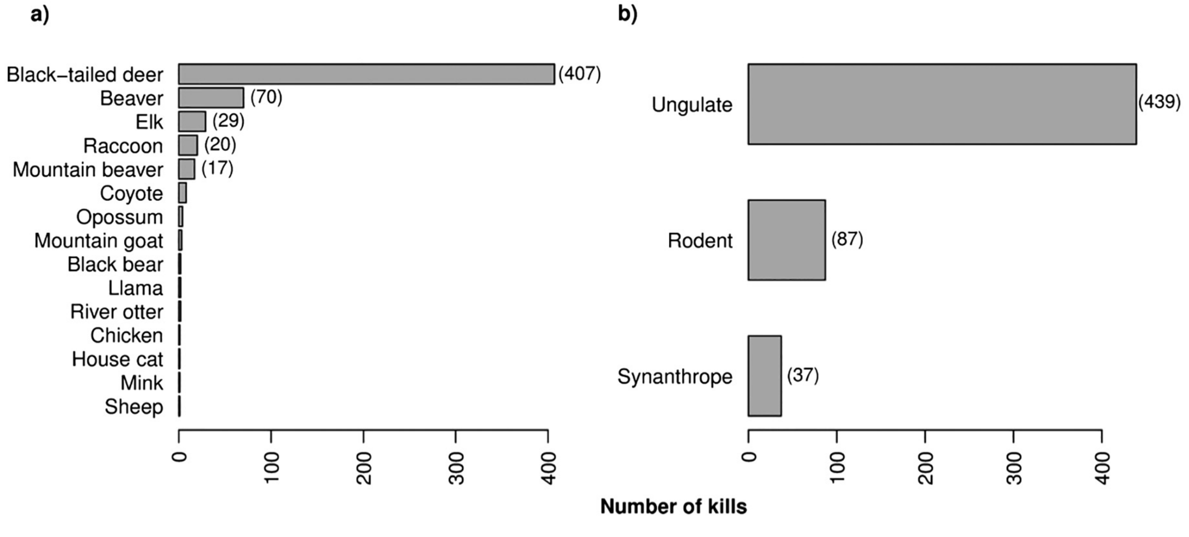

Fig. 2. (a) Numbers of prey individuals killed by cougars (*n* = 568) across all study years, grouped by species; and (b) the numbers of cougar kills included in each of the three prey categories: ungulates (black-tailed deer, elk, mountain goat); rodents (beaver, mountain beaver); and synanthropes (raccoon, coyote, opossum). Two black bear kills, two river otter kills, and one mink kill were removed when grouping prey because these species, though considered wildland mammals, are not rodents or ungulates. Kill numbers for species and prey groups with ≥20 kills are indicated in parentheses.

Table 1. Percentage of kills by prey type (ungulate, rodent, or synanthrope) for each individual cougar.

				Building density			Percentage of kills		
Cat ID	Sex	Period	Kills	Mean	Min.	Max.	Ung.	Rod.	Syn.
136	F	1	64	0.0	0.0	0.1	75	22	3
137	F	1	18	27.7	0.0	126.9	89	11	0
325	F	1	8	3.0	0.0	13.2	62	0	38
327	F	1	18	0.0	0.0	0.0	89	11	0
331	F	1	7	0.0	0.0	0.0	100	0	0
131	M	1	21	11.1	0.0	70.5	95	0	5
309	M	1	10	2.7	0.0	13.4	50	40	10
323	M	1	78	2.5	0.0	38.8	50	45	5
324	M	1	43	10.9	0.0	80.6	49	23	28
326	M	1	7	49.9	0.0	208.2	71	14	14
6	F	2	35	0.0	0.0	0.0	97	3	0
8	F	2	34	0.0	0.0	0.0	94	6	0
12	F	2	21	11.7	0.0	32.5	81	5	14
14	F	2	39	2.2	0.0	26.1	97	3	0
17	F	2	49	0.0	0.0	0.0	86	12	2
30	F	2	12	7.1	0.0	21.5	67	0	33
34	F	2	16	30.7	11.9	57.1	88	0	12
35	F	2	26	1.6	0.0	14.6	85	8	8
137	F	2	33	0.0	0.0	0.2	88	12	0
5	M	2	10	3.6	0.0	36.0	100	0	0
37	M	2	14	12.4	0.0	117.1	79	14	7

Notes: Also shown are sex, study period, number of kills, and building density (mean, minimum, and maximum) across all kill sites for each cougar. Building density is expressed as number of buildings per 100 ha for visualization purposes.

Table 2. All candidate models with a ΔAIC ≤ 2 when compared to the top model for each prey type.

Response variable	Predictor variables	AIC	ΔAIC	Model likelihood	AIC weight
Synanthrope	Building density, r. effect	251.0	0.0	1.00	0.24
	Sex, building density, r. effect	252.4	1.4	0.50	0.12
	Study period, building density, r. effect	252.4	1.4	0.50	0.12
	R. effect only	252.9	1.9	0.40	0.09
	None (null model)	275.0	24.0	0.00	0.00
Ungulate	Sex, study period, r. effect	537.0	0.0	1.00	0.16
	Sex, study period, sex–study period interaction, r. effect	537.6	0.6	0.76	0.12
	Study period, r. effect	537.6	0.6	0.74	0.12
	Sex, r. effect	537.7	0.7	0.71	0.12
	Sex, study period, building density, r. effect	538.6	1.6	0.45	0.07
	R. effect only	539.7	2.7	0.26	0.04
	None (null model)	595.7	58.7	0.00	0.00
Rodent	Sex, study period, building density, r. effect	426.6	0.0	1.00	0.26
	Sex, study period, building density, sex–study period interaction, r. effect	428.1	1.5	0.48	0.12
	Study period, building density, r. effect	428.5	1.8	0.40	0.10
	Sex, study period, building density, study period–building density interaction, r. effect	428.5	1.9	0.39	0.10
	Sex, study period, building density, sex–building density interaction, r. effect	428.6	2.0	0.37	0.09
	R. effect only	440.9	14.3	0.00	0.00
	None (null model)	486.7	60.1	0.00	0.00

Notes: Null models (intercept only) and models only including random cougar effects are shown for reference. Random effect indicated with r. effect. AIC, Akaike information criterion.

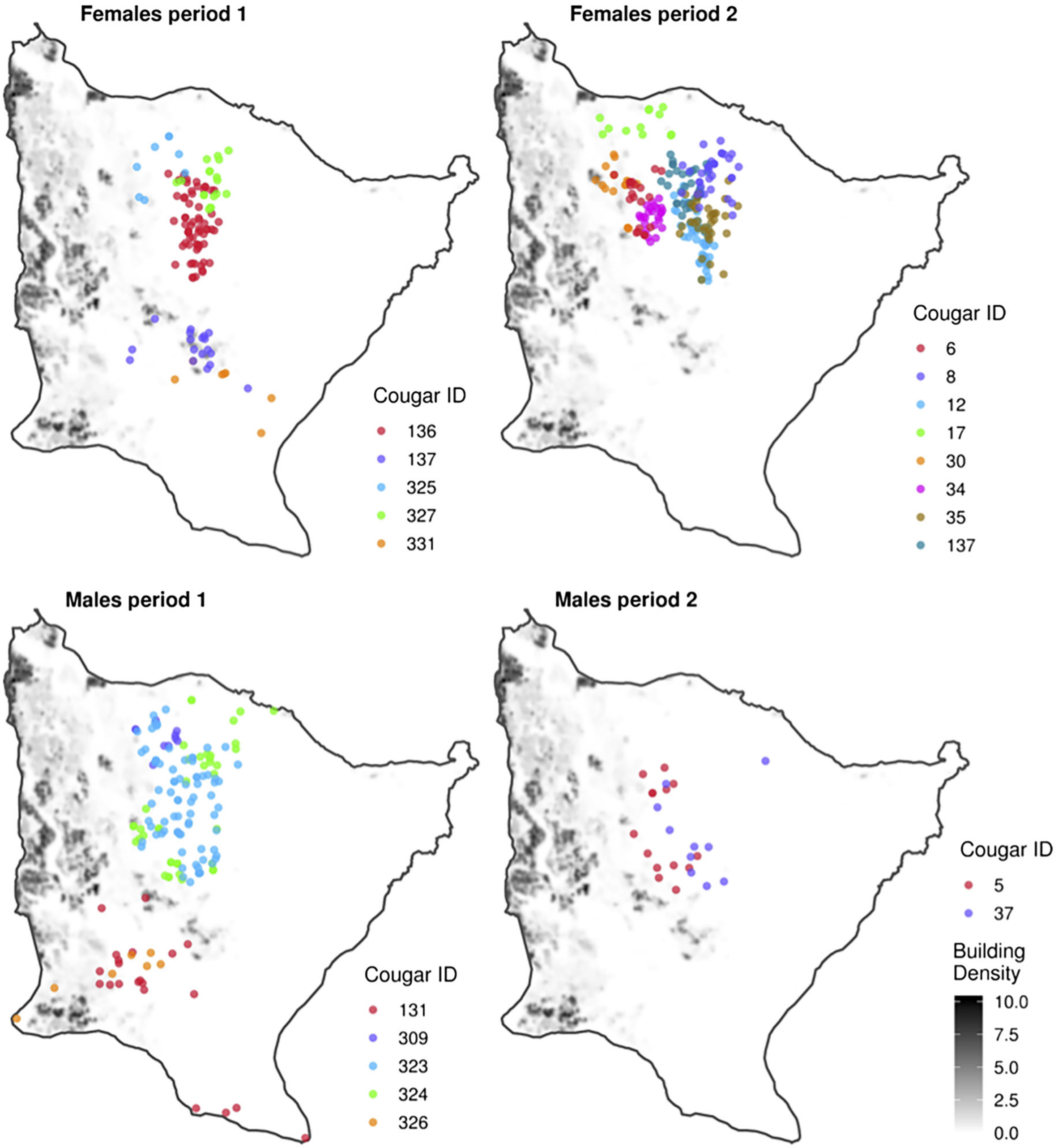

Fig. 3. Cougar kill site distribution across the study area, with panels distinguished by sex and study period (cougar ID indicated). Urbanization across the study area is indicated by the gray scale of 0–10 buildings per hectare.

effects (Table 2). This model suggested that the odds of preying on an ungulate were 2.16 times greater for females compared to males (95% CI: 0.91, 5.15) and were 2.06 times greater in period 2 compared to period 1 (95% CI: 0.92, 4.57), but the 95% CIs for these odds ratios both included 1.0. The estimated standard deviation of the cougar random effect, on the other hand, had a 95% CI that did not overlap zero ($\hat{\sigma} = 0.62$, CI = 0.23, 1.17) indicating significant differences in the use

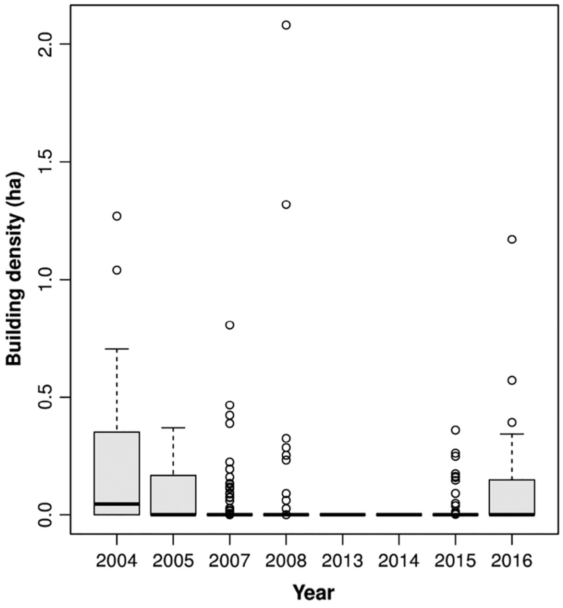

Fig. 4. Average building density at all cougar kill locations during every study year since 2004. Despite a few outlying kills occurring in high-density areas in 2004, 2008, and 2016, kills across years occurred on average in areas with <0.5 built parcels per hectare.

of ungulates among individuals in this study. Specifically, the predicted probabilities of ungulate kills were similar for the majority of cougars; however, three individuals (M309, M323, and M324) exhibited ungulate predation probabilities that were significantly lower than the average study animal (Fig. 6).

The intensity of urbanization (Fig. 5) and individual cougar identity were both important drivers of cougar predation on rodents. Namely, the top rodent model included the fixed effects of sex, study period, and building density, along with the random effect for individual cougars, with no interactions among predictors (Table 2). Additionally, the odds of a rodent kill were estimated to decrease by a multiplicative factor of 1.94 (95% CI: 1.16–3.23) for every increase of just 0.1 buildings per hectare. The odds of a rodent kill for males were 2.49 times greater than those for females (95% CI: 1.07–5.77), and 2.61 times greater in study period 1 than in study period 2 (95% CI: 1.15–5.96). The random effect for cougars had a marginal contribution to the top rodent model after accounting for the other variables ($\hat{\sigma} = 0.49$, 95% CI: 0.00, 1.08). When the

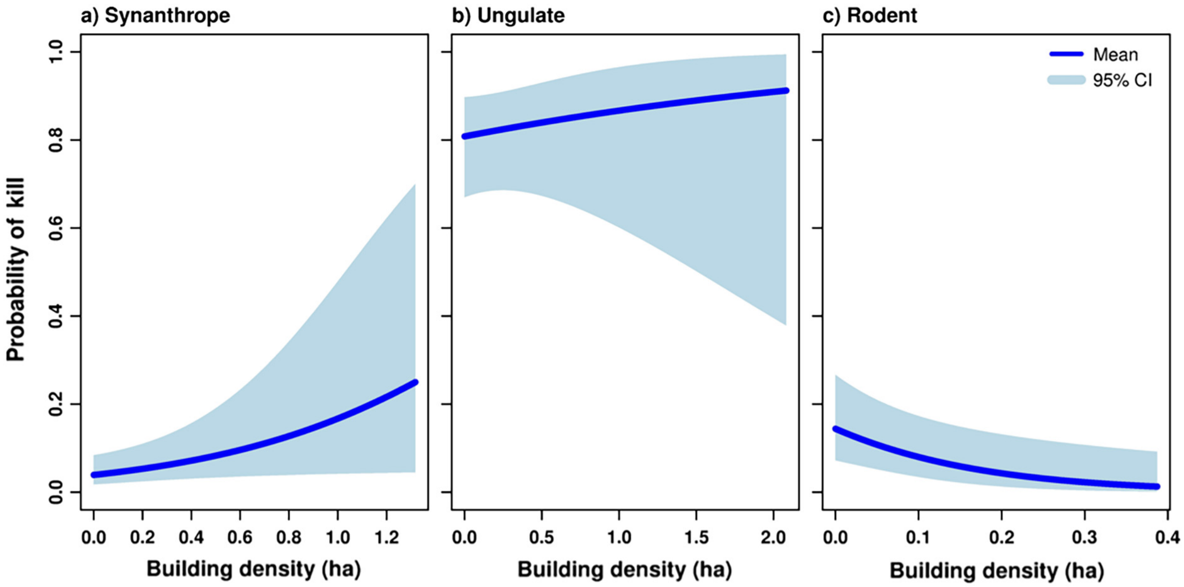

Fig. 5. The probabilities of a cougar kill by prey type (synanthrope (a), ungulate (b), rodent (c)) as a function of increasing building density. Dark blue lines indicate probability estimates and shaded regions indicate 95% confidence intervals. Both ungulate and rodent plots are based on females from study period 1 as probability estimates under both models differed by sex and study period.

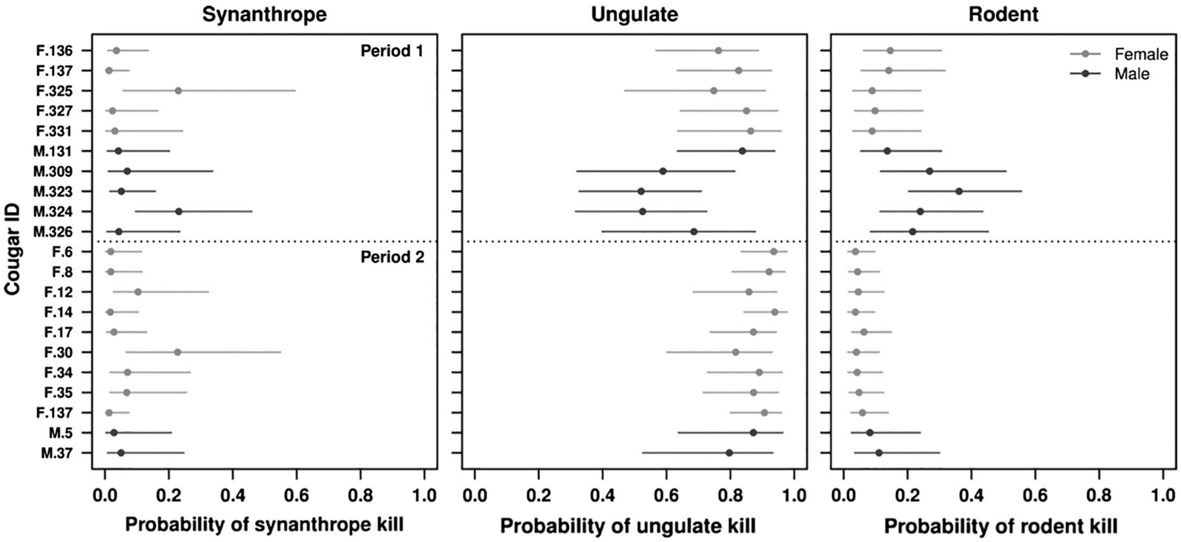

Fig. 6. Predicted probabilities of kills by prey type with associated 95% confidence intervals for each individual cougar. Predictions are from top models, and predictions for the synanthrope and rodent models are calculated at the average building density across all kill sites.

random effect was dropped from the top model, the change in AIC was only 1.57, indicating that the other variables accounted for much of the variability among individual cougars. However, one cougar (M323) had a significantly higher predicted probability of rodent kills at average housing density when compared to the average cougar in this study (Fig. 6).

Discussion

Conflicts with humans remain the key threat to carnivore persistence globally (Chapron et al. 2003, Ripple et al. 2014), and as human populations increase, it is likely that a growing number of species will come into contact with people and anthropogenically altered landscapes (Bateman and Fleming 2012). Urbanization, ranging from low- to high-density residential development, continues to be a principal cause of broad-scale landscape change and can alter animal behavior (Lewis et al. 2015*b*) as well as ecological processes and community structure (Shochat et al. 2006, McKinney 2008, Ordeñana et al. 2010). Based on the findings of Kertson et al. (2011*a*), Smith et al. (2016), Moss et al. (2016*a*), and Blecha et al. (2018), we predicted that cougars foraging along a wildland–urban gradient in western Washington would increase their reliance on synanthropic prey species as a positive function of building density. Consistent with this prediction, building density was a significant predictor of synanthrope predation. The study period variable was not a significant predictor of predation on synanthropic species, suggesting that the study period 1 cougar cohort was similar to the cohort from study period 2 in their predation on synanthropes. As predicted, rodent predation was negatively associated with building density, and rodent predation significantly decreased between the study periods. The change in rodent predation between the study periods may simply be a function of differences in cougar cohorts, as male M323 (study period 1) accounted for 50% of rodent predation during this investigation. Ungulates were consistently the top prey item over the course of the study, and the degree of urban development was not a significant predictor of the use of these prey species, suggesting that under certain conditions, cougars may be able to continually rely on their primary prey even when their environment is subject to anthropogenic changes. Notably, individual differences accounted for a significant amount of variation in the use of all three prey groups. By implication, understanding patterns of individual variability may be key to predicting how adaptable large carnivores respond to urbanization.

The odds of synanthrope predation by cougars increased as a function of building density, confirming our expectation that individuals exposed to increased opportunity to exploit urban prey would do so. Hence, our findings build on several previous studies (Kertson et al. 2011*a*, Moss et al. 2016*a*, Smith et al. 2016, Blecha et al. 2018) that underscore the dietary flexibility of cougars and suggest that individuals in urbanized environments may be able to persist and perhaps mitigate intra-specific competition for traditional prey by exploiting human-associated food. We also observed significant individual variation in synanthrope usage. It is possible that these differences among cougars owed to home range arrangement on the landscape, whereby individual cougar diets differed simply because of variation in the availability of prey items within their respective home ranges (i.e., because of differences in ecological opportunity; Araújo et al. 2011). The kill site locations for cougars in this study overlapped, however, and therefore do not strongly support this idea. We nevertheless acknowledge that the differences in predation on any of the prey types we documented could have stemmed at least in part from intra-specific variation in access to prey but were unable to address this possibility because no prey data were available in our study system. Individual specialization is an alternative explanation for the observed variability in the use of synanthropes, with a recent review of predator selectivity indicating that many generalist predator populations consist of individual dietary specialists, with part of the specialization associated with their phenotype (Pettorelli et al. 2011). Accordingly, the responses of particular cougars to varying degrees of urbanization may depend on divergent prey preferences possibly stemming from inheritance, learning, and/or competition (Araújo et al. 2011).

Contrary to our expectation, the odds of ungulate predation by cougars remained relatively stable across the wildland–urban gradient, suggesting that cougars were able to consistently rely on wild ungulates, particularly black-tailed deer, despite potential differences in ungulate availability as a function of urbanization. Indeed, the three cougars (M309, M323, M324) that deviated significantly from other study animals in their predation on ungulate prey had the majority of their kill site locations in wildland portions of the study area. The availability of black-tailed deer throughout the wildland–urban gradient might be tied to urbanization (Bender et al. 2004*a*, *b*), but contrary to our expectation of an inverse relationship, low-density development may actually augment ungulate use of residential landscapes and these individuals may be particularly susceptible to predation by cougars (Blecha et al. 2018). More importantly, our observations of the continued reliance on black-tailed deer and limited use of livestock by cougars suggest that some predator–prey systems can be maintained at the wildland–urban interface over an extended period of human population growth.

In accordance with our expectation, the odds of rodent predation decreased significantly as building density increased across the wildland–urban gradient. Previous cougar research in western Washington revealed that the majority of beaver and mountain beaver kills occurred within 100m of water and that cougars frequently foraged along hard habitat edges (Kertson et al. 2011*a*). Accordingly, our results suggest that these areas where cougars target beavers and mountain beavers may disappear with urban development and are therefore consistent with the idea that increasing urbanization in western Washington reduces the quality and availability of riparian habitats for cougars. Individual cougars differed in their use of rodents, with males exhibiting significantly greater use of rodents than females. M323 was responsible for a substantial portion of beaver kills during this investigation and may be the primary reason for this demographic disparity in rodent predation. By inference, any dietary shift at the population level induced by diminishing rodent habitat through urbanization is likely to be modest relative to those produced by changes to synanthrope and ungulate availability.

The changes to cougar diets in response to urbanization reported in this study are similar to previous studies elsewhere and suggest widespread applicability of our findings. For example, housing density influenced cougar consumption of small prey (<20 kg) in central California (Smith et al. 2016) and prey switching behavior among cougars in northern Colorado (Moss et al. 2016*b*). Although Kertson et al. (2011*a*) noted individual patterns in foraging behavior among cougars, to our knowledge no study to date has modeled individual differences in the use of particular prey types along a wildland–urban gradient. In the present study, individual differences among cougars were a significant predictor of predation on all three prey groups, and the dominant driver of cougar use of synanthrope and ungulate prey. This pattern of individual variation in cougar diets mirrors the individual differences in space use documented by Kertson et al. (2011*b*) in the same system. It also suggests that cougar population responses to urbanization, and other forms of human disturbance, are unlikely to be uniform, and therefore that understanding the drivers that cause individuals to specialize on certain prey types is key to predicting how cougar populations will be shaped by anthropogenic landscape modification.

Investigation of cougar predation patterns in western Washington using cluster methodology allowed for the detection of non-ungulate prey items but was not without its limitations (Kertson et al. 2011*a*). For example, kill site examination through GPS cluster analysis has been shown to skew detection rates of predation events toward larger-bodied prey in other large carnivores (e.g., gray wolves, *Canis lupus*; Webb et al. 2008). Additionally, despite similar fix rates among GPS collars in study period 1 and study period 2 (80–95%), data transmission rates differed between collar types. The Vectronic GPS Plus GPS collars used during study period 1 achieved 100% data retrieval through the download on demand capability. Full data retrieval during study period 1 provided adequate opportunities for the detection of predation events spanning <24 h (Kertson et al. 2011*a*). The GPS Plus GlobalStar collars used during study period 2, however, frequently had data transmission rates of 60–70%, providing only a subset of the GPS location data and potentially weakening detection of clusters spanning <24 h. It is therefore possible, owing to lower detection probability for small prey, that differences in data transmission between the study periods contributed to a greater proportion of black-tailed deer predation events in study period 2. The individual variation in cougar diets revealed here occurred both during and across the two study periods, however, suggesting that the results of this investigation were not simply a function of methodological variation.

Large carnivores are controversial species whose management and conservation are complicated by broader psychological, political, and socioeconomic issues (Treves and Karnath 2003, Chapron et al. 2014, Ripple et al. 2014). Like many other large carnivores, cougars are periodically involved in conflicts with livestock producers and rural residents (Gilbert et al. 2016). Wildlife professionals also frequently feel considerable pressure to reduce large carnivore populations in an effort to bolster ungulate populations (Todd 2002, Hurley et al. 2011). Experimental efforts to reduce depredations and change ungulate demography through broad-scale predator removal have proven to have minimal effect on prey populations (Hurley et al. 2011), with studies on coyote (Austin et al. 1977, Trainer et al. 1981) and cougar (Robinette et al. 1977, Logan and Sweanor 2001) removal exhibiting variable results on mule deer survival. Alternatively, targeted predator management has proven useful in minimizing livestock depredations by wolves in Montana, Idaho, and Wyoming (Poudyal et al. 2016). Though we focused on a relatively small sample of cougars, our results reveal that certain individuals deviated markedly from the average usage of three prey categories. Thus, they provide additional evidence that management actions targeting individual animals are likely to be more effective in reducing human conflict with cougars, and potentially other large predators, than indiscriminate population reduction.

Cougars in Washington, as well as other predators globally, present unique conservation challenges because of human safety concerns and predation on domestic species (Campbell and Lancaster 2010, Campbell 2013). Yet, our results indicate that despite individual dietary differences, most cougars exhibited similar diets that were dominated by wild ungulates across the wildland–urban gradient and in both study periods. This pattern has implications for wildlife management and human–cougar coexistence. First, cougars in our system relied heavily on black-tailed deer, so promoting healthy native ungulate populations in wildland–urban areas may be a feasible approach to minimizing cougar use of domestic species along urban gradients. By the same token, minimizing anthropogenic subsidies for deer and other food resources for deer near homes could be an effective approach for keeping both deer and foraging cougars away from residences.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2605/full behaviour of the various complexes is the same, but they exhibit profoundly different emission properties, we conclude that the specific nature of the bridge is the key to the colour switching phenomenon. It is well known that electron conduction, stabilization and delocalization on such bridging ligands depend on the geometry, energetics and structural features of the molecules[19–21]. Furthermore, use of different polymers with a higher-energy LUMO level (the HOMO level is chosen to be the same)—so that electron transfer mediated by the Ru complex cannot populate their excited state—did not result in green emission at reverse bias.

Symmetric devices with Au as anode and cathode have symmetric emission properties (that is, they show red emission at both forward and reverse bias), clearly indicating that an asymmetry in the device's charge injection behaviour is needed for the differentiation of the two possible mechanisms of light emission in the [Ru(ph)$_4$-Ru]$^{4+}$ PPV system. As the work functions of the ITO and Au contacts are energetically comparable, and the red/green switching behaviour is also seen when Au is replaced by Al, influences other than simple energetics must also have a role in allowing the stepwise electron transfer at reverse bias; we intend to study these influences in greater detail in the near future. □

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Fingerprints of global warming on wild animals and plants

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Over the past 100 years, the global average temperature has increased by approximately 0.6 °C and is projected to continue to rise at a rapid rate[1]. Although species have responded to climatic changes throughout their evolutionary history[2], a primary concern for wild species and their ecosystems is this rapid rate of change[3]. We gathered information on species and global warming from 143 studies for our meta-analyses. These analyses reveal a consistent temperature-related shift, or 'fingerprint', in species ranging from molluscs to mammals and from grasses to trees. Indeed, more than 80% of the species that show changes are shifting in the direction expected on the basis of known physiological constraints of species. Consequently, the balance of evidence from these studies strongly suggests that a significant impact of global warming is already discernible in animal and plant populations. The synergism of rapid temperature rise and other stresses, in particular habitat destruction, could easily disrupt the connectedness among species and lead to a reformulation of species communities, reflecting differential changes in species, and to numerous extirpations and possibly extinctions.

Many studies have examined biological changes in relation to climatic change[4,5], but generally they are concentrated in particular regions or examine a limited set of taxa. To test whether or not a coherent pattern exists across regions and taxa that is consistent with predictions of expected change, we used two types of meta-analyses on these studies: vote counting and the regression-slope model (see Methods). One advantage of meta-analyses is that a broad spectrum of findings can be combined, including those for which statistical significance has not been shown. We examined thousands of articles, including those assembled by Working Group II of the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC TAR WGII)[6]. Of these, we included in our analyses only those that (1) examined a span of at least 10 years, (2) found that a trait of at least one species shows change over time, and (3) found either a temporal change in temperature at the study site or a strong association between the species trait and site-specific temperature. Because we were looking for trends, we also excluded studies examining climatic cycles, such as North Atlantic Oscillation and El Niño/Southern Oscillation. We divided 143 studies that met our criteria into two 'tiers': those demonstrating a statistically significant trend for at least one species examined (tier 1, most of which were used as the methodological basis for conclusions in the IPCC TAR WGII[6,7]) and those in which statistical significance was not shown by the study's authors (tier 2), usually because no statistical tests were applied. We performed our analyses for each tier taken separately and for the two combined. Appendices 1 and 2 of the Supplementary Information provide the data and citations

Table 1 **Summary statistics for meta-analyses**

	Significant species	Nonsignificant species	Combined species
Number of species changing	586	882	1,468
Number changing in expected direction	482	708	1,190
Percentage in expected direction	82.3%	80.4%	81.1%
90% confidence interval for percentage in expected direction	73.4–88.6%	70.5–87.4%	74.2–86.5%
Effect size (δ)	-0.09	-0.23	-0.23
90% confidence interval for δ	-0.12 to -0.06	-0.30 to -0.14	-0.29 to -0.17
Standard error for δ	0.0004	0.0023	0.0014
Correlation coefficient (r)	-0.05	-0.12	-0.12
90% confidence interval for r	-0.06 to -0.03	-0.16 to -0.07	-0.15 to -0.09
Standard error for r	0.0002	0.0012	0.0007

A breakdown of values for those species or groups of species that were found, in the studies examined, to have statistically significant trends for various traits and for those that were not statistically significant. In addition, values are listed for the combination of these two categories of species or species groups.

for all of the studies used in our meta-analyses.

We focused on temperature change and ignored other climatic changes, such as precipitation, because the biological effects of temperature are often better understood for most of the organisms examined. Explicitly considering drought in our analyses would have allowed us to include many more studies, particularly from the Southern Hemisphere, but attributing local droughts to globally coherent patterns of climatic changes can often be difficult. We do, however, recognize that factors influencing populations interact in complex ways: temperature can exert its influence, for example, by affecting moisture availability.

Four types of change in species' traits due to warming may be possible. First, the density of species may change at given locations, and the ranges of species may shift either poleward or up in elevation as species move to occupy areas within their metabolic temperature tolerances. Second, because many natural history traits of species are triggered by temperature-related cues, changes could occur in the timing of events (phenology), such as migration, flowering or egg laying. Third, changes in morphology, such as body size, and behaviour may occur. Fourth, genetic frequencies may shift.

Attributing observed changes in populations of plants and animals to climatic change, specifically temperature increases, is possible because we expect the trends created by the large-scale pressure of global warming to show widespread, predictable and concordant patterns of change. In addition, we expect these changes to be concentrated in areas where temperature changes are largest (that is, at higher latitudes and altitudes) and for changes to be less evident elsewhere. Climate change is only one of a long list of pressures that influence the distributions and health of populations, as well as traits such as timing of activities and processes. These other pressures (for example, habitat modification, pollinator loss and exotic species introductions) often result in localized (often around centres of human populations) or multidirectional patterns of alterations to populations of species. To document a strong role for climate change in explaining many of the observed changes in animal and plant populations, we looked for repeated examples occurring over long temporal and broad spatial scales that showed unidirectional changes predicted by our understanding of the physiological tolerances of species to temperature. The predicted result, or fingerprint, of an underlying consistent shift in a large-scale pattern shown by many species around the globe, coupled with an understanding of the possible causal mechanisms, provides confidence in attributing observed species changes to climatic change. The 85 tier 1 studies and 58 tier 2 studies found strong changes occurring around the globe in various types (taxa) of animals and plants (see Supplementary Information). The meta-analyses we used to analyse the findings of these studies were the vote-counting method[8] and the regression-slope model[9]. We applied the vote-counting method to three different categories of data: 1) the 587+ species or groups of species ('+' because some studies do not provide numbers) in tier 1 (see Methods) that show statistically significant change; 2 the 886+ species or groups of species in both tier 1 and tier 2 that show statistically nonsignificant change or where the significance was unknown; and 3) the combined species (1,473+) showing change. For all three categories, the percentage of species changing in the expected direction was around 81% with a 90% confidence interval ranging from 71% to 89% (Table 1). The meta-analysis results of effect sizes and correlation coefficients were statistically different from zero ($P < 0.05$), which means that we can reject the null hypothesis of equal change in both the expected and opposite directions. Consequently, even this fairly low-powered vote-counting meta-analysis indicates that most changes are consistent with our understanding of how temperature change influences various traits of a variety of species and populations from around the globe. Hence, we can safely state that there has probably been a discernible impact of recent global warming on animals and plants.

The actual amount of change shown can be determined for those studies that examined shifts in spring phenologies. The 61 studies that investigated the change in timing of events occurring within the

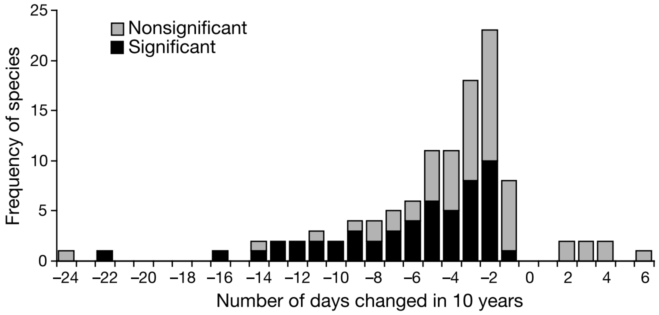

Figure 1 Frequency distribution of species and groups of species (see text) with a temperature-related trait changing by number of days in 10 years. No data were tabulated for species showing zero days changing in ten years (see Methods).

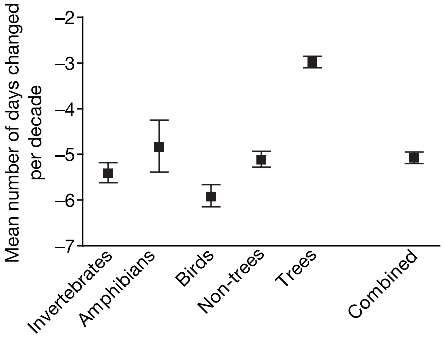

Figure 2 Means ± s.e.m. of days changed for the given groups of species. The 'Combined' category includes only those species tallied in the groups of species (that is, data for the one mammal, two fish and zooplankton are not included).

past 50 years examined a total of 694 species or groups of species. Our meta-analyses of these species indicate that over an average decade within the past 50 years, a statistically significant change towards earlier timing of spring events has occurred. The number of days changed per decade for a given species or species group ranges from 24 days earlier per decade for the breeding of North American common murre (*Uria aalge*) to 6.3 days per decade later for the breeding of North American Fowler's toad (*Bufo fowlen*) (Fig. 1). Using the regression-slope model[9] (see Methods), we found that the estimated mean number of days changed per decade for all species showing change in spring phenology is 5.1 days earlier (s.e.m. ± 0.1; Fig. 1). When the data are grouped by statistical significance, the estimated mean of the species with nonsignificant findings is closer to zero than that for species with significant findings (-3.4 ± 0.1; -6.9 ± 0.1, respectively; negative numbers indicate an earlier shift). The latter mean is understandably earlier than the former, given that regression analysis is more powerful at discriminating steeper slopes than shallower ones. However, all three estimated averages are statistically significantly different from zero, which means that these species are all showing a marked shift towards earlier spring events.

Given that higher latitudes have warmed more than the lower latitudes in the past half century (see Fig. 3d of ref. 1), we expect phenological responses to be larger nearer the poles and not as pronounced closer to the equator. (Unfortunately, our pool of literature did not allow us to test elevational changes.) The latitudes of the spring phenology studies in the Northern Hemisphere extend from 32° N to 72° N, with one study in the Southern Hemisphere at 39°. Because of the unevenness of the location of the data (for example, a preponderance of studies in the United Kingdom), we were able to have large enough sample sizes in each group only by dividing them into two groups along 50° latitude circles. The sample size from 32° to 49.9° was 24 + , which includes the one Southern Hemisphere study. From 50° to 72° N latitude, 85+ species or species groups were examined. As expected, the estimated mean and s.e.m. of the phenological shifts (see Methods) from 32° to 49.9° latitude is smaller (-4.2 ± 0.2) than that between 50° and 72° N latitude band (-5.5 ± 0.1). These two means are statistically significantly different from each other (Kruskal–Wallis test, ($P < 0.0001$), which strongly suggests that species at higher latitudes are indeed reacting more strongly to the more intense change in temperature.

Our spring phenology data set consists of species and populations from major taxa from molluscs to mammals. We had large enough sample sizes to examine the estimated means of the phenological shifts separately for invertebrates, amphibians and birds, and for trees and other plants (Fig. 2). Four of the five means cluster around an earlier shift of 5 days, which is the estimated mean for all taxa combined. Trees, however, show an estimated mean that is later than the cluster (-3.0 ± 0.1). This estimated mean is statistically different from the other means (Kruskal–Wallis test), and the other four means are not statistically different from one another.

Our study shows that recent temperature change has apparently already had a marked influence on many species. Meta-analyses provide a way to combine results, whether significant or not, from various studies, and to find an underlying consistent shift, or fingerprint, among species from different taxa examined at disparate locations. The findings for the nonsignificant species, when aggregated, show nearly as much significant change as the group of species showing statistical significance (Table 1 and Fig. 1). Hence, for the studies we examined, the balance of evidence suggests that a significant impact of recent climatic warming is discernible in the form of long-term, large-scale alterations of animal and plant populations. For example, the average shift in spring phenology (timing) of events, such as breeding or blooming, for temperate-zone species is 5.1 ± 0.1 days earlier in a decade. The observed consistent broad-scale patterns of changes in the expected directions (80% of species showing change) strongly suggest that recent temperature trends are the most likely explanation for these observed phenomena. Clearly, if such climatic and ecological changes are now being detected when the globe has warmed by an estimated average of only 0.6 °C, many more far-reaching effects on species and ecosystems will probably occur in response to changes in temperature to levels predicted by IPCC[1], which run as high as 6 °C by 2100.

Projected future rapid climate change could soon become a more looming concern, especially when occurring together with other already well-established stressors, particularly habitat destruction. During rapid climatic changes in the past, species showed differential movements[10], rather than shifting together as suggested by many authors, including Darwin[11]. Such differential movement could result in a disruption of the connectedness among many species in current ecosystems (for example, a tearing apart of communities[7]). Research and conservation attention needs to be focused not only on global warming and each of the other stressors by themselves, but also on the synergism of several pressures that together are likely to prove to be the greatest challenge to animal and plant conservation in the twenty-first century[3,12]. Because anticipation of changes improves the capacity to manage—by acting proactively rather than reactively—it behoves us to increase our understanding about the responses of plants and animals to a changing climate. This understanding, coupled with further documentation of change, may well indicate a need for actions to modify conservation efforts and future planning to account for climate change, and to slow the projected rate of warming. □

Methods

We used results from 143 studies, each of which found some trait of a species showing a trend over a span of at least 10 years. The geometric mean of the time span for all studies was 30.3 years and the average was 34.5 years. Gaps between years were allowed. Several studies investigated more than one species and some species showed no change. The relative number of species exhibiting change compared with all species reported in the literature sources we examined is not the relevant metric we consider, because we are not trying to determine what percentage of species is responding to current climatic changes. Given that all species examined in this study (and indeed by the entire scientific community) represents only a small proportion of the total number of species that exist in the world (itself unknown), such percentage claims are untenable by any analysis. Rather, a relevant metric to detect a discernible influence of global warming on plants and animals is the fraction of those species exhibiting change that have changed in the direction expected given a temperature trend at their location. For those studies finding change in more than one species and reporting the change as an average for several species, only one entry is used in the various tests performed. For example, Fleming and Tatchell[13] reported the change in flight period of five aphids as 2.6 days earlier per decade. To be conservative, for all our analyses, this group of aphids (and all similarly grouped species) is considered as one entry, rather than as five.

Meta-analyses used

We used two types of meta-analysis, vote counting and regression slope, to determine whether changes observed are consistent with the possibility that one force, global warming, is instigating a noticeable change in species. The vote-counting method is explained in detail in ref. 8. This method is biased towards finding zero or no effect[14]—of global warming, in our case. The various studies have different sampling lengths (K_i) and so we use a geometric mean of these numbers to determine K, the mean length of years the studies examined traits of species or populations. In all three vote-counting analyses that we used—species showing statistically significant change, species showing nonsignificant change, and the combined species that showed change—the value of K is 30.

The regression-slope meta-analysis provides a way to examine directly the shift in spring phenological changes. For this method to work, the various studies examined must have used the same measurement of change, which in these meta-analyses is the number of days changed per decade. We included only those studies that examined more recent spring shifts, from 1951 to 2001. Details of the methods we used here to derive estimated slopes are given in ref. 9. Our only deviation from this formulation is that we did not include the sampling variance term in the calculation of the variance of the slope parameter. This is because most studies examined do not report some of the data necessary to derive the sampling variance. This term acts to reduce the size of the variance of the regression slope. Consequently, the variances presented here are slight overestimates, making our inferences more conservative.

Potential biases

Apart from the problems inherent in summarizing information from diverse studies of numerous subjects and methods, potential biases in the data are also of concern in analyses like ours. We do not claim that all authors of studies in the literature we cite report all species they observe, and there may be a bias to report primarily those species that show change. Even if there were such a bias, however, it would have no influence on our claim of a discernible impact of warming on plants and animals, because our metric of investigation is what fraction of those species that exhibit change has changed in the direction expected with local temperature trends, not what fraction of all species has exhibited change. The only way that observer bias could influence our metric would be if there were a systematic bias among the scores of studies we examine for researchers to select as study subjects only species showing changes in the direction preconceived by the authors to reflect temperature change. In addition, these many authors would have to have deliberately and systematically suppressed reporting on those species that changed in directions opposite to that expected. We find this possibility of widespread and systematic biases far-fetched, and thus believe that the metric we use is adequate for examining in an unbiased manner the existence of a discernible climatic signal in the traits of many plants and animals.

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True navigation and magnetic maps in spiny lobsters

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Animals are capable of true navigation if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey[1,2]. So far, only a few animals, all vertebrates, have been shown to possess true navigation[3]. Those few invertebrates that have been carefully studied return to target areas using path integration, landmark recognition, compass orientation and other mechanisms that cannot compensate for displacements into unfamiliar territory[4,5]. Here we report, however, that the spiny lobster *Panulirus argus* oriented reliably towards a capture site when displaced 12–37 km to unfamiliar locations, even when deprived of all known orientation cues *en route*. Little is known about how lobsters and other animals determine position during true navigation. To test the hypothesis that lobsters derive positional information from the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment. Lobsters tested in a field north of the capture site oriented themselves southwards, whereas those tested in a field south of the capture site oriented themselves northwards. These results imply that true navigation in spiny lobsters, and perhaps in other animals, is based on a magnetic map sense.

In the context of homing behaviour, an animal capable of true navigation must possess both a positional sense to determine its location and a directional or compass sense to orient in the appropriate homeward direction[6,7]. Many animals, both vertebrate and invertebrate, possess diverse compasses based on the Earth's magnetic field, the position of the Sun, patterns of skylight polarization and the positions of stars[4,8]. In contrast, few animals are known to possess the ability to determine position relative to a goal after being displaced to unfamiliar areas under conditions in which

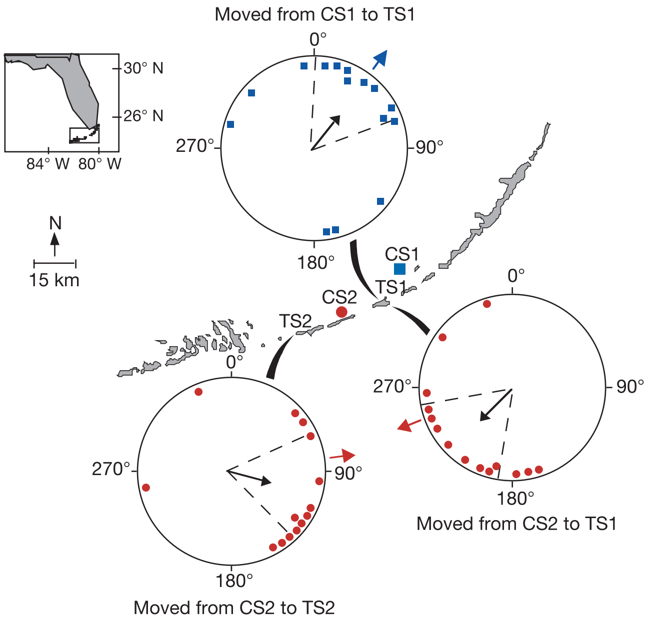

Figure 1 Orientation of displaced lobsters. Lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes (see the text) to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single lobster. Blue squares indicate lobsters captured at CS1, whereas red circles indicate lobsters captured at CS2. The arrow in the centre of each orientation diagram indicates the mean angle of each group; the arrow length is proportional to the mean vector **r**, with the radius of the circle corresponding to $r = 1$. Lobsters transported from CS1 to TS1 were significantly oriented ($r = 0.51$, $Z = 3.92$, $P < 0.02$, Rayleigh test) with a mean angle of 38°. Lobsters transported from CS2 to TS1 were significantly oriented ($r = 0.65$, $Z = 5.96$, $P < 0.01$) with a mean angle of 222°. Lobsters displaced from CS2 to TS2 were also significantly oriented ($r = 0.51$, $Z = 3.89$, $P < 0.02$) with a mean angle of 105°. In all orientation diagrams, the dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north. The blue or red arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction towards the capture site (see the text) and the 95% confidence interval encompassed this 'homeward' direction.

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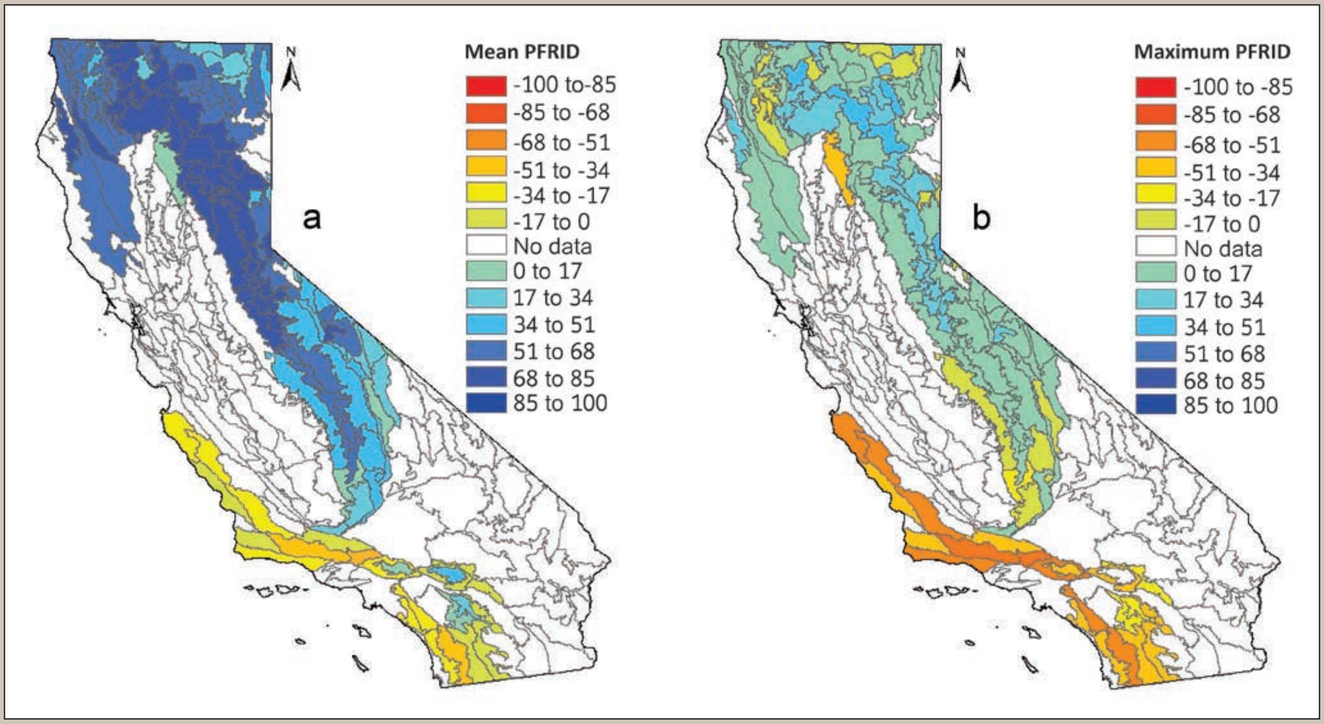
Using Fire Return Interval Departure (FRID) Analysis to Map Spatial and Temporal Changes in Fire Frequency on National Forest Lands in California

Hugh D. Safford and Kip M. Van de Water



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Summary

In the state of California, fire regimes and related ecosystem processes have been altered by land use practices associated with Euro-American settlement, and climate warming is exacerbating the magnitude and effects of these changes. Because of changing environmental baselines, restoration of narrowly defined historical conditions may no longer be an attainable or sustainable long-term management goal, but comparisons between historical and current fire regimes can assist managers in prioritizing areas for ecological restoration and other management actions. Fire return interval departure (FRID) analysis quantifies the difference between current and presettlement fire frequencies, allowing managers to target areas at high risk of threshold-type responses owing to altered fire regimes and interactions with other factors. We assessed FRID variability along geographic, climatic, and vegetation gradients in California on lands managed by the U.S. Department of Agriculture Forest Service and three forest-dominated national parks, using two types of FRID metrics: percent FRID, and the NPS-FRID index. Percent FRID (PFRID) quantifies the extent in percentage to which contemporary fires (i.e., since 1908) are burning at frequencies similar to those that occurred prior to Euro-American settlement. The NPS-FRID index represents the number of intervals missed since the last fire relative to the central tendency of presettlement fire return interval (FRI) distributions. Much of northwestern (NW) California and the Sierra Nevada sensu lato (including the southern Cascades, Modoc Plateau, and White and Inyo Mountains) has missed multiple fire cycles owing to fire suppression, while southern California is characterized by large areas burning at higher frequencies than under presettlement conditions. Ecologically speaking, fire suppression is a management necessity in much of southern California, but it is a major contributor to the growing forest fuels problem in NW California and the Sierra Nevada region. The PFRID exhibited a unimodal (hump-shaped) relationship to elevation in all three regions. The PFRID showed little relationship to precipitation in NW California or the Sierra Nevada region, but it decreased with precipitation in southern California. PFRID trends with temperature were unimodal, reaching a maximum at temperatures that approximate the elevation of the mean freezing line in winter storms, which is also the transition between moist mixed conifer and red fir in most of northern California. Low- and middle-elevation vegetation types supported the greatest departures from presettlement fire frequencies, with oak woodlands, yellow pine, and mixed-conifer forests missing the most fire cycles, and coastal fir, coastal sage scrub, and chaparral tending to experience shorter FRIs than under presettlement conditions. We provide examples of how FRID data may be used in resource management in an age of global change. Our results help refine our understanding of departures from presettlement fire regimes across California, and provide a spatial basis for resource management and planning focused on ecological restoration and adaptation to climate change in a fire-prone region.

Abstract

Safford, Hugh D.; Van de Water, Kip M. 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California. Res. Pap. PSW-RP-266. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 59 p.

In California, fire regimes and related ecosystem processes have been altered by land use practices associated with Euro-American settlement, and climate warming is exacerbating the magnitude and effects of these changes. Because of changing environmental baselines, restoration of narrowly defined historical conditions may no longer be an attainable or sustainable long-term management goal, but comparisons between historical and current fire regimes can assist managers in prioritizing areas for ecological restoration and other management actions. Fire return interval departure (FRID) analysis quantifies the difference between current and presettlement fire frequencies. We assessed FRID variability along geographic, climatic, and vegetation gradients in California on lands managed by the U.S. Department of Agriculture Forest Service and three forest-dominated national parks, using two types of FRID metrics: percent FRID (PFRID), and the NPS-FRID index. Much of northern California north of the Tehachapi Mountains has missed multiple fire cycles owing to fire suppression, while southern California is characterized by large areas burning at higher frequencies than under presettlement conditions. PFRID exhibited a unimodal (hump-shaped) relationship to elevation across our study area. PFRID showed little relationship to precipitation in northwest California or the Sierra Nevada region, but it decreased with precipitation in southern California. PFRID trends with temperature were unimodal, reaching a maximum at temperatures that approximate the elevation of the mean freezing line in winter storms, which also marks the transition between moist mixed conifer and red fir in most of northern California. Low- and middle-elevation vegetation types supported the greatest departures from presettlement fire frequencies, with oak woodlands, yellow pine, and mixed-conifer forests missing the most fire cycles, and coastal fir, coastal sage scrub, and chaparral tending to experience shorter FRIs than under presettlement conditions. Our results help refine our understanding of departures from presettlement fire regimes across California, and provide a spatial basis for resource management and planning focused on ecological restoration and adaptation to climate change in a fire-prone region.

Keywords: Ecological restoration, fire history, presettlement fire regime, Sierra Nevada, time since last fire.

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Introduction

Fire is a keystone ecological process in most of the world's Mediterranean-climate regions (Keeley et al. 2011). In the state of California, which comprises most of the North American Mediterranean-climate region, fire regimes (including fire frequency, severity, extent, spatial patterning, etc.) and related ecosystem processes have been profoundly altered by land use practices associated with Euro-American settlement, especially since American settlement began in earnest after 1849. These changes have in turn led to major modifications in vegetation distribution, structure, and composition (Agee 1993, Barbour et al. 2007, Skinner and Chang 1996, Sugihara et al. 2006). Climate variability at different temporal scales has also been shown to be associated with past, current, and projected changes in fire regimes, vegetation, and other ecosystem properties across California (Lenihan et al. 2003; Miller et al. 2009, 2012; National Research Council 2011; Swetnam 1993; Westerling et al. 2006, 2011). In a drought- and fire-prone region like California, ecological restoration efforts intended to increase ecosystem resilience to global change should consider fire and climate as central organizing principles (Keeley et al. 2011, North et al. 2009).

Practices of ecological restoration traditionally depend on the characterization of reference conditions, which can provide management targets and a means to measure management success (Egan and Howell 2001). Because modern human alteration of many ecosystems has been so profound, reference states must often be derived from historical information from before the onset of anthropogenic change. Maintaining managed ecosystems within the bounds of the "historical range of variation" (HRV) for key ecosystem patterns or processes has traditionally been seen as the best hope for preserving species and landscapes and ensuring long-term ecological sustainability (Egan and Howell 2001, Landres et al. 1999). Our trust in history as a dependable guide to the future has been tempered, however, by the revelation that many key ecosystem processes are not stationary, and that historical environmental baselines may or may not represent conditions that are particularly germane to either contemporary or future circumstances (Millar et al. 2007, Safford et al. 2012, Stephenson et al. 2010). At the same time, there is widespread recognition that the real problem lies not in history itself, which provides our only window into ecological processes operating at longer temporal scales, but rather in how historical information is applied to resource management (Stephenson et al. 2010, Wiens et al. 2012).

Because of the uncertainty surrounding future effects of climate and land use change on ecological processes such as fire, myopic focus on restoration of narrowly defined and static snapshots of historical conditions is probably not a sustainable management option in most California ecosystems (Millar et al. 2007, Safford et al. 2012). Nevertheless, information on fire regimes and ecosystem response to fire before Euro-American settlement is of elementary importance to current and future resource management (Fulé 2008, Millar et al. 2007, North et al. 2009, Van de Water and Safford 2011, Wiens et al. 2012). Such historical information can provide a foundation for understanding status of and trends in fire activity and its ecological effects over time; improve our understanding of the mechanisms that drive ecosystem response to climate and fire, their variability and their interactions with the landscape; furnish data upon which models of "properly functioning" or "resilient" ecosystems might be built; and determine to what extent current conditions may be historically anomalous and worthy of management intervention (Safford et al. 2012, Wiens et al. 2012).

The most commonly used fire regime attribute in reconstructions of historical fire regimes is fire frequency (Agee 1993, Johnson and Gutsell 1994). Disturbance frequency is a major driver of ecological and evolutionary response (Connell 1978, Huston 1994, Pickett and White 1985), and although frequency is only one component of the fire regime, the dependence of fire occurrence and behavior on the growth of vegetation produces a broadly inverse relationship between fire frequency and intensity (within a given ecosystem type, and assuming a constant climate) (Huston 2003, Turner et al. 1989). This relationship has permitted the development of simplistic but useful frequency-based and severity-based (a measure of the effect of fire intensity on the ecosystem) fire regime classifications that underlie mapping and management of wildland fire and fuels in the United States (e.g., Hardy et al. 1998, Heinselman 1978, Kilgore 1981). Within ecosystem types, this relationship also allows some (cautious) inference to be made about the effects of changing fire frequency on other fire regime attributes.

Drawing comparisons between past and current fire frequencies can assist resource managers in prioritizing areas for ecological restoration, fuels reduction, certain fire or habitat management practices, and other activities. Fire return interval departure (FRID) analysis is a method for quantifying the difference between current and presettlement fire frequencies on a management landscape (Caprio et al. 1997, Caprio and Graber 2000, van Wagtendonk et al. 2002). By comparing current fire return intervals (FRIs) with the range of reported pre-Euro-American settlement FRIs from the literature, a sort of rudimentary HRV analysis can be conducted. In such an analysis, quantified current departures from the reference conditions provide a basis to identify areas on the management landscape that are at high risk of type conversion or threshold-type responses owing to either greatly accelerated or greatly decelerated fire frequencies; areas that are within HRV can also be identified and targeted for maintenance management or study.

Several FRID assessments have been conducted in California, focused on individual national parks in the Sierra Nevada (Caprio et al. 1997, Caprio and Graber 2000, van Wagtendonk et al. 2002). These studies are enlightening, but they are of limited use in regional-scale restoration planning applications. In addition, the national park FRID analyses have been focused only on the time since the most recent fire, rather than on the complete record of fire location and size that has been collected since the early 20th century. Restoration of fire as an ecological process, and restoration of other ecosystem properties dependent on fire, will require more than a single application of prescribed fire or the occurrence of a single wildland fire. We therefore developed a complementary set of different FRID measures based on spatial fire records from throughout the last century. These percentage-based measures are less sensitive to the incidence of a single fire, and are more suitable to comparisons of fire frequencies over time between the current and pre-Euro-American settlement periods.

In this study, we determined time since last fire (TSLF) and calculated two sets of FRID measures (percent-based and National Park Service [NPS] calculations) for the approximately 8.1 million ha of land managed by the U.S. Forest Service in California. Except in some wilderness areas, most fires on Forest Service lands in California are subject to fire-suppression efforts, although indirect attack techniques can allow for significant fire spread under some circumstances. For comparison, we also include analyses of three of the largest national parks in California (Sequoia, Kings Canyon, and Yosemite national parks (NPs), 1.6 million ha in total), which encompass large areas where naturally ignited fires are allowed to burn under certain conditions for ecological benefit (van Wagtendonk 2007). In our analysis, we divided the state into three large geographic regions, which exhibit notable differences in climate, geography, and human land use that we expected to affect FRID: northwestern (NW) California; the Sierra Nevada, southern Cascades, Modoc Plateau, and White and Inyo Mountains (the combination of which we refer to as the “Sierra Nevada”); and southern California. Our focus was on identifying and interpreting major patterns in FRID across gradients of geography, climate, vegetation, and management, so as to provide a basis for broad-scale decisionmaking in resource management and planning on Forest Service and neighboring lands across California.

Methods

Study Area

The analysis area for this study, which consisted of the 19 national forests (NFs) and three NPs in California, was divided into three geographic regions: (1) NW

California (Klamath, Mendocino, Shasta-Trinity, and Six Rivers NFs); (2) the Sierra Nevada, including the southern Cascades, Modoc Plateau, and White and Inyo Mountains (El Dorado, Humboldt-Toiyabe [California portion only], Inyo, Lassen, Modoc, Plumas, Sequoia, Sierra, Tahoe, and Stanislaus NFs); the Lake Tahoe Basin Management Unit; and Yosemite, Sequoia, and Kings Canyon NPs; and (3) Southern California (Angeles, Cleveland, Los Padres, and San Bernardino NFs) (fig. 1). Most of California and almost all Forest Service lands in the state (except the eastern Inyo and Modoc NFs) are found in the Mediterranean-climate zone. In this paper, we refer collectively to the NW California and Sierra Nevada regions as “northern California.” In northern California, winters are cool and wet, and summers are warm and dry. In most of southern California, winters are cool but not as wet (except for the northern and central maritime portions of ecological section 261A (Miles and Goudey 1997) (fig. 1), and summers are warmer and drier than in the north. See Major (1988) and Minnich (2007) for information on temperature and precipitation in each region. Elevations in the NW California region range from near sea level to 4320 m; in the Sierra Nevada region, elevations range from 50 to

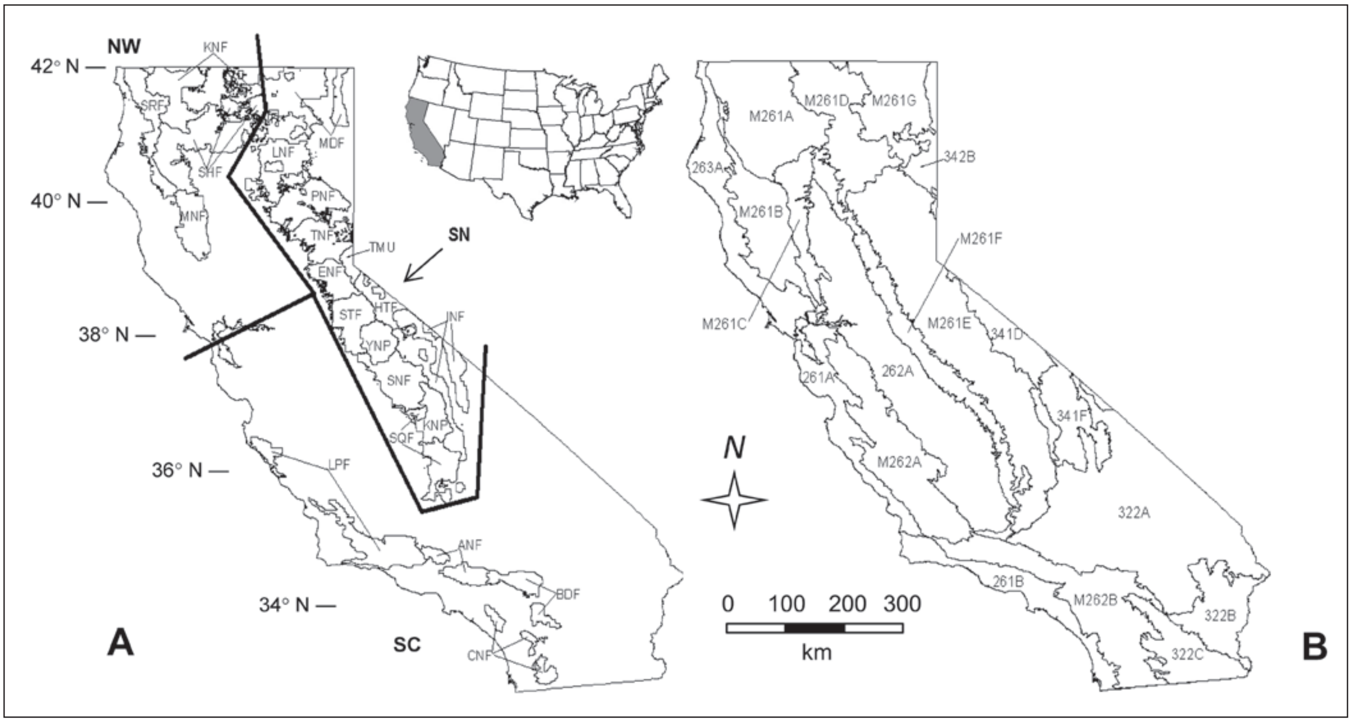

Figure 1—The study area. (A) Federal land management units included in the study area, segregated by geographic region (see text): NW = northwest California region; SN = Sierra Nevada region; SC = southern California region. National forests, clockwise from NW to SC: MNF = Mendocino, SRF = Six Rivers, SHF = Shasta-Trinity, KNF = Klamath; MDF = Modoc, LNF = Lassen, PNF = Plumas, TNF = Tahoe, TMU = Lake Tahoe Basin Management Unit, ENF = Eldorado, STF = Stanislaus, HTF = Humboldt-Toiyabe, SNF = Sierra, INF = Inyo, SQF = Sequoia; BDF = San Bernardino, CNF = Cleveland, ANF = Angeles, LPF = Los Padres. National Parks, in the Sierra Nevada: YNP = Yosemite, KNP = Sequoia-Kings Canyon. (B) Ecological sections in California, from Miles and Goudey (1997), and defined in table 2 on p. 12.

4420 m; in the southern California region, elevations range from near sea level to 3500 m. Vegetation in the analysis area in northern California is dominated by conifer forest, with substantial hardwood presence in lower and middle elevation areas with sufficient precipitation. Vegetation in the analysis area in southern California is dominated by hardwood forests/woodlands and shrublands (Barbour et al. 2007) with conifer forests of relatively small areal extent at high elevations.

Fire Regime Typing

Current existing vegetation types within the analysis area (as identified by the Forest Service's CALVEG classification) (Franklin et al. 2000; see http://www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192) were organized into 28 presettlement fire regime (PFR) groups according to the similarity of their historical relationships with fire (Van de Water and Safford 2011). The PFRs were developed only for vegetation types dominated by woody plants, as our understanding of historical fire regimes in herbaceous vegetation is poor. For each PFR, we conducted an exhaustive review of the published and unpublished literature pertaining to mean, median, minimum, and maximum FRIs that occurred prior to significant Euro-American settlement (i.e., the middle of the 19th century), and the average was taken of all mean, median, minimum, and maximum FRI values to yield a single mean, median, mean minimum, and mean maximum FRI estimate for each PFR (Van de Water and Safford 2011) (table 1). Most of the data used came from composite dendrochronological fire histories including records from multiple trees in a defined area. Our reference period is thus primarily the c. 200 to 500 years before 1850, although some of the records we accessed go back over 2000 years (Van de Water and Safford 2011).

Polygons were created for each area dominated by a given PFR and its associated presettlement mean, median, minimum, and maximum FRIs using ArcGIS 9.3[1] (ESRI 2008). The mapping base was the Forest Service existing vegetation (EVEG) geodatabase (available at http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836), which uses the CALVEG classification. We chose to use existing-vegetation polygons instead of potential natural vegetation (PNV) types because Forest Service PNV mapping was never completed in California and completed PNV mapping (mostly) disregarded disturbances like fire. The LANDFIRE Biophysical Settings (BpS) data are PNV types that incorporate disturbance (Rollins 2009), but the mapped accuracy of this modeled data layer varies across

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[1] Use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Table 1—Mean, mean minimum (min) and mean maximum (max) pre-Euro-American settlement fire return intervals (FRIs) for the presettlement fire regime (PFR) groups, and the current FRIs associated with the boundaries between condition classes (CCs)

PFR	Mean min FRI	CCs-2 and-3	CCs-1 and-2	Mean FRI	CCs 1 and 2	CCs 2 and 3	Mean max FRI
				Years			
Aspen	10	6.3	12.7	19	28.4	57.6	90
Big sagebrush	15	11.6	23.5	35	52.2	106.1	85
Bigcone Douglas-fir	5	10.2	20.8	31	46.3	93.9	95
Black and low sagebrush	35	21.8	44.2	66	98.5	200.0	115
California juniper	5	27.4	55.6	83	123.9	251.5	335
Chaparral and serotinous conifers	30	18.2	36.9	55	82.1	166.7	90
Coastal fir	90	32.7	66.3	99	147.8	300.0	435
Coastal sage scrub	20	25.1	50.9	76	113.4	230.3	120
Curl-leaf mountain mahogany	30	17.2	34.8	52	77.6	157.6	130
Desert mixed shrub	120	201.3	408.7	610	910.4	1,848.5	1,440
Dry mixed conifer	5	3.6	7.4	11	16.4	33.3	50
Fire-sensitive spruce or fir	90	38.6	78.4	117	174.6	354.5	250
Lodgepole pine	15	12.2	24.8	37	55.2	112.1	290
Mixed evergreen	15	9.6	19.4	29	43.3	87.9	80
Moist mixed conifer	5	5.3	10.7	16	23.9	48.5	80
Montane chaparral	15	8.9	18.1	27	40.3	81.8	50
Oak woodland	5	4.0	8.0	12	17.9	36.4	45
Pinyon-juniper	50	49.8	101.2	151	225.4	457.6	250
Port Orford cedar	10	9.9	20.1	30	44.8	90.9	160
Red fir	15	13.2	26.8	40	59.7	121.2	130
Redwood	10	7.6	15.4	23	34.3	69.7	170
Semidesert chaparral	50	21.5	43.6	65	97.0	197.0	115
Shore pine	190	82.5	167.5	250	373.1	757.6	1,025
Silver sagebrush	15	11.6	23.5	35	52.2	106.1	65
Spruce-hemlock	180	90.8	184.3	275	410.4	833.3	550
Subalpine forest	100	43.9	89.1	133	198.5	403.0	420
Western white pine	15	16.5	33.5	50	74.6	151.5	370
Yellow pine	5	3.6	7.4	11	16.4	33.3	40

Note: Mean, mean minimum, and mean maximum FRIs are from Van de Water and Safford (2011).

Forest Service lands in California. We believe the BpS maps are of reasonable accuracy at the regional (e.g., NW California, Sierra Nevada, southern California) or statewide scale, especially when similar vegetation types are pooled (see, e.g., Miller and Safford 2012), but our FRID geodatabase is intended to support planning and management at all spatial scales. Local inaccuracies in the BpS maps make use at or below the scale of a national forest or national park unit challenging. Note that our use of an existing-vegetation map from the 2000s as our base layer means that major changes in vegetation that have occurred since Euro-American settlement will affect the accuracy of our results. We elaborate on this issue in the "Discussion" section.

We carried out a union between the PFR geodatabase and CalFire's Fire Perimeters database (FRAP 2011), which tracks California fire history. The Fire Perimeters database is considered more or less complete for fires larger than 40 ha after 1908, and over 4 ha after 1950 (Miller et al. 2009); many smaller fires are also reported. The resulting geodatabase split the PFR polygons into smaller polygons based on the number of fires that had occurred in each PFR polygon since 1908.

FRID Mapping

Time since last fire was calculated by subtracting the year of the last fire in each polygon from 2010 (the most recent year included in the Fire Perimeters database when we conducted our analysis). Any polygon that had not had a fire since prior to 1908 was assigned a default TSLF value of 103 years; in many cases, TSLF will thus be a conservative measure of the time since last burn. Current FRI was calculated by dividing the number of years in the fire record (i.e., 2010–1908 = 103 years inclusive) by the number of fires occurring in each polygon (according to the Fire Perimeters database) plus one (current FRI = 103/number of times burned + 1). This calculation of current FRI is generally conservative because small fires (<40 ha prior to 1950, <4 ha after 1950) are not included in the Fire Perimeters database (FRAP 2011), prescribed fires are rarely included, and some parts of California have poor fire records for the period before World War II.

Five FRID metrics were calculated for each polygon. Four of them—mean, median, mininum, and maximum percent FRID (PFRID)—were calculated using the following equation when current FRI is longer than presettlement FRI (Hann and Strohm 2003):

$$\text{PFRID} = [1 - (\text{presettlement FRI}/\text{purrent FRI})] \times 100,$$

or, when current FRI is shorter than presettlement FRI:

$$\text{PFRID} = -[1 - (\text{current FRI}/\text{presettlement FRI})] \times 100$$

where presettlement mean, median, mean minimum, and mean maximum FRI are each substituted for their respective PFRID metrics. These PFRID metrics quantify the extent in percent to which contemporary fires (i.e., since 1908) are burning at frequencies similar to the frequencies that occurred prior to Euro-American settlement. To use an example: assuming a presettlement mean FRI of 10 years for some theoretical PFR, a current FRI of 30 years would be a +67 percent departure ([1 – (10/30)] × 100); for the same PFR, a current FRI of 5 years would be a -50 percent departure (-[1 – (5/10)] × 100). PFRID considers the cumulative fire history of each polygon since 1908 and does not return to zero when a fire occurs. For areas dominated by PFRs with a presettlement FRI greater than 103 years and that have not burned in the period of historical record considered in this analysis (i.e., since 1908), PFRID is assumed to equal zero.

Plotted against current FRI, the underlying distribution of the PFRID metric appears approximately linear between -99.9 percent and about +40 percent departure, but above +40 percent departure, increasingly larger leaps in current FRI are required to move the departure statistic (fig. 2), This is because the metric is actually asymptotic (see plot of PFRID against a logarithmic scale of current FRI, fig. 2 inset), owing to the behavior of the PFRID formulas, which divide presettlement FRI by current FRI in cases of positive PFRID and divide current FRI by presettlement FRI in cases of negative PFRID (Hann 2004, Hann and Strohm 2003). This property of the PFRID equations makes them particularly well suited to the analysis of fire frequency distributions where the mean and median FRIs are similar but a small number of high values results in a long tail to the right. This is not an uncommon situation with discrete data sets (Von Hippel 2005) and is the case with many of our nonmaritime forested PFRs (see fig. 1 in Van de Water and Safford 2011).

Mean and median PFRID measure the departure of current FRIs from the central tendency of presettlement FRIs, with median PFRID perhaps better representing the skewed nature of FRI distributions in some vegetation types (i.e., more short or long intervals, depending on the fire regime). Mean PFRID is the standard measure used by the Forest Service in California to spatially map contemporary departure from presettlement fire frequencies (Safford et al. 2011). Mean minimum and mean maximum (hereafter min and max) PFRIDs represent liberal and conservative estimates, respectively, of the departure of current from presettlement FRIs. Min and max PFRIDs are important variables, as they (hypothetically) provide us with approximate lower and upper bounds of sustainability/resilience for the ecosystems represented by our PFRs. Landscapes that are characterized by negative min PFRID values are burning much more frequently today than under presettlement conditions; these landscapes may have undergone or may be undergoing vegetation type conversion and should be focus areas for enhanced fire suppression and public education efforts. In contrast, landscapes that are characterized by positive max PFRID values are usually those that were historically characterized by frequent fire but have not experienced fire for a half century or more. These areas may have experienced major changes in vegetation composition and fuels and should be focus areas for fuel reduction by fire restoration or fire surrogates.

We categorized mean PFRID values into “condition classes” (CCs) (see Safford et al. 2011), where values from 0 to 33 percent and 0 to -33 percent are classified as

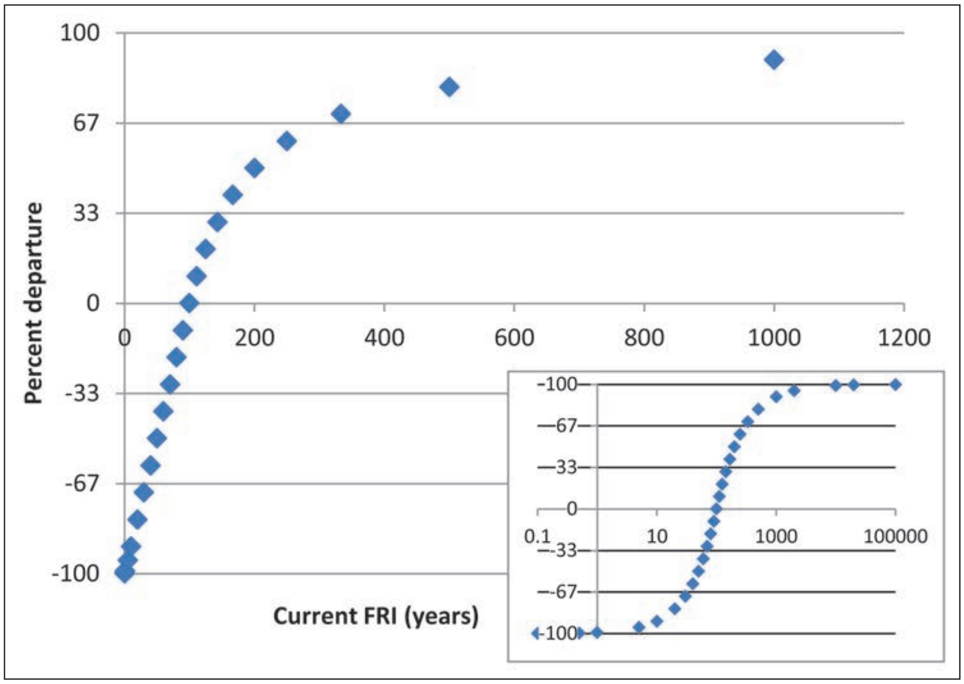

Figure 2—Percent departure versus current fire return interval (FRI) for a presettlement fire regime with a mean presettlement reference FRI of 100 years. The inset plots the departure from -99.9 percent to +99.9 percent against a Log FRI scale.

CC 1 and CC -1 (“low departure”), respectively, while values from 33 to 67 percent and -33 to -67 percent are CC 2 and CC -2 (“moderate departure”), and values greater than 67 percent and more negative than -67 percent are CC 3 and CC -3 (“high departure”). This CC categorization, which simply divides the 0 to 100-percent departure scale into thirds, was developed by the interagency Fire Regime Condition Class (FRCC) program (Hann 2004, Hann and Strom 2003). Positive CCs apply where contemporary fire frequencies are less than presettlement frequencies (Hann and Strohm 2003); negative CCs apply where contemporary fire frequencies are greater than presettlement frequencies (Safford et al. 2011).

Table 1 provides background information to help in the interpretation of the PFRID statistics. Table 1 expands on Van de Water and Safford (2011) to provide the current FRIs associated with the boundaries between the CCs for each PFR. It can be appreciated from table 1 that CC 1 and CC -1 occupy the area between current FRIs that are one-half the frequency of the presettlement FRI and 1.5 times the presettlement FRI. Condition class 2 is found in the area where current FRI is between 1.5 and three times the presettlement FRI; CC 3 is thus defined as any current FRI that is more than three times the presettlement FRI. The boundary between CCs -2 and -3 is found where current FRIs are one-third the presettlement FRIs (i.e., current fires are three times as frequent as the presettlement mean).

The fifth FRID metric we calculated was the NPS FRID index, which represents the number of intervals missed since the last fire relative to the central tendency of presettlement FRI distributions. The NPS-FRID index was calculated using the following equation:

NPS-FRID index = -[(presettlement mean FRI-TSLF)/presettlement mean FRI].

Note that the sign of the equation used in this analysis has been reversed from the original formula (see van Wagtendonk et al. 2002) to facilitate interpretation of FRID trends that is consistent with the sign of our other PFRID metrics. The NPS-FRID metrics were developed by the NPS for the southern Sierra Nevada and do not consider the cumulative fire history of each polygon, but only the time since the last fire (Caprio et al. 1997, Caprio and Graber 2000, Keifer et al. 2000, van Wagtendonk et al. 2002). The NPS-FRID metrics measure the number of presettlement FRIs missed since the first missed cycle, and are thus not helpful in identifying areas where current FRI is shorter than presettlement FRI. The NPS-FRID index values less than 0 are classified as low departure, while values from 0 to 2 are moderate, values from 2 to 5 are high, and values greater than 5 are extreme (van Wagtendonk et al. 2002). Note that the interpretive differences between the two metrics notwithstanding, the numerical boundary between moderate and high NPS-FRID (three missed fires) is equivalent to the boundary between moderate (CC 2) and high (CC 3) departure in the PFRID measure (current FRI = three times the reference FRI).

Fire return interval departure mapping products described above (including PFR, number of fires since 1908, TSLF, and all FRID values) were developed by the Forest Service's Pacific Southwest Region Ecology Program and Remote Sensing Lab (Safford et al. 2011) and are available online at http://www.fs.usda.gov/main/r5/landmanagement/gis.

To provide some geoecological context for our spatial patterns of departure, FRID GIS layers were intersected with a layer consisting of the ecological sections and subsections in California (figs. 1 and 3) (Miles and Goudey 1997). The subsection descriptions in Miles and Goudey (1997) provide information on prevalent environmental conditions in each subsection, including elevations, temperature and precipitation, soils, geology, vegetation, and human uses. The area-weighted average of TSLF and FRID values within each subsection was calculated, using only those Forest Service or analyzed NPS lands that occurred within each subsection, and then TSLF and FRID values were mapped by subsection; the section summaries in table 2 are the summed results from the subsection area-weighting and likewise represent only analyzed federal lands. We report results only for subsections that contained at least 5 percent Forest Service or NPS lands. Figure 3

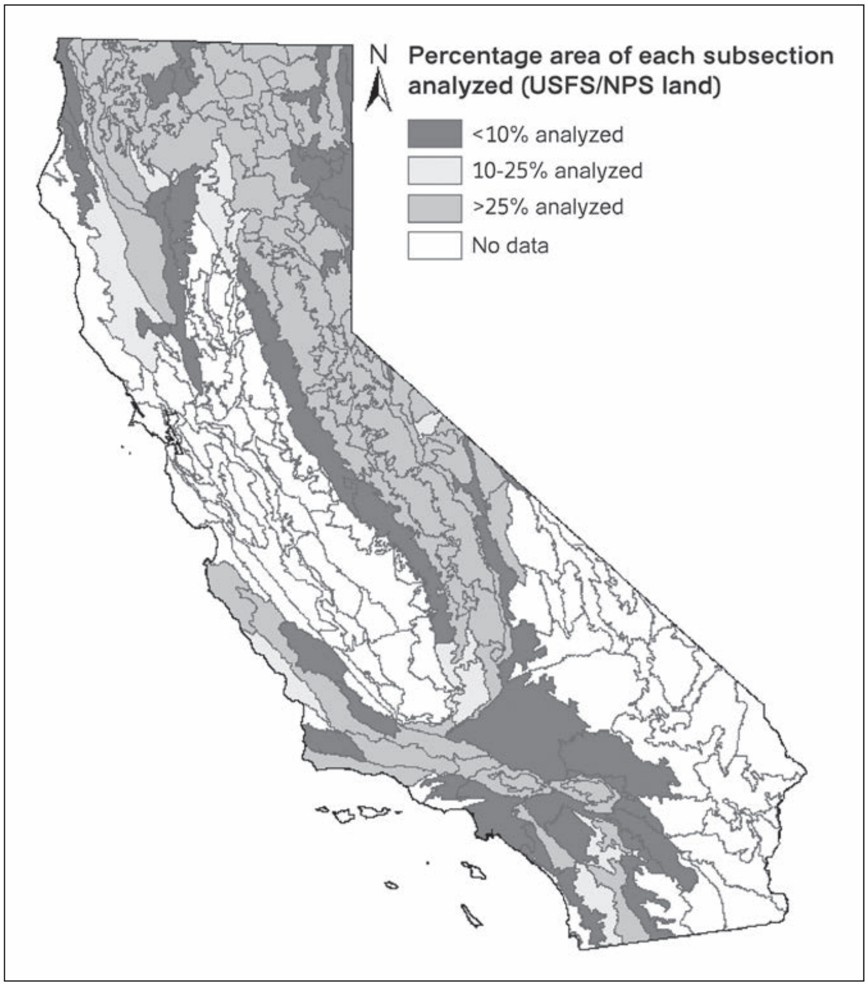

Figure 3—Ecological subsections intersecting with the national forests and national parks analyzed in this study. Dark gray subsections are those where >25 percent of the land base is found within analyzed management units; light gray = 10 to 25 percent of the land base is within analyzed management units; black = ≤ 10 percent of the land base is within analyzed management units. USFS = United States Forest Service, NPS = Natioinal Park Service.

Table 2—Differences in time since last fire (TSLF) and fire return interval departure (FRID)[a] among ecological sections[a], averaged from subsections within the section that contains lands under Forest Service or National Park Service (NPS) (Yosemite or Sequoia-Kings Canyon National Parks) administration

Ecological section	Code	n	Analyzed area	Section area	Percentage of section analyzed	TSLF	Min. PFRID	Mean-PFRID	Median PFRID	Max. PFRID	NPS-FRID Index[b]
			Hectares			*Years*					
Central Coast	261A	2	137 055	1 375 722	10.0	16	25	-19	-7	-57	-0.6
Southern Coast	261B	5	75 765	1 449 424	5.2	33	30	-20	-25	-49	-0.4
Northern Coast	263A	3	11 637	1 722 125	0.7	101	85	71	83	18	3.3
Mojave Desert	322A	3	26 074	6 683 237	0.4	79	16	-1	-4	-17	-0.3
Colorado Desert	322C	1	229	1 185 242	0.0	19	-65	-91	-92	-95	-1.0
Mono	341D	14	402 040	798 345	50.4	98	65	39	39	8	1.0
Southeastern Great Basin	341F	4	83 116	1 103 764	7.5	103	38	21	21	5	0.2
Northwestern Basin and Range	342B	5	3 776	522 403	0.7	94	78	53	51	6	1.8
Klamath Mountains	M261A	16	1 755 085	2 256 796	77.8	77	84	67	79	10	3.3
Northern Coast Ranges	M261B	3	614 783	1 552 449	39.6	77	82	64	70	9	3.3
Northern Interior Coast Ranges	M261C	2	4267	749 443	0.6	69	74	52	60	3	2.3
Southern Cascades	M261D	9	958 842	1 702 525	56.3	90	86	70	73	18	4.6
Sierra Nevada	M261E	21	4 116 267	5 159 316	79.8	84	78	61	66	11	3.3
Sierra Nevada Foothills	M261F	5	152 857	1 819 108	8.4	58	62	31	39	-18	1.8
Modoc Plateau	M261G	11	711 801	1 430 882	49.8	90	75	51	56	13	2.9
Central Coast Ranges	M262A	3	190 822	2 485 244	7.7	22	0	-41	-45	-63	-0.6
Southern Mountains and Valleys	M262B	16	1 193 734	2 755 093	43.3	43	34	-6	-5	-40	0.3

n = Number of analyzed ecological subsections within each section.

[a] Percentage fire return interval departure (PFRID) data are read as percentage departure.

[b] Sign of NPS-FRID Index values reversed to allow consistent interpretation with other FRID measures.

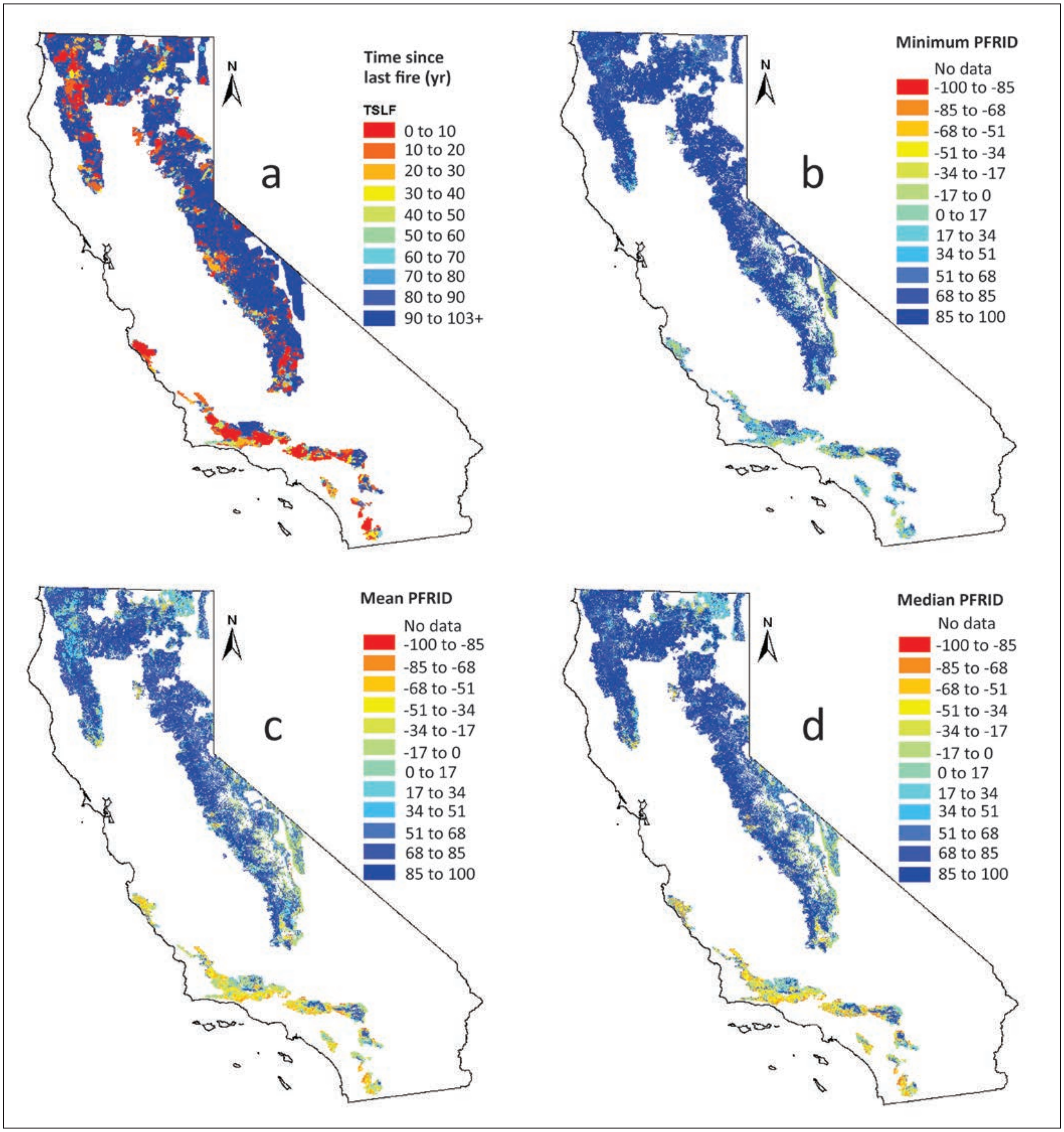

Figure 4—Time since last fire and the five fire return interval departure metrics for federal lands analyzed in this study. Negative percent FRID (PFRID) measures (warm colors) identifies places where current fire return interval (FRI) is shorter than the presettlement FRI; positive PFRID (cool colors) identifies places where current FRI is longer than the presettlement FRI. The PFRID measures are grouped into categories that approximately correspond to the standard condition classes from Hann and Strohm (2003) (see "Methods"). For the National Park Service FRID Index, see "Methods" for interpretation of the index values.

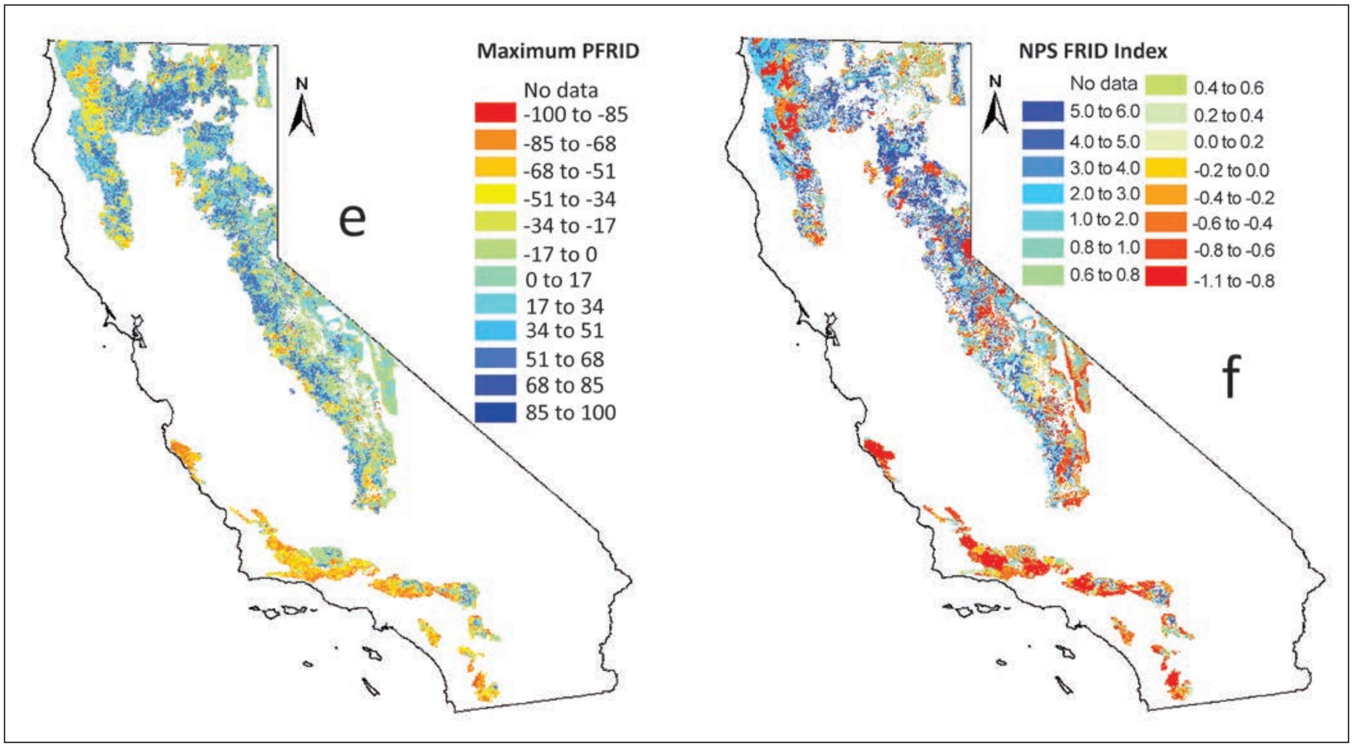

Figure 4—Continued.

identifies those ecological subsections where these federal lands account for < 25 percent and < 10 percent of subsection area. Be careful to avoid overinterpretation of our results in these subsections.

We selected those ecological subsections with the highest positive departure (greater than 17 percent departure, n = 25; the “P” group) as determined by max PFRID (see fig. 4), and those subsections with the most negative departure (more than 33 percent negative departure, n = 17; the “N” group), and used data from Miles and Goudey (1997) to characterize each of the 42 subsections with respect to lowest elevation, mean annual precipitation (from the range given); low mean annual temperature; high mean annual temperature; mean annual frost-free period in days (from the range given); dominant precipitation type (rain = 1, snow = 2, mix = 1.5); soil temperature (thermic = 4, mesic = 3, frigid = 2, cryic = 1; intermediate values given for mixes); and soil moisture (udic = 3, xeric = 2, aridic = 1; intermediate values given for mixes). Each of the 42 subsections was assigned a predominant pre-Euro-American settlement FRI using the predominant vegetation types described by Miles and Goudey (1997) and crosswalking these to the PFRs in Van de Water and Safford (2011). We also assigned each subsection a human population density from the California county that the subsection was found in; in cases of multiple counties, we averaged the densities (data from http://www.csac.counties.org/). The above data were entered into a Principal Components Analysis (PCA) ordination using PC-ORD v. 5 (McCune and Mefford 2006). Before analysis, the input data were relativized by their maximum values. Monte Carlo permutations of the data were carried out 1,000 times in order to calculate correlations of the environmental data with the ordination axes. We also statistically compared the P and N group means for the environmental and population data listed above using the univariate nonparametric Mann-Whitney U test.

In the southern Sierra Nevada, we compared differences in FRID between three large national parks (Yosemite, Sequoia, and Kings Canyon, all of which include large areas where naturally ignited fires are allowed to burn for ecological benefit) and the five adjacent national forests by calculating the area-weighted average of TSLF and FRID values in the two jurisdictions.

Elevational trends in departure were explored using the zonal statistics function of ArcGIS 9.3 (ESRI 2008), which averaged the TSLF and FRID values of all cells of identical elevation in a 100-m digital elevation model. Trends in departure along precipitation, mean, minimum, and maximum temperature gradients were also explored using zonal statistics on averaged annual PRISM climate normal grids, 1971–2000 (PRISM Group 2004).

Results

Geographic Patterns

Geographic patterns of FRI departure on the analyzed Forest Service and NPS lands generally showed positive FRID and longer TSLF in NW California and Sierra Nevada, and negative FRID and shorter TSLF in southern California; trends were relatively consistent across all metrics (table 2, figs. 3 through 6). TSLF strongly reflected the fire seasons of 2003 and 2005–2008 and resulted in very low departure according to the NPS-FRID Index (which is based only on the most recent fire) for much of southern California and scattered portions of the North Coast Ranges, Klamath Mountains, and Sierra Nevada (figs. 4a–4f).

The PFRID measures, which consider fire history across the entire 103-year study period, were much less affected by recent fire seasons (figs. 4b–4e). Min PFRID, which is based on the mean minimum presettlement FRI for the mapped PFRs (Van de Water and Safford 2011), classified most of the study area at high positive departure (fig. 4b). Lower elevation PFRs in the southern California national forests were an exception: some areas in the southern California foothills mapped as high negative departure even using the min PFRID measure, which means they have burned much more frequently over the last century than during any comparable (average) presettlement period in our reference period. Mean and median PFRID were nearly indistinguishable: both showed very high positive departure from presettlement fire frequencies throughout most of NW California and the Sierra Nevada (with some exceptions of low to moderate departure in the central Klamath Mountains, parts of the Modoc Plateau, and the southeastern Sierra Nevada), and a belt of moderate to high negative departures through most of lower and middle elevation southern California (figs. 4c–4d). Max PFRID, based on the mean maximum presettlement FRI, is a more conservative measure of departure for places that are lacking fire and a more liberal measure for places that are seeing much more fire (fig. 4e). Places identified as high positive departure using max PFRID have missed a greater than average number of fire cycles; these tended to be centered in the eastern Klamath Mountains, the southern Cascades, and middle elevations in the main Sierra Nevada. As would be expected, most of southern California is mapped as very large negative departure using the max PFRID measure (fig. 4e).

Figure 5 compares the three major geographic regions by the proportion of area in Forest Service and (in the Sierra Nevada) NPS jurisdiction that falls in each of the CCs, based on the standard mean PFRID measure. It can be readily seen how different southern California is from the northern California regions. Forty-three percent of Forest Service lands in southern California are burning more (CC -2) or much more (CC -3) frequently currently than under the pre-Euro-American settlement fire regime; only 2 percent of the Sierra Nevada and 1 percent of NW California lands fall into this category (fig. 5). About one-third of southern California falls into CCs 1 and -1, within +/- 33 percent of the presettlement mean fire frequency, versus 16 percent in the Sierra Nevada and 9 percent in NW California. More than 85 percent of Forest Service lands in NW California is burning either less frequently (CC 2) or much less frequently (CC 3) currently than under presettlement conditions, compared with 67 percent of Forest Service and NPS lands in the Sierra Nevada and 19 percent in southern California.

Table 2 averages results of the area-weighting procedure among the ecological sections (see fig. 1 for map); figure 6 portrays the geographic results by ecological subsection for mean and max PFRID. After rounding, only seven ecological sections contained more than 40 percent Forest Service or NPS lands (table 2). It is important to remember that our results summarized by ecological units (sections and subsections) are only valid for the Forest Service and NPS lands within those units. As noted above, the highest positive FRID values were consistently on Forest

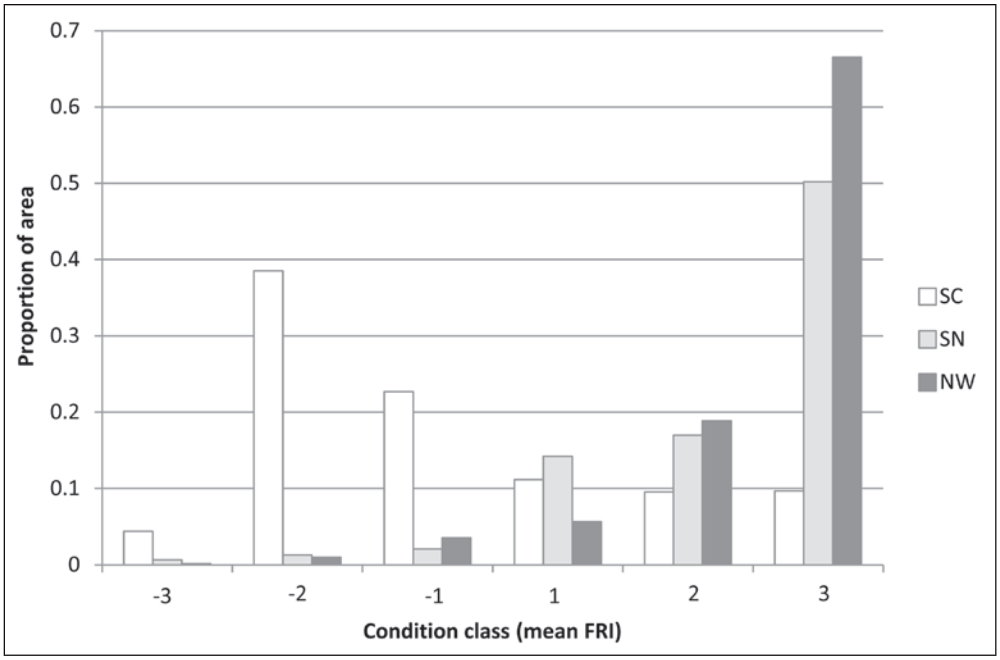

Figure 5—Proportion of total analyzed area in the three geographic regions falling into each of the six condition classes (CCs). Negative CCs represent places where the current fire return interval (FRI) is shorter than the presettlement FRI; positive CCs identify places where current FRI is longer than the presettlement FRI. SC = Southern California, SN = Sierra Nevada, NW = Northwestern California.

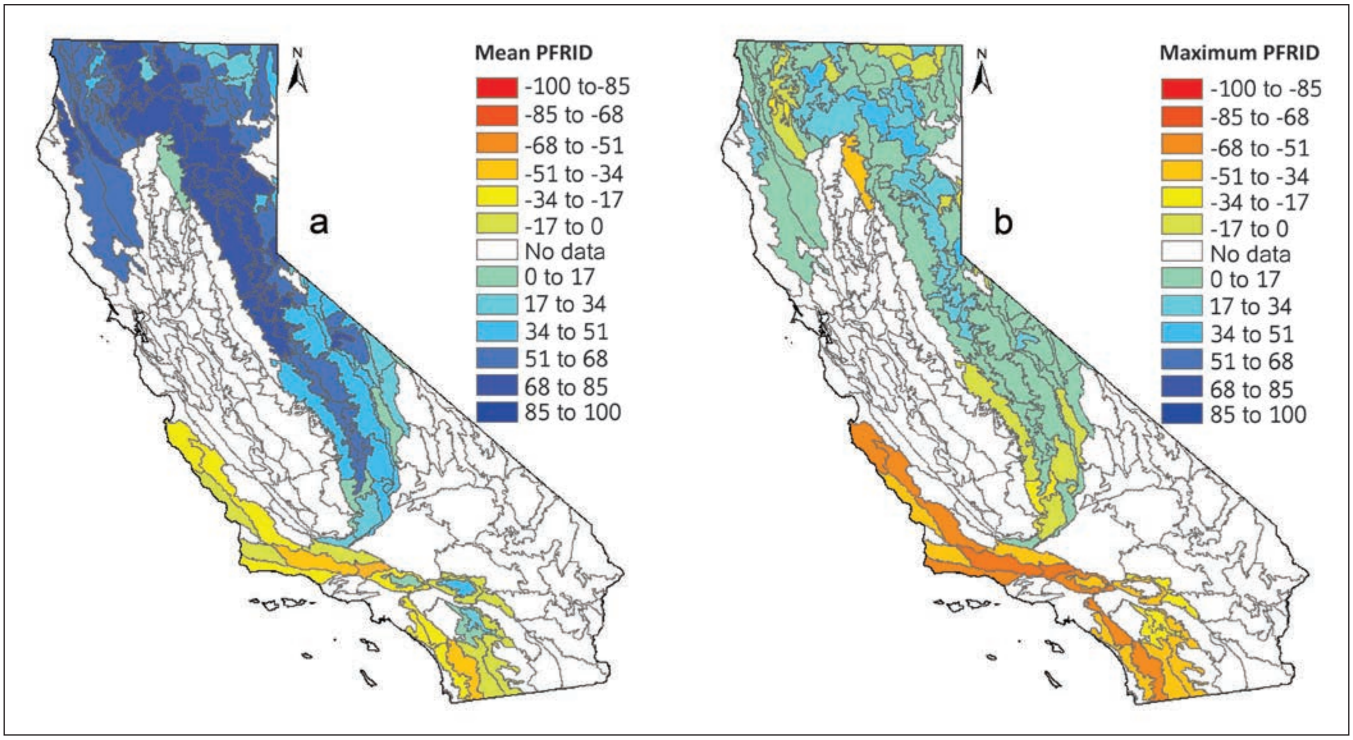

Figure 6—Mean and max percent fire return interval departure (PFRID), with the results of figure 4 extrapolated to the ecological subsection boundaries (Miles and Goudey 1997). See figure 3 for percentages of subsections analyzed; in this figure, subsections with < 5 percent analyzed land have been removed.

Service lands in the eastern Klamath Mountains and the southern Cascades (fig. 6). Mean TSLF averaged 68 years, ranging from 16 years in the Central Coast Ecological Section to 103+ years in the Southeastern Great Basin Section (table 2). The min PFRID measure averaged 50 and ranged from -65 in the very small area of Forest Service land in the Colorado Desert Section to 86 in the Southern Cascades Section (table 2). Mean PFRID averaged 24 across the analyzed subsections, which is high CC 1. Mean PFRID varied from -91 in the Colorado Desert Section to 70 in the Southern Cascades and 71 in the North Coast Section (table 2, fig. 6a). The median PFRID measure averaged 27 and varied from -92 in the Colorado Desert Section to 83 in the North Coast Section (table 2). Max PFRID averaged -14, and ranged from -95 in the Colorado Desert Section to 18 in the Northern Coast and Southern Cascades Sections (table 2, fig. 6b). The NPS-FRID index averaged 1 (moderate departure), ranging from -1.0 in the Colorado Desert Section to 4.6 in the Southern Cascades Section; many northern California Sections fell between 2.9 and 3.3, which fall in the “high” departure category (table 2).

The results of the Principal Components Analysis (PCA) on the subsection environmental data are shown in figure 7. Axis 1 explained 51.3 percent of the variance in the data matrix, axis 2 explained 17.8 percent, and axis 3 explained 11 percent. The subsections supporting strongly positive FRIDs (as determined using max PFRID) were clearly segregated from the subsections supporting strongly negative FRIDs. Of the 25 subsections in the positive FRID (P) group, all but three were from NW California and the Sierra Nevada (the exceptions being P23–25, which are the Upper San Gabriel, Upper San Gorgonio, and San Jacinto Mountains in southern California). Of the 17 subsections in the negative FRID (N) group, all but one (N17—Tuscan Flows [Miles and Goudey 1997]) were from southern California. Along axis 1, all but one of the subsections in the N group were clustered to the right of the ordination center; all but three of the subsections in the P group were grouped to the left of center (fig. 7). Axis 1 was most strongly correlated with environmental variables related to temperature and elevation, with the warmest and lowest subsections (excepting P6) all in the N group. The most strongly correlated variables with axis 1 were: high mean temperature (r = 0.924); lowest elevation (r = -0.919); and mean frost-free period (r = 0.894). Soil temperature was a categorical variable and an r value could not be determined, but it was the most closely associated variable with axis 1. Axis 2 was most closely correlated with moisture (mean annual precipitation [r = -0.745] and soil moisture [categorical variable]) and presettlement FRI (r = 0.542). Along axis 2, the P subsections were evenly distributed above and below the ordination center, but most of the N sites were near or below the center (i.e., N sites tend to be drier and support longer presettlement

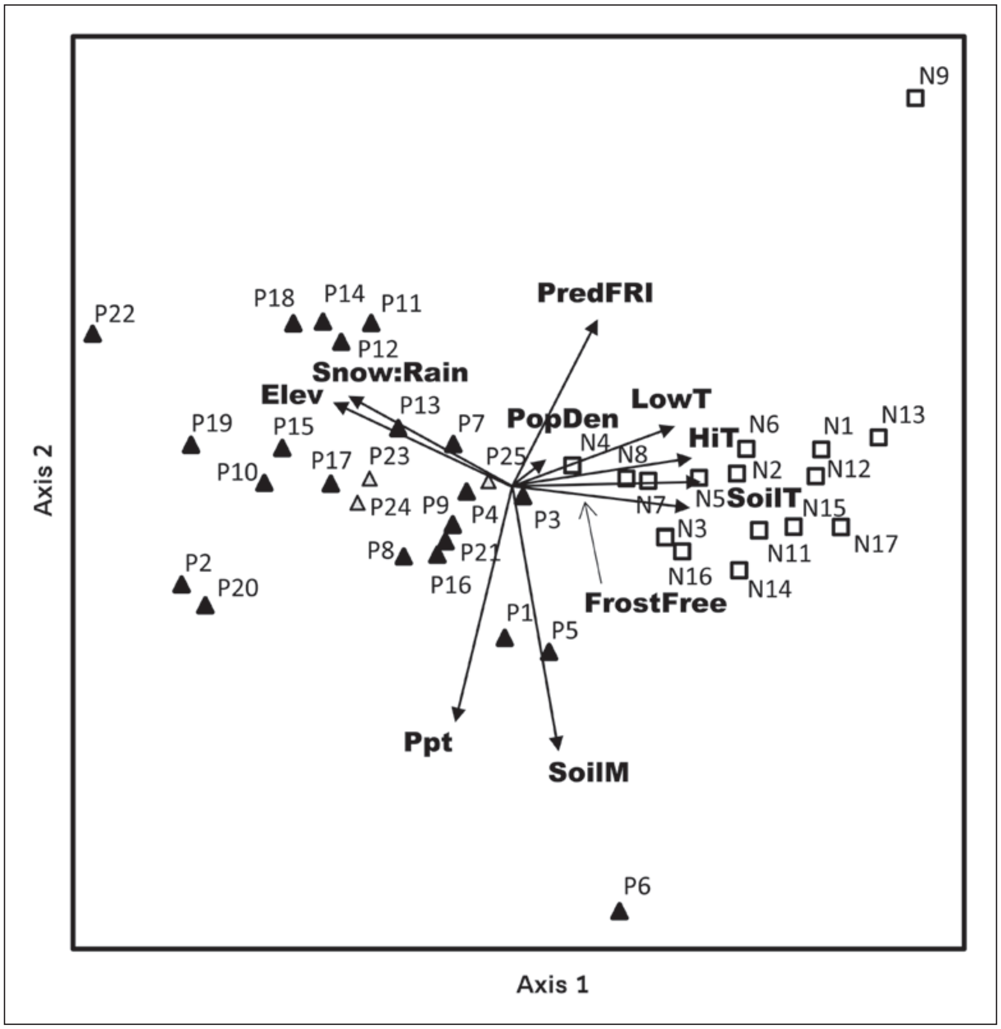

Figure 7—Principal Components Analysis ordination of highly positively (“P,” triangles) and highly negatively departed (“N,” squares) subsections (see “Methods”). The gray triangles are three southern California sites belonging to the P group.

FRIs). Population density was correlated with axis 3 at *r* = 0.960, which was the strongest correlation overall between the environmental variables and any axis; the arrow representing population density in the ordination diagram seems very short because the effect of population density is nearly orthogonal to axes 1 and 2. Along axis 3, the N sites were characterized by high population densities (and are in the distance along axis 3) and the P sites (which are nearer to the observer along axis 3) by low population densities (fig. 7).

We compared the means for the environmental data entered into the PCA for the N and P groups using Mann-Whitney U tests. The results are shown in figure 8. Based on figures 7 and 8 and Miles and Goudey (1997), we can describe the P group as predominantly northern California (plus a few small areas

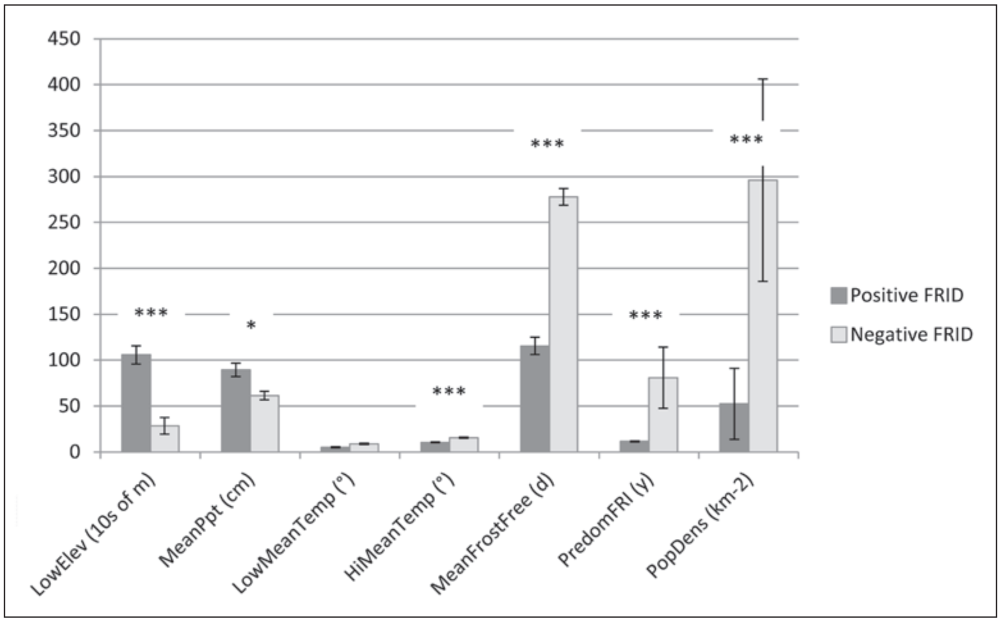

Figure 8—Means comparisons for six environmental variables and human population density between the positive (P) and negative (N) subsection groups from the Principal Components Analysis ordination. LowElev = lowest listed elevation; MeanPpt = mean annual precipitation; LowMeanTemp = lowest listed mean annual temperature; HiMeanTemp = highest listed mean annual temperature; MeanFrostFree = mean length of annual frost free period, in days; PredomFRI = mean presettlement fire return interval (FRI) for the predominant vegetation type in the subsection; PopDens = mean human population density. See "Methods" for data sources. Comparison made with nonparametric Mann-Whitney U-test; * = significantly different at $P < 0.05$; *** = significantly different at $P < 0.001$.

of high-elevation southern California); higher elevation, wetter and cooler, with most precipitation arriving as snow; growing season of 3 to 4 months; conifer forest-dominated vegetation with short presettlement FRIs; mesic to frigid soil temperature regime; and in areas of low population density. The N group can be characterized as predominantly southern California; lower elevation, warmer and drier, with precipitation arriving as rain; growing season of 8 to 10+ months; shrub-dominated vegetation with longer presettlement FRIs; thermic to mesic soil temperature regime; and in areas of high population density.

Differences Among Management Units

Using mean PFRID and considering only those lands for which FRID was calculated (i.e., ignoring barren and rocky areas, lakes, herbaceous vegetation, etc.), the percentage of lands with negative FRI departures (CC -2 and -3) vs. lands within 33 percent of the mean presettlement FRI (CC -1 and 1) vs. lands with positive FRI departures (CC 2 and 3) is different in the three Sierra Nevada national parks (2, 30, and 68 percent) compared to Forest Service-managed lands in the Sierra Nevada (2, 18, and 80 percent). If only the five national forests adjacent to the parks are compared, however (Humboldt-Toiyabe, Inyo, Stanislaus, Sierra, and Sequoia NFs), the national forest percentages are very similar to the national parks (3, 27, and, 70 percent). Most other measures of fire frequency departure in the neighboring national forests are also relatively similar (table 3). Average TSLF is lower in the national parks, although Sequoia NF has the lowest overall TSLF (table 3). The NPS-FRID index is in the “moderate” range (0-2) in the national parks, while the national forests average in the “high” range of departure. Two national forests with large areas of high-elevation wilderness (Inyo and Humboldt-Toiyabe) also fall in the low range (table 3).

Table 3 also highlights the strong differences between NW California plus Sierra Nevada and southern California. The average TSLF in southern California is less than half of the value in the other two regions, and the average PFRID values are all negative in southern California, compared to highly positive numbers in NW California and the Sierra Nevada. The extensive 2008 fires result in a lower TSLF in NW California than the Sierra Nevada, but Min, Mean, and Median PFRID and the NPS-FRID index are all lower in the Sierra Nevada. Averaged across all national forest land, NW California is the region with the greatest FRI departures, but the individual national forest units with the greatest departures are found in the central and northern Sierra Nevada (table 3).

We can also compare management units on the basis of the CC measures derived from mean PFRID. On three national forests in the Sierra Nevada (Lassen, Plumas, and Tahoe), over 70 percent of the landscape falls in CC 3, which is to say that on 7/10 of these lands there has been a greater than 67 percent decrease in fire frequency (i.e., at least three FRIs have been missed) over the last century as compared to the pre-Euro-American settlement period (fig. 9a). The Shasta-Trinity NF in NW California is nearly as extreme. In terms of overall area, the Shasta-Trinity is the only management unit with over 500 000 ha of CC 3 lands; the Klamath, Lassen, Plumas, and Six Rivers NFs all manage more than 300 000 ha of CC 3 lands (fig. 9b).

The lowest percentage and area of CC 3 lands are found in the shrub and hardwood-dominated southern California national forests. At the same time, these four national forests (Angeles, Cleveland, Los Padres, and San Bernardino) contain the only substantial areas of negative CCs (where fire frequencies are currently greater than in presettlement conditions) in California (figs. 4, 6, and 9). In management units dominated by conifer forests, only Yosemite and Sequoia-Kings Canyon National Parks and the Inyo NF have less than one-third of their area in CC 3. Three other national forests in the Sierra Nevada region (Sequoia, Sierra, and Modoc) are 40 to 44 percent CC 3 (fig. 9).

Table 3—Differences in time since last fire (TSLF) and fire return interval departure (FRID) measures between national park (NP) and adjacent national forest (NF) lands in the southern Sierra Nevada, followed by TSLF and FRID measures for the remaining NFs analyzed

Unit	TSLF	Min PFRID	Mean PFRID	Median PFRID	Max PFRID	NPS-FRID Index[a]	Analyzed area[b]	
	Years						*Hectares*	
National parks:								
Sequoia-Kings Canyon NPs	80	60	43	48	-2	1.3	222 045	
Yosemite NP	77	70	51	57	1	1.7	237 318	
National park mean	78	65	47	52	-1	1.5	459 363	Total
Adjacent national forests:								
Humboldt-Toiyabe NF	91	73	50	50	7	1.9	339 646	
Inyo NF	98	55	35	35	7	1.0	766 030	
Sequoia NF	71	71	46	51	-1	2.3	538 316	
Sierra NF	89	71	56	63	10	3.4	529 756	
Stanislaus NF	81	83	68	74	17	4.2	395 477	
Adjacent national forest mean	87	68	49	52	8	2.4	2 569 225	Total
Northwest (NW) California:								
Klamath NF	82	83	65	74	11	3.6	803 959	
Mendocino NF	73	79	60	64	6	3.3	435 526	
Shasta-Trinity NF	81	87	73	80	17	4.3	1 219 109	
Six Rivers NF	79	82	63	79	4	2.4	546 924	
NW California mean	80	84	67	76	11	3.6	3 005 517	Total
Southern California:								
Angeles NF	34	27	-16	-14	-50	0.0	264 271	
Cleveland NF	31	23	-21	-22	-52	-0.2	221 536	
Los Padres NF	35	33	-13	-11	-45	-0.2	753 572	
San Bernardino NF	56	46	13	15	-24	1.1	310 261	
Southern California mean	39	33	-9	-8	-43	0.1	1 549 640	Total
Sierra Nevada:								
El Dorado NF	91	90	76	82	22	4.8	325 558	
Modoc NF	89	75	50	55	11	2.9	835 343	
Lassen NF	86	87	72	76	17	4.4	609 661	
Plumas NF	79	91	77	82	16	4.4	559 398	
Tahoe NF	86	89	75	80	16	4.4	447 880	
Lake Tahoe Basin management unit	99	83	71	74	23	4.0	53 218	
Sierra Nevada mean[c]	87	77	59	63	12	3.2	5 400 282	Total

PFRID = percentage of FRID.

[a] Sign of NPS FRID values reversed for consistent interpretation.

[b] Areas refer only to lands for which FRID was calculated, i.e., they exclude rocky and barren areas, herbaceous vegetation, lakes, etc.

[c] Sierra Nevada means values and local area calculated from 11 Sierra Nevada region forests.

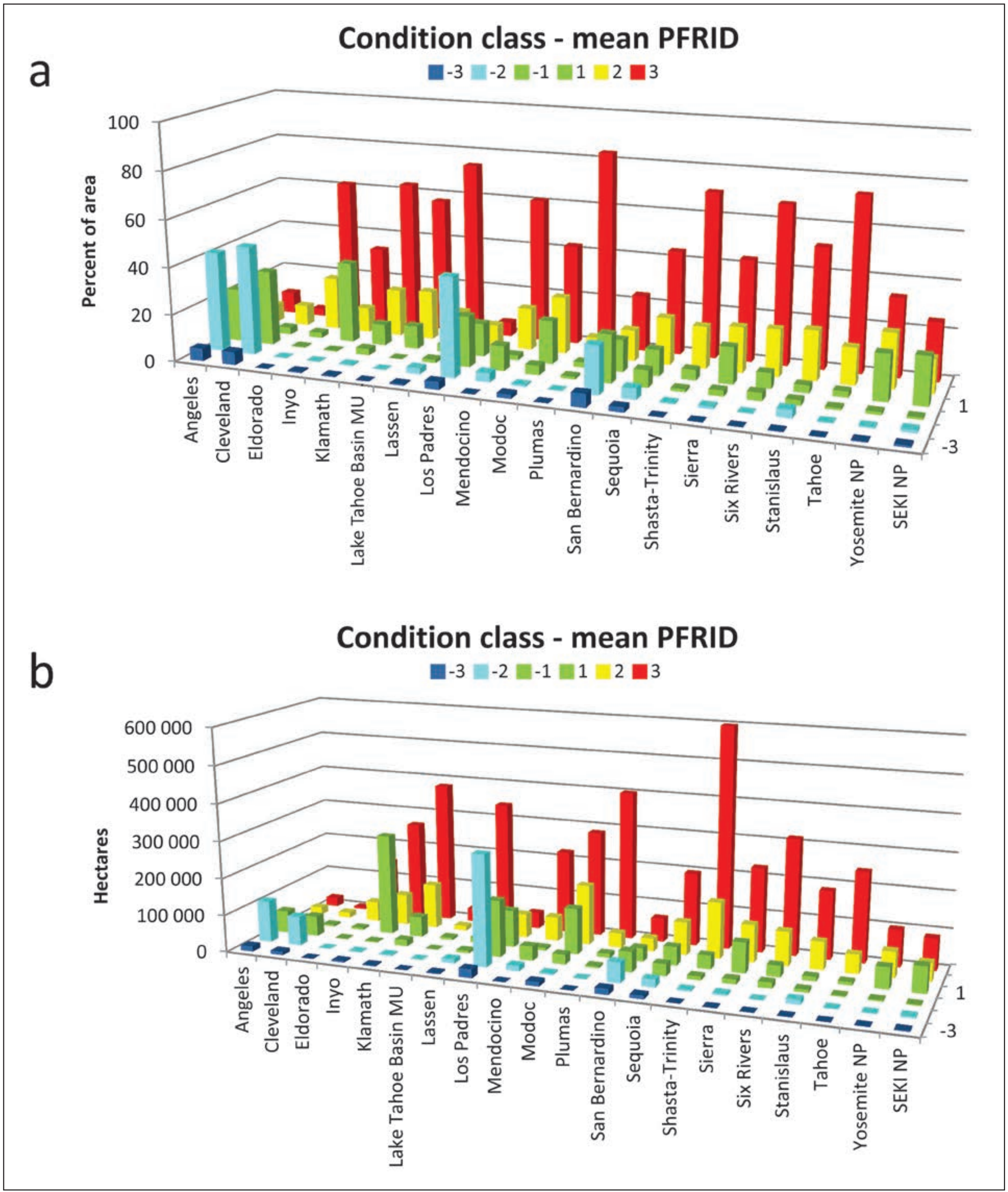

Figure 9—Comparison of condition class (CC) measures (from the mean percent fire return interval departure [PFRID] metric) for the 18 California national forests managed by the Pacific Southwest Region, and Yosemite and Sequoia-Kings Canyon National Parks (NPs); (a) percentage of area; (b) total area. Total area of each management unit includes lands not in woody vegetation (grassland and meadows, barren lands, rocks, etc.), so totals do not add up to 100 percent. Colors are reversed from figures 3 and 5 to correspond to the nationally standard color scheme for CCs 1 through 3 (green-yellow-red).

Elevational Trends

Above 700 m, TSLF rose in all three regions when plotted against elevation (fig. 10). Fire return interval departure measures were mostly unimodally related to elevation, but they rose over most of the elevational gradient in southern California, and dropped over the upper half of the gradient in NW California and the Sierra Nevada. In NW California, the 100-m moving average of TSLF decreased as elevation increased from sea level to 400 m, then increased again at higher elevations (fig. 10a). The 100-m moving averages of mean, median, min, and max PFRID and the NPS-FRID index rose slightly between sea level and 1500–1700 m, then decreased to a minimum at 2900 m. Mean, median, and min PFRID, and NPS-FRID index remained largely positive over the entire elevational range, while max PFRID transitioned from positive to negative at approximately 2400 m. In the Sierra Nevada, TSLF decreased between sea level and 700 m, then increased again at higher elevations (fig. 10b). Mean, median, min, and max PFRID, and the NPS-FRID index decreased between sea level and 700 m, increased until 1750 m, then decreased to a minimum at 3700 m. Mean, median, and min PFRID remained positive over the entire elevation range, while max PFRID was negative from 450 m to 1000 m, and the NPS-FRID index was negative from 3050 m to 3700 m. As elevation increased in southern California, TSLF decreased from sea level to approximately 700 m, then increased again at higher elevations (fig. 10c). Mean, median, min, and max PFRID, and the NPS-FRID index also decreased between sea level and approximately 750 m, then increased to a maximum at around 2500 m before decreasing again. Mean and min PFRID remained largely positive over most of the elevational range. Median PFRID transitioned from negative to positive at approximately 1400 m, max PFRID transitioned at 1800 m, and the NPS-FRID index transitioned at 1600 m.

Using the standard mean PFRID measure as an index of central tendency, the southern California landscape is mostly in CC 2 from about 1500 m to 2900 m elevation (fig. 10c). Averaged across the NW California area, mean PFRID remained above CC 1 throughout the elevational profile until about 2200 m; mean PFRID was in CC 3 between 1200 and 1800 m elevation (fig. 10a). In the Sierra Nevada, mean PFRID showed similar patterns to NW California: it was greater than CC 1 throughout the elevational gradient and in CC 3 between 1600 and 2000 m. Mean PFRID fell to CC 1 values above about 2700 m (fig. 10b). The NPS-FRID index never reached “high” (>2) values in southern California, was >2 between 1000 and 1600 in NW California, and >2 between 900 and 2200 m in the Sierra Nevada.

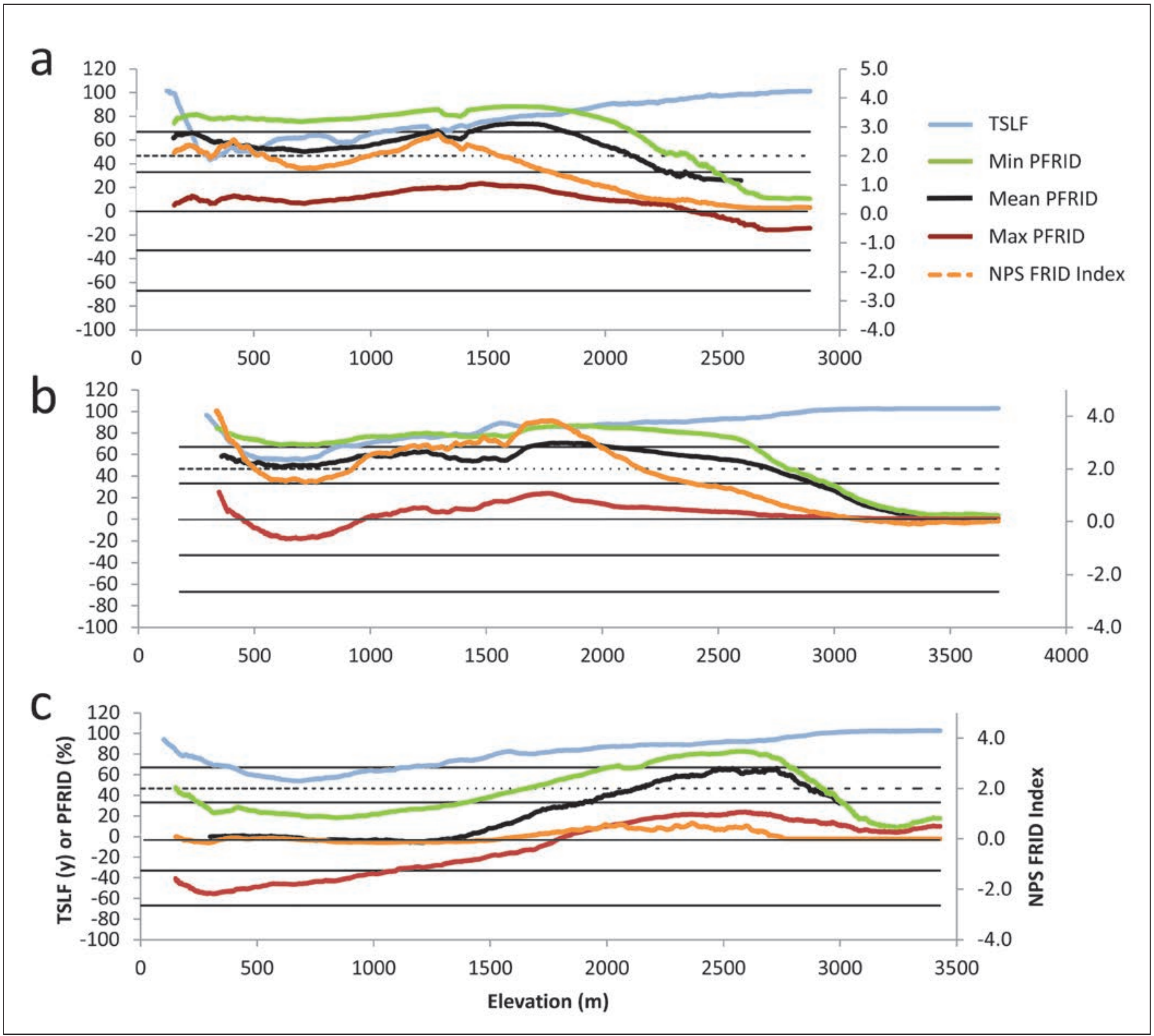

Figure 10—100-m moving averages of time since last fire (TSLF) and fire return interval departure (FRID) versus elevation in (A) northwest California region, (B) Sierra Nevada region, and (C) southern California region. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. For figures 10 through 14, solid horizontal reference lines are provided for PFRID values of -67 (transition from CC -2 to CC -3), -33 (CC -1 to CC -2), +33 (CC 1 to CC 2), and +67 (CC 2 to CC 3). Dotted reference line refers to the National Park Service (NPS) FRID Index value of 2, which is the transition from “moderate” departure to “high” departure.

Precipitation Trends

The TSLF in NW California fluctuated considerably but generally increased with increasing annual precipitation, from 55 years at 25 cm to 103+ years at 420 cm (fig. 11a). As precipitation increased in the Sierra Nevada, TSLF decreased between 10 and 85 cm, increased until 130 cm, decreased until 250 cm, and then increased to a maximum at 300 cm (fig. 11b). Annual precipitation had little relationship to the different FRID measures in either NW California or the Sierra Nevada. In both regions, most FRID measures rose almost imperceptibly across the precipitation gradient (except below 50 cm), although max PFRID decreased gradually with precipitation in NW California. The TSLF and the FRID measures in southern California decreased with precipitation, except between 50 and 100 cm, where they leveled off (fig. 11c). Mean PFRID decreased as precipitation increased from 20 to 50 cm, rose slightly to 100 cm, and then dropped again; the NPS-FRID index stayed near zero, except at the highest precipitation values. Min PFRID remained positive over the entire precipitation gradient, whereas max PFRID remained negative.

In both NW California and the Sierra Nevada, mean PFRID tracked the boundary between CC 2 and 3 across most precipitation values. In southern California, areas with precipitation over 110 cm generally fell in the CC 1 to CC -1 belt (within +/-33 percent of presettlement fire frequency) (fig. 11).

Temperature Trends

Fire return interval departure trends with temperature in NW California and the Sierra Nevada were broadly similar. In both regions, FRID measures were (generally) low at low temperatures, gradually rose to a maximum, then gently declined (figs. 12 and 13). In both regions, the maximum departure between contemporary and presettlement fire frequency was generally reached between -4 and -2 °C mean minimum temperatures, 9 to 11 °C mean temperatures, and 25 to 27 °C mean maximum temperatures. In the Sierra Nevada, a rise in all of the FRID values also occurred again at the highest temperatures (fig. 13). In NW California, mean PFRID exceeded CC 1 along most of the temperature gradient, beginning at about -7 °C mean minimum temperature, 4 °C mean temperature, and 19 °C mean maximum temperature (fig. 12). In the Sierra Nevada, mean PFRID exceeded CC 1 above -10 °C mean minimum temperature, 3 °C mean temperature, and 19° mean maximum temperature; it fell back within CC 1 above 4 °C mean minimum temperature.

In southern California, FRID measures rose with increasing temperature until approximately -6 °C mean minimum temperature, 7 °C mean temperature, and 25 °C mean maximum temperature (fig. 14). Thereafter all measures dropped strongly

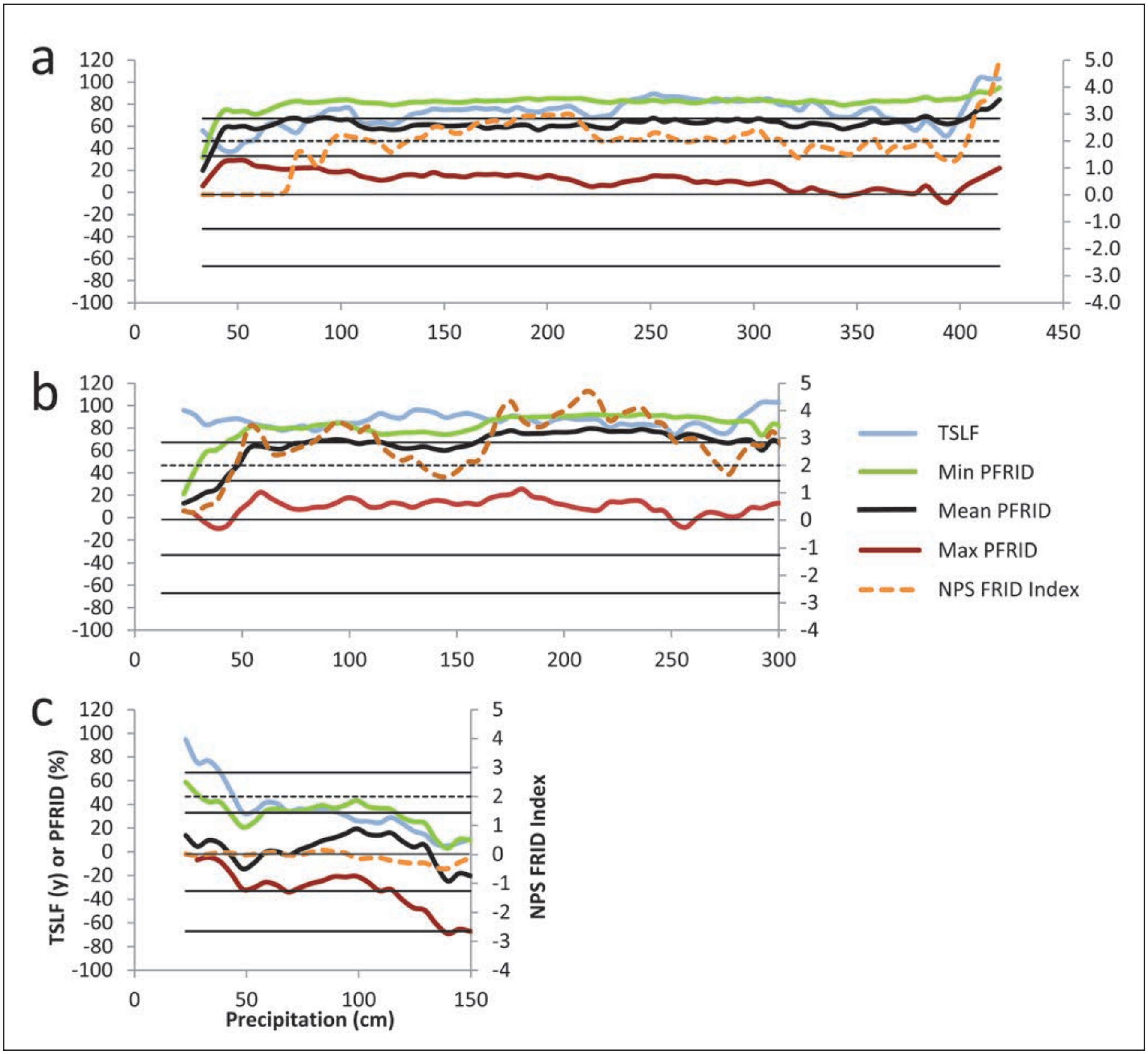

Figure 11—Time since last fire (TSLF) and fire return interval departure (FRID) versus precipitation in (A) northwest California region, (B) Sierra Nevada region, and (C) southern California region. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

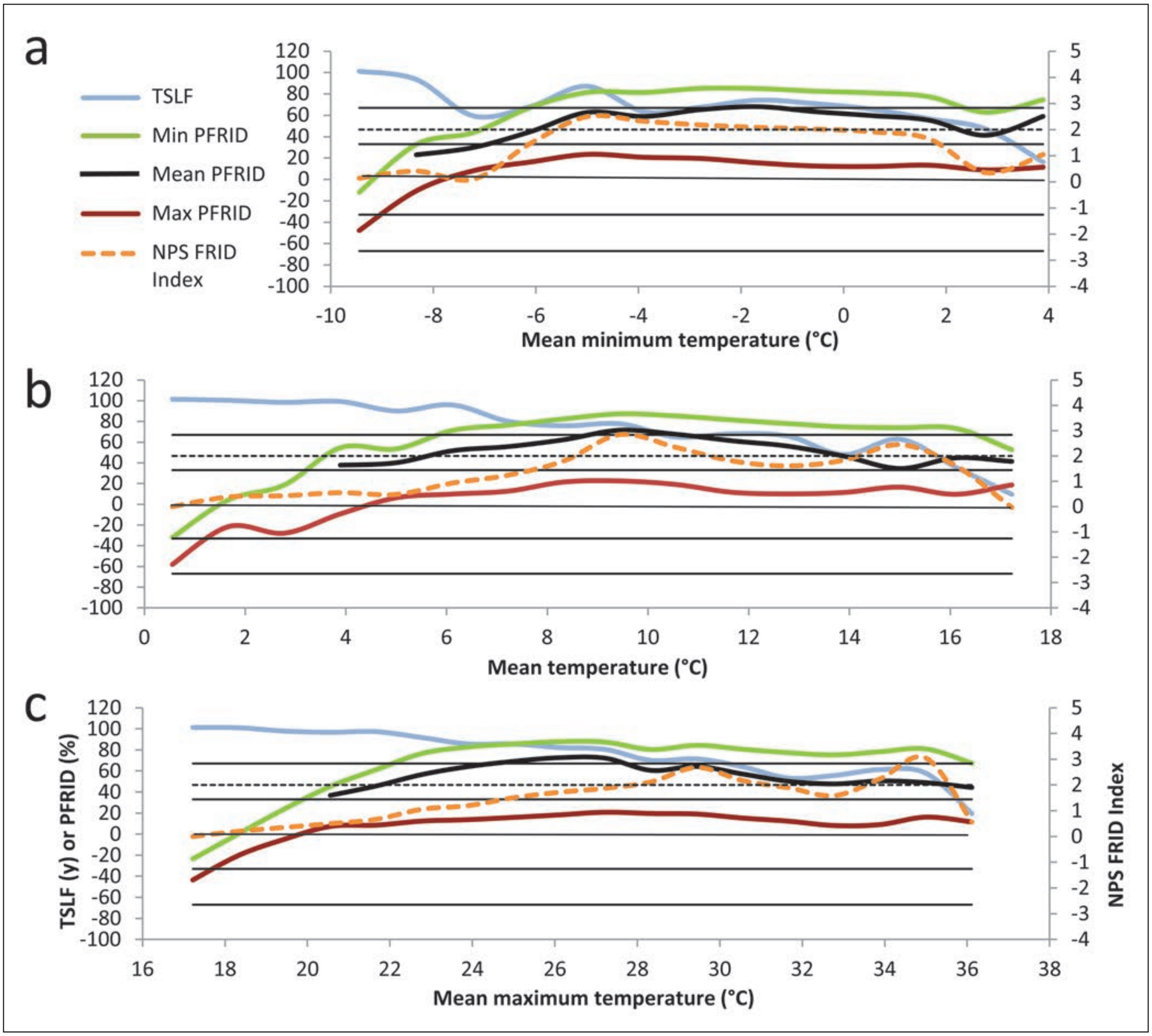

Figure 12—For the northwest California region, time since last fire (TSLF) and fire return interval departure (FRID) versus (A) mean minimum annual temperature, (B) mean annual temperature, and (C) mean maximum annual temperature. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

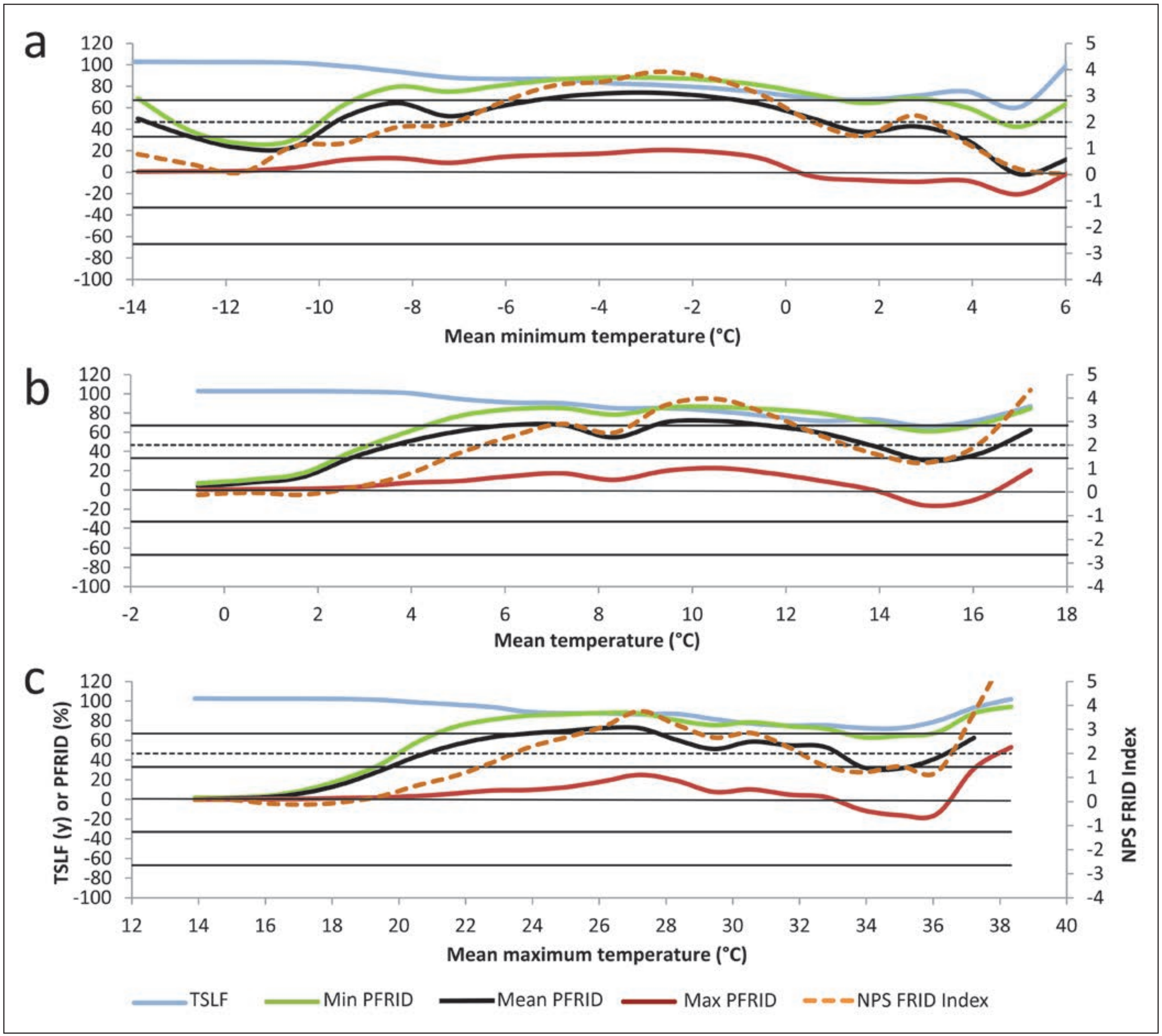

Figure 13—For the Sierra Nevada region, time since last fire (TSLF) and fire return interval departure (FRID) versus (A) mean minimum annual temperature, (B) mean annual temperature, and (C) mean maximum annual temperature. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

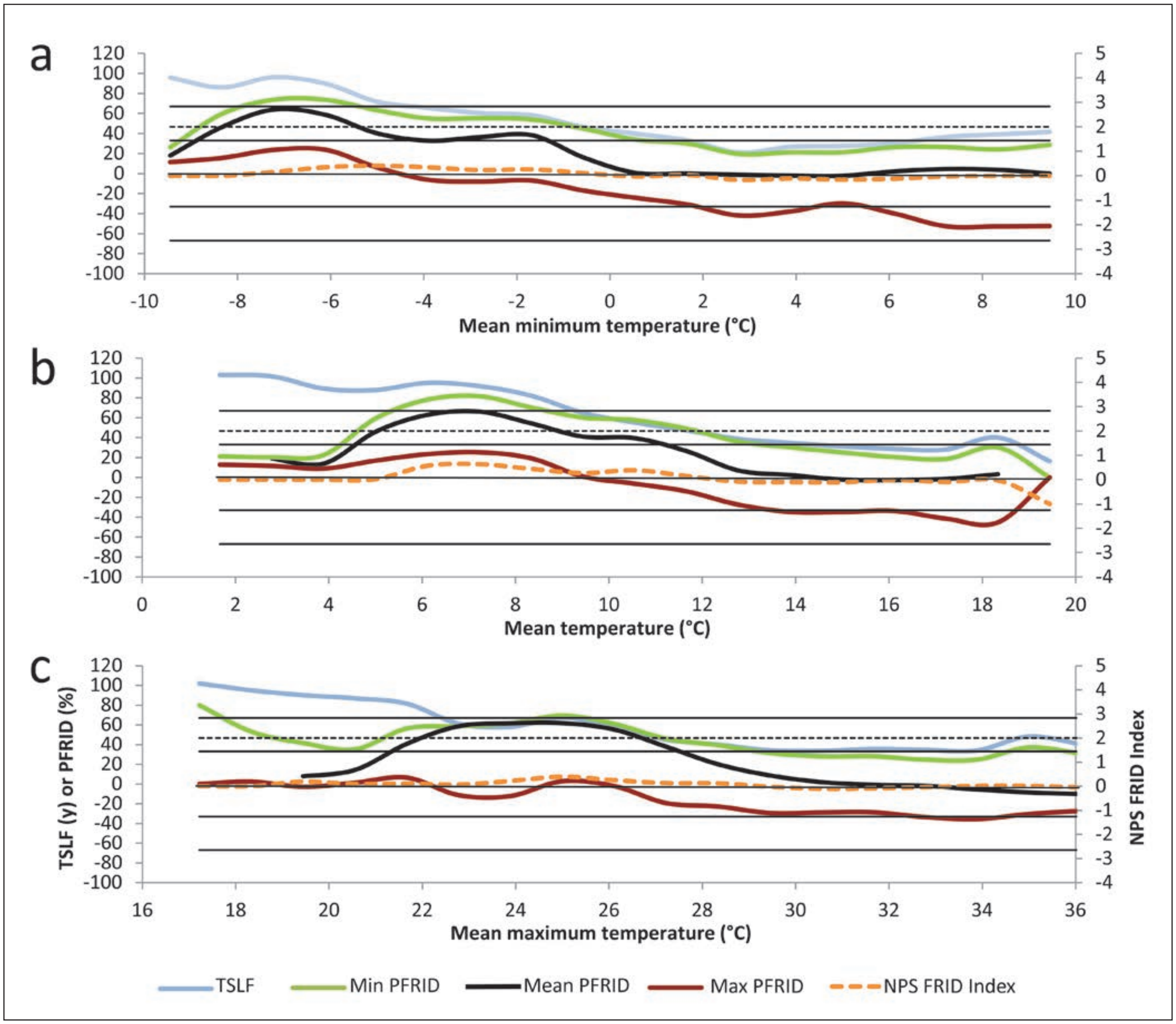

Figure 14—For the southern California region, time since last fire (TSLF) and fire return interval (FRID versus (A) mean minimum annual temperature, (B) mean annual temperature, and (C) mean maximum annual temperature. Median percent FRID (PFRID) closely corresponds to mean PFRID and was removed for clarity. See figure 10 for explanation of horizontal reference lines. NPS = National Park Service.

with increasing temperature. In southern California, mean PFRID (and most other indices) fell in the CC 1 to CC -1 belt above -1 °C mean minimum temperature, 11 °C mean temperature and 27 °C mean maximum temperature (fig. 14).

Differences Among Presettlement Fire Regime (PFR) Types

There were notable differences in departure statistics among the 28 major PFR types (table 4). With respect to PFRs experiencing missed fire events, the most extreme departures (CC 3) were in lower montane and montane forest and woodland types, with the degree of departure decreasing broadly with increasing elevation, precipitation and the snow:rain ratio, and decreasing temperature: yellow pine (*Pinus ponderosa* Dougl. ex Loud. and *P. jeffreyi* Balf.) and dry mixed conifer > moist mixed conifer (all CC 3) > lodgepole pine (*P contorta* Douglas ex Louden) > red fir (*Abies magnifica* A. Murry bis) > western white pine (*P. monticola* ex D. Don) (all CC 2) > subalpine (CC 1) (table 4). Aspen (*Populus tremuloides* Michx.) was another PFR type with mean PFRID in CC 3. With respect to PFRs experiencing enhanced fire activity, there were two groups with high departures: coastal fir and fire-sensitive spruce/fir (both CC -2), which are primarily ± maritime or in areas of higher precipitation; and coastal sage scrub (also CC -2 on average), a shrub type in coastal and near coastal southern California. Much chaparral in southern California is also in CC -2 or -3, but northern California stands are not as prone to anthropogenic fire, and statewide averaging results in an overall mean PFRID of only -19 (CC -1). With respect to Great Basin PFRs, the three sagebrush types were ranked thus: silver sagebrush (*Artemisia cana*; almost CC 3) > big sagebrush (*A. tridentata*; high CC 2) > black and low sagebrush (*A. nova, A. arbuscula*; CC 1). The pinyon-juniper PFR was ranked CC -1 (table 4). Both desert shrubland PFRs (desert mixed shrub and semidesert chaparral) were CC -1, with some geographic areas experiencing much higher current frequencies of fire than under presettlement conditions (e.g., the western Colorado desert), and others not.

Discussion

Our analysis highlights some broad dichotomies and notable gradients in the contemporary occurrence of wildland fire when viewed in the context of the probable “natural” fire frequencies experienced by the ecosystems over the centuries preceding Euro-American settlement. Geographically speaking, there are major differences between northern California and southern California, continental-climate California (Great Basin and desert) and Mediterranean-climate California, and wildland and suburban California. Elevation is unimodally related to most FRID measures, as are mean minimum, mean, and mean maximum temperatures.

Table 4—Total area and spatial averages of time since last fire (TSLF) and fire return interval departure (FRID) measures for the 28 presettlement fire regime (PFR)[a] groups analyzed in this study

PFR	Area	TSLF	Mean PFRID	Median PFRID	Min PFRID	Max PFRID	NPS-FRID Index
	Hectares	*Years*					
Aspen	24 533	96	80	79	89	7	4.0
Big sagebrush	1 105 857	89	57	50	82	5	1.5
Bigcone Douglas-fir	31 939	31	20	23	87	-51	0.0
Black and low sagebrush	336 888	99	32	45	63	-4	0.5
California juniper	7084	71	-4	1	93	-32	-0.2
Chaparral and serotinous conifers	1 575 973	38	-19	-23	24	-47	-0.3
Coastal fir	18 036	20	-57	-67	23	-72	-0.7
Coastal sage scrub	108 323	40	-33	-48	51	-53	-0.5
Curl-leaf mountain mahogany	64 907	96	43	32	67	-8	0.9
Desert mixed shrub	308 386	99	-4	-4	-3	-4	-0.9
Dry mixed conifer	1 398 610	85	85	88	93	35	6.7
Fire-sensitive spruce or fir	159	16	-63	-47	-38	-75	-0.8
Lodgepole pine	186 298	99	62	63	84	-5	1.7
Mixed evergreen	1 302 184	67	51	78	74	-11	1.3
Moist mixed conifer	2 090 128	85	80	85	94	7	4.3
Montane chaparral	519 106	73	61	64	77	27	1.8
Oak woodland	184 673	73	79	79	91	25	5.1
Pinyon juniper	650 199	95	-7	3	46	-8	-0.5
Port Orford cedar	8373	91	65	81	88	-12	2.0
Red fir	522 511	93	55	63	83	-8	1.4
Redwood	7585	60	51	68	78	-38	1.6
Semidesert chaparral	56 233	58	-2	-2	15	-35	-0.1
Silver sagebrush	7921	98	64	69	84	33	1.8
Spruce-hemlock	636	103	0	0	0	0	-0.6
Subalpine forest	335 339	100	-2	-2	1	-3	-0.5
Western white pine	35 066	99	48	57	84	-5	1.0
Yellow pine	1 279 302	80	84	90	93	43	6.3

Note: Results for the shore pine PFR are not reported as it does not occur in the analysis area. Percent fire return interval departure PFRID data are read as percentage departure.

[a] From Van de Water and Safford (2011).

In southern California, precipitation is negatively related to FRID, but elsewhere (both NW California and the Sierra Nevada) it shows little relationship above 50 cm. There are differences among management units and vegetation types as well. We discuss these patterns below.

Vegetation in “northern California” (NW California and Sierra Nevada regions) is dominated primarily by conifer forest and woodland, while shrublands and hardwoods dominate coastal southern California with dryland and desert vegetation covering interior southern California. For any given longitude, precipitation in northern California is generally higher than in southern California, and areas of similar elevation and topographic position are usually warmer and drier in southern California. The fire season in southern California is nearly year-round (compared to 4 to 6 months in most of northern California), and half of the year is characterized by periodic strong, dry easterly winds (e.g., "Santa Ana winds") that are rare north of latitude 35°. About two-thirds of California's human population lives in the southern one-fifth of the state, and fire ignition patterns strongly follow this pattern. The proportion of lightning to human ignitions (on Forest Service lands) is about 1:5 in southern California, but closer to 1:1 in the rest of the state (and 1.3:1 if the Lake Tahoe Basin is excluded) (Keeley 1982). These major ecogeographic differences between southern and "northern" California are key to understanding many of the geographic gradients we see in the FRID data.

Patterns in Southern California

Forest Service lands in 6 of 18 of the ecological sections had average mean and median PFRID values less than 0, and all of these are in southern California. Most of these averaged in the CC -1 range (0 to 33 percent departure), with the exception of Forest Service lands in the Colorado Desert section (a very small area in only one subsection analyzed), which were CC -3 or borderline by all of the PFRID measures, and the central Coast Ranges section, which were CC -2 (almost all Forest Service land in the section is in one subsection, the southern part of the interior Santa Lucia Range). In our analysis, the Colorado Desert section was represented by 521 ha of Forest Service land in the Coachella Valley subsection. Much of the valley is populated or converted to agriculture, and human ignitions are affecting Forest Service lands in areas that are (or were) dominated by the desert mixed shrub PFR, which has the longest reference mean FRI (610 years) of the 28 PFR types in our study (Van de Water and Safford 2011). The Anza-Borrego desert to its south (the Borrego-West Mesa subsection, not in our study area) is also subject to a regime of numerous ignitions by humans. In both subsections, invasion of drylands by exotic grasses and forbs (e.g., red brome [*Bromus madritensis* L. ssp. *rubens*], Mediterranean grass [*Schismus* spp.], Sahara mustard [*Brassica tournefortii* Gouan]) is widespread and leads to fuel continuity that abets fire spread (Brooks and Minnich 2006). Similar invasion by highly flammable exotic species is also occurring in areas of the Mojave Desert Section (which is also mapped predominantly in the mixed desert shrub PFR), but Forest Service lands in the Mojave Desert are only a very small proportion of the section area (fig. 3, table 2) and they are dominated by stands of California juniper (*Juniperus californica*), whose mean presettlement FRI (77 years) is very close to the average TSLF for the section (table 3).

Many areas in the Southern Coast and Southern Mountains and Valleys ecological sections have seen fire frequencies rise dramatically over the last century. Most of this increase in fire activity has occurred since the end of World War II, and temporal and spatial patterns in increasing fire frequency in southern California are strongly correlated with human population growth (Keeley and Fotheringham 2001, Syphard et al. 2007). Interactions between human populations and highly flammable vegetation types like coastal sage scrub and chaparral have led to major changes in fire regimes in and around southern California's urban areas. The ecological subsections surrounding the San Diego, Los Angeles, and Santa Barbara metropolitan areas are among the most negatively departed in the state (figs. 4 and 6; because they did not include Forest Service lands, the coastal subsections including the San Diego and Los Angeles metropolitan areas, Oxnard, and the Santa Monica Mountains were not analyzed in our study, but they have some of the highest fire frequencies in California). In these areas, extensive landscapes characterized originally by dense native shrublands have been converted to degraded, open stands of native shrubs and exotic annual grasses and forbs, which are easily reignited. These fire-mediated changes in vegetation lead to higher rates of erosion, increased exotic species invasion, and higher fire hazard as grass fuels replace shrubs (Merriam et al. 2006, Wells 1987, Zedler et al. 1983).

For its size, southern California between Santa Barbara, San Diego, and San Bernardino is the national leader in average annual wildfire frequency and area, as well as fire-caused human mortality, home loss, and economic damages (Halsey 2004, Hammer et al. 2007, Safford 2007). Although the ecological consequences of the contemporary anthropogenic fire regime in southern California are significant, they receive comparatively little coverage in the popular press, and further degradation of the remaining natural landscapes in southern California will feed back into yet greater human exposure to natural hazards like debris flows, flash floods, and wildfires in suburban settings (Cannon and Gartner 2005, Halsey 2004). Continued high fire frequencies in southern California also threaten the viability of plant and animal species that require longer fire-free periods. High-profile examples of such species include the federally listed California gnatcatcher (*Polioptila californica*) and Tecate and Cuyamaca cypress (*Hesperocyparis forbesii, H. stephensonii*) (Bontrager et al. 1995, Gouvenain and Ansary 2006).

Three small areas of higher mountains (up to 3500 m) rise above southern California south of 35° N latitude. These are found within the Upper San Gabriel, Upper San Gorgonio, and San Jacinto Ecological Subsections. These three subsections can be clearly seen in the mean PFRID map in fig. 6a, where they appear as positive (blue) inclusions in the sea of negatively departed landscapes. These mountain "sky islands" support coniferous PFRs like dry mixed conifer, yellow pine, and lodgepole pine, as well as mixed evergreen forest and montane chaparral. To a great extent, plant communities inhabiting these higher mountains are southern extensions of montane communities in the Sierra Nevada, and their historical relationship with fire is similar (Sugihara et al. 2006). Lightning-ignited fires once burned frequently in these high-elevation forests, but—unlike in lowland chaparral—fire suppression policies have been successful in nearly eliminating wildfire as an ecological force (Keeley et al. 2009). This has resulted in a curious elevational schizophrenia in contemporary southern California fire regimes, where high-elevation forests that once experienced frequent, low- to moderate-severity fire now rarely experience it (and when they do, it is often high severity), while many areas of lower elevation shrublands that experienced relatively infrequent fire before Euro-American settlement (on average maybe every 50 to 80 years) (Van de Water and Safford 2011) are now seeing fire return intervals of 10 to 20 years or less (Safford 2007).

Although it is also part of our southern California block, Forest Service lands in the Central Coast Section are mostly within the probable HRV for fire frequency or are only moderately departed (table 2, figs. 4 and 6) (Moritz 1997). Although a spate of recent large fires in the northern Santa Lucia Range has brought attention to the area, presettlement mean FRIs for the dominant vegetation types in the area were between 23 years (redwood; but this was strongly anthropogenic [Greenlee and Langenheim 1990]) and 76 years (coastal sage scrub) (Van de Water and Safford 2011). Most Forest Service lands in the north and south Santa Lucia Range subsections have burned between two and four times since 1908, so FRIs over the last century are mostly between 25 and 50 years.

Great Basin

In similar fashion to the southern California deserts but to an even greater degree, the Great Basin is experiencing a rash of large fires in lower elevation ecosystems that are driven largely by invasive species (chief among them cheatgrass [*Bromus tectorum* L.] and red brome), which have altered fire regimes by increasing fine fuels, fuel connectivity, and the rate of fire spread (Link et al. 2006). Most PFRs mapped in the small portion of eastern California belonging to the Great Basin sensu lato (ecological sections include Mono, the Southeastern Great Basin, and the Northwestern Basin and Range) (table 2) had presettlement FRIs between 35 and 150+ years (Van de Water and Safford 2011). Some areas in the Great Basin of Nevada and southern Idaho are now burning at intervals of 3 to 5 years (Whisenant 1990). Such extremely high fire frequencies are not yet common in the Great Basin portion of our study area, because the wave of cheatgrass invasion only recently arrived in eastern California, but also because Great Basin lands contained in the California national forests tend to be higher elevation and are less subject to invasion by annual grasses (D’Antonio et al. 2004). Fire frequencies are very high in the Nevada counties east of Lake Tahoe and northeast of Mono Lake (between 38 and 40° N latitude, in Washoe, Douglas, and Lyon Counties and Carson City, just to the east of our study area), and many former stands of single-leaf pinyon pine (*Pinus monophylla* Torr. & Frém.), juniper (*Juniperus* spp.), sagebrush (especially subspecies of *Artemisia tridentate* Nutt.), and even Jeffrey pine have been eliminated and replaced by degraded landscapes of exotic grasses and scattered shrubs. Cheatgrass has recently become an issue in the Mediterranean part of California as well, and it is now a frequent invader of burned areas along the west slope of the Sierra Nevada, especially where the regenerating shrub layer is sparse (McGinnis et al. 2010).

Northwestern California and Sierra Nevada Regions

Unlike most of southern California, the NW California and Sierra Nevada Regions (“northern California”) are experiencing major ecosystem impacts from a century of fire suppression. The effects of fire exclusion on fire frequencies in northern California are the most obvious large-scale pattern in figures 4 to 6 and table 2. Densities of ignitions by humans are much lower in northern California; northern California is less subject to extreme thermal winds than southern California; the northern California fire season is shorter; and fires in contemporary forests in northern California burn largely through woody coniferous fuels, in which relatively low vertical and horizontal continuity in fuel structure makes the occurrence and sustenance of crown fire much less likely than in the more homogeneous and continuous fuels found in southern California chaparral. As a result, the fire suppression policy has been effective in much of northern California, although recent trends in fire activity, burned area, and fire severity suggest that the situation is rapidly changing as climate warms and fuels continue to accumulate (Miller and Safford 2012, Miller et al. 2009, Westerling et al. 2011).

The ecological sections with Forest Service lands having the greatest FRI departures in California are the Southern Cascades, the North Coast (but only a very small part of the section analyzed), the Klamath Mountains, the Northern Coast Ranges and the Sierra Nevada (table 2). The NPS-FRID index, which focuses on the time since last fire, identifies the Southern Cascades as the section with the greatest departure—its 4.6 score is almost in the “extreme” range—while the other sections listed above all scored as 3.3, or “high” departure. There have been very few wildfires in the Southern Cascades section during the contemporary period, largely because—between the volcanoes—much of the landscape is comprised of forests on rolling lava beds and the road density is high, which combine to permit rapid firefighter access to and containment of fire starts (Skinner and Taylor 2006). Another factor contributing to high FRID in certain NW California and Sierra Nevada ecological sections is the high level of fragmentation of federal land ownership. The checkerboard ownership pattern across much of eastern NW California and the northern Sierra Nevada leaves little opportunity for creative fire management to serve ecological purposes, as private land is usually within a burning period of any ignition point.

The only large area of low CC 2 (in some cases CC 1) lands in the Sierra Nevada and NW California regions is found in the southern Sierra Nevada (fig. 6). Here, checkerboard ownership is rare, and Forest Service and NPS lands combine to form one of the largest contiguous blocks of federally managed forest lands in the lower 48 States. The core of this block is formed by Yosemite, Sequoia, and Kings Canyon NPs, all of which include large areas of wilderness managed to promote the occurrence of naturally ignited wildfires. Neighboring national forests (e.g., Sequoia, Sierra, Stanislaus, Inyo, and Humboldt-Toiyabe) also include large tracts of high-elevation wilderness, and wildfires are much more likely to be managed for ecological benefits here than on any other national forests in California. That said, it is noteworthy that the mean PFRID averaged across these southern Sierra Nevada management units still falls into CC 2 (in the case of the Stanislaus NF, CC 3) (table 3). The similarities in PFRID metrics between the adjacent national forest and NPS units are due to the fact that fire was suppressed in both land ownerships for the majority of the time period considered in our analysis (until the early 1970s, when the NPS embarked on a more aggressive wildland fire-use program [note that the term “wildland fire use” is no longer in use]), and relatively few areas have burned a sufficient number of times since 1908 to make up the long-term deficit in fire. If we had based our PFRID comparisons on current FRIs beginning in 1970 instead of 1908, the differences between the NPS units and the national forests would doubtless be much greater. A further consideration is that naturally ignited fires managed for ecological benefit tend to occur in higher elevation forests (e.g., high-elevation mixed-conifer, red fir, subalpine), where fire is more easily controlled owing to lower tree densities, low fuel loadings, and higher fuel moistures, but where FRIs are longer and FRID is generally lower than at lower elevations that are (or were once) dominated by yellow pine, oak, and dry mixed-conifer forests. Fire managers are much less comfortable allowing fires in lower elevation forests to burn, as high fuel loads, drier conditions, and the presence of human communities magnify the consequences of a fire escape. Such lower elevation forests are the core of the fuels problem however, and—at the landscape scale—the use of managed fire in high-elevation forests, while commendable, does nothing to resolve the growing potential for high-severity fire in the yellow pine and mixed-conifer belt (Miller et al. 2009, Miller and Safford 2012). Even under a much expanded managed fire program, it will take many decades of progressive wildfire use in these landscapes to restore them to a compositional and structural state that is reasonably resilient to the probably accelerated disturbance regimes of a warmer future (Overpeck et al. 1990).

The only ecological subsections in NW California and the Sierra Nevada with contemporary fire frequencies approaching presettlement frequencies are in the northern and southern ends of the Sierra Nevada Foothills, the mountain ranges and dry valleys of the Mojave/Southeastern Great Basin, and portions of the Modoc Plateau in the northeastern corner of the state (fig. 6). In the case of the Sierra Nevada Foothills, these are largely landscapes of grasslands and oak woodlands, where contemporary fire frequencies are high owing to intensive human land use and relatively high population densities. The Great Basin and Modoc Plateau subsections support dryland ecosystems (sagebrush, pinyon-juniper, etc.) with longer natural FRIs (35 to 151+ years), and fire frequencies have been relatively low over the last century. The ongoing invasion of cheatgrass into the Great Basin borderlands seems likely to increase fire activity in these subsections as the climate continues to warm (Billings 1994, Brooks and Minnich 2006).

FRID Trends Along Environmental Gradients

Fire return interval departure trends along the analyzed environmental gradients (elevation, precipitation, and temperature) underline the similarities between NW California and the Sierra Nevada, and the different nature of the fire situation in southern California. Along the west coast of North America at 90° W longitude and between 20° and 60° N latitude, the latitudinal gradient in monthly mean temperature averages about 5.6 °C per 1000 km (ranging from 8.7° January to 2.5° July; calculated from isotherms in FAA [1975]). Thus, on average, mean annual temperatures in interior NW California at latitude 41° N are about 1.8 °C cooler than at the same elevation in the central Sierra Nevada (latitude 38° N) and about 4.3 °C cooler than the same elevation in interior southern California (latitude 34° N). The latitudinal increase in warmth to the south results in an upward shift of the major forest types. The elevations and temperatures of the maximum mean PFRID values in NW California and the Sierra Nevada (elevations of 1500 to 1700 m in the former, 1700 to 1900 m in the latter; corresponding temperatures of -2 °C mean minimum, 10 °C mean, 27 °C mean maximum; figs. 10 through 13) correspond broadly to the average elevation of the transition from moist mixed-conifer ("lower montane") to red fir ("upper montane") forest. These elevations are slightly above the level of maximum annual precipitation (Armstrong and Stidd 1967, Barbour et al. 2007), and correspond approximately to the elevations at which the mean freezing level occurs during mid-winter storms (Barbour et al. 2002). Red fir-dominated forests above this transition receive the highest snowfall totals of any vegetation type in California, the growing season is short, and productivity is markedly lower than in lower montane forests (Barbour et al. 2002, 2007). This leads to lower levels of fuel accumulation, moister fuel beds in the early fire season, and lower fire hazard than in the mixed-conifer belt (Cope 1993, Kilgore 1981, Sugihara et al. 2006); the latter is also partly due to the enhanced component of fir needles in surface litter in red fir forest, as fir litter is substantially less flammable than pine litter (Fonda et al. 1998). Presettlement FRIs in the red fir belt averaged 40 years (range of means = 15 to 130), while moist mixed-conifer forests in the lower montane zone supported much more frequent fire (mean = 16 years, range = 5 to 80) (Van de Water and Safford 2011).

In southern California, the behavior of FRID metrics along the environmental gradients was substantially different than in the two northern California regions. The elevations of the maximum mean PFRID values were much higher than in northern California (2500 to 2700 m), and the temperatures much lower (-7 °C mean minimum, 7 °C mean, 25 °C mean maximum; these correspond to about 2600 m). Above these elevations, FRID dropped rapidly (fig. 10), suggesting a threshold type of response. We believe this is because there is no red fir in southern California, so there is no transitional fire regime between the mixed-conifer and subalpine forests, which begin above 2400 to 2700 m in southern California. According to Minnich (2007), the mixed-conifer/subalpine ecotone in southern California represents a shift from frequent surface burns to infrequent stand-replacing burns, and our data support this generalization. As in NW California and the Sierra Nevada, the elevation of the highest mean PFRID values in southern California corresponded broadly to the elevation of the mean freezing level during winter storms, which ranges from 2300 to 2500 m (Minnich 1986) in the San Bernardino Mountains.

The NPS-FRID index is almost invariant along the analyzed environmental gradients in southern California, remaining very near zero in almost all cases. The only slight rises in the NPS-FRID index in southern California are at about those temperatures or elevations that correspond to the maximum mean PFRID values. Because it was developed for assessing departure in fire-suppressed forests, the NPS-FRID index is insensitive to fire frequencies that are occurring at shorter intervals than under reference conditions, which is the case in most of the southern California lowlands that we analyzed. The fact that the NPS-FRID index remains near zero even in fire-suppressed montane forests underlines the recent increase in fire activity that has characterized southern California in general. The PFRID metrics, which depend on FRI information from the entire 103-year record of fire perimeters, show major departures from presettlement conditions and dilute the signal of recent rises in burned area and the incidence of large fires in southern California, which have been ascribed to the effects of increasing drought severities on fuel conditions (Keeley and Zedler 2009).

On its own, precipitation shows no obvious relationship to any of the FRID metrics or TSLF in northern California, but most of the FRID metrics and TSLF appear to decline with rising precipitation in southern California. The range of precipitation in NW California and the Sierra Nevada is at least twice as broad as the range in southern California (fig. 11). All of the regions include some areas with annual precipitation < 50 cm, but none of our southern California analysis area receives more than 150 cm annually, while many areas in the Sierra Nevada and NW California do (fig. 11) (Minnich 2007, Potter 1998). Working in the Sierra Nevada and NW California, Miller et al. (2009, 2012) found that for the period 1908–1910 to 2006–2008 (depending on the region), annual precipitation had no relationship to annual fire number, mean or maximum fire size, or total annual burned area in either region (only forest fires analyzed). However, different seasonal precipitation totals explained substantial variation in the response variables, with the season in question changing over the course of the study period; summer (June through August) or spring (March through May) precipitation had the strongest relationship over the last 20 to 25 years (Miller et al. 2009, 2012). We did not relate seasonal precipitation totals to FRID or TSLF, but Miller et al.'s results, where no single season of precipitation was related to fire number, size, or area measures through the entire study period, make us confident that we would have found no simple relationship. The lower PFRID and NPS-FRID index measures below 50 cm precipitation in NW California and the Sierra Nevada are driven partly by the longer reference FRIs in sagebrush-dominated habitats in the northeastern and southeastern Sierra Nevada regions, and partly by recurrent fires in drier lowland habitats around the Central Valley and elsewhere (fig. 6).

In southern California, the strong drop in TSLF and the PFRID metrics (and the slight dip in the NPS-FRID index) above 100 cm precipitation (fig. 11) is due to the very large 2008 and 2009 southern and central California fires, which burned over 160 000 ha in areas of relatively high precipitation, including the Monterey District of the Los Padres NF (which includes the only part of southern California with mean annual precipitation > 120 cm), and the San Gabriel Mountains around Mount Wilson. Higher PFRID values below 50 cm precipitation (fig. 11) are due primarily to the northeastern, transmontane part of the main body of the Los Padres NF (see figs. 1 and 4), which supports >100 000 ha of pinyon-juniper (presettlement FRI mean = 151 years, range 50 to 250), California juniper (mean = 83 years, range = 5 to 335), and related dryland vegetation and has largely escaped fire for the last century.

Using FRID Data in Resource Management

Using historical data to inform resource management is not simple, and a number of critical limitations must be surmounted. Important limitations include how to account for the roles of humans in reference ecosystems, mismatches in scale within the data and between the data and their application, the quality and quantity of available data, and the lack of stationarity in environmental baselines (Wiens et al. 2012). We discuss these complications below, and then finish with a few examples of how our FRID data can be used in resource management and restoration.

The role of human ignitions prior to Euro-American settlement—
A question that always arises when restoration of fire is discussed is, What role did humans have in the pre-Euro-American settlement regime, and should we be targeting that regime or some version of a fire regime driven only by "natural" (lightning, etc.) ignition sources? The presettlement fire record is derived primarily from fire-caused injury lesions in tree stems or charcoal in layers of sediment or peat, and we are mostly unable to discern lightning-ignited fires from anthropogenic fires. Although lightning occurrence differs temporally at multiple scales, contemporary lightning strike densities (LSDs) can provide some idea as to where on the landscape the ratio of lightning to anthropogenic ignitions was skewed one way or another. California is one of the least lightning-prone states in the United States, with most of the Mediterranean part of the state averaging only 0 to 0.25 strikes per square kilometer per year (compare to the Gulf Coast, with over six strikes per square kilometer per year, or the southeastern and Midwestern United States, with more than three strikes per square kilometer per year [Orville 2008]). The highest LSDs in California are in the deserts of southeastern California and the eastern and higher western slopes of the Sierra Nevada, where average annual LSDs range from 0.3 to 0.55 strikes per square kilometer per year. Highlands in the eastern Klamath Mountains, the southern Cascades, and the interior ranges of southern California average about 0.25 to 0.3 strikes per square kilometer per year (van Wagtendonk and Cayan 2008). Pre-Euro-American settlement fire frequencies in the California Coast Ranges were clearly due primarily to human use of fire, with redwood and

coastal oak woodlands being two of the best examples of ecosystems strongly shaped by human fire management. The relative magnitude of human inputs to the fire regime in the Sierra Nevada before Euro-American settlement is much less certain, although anthropogenic fire was certainly a significant factor within some radius of many Native American cultural sites and as California probably supported more Native Americans than any other Western State (Anderson 2005, Starr 2005), giving consideration to their role in molding California ecosystems seems both wise and justified. (Anderson 2005, Sugihara et al. 2006). Depending on desired conditions and the results of collaborative planning, restoration target conditions in California landscapes might focus on the cultural presettlement landscape, or on some vision of an ecosystem resilient to warming temperatures and higher fire hazard in the future, or even on some conception of how the landscape might have looked in the absence of anthropogenic fire. Whatever the location and the management situation, humans have been in California for more than 10,000 years.

Issues of scale—

We conducted our assessment primarily at the state and regional level, which necessarily hides substantial variability at finer scales. For example, the Sierra Nevada sensu stricto is nearly 700 km long, and precipitation drops and temperature rises from north to south. Forest structure and composition also change. Tree densities and canopy cover decrease to the south, pine dominance increases, and shade tolerant tree species like Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), tanoak (*Notholithocarpus densiflorus* Hook. & Arn.) Manos, CH. Cannon & S. oh), and madrone (*Arbutus menziesii* Pursh) are rare or altogether absent south of 37° 30’ N latitude (Barbour et al. 2007). Other tree species, like giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Bucholz) and foxtail pine (*Pinus balfouriana* Balf.), are restricted primarily or completely to the southern Sierra Nevada. Such clinal changes can have major effects on the fire regime, even within a single vegetation or PFR type. As noted in Van de Water and Safford (2011), different FRI measures (mean, median, minimum, maximum) may be of more use in different parts of the PFR range. Where local data on pre-Euro-American settlement fire regimes are available, they should be consulted (see Van de Water and Safford [2011] for a comprehensive list of pre-2011 references). Spatial relationships between PFRs can also have a major impact on local fire regimes. For example, where vegetation types of very different flammabilities are juxtaposed, fire frequencies will be locally affected. Vegetation patch sizes are also important and can be an important determinant of the local fire regime (Agee 1998, Bond and van Wilgen 1996). Our FRID mapping products are available for all Forest Service units in California, so assessments at finer scales are possible.

Another scalar issue is related to the numerical resolution of the FRID data and the resolution at which they are applied. Condition classes based on some aspect of fire regime or its effects on ecosystem status (e.g., vegetation structure, such as in the FRCC program [Hann and Strohm 2003]) have become widely used measures of ecosystem status and management progress in reducing fuels or restoring forest structure. The green-yellow-red (good-poor-bad) color scheme of many condition class maps or graphics (e.g., fig. 9) is a useful and eye-catching method for highlighting areas in need of management intervention, but it can hide important variation in the analyzed ecosystems and landscapes, and it can suggest one-size-fits-all remedies for situations that require nuanced consideration. Our addition of the negative cc to the classic green-yellow-red (CC1-2-3) scheme for the mean PFRID metric (Safford et al. 2011) was an attempt to allow managers to recognize the very different ecological situations and management challenges created by departures caused by overly frequent fire. Broad categories like condition classes make wide generalizations possible, which may be useful for political, budgetary, and educational purposes. However, we recommend that the PFRID metrics be considered principally in their raw, unclassified form (e.g., 53 percent departure rather than “CC 2”) and with a keen eye to local conditions and information that can provide a more reasoned and realistic assessment at scales that matter to on-the-ground management.

A third scalar issue pertains to the temporal scale of comparison between the reference FRI information and current FRIs. Our PFRID metrics are set up to compare two relatively long-term data sets: the current FRIs, which in this study are obtained from the 103 (inclusive) years between 1908 and 2010, and the pre-Euro-American settlement FRIs, which were primarily derived from the two to five centuries before 1850. Fire management in California has passed through a number of different philosophical and tactical phases (Stephens and Sugihara 2006), and the effects of these different management periods on fire occurrence are masked or diluted by a metric based on averages from 103 years of data. The best example of this effect is in the comparisons we made between Yosemite, Sequoia and Kings Canyon NPs and the adjacent Sierra Nevada national forests. Extensive management of natural ignited fires for resource benefits began in the national parks in the 1970s, and a PFRID comparison using only the current FRIs since that time would probably show much greater differences between the national parks and the national forests, which continue to suppress most wildfires.

Data quality considerations—

The PFR data provided in Van de Water and Safford (2011) are not infallible, and we know of a number of situations where future data collection and finer differentiation of fire regimes are recommendable. For example, Jeffrey pine was placed into the yellow pine PFR by Van de Water and Safford (2011), but it is very stress tolerant and often found in situations where low site productivity notably reduces growth and fuel accumulation. Such sites simply cannot support the very high fire frequencies associated with modal Jeffrey pine sites. Examples include ultramafic "serpentine" soils in NW California and the Sierra Nevada, where Jeffrey pine is often the dominant tree species (Safford and Mallek 2010). The high positive FRID found for the Upper and Lower Scott Mountains ecological subsections in the eastern Klamath Mountains, which are largely underlain by ultramafic substrates, is thus almost certainly an overestimate of departure. In the Sierra Nevada on nonserpentine sites, Jeffrey pine grows extensively on the east side of the range at moderate elevations and on the west side in upper montane forests, where it generally occupies rocky, exposed sites with California juniper and other stress tolerators. The reference FRI in these low-productivity west-side sites, nested in forest with mean presettlement FRIs ≥ 40 years, is likewise surely longer than the standard yellow pine PFR (Van de Water and Safford 2011). The many shrub and closed-cone conifer types grouped together under the huge PFR category "chaparral and serotinous conifers" by Van de Water and Safford (2011) also include variability in FRIs across climatic and edaphic clines that may be better incorporated into a number of groups.

The fire perimeter data upon which the FRID polygons are based are also far from perfect. Because the database focus is on the fire perimeter, many unburned inclusions within fires are missed. Older fire perimeters (pre-World War II) are notoriously inexact, and some fires are represented simply by circular polygons of the appropriate fire size centered on the approximate fire location. Some portions of California are missing records of most fires before 1950. Most prescribed fires are missing from the database, although we are currently working with the Forest Service and NPS to remedy this deficiency. With all of these problems, however, the California Fire Perimeters database (FRAP 2011) is the most extensive and complete data source for fire location, size, and shape in the world to our knowledge. It is considered approximately complete for fires over 4 ha in size back to 1950, and mostly comprehensive for Forest Service fires to about 1908, when the agency began to require the collection of data on fire location and size (see McKelvey and Busse 1996, Miller et al. 2009).

Optimally, we would base an assessment of current FRID from pre-Euro-American settlement conditions on a vegetation map of average presettlement conditions. Obviously such a map does not exist. We considered using potential vegetation maps such as the Küchler map of California from 1976 (Barbour and Major 1988) or the Biophysical Settings (BpS) map from the LANDFIRE project (Rollins 2009), but the former was drawn qualitatively on a very broad-scale map of the state before the advent of geographic information systems, and the latter has too many inaccuracies at the subregional scale. The Forest Service inventoried California's nondesert wildlands in the 1920s and 1930s, but this was 70 to 80 years after settlement (although only a few decades after the beginnings of federal fire suppression), and the project was halted after about 60 percent of the area had been mapped (Wieslander 1935). Our decision to go with the most accurate statewide map of existing vegetation means that any substantial changes in vegetation over the time since 1850 could have an impact on the accuracy of our metrics. One of the best documented widespread changes has been the decrease in pine dominance and the increase in fire-intolerant species in lower and middle elevation forests in northern California (and higher elevation southern California) owing to 19th- and 20th-century timber harvest and 20th century fire suppression (Barbour et al. 2007, Minnich et al. 1995, Sugihara et al. 2006, Thorne et al. 2008). Many forest stands mapped today as mixed conifer would probably have been mapped as yellow pine in the mid-19th century. In these cases, our FRID measures of current departure from presettlement FRIs understate the actual magnitude of change, as the FRID measures are being calculated based on the mixed-conifer reference FRIs, which are up to 45 percent longer (in the case of moist mixed conifer) than the yellow pine reference FRIs (Van de Water and Safford 2011). In other cases, the reverse may be true. For example, comparison of the 1930s Forest Service maps of the Sierra Nevada (Wieslander 1935) with the current EVEG maps suggests that some areas originally mapped as subalpine forest are now dominated by red fir, which would reduce the presettlement baseline mean FRI from 133 years to 40 years. In this case, our FRID measures are somewhat more difficult to interpret, as the vegetation change is more likely due to climate warming than human management (Dolanc et al. 2012), and management attempts to reverse the trend may be counterproductive.

Consideration of changing climate—

Ecosystem transformations caused by directional climate change form the basis for a recent wave of concern regarding the usefulness and applicability of historical data to contemporary and, more importantly, future management problems (Millar et al. 2007, Stephenson et al. 2010, Wiens et al. 2012). The traditional assumption that ecosystem patterns and processes vary about some long-term mean (i.e., that they exhibit stationarity) was always untenable, but it has become even more so in the “Anthropocene” Epoch (Steffen et al. 2007). Changes in the environmental baseline resulting from climate change, or human land use, or invasive species, etc., make the uncritical use of historical data as a management target less and less defensible, but this does not reduce the value of historical data; indeed, the less we know about the future, the more we will have to rely on insight gained from our experiences with the past (Wiens et al. 2012). In the case of fire-suppressed forest types that historically burned at high frequency, human management has pushed the range of variation for fire occurrence far below the HRV. Modeled or inferred considerations of fire frequency over the next 50 to 100 years nearly unanimously project increasing potential for wildfire, perhaps even above levels that reigned when Euro-Americans settled California (see below). In this case, restoration of HRV conditions is a logical first step and might be treated as a waypoint toward the ultimate goal of increasing resilience to a much warmer future (Safford et al. 2012).

Management application of FRID data—
Fire return interval departure data can provide a template for assessing ecosystem conditions and evaluating landscapes for restoration need. Yosemite, Sequoia, and Kings Canyon NPs have used the NPS-FRID index for such purposes for over two decades (Caprio et al. 1997, Keifer et al. 2000, van Wagtendonk et al. 2002). At the simplest level, relationships between FRID and ecosystem type (as represented by our PFRs) can help direct broad landscape-level strategies. In northern California, high-elevation forests (red fir, western white pine, subalpine) are only moderately departed from historical conditions and—ecologically speaking—tend not to be high-payoff landscapes for fuels reduction, wildland fire use for ecological benefit, or other types of restoration management (Agee 2005). However, these are often the safest and easiest places to carry out such management (and climate warming is increasing concern for lower elevation red fir forests, which are transitional from the mixed-conifer belt). Areas of extreme departure, especially when evaluated against min or max PFRID, are probably at or beyond the HRV for fire frequency. These landscapes, mostly shrublands in southern California and low to middle elevation forests in northern California, may seem like logical places to focus ecological restoration efforts, but in some cases, they may be too difficult, too remote, too expensive, or too controversial to actively manage. The projected future environment of the restoration landscape will need to be considered in restoration planning, and management targets may need to be adjusted. The FRIs documented in the database do not need to represent the long-term target condition for the restored landscape, but they provide an idea of the range of fire frequencies that might best promote sustainability of the reference ecosystem type.

Future projections suggest even more ecological potential for wildfire in most Western U.S. forests than was the case during our pre-Euro-American settlement reference period (Lenihan et al. 2003, National Research Council 2011, Westerling et al. 2011), when fire was much more common than today. Climate-driven projections also suggest higher levels of drought and stress-related susceptibility to insect attack and disease (Evangelista et al. 2011, Sturrock et al. 2011). These projections suggest that a serious management effort will be required to increase the resilience of fire- and drought-prone landscapes to future environmental stressors. Our mean PFRID metric can be used in conjunction with the NPS-FRID index to identify recently burned locations that have experienced fire frequencies in the 20th century that are within or near HRV. Lydersen and North (2012) recently used a similar protocol to identify frequently burned mixed-conifer stands in the Sierra Nevada and conducted ground sampling to develop a picture of forest structure in fire-resilient stands. These are places to begin use of prescribed or managed wildland fire to ensure long-term maintenance of fire-resilient composition and structure. Such places could also be used as core areas around which to expand restoration efforts into the surrounding landscape.

As restoration efforts proceed, FRID data can be used to track progress and measure management success. Miller and Davis (2009) carried out fire modeling in two watersheds of Sequoia-Kings Canyon and Yosemite NPs based on suppressed lightning ignitions that had occurred during a previous 20-year period. At the end of their study period, they assessed the outcome of their exercise by generating a hypothetical map of the NPS-FRID index and comparing it to the actual FRID map that existed without the modeled fires. Tracking of fire restoration efforts at the broader landscape scale could be accomplished with a similar comparative protocol. For short-term monitoring, the NPS-FRID index may be the most useful performance measure, as it considers only the time since the most recent fire. In the end, repeated fires at appropriate levels of severity will be required to sufficiently restore the fire regime, vegetation structure and composition, wildlife habitat, and other ecosystem patterns and processes in frequent-fire forest types. In southern California shrubland ecosystems, on the other hand, the focus should be on reducing fire frequencies. Measures like mean, min, and max PFRID, which are better at evaluating the frequency of fire in an ecosystem over time, will be more helpful in targeting and tracking a long-term strategy to promote resilience. The final goal should not be a slavish adherence to the mean pre-Euro-American settlement fire frequencies listed in Van de Water and Safford (2011) and elsewhere. However, these values and their ranges can be used profitably as short- or medium-term targets for restoration efforts, in the understanding that the long-term goal is not some static picture postcard of a presettlement landscape, but a dynamic ecosystem that is more resilient to disturbance, a warming climate, and all of the other stressors that will come with global change.

When using the PFRID measures, managers may have the tendency to focus their restoration efforts on areas mapped as CCs 3 or -3, because current management policies are focused on highly departed lands. In most cases, this is probably a reasonable course of action, although—as noted above—for most situations we recommend use of the raw FRID data rather than the condition class categories. The extent to which the CC 2 and 3 or -2 and -3 boundaries might represent a reliable ecological warning bell can be gauged by the information provided in table 1. Table 1 compares the mean minimum and mean maximum pre-Euro-American settlement FRIs from Van de Water and Safford (2011) with the FRIs associated with the CC 2 and 3 (+67 percent departure) and CC -2 and -3 (-67 percent departure) boundaries. The 33 percent and 67 percent cutoffs used to identify CCs 1, 2, and 3 were based on simple division of the 100 percent maximum departure into thirds (Hann 2004, Hann and Strom 2003), thus there is no underlying statistical distribution of fire frequencies assumed. This leads to different relationships between the range of presettlement FRIs associated with each PFR and the FRIs represented by the CC 2 and 3 and CC -2 and -3 boundaries (table 1, fig. 15).

Looking at table 1, some generalizations can be made about these differences. For example, most tree-dominated PFRs show longer mean maximum FRIs than the FRIs associated with the CC 3 boundary (e.g., fig. 15), while shrub-dominated PFRs in table 1 universally show shorter mean maximum presettlement FRIs than the FRIs represented by the CC 3 boundary (table 1). These differences are probably due both to differences in sample size (there are many fewer studies of fire history in shrub vs. forest ecosystems) (Van de Water and Safford 2011), and inherent differences in the distributions of fire frequencies in the two ecosystem types (e.g., Grissino-Mayer 1999, Moritz 2003). For tree-dominated PFRs with longer mean maximum FRIs, managers might want to treat the mean maximum FRI as a higher class of departure (“extreme?”). For shrub PFRs with shorter mean maximum FRIs, CC 3 is a more conservative measure of departure than the mean maximum FRI. On the negative side of the PFRID scale, for most shrub PFRs the mean minimum presettlement FRI is longer than the FRI represented by the CC -3 boundary (table 1). In practical terms, this means that for PFRs like chaparral/serotinous conifers or semidesert chaparral, both with extensive distributions in southern California, use of the CC -3 category as an ecological alarm bell for overly frequent fire may actually underestimate the magnitude of the ecological departure.

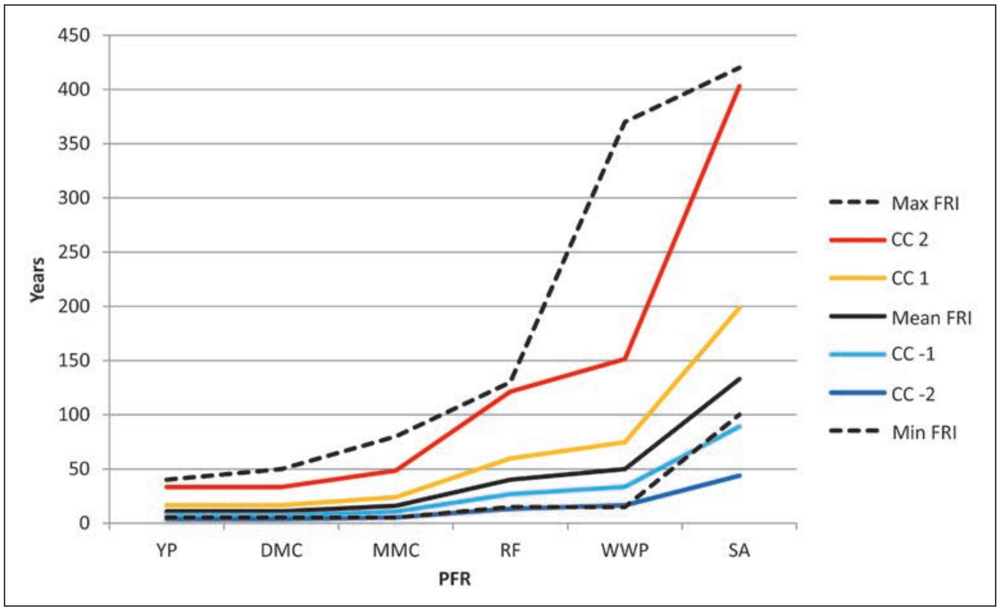

Figure. 15—Elevational gradient (left to right: low elevation to high) of six forest presettlement fire regimes (PFRs) on the west slope of the Sierra Nevada, comparing the condition class (CC) boundaries for each PFR with the approximate range of pre-Euro-American settlement fire return intervals (FRIs) (the area between mean maximum ["max FRI"] and mean minimum ["min FRI"]). Condition class color scheme corresponds to figure 9. YP = yellow pine, DMC = dry mixed conifer, MMC = moist mixed conifer, RF = red fir, WWP = western white pine, and SA = subalpine forest.

Fire return interval departure users should pay careful attention to the various limitations and caveats inherent to the tool. As discussed above, these include scalar issues, issues with data quality and extent, issues with the reference baseline, and issues with interpretation. We finish by reminding the reader that FRID analysis does not include information on aspects of the fire regime other than fire frequency calibrated by vegetation type. Fire occurrence and behavior are driven by such factors as topography, weather, and fuel conditions that were not directly considered in our analysis. FRID is a useful broad-scale planning tool, but proper interpretation at scales meaningful to resource managers will require concurrent consideration of other sources of information as well, such as site history, fuel loading and vegetation structure, topography, weather, and other components of the fire regime, including fire size, severity, and spatial pattern.

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English Equivalents

When you know:	**Multiply by:**	**To find:**
Millimeters (mm)	0.0394	Inches
Meters(m)	0.394	Feet
Kilometers (km)	0.621	Miles
Hectares (ha)	2.47	Acres
Square kilometers (km^2)	0.386	Square miles
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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REVIEW SUMMARY

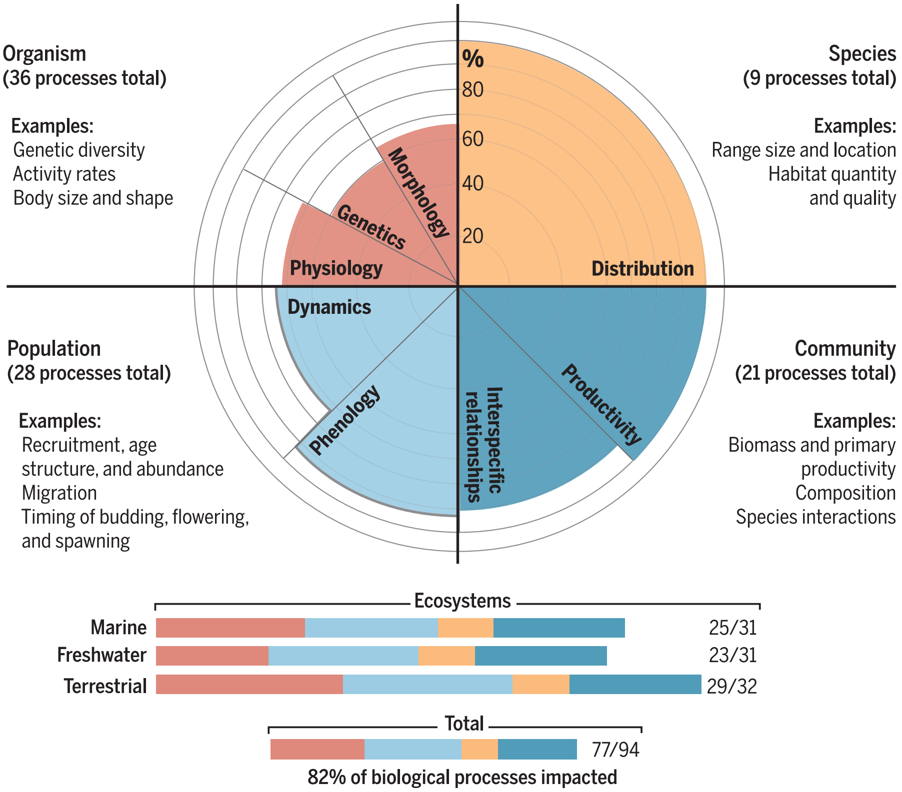
CLIMATE CHANGE

The broad footprint of climate change from genes to biomes to people

Brett R. Scheffers,* Luc De Meester, Tom C. L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H. M. Butchart, Paul Pearce-Kelly, Kit M. Kovacs, David Dudgeon, Michela Pacifici, Carlo Rondinini, Wendy B. Foden, Tara G. Martin, Camilo Mora, David Bickford, James E. M. Watson

BACKGROUND: Climate change impacts have now been documented across every ecosystem on Earth, despite an average warming of only ~1°C so far. Here, we describe the full range and scale of climate change effects on global biodiversity that have been observed in natural systems. To do this, we identify a set of core ecological processes (32 in terrestrial and 31 each in marine and freshwater ecosystems) that underpin ecosystem functioning and support services to people. Of the 94 processes considered, 82% show evidence of impact from climate change in the peer-reviewed literature. Examples of observed impacts from meta-analyses and case studies go beyond well-established shifts in species ranges and changes to phenology and population dynamics to include disruptions that scale from the gene to the ecosystem.

ADVANCES: Species are undergoing evolutionary adaptation to temperature extremes, and climate change has substantial impacts on species physiology that include changes in tolerances to high temperatures, shifts in sex ratios in species with temperature-dependent sex determination, and increased metabolic costs of living in a warmer world. These physiological adjustments have observable impacts on morphology, with many species in both aquatic and terrestrial systems shrinking in body size because large surface-to-volume ratios are generally favored under warmer conditions. Other morphological changes include reductions in melanism to improve thermoregulation, and altered wing and bill length in birds.



Climate change impacts on ecological processes in marine, freshwater, and terrestrial ecosystems. Impacts can be measured on multiple processes at different levels of biological organization within ecosystems. In total, 82% of 94 ecological processes show evidence of being affected by climate change. Within levels of organization, the percentage of processes impacted varies from 60% for genetics to 100% for species distribution.

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Broader-scale responses to climate change include changes in the phenology, abundance, and distribution of species. Temperate plants are budding and flowering earlier in spring and later in autumn. Comparable adjustments have been observed in marine and freshwater fish spawning events and in the timing of seasonal migrations of animals worldwide. Changes in the abundance and age structure of populations have also been observed, with widespread evidence of range expansion in warm-adapted species and range contraction in cold-adapted species. As a by-product of species redistributions, novel community interactions have emerged. Tropical and boreal species are increasingly incorporated into temperate and polar communities, respectively, and when possible, lowland species are increasingly assimilating into mountain communities. Multiplicative impacts from gene to community levels scale up to produce ecological regime shifts, in which one ecosystem state shifts to an alternative state.

OUTLOOK: The many observed impacts of climate change at different levels of biological organization point toward an increasingly unpredictable future for humans. Reduced genetic diversity in crops, inconsistent crop yields, decreased productivity in fisheries from reduced body size, and decreased fruit yields from fewer winter chill events threaten food security. Changes in the distribution of disease vectors alongside the emergence of novel pathogens and pests are a direct threat to human health as well as to crops, timber, and livestock resources. Humanity depends on intact, functioning ecosystems for a range of goods and services. Enhanced understanding of the observed impacts of climate change on core ecological processes is an essential first step to adapting to them and mitigating their influence on biodiversity and ecosystem service provision. ■

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REVIEW

CLIMATE CHANGE

The broad footprint of climate change from genes to biomes to people

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Most ecological processes now show responses to anthropogenic climate change. In terrestrial, freshwater, and marine ecosystems, species are changing genetically, physiologically, morphologically, and phenologically and are shifting their distributions, which affects food webs and results in new interactions. Disruptions scale from the gene to the ecosystem and have documented consequences for people, including unpredictable fisheries and crop yields, loss of genetic diversity in wild crop varieties, and increasing impacts of pests and diseases. In addition to the more easily observed changes, such as shifts in flowering phenology, we argue that many hidden dynamics, such as genetic changes, are also taking place. Understanding shifts in ecological processes can guide human adaptation strategies. In addition to reducing greenhouse gases, climate action and policy must therefore focus equally on strategies that safeguard biodiversity and ecosystems.

Atmospheric concentrations of greenhouse gases from burning fossil fuels and deforestation are approaching levels that have not been detected in the past 20 million years (*1*). This has altered the chemical composition of the Earth's atmosphere, oceans, and fresh waters (*2*). As a result, temperatures in the upper ocean and on land are now ~1°C higher than in preindustrial times, and temperature, wind, and precipitation regimes have become more variable and extreme (*3*, *4*). These changes are having clear impacts on planetary biophysical processes, including desalinization and acidification of the world's oceans (*5*) and melting of permafrost, ice sheets, and glaciers (*6*, *7*). Lakes and rivers have increased in temperature, altering seasonal patterns of mixing and flows (*8*).

Changing climate regimes have been an important driver of natural selection in the past (*9*) and, as in the past, species are responding to the current human-induced climate event in various ways. Previous reviews have covered many of the more obvious changes in species ranges, phenologies, and population dynamics (*10*–*15*) but have usually focused on one ecological system at a time. Here, we discuss the full range and scale of climate change effects on biota, including some of the less obvious disruptions observed in natural systems. We present examples of case studies of observed impacts across terrestrial and aquatic biomes and find evidence that climate change is now affecting most biological and ecological processes on Earth—spanning genetics, organismal physiology and life-history, population distributions and dynamics, community structure, and ecosystem functioning (Fig. 1 and table S1). People depend on intact, functioning ecosystems for a range of goods and services, including those associated with climate adaptation (*16*). Understanding the observed impacts of current climate change on core ecological processes is therefore an essential first step in humans planning and adapting to changing ecosystem conditions.

Although inherently different, marine, freshwater, and terrestrial realms share a common hierarchy of levels of biological organization, ranging from genes to organisms, populations, species, communities, and ecosystems. Broadly adapting from Bellard *et al.* (*17*), we screened the literature (supplementary materials) to evaluate evidence that climate change is affecting ecological components across different levels of biological organization, each of which comprises a core set of ecological processes (Fig. 1, fig. S1, and table S1). We identify a set of core ecological processes on Earth (32 in terrestrial and 31 each in marine and freshwater), which together facilitate ecosystem functioning that supports services to people (*17*). These processes include changes in genetic diversity (genetics), metabolic rates (physiology), body size (morphology), timing of migration (phenology), recruitment (population dynamics), range size (distribution), loss of synchronization (interspecific relationships), and biomass (productivity) (*17*). Because our main goal is to assess what processes are affected by climate change, we define "impact" on each process as an observed change in that process linked to climate change. We do not differentiate between "positive" (adaptive, buffering, or mitigating) and "negative" (stress or damage) responses because responses may be positive at one level of biological organization (such as genetic adaptation to climate change) but negative at another (such as reduced genetic variation and capacity to deal with other stressors). We then consider the relevance of the affected ecological processes in human systems and illustrate observed impacts to ecosystem services such as food and resource security (fisheries, agriculture, forestry, and livestock production), human health, and hazard reduction.

Ecological impacts of climate change

Organisms

Genetics

There is now growing evidence that species are undergoing evolutionary adaptation to human-induced climate change. For example, between the 1960s and 2000s the water flea (*Daphnia magna*) evolved to cope with higher thermal extremes in the UK (*18*), and cornflower (*Centaurea cyanus*) life history traits have recently evolved in response to warmer springs across northern France (*19*). Other examples include the evolution of earlier migration timing in anadromous pink salmon (*Oncorhynchus gorbuscha*), with decreased frequency of incidence of a genetic marker that encodes for late migration (*20*). Time-series data that control for physiological acclimatization also show strong evidence for genetic responses to climate change. For example, Bradshaw and Holzapfel showed that genotypic values for the critical day length that induces diapause in the pitcher plant mosquito (*Wyeomyia smithii*) change with latitude, and that the latitudinal relationship has changed over the period from 1972 to 1996 (*21*). Onset of diapause now occurs later, which is consistent with a longer

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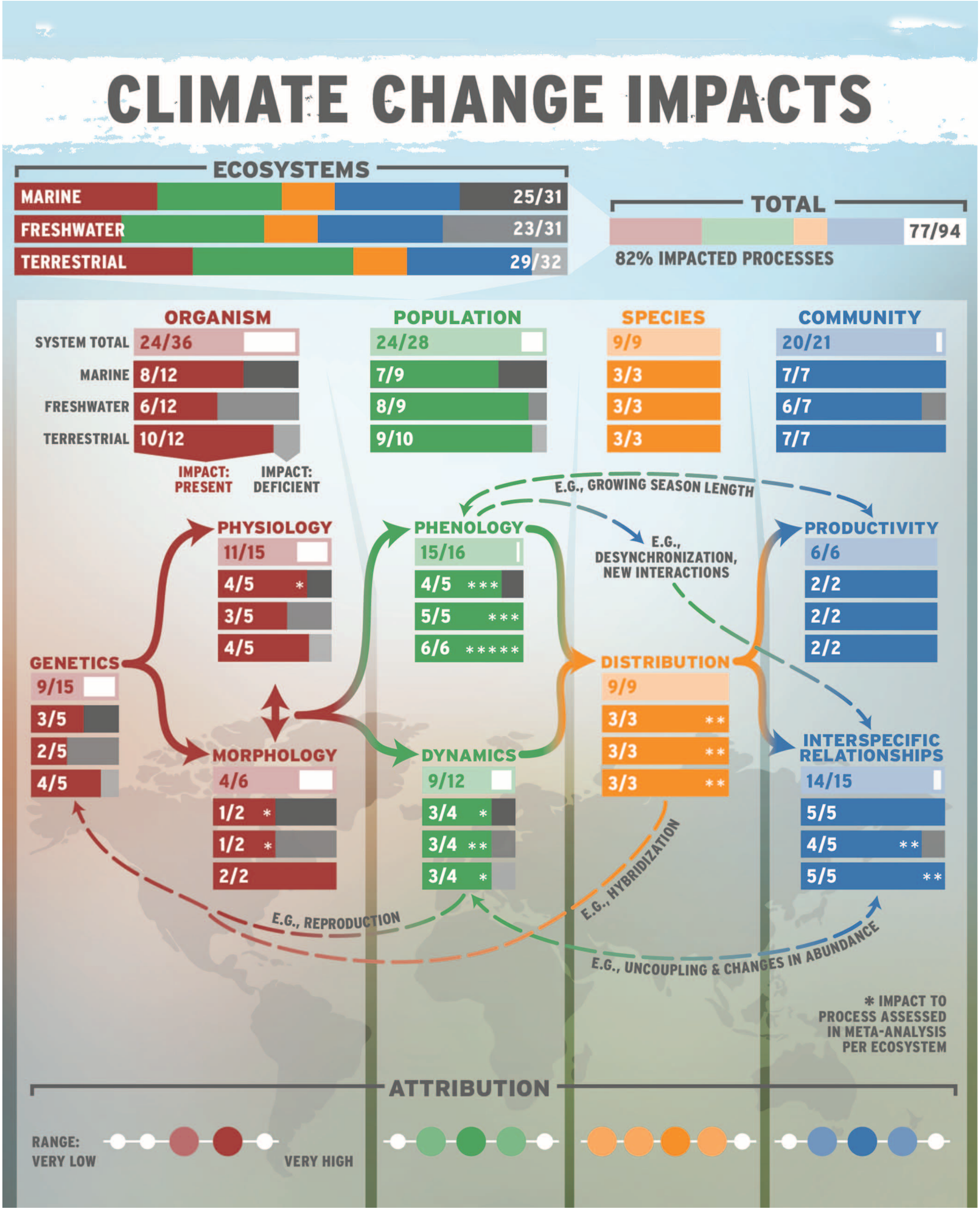

Fig. 1. Climate change impacts on Earth's marine, terrestrial, and freshwater systems. The presence of observed impacts on the different levels of biological organization and its inner components across the Earth's marine, terrestrial, and freshwater ecosystems. The denominator represents the total number of processes that we considered for each group, and the numerator is the number of these processes with evidence of impact (a complete list of processes is provided in fig. S1 and table S1). In total, 82% of all (n = 94) ecological processes that were considered have observed evidence of impact by climate change. Each process has at least one supporting case study. The asterisk indicates whether the affected process was assessed in a meta-analysis in addition to case studies. Thus, double-asterisk indicates that two processes were assessed in at least one meta-analysis. Confidence that the observed impact can be attributed to climate change was assigned for each level of organization and ranges from very low, low, medium, high, to very high; this assessment is based on tables 18-7, 18-8, and 18-11 in (13). The darkest circle indicates confidence level with the most literature support.

IMAGE CREDIT: STACEY JONES/MICHELE WOOD/IFAS

growing season under warmer conditions. Oceanic phytoplankton have adapted to a temperature change of +0.73°C associated with 15 years of climate warming in the Gulf of Cariaco, Venezuela, by adjusting their thermal niche by +0.45°C (*22*). Although such evidence from small organisms with short generation times is accumulating, we found little documented evidence of evolutionary change from species with longer generation times such as birds, mammals, and trees (*14*, *23*), although adaptation appears to be possible in some long-lived reef corals (*24*).

Changes in species ranges have altered or created new "hybridization zones" across the planet. For example, in North America, hybrid zones between black-capped (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*) are shifting in response to warmer winter temperatures (*25*), and because the southern flying squirrel (*Glaucomys volans*) has expanded its range northward in eastern North America, it is now hybridizing with the northern flying squirrel (*G. sabrinus*) (*26*). In North American rivers and streams, hybridization between invasive rainbow trout (*Oncorhynchus mykiss*) and native cutthroat trout (*O. clarkia*) has increased in frequency as the former expand into warming waters (*27*). Such hybridization events have also been observed in some marine fishes, such as the coastal West Coast dusky cob (*Argyrosomus coronus*), and are expected to increase as species shift their ranges poleward in response to rapidly warming ocean conditions (*28*).

Physiology

Many species display temperature-driven trait plasticity in physiological processes such as thermal optima (*29*). Whereas some responses, such as acclimation to high temperatures, maximize fitness, others can reflect failure to cope with temperature stress and other climate-mediated changes. These responses can occur within a generation or between generations through maternal or epigenetic effects (*30*).

There is some observational evidence that warming has affected temperature-dependent sex determination (TSD) of species in marine and terrestrial systems. Snake pipefish (*Entelurus aequoreus*) in the northeastern Atlantic have altered their operational sex ratios and reproductive rates as a consequence of warmer sea surface temperatures (*31*). Most evidence for impacts on TSD in marine systems, however, is derived from experimental studies, which provide strong support for TSD changes in sea turtles and various fish species (*32*, *33*). In terrestrial and freshwater systems, TSD has been implicated in masculinization and feminization, respectively, of lizard and turtle populations (*34*, *35*).

In marine systems, physiological responses to both climate warming and changing ocean conditions are widespread (*36*, *37*). Matching field and laboratory data for the eelpout (*Zoarces viviparus*) show increased metabolic costs associated with warming in the North and Baltic Seas (*38*). In aquatic systems, warming increases oxygen demand but decreases oxygen content of the water, resulting in substantial metabolic costs (*39*). Although climate change per se does not cause acidification of the oceans, both arise directly from higher atmospheric carbon dioxide, and experimental evidence has raised concerns regarding negative effects of ocean acidification on calcification, growth, development, and survival of calcifying organisms (*12*). For example, acidification has led to extensive shell dissolution in populations of the pteropod *Limacina helicina* in northwest North America and in the Southern Ocean off Antarctica (*40*, *41*).

Morphology

Individuals in some species are becoming smaller with increasing warming because large surface-to-volume ratios are generally favored under warmer conditions (*42*)—a phenomenon that is linked to standard metabolic principles (*43*). In the Appalachian Mountains, six species of *Plethodon* woodland salamander have undergone, on average, an 8% reduction in body size over the past 50 years (*44*). Similarly, three species of passerine birds from the northeast United States show an average 4% decrease in wing length correlated with recent warming (*45*), and the long-distance migrant bird the red knot (*Calidris canutus*) is now producing smaller offspring with smaller bills, which reduces survival in juveniles because of altered foraging success on underground bivalves (*46*). In general, decreasing body size with warming is expected, but evidence from cold, high-altitude habitats suggests that increased primary productivity and longer growing seasons from warming have led to increased body size in some mammal species such as American marten (*Martes americana*) and yellow-bellied marmot (*Marmota flaviventris*) (*47*, *48*). In South Australia, leaf width in soapberry (*Dodonaea viscosa*) has decreased compared with the ancestral condition documented under cooler temperatures 127 years ago (*49*). Other climate change impacts on morphology include color changes in butterflies, dragonflies, and birds (*50*–*53*) and pronounced changes in skull shape in the alpine chipmunk (*Tamias alpinus*) (*54*).

Population

Phenology

For most species, migrations and life-history processes (such as budding and flowering in plants, hatching and fledging in birds, and hibernation in mammals) are closely tied to seasonal and interannual variation in climate, and there is now overwhelming evidence that both have been affected by climate change (*10*, *37*, *55*, *56*). Across marine, freshwater, and terrestrial ecosystems, spring phenologies have advanced by 2.3 to 5.1 days per decade (*10*, *57*). A combination of climate warming and higher atmospheric CO_2 concentrations has extended the growing period of many plant populations (*58*). In a large global analysis, which included 21 phenological metrics such as leaf-off and leaf-on dates and growing-season length, plant phenologies were found to have shifted by more than 2 standard deviations across 54% of Earth's land area during the past three decades (*59*).

In marine and freshwater systems, advances in the timing of annual phytoplankton blooms—the basis for many aquatic food webs—have occurred more rapidly than temporal shifts in terrestrial plants (*37*, *60*). Such changes in plankton phenology have been attributed to increases in water temperatures, reduction in the duration of ice cover, and the alteration of the seasonal duration of thermal stability or stratification of the water column.

Shifts in spawning times have been documented for 43 fish species in the northeast Pacific Ocean from 1951 to 2008, with earlier spawning associated with increased sea surface temperature and later spawning associated with delays in seasonal upwelling of nutrients toward the ocean surface (*61*). Similar impacts on breeding have been observed in terrestrial and marine bird species (*62*).

Changes in the timing of migration events have been extensively documented, including advances in spring arrival dates of long-distance migratory bird species in Europe, North America, and Australia (*63*–*65*). Similarly, long-term data on many amphibians and mammals have shown advancements in spring and delays in autumn migration (*66*–*68*) and altered peak calling periods of male amphibians (*67*–*69*). In the largest meta-analysis to date of phenological drivers and trends among species in the southern hemisphere, 82% of terrestrial data sets and 42% of marine data sets demonstrated an advance in phenology associated with rising temperature (*70*).

Abundance and population dynamics

Acute temperature stress can have severe negative effects on population dynamics such as abundance, recruitment, age structure, and sex ratios. Meta-analyses across thousands of species report that ~80% of communities across terrestrial, freshwater, and marine ecosystems exhibited a response in abundance that was in accordance with climate change predictions (*10*, *70*). In a meta-analysis of marine species, 52% of warm-adapted species increased in abundance, whereas 52% of cold-adapted species decreased (*71*). Temperature spikes may cause mass mortality of key ecosystem engineers in both temperate and tropical oceans. Excessive heat kills canopy-forming macroalgae in temperate marine systems (*72*) and causes bleaching and mass mortality of corals in the tropics (*73*). Reductions in sea ice extent have caused declines in abundances of ice-affiliated species in the Arctic [for example, ivory gulls (*Pagophila eburnea*), ringed seals (*Pusa hispida*), and polar bears (*Ursus maritimus*) (*74*)] whereas in some cases, such as on Beaufort Island in the southern Ross Sea, the loss of ice from receding glaciers resulted in increased abundances of Adélie penguins (*Pygoscelis adeliae*) (*75*). In the United States, the bull trout (*Salvelinus confluentus*) has lost >10% of its spawning grounds in central Idaho over the past 13 years because of increased water temperatures (*76*), while the brown trout (*Salmo* *trutta*) has lost habitat in the Swiss Alps (*77*). In western Canada, reduced survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) has been observed with increased water temperatures (*78*), and in eastern Canadian lakes, golden-brown algae dramatically increased in abundance as water temperature increased 1.5°C during the latter part of the 20th century (*79*). Some of the best evidence for climate-change impacts on the abundance of terrestrial species comes from analyses of bird population trends derived from systematic monitoring schemes in Europe, with warm-adapted species having increased in abundance on average since the 1980s and cold-adapted species having declined (*80*).

Climate change can increase the abundance of temperature-sensitive disease vectors, with subsequent effects on disease outbreaks. In the African Serengeti, there is some evidence that a combination of extreme weather, high abundances of ticks carrying *Babesia*-piroplasm, and suppressed immunity to canine distemper virus led to widespread mortality of lions (*Panthera leo*) (*81*). In marine systems, field evidence shows that corals are increasingly susceptible to white band disease at higher temperatures, leading to declines in two of the most important reef-building acroporid (branching) corals in the western Atlantic (*82*).

Species

Distribution

One of the most rapid responses observed for marine, freshwater, and terrestrial species is a shift in their distributions to track optimal habitat conditions (*71*, *83*, *84*). Across land and aquatic ecosystems, species have expanded their leading (cold limit) edge by 19.7 km per decade, with marine species expanding by 72 km per decade compared with 6 km per decade in terrestrial species (*37*). The distributions of many marine taxa have shifted at higher velocities than those of terrestrial taxa (*37*) because areas with rapid changes in climate extend across broader regions of the ocean than on land, and connectivity in marine environments tends to be high (*85*). To illustrate this point, corals around Japan have shifted their range by up to 14 km per year over the past 80 years (*86*), and in waters off the southeast coast of Australia, intertidal invertebrate species have shifted their geographic distributions polewards at an average rate of 29 km per decade (*87*). Where connectivity allows for dispersal, some freshwater fishes are capable of shifting at rates comparable with those of marine and terrestrial taxa (*88*), but mean shifts by river fishes in some regions have been insufficient to compensate for measured temperature rises (*89*).

There has been a consistent overall trend for tropical, warm-adapted species to expand their ranges into environments previously dominated by temperate cold-tolerant species ("tropicalization") (*90*). A similar phenomenon has been documented in the Arctic, where boreal fish communities have responded to warming in the Barents Sea by shifting northward, resulting in a high turnover in Arctic fish communities ("borealization") (*91*). Similarly, on land, increased minimum temperatures have driven rapid changes in the range size (as well as distribution) of Swedish birds, with northern species retracting and southern species expanding northward (*92*).

In addition to latitudinal changes, many observed shifts in species distributions have occured across elevation gradients. In the mountains of New Guinea, birds have shifted their distributions upslope by 95 to 152 m from 1965 to 2013 (*93*). A similar upslope shift was observed in recent decades in mountainous stream-dwelling fish in France (*89*), North American plants (*94*), and Bornean insects (*95*). An analogous response has been the shift to deeper, colder waters among some marine fishes (*91*).

In some cases, species have shown no response or even downhill shifts in their distributions (*96*) or increased frequency of range disjunction rather than poleward or upward range shifts (*97*). Savage and Vellend (*98*) found upward range shifts in North American plant species and an overall trend toward biotic homogenization from 1970 to 2010, but their study also documents considerable time lags between warming and plant responses (*99*, *100*). Delayed community responses to increasing temperature may be in part due to the buffering effects of microhabitats (*101*, *102*) and possibly moisture, which is a critical, but less often studied, driver in the redistribution of species (*103*). For example, Crimmins *et al.* observed downhill movements for North American plants under climate change over an 80-year period, which they attribute to changes in water balance rather than temperature (*104*).

Community

Interspecific relationships

As a by-product of the redistribution of species in response to changing climate, existing interactions among species are being disrupted, and new interactions are emerging (*105*, *106*). These novel biotic interactions can exacerbate the impacts of abiotic climate change (*107*, *108*). Woody plants are invading arctic and alpine herb-dominated communities in response to rapid warming in recent decades, leading to secondary shifts in distribution of other plants and animals (*92*). In the Sierra Nevada Mountains of California, Tingley and Beissinger found high levels of avian community turnover during the past 100 years at the lowest and highest elevations (*109*), and in Greece, Sgardeli *et al.* found similar patterns of temperature-driven turnover in butterfly communities (*110*). There are surprisingly few studies of observed impacts of climate change on competitive interactions (*108*). In one example from Sweden, Wittwer *et al.* found that among four bird species occupying the same ecological guild, resident birds were able to adapt to warmer temperatures and outcompete the sole long-distance migrant, *Ficedula hypoleuca* (*111*).

New interactions among species can also lead to trophic disruptions such as overgrazing. In western Australia, for example, overgrazing of subtropical reefs by the poleward spread of tropical browsing fish has suppressed recovery of seaweeds after temperature-induced mortality (*112*). These types of trophic disruptions are escalating, with range shifts by tropical herbivorous fishes increasing herbivory rates in subtropical and temperate coastal ecosystems where seaweeds are the dominant habitat-forming taxa (*90*).

Phenological mismatches have been observed between butterflies and their annual host plants, with the plants dying before the insect larvae were ready to enter diapause (*113*). Similarly, an analysis of 27 years of predator-prey data from the UK showed asynchronous shifts between the tawny owl (*Strix aluco*) and its principle prey, the field vole (*Microtus agrestis*), which led to reduced owl fledging success (*114*). In Lake Washington, United States, spring diatom blooms advanced by over 20 days since 1962, resulting in predator-prey mismatches with their main grazer, the water flea (*Daphnia pulicaria*), and population declines in the latter (*60*). In Canadian Arctic lakes, asynchronous shifts in diatom blooms resulted in generalist water fleas being replaced by more specialist species (*115*). At higher trophic levels, warming has affected the fry and the juvenile life-history stages of lake char (*Salvelinus umbla*) via direct impacts on their zooplankton and vendace (*Coregonus alba*) food sources (*116*).

Productivity

Changes in productivity are one of the most critical impacts of climate change across aquatic and terrestrial ecosystems (*117*, *118*). In marine systems, climate-mediated changes in chlorophyll-a concentrations as a proxy of phytoplankton biomass have been highly variable (*119*). Depending on location, these include both dramatic increases and decreases in abundance as well as changes in phenology and distribution of phytoplankton over the past several decades. In a global study of phytoplankton since 1899, an ~1% decline in global median phytoplankton per year was strongly correlated with increases in sea surface temperature (*120*), whereas in the Antarctic Peninsula, phytoplankton increased by 66% in southern subregions and decreased by 12% in northern subregions over a 30-year period. These conflicting observations in the Antarctic are in part linked to changes in sea surface temperature but also changes in ice cover, cloudiness, and windiness, which effect water-column mixing (*121*).

In deep tropical freshwater lakes dominated by internal nutrient loading through regular mixing, warmer surface waters confer greater thermal stability, with reduced mixing and return of nutrients to the photic zone, substantially decreasing primary productivity (*122*), phytoplankton growth (*123*), and fish abundance (*122*). In contrast, eutrophication effects are exacerbated by higher temperatures in shallow lakes, resulting in increased productivity and phytoplankton and toxic cyanobacteria blooms (*124*).

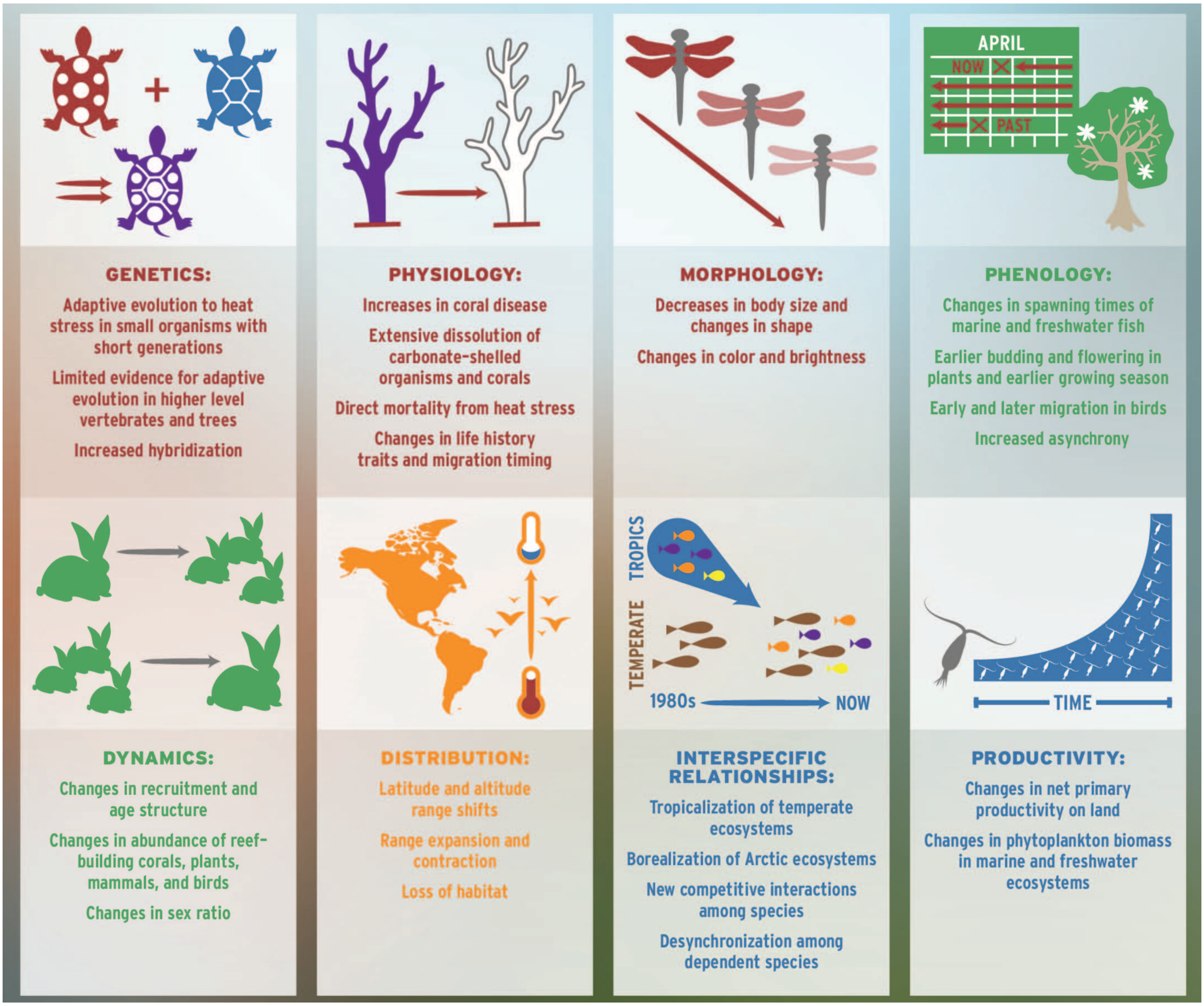

Fig. 2. Climate impacts on ecological processes. Examples of ecological components and processes affected by climate changes across marine, freshwater, and terrestrial ecosystems (fig. S1 and table S1).

IMAGE CREDIT: STACEY JONES/MICHELE WOOD/IFAS

Globally, terrestrial plant growth has increased with increasing temperatures and CO_2 levels. This may in part explain the on average 6% increase in net primary productivity (NPP) from 1982 to 1999 (*125*), although these changes in NPP may also be related to natural variation in El Niño–La Niña cycles (*126*). However, responses are highly variable, and some terrestrial systems are not experiencing increased productivity owing to either extreme temperatures or lack of water. Severe short-term droughts in climatically stable rainforest environments are unusual but in recent years have increased in frequency. These events have led to changes in forest canopy structure in Amazonia (*127*) and decreases in aboveground woody and leaf biomass in the Congo basin (*128*). Across large expanses of the Amazon, there has been an overall reduction in aboveground biomass owing to increased climate variability over the past three decades (*129*).

Impacts across ecosystems

All three biotic realms (terrestrial, freshwater, and marine) are being affected by climate change, and the evidence summarized here reveals that these impacts span the biological hierarchy from genes to communities. Of the 94 processes considered, we found that 82% have evidence of impact by climate change, and this has occurred with just 1°C of average warming globally (Fig. 1). Impacts range from genetic and physiological changes to responses in population abundance and distribution (Fig. 2).

The fact that evidence is missing for some processes is more likely to reflect data deficiencies than the absence of any response to climate change. We only considered field-based case studies that report changes in the processes through time. For many components, such as genetics (*23*) and physiology (*29*), there is strong evidence from experiments on a wide range of species that individuals and populations can and likely will respond to climate change. Thus, even though we found compelling evidence of widespread responses across the biological hierarchy, we still consider our discussion of impacted processes to be conservative. To illustrate this point, Box 1 shows the range of observed responses in the water flea *Daphnia*, which spans the entire hierarchy of biological organization.

Ecosystem state shifts

As ecological systems continue to accumulate stress through compromised ecological processes

Box 1. A complete hierarchy of climate change impact in one model system: the water flea *Daphnia*. Combining time-series data with experimental approaches can lend insights to the breadth of climate change impacts. For water fleas of the genus *Daphnia*, for instance, there is evidence for responses to temperature at all levels of biological organization. *Daphnia* are important grazers in lakes and ponds (180). They adapt to temperature increase through genetic changes in thermal tolerance (18), body size, and life history traits (181, 182). In the laboratory, *Daphnia* exhibit phenotypic plasticity in physiology to changing temperatures [for example, hemoglobin quality and quantity (183) or metabolic activity (184)], behavior [such as swimming activity (184)], life history traits (185), and body size (182). *Daphnia* adjust their phenology (186) and abundance (187) in response to increases in temperature, which results in mismatches with phytoplankton dynamics (60). Warmer, drier weather over two decades can lead to expanded distributions and increased colonization capacity (188). Temperature influences interactions of *Daphnia* with predators (189) and parasites (190), and adaptation to increased temperature influences competitive strength (185). In the absence of fish, high abundances of *Daphnia* in +4°C heated mesocosms exert strong top-down control on phytoplankton (191).

either directly from climate change or interactively with other forced disturbances (discussion is provided in the supplementary materials), diminished resilience may lead to ecological regime shifts—in which one ecosystem state shifts to an alternative and potentially undesirable stable state. For example, some reefs are transitioning from coral- to algal-dominated states as a consequence of mass coral mortality (130), whereas kelp forests are turning into rocky barrens in temperate seas (90, 131, 132). In lakes, climate change has increased the risk of regime shifts from clear-water to turbid states and increased the occurrence of cyanobacteria blooms (124). If sufficient community-based processes are affected at regional scales, wholesale biome shifts can occur such as has been observed in Alaska, where tundra is transitioning to boreal conditions (133). These are clear signs of large-scale ecosystem change and disruption, in which disequilibrium rapidly pushes the system into a new state (134).

Using ecology to better understand climate change impacts on human well-being

Threats to production

The impacts of climate change on marine fisheries have major consequences for human societies because these currently provide ~17% of the global protein for people (135). There is, however, no current consensus on the costs and benefits of the ongoing global redistribution of fisheries because trends are highly variable. In the Arctic, commercially important fish, such as Atlantic cod (*Gadus morhua*) and walleye pollock (*Theragra chalcogramma*), have increased in biomass primarily because of increases in plankton production from reduced sea ice (136, 137), whereas changes in fish biomass in the Southern Ocean are less clear (138). In Switzerland, which has experienced twice the average global temperature increase, trout catches have been halved over two decades because of rising temperatures in Alpine streams (77).

Changes in total marine productivity are not just attributed to abundance shifts but also morphological shifts. Indeed, some fish species appear to be shrinking, but attributing this solely to ocean warming is difficult because size-dependent responses can be triggered by commercial fishing as well as long-term climate change (139). However, long-term trend analyses show convincingly that eight commercial fish species in the North Sea underwent simultaneous reductions in body size over a 40-year period because of ocean warming, resulting in 23% lower yields (140). Reduced body size in fish is also being recorded in lakes and rivers throughout Europe and has been linked to increased temperature and climate-induced shifts in nutrient inputs (141, 142).

Impacts on plant genetics and physiology are influencing human agricultural systems. For example, yields in rice, maize, and coffee have declined in response to the combined effects of rising temperatures and increasing precipitation variability over past decades (143–145). Genetics is being used to counteract decreasing yields in some key crops such as wheat [for which, globally, yields have declined by 6% since the early 1980s (146)] through crossing domesticated crops with wild relatives to maintain the evolutionary potential of varieties (147). Yet, some important wild strains are also showing signs of impact from climate change. Nevo *et al.* documented high levels of genetic changes in the progenitors of cultivated wheat and barley in Israel over the past 28 years (148). These wild cereals exhibited landscape-level changes in flowering time and a loss of genetic diversity in response to increasing temperatures.

Losing genetic resources in nature may undermine future development of novel crop varieties (149) and compromise key strategies that humans use to adapt to climate change. One such strategy is to use assisted gene flow, the managed movement of individuals or gametes between populations to mitigate local maladaptation in the short and long term (150). Where genetic introgression—the movement of genetic material from one species into the genome of another—can occur from unexploited natural populations to managed or exploited populations that are poorly adapted to warmer or drier conditions, adaptive changes may be facilitated (147), as in white spruce (*Picea glauca*), a tree commonly harvested for timber (151). Human-assisted evolution may also be a key strategy in maintaining reef-dependent fisheries by accelerating and enhancing the stress tolerance of corals (152).

Phenological changes due to milder winters are influencing crop and fruit production (153). Climate change has reduced winter chill events in temperate agricultural areas (154), which can desynchronize male and female flowers and trigger delayed pollination, delayed foliation, and reduced fruit yield and quality. To counter this, tree crop industries have developed adaptation measures such as low-chill cultivars with dormancy-breaking chemicals. For example, the "UFBest" peach requires four times fewer chill days than cultivars from more temperate climates (155). Advances in the timing of budding, flowering, and fruiting of plant species has induced earlier harvesting periods in some countries [such as Japan (156)].

Pollination is a key process linked to yields for a large number of crops. The short-lived, highly mobile insect species that provide pollination services to numerous crops have responded rapidly to changing climates by shifting their ranges throughout North America and Europe (157). Additionally, over the past 120 years, many plant-pollinator networks have been lost with overall decline in pollination services, which is attributed to a combination of habitat loss, pollution, and climate warming (158). Yet, observed changes in the phenology, abundance, and distribution of common pollinators have not been directly linked to declines in yields of animal-pollinated crops. This is likely due to limited data that directly link pollination services to crop yield over time and may, in part, reflect resilience provided by the diversity of insect species that pollinate many crops (159, 160). More specialized pollination systems are expected to be more vulnerable to climate change. Humans have adapted to the declines in native pollinators by transporting domesticated pollinators to crop locations.

Pest and disease threats

Climate-induced ecosystem-level changes, such as forest die-offs, have an obvious impact on

PHOTO: JOACHIM MERGEAY

Table 1. Climate change consequences for humans. Affected ecological processes have direct consequences in food systems and human health.

	Organism	Population	Species	Community
	Genetics, physiology, morphology	**Phenology, dynamics**	**Distribution**	**Interspecific relationships, productivity**
Resource security	Rapid genetic adaptation to climate change in timber species	Increased herbivory on crops and timber by pests	Overall distribution shifts in marine and freshwater fisheries	Decline in plant-pollinator networks and pollination services
	Decreased crop yields in hot climates and increases in cool climates	Decreased genetic diversity and altered flowering time in wild cereals and novel crop varieties	Reduced range size or changes in pollinator abundance	Novel pests and invasive species
	Increased weed-crop competition and parasite-livestock interactions	Reduced fruit yields from fewer winter chill events		
	Decreased yield in fisheries from reduced body size	Reduced productivity in commercial fisheries		
Human health	Decline in reef calcifiers threatens coastal communities; loss of protection from storm surges and loss of food/protein sources	Increased costs and risk to subsistence communities from loss of sea ice and permafrost	Expanding and/or new distributions of disease vectors	Increased human-wildlife conflicts
	Rapid adaptation of disease vectors to new climatic conditions		Redistribution of arable land	Novel disease vectors

people, with a reduction in timber supplies and carbon sequestration, and changes in water quality and watershed volume (161–163). Several native insect species from North America, with no prior records of severe infestation, have recently emerged as severe pathogens of forest resources because of changes in population dynamics. These include the Aspen leaf miner (*Phyllocnistis populiella*), the leafblotch miner (*Micrurapteryx salicifoliella*), and the Janet's looper (*Nepytia janetae*), which have decimated millions of hectares of aspen, willows, and spruce-fir forests since the early 1990s (164). Known pests such as mountain and southern pine beetles (*Dendroctonus frontalis* and *D. ponderosae*, respectively) and spruce beetles (*D. rufipennis*) have recently expanded their distribution and infestation intensity on commercially important pine and spruce trees (161, 164). These outbreaks may increase in the future because hundreds of plant pest and pathogen species have shifted their distributions 2 to 3.5 km year^{-1} poleward since the 1960s (165).

An emerging threat to human health under climate change is vector-borne disease (166). Vectors that have shifted their ranges and abundance can be found in marine, freshwater, and terrestrial systems. For example, in marine systems, unprecedented warming in the Baltic Sea led to emergence of *Vibrio* infections in Northern Europe (167, 168), a geographic locality that had limited prior occurrence of this waterborne bacterial pathogen. Mosquitoes (e.g., *Aedes japonicus, A. aegypti, A. albopictus*) are extending their distribution into areas that are much warmer than their original habitats. As a result of ecological adaptation, mosquitos have become more competent vectors for spreading diseases such as chikungunya, dengue, and possibly the emerging Zika virus (169). Last, in terrestrial systems Levi *et al.* found that the nymph stage of the Lyme disease–carrying blacklegged tick (*Ixodes scapularis*) exhibited an overall advancement in nymph and larvae phenology since 1994, shifting the timing of greatest risk for pathogen transfer to humans to earlier in the year (170).

Losing intact ecosystems and their function

Changes in ecological processes might compromise the functionality of ecosystems. This is an important consideration because healthy systems (both terrestrial and marine) sequester substantial amounts of carbon (171), regulate local climate regimes (172), and reduce risks associated with climate-related hazards such as floods, sea-level rise, and cyclones (173). In island and coastal communities, coral reefs can reduce wave energy by an average of 97% (174), and coastal ecosystems such as mangroves and tidal marshes buffer storms (175), while on land intact native forests are important in reducing the frequency and severity of floods (176). In many cases, maintaining functioning systems offers more sustainable, cost-effective, and ecologically sound alternatives than conventional engineering solutions (16).

Science and action in a warmer world

The United Nations Framework Convention on Climate Change (UNFCCC) and the recent COP21 agreement in Paris presently offer the best opportunity for decisive action to reduce the current trajectory of climate change. This latter agreement set global warming targets of 1.5 to 2°C above preindustrial levels in order to avoid "dangerous climate change," yet the current 1°C average increase has already had broad and worrying impacts on natural systems, with accumulating consequences for people (Table 1). Minimizing the impacts of climate change on core ecological processes must now be a key policy priority for all nations, given the adoption of the UN Sustainable Development Goals aiming to increase human well-being. This will require continued funding of basic science focused on understanding how ecological processes are interacting with climate change, and of programs aimed at supporting ecosystem-based adaptations that enhance natural defences against climate hazards for people and nature and ensure ongoing provision of natural goods and services (177).

We must also recognize the role that intact natural ecosystems, particularly large areas, play in overcoming the challenges that climate change presents, not only as important repositories for carbon but also because of their ability to buffer and regulate local climate regimes and help human populations adapt to climate change (16, 173). These systems are also critical for maintaining global biodiversity because the connectivity provided by large, contiguous areas spanning environmental gradients—such as altitude, depth, or salinity—will maximize the potential for gene flow and genetic adaptation while also allowing species to track shifting climate spatially (178).

The overriding priority of the UNFCCC is to set in motion a sustained global reduction in greenhouse gas emissions. This must be achieved alongside an improvement in our understanding of key ecological processes that form the foundation of biological and human systems, and in tandem with efforts to conserve the natural habitats in which such ecological processes operate.

It is now up to national governments to make good on the promises they made in Paris through regular tightening of emission targets, and also to recognize the importance of healthy ecosystems in times of unprecedented change (*179*). Time is running out for a globally synchronized response to climate change that integrates adequate protection of biodiversity and ecosystem services.

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Fig. S1
Table S1
References (*192*–*310*)

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The broad footprint of climate change from genes to biomes to people

Brett R. Scheffers, Luc De Meester, Tom C. L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H. M. Butchart, Paul Pearce-Kelly, Kit M. Kovacs, David Dudgeon, Michela Pacifici, Carlo Rondinini, Wendy B. Foden, Tara G. Martin, Camilo Mora, David Bickford and James E. M. Watson

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Editor's Summary

Accumulating impacts

Anthropogenic climate change is now in full swing, our global average temperature already having increased by 1°C from preindustrial levels. Many studies have documented individual impacts of the changing climate that are particular to species or regions, but individual impacts are accumulating and being amplified more broadly. Scheffers *et al.* review the set of impacts that have been observed across genes, species, and ecosystems to reveal a world already undergoing substantial change. Understanding the causes, consequences, and potential mitigation of these changes will be essential as we move forward into a warming world.

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Review

Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles

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Abstract: *Terrestrial habitats surrounding wetlands are critical to the management of natural resources. Although the protection of water resources from human activities such as agriculture, silviculture, and urban development is obvious, it is also apparent that terrestrial areas surrounding wetlands are core habitats for many semiaquatic species that depend on mesic ecotones to complete their life cycle. For purposes of conservation and management, it is important to define core habitats used by local breeding populations surrounding wetlands. Our objective was to provide an estimate of the biologically relevant size of core habitats surrounding wetlands for amphibians and reptiles. We summarize data from the literature on the use of terrestrial habitats by amphibians and reptiles associated with wetlands (19 frog and 13 salamander species representing 1363 individuals; 5 snake and 28 turtle species representing more than 2245 individuals). Core terrestrial habitat ranged from 159 to 290 m for amphibians and from 127 to 289 m for reptiles from the edge of the aquatic site. Data from these studies also indicated the importance of terrestrial habitats for feeding, overwintering, and nesting, and, thus, the biological interdependence between aquatic and terrestrial habitats that is essential for the persistence of populations. The minimum and maximum values for core habitats, depending on the level of protection needed, can be used to set biologically meaningful buffers for wetland and riparian habitats. These results indicate that large areas of terrestrial habitat surrounding wetlands are critical for maintaining biodiversity.*

Criterios Biológicos para Zonas de Amortiguamiento Alrededor de Hábitats de Humedales y Riparios para Anfibios y Reptiles

Resumen: *Los hábitats terrestres que rodean humedales son críticos para el manejo de recursos naturales. Aunque la protección de recursos acuáticos contra actividades humanas como agricultura, silvicultura y desarrollo urbano es obvia, también es aparente que las áreas terrestres que rodean a humedales son hábitat núcleo para muchas especies semiacuáticas que dependen de los ecotonos mésicos para completar sus ciclos de vida. Para propósitos de conservación y manejo, es importante definir los hábitats núcleo utilizados por las poblaciones reproductivas locales alrededor de humedales. Nuestro objetivo fue proporcionar una estimación del tamaño biológicamente relevante de los hábitats núcleo alrededor de humedales para anfibios y reptiles. Resumimos datos de la literatura sobre el uso de hábitats terrestres por anfibios y reptiles asociados con humedales (19 especies de ranas y 13 de salamandras, representando a 1363 individuos; 5 especies de serpientes y 28 de tortugas representando a más de 2245 individuos). Los hábitats núcleo terrestres variaron de 159 a 290 m para anfibios y de 127 a 289 para reptiles desde el borde del sitio acuático. Datos de estos estudios también indicaron la importancia de los hábitats terrestres para alimentación, hibernación y anidación, y, por lo tanto, que la interdependencia biológica entre hábitats acuáticos y terrestres es esencial para la persistencia de poblaciones. Dependiendo del nivel de protección requerida, se pueden utilizar los valores mínimos y máximos de hábitats núcleo para definir amortiguamientos biológicamente significativos para hábitats de humedales y riparios. Estos resultados indican que extensas áreas de hábitats terrestres que rodean humedales son críticas para el mantenimiento de la biodiversidad.*

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Introduction

Terrestrial habitats surrounding wetlands are critical for the management of water and wildlife resources. It is well established that these terrestrial habitats are the sites of physical and chemical filtration processes that protect water resources (e.g., drinking water, fisheries) from siltation, chemical pollution, and increases in water temperature caused by human activities such as agriculture, silviculture, and urban development (e.g., Lowrance et al. 1984; Forsythe & Roelle 1990). It is generally acknowledged that terrestrial buffers or riparian strips 30–60 m wide will effectively protect water resources (e.g., Lee & Samuel 1976; Phillips 1989; Hartman & Scrivener 1990; Davies & Nelson 1994; Brosofske et al. 1997).

However, terrestrial habitats surrounding wetlands are important to more than just the protection of water resources. They are also essential to the conservation and management of semiaquatic species. In the last few years, a number of studies have documented the use of terrestrial habitats adjacent to wetlands by a broad range of taxa, including mammals, birds, reptiles, and amphibians (e.g., Rudolph & Dickson 1990; McComb et al. 1993; Darveau et al. 1995; Spackman & Hughes 1995; Hodges & Krementz 1996; Semlitsch 1998; Bodie 2001; Darveau et al. 2001). These studies have shown the close dependence of semiaquatic species, such as amphibians and reptiles, on terrestrial habitats for critical life-history functions. For example, amphibians, such as frogs and salamanders, breed and lay eggs in wetlands during short breeding seasons lasting only a few days or weeks and during the remainder of the year emigrate to terrestrial habitats to forage and overwinter (e.g., Madison 1997; Richter et al. 2001). Reptiles, such as turtles and snakes, often live and forage in aquatic habitats most of the year but emigrate to upland habitats to nest or overwinter (e.g., Gibbons et al. 1977; Semlitsch et al. 1988; Burke & Gibbons 1995; Bodie 2001).

The biological importance of these habitats in maintaining biodiversity is obvious, yet criteria by which to define habitats and regulations to protect them are ambiguous or lacking (Semlitsch & Bodie 1998; Semlitsch & Jensen 2001). More importantly, a serious gap is created in biodiversity protection when regulations or ordinances, especially those of local or state governments, have been set based on criteria to protect water resources alone, without considering habitats critical to wildlife species. Further, the aquatic and terrestrial habitats needed to carry out life-history functions are essential and are defined here as "core habitats." No summaries of habitat use by amphibians and reptiles exist to estimate the biologically relevant size of core habitats surrounding wetlands that are needed to protect biodiversity.

For conservation and management, it is important to define and distinguish core habitats used by local breeding populations surrounding wetlands. For example, adult frogs, salamanders, and turtles are generally philopatric to individual wetlands and migrate annually between aquatic and terrestrial habitats to forage, reproduce, and overwinter (e.g., Burke & Gibbons 1995; Semlitsch 1998). The amount of terrestrial habitats used during migrations to and from wetlands and for foraging defines the terrestrial core habitat of a population. This aggregation of breeding adults constitutes a local population centered on a single wetland or wetland complex. Local populations are connected by dispersal and are part of a larger metapopulation, which extends across the landscape (Pulliam 1988; Marsh & Trenham 2001).

Annual migrations centered on a single wetland or wetland complex are biologically different than dispersal to new breeding sites. It is thought that dispersal among populations is achieved primarily by juveniles for amphibians (e.g., Gill 1978; Breden 1987; Berven & Grudzien 1990) or by males for turtles (e.g., Morreale et al. 1984). Dispersal by juvenile amphibians tends to be unidirectional and longer in distance than the annual migratory movements of breeding adults (e.g., Breden 1987; Seburn et al. 1997). Thus, habitats adjacent to wetlands can serve as stopping points and corridors for dispersal to other nearby wetlands. Ultimately, conservation and management plans must consider both local and landscape dynamics (Semlitsch 2000), but core habitats for local populations need to be defined before issues of connectivity at the metapopulation level are considered.

Literature Review

We summarize data from the literature on the use of terrestrial habitats by amphibians and reptiles associated with wetlands. We define wetlands as both lentic (pond) and lotic (stream) habitats that are either permanent or temporary (Cowardin et al. 1979). Also, we use the term riparian in the broadest sense of encompassing the shore, bank, or edge of any wetland. We used data from studies that define habitat use mainly by the adult population and report a mean, mode, or range of distance of migrations from the outer edge of wetlands (Appendices 1 & 2). We used these values to calculate a grand mean for major taxa (Table 1). Rather than calculating a 95% confidence limit, which depends on knowing the distribution of migration distances, and because some studies did not report means, we calculated a mean minimum and maximum distance for amphibians and reptiles from the distance values reported for species in each study (Table 1). These minimum and maximum values likely encompass a large portion of populations and adequately represent the majority of species. We did not use observations of individuals of unknown origin, especially juveniles, found at some distance from a wet-

Table 1. Mean minimum and maximum core terrestrial habitat for amphibians and reptiles.*

Group	*Mean minimum (m)*	*Mean maximum (m)*
Frogs	205	368
Salamanders	117	218
Amphibians	159	290
Snakes	168	304
Turtles	123	287
Reptiles	127	289
Herpetofauna	142	289

**Values represent mean linear radii extending outward from the edge of aquatic habitats compiled from summary data in Appendices 1 and 2.*

land. Such anecdotal observations are relevant to maximum dispersal distances and the probability of recolonization and connectivity for species (Pulliam 1988) but are misleading for the calculation of core terrestrial habitat for the maintenance of local populations. The data we report reflect the size of terrestrial habitats that are biologically necessary for the conservation of amphibian and reptile diversity at individual wetlands. Further, we discuss the use of core habitat sizes in conjunction with a buffer zone and how land-use practices in the surrounding landscape matrix may modify the amount of habitat needed for adequate protection.

Amphibian Core Habitat

Amphibians constitute an important and diverse fauna associated with both isolated wetlands (e.g., Texas, 15 species [Wiest 1982]; Florida, 16 species [Dodd 1992]; South Carolina, 27 species [Semlitsch et al. 1996]; Tennessee, 19 species [Scott & Bufalino 1997]) and stream or river floodplains (e.g., Virginia, 21 species [Buhlmann et al. 1993]; California, 4 species [Panik & Barrett 1994]; Illinois, 14 species [Burbrink et al. 1998]). The studies we reviewed indicate that amphibians use a wide range of terrestrial habitats adjacent to wetlands and streams. Most of these habitats are related to foraging, refuge, or overwintering sites and typically consist of leaf litter, coarse woody debris, boulders, small mammal burrows, cracks in rocks, spring-seeps, and rocky pools. Data on emigration distances from wetlands were found for 19 species of frogs and 13 species of salamanders representing 1363 individuals (Appendix 1).

Patterns of variation in distances traveled appear related to life-history differences between major taxonomic groups. In general, the plethodontid stream salamanders (e.g., *Desmognathus fuscus, Eurycea bislineata, Eurycea longicauda*), although migratory at some stage of their life cycle, remain close to the edges of ponds and streams and seldom move more than 20–30 m from aquatic habitats. Alternatively, some species of frogs, toads, and newts are highly vagile and move 1000–1600 m (e.g., *Bufo bufo, Rana catesbeiana, Notophthalmus viridescens*). The majority of the remaining species use intermediate distances, where they emigrate to find suitable terrestrial habitats. The overall core terrestrial habitat for amphibians ranged from 159 to 290 m from the edge of the aquatic site (Table 1).

Reptile Core Habitat

We summarized data for five snake and 28 turtle species from 25 U.S. states and five countries (Appendix 2). We gathered migration distances from studies of known sample size (total $n = 2245$ individuals) and from those of unknown sample size. Relatively few studies have been conducted on terrestrial migrations of hydrophilic snakes. Snakes migrated into adjacent uplands for the purpose of aestivating, basking, hibernating, or nesting. Although most studies of terrestrial migrations by turtles have focused on nesting, turtles also migrated for the purposes of aestivating, feeding, and hibernating.

Similar to that of amphibians, variation in reptile migration distances appears related to taxon-specific differences in life-history patterns. Some colubrid snakes (e.g., *Nerodia* sp., *Opheodrys aestivus*), trionychid turtles (e.g., *Apalone* sp.), some emydid turtles (e.g., *Graptemys geographica*, *Sternotherus* sp.), and one chelydrid turtle (i.e., *Macroclemys temminckii*) rarely migrate >30 m from aquatic habitats. In contrast, one colubrid snake (i.e., *Coluber constrictor*), viperid snakes (e.g., *Crotalus horridus*, *Sistrurus catenatus*), many kinosternid turtles (e.g., *Kinosternum leucostomum*, *K. subrubrum*), and several emydid turtles (e.g., *Chrysemys picta*, *Clemmys* sp., *Emydoidea blandingi*, *Trachemys scripta*) routinely migrate >100 m. The length of time spent in the terrestrial habitat ranges from <1 hour (e.g., nesting *Chelydra serpentina*; Punzo 1975) to 88% of recorded activity (e.g., *Nerodia sipedon*; Tiebout & Cary 1987). Some migrations into terrestrial habitats occurred following significant rainfall or stream flooding when uplands were temporarily inundated with water (e.g., *Graptemys pseudogeographica* foraging in flooded forest; Bodie & Semlitsch 2000). The overall core terrestrial habitat for reptiles ranged from 127 to 289 m from the edge of the aquatic site (Table 1).

Protection and Management of Terrestrial Habitat

It is not surprising that the terrestrial ecology of semiaquatic species is often underappreciated or overlooked by managers and conservation planners. Some semiaquatic reptiles make only brief visits to terrestrial habitats when nesting, and hibernacula are rarely observed. Additionally, many pond-breeding amphibians are fossorial and are also rarely observed in terrestrial habitats. Surveys and studies of these animals are consequently concentrated within stream and wetland sites, where they are found seasonally, rather than in terrestrial habitats, where detection is extremely difficult but where much of their life history occurs. Aquatic habitats may not be used by semiaquatic species for extended periods of their lives, including between breeding seasons and during droughts. For example, a population of striped newts (*Notophthalmus perstriatus*) in northern Florida was relegated to predominantly terrestrial activity during a 5-year drought (Dodd 1993). Eastern mud turtles (*Kinosternon subrubrum*) in South Carolina often leave aquatic sites after mating in late spring and do not return until the following spring (Bennett et al. 1970). In both cases, the upland forest habitat had obvious importance as a reservoir for adults of these species until breeding and reproduction again occurred.

Although wetlands vary in many characteristics related to type, region, topography, climate, and land-use surrounding them, the data we compiled suggest that a single all-encompassing value for the size of core habitats can be used effectively. Maximum values generated from a taxon with the greatest need for terrestrial habitat—that is, the largest core area or home range (Table 1)—would likely encompass all other taxa and could be used more broadly. On public lands or reserve systems, where first priority is given to conserving biodiversity, this maximum value can facilitate management objectives. On private lands or areas, however, where sustainable land use is the priority, a stratified system of protection zones can minimize impacts on wildlife and support desired land uses. For example, for streams in managed forests in North America, it is recommended by deMaynadier and Hunter (1995) that criteria be adjusted for stream attributes such as width, intensity of logging, and slope adjacent to the stream. Further, the authors recommend a two-tiered approach in which the terrestrial habitat closest to the water is fully protected and a second, outer area provides limited protection (e.g., the forestry practice of light partial cutting and removal of no more than 25% of the basal area).

We propose that stratification should include three terrestrial zones adjacent to core aquatic and wetland habitats (Fig. 1): (1) a first terrestrial zone immediately adjacent to the aquatic habitat, which is restricted from use and designed to buffer the core aquatic habitat and protect water resources; (2) starting again from the wetland edge and overlapping with the first zone, a second terrestrial zone that encompasses the core terrestrial habitat defined by semiaquatic focal-group use (e.g., amphibians 159–290 m; Table 1); and (3) a third zone, outside the second zone, that serves to buffer the core terrestrial habitat from edge effects from surrounding land use (e.g., 50 m; Murcia 1995).

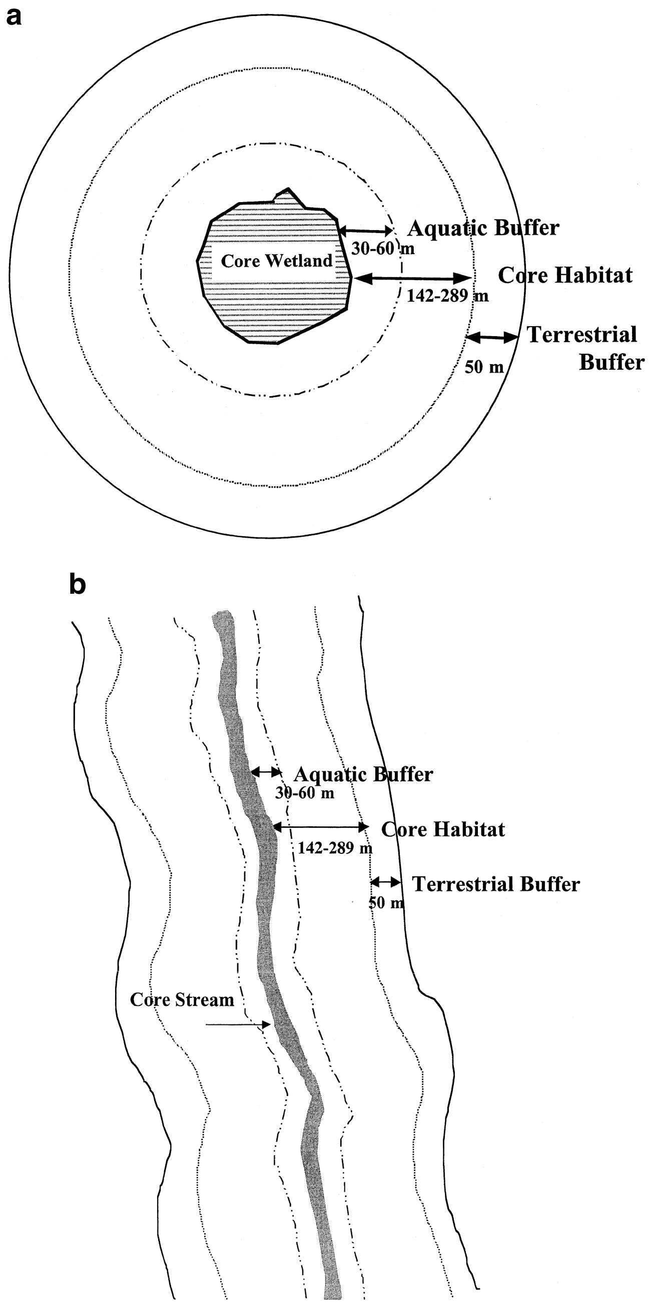

Figure 1. Proposed zones of protection of (a) wetlands and (b) streams. Both core habitat and aquatic buffer requirements are met within the second zone, which may range from 142 to 289 m for amphibians and reptiles (see Table 1 for taxon-specific values). An additional 50-m buffer is recommended to protect core habitat from edge effects (Murcia 1995).

All things being equal, these zones of protection should extend outward from the edge of wetlands far enough to encompass all species populations. However, the habitats used by various species or at different life-history stages are probably not evenly distributed. To protect those habitats essential for species functions, we need to know more about species requirements at each life-history stage and season of the year. We know that special habitats are required by some species, such as the presence of highly aerated pools along small streams or caves for thermal refuges (e.g., overwintering sites for green frogs [*Rana clamitans*; Lamoureux & Madison 1999; Birchfield & Semlitsch unpublished data], yellow-legged frogs [*Rana muscosa*; Matthews & Pope 1999], and pickerel frogs [*Rana palustris*; R.D.S., personal observation]) and mammal burrows for thermal and predatory refuges (e.g., gopher frog [*Rana sevosa*; Richter et al. 2001]), and must be included within protective zones. Habitat generalists probably use whatever habitat is available, and land use such as silviculture may be compatible with maintaining their populations. Little is known, however, about habitat requirements for even common species such as the American toad (*Bufo americanus*), often used as an example of a generalist but which may not be a generalist during all life stages. Newly metamorphosed *B. americanus* exhibit strong selection for forest habitat in the summer in Missouri (Rothermel & Semlitsch 2002). Adjusting the size of terrestrial zones, such as the core habitat, could be done on the basis of protecting different portions of the population (e.g., for turtles 50–90% [Burke & Gibbons 1995]; for ambystomatid salamanders 50–95% [Semlitsch 1998]). It is not known, however, how protecting different amounts of terrestrial habitat affects the population persistence of any species or how habitat quality (e.g., density of mammal burrows; Loredo et al. 1996) might influence that decision.

Decisions about how restrictive each zone might be to land-use practices would depend on management goals and species of concern. Although little data are available on how various amphibians and reptiles might respond to major land-use practices (e.g., logging, farming, residential development), it is reasonable to assume that some activities (e.g., hiking, bicycling), especially those not destroying essential habitats (e.g., for amphibians, vegetation canopy for shade, coarse woody debris and a litter layer used for refuge and food sources), could be conducted in this outer zone of protection and be compatible with the goal of protecting biodiversity. In applying these criteria and bolstering the biological values of core terrestrial habitats, policymakers could develop stratified habitat zones that guide associated protection or management intensity, resulting in more effective conservation of biodiversity along with sustainable land use.

Conclusions

We provide biologically based estimates for the protection of terrestrial habitats surrounding wetlands. Our data clearly indicate that buffers of 15–30 m, used to protect wetland species in many states, are inadequate for amphibians and reptiles. Further, we emphasize that our estimates are derived from the core terrestrial habitats used by amphibians and reptiles and therefore are not buffers per se but necessary habitat. Additional area of terrestrial habitat is needed to fully protect core habitats and minimize edge effects (Fig. 1). For maximum protection, this may be more land than managers can provide, although we do not believe that our estimates are excessive biologically. And we are not naïve enough to believe that all terrestrial land-use activities around wetlands must be excluded. It is our intent, however, to ensure that managers and conservation biologists recognize that both aquatic and terrestrial habitats are essential for maintaining biodiversity and that they must be managed as an integral unit to protect biodiversity. Further, we want managers to know that little is known about the effects of land-use practices on amphibians and reptiles and that without further research it cannot be known whether any such practices used within the core habitat are potentially harmful to their long-term persistence. We hope this discussion generates more research on the effects of land-use practices on plants and animals and that biologists begin testing the effectiveness of various criteria for protecting the core habitats of species. A sustainable balance between continuing economic development and protecting natural resources depends on knowing and responding to species' biological requirements and knowing how tradeoffs affect the maintenance of biodiversity.

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Appendix 1. Summary of terrestrial migration distances from aquatic breeding sites for amphibians.

Species and location	Distance in m (sample size)	*Data source*
Frogs		
Acris crepitans, Illinois	range 8–22 (189)	O'Neil 2001[a]
Bufo americanus, Ontario	range 23–480 (176)	Oldham 1966[a]
Bufo boreas, Colorado	mode = 900	Campbell 1970[b]
Wyoming	maximum = 101	Carpenter 1954[a]
Bufo bufo, Germany	mode 70–760, maximum = 1600	Sinsch 1988[a]
Bufo hemiophrys, Minnesota	range 23–35 (6)	Breckenridge & Tester 1961[b]
Bufo japonicus formosus, Japan	mean = 98.5, range 27–260 (19)	Kusano et al. 1995[c]
Bufo marinus, New Guinea	mean = 150	Zug & Zug 1979[a]
Bufo valliceps, Texas	range 31–72	Blair 1953[a]
Hyla andersoni, New Jersey	mean = 70, maximum = 106 (8)	Freda & Gonzalez 1986[b]
Hyla regilla, Oregon	mode = 92, maximum = 240	Jameson 1956[a]
Pseudacris ornata, Florida	maximum = 55	Ashton & Ashton 1977[b]
Pseudacris triseriata, Indiana	mean = 75, maximum = 213 (9)	Kramer 1973[b]
Rana capito, Florida	range 280–480	Greenberg 2001[a]
Rana catesbeiana, New York	mean = 406, mode = 1046 (22)	Ingram & Raney 1943[a]
Rana clamitans, Ontario	mean = 137, maximum 457	Oldham 1967[a]
New York	mean = 121, maximum = 360	Lamoureux & Madison 1999[c]
Missouri	mean = 485, range 321–570 (6)	Birchfield & Semlitsch 2002[c]
Rana muscosa, California	range 66–142 (81)	Matthews & Pope 1999[a]
Rana pretiosa, Montana	range 41–443	Hollenbeck 1976[a]
Wyoming	maximum = 46	Carpenter 1954[a]
Wyoming	range 369–462	Turner 1960[a]
Rana sevosa , Mississippi	mean = 173, range 49–299 (12)	Richter et al. 2001[c]
Syrrhophus marnocki, Texas	mean = 213, range 114–303	Jameson 1955[a]
Salamanders		
Ambystoma californiense, California	mean = 36, range 8–129 (59)	Loredo et al. 1996[a]
California	mean = 114, maximum = 248 (11)	Trenham 2001[c]
Ambystoma jeffersonianum, Michigan	mean = 39, range 22–108 (6)	Wacasey 1961[a]
Michigan	mean = 92, range 15–231 (45)	Wacasey 1961[d]
Indiana	mean = 252, range 20–625 (86)	Williams 1973[b]
Kentucky	mean = 250 (10)	Douglas & Monroe 1981[b]
Ambystoma maculatum, Michigan	mean = 67, range 26–108 (2)	Wacasey 1961[a]
Michigan	mean = 103, range 15–200 (14)	Wacasey 1961[d]
Indiana	mean = 64, range 0–125 (7)	Williams 1973[b]
Kentucky	mean = 150, range 6–220 (8)	Douglas & Monroe 1981[b]
Michigan	mean = 192, range 157–249 (6)	Kleeberger & Werner 1983[b]
New York	mean = 118, range 15–210 (8)	Madison 1997[c]
Ambystoma opacum, Indiana	mean = 194, range 0–450 (12)	Williams 1973[b]
Kentucky	mean = 30 (6)	Douglas & Monroe 1981[b]
Ambystoma talpoideum, South Carolina	mean = 178, range 13–287 (17)	Semlitsch 1981[b]
Ambystoma texanum, Indiana	mean = 52, range 0–125 (10)	Williams 1973[b]
Ambystoma tigrinum, South Carolina	162 (1)	Semlitsch 1983[b]
South Carolina	mean = 215, range 112–450 (4)	Semlitsch et al., unpublished data[c]
New York	mean = 60, range 0–286 (27)	Madison & Farrand 1998[c]
Desmognathus fuscus, Kentucky	maximum = 17 (14)	Barbour et al. 1969[b]
Ohio	maximum = 20 (16)	Ashton 1975[b]
Eurycea bislineata, Ohio	maximum = 31 (20)	Ashton & Ashton 1978[b]
Eurycea longicauda, New Jersey	mode = 6, maximum = 31	Anderson & Martino 1966[a]
Hynobius nebulosus tokyoensis, Japan	maximum = 100 (48)	Kusano & Miyashita 1984[a]
Notophthalmus viridescens, Massachusetts	mode = 800 (383)	Healy 1975[a]
Taricha torosa granulosa, Oregon	mode = 185	Pimentel 1960[a]

[a] *Uniquely marked individuals.*
[b] *Radioactive tags.*
[c] *Radiotransmitters.*
[d] *Unmarked individuals.*

Appendix 2. **Summary of terrestrial migration distances from aquatic sites for reptiles.**

Species and location	*Distance in m (sample size)*	*Data source*
Snakes		
Crotalus horridus, New Jersey	maximum = 700 (15)	Reinert & Zappalorti 1988[a]
Nerodia harteri, Texas	mean = 2.1, range 0–15 (8)	Whiting et al. 1997[a]
Nerodia sipedon, Wisconsin	maximum = 6 (10)	Tiebout & Cary 1987[a]
Opheodrys aestivus, Arkansas	mode = 3, range 0–5 (31)	Plummer 1981[b]
Sistrurus catenatus, Pennsylvania	mode = 200 (25)	Reinert & Kodrich 1982[a]
Turtles		
Apalone ferox, Florida	22.9 (1)	Goff & Goff 1935[c]
Apalone mutica, Iowa	range 3–18	Muller 1921[c]
Iowa	range 2–8	Goldsmith 1945[c]
Kansas	mean = 38.2, range 4–90 (104)	Fitch & Plummer 1975[c]
Apalone spinifera, Arkansas	mean = 2.5, range 2–3 (4)	Plummer et al. 1997[b]
Indiana	mode = 2	Newman 1906[c]
Minnesota	0.3 (1)	Hedrick & Holmes 1956[c]
Nebraska	4.5 (1)	Gehlbach & Collette 1959[c]
Chelydra serpentina, Florida	mean = 93.7, range 38–141 (7)	Punzo 1975[c]
Michigan	mean = 37.2, range 1–183 (210)	Congdon et al. 1987[b]
Nebraska	mode = 25, maximum =100	Iverson et al. 1997[b,c]
New York	mean = 27.4, range 1–89	Petokas & Alexander 1980[b]
Chrysemys picta, Idaho	mode = 200, maximum = 600	Lindeman 1992[b]
Michigan	mean = 60.4, range 1–164 (185)	Congdon & Gatten 1989[b]
Quebec, Canada	mean = 90.4, range 1–621 (51)	Christens & Bider 1986[a,b]
Clemmys guttata, Connecticut	range = 3–265 (9)	Perillo 1997[a]
Michigan	maximum = 150	Harding & Bloomer 1979[b]
Pennsylvania	range 60–250 (207)	Ernst 1976[b]
Clemmys insculpta, Canada	mean = 27, range 0–500 (10)	Foscarini & Brooks 1993[b]
Pennsylvania	mode = 300, maximum = 600 (50)	Kaufmann 1992[a,b]
New Hampshire	mean = 60.3 (9)	Tuttle & Carroll 1997[a]
New York	maximum = 200 (189)	Carroll & Ehrenfeld 1978[b]
Clemmys marmorata, California	mean = 168, range 39–423 (19)	Reese 1996[a]
Deirochelys reticularia, Texas	30 (1)	David 1975[c]
Virginia	mean = 95, range 32–192 (4)	Buhlmann 1995[a]
Emydoidea blandingi, Illinois	mean = 815, range 650–900 (3)	Rowe & Moll 1991[a]
Michigan	mean = 135, range 2–1115 (105)	Congdon et al. 1983[b]
Wisconsin	mean = 168 (16)	Ross & Anderson 1990[a,b]
Graptemys barbouri, Florida	200 (1)	Ewert & Jackson 1994[c]
Graptemys ernsti, Alabama	range 3–15	Shealy 1976[b]
Graptemys flavimaculata, Mississippi	mode = 100 (20)	Jones 1996[a]
Graptemys geographica, Quebec, Canada	mean = 2.3, range 2–3 (3)	Gordon & MacCulloch 1980[b]
Graptemys oculifera, Mississippi	range 7–17	Jones 1991[c]
Graptemys pseudogeographica, Missouri	mean = 353, range 0–1133 (15)	Bodie & Semlitsch 2000[a]
Kinosternon baurii, Florida	mean = 15.6, range 1–49 (23)	Wygoda 1979[b]
Kinosternon flavescens, Iowa	range 100–450	Christiansen et al. 1985[a]
Nebraska	range 21–191 (33)	Iverson 1990[a]
Kinosternon leucostomum, Mexico	mean = 275, range 0–600 (14)	Morales-Verdeja & Vogt 1997[a]
Kinosternon subrubrum, South Carolina	mean = 103.4, range 1–600 (20)	Bennett et al. 1970[d]
South Carolina	mean = 200, range 100–300 (2)	Bennett 1972[d]
South Carolina	mean = 49.3, range 17–90 (25)	Burke et al. 1994[a]
South Carolina	mean = 61.6, range 18–135 (115)	Burke 1995[a]
Macroclemys temminicki, Florida	mean = 12.2, range 3–22 (12)	Ewert 1976[c]
Florida	maximum = 200 (106)	Ewert & Jackson 1994[c]
Malaclemys terrapin, New Jersey	mode = 150 (40)	Burger & Montevecchi 1975[c]
Podocnemis unifilis, Venezuela	mean = 38.3, range 21–80 (422)	Escalona & Fa 1998[c]
Pseudemys floridana, South Carolina	mean = 106.7, range 62–286 (19)	Burke 1995[a]
Pseudemys rubriventris, Massachusetts	range 10-250	Ernst et al. 1994[b]
Sternotherus depressus, Alabama	6.5 (1)	Dodd 1988[c]
Sternotherus odoratus, Pennsylvania	mean = 6.6, range 3–11 (27)	Ernst 1986[c]
Trachemys scripta, Florida	mode = 180	Carr 1952[c]
Louisiana	maximum = 1600	Cagle 1950[c]
Missouri	mean = 348, range 0–1394 (11)	Bodie & Semlitsch 2000[a]
Panama	mean = 50, range 2–320 (139)	Moll & Legler 1971[b]
South Carolina	mean = 86.5, range 23–299 (11)	Burke 1995[a]

[a] *Radiotransmitters.*
[b] *Uniquely marked individuals.*
[c] *Unmarked individuals.*
[d] *Radioactive tags.*

NATIONAL

Constant Wildfires Leave California Firefighters Strained

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August 4, 2018 · 8:08 AM ET
Heard on Weekend Edition Saturday

California hasn't had a month without a wildfire since 2012. NPR's Scott Simon speaks with Mike Feyh of the Sacramento Fire Department about the strain on firefighters.

SCOTT SIMON, HOST:

The Carr Fire rages in Northern California this weekend, but there's also the Ferguson Fire and the Butte Fire. State emergency management officials say there hasn't been a month without a wildfire in California since 2012. Many firefighters are working 16-hour shifts. Jason Campbell was fighting the Ferguson fire when he learned his house burned in the Carr Fire. He still reported to work.

(SOUNDBITE OF ARCHIVED RECORDING)

JASON CAMPBELL: The only way I felt that I was going to be able to deal with it is just to come out here and deal with the fire personally. You know, it might have taken everything that belongs to me, but it's taken everything from other people. So I made it my personal goal just to get out here and show the guys that, you know, this is what you do. The community comes together, and everybody come out here with a common goal. And that was to get this thing out, so it doesn't happen to other people.

SIMON: Firefighter Jason Campbell, who is a crew boss with the commercial disaster response firm GFP. We're going to turn now to Capt. Mike Feyh of the Sacramento Fire Department.

Captain, thanks so much for being with us.

MIKE FEYH: Sure, it's a pleasure.

SIMON: Help us understand what kind of strain all of these fires have caused firefighters in their departments.

FEYH: Well, it's been a huge strain. I mean, currently here in the city of Sacramento, we have two rigs that are currently deployed - as well as what we call overhead team members. So that's another four individuals. So currently that's just 12, which then impacts our staffing hugely when we're already stretched to the limits.

SIMON: You've been on the fire line yourself, haven't you?

FEYH: Yes, I have. I've been out on these wildland incidents. And typically for our department, which we refer to as local government, we'll go out for 14 to 16 days at a time. And we're out there - and we alternate with 24-hour shifts. But sometimes in the beginning, you'll end up being out on the line for up to 48 hours before you actually get back in and can get some rest and food.

SIMON: Which means, by the time you actually have to fight the fire, you might be - you will be sleep-deprived, exhausted, hungry. And months and months of this must - forgive the phrase - burn out people.

FEYH: And it is. And we're starting to see that among our members. We talk about fire season, but there truly isn't a fire season anymore. Traditionally, that would run from April to May through, you know, September to October here in the state of California. But last year, the Thomas Fire was burning into December. And actually I don't think it was officially put out until March.

SIMON: And is there - as there is in a group of soldiers or police officers, is there some ethic or code of conduct which seems to discourage firefighters from saying they're injured or hungry or need help?

FEYH: And that's one of the other things that we've been battling. And we've tried to raise awareness to firefighters throughout the country - is on the behavioral health side of stuff. We have people who need help. They've got injured. They're suffering from maybe addiction - alcohol, drug. And we've found that if we can actually get out there, do a little bit of preventive education for our members, that we can actually maybe start to reduce the number of firefighter suicides, which has increased drastically over the last 10 to 15 years.

SIMON: I didn't know that. Firefighter suicides have been increasing?

FEYH: Yes. It's almost getting to epidemic proportion. I mean, it's starting to rival our other work-related injuries. And we're finding that a lot of it's due to chronic exposure to multiple trauma and emergency-type response incidents. And then you stack on increased hours, increased workload. And the strain just continues to grow and grow on firefighters to the point where - I mean, it's almost like a rubber band. They're stretched completely thin. Eventually, they're going to snap.

SIMON: If wildfires are going to become a way of life, what do you need?

FEYH: Well, I've been on the Sacramento Fire Department for 24 years. We still have the same number of engines and trucks as we did when I first came on this job. Since then, our call volume has more than tripled. So we need to add resources. We don't have the firefighters and the equipment that we need.

SIMON: We just had a clip from firefighter Jason Campbell, who's with a commercial disaster response company. Is there an increased role for companies like that?

FEYH: I'm sure there is. But some of the things that we're doing with the public agencies is the fact that they will always be there. Civilian agencies, private contractors - there's never that assurance that they're going to be there from the next day.

SIMON: Capt. Mike Feyh of the Sacramento Fire Department. Thanks so much, sir.

FEYH: You're welcome, Scott. Have a nice day.

(SOUNDBITE OF BRONTIDE'S "KNIVES")

More Stories From NPR

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Birdsong and anthropogenic noise: implications and applications for conservation

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Abstract

The dramatic increase in human activities all over the world has caused, on an evolutionary time scale, a sudden rise in especially low-pitched noise levels. Ambient noise may be detrimental to birds through direct stress, masking of predator arrival or associated alarm calls, and by interference of acoustic signals in general. Two of the most important functions of avian acoustic signals are territory defence and mate attraction. Both of these functions are hampered when signal efficiency is reduced through rising noise levels, resulting in direct negative fitness consequences. Many bird species are less abundant near highways and studies are becoming available on reduced reproductive success in noisy territories. Urbanization typically leads to homogenization of bird communities over large geographical ranges. We review current evidence for whether and how anthropogenic noise plays a role in these patterns of decline in diversity and density. We also provide details of a case study on great tits (*Parus major*), a successful urban species. Great tits show features that other species may lack and make them unsuitable for city life. We hypothesize that behavioural plasticity in singing behaviour may allow species more time to adapt to human-altered environments and we address the potential for microevolutionary changes and urban speciation in European blackbirds (*Turdus merula*). We conclude by providing an overview of mitigating measures available to abate noise levels that are degrading bird breeding areas. Bird conservationists probably gain most by realizing that birds and humans often benefit from the same or only slightly modified measures.

Keywords: adaptation, biodiversity, city life, conservation, ecological speciation, homogenization, traffic noise, urbanization

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Introduction

Urbanization concerns all environmental changes associated with urban development and is a global phenomenon affecting animals, including humans, as well as plants (Vitousek et al. 1997; Western 2001). Expectations are that in the next two decades an additional two billion people will need a place to live, and they will not live in the current cities but in newly developed urban areas (Meyer & Turner 1992; World Resources Institute 2004). Urbanization usually has a negative effect on rare species and favours others that become more and more common, which can be native generalist species, but often means non-native urban colonizers (Bolger et al. 1997; Sewell & Catterall 1998; Lim & Sodhi 2004; Marzluff 2005). At a local scale, urbanization does not necessarily lead to a drop in species diversity because the heterogeneous urban habitat does provide quite a variety of niches. However, at a larger scale, urbanization leads to homogenization and a drop in diversity because the typical urban species turn out to be the same everywhere irrespective of the original fauna (Clergeau et al. 2006; McKinney 2006). For species that still occur within and outside of cities, it is known that urban challenges may be relatively stressful as reflected for example by a divergence in heterophil-leucocyte ratios (Ruiz et al. 2002) or increased baseline cortecosterone levels in male birds of city environments (Bonier et al. 2007). Nevertheless, although many species disappear from urban areas because they depend on habitat features that do not exist anymore, others find a new niche among bricks and concrete and adapt to a life in the city (Luniak 2004).

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Cities differ from rural or forested areas in a number of ways (Warren *et al.* 2006; Slabbekoorn *et al.* 2007). Urban areas are usually warmer, have artificial lighting regimes, more chemical pollution, and have relatively little and often exotic vegetation in a landscape dominated by street pavement and concrete buildings. Furthermore, cities harbour a different suit of parasites (Gregoire *et al.* 2002) and predators including domestic cats (Woods *et al.* 2003; Lepczyk *et al.* 2004), and a different set of food sources (Horak & Lebreton 1998). For example, urban house sparrows are reported to have higher cholesterol levels compared to rural ones, and food samples indeed reveal higher fat and protein content in urban diets (Gavett & Wakeley 1986). Consequently, food preferences also affect which species are more likely to do well under the urban food conditions; omnivorous and frugivorous birds are typically more successful than insectivorous and carnivorous species (Clergeau *et al.* 1998; Lim & Sodhi 2004).

One of the most prominent novel urban conditions concerns the ambient noise and the acoustic space available for animals to use acoustic signals (Slabbekoorn & Peet 2003; Katti & Warren 2004). All habitats are noisy to some extent, but the usual urban cacophony produced by cars, mopeds and all sorts of machinery is evolutionarily speaking novel and dramatically different from most natural habitats. Urban noise is typically loud and low in pitch which also applies to anthropogenic noise in areas around highways, railway lines and airports — which together form an ever denser network penetrating deeply into rural and forested areas (Forman & Alexander 1998; Reijnen & Foppen 2006). Anthropogenic noise could be an important factor driving bird species out of cities and away from highways, even when other habitat requirements are still sufficient.

Many studies have reported lower species diversity and lower breeding densities of birds along highways (Van der Zande *et al.* 1980; Reijnen & Foppen 1991, 1994; Illner 1992; Kuitunen *et al.* 1998, 2003). The negative impact of roads on birds has been linked repeatedly with traffic load (Reijnen *et al.* 1995, 1997; Forman *et al.* 2002; Peris & Pescador 2004), showing that the impact is not due to the mere presence of a road. However, direct evidence for traffic noise being the dominant detrimental factor is still lacking and other potential factors are visual disturbance, chemical pollution, road-kills and soil vibration. An interesting study concerns an impact assessment along a German motorway, which revealed a song-frequency-dependent pattern in breeding density in two transects parallel to the road (Rheindt 2003). Bird species with relatively low mean song frequencies were less abundant near the road, while species singing with higher frequencies occurred in higher numbers near the noisy road than in the more quiet transect. Although the lack of replication and statistical significance were limitations to this study, this is the first direct indication that low-frequency traffic noise may constrain breeding opportunities of birds.

Few studies have tried to assess a negative impact of anthropogenic noise on birds while excluding other possibly contributing factors. A study in natural habitat of the Rocky Mountains, USA, showed a negative correlation between the number of species and anthropogenic noise levels (Stone 2000). Another recent study reported the first data on a decline in reproductive success due to anthropogenic noise without confounding parameters typically associated with highway or urban studies (Habib *et al.* 2007). The authors compared ovenbirds (*Seiurus auropilla*) in Canada, in two sets of territories of equal quality, except for either being located next to noise-generating compressor stations or next to noiseless well pads. Significantly more inexperienced first-year breeders were found at the noisy locations, while the pairing success at noisy territories showed a considerable decline, independent of the individual quality. This study unequivocally confirms a negative impact of human-generated ambient noise, but how does the sound affect the birds?

In this paper, we will address in what way birds may be affected by anthropogenic noise as well as how birds may counteract artificially altered noise conditions in their territories. We will discuss a case study of great tits (*Parus major*) which provides insight into how a successful urban species gets at least partly around the noise problem in cities across Europe. Subsequently, we will address to what extent urban habitat may drive divergence of urban populations and how sensible it is to make a case for ecological speciation in this context. The potential emergence of new urban species takes place over an evolutionary time scale and does not relate to conservation of today's biodiversity. Therefore, we will conclude with considering the available options to abate the negative impact of anthropogenic noise on current species at an ecological time scale.

Noise annoys

Extreme noise levels can result in temporary and permanent hearing loss (Ryals *et al.* 1999), but also the ubiquitous condition of more moderate noise levels may have adverse impacts. In humans, traffic noise at the front door of people's houses is a significant predictor of ischemic heart disease (a hospital-based case-control study with controls matched according to sex, age and hospital: Babisch *et al.* 2005), and repetitive exposure to aircraft noise has been shown to reduce performance at school (Stansfeld *et al.* 2005). Even relatively modest noise levels of train- and car traffic can already negatively affect cognitive development and reading skills (Lercher *et al.* 2003). Clearly, humans pay a price for living in noisy cities or along roads with heavy traffic loads with respect to physical and psychological welfare (Miedema & Vos 1998; Nilsson & Berglund 2006). This may also be true for animals, including birds.

Measurements to assess direct and detrimental physical effects of anthropogenic noise on birds, such as an increased heart-beat (Helb & Hüppop 1991), are rare or nonexistent. Nevertheless, a wide variety of animal species has been reported to be affected by anthropogenic noise as indicated by behavioural changes (e.g. birds: Slabbekoorn & Peet 2003; Brumm 2004; whales: Foote *et al*. 2004; Miller *et al*. 2000; frogs: Sun & Narins 2005; ground squirrels: Rabin *et al*. 2006). One of the behavioural changes concerns an increase in vigilance behaviour at the expense of time spent feeding (Rabin *et al*. 2006). For example, chaffinches (*Fringilla coelebs*) spend less time with their head down, pecking at food, during artificially increased noise levels (Quinn *et al*. 2006). The nature of the behavioural change in this experiment suggests that these birds did not change general alertness due to a novel stimulus but have to rely more on visual scanning for predators when the detection of auditory cues is limited by masking noise. Predation risk in noisy conditions may therefore have negative consequences for food-intake rates and ultimately lead to lower survival and lower reproductive success.

Anthropogenic noise may not only hamper the detection of heterospecific predators but also the detection of conspecifics. Many animal species, and especially birds, depend heavily on acoustic signals for intraspecific communication (Catchpole & Slater 1995; Marler & Slabbekoorn 2004). Typically, males defend a territory for access to food, hiding places and nest sites. Singing and song features such as repertoire size or spectral and temporal details may have a direct impact on how well they are able to do so. Encoded in acoustic variation, birds may convey a message about their species identity, fighting ability and motivation to defend a resource (e.g. Ten Cate *et al*. 2002; Ripmeester *et al*. in press). Successful transmission of such a message may prevent competitors from approaching and may save energy, time and risks of injury. In addition, females also pay attention to these messages and are known to select their mates based on male song features (Riebel 2003). Therefore, whether songs are heard properly or not may have serious consequences for territory tenure and mate attraction (Klump 1996), potentially affecting individual fitness and population viability.

However, there are many signalling strategies available to birds to avoid or reduce masking by ambient noise (Brumm & Slabbekoorn 2005). Species-specific abilities in this respect may explain why some species resist urban noise conditions and others do not. A widespread strategy, for example, concerns the Lombard effect: birds as well as humans raise their signal amplitude with noise level. Recently, urban nightingales (*Luscinia megarhynchos*) in the city of Berlin, Germany, were found to raise their song volume in response to traffic noise; as a result they appear to sing louder on weekday mornings than in weekends (Brumm 2004). Another way to adjust to fluctuating noise conditions concerns a temporal shift in singing activity. Several urban bird species are reported to start singing earlier during the day than their forest counterparts (Bergen & Abs 1997), but the potential relationship with avoiding traffic peaks has not been investigated in enough detail yet. However, European robins (*Erithacus rubecula*) sing both, during day and night time, and whether or not birds are active during the night was recently shown to be dependent on day-time noise levels in a study in the city of Sheffield, UK (Fuller *et al*. in press). There was less of an effect in this study of ambient light pollution, to which nocturnal singing in urban birds is frequently attributed. Although it is not clear yet whether nocturnally active robins reduce their day-time activity and whether they gain any fitness benefits by doing so, it seem plausible that this strategy may enable them to avoid masking noise and breed in noisy territories. In general, a division between species surviving in urban conditions and those fleeing the cities may very well depend on how effectively members of a species can adjust their signalling behaviour to the volume, temporal fluctuations or spectral characteristics of traffic noise.

Signalling flexibility in urban great tits

Over the last five years, we have studied patterns of song variation among individual great tits (*Parus major*) within an urban population in Leiden, The Netherlands, and among 20 different urban and forest populations across Europe. We first found in the single-population study that individual variation in the frequency range correlated to local urban noise levels (Slabbekoorn & Peet 2003). Birds of noisier territories sang with higher minimum frequencies, thereby avoiding masking by low-pitched traffic noise (Fig. 1). We speculated at the time that these results could mean that urban birds could have diverged from forest birds, and that flexibility through learning may be the behavioural mechanism underlying the correlation. Subsequently, we confirmed that urban birds across Europe have diverged from nearby forest birds in several parameters, among which the minimum frequency. A surprising 10 out of 10 independent city–forest comparisons revealed a consistent shift (Slabbekoorn & den Boer-Visser 2006).

The habitat-dependent acoustic shift in great tits could be an evolutionary or ontogenetic shift, or it could be based on the ability to adjust at an even shorter temporal

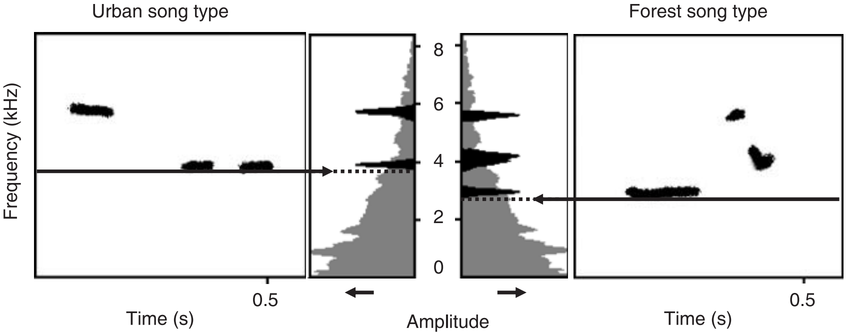


Fig. 1 Sonograms of a three-note song type recorded in an urban habitat, with a relatively high minimum frequency (3.8 kHz, left graph) and of a three-note song type recorded in a forest habitat with a relatively low minimum frequency (2.7 kHz, right graph). The centre panels illustrate the energy concentration of each of the spectral components present in the song, normalized at an equal amplitude and contrasted, at an arbitrary level, against the energy distribution of a typical anthropogenic sound spectrum of urban traffic noise. Noise levels gradually increase towards lower frequencies, and the figure illustrates that critical signal-to-noise ratios leading to perceptual problems are more likely for notes of low frequency. As a consequence, song types without relatively low notes will on average be heard better in noisy cities.

scale (Patricelli & Blickley 2006). It is known from long-term field observations that great tits are probably capable of postdispersal adjustment of song-type repertoires guided by vocal interactions with neighbours (McGregor & Krebs 1989). Noisy conditions may affect such social influences through selective copying or selective reinforcement: song types of neighbours that are not heard well may not be copied, and song types sung but hardly eliciting a response from neighbours may be dropped. Recently, we found that adult males are even more flexible than previously thought. We played back unfamiliar song types and assessed the repertoire of a series of males before and after playback (Franco & Slabbekoorn, unpublished). The song-type repertoire size remained relatively constant over the season, but the rates at which different song types were sung varied and the repertoire composition was sometimes modified dramatically within a week. This shows that great tits have a larger repertoire memorized than they actually sing at a time or that they can make up new song types late in life. Most importantly, this means they have remarkably flexible singing behaviour. They are capable of mobilizing a large set of song types to adjust to new neighbours or possibly to new noise conditions.

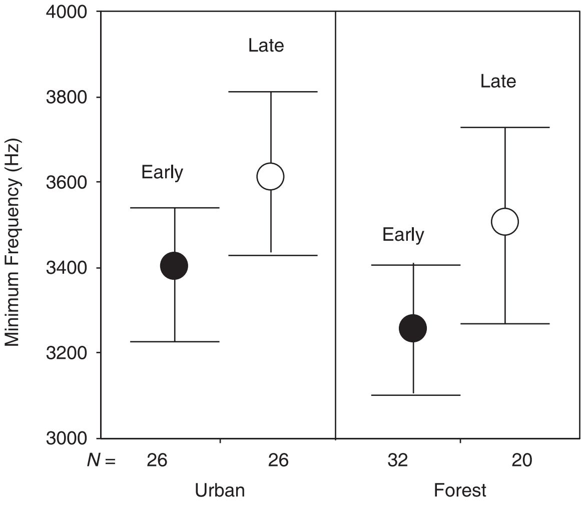
The singing behaviour and repertoire flexibility of great tits has likely evolved to fit their social system in the context of the original forest habitat. They may be just lucky in the sense that these features turn out to be very suitable for coping with dramatic and, evolutionarily speaking, sudden rises in anthropogenic noise levels. The ability to spectrally adjust their song after dispersal to the local circumstances of a breeding territory, and this potentially throughout life, may be key to urban success. At the same time, despite the fact that they remain in cities breeding at relatively high densities, it is not certain that great tits are not at all negatively affected by anthropogenic noise (see Box 1). However, their acoustic counter-strategy seems at least sufficient for urban populations to survive under potentially suboptimal conditions (also see Junker-Bornholdt *et al.* 1998). Our results from the single-population study have now been independently replicated in two other North American bird species that are also very successful in urban environments (house finch, *Carpodacus mexicanus*: Fernández-Juricic *et al*. 2005; song sparrow, *Melospiza melodia*: Wood & Yezerinac 2006). An earlier study on chaffinches did not find a correlation between traffic noise levels and call characteristics (Skiba 2000). Nevertheless, this species, which can be very common in cities, does show the same increase in minimum frequency of their songs with varying levels of natural river noise (Brumm & Slater 2006). We are now waiting for data showing that bird species which are less successful in noisy areas are lacking the ability of spectral adjustment through repertoire changes.

Divergent phenotypes in great tits: a case for urban speciation?

Behavioural plasticity may allow urban birds enough time to evolve and adapt to human-altered environments. Although it is possible, currently there is no evidence that the acoustic divergence between city and forest tits involves any microevolutionary changes and associated genetic differentiation. However, habitat-dependent divergence in a sexual trait like song in birds may play an important role in population divergence and ecological speciation (Slabbekoorn & Smith 2002a, b), and we may be able to consider urban speciation. Species with a distribution across ecological gradients may evolve different subpopulations in different habitats. These

Box 1 Is singing low important to great tits?

There is a general relationship in birds between body size and frequency of pitch: larger species typically sing lower. Small birds with small vocal organs may be lacking the power, the essential size of the vibrating source, or the suitable resonance features of the vocal tract, that allow the production of low-pitched sounds. This creates the possibility of using low frequencies as a way to signal condition or size to competitors and potential mates (Ten Cate *et al*. 2002). However, we do not know whether intraspecific variation in male body measures is related to the minimum frequency in great tits, nor do we know if female great tits prefer males singing low-pitched songs. If it were hard for great tits with a territory to sing low, you may expect that they sing songs relatively high in pitch when the motivation to sing is low. Such a situation occurs at the end of the breeding season, in both urban and forest habitat. Males still sing their stereotypic song types but the resources at stake in their territory have decreased in value until the start of the next breeding season. A decline in motivation to sing is clear from a decline in number of repeated songs (phrases) in a strophe, independent of habitat: in the city of Rotterdam from six to three phrases, and in the forest called the Liesbos from six to four phrases on average (ANOVA: $F_{2,100} = 27.4, P < 0.001$). Interestingly, controlling for habitat differences, we found that the minimum frequency increases dramatically when recordings from relatively early in the season (early April: 'Early') are compared to recordings from late in the season (late May: 'Late', ANOVA: $F_{2,100} = 7.8$, $P < 0.01$). We therefore hypothesize that it may be an important signal of quality to have low-pitched notes in the song type repertoire, which may cause a trade-off especially for the urban birds in noisy territories. Low-frequency noise may constrain the capacity to signal individual qualities: urban birds may need to choose between being heard well or being rated high as a competitor or mate. High noise levels may increase the number of intruding competitors needing physical combat and may affect the number and quality of potential mates that are attracted. Consequently, although great tits are successful in cities, and even though they show a remarkable flexibility in spectral adjustment to local noise conditions, this does not mean that traffic noise interference is not harmful to individual birds.



subpopulations may show genetic divergence in fitness-related traits related to morphology, physiology, neurobiology or life-history. Congruent geographical patterns of variation in sexual and fitness-related traits may arise because varying environmental selection pressures in different habitats shape both types of traits. Congruent patterns may also emerge because acoustic changes are an inherent result of, for example, changes in bill morphology (Slabbekoorn & Smith 2000; Podos *et al*. 2004). As a consequence, under both conditions, songs may guide female birds to the locally adapted males, accelerating the process of reproductive divergence. The fact that many birds learn their songs from conspecifics adds a layer of complexity (Baker & Cunningham 1985; Slabbekoorn & Smith 2002b), as it will accelerate phenotypic divergence among populations but may actually constrain genetic differentiation (Ellers & Slabbekoorn 2003). Nevertheless, divergence in learned song will still increase the rate and chance of speciation for a subset of evolutionary scenarios (Lachlan & Servedio 2004; Ellers *et al*. unpublished).

In terms of gene flow, it may be improbable that urban habitat could generate phenotypically distinct and reproductively isolated subpopulations, as cities are typically scattered geographically and form a patchy network within a matrix of forested and agricultural area (Marzluff 2005). Habitat imprinting, on the other hand, may strongly influence dispersal patterns, and urban-borne birds may preferentially settle in urban territories (see e.g. Septon *et al*. 1995). In terms of consistent directional selection, despite considerable heterogeneity within urban habitat, some urban selection pressures are clearly distinct and dramatically different from those in more natural habitat. These consistent habitat-dependent selection pressures may have the potential for driving divergence of an urban phenotype despite ongoing gene flow.

We are not aware of any publications on gene flow, or dispersal, between urban and nonurban populations of great tits, but there are some studies on urban-related phenotypic divergence. Plastic environmental responses were found for carotenoid-derived plumage coloration, with urban birds being less yellow compared to forest birds (Horak & Lebreton 1998) and also for timing of reproduction and clutch size, with later and smaller broods in (sub)urban great tits compared to their forest counterparts (Riddington & Gosler 1995). Another study, not involving urban habitat, addressed the balance between the response to divergent selection pressures and levels of gene flow over a very short distance. A partial cross-fostering experiment with great tits of two qualitatively different parts of Wytham Woods in Oxfordshire, UK, allowed the separation of genetic and environmental sources of variation (Shapiro *et al*. 2006). Nestlings in the high-quality part of the forest were larger, heavier and in better condition than in the low-quality part irrespective of the part from which they originated. Interestingly, in addition, significant differences in condition and shape could be attributed to area of origin, suggesting genetic differentiation. The areas of varying quality in this comparison were only a few kilometres apart and interconnected by forest, which reveals the evolutionary potential of divergent selection in ecologically distinct habitat for driving populations apart. Another recent and small-scale study on great-tit populations also reported interesting findings with respect to the balance between divergent selection and gene flow. A biased influx of birds from the mainland to only one side of the Dutch island of Vlieland created a local abundance of breeding birds that were not locally adapted (Postma & van Noordwijk 2005).

Evidence for microevolutionary changes in urban habitat

The evidence for genetic differentiation related to anthropogenic selection pressures in cities is also still scarce when we look at bird species beyond great tits. A nice example of selection in an urban environment driving evolutionary change is found in an exceptional urban bird population on the campus of the University of California in San Diego, USA. Dark-eyed juncos (*Junco hyemalis*) have been breeding in this urban setting since the early 1980s (Yeh & Price 2004). The birds were presumably winter visitors that decided to stay instead of return to their natural breeding habitat: montane pine forest at least more than 70 km away (Nolan *et al*. 2002). Population comparisons and a common-garden experiment with hand-raised birds revealed that wing- and tail size, as well as a sexual trait (the amount of white in the tail) has diverged on campus beyond the extend attributable to phenotypic plasticity or drift (Rasner *et al*. 2004; Yeh 2004). However, there was only limited evidence for song divergence between this small urban population of about 70 pairs and four forest populations (Slabbekoorn *et al*. 2007). Although there were strong indications for divergent selection pressures on acoustic signals related to sound transmission, sexual selection based on song may be relaxed, as suggested by a reduced response to playback of junco songs in the urban population (Newman *et al*. 2006). The urban juncos make a strong case for microevolutionary changes related to anthropogenic selection pressures, but they require more study and better replication to increase our insight into the role of song in urban speciation.

Another bird species for which there is growing evidence for urban-related population divergence is the European blackbird (*Turdus merula*), a very common city bird in most parts of Europe (Luniak *et al*. 1990). Urban blackbirds breed in higher densities and start breeding earlier in the year than their forest counterparts (Partecke 2003). A common garden experiment, with nestlings collected in the city of Munich and the nearby Lichtenauer Forest, revealed phenotypically plastic divergence but also suggested that some of the variation reflects genetic differentiation (Partecke *et al*. 2004, 2005, 2006a). The habitat-dependent difference in timing of reproduction corresponds to an earlier initiation of the development of the reproductive system in male and female urban birds (Partecke & Gwinner 2007). The prolonged breeding season allows urban individuals to have more breeding attempts per year than individuals from forests, who on the other hand have a larger clutch size and more fledglings per successful nest (Gregoire 2003). Urban blackbirds also live longer than forest birds (Luniak *et al*. 1990), have a smaller tendency to migrate (Stephan 1999; Partecke & Gwinner 2007) and have a lower acute corticosterone stress response (Partecke *et al*. 2006b). Finally, a pattern of habitat-dependent divergence starts to emerge from several studies at different geographical locations, with blackbirds from cities and forests being distinct from each other in several morphological measures (Lippens & van Hengel 1962; Partecke 2003; Ripmeester & Slabbekoorn, unpublished).

European blackbirds may become the first bird species for which there is evidence for urban habitat-related divergence in both, fitness-related traits (as described above) and acoustic traits (Ripmeester & Slabbekoorn, unpublished). We are in the process of testing with playback recordings whether urban songs trigger stronger responses in city birds than in forest birds and vice versa. At the moment, we do not know yet whether congruent habitat-dependent divergence in song and morphology promotes the process of urban speciation. There is also no information available yet about habitat-guided dispersal, although a first study on divergence in neutral markers between the urban and forest birds of the common garden experiment in Germany could not confirm such a phenomenon (Partecke *et al*. 2006a). It is clear, however, that the aspects of coding and neutral genetic divergence between urban and forest blackbirds warrant further investigation and several complementary studies are on the way.

Considerations on making bird breeding habitat more quiet

It is possible to make bird breeding habitat close to, or surrounded by, anthropogenic noise sources more quiet. We can build noise barriers, make depressed highways or underground tunnels (e.g. Maekawa 1977), or introduce porous road surfaces, speed limitations and restrictions on allowable noise emissions for road traffic related to engine features, break systems and tire types (e.g. Sandberg 1991). There are many examples of successful implementation of these techniques, typically to reduce noise exposure to humans. This means that the main threshold for applications to the benefit of wildlife will likely be the financial costs. However, when considering expensive mitigating measures, it is very important to realize that birds and humans often benefit from the same, or only slightly modified, measures. Urban birds live and breed near human residences, and birds of more natural areas inhabit space often used for recreational activities. The importance to human health and well-being can be used as additional arguments for installing measures to improve bird-breeding areas. In cases where noise barriers are already in place to the benefit of humans, small cost-effective modifications (e.g. increased height, added absorbent) could be a successful strategy (see Box 2).

Urban planners are increasingly aware of the need to consider noise pollution in constructing cities and residential neighbourhoods from a human perspective (Grimm *et al*. 2000; Yli-Pelkonen & Niemelä 2005; Bucur 2006; Nilsson & Berglund 2006). For example, the idea of urban canyons has received considerable attention: the use of relatively continuous rows of office buildings or apartment flats separating noisy human activities from living space in which noise is not appreciated (de Ruiter 2004). This living space may concern pedestrian areas, urban parks and private gardens, all areas in which urban birds would also benefit from reduced noise levels. The strategy of urban canyons also entails concentration of noise sources: canalization of traffic in a limited number of busy through-roads. This will limit the number of canyons to be constructed and make plans economically more feasible (Thorsson & Ögren 2005). Similarly, it is more realistic to concentrate on a restricted set of specified areas which are shielded from noise, instead of trying to reduce noise levels in all public areas (Kihlman & Kropp 2001; Thorsson *et al*. 2004). Urban canyons and 'quiet zones' provide people living in noisy cities with access to at least some quiet areas nearby, which may be a last resort for noise-sensitive bird species at the same time. In the best scenario, bird-breeding data and species-conservation values would be incorporated in the process of selecting the areas to be relieved from urban racket.

More and more tools have been developed to assist policy makers to predict and extrapolate noise levels spatially, based on traffic flow, vehicle types and distance to the road (e.g. Horoshenkov *et al*. 1999; Li *et al*. 2002; de Coensel *et al*. 2005). Spatial extrapolation has also been applied to reveal the impact of traffic noise on bird habitat by using road effect-distances based on general dB-threshold values that are just acceptable for birds, and which depend on habitat type and target species (Reijnen *et al*. 1997). For example, roads with 50 000 vehicles a day result in effect-distances from 75 to 930 meters for grassland species and from 60 to 810 meters for woodland species, as was shown by a meta-analysis combining nine studies (Reijnen & Foppen 2006). Highways may negatively affect bird-breeding habitat in a variety of ways, as stated earlier (e.g. collision, chemical pollution). However, visual disturbance and noise are the primary factors that reach furthest in open habitat, while noise is the single most important factor impacting forested habitat beyond 50 meters from the road (Reijnen & Foppen 2006).

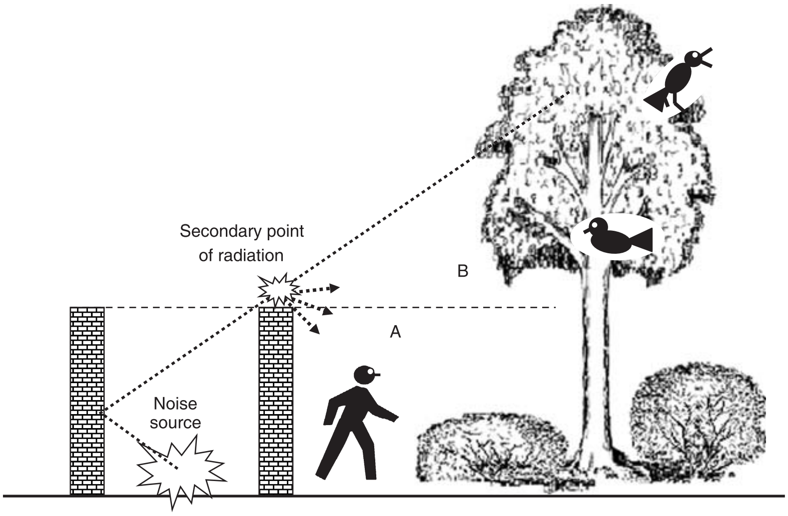
The importance of temporal and spectral overlap

Birds often have a diurnal cycle of vocal activity which matches periods of optimal sound transmission early in the day (Staicer *et al*. 1996; Brown & Handford 2003). Diurnal fluctuations in anthropogenic noise levels are also highly stereotypic with, not surprisingly, noise peaks during the morning and evening rush hour (Jabben *et al*. 2001). Interestingly, traffic jams during these periods may bring down noise levels because of lower driving speeds. Most importantly, however, this means that dawn chorus and rush hour can co-occur at optimal times for sound transmission depending on latitude and season (see Warren *et al*. 2006). Good signalling periods are thus disproportionally affected due to temporal overlap with traffic activity.

The fact that there are often periods during the day in which anthropogenic noise is most detrimental due to concentration of bird singing activity and optimal noise-transmission conditions seems 'bad luck' but also provides the opportunity to ecologically sensible noise control. Reducing traffic flow for short but crucial periods of time, for example, on roads through nature reserves, will raise habitat quality for breeding birds with limited impact on human activities. Similarly, on a slightly larger temporal scale, traffic limitations through sensitive areas during the critical period in spring, when males vocally attract females, could also significantly improve habitat

Box 2 Noise barriers for birds

Raising a barrier between the noise source and bird breeding habitat can lead to a significant reduction in detrimental noise levels. Vegetation is only of limited use, although the effectiveness will increase with stem and leaf density and width of the zone (e.g. Cook & van Haverbeke 1972; Bucur 2006). A solid barrier as close as possible to the noise source will be most effective (Maekawa 1977; Ishizuka & Fujiwara 2004). Adding an overhang on the road side or increasing the height of a barrier which is already in place to benefit pedestrians at ground level (A), could be a very cost-effective measure to the benefit of flying and tree-dwelling birds at a higher level (B). It is usually also easier to filter out the bird-relevant frequency components of traffic or industrial noise than to block the lower frequencies. Construction details and barrier shape especially can have a big impact in the frequency range between 2.0 and 8.0 kHz. For example, sound-pressure levels at the barrier's edge (= secondary point of radiation) can be significantly decreased by installing a soft, absorbent material on top. This will lead to a decrease in the noise level behind the barrier, especially in the field below the barrier height (A). Specific shapes of the barrier top with multiple diffracting edges may add to this effect. For example, T–shaped noise barriers with soft material on top only have to be three meters high to be as effective as a 10-metre high rigid–edged plain barrier (Ishizuka & Fujiwara 2004). This effect steadily gets stronger with frequencies above 250 Hz, also for the sound field above barrier height (B), which concerns the habitat layer typically most important for acoustic signalling in many bird species (Slabbekoorn 2004). Noise barriers at both sides of a road shield areas in both directions, but multiple reflections and scattering effects between the barriers will reduce the shielding capacity. Noise levels become higher especially above the barrier compared to a single barrier situation (Maekawa 1977). Buildings by the side of a busy road typically also increase noise levels within the street or urban canyon (Oldham & Radwan 1994; Heutschi 1995). Both inside and outside urban areas, the problem can be brought down by noise abatement schemes using a more absorbent ground surface and intermittent or continuous absorbers on the walls of buildings or noise barriers (Horoshenkov *et al.* 1999). Placing noise barriers at an angle will also reduce the impact of reflections by beaming them more upward into the sky or downward back towards the tarmac. Finally, the choice of construction material or absorbent matter may make noise barriers also bird-friendly in nonacoustic ways. Combination barriers incorporating trees or shrub layers can reduce the negative impact of an artificial, visual barrier in the landscape, and potentially provide nesting and foraging opportunities.



quality. These critical periods can be quite brief, as in some migratory species, for example, where males arrive at the breeding grounds just before the females. For such species, male singing effort peaks upon arrival and may already decline after one or two weeks.

In addition to seasonal and diurnal fluctuations in bird singing activity and noise levels, more short-term fluctuations may also warrant some attention. Fluctuating noise levels in terms of overall amplitude are usually more annoying to humans than relatively continuous noise levels, especially when areas are relatively quiet overall with sudden unpredictable noise peaks (de Coensel *et al*. 2005). For birds, mean noise levels may similarly not describe the potential for auditory masking or stress levels adequately. Therefore, analyses of sound-level fluctuations in time can add a relevant descriptor capturing more of the dynamics of noise interference.

Traffic-noise fluctuations in terms of frequency are chaotic, but most of the common anthropogenic noise sources show a general decrease in amplitude from low to high frequencies. Bird species in many taxa, such as doves, owls, corvids, woodpeckers, herons and rails use frequencies well below 1.0 kHz. Whether or not species in these groups occur in urban areas or along highways (and some are typically abundant within these habitat types) is probably largely determined by other factors than the impact of noise interference. However, declining signalling efficiency may influence the balance between costs and benefits of city life, especially for those species relying on vocalizations for long-distance communication. Not many noncorvid songbirds use frequencies below 2.0 kHz. The majority of these species uses a bandwidth of 3.0–6.0 kHz, starting at 2.0 or 3.0 kHz and often going up to around 8.0 kHz. The few songbirds that do use very low frequencies down to 1.0 kHz, typically use wideband songs with a bandwidth of about 6.0–9.0 kHz (examples are: European blackbird; nightingale; house sparrow, *Passer domesticus*; European starling, *Sturnus vulgaris*; house martin, *Delichon urbica*), and may therefore be less vulnerable to noise pollution (although we do not know yet whether this is true). Few songbird species rely just on relatively low frequencies, but species that do, like the oriole (*Oriolus oriolus*), the great reed warbler (*Acrocephalus arundinaceus*) and the mistle thrush (*Turdus viscivorus*), may for this reason be relatively sensitive to the masking effect of traffic noise.

A study on distribution and breeding success of great reed warblers in a wetland area in the central part of The Netherlands provides interesting support for the suspected sensitivity to noise in this species (Foppen & Deuzeman 2007). A reed bed in the Vossemeer was known to be inhabited by about 5–10 pairs of reed warblers up until the early 1990s. This reed bed has not changed much since, but it is now situated right beside a road (Vossemeerdijk) with a few thousand cars passing by per day. In the last 15 years, typically only one or two territories each spring have been occupied by singing reed warblers. However, in two years (2003 and 2004) the road was closed to traffic for a substantial time during spring due to road works. The absence of the usual traffic was correlated with an increase from two in 2002 to seven territories in 2003. The return of the noise source was correlated with a decline from five in 2004 back to one territory in 2005. These fluctuations over the course of four seasons constitute only anecdotal evidence, but they do suggest that the vulnerability to a masking of the low-pitched song by traffic noise may have contributed to the overall decline in reed warbler territories in this area since the early 1990s.

Although low-frequency bird songs are most affected by typical anthropogenic noise, it is not true that higher frequencies are free of the impact of anthropogenic noise interference. Masking depends on the amplitude of the acoustic signal relative to the amplitude of the ambient noise within the same frequency range (Lohr *et al*. 2003; Brumm & Slabbekoorn 2005), both measured at the receiver. So, the impact on detection and recognition of acoustic detail can still be serious and deleterious for faint high-pitched notes. Also, high-pitched songs heard at a large distance from the singer, with the receiver potentially being closer to the noise source, may be hampered by the high component of traffic noise which has most energy at low frequencies.

Conclusions

It is becoming more and more clear that the omnipresence of anthropogenic sounds is not only detrimental to human health and well-being, but can also negatively affect birds. Efforts to bring down anthropogenic noise levels to the benefit of bird-breeding areas will almost certainly encounter financial trade-offs. Mitigating measures are typically expensive or counteract economic values, for instance by slowing down, or putting restrictions on, traffic flow. When considering or arguing for expensive noise-reducing actions, it is very important to realize that birds and humans often benefit from the same or only slightly modified measures.

It is obvious from the remarks above on song spectra that we need a thorough comparative study to assess noise sensitivity of bird communities, or at least of those species of high conservation value. Although it may be true in general that making habitat more quiet will improve breeding conditions for many species, we still lack much essential data to guide conservation efforts with adequate detail. Optimally, such data would come from a comparative study that includes experimental assessment of developmental flexibility, tolerance to spectral range reduction and an assessment of the fitness consequences of masking (cf. Habib *et al*. 2007). Data on urban survivors, such as the great tit (Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006), as well as urban 'losers' will be valuable to generate the insight needed to come up with ecologically solid recommendations.

Behavioural flexibility, such as song plasticity in postdispersal adjustment to neighbours under local noise conditions, may allow some species more time to adapt to human-altered environments. Consequently, thriving urban populations may be diverging from their forest counterparts in several traits and may be on a track towards becoming even more successful and potentially an independent urban species. However, this may be true for a 'lucky' few, since many species will not be able to go down this fortunate path. Hopefully in the near future, we will be able to explain which species are negatively affected by anthropogenic noise and why. For those situations for which there is the political will and the financial support to reduce detrimental noise exposure, we hope our considerations on making bird breeding habitat more quiet will prove to be useful.

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Top carnivores increase their kill rates on prey as a response to human-induced fear

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The fear induced by predators on their prey is well known to cause behavioural adjustments by prey that can ripple through food webs. Little is known, however, about the analogous impacts of humans as perceived top predators on the foraging behaviour of carnivores. Here, we investigate the influence of human-induced fear on puma foraging behaviour using location and prey consumption data from 30 tagged individuals living along a gradient of human development. We observed strong behavioural responses by female pumas to human development, whereby their fidelity to kill sites and overall consumption time of prey declined with increasing housing density by 36 and 42%, respectively. Females responded to this decline in prey consumption time by increasing the number of deer they killed in high housing density areas by 36% over what they killed in areas with little residential development. The loss of food from declines in prey consumption time paired with increases in energetic costs associated with killing more prey may have consequences for puma populations, particularly with regard to reproductive success. In addition, greater carcass availability is likely to alter community dynamics by augmenting food resources for scavengers. In light of the extensive and growing impact of habitat modification, our study emphasizes that knowledge of the indirect effects of human activity on animal behaviour is a necessary component in understanding anthropogenic impacts on community dynamics and food web function.

1. Introduction

Anthropogenic disturbance can cause shifts in biotic community dynamics, generally through the loss of native species, introduction of novel species or artificially enhanced populations of native generalists [1]. These changes are characterized most often by quantifying the population size or presence of particular species. However, behaviour-mediated interactions are predicted to have equal or greater impacts on animal populations than purely numerical mechanisms [2–4]. Animal behavioural responses to anthropogenic disturbances have the potential to be cryptic but powerful drivers of ecological change in modified habitats [5].

Large carnivores are widely recognized to be sensitive to human disturbances owing to slow life cycles, large space requirements, direct persecution by humans and avoidance of human-dominated areas, often resulting in their decline or extirpation. Reduced large carnivore density and occupancy in some developed areas has resulted in both mesopredator release [6,7] and overpopulation of primary consumers [8,9]. Yet, some large carnivores do persist in modified landscapes, but alter their behaviour to reduce interactions with humans [10,11]. Owing to the strong regulatory influence large carnivores can exert on their competitors and prey, changes in their behaviour are likely to contribute to whole community responses to anthropogenic disturbances [12].

Hunting and foraging are costly behaviours for carnivores, but are often assumed to be optimized so that individuals gain the most energy (or other limiting nutrients) for the least effort [13]. Animals that choose to expend more energy than what is perceived to be optimal may be responding to risks that increase the long-term pay-off of certain energy-expensive behaviours through decreased chance of non-starvation mortality [14]. Hunting in high-risk habitats can therefore create a risk-foraging trade-off in which animals sacrifice efficient foraging to compensate for increased vigilance and risk avoidance. Giving-up density studies support that an animal's perceived risk is inversely correlated with food intake, suggesting that time spent consuming a food item reflects the fear experienced by forager [15].

Top carnivores generally kill large-bodied prey species, which require a high initial energetic cost during the hunting stage [16], but provide high energy gain during consumption. However, because carnivores are constrained by gut capacity, solitary carnivores can only maximize their caloric yield by repeatedly returning to feed on a prey carcass. In developed habitats, carnivores can be particularly vulnerable to risk-foraging trade-offs because disturbance-induced carcass abandonment can result in food loss owing to scavenging [17] or decomposition [18]. Prey consumption time can therefore be limited by external forces that reduce carnivore access to a carcass. Anthropogenic disturbances can ultimately reduce the net caloric gain carnivores receive from consuming large prey [19] by displacing carnivores from kill sites and decreasing their prey consumption time at kills. If perceived risk increases with human disturbance, the magnitude of human impact should be a predictor of foraging efficiency and consumption time.

We examined puma (*Puma concolor*) behavioural changes associated with perceived risk at kill sites with increasing housing density levels and investigated the relationship between risk-avoidance behaviours and kill rates in disturbed areas. We hypothesized that disturbance would displace pumas more often in highly developed areas, reducing overall prey consumption time and increasing kill rates. In the long term, we anticipate that more frequent risk-avoidance behaviours will increase puma kill rate and subsequently alter interactions with prey, competitors and scavengers.

2. Material and methods

Our research was conducted in the Santa Cruz Mountains, which lie in the Central Coast region of California. We captured 30 pumas from 2008 to 2013 and fitted them with GPS/radio telemetry collars (IACUC no. WILMC1011 Model GPS Plus 1 or 2 D, Vectronics Aerospace, Berlin, Germany). Collars were programmed to record locations every 4 h, and location data were downloaded remotely via UHF once a month. We used a custom cluster generation algorithm integrated in the Geographical Information Systems program ArcGIS (v. 10; ESRI, 2010) using the programming languages R (v. 2.1.3.1; R Development Core Team, 2010) and Python (v. 2.6; Python Software Foundation, 2010) to identify groups of locations in which each location was within 100 m of the cluster centre and 6 days of another location in the cluster (for full details on the algorithm, see [10]). We field-investigated clusters in reverse chronological order from their time of formation using the most recently downloaded GPS data. Clusters were investigated within 30 days of their first recorded locations. At investigated clusters, we recorded whether a kill was present, and if so, the species, age and sex of the kill (if identifiable).

We constructed a mixed-effects binomial logistic regression model to predict deer kill sites from all generated clusters. We chose to only use deer kills because deer are the preferred prey in our study area. In addition, small prey cannot be predicted accurately from location data in our study area owing to high variability in puma behaviours at small kill sites. The variables used to fit the model were behavioural characteristics associated with clusters, including number of night locations (NIGHT), a binary variable indicating greater than 1 day duration (BINARY), the harmonic mean distance of locations from the cluster centre within the cluster (HMDIST), the proportion of locations occurring at night (P.NIGHT), site fidelity measured by the proportion of points occurring within the cluster over the cluster duration (P.ACTIVE) and the farthest distance travelled during a cluster period (DIST). Total duration of a cluster (DUR) was excluded owing to high correlation ($r > 0.7$) with variables already used in the model. We allowed for random slopes and intercepts for individual pumas when fitting the best model. We also constructed a truncated model without behavioural variables that we expected to correlate with housing density in order to allow inference on behavioural influences on kill rates. This model excluded P.NIGHT, P.ACTIVE and DIST. We compared the truncated model and best-fit model to assess if we could confidently use the truncated model. We constructed receiver operating characteristic curves for both full and truncated models and calculated the area under the curve (AUC) to ensure that both models were similar in their predictive abilities. The AUC for the full model (AUC = 0.818) and the truncated model (AUC = 0.820) were nearly identical, and both support good discriminative ability [20]. We assigned each generated cluster as a deer kill or not a deer kill by applying the truncated model to all generated clusters.

We first investigated puma behavioural responses at the population level at four levels of housing density within 150 m of predicted kill sites: no housing, rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to 1.236 houses per hectare) and suburban (greater than 1.236 and up to 9.884 houses ha^{-1}; [21]). Owing to the discrete nature of housing count data, each housing class was rounded up to the nearest number of houses, resulting in housing classes within 150 m of a cluster to be defined as 0 houses for no housing, one house for rural, two to nine houses for exurban and greater than nine houses for suburban. We used the 150 m buffer because this is the scale of development found to most impact puma hunting in our study area [10]. We constrained the response variables to only include behaviours we expected to be associated with risk aversion, which were narrowed down to P.NIGHT, P.ACTIVE, DUR, DIST and a final measure of prey consumption time (P.C.TIME) which was calculated as P.ACTIVE × DUR. We added the prey consumption time measure because it best reflects the energetic gain an animal receives from a kill. We tested the differences in behaviours at all predicted kill sites in different housing density categories using an ANOVA test and examined pairwise comparisons with Tukey's HSD test for all behaviours found to vary significantly with housing density.

To determine kill rates, we calculated the total number of deer predicted to be killed by each puma from the output of the deer kill prediction model using all generated GPS clusters. We divided the predicted number of kills by the total time each puma was actively collecting GPS data to obtain annual deer kill rates. We investigated sex-specific relationships between kill rates and average values for P.NIGHT, P.ACTIVE, DIST, DUR and P.C.TIME for individual pumas using univariate linear regressions owing to high correlation values ($r > 0.7$) among variables.

In order to assess the impact of housing on individual pumas, we calculated housing density within each puma home range. Puma home ranges were obtained using a local convex hull (LOCOH) home range estimator, where the 95% isopleth represented the home range boundary [22,23]. All housing points in the Santa Cruz Mountains were manually digitized from high-resolution satellite imagery. We calculated puma home range housing density as the number of houses per km^2. We tested for the relationship between individual puma kill rates and home range housing densities using univariate linear regression.

3. Results

(a) Behavioural shifts

Of 703 field-investigated clusters, 208 were classified as deer kill sites. The other remaining clusters included 66 non-deer

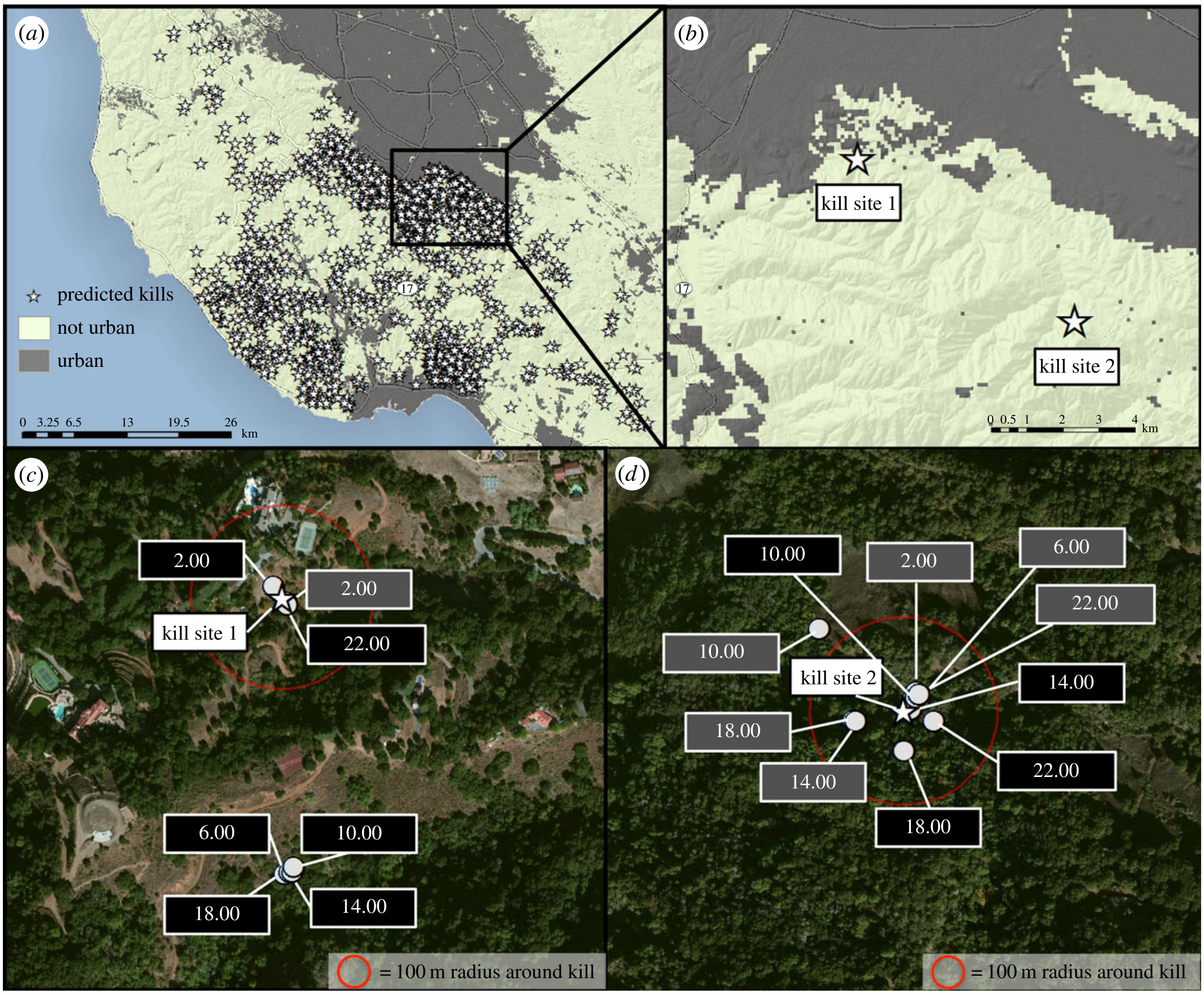

Figure 1. (*a*) Study area and predicted kill sites in relation to housing density. Box shows area (*b*) in which kill site examples (*c*,*d*) are shown. Kill site 1 (*c*) belongs to puma 13F, whose home range is in the top quartile of housing densities among female pumas. Kill site 2 (*d*) belongs to 28F, whose home range in the bottom quartile of housing densities among female pumas. Grey labels depict location times during the first day at the kill site and black labels depict location times during the second day. Note that at kill site 1, the puma has made a kill close to development but spends the majority of time away from the kill, whereas at kill site 2, which has no nearby development, the puma stays within the vicinity of the kill. (Online version in colour.)

kills (e.g. raccoons and house cats) and 429 non-kills (often bed sites). Our best-fit binomial logistic regression model to predict deer kills included NIGHT, BINARY, HMDIST, P.NIGHT and P.ACTIVE. The truncated model included NIGHT, BINARY and HMDIST. Neither the random intercept nor a random slope was included in the best-fit full model or the best-fit truncated model. We used the truncated model to predict 1537 deer kills from 8523 generated clusters (figure 1).

At predicted kill sites, females had lower P.ACTIVE ($F = 67.7, p \ll 0.001$), higher DIST ($F = 16.0, p < 0.001$) and shorter P.C.TIME ($F = 44.2, p \ll 0.001$) as housing density increased (figure 2; example shown in figure 1). In suburban habitat, female P.ACTIVE was 36% lower, DIST was 31% higher and P.C.TIME was 42% lower than in no housing areas. Both males ($F = 19.3$, $p < 0.001$) and females ($F = 144.4$, $p \ll 0.001$) were more nocturnal (higher P.NIGHT) with increasing housing density at kill sites. Males did not show any responses to housing density concerning time spent at kill sites. Identical analyses using only confirmed kills supported each of the reported trends for predicted kills.

(b) Deer kill rates

Male average home range size was 163.0 ± 7.7 s.e. km^2 with 15.6 ± 0.8 s.e. houses km^{-2}. Female average home range size was 53.8 ± 2.1 s.e. km^2 with 25.5 ± 1.3 s.e. houses km^{-2}. Males had an average deer kill rate of 43.7 deer yr^{-1}, whereas females killed on average 67.3 deer yr^{-1}. Male deer kill rates were not correlated with any of our variables of interest (P.ACTIVE, P.NIGHT, DIST, DUR or P.C.TIME), nor with home range housing density ($p = 0.9$, $r^2 = 0.005$; figure 3). Conversely, female deer kill rates showed a strong positive and linear correlation with home range housing density within its observed range ($p = 0.0003$, $r^2 = 0.745$; figure 3). Females with home ranges in the top quartile of housing density killed 36% more deer per year (81.2) than females in the bottom quartile of housing density (59.7). Female kill rates were also negatively correlated with average fidelity to kill sites (P.ACTIVE; $p = 0.05$, $r^2 = 0.322$).

4. Discussion

Our estimate of average male kill rates (43.7 kills yr^{-1}) stayed constant across housing densities and was comparable to previously reported values described by Knopff *et al.* (35 ungulates yr^{-1}, [24]) and Anderson & Lindzey (47 kills yr^{-1}, [25]). However, female kill rates increased positively, strongly and linearly with housing density. Although female kill rates in lower housing density areas (59.7 kills yr^{-1}) were

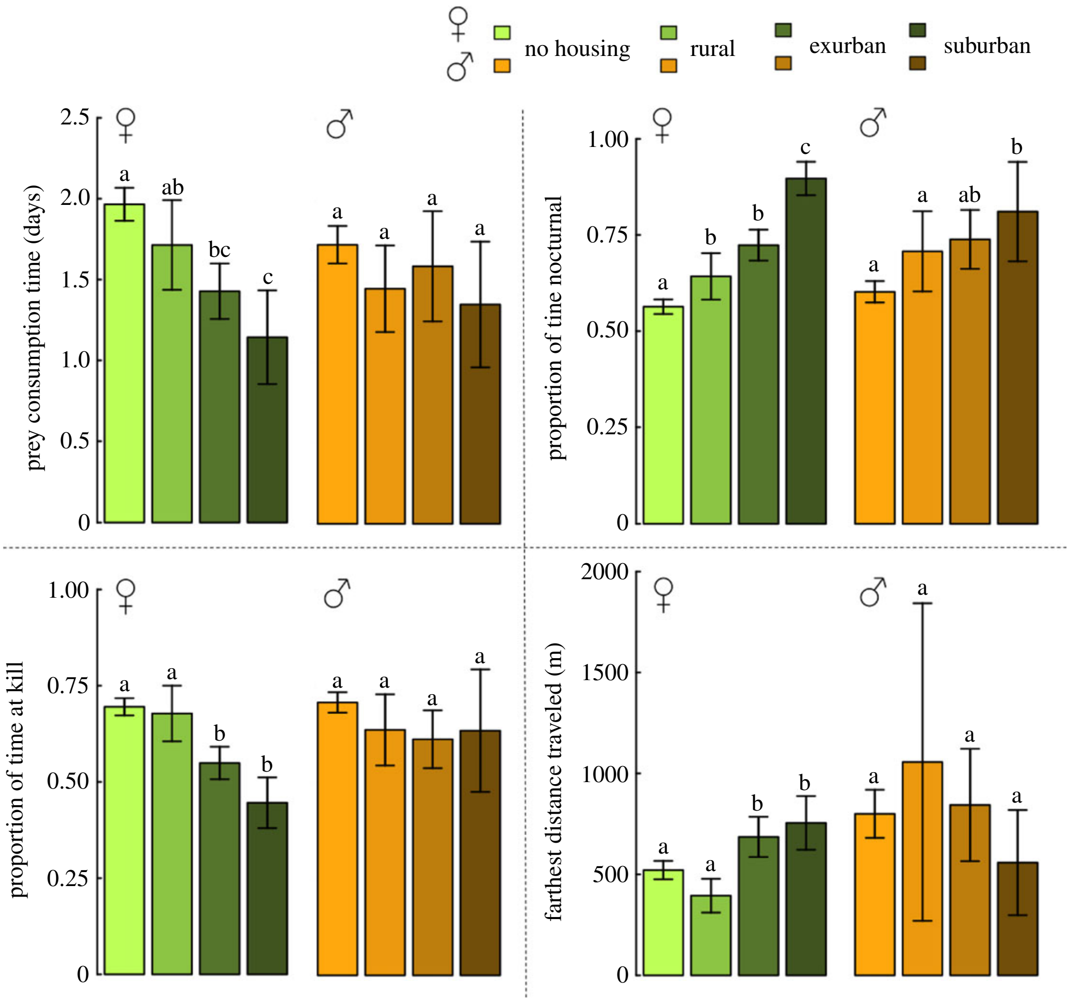

Figure 2. Behaviours that vary with housing density at predicted kill sites. Pairwise comparisons from Tukey's HSD tests reported in superscripts, where different letters represent a statistically significant difference. Error bars represent two standard errors from the mean. Sample sizes of housing classes at female kills are: no housing, 719; rural, 83; exurban, 186; suburban, 71. Sample sizes of housing classes at male kill sites are: no housing, 389; rural, 32; exurban, 42; suburban, 15. (Online version in colour.)

comparable to previously estimated mule deer kill rates for solitary adult females (52.5 kills yr^{-1}, [25]) and females with kittens (62.4 kills yr^{-1}, [26]; 68.1 kills yr^{-1}, [25]; 57.2 kills yr^{-1}, [24]), female kill rates in the highest quartile of home range housing densities were substantially higher (81.2 kills yr^{-1}). This 36% increase in kill rates between the top and bottom quartiles indicates that development may exert a significant energetic cost associated with hunting behaviour.

Hunting deer requires large energetic investments in the stalking, subduing and killing stages for pumas [16]. We have documented a sizable increase in female kill rates that we expect represents higher energetic costs for females in developed landscapes. Although these costs do not appear to influence adult survival (C. C. Wilmers 2014, unpublished data), impacts on reproductive success possibly make development-interface zones sinks for the puma population. Anecdotally, we have observed that the tagged female living in the most developed habitat in our study area has lost at least three litters in the last 3 years, one of which was confirmed as abandonment (C. C. Wilmers 2014, unpublished data). The three other females living in less developed portions of our study area for which we have also documented at least three dens have had the majority of their litters survive. Although there are many stressors in a developed landscape that might influence kitten survival, we expect that higher energetic costs from increased hunting may contribute to this pattern.

Males did not alter their kill rates or prey consumption time at kills with increasing housing density. Because male life histories are constrained by requirements to defend much larger territories [27], this is perhaps not surprising. We found that male pumas have home ranges that are approximately three times as large as female home ranges on average. Male pumas are also known to spend significantly more time performing scent-marking behaviours than females [28]. We found that males have lower DUR at kills than females by 7.2 h on average (males = 2.86 days ± 0.06 s.e., females = 2.56 days ± 0.05 s.e.; $t = 3.83$, d.f. = 1000, $p \ll 0.001$), probably owing to their need to patrol and defend their home range boundaries from encroaching males. Therefore, because males already tend to leave their kills early, they may be less influenced by chronic disturbance. In addition, male home ranges are characterized by much lower overall housing densities, indicating that males may exhibit risk-avoidance behaviours at the landscape scale rather than at the kill site scale.

Higher deer kill rates by females in response to increased housing density appear to be driven by a behavioural shift to a lower proportion of time spent at kill sites over the consumption period. Although females did not alter their total duration spent at clusters, their overall prey consumption times declined owing to a lower proportion of time spent at kills, indicating reduced utilization of carcasses at higher housing densities.

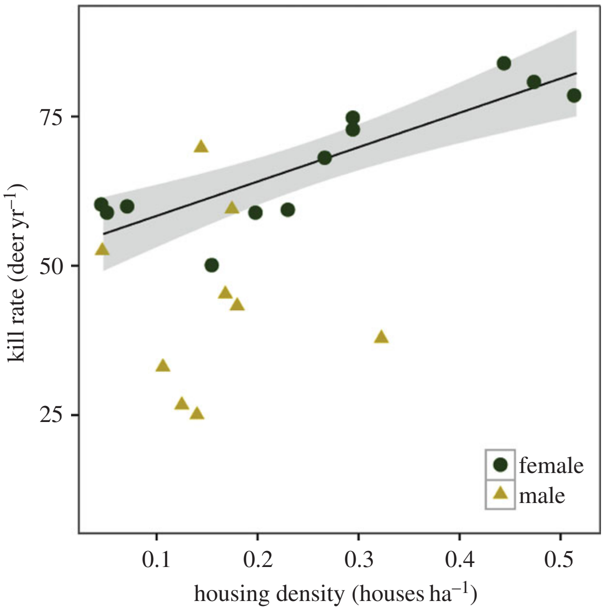

Figure 3. Kill rates of individual male and female pumas in response to housing density per hectare within their 95% LOCOH home range. Regression line and 95% CIs for female kill rates in relation to housing density are shown. Housing density coefficient $\beta_1 = 91.4$. (Online version in colour.)

Other possible explanations for female increase in deer kill rate are not supported by our understanding of puma energetics and reproduction. Deer in our study have lower detection rates in more developed habitats (C. C. Wilmers 2014, unpublished data), therefore variation in deer activity or abundance is unlikely to explain these patterns. In addition, it is unlikely that increased kill rate could be a result of greater reproductive activity in high housing density areas because females in our study area avoid anthropogenic development when denning [10]. We conclude that behavioural risk avoidance is a substantial contributor to female prey consumption time and hence hunting patterns, due to our observation that housing density is associated with decreased prey consumption time. Both food loss and increased movement as a result of these behavioural shifts may contribute to observed increased kill rate in human-modified habitats.

An increase in ungulate carcasses left by female pumas may impact the biotic community by providing additional carrion subsidies to scavengers. By leaving their kills for longer periods of time in more developed areas, female pumas might create greater opportunity for scavenging by mesopredators and birds. Subordinate predators often scavenge kills of apex predators when kills are abandoned or not guarded [29], and carrion can form a large proportion of their diets [30]. Pumas are known to be important sources of food subsidies to mesopredators through carcass abandonment [31]. Our results suggest that mesopredator release may occur not only through the well-documented pathway of apex predator extirpations, but also via behaviour changes in extant apex predators leading to increased food provisioning. The presence of scavengers can exacerbate this pattern by reducing apex predator prey consumption time via food loss [17].

5. Conclusion

The results presented here have bearing on human-modified systems globally. Behavioural responses are often overlooked as ecosystem drivers in modified systems, overshadowed by population declines and extirpations. However, many species are able to persist in developing landscapes, but in an altered behavioural state. Our findings suggest a strong, perceivable impact of observed human-induced behavioural change on species interactions instigated by the presence of development. Risk aversion behaviours that result from anthropogenic disturbances are likely to restructure predator–prey interactions in a variety of contexts, given the large effects risk has been shown to have on foraging across taxa. Behaviour-mediated interactions are powerful forces in biotic systems, often playing an even more impactful role than consumptive interactions. A greater focus on behaviour-mediated effects of habitat alteration can further expand our understanding of community-level processes in human-modified systems.

Ethics statement. The study was carried out under the IACUC approval no. WILMC1011.

Data accessibility. Because pumas are a specially protected species in California, the location data are sensitive and have not been made accessible. However, the data can be available on request by contacting Justine A. Smith at jsmith5@ucsc.edu.

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Author contributions. J.A.S. conceived the study, carried out the data analysis and drafted the manuscript. Y.W. assisted in project development and edited the manuscript. C.C.W. conceived and designed the overall study, supervised data collection, advised on data analysis and edited the manuscript.

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Conflict of interests. We have no competing interests.

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Fear of the human 'super predator' reduces feeding time in large carnivores

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Large carnivores' fear of the human 'super predator' has the potential to alter their feeding behaviour and result in human-induced trophic cascades. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and react strongly enough to have cascading effects on their prey. We conducted a predator playback experiment exposing pumas to predator (human) and non-predator control (frog) sounds at puma feeding sites to measure immediate fear responses to humans and the subsequent impacts on feeding. We found that pumas fled more frequently, took longer to return, and reduced their overall feeding time by more than half in response to hearing the human 'super predator'. Combined with our previous work showing higher kill rates of deer in more urbanized landscapes, this study reveals that fear is the mechanism driving an ecological cascade from humans to increased puma predation on deer. By demonstrating that the fear of humans can cause a strong reduction in feeding by pumas, our results support that non-consumptive forms of human disturbance may alter the ecological role of large carnivores.

1. Introduction

Humans have assumed the role of 'super predator' in animal communities globally, killing terrestrial carnivores at rates as much as nine times higher than their natural predators [1]. In addition to directly killing large carnivores, humans might also elicit fear responses in these species as they do in other wildlife taxa that experience human-caused mortality [2,3]. Indeed, correlative evidence of human-induced changes in large carnivore space use and movement suggests that fear of humans is a common phenomenon among top predators [4–8]. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and whether changes in large carnivore behaviour caused by fear of humans affects ecological communities.

It is increasingly recognized that, even in the absence of direct mortality, fear of predators can itself drive cascading changes across food webs [9,10]. Human-induced fear in large carnivores is likely to have similar cascading effects because of the well-documented top-down effects of large carnivores on their prey and competitors [11–13]. However, different outcomes of human-induced fear in carnivores on prey populations might be expected depending on the nature of the carnivore response. One potential outcome of large carnivore fear of humans is the human shield effect, whereby prey find refuge in human-dominated habitats and are released from top-down forces because carnivores spatially avoid human disturbance [14,15]. However, human disturbance could have the opposite effect on the regulatory role of large carnivores if carnivores persist in human-dominated habitat by instead avoiding humans temporally. This counterintuitive response may actually increase predation pressure on prey by altering carnivore hunting behaviour to accommodate an enhanced risk–foraging trade-off; temporal avoidance could lead to reduced total feeding

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time at a kill, which would require increased kill rates to compensate for lost energetic return from each kill. As land is increasingly transformed by anthropogenic development, quantifying how the fear of humans affects interactions between large carnivores and their prey is essential to understanding novel ecological dynamics emerging in human-dominated landscapes [7,11,16].

We previously reported that pumas (*Puma concolor*) in the Santa Cruz Mountains of Central California spent less time at kill sites in more residential areas and increased kill rates of prey [5]. This increased kill rate could potentially be explained by altered prey communities in human-dominated habitats (either from a perceived human shield or access to anthropogenic food subsidies) leading to more vulnerable [17] or available [18] prey. However, if reduced time at kill sites near residential development is fear-induced, it could also result in increased kill rates to compensate for reduced energy gained per individual predation event. Here, we experimentally test whether pumas exhibit fear responses to the human 'super predator' and whether changes in puma feeding behaviour in response to human-induced fear can explain our previously reported differences in puma feeding time and kill rate between areas of high and low human presence in the Santa Cruz Mountains [5]. To our knowledge this is the first direct experimental test of whether large carnivores respond fearfully to human presence, and whether this response has measurable ecological consequences.

To test the relationship between fear of humans and feeding behaviour, we executed a playback experiment on wild pumas. Predator playback experiments have been used to substantiate fundamental ecological relationships [19], including that the fear of predation reduces reproductive success in birds [20], that fear can have cascading impacts on animal communities [10], and that mesocarnivores exhibit heightened fear responses to human 'super predators' relative to non-human predators [3]. However, no study has linked the fear of humans to feeding behaviour in large carnivores. Our study builds on protocols used in over 200 predator playback experiments [19]. Hearing a predator vocalization signals to prey the direct presence of the predator in relatively close proximity, which is why simulating this using audio predator playbacks provides such a powerful means of directly testing fear responses [3,19,21]. Previous experiments have established that prey hunted by the human 'super predator' react to human vocalizations just as prey react to the vocalizations of any other predator [3], demonstrating that assessing responses to human vocalizations provides the means to directly test the prey's perception of humans *as* predators, rather than humans as simply a source of noise and disturbance (*sensu* [4]). Our experimental approach correspondingly allows us to make direct inferences concerning fear of the human 'super predator' and the resulting consequences of anthropogenic disturbance on risk–foraging trade-offs in a large carnivore. Combined with our previous work [5] our study reveals an ecological cascade from humans to increased predation on deer mediated by fear.

2. Methods

Our experiment was part of a long-term study on puma ecology in the Santa Cruz Mountains of Central California, USA [5,6]. The region has a Mediterranean climate characterized by a rainy season in winter and dry season in summer. Habitat types include mixed hardwood forest, redwood forest, chaparral and grassland. The Santa Cruz Mountains are heavily impacted by human use, particularly residential development and outdoor recreation. Puma exposure to humans here is thus commonplace; all pumas in this study have housing developments in their home range (mean: 21.7 houses km^{-2}) and kill and cache prey as close to 5 m from people's homes [5]. Pumas have a good reason to be fearful of humans in this region, as they were bounty hunted in California for decades and even today humans are their primary source of mortality in the Santa Cruz Mountains (Wilmers unpublished data).

We conducted a playback experiment on pumas at their active kill sites. We first located puma kill sites from recent GPS tracks of collared individuals (IACUC no. WILMC1011). We downloaded recent GPS locations successfully transmitted through GSM or Iridium technologies and identified potential fresh kill sites as clusters of locations within 100 m of one another that occurred between sunset and sunrise. We field-investigated potential kill sites that were no more than 3 days old and at which the puma was present the previous night. If a fresh kill was found, we tied the carcass down so it could not be dragged out of the view of our cameras. Any behavioural effects of tying down the carcass were experienced for both control and experimental playback treatments, therefore baseline disturbance levels should not influence the relative difference in response between treatments.

To test whether pumas fear humans and quantify the cost of this fear, we broadcast predator (human) or non-predator (Pacific tree frog, *Pseudacris regilla*) playbacks at puma kill sites following well-established experimental methods [10,19,20]. Tree frog vocalizations provide an ideal control – like humans, tree frogs occur throughout the study area, but unlike humans they are neither predators, prey, nor competitors of pumas, and thus represent an equally familiar but benign stimulus. Tree frog vocalizations further provide an ideal control because they may naturally be heard both night and day, whenever pumas are active. Controls in other playback studies testing for fear responses in wildlife include running water (study organism: moose; [22]), seals (study organism: raccoon; [10]), sheep (study organism: European badger; [3]) and assorted non-threatening birds (study organism: song sparrow; [20]).

We recorded puma responses to playbacks using an Automated Behavioral Response (ABR) system (i.e. video-enabled camera trap linked to a playback unit triggered by the camera's activation) [21]. We deployed the playback speaker 400–450 cm from the centre of the carcass. Videos were 30 s long, the playback being broadcast for 10 s in the middle of the video. If the puma repeatedly triggered the camera it could hear the playback as often as twice per minute. We used seven exemplars of each playback type [23], the human exemplars all consisting of a single individual speaking conversationally. We edited all exemplars for consistency in amplitude and quality using Audacity® (v. 2.1.0, Audacity Team 2014), and broadcast the playbacks at a consistent peak sound pressure level of 80 dB at 1 m (measured using Radioshack 33-2055 Digital Sound Level Meter set to fast response and C weighting). This volume was chosen to mimic the natural volume of human conversation. Using these exemplars we composed 30 min playlists of each treatment. The playlists alternated between frogs and humans every 30 min; which treatment the puma heard first being determined by when it triggered the camera, and was thus effectively random. An individual puma might be exposed to either or both treatments over 24 h, depending upon its reaction. For pumas that heard both treatments, there was no significant difference in the proportion of each treatment first heard ($Z = 1.63$, $p = 0.103$). Pumas were exposed to each treatment only once over the course of the study.

We tested for the fear response of pumas and its ecological cost as follows: (i) We examined the puma's initial response to

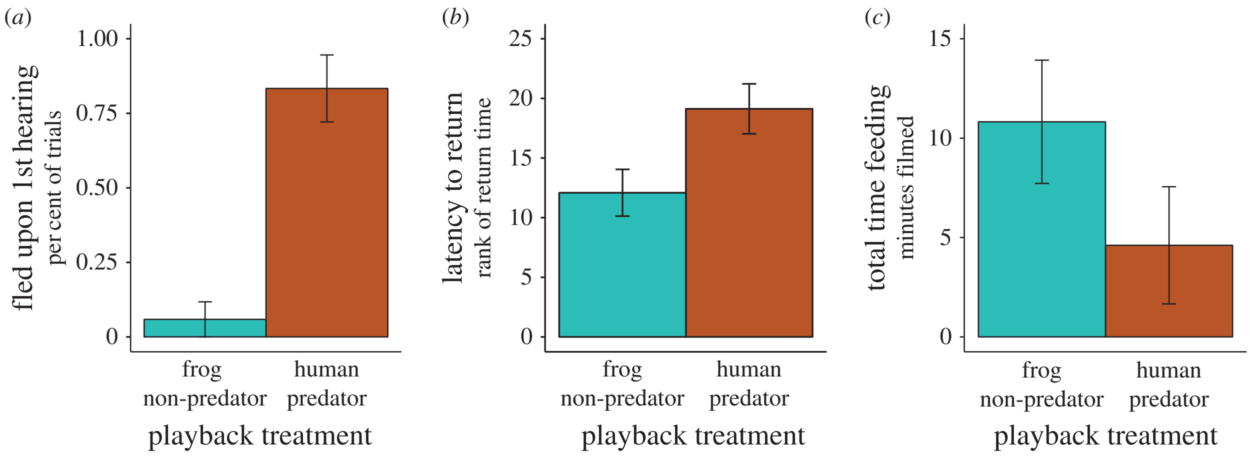

Figure 1. Responses of pumas to predator (human) and non-predator (frog) playbacks at puma feeding sites. (*a*) Proportion of pumas that fled following their first exposure to frog or human playbacks. (*b*) Latency in time to return (rank) after initial payback exposure. (*c*) Total time spent feeding during the first 24 h of playback treatment. Bars represent standard error. Although transformation of feeding data was required to meet normalization assumptions for our analysis, here we show mean and standard error of raw feeding time measures for purposes of visualization. (Online version in colour.)

the playbacks by quantifying whether the puma fled (ran away) upon first hearing a treatment. We tested for significant differences in fleeing using Fisher's exact test. (ii) We assessed recovery time following puma initial exposure to each playback as the time difference between their first exposure to a playback treatment and the next video in which they subsequently appeared (hereafter, 'latency to return time'). We ranked the latency to return time for each trial, assigning the highest rank to individuals who did not return. We tested for a treatment effect by applying a Mann–Whitney *U* test to the ranked return times. Some pumas were exposed to both treatments enabling us to additionally test these two responses (fleeing and latency) using repeated-measures Wilcoxon matched pairs tests, which provided qualitatively the same answers, reinforcing the robustness of the results. Because there is no qualitative difference, but these repeated-measure tests do necessitate excluding some individuals, we report the results of the between-group comparisons to best reflect the full dataset. (iii) We measured the aggregate effect of hearing a playback treatment on feeding time by calculating the total time a puma was observed feeding during each treatment over the course of 24 h. We Box-Cox transformed these data to meet normality assumptions and tested for differences using ANOVA. Again, because some pumas were exposed to both treatments, we began by including individual identity as a random effect in the feeding analysis (the only parametric test), but because this did not explain any additional variation we removed it from the model and accordingly report results from the univariate (predator versus non-predator) fixed effects model.

3. Results

We successfully conducted 29 experimental trials on 17 pumas. All 17 heard non-predator (frog) playbacks and 12 were exposed to both predator (human) and non-predator (frog) playbacks. Pumas fled in the majority of cases (83%) upon first hearing humans and only once upon first hearing frogs (6%; figure 1*a*; Fisher's exact $p < 0.001$). The latency to return time after pumas first heard a treatment was significantly greater in response to human playbacks (figure 1*b*; M-W $U_{12,17} = 151.5$, $p = 0.028$) because pumas returned to the carcass less often following their first hearing of a human playback (42% of trials) than following their first hearing of a non-predator (frog) playback (18%), or if they did return, they took longer to do so after first hearing humans (median = 20 min, range = 0–257) than after first hearing frogs (median = 2 min, range = 0–40). Feeding time was significantly less for the human treatment than the non-predator (frog) treatment ($F_{1,27} = 5.74$, $p = 0.024$; figure 1*c*). Over the course of 24 h, pumas fed for less than half as long when exposed to humans (4.6 ± 2.9 SE min; median = 0.03 min) as when exposed to frogs (10.4 ± 3.1 SE min; median = 4.5 min).

4. Discussion

Our results experimentally demonstrate that fear of the human 'super predator' induces substantial behavioural changes in pumas, ultimately leading to significant reductions in time spent feeding. We observed almost unanimous fleeing behaviour in response to the human playback treatment, directly tying a strong fear response to subsequent declines in feeding. Our previous work showed that pumas nearly halve their feeding time of deer in suburban areas compared to areas with less housing [5]. The halving of feeding time during human trials compared to non-predator trials that we observed in this study suggests that this difference in puma behaviour at kills based on nearby housing densities can be fully accounted for by fear, and that this consequently causes pumas to increase their kill rates by 36% [5]. In a previous study we found that deer occupancy was not influenced by housing density, therefore it is unlikely that relative deer availability explains observed changes in kill rate [18]. Our results support the conclusion that increased kill rates in residential areas are driven by a top-down mechanism (fear of humans), rather than a bottom-up mechanism (availability of prey). Thus, non-consumptive forms of human disturbance may alter the ecological role of large carnivores by affecting the link between these top predators and their prey.

Prey generally respond to both direct (e.g. predator vocalizations) and indirect (e.g. moonlight or cover) cues of predation risk, and the strength of their response depends upon both the nature and number of cues. A single direct cue typically induces a stronger response than a single indirect cue, but multiple indirect cues may induce an equivalent or even stronger response than a single direct one [24–26]. Our experiment demonstrates that pumas respond fearfully to a direct cue indicative of the immediate presence of the human 'super predator' (i.e. hearing human vocalizations). In human-dominated landscapes, pumas are exposed to multiple indirect cues indicative of the presence of the human 'super predator' (e.g. anthropogenic lighting, sounds of vehicles and dogs), and our previous work shows that pumas respond to these indirect cues [5,6,18]. Our purpose in testing the responses of pumas to human vocalizations was to evaluate the perception of humans *as* predator, as explained above. In the present study, exposure to a single direct cue (hearing human vocalizations) had the same magnitude of effect on feeding time as did cumulative indirect (e.g. lighting, vehicles) and less direct (e.g. hearing humans at a distance) cues [5], as might be expected in the response of any prey to any predator. Fear-induced trophic cascades are not caused by responses to a specific cue, but by prey responding to any and every cue signalling the presence of the predator it fears [9,10,25].

Our results are consistent with theoretical predictions made from other playback experiments that have demonstrated the ability for humans to cause fear responses in wildlife [3] and for fear responses in carnivores to cascade to lower trophic levels [10]. We have combined these concepts in context of large carnivores due to their important regulatory role and susceptibility to disproportionately high mortality rates via the human 'super predator' [1]. Our results show that large carnivores are not exempt from human-induced fear, and that human impacts on their feeding behaviour might have surprising cascading effects.

In this study, we implemented a novel ABR playback experiment [21] to quantify a large carnivore's behavioural response to humans. Such direct testing of human disturbance has not previously been done on a large carnivore due to the challenge of observing these animals in the wild. Our use of recent puma kill sites accompanied by the integrated ABR technology allowed us to make inferences on humans as a driver of risk–foraging trade-offs in a large carnivore. Similar methods could be executed on other elusive species to investigate a diversity of risk responses to invasive predators, extirpated predators or competing predators.

Overlap between large carnivores and humans is increasing in regions where continued agricultural and residential development coincides with the recovery of large carnivore populations [27,28]. Although the coadaptation of humans and carnivores can lead to coexistence in human-dominated landscapes [29], carnivore behavioural adaptations might result in unintended indirect effects on other species [11]. Our work suggests that fear-induced trophic cascades instigated by the human 'super predator' are likely to contribute to altered ecological dynamics in human-dominated landscapes. As the habitats used by wildlife and humans are increasingly shared, additional work is needed on the extent to which fear in top predators cascades through ecosystems.

Data accessibility. Data have been made available in the Dryad data repository: http://dx.doi.org/10.5061/dryad.6pn0b [30].

Authors' contributions. J.A.S., M.C., C.C.W. and L.Y.Z. conceived of; J.A.S., J.P.S., M.C., C.C.W. and L.Y.Z. designed; and J.A.S., A.C. and C.C.W. conducted the study. J.A.S., M.C., A.C. and D.R. processed and analysed data. J.A.S. wrote the manuscript, with help from J.P.S., M.C., L.Y.Z. and C.C.W. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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Urban–wildland fires: how California and other regions of the US can learn from Australia

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Abstract

Most urban–wildland interface (UWI) fires in California and the other regions of the US are managed in a similar fashion: fire agencies anticipate the spread of fire, mandatory evacuations are ordered, and professional fire services move in and attempt to suppress the fires. This approach has not reduced building losses in California. Conversely, losses and the associated suite of environmental impacts, including reduced air quality, have dramatically increased over the last three decades. In contrast to California, Australia has developed a more effective ‘Prepare, stay and defend, or leave early’ policy. Using this approach, trained residents decide whether they will stay and actively defend their well-prepared property or leave early before a fire threatens them. Australian strategies have the distinct advantage of engaging and preparing those most affected by such fires: homeowners. Investing more in fire suppression alone, the common response after large UWI fires in California, will not reduce losses. US society has attempted to accommodate many of the natural hazards inherent to the landscapes that we inhabit; by examining the Australian model, we may approach a more sustainable coexistence with fire as well. However, it should be noted that some California communities are so vulnerable that a ‘Prepare and leave early’ strategy may be the only option.

Keywords: fire policy, fire management, wildland urban interface, wildfire, land use planning

1. Introduction

Wildfires in the urban–wildland interface (UWI) continue to devastate communities in California (figure 1) and across the US. Despite known risks, people continue to move into wildfire-prone areas at high rates. The issue is particularly acute in California where a recent analysis indicated that over five million homes are located in the UWI (Radeloff *et al* 2005, Theobald and Romme 2007). This number is the highest in the US, and is expected to increase further as urban dwellers seek the ‘natural amenities’—e.g., open space and recreational opportunities—provided by wildland areas. Similar trends elsewhere in the world are exacerbated by long-term economic conditions, such as the declining value of rural commodities, which result in land being of greater value for housing than for other uses.

Responses after large UWI fires in California have been consistent and largely focused on the procurement of additional

Figure 1. Santiago Canyon Fire in Foothill Ranch, Orange County, California (October 2007). Courtesy of Alex Miroshnichenko (Miro-Foto).

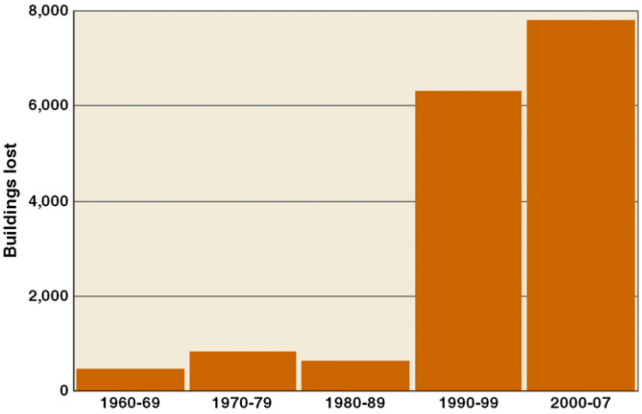

Figure 2. Number of buildings lost from the 25 most destructive UWI fires in California history from 1960–2007.

fire suppression resources, particularly at the state level. The common argument presented is: 'if we had more fire engines, aircraft, and fire fighters then we could have prevented this catastrophic loss of homes'. While fire suppression is a critical component of fire management in the UWI, it alone will not reduce the losses of life and property. A new approach is needed, and that is the goal of our joint examination of the problem by both American and Australian scientists. In a novel collaboration, we present ideas that could be used to fundamentally change fire management in the UWI across the US. Such a new approach must also be examined critically, since it should neither encourage further fragmentation of natural landscapes nor give a false sense of safety to those in the most vulnerable situations.

2. The need for a new approach

As a society we have attempted to accommodate some of the natural hazards inherent to the landscapes that we inhabit. For example, buildings in earthquake-prone areas are designed to withstand events of a given magnitude. Building on floodplains is typically restricted, and land-use planners are familiar with the concept of the 100- or 250-year flood event. In California and the rest of the US we have yet to adopt this line of thinking for fires—instead we focus much more on *fighting* fire than on coexisting with it.

Fuels, topography, and weather determine the level of fire hazard in any given area (Agee and Skinner 2005). Most of California experiences annual summer drought, and there are many different local patterns of fire weather. Some of the most extreme fire weather conditions, however, are generated by 'Santa Ana' winds in southern California (Schroeder *et al* 1964). These foehn winds—generated as air moves downward from a higher elevation—cause hot, dry, and very strong winds for days at a time. When these episodes coincide with dry fuels in autumn, fires can become very large and are unconstrained by the age and spatial patterns of shrubland fuels (Moritz *et al* 2004), pushing fires into the UWI (figure 1). Extreme fire weather can also occur in south east Australia as demonstrated by the 1983, 2003, and 2009 bushfires.

There is a strong link between fire activity and population patterns throughout California and humans are the dominant source of ignitions for UWI fires (Syphard *et al* 2007). Because substantial population increases are projected in coming decades, the problem of human ignitions will only get worse. In addition, some of the largest fires in California and Australia are often those intentionally set by arsonists, who target the worst conditions and most vulnerable locations. The majority of Californian and Australian ecosystems are fire adapted and altered fire regimes have been a negative influence on their sustainability (Pyne 1991, Sugihara *et al* 2006, Stephens *et al* 2007) further confounding management of the UWI and surrounding wildlands (Dombeck *et al* 2004, Donovan and Brown 2007).

Collaborative research between Australia and California on the performance of construction materials and landscaping during wildfires, quantification of fire hazard and risk in changing climates, effectiveness of fuels treatments, and policy development would enable both countries to advance more quickly in developing sustainable UWI areas.

3. Current UWI fire management in California

Most UWI fires in California and other regions in the US are managed in a similar fashion. Fire agencies first attempt to anticipate the spread of the fire, and mandatory evacuations are ordered. With the public evacuated, professional fire services move in and attempt to suppress the fires. This approach has not reduced building losses from UWI fires in California. Instead, losses have dramatically increased over the last three decades (figure 2). Mandatory evacuations may save lives if implemented well before the time a wildfire arrives to a particular location. However, evacuations at the last minute, when people may be overrun by fast-moving fires, create the most deadly periods in UWI fires (Gill 2005, Handmer and Tibbits 2005). Some people pack their cars with possessions and then procrastinate or wait until the wildfire is in close proximity before leaving, this can be very dangerous.

UWI fire policy in California and other regions of the US has developed piecemeal. Historically, large-scale urban conflagrations were the result of structure-to-structure fires, fueled by wood buildings. These types of urban fires, where hundreds of buildings are lost, are uncommon now because urban areas contain fewer wood buildings and most buildings include a multitude of features such as fire alarms, fire-resistant walls, and sprinklers.

As the recent 2007 and 2008 fires in southern California have demonstrated, we still have a long way to go in reducing similar losses in UWI fires (Mutch 2007, Paveglio *et al* 2008). As homes continue to be built in flammable wildland areas, the Californian approach to building has yet to catch up to the types of hazards faced by homeowners (CFRO 2005). For example, it is evident that most homes ignite in UWI fires (figure 1) due to embers that can travel over 1–2 km. At a minimum, therefore, vents that resist ember entry into attics and fire-resistant roofing and other building materials are key. While there is good evidence as to the efficacy of this type of 'fire safe' approach to building and maintaining homes (Cohen 2000, Blanchi and Leonard 2008), it has remained largely unregulated in the US.

4. What California can do reduces losses in the UWI

4.1. UWI building codes

In California, enforcement of new building codes that include ignition-resistant construction standards only began in early 2008 (CBC 2007). These codes will apply only to new buildings in very high hazard UWI areas and areas where the state has financial responsibility for fire protection. Local jurisdictions will have the ability to accept or reject their zoning designation, thereby influencing where stricter building codes apply. While we believe that this new policy is a step forward, much more needs to be done.

Out of necessity, revised building codes are a compromise between science, policy, and economic interests. Even so, a more rigorous and objective approach to assessing structure vulnerabilities is needed, so that each revision to UWI standards and policies is based on the best scientific analysis possible. All UWI policies should be reviewed and updated as new information becomes available.

4.2. Land-use planning

Large portions of California's 58 counties are under local land-use planning control, and several jurisdictions have adopted local ordinances to mandate defensible space and fire-resistant materials in home construction in the UWI (e.g. Ventura and Los Angeles counties). Most local jurisdictions, however, have employed a variety of standards over the years, changing requirements as priorities and economic conditions change. The resulting mixture of different aged housing stock—and thus structural vulnerabilities—makes long-term standardized solutions problematic. The continued expansion of the UWI and fragmentation of fire-prone wildlands is also directly related to increases in the number of ignitions. Importantly, the UWI poses a series of additional environmental challenges, including ecosystem fragmentation, increased exposure to invasive species, and water and air pollution (Alavalapati *et al* 2005).

Alternative policies and/or regulatory approaches aimed at reducing the inconsistencies in local land-use planning should be implemented. For example, one approach would be to move some local, land-use planning authority to the state level. This would mean in reference to fire in the UWI, any new development would have to be reviewed by a state level, land-use planning agency. This standardized review would include both materials used in construction, construction methods, and land-use planning objectives, based on a strategic plan to protect the many public assets that fire affects. This type of comprehensive planning may be especially important in the face of climate change (Moritz and Stephens 2008), an issue that links fire, development patterns, and ecosystem services in broader context.

As a model, in the state of New South Wales in Australia, the Rural Fire Service performs a similar service (albeit at a sub-division level rather than the level of individual houses). In 1997 the Rural Fire Act was passed in New South Wales and this consolidated 142 separate fire municipalities into one organization with similar standards; in 2002 this act was amended to incorporate the review of new housing construction in all wildlands. Such a strategy has advantages because one set of UWI standards is applied to the whole state, and each review includes a mandatory fire perspective. This approach has the best chance of success if planning and building provisions are combined into a holistic process.

4.3. Fire suppression

The costs of fire suppression continue to rise at both federal and state levels in the US (Stephens and Ruth 2005). A large proportion of 'fire' budgets are focused solely on fire suppression with more limited funds for the reduction of hazardous fuels and public education (Steelman and Burke 2007). However, a recent study by the Natural Resources Defense Council reported an average cost of only $2510/home to make the needed improvements (e.g., vent screening and enclosing open eaves to prevent ember intrusion) to create more fire-resistant homes in a community in the Sierra Nevada foothills (Mall and Matzner 2007). Even if subsidized by state or local governments, or insurance companies, these costs are substantively lower than the losses incurred in massive UWI fires.

4.4. Insurance issues

With the numbers of structures lost in California wildfires, many homeowners now risk losing, or never being able to obtain, fire insurance. Although the State of California has developed a program to offer insurance to those homeowners unable to obtain private insurance, the price is higher, and it is not available everywhere it is needed. Regardless, insurers could play a much larger role in providing incentives to homeowners to reduce structure-based wildfire hazards, and therefore losses. However, an insurance-based approach cannot fully solve the UWI fire challenge because a home-based policy disregards non-monetary goods and services (uninsured personal property, recreation, aesthetics) (Talberth *et al* 2006).

In New South Wales and Victoria, Australia, significant components (approximately 17%) of private fire insurance premiums paid by individuals are used in fire mitigation practices. These resources are used to fund rural fire services, neighborhood community groups regarding fire, and public outreach and education (Henri 2003). Connecting fire insurance companies to UWI homeowners can increase incentives to reduce the vulnerability of homes through the marketplace (i.e. lower premiums for houses that resist ember attack, have access to water supplies, include multiple access/egress opportunities).

5. The Australian policy

The 'Stay or Go'—or more accurately 'Prepare, stay and defend, or leave early'—approach has recently been endorsed by all Australian fire services, as well as by most police forces (AFAC 2005); there is a similar approach in southern France although this is not based on a national policy.

The Australian position is that all residents should prepare their property against fire and decide whether to stay and actively defend their property or leave early before a fire threatens the area and road travel becomes dangerous. If they decide to stay, they are advised to prepare their property through vegetation (fuel) management, undertaking house protection measures, and ensuring they have the resources, both physical and psychological, to actively defend their property. The approach does not entail or encourage people to passively 'shelter in place' which is dangerous (Gill 2005). The common American usage of the phrase 'shelter in place' in the context of fire implies a much more passive response than what the Australian policy requires.

There is considerable evidence that well-prepared houses can provide a safe place for people during wildfires, based on the key assumption that a fire front passes quickly and that houses can survive this period and protect occupants from radiant heat, smoke and embers. This is well supported by research on how houses ignite and are destroyed largely through ember attack (Cohen 2000, Blanchi and Leonard 2008). Risk from embers can be reduced by advance preparation, such that when small fires are ignited by embers, they can be extinguished if residents are present and prepared, and actively defending their property.

No option is risk free, but evidence suggests that the most common avoidable cause of death is being caught outside of a structure as the fire front passes with its lethal radiant heat and smoke. Fleeing at the last minute often involves driving or running through flames, ember storms, and intense heat and smoke, with accompanying disorientation and poor visibility. This is the most dangerous option.

Evidence from Australia has come from oral histories, documented practice by fire agencies and those at risk, post-fire public inquiries, scientific publications, and a fatality data-base (Handmer and Tibbits 2005, Gill 2005, Handmer and Haynes 2008, Leicester and Handmer 2008). Most of this material deals with extreme fires—the worst Australian fires in the last 70 years—and their findings indicate:

- *Evidence supports current Australian practice*. The most risky thing to do, and the cause of most fatalities, is to leave at the last moment as the fire front arrives and when roads may be blocked by smoke, electrical power lines, stalled cars, and burning debris.
- Building research confirms that *embers ignite houses* and these fires can be put out by vigilant trained homeowners.
- The critical factor in *building survival is the presence of people.*
- There is *no legal impediment*, but there are some gaps such as some Australian police agencies ordering mandatory evacuations during UWI fires at the same time as fire services want prepared people to stay (Tibbits and Whittaker 2007).
- There are *many implementation issues* to do with information provision, expectations that fire agencies will be at every house, belief that houses explode in fires, confidence, commitment, and high risk decisions. This therefore requires a strong and sustained commitment to public education and outreach.

In Victoria, Australia, the 'Operation Fireguard' program attempts to educate all communities at risk to wildfire attack (CFA 2004, 2007). Training courses are held every year preceding the onset of the fire season, and there are numerous newspaper articles on both preparation and action plans. All residents are exhorted to prepare an 'action plan' prior to the start of the fire season. Within this action plan they select whether they will choose the 'stay and defend' option or the 'leave early' option. The 'Prepare, stay and defend, or leave early' strategy has frequently worked well in Australia, but experience shows that for this to happen all critical components of this strategy must be in place, particularly (a) the effective education of the community, (b) the psychological, infrastructure, landscaping, and equipment preparation of those who plan to stay and (c) an effective early warning system to communicate to those living in the UWI.

6. People living in the UWI: a potential resource regarding wildfire

The Australian approach to UWI fire management has the distinct advantage of engaging those most affected by such fires: homeowners. Homeowners that prepare for inevitable UWI fires can be a positive resource in fire management, instead of simply people to be evacuated, as in the California case. It is recognized that some UWI communities are dominated by vacation homes that are only occupied a few weeks each year. The Australia UWI policy would not directly apply in these areas because of the general absence of people.

In both the US and Australia, most new residents in the UWI have arrived there from cities and have little experience of natural hazards such as fire (Pyne 1991, Moritz and Stephens 2008). This is all the more reason for engagement. By engaging and training those potentially affected by UWI fires, losses could be reduced in California and other regions of the US. However, it is not clear if factors unique to some California UWI communities might make it impossible to implement a policy similar to that in Australia. There may be some regions where the local climate, topography, and infrastructure may render a ‘Prepare, stay and defend or leave early’ option to be inadvisable. In these locations, a focus on preparing your property to resist ignitions and leaving early may be the only viable option. UWI areas surrounded by crown fire adapted ecosystems such as chaparral or mountain ash (*Eucalyptus regnans*) forests could be particularly hazardous.

Investing solely in more resources for fire suppression in an attempt to reduce losses from California UWI fires is not justified. There will never be enough suppression resources alone to reduce losses with an ever-expanding UWI. Part of the solution is a more sustainably designed and built UWI, inhabited by informed and prepared homeowners.

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HUMAN INFLUENCE ON CALIFORNIA FIRE REGIMES

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Abstract. Periodic wildfire maintains the integrity and species composition of many ecosystems, including the mediterranean-climate shrublands of California. However, human activities alter natural fire regimes, which can lead to cascading ecological effects. Increased human ignitions at the wildland–urban interface (WUI) have recently gained attention, but fire activity and risk are typically estimated using only biophysical variables. Our goal was to determine how humans influence fire in California and to examine whether this influence was linear, by relating contemporary (2000) and historic (1960–2000) fire data to both human and biophysical variables. Data for the human variables included fine-resolution maps of the WUI produced using housing density and land cover data. Interface WUI, where development abuts wildland vegetation, was differentiated from intermix WUI, where development intermingles with wildland vegetation. Additional explanatory variables included distance to WUI, population density, road density, vegetation type, and ecoregion. All data were summarized at the county level and analyzed using bivariate and multiple regression methods. We found highly significant relationships between humans and fire on the contemporary landscape, and our models explained fire frequency ($R^2 = 0.72$) better than area burned ($R^2 = 0.50$). Population density, intermix WUI, and distance to WUI explained the most variability in fire frequency, suggesting that the spatial pattern of development may be an important variable to consider when estimating fire risk. We found nonlinear effects such that fire frequency and area burned were highest at intermediate levels of human activity, but declined beyond certain thresholds. Human activities also explained change in fire frequency and area burned (1960–2000), but our models had greater explanatory power during the years 1960–1980, when there was more dramatic change in fire frequency. Understanding wildfire as a function of the spatial arrangement of ignitions and fuels on the landscape, in addition to nonlinear relationships, will be important to fire managers and conservation planners because fire risk may be related to specific levels of housing density that can be accounted for in land use planning. With more fires occurring in close proximity to human infrastructure, there may also be devastating ecological impacts if development continues to grow farther into wildland vegetation.

Key words: California, USA; fire; fire history; housing density; nonlinear effects; regression; wildland–urban interface.

Introduction

Fire is a natural process in many biomes and has played an important role shaping the ecology and evolution of species (Pyne et al. 1996, Bond and Keeley 2005). Periodic wildfire maintains the integrity and species composition of many ecosystems, particularly those in which taxa have developed strategic adaptations to fire (Pyne et al. 1996, Savage et al. 2000, Pausas et al. 2004). Despite the important ecosystem role played by fire, human activities have altered natural fire regimes relative to their historic range of variability. To develop effective conservation and fire management strategies to deal with altered fire regimes, it is necessary to understand the causes underlying altered fire behavior and their human relationships (DellaSalla et al. 2004). Nowhere is this more critical in the United States than in California, which is the most populous state in the nation, with roughly 35×10^6 people. Most of the population lives in lower elevations dominated by hazardous chaparral shrublands susceptible to frequent high-intensity crown fires.

In California, as elsewhere, the two primary mechanisms altering fire regimes are fire suppression, resulting in fire exclusion, and increased anthropogenic ignitions, resulting in abnormally high fire frequencies (Keeley and

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Fotheringham 2003), though climate change, vegetation manipulation, and other indirect factors may also play a role (Lenihan et al. 2003, Sturtevant et al. 2004). For most of the 20th century, fire suppression effectively excluded fire from many western U.S. forest ecosystems, such as ponderosa pine. In these ecosystems, fire exclusion contributed to unnatural fuel accumulation and increased tree density (Veblen et al. 2000, Allen et al. 2002, Gray et al. 2005). Recently, when wildfires have hit many of these forests, hazardous fuel loads have contributed to high-intensity crown fires that are considered outside the historical range of variability (Stephens 1998). While these patterns are widely applicable to many forested landscapes in the western United States, California chaparral shrublands have experienced such substantial human population growth and urban expansion that the increase in ignitions, coupled with the most severe fire weather in the country (Schroeder et al. 1964), have acted to offset the effects of suppression to the point that fire frequency exceeds the historic range of variability (Keeley et al. 1999). Because anthropogenic ignitions tend to be concentrated near human infrastructure, more fires now occur at the urban fringe than in the backcountry (Pyne 2001, Keeley et al. 2004). Profound impacts on land cover condition and community dynamics are possible if a disturbance regime exceeds its natural range of variability, and altered fire regimes can lead to cascading ecological effects (Landres et al. 1999, Dale et al. 2000). For example, too-frequent fire can result in habitat loss and fragmentation, shifting forest composition, reduction of small-mammal populations, and accompanying loss of predator species (Barro and Conard 1991, DellaSalla et al. 2004).

Landscape-level interactions between human activities and natural dynamics tend to be spatially concentrated at the wildland–urban interface (WUI; see Plate 1), which is the contact zone in which human development intermingles with undeveloped vegetation (Radeloff et al. 2005). The WUI has received national attention because housing developments and human lives are vulnerable to fire in these locations and because anthropogenic ignitions are believed to be most common there (Rundel and King 2001, USDA and USDI 2001). The majority of WUI fire research has focused on strategies to protect lives and structures (e.g., Cohen 2000, Winter and Fried 2000, Winter et al. 2002, Shindler and Toman 2003) or on the assessment of fire risk using biophysical or climate variables that influence fire behavior (Bradstock et al. 1998, Fried et al. 1999, Haight et al. 2004). However, it is also important to understand how the WUI itself (or other indicators of human activity) affects fire and to quantify the spatial relationships between human activities and fire (Duncan and Schmalzer 2004).

The influence of proximity to the WUI and other human infrastructure appears to vary markedly with region. In the northern Great Lakes states, areas with higher population density, higher road density, and lower distance to nonforest were positively correlated with fire (Cardille et al. 2001). Also, in southern California, a strong positive correlation between population density and fire frequency was reported (Keeley et al. 1999). However, no relationship between housing count and fire was found in northern Florida counties (Prestemon et al. 2002); population density and unemployment were positively related, and housing density and unemployment were negatively related to fire in a different analysis of Florida counties (Mercer and Prestemon 2005). A negative relationship between housing density and fire was also found in the Sierra Nevada Mountains of California (CAFRAP 2001).

In addition to potential regional differences, it is also difficult to draw general conclusions from these studies because they used different indicators of human activities, their data sets differed in spatial and temporal scale, and they were conducted in small areas where ranges of variability in both fire frequency and level of development were limited. Human–fire relationships may also vary based on factors that were not accounted for, such as pattern of development. Another explanation for the discrepancy is that relationships between human activities and fire may be nonlinear in that humans may affect fire occurrence positively or negatively, depending on the level of influence. These nonlinear effects were apparent in data from a recent study in the San Francisco Bay region, where population growth was positively related to fire frequency over time up to a point, but then fire frequency leveled off as population continued to increase (Keeley 2005).

Whether positive or negative, the significance of the relationships between human activities and fire that were detected in previous studies stresses the importance of further exploring links between anthropogenic and environmental factors and their relative influence on wildfire patterns across space and time. Therefore, our research objective was to quantify relationships between human activities and fire in California counties using temporally and spatially rich data sets and regression models. Although fire regimes encompass multiple characteristics, including seasonality, intensity, severity, and predictability, we restricted our analysis to questions about fire frequency and area burned to determine: (1) what the contemporary relationship between human activities and fire is; (2) how human activities have influenced change in fire over the last 40 years; and (3) whether fire frequency and area burned vary nonlinearly in response to human influence.

Humans are responsible for igniting the fires that burn the majority of area in California (Keeley 1982); therefore, we expected our anthropogenic explanatory variables to significantly explain fire activity on the current landscape and over time. In addition to population density (which simply quantifies the number of people in an area), we expected the spatial pattern of human development (indicated by housing density and

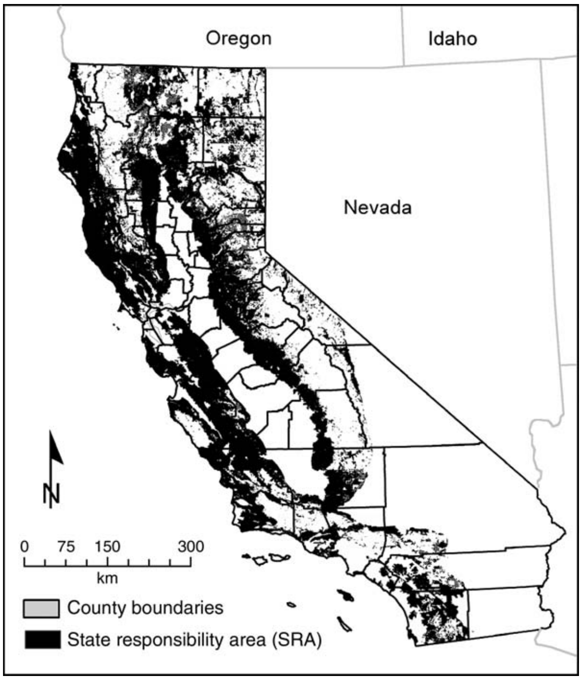

FIG. 1. Map of California Department of Forestry and Fire Protection (CDF) state responsibility areas (SRAs) within county boundaries of California, USA.

land cover combinations and distance variables) to be an important influence on fire because we assumed that anthropogenic ignitions are most likely to occur where human presence is greatest. We also expected that the relationships between human activities and fire would be both positive and negative because humans ignite fires, but development patterns affect fuel continuity and the accessibility of fire suppression resources. Finally, we included several environmental variables in the analysis because we expected the human relationships to be mediated by these other biophysical variables that shape the pattern and frequency of fire (Wells et al. 2004).

METHODS

Study area

California is the second largest state in the continental United States and is the most populous and physically diverse. Most of the state has a mediterranean climate, which, along with a heterogeneous landscape, contributes to tremendous biodiversity (Wilson 1992). Because the state contains a large proportion of the country's endangered species, it is considered a "hotspot" of threatened biodiversity (Dobson et al. 1997). There is extensive spatial variation in human population density: large areas in the north are among the most sparsely populated in the country, but metropolitan regions in the south are growing at unprecedented rates (Landis and Reilly 2004). Much of the landscape is highly fire-prone, but fire regimes vary, and fire management is divided among many institutions. Humans have altered California's fire regimes, and its fire-related financial losses are among the highest in the country (Halsey 2005).

Data

Dependent variables: fire statistics.—We assembled our fire statistics from the California Department of Forestry and Fire Protection (CDF; Sacramento, California, USA) annual printed records, which included information on all fires for which the CDF took action between 1931 and 2004. For all state responsibility areas (SRA; Fig. 1), fire statistics are recorded by county and include numbers by size class, total area burned, vegetation type, and cause. Because the statistics did not include spatially explicit information on individual fires, we weighted the data by the area within the SRA in each county by calculating proportions to use as our dependent variables. These fire statistics were substantially more comprehensive than the readily available electronic Statewide Fire History Database, which excludes most fires <40 ha, which in many counties represents >90% of the fires. Although both anthropogenic and lightning ignitions would be important to consider for fully understanding fire patterns in other regions (e.g., Marsden 1982), humans were responsible for ~95% of both the number of fires and area burned in California in the last century. We restricted our analysis to these anthropogenic fires because our focus was on human relationships with fire. Although the fire statistics were not spatially explicit, we developed GIS grids at 100-m resolution to derive data for all of the explanatory variables. The data for these explanatory variables were only extracted and averaged from within the SRA boundaries corresponding to the fire data.

Out of the 58 counties in California, we had fire statistics for 54 of them for the year 2000. Therefore, to assess the contemporary relationship between fire and human activities (hereafter referred to as the "contemporary analysis"), we analyzed the data from these counties using the annual number of fires and area burned as our dependent variables (Table 1).

Based on a preliminary exploration of the fire history data (averaged across all counties), we observed two distinct trends during the last 50 years. First, the number of fires substantially increased until 1980 and then decreased until 2000; and second, the average area burned changed inversely to the number of fires, but the differences over time were less dramatic and not statistically significant (Fig. 2). Considering these trends, we broke the historic analysis into two equal time periods (1960–1980 and 1980–2000) to compare the relative influence of the explanatory variables on both the increase (i.e., from 1960 to 1980) and decrease (from 1980 to 2000) in fire activity. The year 1980 is used to compute differences for both time periods because the census data that formed the basis for many of our explanatory variables were only available by decade. We averaged the number of fires and the area burned for 10-

TABLE 1. Variables analyzed in the regression models.

Variable	Source	Processing
2000 data		
Dependent variables		
Number of fires	CDF	proportion in SRA, square-root transformed
Area burned	CDF	proportion in SRA, square-root transformed
Explanatory variables		
Human		
Intermix WUI	SILVIS	proportion in SRA
Interface WUI	SILVIS	proportion in SRA
Low-density housing	SILVIS	proportion in SRA
Distance to intermix WUI	SILVIS	mean Euclidean distance in SRA
Distance to interface WUI	SILVIS	mean Euclidean distance in SRA
Population density	SILVIS	proportion in SRA
Road density	TIGER	mean km/km^2 in SRA
Distance to road	TIGER	mean Euclidean distance in SRA
Biophysical		
Ecoregion	CDF	discrete class
Vegetation type	CDF	area burned in vegetation type/area burned in SRA
Historic data, 1960–1980 and 1980–2000		
Dependent variables		
Change in number of fires	CDF	difference between decadal averages, proportion in SRA, square-root transformed
Change in area burned	CDF	difference between decadal averages, proportion in SRA, square-root transformed
Explanatory variables		
Human		
Change in housing density	SILVIS	difference between decades
Change in distance to low-density housing	SILVIS	difference between mean Euclidean distance in SRA
Initial housing density	SILVIS	mean housing density in either 1960 or 1980
Initial distance to low-density housing	SILVIS	mean Euclidean distance in SRA in either 1960 or 1980
Biophysical		
Ecoregion	CDF	discrete class
Vegetation type	CDF	mean area burned in vegetation type/area burned in SRA over time period

Notes: Key to abbreviations: WUI, wildland–urban interface; SRA, state responsibility area. Sources are as follows: CDF, California Department of Forestry and Fire Protection, Sacramento, California, USA, *unpublished data*; SILVIS, Radeloff et al. (2005); TIGER, U.S. Census Bureau (2000).

year time periods that bracketed the dates of the census data (e.g., 1955–1964 [1960], 1975–1984 [1980], 1995–2004 [2000]) and then calculated the difference in averages from the 1960–1980 and 1980–2000 periods for our dependent variables (Table 1). By averaging the fire data, we smoothed some of the annual variability that may have occurred due to stochastic factors such as weather.

Explanatory variables: housing data.—Data for most of the anthropogenic variables were available through a nationwide mapping project that produced maps of the WUI in the conterminous United States using housing density data from the 1990 and 2000 U.S. Census (U.S. Census Bureau 2002) and land cover data from the USGS National Land Cover Dataset (Radeloff et al. 2005). The maps were produced at the finest demographic spatial scale possible, the 2000 decennial census blocks. The vegetation data were produced at 30-m resolution. These maps delineated two types of WUI in accordance with the Federal Register definition (USDA and USDI 2001). "Intermix WUI" is defined as the intermingling of development with wildland vegetation; the vegetation is continuous and occupies >50% of the area. "Interface WUI" is defined as the situation in which development abuts wildland vegetation; there is <50% vegetation in the WUI, but it is within 2.4 km of an area that has >75% vegetation. In both types of WUI communities, housing must meet or exceed a density of more than one structure per 16 ha (6.17 housing units/km^2). Interface WUI tends to occur in buffers surrounding higher-density housing, whereas intermix WUI is more dispersed across the landscape (Fig. 3A, B).

The WUI data were only produced for 1990 and 2000 due to the lack of historic land cover data, but housing density data were available from 1960 to 2000. Historic housing density distribution was estimated using back-casting methods to allocate historic county-level housing unit counts into partial block groups (as described in Hammer et al. 2004). We used both intermix and interface WUI as explanatory variables (proportions within the county SRAs) in the current analysis to evaluate how these different patterns of vegetation and housing density affected fire activity. We also used low-density housing (housing density $\geq$6.17 housing units/km^2 and <49.42 housing units/km^2) to determine whether it could act as a substitute for WUI as an explanatory variable in the historic analysis (Table 1).

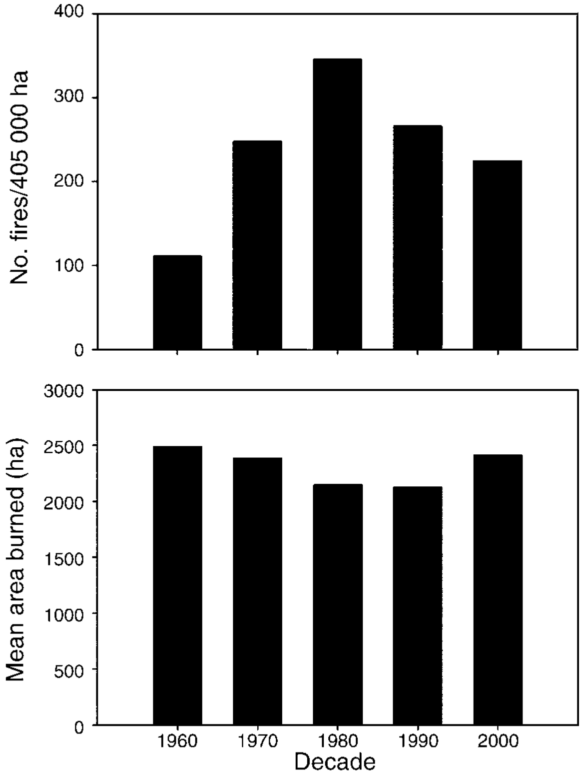

FIG. 2. Trends in number of fires and area burned for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

Looking at an overlay of fire perimeters from the electronic Statewide Fire History Database (from the last 25 years; *available online*)[7] on the WUI data, it was apparent that many fires occurred close to the WUI, but not necessarily within the WUI (Fig. 3C, D). Therefore, we calculated the mean distance to intermix and interface WUI to evaluate as explanatory variables (Table 1). These means were calculated by iteratively determining the Euclidean distances from every grid cell in the county SRA boundaries and then averaging the distances across all cells to determine means for the counties. We also included population density data from the 2000 Census.

For the historic analysis, we calculated changes in mean housing density and mean distance to low-density housing between the 1960–1980 and 1980–2000 periods to relate to change in the dependent variables. We excluded the proportion of low-density housing from our analysis because it was highly correlated with mean housing density ($r = 0.84$). Unlike the historical fire data that switched in their direction of change over time, housing density continued to increase while the mean distance to low-density housing continued to decline (Fig. 4). We included the initial values of these data (e.g., 1960 and 1980) to account for the fact that the same magnitude of change may have different effects on the dependent variables depending on the starting value of the explanatory variables (Table 1).

Explanatory variables: road data.—The quality of road data can vary according to data source (Hawbaker and Radeloff 2004), so we compared the U.S. Geological Survey digital line graph (DLG; U.S. Geological Survey 2002) and the US TIGER 2000 GIS (U.S. Census Bureau 2000) layers of roads to determine whether there were substantial differences that could affect the interpretation of the results. After calculating and summarizing road density by county, we found a strong positive correlation ($r = 0.97$). Therefore, we used the TIGER data because they were produced in 2000, the same year as the contemporary analysis. The more current TIGER data generally capture new development that might not be included in the DLG data. We evaluated mean road density and mean distance to roads in the current analysis (Table 1), but road data were unavailable for the historic analysis.

Explanatory variables: environmental.—In the absence of human influence, fire behavior is primarily a function of biophysical variables (Pyne et al. 1996, Rollins et al. 2002). These can vary widely across a county, but ecoregions capture broad differences by stratifying landscapes into unique combinations of physical and biological variables (ECOMAP 1993). Our ecoregion data were the geographic subdivisions of California defined for The Jepson Manual (Hickman 1993), designated through broadly defined vegetation types and geologic, topographic, and climatic variation (Fig. 5).

Because vegetation type influences the ignitability of fuel and the rate of fire spread (Bond and van Wilgen 1996, Pyne et al. 1996), we also evaluated the proportion of area burned within three broad vegetation types: shrubland, grassland, and woodland (Fig. 5). Differences in fire regimes between broadly defined vegetation types can be striking, particularly between shrubland and woodland in southern California (Wells et al. 2004). The CDF fire statistics included information on the proportion of area burned in these vegetation types. For the historic analysis, we averaged the proportion of fires burned within different vegetation types over the entire decade (Table 1).

Analytical methods

Diagnostics and data exploration.—Before developing regression models, we examined scatter plots for each variable. Nonlinear trends were apparent (e.g., Fig. 6), suggesting that we needed to include quadratic terms for the explanatory variables in the regressions. Unequal variances in the residual plots prompted us to apply a square-root transformation to the dependent variables. We also plotted semivariograms of the models' residuals (using centroids from the SRA boundaries) and found no evidence of spatial autocorrelation. To check for

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[7] ⟨http://frap.cdf.ca.gov/data/frapgisdata/select.asp⟩

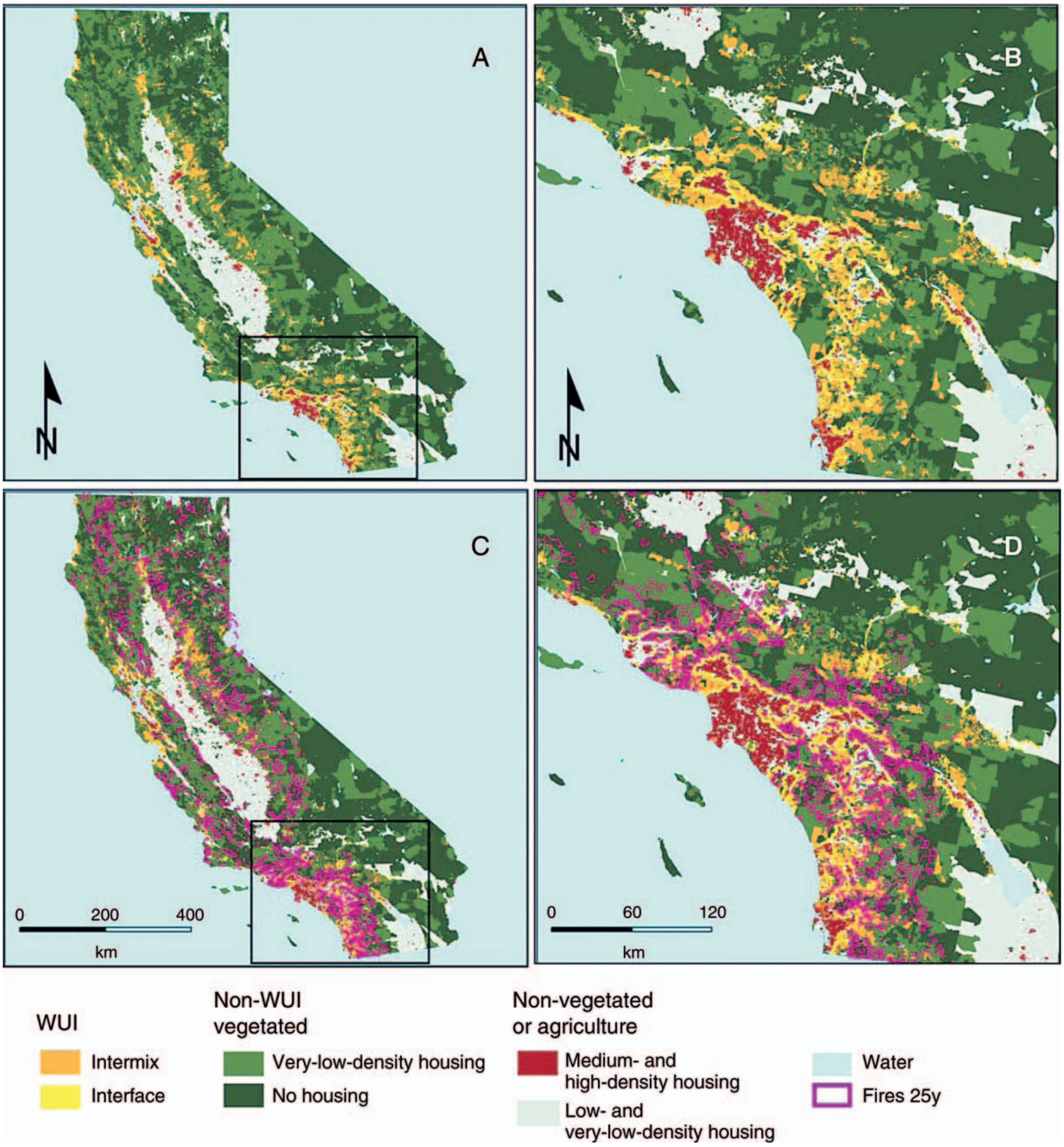

FIG. 3. The wildland–urban interface (WUI) in 2000 with and without fire perimeter overlays (from 1979 to 2004) in (A, C) California and (B, D) southern California. Housing density is defined as follows: very low, >0–6.17 housing units/km^2; low, 6.17–49.42 housing units/km^2; medium, 49.42–741.31 housing units/km^2; and high, >741.31 housing units/km^2 (USDA and USDI 2001). "Fires 25y" refers to 25 years of fire perimeters, from 1980 to 2005.

multicollinearity, we calculated the correlation coefficients between all of the explanatory variables and only included noncorrelated variables ($r \leq 0.7$) in the multiple regression models.

The areas of CDF jurisdiction for each county varied slightly over time. Therefore, we compared separate regressions from the full historic data set ($n = 37$) to a subset of the data excluding counties that experienced a greater than 20% change in area over time ($n = 23$). For both the 1960–1980 regressions and the 1980–2000 regressions, every one of the explanatory variables that was significant in the subset was also significant in the full data set, with very similar R^2 values; therefore, we felt confident proceeding with the full data set for the historic analysis because we had greater power with the larger sample size.

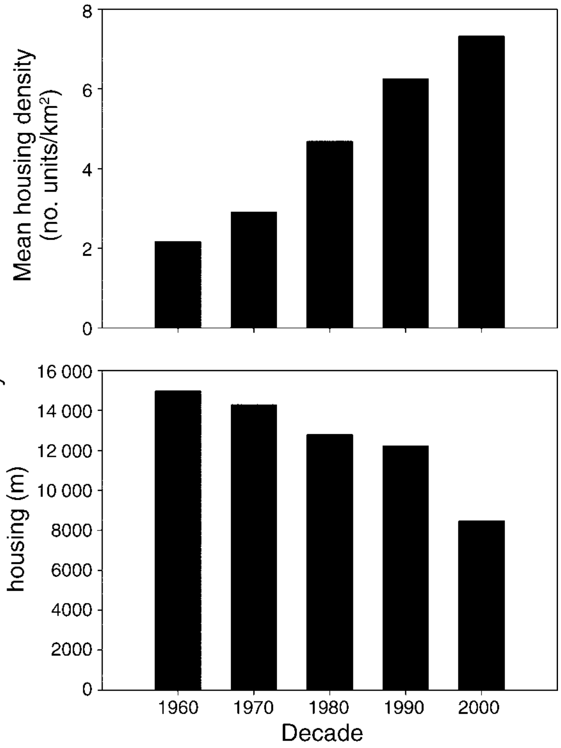

FIG. 4. Trends in housing density and distance to low-density housing (6.17–49.42 housing units/km^2) for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

Statistical analysis

We used the same regression modeling approach for both the current and historic analyses. First, we developed bivariate regression models for all of the explanatory variables and their quadratic terms so that we could evaluate their independent influence on fire frequency and area burned. To account for the interactions between variables (and their quadratic terms), we also built multiple regression models using the R statistical package (R Development Core Team 2005). For all models, we first conducted a full stepwise selection analysis (both directions) using Akaike Information Criteria to identify the best combination of predictor variables (Burnham and Anderson 2002). Some of the models retained a quadratic term without including the lower-order variable. In these models, we added the lower-order term, rebuilt the model, and then proceeded with a backwards elimination process until all predictor variables in the model were significant with P values ≤ 0.05.

RESULTS

Current analysis

Bivariate regressions.—Many of the anthropogenic variables were highly significant in explaining the number of fires in 2000. The quadratic term for each of these variables was also significant, and the direction of influence was both positive and negative (Fig. 7). Compared to the other variables, population density explained the greatest amount of variability. The proportion of intermix WUI and low-density housing in the counties also explained significant variation in the number of fires; but the proportion of interface WUI was insignificant. The number of fires was significantly related to the mean distance to both types of WUI, but neither of the road variables was significant. All three vegetation types, particularly shrubland, significantly influenced the number of fires, but ecoregion was insignificant.

For the anthropogenic variables, the number of fires was highest at intermediate levels of population density (from ~35 to 45 people/km^2; Fig. 6), proportion of intermix WUI (~20–30% in the county), and proportion of low-density housing (~25–35% in the county). It was also highest at the shortest distances to intermix and interface WUI, but started to level off at ~9–10 km for intermix (Fig. 6) and 14–15 km for interface WUI.

Unlike the number of fires, none of the anthropogenic variables were significantly associated with the area burned in 2000. In fact, shrubland was the only variable that explained significant variation in area burned.

Multiple regression.—When all of the variables were modeled in the multiple regressions, the resulting model for number of fires in 2000 included population density, the proportion of intermix WUI and its quadratic term, grassland and its quadratic term, and shrubland (Table 2). The model was highly significant with an adjusted R^2 value of 0.72.

The multiple regression model for area burned in 2000 included distance to road, shrubland, and woodland, and all three variables had significant positive relationships (no quadratic terms were retained). This model was also highly significant with an adjusted R^2 of 0.50.

Historical analysis 1960–1980

Bivariate regressions.—Change in the number of fires (net increase) from 1960 to 1980 was significantly explained by each of the human-related variables except for change in the mean distance to low-density housing (Fig. 8). The quadratic term was also significant in the separate models, except for the initial distance to low-density housing (in 1960), which had a negative influence on the change in number of fires. Change in number of fires was also significantly related to ecoregion and shrubland vegetation.

The only three variables with significant influence on the change in area burned (net decrease) were the three vegetation types.

Multiple regression.—The explanatory variables that were retained in the multiple regression model for change in the number of fires from 1960 to 1980 included mean housing density in 1960 and its quadratic term, grassland vegetation, and ecoregion (Table 2). The adjusted R^2 value was highly significant at 0.72.

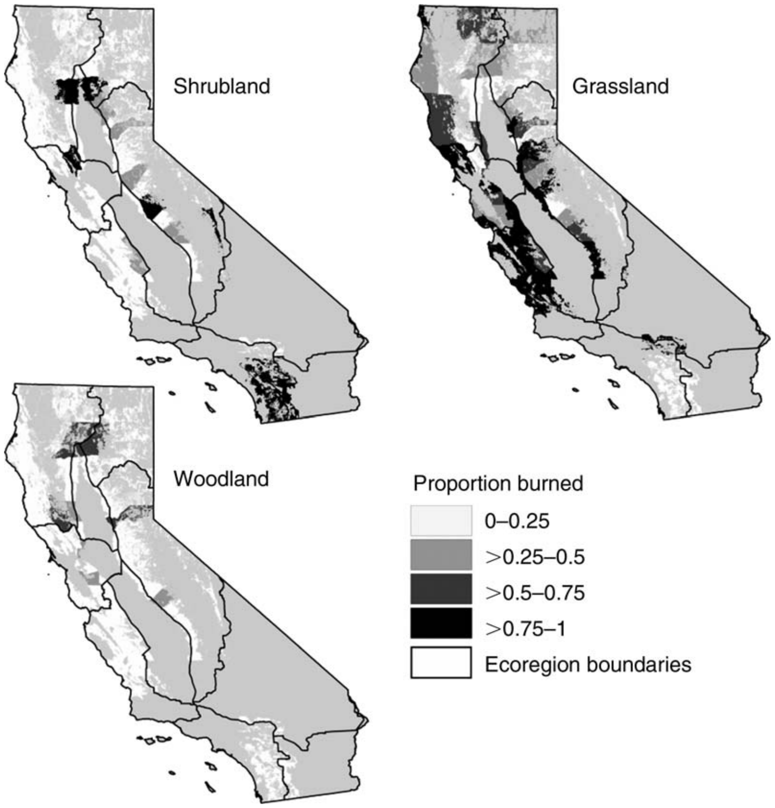

FIG. 5. Maps showing ecoregion boundaries and the proportion of area burned in shrubland, grassland, and woodland in 2000.

Mean housing density in 1960 was positively associated with change in area burned from 1960 to 1980, and the distance to low-density housing had first a positive, then a negative influence because the quadratic term was included. Other variables retained in the multiple regression model included shrubland and its quadratic term, grassland, woodland, and ecoregion.

Historical analysis 1980–2000

Bivariate regressions.—Initial housing density (in 1980) was the only significant explanatory variable explaining change in number of fires (net decrease) from 1980 to 2000 (Fig. 9). Woodland vegetation was the only significant variable out of the separate models explaining change in area burned from 1980 to 2000 (net increase). The quadratic terms were significant for both of these models.

Multiple regression.—The multiple regression model explaining change in number of fires from 1980 to 2000 included change in housing density, initial housing density (in 1980), and woodland vegetation; the quadratic term was also significant for these three variables (Table 2). Although the model was significant, the R^2 was substantially lower than the 1960–1980 model, at 0.26.

The multiple regression model explaining change in area burned included initial housing density (in 1980) and its quadratic term, initial distance to low-density

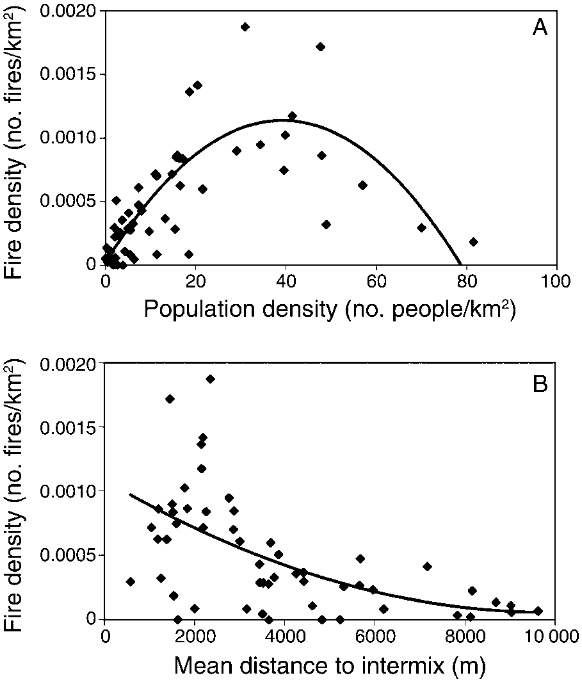

FIG. 6. The relationships between (A) the proportion of the number of fires and population density and (B) the proportion of the number of fires and mean distance to intermix wildland–urban interface (WUI).

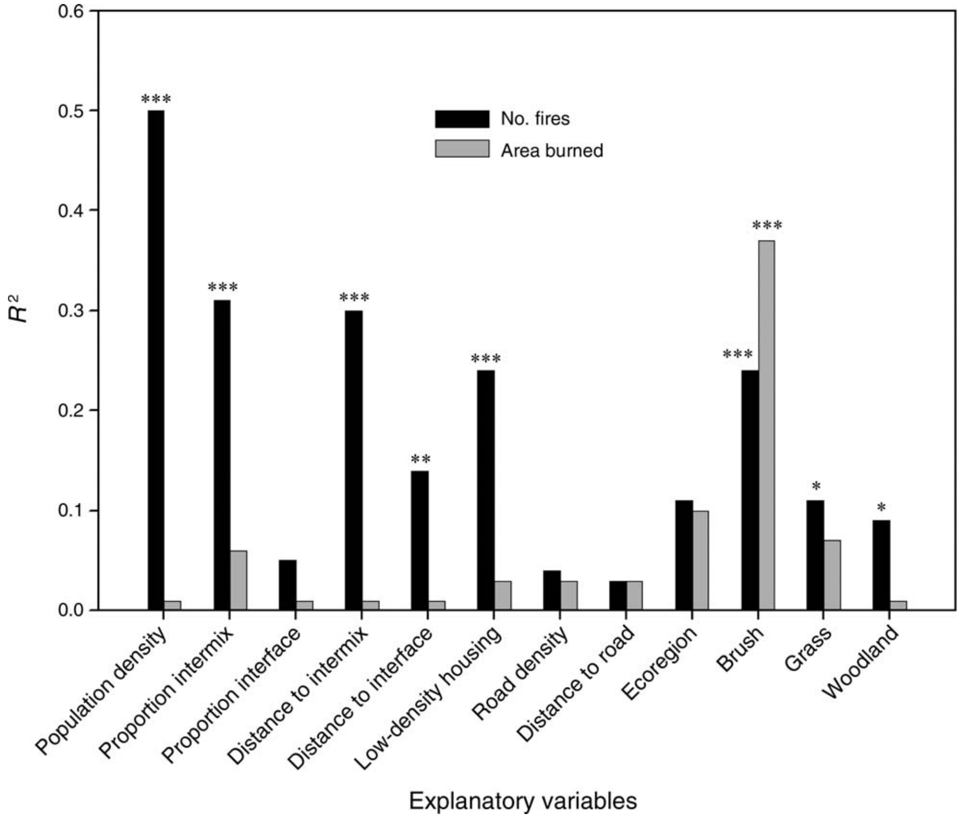

FIG. 7. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned in 2000.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

housing, woodland vegetation and its quadratic, and ecoregion. This model had better explanatory power than the number of fires model, with an R^2 of 0.41.

DISCUSSION

The expression of fire on a landscape is influenced by a combination of factors that vary across spatial and temporal scales and involve both physical and biological characteristics. Fire behavior has long been viewed as a largely physical phenomenon illustrated by the classic fire environment triangle that places fire as a function of weather, fuels, and topography (Countryman 1972), but clearly the human influence on modern fire regimes must also be understood to meet fire management needs (DellaSalla et al. 2004). We first asked what the current relationship is between human activities and fire in California and found that humans and their spatial distribution explained a tremendous proportion of the variability in the number of fires, but that area burned was more a function of vegetation type. Anthropogenic ignitions are the primary cause of fire in California and were the focus of our analysis, so we were not surprised by the strong human influence. Nevertheless, the high explanatory power of the models underscores the importance of using locally relevant anthropogenic factors as well as biophysical factors in fire risk assessments and mapping. The models also identify which indicators of human activity are most strongly associated with fire in California. For number of fires, the proportion of intermix WUI explained more variation than any other variable except for population density, suggesting that the spatial pattern of housing development and fuel are important risk factors for fire starts.

Human-caused ignitions frequently occur along transportation corridors (Keeley and Fotheringham 2003, Stephens 2005), so it was surprising that neither road density nor average distance to road were significant in explaining fire frequency. Although roads are important in local-scale ignition modeling, detecting their influence on fire ignitions may be difficult at an aggregated, county level since they are narrow, linear features. On the other hand, distance to roads was the only anthropogenic variable associated with area burned, having a positive influence when grassland and shrubland were also accounted for in the multiple regression model, which may reflect the difficulty of fire suppression access contributing to fire size.

Humans influence fire frequency more than area burned because anthropogenic ignitions are responsible

Table 2. Variables retained in the multiple regression models for the current and historic analyses.

Analysis and explanatory variable	Coefficient and intercept	P
Current		
2000		
No. fires		
Population density	0.0006	<0.01
Proportion intermix	0.0702	<0.01
(Proportion intermix)^2	−0.2629	<0.01
Grassland	0.0496	<0.01
(Grassland)^2	−0.0441	<0.01
Shrubland	0.0093	0.02
Overall model (adjusted R^2: 0.72)	0.0001	<0.01
Area burned		
Distance to road	0.00004	<0.01
Shrubland	0.0833	<0.01
Woodland	0.0559	<0.01
Overall model (adjusted R^2: 0.50)	−0.0052	<0.01
Historic		
1960–1980		
No. fires		
Initial housing	2.7649	<0.01
(Initial housing)^2	−0.1523	<0.01
Grassland	4.6311	0.05
Ecoregion	…†	<0.01
Overall model (adjusted R^2: 0.72)	0.6443	<0.01
Area burned		
Initial housing	0.0188	<0.01
Initial distance	0.00002	<0.01
(Initial distance)^2	-2×10^{-10}	<0.01
Shrubland	−0.3641	0.12
(Shrubland)^2	0.8778	0.01
Grassland	0.0371	<0.01
Woodland	0.0449	0.01
Ecoregion	…†	0.03
Overall model (adjusted R^2: 0.51)	−0.373	<0.01
1980–2000		
No. fires		
Change housing	3.0666	0.01
(Change housing)^2	−0.2661	0.01
Initial housing	−1.8269	0.01
(Initial housing)^2	0.0505	0.03
Woodland	38.1957	0.03
(Woodland)^2	−107.0112	0.02
Overall model (adjusted R^2: 0.26)	−1.894	0.01
Area burned		
Initial housing	−0.0114	0.01
(Initial housing)^2	0.0003	0.05
Initial distance	−0.000003	<0.01
Woodland	0.0292	0.18
(Woodland)^2	−1.2831	0.02
Ecoregion	…†	0.05
Overall model (adjusted R^2: 0.41)	0.0409	<0.01

† Coefficients are not listed for categorical variables.

for fire initiation, but fire spread and behavior is ultimately more a function of fuel availability and type (Bond and van Wilgen 1996, Pyne et al. 1996). Yet humans do have some control over fire size through suppression and, indirectly, through fuel connectivity (Sturtevant et al. 2004), although fires are extremely difficult to suppress in California shrublands under high-wind conditions that typify the most destructive fires (Keeley and Fotheringham 2003). Therefore, human effects on area burned may cancel one another out to some extent because fire suppression can minimize the increase in area burned that would result from increased ignitions, at least at the WUI. Fire suppression resources are more likely to be concentrated on structural protection in developed areas (Calkin et al. 2005), which would explain the positive relationship between area burned and distance to road. Roads can serve as firebreaks and can also provide access routes for firefighters.

The inclusion of vegetation type in the multiple regression models illustrates that, despite the strong influence of humans, fire occurrence remains a function

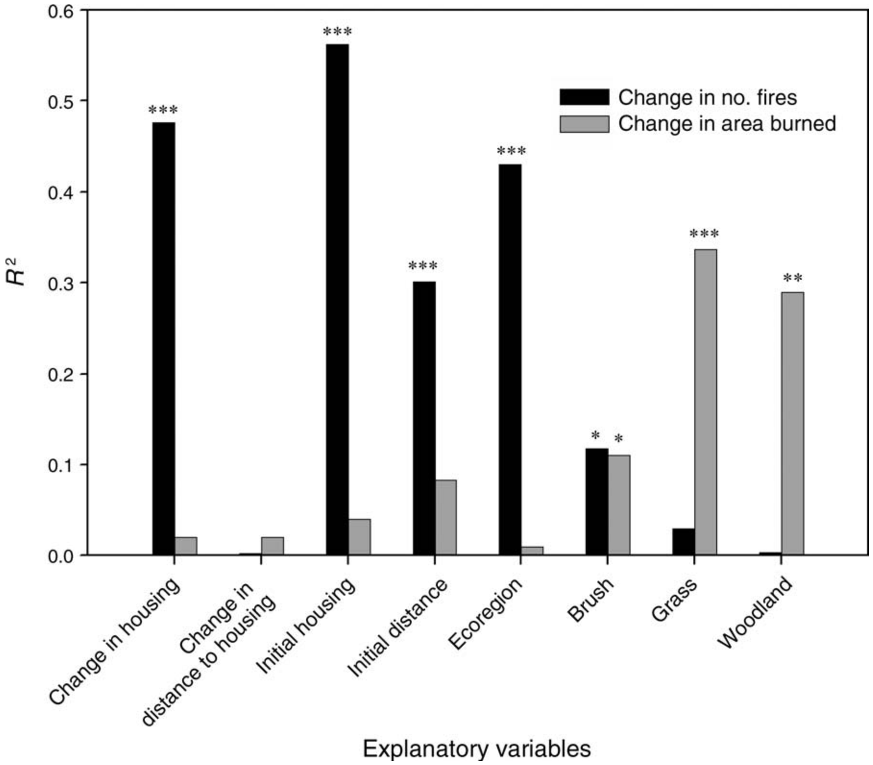

FIG. 8. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1960 to 1980.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

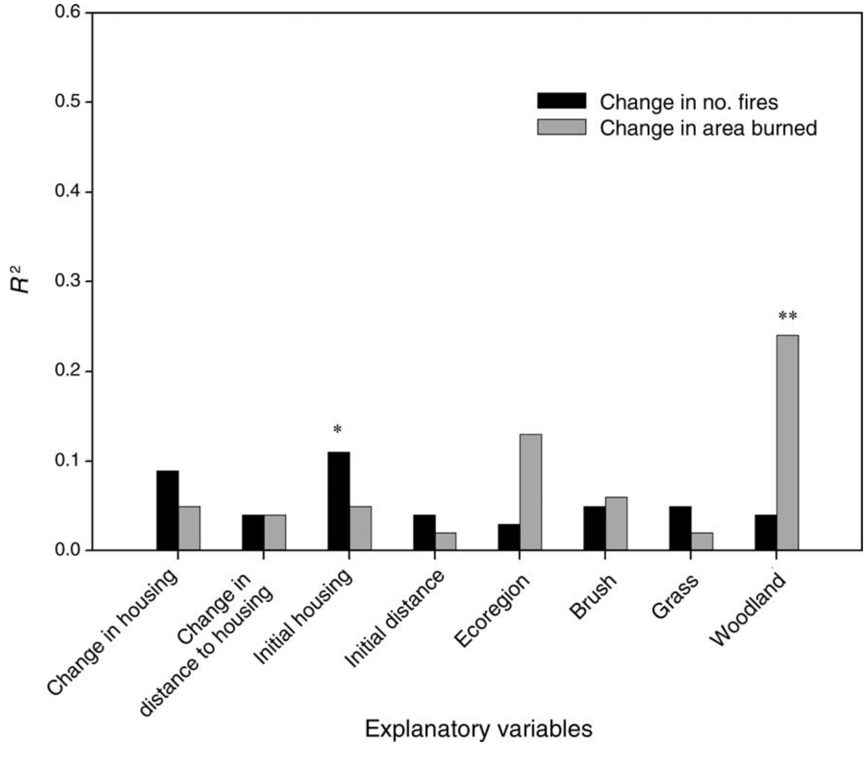

FIG. 9. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1980 to 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Plate 1. (Left) Wildland–urban interface (WUI) and (right) burned-over fuel break, both at the eastern end of Scripps Ranch (San Diego County, California, USA) after the autumn 2003 Cedar Fire (largest fire in California since the beginning of the 20th century). Photo credits: J. E. Keeley.

of multiple interacting social and environmental variables. For number of fires and area burned, shrubland had the strongest explanatory power of the vegetation types. Chaparral and coastal sage scrub are both extremely fire-prone vegetation types and high human population density tends to be distributed in these types; other studies have shown that they have experienced a higher rate of burning than other vegetation types in the southern part of the state in the last century (Keeley et al. 1999, Keeley 2000, Wells et al. 2004). Increased ignitions in highly flammable vegetation types can lead to very hazardous conditions (Halsey 2005).

The second question we asked was "How do human activities relate to change in fire?" In the last 40 years, the most substantial change was the increase in number of fires from 1960 to 1980. The decrease in number of fires was less dramatic between 1980 and 2000; and the change in area burned was relatively small in both time periods. Housing development patterns were most influential when change was greatest, from 1960 to 1980, and for trends in fire frequency (vs. area burned).

Although anthropogenic influence was partially responsible for the change in area burned, the apparent inverse relationship between change in fire frequency and change in area burned may be spurious. In other words, the explanation for a decrease in number of fires may be independent of the concurrent increase in area burned. Trends in area burned are naturally cyclic due to broad-scale factors such as climate. Recent research has shown that change in climate was a major factor driving fire activity in the western United States in the last several decades (Westerling et al. 2006); however, that research was restricted to large montane fire events on federally owned land above 1370 m. Therefore, while climate change may have played some role in our observed change in area burned, we cannot extend those results to our analysis because we included fires of all sizes under multiple land ownership classes, and historical fire patterns in the lower elevations do not correspond to patterns in montane forests (Halsey 2005).

Fire both constrains and is constrained by the fuel patterns it creates, resulting in cycles of fire activity and temporal autocorrelation in area burned, in part because young fuels are often less likely to burn (Malamud et al. 2005). Temporal autocorrelation effects vary with ecosystem, fuel type, and the area of analysis; but in all vegetation types, temporal dependence diminishes over time due to post-fire recovery. Therefore, we assumed that the effects would be low in our study because we were looking at change over 20-year time periods. Furthermore, the chaparral vegetation that dominates much of California recovers very quickly following fire, meaning that the effect of temporal autocorrelation in this vegetation type would last for only brief periods of time. Also, under extreme weather conditions, young age classes are capable of carrying fires in the southern portions of California (Moritz 1997, Moritz et al. 2004).

In general, the anthropogenic influence on fire frequency and extent was complicated through the combination of positive and negative effects, which helps to answer our third question: "Do fire frequency and area burned vary nonlinearly in response to human influence?" Nonlinear effects were evident in the scatter plots and confirmed by the significance of quadratic terms in most of the models. The regression models indicate that humans were responsible for first increasing and then decreasing fire frequency and area burned. These dual influences may explain why prior studies presented conflicting results, because a positive or negative response was dependent on the level of human presence. Aside from the fact that we intentionally tested hypotheses regarding nonlinear relationships, our data also contained a wide range of human presence due to the large extent and diversity of the state of California.

The scatter plots illustrate how these human–fire relationships occurred. For both the number of fires and area burned, and in the current and historic analyses, the maximum fire values occurred at intermediate levels of human presence (as in Fig. 6A); and when human activity was either lower or higher, fire activity was lower. Initial increase in fire occurrence with increasing population is reasonable since human presence results in more ignitions. However, it appears that when human population density and development reach a certain threshold density, ignitions decline, and this is likely the result of diminished and highly fragmented open space with fuels insufficient to sustain fire. In addition, above a certain population threshold, fire suppression resources are likely to be more concentrated in the WUI. Inverse relationships were evident in the scatter plots of distance (Fig. 6B). In these, fire frequency and area burned were greatest at short distances to WUI; and at longer distances, the trend lines leveled off. These distance relationships indicate that more fires would be expected in close proximity to settled areas where ignitions are likely to occur.

The inclusion of quadratic terms in the multiple regression models supports the concept that fire frequency and area burned were dependent on the level of human activity. Initial housing density was important in all four historic multiple regression models, and initial distance to low-density housing was important in both of the historic area-burned models. The change in number of fires for both periods was also related to change in housing density, in bivariate regression models for the earlier period and in the multiple regression model for the later period (1980–2000). These results further emphasize that fire activity was a function of a certain level of human presence. In addition to the strong influence of human presence, ecoregion and vegetation types were also highly significant in the multiple regression models, suggesting that the particular level of human activity that was most influential in explaining fire activity was dependent upon biophysical context.

The primary value of the multiple regression models was to identify the most influential variables and their direction of influence when accounting for other factors. While they explained how fire activity varied according to context-dependent interactions, their purpose was not to provide a formula for determining fire risk at a landscape scale. Environmental and social conditions differ from region to region, and processes such as fire and succession are controlled by a hierarchy of factors, with different variables important at different scales (Turner et al. 1997). Nevertheless, these models provide strong evidence about the strength and nature of human–fire relationships. That these relationships are significant across a state as diverse as California suggests that human influence is increasingly overriding the biophysical template; yet, managers must account for the interactions with ecoregion and vegetation type when making management decisions. Determining the conditions (e.g., thresholds) for nonlinear anthropogenic relationships will be important to understand how fire risk is distributed across the landscape.

At the coarse scale of our analysis, we can estimate these thresholds based on the nonlinear relationships in our scatter plots (as in Fig. 6) and suggest that fire frequency is likely to be highest when population density is between 35 and 45 people/km^2, proportion of intermix WUI is ~20–30%, proportion of low-density housing is ~25–35%, the mean distance to intermix WUI is $<$9 km, and the mean distance to interface WUI is $<$14 km. Our next step is to more precisely define these relationships at scales finer than the county level (where management decisions often occur) and to understand the conditions under which human activities positively or negatively influence fire.

These results imply that fire managers must consider human influence, together with biophysical characteristics such as those represented in the LANDFIRE database, when making decisions regarding the allocation of suppression and hazard mitigation resources. If human presence is not explicitly included in decision making, inefficiencies may result, because fire occurrence is related to human presence on the landscape. In particular, we identify an intermediate level of housing density and distance from the WUI at which the effects of human presence seem to be especially damaging, i.e., a point at which enough people are present to ignite fires, but development has not yet removed or fragmented the wildland vegetation enough to disrupt fire spread. This intermediate level of development is one that large areas of the lower 48 states, particularly in the West and Southwest, will achieve in the coming decade. Hence, the WUI's location, extent, and dynamics will continue to be essential information for wildland fire management.

CONCLUSION

In addition to the risk to human lives and structures, changing fire regimes may have substantial ecological impacts, and the results in this analysis support the hypothesis that humans are altering both the spatial and temporal pattern of the fire regime. Although the overall area burned has not changed substantially, the distribution of fires across the landscape is shifting so that the majority of fires are burning closer to developed areas, and more remote forests are no longer burning at their historic range of variability (Pyne 2001). In either case, the ecological impacts may be devastating. Due to lack of dendrochronological information, historic reference conditions are difficult to determine in stand-replacing chaparral shrublands. Although chaparral is adapted to periodic wildfire, there is substantial evidence that fires are burning at unprecedented frequencies, and this repeated burning (at intervals closer than 15–20 years apart) exceeds many species' resilience and has already resulted in numerous extirpations (Zedler et al. 1983, Haidinger and Keeley 1993, Halsey 2005).

If present trends continue in California, the population may increase to 90×10^6 residents in the next 100 years. Recent trends in housing development patterns also indicate that growth in area and number of houses in intermix WUI has far outpaced the growth in interface WUI (Radeloff et al. 2005; Hammer et al., *in press*). Our results showing that fire frequency and area burned tend to be highest at intermediate levels of development (more typical of intermix than interface) suggest that fire risk is a function of the spatial arrangement of housing development and fuels. Therefore, in addition to more people in the region that could ignite fires, future conditions that include continued growth of intermix WUI may also contribute to greater fire risk. Land use planning that encourages compact development has been advocated to lessen the general impacts of growth on natural resources (Landis and Reilly 2004), and we suggest that reducing sprawling development patterns will also be important to the control of wildfires in California.

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Conservation Biology

Contributed Paper

Conservation Threats Due to Human-Caused Increases in Fire Frequency in Mediterranean-Climate Ecosystems

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Abstract: *Periodic wildfire is an important natural process in Mediterranean-climate ecosystems, but increasing fire recurrence threatens the fragile ecology of these regions. Because most fires are human-caused, we investigated how human population patterns affect fire frequency. Prior research in California suggests the relationship between population density and fire frequency is not linear. There are few human ignitions in areas with low population density, so fire frequency is low. As population density increases, human ignitions and fire frequency also increase, but beyond a density threshold, the relationship becomes negative as fuels become sparser and fire suppression resources are concentrated. We tested whether this hypothesis also applies to the other Mediterranean-climate ecosystems of the world. We used global satellite databases of population, fire activity, and land cover to evaluate the spatial relationship between humans and fire in the world's five Mediterranean-climate ecosystems. Both the mean and median population densities were consistently and substantially higher in areas with than without fire, but fire again peaked at intermediate population densities, which suggests that the spatial relationship is complex and nonlinear. Some land-cover types burned more frequently than expected, but no systematic differences were observed across the five regions. The consistent association between higher population densities and fire suggests that regardless of differences between land-cover types, natural fire regimes, or overall population, the presence of people in Mediterranean-climate regions strongly affects the frequency of fires; thus, population growth in areas now sparsely settled presents a conservation concern. Considering the sensitivity of plant species to repeated burning and the global conservation significance of Mediterranean-climate ecosystems, conservation planning needs to consider the human influence on fire frequency. Fine-scale spatial analysis of relationships between people and fire may help identify areas where increases in fire frequency will threaten ecologically valuable areas.*

Keywords: fire, land cover, Mediterranean, MODIS, population density, remote sensing

Amenazas a la Conservación Debido a Incrementos en la Frecuencia de Incendios Causados por Humanos en Ecosistemas de Clima Mediterráneo

Resumen: *El fuego periódico es un proceso natural importante en los ecosistemas de clima mediterráneo, pero el incremento de la recurrencia de fuego amenaza la frágil ecología de esas regiones. Debido a que la mayoría de los incendios son causados por humanos, investigamos el efecto de los patrones de población humana sobre la frecuencia del fuego. Investigaciones previas en California sugieren que la relación entre la densidad poblacional y la frecuencia de incendios no es lineal. Hay pocas igniciones humanas en áreas con baja densidad poblacional, así que la frecuencia de incendios es baja. A medida que aumenta la densidad poblacional, los incendios causados por humanos y la frecuencia de incendios también incrementa; pero al*

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llegar a un umbral de densidad, la relación se vuelve negativa ya que los combustibles son escasos y se concentran recursos para la supresión de fuego. Probamos sí esta hipótesis también aplica a los otros ecosistemas de clima mediterráneo en el mundo. Utilizamos bases de datos de satélite de población, actividad de fuego y cobertura de suelo para evaluar la relación espacial entre humanos y fuego en los cinco ecosistemas de clima mediterráneo en el mundo. Tanto las densidades medias y medianas fueron consistente y sustancialmente más altas en áreas con fuego como sin fuego, pero los incendios alcanzaron su máximo en densidades poblacionales intermedias, lo que sugiere que la relación espacial es compleja y no lineal. Algunos tipos de cobertura de suelo tuvieron incendios más frecuentemente de lo esperado, pero no se observaron diferencias significativas en las cinco regiones. La asociación consistente entre mayores densidades poblacionales y fuego sugiere que, independientemente de las diferencias entre tipos de cobertura de suelo, los regímenes de fuego naturales o la población total, la presencia de gente en regiones de clima mediterráneo afecta fuertemente a la frecuencia de incendios; por lo tanto, el crecimiento poblacional en áreas escasamente pobladas es preocupante para la conservación. Considerando la sensibilidad de las especies de plantas a incendios recurrentes y la significancia para la conservación de los ecosistemas de clima mediterráneo, la planificación de la conservación requiere que se considera la influencia humana sobre la frecuencia de incendios. El análisis espacial a fina escala de las relaciones entre gente y fuego puede ayudar a identificar áreas en las que el incremento en la frecuencia de fuego amenazará a áreas valiosas ecológicamente.

Palabras Clave: cobertura de suelo, densidad poblacional, fuego, Mediterráneo, MODIS, percepción remota

Introduction

The biodiversity of Mediterranean-climate ecosystems is among the highest of any biome in the world. The five regions in the world with Mediterranean climates (the Mediterranean Basin, central Chile, the Cape Region of South Africa, southwestern Australia, and parts of California and northern Baja California in North America) collectively occupy <5% of the Earth's unglaciated land surface, yet they contain 20% of the world's flora (Cowling et al. 1996), and many species are endemic (Mittermeier et al. 1998). Because of rapid global change and increasing anthropogenic pressure, all Mediterranean regions are of high global conservation concern (Médail & Quézel 1999; Olson & Dinerstein 2002; Vogiatzakis et al. 2006).

Although Mediterranean-climate ecosystems are geographically disjunct, they are classic examples of convergence in ecosystem structure and dynamics (Cody & Mooney 1978). The Mediterranean climate is characterized by cool, wet winters and warm to hot, dry summers, and the summer drought produces water stress that affects the seasonal distribution of wildfires. Vegetation in Mediterranean-climate regions is dominated by evergreen, woody, sclerophyllous shrubs that are very flammable and support crown fires (Christensen 1985). Nevertheless, specialized postfire persistence traits (e.g., seed banking in the soil and canopy and resprouting) make plant species resilient to periodic wildfire (Naveh 1975). The presence of fire-stimulated reproduction indicates an adaptive response to fire, and seed banking evolved independently in all Mediterranean-climate ecosystems except Chile (Bond & van Wilgen 1996). Nevertheless, all the woody shrubs in Chile resprout in response to fire, which is now frequent due to anthropogenic ignitions (Montenegro et al. 2004).

Fire in Mediterranean-climate ecosystems predates humans (except in Chile), and natural fire frequencies have varied between and among regions over time and in response to climate fluctuations (Rundel 1998). The history of human impact on fire regimes also differs among regions. For example, humans ignited fires in the Mediterranean Basin for thousands of years to support agropastoral activities (Lozano et al. 2008), Native Americans ignited fires in California since the early Holocene (Keeley 2002), and small populations of hunter-gatherers ignited fires in other regions until a few centuries ago (Rundel 1998). Evidence regarding early human influence on fire is circumstantial and controversial, but human activity is now thought to be a major determinant of the timing and location of fire. In fact, humans ignite most fires in Mediterranean regions (Bond & van Wilgen 1996). Current human influence on fire regimes and the potential ecological impact of their influence on fire is similar among Mediterranean-climate regions and differs strongly from fire problems in other forested systems.

In dry coniferous forests, like those in the western United States, the primary concern is a lack of fire primarily due to 20th-century fire suppression. Lower fire frequency in forests that naturally experienced high-frequency, low-intensity surface fires resulted in high accumulation of surface and canopy fuels (Parsons & Landres 1998). Fuel accumulation increases the likelihood fires will become uncharacteristically large and intense, which can kill even large, surface-fire-resistant trees.

Conservation threats and changes in fire regimes in Mediterranean-climate regions, however, are different. The shrublands are adapted to fire-return intervals that are generally longer than those historically experienced in conifer forests (Sugihara et al. 2006). Despite their capacity for rapid postfire regeneration, many shrubland plant species are sensitive to repeated burning. Serotinous species are particularly vulnerable (e.g., Wark et al. 1987; Pausas 1999; Syphard et al. 2006), but repeated burning may also extirpate resprouting species by reducing their capacity to regenerate and constraining their reproductive ability (e.g., Haidinger & Keeley 1993; Montenegro et al. 2004; Espelta et al. 2008). A related issue is that exotic species may facilitate fire and may expand under frequent fire (Mack & D'Antonio 1998). In California biodiversity is critically threatened by shrubland conversion to exotic annual grasses caused by atypically frequent fire (Keeley et al. 2005). Therefore, where the primary concern in dry coniferous forests is fire exclusion, the problem in Mediterranean-climate regions is repeated fires in the same location (Montenegro et al. 2004; Badia-Perpinyà & Pallares-Barbera 2006; Forsyth & van Wilgen 2008), although the intensity of fires may vary from region to region because of differences in prescribed management practices. Thus, understanding the causes and spatial distribution of altered fire regimes in Mediterranean-climate ecosystems has become a major research priority with strong conservation implications (Lavorel et al. 1998) and is particularly important given population growth in Mediterranean-climate ecosystems.

Studies in California show that area burned and number of fires are highest when population and housing densities are intermediate (Keeley 2005; Syphard et al. 2007). Fires initially increase with population and housing density and then decline where a threshold density is reached. There are several interrelated reasons for this. Ninety-five percent of California's fires are human caused; therefore, anthropogenic ignitions are lower in areas with low population density. As population and housing densities increase, fuels are still abundant and contiguous enough to carry fire, and the number and frequency of fires increase (Syphard et al. 2007). As population density increases further and an area is developed, wildland fuel is reduced and fragmented and fire-suppression resources are concentrated, resulting in lower fire frequencies at high population densities. Finally, even if fire frequency remains stable, fires may cluster in certain areas (e.g., human settlements) or land-cover types (Nunes et al. 2005; Forsyth & van Wilgen 2008), resulting in high fire frequency in localized areas.

Although the relationship between human population densities and fires has been studied in California, less is known about fire trends and patterns in other Mediterranean ecosystems. In recent years, fire frequency has escalated because of population growth and human ignitions in Chile (e.g., Montenegro et al. 2004) and South Africa (Forsyth & van Wilgen 2008), and fires increased exponentially in many areas in the Mediterranean Basin, in part due to the abandonment of traditional land-use practices (Pausas & Vallejo 1999). Interactions between fire and exotic species have been exacerbated by recurrent human-caused fires in Chile (Montenegro et al. 2004), South Africa (Bond & van Wilgen 1996), the Mediterranean Basin (Kark & Sol 2005; Vogiatzakis et al. 2006), and Australia (Offor 1990). In Spain fire ignitions cluster near urban areas (Badia-Perpinyà & Pallares-Barbera 2006), and population density has been correlated with the number of fires and area burned (Vázquez de la Cueva et al. 2006). Results of previous studies thus suggest that the relationship between human populations and fire frequency may be similar in all Mediterranean-climate ecosystems, but this idea has not been examined systematically across the different areas. Whether fire frequencies consistently peak at intermediate densities of human population is unclear. Nor is it clear whether certain land-cover types are more likely to burn.

Our objective was to quantify the relationship between humans and fire in Mediterranean-climate ecosystems across the globe. We asked, Are population densities higher in places where fires occur than in places without fires? Are fires consistently most frequent at intermediate population densities? Are certain land-cover types in each region more prone to fires?

Methods

Study Area

We used Bailey's ecoregion boundaries to demarcate Mediterranean-climate ecoregions (Bailey 1989). (Table 1). This is a hierarchical system with four levels (domains, divisions, provinces, and sections). For all five

Table 1. Number of Bailey's ecoregions, total area, and biogeographic characteristics* of Mediterranean-climate regions.

	Number of ecoregions	*Total area (km^2)*	*Number of native vascular plants*	*Endemic species (%)*	*Threatened species (%)*
Mediterranean Basin	25	2,392,048	23,300	50	18
North America	5	407,654	4,300	35	17
Chile	2	74,863	2,100	23	unknown
South Africa	1	69,401	8,550	68	15
Southwest Australia	1	118,882	8,000	75	18

**Biogeographic characteristics based on Calow (1998) and Vogiatzakis et al. (2006).*

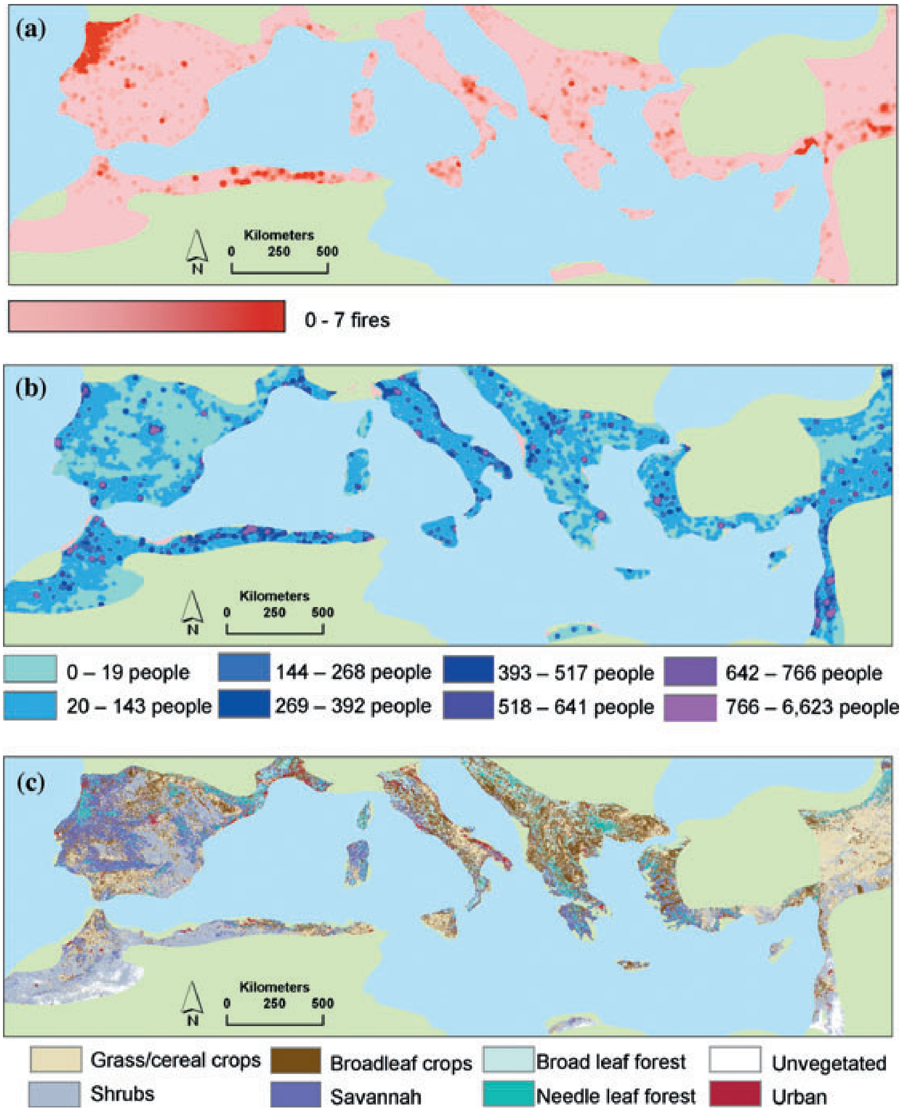

Figure 1. For the Mediterranean Basin, (a) MODIS active-fire detections in 2005, (b) LandScan population density in 2005, and (c) MODIS land-cover data. Fire and population density values are averaged across 225-km^2 pixels.

continents, we selected all ecoregions classified as either the Mediterranean Division or the Mediterranean Regime Mountains. To ensure comparability of area calculations, all spatial data were projected into an Albers equal area projection.

Processing of Population Data

We used population data from the LandScan Global Population Product because it has the finest resolution (<1 km) of any global population data set (Dobson et al. 2000). The LandScan database represents ambient population, accounting for diurnal movement and travel patterns. Every grid cell is allocated a population count based on a distribution model that incorporates the best available data on human population for every country, proximity of people to roads, land cover, nighttime lights, and urban density.

Because the accuracy and precision of LandScan are continually being improved, we restricted our analysis to 2005, the year with the most current data (Fig. 1). For comparison purposes, we divided the population counts by area and analyzed population density.

Processing of MODIS Fire Data

We used fire data from the Moderate Resolution Imaging Spectroradiometer (MODIS) to assess fire activity in Mediterranean-climate ecoregions because of its unmatched spatial and temporal detail (Justice 2002). With two polar-orbiting satellites, the MODIS active-fire product provides daily global information on fires. These data show actively burning fires based on radiant energy and comparisons of target pixels with surrounding pixels (Giglio et al. 2003).

Instead of mapping individual fires and area burned, MODIS indicates pixels in which fire activity was detected. Thus, there could be more than one fire active within a 1-km^2 MODIS pixel (Csiszar et al. 2006). In addition, fires occupying only a portion of a pixel can be detected (Dozier 1981). Although many small fires are missed, MODIS consistently detects larger fires that are ecologically relevant (Hawbaker et al. 2008), and the number of contiguous MODIS fire pixels tends to correlate with fire size (Giglio et al. 2006).

We analyzed MODIS fire data from the Land Processes Distributed Active Archive Center (LPDAAC, http://edcdaac.usgs.gov/modis/dataproducts.asp) for both sensors every day in 2005 to match the date of the population data. Using the boundaries of the Mediterranean ecoregions, we put all images into a mosaic (i.e., joined them together to form daily continuous tiles) for both sensors and summarized the daily data to create annual maps of fire for each region (Fig. 1). We included fire detections from all classified confidence levels because detection accuracy varies little whether fires are classified as low or high confidence (Hawbaker et al. 2008).

Processing of MODIS Land-Cover Data

In addition to the active-fire product, we used the 2003 MODIS 1 km Land Cover Dataset (Friedl et al. 2002) to analyze fire activity by land-cover class (Fig. 1). We used the LAI/fPAR Biome land-cover classification scheme because it was designed to capture differences in vegetation structural types (grasslands and cereal crops, shrubs, broadleaf crops, savannah, broadleaf forest, needle leaf forest, unvegetated, and urban; Myneni et al. 1997).

Analysis

In California fires are most likely to occur when the distance to housing is <15 km (Syphard et al. 2007). Because scale dependencies of ecological patterns and processes vary by region (Shugart 1998) and because people are mobile and affect their surroundings, we conducted our analysis of humans and fire at three levels of resolution (1, 15, and 45 km). Land-cover analyses were conducted only at the 1-km resolution, however, because we did not consider relationships between land cover and population measures.

We conducted a moving-window GIS analysis to summarize data across the entire land area. Within each window and at each resolution, we summarized the population density and the number of fires. Satellite fire detections can be obscured by clouds, and the MODIS active-fire product explicitly masks cloud cover in every daily image (Giglio et al. 2003). Therefore, we excluded cloud pixels, calculated the number of "observable days" within each window, and used this number to calculate average fire frequency. Uncertainty due to land-cover misclassification, undetected fires, and errors in population distribution was assumed to be consistent among the Mediterranean-climate ecoregions.

To determine whether population densities were higher in areas with fires, we selected all pixels and windows where there was one or more fires and calculated the mean and median population densities. We compared those with mean and median population densities in pixels and windows where no fires occurred. If there is a relationship between humans and fire, the proportion of fire should be higher where population is higher and lower where population is lower. We did not conduct a statistical test to determine whether the distributions differed because our data represent a complete enumeration, not a sample, and any difference would be statistically significant. Instead, we distributed the population data into 25 equally spaced categories and plotted the proportion of fires that occurred within each category for the three window sizes. The resulting bar charts showed whether more fires occurred at low, intermediate, or high population densities.

To determine whether fires burned more often (selectively) in different land-cover types, we calculated the total proportion of land-cover types in each region, then selected only the pixels with fires and recalculated the proportion. We calculated the ratio of the proportion of fires in the land-cover types and the proportion of the land-cover types in the landscape. A ratio of 1.0 means fire occurred in a land-cover type as often as would be expected by chance, >1.0 means fire occurred in the land-cover type more often, and <1.0 means fire occurred less often than expected by chance.

Results

We observed substantial differences in population density among the regions. Both the mean and median population densities in southwestern Australia were lowest of all the regions, and those in the Mediterranean Basin were highest. Although median population densities were substantially lower than mean population densities for all regions, the difference in North America was so substantial that mean population density was highest among the regions, but median population density was equal to that in southwestern Australia.

Pixels or windows with fires typically had higher population densities than pixels or windows without fires (Fig. 2). The only exception was in the 1-km pixels in North America, where mean population density was higher in the pixels without fires. Median population densities were nearly equal with and without fire in 1-km pixels in North America, South Africa, and southwestern Australia.

The relationship between population density and fire was more pronounced at 15 km than at 1 km, and at 45 km the mean population densities in areas with fires were much higher than where there were no fires (Fig. 2a). The median population density with fire was almost 3 times larger than the population density without fire at 45-km resolution.

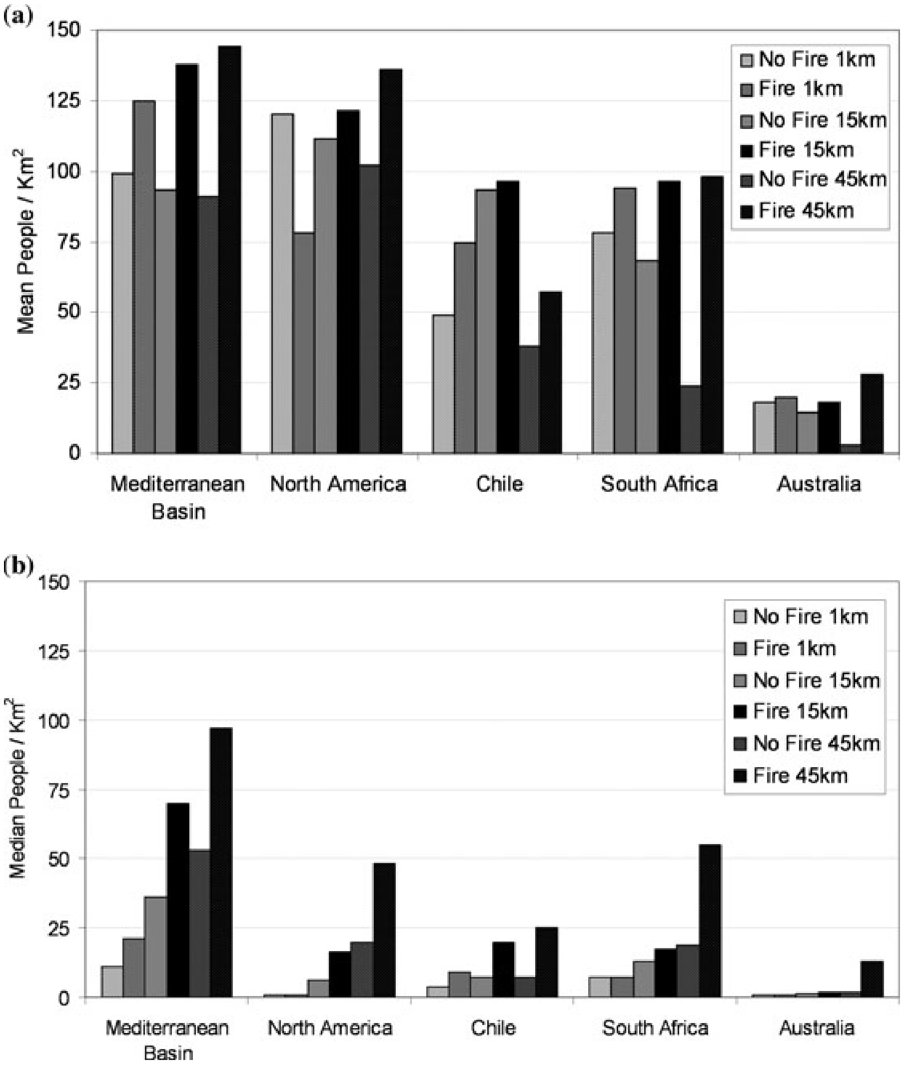

Figure 2. (a) Mean and (b) median population densities in areas with and without fires for 1-, 15-, and 45-km resolution windows. The y-axis scales differ.

Although population densities were, on average, higher where there were fires, the largest proportion of fires peaked at intermediate population densities (Fig. 3). Patterns of variation and peak population densities varied from region to region though, particularly at the 1- and 15-km window sizes. In addition, the peak in proportion of fires occurred in areas of lower population densities in North America at the 1-km resolution. In Chile and southwestern Australia, peak in proportion of fires occurred at the higher end of the population density distribution in the 1- and 45-km window sizes. The most consistent trend was apparent at the 45-km window size, where the highest proportion of fires occurred between 100 and 250 people per 45 km^2.

Land cover in the five regions included grasslands and cereal crops, shrubs, and savanna, with lower proportions of broad-leaf crops, broad-leaf forest, needle-leaf forest, unvegetated, and urban cover (Fig. 4). Distribution of these land-cover types, however, varied widely from region to region. Grasslands and cereal crops accounted for 40% of land cover in South Africa and southwestern Australia, but in Chile and North America they were just 20% of land cover. Substantially more needle-leaf forest was present in North America (21%) than in the other regions (<10%), and much of Chile was unvegetated (23%).

Some land-cover classes burned proportionately more than expected by chance given their areal distribution in the regions, but patterns were not consistent (Table 2; Fig. 4). In North America and Chile grasslands and cereal crops burned substantially more than expected but only as much as expected in the other three regions. Broad-leaf forest burned more than expected in southwestern Australia but not in the other regions. In North America shrubs burned more than expected and needle-leaf forest burned less than expected, but in the Mediterranean Basin, shrubs burned less than expected and needle-leaf forest burned more. In all regions, except for North America, more fires occurred in savannah than expected. Overall, very little fire occurred in unvegetated or urban areas.

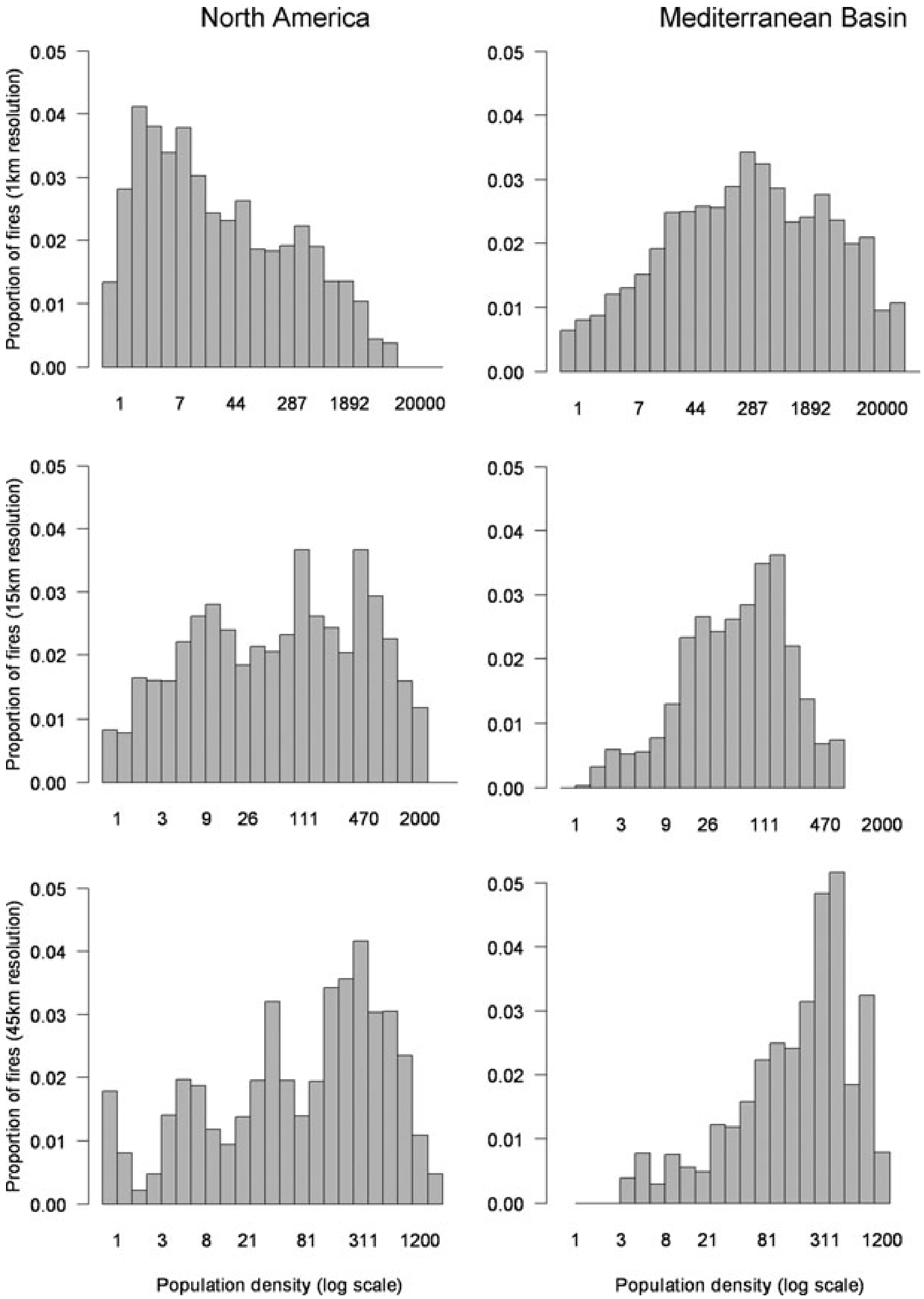

Figure 3. Proportion of fires within population density classes for 1-, 15-, and 45-km resolution windows.

Discussion

We found strong evidence that people are associated with the frequency and spatial distribution of fire similarly in all five Mediterranean-climate regions. Both mean and median population densities were consistently and substantially higher in areas with fire than in areas that did not burn; fires in Mediterranean-climate regions tended to occur close to people. Despite their convergence in ecosystem structure and function, Mediterranean-climate regions do vary in fire history, land-use history, or socioeconomic and political conditions (Pignatti et al. 2002; Carmel & Flather 2004; Vogiatzakis et al. 2006). Because of these differences, variations among the regions in population densities and land cover are not surprising. But these differences make the consistency of spatial relationships between people and fire across the five regions even more striking. The spatial pattern of fires

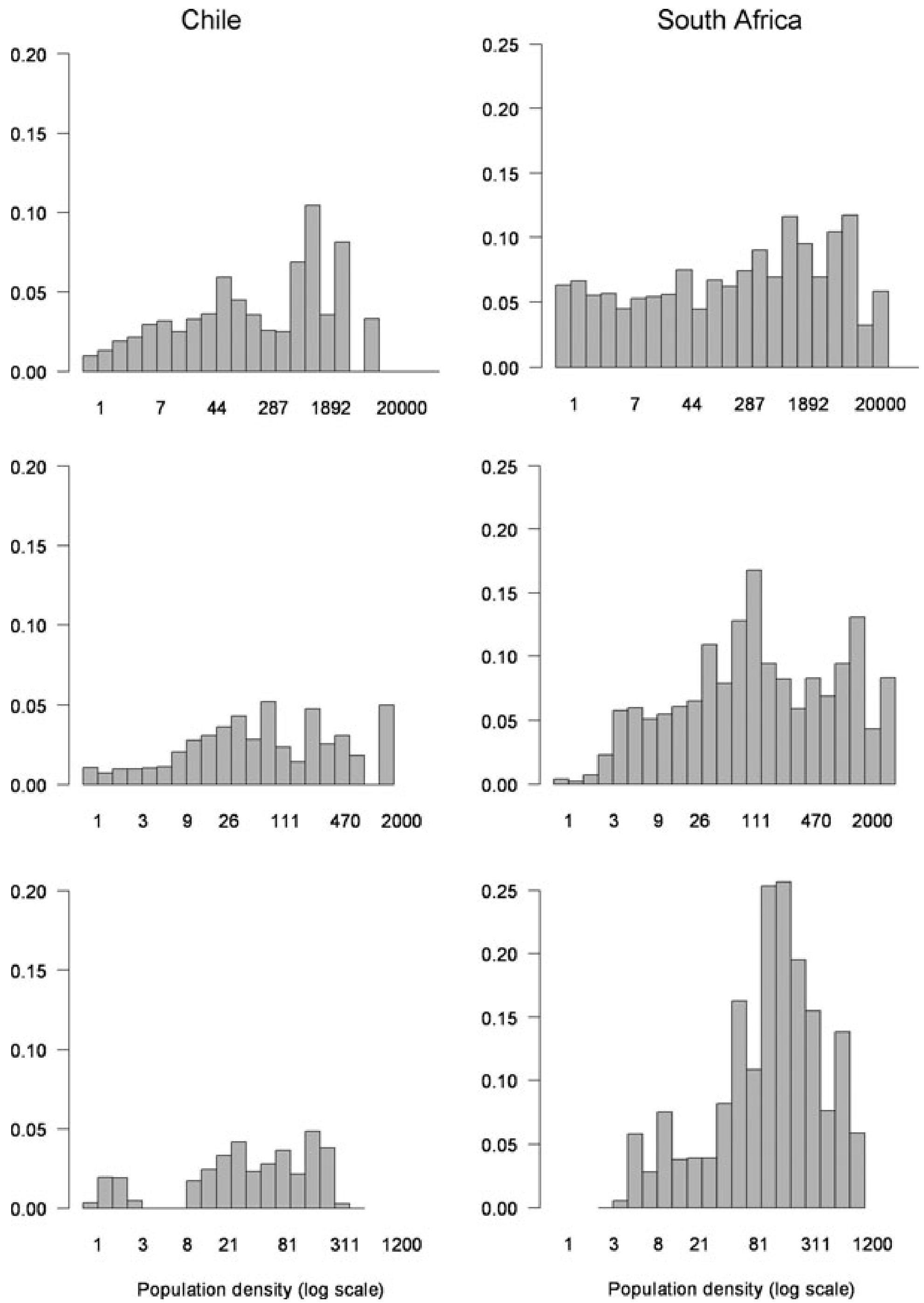

Figure 3. (continued)

in any region depends on complex interactions between ignition sources, landscape characteristics, and fuel continuity (Whelen 1995). So the consistent relationship between fire and population density suggests that the presence of people in Mediterranean-climate regions overrides these other factors.

Understanding the distribution of fire in Mediterranean-climate ecosystems is critical due to the vulnerability of its unique vegetation to repeated burning. Unlike other ecoregions in which decreased fire frequency threatens some species (Allen et al. 2002), in Mediterranean-climate ecoregions, the conservation concern is increased fire frequency (e.g., Keeley et al. 1999; Montenegro et al. 2004; Badia-Perpinyà & Pallares-Barbera 2006). The persistence of native plants is threatened and may have cascading ecological effects (Barro & Conard 1991; DellaSalla et al. 2004). Because Mediterranean regions are highly heterogeneous, the

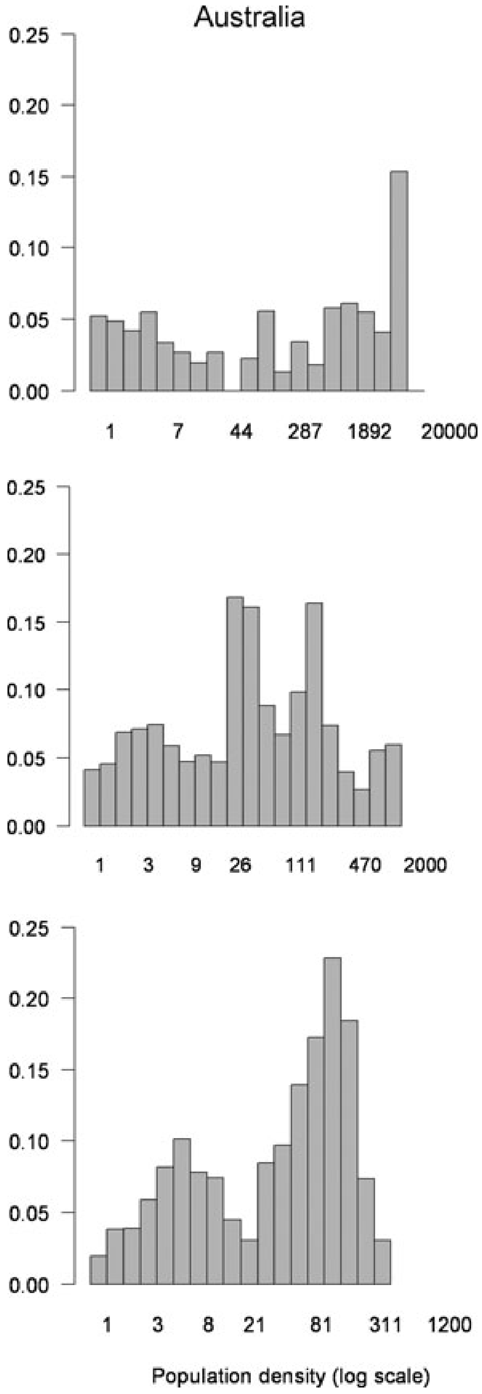

Figure 3. (continued)

sensitivity of different plant species to specific fire frequencies will vary (Public Library of Science ONE DOI:10.1371/journal.pone.0000938. 2007). Nevertheless, identifying where the landscape is likely to burn frequently is an important step in identifying areas vulnerable to the extirpation of native species.

Table 2. Ratio of the proportion of fires by land-cover type and proportion of land-cover type in the landscape.*

Land-cover type	*Mediterranean Basin*	*North America*	*Chile*	*South Africa*	*SW Australia*
Grass/cereal	0.79	1.76	1.72	1.09	0.85
Broad crops	1.07	1.70	1.65	0.55	0.49
Shrubs	0.42	1.35	1.00	0.79	0.43
Savannah	2.01	0.72	1.51	1.46	1.35
Broad leaf	0.80	0.45	1.02	1.62	1.90
Needle leaf	2.01	0.54	1.03	0.94	2.64
Unvegetated	0.06	0.17	0.03	0.13	0.06
Urban	1.92	0.89	1.88	1.41	0.96

**A ratio of 1.0 means fire occurred in a land-cover type as often as would be expected by chance, >1.0 means that fire occurred more often than expected, and <1.0 less often than expected by chance.*

The association of people with the spatial distribution of fire occurrence is likely due to the fact that humans now cause the majority of ignitions in all five Mediterranean-climate regions (Bond & van Wilgen 1996), and human ignitions are likely to occur close to roads and human infrastructure (e.g., Yang et al. 2007; Syphard et al. 2008). Nevertheless, our results also showed that fire occurrence consistently peaked where population densities were intermediate, which suggests that fire patterns in Mediterranean-climate regions are related to the spatial arrangement between people, urban development, and fuel. When population density is lowest, human ignitions are also low but increase with population density. Nevertheless, there appears to be a threshold above which fire occurrence declines, possibly due to less open space and fuel fragmentation caused by urban development or other land-use change. Fire-suppression resources also tend to be concentrated near urban areas (Calkin et al. 2005), and intermediate-density housing when located within wildland vegetation is classified as the wildland–urban interface (WUI) in the United States and given special fire-management considerations (Radeloff et al. 2005).

The relationship between people and fire in our study was most pronounced at the 15- and 45-km scales of analysis. Many ecological processes and spatial relationships have characteristic scales or space and time intervals over which the process can be detected (Shugart 1998). One explanation for the scale effect in our results is that analysis with the 15- and 45-km window sizes could include pixels where fires did, and did not, burn. The observed relationship and scale dependence of the results may therefore have been related to the relative proportion of burned cells within a window. At the 1-km resolution, the pixel either burned or it did not, and the analysis did not account for neighborhood effects.

Although our primary focus was to assess the relationship between population density and fire, other researchers have shown that land use and land cover may be important covariates of fire patterns due to their effects on fuel types, flammability, and human use of fire (e.g., Viedma et al. 2006; Baeza et al. 2007). In our analysis some land-cover types burned more frequently than expected, but no systematic differences were observed.

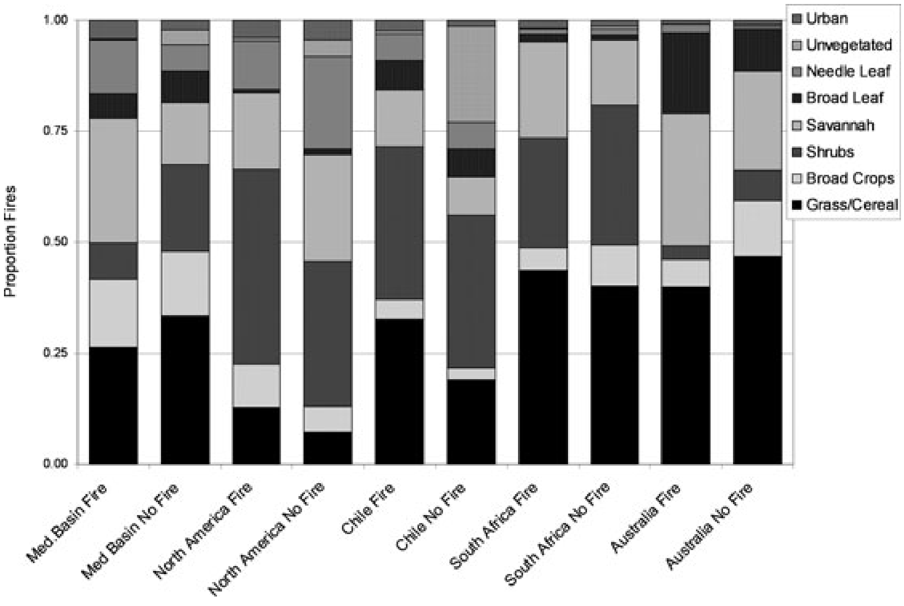

Figure 4. Aerial proportion of land-cover classes in the ecoregions and within pixels with an active fire in 2005.

Therefore, the patterns we observed in land-cover types were likely related to unique combinations of human land use and management practices within each region. For example, in North America, needle-leaf forest burned less than expected, whereas shrublands burned more. Fire suppression has successfully excluded fire from California's high-elevation-mixed conifer forests. On the other hand, the disproportionately high level of fire in shrubs is likely due to housing development and increased human ignitions in low-elevation areas where these shrubs (i.e., chaparral) are common (Keeley et al. 1999). More fires than expected in needle-leaf forests in the Mediterranean Basin may be due to land abandonment, which has resulted in substantial increases of fire in pine forests (Pausas & Vallejo 1999).

In North America and Chile fire burned more in grasslands and cereal crops than expected. Grasslands can sustain and even promote higher fire frequencies than other land-cover types (Mack & D'Antonio 1998), a major conservation concern in southern California, where exotic annual grasses have replaced native shrublands under unnaturally high fire frequencies (Haidinger & Keeley 1993). Problems with exotic annual grasses have also been reported in Chile and Australia (Pignatti et al. 2002) and may become more pronounced if fire frequency continues to increase.

Conclusions

Mediterranean-climate ecosystems are among the most biologically diverse regions in the world with rates of endemism ranging from 23% (Chile) to 75% (southwestern Australia), and at least 15% of the taxa in Mediterranean-climate ecosystems are threatened (Calow 1998). Our results suggest that conservation planners in Mediterranean-climate regions should seriously consider human alteration of fire patterns. Although we used fire data for only 1 year, the consistency in our results demonstrates that, regardless of the overall fire frequency in a region and its annual weather-driven variations, it may be possible to predict where fires are concentrated. Our results therefore provide a foundation for further research and planning to identify where frequent fire threatens vulnerable Mediterranean-climate plant species.

Future research should identify regionally specific ranges of population densities where fire occurrence is highest, be conducted at the scales most relevant to planning and management, and incorporate other drivers of fire pattern, such as biophysical variables. Finally, compact development should be studied for its potential to mitigate the effects of human presence by limiting expansion into undeveloped vegetation. Education efforts to reduce human-caused ignitions were once the foundation of outreach programs, such as Smokey Bear; perhaps the time has come to bring the bear back from semiretirement.

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Comparing the role of fuel breaks across southern California national forests

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ABSTRACT

Fuel treatment of wildland vegetation is the primary approach advocated for mitigating fire risk at the wildland–urban interface (WUI), but little systematic research has been conducted to understand what role fuel treatments play in controlling large fires, which factors influence this role, or how the role of fuel treatments may vary over space and time. We assembled a spatial database of fuel breaks and fires from the last 30 years in four southern California national forests to better understand which factors are consistently important for fuel breaks in the control of large fires. We also explored which landscape features influence where fires and fuel breaks are most likely to intersect. The relative importance of significant factors explaining fuel break outcome and number of fire and fuel break intersections varied among the forests, which reflects high levels of regional landscape diversity. Nevertheless, several factors were consistently important across all the forests. In general, fuel breaks played an important role in controlling large fires only when they facilitated fire management, primarily by providing access for firefighting activities. Fire weather and fuel break maintenance were also consistently important. Models and maps predicting where fuel breaks and fires are most likely to intersect performed well in the regions where the models were developed, but these models did not extend well to other regions, reflecting how the environmental controls of fire regimes vary even within a single ecoregion. Nevertheless, similar mapping methods could be adopted in different landscapes to help with strategic location of fuel breaks. Strategic location of fuel breaks should also account for access points near communities, where fire protection is most important.

1. Introduction

Wildfire is a key natural process in many ecosystems, but fire frequency, extent, and/or severity have surged across the globe in recent decades (Bowman et al., 2009; Flannigan et al., 2009; Westerling et al., 2006). The social and economic consequences of these fires are immense, with dramatic increases in property destruction and firefighting expenditures (Butry et al., 2001; NIFC, 2009). Altered fire regimes also threaten ecosystem integrity and biodiversity (Pausas and Keeley, 2009; Pyne, 2004). In many parts of the world the fire problem has been exacerbated by the continued expansion of the wildland–urban interface, where homes and lives are most vulnerable to wildfires, and where human ignitions increase the likelihood of fire occurring (Radeloff et al., 2005; Syphard et al., 2007). Mitigating the risk of wildfire at the wildland–urban interface, therefore, is now described as a major objective in the National Fire Plan (2001), the Healthy Forests Restoration Act (2003), and other federal fire management documents. The primary approach advocated for mitigating fire risk is to reduce hazardous fuel loads through fuel treatments of vegetation in wildland areas. In the last decade, expenditures on fuel treatments and area treated has increased markedly (Mell et al., 2010), with U.S. federal land management agencies receiving billions of dollars and treating millions of hectares of land (Schoennagel et al., 2009).

Despite this recent surge in treatment area and expenditure, fuel treatments have been a cornerstone of fire management in the U.S.A. for the better part of the 20th century. Yet, little systematic research has been conducted to understand what role fuel treatments have played in controlling fire, which factors influence this role, or how the role of fuel treatments may vary over space and time. A number of simulation studies have improved our understanding of potential fuel treatment effectiveness in modifying forest fire behavior (e.g., Finney et al., 2007; Miller and Urban, 2000; Schmidt et al., 2008). However, most empirical studies have focused on relatively localized effects when fires have intersected fuel treatments on forests (e.g., Finney et al., 2005; Martinson and Omi, 2003; Raymond and Peterson, 2005; Schoennagel et al., 2004). Due to this relatively small temporal and spatial scale (but see

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Syphard et al., in press-b), these studies have not contributed to an understanding of factors that influence sustainable fuel treatment performance over broad landscapes. This is important because many parts of the western U.S. that intersect with urban environments comprise heterogeneous landscapes that include forest and non-forested ecosystems and because strategic planning requires an understanding of how repeated fire events over time are affected by fuel treatments.

Due in part to the paucity of appropriate research, there is no comprehensive fire policy in the United States that provides forest mangers with science-based guidance on where, how, and when fuel treatments should be conducted (Agee et al., 2000; Franklin and Agee, 2003). Instead, within-agency policies are established and implemented according to the agencies' missions and objectives, and many policies are not publicly reviewed or debated (Franklin and Agee, 2003). Developing scientifically based general principles and guidelines for using fuel treatments to control fires could benefit managers if these guidelines were to facilitate decision-making with regards to strategic placement and tactical response. Given limits in time and money, managers need to prioritize where to place new fuel treatments and to determine the level of maintenance needed for current fuel treatments (Dellasala et al., 2004). Thus, a scientifically based methodology and set of principles could make the decision-making process not only easier but more defensible as well. Furthermore, a better understanding of the factors that influence the role of fuel treatments could lead to the identification of additional management considerations and the development of improved management practices.

The primary problem with development of general guidelines for fuel treatments is that fire-prone regions are highly variable with regards to their natural fire regimes and the factors that control them. Fire regimes vary as a function of forest type, fuels, terrain, climate, and ignition sources (Pyne et al., 1996; Keeley et al., 2009), and fuel treatment effectiveness may also vary according to these factors (Schoennagel et al., 2004). In addition, human development and other infrastructure strongly influence fire regimes and vulnerability to fire. Humans start and stop fires both directly (e.g., via suppression or accidental ignitions) and indirectly (e.g., via land use planning, land cover change, exotic species introduction, climate change), and their influence varies by scale and by locale (Cardille et al., 2001; Prestemon et al., 2002; Syphard et al., 2009). These variations in fire regime and human influence complicate the notion of general principles because management programs need to account for these differences (Noss et al., 2006).

Another reason that a "one size fits all" approach to fire management is problematic is that fuel treatment objectives are likely to vary from region to region, particularly for wildland areas versus the wildland–urban interface (Keeley et al., 2009). In wildland areas, particularly in western U.S. forests, fuel treatments are intended to change fire behavior and to reduce the severity of fire effects, whereas fuel treatments in the wildland–urban interface are intended to prevent fire from spreading into communities (Radeloff et al., 2005; Reinhardt et al., 2008). Therefore, the effectiveness of fuel treatments, and the factors that contribute to their effectiveness, may change as a function of fuel treatment objectives.

One way to determine how well certain guidelines may transfer from region to region is to identify which factors affecting fuel treatment outcome are most likely to vary. Identifying these could help to determine what aspects of plans need to be developed separately for each management area. Common decision-making tools could be developed that account for regional differences in those variables. If there are factors that are universally influential across different regions or landscapes, these could help in the development of general management considerations.

In California, where a substantial portion of the landscape comprises non-forested ecosystems such as chaparral and sage scrub, fuel breaks have been a major part of fire management activities since the 1930s (Davis, 1965). Unlike forests where mechanical fuel treatments remove only surface fuels (preserving larger, older trees), fuel break construction in chaparral typically involves complete removal of vegetation, chemical herbicides, and permanent conversion of native shrublands to weedy herbaceous associations (Wakimoto, 1977).

In southern California, differences in natural fire regimes and the way fire regimes have been altered by past land use complicate fire management in the region. In the shrubland-dominated foothills and coastal valleys, fire frequency has substantially increased along with population growth and urban expansion (Keeley et al., 1999; Syphard et al., 2007). This increased fire frequency not only threatens homes and lives, but many shrublands cannot tolerate repeated fires and under such conditions are often replaced with non-native grasslands (Keeley and Fotheringham, 2003; Syphard et al., 2006). In shrubland-dominated regions, fuel manipulation projects involve a trade-off. On one hand, fuel breaks are needed to protect homes and lives, which are at an elevated risk in these crown fire shrublands; on the other hand, construction of fuel breaks typically involves complete removal of vegetation and may result in a range of ecological impacts. Thus, fire management in the region is greatly complicated by the need to balance both fire and resource management.

In the less extensive montane coniferous forests in the region, fire frequency has been unnaturally low during the last century, and fire hazard has consequently increased due to accumulated fuels associated with fire suppression and logging (Keeley, 2006), problems similar to other forests in the western U.S. (Miller et al., 2009). Because thinning and fuel manipulation is intended to improve forest vigor and reduce risk of catastrophic loss to wildfire (often by restoring forests to more historic conditions), fuel treatments and resource benefits are likely to be compatible in these forested regions (Schwilk et al., 2009). However, this model of fuel accumulation and ecological compatibility with fuel treatments has often been inappropriately applied to chaparral (Keeley and Fotheringham, 2004, 2006).

To better understand the factors that influence the role of fuel treatments in controlling large fires in southern California, and how the role of fuel treatments varies across different landscapes, we assembled a spatial database of fuel breaks and fires from the last 30 years in four national forests. For this analysis, we only considered fuel manipulation projects that were clearly intended to serve as fuel breaks, which are defined as wide blocks, or strips, on which vegetation was manipulated to create lower fuel volume and reduced flammability (Green, 1977). Thus, prescribed fires and burn piles were excluded, as were any dozer lines created to aid suppression activities during the time that a fire was burning. We analyzed relationships among fires and fuel breaks to answer:

(1) What are the most important environmental and management variables affecting the role of fuel breaks in controlling large fires, and do these factors vary among national forests?
(2) What are the primary factors affecting the spatial pattern of fires and fuel break intersections, and do they vary among national forests?

Because we restricted our analysis to U.S. Forest Service national forests, we assumed these landscapes would be broadly similar in the tactical approaches used in the construction and maintenance of fuel breaks. Thus, this study could help determine how well management approaches for one national forest may transfer to other national forests. Also, on these largely non-forested landscapes we assumed that the primary management objective for fuel breaks in the region is to control the spread of fire and protect communities.

Table 1
Characteristics of fires and fuel breaks in the four southern California national forests. Fire rotation was calculated from 1980 to 2007.

	Angeles	Cleveland	Los Padres	San Bernardino
Area (ha)	26,375	21,117	61,464	30,408
Number of fires since 1980	175	118	96	253
Fire rotation period (years)	32	14	35	30
Fuel break length (km)	1834	482	550	1199

2. Methods

2.1. The national forests of southern California

The area of study included the Los Padres, Angeles, San Bernardino, and Cleveland National Forests (Table 1), an area spanning the extent of the state's South Coast Ecoregion (Keeley, 2006), which encompasses approximately 3.4 million ha (8% of the state) and is home to more than 19 million people (US Census 2000) (Fig. 1). Although the region is the most threatened hotspot of biodiversity in the continental US (Hunter, 1999), the national forest lands together occupy more than 1.5 million ha and offer some measure of protection for the region's biodiversity.

The South Coast Ecoregion is characterized by a Mediterranean-type climate, with cool, wet winters and warm, dry summers. Chaparral shrublands are the most extensive vegetation type, but there is extraordinary ecosystem diversity in the region, owing largely to a relatively sharp elevational gradient from sea level to more than 3500 m. Therefore, chaparral forms a mosaic with other vegetation types, including coastal sage scrub shrublands, grasslands, oak woodlands, and montane coniferous forests, and natural fire regimes are correspondingly variable (Keeley, 2006; Wells et al., 2004).

Fire management on the national forests is the responsibility of the U.S. Forest Service. The two primary strategies for management are to (1) suppress all actively burning fires, and (2) reduce the extent of future fires through mechanical construction of fuel breaks and limited use of prescription burning. We focus exclusively on fuel breaks in this study.

2.2. Data for dependent variables: fuel break outcome and fire/fuel break intersections

We acquired information on historic fuel breaks and their location from U.S. forest service staff on each of the four forests. We developed a digital spatial database of fuel breaks for the four forests by combining existing GIS layers with files that we created ourselves by digitizing fuel breaks that had been drawn on paper maps. Due to the substantial number of fuel breaks that were hand drawn, we conducted follow-up interviews to validate the newly digitized data.

On all the forests, we overlaid the fuel break GIS layer with fire perimeter polygons compiled by the California Department of Forestry-Fire and Resource Assessment Program (CALFIRE). The fire perimeter data represent the largest fires, with a minimum mapping unit of 4.04 ha (10 acres).

To evaluate factors affecting fuel break outcome, we first used a GIS overlay to identify all events in which a fire intersected a fuel break (within a 100 m buffer distance to account for potential data uncertainty). These events were considered potential case studies to retain for subsequent analysis. To be included for consideration, the date of the fire had to be later than the date of fuel break construction. For the case studies, we conducted a preliminary assessment as to whether fires stopped or crossed over fuel breaks, and then confirmed the outcome during personal interviews with firefighters who had first-hand knowledge of the event.

Table 2
Variables considered and retained in the multiple regression models explaining number of fire and fuel break intersections in three national forests. All variables retained in the models are designated through a significance symbol.

	Angeles	Los Padres	San Bernardino
Elevation	*		*
Slope			
Solar radiation		*	
USFS fuel model	*		*
Distance road		**	
Distance development			
Distance trails		**	
Historic fire frequency	***	**	***
Ignition density	*	*	
Deviance explained	37.27	27.55	54.7

[*] $p = 0.05$.
[**] $p = 0.01$.
[***] $p = 0.001$.

Although data for some of the explanatory variables were acquired during personal interviews, we also used a GIS to extract information for other explanatory variables to relate to the fuel break outcome. See below for description of explanatory variables. For this analysis, we extracted data only from the portion of the fuel break that intersected the fire and averaged values across that area. In some cases, fires stopped at a portion of the fuel break, but ultimately crossed over the fuel break. For those cases, we classified the fuel break as not having stopped fire (for statistical analysis purposes only), and we only extracted explanatory variables for the section of the fuel break where the fire crossed over.

To analyze factors influencing the number of times fires intersected fuel breaks, we spatially stratified and classified all fuel breaks according to the number times they intersected fires during the study period. We only considered fires that had occurred since 1980, and to ensure that all fuel breaks had an equal chance of experiencing a fire, we only looked at fuel breaks that had been constructed before 1980. From this spatially stratified layer, we randomly selected point samples (greater than 1 km apart, to avoid spatial autocorrelation) to extract environmental data used as explanatory variables. The dependent variable was number of intersections at each sample location.

2.3. Explanatory variables for role of fuel breaks

The factors we considered as potentially influencing the role of fuel breaks on the forests included human and biophysical variables that have previously explained landscape-scale fire patterns in the region (Syphard et al., 2008), and that we used in a previous study of fuel breaks on a single national forest (Table 2, Syphard et al., in press-a). In addition to static landscape features, we also considered variables related to the actual event when a fire intersected a fuel break, including characteristics of fires, fuel breaks, vegetation age, and firefighting activities.

For the human variables, we considered distance to roads, trails, and development (Table 2) because fire ignitions in the region tend to occur near human activities (Syphard et al., 2008). We also hypothesized that these human variables may influence firefighting access and resources. For these three variables, we developed continuous grid surfaces reflecting the Euclidean distance to the nearest feature (road, trail, or development) and extrapolated values from those grids for the areas where fuel breaks intersected fires.

Biophysical variables (including climate, terrain, and fuels) influence fire spread rate, fuel moisture, flammability, and fire intensity (Pyne et al., 1996; Whelan, 1995). Therefore, we evaluated the potential influence of elevation, slope, solar radiation, vegetation age, and fuel model on fuel break outcome (Table 2). After

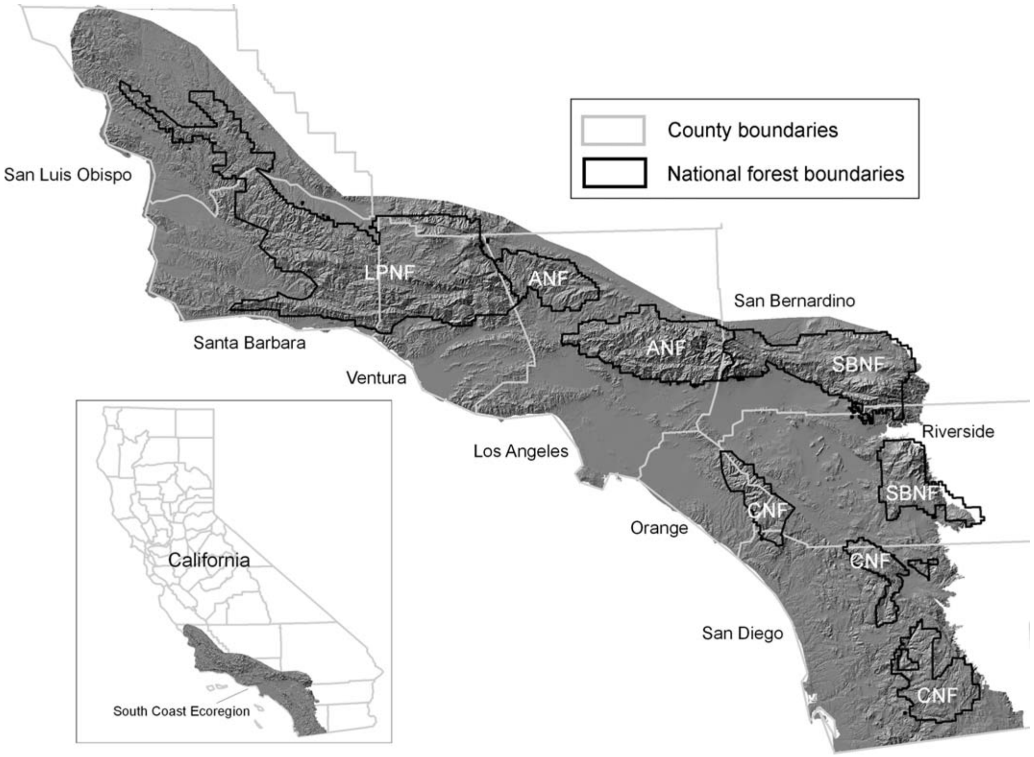

Fig. 1. Study area showing the four national forests of southern California. ANF is Angeles National Forest, CNF is Cleveland National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

preliminary regression analysis, we found that climate variables were significantly correlated with terrain variables, so we did not include them. Because most fires are stand-replacing in southern California shrublands, we determined vegetation age by calculating the time since last fire in the area immediately adjacent to the fuel break before the fire intersected it.

Severe weather conditions are likely to strongly influence fire spread rates and intensity (Moritz et al., 2004; Keeley and Zedler, 2009), and lead to conditions that are dangerous for firefighters (Halsey, 2005). However, previous analysis indicated that, because weather is highly variable over space and time, it is difficult to attribute exact weather conditions to the moment of intersection (Syphard et al., in press-a). Instead, we considered fire size and season as potential explanatory variables because they indirectly reflect the severity of weather conditions (Finney, 2003; Westerling et al., 2004), particularly because of the importance of autumn Santa Ana winds in this region (Moritz et al., 2010). We calculated fire size from the fire perimeter data through GIS calculations, and we derived fire season from the attributes of the fire perimeter data. We reclassified the months of the fires into winter and spring (January through May), summer (June through August), and autumn (September through November) to reduce the degrees of freedom in the data.

We obtained information on fuel break condition and firefighting activities through personal interviews with firefighters and managers who were most familiar with the fire events. Fuel break length was calculated from the GIS files, but data on fuel break width were largely unavailable for all four forests. Because written fuel break maintenance records were often unavailable, we determined how well the fuel break had been maintained by asking fire personnel to indicate the condition of the fuel break at the time the fire intersected it on a scale from one to three. The ranking reflected poor to excellent conditions, with poor reflecting fuel breaks where the vegetation had almost entirely regrown, and excellent reflecting fuel breaks that were either entirely grass, or no vegetation had regrown. To evaluate the importance of management activities, we also asked personnel to indicate whether they were able to gain access to the fuel break for firefighting (yes or no) and whether they had sufficient resources available (including manpower and equipment) to fight the fire, again on a scale of one to three, from poor (no resources) to excellent (full resources).

2.4. Explanatory variables for mapping number of intersections

To explain and map areas where fires and fuel breaks are most likely to intersect, we evaluated the same human and biophysical variables as for the fuel break outcome (Table 2). However, we did not consider fire and management variables related to single events because we were interested in trends across the entire study period (1980–2007). In addition, we hypothesized that significantly more fire and fuel break intersections would occur in areas that were historically fire-prone. Therefore, we additionally explored historic fire frequency (derived through overlay of fire perimeters from 1878 to 2007) as well as spatially interpolated ignition density as explanatory variables.

2.5. Fuel treatment outcome: structural equation modeling

Structural equation modeling provides advantages over traditional multiple regression analysis because it uses existing information to examine potential causal pathways among intercorrelated variables and identify indirect relationships (Bollen, 1989; Grace and Pugesek, 1998). The model is statistically evaluated to determine the degree of consistency with empirical data and compare the outcomes of alternative models. Although structural equation modeling is a confirmatory approach that tests a priori hypotheses of about interrelationships among variables, it is often essential to use exploratory regression and correlation analysis to suggest which pathways to explore (Grace, 2006).

For the different national forests, we initially conducted correlation analyses and built simple and multiple logistic regression models to explore the relationships among the explanatory variables and fuel break outcome. We used logistic regression because the response variable for fuel treatment outcome was binary, indicating whether the fuel treatment stopped the fire or not. Based on the hypothesized interrelationships developed through correlation and regression analysis, we developed and tested structural equation models using Mplus version 5.1 software. Because we modeled categorical outcomes, we used the weighted least-squares with mean and variance adjustment (WLSMV) estimator. To ensure that we retained only the important pathways in the final models, we sequentially removed one path at a time to ensure that, if a path were removed, the chi-square did not increase more than 3.84 points (the single degree-of-freedom test) (James B. Grace, personal communication). We also examined the fit of alternative models through *p*-values, root mean square error of approximation, and weighted root mean square residual (Hooper et al., 2008).

2.6. Number of intersections: multiple regression and predictive mapping

To evaluate the relative influence of the explanatory variables on the number of times fires intersected fuel breaks on the forests, we developed simple and multiple Poisson regression models that were appropriate for count response variables (Agresti, 1996). Because the objective of this part of our study was to create predictive maps (rather than explore causal pathways), we only used multiple regression analysis, as opposed to structural equation modeling. We first conducted simple regression models with each variable (and quadratic terms for continuous variables) to establish rankings for entering the variables into a multiple regression.

For the multiple regression models, we entered variables according to the amount of deviance they explained [D^2, equivalent to the R^2 in ordinary least square models (Guisan and Zimmermann, 2000)] and only considered those variables that were significant at $p \leq 0.15$. We evaluated correlation coefficients in the models for all of the forests and avoided including two variables with a bivariate correlation ≥ 0.3. For each forest, we evaluated alternative plausible multiple regression models with different combinations of predictor variables and selected the best model as the one that explained the highest percentage deviance with the lowest Akaike information criterion (AIC) (Quinn and Keough, 2002). We also checked to ensure that overdispersion was not present in the models.

After selecting the best multiple regression models, we converted them into continuous map surfaces that reflected the predicted number of fires that would intersect fuel breaks across the entire forest. We created these maps by applying the Poisson regression formula and predicted coefficients onto the GIS layers of the significant explanatory variables (as in Syphard et al., 2008). We evaluated the correspondence of the predicted number of intersections to the actual intersections that occurred through Pearson correlation coefficients. We also quantified the magnitude of discrepancy among predicted and observed values by calculating the root mean square error (RMSE).

To test how well the models that explained the number of intersections on one national forest matched the models in the other forests, we applied the models developed on each forest to the entire South Coast Ecoregion and compared the maps. To quantify the spatial correspondence among the maps, we used a Pearson's correlation coefficient to calculate pairwise correlations (Termansen et al., 2006; Syphard and Franklin, 2009). High correlations among maps would indicate that the factors controlling the spatial pattern of fire and fuel break intersections were similar among the forests, and low correlations would suggest that those factors vary.

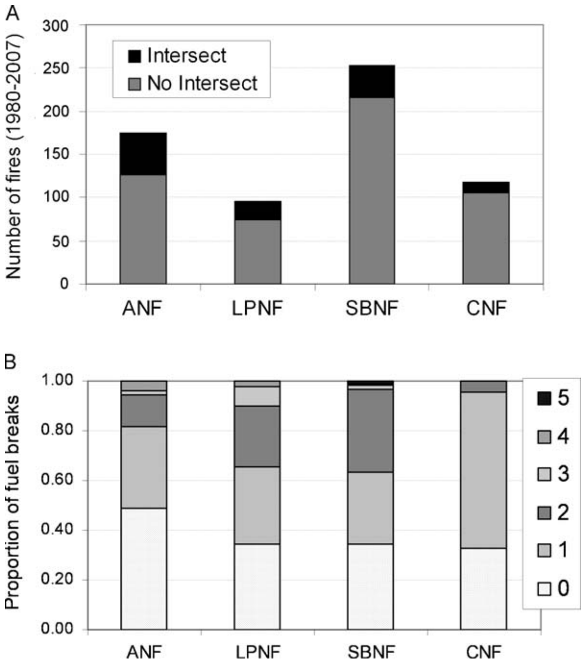

Fig. 2. Number of fires that occurred in four national forests divided into those that intersected a fuel break and those that did not intersect a fuel break (A); and proportion of fuel break area intersected by 0–5 fires from 1980 to 2007 (B). ANF is Angeles National Forest, CNF is Cleveland National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

3. Results

3.1. Summary of fuel break and fire intersections and outcomes

During the 28 years of the analysis, 641 fires occurred within the boundaries of the four national forests. On average, 23% of those fires intersected a fuels treatment, but the proportion of intersections varied among the forests (Fig. 2A). In fact, the number of intersections among fires and fuel breaks on the Cleveland National Forest was only 13 (11% of the intersections), and this small number precluded us from including that forest in our statistical analyses.

For the fuel breaks that we considered in our spatial analysis of intersections (i.e., those constructed on or before 1980), approximately 25–50% of the fuel break area never intersected a fire. On the other hand, approximately 10–45% of the fuel break area intersected multiple (two or more) fires. The proportion of fuel break area that intersected fires varied among the four forests (Fig. 2B).

When fires intersected fuel breaks, the percentage that stopped at the fuel breaks ranged from 22 to 47%, and the percentage that crossed over the fuel breaks ranged from 29 to 65%, depending on the forest (Fig. 3). We distinguished another group of fuel break intersections where fires crossed over fuel breaks, but the fuel breaks did change fire behavior enough to facilitate firefighter access and eventually help with the suppression of the fire. When this group is considered along with the other cases in which the fuel break held a portion of the fire, the percentage ranged from 10 to 23% (Fig. 3).

3.2. Fuel treatment outcome: structural equation modeling

Among the three national forests that we analyzed, there were seven variables that significantly affected fuel break/fire outcomes. However, the structural equation models revealed differences in the number and combination of important variables as well as

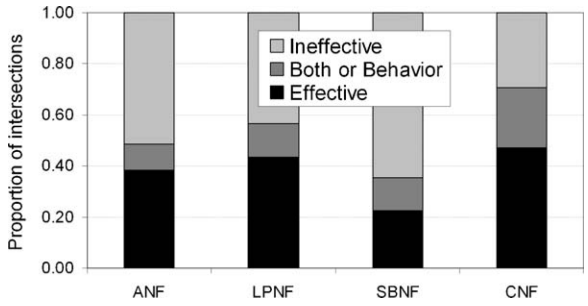

Fig. 3. Proportion of fire and fuel break intersections in four forests divided into those that effectively stopped a fire (Effective); those in which only a portion stopped a fire or that changed fire behavior (Both or Behavior); and those in which the fires crossed over the fuel break (Ineffective). ANF is Angeles National Forest, CNF is Cleveland National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

differences in the interrelationships among them. We tested alternative models with different explanatory variables and different direct and indirect effects. The final model varied among the forests (Fig. 4). Despite these differences, most of the variables were common to at least two of the three forests; and three variables were common to all forests: firefighter access, fire size, and fuel break condition.

Firefighter access was the only variable to directly improve the outcome in all three forests, and it was the most influential variable for the Los Padres and Angeles National Forests. The proportion of events in which firefighters had access to fuel breaks was slightly lower in the Angeles than in the other two forests (Fig. 5C). On the Los Padres and San Bernardino forests, fire size was directly and negatively related to fuel break outcome; in the Angeles, fire size negatively affected firefighter access and thus indirectly influenced fuel break outcome. On average, the fires were smaller in the Angeles, but fire sizes were highly variable on all of the forests (Fig. 6). On the Los Padres and Angeles forests, fuel break condition facilitated firefighter access to fuel break and thus indirectly improved fuel break outcome; the relationship was direct in the San Bernardino, which reported the largest proportion of fuel breaks with low scores for fuel break condition (Fig. 5B).

The Los Padres was the only forest for which season was not important in explaining fuel break outcome, as later-season fires (i.e., September through November) had a direct negative influence on outcome for the Angeles; and for the San Bernardino, later-season fires contributed to increased fire size, so the effect was indirectly negative. Most of the fires on the Los Padres occurred in the summer months, whereas fires in the autumn were most common for the other two forests (Fig. 5E). The Los Padres was the only forest in which firefighting resources were not influential in explaining outcome. On both the Angeles and San Bernardino, resources indirectly improved fuel treatment outcome; but on the Angeles, the primary relationship was by improving access and on the San Bernardino, the primary relationship was through reduction in fire size. The overall distribution of firefighting resources, according to the interviews, was variable among the forests (Fig. 5A). Finally, the Los Padres was the only forest in which fuel break length had a significant direct and positive impact on fuel treatment outcome, and this forest had longer fuel breaks, on average, than the other two forests (Fig. 6).

The Angeles was the only forest in which vegetation age was not important. On the Los Padres, younger vegetation surrounding the fuel breaks improved firefighter access to the treatment, so the relationship was indirectly negative. On the San Bernardino, the relationship was direct and positive. Although the average vegetation age was lowest on the San Bernardino, there was a lot of variability in age for all the forests (Fig. 6).

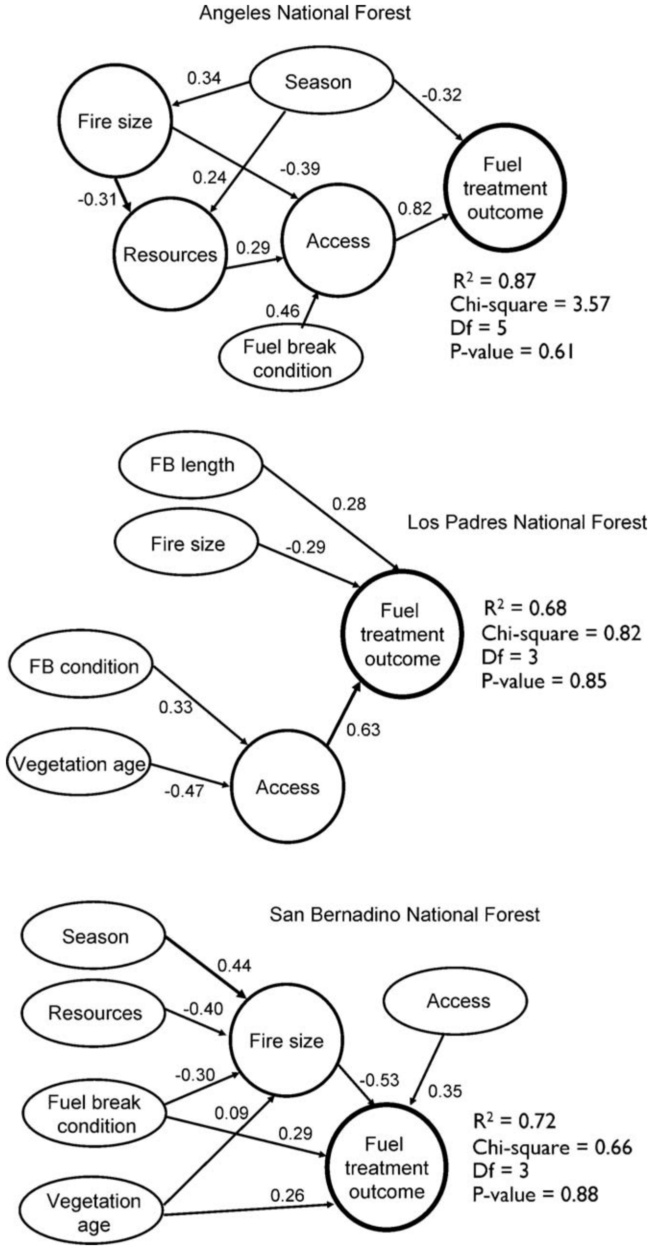

Fig. 4. Structural equation model of factors that directly and indirectly explain why fires stopped at fuel breaks in the Angeles, Los Padres, and San Bernardino National Forests. Solid arrows represent direction of effect, and coefficients shown along arrows are standardized values. Circles represent endogenous (or dependent) variables in the models. Due to insufficient number of fuel break/fire intersections the Cleveland National Forest was not included.

3.3. Number of intersections: multiple regression and predictive mapping

Of the variables we considered for explaining the number of fire and fuel break intersections in the forests, historic fire frequency was the only one that was retained in all three of the multiple regression models (Table 2). For all three forests, the number of intersections was strongly and positively related to the number of fires that had occurred since 1878 (date of the earliest fire in the database). Ignition density was also positively related to the number of intersections on the Angeles and Los Padres National

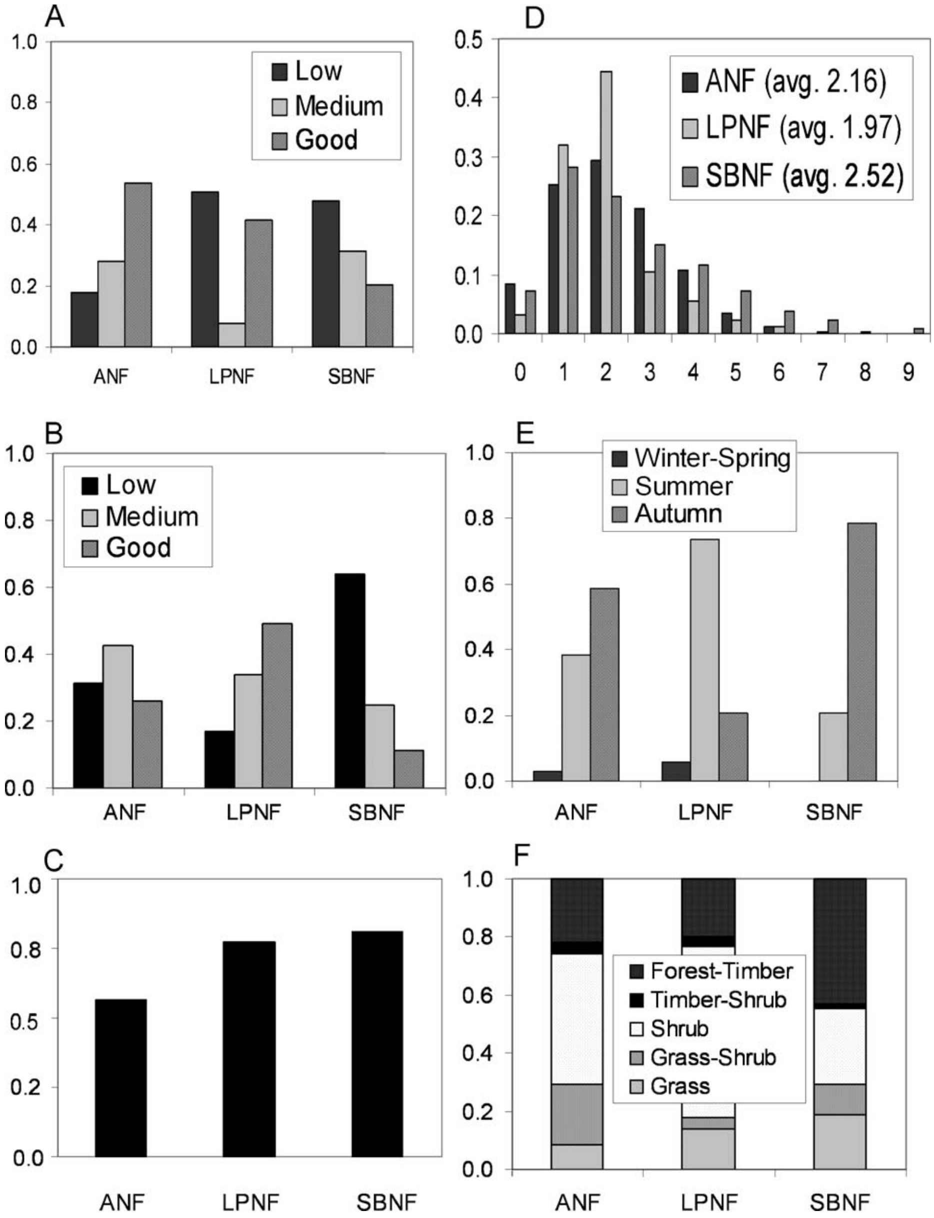

Fig. 5. Distribution of categorical variables for three national forests that were significant in any of the statistical models. The *y*-axis for all charts represents the proportion of observations within each forest. The charts represent (A) firefighting resources; (B) fuel break condition; C) Access to fuel break; (D) historic fire frequency (with the average for each forest indicated in the legend); (E) season when intersection occurred; (F) fuel type. ANF is Angeles National Forest, LPNF is Los Padres National Forest, and SBNF is San Bernardino National Forest.

Forests, but was not retained in the model for the San Bernardino National Forest. The Los Padres had the lowest average number of fires and lowest ignition density, whereas the San Bernardino had the highest fire frequency and ignition density (Figs. 5D and 6).

For both the Angeles and San Bernardino National Forests, the number of intersections was negatively related to elevation, which was slightly higher on average on the San Bernardino than the other forests (Fig. 6). The fuel model parameter was also significant in explaining model variation for only the Angeles and San Bernardino. A larger number of intersections occurred in forest and timber fuel models on the San Bernardino National Forest (“TU” or “TL”, Scott and Burgan (2005)), whereas the shrub models (“SH”, Scott and Burgan (2005)) were more influential in the Angeles (Fig. 5F). Three variables were retained in the multiple-regression model for the Los Padres that were not important in the other forests. On the Los Padres, fires were more likely to intersect fuel breaks when fuel breaks were in close proximity to trails, distance to roads was intermediate, and winter solar radiation was low. Both the average distance to trails and solar radiation were lower on the Los Padres than in the other two forests, but the average distance to roads was similar, with high variation in the three forests (Fig. 6).

The three map surfaces developed by applying the multiple-regression model formulas and coefficients to the GIS maps of the significant variables reflect a continuous probability distribution of where fires and fuel breaks are most likely to intersect (Fig. 6). The Pearson’s correlation coefficients between the observed number of intersections and the number of intersections predicted by the model ranged between 0.59 and 0.74 (Table 3), and the root mean squared error ranged from 0.28 to 1.31 intersections. The correlations among the three maps generated by the differ-

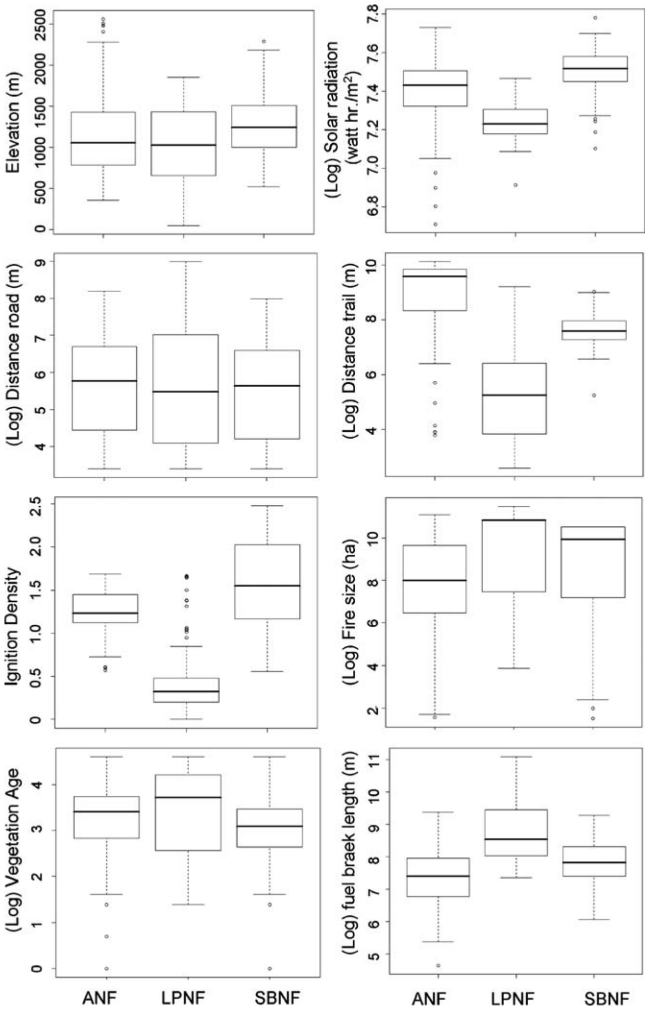

Fig. 6. Distribution of continuous variables for three national forests that were significant in any of the statistical models.

ent multiple-regression models were lower, particularly for the Los Padres model (correlation of 0.21 with the Angeles and 0.16 with the San Bernardino). The Angeles and San Bernardino maps, however, had a much stronger correlation (0.54) (Fig. 7).

4. Discussion

The four southern California national forests studied here all share several features in common; they are in rugged terrain, are dominated by non-forested ecosystems, and contain a substantial amount of wildland–urban interface. These national forests, however, differ in the proportions of vegetation types, biophysical characteristics, and the relative proportions of wildland–urban interface and intermix landscapes. These differences are part of the reason the significant factors explaining fuel break/fire outcomes and number of intersections were different among forests. Nevertheless, several factors were consistently important across all forests in explaining the number of intersections between fuel breaks and big fires and the role of fuel breaks in altering fire spread. These similarities support several general conclusions about the role of fuel breaks in controlling large fires in southern California.

Table 3
Pearson correlation coefficients among prediction maps for three national forests and among predicted and observed number of intersections within each forest. Root mean squared error (RMSE) is calculated between the observed and predicted number of intersections within each forest.

	Angeles	Los Padres	San Bernardino
Angeles map	1.00	0.21	0.54
Los Padres map	0.21	1.00	0.16
San Bernardino map	0.54	0.16	1.00
Observed *N* intersections	0.61	0.59	0.74
RMSE	1.31	0.76	0.28

One conclusion is that the primary role of fuel breaks in the region is to facilitate fire management activities. Two of the three fire management variables we considered (access and fuel break condition) were important in all three structural equation models (Fig. 4), and firefighter resources was important for two of the forests (Angeles and San Bernardino). Furthermore, while other important variables in the models (related to vegetation structure, fire size, and season) were not directly related to management, these variables often indirectly influence management, for example, by affecting access to treatment areas. Demonstrating the strength of these indirect effects is one of the benefits to structural equation modeling (Grace, 2006).

Firefighter access to fuel breaks was the most influential factor in fuel treatment outcome for the Los Padres and Angeles, and was also highly significant for the San Bernardino. The high level of significance for this variable supports the notion that, without firefighters present to control fires, fires will generally not stop at fuel breaks. Although three fires stopped on their own at the top of ridges on the San Bernardino, these fires constituted less than 1% of the cases. Only one fire stopped passively on the Los Padres, and none of the fires in our analysis stopped without firefighters on the Angeles. Despite this conclusion, it is important to point out that the fire perimeter database only includes fires greater than 10 ha; therefore, it is possible that some smaller fires do stop passively (i.e., without fire fighting actions) at fuel breaks. Many fire management personnel understand that fuel breaks are unlikely to passively stop most fires, particularly during extreme weather conditions, but the public, news media, and policy-makers may unrealistically expect otherwise. Our results show that such beliefs could lead to a false sense of security about the protective value of fuel breaks.

Most of the largest fire events in southern California occur during severe weather conditions in autumn, prior to winter rains, when dry, offshore Santa Ana winds can exceed 30 ms^{-1} (Miller and Shlegel, 2006; Moritz et al., 2010). Fighting fires during these weather conditions can be extremely dangerous, and during these wind events, multiple fires often break out simultaneously. These severe weather conditions likely explain why fire size was another variable that was highly significant in explaining fuel treatment outcome in all three forests. Discussions during the interviews confirmed that fires were more difficult to control, and likely to become large, under severe weather conditions. There are a number of reasons for this: the speed of such fires, which can cover 10,000 ha within a day or two, and thus the lack of time for accessing fuel breaks, the danger of aggressively attacking fires under such conditions, and firefighting resources spread too thin because of multiple fire fronts. Consistent with the effect of fire size, fire season was significant on the Angeles and San Bernardino because Santa Ana winds typically occur during the fall (and this was the season when fuel treatment/fire outcomes were poorest). The reason that season was not important for the Los Padres, but fire size was, is that Santa Ana winds are much less predictable there (Moritz et al., 2004, 2010). The Los Padres regularly experiences strong, hot wind downcanyon wind events known as “sundowners,” typically in summer (Ryan, 1996), but these are not annual events as are Santa Ana winds. It is possible for severe-weather fire events to occur in any season, not just the fall, across the entire southern California region. This explains why fire size was important on all three forests.

In addition to fire management and fire weather (i.e., size and season), there was evidence that vegetation structure played an

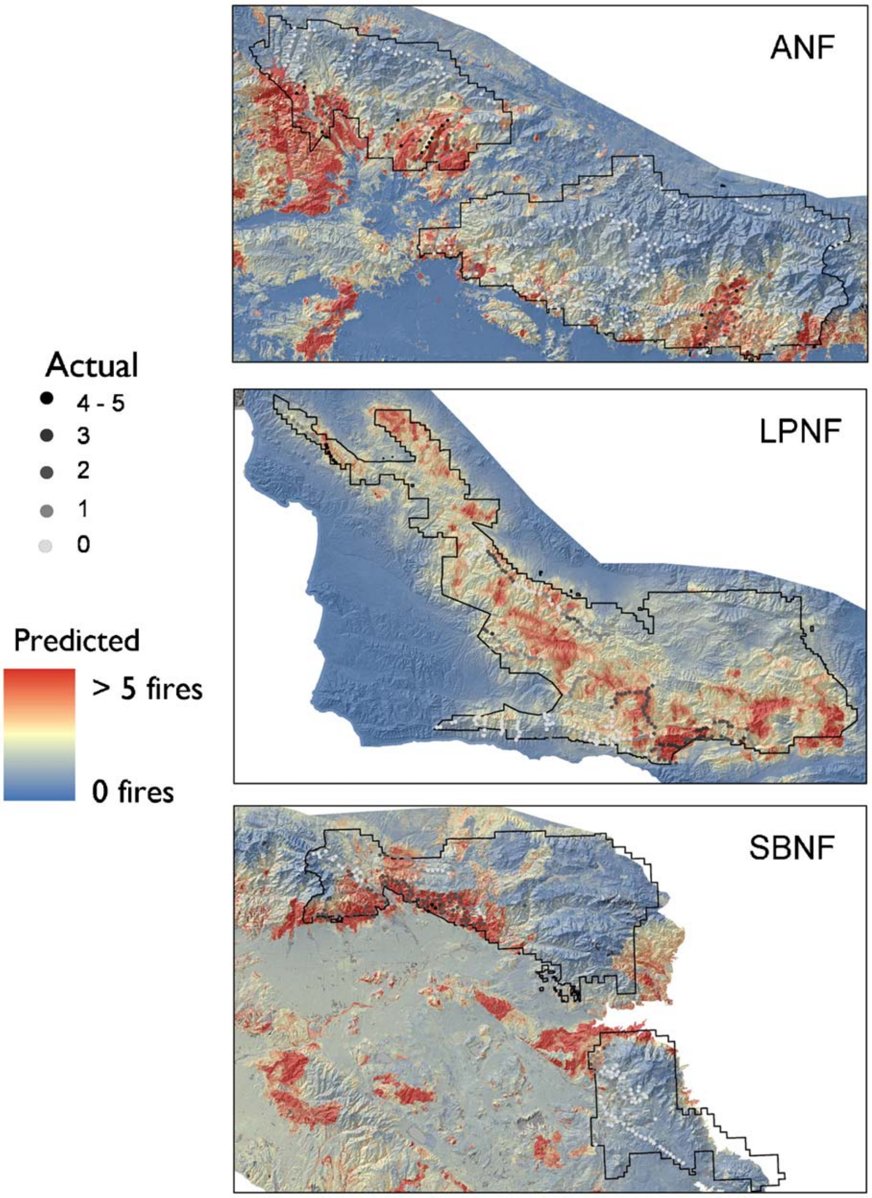

Fig. 7. Maps showing predicted distribution of areas most likely to intersect fuel breaks in the Angeles, Los Padres, and San Bernardino National Forests. The sample points along the fuel breaks also show the actual number of times fires intersected fuel breaks at those locations from 1980 to 2007.

important role in improving fuel break outcome in all three forests, and this was generally because well-maintained fuel breaks were much easier for firefighters to access in time to prepare the fuel break for suppression activities. Because young vegetation typically has a lower fuel load than old vegetation, one of the premises of conducting fuel manipulation is that young vegetation can directly slow or stop the spread of fire. However, in southern California shrublands, stand age and fuel loads play a limited role in stopping the spread of fire, particularly during extreme weather conditions, when fires often spread through or over very young age classes (Keeley and Zedler, 2009; Moritz, 1997; Moritz et al., 2004). Accordingly, while vegetation age was significant in the Los Padres, younger vegetation did not directly prevent fires from spreading, but helped facilitate firefighter access to fuel breaks. There are some parts of the Los Padres where, because of the lack of consistent Santa Ana influence, fuel age may play a role in controlling fire spread (Moritz, 1997). This particularly applies to the coastal area near the city of Santa Barbara. Regardless, the most significant relationship was between vegetation age and firefighter access.

Fuel break condition (i.e., how well it was maintained) played a similar role as vegetation age, and it was influential in all three forests. While the relationship was direct on the San Bernardino, better-maintained fuel breaks improved access to fuel breaks in the Los Padres and the Angeles, and thus, the relationship was indirect. Southern California chaparral forms a dense, continuous cover that is extremely difficult to maneuver in (Halsey, 2005), which likely explains why well-maintained fuel breaks improved the outcome.

As in the models for fuel break outcome, the models explaining the number of fire and fuel break intersections reflected regional landscape diversity and differences among the forests, while nevertheless suggesting several general conclusions. By far the most significant variable, and the only variable consistently significant for all forests, was historic fire frequency. This result is not surprising because areas that have burned most frequently in the past are likely to be most fire-prone in general. Ignition density patterns were also significant for two of the forests. Nevertheless, fire history was not the only factor explaining why fuel breaks intersect fires more in some places than in others. Fire and fuel break intersections were a function of a combination of biophysical and human variables for all the forests, but the biophysical variables were generally more important than the human ones. This is consistent with other regional studies that have shown biophysical factors to be strongly related to patterns of fire occurrence and area burned, whereas human variables are most significant for explaining ignition patterns and fire frequency (Parisien and Moritz, 2009; Syphard et al., 2007, 2008).

The maps of predicted distribution of areas where fuel breaks are most likely to intersect with large fires did not correlate well among the forests, yet there was good correlation among observed and predicted number of intersections within the forests. In other words, the combination of factors that best predicted the number of intersections in one forest did not match well with the combination of factors that best predicted the intersections in the other forests. These differences reflect how the environmental controls of fire regimes vary from region to region, even within a single ecoregion. Therefore, a “one size fits all” management approach would be inappropriate if the objective were to map likely areas for fires and fuel treatments to intersect. While developing a model for one region and applying it to a different region may be inappropriate, the modeling methodology adopted here could easily be applied anywhere. These types of maps could be part of a manager’s toolset in helping to identify areas where new fuel breaks could be constructed or where current fuel breaks should be maintained.

We cannot directly attribute differences in the influential variables of our models to differences among the forests because we only statistically analyzed three national forests. Nevertheless, the differences among the national forests do provide a perspective on the variability of the region, despite the fact that it all falls within the same ecoregion. This is striking considering that southern California has a distinctive fire regime, owing to the defining characteristics of the region’s Mediterranean-type climate. Because of the cool, wet winters and hot, dry summers, and the specific properties of chaparral, this vegetation is particularly flammable for a substantial portion of the year and burns in large, stand-replacing, high-intensity fires (Pyne et al., 1996). The region’s fire regime and fire management issues are typically most starkly contrasted against those in forested regions (Keeley et al., 2009). While it has been recognized that many fire management practices in forested regions are inappropriate for southern California shrublands (Halsey, 2005; Keeley and Fotheringham, 2006), this study shows how certain aspects of fire management may need to be individually tailored at even finer scales, dependent on terrain, proximity to urban environments, regional weather patterns, and fuel type composition.

In southern California, fuel treatments can lead to ecological degradation because they often involve complete removal of vegetation, facilitate the spread of exotic species, and may thus indirectly contribute to increased fire frequency in a region where recurrent fire already threatens the native shrublands (Merriam et al., 2006, 2007). These resource costs should be considered relative to the benefits of protecting communities, and these trade-offs should be considered when constructing new fuel breaks in the region. This is in contrast to forested regions, where the objective of protecting communities is often coupled with the objective of reshaping the age structure and composition of forests to resemble historic conditions (Reinhardt et al., 2008). In these forests, fuel breaks and resource benefits generally are mutually beneficial. Regardless of the region, mitigating fire risk to communities is a priority for federal land managers, yet most fuel treatments are not placed within the wildland–urban interface where they may have the greatest potential for protecting homes. Across the western United States, only 3% of the area treated from 2004 to 2008 was located in this interface (Schoennagel et al., 2009).

Many new fuel breaks are currently being constructed in southern California. In fact, the most likely reason there were not enough fire and fuel break intersections to complete a statistical analysis in the Cleveland National Forest is because a large proportion of the fuel treatments have been recently constructed. Despite the large amount of new fuel break construction, the results of this study show that many fires never actually intersect fuel breaks, and large areas of fuel breaks never intersect fire. Also, the forests that had the highest density and area of fuel breaks did not have the highest overall effectiveness of fuel breaks, suggesting that treating more area alone does not necessarily increase the safety of a region. It may be more effective to have fewer fuel breaks in strategically placed locations than to have greater area of fuel breaks overall, at least in terms of protecting communities. The results from all three forests show that fuel breaks played an important role in controlling large fires primarily where they provided access for firefighting activities. Strategically locating fewer fuel breaks could also reduce the potential for resource costs.

Discussion in the interviews revealed that many strategic decisions do go into placing fuel breaks. While these decisions are often based on years of fire management experience, quantitative and spatially explicit analyses could potentially be helpful in refining these strategic decisions. For example, maps like the ones generated here, showing where fuel treatments are mostly likely to intersect fires, could be combined with further spatial analyses of where access is best and where communities need the most protection. In particular, this study strongly supports the notion of constructing fuel breaks along the wildland–urban interface where firefighters will have better access to the fuel breaks, and where the fuel breaks will provide an immediate line of defense adjacent to homes that are at risk. The case studies from all four national forests demonstrate that fuel breaks will not stop fires without firefighter presence. Therefore, constructing fuel breaks in remote, backcountry locations will do little to save homes during a wildfire because most firefighters will be needed to protect the wildland–urban interface, and fires will not be stopped by those fuel breaks that are located farther away. Finally, because access to fuel breaks was consistently improved when vegetation structure was favorable, this study suggests that maintaining fuel breaks in strategic locations may be just as important as constructing new fuel breaks.

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Housing Arrangement and Location Determine the Likelihood of Housing Loss Due to Wildfire

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Abstract

Surging wildfires across the globe are contributing to escalating residential losses and have major social, economic, and ecological consequences. The highest losses in the U.S. occur in southern California, where nearly 1000 homes per year have been destroyed by wildfires since 2000. Wildfire risk reduction efforts focus primarily on fuel reduction and, to a lesser degree, on house characteristics and homeowner responsibility. However, the extent to which land use planning could alleviate wildfire risk has been largely missing from the debate despite large numbers of homes being placed in the most hazardous parts of the landscape. Our goal was to examine how housing location and arrangement affects the likelihood that a home will be lost when a wildfire occurs. We developed an extensive geographic dataset of structure locations, including more than 5500 structures that were destroyed or damaged by wildfire since 2001, and identified the main contributors to property loss in two extensive, fire-prone regions in southern California. The arrangement and location of structures strongly affected their susceptibility to wildfire, with property loss most likely at low to intermediate structure densities and in areas with a history of frequent fire. Rates of structure loss were higher when structures were surrounded by wildland vegetation, but were generally higher in herbaceous fuel types than in higher fuel-volume woody types. Empirically based maps developed using housing pattern and location performed better in distinguishing hazardous from non-hazardous areas than maps based on fuel distribution. The strong importance of housing arrangement and location indicate that land use planning may be a critical tool for reducing fire risk, but it will require reliable delineations of the most hazardous locations.

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Introduction

As the frequency, extent, and severity of wildfires are surging across the world [1,2], so too are the ecological, social, and economic consequences. Residential losses associated with wildland fire have escalated globally [3–5], and recent fire events have resulted in billions of dollars of damage per event [6]. The problem is particularly critical in Mediterranean-climate regions of the world, where major metropolitan centers are juxtaposed with highly flammable ecosystems [7]. Since the 1950s, southern California has experienced the highest losses in property and life in the U.S., averaging 500 homes per year [8]. Here we show that the arrangement and location of structures strongly affects their susceptibility to being destroyed in a wildfire, and that empirically based maps developed using housing density and location can better identify hazardous locations than fuel-based maps.

The escalation of wildland fire losses is typically attributed to housing development within or adjacent to wildland vegetation (i.e., the "wildland-urban interface") [6,9], changing climate conditions [1], or an accumulation of hazardous wildland fuels [10]. The primary preventive strategy used for reducing fire impacts has been the manipulation of wildland vegetation to reduce hazardous fuels. The U.S. federal government has strongly promoted and funded fuel reduction treatments to mitigate fire hazard, and federal land management agencies spent billions of dollars (e.g., $2.7 billion from 2001–2006) to treat millions of hectares within the last decade [10]. Yet, while costs for suppression and treatment have nearly tripled since 1996 [11], the fire problem has only gotten worse.

With the growing realization that wildland fuel manipulations can alter fire outcomes only to a limited extent, the need for alternatives has risen. For example, a structure's survival during a wildfire depends largely on its building materials and the characteristics of fuels in its immediate surroundings [3], suggesting that fire hazard can be reduced by homeowner actions to protect the structure [12].

However, what remains unclear is to what extent property loss depends on the role of land planning and the placement and arrangement of homes relative to the spatial patterns of wildland fire hazards. Past land-use decision-making has allowed homes to be constructed in highly flammable areas, and this may be one of the roots of the fire problem [13]. Although it is not feasible to change current housing patterns, homes in the most hazardous locations could be identified and prioritized for fire protection efforts, and land use planning and regulation may potentially be a powerful tool for reducing future property loss [14], especially in areas such as southern California where substantial future housing growth is expected [15], and across the western US, where further development is expected in a substantial proportion of the wildland-urban interface [16].

If land use regulation and planning are to effectively reduce wildland fire loss, they have to be based on solid understanding of what landscape factors most significantly contribute to wildfire danger and where to locate and arrange homes to reduce fire hazard. Currently, most fire hazard maps are based on expert knowledge of how fuel and fire history determine threats to a given community e.g., [17–19]. Similar fire hazard maps have been created for the state of California that identify communities at risk and areas of substantial fire threat to people. These maps are readily available [20] and widely used. Fire hazard maps, however, are only effective if they accurately delineate areas where property loss is most likely to occur. Whether this is the case or not is unknown since most have never been evaluated against empirical data.

We constructed a complete database of structure locations in two extensive, fire-prone regions of southern California and identified which structures were destroyed or damaged by wildfires since 2001 (Fig. 1). These two regions were the Santa Monica Mountains, one of the largest wildland open space areas adjacent to the Los Angeles metropolitan area and San Diego County, site of major wildfire losses in both 2003 and 2007 [20]. Based on these data, we used logistic regression and maximum entropy analysis to answer three questions: 1) What is the relative importance of housing arrangement (i.e., the spatial pattern of residential structures), location, and environment in explaining property loss from fire? 2) How well do currently available statewide fuel-based maps of fire hazard correspond to actual wildfire impacts? 3) Can fire hazard maps based on empirical data and an expanded set of explanatory variables successfully predict local-scale housing losses?

Results

In the Santa Monica Mountains, 3% of 36,399 structures were located within the boundaries of 10 large fires that occurred from 2001 to 2009. In these fires, 173 homes, guest houses, or outbuildings were destroyed and an additional 140 were damaged. For the second study region in San Diego County, 4% of 687,869 structures were located within one of 40 fire perimeters. In these fires, 4315 structures were completely destroyed and an additional 935 were damaged.

In both study regions, the spatial arrangement of structures (Table 1) significantly influenced the likelihood of property loss (i.e., destruction or damage) (Figs. 2 and 3). Property loss was more likely in smaller, more isolated housing clusters with low- to intermediate housing density and fewer roads, although road density was insignificant after accounting for spatial autocorrelation in the Santa Monica Mountains (Table 2). Structures located near the edges of developments, or in housing clusters on steep slopes, were also more susceptible. Many relationships were nonlinear, with the highest property loss occurring when structures were at intermediate distances to other structures or housing clusters.

In addition to spatial arrangement, a structure's location on the landscape was also a highly significant predictor of property loss (Fig. 2). In both study regions, property loss was significantly related to a structure's distance from the coastline, but the relative effect varied. In the Santa Monica Mountains, property loss occurred disproportionately closer to the coast, whereas structures farther from the coast were most susceptible in San Diego County (Tables 2 and 3).

The other significant location-dependent variable affecting property loss was historical fire frequency (Fig. 2). In the Santa Monica Mountains, this was the single most important predictive variable. Here, property loss was most likely in areas of historical high fire frequency, which corresponded with wind corridors. Fire frequency was also a significant variable in San Diego County, but here the relationship was nonlinear.

Property loss was more likely to occur when structures were surrounded by wildland vegetation rather than by urban or impervious areas (Fig. 4). However, property loss was also more (Santa Monica Mountains) or as likely (San Diego County) to

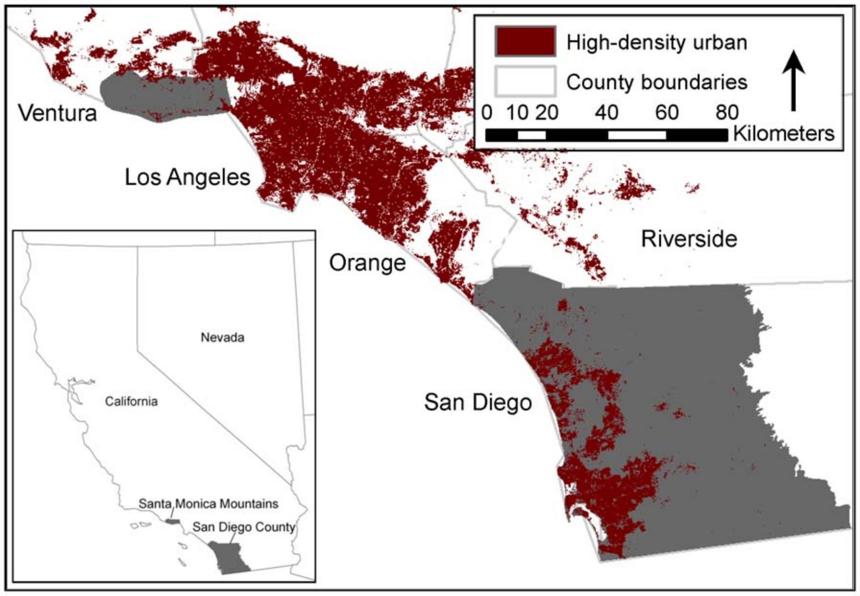

Figure 1. The Santa Monica Mountains and San Diego County, California, USA. Study areas in gray. The Santa Monica Mountains are located in Ventura and Los Angeles counties, and both study areas are located within the South Coast Ecoregion of California, USA. Study areas in gray.
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Table 1. Variables analyzed for explaining structure loss in the Santa Monica Mountains and San Diego County.

Variable	*Source*	*Description*
Fire frequency 2001	CDF* Fire perimeter overlays	Number of fires (2001–2010)
Distance to coast	Derived from coastline of county	Continuous distance in meters
Fire threat	CDF*	Ranking from 1 to 5
Fire threat to people	CDF*	Ranking from 1 to 5
Communities at risk	CDF*	Binary, at risk or not at risk
Housing density	Derived from digitized structures	Structures per hectare
Distance nearest housing cluster	Derived from 100 m buffer of structures	Continuous distance in meters
Housing dispersion	Derived from 100 m buffer of structures	Standard deviation/mean distance between structures in housing cluster
Distance to nearest structure	Derived from digitized structures	Continuous distance in meters
Distance to edge of housing cluster	Derived from digitized structures	Continuous distance in meters
Area of housing cluster	Derived from 100 m buffer of structures	Squared meters
Elevation	US Geological Survey digital elevation model (DEM	30 meters
Slope	Derived from the DEM	Percent slope
Southwestness	Derived from the DEM	SW = con(aspect(<dem>) = = −12, 201,(cos(((aspect(<dem>)−255) div deg)+1) * 100)))
Road length	US Census Bureau TIGER/Line files	Meters

*California Department of Forestry Fire and Resource Assessment Program.
doi:10.1371/journal.pone.0033954.t001

occur within herbaceous fuel types than within the higher fuel-volume woody types that are typically considered as the most hazardous fuels.

Variables with correlation coefficients greater or equal to 0.7 in the Santa Monica Mountains included road length and area of housing cluster (0.95) and elevation and distance to coast (0.72). In San Diego County, pairs of correlated variables also included road length and area of housing cluster (0.99), distance to nearest structure and distance to nearest housing cluster (0.71). Distance to coast was correlated with housing density (−.71) and elevation (0.89). To develop multiple-regression models, we removed elevation and road length from consideration in the Santa Monica Mountains, because they explained less variation than the variable with which they were correlated. For the San Diego County analyses, we removed distance to coast, road length, and distance to nearest housing cluster.

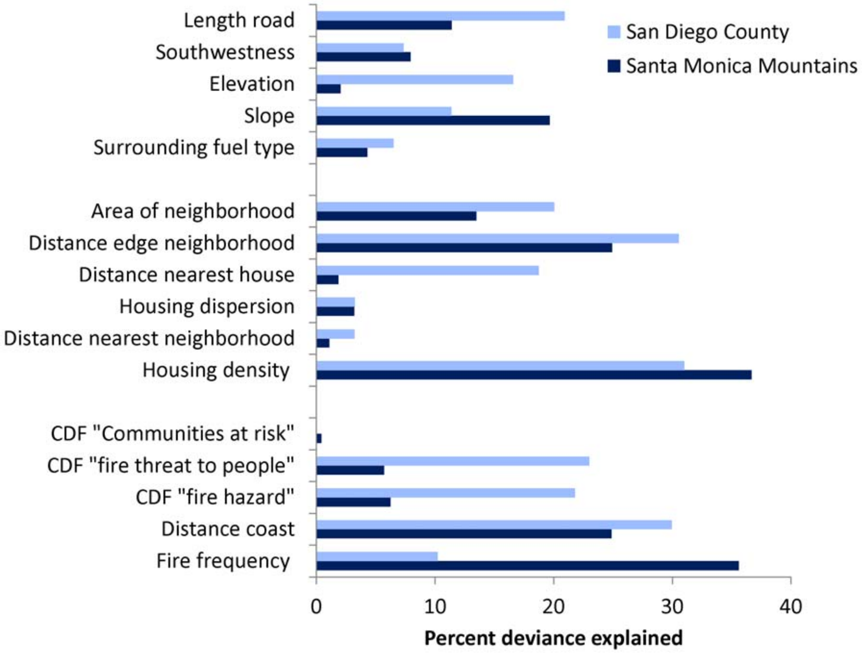

Figure 2. Percent deviance explained for generalized additive models (GAMs). GAMs explain the influence of firefighter access, biophysical variables, structure arrangement, and structure location on burned structures from fires during 2001–2010 in the Santa Monica Mountains, CA and San Diego County, CA. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g002

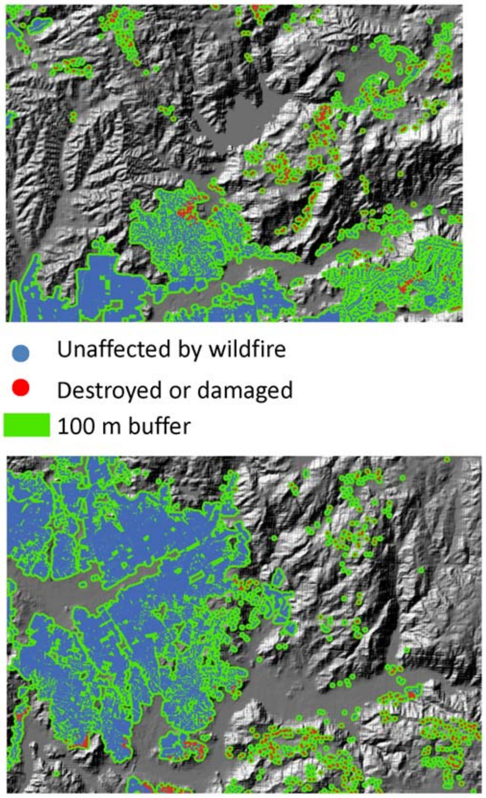

Figure 3. Maps from portions of San Diego County illustrating how housing arrangement influences the likelihood that a house will be lost from wildfire. Structures most likely to be burned by fires (in red) were: in areas with low to intermediate structure density; in small, dispersed housing clusters, close to the edge of the housing cluster, at intermediate distance to the nearest structure or housing cluster than structures that were unaffected (in blue).
doi:10.1371/journal.pone.0033954.g003

The multiple-regression GAM model for the Santa Monica Mountains included fire frequency, housing density, distance to edge of housing cluster, distance to coast, slope, area of housing cluster, southwestness, fuel type, housing dispersion, distance to nearest structure and housing cluster. Only nonparametric terms were selected, except fuel type, which was categorical. The deviance explained for the model was 65.7%, and the area under the curve (AUC) of receiver operating characteristic (ROC) plots, indicating the ability of the model to discriminate between burned and unburned structures on test data (20%), was 0.82.

The multiple-regression GAM model for San Diego County included housing density, distance to edge of housing cluster, area of housing cluster, elevation, fire frequency, fuel type, and housing dispersion. All terms included in the model were nonparametric except for distance to edge of neighborhood, which was linear, and fuel type. The deviance explained for the model was 45.5%, and the AUC was 0.87.

Our fire-hazard maps developed with the Maxent model using empirical data and multiple explanatory variables (Figs. 5 and 6) performed well. The AUC of receiver operating characteristic (ROC) plots on test data (15% withheld) was 0.987 for the Santa Monica Mountains and 0.923 for San Diego County.

In contrast, statewide fire-hazard maps developed using fuel rank and fire rotation were unable to predict which structures were burned by fire (Fig. 7). This poor performance of the statewide maps was also evident through visual comparison with maps of actual property loss (Figs. 5 and 6). Similarly, property loss was not substantially higher in the highest hazard or communities-at-risk areas of the statewide maps. In most cases, property loss was evenly divided among hazard levels (Fig. 8A and 8B), and even where a substantial proportion of burned structures were located in areas mapped as high fire hazard, most of the unaffected structures were also distributed in these high-hazard areas, suggesting high commission error (Fig. 8C and 8D). The most worrisome finding was that the majority of property loss occurred in areas not designated as at-risk (Fig. 8E and 8F).

The results of all sensitivity analyses indicated that the results were robust: the importance and ranking of variables remained essentially the same for all data sets at different buffer distances and certainty classifications (Table 3). Differences in results were slightly larger using different buffer distances than using all burned structures across a range of certainty levels versus all destroyed structures classified at the highest level of certainty. The main difference between the 200 and 100-m buffer analysis was that housing density was somewhat less important while distance to nearest housing cluster and southwestness were somewhat more important using the 200-m buffer in the Santa Monica Mountains. In San Diego County, housing dispersion and distance to the edge of housing cluster were somewhat more important using the 200-m buffer. We also found no substantial difference in results for the Maxent models.

After adding a spatial term, spatial autocorrelation was no longer present in the residuals of any of the models (Table 2). Also, although there were small differences in the coefficients between spatial and non-spatial models, the direction of influence consistently remained the same. The only variables that were no longer significant after accounting for spatial autocorrelation included the CDF communities at risk map, the distance to the nearest housing cluster, southwestness, and road length for the Santa Monica Mountains, and southwestness for San Diego County.

Discussion

Wildfire is a key process that interacts with all major components of the earth system, but fire frequency, extent, and/or severity are on the rise [1,2,21,22]. Residential losses to wildfire have also escalated despite enormous investments in wildland fuel manipulation, improvements in fire-safe codes and building regulations, and advanced fire suppression tactics. Therefore, our finding that housing arrangement and location were the most important contributors to property loss supports the notion that patterns of land use may be partly responsible for property loss in the wildland-urban interface [13].

One reason that property loss is related to the arrangement of housing across the landscape may be that the amount and arrangement of human infrastructure also strongly and nonlinearly influence wildfire ignitions and frequency [7,23,24]. Therefore, the places where homes are most likely to burn may also be the places where fires are most likely occur, which is partly a function of the distribution of people. Thus, there may be spatial interactions and feedbacks between fire and housing patterns.

In southern California, as in many regions, humans cause most fires [7,23–25]. Thus, population growth and housing development increase fire frequency. Yet, although urban expansion increases fire frequency in general, the highest hazard tends to be in low-density housing areas, where structures are interspersed with wildland vegetation [9]. Scattered, isolated structures are more difficult for firefighters to defend, and poor firefighter access may explain why housing clusters with fewer roads were more vulnerable in San

Table 2. Model coefficients for generalized linear models (GLMs) estimated with and without autocovariate terms in the Santa Monica Mountains and San Diego County.

	Linear	*Autocovariate linear*	*Quadratic*	*Autocovariate quadratic*	*P-value*
Santa Monica Mountains					
Fire frequency 2001	0.860	0.440			<0.001
Distance coast	0.004	0.002	−7.0E-07	−4.0E-07	<0.001
CDF Fire threat	5.900	2.880	−8.5E-01	−3.9E-01	<0.001
CDF Fire threat people	3.070	1.540			<0.01
CDF Communities risk	−0.540	−0.280			NS
Housing density	1.010	1.130	−3.9E-01	−4.0E-01	<0.001
Distance housing cluster	0.006	0.004	−1.0E-05	−7.0E-06	NS
Housing dispersion	2.280	2.670			<0.001
Distance structure	0.020	0.020	−3.0E-05	−2.0E-05	<0.001
Distance edge	−0.021	−0.017			<0.001
Area housing cluster	−2.0E-07	−8.0E-08			<0.001
Slope	0.033	0.016			<0.001
Elevation	−0.001	−0.001			0.01
Southwestness	−0.002	0.002			NS
Road length	−2.0E-05	−2.0E-05			NS
San Diego County					
Fire frequency 2001	1.53	1.05	−0.33	−0.22	<0.001
Distance to coast	3.0E-04	3.0E-09	2.0E-04	2.0E-09	<0.001
CDF Fire threat	−0.54	−0.68	0.189	0.17	<0.001
CDF Fire threat people	2.27	1.69			<0.001
CDF Communities risk	−0.93	−0.51			<0.001
Housing density	−0.99	−0.47			<0.001
Distance housing cluster	0.005	0.004	−4.0E-06	−1.0E-06	<0.001
Housing dispersion	−3.08	−1.68	0.865	0.542	<0.001
Distance structure	0.007	0.004	−5.0E-06	−2.0E-06	<0.001
Distance edge	−0.02	−0.01			<0.001
Area of housing cluster	−2.0E-08	−7.0E-09			<0.001
Slope	0.17	0.12			<0.001
Elevation	0.001	0.003			<0.001
Southwestness	−0.005	−0.003			NS
Road length	−1.0E-06	−7.0E-07			<0.001

Quadratic terms were evaluated for all models, and coefficients are only provided for those models in which the quadratic term was significant in the non-spatial model.

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Diego County. However, there can also be situations in which high housing density contributes to structure-to-structure fire spread e.g., [26], depending on their flammability [27].

The importance of a structure's location on the landscape relative to the coast and historical patterns of fire frequency shows that certain places are more fire-prone than others, which in turn reflects how biophysical and human variables together create conditions that are particularly conducive to wildfire occurrence [2]. In our study areas, these relationships are also likely a function of a structure's location relative to predominant wind patterns and direction [28]. In the Santa Monica Mountains, certain fire corridors tend to burn repeatedly, and winds funnel down these corridors toward vulnerable structures located directly in their path. Here, the high-density coastal strip is narrow, and homes are closer to continuous vegetation than in San Diego County, where high-density development extends inland for much greater distances. This may be why houses were more likely to burn at a closer distance to the coast in the Santa Monica Mountains than in San Diego County. The low-density, high-risk areas in San Diego County are located farther inland where, if an ignition occurs there under extreme wind conditions, the fire is in its initial stages. Santa Ana winds blow from west toward the coast, and they are particularly dangerous in the beginning because they are usually most explosive and fast-moving right after they start, and it takes time to mobilize firefighting resources. Thus, the significance of distance to coast may be a proxy for other variables, such as the juxtaposition of housing density, contiguous fuels, and location relative to predominant wind patterns.

The importance of historical fire frequency suggests that, at least in non-forested ecosystems, fuel age may not be an important predictor of home loss [25], despite the fact that fuel age and time-since-fire maps are often used to delineate fire hazard. In fact, substantial property loss occurred when the primary surrounding fuel type was low fuel-volume grasslands. Although this result may seem counter-

Table 3. Percent deviance explained in generalized additive models (GAMs) for structures that were destroyed or damaged (Burned) and destroyed with the highest certainty (Destroyed); and for burned structures analyzed using a 200 m buffer distance (200 m).

	Burned	*Destroyed*	*200 m*	*Relationship*
Santa Monica Mountains				
Fire frequency 2001	35.59	31.63	NA	Positive
Distance coast	24.86	22.85	NA	Intermediate
CDF fire threat	6.23	4.37	NA	Intermediate
CDF fire threat people	5.69	5.01	NA	Positive
CDF Communities at risk	0.42	0.81	NA	Negative
Housing density	36.68	33.19	14.04	Intermediate
Distance housing cluster	1.08	1.46	14.23	Intermediate
Housing dispersion	3.18	2.23	4.24	Positive
Distance structure	1.85	2.17	NA	Intermediate
Distance edge	24.92	33	16	Negative
Area of housing cluster	13.47	12.88	18.06	Negative
Surrounding fuel type	4.3	3.18	NA	NA
Slope	19.66	17.79	18.31	Positive
Elevation	2.04	0.78	1.62	Negative
Southwestness	7.93	8.91	16.1	NA
Road length	11.4	11.2	13.98	Negative
San Diego County				
Fire frequency 2001	10.2	10.6	NA	Intermediate
Distance coast	30.0	28.19	NA	Intermediate
CDF fire threat	21.8	20.4	NA	Intermediate
CDF fire threat to people	23.9	24.1	NA	Positive
CDF Communities at risk	0.0	0.02	NA	Negative
Housing density	31.0	28.16	21.59	Negative
Distance housing cluster	3.2	2.92	0.97	Intermediate
Housing dispersion	3.3	2.85	8.62	Parabolic
Distance structure	18.7	15.73	NA	Intermediate
Distance edge	30.5	28.74	54.76	Negative
Area of housing cluster	20.1	16.41	10.63	Negative
Surrounding fuel type	6.5	4.90	NA	NA
Slope	11.4	13.94	10.61	Positive
Elevation	16.6	25.5	19.75	Positive
Southwestness	7.3	6.98	4.17	NA
Road length	20.9	19.6	15.4	Negative

The buffer distance used in all other analysis was 100 m. Relationship describes the shape of the response curve for all models. Ïntermediate signifies a nonlinear relationship in which values were highest at intermediate levels of the variable. Values listed as NA in 200 m were for variables that were only analyzed at the level of the individual house.

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intuitive, herbaceous fuels tend to have low fuel moisture, facilitate high wind speeds and fire spread, and have low heat requirements for ignition, thus promoting longer fire seasons and high fire frequency [29,30]. Grasslands also tend to ignite quickly, then carry fires into shrublands or woodlands [31]. These results suggest a need to reexamine the assumptions used in existing hazard maps and the management practice of converting shrublands to grasslands.

Fire hazard in the CDF statewide maps, as with most hazard maps [17–19,32], depends largely on the assumption that fuel properties are the primary contributors to fire danger. However, our empirical data indicate that, at least at the local scale considered here, fuel was not as significant as measurable factors related to the arrangement and location of structures. This is likely because the influence of fuel is complex and interacts with other risk factors [33]. Therefore, our empirical maps developed using a more comprehensive set of predictor variables, including fuel type, housing arrangement and location, and other environmental variables, performed better in distinguishing hazardous from non-hazardous areas.

Another reason for the discrepancy in map performance may be related to differences in mapping approach: while our approach used empirical data on actual structure loss, the statewide maps were developed based on a priori assumptions of where hazard is expected to be highest. At larger scales, such as the state level, the CDF fuel-based maps would likely perform better at picking out where homes are most vulnerable to fires. We also did not evaluate the CDF maps developed for local responsibility areas, which may better capture finer-scale patterns of hazard in local jurisdictions.

The fact that unburned structures in our analysis were more likely to be located in "communities at risk," whereas burned structures were more likely to be located outside of high-risk areas is potentially due to two reasons. At the most basic level, this may simply be caused by an incorrect identification of communities at risk. However, we caution that the discrepancy may also be due to scale effects and the definition of "community at risk." At a broad scale, "communities at risk" are likely located within areas that generally have the potential for hazardous fires, and places with more houses in such a danger zone are more likely to be identified as a "community at risk." However, at the structure level, low-housing density significantly increases the chance a house will burn – while it decreases the likelihood that at home will be included in a "community at risk." In summary, our results support the notion that property loss is a function of many physical and biological factors, in addition to characteristics of home construction and maintenance that we did not consider, such as roofing, construction materials, and home landscaping.

The effects of housing arrangement and location on the likelihood that a house will be destroyed or damaged by wildfire suggest that land use planning may be a critical tool for reducing fire hazard. Restricting development from hazardous locations has been effective for other hazards, such as flooding and the prevention of building on floodplains [34]. In the case of fire, new structures should be located and arranged in ways that not only minimize their exposure to hazard, but may also limit the increase in fire occurrence that often accompanies urban development. For example, our results suggest that in both study areas, new development would have a lower likelihood of burning if it were located away from fire-prone areas, such as wind corridors or steep slopes, and if new structures were arranged in intermediate-to high-density neighborhoods designed to minimize the amount of interface between homes and wildland vegetation. New development within large, existing urban areas, which typically also have better firefighter access, would also lower the likelihood of burning, compared to new development in more isolated, remote settings. Land use planning that considers minimizing future structure loss and prioritizing other fire prevention actions would be more informed with maps that reliably differentiate the most hazardous locations than with maps currently used for this purpose. Although the direction of influence was the same for most variables in the two study regions, the relative importance varied, and the distance from coast and elevation had opposite effects. This supports the notion that hazard is place-specific [35], and fire hazard mapping should therefore be individualized for specific landscapes.

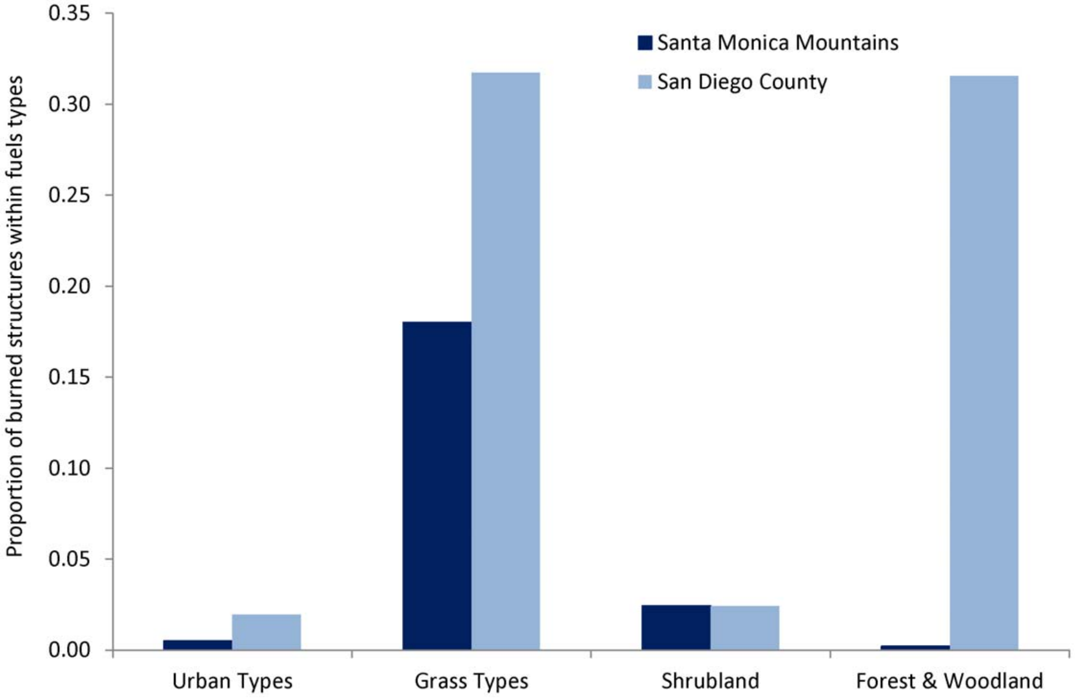

Figure 4. Proportion of burned structures within broad fuels types in the Santa Monica Mountains and San Diego County.
doi:10.1371/journal.pone.0033954.g004

Materials and Methods

Data and digitizing structures

We explained property loss by comparing structures that were burned (i.e., destroyed or damaged) by wildfires to those structures that were unaffected. The likelihood of a house burning in a fire has two major components: the first is the likelihood that there will be a fire, and the second is the likelihood that a structure will burn if there is a fire. That 'total' likelihood required us to include both structures inside and outside of fire perimeters in the model. We

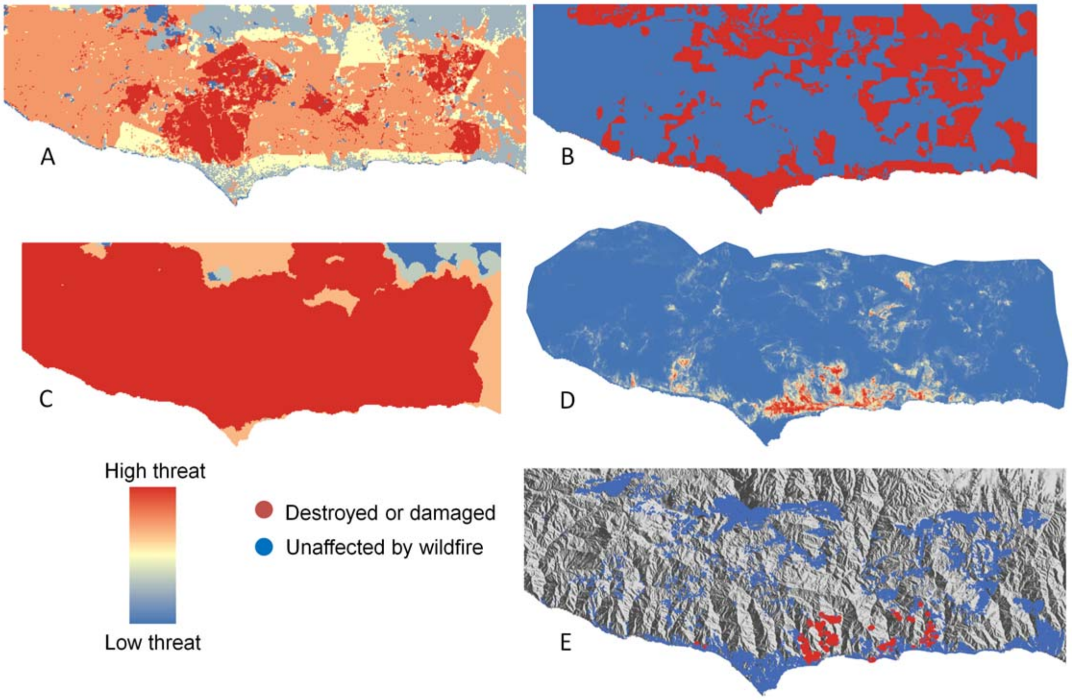

Figure 5. Fire hazard maps versus actual burned structures in the Santa Monica Mountains. (A) CDF "Fire threat" (B) CDF "Communities at risk" (C) CDF "Fire threat to people (D) Empirically based map showing probability of structure being burned by fire (E) Structures that were destroyed or damaged (red) and unaffected (blue) by wildfire from 2001–2010. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g005

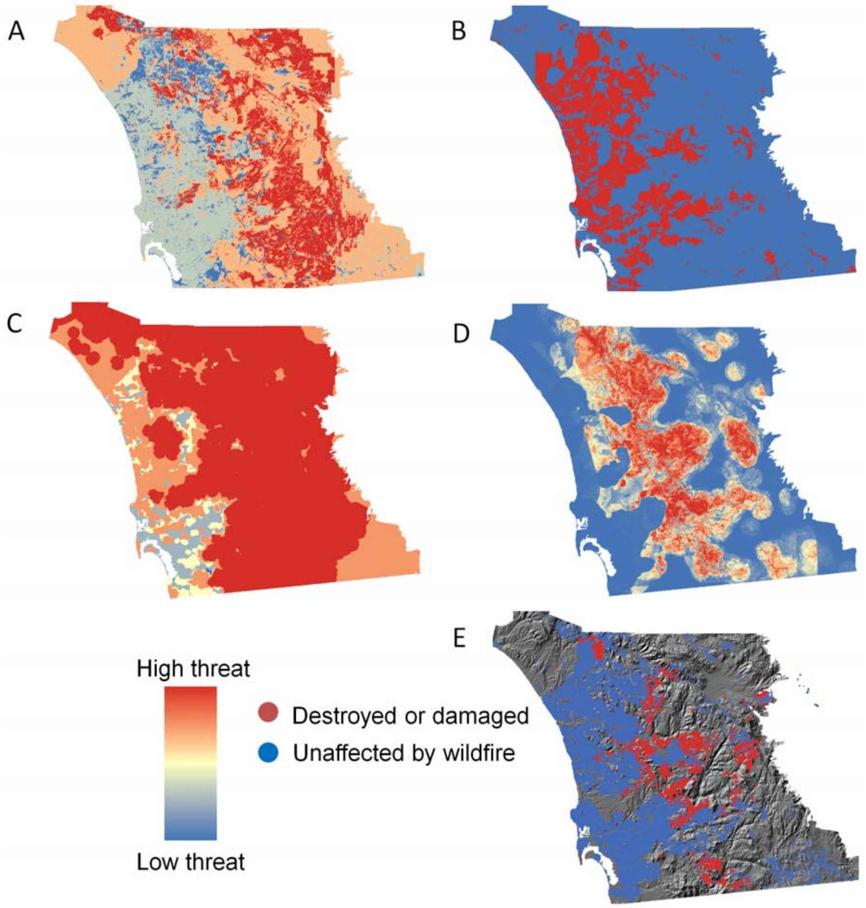

Figure 6. Fire hazard maps versus actual burned structures in San Diego County. (A) CDF "Fire threat" (B) CDF "Communities at risk" (C) CDF "Fire threat to people (D) Empirically based map showing probability of structure being burned by fire (E) Structures that were destroyed or damaged (red) and unaffected (blue) by wildfire from 2001–2010. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g006

also wanted to account for the full range of variation for the explanatory variables because planning decisions occur at a landscape scale, not just for a subset of structures within fire perimeters. Therefore, we digitized and analyzed all residential structures within the Santa Monica Mountains National Recreation Area in Ventura and Los Angeles counties, California as well as the portion of San Diego County that falls within the South Coast Ecoregion. Using onscreen digitizing, we carefully scanned the most recent aerial imagery available in Google Earth for each study area and placed a point over every visible structure. We digitized all structures, including homes, outbuildings, and guest houses, because we assumed that the factors explaining which homes burned were similar to those explaining the burning of other structures. Because most of the vegetation in our study areas is non-forested, there were very few occasions in which vegetation canopy obscured structures in the imagery. Structures were in all cases at least partly visible, even if they were covered by vegetation, and we looked at earlier images available in Google Earth to confirm where structures were located. The canopy cover was generally lower farther back in time.

Due to the large number of structures in San Diego County, many of which are located in high-density urban core areas, we used a parcel map to facilitate the digitizing process. For small parcels (area <900 m^2, equivalent to one 30×30 m pixel of the environmental data, see below), we placed the point representing the structure in the centroid of the polygon instead of digitizing the exact location of the structure within the parcel boundary. We assumed the location of the structure within the boundary of small parcels would not significantly alter the overall calculations of spatial pattern among structures. However, for large parcels, the location of the structure within the parcel boundary may be important because the parcel may include more than one pixel, and thus, the environmental data are associated with the structure may depend on structure location. Distance calculations to other structures could also be more substantially influenced by the location of structures in large parcels, which is why we analyzed the Google Earth imagery to place those structures accurately. We did not digitize houses under construction at the date the remote sensing imagery was recorded.

To identify burned structures, we developed an initial address list and spatial database of structures destroyed or damaged by fires from a variety of records, including official incident reports, county assessors' offices, public works departments, city records, and newspaper reports. Because these records were incomplete, we also used Google Earth imagery for a systematic visual analysis to correct geocoded locations and to identify additional structures that had not been documented. For this analysis, we identified burned structures by comparing pre-fire to post-fire images that are available in Google Earth. To develop a data set of houses to inspect for property loss, we selected all structures that fell within and up to 80 m outside any perimeter of a fire that occurred since 2001 in both study areas. We used 80 m because it is twice the distance beyond which flame fronts are not expected to ignite

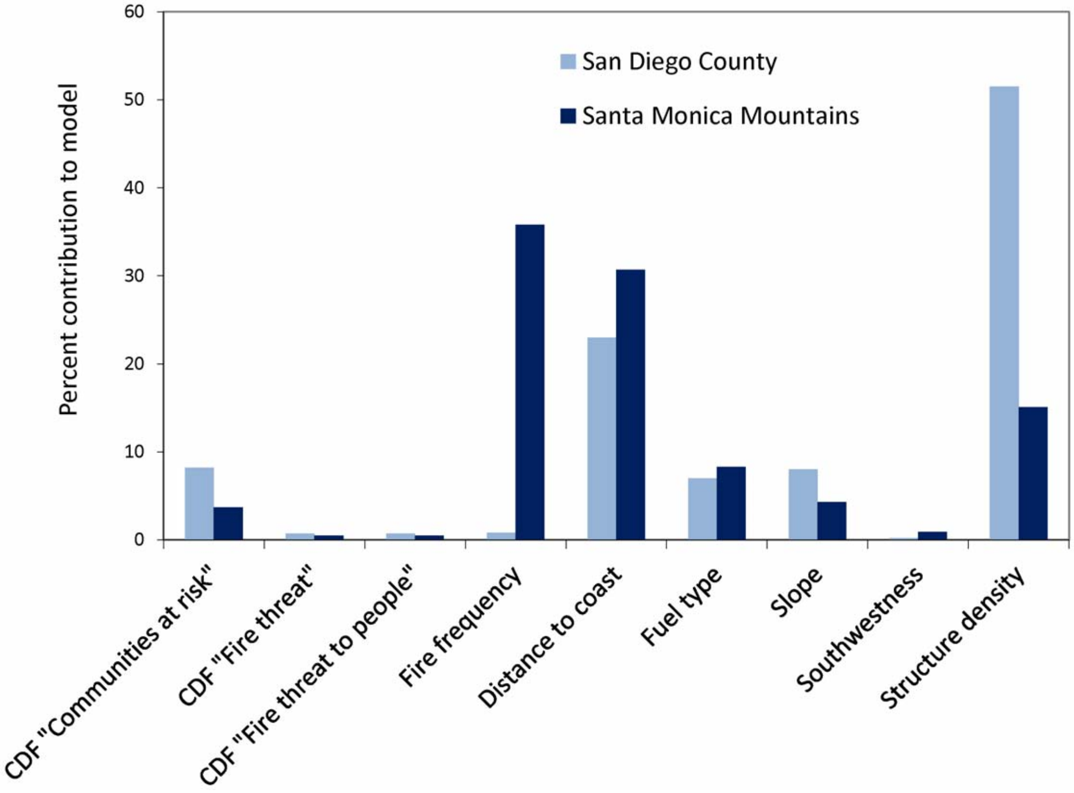

Figure 7. The percent contribution of explanatory variables in Maxent empirical fire hazard model. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g007

wood [36].The determination of destroyed or damaged structures was based on data collected from official records combined with visual inspection of imagery. Destroyed structures were those in which the house had completely burned to the ground, whereas damaged structures where those that had partially burned. Because damaged structures were more difficult to identify in the imagery, we ruled that if a fire had clearly burned into the property (i.e., if vegetation had visibly been burned), the structure was classified as damaged.

For both the destroyed and damaged structures, we assigned an estimate of certainty for the classification and conducted sensitivity analyses to test if results were similar for destroyed structures that were classified with the highest level of certainty versus a complete dataset with all destroyed and damaged homes at all certainty levels. In our classification, we indicated “1” for uncertain if the house was damaged or destroyed; “2” for fairly certain; “3” for absolutely certain. Since the results were similar (Table 3), we used the full dataset in our analyses to obtain the largest sample size. Although rare, if two buildings burned on a parcel, we only included one in our analysis. For those structures that burned in more than one fire, which only occurred in San Diego, we only used the data for the first fire to avoid double counting of structures in the spatial analysis.

Explanatory variables

To fully explore the influence of housing arrangement and pattern, we analyzed both the spatial relationships among individual structure locations and the arrangement of structures within housing clusters. Housing clusters were defined as groups of houses with a maximum distance of 100 m from each house to any other house [24]. We calculated these housing clusters by creating a 100 m buffer around each structure and dissolving overlapping boundaries. Thus, areas with many homes within 100 m of each other constituted one large housing cluster, while smaller housing clusters contained fewer or more isolated homes. This allowed spatial analysis based on the spatial and biophysical properties of the structure locations as well as spatial and biophysical properties of the housing clusters within which structures were located. Thus, some variables were calculated for the housing cluster in which the structure was located and the values for that housing cluster were assigned back to the structure. Other variables were calculated only for the location in which the structure was located.

Because our objective was to better understand the landscape factors that significantly contribute to the likelihood that a house will burn in a wildfire, particularly focusing on those factors that are relevant to land use planning, we only assessed variables affecting exposure of structures to wildfires (i.e., fires spreading into the property and reaching the structure, or embers landing on a structure). We did not consider factors such as urban landscaping or housing construction materials within the home ignition zone that determine whether the house survived the exposure. To evaluate the influence of housing arrangement and location on susceptibility to wildfire, we considered a suite of variables representing different spatial configurations and locations of structures as well as additional environmental variables that may affect property loss due to their potential control over fire spread behavior, fuel moisture, or flammability [23,37] (Table 1).

Housing arrangement variables. We evaluated the area of the housing cluster to test the hypothesis that small, isolated groups of structures are more susceptible to wildfire than large groups of structures. Housing density was calculated as the number of structures divided by the area of the housing cluster. For every

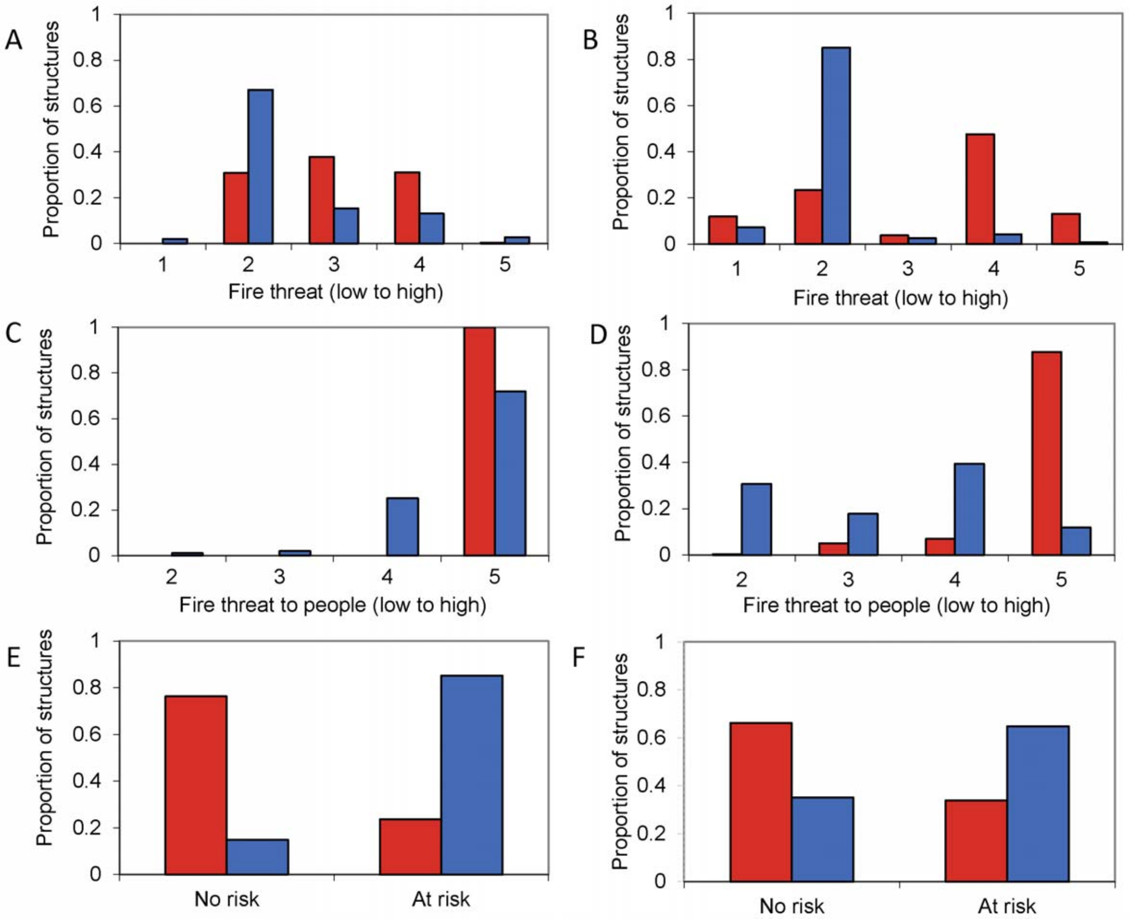

Figure 8. Distribution of actual burned structures in classes of statewide fire hazard maps. Proportion of structures burned (in red) or unaffected (in blue) distributed within map classes of: (A) CDF "Fire threat" in Santa Monica Mountains. (B) CDF "Fire threa" in San Diego County. (C) CDF "Fire threat to people" in Santa Monica Mountains (D) CDF "Fire threat to people" in San Diego County (E) CDF "Communities at risk" in Santa Monica Mountains (F) CDF "Communities at risk" in San Diego County. CDF – California Department of Forestry and Fire Protection.
doi:10.1371/journal.pone.0033954.g008

structure, we calculated the distance to the edge of the housing cluster to evaluate whether structures in the interior of housing clusters were less susceptible to wildfire than structures at the edge. To assess local spatial patterns, we calculated the distance from each structure to its nearest neighbor, and for overall landscape configuration of structures, we calculated the distance from each housing cluster to the next nearest housing cluster. Finally, we calculated the coefficient of variation, or, the standard deviation of distance among structures in a housing cluster divided by the mean to assess housing dispersion, or, regularity of housing pattern.

Housing location variables. To test whether structures located in fire-prone parts of the landscape were more likely to be burned, we overlaid fire perimeter polygons compiled by the California Department of Forestry (CDF)-Fire and Resource Assessment Program and created a continuous raster map representing the number of times an area had burned from the beginning of record-keeping, 1878, until 2001. We did not include any fires that occurred after 2001 to ensure that our count of fire frequency was independent of those fires that burned the structures in our analysis. We calculated the distance from the coast for every structure as another way to test whether a structure's location influences its likelihood to be burned. In southern California, a number of variables that influence fire patterns, including climate, terrain, and vegetation distribution, are correlated with the distance to the coast. Distance to the coast is also correlated with housing patterns, and may influence how a house is arranged relative to the major wind corridors in the region [38]. Although the inclusion of weather data at the time of fires would be more directly related to fire behavior and danger, the high variability of weather over space and time limits the ability to relate specific weather data to the place and time that fires burn structures. First, we did not know the exact time that fires burned structures, and thus could not retrieve the temporally matching weather data. Second, weather stations are generally located too far away from where fires burned homes to reflect local variability in weather conditions.

Biophysical variables. Terrain-derived variables included the average elevation and percent slope of the housing cluster as well as a cosine-transformation of aspect to create an index of 'southwestness,' which could account for the influence of solar radiation and aspect on fuel properties and fire behavior. For each structure, we also determined fuel type in the surrounding by identifying the most common fuel model within a 1 km buffer of the structure. This buffer allowed us to identify the vegetation types fires spread through before reaching the property. Our objective for this analysis was to determine which broad-based fuel classes were most closely associated with structure loss. If more than one fuel type occurred in the buffer, we used the fuel type present in the majority of the area. We obtained spatial fuel model data, developed for fire behavior modeling, from statewide maps developed by the U.S. Forest Service (N. Amboy) at 30 m resolution. The fuel models provided in the USFS maps were created through remote sensing and classified according to Scott and Burgan [39]. From this map, we grouped together the fuel models from broad fuel types (representing grassland, shrubland, and timber). We also grouped agriculture, barren land, and urban land into one type representing mostly urban landscaping and impervious surface (i.e., with little wildland vegetation).

Firefighter access. As a way of indirectly assessing firefighter access to the structure, we calculated the length of road within each housing cluster using the 2000 US Topologically Integrated Geographic Encoding and Referencing system TIGER/line files from the US Census.

Statewide fire hazard maps

Statewide fire hazard maps were available online from the California Department of Forestry and Fire Protection (CDF) [20].We downloaded the Wildland Urban Interface (WUI) "fire threat" data product that includes a series of maps that rank the wildland fire threat to human development. The term "fire threat" in these maps is used analogously to the way we use the term fire "hazard" or, a phenomenon or place where harm is likely to occur.

The "fire threat" map is based on the hazard ranking of different fuels types combined with the fire rotation period, or, the average area burned during the period of record for different vegetation types. Fuels types with higher fuel loads and vegetation types that burned most frequently were considered most hazardous. The "fire threat to people" map is based on a cost-distance calculation that estimates distances from areas of high fire hazard. As an example, the highest "fire threat to people" is calculated as a maximum of 2400 m from "extreme threat" in the fire threat map. Finally, the "communities at risk" map depicts U.S. Census communities with more than 1 house per 8.09 ha (20 acres) that are located in areas with "high fire threat to people."

The CDF provides additional fire hazard severity maps developed separately for state and local responsibility areas. The finer-scale maps for local responsibility areas, which include incorporated cities, cultivated agricultural lands, and portions of the desert, are limited in extent and only overlap a small portion of our study areas. Due to the limited extent of the local responsibility area maps, and the fact that the state responsibility maps were still being refined, we did include these in our analysis. Their proposed modeling approach will be based upon the existing fire threat and communities at risk maps and will be refined to include additional methods that characterize brand production from vegetative fuels.

To evaluate how well the CDF statewide fire hazard maps corresponded to actual burned structures, we included the three maps as predictor variables in our statistical analyses and quantified the distribution of burned and unaffected structures within the different classes of each map.

Analysis

To identify the variables that best explain property loss and to estimate the relative contribution of each variable, we developed generalized additive models (GAMs) using a binary response (i.e., house burned or unaffected by fire) and logit link. We used three target degrees of freedom for smoothing splines for our continuous explanatory variables. Because we wanted to compare the independent relative variance explained for all explanatory variables, we estimated separate regression models for each variable. However, we also calculated the correlation coefficients among all variables and developed multiple-regression models with non-correlated variables for each study area. We used a stepwise selection procedure, entering variables according to amount of deviance explained and exploring both forward and backwards directions. We used AIC as the selection criterion for variable selection. To develop the models, we split the data for training and testing (withholding 20% of the data for testing) so we could calculate the area under the curve (AUC) of receiver operating characteristic (ROC) plots on an independent dataset to quantify model performance.

We used GAMs because prior studies reported nonlinear relationships between fire patterns and many of our predictor variables [7,23,24]. Unlike parametric statistical methods, such as generalized linear models (GLMs), in which nonlinear relationships are specified *a priori* (e.g., through polynomial terms) in the model, GAMs allow the structure of the data to determine the shape of the response curves. Thus, GAMs provide a more flexible and automated approach for identifying and describing nonlinear relationships [40,41]. We used the GAMs to estimate the shape of response curves and to calculate deviance explained (D^2, analogous to R-squared in linear regression) for all explanatory variables.

Although non-parametric methods, such as GAMs, tend to be less sensitive to the effects of spatial autocorrelation than other model approaches [42], we wanted to ensure that spatial autocorrelation did not significantly influence the results of our analysis. The main concerns about spatial autocorrelation in regression models are inflated significance values and biased coefficients [42,43]. GAMs do not estimate regression coefficients, which are replaced with smoothing functions. This is why we also fit GLMs to our data because they are parametric models similar to GAMs, but they estimate coefficients. Therefore, the GLMs allowed us tocheck the influence of autocorrelation on both coefficients and the significance of variables. The GLMs also allowed us to test whether our results were robust by comparing two modeling methods. We first developed non-spatial GLMs, and fit linear and quadratic terms for all variables (except for fuel type, which was categorical). After detecting residual autocorrelation in these nonspatial models using Moran's I [43], we calculated an autocovariate term to account for the influence of neighboring values on predictions, and included as the term as an additional explanatory variable in models. To calculate the autocovariate term, we specified a neighborhood radius of 1, which finds the minimum distance for which all observations (i.e., structure locations) are linked to at least one neighbor. The influence of structures located within any neighborhood radius was weighted by inverse distance. . After fitting these autocovariate models, we used Moran's I to recheck for spatial autocorrelation of model residuals, compared the coefficients to the nonspatial models, and checked variable significance after incorporating the autocovariate term..All model fitting and evaluation were accomplished using the gam, spdep, vegan, and ROCR packages for R [44].

Empirical fire mapping

To develop empirical fire hazard models and maps, we selected Maxent [45], a machine-learning method that is best recognized for creating species distribution models and maps. We selected Maxent because it outperforms other presence-only and presence-background species distribution modeling methods [41] and has been applied successfully to map the distribution of fire [46]. Maxent assumes that the best approximation of an unknown distribution (e.g., fire hazard) is the one with maximum entropy. The model iteratively evaluates contrasts between values of explanatory variables at locations of the response variable (i.e., burned structures) and for averages of the explanatory variables across the entire study area. The output is an exponential function that assigns a hazard probability (i.e., probability of structure being burned) to each site or cell of a map. In the output map, areas of predicted high risk that do not have structures on them represent environmental conditions similar to those in which structures have actually burned.

Because mapped predictor variables were required for the modeling, so that conditions similar to those where structures were burned could be delineated continuously across the landscape, we created maps representing a subset of the variables that we explored with the regression analysis. These variables represented a combination of structure arrangement, location, and biophysical variables, including: interpolated structure density, distance to coast, fuel type, slope, historical fire frequency, and southwestness. We developed models that included CDF fire hazard maps as predictors to test their importance relative to the other predictor variables. However, for generating maps and quantifying model performance, we only used models that did not include CDF predictor variables.

Sensitivity tests

The results of our analysis may have been affected by the size of the buffer that we used around structures to create housing clusters, the degree of impact of fire on the structure (i.e., destroyed or damaged), and certainty of the classification (i.e., 1–3). Therefore, to evaluate how sensitive our results were to these variables, we created housing clusters around structures using a 200 m buffer and compared the regression results for which housing cluster was relevant in the to those obtained when using a 100 m buffer. We also performed separate regressions using only those structures that had been destroyed with complete certainty (a "3") and compared those to the regressions of all burned structures at all certainty levels. For the Maxent analysis, we also compared models using only structures that were destroyed with the highest level of certainty to models using all burned structures at all certainty levels.

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Author Contributions

Conceived and designed the experiments: ADS JEK ABM TJB VCR. Performed the experiments: ADS ABM TJB. Analyzed the data: ADS JEK ABM. Wrote the paper: ADS JEK ABM TJB VCR.

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Land Use Planning and Wildfire: Development Policies Influence Future Probability of Housing Loss

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Abstract

Increasing numbers of homes are being destroyed by wildfire in the wildland-urban interface. With projections of climate change and housing growth potentially exacerbating the threat of wildfire to homes and property, effective fire-risk reduction alternatives are needed as part of a comprehensive fire management plan. Land use planning represents a shift in traditional thinking from trying to eliminate wildfires, or even increasing resilience to them, toward avoiding exposure to them through the informed placement of new residential structures. For land use planning to be effective, it needs to be based on solid understanding of where and how to locate and arrange new homes. We simulated three scenarios of future residential development and projected landscape-level wildfire risk to residential structures in a rapidly urbanizing, fire-prone region in southern California. We based all future development on an econometric subdivision model, but we varied the emphasis of subdivision decision-making based on three broad and common growth types: infill, expansion, and leapfrog. Simulation results showed that decision-making based on these growth types, when applied locally for subdivision of individual parcels, produced substantial landscape-level differences in pattern, location, and extent of development. These differences in development, in turn, affected the area and proportion of structures at risk from burning in wildfires. Scenarios with lower housing density and larger numbers of small, isolated clusters of development, i.e., resulting from leapfrog development, were generally predicted to have the highest predicted fire risk to the largest proportion of structures in the study area, and infill development was predicted to have the lowest risk. These results suggest that land use planning should be considered an important component to fire risk management and that consistently applied policies based on residential pattern may provide substantial benefits for future risk reduction.

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Introduction

The recognition that homes are vulnerable to wildfire in the wildland-urban interface (WUI) has been established for decades [e.g., 1,2]; but with a recent surge in structures burning, this issue is now receiving widespread attention in policy, the media, and the scientific literature. Single fire events, like those in Greece, Australia, southern California, and Colorado have resulted in scores of lost lives, thousands of structures burned, and billions of dollars in expenditures [3–6]. With the potential for increasingly severe fire conditions under climate change [7] and projections of continued housing development [8], it is becoming clear that more effective fire-risk reduction solutions are needed. "Fire risk" here refers to the probability of a structure burning in a wildfire within a given time period.

Traditional fire-risk reduction focuses heavily on fire suppression and manipulation of wildland vegetation to reduce hazardous fuels [9]. Enormous resources are invested in vegetation management [10], but as increasing numbers of homes burn down despite this massive investment, the "business-as-usual" approach to fire management is undergoing reevaluation. One issue is that fuel treatments may not be located in the most strategic positions, i.e., in the wildland-urban interface [11]. Yet, even if treatments surrounded all communities, scattered development patterns are difficult for firefighters to reach [12–14], and fuel treatments do little to protect homes without firefighter access [15–16]. Fuel treatments may also be ineffective against embers or flaming materials that blow ahead of the fire front [17].

One alternative to traditional fire management that is receiving widespread attention is to prepare communities through the use of fire-safe building materials or creating defensible space around structures [17–18]. These actions represent an important shift in emphasis from trying to prevent wildfires in fire-prone areas to better anticipating fires that are ultimately inevitable. Nevertheless, the cost of building and retrofitting homes to be fire-safe can be prohibitive, and these actions do not guarantee immunity from fire [19].

Land use planning is an alternative that represents a further shift in thinking, beyond the preparation of communities to withstand an inevitable fire, to preventing new residential structures from being exposed to fire in the first place. The reason homes are vulnerable to fires at the wildland-urban interface is a function of its very definition: "where homes meet or intermingle with wildland vegetation" [20]. In other words, the location and pattern of homes influence their fire risk, and past land-use decision-making has allowed homes to be constructed in highly flammable areas [21]. Land use planning for fire safety is beginning to receive some attention in the literature [22–23], and there is growing recognition of the potential benefits of directing development outside of the most hazardous locations [8,19,24].

Despite recent attention in the literature, land use planning for wildfire has yet to gain traction in practice, particularly in the United States. However, fire history has been used to help define land zoning for fire planning in Italy [22], and bushfire hazard maps are integrated into planning policy in Victoria, Australia [25]. Although some inertia inevitably arises from complications with existing policy and plans, a primary impediment to the design and implementation of fire-smart land use planning is lack of guidance about specific locations, patterns of development, or appropriate methodology to direct the placement of new development. Without a solid knowledge base to draw from, planners will be misinformed about which planning decisions may result in the greatest overall reduction of residential landscape risk. Even worse, poor science could result in placement of homes in areas that actually have high fire hazard.

Research on how planning decisions contributed to structures burning in the past provides some guidance about what actions may work in the future. Analysis of hundreds of homes that burned in southern California the last decade showed that housing arrangement and location strongly influence fire risk, particularly through housing density and spacing, location along the perimeter of development, slope, and fire history [26]. Although high-density structure-to-structure loss can occur [27–28], structures in areas with low- to intermediate- housing density were most likely to burn, potentially due to intermingling with wildland vegetation or difficulty of firefighter access. Fire frequency also tends to be highest at low to intermediate housing density, at least in regions where humans are the primary cause of ignitions [29–30].

These results suggest, for example, that placing new residential development within the boundaries of existing high-density developments or in areas of low relief may reduce fire risk. However, it is difficult to know whether broad-scale planning policies would actually result in the intended housing arrangement and pattern at the landscape scale, and whether those patterns would result in lower fire risk. Our objective here was to simulate three scenarios of future residential development, and to project wildfire risk, in a rapidly urbanizing and fire-prone region where we have studied past structure loss [25]. We based all future development on an econometric subdivision model, but we varied the emphasis of subdivision decision-making based on three broad and common growth types.

Although cities vary in extent, fragmentation, and residential density [31–32], urban form typically adheres to a set of common patterns [33–34], and we based our development scenarios on the three primary means by which residential development typically occurs: infill, expansion, or leapfrog [34]. Infill is characterized by development of vacant land surrounded by existing development, typically in built-up areas where public facilities already exist. [35–36], and should result in higher structure density rather than increased urban extent. Expansion growth occurs along the edge of existing development, extends the size of the urban patch to which it is adjacent, and may have variable influence on structure density. Leapfrog growth occurs when development occurs beyond existing urban areas such that the new structure is surrounded by undeveloped land. This type of growth would expand the urban extent and initially result in lower structure density; but these areas may eventually become centers of growth from which infill or expansion can occur. We asked:

1) Do residential development policies reflecting broad growth types affect the resulting pattern and footprint of development across the landscape?
2) Do differences in extent, location, and pattern of residential development translate into differences in wildfire risk, based on the current configuration of structures?
3) Which development process, infill, expansion, or leapfrog, results in the lowest projected fire risk across the landscape?

Methods

Study Area

The study area included all land within the South Coast Ecoregion of San Diego County, California, US, encompassing an area of 8312 km^2. The region is topographically diverse with high levels of biodiversity, and urban development has been the primary cause of natural habitat loss and species extinction [37]. Owing to the Mediterranean climate, with mild, wet winters and long summer droughts, the native shrublands dominating the landscape are extremely fire-prone. San Diego County was the site of major wildfire losses in 2003 and 2007 [38], although large wildfire events have occurred in the county since record-keeping began, and are expected to continue, as fire frequency has steadily increased in recent decades [29,39]. The county is home to more than three million residents, and approximately one million more people are expected by 2030 [40]. Although most residential development has been concentrated along the coast, expansion of housing is expected in the eastern, unincorporated part of the county.

Econometric Subdivision Model

A host of alternative modeling approaches exist to simulate future land use scenarios [41], including a cellular automaton model that we previously applied to the study area [42]. We chose to use an econometric modelling approach for this study because we wanted to capture fine-scale, structure-level patterns and processes that are correlated with housing loss to wildfire [26]; and econometric models may perform better at the scale of individual parcels [43].

Although we based the three development scenarios on generalized planning policies, we also wanted to ensure that the residential projections were realistic and adhered to current planning regulations. The objective of the econometric modeling was to estimate the likelihood that residential parcels will subdivide in the future. Therefore, we used a probit model to estimate the transition probability of each parcel based on a range of potential explanatory variables typically associated with parcel subdivision and housing development [44–45].

To develop the model of subdivision probability, we acquired GIS data of the county's parcel boundaries in years 2005 and 2009 from the San Diego Association of Governments (SANDAG). The dependent variable was equal to 1 if a parcel subdivided between 2005 and 2009, and zero otherwise. Using these data layers we first determined which parcels were legally able to subdivide given current land use regulations. Minimum lot size restrictions are typically considered the most import restriction for determining future land use. We deemed a parcel eligible for subdivision if the current lot size was greater than twice the minimum legal size given the land class. To determine which parcels subdivided between 2005 and 2009, we queried parcel IDs where the total area was reduced by at least the minimum lot size between the two time periods. Finally, we were able to generate a suite of variables that determine the likelihood of a parcel developing in the future (Table S1).

We overlaid the parcel boundaries over a range of GIS layers representing our explanatory variables. These data are available to download at (http://www.sandag.org/index.asp?subclassid = 100&fuseaction = home.subclasshome). Our explanatory variables included: parcel size, parcel size squared, six dummy variables which capture non-linear effects of parcel size, distance to the coast, distance to the coast squared; distance to city center and its square, current zoning, slope, land use, roads, if the parcel is in a protected area, if the parcel is in a development area, if the parcel is in the redevelopment area (Table 1).

Spatial Model of Future Development under Planning Alternatives

The outcome of the land use change econometric model is the subdivision probability for each parcel for a five-year time step. Based on these probabilities, we developed a GIS spatial simulation model of future land use under three distinct planning scenarios: infill (development in open or low density parcels within already developed areas), expansion (development on the fringe of developed areas), and leapfrog (development in open areas). The model runs in four 5-year time steps from 2010 to 2030, and generates the spatial locations of new housing units in the county.

Although development decisions could feasibly depend on fire risk, we did not model that here. There is no evidence that fire has influenced past regional planning decisions, so it was not used as an explanatory variable in the econometric model. Although we could have evaluated the potential for future development decisions to be based in part on fire risk, this would have required simulation of feedbacks between fires and probability of development. Because our objective in this study was to isolate the effects of the three distinct growth types, we modeled fire risk only as a function of development pattern and not vice versa.

We constructed a complete spatial database of existing residential structures in the study area [26]. These structures and their corresponding parcel boundaries served as the initial conditions for all three scenarios of the spatial simulation model. The current and projected future GIS layers of structures were also subsequently used in the fire risk model (see below). The

Table 1. Variables and results from the probit regression model of parcel subdivision in San Diego County.

Subdivided (1 = yes,0 = no)	**Coefficient**	**Std. Err.**	**z**	**P>|z|**	**[95% Conf. Interval]**	
Acres of lot	0.0026342	0.00075	3.51	0	0.001164	0.004105
Acres of lot ^{2}	−3.02E-06	1.29E-06	−2.34	0.019	−5.55E-06	−4.93E-07
Distance to ocean	−7.42E-06	1.33E-06	−5.59	0	−0.00001	−4.82E-06
Distance to ocean ^{2}	2.33E-11	8.28E-12	2.82	0.005	7.11E-12	3.96E-11
Distance to major road	2.17E-07	2.74E-06	0.08	0.937	−5.16E-06	5.59E-06
Distance to major road ^{2}	−1.94E-11	1.70E-11	−1.14	0.252	−5.27E-11	1.38E-11
Distance to nearest city center	−0.0000115	1.70E-06	−6.76	0	−1.5E-05	−8.16E-06
Distance to nearest city center ^{2}	2.89E-11	9.70E-12	2.98	0.003	9.91E-12	4.79E-11
Slope between 0–5%	0.6211289	0.211761	2.93	0.003	0.206085	1.036173
Slope between 5–10%	0.3911427	0.210684	1.86	0.063	−0.02179	0.804076
Slope between 10–25%	0.0716669	0.212725	0.34	0.736	−0.34527	0.4886
Rural Residential	−0.3563149	0.071512	−4.98	0	−0.49648	−0.21615
Single Family	0.1361149	0.068678	1.98	0.047	0.001509	0.270721
Multi-Family	−0.2505093	0.151486	−1.65	0.098	−0.54742	0.046397
Road	0.015329	0.086094	0.18	0.859	−0.15341	0.184069
Open Space	−0.7440933	0.099145	−7.51	0	−0.93841	−0.54977
Orchard/Vineyard	−0.5813305	0.097867	−5.94	0	−0.77315	−0.38951
Agriculture	−0.9785208	0.132734	−7.37	0	−1.23867	−0.71837
Vacant Land	−0.5222501	0.074586	−7	0	−0.66844	−0.37606
Zoned protected	0.253769	0.076881	3.3	0.001	0.103086	0.404452
Area marked for redevelopment	−0.2680261	0.14069	−1.91	0.057	−0.54377	0.007722
Area marked for development	0.5780101	0.064103	9.02	0	0.452371	0.703649
Parcel between 10–20 acres	−0.3379532	0.065899	−5.13	0	−0.46711	−0.20879
Parcel between 5–10 acres	−0.6119036	0.067012	−9.13	0	−0.74325	−0.48056
Parcel between 2–5 acres	−1.16297	0.07062	−16.47	0	−1.30138	−1.02456
Parcel between 1–2 acres	−1.563956	0.090286	−17.32	0	−1.74091	−1.387
Parcel between.5–1 acres	−1.999939	0.099893	−20.02	0	−2.19573	−1.80415
Parcel between.25–.5 acres	−2.178273	0.117101	−18.6	0	−2.40779	−1.94876
Constant	−1.397931	0.227467	−6.15	0	−1.84376	−0.9521

Sample size 113 001, LR Chi^2 1535.23, pro>chi 0, pseudo R^2 0.22. Further description of the variables is provided in Table S1.
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dataset of existing housing includes locations of 687,869 structures, of which 4% were located within the perimeter of one of 40 fires that burned since 2001. During these fires, 4315 structures were completely destroyed, and another 935 were damaged.

For future development scenarios, we wanted to allocate an equal number of new structures to the landscape. This was to ensure that any predicted difference in fire risk was a function of the arrangement and location of structures, not the total number of structures. Nevertheless, differences in the total number of structures were simulated with each of the 5-year time steps. We determined the number of housing units to add during the simulations based on projections made by San Diego County [46]. Using factors such as development proposals, general plan densities, and information from jurisdictions, the county estimated that between 331,378 units and 486,336 units could be supported within the developable residential land by 2030. Because the eastern, desert portion of the county was not included in our study area, we used a conservative approach and simulated the addition of 331,378 new dwelling units. We divided this number by four to define the number of new dwelling units to add at each time step, assuming a linear growth rate.

One output of the econometric model was the prediction of the maximum number of new dwelling units that could be added to each parcel. However, dwelling units may consist of apartments as well as single family homes. The mix of single and multifamily units in the region has remained relatively constant over time, and the overall trend has been a mix of roughly 1/3 multifamily and 2/3 single family units. Because the fire risk model is based on points representing structure locations across the landscape, regardless of the number of dwelling units per structure, we needed to generate a conversion factor from dwelling units to structures. We therefore defined a minimum lot size of 0.25 acre on which no more than a single structure could be built, regardless of the number of dwelling units in it (i.e., a single family home or apartment complex). Then, once a parcel was selected for development by the model (see details below), we divided its total area by the maximum number of dwelling units to be added, according to the econometric model. If the result was larger than 0.25, we subdivided parcels according to the result. If not, we quantified how many 0.25 acre parcels fit into the original parcel, and generated the new parcel boundaries accordingly.

Using the initial map of parcels (year 2010), we classified each parcel that was defined as eligible for development (in the previous stage) as suitable for one of the three planning scenarios described above, according to the number of developed parcels in its immediate neighborhood (i.e., those parcels that share a boundary with the focal parcel). We defined ‘developed parcels’ as ones that had more than one house per 20 acres (8.09 ha). Therefore, according to these density thresholds, we allowed some parcels with nonzero housing density to be considered as ‘undeveloped’ because these large, rural parcels might contain a single or a handful of houses but they exist within a large open area. In other words, the overall land cover of these parcels was effectively undeveloped, and we therefore assumed that development in adjacent parcels would be akin to development in open areas.

We defined infill parcels as those that were completely surrounded by developed parcels. Expansion parcels had at least one neighboring parcel that was undeveloped; and leapfrog parcels were those with no developed parcels in their immediate surroundings. We reclassified the type of each available parcel in the same manner after each time step, to account for changing dynamics in the development map of the county.

We conducted three simulations, one for each development scenario (infill, expansion, and leapfrog). In each simulation, all parcels were eligible to subdivide, regardless of their class. Therefore, to build a simulation for a specific scenario, we increased the development probability of parcels of the selected scenario by 20%, to favor their development compared to the other types of parcels, without prohibiting development in the other parcel types. This approach was necessary because the projected number of dwelling units was much larger than it would be possible to fit in infill and leapfrog class parcels solely. For example, as the spatial coverage of developed parcel expands, there is less contiguous area that is undevelopable and suitable for leapfrog development. Therefore, the scenarios are not exclusive, but rather a mixture of the three development types. Yet, in each scenario, there is one main type of development, and smaller amounts of development events of the other two types.

Due to the immense computational demand of the simulations, we adopted a deterministic, rather than a stochastic approach to decide on which parcels were subdivided. After enhancing the transition probability according to the corresponding scenario, we ranked and then sorted all parcels according to their probability of subdivision. We then sequentially selected parcels, while simultaneously tallying the number of dwelling units in them, until the development target in that time step (one fourth of the total number of dwelling units to be added: 82,795) was reached. Once the development target was reached, we moved to the next time step. After each time step, the remaining parcels that were still eligible for development were re-classified to development types according to the new spatial configuration of the landscape.

Once a parcel was selected for subdivision, and the number of new parcels to develop in it was calculated (as detailed above), an equal-area spatial splitting model was employed to split the parent parcel to the predefined number of equal-area child parcels. We developed a simple splitting model which is based on iterative splitting of larger parcels into two smaller parcels using a straight line splitting boundary. Once the parcel was fully split into the needed number of sub-parcels, we allocated a new structure inside each new parcel by generating a point at its centroid (center of gravity). The point datasets of all structure locations per time step per scenario were passed over to the fire risk model, which is described below.

Fire Risk Modeling and Analysis

To project the distribution of fire risk under alternative scenarios, we used MaxEnt [47–48], a map-based modeling software used primarily for species distribution modeling [48], but we have used it successfully for ignition modeling [50] and for projecting current fire risk in the study area [26]. For this study, we slightly modified the model from Syphard et al. [26]. The dependent variable was the location of structures destroyed by fire between 2001 and 2010. Although inclusion of damaged structures in the data set does not significantly affect results [26], we only included completely destroyed structures to avoid the introduction of any uncertainty.

The MaxEnt software uses a machine-learning algorithm that iteratively evaluates contrasts among values of predictor values at locations where structures burned versus values distributed across the entire study area. The model assumes that the best approximation of an unknown distribution (i.e., structure destruction) is the one with maximum entropy. The output is an exponential function that assigns a probability to every cell of a map. Thus, the resulting continuous maps of fire risk represented the probability of a structure being destroyed by fire. In these output maps, areas of predicted high fire risk that did not have structures on them represented environmental conditions similar to those in which structures have actually burned.

We based the explanatory variables on those that were significantly related to burned structures in Syphard et al. [26], including maps depicting housing arrangement and pattern, housing location, and biophysical factors. Housing pattern variables reflected individual structure locations as well as the arrangement of structures within housing clusters. We calculated housing clusters, defined as groups of structures located within a maximum of 100 m from each other, by creating 100 m buffers around all structures and dissolving the overlapping boundaries [51].

Because burned structures were significantly related to small housing clusters [26], we calculated the area of every cluster as an attribute, and then created raster grids based on that attribute. Low-to intermediate housing density and distance to the edge of the cluster were also significant explanatory variables relative to housing pattern and location [26], so we also created raster grids for those. GIS buffer measures at 1-km have been found to explain approximately 90% of the variation in rural residential density [52], so we developed density grids using simple density interpolation based on a 1-km search radius, with area determined through square map units. To create grids representing distance to the edge of clusters, we first collapsed the cluster polygons into vector polyline files, and then created grids of interpolated Euclidean Distance to the edge within each cluster.

Because the MaxEnt model randomly selects background samples in the map to compare with locations of destroyed structures, we used a mask to restrict sampling to the developed environment within cluster boundaries; the distance to the edge of the cluster would represent a different relationship inside a cluster boundary versus outside in the wildland. We also modified the grids to ensure that any random sample located within the 100m buffer zone would receive a value of 100m; thus, all points within the buffer were considered "the edge of the development".

After creating the grids representing housing pattern and arrangement of the current configuration of structures, we applied the same algorithms to the maps of simulated future structure locations. We thus generated grids representing future housing pattern and arrangement under alternative development scenarios. The other explanatory variables, including fire history, slope, fuel type, southwest aspect, and distance to coast [26] remained constant through time for current and future scenarios. Although historic fire frequency and fuel type typically change through time, we did not simulate their dynamics here because we wanted to isolate the effect of planning decisions on housing pattern and arrangement while holding everything else constant.

We conditioned the MaxEnt model on present distributions of housing using ten thousand random background points and destroyed structures located no closer than 500-m to minimize any effect of spatial autocorrelation. We used 80% (260 records) of these data for model training, and 20% [66 records) for testing. We repeated the process using cross-validation with five replicates and used the average of these five models for analyses. For smoother functions of the explanatory variables, we used hinge features, linear, and quadratic with an increase in regularization of beta set at 2.5, based on Elith et al. [48]. The smoother response curves minimize over fitting of the model. We conducted jackknife tests of explanatory variable importance.

We first developed the model using mapped explanatory variables derived from the current configuration of structures. To project fire risk under the different time steps of the alternative development scenarios, projected the model conditioned upon current conditions onto maps representing future conditions by substituting the grids representing future housing pattern and arrangement. This is similar to how potential future distributions of species are projected under climate change scenarios [49].

To quantify differences among current and future alternative scenarios, we calculated metrics representing housing density, pattern, and footprint to determine the extent to which the planning policies produced differences in housing pattern and location. We compared the modeled structure fire risk of the scenarios by overlaying all maps of structure locations with their respective mapped output grids from the MaxEnt models and calculating probability of burning for every structure point. We also calculated total area of risk by selecting three threshold criteria [53]. These criteria, at 0.05, 0.25, and 0.5 represented three different degrees of risk, and we calculated the proportion of structures that were located in risk areas for every time step in all scenarios.

Results

The probit econometric model, run on 113 001 observations, showed that larger parcels were most likely to subdivide, although the relationship between parcel size and subdivision probability was non-linear (Table 1). Parcels closer to existing roads, the ocean, those with lower slopes, and those designated as fit for development were all most likely to develop. Parcels designated in redevelopment areas were less likely to develop. Overall, the model had a pseudo r –squared of 0.22.

The land use simulation model, based on a combination of the econometric subdivision model and three different growth policies, resulted in substantial differences in the extent and pattern of housing of the three scenarios. The total area of housing development, or the housing footprint, was largest for simulations where leapfrog growth dominated, followed by expansion-type development, and then infill (Figure 1a). The differences in the housing footprint became larger among the scenarios over time, but the largest difference was between infill and the other two development types. As the housing footprint expanded in the three scenarios, the corresponding housing density declined, so that leapfrog growth resulted in the lowest housing density per 1-km, followed by expansion and then infill (Figure 2b). Despite the near inverse of this relationship, there was generally a larger separation among scenarios with regard to housing density. With larger housing footprints and lower housing density, the number of separate housing clusters increased while their size decreased (Figure 2c).

In the first two time steps of the model (2015 and 2020), the simulated development pattern closely followed the desired pattern in the scenario, although some of the growth in the infill scenario ended up becoming expansion or leapfrog (Table 2). In the last two time steps (2025 and 2030), there were not enough infill parcels left, and thus, the majority of growth in these simulations became expansion, followed by infill, and then leapfrog. In the last time step, there were not enough isolated parcels in the leapfrog scenario and thus, the majority of development became expansion. Thus in general, as more development occurred in the simulations by the year 2030, the majority took the form of expansion.

The area under the curve (AUC) of receiver operating characteristic (ROC) plots, indicating the ability of the MaxEnt model to discriminate between burned and unburned structures, averaged across five cross-validated replicate runs was 0.91. The AUC represents the probability that, for a randomly selected set of observations, the model prediction was higher for a burned structure than for an unburned structure [49].The two most important variables in the model according to the internal jackknife tests in MaxEnt [47] were related to housing pattern:

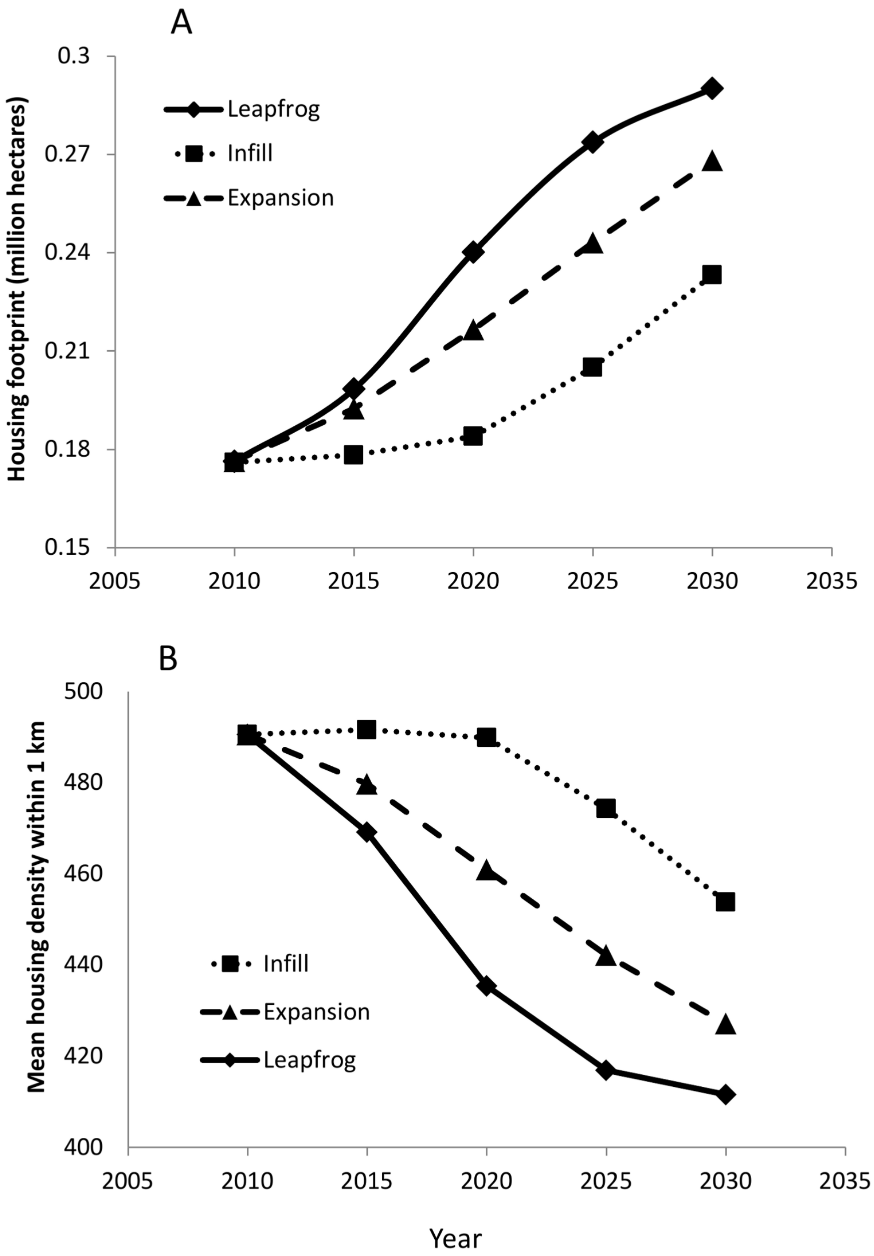

Figure 1. Trends of development extent and pattern for three planning policy simulations from 2010–2030, including A) total housing footprint representing the area of land within all housing clusters, and B) mean housing density averaged across all housing clusters.
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low to intermediate housing density and small cluster size and housing density (Figure 3). The distance to the edge of housing cluster was a less important contribution.

Maps showing the probability of a structure being destroyed in a wildfire, displayed as a gradient from low to high risk, show broad agreement relative to the general areas of the landscape that are riskiest, with correlation coefficients ranging from 0.85–0.91 (Figure 4). Nevertheless, subtle differences are apparent in the three development-scenario maps by year 2030, with the highest-risk areas in the expansion scenario located farther east than infill, and the highest-risk areas in leapfrog occupying a wider extent than either of the other two scenarios.

Differences among current housing and the three development scenarios are clearly illustrated through the mean landscape risk, or total probability of all structures burning (Figure 5). All three development scenarios were predicted to experience an increase in mean landscape risk over the duration of the simulations, except for infill at year 2015. The highest landscape risk to structures was predicted for the leapfrog scenario, followed by expansion, and then infill. The increase in risk over time is more gradual for the infill scenario than the other two scenarios.

The ranking of scenarios varied according to the proportion of structures located within different levels of risk defined through binary thresholding (Figure 6). When the continuous risk maps were thresholded at the lowest number of 0.05, a large proportion

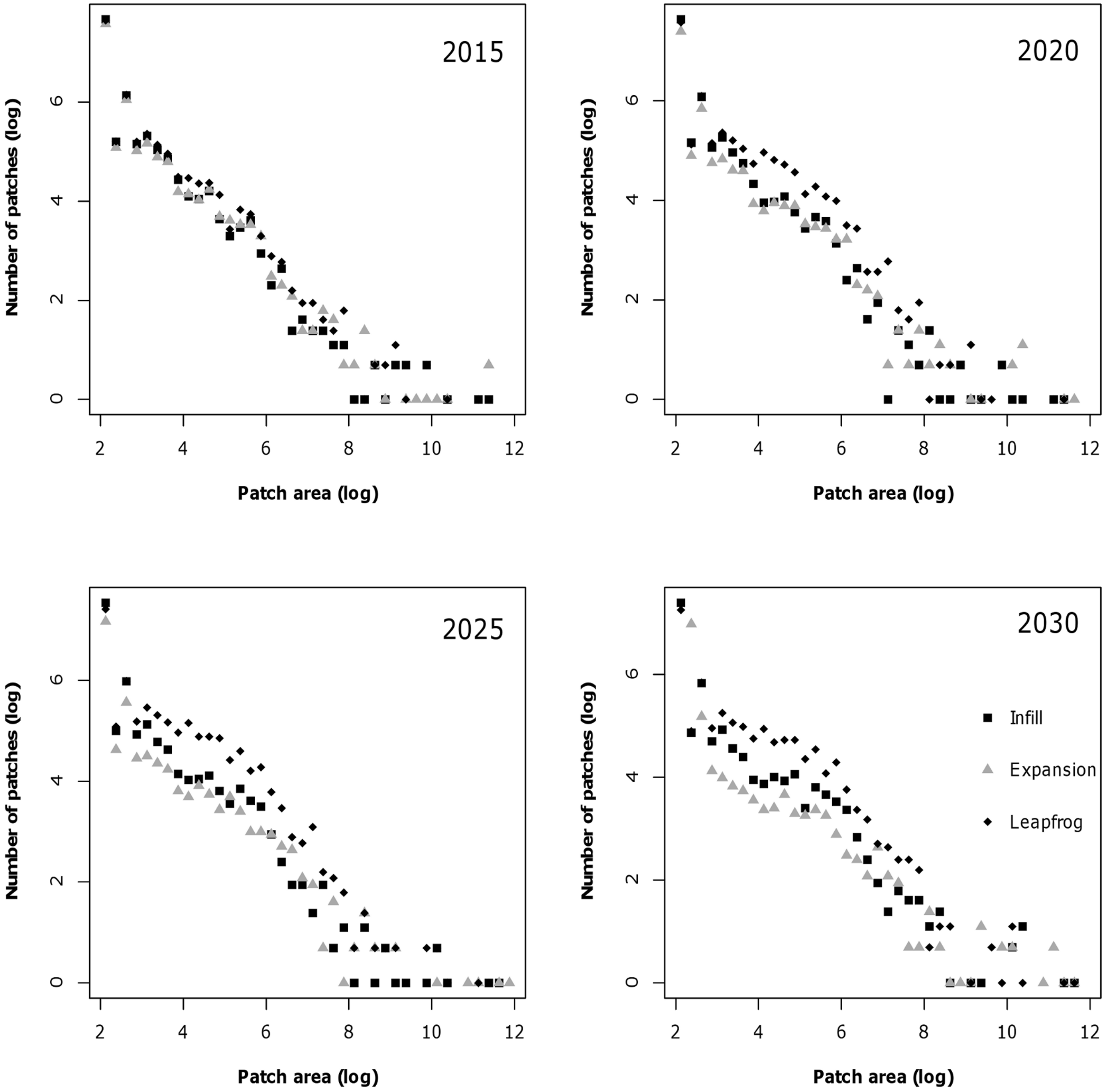

Figure 2. Trends in number of patches and patch area for three planning policy simulations from 2010–2030. Numbers were log-transformed for better visual representation of the scenarios.
doi:10.1371/journal.pone.0071708.g002

of structures in all scenarios fell within areas defined as risky according to this criterion. At this threshold, the proportion of structures in high-risk areas increased linearly for the expansion and leapfrog development scenarios while the proportion of infill homes increased more gradually. When risk was defined more conservatively at 0.25, temporal trends for the leapfrog and infill scenarios were similar to the 0.05 threshold. However, the proportion of structures at risk in the expansion scenario initially increased to 2020, but this proportion leveled off and declined by 2030. When the threshold was highest at 0.50, a very low proportion of structures in any scenario were located in areas at risk. But in these high-risk areas, the expansion scenario switched places with infill to have the lowest proportion of structures at risk in all time steps. Leapfrog had the largest proportion of homes at risk. This proportion of homes located in areas at risk with a threshold at 0.5 declined over time for all three scenarios.

Discussion

Our simulations of residential development showed that planning policies based on different growth types, applied locally for subdivision of individual parcels, will likely produce substantial and cumulative landscape-level differences in pattern, location, and extent of development. These differences in development pattern, in turn, will likely affect the area and proportion of

Table 2. Pattern of simulated development under infill, expansion, and leapfrog growth policies.

		Actual development		
Development scenario	**year**	*Infill*	*Expansion*	*Leapfrog*
Infill	2015	9450	18	6
	2020	11787	153	29
	2025	236	624	144
	2030	325	890	179
Expansion	2015	0	772	0
	2020	0	1243	2
	2025	0	1871	1
	2030	0	2662	0
Leapfrog	2015	0	10	408
	2020	0	5	1132
	2025	1	83	3563
	2030	34	917	0

The numbers in the table denote the numbers of patches of a given development type.
doi:10.1371/journal.pone.0071708.t002

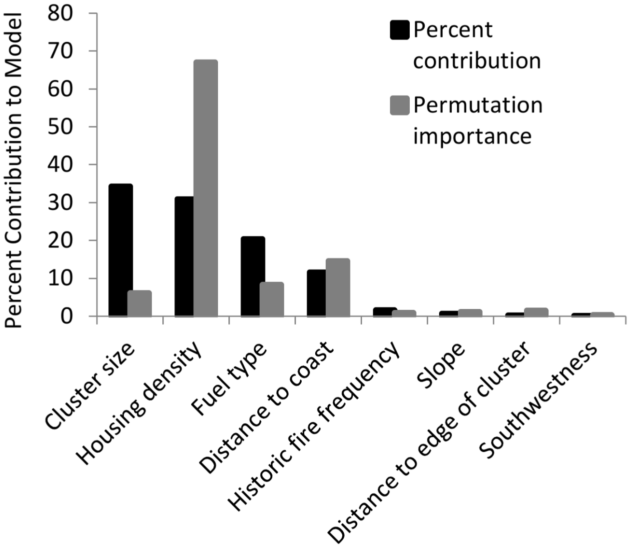

Figure 3. The importance of explanatory variables averaged across five cross-validated replications in the MaxEnt fire risk model. Percent contribution is determined as a function of the information gain from each environmental variable throughout the MaxEnt model iterations. Permutation importance reflects the drop in model accuracy that results from random permutations of each environmental variable, normalized to percentages.
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structures at risk from burning in wildfires. In particular, the scenarios with lower housing density and larger numbers of small, isolated clusters of development, i.e., leapfrog followed by expansion and infill, were generally predicted to have the highest predicted fire risk to the largest proportion of structures in the study area. Nevertheless, rankings of scenarios were affected by the definition of risk.

Theoretically, it makes sense that leapfrog development produced fragmented development with larger numbers of small patches, lower housing density, and a larger housing footprint; and that infill resulted in the opposite, with expansion in the middle. By definition, leapfrog development requires open space around all sides of the newly developed parcel, whereas infill requires development on all sides, and expansion requires development on one side and open space on another. Implementing these planning policies on real landscapes, however, can be complex if there are more houses to build than there are parcels that meet the definitions of the three planning rules, and thus not all development conforms strictly to the policy [54]. In our simulations, parcels meeting the definition of each growth type had a higher probability of subdividing; yet, as we were simulating a real landscape, many newly developed parcels did not meet the scenario criteria. That the three scenarios nevertheless produced substantial differences in landscape-level development patterns shows that decision-making at the individual level can lead to meaningful broad-scale effects.

The objective of the econometric model was to provide a baseline probability to predict which parcels were most likely to subdivide; thus, the econometric model itself provides no explanation of how a given policy affects likelihood of subdivision, although it does indicate the correlation between the policy and the outcome. In our setting, which areas are protected, marked for redevelopment, or marked for development may be endogenous to the land owner decision to subdivide. In the case of these variables especially, our results should not be interpreted as causal predictors. Likewise, we use data only from 2005–2009 to predict changes to 2030. If major changes in the land market take place over this time horizon our model will not be able to take this into account.

Although some differences in predicted fire risk among the three scenarios likely stemmed from location of new structures relative to variables such as distance to coast, fuel type, or slope, the most important variables in the fire risk model were housing density and cluster size, with most structure loss historically occurring in areas with low housing density and in small, isolated housing clusters. Thus, leapfrog development was generally the riskiest scenario and infill the least risky. The most surprising result was the variation in predicted risk for the expansion scenario over time and at different thresholds. While leapfrog and infill showed similar trajectories across thresholds, expansion went from being the highest-risk scenario at the low threshold to being the lowest-risk scenario at the highest threshold. Because the threshold is merely a way to group structures into a binary classification, this means that, while the average risk calculated across all homes shows expansion to rank in the middle of infill and leapfrog throughout the simulation (Figure 5), the other two scenarios have a relatively larger proportion of homes that are modeled to be at a very high risk (i.e., 0.25 or 0.5), particularly by the end of the simulations. Because the total number of structures with a risk greater than 0.25 or 0.5 is relatively low in all scenarios, this difference in distribution of homes at the highest risk is not reflected in the mean. Another reason for the shift in rank of expansion over time is that, as more development occupied the landscape, there were fewer parcels remaining to accomplish infill or leapfrog type growth in the other scenarios. Thus, by the end of the simulations in year 2030, the majority of growth in all scenarios was expansion, and there was some convergence between scenarios. Finally, the change in risk of expansion growth over time may reflect that, despite the relatively low importance of distance to edge of cluster as an explanatory variable, expansion growth is characterized as having an initially fragmented landscape pattern that eventually merges into large patches with low edge.

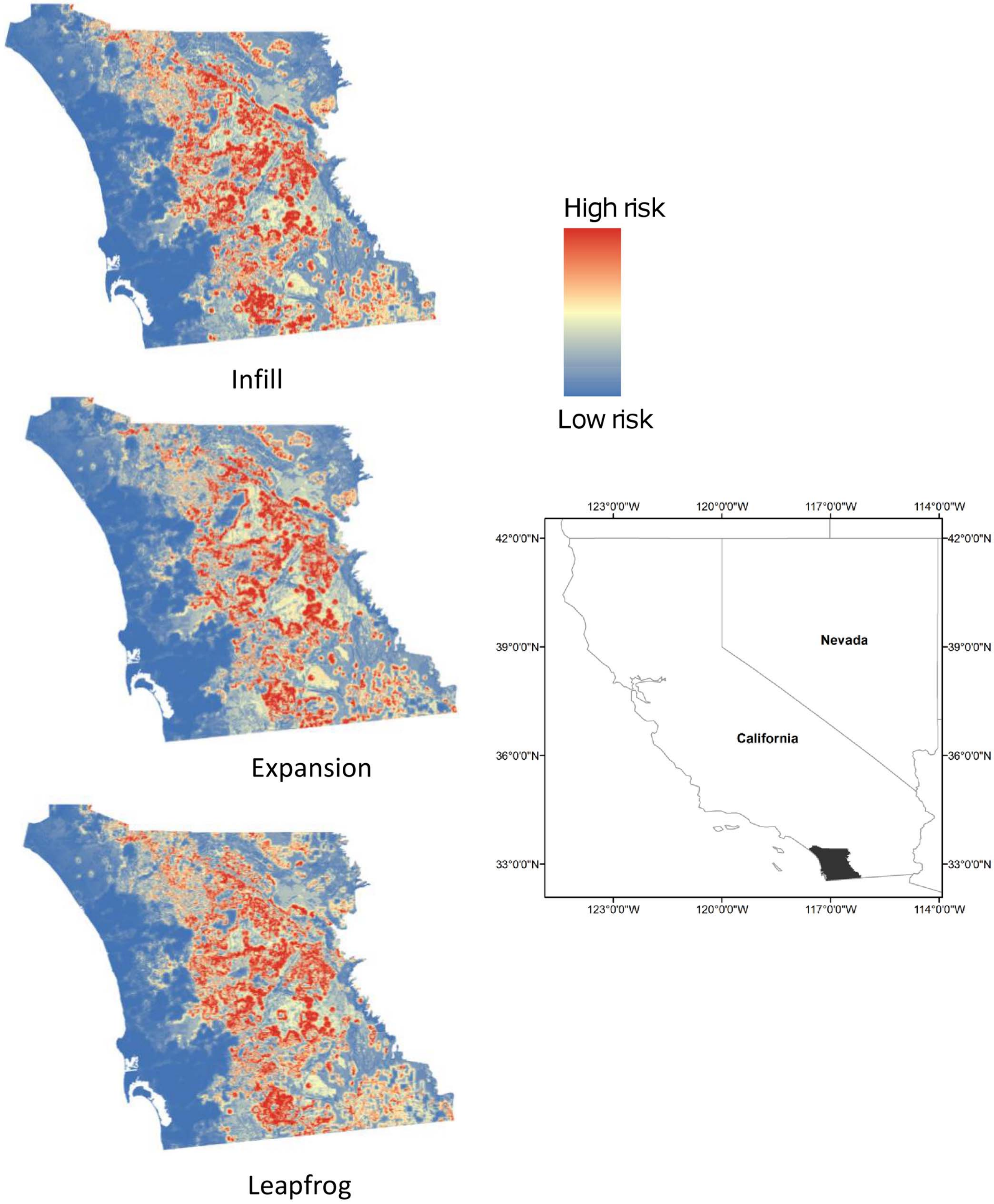

Figure 4. Maps of the study area showing projected wildfire risk at year 2030 for simulations of residential development under policies emphasizing infill, expansion, or leapfrog growth.
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Although leapfrog development clearly ranked highest in terms of fire risk, the interpretation of which planning policy is best may depend on fire management objectives and resources, as well as other considerations such as biodiversity or ecological impacts.

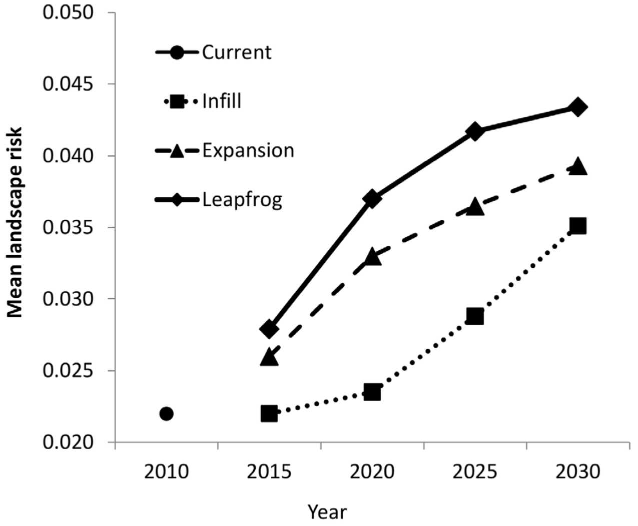

Figure 5. Projected landscape fire risk, reflecting the probability of burning in a wildfire averaged across all residential structures on the current landscape and in three development scenarios of infill, expansion, and leapfrog for year 2030.
doi:10.1371/journal.pone.0071708.g005

The spatial pattern of development affects multiple ecological functions and services [55], with potentially varying conservation implications; both leapfrog and expansion development consumed more land than infill, which would likely lead to more ecological degradation [56]; nevertheless, higher-density clustered development may be dominated by more invasive species [57]. Trade-offs between fire protection and conservation are common, but techniques are available for identifying mutually beneficial solutions [58].

Different perceptions of the fire risk results could also potentially translate into different planning priorities for management. For example, if the priority is to plan for the lowest overall risk to structures, then the mean landscape risk clearly delineates the rankings of options, with infill being the winner. However, if the objective is to reduce the number of structures at the highest risk threshold, i.e., > = 0.5, then expansion is the best option, at least by 2030. An important consideration for fire management is the total area that needs to be protected, as well as the length of wildland-urban interface [8,13]. Therefore, despite the lower number of structures at the highest risk thresholds, expansion creates more edge than infill and may translate into greater challenges for firefighter protection.

Although we did not create separate scenarios for high or low growth, the results at different time steps can be substituted to envision the potential outcome of developing more or fewer houses. In the short term, the total fire risk is projected to increase proportionately as more land is developed. However, given the inverse relationship between housing density and fire risk, it is possible that this trend could reverse if housing growth eventually resulted in expansive high-density development.

Land use planning is one of a range of options available for reducing fire risk, and the best outcome will likely be achieved through a combination of strategies that include homeowner actions, improvements in fire-safe building codes, and advanced fire suppression tactics. Although we isolated the effect of land use planning policy in the three development scenarios, the fire risk model nevertheless showed that the pattern and location of structures in this study area were the most important out of a suite of factors influencing structure loss. We used a correlative approach that did not incorporate mechanisms or feedbacks, but our models clearly illustrated differences in the cumulative effects of individual planning decisions. The relationship between spatial pattern of development and fire risk is likely related to the intermixing of development and wildland vegetation [29,59]; thus, these results likely apply to a wide range of fire-prone ecosystems with large proportions of human-caused ignitions. Nevertheless, because fire risk is highly variable over space and time, and due to a range of human and biophysical variables [60], we recommend planners develop their own models for the best understanding of where the most fire-prone areas are in their region [19].

With projections of substantial global change in climate and human development, we recommend that land use planning should be considered as an important component to fire risk management, potentially to become as successful as the prevention of building on flood plains [61]. History has shown us that preventing fires is impossible in areas where large wildfires are a natural ecological process [4,9]. As Roger Kennedy put it, "the

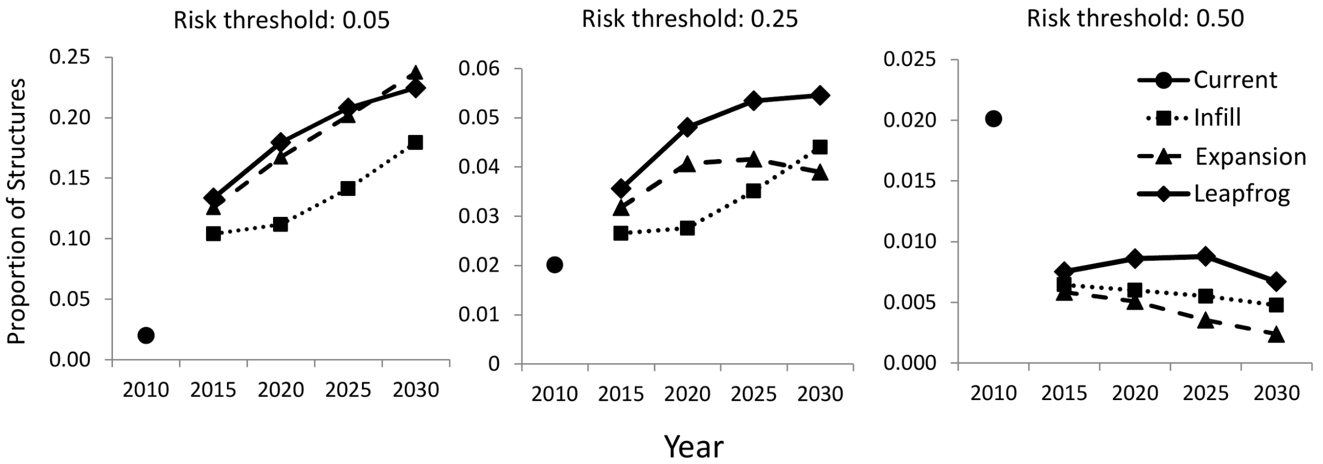

Figure 6. Proportion of residential structures that are located in areas of high fire risk defined using thresholds from the fire risk model of 0.05, 0.25, and 0.5 for current structures and for structures simulated under infill, expansion, and leapfrog growth policies.
doi:10.1371/journal.pone.0071708.g006

problem isn't fires; the problem is people in the wrong places [62]."

Supporting Information

Table S1 Definitions and summary statistics for variables used in the probit model.
(DOCX)

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Author Contributions

Conceived and designed the experiments: ADS JEK ABM VB. Performed the experiments: ADS ABM VB. Analyzed the data: ADS ABM VB. Wrote the paper: ADS JEK ABM VB.

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The role of defensible space for residential structure protection during wildfires

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Abstract. With the potential for worsening fire conditions, discussion is escalating over how to best reduce effects on urban communities. A widely supported strategy is the creation of defensible space immediately surrounding homes and other structures. Although state and local governments publish specific guidelines and requirements, there is little empirical evidence to suggest how much vegetation modification is needed to provide significant benefits. We analysed the role of defensible space by mapping and measuring a suite of variables on modern pre-fire aerial photography for 1000 destroyed and 1000 surviving structures for all fires where homes burned from 2001 to 2010 in San Diego County, CA, USA. Structures were more likely to survive a fire with defensible space immediately adjacent to them. The most effective treatment distance varied between 5 and 20 m (16–58 ft) from the structure, but distances larger than 30 m (100 ft) did not provide additional protection, even for structures located on steep slopes. The most effective actions were reducing woody cover up to 40% immediately adjacent to structures and ensuring that vegetation does not overhang or touch the structure. Multiple-regression models showed landscape-scale factors, including low housing density and distances to major roads, were more important in explaining structure destruction. The best long-term solution will involve a suite of prevention measures that include defensible space as well as building design approach, community education and proactive land use planning that limits exposure to fire.

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Introduction

Across the globe and over recent decades, homes have been destroyed in wildfires at an unprecedented rate. In the last decade, large wildfires across Australia, southern Europe, Russia, the US and Canada have resulted in tens of thousands of properties destroyed, in addition to lost lives and enormous social, economic and ecological effects (Filmon 2004; Boschetti *et al.* 2008; Keeley *et al.* 2009; Blanchi *et al.* 2010; Vasquez 2011). The potential for climate change to worsen fire conditions (Hessl 2011), and the projection of continued housing growth in fire-prone wildlands (Gude *et al.* 2008) suggest that many more communities will face the threat of catastrophic wildfire in the future.

Concern over increasing fire threat has escalated discussion over how to best prepare for wildfires and reduce their effects. Although ideas such as greater focus on fire hazard in land use planning, using fire-resistant building materials and reducing human-caused ignitions (e.g. Cary *et al.* 2009; Quarles *et al.* 2010; Syphard *et al.* 2012) are gaining traction, the traditional strategy of fuels management continues to receive the most attention. Fuels management in the form of prescribed fires or mechanical treatments has historically occurred in remote, wildland locations (Schoennagel *et al.* 2009), but recent studies suggest that treatments located closer to homes and communities may provide greater protection (Witter and Taylor 2005; Stockmann *et al.* 2010; Gibbons *et al.* 2012). In fact, one of the most commonly recommended strategies in terms of fuels and fire protection is to create defensible space immediately around structures (Cohen 2000; Winter *et al.* 2009). Defensible space is an area around a structure where vegetation has been modified, or 'cleared,' to increase the chance of the structure surviving a wildfire. The idea is to mitigate home loss by minimising direct contact with fire, reducing radiative heating, lowering the probability of ignitions from embers and providing a safer place for fire fighters to defend a structure against fire (Gill and Stephens 2009; Cheney *et al.* 2001). Many jurisdictions provide specific guidelines and practices for creating defensible space, including minimum distances that are required among trees and shrubs as well as minimum total distances from the structure. These distances may be enforced through local ordinances or state-wide laws. In California, for example, a state law in 2005 increased the required total distance from 9 m (30 ft) to 30 m (100 ft).

Despite these specific guidelines on how to create defensible space, there is little scientific evidence to support the amount and location of vegetation modification that is actually effective at providing significant benefits. Most spacing guidelines and laws are based on 'expert opinion' or recommendations from older publications that lack scientific reference or rationale (e.g. Maire 1979; Smith and Adams 1991; Gilmer 1994). However, one study has provided scientific support for, and forms the basis of, most guidelines, policy and laws requiring a minimum of 30 m (100 ft) of defensible space (Cohen 1999, 2000). The modelling and experimental research in that study showed that flames from forest fires located 10–40 m (33–131 ft) away would not scorch or ignite a wooden home; and case studies showed 90% of homes with non-flammable roofs and vegetation clearance of 10–20 m (33–66 ft) could survive wildfires (Cohen 2000). However, the models and experimental research in that study focussed on crown fires in spruce or jack pine forests, and the primary material of home construction was wood. Therefore, it is unknown how well this guideline applies to regions dominated by other forest types, grasslands, or nonforested woody shrublands and in regions where wooden houses are not the norm.

Some older case studies showed that most homes with non-flammable roofs and 10–18 m (33–ft) of defensible space survived the 1961 Bel Air fire in California (Howard *et al.* 1973); most homes with non-flammable roofs and more than 10 m (33 ft) of defensible space also survived the 1990 Painted Cave fire (Foote and Gilless 1996). Also, several fire-behaviour modelling studies have been conducted in chaparral shrublands. One study showed that reducing vegetative cover to 50% at 9–30 m (30–ft) from structures effectively reduced fireline intensity and flame lengths, and that removal of 80% cover would result in unintended consequences such as exotic grass invasion, loss of habitat and increase in highly flammable flashy fuels (A. Fege and D. Pumphrey, unpubl. data). Another showed that separation distances adequate to protect firefighters varied according to fuel model and that wind speeds greater than 23 km h^{-1} negated the effect of slope, and wind speed above 48 km h^{-1} negated any protective effect of defensible space (F. Bilz, E. McCormick and R. Unkovich, unpubl. data, 2009). Results obtained through modelling equations of thermal radiation also found safety distances to vary as a function of fuel type, type of fire, home construction material and protective garments worn by firefighters (Zárate *et al.* 2008).

Although there is no empirical evidence to support the need for more than 30 m (100 ft) of defensible space, there has been a concerted effort in some areas to increase this distance, particularly on steep slopes. In California, a senate bill was introduced in 2008 (SB 1618) to encourage property owners to clear 91 m (300 ft) through the reduction of environmental regulations and permitting needed at that distance. Although this bill was defeated in committee, many local ordinances do require homeowners to clear 91 m (300 ft) or more, and there are reports that some people are unable to get fire insurance without 91 m (300 ft) of defensible space (F. Sproul, pers. comm.). In contrast, homeowner acceptance of and compliance with defensible space policies can be challenging (Winter *et al.* 2009; Absher and Vaske 2011), and in many cases homeowners do not create any defensible space.

It is critically important to develop empirical research that quantifies the amount, location and distance of defensible space that provides significant fire protection benefits so that guidelines and policies are developed with scientific support. Data that are directly applicable to southern California are especially important, as this region experiences the highest annual rate of wildfire-destroyed homes in the US. Not having sufficient defensible space is obviously undesirable because of the hazard to homeowners. However, there are clear trade-offs involved when vegetation reduction is excessive, as it results in the loss of native habitats, potential for increased erosion and invasive species establishment, and it potentially even increases fire risk because of the high flammability of weedy grasslands (Spittler 1995; Keeley *et al.* 2005; Syphard *et al.* 2006).

It is also important to understand the role of defensible space in residential structure protection relative to other factors that explain why some homes are destroyed in fires and some are not. Recent research shows that landscape-scale factors, such as housing arrangement and location, as well as biophysical variables characterising properties and neighbourhoods such as slope and fuel type, were important in explaining which homes burned in two southern California study areas (Syphard *et al.* 2012; 2013). Understanding the relative importance of different variables at different scales may help to identify which combinations of factors are most critical to consider for fire safety.

Our objective was to provide an empirical analysis of the role of defensible space in protecting structures during wildfires in southern California shrublands. Using recent pre-fire aerial photography, we mapped and measured a suite of variables describing defensible space for burned and unburned structures within the perimeters of major fires from 2001 to 2010 in San Diego County to ask the following questions:

1. How much defensible space is needed to provide significant protection to homes during wildfires, and is it beneficial to have more than the legally required 30 m (100 ft)?
2. Does the amount of defensible space needed for protection depend on slope inclination?
3. What is the role of defensible space relative to other factors that influence structure loss, such as terrain, fuel type and housing density?

Methods

Study area

The properties and structures analysed were located in San Diego County, California, USA (Fig. 1) – a topographically diverse region with a Mediterranean climate characterised by cool, wet winters and long summer droughts. Fire typically is a direct threat to structures adjacent to wildland areas. Native shrublands in southern California are extremely flammable during the late summer and fall (autumn) and when ignited, burn in high-intensity, stand-replacing crown fires. Although 500 homes on average have been lost annually since the mid-1900s (Calfire 2000), that rate has doubled since 2000. Most of these homes have burned during extreme fire weather conditions that accompany the autumn Santa Ana winds. The wildland–urban interface here includes more than 5 million homes, covering more than 28 000 km^2 (Hammer *et al.* 2007).

Property data

The data for properties to analyse came from a complete spatial database of existing residential structures and their

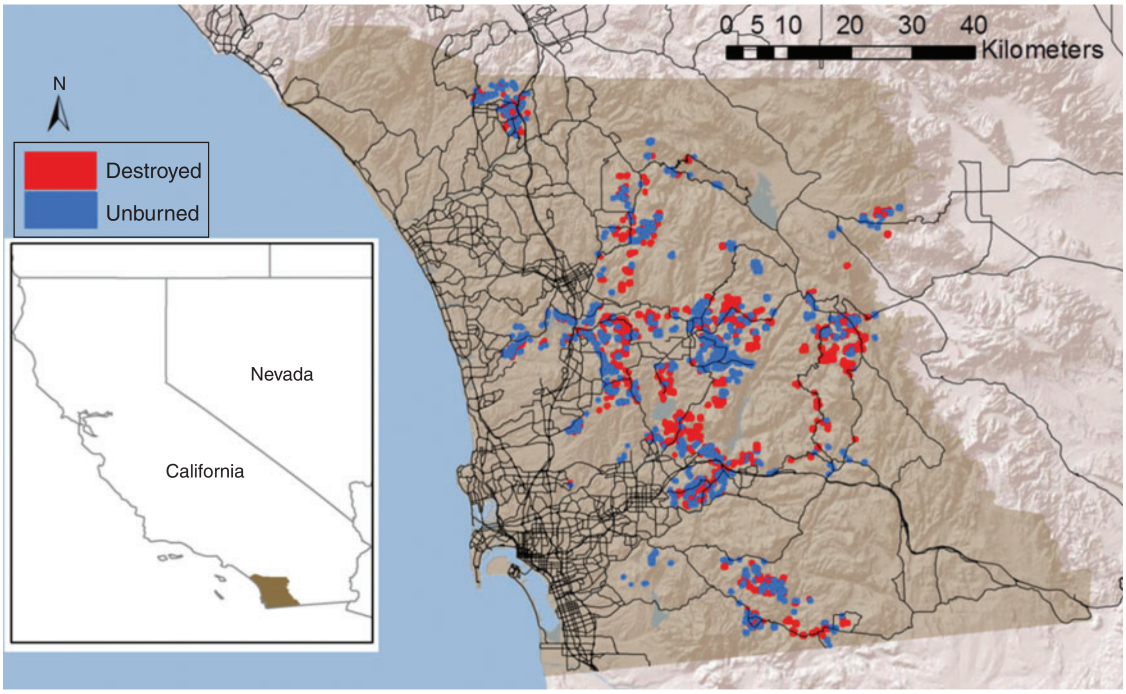

Fig. 1. Location of destroyed and unburned structures within the South Coast ecoregion of San Diego County, California, USA.

corresponding property boundaries developed for San Diego County (Syphard *et al.* 2012). This dataset included 687 869 structures, of which 4315 were completely destroyed by one of 40 major fires that occurred from 2001 to 2010. Our goal was to compare homes that were exposed to wildfire and survived with those that were exposed and destroyed. To determine exposure to fire, we only considered structures located both within a GIS layer of fire perimeters and within areas mapped as having burned at a minimum of low severity through thematic Monitoring Trends in Burn Severity produced by the USA Geological Survey and USDA Forest Service. From these data, we used a random sample algorithm in GIS software to select 1000 destroyed and 1000 unburned homes that were not adjacent to each other, to minimise any potential for spatial autocorrelation. Our final property dataset included structures that burned across eight different fires. More than 97% of these structures burned in Santa Ana wind-driven fire events (Fig. 1).

Calculating defensible space and additional explanatory variables

To estimate defensible space, we developed and explored a suite of variables relative to the distance and amount of defensible space surrounding structures, as well as the proximity of woody vegetation to the structure (Table 1). We measured these variables based on interpretation of Google Earth aerial imagery. We based our measurements on the most recent imagery before the date of the fire. In almost all cases, imagery was available for less than 1 year before the fire.

Our definition of defensible space followed the guidelines published by the California Department of Forestry and Fire Protection (Calfire 2006). 'Clearance' included all areas that were not covered by woody vegetation, including paved areas or grass. Although Google Earth prevents the identification of understorey vegetation, woody trees and shrubs were easily distinguished from grass, and our objective was to measure horizontal distances as required by Calfire rather than assess the relative flammability of different vegetation types. Trees or shrubs were allowed to be within the defensible space zone as long as they were separated by the minimum horizontal required distance, which was 3 m (10 ft) from the edge of one tree canopy to the edge of the next (Fig. 2). Although greater distances between trees or shrubs are recommended on steeper slopes, we followed the same guidelines for all properties. For all structures, we started the distance measurements by drawing lines from the centre of the four orthogonal sides of the structure that ended when they intersected anything that no longer met the requirements in the guidelines. A fair number of structures are not four sided; thus, the start of the centre point was placed at a location that approximated the farthest extent of the structure along each of four orthogonal sides.

We developed two sets of measurements of the distance of defensible space based on what is feasible for homeowners within their properties *v.* the total effective distance of defensible space. We made these two measurements because homeowners are only required to create defensible space within their own property, and this would reflect the effect of individual homeowner compliance. Therefore, even if cleared vegetation extended beyond the property line, the first set of distance measurements ended at the property boundary. The second set of measurements ignored the property boundaries and accounted for the total potential effect of treatment. For all measurements, we recorded the cover types (e.g. structure >3 m (10 ft) long, property boundary, or vegetation type) at which the distance measurements stopped (Table 1). Because property

Table 1. Defensible space variables measured for every structure

Urban veg, landscaping vegetation that was not in compliance with regulations within urban matrix; wildland veg, wildland vegetation that was not in compliance with regulations; orchard, shrub to tree-sized vegetation in rows; urban to wildland, landscaping vegetation that leads into wildland vegetation; structure, any building longer than 3 m (10 ft)

Variable	Definition
Distance defensible space within property	Measure of clearance from side of structure to property boundary calculated for four orthogonal directions from structure and averaged
Total distance defensible space	Measure of clearance from side of structure to end of clearance calculated for four orthogonal directions from structure and averaged
Cover type at end of defensible space	Type of cover encountered at end of measurement (urban veg, wildland veg, orchard, urban to wildland, structure)
Percentage clearance	Percentage of clearance calculated across the entire property
Neighbours' vegetation	Binary indicator of whether neighbours' uncleared vegetation was located within 30 m (100 ft) of the main structure
Vegetation touching structure	Number of sides on which woody vegetation touches main structure (1–4) Structure with more than 4 sides were viewed as a box and given a number between 1 and 4
Vegetation overhanging roof	Was vegetation overhanging the roof? (yes or no)

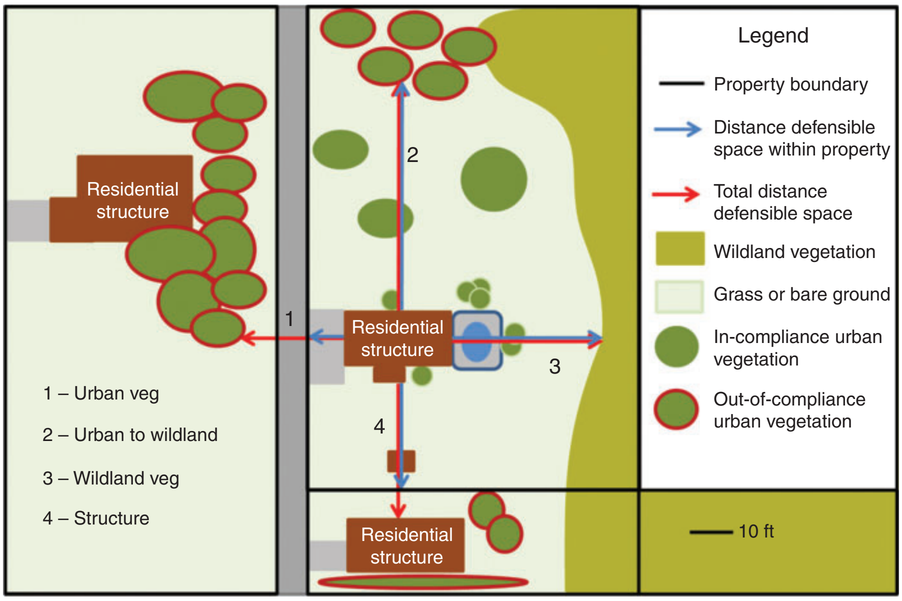

Fig. 2. Illustration of defensible space measurements. See Table 1 for full definition of terms.

owners usually can only clear vegetation on their own land, it is possible that the effectiveness of defensible space partly depends upon the actions of neighbouring homeowners. Therefore, we also recorded whether or not any neighbours' un-cleared vegetation was located within 30 m (100 ft) of the structure.

To assess the total amount of woody vegetation that can safely remain on a property and still receive significant benefits of defensible space, we calculated the total percentage of cleared land, woody vegetation and structure area across every property. This was accomplished by overlaying a grid on each property and determining the proportion of squares falling into each class. Preliminary results showed these three measurements to be highly correlated, so we only retained percentage clearance for further analysis. To evaluate the relative effect of woody vegetation directly adjacent to structures, we also calculated the number of sides of the structure with vegetation touching and recorded whether any trees were overhanging structures' roofs.

In addition to defensible space measurements, we evaluated other factors known to influence the likelihood of housing loss to fire in the region (Syphard *et al.* 2012, 2013). Using the same data as in Syphard *et al.* (2012, 2013), we extracted spatial information from continuous grids of explanatory variables for the locations of all structures in our analysis. Variables included interpolated housing density based on a 1-km search radius; percentage slope derived from a 30-m digital elevation model (DEM); Euclidean distance to nearest major and minor road and fuel type, which was based on a simple classification of US Forest Service data (Syphard *et al.* 2012), including urban, grass, shrubland and forest & woodland.

Analysis

We performed several analyses to determine whether relative differences in home protection are provided by different distances and amounts of defensible space, particularly beyond the legally required 30 m (100 ft), and to identify the effective treatment distance for homes on low and steep slopes.

Categorical analysis

For the first analysis, we divided our data into several groups to identify potential differences among specific categories of defensible space distance around structures located on shallow and steep slopes. We first sorted the full dataset of 2000 structures by slope and then split the data in the middle to create groups of homes with shallow slope and steep slope. We divided the data in half to keep the number of structures even within both groups and to avoid specifying an arbitrary number to define what constitutes shallow or steep slope. The two equal-sized subsets of data ranged from 0 to 9%, with a mean of 8% for shallow slope, and from 9 to 40%, with a mean of 27% for steep slope. Within these data subsets, we next created groups reflecting different mean distances of defensible space around structures. We also performed separate analyses based on whether defensible space measurements were calculated within the property boundary or whether measurements accounted for the total distance of defensible space.

Within all groups, we calculated the proportion of homes that were destroyed by wildfire. We performed Pearson's Chi-square tests of independence to determine whether or not the proportion of destroyed structures within groups was significantly different (Agresti 2007). We based one test on four equal-interval groups within the legally required distance of 30 m (100 ft): 0–7 m (0–25 ft), 8–15 m (26–50 ft), 16–23 m (51–75 ft) and 24–30 m (76–100 ft). A second test was based on three groups (24–30 m (75–100 ft), 31–90 m (101–300 ft) and $>$90 m ($>$300 ft) or $>$60 m ($>$200 ft)) to evaluate whether groups with mean defensible space distances $>$30 m ($>$100 ft) were significantly different from groups with $<$30 m ($<$100 ft). When defensible space distances were only measured to the property boundary, few structures had mean defensible space $>$90 m ($>$300 ft). Therefore, we used a cut-off of 60 m (200 ft) to increase the sample size in the Chi-square analysis. In addition to the Chi-square analysis, we calculated the relative risk among every successive pair of categories (Sheskin 2004). The relative risk was calculated as the ratio of proportions of burned homes within two groups of homes that had different defensible space distances.

Effective treatment analysis

In addition to comparing the relative effect of defensible space among different groups of mean distances, as described above, we also considered that the protective effect of defensible space for structures exposed to wildfire is conceptually similar to the effect of medication in producing a therapeutic response in people who are sick. In addition to pharmacological applications, treatment–response relationships have been used for radiation, herbicide, drought tolerance and ecotoxicological studies (e.g. Streibig *et al.* 1993; Cedergreen *et al.* 2005; Knezevic *et al.* 2007; Kursar *et al.* 2009). The effect produced by a drug or treatment typically varies according to the concentration or amount, often up to a point at which further increase provides no additional response. The effective treatment (ET50), therefore, is a specific concentration or exposure that produces a therapeutic response or desired effect. Here we considered the treatment to be the distance or amount of defensible space.

Using the software package DRC in R (Knezevic *et al.* 2007; Ritz and Streibig 2013), we evaluated the treatment–response relationship of defensible space in survival of structures during wildfire. To calculate the effective treatment, we fit a log-logistic model with logistic regression because we had a binary dependent variable (burned or unburned). We specified a 2-parameter model where the lower limit was fixed at 0 and the upper limit was fixed at 1. We again performed separate analyses for data subsets reflecting shallow and steep slope, as well as from measurements of defensible space taken within, or regardless of, property boundaries. We also performed analyses to find the effective treatment of percentage clearance of trees and shrubs within the property.

Multiple regression analysis

To evaluate the role of defensible space relative to other variables, we developed multiple generalised linear regression models (GLMs) (Venables and Ripley 1994). We again had a binary dependent variable (burned versus unburned), so we specified a logit link and binomial response. Although the proportion of 0s and 1s in the response may be important to consider for true prediction (King and Zeng 2001; Syphard *et al.* 2008), our objective here was solely to evaluate variable importance. We developed multiple regression models for all possible combinations of the predictor variables and used the corrected Akaike's Information Criterion (AICc) to rank models and select the best ones for each region using package MuMIn in R (R Development Core Team 2012; Burnham and Anderson 2002). We recorded all top-ranked models that had an AICc value within 2 of that of the model with lowest AICc to identify all models with empirical support. To assess variable importance, we calculated the sum of Akaike weights for all models that contained each variable. On a scale of 0–1, this metric represents the weight of evidence that models containing the variable in question are the best model (Burnham and Anderson 2002). The distance of defensible space measured within property boundaries was highly correlated with the distance of defensible space measured beyond property boundaries ($r = 0.82$), so we developed two separate analyses – one using variables measured only within the property boundary and the other using variables that accounted for defensible space outside of the property boundary as well as the potential effect of neighbours having uncleared vegetation within 30 m (100 ft) of the structure. A test to avoid multicollinearity showed all other variables within each multiple regression analysis to be uncorrelated ($r < 0.5$).

Surrounding matrix

To assess whether the proportion of destroyed structures varied according to their surrounding matrix, we summarised the most common cover type at the end of defensible space measurements (descriptions in Table 1) for all structures. These summaries

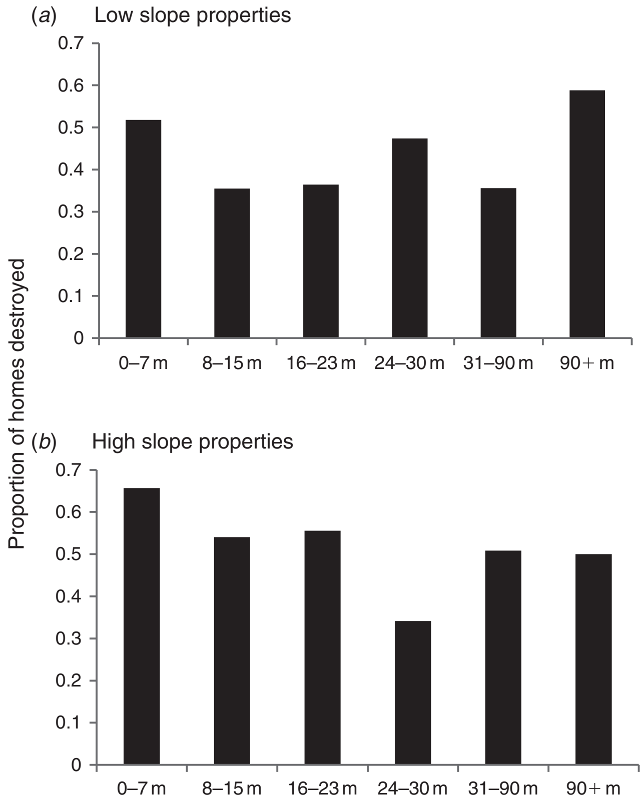

Fig. 3. Proportion of destroyed homes grouped by distances of defensible space based upon total distance of clearance within property boundary, for structures on (*a*) shallow slopes (mean 8%) and (*b*) steep slopes (mean 27%).

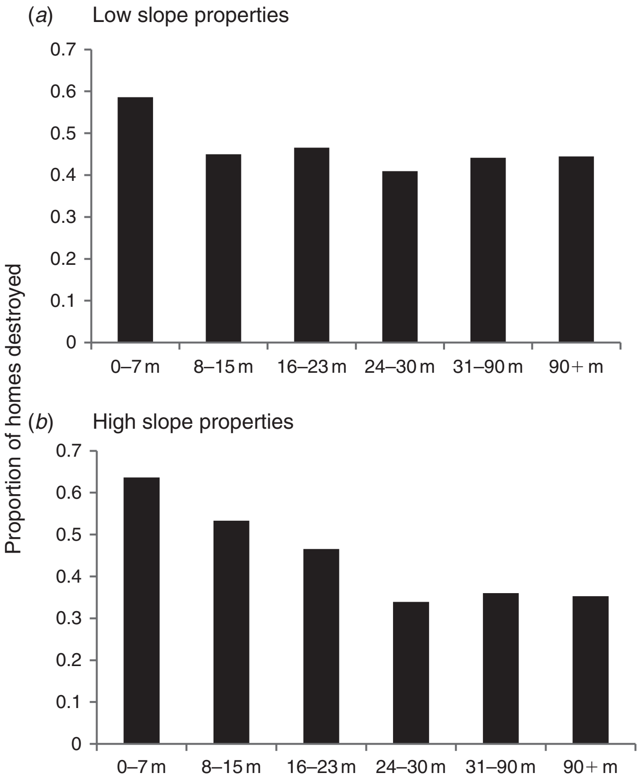

Fig. 4. Proportion of destroyed homes grouped by distances of defensible space based upon total distance of clearance regardless of property boundary, for structures on (*a*) shallow slopes (mean 8%) and (*b*) steep slopes (mean 27%).

were based on the majority surrounding cover type from the four orthogonal sides of the structure. We also noted cases in which there was a tie (e.g. two sides were urban vegetation and two sides were structures).

Results

Categorical analysis

When the distance of defensible space was measured both 'only within property boundaries' (Fig. 3) and 'regardless of property boundaries' (Fig. 4), the Chi-square test showed a significant difference ($P < 0.001$) in the proportion of destroyed structures among the four equal-interval groups of distance ranging from 0 to 30 m (0–100 ft). This relationship was consistent on both shallow-slope and steep-slope properties, although the relative risk analysis showed considerable variation among classes (Table 2) There was a steadily decreasing proportion of destroyed structures at greater distances of defensible space up to 30 m (100 ft) on the steep-slope structures with defensible space measured regardless of property boundaries (Fig. 4*b*). Otherwise, the biggest difference in proportion of destroyed structures occurred between 0 and 7 m (0–25 ft) and 8–15 m (26–50 ft) (Figs 3*a*–*b*, 4*a*).

When the distance of defensible space was measured in intervals from 24 m (75 ft) and beyond, the Chi-square test showed no significant difference among groups ($P = 0.96$ for shallow-slope properties and $P = 0.74$ for steep-slope properties) (Figs 3, 4), although again, the relative risk analysis showed considerable variation (Table 2).There was a slight increase in the proportion of homes destroyed at longer distance intervals when the defensible space was measured only to the property boundaries (Fig. 3*a*–*b*). This slight increase is less apparent when distances were measured regardless of boundaries (Fig. 4*a*–*b*).

The relative risk calculations showed that the ratio of proportions was generally more variable among successive pairs when the distances were measured within property boundaries (Table 2). For these calculations, the risk of a structure being destroyed was significantly lower when the defensible space distance was 8–15 m (25–50 ft) compared to 0–7 m (0–25 ft) on both shallow- and steep-slope properties. On the steep-slope properties, there was an additional reduction of risk when comparing 24–30 m (75–100 ft) to 16–23 m (50–75 ft). However, the risk of a home being destroyed was slightly significantly higher when there was 31–90 m (101–225 ft) compared to 16–23 m (50–75 ft). For distances that were measured regardless of property boundary (total clearance), the only significant differences in risk of burning were a reduction in risk for 8–15 m (25–50 ft) compared to 0–7 m (0–25 ft).

Table 2. Number of burned and unburned structures within defensible space distance categories (m), their relative risk and significance

A relative risk of 1 indicates no difference; <1 means the chance of a structure burning is less than the other group; >1 means the chance is higher than the other group. The relative risk is calculated for pairs that include the existing row and the row above. Confidence intervals are in parentheses

	Distance within property				Total distance			
	Burned	Unburned	Relative risk	*P*	Burned	Unburned	Relative risk	*P*
Shallow slope								
0–7	200	186			162	114		
8–15	109	198	0.69 (0.12)	<0.001	108	132	0.77	0.002
16–23	51	89	1.03 (0.30)	0.850	78	90	1.03	0.770
24–30	36	40	1.30 (0.39)	0.110	50	70	0.90	0.430
31–90	28	47	0.79 (0.24)	0.220	79	99	1.06	0.640
60 or 90+	10	6	1.67 (0.63)	0.040	8	9	1.01	0.830
Steep slope								
0–7	245	128			224	128		
8–15	174	148	0.82 (0.10)	0.001	158	139	0.84	0.008
16–23	85	68	1.03 (0.16)	0.750	73	83	0.87	0.210
24–30	29	56	0.61 (0.17)	0.004	26	50	0.73	0.080
31–	29	28	1.49 (0.48)	0.050	39	68	1.06	0.760
60 or 90+	5	5	0.98 (0.47)	0.950	4	8	0.91	0.830

Table 3. Effective treatment results reflecting the distance (in metres, with feet in parentheses) and percentage clearance within properties that provided significant improvement in structure survival during wildfires

The property mean is the average distance of defensible space or percentage clearance that was calculated on the properties before the wildfires and provides a means to compare the effective treatment result to the actual amount on the properties

	All parcels effective treatment ($n = 2000$)	Parcel mean	Shallow slope (mean 8%) effective treatment ($n = 1000$)	Parcel mean	Steep slope (mean 27%) effective treatment ($n = 1000$)	Parcel mean
Defensible space within parcel	10 (33)	13 (44)	4 (13)	14 (45)	25 (82)	11 (35)
Total distance defensible space	10 (32)	19 (63)	5 (16)	20 (67)	20 (65)	18 (58)
Mean percentage clearance on property	36	48	31	51	37	35

Effective treatment analysis

Analysis of the treatment–response relationships among defensible space and structures that survived wildfire showed that, when all structures are considered together, the mean actual defensible space that existed around structures before the fires was longer than the calculated effective treatment (Table 3). Regardless of whether the defensible space was measured within or beyond property boundaries, the estimated effective treatment of defensible space was nearly the same at 10 m (32–33 ft).

The effective treatment distance was much shorter for structures on shallow slopes (4–5 m (13–16 ft)) than for structures on steep slopes (20–25 m (65–82 ft)), but in all cases was <30 m (<100 ft). Although longer distances of defensible space were calculated as effective on steeper slopes, these structures actually had shorter mean distances of defensible space around their properties than structures on low slopes (Table 3).

The calculated effective treatment of the mean percentage clearance on properties was 36% for all properties, 31% for structures on shallow slopes and 37% for structures on steep slopes (Table 3). In total, the properties all had higher actual percentage clearance on their property than was calculated to be effective. However, this mainly reflects the shallow-slope properties, as those structures on steep slopes had less clearance than the effective treatment.

Multiple regression analysis

When defensible space was measured only to the property boundaries, it was not included in the best model, according to the all-subsets multiple regression analysis (Table 4). However, it was included in the best model when factoring in the distance of defensible space measured beyond property boundaries (Table 5). In both multiple regression analyses, low housing density and shorter distances to major roads were ranked as the most important variables according to their Akaike weights. Slope and surrounding fuel type were also in both of the best models as well as other measures of defensible space, including the percentage clearance on property and whether vegetation was overhanging the structure's roof. The number of sides in which vegetation was touching the structure was included in the best model when defensible space was only measured to the property boundary. The total explained deviance for the multiple regression models was low (12–13%) for both analyses.

Table 4. Results of multiple regression models of destroyed homes using all possible variable combinations and corrected Akaike's Information Criterion (AICc)

Includes variables measured within property boundary only. Top-ranked models include all those ($n = 12$) with AICc within 2 of the model with the lowest AICc. Relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable

Variable in order of importance	Relative variable importance	Model-averaged coefficient	Number inclusions in top-ranked models
Housing density	1	−0.003	12
Distance to major road	1	−0.0005	12
Percentage clearance	1	−0.02	12
Slope	1	0.03	12
Vegetation overhang roof	1	0.5	12
Fuel type	0.67	Factor	9
Vegetation touch structure	0.49	0.07	6
Distance defensible space within property	0.45	−0.0002	5
South-westness	0.36	−0.0007	3
Distance to minor road	0.28	−0.0002	1
D^2 of top-ranked model			0.123

Table 5. Results of multiple regression models of destroyed homes using all possible variable combinations and corrected Akaike's Information Criterion (AICc)

Includes variables measured beyond property boundary. Top-ranked models include all those ($n = 6$) with AICc within 2 of the model with the lowest AICc. Relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable

Variable in order of importance	Relative variable importance	Model-averaged coefficient	Number inclusions in top-ranked models
Housing density	1	−0.003	6
Distance to major road	1	−0.0005	6
Total distance defensible space	1	−0.004	6
Percentage clearance	1	−0.01	6
Vegetation overhang roof	0.99	0.4	6
Slope	0.99	0.03	6
Fuel type	0.86	Factor	4
South-westness	0.42	−0.0009	2
Distance to minor road	0.36	−0.0009	2
Neighbours' vegetation	0.27	0.08	1
Vegetation touch structure	0.27	0.18	1
D^2 of top-ranked model			0.125

Surrounding matrix

The cover type that most frequently surrounded the structures at the end of the defensible space measurements was urban vegetation, followed by urban vegetation leading into wildland vegetation, and wildland vegetation (Fig. 5). Many structures were equally surrounded by different cover types. There were no significant differences in the proportion of structures destroyed depending on the surrounding cover type. However, a disproportionately large proportion of structures burned (28 *v.* 9% unburned) when they were surrounded by urban vegetation that extended straight into wildland vegetation.

Discussion

For homes that burned in southern Californian urban areas adjacent to non-forested ecosystems, most burned in high-intensity Santa Ana wind-driven wildfires and defensible space increased the likelihood of structure survival during wildfire. The most effective treatment distance varied between 5 and 20 m (16–58 ft), depending on slope and how the defensible space was measured, but distances longer than 30 m (100 ft) provided no significant additional benefit. Structures on steeper slopes benefited from more defensible space than structures on shallow slopes, but the effective treatment was still less than 30 m (100 ft). The steepest overall decline in destroyed structures occurred when mean defensible space increased from 0–7 m (0–25 ft) to 8–15 m (26–50 ft). That, along with the multiple regression results showing the significance of vegetation touching or overhanging the structure, suggests it is most critical to modify vegetation immediately adjacent to the house, and to move outward from there. Similarly, vegetation overhanging the structure was also strongly correlated with structure loss in Australia (Leonard *et al.* 2009).

In terms of fuel modification, the multiple regression models also showed that the percentage of clearance was just as, or more important than, the linear distance of defensible space.

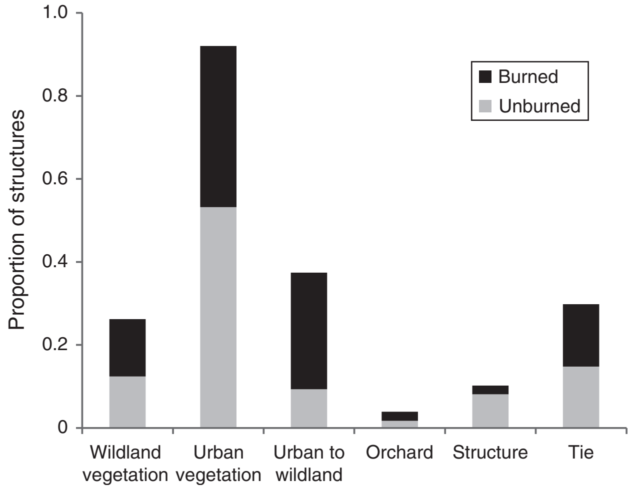

Fig. 5. Proportion of destroyed and unburned structures based on the primary surrounding cover type at the end of defensible space measurements. There were no significant differences in the proportion of burned and unburned structures within cover types ($P = 0.14$). Cover types are defined in Table 1.

However, as with defensible space, percentage clearance did not need to be draconian to be effective. Even on steep slopes, the effective percentage clearance needed on the property was <40%, with no significant advantage beyond that. Although these steep-slope structures benefited more from clearance, they tended to have less clearance than the effective amount, which may be why slope was such an important variable in the multiple regression models. Shallow-slope structures, in contrast, had more clearance on average than was calculated to be effective, suggesting these property owners do not need to modify their behaviours as much relative to people living on steep slopes.

Although the term ‘clearance’ is often used interchangeably with defensible space, this term is incorrect when misinterpreted to mean clearing all vegetation, and our results underline this difference. The idea behind defensible space is to reduce the continuity of fuels through maintenance of certain distances among trees and shrubs. Although we could not identify the vertical profile of fuels through Google Earth imagery, the fact that at least 60% of the horizontal woody vegetative cover can remain on the property with significant protective effects demonstrates the importance of distinguishing defensible space from complete vegetation removal. Thus, we suggest the term ‘clearance’ be replaced with ‘fuel treatment’ as a better way of communicating fire hazard reduction needs to home owners.

The percentage cover of woody shrubs and trees was not evenly distributed across properties, and we did not collect data describing how the cover was distributed. Considering the importance of defensible space and vegetation modification immediately adjacent to the structure, it should follow that actions to reduce cover should also be focussed in close proximity to the structure. The hazard of vegetation near the structure has apparently been recognised for some time (Foote *et al.* 1991; Ramsey and McArthur 1994), but it is not stressed enough, and rarely falls within the scope of defensible space guidelines or ordinances.

In addition to the importance of vegetation overhanging or touching the structure, it is important to understand that ornamental vegetation may be just as, if not more, dangerous than native vegetation in southern California. Although the results showed no significant differences in the cover types in the surrounding matrix, there was a disproportionately large number of structures destroyed (28% burned *v.* 9% unburned) when ornamental vegetation on the property led directly into the wildland. Ornamental vegetation may produce highly flammable litter (Ganteaume *et al.* 2013) or may be particularly dangerous after a drought when it is dry, or has not been maintained, and species of conifer, juniper, cypress, eucalypt, *Acacia* and palm have been present in the properties of many structures that have been destroyed (Franklin 1996). Nevertheless, ornamental vegetation is allowed to be included as defensible space in many codes and ordinances (Haines *et al.* 2008).

One reason that longer defensible space distances did not significantly increase structure protection may be that most homes are not destroyed by the direct ignition of the fire front but rather due to ember-ignited spot fires, sometimes from fire brands carried as far as several km away. Although embers decay with distance, the difference between 30 and 90 m (100 and 300 ft) may be small relative to the distance embers travel under the severe wind conditions that were present at the time of the fires. The ignitability of whatever the embers land on, particularly adjacent to the house, is therefore most critical for propagating the fire within the property or igniting the home (Cohen 1999; Maranghides and Mell 2009).

Aside from roofing or home construction materials and vegetation immediately adjacent to structures (Quarles *et al.* 2010; Keeley *et al.* 2013), the flammability of the vegetation in the property may also play a role. Large, cleared swaths of land are likely occupied at least in part by exotic annual grasses that are highly ignitable for much of the year. Conversion of woody shrubs with higher moisture content into low-fuel-volume grasslands could potentially increase fire risk in some situations by increasing the ignitability of the fuel; and if the vegetation between a structure and a fire is not readily combustible, it could protect the structure by absorbing heat flux and filtering fire brands (Wilson and Ferguson 1986).

The slight increase in proportion of structures destroyed with longer distances of defensible space within parcel boundaries was surprising. However, that increase was not significant in the Chi-square analysis, although there were some significant differences in the pairwise relative risk analysis. Nevertheless, the largest significant effect of defensible space was between the categories of 0–7 m (0–25 ft) to 8–15 m (26–50 ft), and it may be that differences in categories beyond these distances are not highly meaningful or reflect an artefact of the definition of distance categories. These relationships at longer distances are likely also weak compared to the effect of other variables operating at a landscape scale. Although the categorical analysis allowed us to answer questions relative to legal requirements and specific distances, the effective treatment analysis was important for identifying thresholds in the continuous variable.

The multiple regression models showed that landscape factors such as low housing density and longer distances to major roads were more important than distance of defensible space for explaining structure destruction, and the importance of these variables is consistent with previous studies (Syphard *et al.* 2012, 2013), despite the smaller spatial extent studied here. Whereas this study used an unburned control group exposed to the same fires as the destroyed structures, previous studies accounted for structures across entire landscapes. The likelihood of a fire destroying a home is actually a result of two major components: the first is the likelihood that there will be a fire, and the second is the likelihood that a structure will burn in that fire. In this study, we only focussed on structure loss given the presence of a fire, and the total explained variation for the multiple regression models was quite low at ~12%. However, when the entire landscape was accounted for in the total likelihood of structure destruction, the explained variation of housing density alone was >30% (Syphard *et al.* 2012). One reason for the relationship between low housing density and structure destruction is that structures are embedded within a matrix of wildland fuel that leads to greater overall exposure, which is consistent with Australian research that showed a linear decrease of structure loss with increased distance to forest (Chen and McAneney 2004). That research, however, only focussed on distance to wildland boundaries and did not quantify variability in defensible space or ornamental vegetation immediately surrounding structures. Thus, fire safety is important to consider at multiple scales and for multiple variables, which will ultimately require the cooperation of multiple stakeholders.

Conclusions

Structure loss to wildfire is clearly a complicated function of many biophysical, human and spatial factors (Keeley *et al.* 2009; Syphard *et al.* 2012). For such a large sample size, we were unable to account for home construction materials, but this is also well understood to be a major factor, with older homes and wooden roofs being most vulnerable (Franklin 1996; Cohen 1999, 2000). In terms of actionable measures to reduce fire risk, this study shows a clear role for defensible space up to 30 m (100 ft). Although the effective distances were on average much shorter than 30 m (100 ft), we recognise that additional distance may be necessary to provide sufficient protection to firefighters, which we did not address in this study (Cheney *et al.* 2001). In contrast, the data in this study do not support defensible space beyond 30 m (100 ft), even for structures on steep slopes. In addition to the fact that longer distances did not contribute significant additional benefit, excessive vegetation clearance presents a clear detriment to natural habitat and ecological resources. Results here suggest the best actions a homeowner can take are to reduce percentage cover up to 40% immediately adjacent to the structure and to ensure that vegetation does not overhang or touch the structure.

In addition to defensible space, this study also underlines the potential importance of land use planning to develop communities that are fire safe in the long term, in particular through their reduction to exposure to wildfire in the first place. Localised subdivision decisions emphasising infill-type development patterns may significantly reduce fire risk in the future, in addition to minimising habitat loss and fragmentation (Syphard *et al.* 2013). This study was conducted in southern California, which has some of the worst fire weather in the world and many properties surrounded by large, flammable exotic trees. Therefore, recommendations here should apply to other non-forested ecosystems as well as many forested regions.

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Chapter 12

Chaparral Landscape Conversion in Southern California

Alexandra D. Syphard, Teresa J. Brennan, and Jon E. Keeley

> *Southern California, where the American Dream came too true*
>
> *–Lawrence Ferlinghetti*

Abstract The low-elevation chaparral shrublands of southern California have long been occupied and modified by humans, but the magnitude and extent of human impact has dramatically increased since the early 1900s. As population growth started to boom in the 1940s, the primary form of habitat conversion transitioned from agriculture to urban and residential development. Now, urban growth is the primary contributor, directly and indirectly, to loss and fragmentation of chaparral landscapes. Different patterns and arrangements of housing development confer different ecological impacts. We found wide variation in the changing extent and pattern of development across the seven counties in the region. Substantial growth in lower-density exurban development has been associated with high frequency of human-caused ignitions as well as the expansion of highly flammable non-native annual grasses. Combined, increases in fire ignitions and the extent of grassland can lead to a positive feedback cycle in which grass promotes fire and shortens the fire-return interval, ultimately extirpating shrub species that are not adapted to short fire intervals. An overlay of a 1930s vegetation map with maps of contemporary vegetation showed a consistent trend of chaparral decline and conversion to sage scrub or

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grassland. In addition, those areas type-converted to grassland had the highest fire frequency over the latter part of the twentieth century. Thus, a continuing trend of population growth and urban expansion may continue to threaten the extent and intactness of remaining shrubland dominated landscapes. Interactions among housing development, fire ignitions, non-native grasses, roads, and vehicle emissions make fire prevention a complex endeavor. However, land use planning that targets the root cause of conversion, exurban sprawl, could address all of these threats simultaneously.

Keywords Chaparral · Fire · Housing development · Land use change · Non-native species · Vegetation change

12.1 Introduction

For thousands of years, humans have occupied the vast shrublands blanketing the foothills and mountains of southern California. Native Americans altered their environment to protect and sustain themselves, particularly via controlled burning to open up shrubland landscapes (see Chap. 4). Subsequently, the arrival of Euro-American settlers in the late eighteenth century brought about a sequence of progressively intense phases of rapid population growth and landscape conversion. The California Gold Rush and statehood brought one of the first population booms in 1850, and shortly thereafter, the region was linked to the railroad, enabling faster and safer immigration to the region from the rest of the country. Transportation via automobile soon became possible in the early 1900s, which facilitated even more immigration; plus, it enabled the beginning of suburban development outside of the region’s main urban centers, such as Los Angeles and San Diego.

Throughout the progression of the twentieth century, southern California has continued to offer a wide range of economic opportunities. When coupled with the mild Mediterranean-type climate, these have made the region one of the most desirable places to live in the US. In particular, people flocked to the region with the discovery of oil at the turn of the century, which was then followed by growth in numerous other industries, including military defense production, agriculture, and the film industry. In the middle of the century, human population growth exploded; the accompanying massive change in land use dramatically altered the extent and composition of the native vegetation communities in the region. Although large expanses of native shrublands still exist in many areas, southern California has come to be viewed by the world as the land of freeways, strip malls, and endless housing developments.

In this chapter, we explore the trends and drivers of vegetation change in southern California since the early 1900s. In particular, we focus on the interactions between direct habitat conversion through urban growth and indirect changes brought on by non-native annual grasses, increased frequency of fires, and the resultant loss of native shrublands.

12.2 Habitat Conversion

12.2.1 Overview of Land Use Change

By the middle Holocene, Indian populations dominated much of coastal California, and they had a significant impact on landscape patterns through repeated burning and displacement of chaparral with more productive herbaceous communities (see Chap. 4). In the late eighteenth century, Spanish settlements initiated a new wave of changes with the introduction of a wide selection of non-native annual grasses and forbs (Mack 1989). The economy of these early settlements was based on cattle production, and the Mexican vaqueros would often burn off shrublands to increase grazing lands (Kinney 1887). Ever since then, rangeland management has had a significant component of repeated burning of shrublands to increase forage for livestock (Keeley and Syphard 2018).

One of the most significant changes in plant community composition with Euro-American settlement was the replacement of native vegetation with non-native grassland. As a result, non-native annuals were likely a large component of California grasslands by the 1850s (Burcham 1956). Livestock grazing undoubtedly has contributed substantially to this shift (D'Antonio et al. 1992), often in combination with severe droughts (Burcham 1956). Nevertheless, even in the absence of grazing, non-native annuals introduced by Euro-American settlers likely outcompeted native bunch grasses (Bartolome and Gemmill 1981). Intentional conversion of shrublands to create grassland for grazing was common across California (Burcham 1956; Keeley and Fotheringham 2003). Similar patterns of type-conversion have occurred over the 10,000-year history of human occupation in the Mediterranean Basin, where transitions from woody to herbaceous species have also been caused by human disturbance via livestock grazing and accelerated burning due to anthropogenic ignitions. However, in California, this loss of woody cover degrades natural systems and diminishes their conservation value by displacing native flora with non-native species. In the Mediterranean Basin, type-conversion replaces woody natives with herbaceous natives, and thus, native biodiversity increases.

In the early twentieth century, conversion of natural habitat into agricultural lands was the most dominant form of land use change, and by the 1930s, approximately 20% of the land within the South Coast Ecoregion had become croplands, with citrus and other fruit trees becoming especially extensive. At this time, southern California was considered one of the top agricultural regions in the US. However, with population growth and evolving economic opportunities, farming was largely wiped out in the middle of the century in favor of commercial and residential development, a trend that was common nationwide (Alig and Plantinga 2004). In the South Coast Ecoregion of California, less than five percent of the croplands mapped in the 1930s were still present by the early 2000s (derived from data described in next section).

Urban and residential development is now the top contributor to both direct and indirect habitat conversion in southern California. Not only have the major metropolitan areas become denser, but the freeway system developed in the 1940s initiated what has been an ongoing trend of "sprawl" outward from coastal cities into the inland foothills and mountains. This growth was so rapid and extensive that the San Fernando Valley outside of Los Angeles took on the name of "America's Suburb" (Roderick 2002). Across the world, southern California is still perceived as synonymous with urban sprawl.

12.2.2 Spatial and Temporal Patterns of Housing Growth

The spatial pattern of housing development has important implications for landscape conversion because low-density, sprawling-type development typically consumes more land and wildlife habitat than high-density development (Odell et al. 2003). As a consequence, low-density development may have a more negative impact on biodiversity and ecosystem services (Hansen et al. 2005). On the other hand, higher-density, clustered development may be more ecologically degraded with a larger dominance of non-native species (Lenth et al. 2006). Despite these trade-offs, compact urban development has been shown to minimize ecological disruption relative to sprawling development (Sushinsky et al. 2013).

The term wildland-urban interface (WUI) has emerged in the last couple of decades to describe the characteristics and social-ecological effects of those areas where housing development is adjacent to or interspersed with wildland vegetation (Radeloff et al. 2005). Two types of WUI are typically defined, largely as a function of housing density and the extent to which houses are surrounded by wildland vegetation. The "interface WUI" describes those areas where human settlements are denser and form an edge with wildland vegetation, whereas "intermix WUI" reflects areas where sparser, lower-density housing is interspersed with wildland vegetation. Although the exact definition of intermix or interface WUI may vary slightly with regards to how it is mapped (Stewart et al. 2007), these terms have provided a useful framework for understanding how and where human settlements interact with the natural environment, and how different forms of development may differentially affect habitat change and ecological impacts (Bar-Massada et al. 2014).

The spatial pattern of urban development in any given area can vary dramatically over time, but it typically emerges as a result of different characteristic growth types (Herold et al. 2003; Dahal et al. 2017). At one end, compact and high-density development patterns usually result from infill-type growth, where new structures are built within or expand outward from existing urban areas. At the other end, low-density, fragmented, exurban development patterns result from leapfrog-type growth in which new development occurs outside of urban areas and is typically surrounded by wildland vegetation. This lower-density exurban development, characteristic of the intermix WUI, is often the result of homeowner preferences and behaviors, including a desire to live closer to natural amenities (Netusil 2005) or lower land prices at greater distances from the urban core (Wu and Plantinga 2003).

Given the importance of both spatial extent and pattern of housing growth in terms of natural habitat conversion, we quantified historical housing trends in the South Coast Ecoregion from 1940 to 2010. To do this, we evaluated historical housing density maps (Hammer et al. 2004, available at http://silvis.forest.wisc.edu/maps/housing) within the footprint of a modified South Coast Ecoregion boundary (i.e., as in Syphard et al. 2011) that includes the full extent of the Los Padres National Forest. The maps were developed as part of a national data product in which housing density was mapped within partial census block groups and reported as housing units per square kilometer.

We quantified the extent of both low- and medium- to high-density housing from 1940 to 2010 within the seven counties that are located within the ecoregion. Instead of clipping the counties to the ecoregion boundary, we assessed housing growth for the complete extent of each county. To threshold the continuous housing data into classes of low- and medium-high-density, we selected all areas with a housing density between 6.17 and 49 houses per km^2 and classified them as "low density." The number 6.17 corresponds to the minimum housing density cutoff for defining low-density WUI (Radeloff et al. 2005). The threshold of ≥50 houses per square kilometer corresponds to those areas defined as medium- or high-density WUI. For each county in each decade, we summarized the total extent of each housing density type and calculated its proportion of the county area.

In all seven counties, housing development, and hence direct habitat conversion, increased substantially from 1940 to 2010 across the region, but the extent of development and pattern of housing growth varied over time and by county (as can be seen in the widely varying range of the Y axis in Fig. 12.1). Medium- to high-density development has dominated the counties closest to Los Angeles, but low-density housing growth has predominated in San Luis Obispo, Riverside, and San Diego counties (Figs. 12.1 and 12.2). Except for Los Angeles, which exhibited slow, steady growth in both housing-density types over time, a pulse in growth was apparent during and shortly after the 1990s for the other counties, which is consistent with nation-wide trends (Glaeser and Shapiro 2003). Orange County stands out in that, as medium-high density increased over time, low-density development has shown a slight decline across most of the record. This also has been evident in recent decades for Santa Barbara and San Luis Obispo Counties, suggesting that, in addition to urban expansion, existing urban areas in these counties may also be infilling and becoming denser. The two southern-most counties (San Diego and Riverside), on the other hand, show no sign of slowing in the expansion of low-density development.

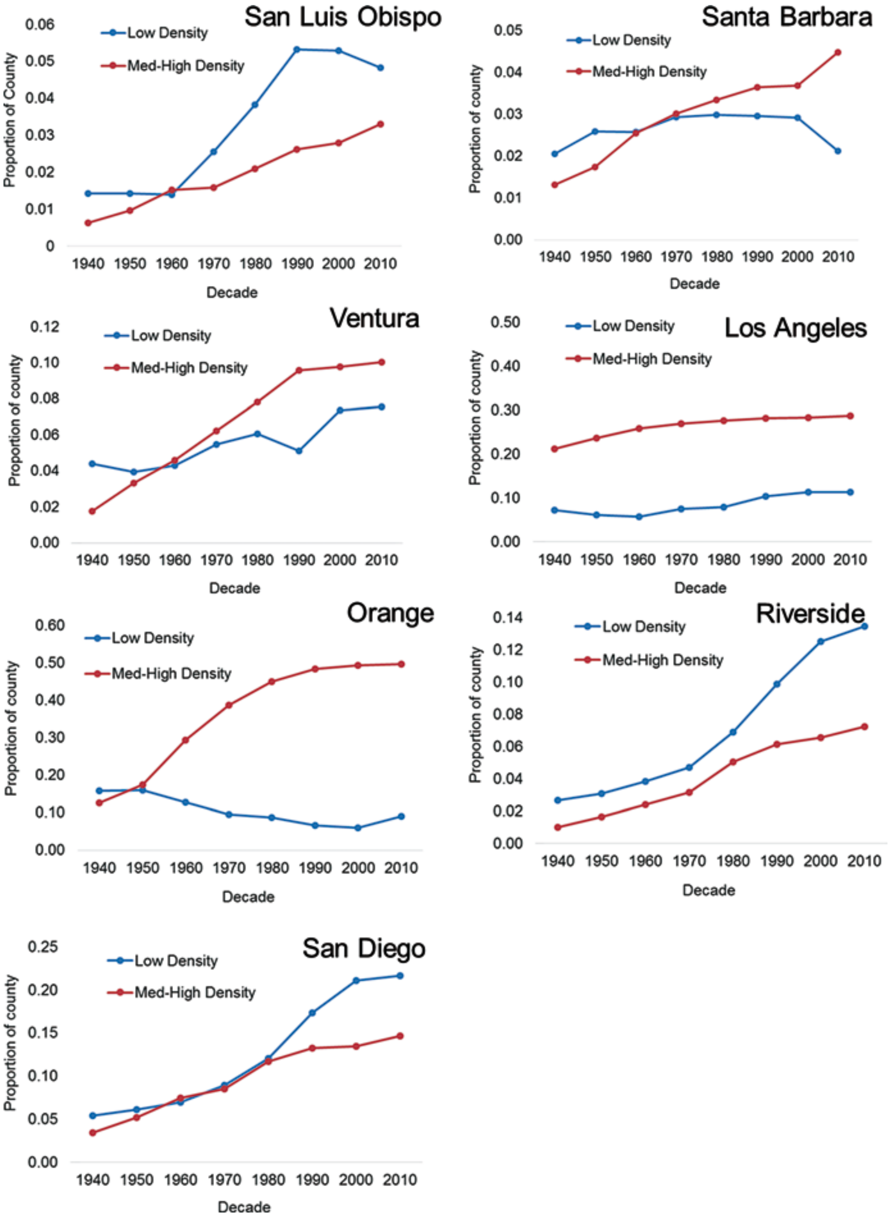


Fig. 12.1 Growth in area (proportion of county) of low and medium-high housing density from 1940 to 2010 within the full boundaries of the seven counties overlapping the South Coast Ecoregion of southern California

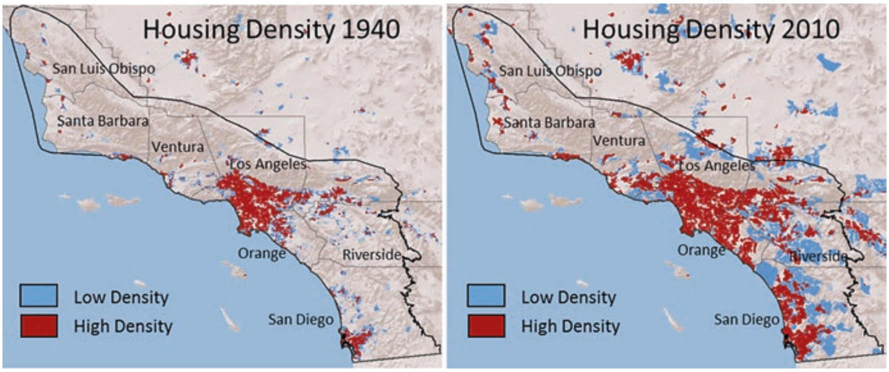


Fig. 12.2 Maps of low and medium-high housing density in 1940 and 2010 in the South Coast Ecoregion of southern California

12.2.3 Indirect Habitat Loss and Conversion

In addition to causing direct conversion of native habitat, housing development in southern California indirectly contributes to chaparral conversion, primarily by facilitating an interaction between increased fire frequency and the expansion of weedy non-native annual grasslands.

Although periodic wildfire is an essential component of chaparral ecosystems, fire frequency has been increasing in southern California to the extent that most of the landscape is burning at fire-return intervals (i.e., the time between fires at a defined area) that are uncharacteristically short relative to pre-EuroAmerican settlement conditions (Safford and Van de Water 2014). In some areas, fires are now so frequent that they outpace the historical baseline by a wide margin; for example, return intervals that once averaged 30 to more than 150 years are now shorter than 10 years in some areas (Keeley and Syphard 2018).

Given that humans cause more than 95% of the fires in the region (Syphard et al. 2007), the trend of increasing fire frequency is primarily explained by population growth and expansion of development into wildland vegetation. Although human-caused fires generally increase with human population, this relationship is mediated by population or housing density. That is, across California and other Mediterranean-type climate regions, studies show that the ignition frequencies tend to peak at low-intermediate population density, such as the WUI intermix areas (Syphard et al. 2007, 2009; Archibald et al. 2010; Syphard and Keeley 2015). The likely explanation for this is that these intermix WUI areas have both enough people to start frequent fires, which wild areas lack, and sufficient wildland areas to facilitate fire spread, which urban areas lack. These are also the areas most difficult to access for fire suppression (Gude et al. 2008).

In addition to increased fire frequency, exurban development provides conduits for non-native species to expand into wildland vegetation, via land disturbance, road networks, and residential landscaping (Gavier-Pizarro et al. 2010). Even fuelbreaks designed to control wildfires facilitate establishment and spread of non-native species (Merriam et al. 2006). In recent studies, which assessed the ecological effects of mechanical fuel treatments on chaparral (such as removing vegetation with bulldozers), it was found that treated sites had a significantly lower cover and density of shrubs and a significantly higher cover and density of herbaceous plants (Brennan and Keeley 2015). The increase in herbaceous plants was dominated by non-native species and in particular by non-native annual grasses. Sites that were treated a second time had more than twice the cover and density of non-native species than single treatments and were clearly showing more signs of degradation and type-conversion, that is, a shift in physiognomic structure from woody shrubland to herbaceous cover. These treatments are frequently used near housing developments within the WUI; and over time, with periodic retreatment, will most likely be completely type-converted to non-native annual grasslands.

The weedy annual grasses that have invaded vast portions of southern California are highly flammable and tolerant of rapidly repeating fires. In the absence of disturbance, chaparral shrublands are relatively resistant to invasion by non-native species, in part due to their dense cover and closed canopy. However, increased human ignitions in these fire-prone grasslands has lengthened the fire season, thereby increasing canopy opening and providing new establishment opportunities for these well-dispersed grasses. This positive feedback process between fires and grass expansion is typically referred to as a grass-fire cycle, and it is recognized as a potential problem in ecosystems across the world (e.g., D’Antonio and Vitousek 1992; Rossiter et al. 2003; Brooks et al. 2004; Bowman et al. 2014), including southern California shrublands (Keeley et al. 2012).

The larger ecological issue is that, despite native shrublands’ resilience to periodic wildfire, too-short intervals between fires can lead to their extirpation. This is because many species require a minimum amount of time between fires to recover and regenerate. Non-resprouting species—i.e., obligate seeders—may require up to 25 years to fully establish a seedbank that can effectively recruit new plants after fire (Keeley 1986). Although re-sprouting chaparral species are resilient to shorter intervals between fires than non-re-sprouters, even re-sprouters were reduced when multiple fires occurred within in a six-year interval (Haidinger and Keeley 1993). Thus, as native shrubland species are extirpated, providing opportunities for further grass expansion, the potential exists for large scale vegetation type-conversion.

A number of studies in southern California have provided evidence of vegetation type-conversion from shrubland to grassland. Particularly widespread has been the conversion of coastal sage scrub to non-native grasses (Minnich and Dezzani 1998; Cox et al. 2014). Talluto and Suding (2008) found nearly 50% replacement of sage scrub by annual grasses within a 76-year study period in parts of Orange and Riverside Counties, with a substantial amount being due to fire frequency. Because sage scrub is generally more tolerant of higher fire frequencies than chaparral, chaparral may be even more vulnerable to vegetation type-conversion, depending on species composition and site factors. In some cases, it may even transition to sage scrub vegetation before finally transitioning to herbaceous cover (Syphard et al. 2006).

Chaparral conversion to grasslands after repeated fires has been documented in many localized studies (e.g., Zedler et al. 1983; Haidinger and Keeley 1993; Lippitt et al. 2012; Keeley and Brennan 2012). Given the consistency in these findings across the southern California region, and the fact that large areas across the region have experienced short fire-return intervals, there is reason to suspect that widespread conversion due to repeated fires has already occurred (Keeley 2010). Nevertheless, the empirical evidence for larger landscape scale changes in chaparral has been sparse, with one recent study even questioning the potential for widespread vegetation type change in chaparral to occur (Meng et al. 2014).

12.3 Landscape Scale Vegetation Type-Conversion

As a general means of quantifying historical vegetation change in concert with mean historical fire frequency in southern California, we overlaid contemporary maps of existing vegetation with an historical map delineating broad scale vegetation types and then integrated data on fire frequency. We estimated change using maps from multiple data sources because of the potential for vegetation to be mapped differently. Although variation is much more likely given finer scale vegetation classification schemes, there may even be differences in the way broad vegetation types are mapped due to differences in mapping methods, scales, and definitions.

The historical vegetation type maps (VTM) were developed between the years 1929 and 1934 (Wieslander 1935) as part of an extensive statewide mapping project. In addition to detailed species level plot information, vegetation types and dominant species were mapped on 15-minute topographic quadrangles in the field with a minimum mapping unit of 16 ha (39.5 acres) (Kelly et al. 2005; Kelly 2016). The first contemporary map we evaluated represents existing vegetation and was produced by the US Forest Service using a combination of satellite imagery, field verification, and expert guidance (CalVeg, http://www.fs.fed.us/r5/rsl/projects/classification/system.shtml). The majority of the area in this map was most recently updated in 2002. However, the national forest lands were updated more recently, in 2003, 2009, or 2010. The entire region was mapped at a scale of 1:24,000.

Both the VTM and CalVeg maps provide classification according to the California Wildlife Habitat Relationships System (Mayer and Laudenslayer 1988). Therefore, for both of these maps, we grouped vegetation classes into life-forms, including tree, shrub, coastal sage scrub, and herbaceous. For the other categories, which are mostly unvegetated (e.g., urban/developed land) or wetland, we lumped them into a class named “other.”

We also evaluated the 2013 Landfire existing vegetation maps, which were developed based on a combination of decision tree models, field data, Landsat 7 imagery, elevation, and biophysical gradient data (http://landfire.cr.usgs.gov/viewer/ [2013, May 8]). The map comes as a grid at 30 m (0.2 acres) resolution. We developed map classes to match the vegetation types in the other two maps using the map

Table 12.1 Proportion of vegetation types within the historical (VTM) and contemporary (San Diego County, CalVeg, and Landfire) maps

Vegetation Type	VTM	San Diego	CalVeg	Landfire
Grass	0.06	0.09	0.12	0.27
Sage scrub	0.29	0.24	0.10	0.06
Shrubland	0.45	0.35	0.43	0.19
Tree	0.08	0.09	0.12	0.18
Other	0.13	0.23	0.23	0.29
Total	1.0	1.0	1.0	1.0

attribute based on the National Vegetation Classification System Physiognomic Order. Any area that was classified as "sparsely vegetated," "barren," "water," "developed," or "agriculture" in the Landfire vegetation type classification, we converted to the "other" class.

At a finer resolution for a subset of the South Coast Ecoregion, we compared the VTM map to a detailed 2012 vegetation community map that spans part of San Diego County (https://databasin.org/datasets/bcd5db8e6aa540e6b06a371bde0afde3). This map was developed with a 1 ha (2.5 acre) minimum mapping unit for terrestrial vegetation and has an accuracy of at least 80% as determined through extensive field verification reports. The map was classified according to Sproul et al. (2011), and again, we grouped these into the same life-form vegetation classes and an "other" class.

After re-classifying the vegetation maps into physiognomic types, we quantified the proportion of each vegetation or cover type within each map. We then overlaid the contemporary maps with the VTM map and summarized the mean historical fire frequency that occurred within each change class up to 2013. To estimate the transitions between life-form classes, we assessed changes from shrub to grass, sage scrub to grass, shrub to sage scrub, tree to earlier successional class (shrub, sage scrub, or grass), successional (e.g., grass to sage scrub, sage scrub to shrub, shrub to tree), no change in vegetation, or other (i.e., unvegetated in either map. We used the California Department of Forestry–Fire and Resource Assessment Program (CDF-FRAP 2013) map of overlapping historical fire perimeters (wildfire only) to create a continuous 30 m grid with each cell representing the number of times it had burned since 1878 (http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download). In this database, any grid cell location may have burned 0–13 times during the time period, although this may under-estimate fire frequency due to the minimum mapping unit of this dataset (Syphard and Keeley 2017).

The contemporary vegetation maps showed consistent trends of increasing grass, tree, and other cover types and decreasing sage scrub and shrubs over time (Tables 12.1 and 12.2, Fig. 12.3). There were substantial areas of agreement in the delineation of all vegetation types that did not change between the VTM map and contemporary maps (Figs. 12.4 and 12.5), particularly in CalVeg and the higher-resolution San Diego County map. The Landfire map, however, delineated a much larger pro-

Table 12.2 Proportion of chaparral in the historical (VTM) map that transitioned to other vegetation types in contemporary (San Diego County, CalVeg, and Landfire) maps

Chaparral Change Class	San Diego	CalVeg	Landfire
Chaparral to chaparral	0.33	0.22	0.24
Chaparral to sage scrub	0.07	0.22	0.26
Chaparral to grass	0.12	0.10	0.26
Chaparral to tree	0.40	0.27	0.17
Chaparral to other	0.09	0.20	0.07
Total	1.0	1.0	1.0

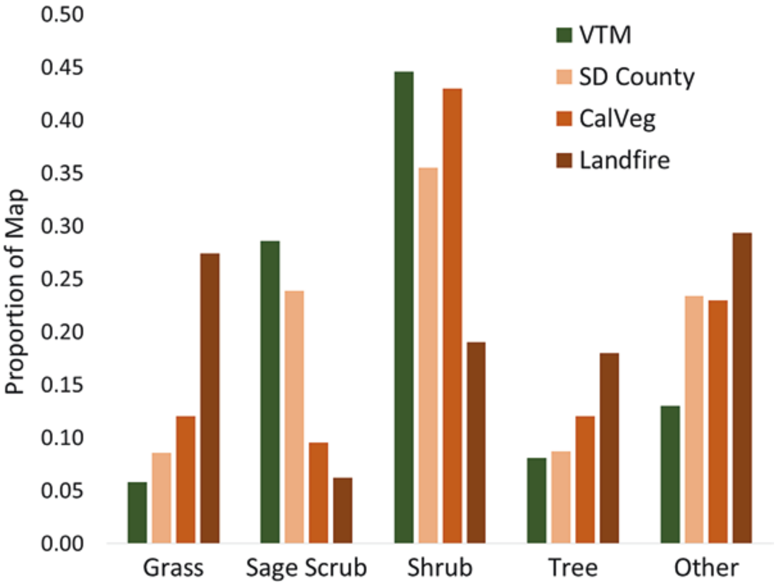


Fig. 12.3 Proportion of vegetation type within four vegetation maps of the South Coast Ecoregion (VTM 1930s; CalVeg 2002; Landfire 2013) and San Diego County (2012)

portion of the landscape as grassland than the other two contemporary maps (Fig. 12.4c). This is reflected in the vast areas of the landscape that were mapped as having changed from sage scrub or shrub to grass (Fig. 12.6a).

In terms of fire frequency, the analysis showed highest mean fire frequencies in classes where either sage scrub or shrub converted to grass, or where shrub converted to sage scrub (Fig. 12.7). The mean number of fires summed across grid cells in each change class ranged from 1.55 to 2.41, but the actual number of times areas burned during the 135-year span of the fire history data ranged from 0 to13.

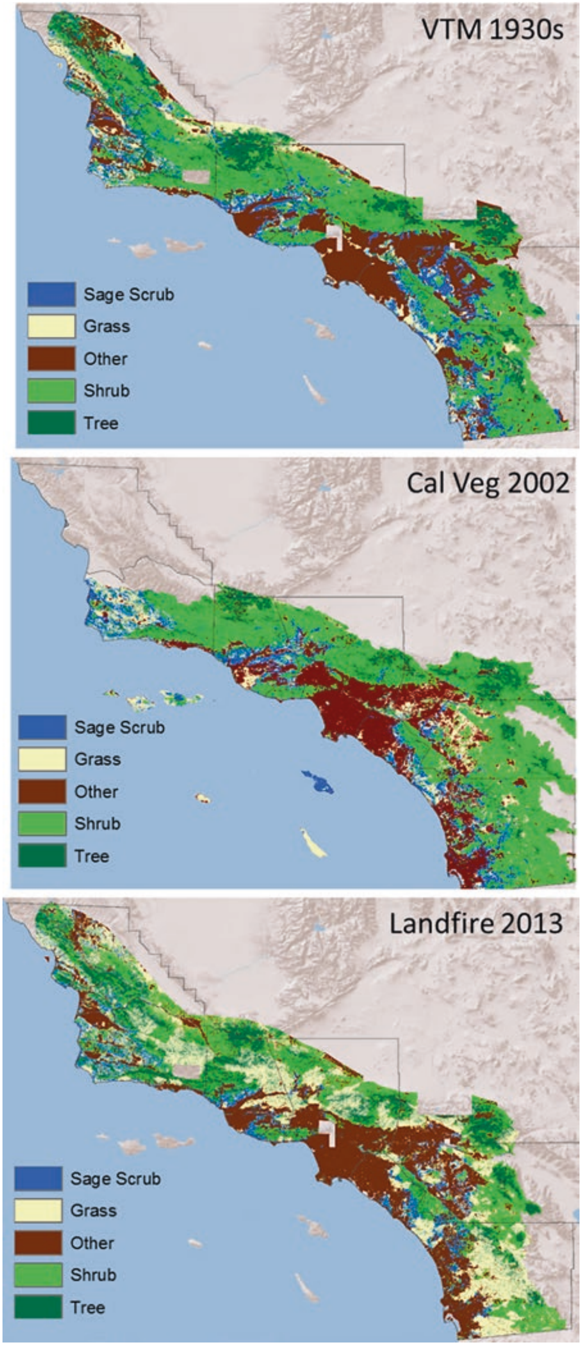


Fig. 12.4 Vegetation types as mapped in the 1930s (VTM), 2002 (CalVeg maps), and 2013 (Landfire)

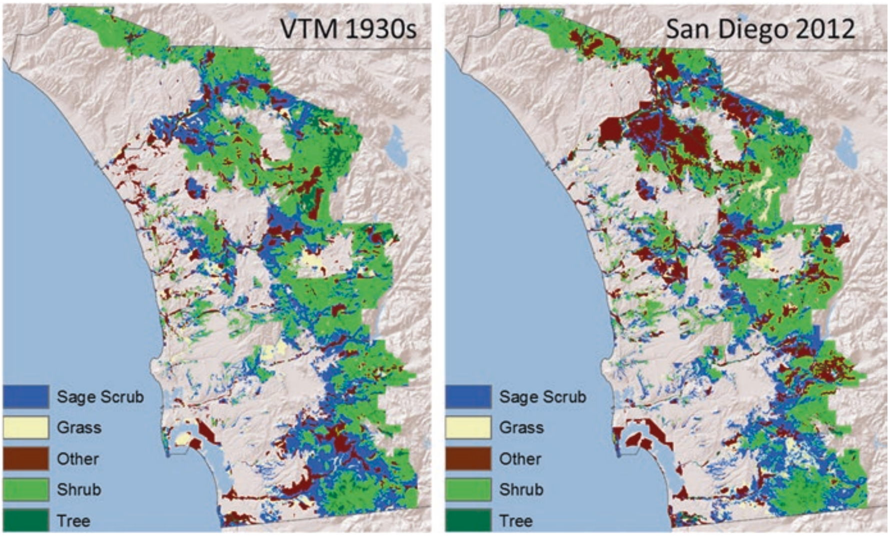


Fig. 12.5 Comparison of vegetation type classes as mapped in the 1930s (VTM) and in 2012 (San Diego County map)

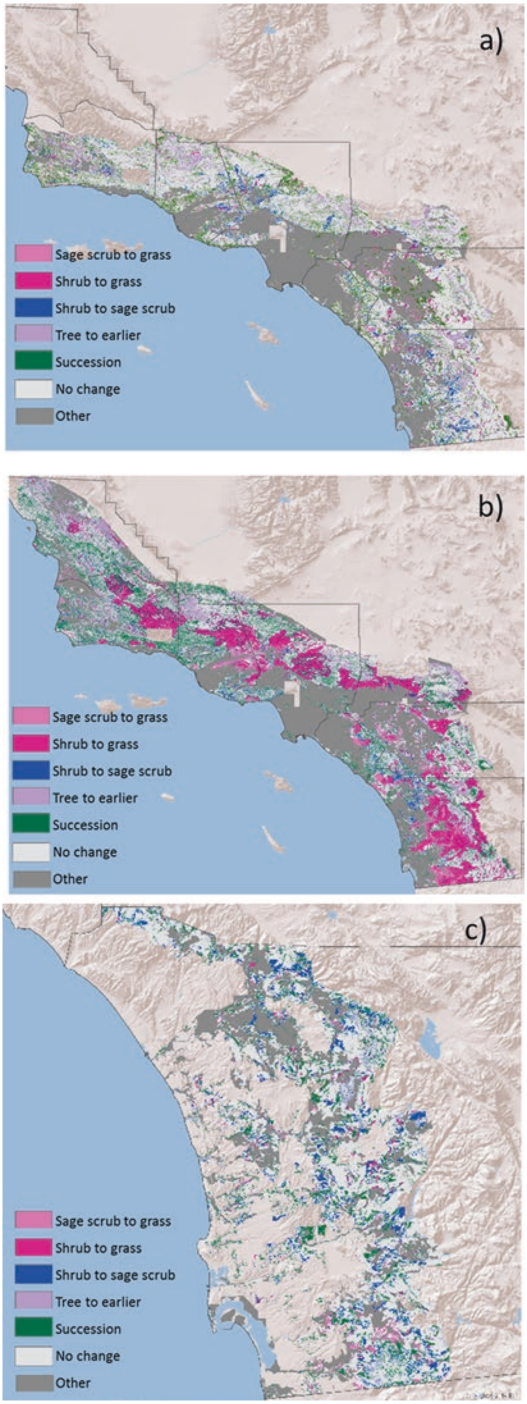
12.3.1 Challenges in Quantifying Vegetation Change

The wide variation apparent among the three contemporary maps illustrates the challenge in overlapping different vegetation maps to accurately delineate and quantify vegetation change, particularly if the objective is to map change at a fine scale. There are multiple sources of uncertainty inherent in any ecological analysis (Regan et al. 2002), and spatial data are particularly susceptible to errors in map boundaries and classification (Goodchild and Gopal 1989). Nevertheless, when vegetation map classes are collapsed into broad categories reflecting vegetation formations, map accuracy can be relatively high (Goodchild et al. 1991).

Clearly, the extent and location of vegetation type-conversion cannot be precisely determined from our analysis, and the vast areas of type change from shrub or scrub to grass mapped using the Landfire data should be interpreted with some caution given that many of these areas were not mapped as grass in the other two contemporary maps. Nevertheless, despite the variation among contemporary maps, the results of all three overlays were remarkably consistent in the kind of change measured. Thus, even using the most conservative estimates, there has been a clear trend of chaparral decline and conversion to either sage scrub or grassland over the last 70–80 years. Furthermore, fire frequency tends to be highest where these changes have been mapped (Fig. 12.7).

In the southern California landscape, the most likely explanation for the differences in maps is the treatment of mixed classes. Depending on the scale of the analysis relative to the heterogeneity of the vegetation, mixed grass and shrub stands must often be lumped into one class or the other. Thus, many of the areas mapped

Fig. 12.6 Maps of vegetation type change from (**a**) the 1930s to 2002 (CalVeg), (**b**) the 1930s to 2013 (Landfire), and (**c**) the 1930s to 2012 (San Diego County map)



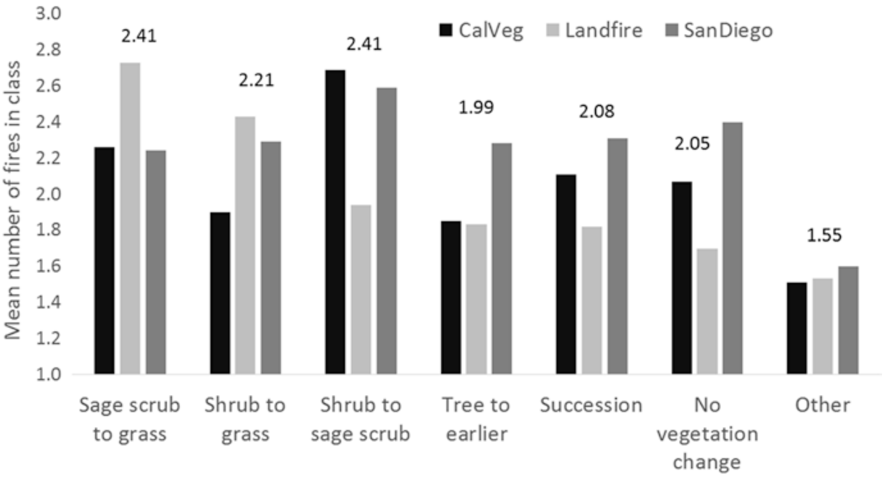


Fig. 12.7 Mean number of fires from 1878–2013 within each vegetation type change class between the 1930s and 2002, using data from CalVeg (2002), Landfire (2013), and San Diego County maps (2012). Numbers above the bars indicate the mean fire frequency averaged across the three maps. "Tree to other" reflects any changes in which trees changed to shrub, sage scrub, or grass. "Succession" reflects any changes in which grass changed to shrub or sage scrub, or sage scrub changed to shrub

as grass in the Landfire map, and mapped as some type of shrubland in the CalVeg or San Diego County map, were probably some mixture of shrub and grass.

Whether these classes were purely grass or represented some mixture with shrubs is one of the central challenges in quantifying landscape scale vegetation change. It also provides one reason for questioning Meng et al.'s (2014) conclusion that widespread vegetation type-conversion is not an immediate threat in southern California, as vegetation type-conversion does not occur as a complete shift at one moment in time. Instead, it occurs as a gradual and cumulative process, which often begins with the elimination of non-resprouting species within mixed stands, habitat simplification, and biodiversity loss (Keeley et al. 2005). In addition, because sage scrub can withstand higher fire frequencies than chaparral, vegetation change may begin with a gradual shift from stands of pure chaparral to mixed stands of chaparral, sage scrub, and grass. This type of transition is suggested in the results here that show substantial change from shrub to sage scrub under higher mean fire frequencies. Given that different species have varying sensitivities to repeat fires, and that overlapping fires exhibit fragmented spatial patterns, multiple repeat fire events are probably necessary for significant vegetation change to be discernable. Thus, one of the methodological challenges in landscape scale analyses like those in Meng et al. (2014) is that type-conversion is only inferred, and the gradual process of vegetation change cannot be documented at a specific location over time the way it can in field studies (Halsey and Syphard 2015). Another challenge is that substantial chaparral conversion had already occurred before vegetation maps became available for modern analysis. There is evidence of chaparral conversion prior to the twentieth century (Cooper 1922), and evidence has also been documented in field studies. In summary, vegetation change is complex, gradual, and related to site factors in addition to long-term fire history and plant community composition. These factors need to be resolved and better understood when considering the potential for future chaparral conversion.

12.4 Ecological and Social Consequences of Chaparral Loss

In addition to the loss of plant biodiversity that occurs with habitat conversion, many rare and sensitive animal species depend on vegetation structure for their habitat (see Chaps. 2 and 3). The native coastal sage and chaparral shrublands, as well as riparian areas and oak woodlands, provide important habitat for a wide range of bird, insect, mammal, and herpetofauna species, and the negative effects of habitat loss and fragmentation have been documented for decades in numerous studies (e.g., Bolger 1991; Soulé et al. 1992; Bolger et al. 2000; Riley et al. 2003; Ruell et al. 2012). Recent studies are also beginning to show how interactions among direct and indirect effects (e.g., fire, climate change, non-native species) of urban development contribute to biodiversity loss (e.g., Franklin et al. 2014; Conlisk et al. 2015; Jennings et al. 2016).

Changes in vegetation structure that occur with the conversion of shrublands to grasslands also impact the physical and hydrological properties of the soil (Martinez-Fernandez et al. 1995; Williamson et al. 2004). The increased density of plants combined with changes in the canopy shape and root distribution of individuals significantly alter how rainfall and organic matter are channeled into and through the soil (Lee and Lauenroth 1994; Martinez-Meza and Whitford 1996). The resultant changes affect the infiltration capacity and water retention of the soil as well as the concentration and dispersal of nutrients and carbon (Gutierrez et al. 1995; Martinez-Fernandez et al. 1995). Shrublands that have been converted to grasslands have more extreme soil temperatures and they tend to develop a thicker, more variable surface (A) horizon with a significantly higher soil bulk density (Williamson et al. 2004). These changes in root distribution decrease the stability of slopes while increasing the potential for hazardous debris flows (Gabet and Dune 2002). External factors such as fire and flooding can further exacerbate the system by increasing runoff and soil erosion, which in turn have the potential to affect water quality and reservoir infilling (Hubbert et al. 2012). Finally, shrublands have substantially better capacity for ecosystem carbon sequestration than grasses (Petrie et al. 2015), which has critical implications in this era of rapid climate change.

Development patterns and chaparral conversion are not only important in terms of ecological effects, but from a social perspective, the intermix WUI areas are also the locations where houses are most likely to be destroyed by wildfire in southern California (Syphard et al. 2012). Large fires at the WUI have been occurring for decades in the region, with an average of 500 houses lost per year in the last 50 years. Furthermore, the rate of destroyed houses and lost lives in the last 10–15 years has been unprecedented (Keeley et al. 2013).

12.5 Discussion and Future Changes

As we march into the twenty-first century, the acceleration of global change is bound to occur, especially given the projections of continued population growth. For example, the San Diego Association of Governments expects a 140% increase in population by 2050 across the county (www.sandag.org/2050forecast). Thus, continuation of direct habitat conversion, particularly in the form of urban development, will continue to reduce and fragment chaparral habitat, as well as increase the length and extent of the WUI (Landis and Reilly 2003; Hammer et al. 2009). Furthermore, these land use changes will likely continue to interact with indirect drivers of conversion, including fire and invasion by non-native grasses.

Climate change will also likely result in chaparral species' range shifts, and possibly type-conversion, through habitat shifts and modifying phenology (Chen et al. 2011; Beltrán et al. 2014, see Chap. 14). However, it is the interaction of climate with the drivers discussed here that may be of most concern (Syphard et al. 2013b; Franklin et al. 2014). For example, future projections suggest that land use change will likely either override or compound the impacts of climate change on shrubland habitat conversion across the state of California (Mann et al. 2014; Riordan and Rundel 2014), and in southern California, loss of chaparral species' suitable habitat may be exacerbated by urban growth, with fire being the most serious threat for obligate seeding chaparral species (Syphard et al. 2013b; Bonebrake et al. 2014). Fire regimes, however, are more likely to be altered due to land use change rather than climate change in chaparral shrublands, as fire activity has not been significantly correlated with historical patterns of temperature and precipitation in these areas (Keeley and Syphard 2015, 2016, 2018). This may be due to the fact that climatic conditions are already suitable for extreme fire activity every year on these landscapes. On the other hand, changing patterns and timing of ignitions may have profound impacts on fire activity and its social and ecological consequences (Syphard and Keeley 2015).

Although the South Coast Ecoregion is relatively homogenous in terms of broad scale climatic and vegetation patterns, questions of scale and geographical context will be important when considering future management needs and priorities. For example, species with similar functional traits and sensitivities to certain threats may be differentially exposed to those threats depending on their distributions (Syphard et al. 2013b). That is, areas with the fastest climate change may not always be the same as the areas of fastest land use change or disturbance regime shifts.

Within the South Coast Ecoregion, different counties have unique histories of development and urban growth, which explains why our data show such variation in the extent and spatial pattern of housing density. Accordingly, habitat loss and fragmentation have and will continue to vary across the region. One of the most serious concerns related to chaparral conversion may be the ongoing expansion of low-density development in counties like San Diego, which still contain substantial areas of intact chaparral. Not only does continued development threaten to reduce shrubland extent and continuity, but intermix WUI is the area most prone to non-native annual grass expansion, increased fire frequency, and corresponding fire risk.

One major concern associated with the increase in fires in the southern California region is that vast areas are now covered with very young chaparral due to the enormous extent of recent wildfires. Also, there have already been extensive areas within southern California that have recently burned at anomalously short intervals (Keeley et al. 2009). These trends greatly increase the risk for future conversion to annual non-native grass. An additional potential factor is increased atmospheric pollution. Non-native grasses respond favorably to elevated atmospheric nitrogen deposition, which will likely accelerate with ongoing development (Cox et al. 2014).

Given the profound recent loss of human lives and property in southern California associated with wildfire, there has been a growing sense of urgency to identify new ways to reduce fire risk and ensure community safety. Aside from active fire suppression to control burning wildfires, the most prevalent form of management has been to burn, modify, or clear wildland vegetation to control fire behavior. While fuelbreaks can be safe and effective tools for firefighter access to chaparral communities, research shows that vegetation management in terms of prescribed fire and fuelbreaks provide little benefit for controlling the most damaging weather-driven fires (Syphard et al. 2011; Price et al. 2012; Penman et al. 2014). Given that vegetation management is a driver of chaparral conversion, trade-offs could be carefully considered in the design and placement of fuelbreaks, which ideally could be strategically placed for firefighter defense of communities.

In addition to strategically placed fuelbreaks, homeowner property preparation in terms of building construction and design and defensible space may significantly reduce the risk of a house being destroyed in a wildfire (Cohen 2004; Quarles et al. 2010; Syphard et al. 2014, 2016a). However, while defensible space does provide significant protection, the effect results primarily from modifying vegetation immediately adjacent to the structure. Research has shown there is no added benefit of treating areas farther than 100 ft. (30 m) from the property, even on steep slopes. In addition, only 40% reduction in woody cover was needed for significant protection (Syphard et al. 2014). This is important with regards to habitat, as there has been a recent push from county governments and insurance companies for homeowners to clear up to 300 ft. (60 m) of defensible space around their houses, which cumulatively could result in substantial areas of habitat loss (Keeley et al. 2013).

Considering house losses from wildfire at both local and landscape scales, the most significant factor that explains whether or not a house is destroyed has been its location and arrangement relative to other houses on the landscape (Syphard et al. 2012; Alexandre et al. 2015). Therefore, land use planning may be the most effective long-term solution for not only preventing house loss to wildfires, but also for maximizing biodiversity. Simulation studies showed that land use planning decisions, either through growth policies or through private land acquisition, could result in mutual benefits for both fire risk reduction and biodiversity conservation (Syphard et al. 2013a, 2016b; Butsic et al. 2017). In particular, both house loss and ecological impacts are likely to be most effectively minimized if future development is designed to be compact and clustered, with development restricted in either high-fire-hazard or species-rich areas, which tend to occur in the same areas (Syphard et al. 2016b). Ignition prevention efforts may also be highly effective as part of a comprehensive fire management program (Prestemon et al. 2010; Syphard and Keeley 2015).

12.6 Conclusion

The sprawling development pattern in southern California has been the primary driver of contemporary chaparral conversion, both through the direct removal and fragmentation of habitat, but also through its indirect role in driving annual grass expansion associated with increased fire frequency. It is also indirectly responsible for other factors such as fuelbreaks to protect communities scattered throughout the wildland, climate change, and perhaps even the increase of nitrogen deposition. For example, the increasing road density and traffic volumes associated with increased population and urban development have and will continue to have numerous effects that threaten chaparral ecosystems. Roads are often the source of fire ignitions (Syphard and Keeley 2015), promote the spread of non-native species (Bar-Massada et al. 2014), contribute to elevated ozone and nitrogen deposition that favors grasses over shrubs (Fenn et al. 2010), and fragment habitat needed for sensitive fauna (Poessel et al. 2014).

Thus, as we move into the future, it may be well worth the effort to seriously consider how developments are designed and arranged across the landscape. Land use planning could systematically address the root causes of fire risk as well as habitat loss (Moritz et al. 2014). It could lower ignitions through reduced human presence in flammable areas, lower non-native species expansion by reducing corridors to invasion, and lower the risk of property loss by arranging houses so that they are less fire-prone (Syphard et al. 2012, 2013a). Land use planning can thus address multiple impacts of global change across California shrublands, and may ultimately be the most powerful tool for a sustainable future.

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The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes

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ABSTRACT

Climate and land use patterns are expected to change dramatically in the coming century, raising concern about their effects on wildfire patterns and subsequent impacts to human communities. The relative influence of climate versus land use on fires and their impacts, however, remains unclear, particularly given the substantial geographical variability in fire-prone places like California. We developed a modeling framework to compare the importance of climatic and human variables for explaining fire patterns and structure loss for three diverse California landscapes, then projected future large fire and structure loss probability under two different climate (hot-dry or warm-wet) and two different land use (rural or urban residential growth) scenarios. The relative importance of climate and housing pattern varied across regions and according to fire size or whether the model was for large fires or structure loss. The differing strengths of these relationships, in addition to differences in the nature and magnitude of projected climate or land use change, dictated the extent to which large fires or structure loss were projected to change in the future. Despite this variability, housing and human infrastructure were consistently more responsible for explaining fire ignitions and structure loss probability, whereas climate, topography, and fuel variables were more important for explaining large fire patterns. For all study areas, most structure loss occurred in areas with low housing density (from 0.08 to 2.01 units/ha), and expansion of rural residential land use increased structure loss probability in the future. Regardless of future climate scenario, large fire probability was only projected to increase in the northern and interior parts of the state, whereas climate change had no projected impact on fire probability in southern California. Given the variation in fire-climate relationships and land use effects, policy and management decision-making should be customized for specific geographical regions.

1. Introduction

As one of the most fire-prone places in the world, California is globally recognized for its long history of wildfire-related losses of homes and human lives. Wildfire is also important for shaping ecological structure and function (van Wagtendonk, 2018), but many of California's diverse fire regimes, as those across the world, are changing in response to past fire management (e.g., Steel et al., 2015), invasive species (e.g., Syphard et al., 2017a), land use change (e.g., Mann et al., 2016), and climate change (e.g., Westerling and Bryant, 2008). Climate and land use patterns, in particular, are expected to change dramatically in the coming century, raising concern about their effects on fire regimes and subsequent impacts to human communities across the world. California is expected to embody a wide range of these changes and their impacts, and the risk to human communities is complex because it requires predicting how and where climate or land use change will alter fire patterns, i.e., the long-term spatial and temporal characteristics of fire events on a landscape. Manifestation of change will depend upon both the nature and

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strength of the drivers and their relative impacts in different regions.

There is evidence from historical patterns and modeling studies that climate change will lead to large changes in fire extent and severity (e.g., Westerling et al., 2006; Jolly et al., 2015; Abatzoglou and Williams, 2016; Restaino and Safford, 2018). However, the relationships between climate and fire are nuanced and complex (Krawchuk et al., 2009; Bradstock, 2010; Doerr and Santín, 2016) and vary in nature and strength geographically (Littell et al., 2009; Hessl, 2011; Keeley and Syphard, 2017). One of the clearest factors that determines whether a fire becomes large is wind speed (Abatzoglou et al., 2018). Large, wind-driven fire events have been responsible for the vast majority of structures lost in California wildfires (Keeley et al., 2009), including the recent fires in 2017 and 2018. Beyond weather, climate controls fire size directly via temperature, and also via its short and long-term effects on fuel volume and moisture content, which are important controls on fire behavior (Keeley and Syphard, 2016). Thus, given that hot, dry conditions are generally associated with fire, and that temperatures and moisture deficit are projected to increase globally, there is widespread concern that climate change will lead to greater fire activity. However, feedbacks between climate, vegetation, and fire are likely to mediate these effects (Bowman et al., 2014; Parks et al., 2016; Syphard et al., 2018).

Adding to the complexity, changes in human land use and population are also expected to alter spatial and temporal characteristics of future wildfires, and these effects may also interact with climate-driven effects. Humans affect fire patterns in a variety of ways, including deliberate or accidental ignitions, prescribed burning and mechanical vegetation treatments, and suppression activities; humans also change fire behavior and extent through landscape fragmentation, cultivation practices, landscaping, and flammability of buildings. Given the diversity of these effects, recent studies highlight that one of the main problems for prediction of fire patterns and related human impact is that human presence may dampen or override the influence of climate in driving fire activity (Higuera et al., 2015; Ruffault and Mouillot, 2015; Mann et al., 2016; Syphard et al., 2017b). Another complexity is that the anthropogenic and biophysical factors that influence patterns of small fires have been shown to differ from the factors that drive large fires, particularly in areas where most fires are caused by humans (Syphard et al., 2008, 2017, Barros and Pereira, 2014). This is likely due to inherent geographical and biophysical differences between those fires that are easily suppressed and those that escape control (Moritz, 1997; Hantson et al., 2015).

In California, the vast majority of fires are human-caused (Syphard et al., 2007; Balch et al., 2017), but the spatial and temporal pattern of ignition causes and patterns varies widely across the state (Keeley and Syphard, 2018). Contrary to what might be expected, fire activity is not highest where population is highest. Instead fire frequency, and to a lesser extent, area burned, tend to peak at low- to intermediate population and housing density (Syphard et al., 2007; Westerling and Bryant, 2008; Mann et al., 2016); this relationship has also been observed in other areas across the globe (Syphard et al., 2009; Aldersley et al., 2011; Bistinas et al., 2013). This hump-shaped relationship reflects, in part the increased ignitions in rural and residential areas (compared to wildlands), balanced against lower potential for fire spread and/or greater suppression in urban areas (Butsic et al., 2015).

Beyond housing density's effect on fire patterns, studies have shown that structure loss in southern California is significantly correlated with low-to-intermediate housing density (Syphard et al., 2012, 2013, 2016). Other work in southern California and Colorado (Alexandre et al., 2016a), and a national analysis across the U.S. (Alexandre et al., 2016b), identified the spatial arrangement of housing development, in addition to topographic conditions, as consistently more important than vegetation-related variables in explaining structure loss to wildfire. Although small, isolated clusters of development were consistently associated with structure loss, in some cases, high housing density in those clusters contributed to higher structure loss. In addition, high-density development has been implicated in structure loss in some fires due to fire spread among structures (Cohen and Stratton, 2008; Price and Bradstock, 2013), as seen recently in the Coffey Park neighborhood in Sonoma County, CA in 2017 (Nauslar et al., 2018). House-to-house spread is also suspected for contributing to massive structure loss in the Camp Fire in Butte County in 2018. The role of building codes and ignition resistance has yet to be examined in such loss patterns, however.

Despite clear evidence of a nonlinear relationship between housing density and patterns of fire, and subsequently on patterns of structure loss, much is unknown regarding the scale and potential thresholds that define the relationship between housing density and fire. For example, Bistinas et al. (2013) reported regionally varying thresholds determining the shape of the nonlinear relationship between population density and area burned across the globe. Much more work is needed to identify the relative roles of climate and human presence in determining fire and structure loss patterns, and to determine the extent to which these relationships vary regionally. This is particularly critical considering there have already been rapid changes in both climate patterns (Swain et al. (2018)) and land use patterns in flammable landscapes (Radeloff et al. (2018)).

To better understand the relative importance of climatic and land use factors on long-term spatial and temporal patterns of fire and structure loss and how these patterns vary from region to region, we developed an integrated modeling framework to quantify variable importance and to map the distribution of current and future projected probability of fires and structure loss in three California study areas. These regions vary biophysically but have all experienced substantial residential losses from wildfire. We first developed statistical models and maps based on the association of climate, biophysical, and anthropogenic variables with small and large fire patterns, and then we modeled structure loss as a function of those variables and the projected probabilities of large fires. After quantifying and mapping current relationships, we projected future large fire and structure loss probability under different climate and housing growth scenarios. We address the following questions:

1) How do fire patterns vary by housing density and climate?
2) How do structure loss patterns vary by housing density and climate?
3) Do these relationships vary from region to region?
4) Which is likely to be the most influential driver of future change, climate or housing development, across our study regions?

2. Methods

2.1. Study areas

The northern coastal study area (NC) includes more than 1.4 million ha of land spanning all of Lake, Sonoma, and Napa Counties, in addition to small parts of Mendocino, Glenn, Colusa, Yolo, and Solano Counties (Fig. 1). The vegetation is characterized by a mosaic of oak woodlands, grassland, chaparral, and Douglas fir/hardwood ("mixed evergreen") forests, with montane conifer forests at higher elevations. Extensive exurban development has occurred in recent decades, and numerous homes have been destroyed by fire here; in particular, the 2017 'wine country' wildfires in this region resulted in 44 lost lives and nearly 9000 destroyed buildings.

The Butte and Plumas Counties study area (BP) included the full counties, plus a 20 km buffer to incorporate a larger urban-wildland gradient (2.2 million ha). Across this gradient spanning from the Central Valley to the northern cismontane Sierra Nevada, the vegetation transitions from grassland and chaparral to mixed evergreen and then pine- and fir-dominated forests, with a very small component of subalpine forest on the highest peaks (Fig. 1). Although the higher-elevation forests are mostly protected by the U.S. Forest Service and National Park Service, substantial residential development has been

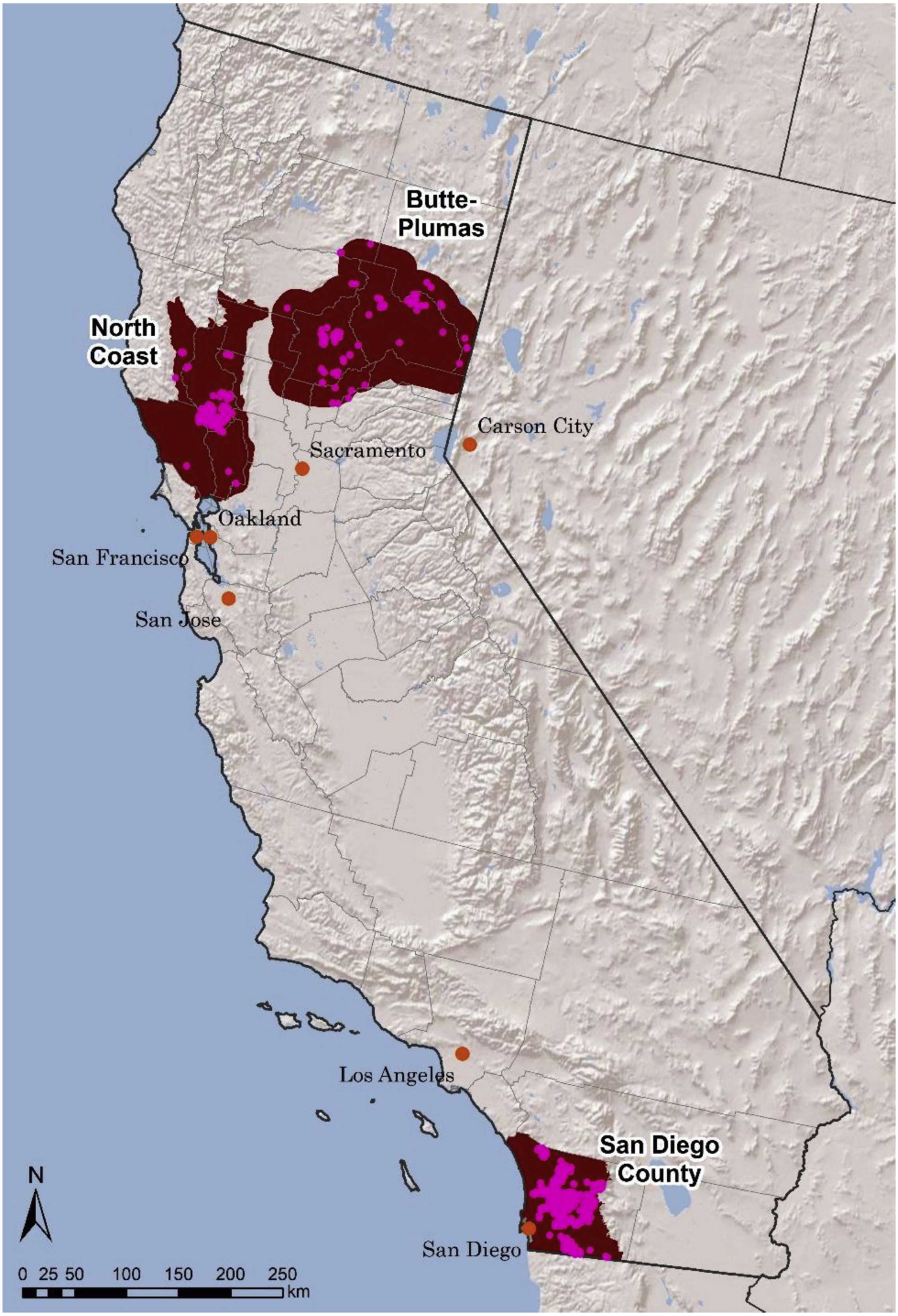

Fig. 1. Boundaries of three California study areas, with destroyed structure locations (2000–2015) in pink (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

occurring in the foothills. Wildfires destroyed more than 1000 structures here between 2000 and 2015 (the period we used for modeling); in 2018, the Camp Fire alone resulted in 86 fatalities and more than 18,000 destroyed structures. While all three study areas are characterized by Mediterranean climates, with warm to hot, dry summers and wet winters, BP is the only study area to receive substantial precipitation in the form of snowfall.

The third study area, coastal San Diego County (SD), is a rapidly developing, highly fire-prone region with an extensive wildland-urban interface. The majority of the study area is dominated by coastal sage and chaparral shrublands intermixed with grasslands and mixed oak woodlands, and some montane conifer forests at the highest elevations. Native shrubs are threatened by too-frequent fire, typically human-caused, which could lead to extensive replacement with more fire-prone herbaceous vegetation (Syphard et al., 2018b). Thousands of structures have been destroyed during large, Santa Ana wind-driven fire events (Keeley et al., 2009).

2.2. Data

For all dependent and independent variables (Table 1), we first assembled consistent statewide spatial data coverage, which we then clipped to the boundaries of the three study areas. We also rasterized all vector data, or resampled all grid data, to match the resolution of the climate variables (270 x 270 m).

2.2.1. Fire data

To determine whether different factors influence fire ignitions and large fire patterns across the study areas, we created statistical models based on two sources of data (Table 1). The first dataset included the location of origin for all fires of any size from the most recent decade of data available, 2003–2013 and was available via spatial coordinates indicating the point location of fire ignition. The data, from the National Interagency Fire Program Analysis, Fire-Occurrence Database (FPA FOD), include fire size and date as attributes and are publicly available for the whole country (Short 2014). Spatial clustering of points has the potential to lead to autocorrelation, which can inflate the accuracy of statistical distribution models (Veloz, 2009). Although we were less interested in model accuracy than we were in variable importance and maintaining comparability of model results, we nevertheless spatially filtered the presence data to ensure no duplicate points within a 500-m radius, as spatial filtering can reduce the effect of sample bias (Veloz, 2009). While this distance was not systematically determined, this was the radius used in Syphard et al. (2018) that best attained the appropriate number of samples per fire, using the method described in Davis et al. (2017).

We developed a second dataset for large fire locations using a separate comprehensive statewide fire perimeter database, provided by the State of California Fire and Resource Assessment Program (FRAP, http://frap.fire.ca.gov/data/frapgisdata-subset). We only considered large fires from these data (> =40 ha), and, based on the method developed by Davis et al. (2017), we generated a random sample of points within all fire perimeters from a baseline period of 1985–2015, the most recent 30 years available. That is, to calculate the number of random points to generate for each fire in the database, we took the square root of the ratio of the given fire's area to the area of the smallest fire in the study area as recorded in this dataset. Because a filter distance of 500 m resulted in too-small sample sizes for many of the fires, we reduced the filter distance to 400 m.

We considered the two fire datasets to capture two different processes, where each process potentially has its own set of drivers. The 'fire ignitions' dataset reflects the spatial patterns of ignitions (which is an outcome of fire initiation processes), whereas the 'large fires' dataset reflects a discrete sample of burnt locations (which is an outcome of fire spread processes).

2.2.2. Structure loss data

The dependent variable for the structure loss models was the location of any structure that had been destroyed in a fire from 2000 to 2015 (Table 1). The baseline data were developed by Alexandre et al. (2016), and included all destroyed structure locations across fires in the U.S. from 2000 – 2010. These data were created by examining, for all wildfires recorded in the Monitoring Trends and Burn Severity dataset (MTBS, https://mtbs.gov), Google Earth historical imagery from the closest dates before and after the fires. Within each fire perimeter, Alexandre et al. digitized all buildings before the wildfire; then, any building that had been completely removed in the post-fire image was considered destroyed. To update and extend these data, we followed the same methods using pre- and post-fire Google Earth imagery and digitized buildings in all three study areas that were present through 2015. Additionally, we selected all fires from the most recent Cal Fire historical perimeter database (2015 at the time of completion) and added new structures that may have been missed by Alexandre et al. (e.g., due to small fire size) or had occurred after 2010.

2.2.3. Topographic data

Terrain-related variables are typically included in fire behavior and distribution models due to their direct influence on fire behavior and indirect influence on fuel characteristics and flammability (Bond and van Wilgen 1996, Pyne 1996); and they have also been significantly associated with structure loss to wildfire due to exposure (Syphard et al., 2012, Alexandre et al. 2016). Therefore, we considered a range of topographic variables in both the fire and structure loss models, including slope, topographic variability, and topographic position (Table 1).

2.2.4. Climate data

We considered a range of historical and projected future climate variables, which were developed by Flint and Flint (2012) and updated through 2017 using the California Basin Characterization Model (https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html (Table 1). The data were available annually at 270 m resolution. We processed the annual data to create 30-year baseline statistical summaries from 1981 to 2010 as well as decadal future projections from 2020 to 2050. To ensure consistency with state recommendations (Kravitz, 2017), we compared two scenarios of future climate conditions from complementary CMIP-5 General Circulation Model projections regarded as relevant for California. The scenarios were CNRM-CM5 and MIROC5, which represent "warm/wet" and "hot/dry" conditions, respectively. Despite this characterization both scenarios have substantial spatial and temporal variation in projected conditions, but should still provide meaningful bookends for representative climate spaces. For both scenarios, we used the RCP 8.5 "business as usual" emissions scenario (RCP scenarios are generally similar through 2050 and only diverge in the second half of the century).

For the fire models, we considered a combination of temperature and moisture-related climate variables that have had significant associations with fire patterns in other studies due to their effects on energy and moisture gradients that influence wildland fuel condition and abundance (e.g., Whitman et al., 2015; Parisien et al., 2016; Davis et al., 2017). We also included actual evapotranspiration (AET) and climatic water deficit (CWD) in all models, as these variables have been used to account for changes in fuel abundance (AET) and moisture (CWD) (Krawchuk et al., 2014, Parks et al., 2016, Mann et al., 2016). We did not include temperature and precipitation in the structure loss models because we assumed their influence on structure loss would be indirect, via their effects on large fire probability. On the other hand, given that AET and CWD served as proxies for vegetation, and that vegetation adjacent to structures could be influential beyond the effect on large fire probability, we did include these variables.

Table 1
Dependent and explanatory variables used to model fire and structure loss distribution in three California study areas.

Category	Fire models	Structure loss model	Data layer	Description and source	Time Variant
Dependent variable	x		Fire ignitions	Fire occurrence locations delineating point of ignition from 2003 - 2013 (Short 2014)	NA
	x		Large fires	Cal Fire fire perimeter database 1985 – 2015 (Department of Forestry and Fire Protection	NA
		x	Structure loss	Digitizing, Alexandre et al. (2016)	NA
Terrain					
	x	x	Slope	LANDFIRE, 30-m native resolution, aggregated by mean to 270m	No
	x	x	Topographic roughness	Range of slope values within 810-m radius from center cell (Derived from 30-m digital elevation model)	No
	x	x	Topographic position index	Index of slope position and landform, Jenness 2006 (Derived from 30-m digital elevation model)	No
	x	x	Topographic heterogeneity	Range of elevation values within 810-m radius from center cell (Derived from 30-m digital elevation model)	No
Climate					
	x		Temperature seasonality	Coefficient of variation across calendar year of temperatures (Derived from Flint and Flint, 2014)	Yes
	x		Annual precipitation	Sum over calendar year (mm) (Flint and Flint, 2014)	Yes
	x		Summer precipitation	Sum over June, July, August (mm) (Flint and Flint, 2014)	Yes
	x		Annual minimum temperature	Mean low temperature of coldest month (degrees C) (Flint and Flint, 2014)	Yes
	x	x	Actual evapotranspiration	Total annual water evaporated from surface and transpired by plants (Flint and Flint, 2014)	Yes
	x	x	Climatic water deficit	Annual evaporative demand exceeding water availability (Flint and Flint, 2014)	Yes
Land use					
	x	x	Housing density	Based on 2000 U.S. Census data using the baseline projection at 2009 (Mann et al., 2014)	Yes
		x	Housing cluster area	Boundaries around areas with housing density > = 0.02 units per ha (Derived)	Yes
		x	Distance to cluster edge	Mean Euclidean distance to boundary of housing clusters (Derived)	Yes
	x	x	Distance to populated places	Census populated places of at least 10,000 inhabitants in 2010 (Derived)	No
	x	x	Distance to roads	TIGER line files 2015, U.S. Department of Commerce, U.S. Census Bureau	No
	x	x	Distance to public land	Cal Fire land ownership database 2015 (Department of Forestry and Fire Protection)	No
Fire					
		x	Predicted large fire suitability	Output from large fire model (this paper)	Yes

2.2.5. Land use projections and anthropogenic data

Our primary source of land use data were maps of current and future projected housing density that were published in Mann et al. (2014). The historical data were collected from the U.S. Census long form with models trained using historical trends from 1940 to 2000 (the latest date that the long form was available). The predictions of housing density were provided in decadal time steps, and we used the 2009 forecast as our baseline here. Created using longitudinal census data, the model calculated the total number of new houses based on demographic forecasts at the national level, and then allocated them to split-block units based on a spatio-temporal estimate of housing density. We considered two scenarios, one with concentrated urban development ("urban scenario") and the other that favored rural expansion ("rural scenario"). In the "urban development" scenario, an additional 25% of all new housing was added into urban areas (density greater than 1 house per acre), while the "rural growth" scenario pushed the 25% into areas with less than 1 house per acre.

Housing density data were initially provided as vector data, with housing density listed as an attribute for each polygon. We converted these data into 270 m raster layers using housing density as the value to grid. In previous studies of structure loss to wildfire, two additional variables, the size of the housing cluster and the distance from each structure to the edge of development, were found to be highly significant (Syphard et al., 2012; Alexandre et al., 2016a, 2016b). Given that those data had been created using point locations of all structures, we developed an approach to devise similar housing clusters by thresholding and creating borders around polygons with at least 0.01 housing units per ha, which was the value that resulted in the best fit to the data created for San Diego County (Syphard et al., 2012). The housing density variables were available for the same time periods as the climate data, with 2009 representing current conditions, and decadal projections until 2050 for the two growth scenarios. Thus, for models using baseline climate data for 1981–2010, we used housing data from 2009; and for models using climate projections from 2019 to 2029, we used the housing projection for 2029, etc.

In addition to the housing projections, we included three other variables that have been significantly associated with fire occurrence patterns in other studies (e.g., Mann et al., 2016; Syphard et al., 2018). These included proximity to primary and secondary roads, which are often associated with human-caused ignitions (Syphard and Keeley, 2015); proximity to public land, which typically consists of large uninterrupted swaths of wildland vegetation; and distance to census populated places where the city includes at least 10,000 residences (Mann et al., 2016). These maps remained static for future projections.

2.3. Statistical modeling

We used Maxent 3.3.3k to estimate variable importance and project mapped probabilities of current and future fires and structures loss (Phillips and Dudik, 2008; Elith et al., 2011). A statistical machine learning method, MaxEnt estimates the best approximation of a distribution via iterative comparisons between values of the environmental predictor variables at the location of presence locations (i.e., all fires, large fires, destroyed structures) versus the values of the same variables at 10,000 randomly located background points. The best distribution is identified as the one with maximum entropy, and the model outputs a continuous grid with each cell assigned a relative suitability of occurrence from an exponential function. Recognized as one of the top-performing species distribution models (Elith et al., 2006), MaxEnt has also been successfully used in a range of wildfire analyses and mapping applications (e.g., Bar-Massada et al., 2012; Batllori et al., 2013; Parisien et al., 2016; Davis et al., 2017; Tracy et al., 2018).

We developed separate models for all fires and large fires to investigate potential differences in variable importance. We also tested the output of both models as potential predictors for the structure loss model, but we found significant correlation between the output of the small fire model and distance to roads. Given that most homes are destroyed in large fires, we decided to only use the output of the large fire probability model as a predictor variable for the structure loss model.

We initially developed all models with the full range of climatic, topographic, and anthropogenic explanatory variables to compare variable importance. For projecting future conditions, we employed a variable selection and model tuning process separately for each of the three study regions to ensure the best model fit. We first used ENMTools (Warren et al., 2010) to calculate Pearson correlation coefficients for all explanatory variables using current conditions (baseline) in each study area. For any pair of variables with a correlation coefficient of $r > = 0.8$, we retained the one that had a higher mean cross-validated receiver operating characteristic curve (AUC, Fielding and Bell, 1997), based on univariate models.

We used most of the default parameters for the MaxEnt modeling, except that we used only linear, quadratic, and product features for all models, and selected regularization multipliers, that avoid overfitting by penalizing complex solutions, by running models in 0.5 increments from 0.5 to 5. The final model was chosen by selecting the multiplier that resulted in the lowest Bayesian Information Criterion (BIC). For the baseline models of all and large fires, and structure loss, we ran five cross-validated model replicates to obtain mean permutation importance values and mean out-of-sample AUCs. We averaged the predicted values from the five replicate output maps to produce the baseline maps, which are interpreted as grids of mean predicted probability of large fires or structure loss given the environment in each study area.

After conditioning the models on the baseline time period, we then projected the averaged baseline models of large fires and structure loss onto maps representing future conditions at each time step for all combinations of future climate (two scenarios) and land use (two scenarios) projections. For each future time step, we first projected large fires, and then used those projections as input to the structure loss models.

2.4. Analysis

We averaged large fire probability and structure loss probability for all maps generated as model output by first summarizing the predicted probabilities across all grid cells in every map, then dividing this sum by the total number of cells in the maps of the three study areas. We calculated these numbers for all model replicates in all time periods and for all climate/land use scenario combinations. The probability averages for current conditions served as a baseline to compare with the probability averages of future scenarios, which allowed an overall estimate of whether fire or structure loss probability went up or down across the region.

To identify the housing density where most structure loss occurs in each study area, we extracted the housing density of destroyed structures from the baseline housing density maps generated by Mann et al. (2014). We then compared the mean housing density of destroyed structures in each study area with the underlying housing density in each region (i.e., all burned and unburned structures), which we determined by multiplying the area of each polygon in the study area by its housing density as indicated in the attribute table. This calculation assumed housing density was evenly distributed across polygons. For polygons that overlapped the study area boundary, we calculated the number of units in the entire polygon, then prorated by the percentage of the polygon within the study area. For both destroyed and the total structures in each study area, we plotted and compared their mean and distribution across housing density classes.

To compare the mean housing density data in our study areas to the recent destructive fire events of 2017 and 2018, we additionally acquired point locations for the destroyed structures in the 2017 Tubbs, Nunn, Atlas, and Pocket Fires in Sonoma and Napa Counties (number destroyed = 8022; http://sonomamap.maps.arcgis.com/apps/webappviewer/index.html?id=5af1dd01cb9b446db928abe51a259763), the 2018 Camp Fire in Butte County (number destroyed = 18,804; https://calfire.app.box.com/s/z03vd6hoikxa94ey25m0kuq2fsq2ln5e/folder/64813192070), the 2018 Carr Fire in Shasta County (number destroyed = 1614; https://www.arcgis.com/home/item.html?id=17d44552e0ea4c6ab2c43e80246e05b9), and the 2018 Woolsey Fire in Los Angeles and Ventura Counties (number destroyed = 1673; provided from Cal Fire to the National Park Service, Robert Taylor personal communication). All of these data were provided as part of the Cal Fire Damage Assessment and Fatality Totals (**DINS**) program. We used the same methods as above to calculate the mean housing density for destroyed and total number of structures. We calculated the total number of structures within the county boundaries where the fires were located.

To map geographical variation in structure loss probability by land use scenario, we subtracted the mapped probability of structure loss projected in the rural growth scenario models for year 2049 from the corresponding mapped probability of structure loss in the urban growth scenarios.

3. Results

3.1. Baseline statistics

From 2000–2015, there were 2081 structures destroyed in the NC study area. These destroyed structures were distributed across 17 out of a total of 202 fires during the same time period (based on the Cal Fire perimeter data). The mean size of fires where structures were destroyed (includes entire perimeters of those intersecting study area) was 5525 ha versus an overall mean fire size of 896 ha. In the BP study area, there were 451 destroyed structures that burned through 2015 in 39 out of 241 fires. The mean fire size with destroyed structures was 4018 ha versus a mean of 905 ha overall. In SD, 4338 structures were destroyed, across 20 fires out of a total 206 fires. The mean fire size when structures were destroyed was 150,647 ha versus a total mean of 1877 ha.

The mean density of destroyed structures was much lower than that of all structures in all study areas, by orders of magnitude (Fig. 2). This pattern was the same for density of destroyed structures versus all structures within counties in the recent fire events of 2017 and 2018 (Fig. 2), although the difference between destroyed and all structures was only about half for the Camp Fire and about a third for the 2017 North Coast fires. The distribution of housing density for both destroyed and all structures varied by study region, but destroyed structures were consistently located in low-density classes (Fig. 3).

Projected future trends in temperature and precipitation varied across regions for the two different climate scenarios, as did the overall housing density change. In the NC and BP study areas, the mean annual precipitation resulted in conditions with consistently more moisture in the CNRM scenario and consistently drier conditions in the MIROC scenario by 2049, with slight geographical variability (Fig S1a&b). Both GCMs projected decreased annual precipitation in the SD study area, but the drying was stronger for the MIROC scenario (Fig. S1c). The changes in summer precipitation showed much more geographical variability within study regions, but the differences in GCMs were flipped such that CNRM was projected to be drier in the summer than MIROC (Fig. S2a-c). Annual temperature was projected to increase much more substantially in the MIROC than the CNRM scenario for all three study areas by 2049, with substantially more geographical variation in the CNRM scenario (Fig. S3a-c). Decadal fluctuations, reflecting idiosyncrasies of the model run, were strongest in MIROC in the North Coast.

Changes in projected housing density patterns from 2009 to 2049 show substantial geographical variability across all three study regions (Fig. 4). For all regions, the rural scenario showed a larger areal increase of housing densities within the range where houses have been destroyed historically (Fig. 4); but the difference in rural versus urban scenarios was most substantial in NC, followed by SD, then BP. In the rural scenario, most of this increase in low-density housing occurred via growth (i.e., increased housing density) across more rural parts of the landscape, whereas in the urban scenario, a larger portion of exurban areas declined in housing density as there was a shift to more

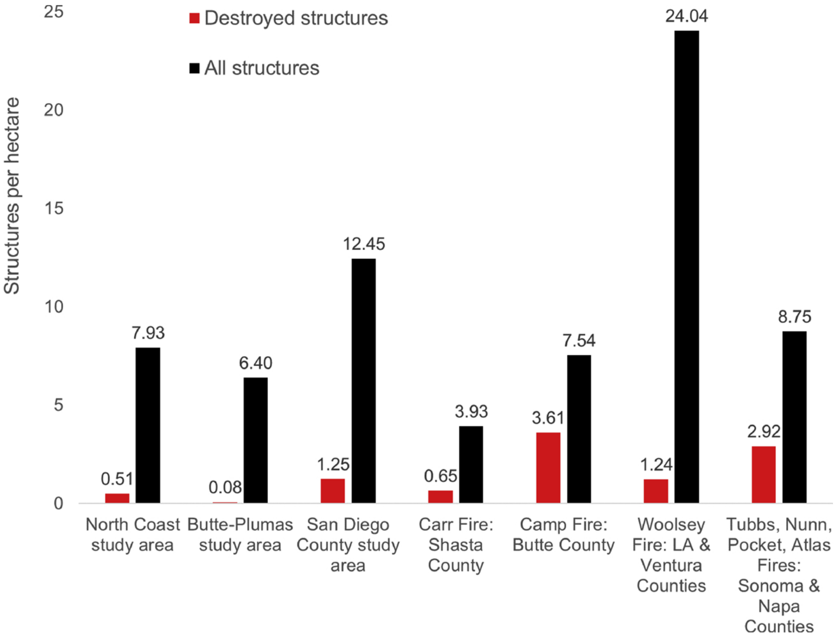

Fig. 2. Mean housing density for destroyed and all structures in three California study areas (using data through 2015) and for the four largest destructive fire events in 2017 and 2018.

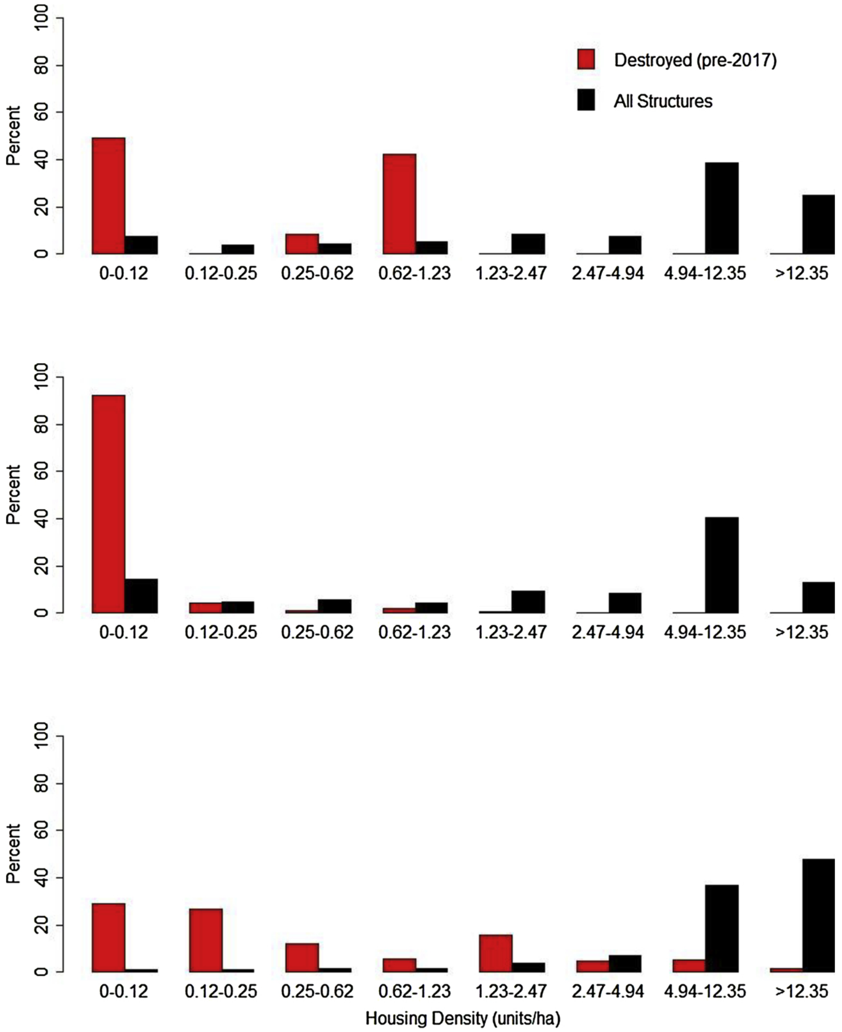

Fig. 3. Distribution of housing density classes (structures/ha) for destroyed and all structures in the a) North Coast, b) Butte-Plumas, and c) San Diego County study areas.

concentrated high-density housing near urban areas (Fig.4). One exception is the northern coastal portion of the SD study area, where there was some housing density decline in the rural scenario.

3.2. Variable importance

There were large differences in model variable importance for fire ignitions vs. large fires for all three study areas, and these were much larger than differences among regions (Table S1 – S2,Fig. 5). In particular, anthropogenic variables, particularly proximity to roads, dominated the patterns of fire ignitions, whereas topography and climate variables dominated the patterns of large fires, except in SD, where both housing density and distance to roads had about the same importance as topography and climate for large fires. In SD, housing density was almost equally as important as climate for explaining large fires. The directions of relationships differed such that fire ignitions tended to occur in close proximity to roads or populated places, but large fires occurred closer to public lands and farther from roads and populated places.

Whereas climate variables had a strong influence on fire ignitions and especially large fires, the vegetation productivity and moisture variables (AET and CWD) were not important for explaining structure loss patterns in NC or BP (Table S3 – S4, Fig. 5), and were less important than fire suitability for SD. Instead, housing variables and large fire suitability were the two most important factors explaining structure loss across all regions, with higher structure loss Univariate response curves showing the probability at low housing density (Fig. 6). SD was again different than NC or BP in that housing variables were more important than fire suitability.

3.3. Future projections

Overall, NC had a slightly lower baseline probability of large fires across the study area (Fig. 7a) than BP or SD, which had similar baselines (Fig. 7 b & c). Projections of future large fire probability were higher than the baseline for most time periods and climate scenarios for both the NC and BP study areas, except for MIROC in 2029 and 2049 in NC and CNRM 2019 in BP, and the results from these decades reflected oscillations that stemmed from decadal variability in the climate model projections. Large fire probability did not significantly change under either climate scenario in SD (Fig. 7c), but there was also slight decadal variability in the model run for CNRM. In all cases, differences in projected large fire suitability between the two land use scenarios were virtually absent due to the small relative importance of these variables to the model.

Compared to NC and BP (Fig. 8a & b respectively), SD had a relatively high baseline structure loss probability across the landscape (Fig. 8 c). Differences in structure loss probability for the two climate scenarios in NC and BP generally mimicked the large fire probability results in ranking and magnitude, and the decadal variability in fire

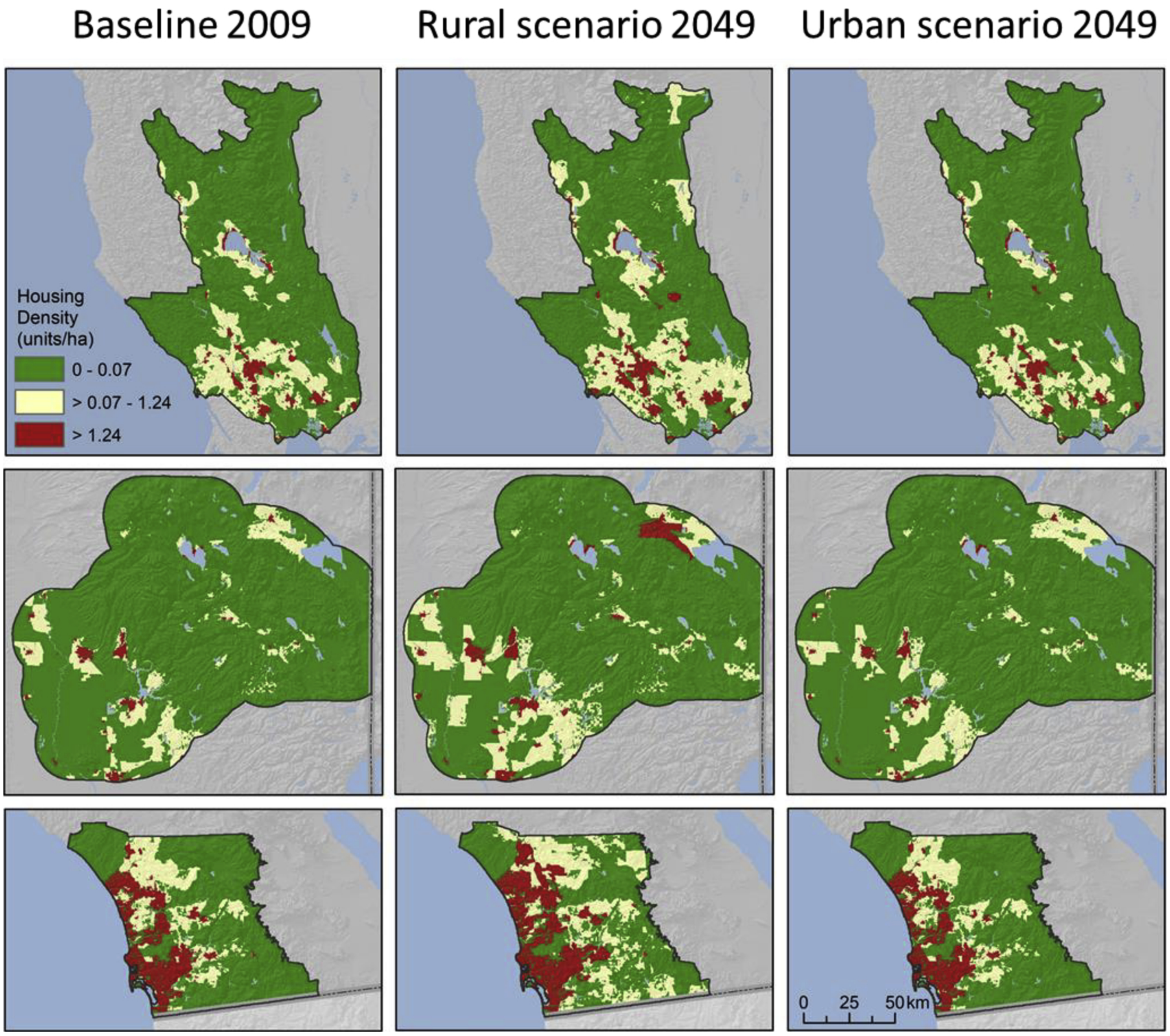

Fig. 4. Classified housing density in 2009, 2049 for the rural, and 2049 for the urban scenarios in the a) North Coast, b) Butte-Plumas, and c) San Diego County study areas. The middle (yellow) class represents the housing density range across the three study areas where structures have been destroyed in the past (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

probability for SD that came from climate model projections was reflected in the CNRM result. Compared to large fire probability, there was a much stronger effect of land use scenario on structure loss projections, and more variation in which scenarios exceeded baseline for NC (Fig. 8a) and SD (Fig. 8b). BP showed little variation in either climate or land use scenario probabilities. In NC, the rural land use scenario had a much larger probability of structure loss overall, and for CNRM, this difference generally determined whether probability would increase or decrease relative to the baseline. The rural scenario also resulted in higher overall structure loss probabilities in SD, but this was mostly apparent in 2049.

While structure loss was higher overall across regions and climate scenarios in the rural land use scenario (Fig. 8), there was considerable spatial heterogeneity in the effect of the land use scenario (Fig. 9). Comparing the rural land use scenario to the urban scenario in NC and SD, there were small changes to structure loss probabilities across most of the currently semi-urban and urban areas and large increases in structure loss probabilities in the currently rural areas (compare Fig. 9 to Fig. 4). In contrast, BP had locations of large increases and decreases in structure loss probabilities under the rural land use scenario compared to the urban land use scenario. However, all three regions had higher predicted structure loss in areas where there was an increase in low-density housing.

4. Discussion

Our projections suggest that both climate and land use will drive future changes in patterns of wildfire and subsequent likelihood of structure loss; but the relative importance and strength of different drivers will vary across and within different regions. Future changes will depend upon the nature and degree of change in both climate and land use relative to current conditions. For example, locations with increased low density rural housing are likely to see increased structure loss even in decades with lower large fire probabilities (compare decades 2029 and 2049 in Figs. 7a and 8a). Changes will also vary according to the strength and nature of regional relationships among climate, land use, fire patterns, and structure loss, with potential feedbacks among these drivers. Despite these complexities, which underscore the importance of customizing policy and management by geographical location (Keeley et al., 2009; Moritz et al., 2014), there were also key commonalities across regions. In particular, structure loss mostly occurred at fairly low housing densities. While more work needs to be done to create models that incorporate short-term weather conditions, such as wind, and feedbacks among drivers, we believe that the central importance of housing density to structure loss may be generally applicable to fire-prone landscapes.

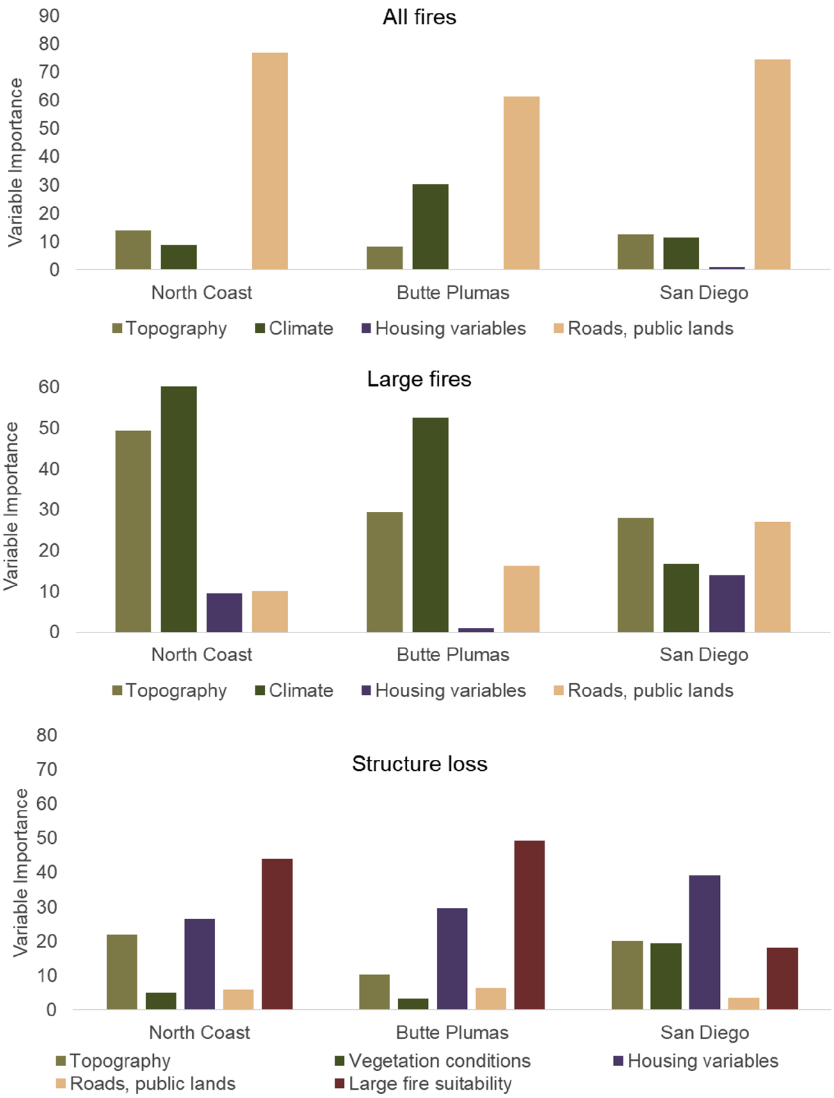

Fig. 5. MaxEnt variable permutation importance for fire and structure loss models in three California study areas, with variables grouped into categories. The fuel category for structure loss consisted of actual evapotranspiration and climatic water deficit.

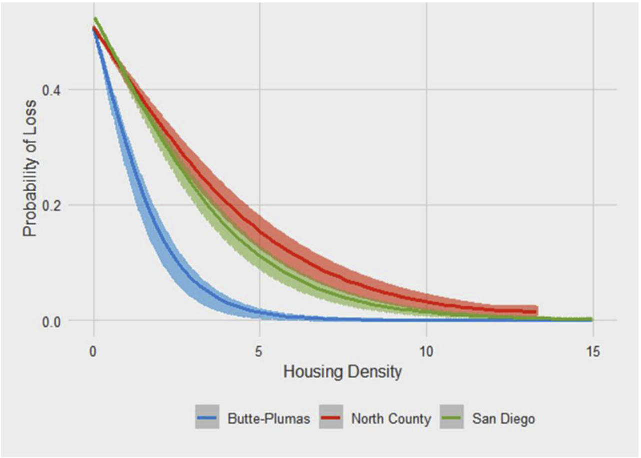

Fig. 6. Probability of structure loss relative to housing density (units/ha) for three California study areas, averaged across 5 model replicates.

4.1. *High anthropogenic variable importance for fire ignitions, but not large fires*

One commonality across regions was that anthropogenic variables were most important in explaining patterns of fire ignitions, whereas large fires were more related to topography, climate, and fuel (via AET and CWD). This finding is not surprising given that most fires in California are started by humans (Syphard et al., 2007; Balch et al., 2017), near human infrastructure (Syphard and Keeley, 2016). The finding is also consistent with other studies that have shown differences between the drivers of small and large fires (e.g., Syphard et al., 2008, 2016, Barros and Perreira, 2014; Abatzoglou et al., 2018) and that large fires are more likely to occur in remote areas where fuel continuity is greater, with severe winds better able to propagate fires via long-distance ember production, and access to suppression is lower (Gray et al., 2014). The consistency with other studies, and across divergent regions in this study, has important considerations for management. For example, ignition prevention efforts may be most effective if geographically concentrated near roads and development. Thus, land use change may generally be the biggest concern for preventing fires from starting; but climate change, in addition to weather and fuel patterns, may be more critical in the consideration of large fire behavior. One exception is that, unlike other human-caused fire sources, powerline-

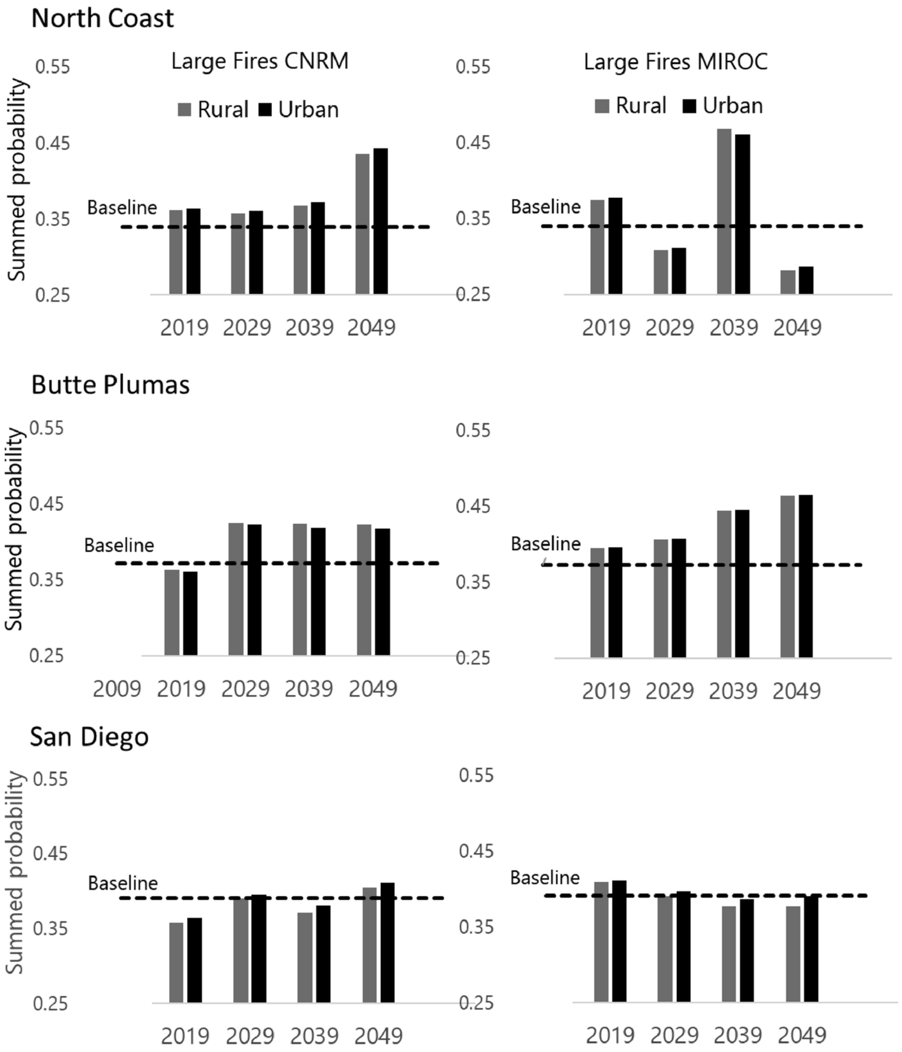

Fig. 7. Total projected probability of large fires under two climate and two land use scenarios for a) North Coast, b) Butte Plumas, and c) San Diego.

ignited fires tend to occur in more remote areas during severe weather, and these fires often result in large areas burned with substantial human losses (Keeley and Syphard, 2018). Understanding the relative importance of anthropogenic variables is critical given expected changes in human land use with resulting downstream impacts on deliberate or accidental ignitions, prescribed burning, mechanical vegetation treatments, and fire suppression.

The timing of ignitions, particularly corresponding with extreme fire weather, may be the most important variable to consider in determining whether fires become large and potentially destructive to human assets (Syphard et al., 2016; Abatzoglou et al., 2018). Historical analysis has also shown there to be an overall low correlation between fire frequency and area burned in California (Keeley and Syphard, 2018). Thus, small, frequent fires caused by human ignitions do not necessarily lead to highly destructive fires. Instead, the fires most likely to cause structure loss tend to be ignited in low-intermediate population or housing density (Syphard et al., 2007, 2009), adjacent to areas of high fuel loading.

Studies of historical fire-climate relationships in California (Keeley and Syphard, 2015, 2016) and across the U.S. (Littell et al., 2009; Parisien and Moritz, 2009; Syphard et al., 2017a; Littell et al., 2018) show differences in the strength and nature of climatic control over fire activity. In particular, those areas where fire is most strongly explained by climate in California are in northern, higher-elevation parts of the state, whereas in southern CA, fire-climate relationships have historically been weak (Keeley and Syphard, 2016). Other studies have shown fire-climate relationships to be weaker in areas with higher human presence (Higuera et al., 2015; Ruffault and Mouillot, 2015; Mann et al., 2016; Syphard et al., 2017b), and this is supported in our results, with the SD study area having both the highest overall housing density and the weakest link between climate and large fire suitability. SD was also the study area with the strongest relationship between anthropogenic variables and patterns of large fire suitability.

4.2. Predicted future wildfire varied less across scenarios than structure loss

Given the weak ties between climate and large fire suitability in SD, there were no major changes projected for large fires here, which is an important result given widespread concern that climate change will be responsible for increasing future fire activity across the western U.S. (Westerling et al., 2006; Barbero et al., 2015; Abatzoglou and Williams, 2016). Nevertheless, there could be other types of indirect climate change effects on fires in southern CA, such as long-term drought (Keeley and Zedler, 2009), vegetation type conversion facilitated by drier conditions (Jacobsen et al. (2007); Park et al., 2018; Syphard et al., 2018b), or changes in wind patterns (Guzman-Morales et al. (2016)). For the other two study areas, climate change was projected to increase large fire probability by the middle of the century, which corresponded to at least part of the increase in structure loss probability in these regions. In all regions, it is important to acknowledge that,

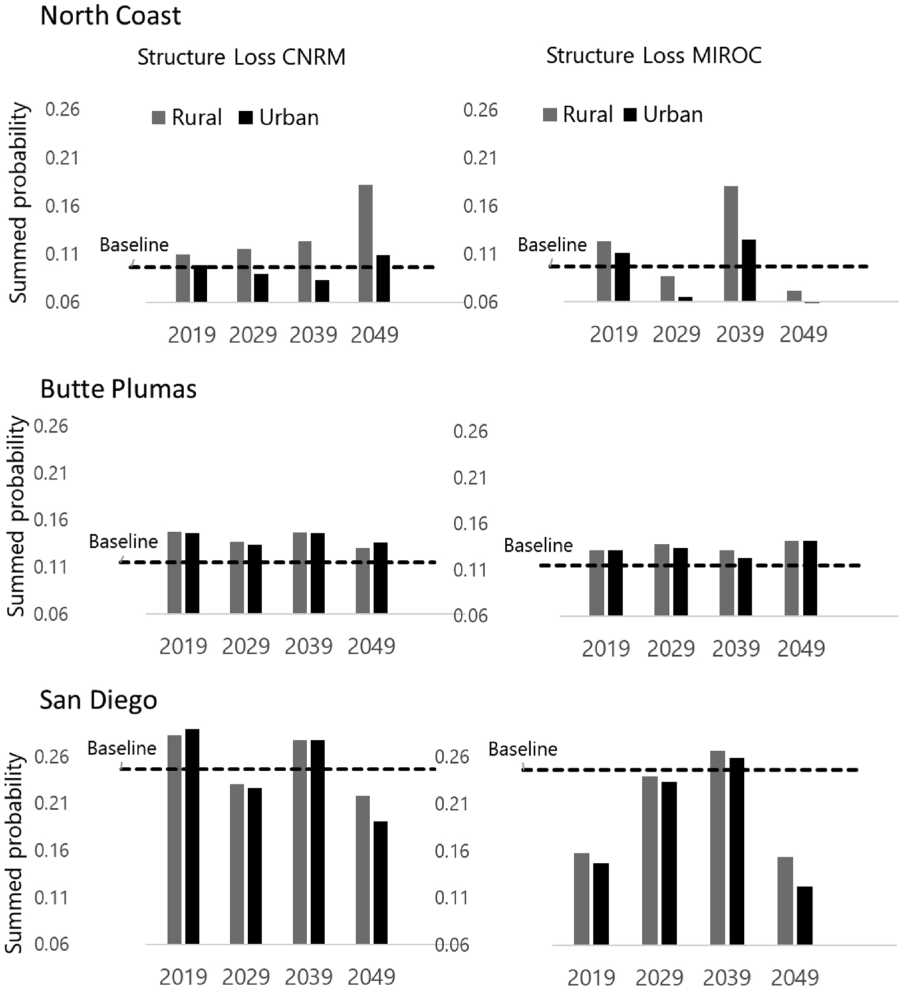

Fig. 8. Total projected probability of structure loss under two climate and two land use scenarios for a) North Coast, b) Butte Plumas, and c) San Diego.

despite inclusion of AET and CWD as proxies for fuel amount and condition, fire-vegetation feedbacks or vegetation type changes were not accounted for, and these could play an important, yet undetermined role in future fire activity (Syphard et al., 2018).

Particularly in the NC study area, land use change scenario played a major role in differences in structure loss probability, due to the significant relationships found in the baseline models as well as the nature of projected change in the rural versus urban scenarios. That is, there was substantially more expansion of low-density housing in the rural scenario versus the urban scenario in the NC study area, corresponding with the densities where most structures have been destroyed (i.e., the middle class in Fig. 4). This was true in BP and SD as well, but to a lesser extent. Also, for the urban scenario projections in all regions, and the rural projections for SD, there were both increases and decreases in housing density across the landscape; this patchwork of change may have dampened the apparent effect of land use on future projections of either fire or overall structure loss probability. Another important consideration is that structure loss probability may shift over time in response to changing density patterns. In other words, as some lower-density developments fill in with new homes, they may become less susceptible in the future; this is the likely reason that structure loss probability was projected to decline in some scenarios and time periods.

In modeling the decadal projections, we attempted to understand how different growth trajectories influenced model outcomes. For example, a region may initially experience low-density housing development in 2020–2030 that transitions to high density development by 2050. We hypothesized that either large fire or structure loss probability might thus vary through time as a function of the underlying housing density. However, given that land use was not one of the most important predictors of large fires, we did not observe a strong effect of oscillating housing density on fire projections. Instead, the up and down behavior in large fires, particularly in NC under MIROC, was due to idiosyncratic oscillations in climate projections that resulted from the climate model. For projections of structure loss, there was continued growth of low-density housing in the rural scenario for NC, which resulted in consistently higher structure loss probabilities over time. On the other hand, some areas of low-density development converted into high density development in San Diego County, which led to a net decline of structure loss probability by 2049. Overall, however, the biggest differences in effect of housing density was via the higher concentration of high-density development in the urban versus rural scenarios.

It is important to clarify that the land use scenarios were not meant to reflect precise changes but were designed to emphasize possible differences based on housing density and general trends towards urban or rural development. The land use change model tended to emphasize temporal and spatial spillovers; that is, any projection of housing density change in largely uninhabited areas first required either a history of growth or a spillover of growth from neighboring polygons, and this may have limited spatial expansion of housing in those areas. In other words, the model results, particularly for the rural growth scenario may understate the risks associated with low-density development. Further, we also assumed that road proximity, the distance to urban areas (areas with $\geq$10,000 residences), and the proximity to public land would remain unchanged over time, suggesting the results here are conservative.

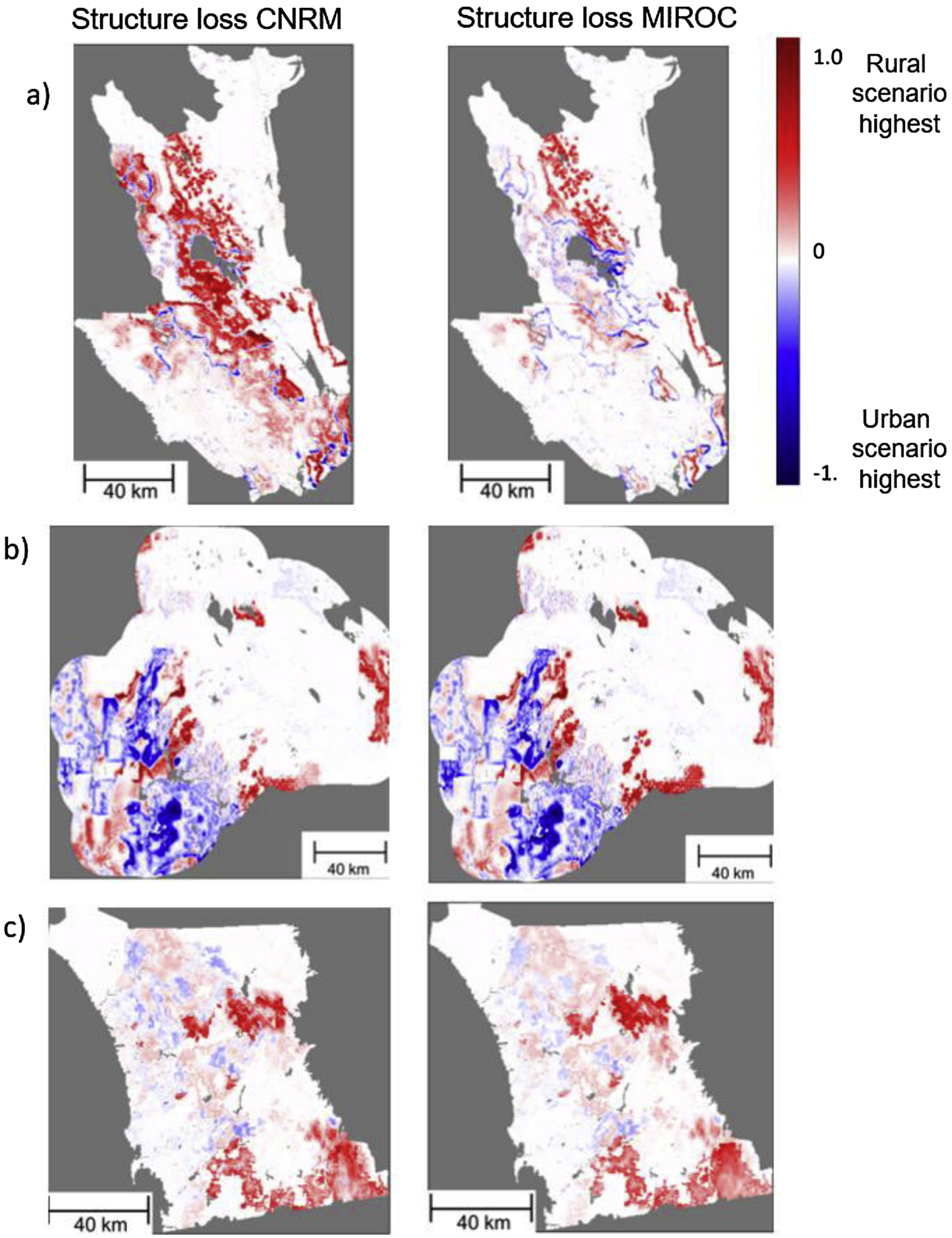

Fig. 9. Projected differences in structure loss probability at 2049 between the rural and urban density land use scenarios for CNRM and MIROC in the a) North Coast, b) Butte Plumas, and c) San Diego study areas.

4.3. Higher structure loss was seen in low density development

Regardless of future projections, one of the striking commonalities in the results was that observed structure loss occurred in larger fires and at lower housing densities than the averages for the regions. There are two different statistics related to housing density that are closely related but distinct. The first is the probability of structure loss for any house given its density (i.e., Fig. 6), and the other is the total number of structures lost at different housing densities (i.e., Fig. 3). Our results showed that probability of structure loss is negatively related to housing density in all regions, and while most destroyed structures were located in lower housing density classes, some structures were also destroyed at high densities. The association between structure loss and housing pattern has been documented in recent studies (Syphard et al., 2012, Alexandre et al. 2016, Kramer et al., 2018), and there has long been an assumption that fire risk is highest at the Wildland-Urban Interface (WUI), where houses meet or intermingle with wildland vegetation, both in the U.S. (e.g., Radeloff et al., 2018, Mell et al., 2010) and internationally (e.g., Lampin-Maillet et al., 2010; Montiel Molina and Galiana-Martín, 2016; Argañaraz et al. (2017)). However, the occurrence of several highly catastrophic wildfire events within high-density developments (e.g., Cohen and Stratton, 2008; Price and Bradstock, 2013; Nauslar et al., 2018), including recent California events, combined with previous lack of data associating changes in fire losses to changes in development patterns (McCaffrey et al. https://fireadaptednetwork.org/fire-narratives-accurate/) have led to questions and debate over which are the most dangerous development patterns.

Thus, one of the most important results of this study is that, even considering the massive numbers of structures that were destroyed in the last two years in wind-driven fire events, the overall mean housing density where houses are most likely to be destroyed (0.08 to 2.01 structures/ha pre-2015 and 1.24–3.61 in recent events) was more than an order of magnitude lower than the average housing density on the landscape for most cases (except the Camp Fire where the destroyed structure density was about 50% lower and the 2017 North Coast Fires, where the destroyed structure density was about 66% lower than total structures). The recent wildfires were uncharacteristic in the sheer number of structures and lives lost relative to historical numbers, in addition to the fact that wildfires did reach and enter parts of high-density urban areas in Coffey Park (Tubbs Fire), Paradise (Camp Fire), and the city of Malibu (Woolsey Fire). Thus, a lot more research is needed to understand how and why so many structures were lost. One clear factor were the wind speeds in these events, in addition to apparently substantial structure-to-structure spread and incendiary ember ignitions in which the houses themselves were more flammable than the nearby vegetation. Nevertheless, the losses in urban areas were still only a portion of the total number of structures destroyed in these fires, and thus they do not change the main conclusions of our study: overall, most structure loss tends to occur in areas of low-density development. One caveat is that we calculated housing density using data from the 2000 Census projected to 2009 as a baseline, and thus housing density has likely changed since then. However, the relative comparisons likely still hold because we consistently used the same housing data. Another recent study reported that the majority of threatened and destroyed structures from the last 30 years in the U.S. were located within the WUI; furthermore, when destroyed houses were not located in the WUI, the most common reason was that the housing density was lower than that in the WUI definition (Kramer et al., 2018).

The most likely explanation for this striking consistency is that housing patterns largely reflect exposure to wildfire. That is, wildfires typically burn through vegetation; and thus, those homes most interspersed with vegetation are most likely to encounter a wildfire in the first place, or be hit by incendiary embers. The reason for occasional catastrophic wildfire losses in high density areas is that, once exposed to a fire, a community with closely spaced homes made of flammable materials can lead to rapid house-to-house spread, particularly during severe weather conditions. In these cases, like the Tubbs fire in 2017 and Camp fire in 2018, the house itself becomes the fuel that propagates the fire.

Therefore, in terms of addressing conflicts between housing and wildfire in the future, the most effective mitigation may be land use and urban planning decisions that reduce the exposure of homes to wildfires (Syphard et al., 2013, 2016, Butsic et al., 2017). However, mitigation measures focused on defensible space and fire-safe construction materials, particularly when houses are closely spaced, are also critical for preventing future losses (Syphard et al., 2015, 2017c), as are other traditional fire management practices such as fire suppression and strategic location of fuel breaks to allow safe firefighter access to defend homes.

4.4. *Conclusion*

Looking at fire ignitions, large fires, and structures burned, we explored the importance of climatic and human variables for explaining fire and structure loss patterns across three diverse California landscapes, under current and future climate (hot-dry or warm-wet) and land use (rural or urban residential growth) scenarios. Across regions, we found that housing and human infrastructure were more responsible for explaining fire ignitions and structure loss probability. Large fires were better explained by climate, topography, and fuel variables. The differing strengths of these relationships interacted with the climate and land use scenarios, resulting in variability across regions in the relative importance of climate and housing patterns on fire and structures burnt. Focusing only on empirical housing density and structures burnt, we found that most structure loss occurred in areas with low housing density (from 0.08 to 2.01 units/ha), and as such, expansion of rural residential land use generally increased projected structure loss probability in the future. Both the historical results and the future projections highlight that future changes are likely to be complex and will result from a range of interacting factors. Climate change will be important to consider for managers and policy makers in some, but not all regions. In all areas, land use change merits increased attention, as local policy decisions can influence future patterns of development and exposure of structures to risk of loss in large wildfires.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.gloenvcha.2019.03.007.

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AMPHIBIAN UPLAND HABITAT USE AND ITS CONSEQUENCES FOR POPULATION VIABILITY

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Abstract. To predict the effects of habitat alteration on population size and viability, data describing the landscape-scale distribution of individuals are needed. Many amphibians breed in wetland habitats and spend the vast majority of their lives in nearby upland habitats. However, for most species, the spatial distribution of individuals in upland habitats is poorly understood. To estimate the upland distribution of subadult and adult California tiger salamanders (*Ambystoma californiense*), we used a novel trapping approach that allowed us to model the spatial variation in capture rates in the landscape surrounding an isolated breeding pond. As expected, we found that captures of adults declined with distance from the breeding pond. However, captures of subadults increased steadily from 10 to 400 m from the breeding site, but there were no captures at 800 m. A negative exponential function fit to the adult capture data suggested that 50%, 90%, and 95% were within 150, 490, and 620 m of the pond, respectively. For subadults, the quadratic function fit to the data similarly suggested that 95% were within 630 m of the pond, but that 85% of this life stage was concentrated between 200 and 600 m from the pond. To investigate the population-level consequences of reducing the amount of suitable upland habitat around breeding ponds, we used a stage-based stochastic population model with subadult and adult survival parameters modified according to our empirical observations of upland distribution. Model simulations suggested that substantial reductions in population size are less likely if upland habitats extending at least 600 m from the pond edge are maintained. Model elasticities indicated that quasi-extinction probabilities are more sensitive to reductions in subadult and adult survivorship than reproductive parameters. These results indicate that understanding the upland ecology of pond-breeding amphibians, especially the distribution and survivorship of subadults, may be critical for designing protective reserves and land use plans.

Key words: Ambystoma californiense; *California tiger salamander; declining amphibian; drift fence; matrix simulation model; pitfall trap; population viability analysis; reserve design; terrestrial; upland spatial distribution.*

Introduction

In the United States, wetland habitats are protected against draining and filling by state and federal regulations. A few states further require maintenance of a 30–60 m wide upland buffer of undeveloped habitat around some or all wetlands. These buffers capture silt and chemical pollutants before they reach the wetlands, and are generally recognized as effective in protecting water resources (e.g., Phillips 1989, Brosofske et al. 1997). An additional benefit of upland buffers is that they provide essential habitat for a variety of wildlife species. While the contribution of buffers towards the maintenance of viable populations is intuitively obvious, there has been relatively little quantitative evaluation of exactly how buffers may enhance the value of wetlands for wildlife. Recently there have been attempts to estimate the amount of ''core upland habitat'' needed to accommodate populations of semi-aquatic wetland-breeding amphibians (Semlitsch 1998, Semlitsch and Bodie 2003). Summarizing across 32 species, Semlitsch and Bodie (2003) estimated that the core upland habitat used by amphibians extends 159 to 290 m from the wetland edge, revealing that buffers designed to protect water quality encompass only a small fraction of the habitat used by most amphibians. While the Semitsch and Bodie (2003) review provides strong rationale for greater protection of upland habitat around wetlands to enhance habitat values for amphibians, it also emphasizes our rudimentary understanding of amphibian upland ecology.

Losses of wetland and upland habitats are recognized as key contributors to the widespread decline of amphibian populations (Semlitsch 2002, Collins and Storfer 2003). However, experimental research on amphibian declines has continued to focus on the aquatic embryonic and larval stages, while the equally important terrestrial stages are rarely studied (Storfer 2003). This research inequity between aquatic and upland amphibian ecology is not a new phenomenon, and is probably

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PLATE 1. An adult California tiger salamander (*Ambystoma californiense*). Photo credit: Bret Stewart.

due to the relative difficulty of terrestrial studies. Particularly for the diverse array of amphibians that breed in aquatic habitats but spend most of their lives in underground terrestrial retreats, even basic elements of upland ecology have remained essentially a ‘‘black box.’’ For example, we know almost nothing about interspecific interactions, density dependent effects on growth and maturation, and how these factors may influence dispersion in the uplands. Further, two recent papers indicate that amphibian population viability is often extremely sensitive to reductions in survivorship of upland stages (Biek et al. 2002, Vonesh and de la Cruz 2002). Clearly, additional experimental and observational studies of upland ecology are warranted (Storfer 2003).

Although population modeling studies have demonstrated that amphibian populations are sensitive to reductions in upland survival parameters, we know of no attempts to estimate the effects of upland habitat loss or modification on populations. For conservation planning, a model reflecting the likely population-level consequences of converting upland habitat to non-habitat or habitat where survival is substantially reduced, would greatly improve our ability to estimate the effects of human modification of landscapes. This would require both a demographic population model and a model describing the spatial distribution of individuals in the uplands. Unfortunately, either of these pieces is available for very few species, mainly due to the rarity of detailed upland distribution data.

The federally threatened California tiger salamander (*Ambystoma californiense*; CTS; see Plate 1) is a species for which there is a pressing need for a realistic analysis of the likely population-level effects of upland habitat conversion. Currently, the best available evidence suggests that this pond-breeding species has declined primarily due to the conversion of its aquatic and upland habitats to intensive land uses (Fisher and Shaffer 1996, U.S. Fish and Wildlife Service 2000, Davidson et al. 2002). In 2004, the U.S. Fish and Wildlife Service listed the CTS as a federally threatened species throughout its range, which includes parts of 22 California counties (U.S. Fish and Wildlife Service 2004*a*). Researchers have characterized many critical aspects of CTS life history, demography, ecology, and genetics (Shaffer et al. 1991, Austin and Shaffer 1992, Fisher and Shaffer 1996, Loredo and Van Vuren 1996, Trenham et al. 2000, 2001, Trenham 2001, Shaffer et al. 2004). We used data from those studies to parameterize a stage-based demographic population model that includes density dependent larval survival and environmental stochasticity. However, our knowledge of upland distribution, based two short-term studies that tracked metamorphosed CTS either visually (Loredo et al. 1996) or with radio transmitters (Trenham 2001), was inadequate to confidently project the population-level impacts of upland habitat loss.

We had two goals for the current study. First, we sought to collect field data that would allow us to derive an empirical model reflecting the distribution of salamanders in the uplands around an isolated breeding pool. Because CTS are usually at least four years old when they breed for the first time (Trenham et al. 2001), we sought to design a study that would yield relevant upland distribution data for adults and subadults. Rather than tracking individuals, we used an upland trap grid to capture salamanders. We modeled trap capture rates as a function of distance from the breeding pond, and based on those relationships estimated the width of surrounding upland habitat needed to encompass

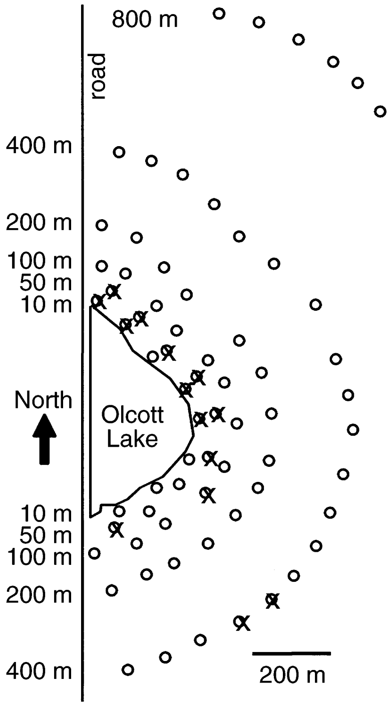

FIG. 1. Map of trap locations east of Olcott Lake, Solano County, California, USA (38.2712° N, 121.8224° W). Small circles indicate the location of each trap. An × is superimposed over traps consistently flooded and thus excluded from analyses.

specific proportions of CTS movements. Second, we used this newly derived model describing upland distribution and our demographic model to simulate the population-level effects of upland habitat loss/conversion around an isolated breeding pond. We explored the behavior of the model across a range of realistic parameter values and conducted an elasticity analysis to determine which parameters had the greatest incremental influence on the probability of quasi-extinction (Morris and Doak 2002). We discuss the implications of our results for the management and recovery of the CTS and other pond-breeding amphibians.

MATERIAL AND METHODS

Field methods

We collected field data at the Jepson Prairie Preserve, Solano County, California, USA. The site is essentially flat with less than 2.5 m of elevation variation across the entire 625-ha preserve. The uplands are dominated by grassland with a remnant stand of introduced blue gum (*Eucalyptus globulus*). The dominant feature in this landscape is Olcott Lake, a 36-ha playa vernal pool (Fig. 1). This pool fills with winter rainfall and runoff to a maximum depth of ~1 m, and dries every year, typically between May and July. In addition to harboring several endangered crustaceans (U.S. Fish and Wildlife Service 2002), this pool consistently contains large numbers of CTS larvae (H. B. Shaffer, *unpublished data*). Although CTS are known to use the burrows of both California ground squirrels (*Spermophilus beecheyi*) and pocket gophers (*Thomomys bottae*), only gopher burrows were present and abundant in all upland areas of the preserve. The pool is split by a north–south dirt road. We focused our trapping effort east of this road because there are no other suitable breeding pools for several kilometers to the east, whereas there are other breeding pools to the west. Based on prior tracking (Trenham 2001) and interpond movement (Trenham et al. 2001) studies at other sites, we assume that terrestrial salamanders captured east of the road originated exclusively from Olcott Lake.

We installed a total of 68 trap systems around the eastern half of Olcott Lake at locations 10, 50, 100, 200, 400, and 800 m away from the high-water line (hereafter, traps; Fig. 1). The distribution of traps was based on prior observations of CTS movements (Trenham 2001, Trenham et al. 2001). Each trap consisted of a 10 m long section of 0.9 m tall silt fence supported by wooden stakes. The bottom 15–30 cm of the silt cloth was buried in a shallow trench and anchored in place. Fence sections were oriented parallel to the perimeter of Olcott Lake. At both ends of each fence, one 3.8-L plastic bucket with 5 mm diameter drain holes was buried with its lip flush with the ground surface. To allow us to determine the direction of travel of captured animals, a tight-fitting piece of 4 mm thick plywood divided each bucket along the axis of the silt fence. A block of wood was attached to the top side of each bucket lid, such that when the lid was inverted it was supported 3 cm above the bucket lip, providing shade over the entire bucket. To allow the escape of nontarget animals, 15 cm long sections of rope were attached to the lids and hung in each bucket (Karraker 2001). When not in use, the bucket lids were closed to prevent the entry of animals.

Traps were spaced 90 m apart to achieve consistent fence coverage of ~10% at each distance. We shifted the spacing between some traps to avoid low areas subject to flooding. The portion of Olcott Lake east of the road is roughly half-circular with a radius of 240 m and a 754-m perimeter (Fig. 1). An arc 10 m beyond the high-water line has a radius of 250 m and a hemispherical perimeter of 785 m, so the eight 10 m long traps that we installed here encompassed just over 10% of that arc. Along the 50-, 100-, 200-, and 400-m arcs, we installed nine, 12, 14, and 19 traps, respectively, thus keeping coverage between 9.5% and 11.2% of each arc. The six traps installed at 800 m represent 1.8% coverage east of the road at this distance. We did not initially plan for traps at 800 m and only added them after we captured substantial numbers of CTS at 400 m. We constructed the 800 m traps northeast of Olcott Lake because initial captures were generally greater in this direction. We chose the 800 m distance to continue the pattern of doubling distances between

TABLE 1. Demographic information used to construct and parameterize the California tiger salamander population model.

Parameter	Estimate
Age of reproductive females	≥4 yr
Annual subadult survival probability	0.6†, 0.66
Annual adult survival probability	0.6†, 0.66
Probability of breeding in typical pond-filling years	0.5
Probability of breeding in late pond-filling years	0.1
Probability of late pond-filling years	0.0, 0.1, 0.3†, 0.5
Probability of complete reproductive failure	0.0, 0.1†, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9
Eggs deposited per breeding female	814
Survival from egg to metamorphosis	$0.131 \times (\text{no. eggs per m}^2)^{-0.6803}$; maximum = 0.20
Pond areas considered	700 m^2, 3500 m^2, 7000 m^2

Note: Where multiple parameter values are listed, daggers (†) indicate best estimates based on Trenham et al. (2000, 2001).

trap lines (Turchin 1998). The decision to construct all six traps in this area was purely for logistical reasons; we wanted to provide a reasonable probability of detection while not dramatically increasing the time to check all traps.

The first appreciable rain of the 2002–2003 season came on 13 December. We began installing traps on 14 December, and captured our first CTS that night. Traps 10 to 400 m from Olcott Lake were installed between 14 December 2002 and 4 January 2003; we added the 800-m traps on 20 January 2003. Beginning on 14 December, traps were opened each day prior to predicted rain, and kept open for several days thereafter. We installed a rain gauge to measure precipitation received between site visits. When open, we checked traps each morning by 07:30. Because we never caught more than one animal if no rain fell during the 24 hours prior, we closed traps after several days without rain or captures. Trapping of subadults and adults was terminated on 21 March 2003.

For each captured CTS, we noted trap number and direction of travel (i.e., moving towards or away from the pond). We also photographed each individual next to a metric ruler, clipped a single toe that was preserved in 70% ethanol, and recorded the sex of adult animals. Animals were immediately released into nearby dense vegetation or pocket gopher burrows. We measured the snout–vent length of each animal from the photographs.

Data analysis and modeling

The dependent variable that we modeled in our analyses was the capture rate of each trap, with the two buckets on each fence considered elements of the same trap. To determine capture rates for each trap we divided the number of adults or subadults captured by the number of nights the trap was open. We took this approach because there was some variability in the number of nights each trap was open. Capture rates were square root transformed prior to further analysis, and traps that were consistently flooded ($n = 14$; Fig. 1) and from which salamanders could easily escape were excluded from these analyses. We used linear and nonlinear regression to fit statistical models relating capture rates to distance from Olcott Lake. Based on these functions we estimated capture rate at 10 m intervals to the point where no further captures were predicted. We summed the capture rates across all distances, and then estimated the cumulative proportion of captures encompassed by upland habitat rings of increasing width.

To investigate the potential effects of increased mortality due to upland habitat loss on adult population size and population persistence, we used a stage-based matrix population model with six stages: new metamorphs, 1-yr-old subadults, 2-yr-old subadults, 3-yr-old subadults, new adults, and older adults (Caswell 2001). We parameterized the basic model with demographic data from our long term study of this species in Monterey County, California, USA (Trenham et al. 2000; P. C. Trenham, *unpublished data*; Table 1, Fig. 2). Because adult males are not presumed to be limiting, the model tracks only females. In the model, salamanders mature at four years old and, in each year, a fraction the surviving adults breed. Each breeding female lays a clutch of 814 eggs, half of which are assumed to be female, and survival from laying to metamorphosis depends on egg density in the pond (Fig. 2). After metamorphosis, upland survival of subadults and adults are fixed, but can be adjusted independently. In reality, subadult survival is poorly characterized. However, assuming that subadults survive at the same rate as adults (0.60) and mature at four years old, approximately 13% would survive to maturity, which matches the available data for this and related species (Scott 1994, Loredo and Van Vuren 1996, Trenham et al. 2000).

At the start of each model run, the population was composed of 100 new metamorphs, 50 1-yr-old subadults, 25 2-yr-old subadults, 13 3-yr-old subadults, seven new adults, and seven older adults. The model included two forms of environmental stochasticity to match observations from our long-term study (Trenham et al. 2000). First, because we found that in years when ponds fill late, females are much more likely to skip breeding, late pond-filling years occurred with a defined probability and the probability that an adult female bred in these years was reduced. Second, in some years model reproduction failed completely, as is com-

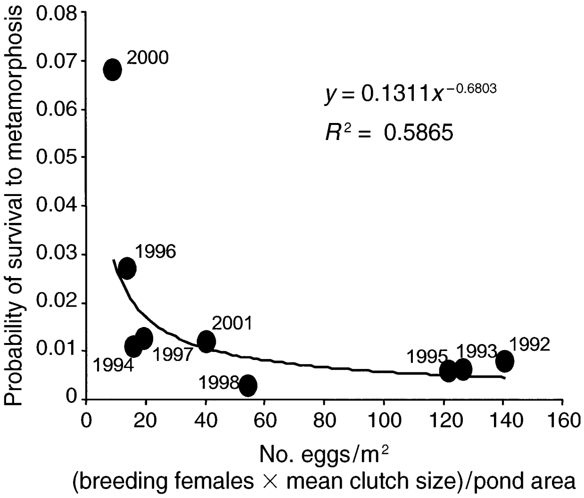

FIG. 2. Data from our long-term study in Monterey County, California, USA, suggest that larval survival is density dependent (Trenham et al. 2000). We fit a negative power function to these data to approximate this relationship. Symbols are labeled with the year for each data point; in 1999 California tiger salamander (CTS) breeding failed completely. Probability of survival to metamorphosis for each year was calculated as the number of newly metamorphosed salamanders emerging from the pond divided by the product of the number of breeding females and the average clutch size. Initial egg density was calculated as product of the number of breeding females and the average clutch size divided by 700 m^2, the area of our long-term study pond.

monly observed when ponds dry prior to metamorphosis (Gill et al. 1983, Semlitsch et al. 1996). Each year the program selected one random number to determine if pond-filling was late, and a second random number to determine if reproduction failed. Depending on the random values generated, the program used one of three alternate forms of the transition matrix—the first for typical pond-filling years, the second for late pond-filling years, and the third for years when reproduction failed completely—to project the population at the next time step. We initially evaluated model behavior with the probabilities of late filling and reproductive failure set to zero, and then with these probabilities set at a range of values (Table 1). For each set of parameter values considered we ran the model 100 times, recording for each the mean and variance in the number of adult females at 100 years, and the number of runs that went to zero. Because our model did not include random variation in upland survival probabilities and reproductive output, the probability of extinctions was underestimated.

To determine which parameters had the greatest proportional effect on modeled population viability, we used a simulation approach to estimate the elasticity values for cumulative quasi-extinction probabilities (Morris and Doak 2002). The quasi-extinction threshold was set at five adult females. To obtain elasticities we first ran the model with a baseline set of parameters, and then with each parameter reduced to 95% of its baseline value. For each parameter set, we made 1000 model runs of 100 years each, recording for each run where the adult population dipped to or below the quasi-extinction threshold, the year in which this occurred. Elasticities for each parameter were estimated based on the difference between the baseline and perturbed cumulative quasi-extinction probability at each year (Morris and Doak 2002).

After evaluating model behavior assuming intact upland habitat, we investigated the population-level consequences of maintaining increasingly narrow bands of unaltered upland habitat adjacent to 700-, 3500-, and 7000-m^2 breeding ponds. For these simulations, we fixed the probabilities of late pond-filling years and reproductive failures at 0.30 and 0.10, respectively, to match our long-term observations of environmental variation (Trenham et al. 2000; P. C. Trenham, *unpublished data*). We began with the same three alternative forms of the transition matrix described previously. However, based on the estimated cumulative distribution of subadults and adults in the uplands around Olcott Lake, survival parameters were adjusted accordingly. Because actual survival in altered habitat is unknown, we investigated two scenarios for animals moving beyond the protected habitats: (1) no survival and (2) survival reduced by 50%. For example, assuming that 10% of adults remain within 100 m of the breeding pond, an unaltered upland survival probability of 0.60 would be reduced to 0.06 for scenario one, or 0.33 (i.e., 0.06 + [0.54/2]) for scenario two. The first scenario approximates what we imagine occurs with intensive residential development, the second may be representative of some agricultural land uses or low-density housing. We assumed that movement is independent of habitat suitability. Because subadults do not migrate to and from the pond each year, the reduction in survival due to habitat alteration was assessed only once prior to maturity for each cohort. We also compared the effects of basing the cumulative distribution functions on different functional forms of the relationship between density and distance for the Olcott Lake data.

RESULTS

Upland trapping results

Between 14 December 2002 and 21 March 2003, we captured 74 female, 53 male, and 62 subadult CTS in 2696 trap-nights (see Appendix A for a complete listing of capture data). Only three salamanders were recaptured; for these individuals we used only their initial capture data in the analyses that follow. We captured at least one male, female, and subadult salamander in traps at each distance from 10 to 400 m from Olcott Lake. We captured no CTS in our traps at 800 m. Comparisons of the distributions of adult and subadult captures, however, indicate divergent relationships be-

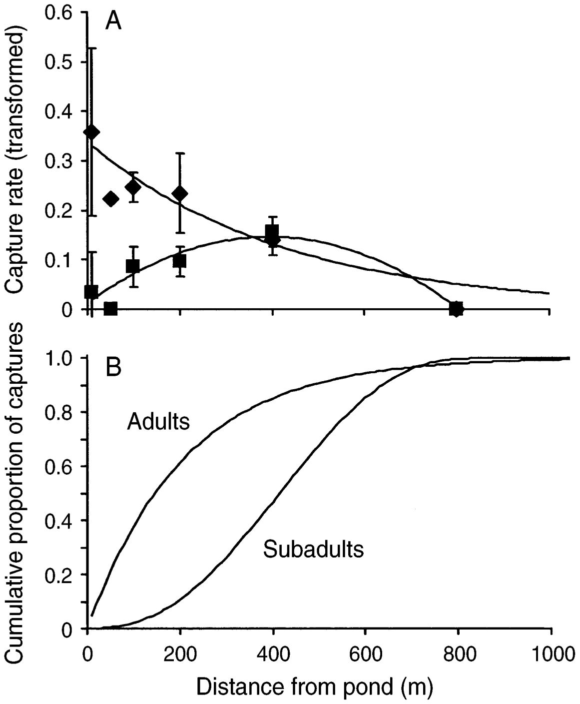

FIG. 3. Spatial distribution of California tiger salamander captures for all non-flooded traps. (A) Square-root-transformed number of adult (diamonds) and subadult (squares) captures per trap-night summarized for each distance (mean ± 2 SE). Lines represent exponential (adults) and second-order polynomial (subadults) regressions fit to the data; parameters are provided in *Upland trapping results.* (B) Using the regression functions represented in Fig. 3A, we estimated the cumulative proportion of subadults and adults encompassed within increasingly wide upland buffers around Olcott Lake.

tween capture rate and distance for these two groups. Adult capture rates declined from a maximum at 10 m, whereas subadult captures increased steadily from 10 to 400 m (Fig. 3A).

To make quantitative predictions about the distribution of adults in the uplands, we fit linear and exponential functions to the full adult data set. Although there was substantial heterogeneity in capture rates among traps at each distance, both the linear ($\sqrt{y} = 0.300 - 0.00039 \cdot x$; $F_{1,52} = 37.7$, $P < 0.0001$, $R^2 = 0.408$) and the exponential ($\sqrt{y} = 0.339 \cdot e^{-0.00236x}$; $F_{2,51} = 104.9$, $P < 0.0001$, $R^2 = 0.402$; Fig. 3A) fits were highly significant and explained roughly 40% of the variance in the data. Because there is a history of biological support for an exponential relationship between density and distance (Turchin 1998), we focus our further investigations on this form. Extrapolating from the exponential fit, we estimate that to encompass 50%, 90%, and 95% of the adults would require upland habitats extending 150, 490, and 620 m from the edge of Olcott Lake, respectively (Fig. 3B). A potential issue of concern with our sampling was the presence of only six traps at 800 m. To assess the influence of our lack of captures at 800 m on the predicted relationship we reanalyzed the data with those traps excluded. Extrapolating from the resulting function ($\sqrt{y} = 0.326 \cdot e^{-0.00205x}$; $F_{2,45} = 96.7$; $P < 0.0001$; $R^2 = 0.235$) the predicted upland habitat areas to encompass the same proportions of adults as above are roughly 13% wider: 170, 550, and 700 m, respectively.

Because subadult captures increased steadily from 10 to 400 m but declined to zero at 800 m we fit a quadratic function to the subadult dataset. Although the true shape of the function between 400 and 800 m cannot be determined from our data, quadratic regression provides a reasonable approximation. Fitting this function to the data resulted in a statistically significant relationship which explained only 18% of the variation ($\sqrt{y} = 0.084 + (1.8 \cdot 10^{-4}x) - (9 \cdot 10^{-7}(x - 290)^2)$; $F_{2,51} = 5.52$, $P = 0.007$, $R^2 = 0.178$; Fig. 3A). Extrapolating from this function the widths of upland habitat to encompass 50%, 90%, and 95% of subadults are 380, 590, 630 m, respectively (Fig. 3B). Upon further inspection, we noticed that very few subadults were captured in the traps south of Olcott Lake; dividing the traps into a northern and southern half there were 53 northern and nine southern captures. Reanalyzing only the northern trap data resulted in a substantially improved fit ($\sqrt{y} = 0.208 + (4.4 \cdot 10^{-5}x) - (1.3 \cdot 10^{-6}(x - 359)^2)$; $F_{2,26} = 10.12$, $P = 0.0006$, $R^2 = 0.438$). However, the predicted upland habitat widths to encompass 50%, 90%, and 95% of subadult CTS were nearly identical at 390, 600, 650 m, respectively.

Population model output

Before attempting to assess the population-level effects of upland habitat alteration for CTS, we investigated the model response to variation in parameters other than upland survival. With no stochastic elements, because larval survival was density dependent the number of adult females in the population rapidly reached an equilibrium determined by upland survival probabilities and pond area. With subadult and adult survival both set at 0.60, half of adult females breeding each year, and no stochastic reproductive failures, the equilibrium adult female population increased by one for each additional 8.1 m^2 of pond area.

Next, we investigated how population size and extinction risk responded to a range of stochastic conditions. Fig. 4A shows that, for a given pond area and probability of late pond filling, the average adult population size declines linearly as the probability of reproductive failure increases. Similarly, if the probability of reproductive failure is held constant while the probability of late pond-filling years is increased the mean adult population size declines linearly. Fig. 4B shows that the proportion of model runs going to zero within 100 years accelerates as the probability of reproductive failure increases. Because larvae may survive to metamorphosis in late pond-filling years, but not with reproductive failure, increasing the probability

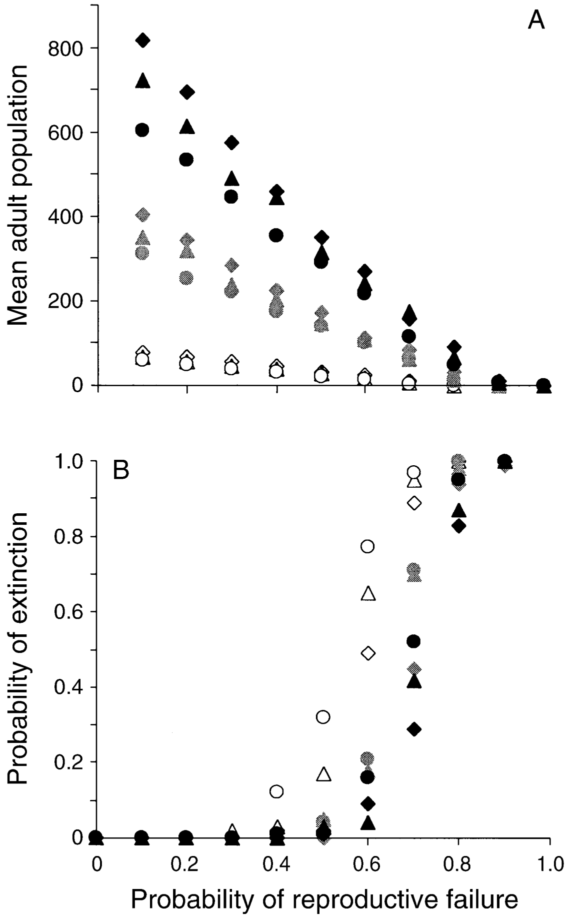

FIG. 4. Using our simulation model, we explored how (A) average California tiger salamander population size and (B) local extinction risk responded to increasing degrees of environmental stochasticity. Environmental stochasticity entered the model as (1) the probability of complete reproductive failure due to early pond drying (range 0–0.9; *x*-axis), and (2) the probability of late pond-filling years when only 10% of surviving females bred (diamonds = 0.1; triangles = 0.3; circles = 0.5). The probabilities of these perturbations were modeled as independent events. Symbol colors indicate the three different pond sizes modeled: 700 m^2 (open symbols), 3500 m^2 (gray symbols), and 7000 m^2 (black symbols). Upland survival of subadults and adults was set to 0.6. Females could breed beginning at four years old, and 50% of surviving females bred in each typical pond-filling year. Probability of survival to metamorphosis declined from a maximum of 0.2 in response to the density of eggs deposited in the pond (Fig. 2).

of the latter produced a larger effect on average population size and the frequency of runs that went to zero.

Fig. 5 summarizes the results of an elasticity analysis of the probability of quasi-extinction in model simulations. This analysis indicated that the probability of quasi-extinction was relatively insensitive to parameters influencing larval survivorship, but highly sensitive to small perturbations of upland survivorship. Of the two upland survivorship parameters, quasi-extinction probability was more than twice as sensitive to shifts in subadult as adult survivorship. Quasi-extinction probability was similarly insensitive to perturbation of each of the two parameters controlling larval survival.

The ultimate goal of this modeling exercise was to investigate the potential population-level consequences of converting upland habitat to nonhabitat or to habitat where survival is substantially reduced. Because there is uncertainty in the model parameters, we conducted simulations for a range of baseline survival parameters, mortality scenarios, and functional relationships between upland distribution and distance (see Table 1). In Fig. 6, we present model results illustrating the estimated effects on adult population size of maintaining increasingly wide areas of undisturbed upland habitat around a 700-m^2 pond; the results of model runs for 3500- and 7000-m^2 ponds were qualitatively identical (not shown). Consistent with the elasticity analysis results (Fig. 5), increasing annual subadult survivorship from 0.6 to 0.66 resulted in a larger average adult population than did similarly increasing adult survivorship (Fig. 6). Assuming a linear rather than an exponential decline in adult upland densities, resulted in small increases to estimated average population sizes of about 10–20% (Fig. 6).

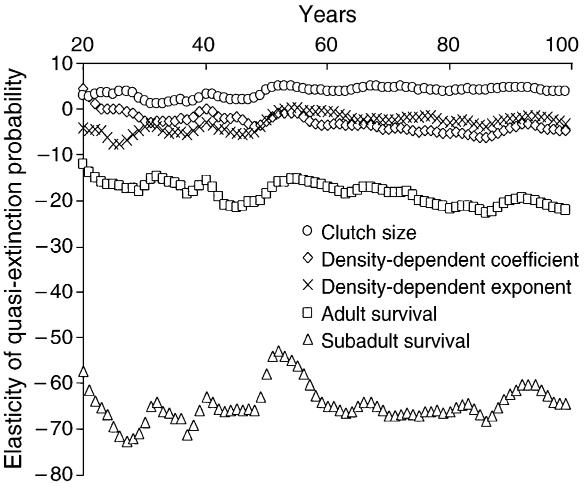

FIG. 5. Estimated elasticity values for cumulative quasi-extinction probabilities in response to perturbations of mean vital rates. Symbols represent elasticity in response to perturbation of various model parameters: subadult survival, adult survival, coefficient and exponent in larval density-dependent survival function, and number of eggs deposited per breeding female. Five adult females was the quasi-extinction threshold. The baseline model parameter values for this analysis were those indicated in Table 1. Elasticities for <20 years are not plotted because few extinctions occurred before this time, and as a result estimates of extinction probabilities and elasticities during this interval are highly variable and unreliable. Methods for elasticity analysis of density-dependent stochastic models are adapted from Morris and Doak (2002).

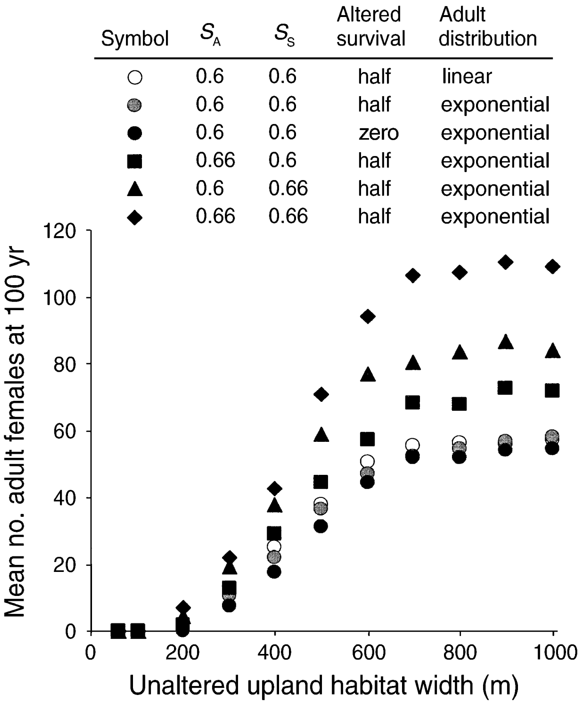

FIG. 6. Simulation model results showing the response of adult population size to the maintenance of increasingly wide bands of unaltered habitat around breeding ponds. Each point represents the mean number of adult females present in the simulated population at time step 100 based on a total of 100 runs with each set of parameter values. Different symbols represent different initial values for upland survival (i.e., with completely intact upland habitat), different mortality scenarios for animals moving into altered habitats (i.e., zero vs. halved survivorship), and adult survivorship (S_A) reduced either according to the cumulative distribution function in Fig. 3B (exponential) or a cumulative distribution function based on a linear relationship between adult captures and distance (linear; not shown). Subadult survivorship (S_S) was always reduced according to the subadult cumulative distribution function in Fig. 3B. Results shown are for a 700-m^2 breeding pond, with late pond-filling years and reproductive failures in 30% and 10% of years, respectively.

In general, as subadult and adult survival were reduced in response to simulated habitat loss, average population sizes declined, with accelerating declines when adjacent habitats extending less than 600 m from the pond edge were maintained (Fig. 6). Although estimated adult population sizes were sensitive to the particular set of parameter values, the proportional effects of a given amount of habitat loss were consistent. For example, under all scenarios considered, maintaining only a 400 m wide ring of upland habitat resulted in population declines of >50% when compared with the unaltered condition. Predicted declines approached 70% when animals moving into altered habitat all died. Leaving 200 m of upland habitat resulted in declines in average population size of 90–100%. Finally, if only 60 m of upland habitat was left intact, populations are generally predicted to go extinct within 100 years, or occasionally persist but at <1% of their estimated capacity in an intact landscape.

DISCUSSION

To confidently manage wetland habitats for viable populations of semi-aquatic animals requires a more detailed understanding of how these animals use upland habitats (Semlitsch and Bodie 2003). For researchers attempting to understand amphibian population ecology, penetrating the upland ecology of small, secretive, and often fossorial amphibians has remained a daunting empirical challenge (Taub 1961, Semlitsch 1998). While no single method or strategy will provide all of the critical data, our quantitative drift fence analysis of CTS at Jepson Prairie provides at least two novel results. First, adult dispersion appears to be far greater than indicated by earlier projections based on direct observations (Loredo et al. 1996) and radio tracking data (Trenham 2001), and is more in line with estimates based on observations of interpond dispersal over several years (Trenham et al. 2001). Second, the spatial distribution of subadults appears to be very different from that of adults.

To date, radio tracking has been the primary method used to obtain data on the distribution of adult amphibians in the uplands. Semlitsch (1998) and Trenham (2001) used tracking data to estimate the upland distribution ambystomatid salamanders. In a review of six eastern U.S. *Ambystoma* species, adults captured at breeding ponds and tracked directly via radio transmitters or radioactive implants moved an average of 125 ± 73 m (mean ± 1 SD) from ponds (Semlitsch 1998). Similarly, Trenham (2001) documented an average emigration distance of 114 ± 83 m for radio-tracked adult CTS. Assuming that movements are normally distributed, the means approximate the width of upland habitat required to encompass 50% of salamander movements. The means plus 1.645 standard deviations approximate the width of upland habitat needed to encompass 95% of movements (i.e., 245 and 250 m for these two studies). Our trapping results similarly suggest that 50% of adults are within 150 m of Olcott Lake. However, our analyses suggest that to encompass 95% of adults a 620 m wide upland habitat area is needed.

Although direct-tracking data provide valuable information on individual behavior and movements, we place more confidence in our trap-based projections of population distribution in the landscape for several reasons. First, there are always concerns that radio-equipped animals may not behave naturally, which is not an issue with our trap-based approach. Second, rather than assuming a normal distribution for salamander migration distances (Semlitsch 1998, Trenham 2001), we fit statistical models to the spatial distribution of actual capture rates. Finally, whereas radio tracking studies generally follow animals for only a few months after breeding, longer studies suggest that movement during these initial periods may not be representative of total adult displacement (e.g., Madison 1997, Madison and Farrand 1998). Because CTS adults frequently skip breeding for one or more years (Trenham et al. 2000), following post-breeding movements for just a few months is likely to underestimate overall movement patterns. Trap arrays, in contrast, register upland movements in proportion to their occurrence in the landscape. Interestingly, our projections in the current study closely resemble the spatial distribution of interpond dispersal events in our Monterey County study. In that system we observed adult and subadult dispersal among ponds separated by 60–670 m, but not farther (Trenham et al. 2001).

Because newly metamorphosed and subadult amphibians are generally too small to equip with radio transmitters, almost nothing is known about the upland ecology of these intermediate life stages. Whereas Semlitsch (1998) found tracking data for 265 individual adult *Ambystoma*, he found data for only 18 newly metamorphosed juveniles, and no data on subadults. CTS most commonly require three to five years to reach sexual maturity (Trenham et al. 2000; P. C. Trenham, *unpublished data*), and during this time they are completely terrestrial and rarely encountered. In contrast to the decline in adult capture rates at increasing distances from Olcott Lake, subadult capture rates increased from 10 to 400 m, and then declined to zero at 800 m. The apparent overall greater dispersion of subadults could potentially be a response to size-structured competition, which has been documented in related species (Smyers et al. 2002), or simply a consequence of diffusion-like movement over the lengthy subadult phase compared to the shorter interval between adult breeding events. Regardless of the cause, our data suggest that to encompass 95% of subadults an upland area on the order of 630 m wide would be required.

Although recommending upland habitat protection guidelines to encompass specific proportions of populations is a logical approach (Semlitsch 1998, Faccio 2003), this may not maintain population viability. We used a stochastic population model to evaluate this goal more directly. The results of our model, represented in Fig. 6, suggest that protecting at least 600 m of upland habitat would maintain populations with ~10% reduction in mean population size. Extrapolating from Fig. 3B, this translates to 90% and 92% protection of adults and subadults, respectively, and thus supports the protective value of the 95% protection benchmark. From a management perspective, this is a useful benchmark in situations where the goal is to maintain populations on lands containing one or a few breeding ponds isolated from immigrants. The upper bound on core upland habitat width of 290 m suggested by Semlitsch and Bodie (2003) may adequately protect other species, but our analyses suggest that if it were applied to CTS average population sizes would be reduced by >80% (Fig. 6). Therefore, for long-term preservation of individual CTS populations, the currently best-supported strategy is establishing protected landscapes with breeding ponds buffered by at least 630 m from incompatible upland land uses.

In many situations, due to historic habitat losses, protecting such broad areas of upland habitat will not be possible. Although breeding ponds nested in suboptimal uplands will be more likely to experience local extinctions, if linked to other ponds by dispersal they could contribute to the maintenance of a regional metapopulation (Sjögren-Gulve and Ray 1996, Marsh and Trenham 2001). Experimental metapopulation approaches to conservation may be the only viable option for CTS preservation highly fragmented regions and for the broader recovery of this species. Studies of a wide variety of amphibian species suggest that interpond distances of less than one kilometer should be maintained to avoid isolating breeding ponds (Marsh and Trenham 2001, Semlitsch 2002; but see also Smith and Green 2005). Strategies worth considering may include protecting corridors of marginal upland habitat between breeding sites, pond creation to enhance connectivity among distant sites, and even translocation of individuals to currently isolated unoccupied sites (Trenham and Marsh 2002, Seigel and Dodd 2002).

Ideally, before more detailed guidelines are drawn and predictions made, data from multiple sites and multiple years would be available to evaluate spatial and temporal variation in upland distribution, upland survival, and reproduction. Our model results suggest that obtaining additional data on upland survival should be a priority. In this and similar studies, pond-breeding amphibian populations are sensitive to upland survivorship of adults and subadults (Taylor and Scott 1997, Biek et al. 2002, Vonesh and de la Cruz 2002). Recognizing that upland survivorship of subadults is the parameter in which we have the least confidence and to which model results were most sensitive, this is an important area for additional study. Estimates of survivorship in different land use treatments would be of both basic and applied value (e.g., Rothermel and Semlitsch 2002).

Although we constructed our model as a tool to investigate the effects of upland habitat alteration, the results address some broader patterns of interest. Marsh and Trenham (2001), in reviewing the fit between theoretical metapopulations and pond-breeding amphibians, found little evidence that random extinctions of local populations are common as long as upland habitats were intact. This was also true of our model populations (Fig. 4B), and is due to strong density dependence in larval survivorship. In models where reproduction is enhanced at low densities, there is a strong tendency to recover from stochastic reductions in population size (Taylor and Scott 1997, Vonesh and de la Cruz 2002, Ferrer et al. 2004). From a practical perspective, our model results should also inform attempts to create breeding habitat for CTS or to assess the value of existing habitats. Our simulations emphasize the value of breeding habitats with large surface areas and those that hold water until metamorphosis in most years. In habitats where the probability of reproductive failure exceeds 0.50, simulations suggest that the result will be frequent local extinctions. However, it is important to note that, due to the potential for the establishment of fishes and other predator populations, reproductive failure is common in both permanent and highly ephemeral pools (Fisher and Shaffer 1996, Semlitsch 2002). Recent work indicates that even pond ‘‘improvement’’ that reduces the probability of annual drying, increases invasability by exotic fishes, crayfish and non-native tiger salamanders (*A. tigrinum*) decreasing the biological value of these sites (Fitzpatrick and Shaffer 2004).

The CTS was initially emergency listed as endangered in both Santa Barbara and Sonoma counties due to rapid conversion of its remaining habitat (U.S. Fish and Wildlife Service 2000, 2003). Because habitat loss was the main threat that brought about both of these actions and the statewide listing, a primary recovery objective should be the establishment of preserve areas with sufficient breeding and upland habitat for long-term persistence. To encompass a single isolated breeding pond with a 630 m wide ring of upland habitat (i.e., 95% protection) would require at least 125 ha. In Santa Barbara County, where all known CTS breeding ponds are on privately owned land, the U.S. Fish and Wildlife Service recently determined that about 4500 ha of critical habitat is needed to protect the salamander in perpetuity (U.S. Fish and Wildlife Service 2004*b*). In Sonoma County, confirmed breeding ponds existed on several preserves at the time of the emergency listing, but the largest of these protected areas is just 73 ha, and most are much smaller (U.S. Fish and Wildlife Service 2003). Thus, particularly in Sonoma County, experimental metapopulation approaches may be the only solution to the long-term viability of the remaining populations. Although the study of amphibians in the uplands remains challenging, new approaches are emerging that promise to yield further basic insights and data essential for improved conservation planning and management (Regosin et al. 2003, Rothermel and Semlitsch 2002). The pursuit of guidelines for upland habitat protection around wetlands will benefit from additional quantification of the consequences of habitat loss and appropriate data collection to reduce the assumptions required.

ACKNOWLEDGMENTS

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APPENDIX A

A table showing raw trapping data is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-031-A1.

APPENDIX B

A photograph of the study area and some representative traps is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-031-A2.

Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities

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Abstract: *Roads are a widespread and increasing feature of most landscapes. We reviewed the scientific literature on the ecological effects of roads and found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. Roads of all kinds have seven general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotics, and increased use of areas by humans. Road construction kills sessile and slow-moving organisms, injures organisms adjacent to a road, and alters physical conditions beneath a road. Vehicle collisions affect the demography of many species, both vertebrates and invertebrates; mitigation measures to reduce roadkill have been only partly successful. Roads alter animal behavior by causing changes in home ranges, movement, reproductive success, escape response, and physiological state. Roads change soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads promote the dispersal of exotic species by altering habitats, stressing native species, and providing movement corridors. Roads also promote increased hunting, fishing, passive harassment of animals, and landscape modifications. Not all species and ecosystems are equally affected by roads, but overall the presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems. More experimental research is needed to complement post-hoc correlative studies. Our review underscores the importance to conservation of avoiding construction of new roads in roadless or sparsely roaded areas and of removal or restoration of existing roads to benefit both terrestrial and aquatic biota.*

Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas

Resumen: *Las carreteras son una característica predominante y en incremento de la mayoría de los paisajes. Revisamos la literatura científica sobre los efectos ecológicos de las carreteras y encontramos sustento para la conclusión general de que las carreteras están asociadas con efectos negativos en la integridad biótica tanto de ecosistemas terrestres como acuáticos. Las carreteras de cualquier tipo ocasionan siete efectos generales: mortalidad ocasionada por la construcción de la carretera; mortalidad debida a la colisión con vehículos; modificaciones en la conducta animal; alteración del ambiente físico; alteración del ambiente químico; dispersión de especies exóticas e incremento en el uso de áreas por humanos. La construcción de carreteras elimina a organismos sésiles y a organismos de lento movimiento, lesiona a organismos adyacentes a la carretera y altera las condiciones físicas debajo ella misma. Las colisiones con vehículos afectan la demografía de muchas especies tanto de vertebrados como invertebrados; las medidas de mitigación para reducir la pérdida de animales por colisiones con vehículos han sido exitosas solo de manera parcial. Las carreteras alteran la conducta animal al ocasionar cambios en el rango de hogar, movimientos, éxito reproductivo, respuesta de escape y estado fisiológico. Las carreteras cambian la densidad del suelo, temperatura, contenido de agua en el suelo, niveles de luz, polvo, aguas superficiales, patrones de escurrimiento y sedimentación, además de agregar metales pesados (especialmente plomo), sales, moléculas orgánicas, ozono y mutrientes a los ambientes que atraviesan. Las carreteras promueven la dispersión de especies exóticas al alterar los hábi-*

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tats, al estresar a las especies nativas y proveer corredores para movimiento. Las carreteras también promueven el incremento de la caza y la pesca, el hostigamiento pasivo de animales y modificaciones del paisaje. No todas las especies ni todos los ecosistemas son afectados por las carreteras de igual forma, pero en general la presencia de carreteras está altamente correlacionada con cambios en la composición de especies, los tamaños poblacionales y los procesos hidrológicos y geomorfológicos que afectan a la estructura de sistemas acuáticos y reparios. Se necesita más investigación experimental para complementar estudios correlativos post-hoc. Nuestra revisión hace énfasis en que en trabajos de conservación es importante evitar la construcción de nuevas carreteras en áreas carentes de ellas o en áreas con pocas carreteras, además de remover o restaurar carreteras existentes con la finalidad de beneficiar tanto a la biota acuática como la terrestre.

Introduction

Among the most widespread forms of modification of the natural landscape during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of populations and the overall health of ecosystems, it is important that we understand the scope of the ecological effects of roads of all types, especially important as conservation biologists are asked to participate in the development and implementation of strategies to protect or restore elements of biological diversity and integrity.

Roads of all kinds affect terrestrial and aquatic ecosystems in seven general ways: (1) increased mortality from road construction, (2) increased mortality from collision with vehicles, (3) modification of animal behavior, (4) alteration of the physical environment, (5) alteration of the chemical environment, (6) spread of exotic species, and (7) increased alteration and use of habitats by humans. These general effects overlap somewhat. In some cases animals modify their behavior and avoid roads because of concentrated human activity along roads. Roads may facilitate the spread of invasive species by disrupting native communities and changing physical habitats. Roads may fragment populations through roadkill and road avoidance. Despite the difficulty of categorizing discretely the causal basis in every example, these seven categories provide a useful framework for assessing what is known and unknown about the ecological effects of roads.

Selective road removal, relocation, or remediation may provide ecological benefits in certain situations. Yet, although roads are commonly identified as important correlates or indicators of loss of ecological health (e.g., Noss & Cooperrider 1994), the specific mechanisms by which biota are affected are often complicated or uncertain. Therefore, mitigation or treatment of specific effects, whether during road design or in post-construction remediation, can be costly and fraught with uncertainty.

Mortality from Road Construction

Road construction kills any sessile or slow-moving organism in the path of the road. The extent to which road construction contributes to direct mortality has not been estimated as has direct mortality from other forms of habitat destruction (e.g., Petranka et al. 1993). The fact that road construction kills individual organisms is obvious, however. The magnitude of such construction is not trivial; the 13,107,812 km of road lanes of all types in the conterminous United States, with an average width of 3.65 m per lane, have destroyed at least 4,784,351 ha of land and water bodies that formerly supported plants, animals, and other organisms (U.S. Department of Transportation 1996). The actual number is likely much higher because this estimate does not include shoulder pavement and land peripheral to the roadbed that is cleared during construction.

Construction may physically injure organisms adjacent to the path of construction. Roads built for extraction of white fir result in damage to trees that is visible up to 30 m from the road (Trafela 1987). Such damage contributes to a decline of up to 30% in forest productivity per rotation, due in part to a decline in growth of damaged trees. Construction also alters the physical conditions of the soil underneath and adjacent to the road. Riley (1984) showed that road construction increases soil compaction up to 200 times relative to undisturbed sites. These changes likely decrease the survival of soil biota that are not killed directly. Direct transfer of sediment and other material to streams and other water bodies at road crossings is an inevitable consequence of road construction (Richardson et al. 1975; Seyedbagheri 1996). High concentrations of suspended sediment may directly kill aquatic organisms and impair aquatic productivity (Newcombe & Jensen 1996).

Mortality from Collision with Vehicles

Mortality of animals from collision with vehicles is well documented. Many reviews of the taxonomic breadth of the victims of vehicle collision have been published (e.g., Groot Bruinderink & Hazebroek 1996). Few if any terrestrial species of animal are immune. Large mammals ranging in size from moose (*Alces alces*) to armadillos (*Dasypus novemcinctus*) are the best-documented roadkills, probably due to interest in their demography and to their size (Bellis & Graves 1971; Puglisi et al. 1974;

Reilly & Green 1974; Holroyd 1979; Wilkins & Schmidly 1980; Bashore et al. 1985; Davies et al. 1987; Bangs et al. 1989; Palomares & Delibes 1992).

Roadkill among many other species includes American Kestrels (*Falco sparverius*; Varland et al. 1993), Barn Owls (*Tyto alba*; Newton et al. 1991), Northern Saw-whet Owls and Eastern Screech Owls (*Aegolius acadicus and Otis asio*; Loos & Kerlinger 1993), tropical forest birds (Novelli et al. 1988), garter snakes (Dalrymple & Reichenbach 1984), granivorous birds (Dhindsa et al. 1988), American crocodile (*Crocodylus acutus*; Kushlan 1988), green iguanas (*Iguana iguana*; Rodda 1990), desert snakes (Rosen & Lowe 1994), toads (van Gelder 1973), plus a wide range of invertebrates, especially insects (H. C. Seibert & Conover 1991).

This form of mortality can have substantial effects on a population's demography. Vehicle collision is the primary cause of death for moose in the Kenai National Wildlife Refuge in Alaska (Bangs et al. 1989) and for Barn Owls in the United Kingdom (Newton et al. 1991), the second highest form of mortality for Iberian lynx (*Felis pardina*) in southwestern Spain (after hunting; Ferreras et al. 1992), and the third highest form for white-tailed deer (*Odocoileus virginianus*) in New York (Sarbello & Jackson 1985) and wolves (*Canis lupus*) in Minnesota (Fuller 1989). Roadkill is a limiting factor in the recovery of the endangered American crocodile in southern Florida (Kushlan 1988) and is contributing to the endangerment of the prairie garter snake (*Thamnophis radix radix*; Dalrymple & Reichenbach 1984). Roadkill is often nonspecific with respect to age, sex, and condition of the individual animal (e.g., Bangs et al. 1989).

Amphibians may be especially vulnerable to roadkill because their life histories often involve migration between wetland and upland habitats, and individuals are inconspicuous and sometimes slow-moving. Roads can be demographic barriers that cause habitat and population fragmentation (Joly & Morand 1997). In the Netherlands, for example, roads with high traffic volume negatively affect occupancy of ponds by moor frogs (*Rana arvilis*; Vos & Chardon 1998). In Ontario, the local abundance of toads and frogs is inversely related to traffic density on adjacent roads, but the incidence of roadkill relative to abundance is higher on highly trafficked roads (Fahrig et al. 1995). Thus, even though populations in high-traffic areas have apparently already been depressed from cumulative road mortality, they continue to suffer higher proportionate rates of roadkill.

Mitigation measures have been employed in different locations with varying degrees of success (e.g., Yanes et al. 1995). For example, underpasses on Interstate 75 have been only partially successful in reducing roadkill of Florida panthers (*Felis concolor coryi*; Foster & Humphrey 1991). Despite mitigation efforts, roads are likely to be a persistent source of mortality for many species. In general, mortality increases with traffic volume (e.g., Rosen & Lowe 1994; Fahrig et al. 1995). Some species are less likely to be killed on high-speed roads than on medium-speed roads because the former usually have vegetation cleared back further from the road's shoulder, creating less attractive habitat and greater visibility for both animals and drivers. Other species, however, are attracted to the modified habitat alongside and in the meridians of high-speed roads (Cowardin et al. 1985), making them population sinks.

Modification of Animal Behavior

The presence of a road may modify an animal's behavior either positively or negatively. This can occur through five mechanisms: home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological state.

Black bears (*Ursus americanus*) in North Carolina shift their home ranges away from areas with high road densities (Brody & Pelton 1989), as do grizzly bears in the Rocky Mountains (*Ursus horribilis*; McLellan & Shackleton 1988). Elk (*Cervus elaphus*) in Montana prefer spring feeding sites away from visible roads (Grover & Thompson 1986), and both elk and mule deer (*Odocoileus hemionus*) in Colorado in winter prefer areas 200 m from roads (Rost & Bailey 1979). Wolves will not establish themselves in areas with road densities greater than a region-specific critical threshold (Jensen et al. 1986; Thurber et al. 1994), probably as a result of a relationship between road density and hunting pressure. Mountain lion (*Felis concolor*) home ranges are situated in areas with lower densities of improved dirt roads and hard-surface roads (Van Dyke et al. 1986), suggesting that either mountain lions avoid these areas or road construction tends to avoid their prime habitat. Elephants (*Loxodonta africana*) in northeastern Gabon preferentially locate in forests away from both roads and villages (Barnes et al. 1991). Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), on the other hand, preferentially establish home ranges in areas with greater road densities (Coleman & Fraser 1989), probably because of the increase in carrion.

Roads may also alter patterns of animal movement. Caribou (*Rangifer tarandus*) in Alaska preferentially travel along cleared winter roads that lead in the direction of their migration (Banfield 1974). Although the road may enhance caribou movement, it results in increased mortality from vehicle collisions and predation by wolves. After calving, female caribou with calves avoid roads (Klein 1991). The land snail *Arianta arbustorum* avoids crossing roads, even those that are unpaved and as narrow as 3 m (Baur & Baur 1990), and extend their movements along road verges. Reluctance to cross roads is also seen in white-footed mice (*Peromyscus* *leucopus*; Merriam et al. 1989) and many other rodent species (Oxley et al. 1974), even when the road is narrow and covered only with gravel. Cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*) avoid roads as narrow as 3 m (Swihart & Slade 1984). Black bear almost never cross interstate highways in North Carolina (Brody & Pelton 1989) but will cross roads with less traffic volume. Roads act as barriers to gene flow in the common frog (*Rana temporaria*) in Germany, leading to significant genetic differentiation among populations (Reh & Seitz 1990). Other animals that show a reluctance to cross roads include pronghorn antelope (*Antilocapra americana*; Bruns 1977) and mountain lions (Van Dyke et al. 1986).

Some animals seem unaffected by the presence of roads, at least at some spatial scales. Based on a study of 20 wolverines, Hornocker and Hash (1981) concluded that the sizes and shapes of home ranges of wolverines where they are still found in northwestern Montana are independent of the presence of highways. Similarly, the presence of highways explained none of the allelic differentiation among populations of brown hares (*Lepus europaeus*) in Austria (Hartl et al. 1989).

Roads may affect an animal's reproductive success. Productivity of Bald Eagles (*Haliaeetus leucocephalus*) in Oregon (Anthony & Isaacs 1989) and Illinois (Paruk 1987) declines with proximity to roads, and they preferentially nest away from roads. Golden Eagles (*Aquila chrysaetos*) also prefer to nest away from human disturbances, including roads (Fernandez 1993). The reduced nesting success of eagles in proximity to roads may be more a function of the presence of humans than of the road itself; nesting failure by Golden Eagles in Scotland correlates with how easy it is for people to approach but not with proximity to roads themselves (Watson and Dennis 1992). Relative to habitat availability, Sandhill Cranes (*Grus canadensis*) avoid nesting near paved and gravel public roads (Norling et al. 1992); they do not avoid private roads with low-traffic volume (Norling et al. 1992) and can habituate to roads over time (Dwyer & Tanner 1992). Mallards (*Anas platyrhynchos*) in North Dakota, on the other hand, prefer road rights-of-way for nesting (Cowardin et al. 1985), perhaps because of a lower level of predation there.

Roads can also alter escape responses. Pink-footed Geese (*Anser brachyrhynchus*) in Denmark are more easily disturbed when feeding near roads, flying away when humans approach within 500 m, a greater distance than when feeding in areas without roads (Madsen 1985). Both the Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) are more easily disturbed near roads and have disturbance distances of 480–2000 m depending on traffic volume (Van der Zande et al. 1980). Less well known is the effect of roads and vehicles on an animal's physiological state. MacArthur et al. (1979) showed that heart rate and therefore metabolic rate and energy expenditure of female bighorn sheep (*Ovis canadensis*) increase near a road independent of any use of the road. Roads contribute to fragmentation of populations through both increased mortality and modification of behavior that makes animals less likely to cross roads. Fragmentation may be accelerated by roads when spatially critical habitat patches (e.g., "stepping stones") become unoccupied as a result of increased local mortality or reduced recolonization.

Disruption of the Physical Environment

A road transforms the physical conditions on and adjacent to it, creating edge effects with consequences that extend beyond the time of the road's construction. At least eight physical characteristics of the environment are altered by roads: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of runoff, and sedimentation.

Long-term use of roads leads to soil compaction that persists even after use is discontinued. Soil density on closed forest roads continues to increase, particularly during winter months (Helvey & Kochenderfer 1990). Increased soil density can persist for decades: logging skid trails in northeastern California over 40 years old have soil that is 20% more compacted than soil in nearby areas that have not been used as trails (Vora 1988).

The reduction of water vapor transport on a road with a hard surface increases the surface temperature of a road compared to bare soil, an effect that increases with thickness of the road surface (Asaeda & Ca 1993). The heat stored on the road surface is released into the atmosphere at night, creating heat islands around roads. Animals respond to these heat islands: small birds (Whitford 1985) and snakes, for example, preferentially aggregate on or near warm roads, increasing their risk of being hit by cars and, at their northern range limits, reducing energetic demands for breeding.

During the dry season, the moisture content of soils under roads declines even if the roads are not in use (Helvey & Kochenderfer 1990), probably in response to changes in soil porosity. Roads through forests also increase the amount of light incident on the forest floor. The amount of increase depends on how much of the original canopy and lower strata remain, which depends in turn on the width of the road and roadside verge. The increase in light increases the density of species that preferentially grow where light levels are high, such as early-successional, disturbance-adapted species such as the North American orchid *Isotria medeoloides* (Mehrhoff 1989).

Road traffic mobilizes and spreads dust, which when settled on plants can block photosynthesis, respiration, and transpiration and can cause physical injuries to plants (Farmer 1993). These effects are sufficient to alter plant community structure, especially in communities dominated by lichens and mosses (Auerbach et al. 1997). Although most sediment enters water bodies through overland flow or mass failure, dust from highly trafficked roads can serve as a source of fine sediments, nutrients, and contaminants to aquatic ecosystems (Gjessing et al. 1984).

Roads and bridges can alter the development of shorelines, stream channels, floodplains, and wetlands. Because of the energy associated with moving water, physical effects often propagate long distances from the site of a direct road incursion (Richardson et al. 1975). Alteration of hydrodynamics and sediment deposition can result in changes in channels or shorelines many kilometers away, both down- and up-gradient of the road crossing. The nature of such responses to channel and shoreline alteration is not always predictable; it may depend on the sequence of flood and sedimentation events after the alteration is made. Roads on floodplains can redirect water, sediment, and nutrients between streams and wetlands and their riparian ecosystems, to the detriment of water quality and ecosystem health. Roads are among the many human endeavors that impair natural habitat development and woody debris dynamics in forested floodplain rivers (Piégay & Landon 1997).

Road crossings commonly act as barriers to the movement of fishes and other aquatic animals (Furniss et al. 1991). Although many headwater populations of salmonid fishes are naturally migratory, they often persist today as fragmented headwater isolates, largely because of migration barriers created by road crossings and other human developments that fail to provide for fish passage (Kershner et al. 1997; Rieman et al. 1997). Salmonids and other riverine fishes actively move into seasonal floodplain wetlands and small valley-floor tributaries to escape the stresses of main-channel flood flows (Copp 1989), but valley-bottom roads can destroy or block access to these seasonally important habitats (Brown & Hartman 1988). Persistent barriers may encourage local selection for behaviors that do not include natural migration patterns, potentially reducing both the distribution and productivity of a population.

Roads directly change the hydrology of slopes and stream channels, resulting in alteration of surface-water habitats that are often detrimental to native biota. Roads intercept shallow groundwater flow paths, diverting the water along the roadway and routing it efficiently to surface-water systems at stream crossings (Megahan 1972; Wemple et al. 1996). This can cause or contribute to changes in the timing and routing of runoff (King & Tennyson 1984; Jones & Grant 1996; Ziemer & Lisle 1998), the effects of which may be more evident in smaller streams than in larger rivers (Jones & Grant 1996). Hydrologic effects are likely to persist for as long as the road remains a physical feature altering flow routing—often long after abandonment and revegetation of the road surface. By altering surface or subsurface flow, roads can destroy and create wetland habitats.

Changes in the routing of shallow groundwater and surface flow may cause unusually high concentrations of runoff on hillslopes that can trigger erosion through channel downcutting, new gully or channel head initiation, or slumping and debris flows (Megahan 1972; Richardson et al. 1975; Wemple et al. 1996; Seyedbagheri 1996). Once such processes occur, they can adversely affect fishes and other biota far downstream for long periods of time (Hagans et al. 1986; Hicks et al. 1991). Roads have been responsible for the majority of hillslope failures and gully erosion in most steep, forested landscapes subject to logging activity (Furniss et al. 1991; Hagans et al. 1986). Because most of these more catastrophic responses are triggered by the response of roads during infrequent, intense storm events, lag times of many years or decades pass before the full effects of road construction are realized.

Chronic effects also occur, however. The surfaces of unpaved roads can route fine sediments to streams, lakes, and wetlands, increasing the turbidity of the waters (Reid & Dunne 1984), reducing productivity and survival or growth of fishes (Newcombe & Jensen 1996), and otherwise impairing fishing (Buck 1956). Existing problem roads can be remediated to reduce future erosion potential (e.g., Weaver et al. 1987; Harr & Nichols 1993). The consequences of past sediment delivery are long-lasting and cumulative, however, and cannot be effectively mitigated (Hagans et al. 1986).

Alteration of the Chemical Environment

More has been written about the effects of roads on the chemical environment than on all other effects combined. Maintenance and use of roads contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone, and nutrients.

A variety of heavy metals derived from gasoline additives and road deicing salts are put into the roadside environment. The most widely documented is lead, but others include aluminum, iron, cadmium, copper, manganese, titanium, nickel, zinc, and boron (Garcia-Miragaya et al. 1981; Clift et al. 1983; Gjessing et al. 1984; Oberts 1986; Araratyan & Zakharyan 1988).

Heavy metal contamination exhibits five patterns. First, the amount of contamination is related to vehicular traffic (Goldsmith et al. 1976; Dale & Freedman 1982; Leharne et al. 1992). Second, contamination of soils, plants, and animals decreases exponentially away from the road (Quarles et al. 1974; Dale & Freedman 1982). Most studies indicate that contamination declines within 20 m but that elevated levels of heavy metals often occur 200 m or more from the road. The pattern of decline is influenced by prevailing wind patterns (Haqus & Hameed 1986). Once metals reach aquatic environments, transport rates and distances increase substantially (Gjessing et al. 1984).

Third, heavy metals can be localized in the soil, either close to the surface if downward transport has not occurred (Indu & Choudhri 1991) or deep below the surface if pollution levels in the past exceeded those in the present (Byrd et al. 1983). Transportation and localization is largely affected by the physical properties of the soil (Yassoglou et al. 1987). Metals and other persistent chemicals fixed to soils may become remobilized once they are inundated or transported to freshwater environments by wind, water, or gravity.

Fourth, heavy metals accumulate in the tissues of plants (Datta & Ghosh 1985; Beslaneev & Kuchmazokova 1991) and animals (Collins 1984; Birdsall et al. 1986; Grue et al. 1986). As with soil, contamination of plant tissue occurs up to at least 200 m from a road and is greatest for individuals along roads with high traffic volume.

Fifth, heavy metal concentrations in soil decline over time where use of leaded gasoline has been stopped and surface-water flow carries the metal ions away (Byrd et al. 1983; Tong 1990). After they leave the terrestrial environment, however, the mobilized metals may cause additional harm to aquatic biota. Also, some of the processes of metal demobilization may be reversed rapidly if environmental conditions, such as acidity of the soils, sediments, or water, change (Nelson et al. 1991).

Deicing salts, particularly NaCl but also $CaCl_2$, KCl, and $MgCl_2$, contribute ions to the soil, altering pH and the soil's chemical composition (Bogemans et al. 1989). As with lead, discontinuation of the use of deicing salts allows plants damaged by salt stress to recover (Leh 1990). The effects on aquatic biota of temporary surges of salt that often accompany runoff from roads to surface and groundwaters have received little study. Deicing salts on roadways elevate chloride and sodium concentrations in streams (Molles & Gosz 1980; Hoffman et al. 1981; Peters & Turk 1981; Mattson & Godfrey 1994) and in bogs, where road salts can alter patterns of succession in aquatic vegetation (Wilcox 1986). Accumulation of salts from chemicals used for road deicing or dust control can disrupt natural stratification patterns and thus potentially upset the ecological dynamics of meromictic lakes (Hoffman et al. 1981; Kjensmo 1997).

Organic pollutants such as dioxins and polychlorinated biphenyls are present in higher concentrations along roads (Benfenati et al. 1992). Hydrocarbons may accumulate in aquatic ecosystems near roads (Gjessing et al. 1984). In one stream along a British highway, numerous contaminants were present at elevated levels in the water column and sediments, including copper, zinc, and various hydrocarbons, but polycyclic aromatic hydrocarbons associated with stream sediments accounted for most of the observed toxicity to aquatic amphipods (Maltby et al. 1995). Comparatively little research has focused on the questions of the fate and effects of the organic chemicals associated with roads.

Vehicles produce ozone, which increases the concentration of this harmful molecule in the air, especially in areas where vehicle exhaust accumulates (Flueckiger et al. 1984). Roads are also especially important vectors of nutrients and other materials to aquatic ecosystems, because the buffering role normally played by riparian vegetation (Correll et al. 1992) is circumvented through direct runoff of materials in water and sediment where roads abut or cross water bodies. Water moving on and alongside roadways can be charged with high levels of dissolved nitrogen in various forms, and sediment brings a phosphorus subsidy when it reaches surface waters. Road deicing salts are an additional source of phosphorus (Oberts 1986). The degree to which roads directly contribute to eutrophication problems in aquatic ecosystems has been little investigated. Because roads deliver nutrients that originate in the contributing slope area, the nutrient burden is probably largely controlled by surrounding vegetation and land use. An increased density of road crossings of water bodies can be expected to increase delivery of nutrients.

The alteration of the chemical environment by roads results in a number of consequences for living organisms. First, in the terrestrial environment the chemical composition of some woody plants changes in response to pollution. These changes include increased concentrations of chemicals produced by plants, such as terpenoids, which help them resist the toxic effects of pollution (Akimov et al. 1989) and salts (Bogemans et al. 1989), and decreased production of other chemicals, such as soluble protein and chlorophyll *a*, which are necessary for plant function (Banerjee et al. 1983).

Second, organisms may be killed or otherwise displaced as a result of chemical exposure. Virtually all measures of soil biotic diversity and function decline in contaminated soil, including abundance, number of species, species composition, index of species diversity, index of equability, and bulk soil respiration (Muskett & Jones 1981; Guntner & Wilke 1983; Krzysztofiak 1991).

Third, the growth (Petersen et al. 1982) and overall physical health (Flueckiger et al. 1984; Moritz & Breitenstein 1985) of many plants is depressed, even to the point of death (Fleck et al. 1988). The sensitivity of plants to pollutants may change during development; for example, seedlings are more sensitive to salt than are adults (Liem et al. 1984), which influences juvenile recruitment. Pollutants may affect plant health by damaging fine roots, mycorrhizae (Majdi & Persson 1989), and leaves (Simini & Leone 1986) and by changing salt concentrations in plant tissues (Northover 1987). Secondary effects on plant health include decreased resistance to pathogens (Northover 1987), causing further declines. In aquatic environments, plant (and animal) assemblages may change due to direct and indirect responses to nutrient increases and due to growth suppression or mortality caused by other chemicals introduced by roads.

Fourth, plants (Graham & Kalman 1974; Nasralla & Ali 1985; Dickinson et al. 1987; Guttormsen 1993) and animals (Robel et al. 1981; Collins 1984; Harrison & Dyer 1984; Krzysztofiak 1991; Marino et al. 1992), including those cultivated or raised for agriculture, may accumulate toxins at levels that pose health hazards, including those for humans that consume exposed organisms (Jarosz 1994).

Fifth, increased concentrations near roadsides of some pollutants, particularly salt, attract large mammals, putting them more at risk of being killed by vehicles (Fraser & Thomas 1982). Spills of edible products from trucks and trains also attract wildlife to roadsides. Finally, evolutionary processes may be affected through altered selection pressures that result in local differentiation of populations of both plants (Kiang 1982) and animals (Minoranskii & Kuzina 1984).

Spread of Exotic Species

Roads provide dispersal of exotic species via three mechanisms: providing habitat by altering conditions, making invasion more likely by stressing or removing native species, and allowing easier movement by wild or human vectors. It is often difficult to distinguish among these factors. Soils modified during road construction can facilitate the spread of exotic plants along roadsides (Greenberg et al. 1997). Some exotic plants establish themselves preferentially along roadsides and in other disturbed habitats (Wester & Juvik 1983; Henderson & Wells 1986; Tyser & Worley 1992; Wein et al. 1992). The spread of exotic diseases (Dawson & Weste 1985; Gad et al. 1986) and insects (Pantaleoni 1989; Schedl 1991) is facilitated by increased density of roads and traffic volume. Road construction that alters the canopy structure of forests promotes invasion by exotic understory plants, which affects animal communities (Gaddy & Kohlsaat 1987). Some roadside verges have been invaded by maritime plants because of their ability to tolerate saline soil (Scott & Davison 1982). Feral fruit trees are found preferentially along roadsides, and some populations are maintained solely by seeds in fruit waste thrown from vehicles (Smith 1986).

Exotic species are sometimes introduced along roadsides for the purpose of erosion control (Niordson 1989). Native species are now more widely preferred for this purpose, but Dunlap (1987) argues that in some cases the need for rapid establishment of plant cover requires the use of exotic species.

In another form of deliberate introduction, roads provide easy access to streams and lakes for fishery managers to stock nonnative hatchery fish (Lee et al. 1997), which adversely affect native biota and disrupt aquatic ecosystems in many ways (Allan & Flecker 1993). Unsanctioned, illegal, and unintentional introductions of fishes, mollusks, plants, and other aquatic organisms also occur frequently (Allan & Flecker 1993), and they are facilitated by public road access to water bodies.

The dispersal of a biological agent such as a pathogen along a roadway can affect both terrestrial and aquatic ecosystems far from the road. In northern California and southwest Oregon, for example, vehicle traffic and roadway drainage along logging and mining roads during the wet season disperse spores of an exotic root disease (*Phythoptera lateralis*) that infects the endemic Port Orford cedar (*Chamaecyparis lawsoniana*; Zobel et al. 1985). Transfer of the water-borne spores from forest roads into headwater stream crossings can result in the infection and nearly complete mortality of Port Orford cedars along a much larger network of downstream channel margins and floodplains, even deep inside otherwise roadless areas. The progressive loss of this important conifer species from riparian ecosystems may engender substantial long-term consequences for the integrity of stream biota, including endangered salmon species, for which the Port Orford cedar provides shade, large and long-lasting coarse woody debris, and stabilization of channels and floodplains.

Changes in Human Use of Land and Water

Roads facilitate increased use of an area by humans, who themselves often cause diverse and persistent ecological effects. New roads increase ease of access by humans into formerly remote areas. Perhaps more important, roads often increase the efficiency with which natural resources can be exported. At least three different kinds of human use of the landscape, made increasingly possible by roads, can have major ecological effects: hunting and fishing, recreation, and changes in use of land and water.

Roads open up areas to increased poaching and legal hunting. Hunting reduces population sizes of many game species, including brown bear (*Ursus arctos*; Camarra & Parde 1990), Iberian lynx (Ferreras et al. 1992), wolves (Fuller 1989), black bear (Manville 1983), and Egyptian mongooses (*Herpestes ichneumon*; Palomares & Delibes 1992). Roads also increase both legal and illegal fishing in streams and lakes. Native fish populations in previously inaccessible areas are often vulnerable to even small increases in fishing effort. Increased fishing then often gives rise to public demand for fish stocking as an attempt to artificially compensate for the effects of unsustainable harvest, at the further expense of native fishes and other species (e.g., Gresswell & Varley 1988).

Visitors increase when roads make areas more accessible, leading to increased passive harassment of animals—such as elk on Mount St. Helens in Washington State (Czech 1991) and the Oregon Coast Range (Witmer & DeCalesta 1985), brown bear in Europe (Del Campo et al. 1990), and mountain goats (*Oreamnos americanus*) in Montana (Pedevillano & Wright 1987)—and damage to plant communities (Matlack 1993).

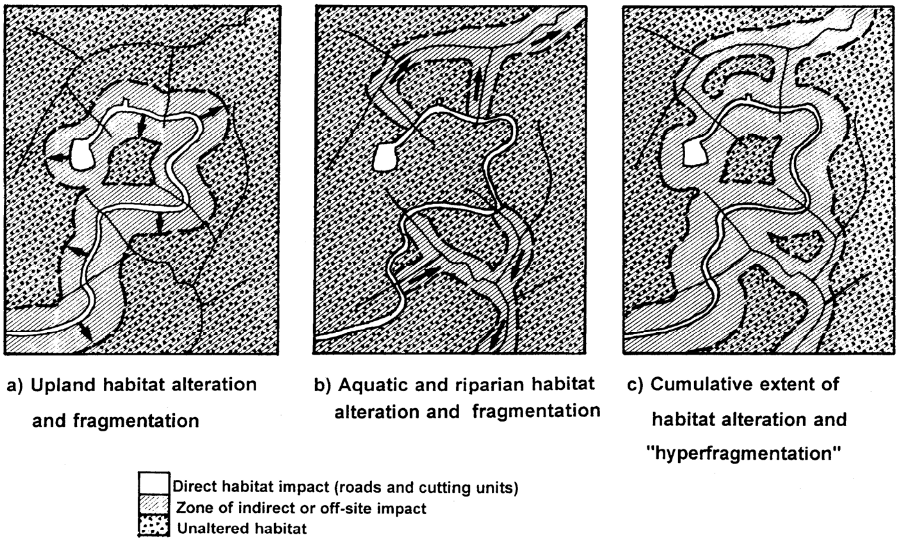
Roads are often built into areas to promote logging, agriculture, mining, and development of homes or industrial or commercial projects. Such changes in land cover and land and water use result in major and persistent adverse effects on the native flora and fauna of terrestrial (Van Dyke et al. 1986; Karnefelt & Mattsson 1989; P. Seibert 1993) and freshwater ecosystems (Schlosser 1991; Allan & Flecker 1993; Roth et al. 1996).

Numerous studies have demonstrated declines in stream health associated with roads. Because the nature and extent of land use within a region tend to be highly correlated with road networks, however, it is often difficult or impossible to separate the direct ecological effects of roads from those of the accompanying land-use activities. For example, Eaglin and Hubert (1993) reported that trout biomass and streambed habitat quality in Wyoming streams declined in relation to the number of road crossings and to the proportion of area logged in the contributing catchment. Findlay and Houlahan (1997) found that herptile species diversity in wetlands declined in relation to the density of roads within 2 km of the perimeter. Among streams in the Pacific Northwest, the status or abundance of bull trout populations has been inversely correlated to road density (Rieman et al. 1997; Baxter et al. 1999); these studies used roads as the best available general proxy of cumulative effects associated with land use and human access. On the other hand, some studies (e.g., Roth et al. 1996) have demonstrated correlations of stream biotic integrity with land-use patterns across large catchments but did not investigate the specific roles that roads might play in mediating the causes and effects.

It appears that roads can serve as useful indicators of the magnitude of land-use changes, but it remains unclear to what degree the associated ecological responses result directly from roads themselves. If roads are largely responsible, effects could be ameliorated through altered road design, placement, remediation, or road removal. Strong interactions between roads and land use are likely, however. Forest roads in Idaho, for example, are less prone to erosion when the surrounding landscape remains in natural forest cover (Seyedbagheri 1996).

Discussion and Conclusions

Roads have diverse and systemic effects on many aspects of terrestrial and aquatic ecosystems. The ecological effects of roads can resonate substantial distances from the road in terrestrial ecosystems, creating habitat fragmentation and facilitating ensuing fragmentation through support of human exploitative activities (Fig. 1a). Habitat deterioration is not widely appreciated as an aspect of ecological fragmentation in aquatic ecosystems. At the scale of an extensive landscape or stream network, however, roads produce a pattern of aquatic habitat loss that differs from the terrestrial pattern yet nevertheless results in the ecological fragmentation of aquatic ecosystems (Fig. 1b). We coin the term *hyperfragmentation* to describe the multidimensional view of ecological fragmentation and habitat loss that emerges when the consequences of roads or any habitat alteration for terrestrial and aquatic ecosystems are considered simultaneously (Fig. 1c). Hyperfragmentation is the result of a spatial footprint of ecological effect that propagates across the landscape differently in freshwater and


a) Upland habitat alteration and fragmentation

b) Aquatic and riparian habitat alteration and fragmentation

c) Cumulative extent of habitat alteration and "hyperfragmentation"

Figure 1. Spatial pattern of direct and indirect habitat alteration caused by human disturbance in a forested watershed: (a) classical forest edge effects contributing to terrestrial habitat fragmentation, (b) downstream-propagating hydrologic and biotic effects leading to large-scale fragmentation of freshwater habitats and populations, (c) combined terrestrial-aquatic view of landscape alteration that we term hyperfragmentation *because it considers multiple ecosystem dimensions on the same landscape. Arrows indicate predominant spatial vector of effects.*

aquatic ecosystems than in terrestrial systems. Even where only a small percentage of the land's surface is directly occupied by roads, few corners of the landscape remain untouched by their off-site ecological effects. The breadth of these effects cannot be appreciated unless one takes a broadly transdisciplinary view of ecosystems and biological communities.

Road design, management, and restoration need to be more carefully tailored to address the full range of ecological processes and terrestrial and aquatic species that may be affected. Deliberate monitoring is necessary to ensure that projects have robust ecological benefits and minimal adverse effects and that they are cost-efficient relative to their actual benefits (e.g., Weaver et al. 1987). Of course, such assessments require time and money that are usually unavailable. Most funds used to remediate problem roads are earmarked for actual field operations and are not available to support such assessment and monitoring. Few of the experts building roads or "restoring" them are trained to recognize and address the full spectrum of ecological issues that we have identified. Moreover, by their nature roads have systemic ecological effects that, even if recognized, cannot be overcome.

If a broad view of the ecological effects of roads reveals a multiplicity of effects, it also suggests that it is unlikely that the consequences of roads will ever be completely mitigated or remediated. Thus, it is critical to retain remaining roadless or near-roadless portions of the landscape in their natural state. Because of the increasing rarity of roadless areas, especially roadless watersheds, conservation efforts cannot rely entirely on protection of existing natural areas. But neither can conservation efforts depend entirely on tenuous and unexamined assumptions about the capability of site- and species-specific mitigation and remediation measures to reduce the ecological consequences of existing and proposed roads.

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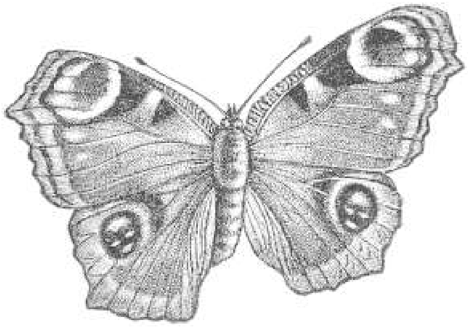

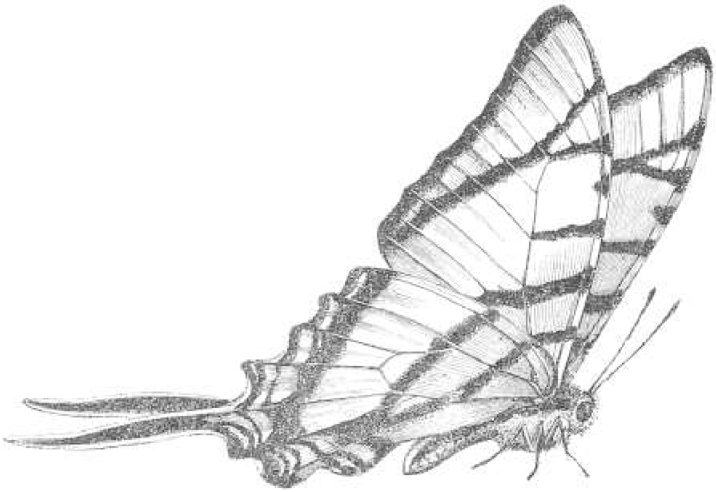

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Guest Editorial, part of a Special Feature on Effects of Roads and Traffic on Wildlife Populations and Landscape Function

Effects of Roads and Traffic on Wildlife Populations and Landscape Function: Road Ecology is Moving toward Larger Scales

Rodney van der Ree [1], *Jochen A. G. Jaeger* [2], *Edgar A. van der Grift* [3], *and Anthony P. Clevenger* [4]

ABSTRACT. Road ecology has developed into a significant branch of ecology with steady growth in the number of refereed journal articles, books, conferences, symposia, and “best practice” guidelines being produced each year. The main objective of this special issue of *Ecology and Society* is to highlight the need for studies that document the population, community, and ecosystem-level effects of roads and traffic by publishing studies that document these effects. It became apparent when compiling this special issue that there is a paucity of studies that explicitly examined higher order effects of roads and traffic. No papers on landscape function or ecosystem-level effects were submitted, despite being highlighted as a priority for publication. The 17 papers in this issue, from Australia, Canada, the Netherlands, and USA, all deal to some extent with either population or community-level effects of roads and traffic. Nevertheless, many higher order effects remain unquantified, and must become the focus of future studies because the complexity and interactions among the effects of roads and traffic are large and potentially unexpected. An analysis of these complex interrelations requires systematic research, and it is necessary to further establish collaborative links between ecologists and transportation agencies. Many road agencies have “environmental sustainability” as one of their goals and the only way to achieve such goals is for them to support and foster long-term and credible scientific research. The current situation, with numerous small-scale projects being undertaken independently of each other, cannot provide the information required to quantify and mitigate the negative effects of roads and traffic on higher levels. The future of road ecology research will be best enhanced when multiple road projects in different states or countries are combined and studied as part of integrated, well-replicated research projects.

Key Words: *animal movement; animal-vehicle collisions; barrier effect; ecological threshold; gene flow; habitat fragmentation; mitigation; population viability analysis; road ecology; road-effect zone; traffic mortality; traffic noise; traffic volume; transportation planning*

INTRODUCTION

Humans are responsible for the current unprecedented rate of biodiversity loss across the globe with climate change, pollution, and the loss, fragmentation, and degradation of habitat being the major drivers of extinction (Vitousek et al. 1997). Roads and other linear infrastructure are a major cause of habitat loss, fragmentation, and degradation and are ubiquitous in most landscapes around the world. Worldwide, there are already an estimated 750 million vehicles travelling on approximately 50 million km of public road (T. Langton, *personal communication*), and the road network and traffic volumes are still increasing, particularly in eastern Europe, China, India, and Latin America.

Linear infrastructure is important for society because it provides connectivity for people. However, linear infrastructure also exerts significant negative effects on adjacent habitats, wildlife populations, communities, and ecosystems. Research about the ecological effects of roads and traffic on the natural environment began in 1925 when Dayton Stoner documented the 225 traffic-killed vertebrates from 29 species that he observed during a 632 mile trip in Iowa, USA (Stoner 1925).

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The term “road ecology” was first used in German (“Straßenökologie”) in 1981 (Ellenberg et al.), and was later translated into English by Forman et al. (2003) for their book *Road Ecology: Science and Solutions*. Since the mid 1990s, there has been a rapid increase in the number of studies, publications, and symposia, particularly from Europe, North America, and Australia. These include major national and international reports and best practice guidelines (Iuell et al. 2003, Trocmé et al. 2003, National Research Council 2005, Clevenger and Huijser 2009), regular dedicated conferences such as the biennial International Conference on Ecology and Transportation (ICOET), Infra-Eco Network of Europe (IENE), and symposia and special issues of peer-reviewed journals, e.g., *Biological Conservation* (Mader 1990), *Conservation Biology* (Hourdequin 2000), *GAIA* (Jaeger et al. 2005), and *Naturschutz and Landschaftsplanung* (Roedenbeck and Jaeger 2006).

The overall aim of road ecology research is to quantify the ecological effects of roads, with the ultimate aim of avoiding, minimizing, and compensating for their negative impacts on individuals, populations, communities, and ecosystems. This research has demonstrated the numerous and diverse effects of roads and traffic on plants and animals, with most studies focusing at the level of the individual animal. These effects include the loss and fragmentation of habitat, increased rates of wildlife mortality because of collision with vehicles, alterations to light, moisture and wind regimes due to the creation of edges, pollution from traffic, e.g., light, noise, and chemical, and facilitating the spread and dispersal of weeds and feral animals. Roads also affect the aesthetic and recreational quality of landscapes for humans (Di Giulio and Holderegger 2009). Consequently, roads have been described as the single most destructive element in the process of habitat fragmentation (Noss 1993) and their ecological effects are considered “the sleeping giant of biological conservation” (Forman 2002:viii).

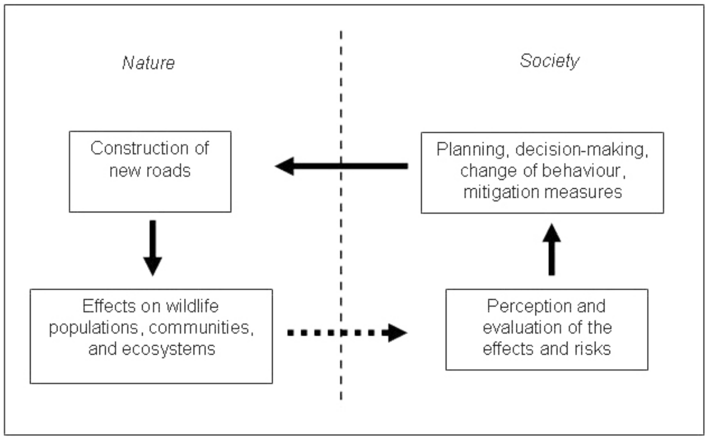
Understanding the impacts of roads and traffic at higher levels is necessary for a number of good reasons. Most governments have agreed that conservation of biodiversity is important and therefore road agencies must endeavor to ensure that they are contributing to achieving this goal. Counting the number of dead animals on the side of the road or measuring the size of the ecological road-effect zone will not, by itself, inform whether roads and vehicles are endangering the existence of populations or species. The important parameter must be the long-term viability of adjacent populations, and this requires data on the sizes of the populations, vital rates, and level of connectivity among subpopulations. Similarly, a critical question when evaluating mitigation works is the extent to which populations have become more viable, and whether they are now sufficiently viable, not simply how many animals pass through an underpass (van der Ree et al. 2007). The extent to which the results from the numerous local studies can be extrapolated to larger spatial and temporal scales is unknown. Therefore, an important next step is to evaluate how the density and configuration of entire road networks affect the functional relationships within and among ecosystems at the landscape scale. Answers to this question will inform cumulative environmental assessments and transportation planning (Roedenbeck et al. 2007). Roads also affect humans in a range of ways but little research on this topic has been completed (Di Giulio and Holderegger 2009).

Reducing the negative effects of roads and traffic will only be possible if more dialogue is achieved between the scientific community and the planners and political decision makers (Fig. 1). The majority of people in the world live in cities and increasingly, their encounters with wildlife involve animals that have died after collision with vehicles. Novel approaches to engage the public, and hence, governments, are required. A recent example was an award-winning exhibition in the Whyte Museum in Banff, Alberta, Canada in 2006 of images of wildlife using the now famous overpasses and underpasses in Banff National Park. A second example was a creative arts competition as part of the IENE 2010 conference for Hungarian school children to portray the conflict, and solutions, between roads and wildlife (Fig. 2).

ABOUT THIS ISSUE: THE EFFECTS OF ROADS AND TRAFFIC ON POPULATIONS, COMMUNITIES, AND ECOSYSTEMS

The two main objectives of this special issue of *Ecology and Society* were to (1) highlight the need for studies that document the population, community, and ecosystem-level effects of roads and traffic, and (2) publish studies that document

Fig. 1. Society’s ability to address the negative effects of road networks on wildlife populations and ecosystems depends on the perception of the ecological effects and risks. As the perception of the effects by society has been severely limited (as indicated by the dotted line), alternative approaches may be required that would be based on more indirect indicators of ecological risk and on the precautionary principle.



these effects. The special issue consists of 17 papers from four countries, i.e., Australia, Canada, the Netherlands, and U.S.A., that all deal to some extent with either population or community-level effects of roads and traffic. It became apparent when compiling the special issue that there is a paucity of road ecology studies that explicitly examined higher order effects of roads. No papers on landscape function or ecosystem-level effects were submitted, despite being highlighted as a priority for publication.

The special issue begins with a synthesis paper (Fahrig and Rytwinski 2009) and ends with an insight paper (Simmons et al. 2010). The synthesis is an appropriate first paper because it assesses the widely held assertion that “there are very few studies that assess the population-level effects of roads and traffic.” The assertion was found to be partly true and partly false; the authors located 79 studies that provide data on population-level effects (abundance and density) but found that in most cases, the population-level effect was ‘hidden’ in many of the papers reviewed. Nevertheless, Fahrig and Rytwinski (2009) found that overwhelmingly, roads and traffic had a negative effect on animal abundance, with negative effects outnumbering positive effects by a factor of five. The final paper in the special issue reviews some of the genetic methods used in road ecology and provides an insight into how conservation genetics can be better utilized in future studies. Simmons et al. (2010) argue that conservation genetics is a rapidly evolving field and that many of the widely perceived limitations to the use of genetics are either misconceptions or no longer apply. They conclude with strong recommendations that genetic approaches be combined with field studies to increase the inferential strength of whichever study design is adopted (sensu Roedenbeck et al. 2007).

The road-effect zone is the distance from the edge of the road over which significant ecological effects can be detected (Forman and Alexander 1998). Eigenbrod et al. (2009) quantified threshold effects of a motorway on anuran populations in Canada, and Bissonette and Rosa (2009) investigated the effects of a motorway on the composition and abundance of a small-mammal community in the deserts of Utah, USA. Eigenbrod et al. (2009) were the first to quantify the road-effect zone on the species richness and relative abundance of anurans, and found strong negative effects for four of seven species, extending 250 – 1000 m from the road edge. They conclude that although most anurans are likely to have reduced abundances near motorways, the extent and cause of this relationship will vary among species (Eigenbrod et al. 2009). In contrast, Bissonette and Rosa (2009) found that roadside vegetation in desert environments often provides

Fig. 2. Runner up of the "On Dangerous Roads" Competition organized by Varangy Akciócsoport Egyesület for the 2010 Infra-Eco Network of Europe Conference showing an overpass used by wildlife. An ongoing project in the Netherlands is studying the effectiveness of an overpass for amphibians, in combination with fences along the road. This overpass is equipped with a cascading series of small ponds fed with water pumped into the highest pond in the center of the overpass.

suitable habitat for small mammals. Only 2 of 13 species of small mammals were never captured near roads, and the remaining 11 species' numbers were either similar or more abundant near the road than further away.

Vegetation adjacent to roads often provides habitat (e.g., Bissonette and Rosa 2009), and in some landscapes, even the majority of habitat (van der Ree and Bennett 2003). Wildlife that use this habitat will experience traffic noise and may be affected by it. Anthropogenic noise has the potential to severely disrupt the communication of species by acoustic interference or masking. Three studies in this special issue investigate this effect on frogs and birds. Parris and Schneider (2008) found that the Grey Shrike-thrush (*Colluricincla harmonica*) sang at a higher frequency in areas with traffic noise than the Grey Fantail (*Rhipidura fuliginosa*) and that the probability of detecting either species declined substantially with increasing traffic noise and traffic volume. The effects of traffic noise on frogs were assessed by Parris et al. (2009) in an urban landscape in southeast Australia and by Hoskin and Goosem (2010) in tropical rainforest in northeastern Australia. One species of urban frog in and around Melbourne called at a higher pitch in traffic noise, while the second species studied may also call at a higher pitch, but more data is required to be sure (Parris et al. 2009). *Litoria rheocola* in tropical rainforest also called at a higher pitch when closer to the road, as well as calling at a higher rate when near roads (Hoskin and Goosem 2010). The abundance of some species of rainforest frogs was also lower near roads.

A significant proportion of the road ecology literature is focused on evaluating the use and effectiveness of mitigation measures that aim to restore connectivity for wildlife or reduce rates of animal-vehicle collisions. A review presented at the ICOET conference in 2007 concluded that most studies in the scientific and grey literature had focused almost exclusively on documenting rates of use of wildlife passages, and that few had explicitly evaluated the effectiveness of mitigation measures at enhancing population viability (van der Ree et al. 2007). In this special issue, five papers have addressed the topic of mitigation of road effects on wildlife in differing perspectives. Thorne et al. (2009) highlight the importance of landscape-scale planning to better integrate the needs of wildlife into regional transportation plans. Using two examples from California, USA, they show how road projects can benefit financially and ecologically when road agencies and conservation groups collaborate early in the planning stages. Approximately 1 – 2 million mammal-vehicle collisions occur annually in North America, causing in excess of 200 human fatalities and over one billion U.S. dollars in property damage each year (references in Huijser et al. 2009). Huijser et al. (2009) reviewed the effectiveness and cost of 13 measures considered effective at reducing collisions with large ungulates and found that for many sections of road, the effectiveness, measured as money saved, exceeds the costs to install the mitigation. The results of their cost-benefit model suggests that there must be many locations in North America where the mitigation measures are cost-effective, and thereby would save society money and improve road safety for humans and wildlife if implemented more often. At a smaller spatial scale, Grosman et al. (2009) combined real data on the movement of moose (*Alces alces*) with agent-based computer simulations to investigate if the removal of salt pools or their relocation from adjacent to the highway to 100 – 1500 m away from the road would result in fewer moose-vehicle collisions. Their model predicted that the removal of salt pools from near the edge of the highway would result in an almost 50% reduction in moose-vehicle collisions (Grosman et al. 2009).

The viability of populations adjacent to wildlife crossing structures is one of the fundamental measures of success of mitigation (van der Ree et al. 2007). Two papers in this special issue explicitly investigated the increase in the viability of a population of wildlife after mitigation (Taylor and Goldingay 2009, van der Ree et al. 2009). Taylor and Goldingay (2009) used population modeling to assess the viability of the Greater Glider (*Petauroides volans*) in Brisbane, a rapidly urbanizing area of Australia. They concluded that even a relatively low rate of dispersal across the road was sufficient to substantially reduce the risk of extinction of the smaller subpopulation isolated by the road. Similarly, van der Ree et al. (2009) used population viability modeling to assess the effectiveness of under-road tunnels installed in 1985 to restore connectivity for the critically endangered Mountain Pygmy-possum (*Burramys parvus*; Mansergh and Scotts 1989). They found that the tunnels reduced, but did not completely eliminate the negative effect of the road, with the density of the population affected by the road still 15% lower than a comparable undivided population nearby (van der Ree et al. 2009).

The majority of studies that assess the use of wildlife crossing structures have utilized two primary methods to detect and record wildlife passage, namely remotely triggered cameras, and/or the detection of tracks in a suitable substrate (van der Ree et al. 2007). Clevenger and Sawaya (2010) have used the suggestions of Simmons et al. (2010) and tested the feasibility of a noninvasive genetic sampling approach to identify the species as well as the sex, individual, and relatedness of different individuals using the crossing structure. The technique, if successful, would be applied at a larger scale to determine the level of genetic fragmentation and natural and anthropogenic factors influencing gene flow. They tested their approach on Black Bears (*Ursus americanus*) and Grizzly Bears (*U. arctos*) at two underpasses in Banff National Park. Hair was collected from 90% of crossing events (determined from cameras), and 70% of hair samples had sufficient DNA for extraction, resulting in the identification of five individual bears at each underpass, and highlighting the potential of this method for population-level analysis of the efficacy of wildlife crossing structures (Clevenger and Sawaya 2010).

There is still a paucity of data on the behavior and movement of animals near roads. Bouchard et al. (2009) evaluated the behavioral response of the Northern Leopard Frog (*Rana pipiens*), a species known to be negatively affected by roads and traffic. They studied the movement of frogs during their spring migration and also undertook short distance translocations of migrating frogs and found frogs near roads with more traffic took longer to move and tended to deviate more from straight-line movements when released near roads (Bouchard et al. 2009). The combination of the Northern Leopard Frog's apparent inability to avoid roads and their slow rate of movement make them highly vulnerable to road mortality. The second study in this special issue on the movement behavior of wildlife near roads was for the Squirrel Glider (*Petaurus norfolcensis*) in southeast Australia (van der Ree et al. 2010). The authors found that the size of the gap in the canopy was the primary determinant of the rate of crossing in their study, with similar rates of crossing across the dual-roadway with tall trees in the median and across single-lane roads. In this study, traffic volume, i.e., approximately 5000 vehicles per day per roadway of which about 25% occurs at night when the gliders are active, did not appear to greatly influence crossing rates.

The traffic volume on minor roads is expected to continue to increase in areas with high human population densities because existing motorways are nearing capacity and the minor roads are expected to accommodate the excess flows (references in van Langevelde and Jaarsma 2009). Traffic calming is a regional planning approach to concentrate these flows onto a few roads, and ensure low-volume and low-speed roads are maintained. The conclusions of population viability modeling suggest that the results are species specific and depend upon the size of the traffic-calmed area as well as the area and quality of habitat (van Langevelde and Jaarsma 2009).

ROAD ECOLOGY: THE ROAD AHEAD

The research presented in this special feature shows that road ecology is moving toward larger scales. However, it also became evident while compiling this special issue that many higher order, e.g., population, community, ecosystem, or landscape-level, effects remain unquantified. These higher order effects must become the focus of future studies because the complexity and interactions among the effects of roads and traffic are large and potentially unexpected. An analysis of these complex interrelations requires systematic research. Therefore, a promising avenue to further develop the field of road ecology is to establish collaborative links with road and transportation agencies. Experience shows that the level of engagement with each local, state, or national road agency depends largely on the presence of interested people, rather than an institutionalized approach to environmental matters. However, institutional mandates are important as they are often a precondition for interested people to spend their efforts during work hours on these issues. Many road agencies have “environmental sustainability” as one of their goals and the only way to achieve such goals is for them to support and foster long-term and credible scientific research. Every road project is essentially an experiment and when combined with other road projects, they become replicated. The challenge we face as researchers is to (1) use good scientific approaches to design studies that are scientifically robust and maximize the individual value of each road project within a larger experimental scope; (2) ensure our research is applied and has tangible value for road agencies and for ecological outcomes; (3) address the higher order effects of roads, traffic, and mitigation measures.

This special feature demonstrates that the emerging field of road ecology is confronted with many important unanswered questions. Research needs to address large spatial and temporal scales that are not compatible within most postgraduate programs, i.e., single MSc or PhD theses, or short-term research contracts. The synergistic effects of roads and other factors that operate simultaneously, e.g., agricultural intensification and increased urbanization, have rarely been investigated. However, empirical studies are limited by the delayed response of wildlife to many environmental changes, i.e., there is an extinction debt such that wildlife populations will continue to decline for many years, in the order of decades, before they will reach a new equilibrium (Tilman et al. 1994, Findlay and Bourdages 2000). This lack of knowledge is often used as a justification to build more roads by arguing that not enough is known and more research is needed before road construction may slow down. This constitutes a “fragmentation spiral” (Jaeger 2002), because research has been unable to catch up with the ecological effects of the rapid increase in road densities. This situation is contrary to the precautionary principle and flies in the face of the principles of sustainability. The use of computer models may help overcome these limitations. For example, simulation models have demonstrated that there are thresholds in the effects of road density on the viability of wildlife populations above which populations are prone to extinction (Jaeger and Holderegger 2005, Frair et al. 2008). In addition, a research approach is required that will address the remaining uncertainties that to a large degree are irreducible, e.g., through building on the precautionary principle (e.g., Jaeger 2002). This would open up promising new lines of action for landscape management. For example, the German Federal Environment Agency recently suggested that region-specific limits to control landscape fragmentation should be introduced (Penn-Bressel 2005).

With this issue, we hope to contribute to the field of road ecology and to highlight both its appealing theoretical insights and its high practical relevance. Most importantly, we hope that this special issue will inspire further research in road ecology at the scale of populations, communities, and ecosystems. We are looking forward to these exciting research studies to come.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/vol16/iss1/art48/responses/

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RESEARCH ARTICLE

Survival and Mortality of Pumas (*Puma concolor*) in a Fragmented, Urbanizing Landscape

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Abstract

Wide-ranging large carnivores pose myriad challenges for conservation, especially in highly fragmented landscapes. Over a 13-year period, we combined monitoring of radio collared pumas (*Puma concolor*) with complementary multi-generational genetic analyses to inform puma conservation in southern California, USA. Our goals were to generate survivorship estimates, determine causes of mortality, identify barriers to movement, and determine the genetic and demographic challenges to puma persistence among >20,000,000 people and extensive urban, suburban, and exurban development. Despite protection from hunting, annual survival for radio collared pumas was surprisingly low (55.8%), and humans caused the majority of puma deaths. The most common sources of mortality were vehicle collisions (28% of deaths), and mortalities resulting from depredation permits issued after pumas killed domestic animals (17% of deaths). Other human-caused mortalities included illegal shootings, public safety removals, and human-caused wildfire. An interstate highway (I-15) bisecting this study area, and associated development, have created a nearly impermeable barrier to puma movements, resulting in severe genetic restriction and demographic isolation of the small puma population (n ~ 17–27 adults) in the Santa Ana Mountains west of I-15. Highways that bisect habitat or divide remaining "conserved" habitat, and associated ongoing development, threaten to further subdivide this already fragmented puma population and increase threats to survival. This study highlights the importance of combining demographic and genetic analyses, and illustrates that in the absence of effective measures to reduce mortality and enhance safe movement across highways, translocation of pumas, such as was done with the endangered Florida panther (*P*. *c*. *coryi*), may ultimately be necessary to prevent further genetic decline and ensure persistence of the Santa Ana Mountains population.

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Introduction

Many large carnivores have been extirpated from substantial portions of their historic range, and extant populations are threatened by habitat loss and fragmentation, and conflict with humans [1]. Human population growth expected over the next century exacerbates these threats [2–5], and exurban development will have substantial impacts on habitat that today is still relatively intact [6]. Because large carnivores pose myriad challenges for conservation in urbanizing landscapes, we began a long-term study of pumas (*Puma concolor*) in 2001 in southern California, USA, to provide quantitative insights and guidance for conservation of pumas and other large carnivores in human-dominated habitats.

Pumas, also known as mountain lions, cougars, or panthers, are wide-ranging carnivores that historically occurred throughout the Americas. Humans have extirpated or greatly reduced puma numbers in much of their former range in the past 200 years [2]. The only documented breeding population of pumas remaining in the eastern United States is in Florida, where a small population of federally endangered pumas (Florida panthers–*Puma concolor coryi*) persists, largely because their endangered status spurred intensive management including translocation and genetic introgression [7, 8]. In the western United States, pumas are hunted for sport in several states, but there is considerable controversy and uncertainty about the long-term consequences of hunting on population persistence. For example, a recent study of heavily-hunted and semi-protected puma populations in Utah [9] did not detect a compensatory decrease in natural mortality in response to heavy hunting pressure, and concluded that uncertainties in the functional relationship between natural and anthropogenic mortality could lead to biased conclusions and mismanagement.

In California, pumas are considered a “specially protected mammal” and hunting is prohibited [10]. Despite these protections, recent genetic studies of pumas in southern California show that the genetic viability and long-term persistence of some populations are in jeopardy [11, 12]. The threats facing pumas in southern California—habitat loss, increased conflict with humans, demographic isolation, and genetic restriction [11–15]—mirror the challenges facing large carnivores in urbanizing landscapes around the world [3], and long-term studies intended to guide conservation and management in these settings are difficult and expensive to conduct. We addressed this information gap by conducting a 13-year study of pumas in the California south coast ecoregion, USA, a biodiversity hotspot [16, 17] with a growing population of $>$20,000,000 people [18].

Sandwiched between the sprawling metropolitan areas of greater Los Angeles and San Diego, much of the available puma habitat in our study area is not protected from new highways and development, and is subject to ongoing habitat loss and fragmentation [15]. Our goals for this study were to generate survivorship estimates and cause-specific mortality data for pumas in this region, and identify options for improving survivorship and facilitating movement within and among conserved and non-conserved areas. This demographic study builds upon and complements our recent genetic analysis [11], and provides the essential ecological context for understanding the causes and potential solutions to the genetic restriction we found in pumas in the Santa Ana Mountains.

Materials and Methods

Statement

We operated under Protocol 10950/PHS, Animal Welfare Assurance number A3433-01, with capture and sampling procedures approved in Protocol number 17233 by the Animal Care and Use Committee at the University of California, Davis, and Memoranda of Understanding and

Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). Permits and permissions for access to conserved lands where captures and monitoring were conducted were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (U.S.) Fish and Wildlife Service, U.S. Forest Service, U.S. Bureau of Land Management, U.S. Navy / Marine Corps, U. S. Fish and Wildlife Service, Orange County Parks Department, San Diego County Parks Department, Riverside County Parks Department, San Diego State University, University of California—Riverside, Audubon Starr Ranch, Vista Irrigation District, Rancho Mission Viejo / San Juan Company, Sweetwater Authority, California Department of Transportation, the City of San Diego Water Department and Parks Department, and the Irvine Ranch Conservancy. Anesthetic drug combinations used in capture procedures were either teletamine / zolazapam (Telazol) or medetomidine / ketamine at dosages prescribed in the scientific literature.

Study Area and Population

The study area encompassed the Santa Ana Mountains (a portion of the Peninsular Ranges) and the remainder of the Peninsular Mountain Ranges and surrounding foothills to the east (hereafter referred to as the eastern Peninsular Range). These areas constitute the majority of occupied puma habitat in southern California south of greater Los Angeles (Fig 1). Pumas are the primary large carnivore remaining in the study area since grizzly bears (*Ursus arctos californicus)* were extirpated in the early 1900s [19, 20].

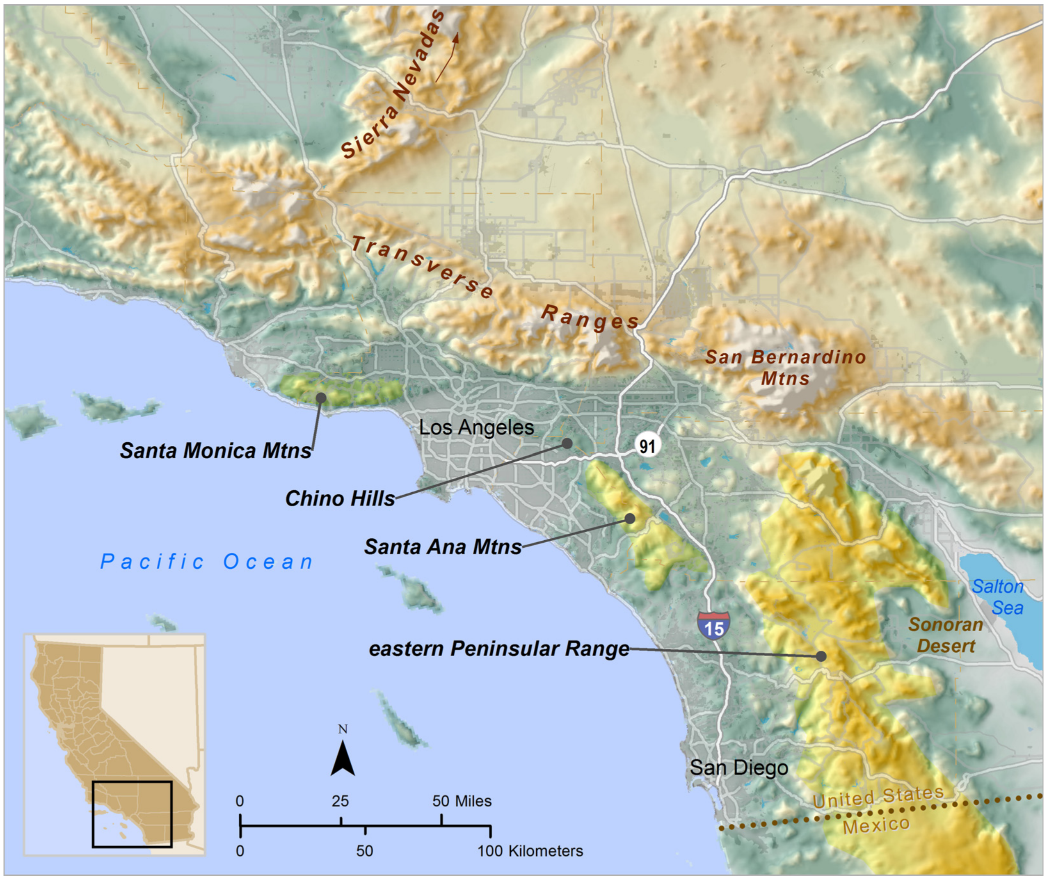

Fig 1. Puma study area in southern California, USA, and regional context. The focal area of this study includes the Santa Ana Mountains and the eastern Peninsular Range. Inset shows location within California.

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An extensive and growing network of roads, some carrying more than 250,000 vehicles per day, encircles and fragments the study area [21] (Fig 1). Interstate highway 15 (I-15) connects the greater Los Angeles, Riverside, and San Diego metropolitan areas, and the highway and associated development have been hypothesized to be a barrier to puma movement between the Santa Ana Mountains in the west and the eastern Peninsular Ranges [11, 13, 22, 23]. Therefore, we assigned pumas that were captured or found dead west of I-15 to a putative "Santa Ana Mountains" source population, and those east of I-15 to a putative "eastern Peninsular Range" source population.

Land use varies considerably across the study area, with the eastern Peninsular Ranges generally having less intensive development and more rural, undeveloped, and protected lands. Burdett et al. [15] classified land use and urbanization in the study area into five categories: protected public lands (55% of the study area), private undeveloped (9.5%), rural (14.4%; >16.18 ha per housing unit), exurban (15.7%; 0.68–16.18 ha per housing unit), and suburban/urban (5.4%; <0.68 ha per housing unit). The Santa Ana Mountains have substantial protected public lands, but new highway construction, development, and land use practices tend to be much more intensive immediately adjacent to remaining high quality puma habitat [15].

Capture and Monitoring Methods

We captured, marked, and monitored radio collared pumas from 2001 through 2013. Pumas were captured primarily using baited cage traps [24], and to a lesser extent using hounds or foothold snares [25, 26]. Each captured animal was tattooed in one ear with a unique numerical identifier ("marked") and a numbered tag was placed in the opposite ear. Age was determined from dental characteristics and body morphometrics as described in Ashman et al. [27] and Laundre et al. [28, 29]. We classified pumas <18 months as kittens, 18–30 months as subadults, and >30 months as adults [30]. We applied Very High Frequency ("VHF"; MOD500 Telonics, Mesa, AZ), and/or Global Positioning System ("GPS"; Simplex P-1D, Televilt, Lindesberg, Sweden; TGW 3580, Telonics, Mesa, AZ; GPS4400S, GPS3300S, and GlobalstarTrack S, Lotek, Ontario, Canada) radio collars to pumas if their body weight exceeded 22.7 kg. GPS locations were collected at varying time intervals from every 5 minutes to every 6 hours depending on specific study objectives.

Puma Movements

We hypothesized that the Pacific Ocean, Sonoran Desert, major highways, and urban centers would form barriers that constrained pumas in our study area into one or more discrete populations. To test this hypothesis, we examined movements of radio collared pumas from 2001–2013 to determine the degree of interchange within and between the Santa Ana Mountains and eastern Peninsular Range populations, and whether monitored pumas emigrated out of the entire study area. We were particularly interested in determining if ongoing habitat fragmentation had created or hardened existing barriers, and in evaluating puma movements relative to corridors or linkages identified through previous modeling efforts. These included: 1) the east-west "Santa Ana—Palomar Mountains Linkage" across I-15 that connects the Santa Ana Mountains and eastern Peninsular Range puma populations [31]; 2) the "Coal Canyon Corridor" under California State Route 91 (SR-91) linking the Santa Ana Mountains and the Chino Hills to the north [17, 32]; and 3) the "Parque-to-Park Linkage" connecting California and Baja California, Mexico to the south [33].

Mortality and Survival Analyses

The distribution of radio collared pumas in the populations west and east of the I-15 freeway were compared using the Fisher exact test to determine if they differed by sex or age class, and a two-sample t-test was used to determine if they differed by average age at entry or exit to the study (in months), or the average number of days monitored (STATA IC 13.0, STATACorp, College Station, Texas, USA). A P value of ≤ 0.05 was used as the cutoff for significance for all analyses.

Deaths of radio collared pumas from 2001–2013 were detected when VHF or GPS data indicated a lack of movement, and the cause of death was determined by field investigation and necropsy. In addition, we combined mortality data for our marked (n = 36) pumas with "unmarked" (n = 218) pumas that were confirmed to have died in the study area from 1981–2013 based on CDFW records. Age determination was less precise for unmarked animals due to conditions of carcasses at discovery or variable experience of reporting parties in the aging of pumas. Therefore, we classified unmarked pumas as either subadults ($\leq$30 months) or adults ($>$30 months) [30].

We compared long-term trends in the number of pumas being killed under depredation permits in our dataset to the total number of puma mortalities across all of California during the same time period, as reported by CDFW [34], by plotting 5-year simple moving averages for each dataset. For each calendar year, the number of puma mortalities was averaged for the current year and previous 4 years. This allowed us to smooth short-term fluctuations and visualize long-term trends in the data.

Radio collared pumas entered the study on the date they were first captured, and exited on the date of mortality or the last date of detection by radiotelemetry. The number of days each animal was monitored was calculated as the time between entry and exit dates. Cause of death was determined at necropsy for both marked and unmarked animals unless the state of carcass decomposition precluded definitive diagnosis. In those cases, cause of death was classified as "unknown". Because numbers of at-risk individuals varied across the course of the study, a formal cause-specific mortality analysis was not possible [35]. However, source population, sex, and age class (at time of mortality) were evaluated in both marked and unmarked populations for associations with the various causes of mortality using the Fisher exact test (STATA IC 13.0, STATACorp, College Station, Texas, USA).

We estimated survival using the known-fate model in Program MARK (Version 7.1) [36]. We chose a set of 8 models a priori for analysis that included combinations of population, sex, and age class (at the time of collaring) as parameters. Support for each model was assessed using Akaike's Information Criterion (AIC), corrected for small sample size (AIC_c). The *sin* link function was used to run all models. If no model was clearly superior to all others (AICc weight $>$90% andΔAIC $>$2) [36–38], we performed model averaging to reduce the uncertainty in our parameter estimates.

We used a Cox proportional hazards model (STATA IC 13.0) to evaluate the relationship of biologically important covariates (source population, sex, age, and year of mortality) to the length of time pumas survived during the study. Adult age class ($>$30 months old) and mortality years 2007 and 2008 were used as reference categories in the models. Staggered entry into the study was addressed by including the Andersen-Gill formulation [39, 40]. The Breslow approximation method was used to address tied failure times [41], and Schoenfeld residuals were used to test the proportional hazards assumption that relative risk for each variable of interest was the same for the duration of the study.

Results

Puma Monitoring and Movements

Our analyses included 74 pumas that were captured, marked, and radio collared between March 2001 and December 2013 (Table 1). The distribution of these marked pumas in the

Table 1. Demographic characteristics of radio collared pumas in southern California, USA from 2001–2013.

Variable	Number of pumas		
	Total	Santa Ana Mountains	Eastern Peninsular Ranges
Sex			
Females	37	17	20
Males	37	14	23
Outcome			
Survived	38	18	20
Died	36	13	23
Age class at entry			
<18 months	19	6	13
18 to 30 months	19	9	10
>30 months	36	16	20
Age class at exit			
<18 months	2	0	2
18 to 30 months	16	7	9
>30 months	56	24	32

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eastern Peninsular Range (n = 43) and Santa Ana Mountains (n = 31) did not differ significantly by sex, age class, average age at entry or exit to the study, or the average number of days monitored.

We detected numerous long distance (>80 km) movements by radio collared pumas from 2001–2013, but only one radio collared puma moved out of the overall study area. In 2009, a young adult male (M53) traveled approximately 150 km south from his capture site in the eastern Peninsular Range, utilizing the Parque-to-Park Linkage to cross the U.S.-Mexico border (Fig 2). He reached a point 70 km south of the border before returning to his original location in the U.S. Several other radio collared pumas were detected near, but not across, the U.S.-Mexico border (Fig 2).

Radio collared puma movements between the eastern Peninsular Range and Santa Ana Mountains were limited, indicating the pumas in these regions formed relatively discrete populations. In 2010, a dispersing sub-adult male (M56) crossed I-15 from west to east several miles south of the proposed Santa Ana Mountains—Palomar Mountains Linkage (Fig 2), but he was killed 25 days later for depredating domestic sheep.

None of the radio collared pumas used the Coal Canyon undercrossing beneath SR-91 at the northern tip of the Santa Ana Mountains to move into the Chino Hills to the north (Fig 2). However, two unmarked pumas were killed from 2001–2013 while attempting to cross this major freeway within 3 km of the Coal Canyon undercrossing.

Puma Mortality

The number of pumas alive (n = 38) vs. dead (n = 36) by the end of the study did not differ between source populations, sexes, or age class at entrance or exit (Table 1). Though time-at-risk and sample size constraints prevented a formal cause-specific mortality analysis, we report here proportional mortality of both marked and unmarked pumas over the entire study period. Over the course of the entire study period, proportional mortality due to vehicle collisions and depredation permits was greater than for all other causes of mortality. Other known sources of mortality included disease, illegal shooting, arson-caused wildfire, public safety removal, and intraspecific aggression (Table 2). Proportional mortality due to vehicle strikes and

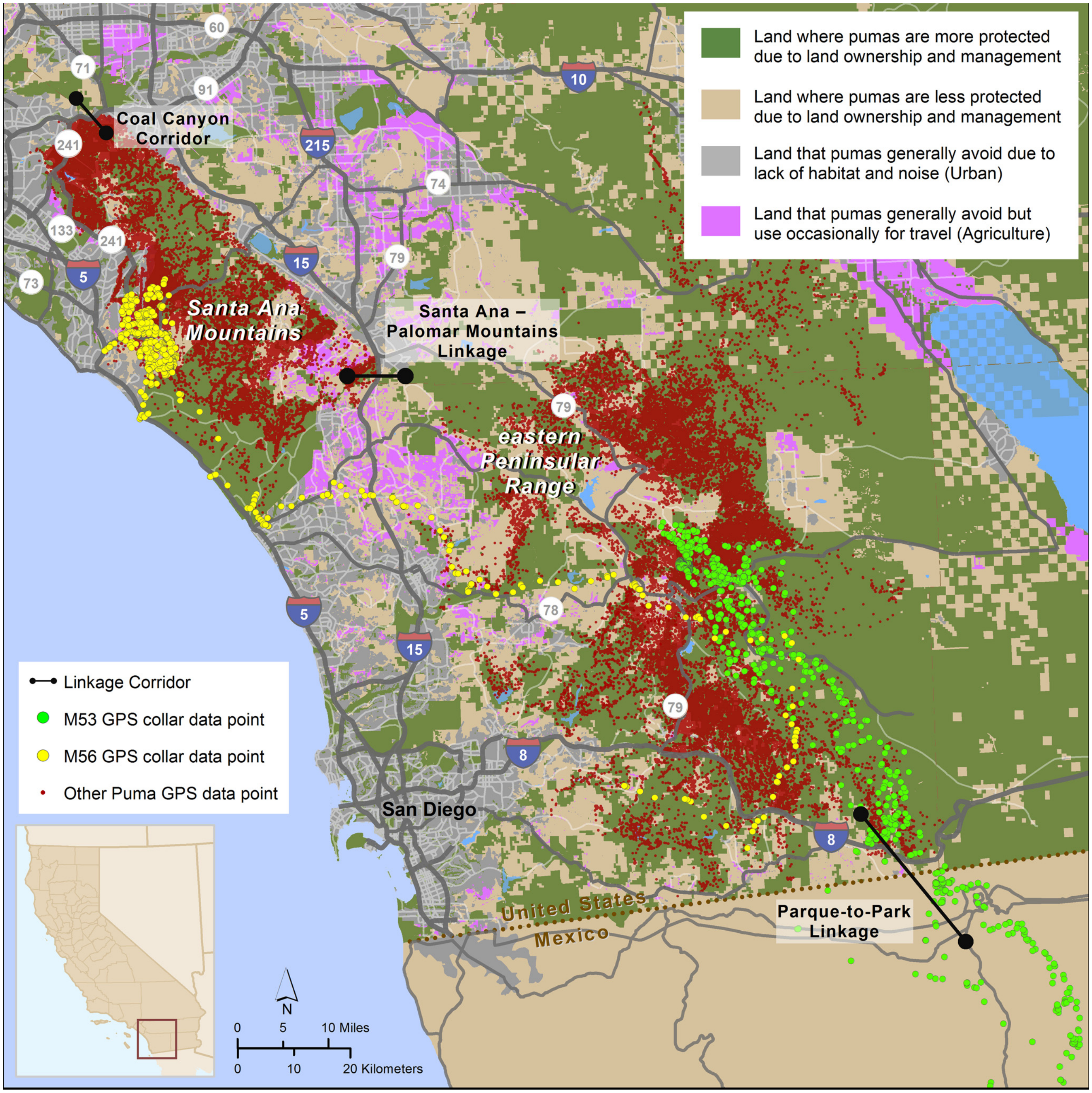

Fig 2. Puma GPS collar data points collected from 2001–2013 in southern California, USA. GPS collar data points are overlaid on lands classified (by color) based on their relative levels of puma protection and typical usage. Primary linkages within the study area are noted and GPS collar data points from pumas M53 and M56 are highlighted. Inset shows location within California.

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depredation permits differed between pumas from the eastern Peninsular Range and Santa Ana Mountains populations ($P = 0.034$), but did not differ by sex or age class. In fact, all mortalities of marked pumas due to depredation permits occurred in the eastern Peninsular Range, while 60% of mortalities due to vehicle collisions were in the Santa Ana Mountains (Table 2; Figs 3 and 4). With the exception of vehicle strikes and depredation, the data were too sparse to evaluate relationships between specific causes of mortality and various risk factors.

Table 2. Proportions and numbers of radio collared pumas that died from different causes in Southern California study areas from 2001–2013.

Cause of mortality	Total	Santa Ana Mountains	Eastern Peninsular Ranges
Vehicle Strike[a]	0.28 (10)	0.46 (6)	0.17 (4)
Depredation Permit[a]	0.17 (6)	0.00 (0)	0.26 (6)
Killed illegally	0.11 (4)	0.23 (3)	0.04 (1)
Disease suspected	0.11 (4)	0.08 (1)	0.13 (3)
Disease confirmed	0.06 (2)	0.00 (0)	0.09 (2)
Fire	0.06 (2)	0.08 (1)	0.04 (1)
Public safety	0.03 (1)	0.00 (0)	0.04 (1)
Killed by other puma	0.03 (1)	0.00 (0)	0.04 (1)
Capture related	0.03 (1)	0.00 (0)	0.04 (1)
Unknown	0.14 (5)	0.15 (2)	0.13 (3)
Total	36	13	23

[a] Mortalities secondary to depredation permits and vehicle strikes differed between the two populations (P = 0.034; Fisher's exact test).

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In the combined dataset (marked and unmarked pumas; n = 254), proportional mortality due to depredation permits was approximately 3.4 times higher for males than females (54M:16F; $P = 0.001$), while proportional mortality due to vehicle collisions was equal for both sexes (45M:45F). In the combined dataset, proportional mortality varied between the eastern Peninsular Range and Santa Ana Mountains populations ($P < 0.001$). There were more mortalities due to depredation permits in the eastern Peninsular Range (n = 62, compared to n = 11 in the Santa Ana Mountains), and almost equal numbers of mortalities due to vehicle collisions in the two populations (n = 46 in the eastern Peninsular Range, compared to n = 50 in the Santa Ana Mountains; Fig 5). Mortality varied substantially year by year in the combined dataset, but the trend for mortalities due to depredation permits tended to increase from 1981 to 2004 and then began to decline, before trending upward again through 2013 (Fig 6), a pattern generally similar to that seen in CDFW's graph of statewide depredation data (http://www.dfg.ca.gov/wildlife/lion/depredation.html). In contrast, the trend for deaths due to vehicle collisions increased steadily through 2013, with no decline or downward trend detected after 2004 (Fig 6). Vehicle mortalities occurred throughout the study area (Figs 3 and 4), however the majority of vehicle-related mortalities in the Santa Ana Mountains occurred on California State Highway 241 (SR-241) and SR-74, two highways that traverse puma habitat, and I-15 in the Santa Ana Mountains to Palomar Mountains Linkage area (Fig 3).

Puma Survival

Survival estimates were calculated using data from the 74 radio collared pumas that were monitored from 2001–2013 for a total of 29,578 puma days (mean = 400, SE = 38 days per animal). Using the known-fate model within Program MARK, the estimated mean annual survival rate was 55.8%, (95% CI = 44.5–65.6%). In the most parsimonious model survival was constant across populations, sexes, and ages ("S(.)"; Table 3). Two models had ΔAIC values <2: model "S(Sex)" which included sex as a parameter (model likelihood = 0.43), and model "S(Population)" which included population as a parameter (model likelihood = 0.37; Table 3). These models yielded annual survival estimates of 58.6% for females and 52.5% for males across the entire study area, and 56.5% for the Santa Ana Mountains population and 55.4% for the eastern Peninsular Range population across all sexes and age groups (Table 3). Due to the distribution of AICc weights among the top models (Table 3), we performed model averaging of similarly

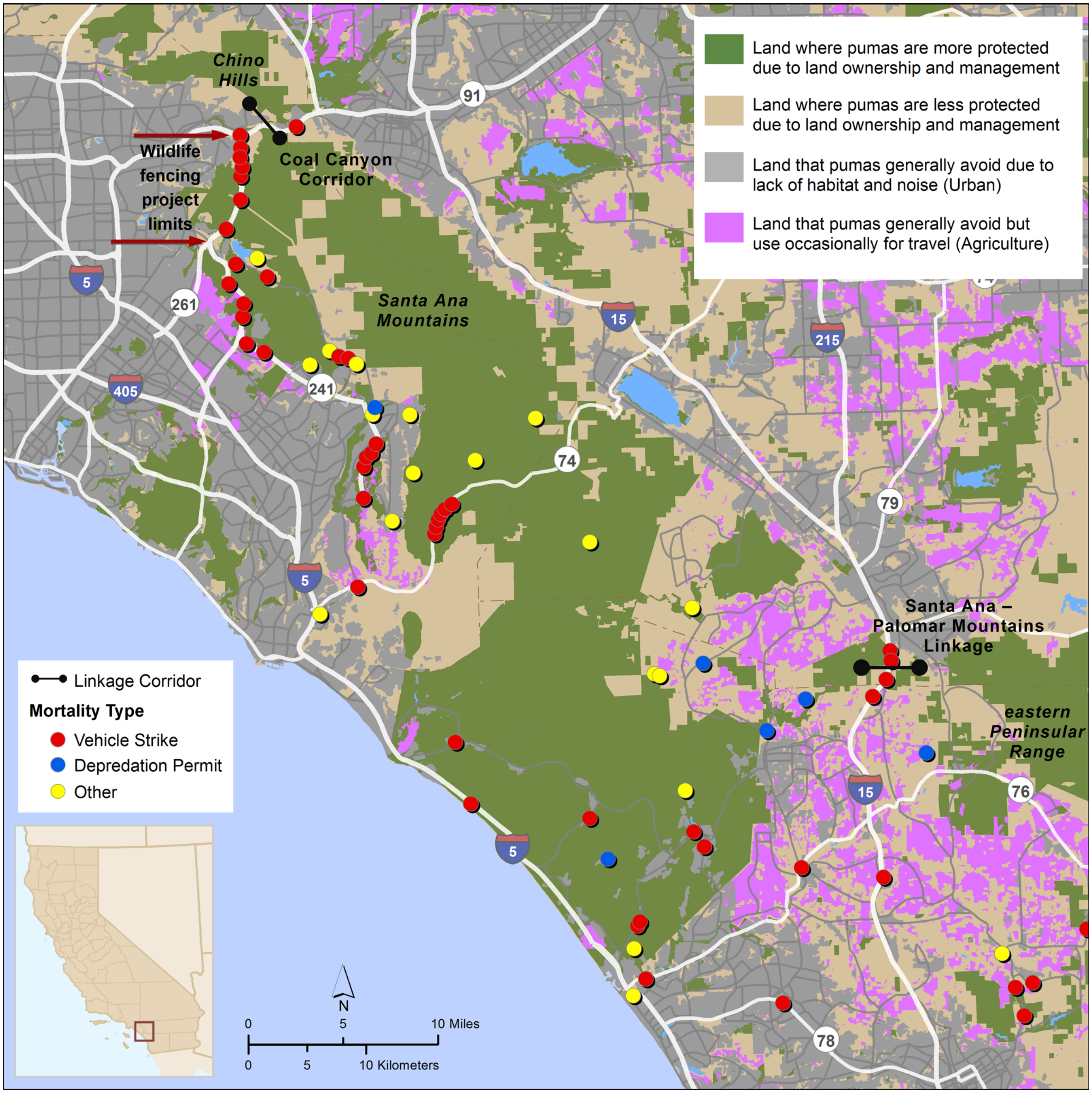

Fig 3. Sites and causes of puma mortalities in the Santa Ana Mountains, 1981–2013. The Coal Canyon Corridor and Santa Ana—Palomar Mountains Linkage are noted, as well as the limits of a wildlife fencing project on SR 241. Inset shows location within California.

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parameterized models but did not detect any differences among groups (95% CI of survival estimates overlapped).

Survival rates varied widely among years, and the Cox proportional hazards model identified calendar years 2001, 2003 2005, 2006, and 2009 as having significantly higher hazard ratios compared to years 2007 and 2008 (Table 4). All other covariates, including source population, sex, and age at entry were not significantly associated with time to death. Evaluation of the proportional hazards assumption for the final model based on a test of Schoenfeld residuals

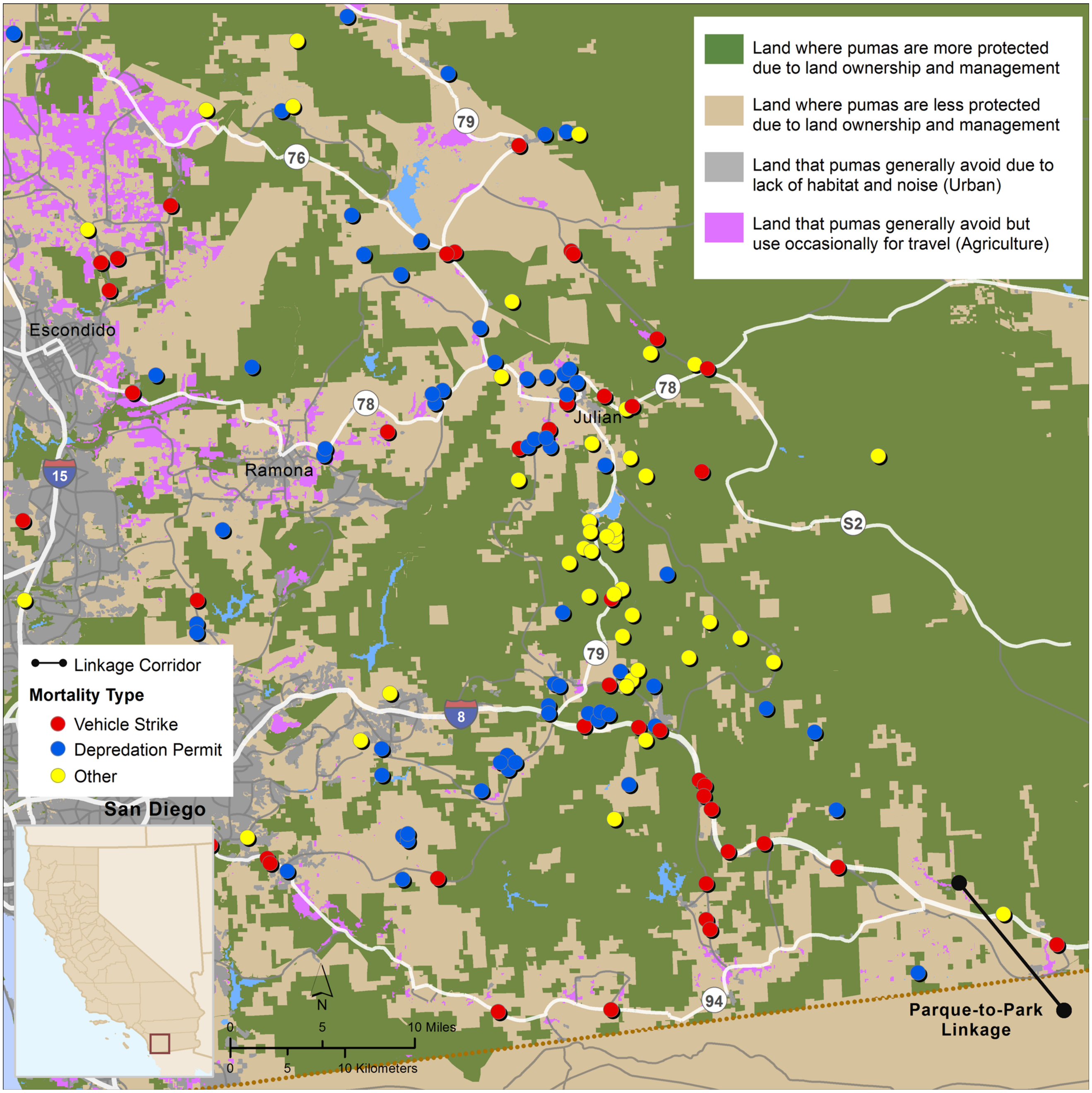

Fig 4. Sites and causes of puma mortalities in the eastern Peninsular Range, 1981–2013. Area depicted is generally east of Interstate 15, with the Parque to Park linkage noted. Inset shows location within California.

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indicated that the relative risk for each variable of interest, after including year as a variable in the model, did not differ for the duration of the study (*P* = 0.99).

Discussion

This 13-year study demonstrates the high risk of mortality for pumas associated with fragmentation and urbanization, and coupled with our genetic analyses [12], we conclude that puma

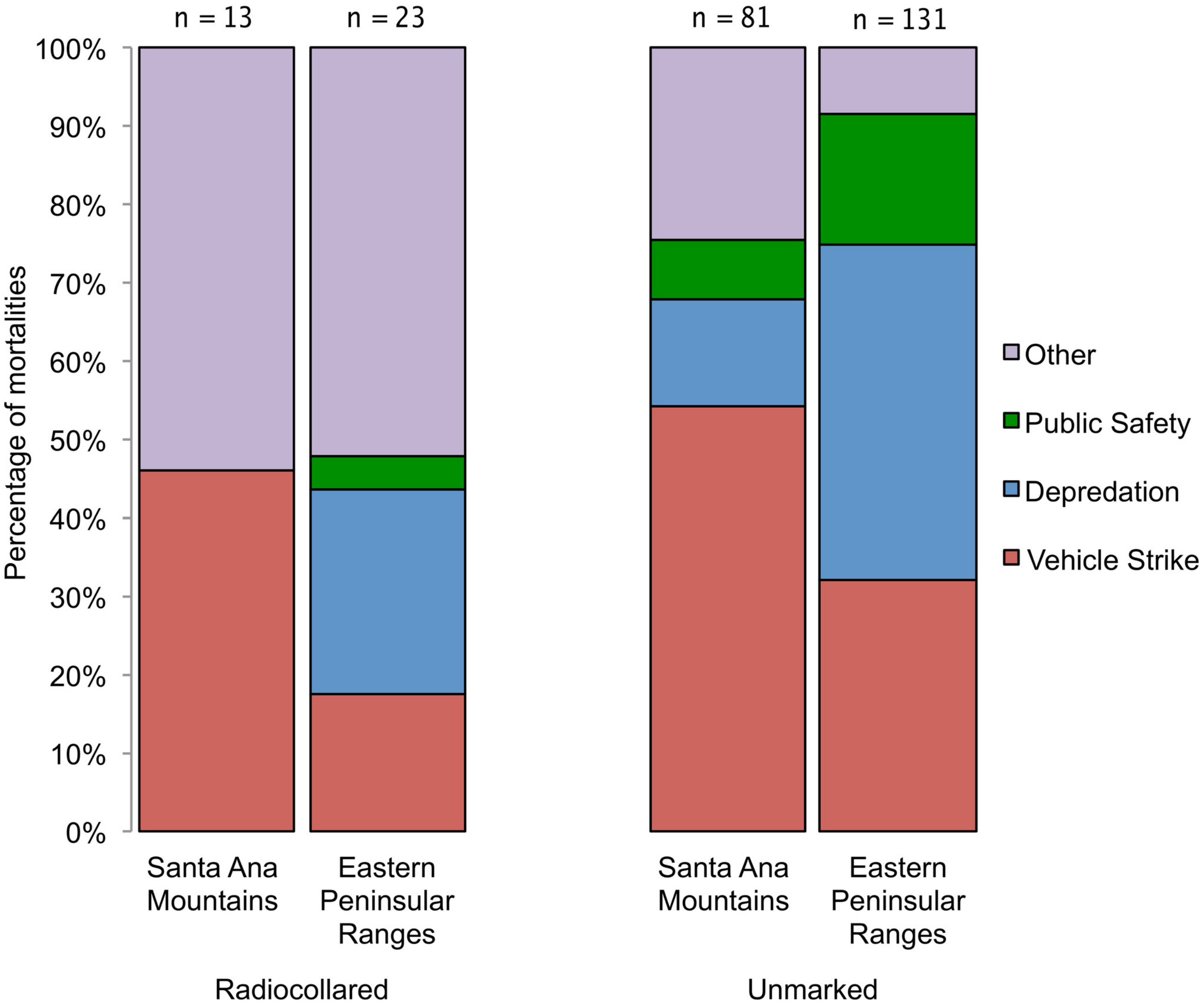

Fig 5. Percentages of pumas dying from different causes of mortality in southern California, USA. Mortalities of radiocollared (n = 36; 2001–2013) and unmarked (n = 212; 1981–2013) pumas were assigned to the Santa Ana Mountains or the eastern Peninsular Ranges subpopulation. Six unmarked pumas were not included in this figure because they were found on the I-15 freeway and could not be assigned to a population.

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persistence in this human-dominated landscape is threatened [42–46]. Annual puma survival rates for radio collared pumas in the Santa Ana Mountains (56.5%) and eastern Peninsular Range (55.4%) were very low from 2001–2013, and were similar to those in heavily hunted populations [2, 9, 43]. Indeed, annual survival rates for our study population were lower than rates for pumas in the peri-urban Santa Monica Mountains population northwest of Los Angeles (>75%) [12], and are within the range that is considered a threat to persistence of puma populations [13].

Our movement data (this paper) and our genetic findings [11] support the hypothesis that pumas in the Santa Ana Mountains and eastern Peninsular Range effectively form two subpopulations, bisected by an interstate highway and neighboring development. Our data demonstrate that both subpopulations had low survival; and though proportional mortality is a crude measure of causes of death in a population, the major causes of puma proportional mortality

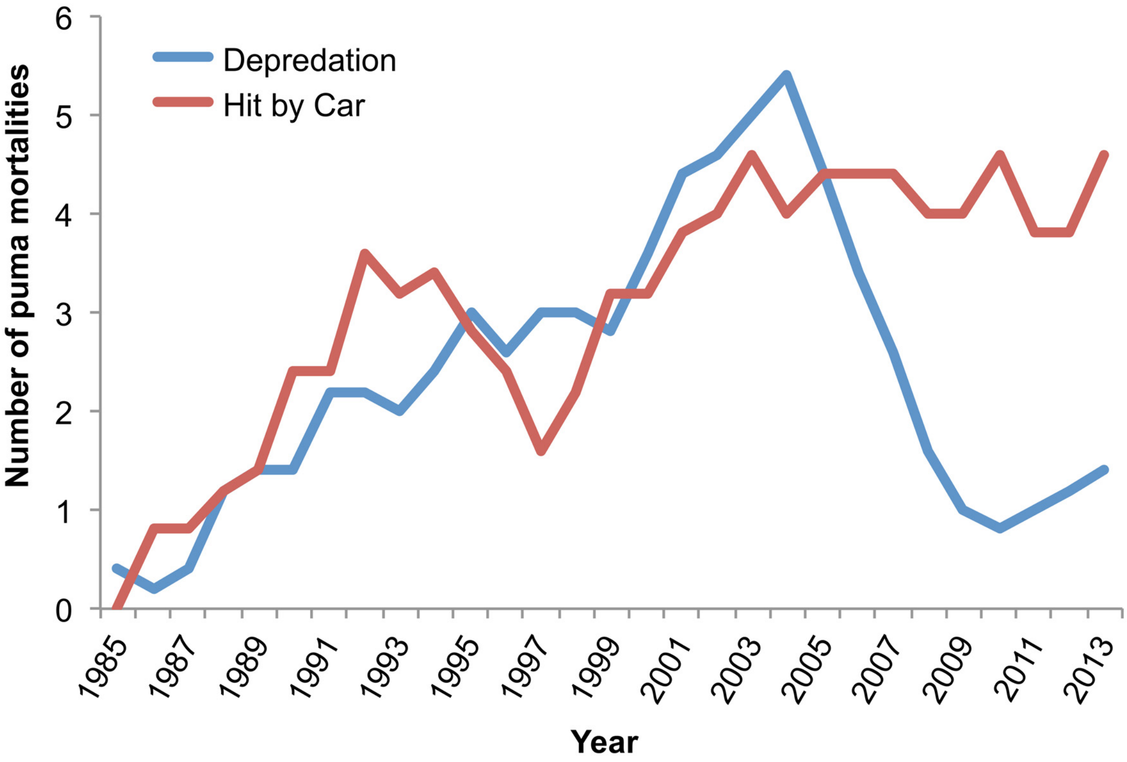

Fig 6. Pumas killed secondary to vehicle collisions or depredation permits from 1981–2013 in southern California, USA. Five year moving average of pumas killed secondary to vehicle collisions or depredation permits (n = 174) in the Santa Ana Mountains and eastern Peninsular Ranges.

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differed between these areas. Depredation permits were the most common proportional mortality factor in the eastern Peninsular Range and primarily affected males, whereas vehicle strikes were the main source of proportional mortality in the Santa Ana Mountains, affecting males and females equally. Conservation biologists have long expressed concern about demographic and genetic isolation of pumas in the Santa Ana Mountains [11, 13], and this study, coupled with our companion genetic study [11], provides a comprehensive view of the fractured demographic and genetic connectivity among pumas in this region.

Ernest et al. [11] concluded that Santa Ana Mountains pumas monitored in this study "had high average pairwise relatedness, high individual internal relatedness, a low estimated effective population size, and strong evidence of a bottleneck and isolation from other populations in California." Genetic restriction and isolation were pronounced even though limited gene flow

Table 3. Results of the known-fate model (Program MARK) for survival (S) for radio collared pumas in southern California, USA.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Number Parameters	Deviance
S(.)	397.21	0.00	0.4668	1.00	1	327.25
S(Sex)	398.89	1.68	0.2012	0.43	2	326.93
S(Population)	399.20	1.99	0.1724	0.37	2	327.24
S(Age)	400.24	3.03	0.1026	0.22	3	326.27
S(Population*Sex)	402.69	5.48	0.0301	0.06	4	326.72
S(Population*Age)	403.68	6.48	0.0183	0.04	6	323.70
S(Sex*Age)	405.22	8.01	0.0085	0.02	6	325.24
S(Population*Sex*Age)	414.57	17.37	0.0001	0.00	12	322.52

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Table 4. Variables related to time to death in the Cox proportional hazards model of survival of radio collared pumas in southern California, USA.

Covariate[a]	Hazard Ratio	SE	Z	P>|z|	95% CI
Age at Entry[b]					
<18 months	0.53	0.28	-1.21	0.23	0.19–1.48
18–30 months	1.56	0.75	0.93	0.35	0.61–3.99
Year at Exit[c]					
2001*	149.20	209.78	3.56	0.00	9.48–2347.27
2002	5.16	6.85	1.24	0.22	0.38–69.63
2003*	9.86	8.34	2.71	0.01	1.88–51.73
2004	5.41	6.98	1.31	0.19	0.43–67.91
2005*	12.75	11.51	2.82	0.01	2.18–74.76
2006*	7.10	6.82	2.04	0.04	1.08–46.64
2009*	8.02	7.79	2.14	0.03	1.20–53.77
2010	1.70	1.71	0.53	0.60	0.24–12.16
2011	3.03	4.03	0.84	0.40	0.23–40.89
2012	6.16	6.14	1.82	0.07	0.87–43.44
2013	3.55	3.48	1.29	0.20	0.52–24.23

*Covariates significant at $P \leq 0.05$.

[a] The final model controlled for population and sex which were not significantly associated with time to mortality

[b] Oldest age class (>30 months old) designated as reference category.

[c] Years 2007 and 2008 designated as reference category

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did occur from the eastern Peninsular Ranges into the Santa Ana Mountains. Genetic analysis showed that a male puma (M86) captured in the Santa Ana Mountains was likely born in the eastern Peninsular Ranges, and successfully migrated into the Santa Ana Mountains during our study. This male, and two females (F61 and F89) captured in the Santa Ana Mountains, were the likely parents of four pumas born in the Santa Ana Mountains in 2010–2011 (M91, F92, M93, and M97) [11]. However, this is the only evidence of successful genetic interchange between the two populations during the study period other than an 8 month old kitten (F102) [11] killed by a car in the Santa Ana Mountains in August 2003. In 13 years, none of the pumas radio collared in the eastern Peninsular Range were observed to move west into the Santa Ana Mountains, and the single radio collared male that did move from the Santa Ana Mountains into the eastern Peninsular Range was killed for depredating domestic sheep within weeks of crossing I-15. This suggests that the estimated 17–27 adult pumas in the Santa Ana Mountains [13] have become an insular population, much like the small population of pumas located in the Santa Monica Mountains [12]. The combination of small population size, limited potential for immigration of new individuals (male and female) into the area, female mortality rates that are similar to males, and negative effects of genetic restriction [11], collectively put the Santa Ana Mountains population at risk for demographic collapse [13, 22, 47].

Southern California has been the focus of multiple regional-scale conservation planning efforts aimed at protecting a network of natural habitats, among extensive urban, suburban, and exurban development and a burgeoning population of >20,000,000 people [48]. Pumas have been a focal species for these efforts because of their ecological value, their inherent value to humans, and their utility as surrogates for other wide-ranging taxa in conservation planning [13, 22, 42, 49–52]. Despite some concerted conservation efforts (e.g. [14]), this study shows that pumas are currently subject to high levels of human-caused mortality, and that wildlife corridors that facilitate safe movement through the landscape are lacking or insufficient. These threats will only grow worse without further action. For example, additional urban development is underway or proposed on both the east and west sides of I-15 in the Santa Ana–Palomar Mountains Linkage (Figs 2 and 3) [53, 54], and 14,000 new homes and associated highways will be constructed at the south end of SR-241 in the center of puma habitat in the Santa Ana Mountains [55].

Conserving core habitat areas and functional wildlife corridors has been the main focus of conservation efforts for pumas in southern California [15, 31, 32, 56, 57] and coordinated regional action in the form of targeted investment in habitat protection is especially urgent to maintain viability of the Santa Ana Mountains population. However, our analysis highlights that land protection alone will not be sufficient to ensure puma persistence in the region. Also important will be directed focus on improving road infrastructure to facilitate safe wildlife crossings, and reducing depredation conflicts that precipitate puma deaths. Options for enhancing movements across I-15 and other highways include protection of additional lands on both sides of the highway, improving or adding large culverts, adding exclusionary fencing [58] such as that currently being constructed on SR 241 (Fig 3) [59], and possibly constructing vegetated overpasses for wildlife use [60, 61]. Strategies to reduce mortalities stemming from depredation permits include education activities to promote wider use of predator-proof enclosures for their domestic animals during the crepuscular periods and at night [62–65]. A focus on land protection, roadway and wildlife crossing design, and landowner outreach will be critical for persistence of puma in southern California, and may well be a formula for conserving large carnivores in highly populated and fragmented landscapes generally.

The combination of long term field monitoring of radio collared animals coupled with genetic analyses was critical for understanding puma biology and providing directions for conservation efforts in southern California. The movement of puma M86 across I-15 from the eastern Peninsular Ranges may aid in the genetic rescue of the Santa Ana population, but only if his offspring survive and reproduce. To date, only one of his four known offspring are still alive in the wild—a female with two dispersal-age offspring, and evidence points towards pumas being less likely to successfully navigate this human-dominated landscape in the future. In the absence of effective measures to reduce mortality and enhance safe movement across highways, translocation of pumas, such as was done with the Florida panther [66], may ultimately be necessary to prevent further genetic decline and assure persistence of the Santa Ana Mountains population.

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Author Contributions

Conceived and designed the experiments: TWV WMB RB SAM PRH TS HBE. Performed the experiments: TWV WMB RB HBE JNS. Analyzed the data: TWV WMB JNS CKJ BSC HBE PRH RB. Contributed reagents/materials/analysis tools: JNS CKJ HBE SAM BSC. Wrote the paper: TWV JNS CKJ SAM RB TS BSC PRH HBE WMB.

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RE: [Federal Register Volume 84, Number 232 (Tuesday, December 3, 2019)]
[Notices]
[Pages 66268-66269]
From the Federal Register Online via the Government Publishing Office [www.gpo.gov]
[FR Doc No: 2019-26117]
======================================================================
-----------------------------------------------------------------------
DEPARTMENT OF TRANSPORTATION
Federal Highway Administration
Environmental Impact Statement: San Diego and Orange Counties,
California
AGENCY: Federal Highway Administration, U.S. Department of
Transportation.
ACTION: Notice of Intent.
-----------------------------------------------------------------------
SUMMARY: The Federal Highway Administration (FHWA), on behalf of the
California Department of Transportation (Caltrans), is issuing this
notice to advise the public that a Draft Environmental Impact Statement
(Draft EIS) will be prepared for a proposed highway project in Orange
County and San Diego County, California.
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January 8, 2020

To Whom It May Concern

Please accept this letter as comment on the Draft Environmental Impact Statement that will be prepared in relation to the proposed highway project as presented in this publication in the Federal Register. I would request that my comments be considered during the development of the project Draft EIS.

Comments:

As a wildlife veterinarian and researcher who has conducted scientific studies for over a decade in the south Orange County region where the proposed project is planned, I have significant concerns with the negative impacts that several of the proposed alternatives may have on mountain lion (*Puma concolor*) and other wildlife movement and connectivity. My special expertise and knowledge relates to mountain lions in that area, but their movement patterns can illuminate the patterns of numerous other wild species as well.

It is well established by multiple peer reviewed studies and published reports to government agencies (1-4) that mountain lions in the Santa Ana Mountain Range are seriously genetically restricted and have unusually low annual survival rates, with the number one source of mortality being collisions with cars (5). This has resulted in a population under serious threat of extirpation within less than two decades if inbreeding depression begins to reduce reproductive success in the population (3). As a result of the aforementioned studies, the Santa Anas mountain lion population has been petitioned for listing under the California Endangered Species Act, and its status is currently being studied intensively by our research group at the University of California–Davis, as well as by the California Department of Fish and Wildlife. Connectivity across highways has emerged as the most important factor in restriction of connectivity, and extensive study has been done and is ongoing by our group and collaborators that is related to this issue across the region (4, 6-7, Vickers unpublished data).

The majority of the mountain lion deaths from vehicle collisions in the last two decades have been on the SR 241 Toll Road, but SR 74 and other regional highways that are less busy have also been sites of mountain lion mortalities. The toll road agency has built additional fencing on SR 241 in one 6 mile section to reduce the rate of vehicle collisions, and that has been quite successful in that goal, but other sections of both SR 241, as well as sections of SR 74, remain a danger to mountain lions and other wildlife.

In the area of the proposed project, movement of mountain lions between habitat patches is already compromised in both the north-south and east-west directions by existing housing and roads, with more approved and under construction in Rancho Mission Viejo. Connections between Chiquita Canyon and Bell Canyon habitat areas north of SR 74, and habitat areas to the south of SR 74 are already affected negatively by increasing traffic on SR 74 itself and expanding development in Ranch Mission Viejo, including Los Patrones Parkway. Though passageway structures for wildlife and fencing are present on Los Patrones Parkway, to my knowledge movement studies have not been done with GPS collars to determine if that roadway is having any barrier effect on east-west movement.

Mountain lions must move north and south in the region of the proposed project in order to utilize habitat specifically set aside for conservation. Increasing restriction of access to those habitats is anathema to the effort and expense of conserving those habitat areas originally and maintaining their function for wildlife. Thus any project that is built in that region should be extremely sensitive to negative impacts on mountain lions and other wildlife. Our studies of the impacts of SR's 241, 74, 78, 79, 76, and 67, and large freeways such as SR 91 and I-15, all confirm that essentially any significant highway can be both a barrier and a mortality source. Preliminary results from studies underway by our research team and other UC Davis and University of Southern California researchers, as well as those by other researchers, suggest that the light, noise, and other aspects of highways can have negative impacts on wildlife numbers and diversity near the highways. Thus highways can exert negative effects at some level even when adequate wildlife passageways and fencing are well designed. This should be kept in mind when considering the different alternatives in the Environmental Impact Statement.

As such, all of the Alternatives should be closely evaluated to ascertain that they would not further fragment the mountain lion population in the Santa Ana Mountains and put it at further risk via increased road mortality, or worsen its genetic connectivity.

The Alternatives listed in the Federal Register notice are:

Alternative 1/No Build Alternative; taking no action.
Alternative 13; connect SR 241 to I-5 via a connection from
Los Patrones Parkway to La Novia Avenue, I-5 widening and improvements,
and the addition of HOT lanes in each direction on I-5
Alternative 17; connect SR 241 to I-5 via a connection from
Los Patrones Parkway to Avenida Vaquero, I-5 widening and improvements,

and the addition of HOT lanes in each direction on I-5
Alternative 14; connect SR 241 to I-5 via a connection from Los Patrones Parkway to Avenida Pico, I-5 widening and improvements, and the addition of HOT lanes in each direction on I-5
Alternative 11; add I-5 general purpose lanes from I-405 to San Diego County
Alternative 12; add I-5 HOT/toll lanes from I-405 to San Diego County
Alternative 9; connect Ortega Highway and Antonio Parkway to Avery Parkway and SR 73
Alternative 18; connect SR-241 to SR-73 and extend Crown Valley Parkway to SR 241
Alternative 21; extend Los Patrones Parkway to Avenida La Pata and add HOT lanes in each direction on I-5
Alternative 22; extend Los Patrones Parkway to Avenida La Pata
Alternative 23; extend I-5 managed lanes from SR 73 to Basilone Road or from Avenida Pico to Basilone Road (depending on the design option)

In my view, several of the alternatives would have minimal negative impact on the Santa Ana Mountains mountain lion population. These include Alternatives 1, 11, 12, and 23c and 23d.

In my view, Alternatives 9, 13, 14, 17, 18, 21, and 22 all would potentially disrupt some mountain lion movement through this already fragmented landscape, and further disrupt local gene flow in this imperiled species unless structural plans are such that permeability is assured. All of these alternatives place the highway footprint in lands that currently host many wildlife species including mountain lions and others. Some of the named alternatives would potentially have a negative effect on subsequent major north-south or east-west movement. Alternative 18 for instance would cut a major habitat block (Chiquita Canyon) into 3 pieces, and Alternatives 14, 17, 21, and 22 would all erect another barrier to north-south movement.

In my view, Alternative 21's hot lanes could be added to I-5 without mountain lion habitat disruption, but Alternative 21's extension of Los Patrones Parkway to Avenida La Pata would likely have some detrimental impact on the local mountain lion population.

In my view, of the Alternatives that involve construction of new wide highway segments south of SR 74, Alternative 13 would appear to be least disruptive of large wildlife habitat patches, but like the other Alternatives south of SR 74, some barrier effect on north-south movement of mountain lions may occur unless extraordinary design elements are included that maximize safe travel potential and eliminate mortality potential, but that also eliminate other negative impacts of sound, light, etc from vehicles and infrastructure along the highway. These can include freeway light shielding and design, berms and walls to reflect sound and light away from the habitat, and other measures.

I feel that it is critical that any Alternative that is accepted by the various agencies involved, and the public, keep the interests of wildlife on an even par with transportation improvement in the list of goals of any project.

Thank you,

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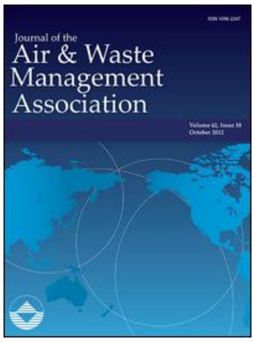

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An Analysis of Effects of San Diego Wildfire on Ambient Air Quality

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An Analysis of Effects of San Diego Wildfire on Ambient Air Quality

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ABSTRACT

The impact of major gaseous and particulate pollutants emitted by the wildfire of October 2003 on ambient air quality and health of San Diego residents before, during, and after the fire are analyzed using data available from the San Diego County Air Pollution Control District and California Air Resources Board. It was found that fine particulate matter (PM) levels exceeded the federal daily 24-hr average standard during the fire. There was a slight increase in some of the gaseous pollutants, such as carbon monoxide, which exceeded federal standards. Ozone (O_3) precursors, such as total hydrocarbons and methane gases, experienced elevated concentration during the fire. Fortunately, the absence of sunlight because of the cloud of thick smoke that covered most of the county during the fire appears to have prevented the photochemical conversion of the precursor gases to harmful concentrations of O_3. Statistical analysis of the compiled medical surveillance data has been used to establish correlations between pollutant levels in the region and the resultant health problems experienced by the county citizens. The study shows that the increased PM concentration above the federal standard resulted in a significant increase in hospital emergency room visits for asthma, respiratory problems, eye irritation, and smoke inhalation. On the basis of the findings, it is recommended that hospitals and emergency medical facilities engage in pre-event planning that would ensure a rapid response to an impact on the healthcare system as a result of a large wildfire and appropriate agencies engage in the use of all available meteorological forecasting resources, including real-time satellite imaging assets, to accurately forecast air quality and assist firefighting efforts.

IMPLICATIONS

The purpose of this research project is to document the amounts and effects of major gaseous pollutants and particulate matter emitted into the ambience of San Diego County by the wildfire of October 2003. In addition, establish correlations between pollutant levels in the region and resultant health problems experienced by the county citizenry using the medical surveillance report compiled in collaboration with area hospitals. Establishing a nexus between the major pollutants emitted and air quality related health problems would be useful in preparing for similar events and developing preventive strategies for the future.

INTRODUCTION

San Diego, the sixth largest county in the United States, is home to 2.8 million residents, and is the third most populous city in California. The county encompasses 4300 square miles and includes a mixture of urban and rural communities that live in the coast, the mountains, and the desert. It borders Orange and Riverside counties to the North, Mexico to the south, Imperial County to the East, and the Pacific Ocean to the West. San Diego enjoys desirable weather receiving only approximately 20–30 days of rain per year. Around October, this region experiences persistent dry weather and low moisture that create conditions conducive for fire that are reinforced by Santa Ana winds. It was precisely that these conditions that were partially responsible for the 2003 wildfires that besieged Southern California. These turned out to be the most disastrous in the history of the state, as they was characterized by 14 fires in the counties of San Diego, Los Angeles, San Bernardino, and Ventura.

The fires that occurred in San Diego mainly took place in three different locations. The Cedar Fire was the most intense and largest of the fires. The other two were the Paradise and Otay Fires. The Cedar Fire spread ~20 miles to the east of Interstate Route 805, then moved on toward Pine Valley and Julian to the North, and soon spread over the entire area that demarcates the communities of Ramona, Poway, Miramar, Tierrasanta, and Grossmont. The Paradise Fire covered the area of Valley Center, and the Otay Fire burnt the mountainous area close to the U.S.–Mexico border and East Chula Vista. The Santa Ana winds took the fires toward the west, directly into wild vegetations and the residential areas. The task of fighting the fires was made difficult as local wind patterns sporadically changed the direction of the fire. The whole region was blanketed with clouds of smoke, and ashes were carried over hundreds of miles. The San Diego Air Pollution Control District issued a health advisory recommending that all of the schools in the county be closed and all outdoor activities be limited for over a week. Mass attention was focused, by the increased number of hospital admissions, on what was emitted into the regional atmosphere from the fires.

The wildfire of October 2003 brought residents of San Diego and neighboring cities unprecedented devastating effects far beyond the short-term and long-term harmful suffering done to the environment, flora, and fauna. The San Diego fire consumed an area of >390,000 acres; burned 5597 homes, commercial, and accessory buildings; destroyed 3773 automobiles, trucks, and boats;[1] and caused 16 deaths.[2] The incident became a catalyst for instituting legislations that would ensure that different private and public agencies would be ready to respond to similar catastrophes in the future.

The Cedar Fire released ~300,150 t of PM and other pollutants into the atmosphere.[3] These pollutants are known to cause serious adverse health effects in the human respiratory system. If the government air quality standards are met, a healthy person can expect minimal adverse epidemiological consequences. However, when natural disasters, such as wildfires, occur, they produce such unpredictable, uncontrollable pollutant masses in the atmosphere that no living, breathing creature can escape from its poisonous effects. The purpose of this research project was to document the amounts and effects of major gaseous pollutants and PM emitted into the ambience of San Diego County by the wildfire of October 2003. Another objective was to establish correlations between pollutant levels in the region and resultant health problems experienced by the county residents, by using the medical surveillance report that was compiled in collaboration with area hospitals. It is assumed that establishing a nexus between the major pollutants emitted and air quality-related health problems would help both private and public agencies develop preventive strategies and, thus, be better prepared for similar events in the future.

Literature Review

Biomass burning and wildfires emit a substantial amount of gaseous pollutants and PM into the environment and cause people to suffer from respiratory illnesses. The seriousness of illness that they may suffer from depends not only on the concentration levels but also on individual sensitivity, physiological characteristics, and susceptibility. Other consequences include nuisance, visibility impairment, ozone (O_3) generation, and greenhouse effects. In recent years, air pollution has been considered to be an important cause or risk factor for reproductive health. There have been growing concerns about the adverse effects of air pollution on birth outcomes, such as low birth weight (LBW), intrauterine growth retardation, preterm births, and birth defects.[4–7] Coarse PM (PM_{10}) exposure in the second and fourth months has been associated with LBW.[8] Particulate air pollution has been associated with both acute and chronic exacerbation of childhood asthma. More chronic symptoms of bronchitis have been observed in previous cross-sectional studies of children with asthma exposed to PM[9–14].

Wildfire smoke is comprised of a complex mixture of particles, liquids, and gaseous compounds. These include PM_{10}, carbon monoxide (CO), nitrogen oxides (NO_x), and sulfur dioxide (SO_2), oxidants that may include small amounts of O_3, polycyclic organic material,[15] and toxic pollutants. These emissions may significantly impact air quality on local, regional, and global scales. Some events are extreme, and the contributions of fires to air pollutant concentrations are readily observable.[16] For instance, the 1997 Indonesia forest fire caused massive transboundary air pollution, producing large amounts of haze in the region and causing visibility and health problems within Southeast Asia. Furthermore, fires of such magnitude have the potential to contribute to global warming and climate change as they emit large amounts of greenhouse gases and other pyrogenic products.[17,18]

PM is the pollutant that has most consistently been associated with short-term effects on mortality.[19] Recent findings tend to relate particulate pollution to an increased plasma viscosity,[20] increased risks of heart rate,[21] electrocardiographic changes in humans,[22–24] and the triggering of myocardial infraction.[25] A high degree of human exposure to concentrated air particles has also been associated with plasma fibrinogen.[26] Several studies have indicated that the smaller particles, which are <2.5 μm in diameter, are mainly responsible for the above effects.[19]

Long-term exposure to combustion-related fine particulate and sulfur oxide (SO_x)-related air pollution has been identified as an important environmental risk factor for cardiopulmonary and lung cancer mortality. Each 10 $\mu g/m^3$ increase in fine particulate air pollution is associated with an ~4, 6, and 8% increased risk of all cause, cardiopulmonary, and lung cancer mortality, respectively. However, measures of coarse particle fraction and total suspended particles are not consistently associated with mortality.[27]

Time-series and panel studies have shown acute increases in ambient PM to be associated with increases in emergency room visits,[28] hospital admissions for asthma,[29,30] acute symptoms,[31–35] medication use,[31,33] and a decline in peak exploratory flow rates.[31,32,34] There was a 91% increase in asthma and chronic bronchitis incidences during a fire in central Florida in 1998. On average, there was a 1–1.5 day lag between the fire event and the increased emergency room visits and in-patient admissions for asthma.[36]

The most abundant air pollutant from wild land fires is CO. This, coupled with carbon dioxide and methane (CH_4), has been found to be a significant source of greenhouse gases. Besides CO, NO_x can also form at lower temperatures, although the amount primarily depends on the nitrogen content of the fires burnt. However, the SO_x produced are in negligible quantities, because forest fires normally contain low sulfur content. Fires also emit a large amount of semivolatile organic compounds (VOCs), which are partitioned between the gaseous and liquid or solid phase at ambient temperatures. Some VOCs are carcinogenic and can condense or absorbed into the surface

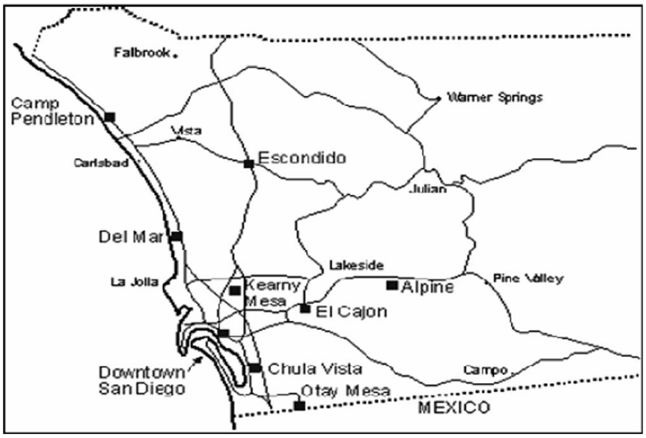

Figure 1. San Diego APCD-chosen monitoring stations.

of the particulate. Incomplete combustion produces hydrocarbons, including ethylene, alkynes, aldehydes, furans, and carboxylic acids.[15]

The main health impact is from the exposure to PM. It is a major component of smoke and is comprised of a complex mixture of soot, tars, and volatile substances and, thus, is harmful to human health.[15] In many cases, pollutant gases, such as SO_x, NO_x, and VOCs, interact with other compounds in the air to form fine particles. Their chemical and physical compositions vary depending on location, time of the year, and weather.[37] Fine PM ($PM_{2.5}$) is becoming more commonly measured during fire-related incidents, because the fine fraction predominates in the smoke and haze, and it is thought to be more responsible than larger particles for the observed health effects.[38,39]

Methodology

San Diego Air Pollution Control District (APCD) has established nine air monitoring stations that are strategically located to evaluate pollution levels that affect the county residents (Figure 1). Each station monitors specific pollution levels borne by sources pertaining to the area, such as stationary and mobile sources (Table 1).

To assess the impact of the pollutants emitted by the San Diego Wildfire, a 4-week baseline surveillance period before the start of fire (October 25, 2003), a 10-day period during the fire, and a 4-week post-fire surveillance period immediately after the fire were established. For the purpose of analysis, data were primarily obtained from two urban and one remote monitoring locations: Downtown San Diego, Escondido, and Alpine. Downtown San Diego and Escondido are heavily urbanized with a high density of vehicular population. Alpine is a rural town ~25 miles east-northeast of the city of San Diego. It is in the foothill zone, and its western sloping terrain traps air pollutants. For the purpose of this study, average daily, 1-hr maximum and 8-hr maximum readings were referenced to analyze the resultant effects of gaseous pollutants. Standard and local conditions for PM were also noted. Contributions by O_3 precursors, such as total hydrocarbons (THC), CH_4, and non-CH_4 hydrocarbons, were analyzed to determine the behavior of the major pollutants. The conditions for each criteria pollutant of concern in 2002 were recorded by San Diego County as described below.[40]

Table 1. Pollutants monitored by the nine monitoring stations in the San Diego APCD.

Station	Pollutant Measured
Alpine	O_3, NO_2, NO, NO_x, PM_{10}
Camp Pendleton	O_3, NO_2, NO, NO_x
Chula Vista	O_3, NO_2, NO, NO_x, PM_{10}, $PM_{2.5}$
Del Mar	O_3
El Cajon	O_3, NO_2, NO, NO_x, PM_{10}, $PM_{2.5}$, CH_4, non-CH_4 hydrocarbon, THC
Escondido	O_3, NO_2, NO, NO_x, CO, $PM_{2.5}$
Otay Mesa	O_3, NO_2, NO, NO_x, CO, SO_2, PM_{10}
San Diego–Downtown	O_3, NO_2, NO, NO_x, CO, SO_2, PM_{10}, $PM_{2.5}$
Kearny Mesa	O_3, NO_2, NO, NO_x, CH_4, THC, PM_{10}, $PM_{2.5}$

O_3. O_3 levels were measured in all nine of the locations. The county did not exceed the federal 1-hr concentration of 0.125 ppm. However, the federal 8-hr concentration of 0.085 ppm was exceeded for a total of 13 days. The Alpine station measured the greatest number of days exceeding the 8-hr standard[12] days for O_3. This was because emissions from motor vehicles, industry, and anthropogenic activities were blown inland through dense urban areas by the onshore breeze and tended to stay along the west-facing mountain slopes ~2000 ft above sea level. There were also enough pollutant generators in San Diego County to contribute to higher pollution concentrations. The region has adequate conducive atmosphere to produce higher O_3 levels, such as persistent light winds, hot temperature, and plenty of sunlight.

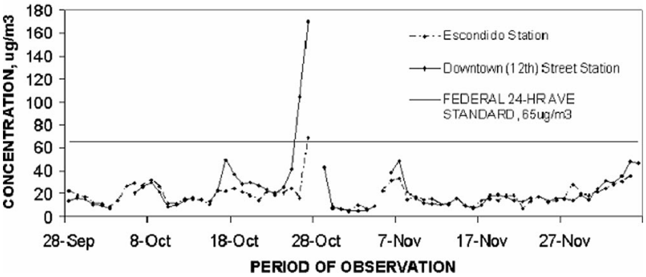

Figure 2. $PM_{2.5}$ daily 24-hr average measurements during the surveillance period.

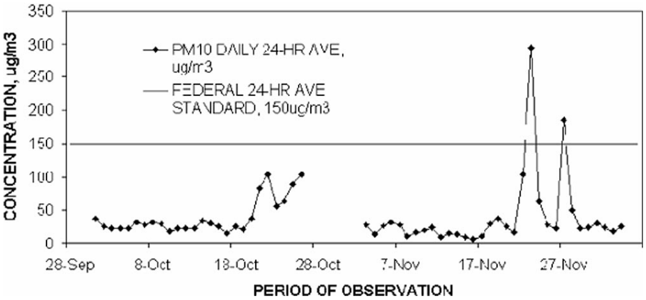

Figure 3. PM_{10} measurement in Alpine station during the surveillance period.

PM_{10}. San Diego APCD measured PM_{10} standards as mandated by both federal and state governments in six locations as shown in Table 1. The stations collected 24-hr samples on specific filters and compared data to air quality standards (annual arithmetic mean: federal –50 μg/m^3 and state –20 μg/m^3; and maximum 24-hr, federal –150 μg/m^3 and state –50 μg/m^3). The results indicate that the county did not exceed the federal standards except for one location, Otay Mesa, where a high volume of border crossings occurred, and this contributed to a high generation of PM_{10}. However, most locations failed to meet state standards, which are more stringent than federal standards.

$PM_{2.5}$. $PM_{2.5}$ samples were collected daily in three sites, El Cajon, Escondido, and downtown San Diego. Samples from Kearny Mesa and Chula Vista were taken for measurements every third day. All of the locations met the federal 24-hr standard of 65 μg/m^3 for $PM_{2.5}$. Three sites exceeded the annual standard, arithmetic mean 15 μg/m^3, and the more stringent state standard of 12 μg/m^3.

CO. The county attained all of the federal and state standards for CO (maximum 1-hr concentration of 35 ppm for federal and 20 ppm for state, and maximum 8-hr concentrations of 9 ppm for federal and state). The emissions of CO came primarily from automotive vehicles. Strict motor vehicle emission requirements controlled CO emissions formed during combustion.

NO_2. The annual average federal allowable standard is 0.053 ppm, and the California maximum 1-hr standard is 0.25 ppm. The county has not exceeded either of these limits in more than a decade.

SO_2. There has never been a violation of SO_2 exceeding the standards in San Diego County, although three federal standards and two state standards are in place to limit SO_2 pollution. The three federal standards include an annual average of 0.030 ppm, a maximum 24-hr concentration of 0.14 ppm, and a maximum 3-hr concentration of 0.5 ppm. More stringent state standards are a maximum 24-hr concentration of 0.05 ppm and a maximum 1-hr concentration of 0.25 ppm.

The San Diego APCD archives the data on the pollutants, which were measured from the nine monitoring stations. In addition to this source of raw data, similar data are available from the California Air Resources Board (CARB). The meteorological impact on the behavior of pollutant dispersion and movement during the fire was based on the daily forecast generated by San Diego APCD meteorologists. Real-time observations of the meteorologists were also taken into consideration in the analysis of the overall impact to ambient air quality from the fires.

Before October 1, 2003, San Diego County APCD was using the Federal Reference Method (FRM) samplers to collect $PM_{2.5}$ data for data analysis and archiving. The FRM is based on statistical analyses of filter samples collected at the five monitoring stations located throughout the county. These five stations are located in downtown San Diego (Twelfth Avenue), Chula Vista, El Cajon, Kearny Mesa (Overland Avenue), and Escondido. When San Diego APCD became part of the national forecasting program on October 1, 2003, district meteorologists began relying on data collected from the two $PM_{2.5}$ Beta Attenuation Monitor (BAM) samplers for real-time data reporting and forecast verification. Statistical analysis of the FRM data did not show sharp gradients across the county or radical departures from mean conditions. As a result, the two BAM samplers were thought to be adequate for ambient conditions expected in the county. These two BAM samplers are located at downtown San Diego and Escondido monitoring stations. The only real-time PM_{10} Tapered Element Oscillating Microbalance (TEOM) sampler is located at the Alpine monitoring station. Meteorological data were provided by the District Radar Wind Profilers (RWPs) and the Radio-Acoustic Sounding Systems (RASS) located in Miramar and Point Loma.

Medical Surveillance Methods

Health effects to county residents were assessed through the efforts of San Diego County Health and Human Services Agency, Public Health Services. On Tuesday, October 28, 2003, in response to the fires, smoke, and circulating ashes, a fire-related surveillance process was developed, and by Thursday, October 30, 2003, 15 of the 19 civilian hospital emergency departments in the county (two Navy hospitals were excluded from this surveillance) were asked to participate in this fire-related surveillance. A 3-week surveillance period was established, including 1 week of baseline (pre-event) and 2 weeks following the fires. Because this surveillance was conducted during the fires, the intent was to capture critical information from a limited time period to quickly assess the impact of the fires.

A number of potential fire-related indicators were identified as categories to be monitored. These surveillance categories included the following: asthma, bronchitis, or emphysema; other respiratory conditions with no fever; eye irritation; smoke inhalation; burns; chest pain or cardiac arrests; and diarrhea. The total number of visits made by patients to the hospital was also considered. Each hospital was asked to provide the necessary data to support these surveillance activities.

A standard univariate approach to analysis of the surveillance data using a variety of statistical quality control charts was used in this project. Atypical increases in the number of emergency department (ED) visits, in terms of raw numbers and as a proportion of total ED visits, were monitored with U-charts and P-charts, respectively. Additionally, exponentially weighted moving average (EWMA) charts were generated to detect small shifts in the mean of a variable over time. Time series graphs were generated to evaluate the behavior of the variable over time, and detailed descriptive statistics were inspected to gain insight into the long-term behavior and distributional properties of the variable, including measures of central tendency, dispersion, and degree of normality.

Estimated Amount of Emissions Computation Method

In a study conducted by the University of California, Berkeley,[3] for the CARB, researchers used the U.S. Department of Agriculture Forest Service First-Order Fire Effects Model

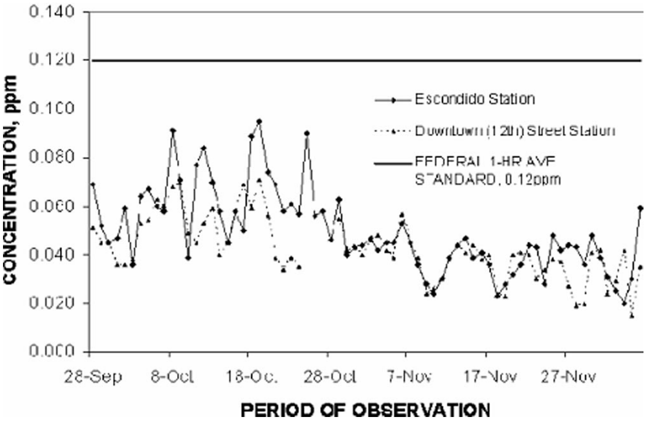

Figure 4. O_3 daily max. 1-hr average measurements during the surveillance period.

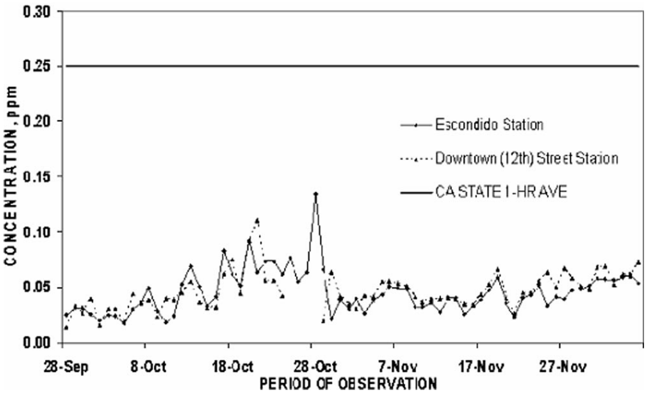

Figure 6. NO_2 California State 1-hr average standard measurements during the surveillance period.

(FOFEM), adapted to run in a Geographic Information System, to assess the fuels that contributed to the fires and the emission amounts and components that resulted from the combustion. The model requires the following inputs: (1) a spatial fuel, vegetation, or land cover map, which should contain vegetation types that can be linked to the FOFEM fuel model library to determine preburn fuel loadings in terms of tons per acre; (2) a fuel model look-up table, which is a relational database table that contains characteristic loadings in several fuel categories and a link to the vegetation-type map that establishes the loadings to be used for each vegetation type; (3) a fire perimeter map, which establishes the spatial extent of the burn area and can be decomposed temporally (into daily perimeters, for example) if those data exist; and (4) user-defined parameters of fuel moisture, seasonality, and fuel loadings.

RESULTS AND DISCUSSION

Data on pollutants between the period of September 28 and December 6, 2003, from Escondido, downtown (12th Avenue), Kearny Mesa (Overland Avenue), and Alpine monitoring stations were analyzed. The Escondido and downtown stations provided gaseous pollutants and $PM_{2.5}$ data. The PM_{10} data from Alpine station and gaseous pollutant data from Kearny Mesa station, along with meteorological data recorded by San Diego APCD RWPs and RASS located in Miramar and Point Loma were analyzed. Statistical analysis of medical surveillance data compiled by San Diego County Health and Human Services Agency in collaboration with area hospitals was used to establish correlations between pollutant levels in the region and resultant health problems experienced by the county citizens.

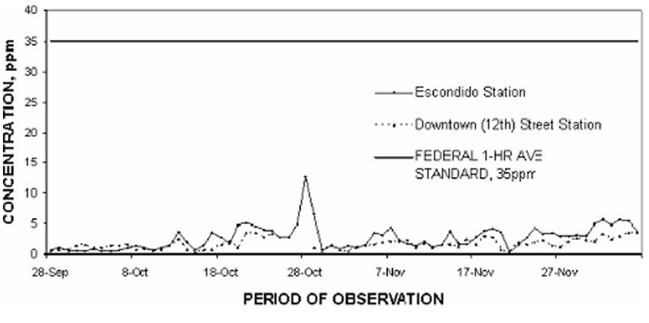

Figure 5. CO federal 1-hr average standard measurements during the surveillance period.

PM

$PM_{2.5}$. The $PM_{2.5}$ trend during the observation period is shown in Figure 2. On October 27, 2003, during the fire, the $PM_{2.5}$ U.S. Environmental Protection Agency (EPA) limit of 65 $\mu g/m^3$ was exceeded in the Escondido station. This measurement was recorded by the FRM monitor. The recorded readings during the period before and after the fire episode did not exceed the EPA limit. The data plot before and after the fire episode reveals a consistent trend.

The $PM_{2.5}$ trend during the observation period in the downtown station is shown in Figure 2. During the fire episode on October 26, 2003, the first full day of the fire, $PM_{2.5}$ daily 24-hr average measurement rose sharply to 104.6 $\mu g/m^3$. On October 27, 2003, $PM_{2.5}$ daily 24-hr average measurement recorded was $>$2.5 times the EPA limit at 170 $\mu g/m^3$. However, similar to the Escondido station, the EPA limit was not exceeded during the surveillance period, the period before and after the fire episode. The data plot revealed a consistent trend before and after the fire episode.

PM_{10}. The Alpine station monitors real-time PM_{10} using the TEOM monitor. The PM_{10} trend measurement for the

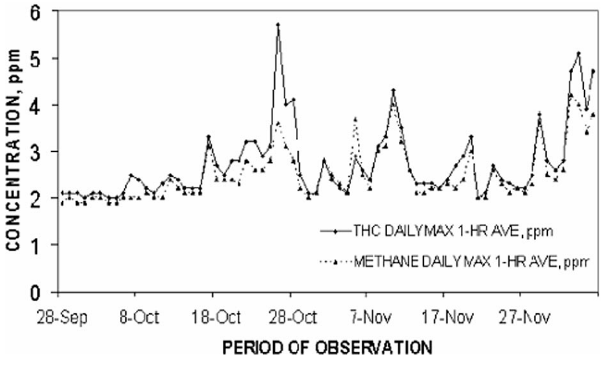

Figure 7. CH_4 and total THC measurement at the Overland station (Kearny Mesa) during the surveillance period.

Figure 8. Photograph of the localized turbulence near the fire.

Alpine station is shown in Figure 3. There was no real-time measurement recorded between October 27 and November 2, 2003, because power supply to the Alpine monitoring station was interrupted by the fire. Just before data recording was lost, the trend showed a steady increase, although it did not reach the maximum 24-hr average federal standard of 150 μg/m^3. However, the FRM PM_{10} measurement from the Escondido station recorded 179 μg/m^3 on October 29, 2003. This level exceeded the federal maximum 24-hr average limit. Therefore, it could be inferred that if the Alpine real time monitor was functional at that time, it would have recorded a much higher concentration because of its close proximity to the fire. Real-time measurement indicated an unusually high concentration of PM_{10} on November 23 and 27, 2003, at 294 μg/m^3 and 184 μg/m^3, respectively. This was because of the Santa Ana wind condition during that time frame. The strong offshore wind direction stirred and carried the ashes deposited in the burned areas.

Gaseous Pollutants

Three gaseous pollutants of concern namely O_3, CO, and NO_2 were analyzed at the Escondido and downtown (Twelfth Avenue) stations based on data recorded by the station monitoring equipment. No data were available between October 25 and October 28, 2003, the period when the fires were burning. The station equipment monitoring these parameters was powered down to support construction efforts of the ballpark nearby.

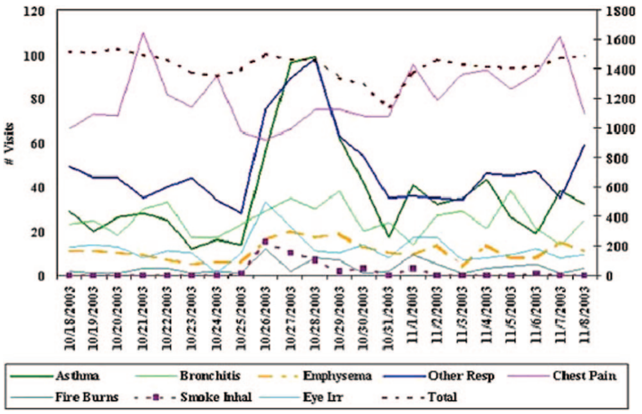

Figure 9. Frequency of selected types of visits to San Diego hospital EDs.

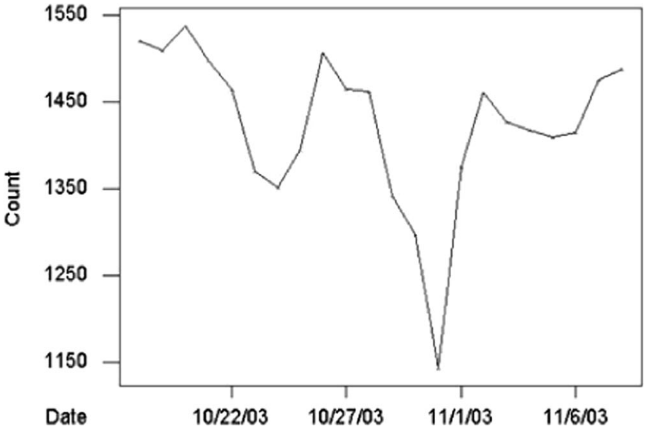

Figure 10. Time-series plot for total visits (interval: October 18–November 8, 2003).

O_3. The O_3 trend during the observation period is shown in Figure 4. Throughout the surveillance period, the federal 1-hr O_3 concentration of 0.12 ppm was not exceeded on either the Escondido or downtown station. The trend showed a relative decrease in concentration after the start of the fire and continued until the end of the surveillance period.

CO. The CO trend during the surveillance period at the Escondido and downtown stations is shown in Figure 5. Recorded data showed that CO concentrations before, during, and after the fire were well below and did not exceed the federal 1-hr standard of 35 ppm. However, on October 28, 2003, the state and federal 8-hr standard was exceeded by 1.6 ppm over the 9-ppm maximum.

NO_2. The NO_2 trend during the surveillance period in Escondido station is shown in Figure 6. There is no federal 1-hr maximum concentration for NO_2. However, the state of California mandates a 1-hr maximum concentration

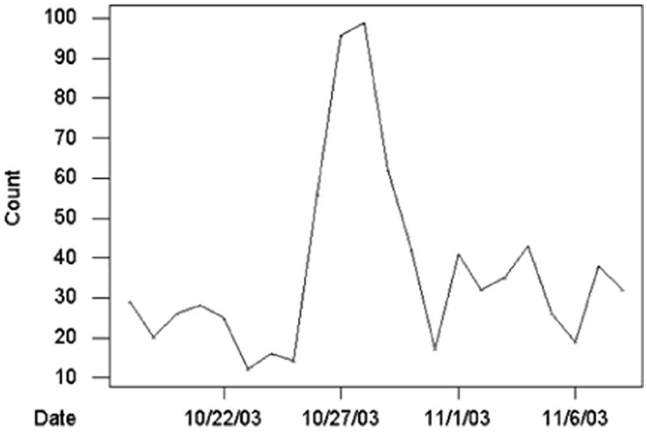

Figure 11. Time-series plot for asthma. (interval: October 18–November 8, 2005)

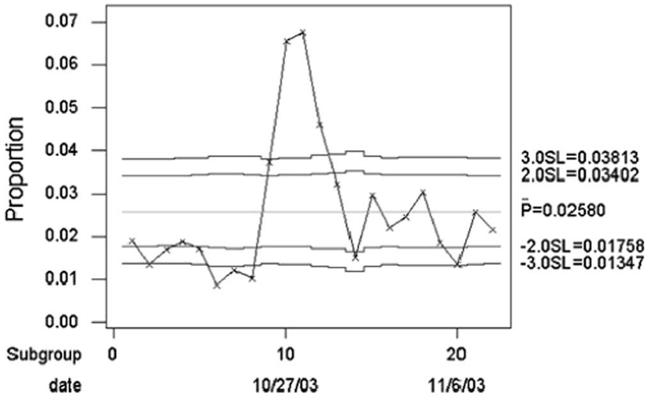

Figure 12. P-chart plot for asthma (interval: October 18–November 8, 2003).

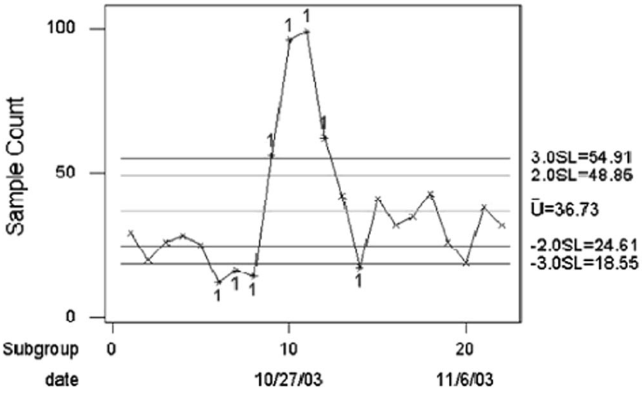

Figure 13. U-chart plot for asthma (interval: October 18–November 8, 2003).

level for NO_2 of 0.25 ppm. Recorded data showed that NO_2 concentrations before, during, and after the fire did not exceed the California state 1-hr standard of 0.25 ppm in both the Escondido and downtown stations.

CH_4 and THC. The CH_4 and THC trend during the surveillance period is shown in Figure 7. The Overland Avenue station is the station closest to the Cedar Fire in which CH_4 and THC were measured.

Meteorological Influence

The San Diego APCD forecasted for a moderate level of $PM_{2.5}$ throughout the county from Saturday, October 25, 2003, through Sunday, October 26, 2003, because of the Santa Ana winds. Santa Ana winds are warm, dry winds that blow from the east (offshore) and have wind speeds $>$25 knots (12.9 m/sec). The Cedar Fire began at ~5:30 p.m. on Saturday, October 25, 2003. On Saturday evening, at ~7:30 p.m., data recorded by the San Diego APCD RWP indicated a wind direction shift that was consistent with Santa Ana condition.

Although on October 26, 2003, the fire was driven in the southwest direction by the Santa Ana winds, there was no significant surface smoke impact except in the areas immediately around the fire. The wind condition near the coast was not strong. The Point Loma RASS recorded a shallow mixed layer during the morning followed by a weak neutral atmosphere later in the day. These conditions were not conducive to heavy smoke impacts at the surface level from a lofted plume of smoke.

As the first full day of the fire progressed on October 26, 2003, conditions in the close proximity of the fire recorded a different result. Throughout the morning, the fire advanced rapidly in a southwesterly direction and burned the heavily populated communities of Poway, Miramar, and Tierrasanta. Flames and a vortex of heavy smoke prevailed in the vicinity of the fires, particularly downwind and on the leading edge of the fire. Figure 8 shows the localized turbulent condition as the wind fanned the fire. In addition, the intense fire produced its own circulation, an indication of a firestorm.

The Santa Ana wind condition decreased in strength toward the end of the day on October 26, 2003. Consequently, the westward progression of the fire was either stopped or was put under control. At dawn of October 27, 2003, the fire progression was shifted toward the east, away from major population centers and into the mountain communities. Data recorded on October 27, 2003, showed offshore winds aloft during the first half of the day followed by a turning of the winds to weak onshore in the early afternoon and then general stagnation conditions during the evening and nighttime. At the same time, the recorded data showed an isothermal atmosphere during the early morning with surface-based inversion forming later in the day. These meteorological conditions were more conducive to trapping smoke in the surface layer.

On October 28, 2003, the data recorded showed wind conditions becoming stagnant during the day with low-level winds becoming southerly in the evening. The data also showed a surface-based inversion during most of the day. These stable conditions were conducive for trapping the smoke in the surface layer. Even as the fires continued burning eastward into the more rural areas of the county, satellite imaging taken by the National Oceanographic and Atmospheric Administration showed an abrupt stop and slow smoke movement offshore.

Data recorded on Wednesday, October 29, 2003, showed southerly winds in the low levels during the early morning hours, turning to offshore during the day and south-southwest and southerly winds at night. For the same day, the recorded data showed a shallow marine layer capped by an inversion that lifted during the day and dissipated at night. These conditions were consistent with air mass change and improved air quality conditions. Although the fires continued to burn in the inland, mountain areas of the county, similar meteorological conditions continued until the fire was out on November 4, 2003.

Medical Surveillance

During the surveillance period, 15 of the 19 hospitals (79%) participated by providing the following surveillance information from October 18 through November 8, 2003: (1) number of patients admitted to the hospital; (2) date of admission; and (3) type of medical problems encountered (asthma, bronchitis, emphysema, other respiratory problems, and/or chest pain).

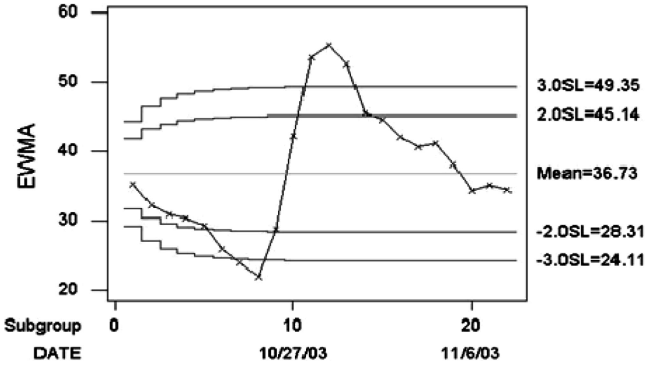

Figure 14. EWMA plot for asthma (interval: October 18–November 8, 2003).

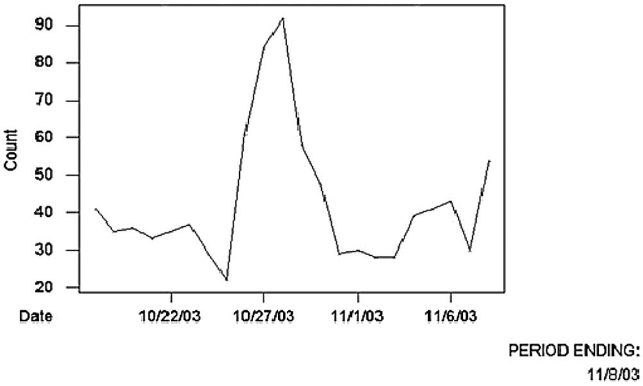

Figure 15. Time-series plot for other respiratory conditions with no fever (interval October 18–November 8, 2003).

The participating hospitals represented geographic diverse locations and included several hospitals near the fire-impacted areas. As seen in Figure 9, several of the surveillance indicators increased significantly during the periods of the fire. The most dramatic increase was asthma and other respiratory complaints with no fever. Each of the surveillance indicators is additionally described below.

Total Visits. The impact of the fires on area ED visits varied across hospitals. In total, information on 31,321 visits was recorded and analyzed. For the surveillance time period, the mean number of cases was 1423 visits per day among 15 hospitals. In general, the total number of ED visits declined (Figure 10) during selected periods of the fire. The day with the minimum number of total visits was October 31, 2003. The period of greatest decrease in total volume of patients corresponds with the days that the schools and employees were asked to remain at home (October 27–31, 2003). When the total visits were analyzed using the EWMA method, the mean number of total visits continued to remain lower for over a week after the fires began. During this period, the moving average decreased substantially.

Asthma. Several respiratory indicators were monitored at EDs throughout the county, and related visits were assessed. In general, each of the respiratory indicators demonstrated significant increases during the fire period with expected postfire levels approaching prefire levels with the decline in the fires and subsequent improvement in air quality.

Asthma-related visits increased significantly, particularly during the days of greatest fire burn and unhealthy air quality. Both the total number of asthma visits and the proportion of asthma visits increased. These increases correspond well with the increases in the air quality index. Figure 11 displays the number of asthma-related visits over time with the days of greatest number of asthma-related visits occurring on Tuesday, October 28. Controlling for the total number of visits, Figure 12 includes the proportion of asthma-related visits during the surveillance period. Additional information about the asthma-related results are detailed in Figures 13 and 14.

Bronchitis. Bronchitis-related visits were monitored, and they showed a slight increase during the surveillance period when they were measured using the same methodology as the one used for asthma-related cases. The mean number of cases across all of the participating hospitals was 25 per day. Although a slight increase in bronchitis-related visits was noted in each of the analyses, the increase was neither significant nor sustained.

Other Respiratory with No Fever. The surveillance category for other respiratory illness/problems with no fever-related visits were analyzed. The intention of this indicator was to track people with a multitude of respiratory-related symptoms not previously identified as asthma, bronchitis, or respiratory illness that occur along with fever, such as influenza and pneumonia. A dramatic increase in visits with complaints primarily associated with the other respiratory illnesses without fever observed after the beginning of fires on October 25 is likely a direct result of the increasingly poor air quality. Analysis of this indicator reveals that both the total number of visits and the proportion of visits increased significantly, particularly during the days of greatest fire burn and ash fallout (Figures 15 and 16, respectively).

Smoke Inhalation. Because of the large area of fire burn in both densely and rural populated areas, it was expected

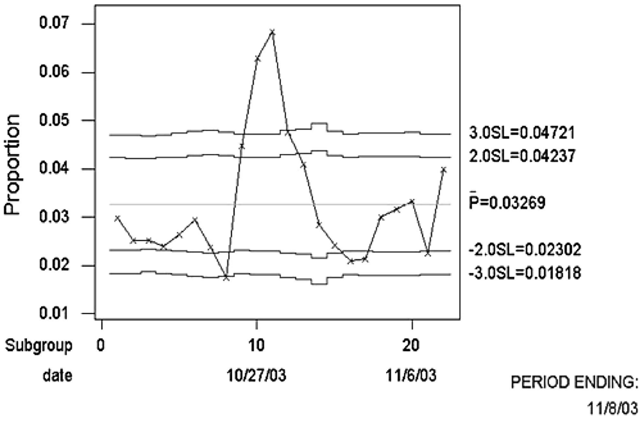

Figure 16. P-chart plot for other respiratory conditions with no fever.

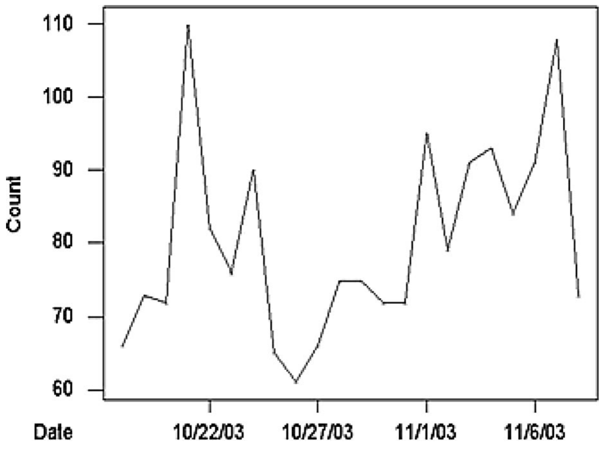

Figure 17. Time series plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

that hospitals would experience a number of patients with smoke inhalation. Although the overall number of smoke inhalation-related visits across participating hospitals was small each day during the surveillance period, smoke inhalation-related visits increased markedly. Both the total number of smoke inhalation visits and the proportion of visits increased for a brief period during the periods of greatest fire burn.

Eye Irritation. Because of several days of large ash fall throughout San Diego County, it was expected that a number of patients would seek treatment for eye irritation at EDs. The indicator for eye irritation was analyzed. Although very few patients experiencing eye irritation problems were reported during the prefire period, a brief increase in those with eye irritation occurred during the days of greatest fire burn and ash fallout.

Chest Pain/Cardiac Arrest. Because of the uncertainty of determining how the fire and air quality would impact patients suffering from chest pain or cardiac arrest, an indicator was selected to assess the same during the surveillance period. The indicator for chest pain was analyzed. As seen in Figures 17 and 18, the number of chest pain and cardiac arrest visits does not appear to have noticeably increased as a result of the fire. Figure 19 describes the U-chart and Figure 20 describes the EWMA during this time. Although the time period is limited to ~3 weeks, it is difficult to determine whether this pattern is typical during nonfire periods.

Diarrhea/Gastroenteritis. During the fires, selected parts of the county were without power for several days. Because of the increased chance of people consuming spoiled food or contaminated water, an indicator for diarrhea/gastroenteritis was monitored. This indicator was analyzed using the same criteria explained before. In general, diarrhea-related visits during this surveillance period did not increase or decrease from the usual trend.

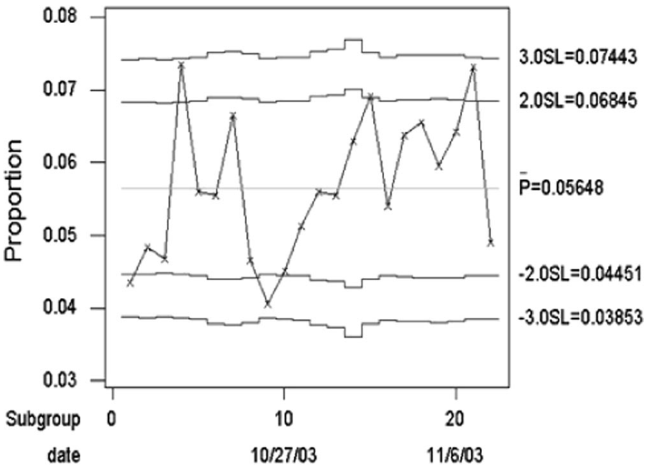

Figure 18. P-chart plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

Sources and Estimated Amount of Emissions

The estimated prefire fuel loading for the Cedar and Paradise fires, the predominant fires that occurred about the same time, is shown in Table 2. Table 3 shows the estimated emission amounts of selected pollutants. The data

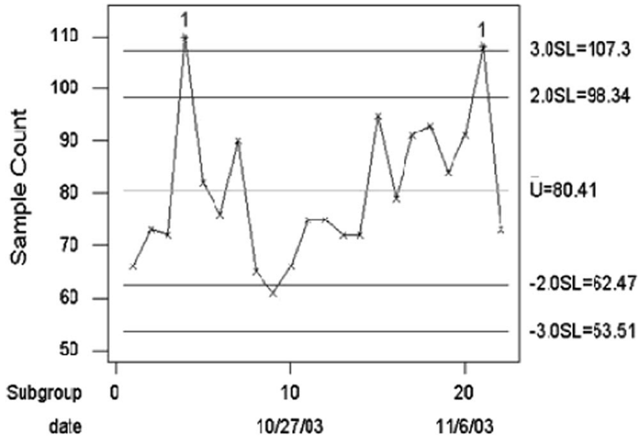

Figure 19. U-chart plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

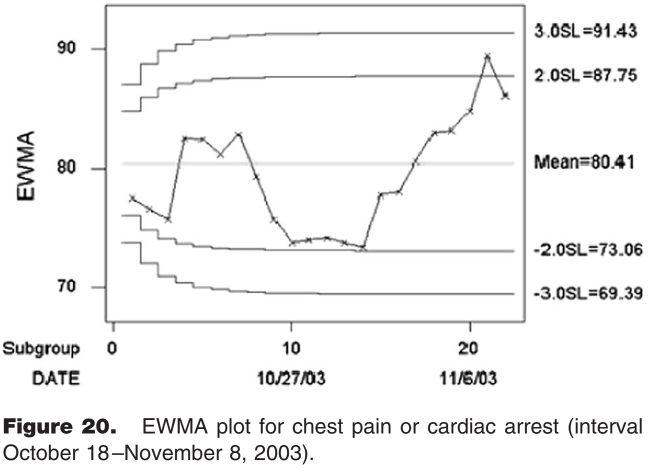

Figure 20. EWMA plot for chest pain or cardiac arrest (interval October 18–November 8, 2003).

Table 2. Estimated prefire fuel loading in tons.

Fuel Component	Paradise Fire	Cedar Fire	Total Both Fires
Canopy branch wood	0	12,104	12,104
Canopy foliage	0	85,399	85,399
Duff	86,059	509,287	595,346
Herbs	6562	43,983	50,545
Litter	27,458	151,329	178,814
Regen	286	3447	3733
Shrubs	321,020	1,585,703	1,906,723
Wood 0–1 inch	2861	23,483	26,344
Wood 1–3 inch	0	12,115	12,115
Wood >3 inches	0	87,059	87,059
Total all fuel types	444,246	2,513,909	2,958,155

output for preburn conditions and emissions tabulated in Tables 2 and 3 was based on the Cedar and Paradise fire perimeter input and processed by the FOFEM. The model determined the emissions based on the moisture content of the fuel and the moisture in the burning environment and the preburn fuel loading from the fuel models.[3]

CONCLUSIONS

On the first full day of the San Diego Wildfire on October 26, 2003, the Overland Avenue station recorded the highest THC concentration level, about twice the average concentration of the period before the fire. THC is a precursor to the formation of ground-level O_3. However, the meteorological condition during this phase of the fire progression was such that the heavy smoke produced by the fire was allowed to rise and blanket the entire county. Photochemical reaction provided by sunlight did not happen. Therefore, O_3 levels on this day and subsequent days during the fire remained below the allowable levels set by EPA at 0.12 ppm.

The CO concentration level rose by 250% on October 28, 2003, at the Escondido station, the highest recorded level during the fire and during the surveillance period, which slightly exceeded the state and federal 8-hr average. There was a 100% increase in the NO_2 level recorded on October 28, 2003, at the Escondido station. However, this level is within the allowable limit of 0.25 ppm according to the California state daily maximum 1-hr average standard. Although there were no data available on O_3, CO, and NO_2 at the downtown station on October 25–28, 2003, other stations that monitor these pollutants of concern did not record concentrations that exceeded the allowable limits during the entire period that the downtown station was offline.

Table 3. Emissions mass estimate totals, in tons.

Pollutant	Paradise Fire	Cedar Fire	Total Both Fires
PM_{10}	3951	22,610	26,561
$PM_{2.5}$	3,354	19,188	22,542
CO	38,963	222,190	261,153
CH_4	1558	8886	10,444
TNMHC	2727	15,549	18,276
NH_3	388	2221	2609
N_2O	69	399	468
NO_x	1198	6958	8156
SO_2	371	2147	2518

TNMHC = total non-CH_4 hydrocarbon.

The meteorological condition that allowed the heavy smoke to lift and create a thick blanket that turned day almost into night let the PMs settle over most of the county. Consequently, the downtown and Escondido stations recorded the highest level of $PM_{2.5}$ concentration. The downtown station recorded a $PM_{2.5}$ concentration of 104.6 $\mu g/m^3$ on the first full day of the fire on October 26, 2003, and 170.1 $\mu g/m^3$ on October 27, 2003. The Escondido station recorded a 69.2 $\mu g/m^3$ $PM_{2.5}$ concentration on October 27, 2003. All of these readings exceeded the federal daily maximum 24-hr average.

The ability of the fire to create a localized weather condition, such as a different wind pattern from the general prevailing condition, suggests that actual levels of pollutants in random points within the surveillance area may vary from measured levels recorded by the monitoring stations. During the fire, actual air quality depended on where one was located in the affected areas of the county. This also accounted for the variance in the concentration levels above the allowable range for those pollutants that exceeded established standards as recorded in different monitoring stations.

Meteorological conditions that allowed for massive air mass change, such as that which began to prevail on October 29, 2003, during the fire, helped mitigate the effects of pollutants to affected areas. This was indicated by the decrease in concentration of pollutants to allowable levels and the decrease in ED admissions during the surveillance period.

The total number of ED visits declined during the period of the fire, and these correspond with the days that the school children and employees were asked to remain at home. In addition, many roads and freeways were closed because of the fires. Each of these is likely to have influenced the behavior of people seeking treatment or refuge at local EDs. These results presented in the medical surveillance demonstrated that selected increases in certain types of ED visits did occur during this period. Particularly, selected respiratory-related conditions increased significantly. Communication with various medical providers during the fires indicated that the ash, smoke, and unhealthy air quality resulted in an increase in asthma-related medical visits and inquiries.

There are a number of limitations associated with an assessment related to the disaster. The medical surveillance was primarily based on the chief complaint of the patient on arrival at the ED. Because this is not the final diagnosis of the patient's reason for visit, it is possible, although unlikely, that the final results may have been slightly different from that presented by this study. Additional studies are needed to additionally assess the impact of the fire on ED utilization trends, long-term impact of the fire on health outcomes, and the effect of a local disaster on health service options.

The results indicated that there was a direct correlation between the increase in PM, specifically $PM_{2.5}$, concentration level and the significant increase in ED visits for asthma, other respiratory with no fever, eye irritation, and smoke inhalation. The pattern for increase in emergency visits for asthma was consistent with documented studies from previous wildfires[36] in which there was a 1–1.5-day lag between the periods of exposure to high concentrations of PM from wildfires to the actual time of admission.

The FOFEM results indicated that shrubs and duff were the predominant sources of combustion, totaling ~2.5 million t or ~85% of the fuel components of the San Diego wildfire. Clearly, these were catastrophic fire events that burned, for the most part, in chaparral and other shrub-dominated ecosystems.[3]

RECOMMENDATIONS

The following recommendations are made in the event a similar catastrophe occurs in the future: (1) improve the capability of accurate real-time monitoring of PMs, because it is the pollutant of concern that has an immediate impact on the health of county residents; mobile monitoring capability is an added resource, because it can better assess the actual condition independent of prevailing meteorological condition; (2) encourage hospitals and emergency medical facilities to engage in preevent planning that would ensure a rapid response to an impact on the healthcare system as a result of a large wildfire; and (3) use all available meteorological forecasting resources, including real-time satellite imaging assets to accurately forecast air quality, assist firefighting efforts, and mobilize emergency service providers.

ACKNOWLEDGMENTS

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RESEARCH ARTICLE

Residential development alters behavior, movement, and energetics in an apex predator, the puma

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Abstract

Human development strongly influences large carnivore survival and persistence globally. Behavior changes are often the first measureable responses to human disturbances, and can have ramifications on animal populations and ecological communities. We investigated how a large carnivore responds to anthropogenic disturbances by measuring activity, movement behavior, and energetics in pumas along a housing density gradient. We used log-linear analyses to examine how habitat, time of day, and proximity to housing influenced the activity patterns of both male and female pumas in the Santa Cruz Mountains. We used spatial GPS location data in combination with Overall Dynamic Body Acceleration measurements recorded by onboard accelerometers to quantify how development density affected the average distances traveled and energy expended by pumas. Pumas responded to development differently depending on the time of day; at night, they were generally more active and moved further when they were in developed areas, but these relationships were not consistent during the day. Higher nighttime activity in developed areas increased daily caloric expenditure by 10.1% for females and 11.6% for males, resulting in increases of 3.4 and 4.0 deer prey required annually by females and males respectively. Our results support that pumas have higher energetic costs and resource requirements in human-dominated habitats due to human-induced behavioral change. Increased energetic costs for pumas are likely to have ramifications on prey species and exacerbate human-wildlife conflict, especially as exurban growth continues. Future conservation work should consider the consequences of behavioral shifts on animal energetics, individual fitness, and population viability.

Introduction

Habitat conversion is a primary driver of species extinctions and increases exposure of wildlife to anthropogenic disturbances [1]. These disturbances influence many integral animal behaviors (e.g., foraging, mating, and movement) [2] and transform species interactions [3–4].

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Conversion to low-density development at the wildland-urban interface is the fastest growing type of land use change in the continental United States [5] and is expected to continue expanding in the coming decades [6]. Although many species, including mammalian apex predators, continue to live at the wildland-urban interface [7], these regions may prove to be population sinks due to the increased risk of human-caused mortality or from the costs of adopting behavioral adaptations in response to human disturbances [8].

Behavioral changes by animals often provide the first measurable indication that individuals are responding to anthropogenic disturbance [9–11]. These behavioral responses can alter energetic budgets with important effects on individual fitness that may lead to population and community level changes. Movement behavior in particular carries rich information about where, when, and how an animal interacts with its surroundings, providing insight into the relationship between internal state and environmental factors [12]. Technological advances with GPS and accelerometer tracking devices now allow scientists to link animal movement behavior to caloric expenditure, which greatly increases our understanding of how animal energetics are impacted by human development at the landscape level. With the integration of accelerometers and traditional biologgers, we can monitor how natural and anthropogenic landscape structures change behavioral patterns and energy allocation in wild animals [13], with far ranging conservation implications for species living at the wildland-urban interface.

Large carnivores are frequently the first species to be lost from ecosystems as humans transform and develop landscapes [14]. Despite this, comparatively little is known about the behavioral and energetic responses of predators to development that could eventually lead to their local extirpation [15]. Large carnivores often respond to human disturbance and persecution through behavioral modifications much like prey species respond to predators [10]. Pumas (*Puma concolor*) have demonstrated behavioral responses to human developments by avoiding roads, moving quickly through developed areas, and changing temporal feeding patterns [8,16]. As human development continues to fragment previously intact landscapes, it becomes increasingly vital to understand how large carnivores adjust their behavior and energetic responses to anthropogenic perturbations. Only by better understanding these relationships can we implement protective policies that reduce human-wildlife conflict and promote their continued co-existence with humans [17].

Here we examined how human development alters daily behavior and energetics of pumas in the Santa Cruz Mountains of central California. We investigated the extent to which proximity to houses affected puma movements and daily activity budgets. These behavioral differences translate into differential energetic costs that progressively accumulate over time, which may have lasting repercussions on individual fitness[18]. We also investigated whether habitat type and time of day influenced how pumas responded to human development. In order to link behavior change to energetic impacts, we evaluated how human development affected the daily movement patterns and caloric expenditures of pumas using GPS tracks, which we calibrated using accelerometer data from a much finer temporal scale. Lastly, we explored the extent to which puma prey demands are altered in human-modified habitats and discuss potential consequences for recruitment of future generations.

Methods

Study species and area

Pumas are territorial, apex predators which live throughout diverse habitats in the Americas [19]. Individuals are primarily nocturnal and solitary, although females will typically raise and accompany cubs for up to 15–21 months after birth. In our study area in the Santa Cruz Mountains of California, pumas predominantly feed on black-tailed deer (*Odocoileus* *hemionus columbianus*, 90% by biomass), but occasionally on other species, including wild boars (*Sus scrofa*), raccoons (*Procyon lotor*) and house cats (*Felis catus*) [20].

Our 1,700 km^2 study area encompasses a diverse landscape ranging from dense, urban development to large tracts of intact and relatively undisturbed native vegetation. Puma home ranges contain both protected and developed lands, with an average home range housing density of 21.7 ± 3.0 SE houses/km^2 (range 4.6–51.5) [8]. Even pumas that regularly move through or near residential areas also use nearby protected areas, allowing for comparison of movement behavior across a disturbance gradient within individual pumas. The vegetation is primarily forested (e.g., woodlands, hardwood and conifer forests) and shrubland (e.g., scrub and chaparral) habitats. It is bisected by a large freeway and further crisscrossed by numerous other smaller roads providing access to rural houses and developments. The climate is Mediterranean, with precipitation concentrated between November and April, and elevation ranges from sea level to 1155m.

Data collection

We captured 22 wild pumas (11 males, 11 females) from June 2010—March 2013 using trailing hounds, cage traps, or leg hold snares. Each animal was tranquilized using Telazol at a concentration of 100mg/mL (3.3–6.0 mg/kg estimated body weight) and outfitted with a GPS/VHF collar (3.7 kg; Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany). Six of the 22 animals were also equipped with a custom-built archival 3-axis accelerometer sampling continuously at 64Hz when activated [21]. The tri-axial accelerometer was mounted such that the x-axis was parallel to the anterior-posterior plane of the animal, the y-axis to the transverse plane, and the z-axis to the dorsal-ventral plane.

Accelerometers on pumas were programmed to record at a duty-cycle of 2 days on and five days off to maximize battery life. The GPS was programmed to acquire locations every 15 minutes during a 24-hour intense sampling period starting from noon one day each week. The Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures (Protocols Wilmc0709 and Wilmc1101).

Data processing

During each 15-minute GPS sampling interval, we assigned one behavioral state (active or inactive) to each collared individual and considered these states to be mutually exclusive. We considered any distance greater than 70m between successive 15 minute GPS fixes to be an active period, and a distance smaller than 70m to be an inactive period. We used accelerometer measurements to determine the distance cutoff between activity states as follows. We used a random forest algorithm described in Wang et al. [22] to categorize 2-second increments of accelerometer measurements into mobile or non-mobile behaviors. These were then aggregated into 15-minute observation periods to match the GPS sampling periods. After inspecting the data visually, we identified 10% activity (i.e., 10% of accelerometer measurements categorized as mobile out of 15 minutes) as the cutoff between active and inactive periods. Because of the strong linear relationship ($r = 0.89$) between accelerometer defined activity and the distance traveled between GPS fixes, 10% activity recorded by accelerometers corresponded to 70 meters between GPS fixes.

Environmental and anthropogenic measurements

Our study animals inhabit a landscape primarily comprised of forested or shrubland habitats interspersed with developed areas. To examine how human development and habitat type affected puma behavior, we collected spatial information on buildings and habitat types surrounding each puma GPS location. Using the Geographic Information Systems program ArcGIS (v.10, ESRI, 2010), we digitized house and building locations manually from high-resolution ESRI World Imagery basemaps for rural areas and with a street address layer provided by the local counties for urban areas. For each puma GPS position recorded, we calculated the distance in meters to the nearest house. We placed circular buffers with 150m radii around each GPS location and used the California GAP analysis data [23] to categorize the local habitat as either predominantly forested or shrubland. We chose a buffer size of 150m based on a previous analysis of puma movement responses to development [24].We also classified the time each GPS location was recorded as diurnal or nocturnal based on sunset and sunrise times.

Markov chains

We modeled puma behavior sequences as discrete-time Markov chains, which are used to describe activity states that depend on previous ones [25]. Here, we used first-order Markov chains to model a dependent relationship between the succeeding behavior and the preceding behavior. First-order Markov chains have been successfully used to describe animal behavioral states in a variety of systems, including sex differences in beaver behavior [26], behavioral responses to predators by dugongs [27], and impacts of tourism on cetacean behavior [28–29]. Because we were modeling behavior transitions with respect to spatial characteristics, we recorded the states of the puma (active or inactive) in the 15 minutes prior to and succeeding each GPS acquisition. We populated a transition matrix using these preceding and succeeding behaviors and examined whether proximity to houses influenced the transition frequencies between preceding and succeeding behavior states. Transition matrices are the probabilities that pumas remain in a behavioral state (active or inactive) or transition from one behavior state to another.

We built multi-way contingency tables to evaluate how sex (S), time of day (T), proximity to house (H), and habitat type (L) affected the transition frequency between preceding (B) and succeeding behaviors (A). Because high-dimensional contingency tables become increasingly difficult to interpret, we first used log linear analyses to evaluate whether sex and habitat type influenced puma behavior patterns using two three-way contingency tables (Before × After × Sex, abbreviated as BAS). Log linear analyses specifically test how the response variable is influenced by independent variables (e.g., sex and habitat) by using Likelihood Ratio Tests to compare hierarchical models with and without the independent variable [25]. We found that there were strong sex differences in activity patterns because adding S to the model greatly increased the goodness-of-fit (G^2) compared to the null model ($\Delta G^2 = 159.8$, d.f. = 1, $P<0.0001$), which assumed that succeeding behaviors only depend on preceding ones. Therefore, we evaluated data from male pumas separately from those of female pumas.

We then used another three-way contingency table for each sex to evaluate whether behavior patterns differed between habitats (L). We found that including habitat type significantly improved model fit for male ($\Delta G^2 = 7.9$, df = 1, $P<0.005$) but not female pumas ($\Delta G^2 = 3.18$, df = 1, $P = 0.0744$). Thus we evaluated three sets of data: all females, males in forests, and males in shrublands. For each dataset, we created four-way contingency tables (Before × After × House × Time) to evaluate how development and time of day affected behavioral transitions using the likelihood ratio methods described above.

Our null model (BA, BHT) is built such that succeeding behaviors (A) are only affected by behaviors in the previous time steps (B) and independent of proximity to houses and time of day. We tested whether including additional factors (proximity to house and time of day) improved model fit by comparing the null model with hierarchically more complex models. For example, the effects of proximity to housing on succeeding behaviors are evaluated by comparing the goodness-of-fit (G^2) values for the null model and the model containing an interaction between succeeding behaviors and houses (*BAH*, *BHL*). We also tested the interaction between proximity to houses and time of day by comparing the saturated model (*BAHT*), which fits the data fully, to a less complex model without the interaction term (*BAH*, *BAT*, *BHT)*. Finally, we selected the best fitting model by minimizing the Akaike Information Crtierion (AIC) estimate.

Behavioral budgets

We tested whether transition matrices differed when pumas were close to houses or roads using the Z test for proportions [30]. We also estimated the amount of time pumas spent in each behavioral state by conducting an eigenanalysis on the transition matrix. Because Markov chains are ergodic matrices, we used the left eigenvector of the transition matrix to estimate the proportion of time pumas spent in each state [25]. We compared these values using a Z test of proportions and calculated 95% confidence intervals using the Wilson's score test [31].

Puma travel and energetic costs

For each puma, we identified all 24-hour intensive sampling periods during which GPS points were recorded every 15 minutes. At a fix rate of 4 times an hour, up to 96 GPS points are recorded throughout the day, equating to a total of 95 travel segments (straight lines between consecutive points). We removed any days from analyses that were missing more than 10% (i.e., 9 points) of potential GPS fixes. We determined the linear length of all travel segments and calculated the total daily distance (*D*) in km traveled by pumas by summing all travel segments and correcting for any missing GPS fixes using the formula:

$$D_{total} = D_{summed} \times 95/n \tag{1}$$

in which n represents number of actual recorded segments. Next, we calculated the minimum cost of transport (*COT*, W/kg) expended daily for each puma by adapting the equation developed by Taylor et al. [32]:

$$\mathrm{COT} = \sum\nolimits_{\mathrm{i}}^{\mathrm{n}} 10.7(\mathrm{wt})^{-0.316} \times \mathrm{v_i} + 6.03(\mathrm{wt})^{-0.303} \tag{2}$$

in which *wt* is the weight (kg) of the animal when captured and v_i is the velocity of travel (m/s) between consecutive GPS points. *COT* has the units Watts/kg, which we converted to kcal/kg by applying the conversion factor 4.1868 Watt = 1 cal/s.

Lastly, we estimated the minimum number of black-tailed deer, the primary prey of pumas in our area, needed to sustain each puma given their daily minimum *COT*. We calculated the daily deer biomass (*DB*) needed to fulfill each puma's prey requirements using Eq 3 [33]:

$$DB\left(\frac{kg}{day}\right) = \frac{COT\ (kcal)}{1890\left(\frac{kcal}{kg}\right) \times 0.86 \times 0.88} \tag{3}$$

in which 1890 kcal represents the caloric content in each kg of wet deer tissue [34], and this value is then modified by multiplying it by the conversion efficiency (0.86) and the proportion of deer in a puma's diet—here estimated as 88% [20]. Finally, we used Eq 4 to convert the daily deer biomass into an estimate of the yearly deer requirements [33]:

$$\frac{Deer}{year} = \frac{DB\left(\frac{kg}{day}\right) \times 365\ days}{36.5\ kg \times 0.79} \tag{4}$$

in which 36.5 kg is the average weight of a black-tailed deer doe [35] and 0.79 is the edible proportion of the deer [34].

It is broadly understood that the energetic estimates generated using the equation developed by Taylor et al. [32] are the minimum estimates for *COT*. Even at 15-minute GPS sampling intervals, animals can deviate greatly from straight-line travel paths, thus expending many more kcals than estimated. In contrast, Overall Dynamic Body Acceleration (ODBA) measurements recorded by accelerometer collars, which sums the dynamic acceleration of the subject across three dimensions, provide a more precise measurement of energetic expenditure because it takes measurements at a rate of 64Hz [36]. Not all pumas were outfitted with accelerometer collars and we were unable to use ODBA alone to estimate energetic budgets. Instead we recorded ODBA values from two wild pumas whose accelerometers were active concurrent to the GPS intensive sampling periods. Using those values, we calculated the correlation between COT estimates from ODBA measurements and those estimated using velocities generated from intensive GPS sampling by Eq 2. This resulted in a correction factor that we applied to the energetic estimates of each puma in the study.

Development influences on puma movement

To quantify puma exposure to human development, we used ArcGIS (v. 10.1, ESRI, 2012) to create buffers of 150m around all GPS points within each 24-hour intensive GPS sampling period. We then calculated the number of houses encompassed within each buffer polygon and also recorded the time of day. For each day, we recorded the average housing density individual pumas were exposed to and the average distance pumas traveled between successive GPS locations during both nocturnal and diel periods. We hypothesized that pumas would use more calories by moving faster and further through areas with more houses in order to minimize their exposure to development [24,37]. However we also predicted that this relationship might be affected by time of day because pumas may prefer to stay hidden if they are in more developed areas during the day.

We used linear mixed effects models using restricted maximum likelihood estimation with the average diurnal and nocturnal calories burned between successive GPS points as the dependent variable. To select the best model, we used a top-down model selection approach to compare models with no random terms, with random intercepts, and with both random intercepts and slopes [38]. We started by fitting a linear model that included the full complement of fixed effects terms: sex of the puma (male coded as 1 and female as 0), time of day (day coded as 1 and night as 0), the average number of houses (log-transformed to account for all distributions being bound at zero), the interactions between sex and time of day, and the interaction between time of day and housing. In a second model, puma identity was included as a factor in the model to allow for random intercepts. For the third model, we also tested whether individual pumas responded to time of day, the log average number of houses, and their interaction differently by including random slopes for those terms. We used AIC to compare the three models to determine the optimal model structure. We examined the residuals for our final model visually to identify any obvious deviations from normality.

To quantify the difference in puma energetic expenditure between areas with low and high housing density, we calculated the average caloric expenditure by individual pumas in the top and bottom housing density quartiles of their home range for both days and nights. To maximize statistical power, only pumas with a minimum of 20 day and 20 night measurements were included in this analysis. We added day and night averages to get total daily difference in caloric expenditure. We calculated the percentage increase in calories used as the total daily difference between caloric expenditure for high and low housing density divided by the average daily caloric expenditure for the individual puma. In order to conceptualize variation of human disturbances for individual pumas, we classified average housing density in the top and bottom quartiles into the following categories described by Theobald [5]: rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to1.236 houses per hectare), suburban (greater than 1.236 and up to 9.884 houses/hectare), or no housing. We used the package *nlme* [39] in R (v. 3.0.2, R Core Team, 2013) for all analyses.

Results

Log linear analyses

We recorded 78,242 GPS locations for 22 pumas, comprised of 6,967 behavioral transitions (e.g. active to inactive) for males in shrubland habitats, 11,379 transitions for males in forested habitats, and 21,977 transitions for females in all habitats. Log linear analyses revealed that both proximity to houses and time of day influenced puma activity levels, but this effect differed by sex, and by habitat type for males. Proximity to houses and time of day had a significant positive effect on the number of behavior transitions of male pumas in forests (Table 1). However, for males in forests, support for the interaction term (proximity to houses × time of day) was ambiguous because the two models had a ΔAIC of less than 0.2, indicating that they were statistically indistinguishable [40]. AIC comparison revealed that the best models for all female pumas and males in shrublands included the proximity to houses, time of day, and an interaction between the two (Table 1). This indicates that the time of day determined how pumas altered their movement patterns near development, which we discuss next.

Table 1. Results of log-linear analysis for all puma behavioral transition models.

Study Group	Model[a][b]	ΔAIC[c]	Components added[a]	ΔG^2, *df*, *P*-value
Males, Forests	Null (BA, BHT)	72.0		84, 6, —
	Previous Location × House (BAH, BHT)	63.8	BAH	71.8, 4, 0.002
	Previous location × Time (BAT, BHT)	2.2	BAT	10.2, 4, <0.001
	Previous location × Time + Previous location × House (BAT, BAH, BHT)	0.01	BAT	4.01, 2, 0.001
			BAH	4.01, 2, 0.045
	Time × House (BAHT)	0.00	TH	0, 0, 0.135
Males, Shrubland	Null (BA, BHT)	53.4		65.4, 6, —
	Previous Location × House (BAH, BHT)	54.0	BAH	62, 4, 0.002
	Previous location × Time (BAT, BHT)	8.4	BAT	16.4, 4, <0.001
	Previous location × Time + Previous location × House (BAT, BAH, BHT)	11.5	BAT	15.5, 2, <0.001
			BAH	15.5, 2, 0.64
	Time × House (BAHT)	0.00	TH	0, 0, < 0.001
Females, All habitat	Null (BA, BHT)	90.8		102.8, 6, —
	Previous Location × House (BAH, BHT)	66.6	BAH	76.4, 4, <0.001
	Previous Location × Time (BAT, BHT)	41.3	BAT	49.3, 4, <0.001
	Previous Location × Time + Previous location × House (BAT, BAH, BHT)	24.5	BAT	28.5, 2, <0.001
			BAH	28.5, 2, <0.001
	Time × House (BAHT)	0.00	TH	0, 0, < 0.001

[a] A: Succeeding behavior; B: Previous behavior; T: Time; and H: Number of Houses.

[b] In null models, effects of time and number of houses were assumed to be independent of behavioral transitions. Succeeding behaviors (A) are only dependent upon preceding behaviors (B), and not on time of day (T) or proximity to housing (H). Subsequent models which incorporate the housing and time covariates and their interactions are listed below the null.

[c] ΔAIC values are in comparison to the top model for each study group.

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Behavioral budgets

All puma behavioral transitions showed contrasting responses to housing depending on the time of day (Fig 1). At night, all pumas regardless of sex or habitat were less likely to remain inactive, more likely to remain active, and more likely to transition between behavioral states near houses. In contrast, male and female pumas were more likely to stay inactive near houses during the daytime. However, male pumas in forests were also less likely to remain active near houses in the forest during the day whereas male pumas in shrublands were unaffected.

Both male and female pumas were generally more active at night than during the day. Male pumas near houses at night were active 26.9% and 21.1% of the time in forested and shrubland habitats, respectively, compared with 17.2% and 13.2% when they weren't close to human structures (Fig 2). Females were active 13.3% of the time when near houses at night, compared with only 7.5% when further away (Fig 2). In the daytime, puma activity was generally low, with females and males in forests exhibiting no difference in activity level in relation to proximity to houses (Fig 2). However, males in shrubland habitats were less likely to be active near houses (2.8%) than when far from houses (8%) during the day.

Energetic costs

Our COT estimates based on ODBA measurements from accelerometers for pumas 16M and 28F showed that our energetic expenditure estimates from GPS movement data greatly underestimated caloric intake. Applying the COT formula from Taylor et al. [32] to the intensive GPS sampling period, we estimated that 16M expended 2,492 and 2,296 kcals over two days and that 28F expended 1,793 kcals. In contrast, our COT estimates from ODBA for the same three days were about 2–2.5 times higher at 6,079 and 5,492 kcals, and 3,608 kcal, respectively. We used the results from a linear regression between the COT values calculated using 15 min GPS and ODBA measurements (intercept = 8.21, slope = 1.88; $r = 0.75$) to apply corrections factor to all puma energetic calculations.

We used 19 pumas (10 males and 9 females) to evaluate movement activities and energetics over 369 24-hour intense sampling periods (216 for females and 153 for males) (Table 2). Male pumas, averaging 53.3 kg ± 7.82kg (SD), traveled a mean of 7.43 km ± 2.2 km daily and expended 5,145 kcal ± 542 kcal (after factoring the correction factor). Females, averaging 39.8 kg ± 2.73 kg, were more sedentary and traveled a mean of 4.12 km ± 0.5 km daily and expended 4,760 kcal ± 555 kcal. If a puma only subsisted on a diet of black-tailed deer, we calculated that a male puma would need to kill a minimum average of 45.5 doe equivalents/year and that a female puma would need to kill 42 doe equivalents/year.

Development influences on puma energetics

We found that the model structure that included random intercepts and slopes for Puma ID minimized AIC values and fit the data better compared to a fixed-effects model (ΔAIC = 632) and the model with random intercepts only (ΔAIC = 23.4). The final model included all original fixed effects terms for sex, time, the log-transformed number of houses, the interaction between sex and time, and the interaction between time and number of houses (Table 3). As expected, males burned more calories than females during both nocturnal and diurnal hours (Fig 3). However, the influence of increased housing density on puma energetic expenditures differed depending on time of day, with pumas burning more calories between GPS points in more developed areas during nocturnal hours but not during diurnal hours.

Average daily caloric expenditure for individual pumas was consistently higher on days when pumas were in high housing density areas than in low housing density areas, constituting a 434.3 ± 130.3 SE kcal increase for females and a 513.3 ± 83.1 SE kcal increase for males

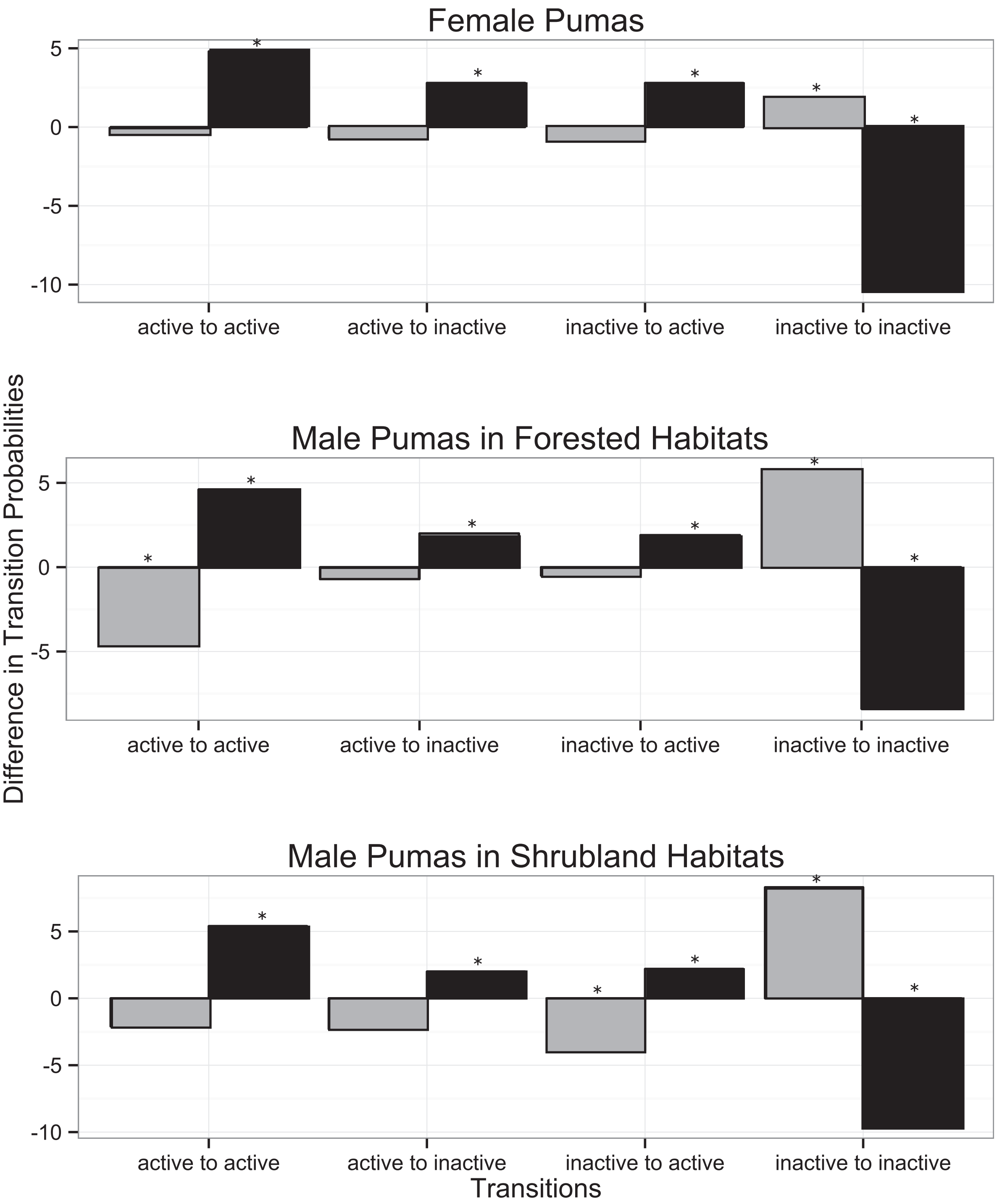

Fig 1. The effect of proximity to houses on the daytime (gray) and nighttime (black) transition probabilities between activity states for female pumas, male pumas in forested areas, and male pumas in shrubland habitats. Difference in transition probabilities is calculated as probability of transitioning between states when pumas are ≤150m from buildings subtracted by the probabillity of transitioning between states when pumas are >150m from buildings. A positive value means pumas are more likely to engage in those transitions when close to buildings than when further away. Asterisks above columns represent significant differences between transition probabilities close and far from houses ($P < 0.05$).

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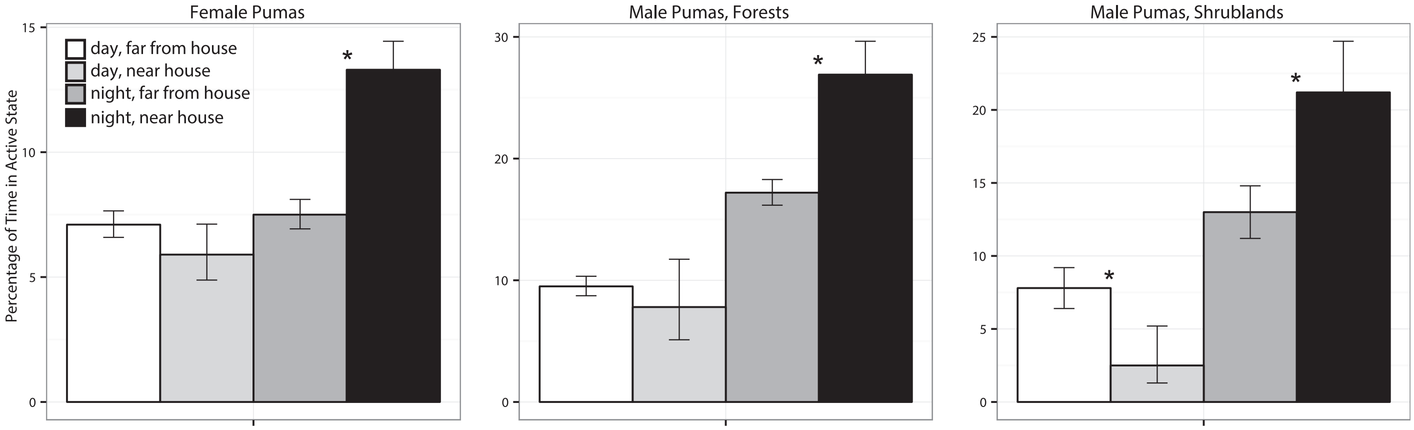

Fig 2. Proportion of time spent active for female pumas,male pumas in forests, and male pumas in shrublands ≤150m from buildings during the day (light gray) or night (black bars) and >150m from buildings during the day (white) or night (dark grey bars). Asterisks between paired columns represent significant differences between activity levels near houses and far from houses ($P < 0.05$). Error bars represent 95% confidence intervals.

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(Table 4). These differences in average daily caloric expenditure were equivalent to a mean total percentage increase of 10.1 ± 3.1 SE% of daily kcals used by individual females and 11.6 ± 1.8 SE% of daily kcals used by males. When the increase in daily calories is converted to the extra number of deer required annually by each puma, females would need to kill an additional 3.4 deer annually to meet higher energetic requirements, and males would need to kill 4.0 more deer.

Table 2. Mean (± standard error) of daily distanced traveled, daily caloric expenditure, and projected annual deer requirements of 9 female (F) and 10 male (M) pumas.

Puma ID	Days monitored	Daily distance (m)	Daily kcal/kg	Deer/year
7F	42	3236 ± 378	97.8 ± 0.6	36.3 ± 0.2
11F	22	3935 ± 489	104.5 ± 0.8	35.2 ± 0.3
18F	8	4001 ± 939	119.3 ± 1.7	40.0 ± 0.6
19F	35	3927 ± 495	107.9 ± 0.8	39.9 ± 0.3
23F	38	4389 ± 373	133.3 ± 0.8	48.0 ± 0.3
24F	15	3966 ± 462	145.0 ± 1.0	47.7 ± 0.3
25F	14	4493 ± 941	138.2 ± 2.0	48.1 ± 0.7
28F	24	4111 ± 606	129.9 ± 1.2	41.6 ± 0.4
29F	18	5060 ± 511	124.8 ± 1.0	42.2 ± 0.3
Female total	216	4132 ± 176	118.9 ± 1.1	41.6 ± 0.3
16M	12	10760 ± 1140	96.2 ± 1.5	50.4 ± 0.8
17M	8	4297 ± 706	95.0 ± 1.0	40.2 ± 0.4
22M	29	9830 ± 1091	91.2 ± 1.4	52.0 ± 0.8
26M	28	6743 ± 810	103.0 ±1.2	39.6 ± 0.5
27M	22	6853 ± 1000	99.5 ± 1.4	43.4 ± 0.6
31M	10	7047 ± 1298	94.8 ±1.8	46.1 ± 0.9
34M	17	6504 ± 727	90.1 ± 1.0	47.1 ±0.5
35M	19	4215 ± 484	97.3 ±0.7	38.8 ±0.3
36M	6	9192 ± 1874	96.4 ± 2.6	49.4 ± 1.3
37M	2	8877 ± 3	98.23 ± 0.1	48.4 ± 0.0
Male total	153	7334 ± 373	96.3 ± 0.6	45.0 ± 0.5

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Table 3. Results of final mixed effects model to predict puma activity.

Model Parameter	β	SE	t	*P*
Sex	5.50	2.84	1.94	0.069
Time	- 0.66	0.78	-0.85	0.395
Number of Houses (log-transformed)	1.21	0.28	4.26	< 0.001
Sex X Time	-3.10	0.97	-3.21	0.001
Time X Number of Houses	- 1.45	0.49	-2.95	0.003

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Discussion

This study explores how housing development influences puma behavior and energetics in a fragmented landscape. Our results suggest a clear relationship between proximity to houses and puma movement activity. This effect was modulated by the time of day, whereby pumas were more likely to be active and remain active when within 150m of development at night. We also found that pumas were more likely to transition between behavioral states when close to houses. These activity shifts may reflect discomfort with being in close proximity to humans and domestic animals or reaction to other abiotic disturbances from these sources, such as light pollution or human-associated sounds [41].

As we predicted, there was a significant positive relationship between distance traveled and the number of houses surrounding each puma's travel path. This pattern resulted in greater metabolic demand associated with higher densities of residential development. Both male and female pumas moved further and expended more calories in developed areas at night but not during the day, providing evidence that puma response to development was strongly influenced by the time of day. Although pumas only increased their movement activity near houses at night, we found that this still resulted in increased net energetic expenditure. Increases in distance traveled are unlikely to be influenced by deer availability, as occupancy of deer is ubiquitous across our study site in both developed and protected areas [20].

The increases in caloric expenditure we observed could in part explain observed increases in puma kill rate in developed areas [8]. To compensate for the higher energetic costs of living in developed areas alone, we found that pumas would need to kill on average a minimum of 3.4 and 4.0 more deer annually for female and male pumas, respectively. This estimated increase is likely conservative, as we have previously found that pumas in the most developed parts of our study area kill over 20 more deer per year than pumas in less disturbed areas [8]. Higher kill requirements based on increased movement may exacerbate other behavioral influences on energetics, including changes in feeding rates and handling time of prey [8] and altered diet composition [20].

Although pumas in our study area are not legally harvested, human-caused mortality is the leading cause of death for collared pumas. Hence, even in the absence of puma hunting, which is illegal in California, high human-induced mortality rates due to depredations give pumas strong incentive to alter their behaviors to minimize contact with people. Pumas fear humans in this human-dominated ecosystem, demonstrated by immediate responses to human stimuli [41], altered feeding behavior [8,24,41], reduced occupancy of developed areas [7], and strong avoidance of development when engaged in reproductive behaviors [24]. As large tracts of land increasingly transition from undeveloped to exurban development, non-lethal human disturbances will likely continue to alter puma behavior. As demonstrated here, changes in puma movement behavior has energetic consequences. The cumulative energetic cost of all behavior change in human-dominated systems is likely to exceed even the substantial estimated energetic requirements reported here.

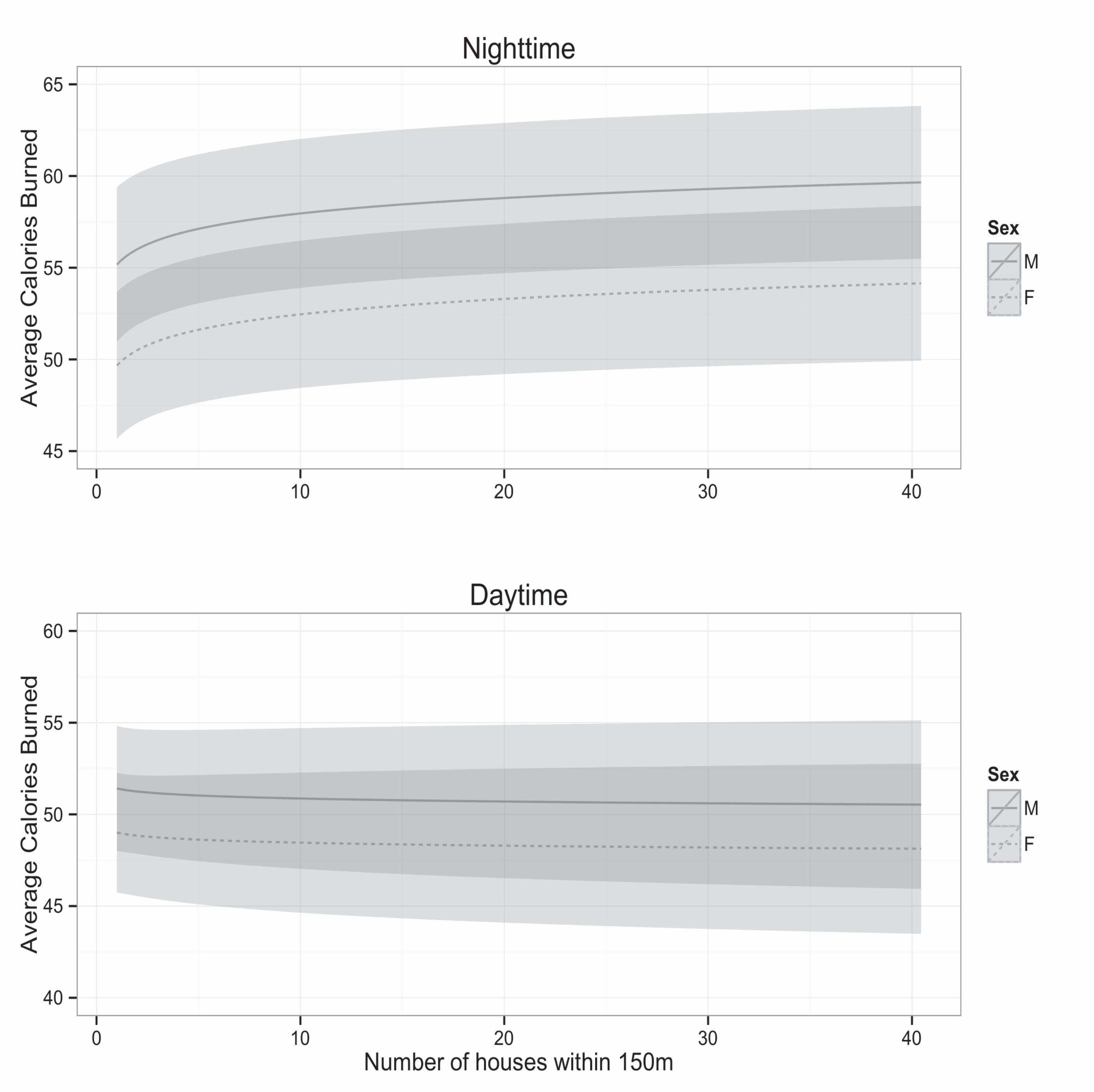

Fig 3. Predicted curves bounded by 95% confidence intervals relating the average calories expended between 15-minute GPS points and the average number of houses in a 150m radius around locations in nighttime and daytime. Predictions for males are indicated by the solid line and females are indicated by the dashed line.

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Increased energetic requirements are likely to disproportionalty impact females with kittens, given their higher energetic demands [34]. Kittens older than 6 months follow their mothers to kill sites to feed [42]; if these locations are close to development, their feeding times

Table 4. Caloric difference between time spent in high and low housing density areas relative to each puma.

Puma Sex	Puma ID	Difference in kcals (day)[a]	Difference in kcals (night)[a]	Total Difference (kcal)	Increase in Daily Calories (%)[b]	Change in annual deer consumption	Bottom 25% Housing Density[c]	Top 25% Housing Density[c]
Female	23F	-754.5	809.5	55.1	1.1	0.4	Rural	Suburban
	11F	94.1	19.8	113.9	2.9	0.9	No Housing	Exurban
	28F	128.7	128.3	256.9	5.7	2.0	No Housing	Exurban
	7F	124.9	206.3	331.2	8.3	2.6	No Housing	Exurban
	19F	509.1	10.5	519.6	12.3	4.0	No Housing	Rural
	25F	54.7	736.1	790.9	16.2	6.2	No Housing	Exurban
	29F	21.2	951.3	972.6	24.4	7.6	No Housing	Exurban
Male	26M	-23.5	328.6	305.1	7.2	2.4	No Housing	Exurban
	22M	114.9	288.1	403.0	7.5	3.1	No Housing	Rural
	17M	418.8	40.2	459.0	11.8	3.6	No Housing	Exurban
	27M	63.0	408.4	471.4	10.9	3.7	No Housing	Rural
	35M	2.8	543.6	546.3	12.9	4.3	No Housing	Exurban
	16M	343.1	551.9	895.0	19.3	7.0	Rural	Exurban

[a] Differences are calculated from average caloric expendature during days and nights spent in the top and bottom quartiles of housing density per puma.

[b] Increase in daily calories are measured as the total increase in caloric expendature divided by individual average daily caloric expendature.

[c] Housing density classifications are derived using categories described in Theobald (2005).

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may decline in response to disturbances [8]. Additionally, females may choose daytime resting locations further away from kill sites in developed areas, thus reducing the energetic gains kittens receive from carcasses. Although we could not track kitten survival during our study, most female pumas we tracked had kittens and lived in home ranges that encompassed developed areas. Future studies that measure kitten recruitment will shed light on the added energetic and survival costs of raising kittens in human-modified landscapes.

Our approach of using GPS and accelerometer data allowed us to obtain more accurate estamates of energetic use and requirements, which were likely underestimated in previous studies using GPS or telemetry data alone. The average activity levels of our study animals (20.8%) was relatively low compared to Beier et al.'s [37] estimates of 25% diel activity for pumas in southern California. This discrepancy may be due to methodological differences; Beier et al. [37] used the radio-telemetry to estimate the locations of animals, which is characterized by lower precision and sampling in comparison to GPS data. Pumas tracked in our study have some of the lowest travel distances (4–7 km/day) of any pumas studied, traveling less than half as far as those monitored by other studies [34,43]. However, despite their relatively short travel distances, our corrected estimates of puma energetic expenditures (average of 4,760 kcal for females and 5,145 kcal for males) was nearly twice as high as those of Laundré [34] (average of 2,420 kcal for females and 3,144 kcal for males), which suggests that previous estimates of puma energetics from GPS or radio-tracked animals have considerably underestimated true field energetics. Metabolic costs derived soley from mimimum COT equations or telemetry-only tracking studies may woefully underestimate true large predator hunting costs due to their inability to account for additional energy demand associated with topographic complexity, substrate type, intermittent locomotion, maneuvering, feeding and weather [13,44,45].

Incorporating calibrated accelerometer datasets alongside GPS locations, as demonstrated here for pumas, allows for significantly finer-scale reconstruction of behavioral and energy budgets. Our accelerometer-corrected estimates for minimum annual deer consumption (42 deer/yr for females without kittens and 45.5 deer/yr for males) are likewise much higher than those predicted by Laundré [34] (14.9 deer/yr for females and 19.4 deer/yr for males). Instead, our estimates are similar to the field-estimated kill rates of 25–84 deer/yr for pumas in our population [8].

Our study provides evidence that behavioral responses to human disturbance have energetic consequences to individuals. While previous research had focused primarily on how urbanization and development affect the persistence or declines in wildlife populations, more studies now examine the behavioral responses of these species as they adapt to increased human presence [8,46]. Understanding how animal motivations and behaviors are altered by human influences can shed light on why some species can continue to persist in human dominated landscapes while others become extirpated [47,48]. New technologies such as accelerometers can reveal much more than whether or not an animal is in an area, but elucidate how successfully the individual is able to move, feed, and reproduce [49]. Increasing awareness of the consequences of human-induced behavioral change in wildlife can contribute to more robust wildland-urban interface planning and reductions in human-wildlife conflict.

Currently, exurban or low density development is the fastest growing type of land-use change in the United States [50]. As low density development fragments previously intact landscapes, it could pose significant challenges to survival for wildlife due to cummulative effects of increased non-lethal human disturbance. By incorporating energetic measurements from accelerometers, we showed the substantial consequences of these changes in behavior on energetic costs and requirements. Changes in movement activity and behavior can provide the first indications of predator energetic responses to development. Large carnivores such as pumas occupy pivotal roles in ecosystems, and changes to their behaviors can lead to demographic effects that reverberate throughout the ecological community. In addition, as energetic needs increase with development, large carnivores may switch to domestic or synanthropic prey sources, exacerbating conflict with humans and threatening carnivore survival and population persistence. For all large carnivores, accounting for human-induced behavioral change should play a larger role in any conservation management strategy.

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Writing – original draft: Yiwei Wang, Justine A. Smith.

Writing – review & editing: Yiwei Wang, Justine A. Smith, Christopher C. Wilmers.

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OPINION

Op-Ed: There's a quick way to help prevent wildfires: Shut off the power grid

Flames burn near power lines in Montecito, Calif. on Dec. 16, 2017. (Mike Eliason / Associated Press)

By MICHAEL W. WARA

DEC. 10, 2018
3:05 AM

The challenge created by wildfires in California — and our need to adapt to a hotter, drier climate — cannot be overstated. The state, which leads the nation on environmental issues, must call upon the creativity of its innovators and the adaptability of its citizens to secure its future. The reality of climate change means we need to make urgent big investments in infrastructure that will keep us safe.

The Legislature began to implement wildfire solutions last session that, over time, will make California safer. Gov. Jerry Brown added more than $250 million to this year's budget, doubling the state's forest-thinning efforts and increasing prescribed burns, which could make parts of the state less combustible. Stricter building codes are also under discussion, along with limiting new construction and rebuilding in the likely path of fires. There are also calls to put power lines underground — at tremendous cost.

But these strategies will take time — probably a decade or more. And we cannot afford more firestorms like the ones that swept through Santa Rosa and Ventura in 2017, and Paradise and Malibu in November.

The most destructive fires in recent California history have been traced, to a high degree of probability, to downed utility power lines or electrical equipment malfunctions. (The causes of last month's Camp fire and Woolsey fire have yet to be determined, but electrical infrastructure problems are the suspected cause.) In the fires' terrible wake, California residents are also faced with bailing out utilities when they are found liable for the conflagrations.

Deploying clean "distributed energy" — individualized power generation and storage — could be a kind of green New Deal.

There is a simple and effective way to reduce the risk of utility-caused wildfire, and it doesn't take decades to implement: Shut the power off when and where wind and drought create wildfire risk. All other options for preventing these fires — such as putting power lines underground or trimming trees that threaten power infrastructure — will take too long or are too prone to error to adequately address the crisis we're facing.

To make it acceptable to turn off whole sections of the electricity grid, the state will have to start a crash program to build a backup power supply for households and businesses in high-risk wildfire areas. The logical choices are individual solar and battery setups for households, and "microgrids" linking business districts. We need to make it OK for the utilities to take decisive action to avoid wildfire threats: When the main grid has to go down for safety, backup power must be available to keep medical devices, refrigerators and the internet up and running.

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Deploying clean "distributed energy" — individualized power generation and storage — could be a kind of green New Deal. It would not only cut down on destructive wildfires, it could create enormous numbers of new jobs all over the state. And it could speed up our pursuit of statewide emissions-free energy. Establishing an alternative to the massive, interconnected grid that delivers power would also add security to a system vulnerable to other natural disasters as well as cyber threats. It might expand over time to include areas not threatened by wildfire.

Setting up off-the-grid power sources would be costly, but it's a much smarter investment than repeatedly bailing out utilities after fires. As massive as the project would be, it compares in scale and cost to wildfire losses in just the last two years.

By my back-of-the-envelope calculation, it would cost something like $30 billion to install individualized backup power for 1 million of the highest-risk homes if the costs were fully funded by the state. But the state wouldn't have to foot the whole bill; it could provide very low-cost financing, paid back over many years on customer utility bills, while providing additional assistance to low- and moderate-income customers.

California can't afford to have more towns and neighborhoods destroyed or hollowed out by fire. Spending billions on alternatives to utility-delivered power might have seemed like an unaffordable luxury once, but now it's clear what doing nothing will mean: more lives, livelihoods and communities lost in what the governor calls the "new abnormal."

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Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise

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Santiago de la Nava Santos · Guy Midgley

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Abstract In a meta-analysis we integrate peer-reviewed studies that provide quantified estimates of future projected ecosystem changes related to quantified projected local or global climate changes. In an advance on previous analyses, we reference all studies to a common pre-industrial base-line for temperature, employing up-scaling techniques where necessary, detailing how impacts have been projected on every continent, in the oceans, and for the globe, for a wide range of ecosystem types and taxa. Dramatic and substantive projected increases of climate change impacts upon ecosystems are revealed with increasing annual global mean temperature rise above the pre-industrial mean (ΔT_g). Substantial negative impacts are commonly projected as ΔT_g reaches and exceeds 2°C, especially in biodiversity hotspots. Compliance with the ultimate objective of the United Nations Framework Convention

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on Climate Change (Article 2) requires that greenhouse gas concentrations be stabilized within a time frame “sufficient to allow ecosystems to adapt naturally to climate change”. Unless ΔT_g is constrained to below 2°C at most, results here imply that it will be difficult to achieve compliance. This underscores the need to limit greenhouse gas emissions by accelerating mitigation efforts and by protecting existing ecosystems from greenhouse-gas producing land use change processes such as deforestation.

1 Introduction

Effects of climate change are already being observed on a wide range of ecosystems and species in all regions of the world (Rosenzweig et al. 2007), in response to the 0.74°C rise (ΔT_g) in global mean temperature (GMT) that has been experienced since pre-industrial times (Solomon et al. 2007). Such responses include changes in phenology and shifts in species ranges (e.g. Walther et al. 2002; Root et al. 2003), whilst the first extinctions which are likely to be attributable to climate change—acting synergistically with disease—have already occurred in amphibians (Pounds et al. 2006; Bosch et al. 2006). Coral reef bleaching is expected to increase strongly with rising sea surface temperatures (Hughes et al. 2003). At the same time, the ocean has already acidified by 0.1 pH units since pre-industrial times (Solomon et al. 2007) due to the direct effects of increasing atmospheric concentrations of carbon dioxide from the pre-industrial level of 280 ppm to the 2005 level of 379 ppm CO_2 (Solomon et al. 2007).

The literature contains a growing number of studies that project for the future increasingly severe impacts that further anthropogenic climate change would have on ecosystems and species around the world (see the 71 studies referenced in Tables 2, 3, 4 and 5). Such studies typically identify the onset of some positive, but predominantly negative, impacts upon a species or ecosystem as the climate changes. However, these studies have largely been carried out independently from each other and have used a wide range of future climate scenarios. This makes it difficult to compare results and obtain a clear and aggregated picture of how impacts accrue with increasing global mean temperature rise. Such an aggregated picture is important for two reasons: firstly it addresses climate change at the appropriate scale, i.e. as a global phenomenon; and secondly it enables the evaluation of major policy recommendations, such as the much discussed 2°C limit suggested by the EU as both a “safe” and achievable level of global temperature increase. Existing reviews (Houghton et al. 2001; Thomas et al. 2004a; Hare 2006; Warren 2006) have not included the full range of recent literature and have not estimated uncertainties. Similarly to the summary given in Fischlin et al. (2007), this paper integrates the dispersed and fragmented literature on ecosystem impacts of projected climate change, often expressed at a regional level, into a set of tables of projected impacts for different levels of global mean temperature rise with respect to pre-industrial times, ΔT_g, providing an estimate of uncertainty in these levels. The tables report the main findings in terms of: range losses for species, habitats or entire ecosystems; extinction risks; and other biodiversity impacts caused by ecosystem degradations or declines in key populations due to anticipated climate changes.

2 Materials and methods

2.1 Literature search

A literature search was made to assess pertinent impacts of climate change on both terrestrial and marine ecosystems across the globe (Fischlin et al. 2007). Search engines were first used to identify references in the peer reviewed literature, and further references were then derived from information provided within these. Existing reviews (Gitay et al. 2001; Thomas et al. 2004a; Hare 2006; Warren 2006) were particularly useful in identifying additional references. All references were then reviewed for specific information about thresholds in local or global temperature change/sea level rise above which adverse consequences could be expected, and also for quantified projections of ecosystem or species changes associated with quantified local or global climate changes, taking note of the climate scenario and any general circulation model (GCM) used, and the treatment of dispersal and migration. Thus studies that contained insufficient detail about the climate scenario used, or that did not provide quantitative estimates of the resultant ecosystem or species changes, could not be included in the analysis. In particular, studies which reported only the general direction of trends in response to changing temperature or precipitation were deliberately excluded. In cases where more than one study addressed similar species or ecosystems, each study was included separately in the summary table, since it may be projecting different sensitivities due to the use of other climate change scenarios and/or assessing other kinds of impact responses.

2.2 Converting to a pre-industrial reference point for global mean temperature change

Information on the climate change scenario simulated by each original study was converted to a common pre-industrial reference point for temperature. Studies often refer to baselines of pre-industrial (<1850), 1960–1990 mean, 1990, or "present day" (e.g. 1980–1999). In this study the temperature rise between pre-industrial and the 1960–1990 mean is taken as 0.3°C and the temperature rise between pre-industrial and 1990 is taken as 0.6°C (Houghton et al. 2001); whilst that from the mid 1970s to 1990 is taken as 0.2°C (Houghton et al. 2001). Where studies report impacts as caused by a particular GCM simulation using the HadCM3 model, Table 7 of Arnell et al. (2004) was used to convert the temperatures to a common pre-industrial baseline.

While some of the literature relates impacts directly to global mean temperature increases, many studies refer only to local temperature rise, and hence upscaling from a local to a global scale is required. Upscaling was carried out as detailed below for the different classes of studies identified (Table 1) and also provided an opportunity to estimate the uncertainties arising from the use of different GCMs in climate projection. Whenever possible it was also considered whether the impact had been estimated based only on temperature change, or also on associated precipitation change.

When studies gave minimal detail about GCM scenarios, such as referring to them only as "CO_2 doubling scenarios", the original literature publishing that scenario was traced, and/or the model authors were contacted, in order to verify the global mean

Table 1 Detail of the upscaling methodology used to derive global mean temperature (GMT) change (ΔT_g) for the eight study classes a–h

Class	Description of study	Derivation of central estimate of GMT change ΔT_g	Derivation of range of GMT change
a	Relates global impacts directly to ΔT_g	ΔT_g by definition already provided: harmonised if necessary to pre-industrial	Not derived unless provided in original study
b	Relates local impact (e.g. x% species at risk of extinction) to regional temperature change without using GCM output	ΔT_g is the mean of values derived via upscaling procedure, using the cited regional temperature change	Range of values derived via upscaling procedure using the cited regional temperature change
c	Relates a local impact (e.g. y% species at risk of extinction) to regional temperature change while using the output of specific GCM(s)[2]	As not all studies provide the regional temperature change this may need to be derived by first downscaling for the appropriate timeslice (e.g. Gyalistras and Fischlin 1999). ΔT_g is then the mean of values derived via a subsequent upscaling of the downscaled regional temperature change	Range of values derived via upscaling procedure, using the downscaled regional temperature change
d	As b but regional precipitation change also used	As b	As b
e	As c but study uses also GCM simulated precipitation as well as temperature	Upscaling is not applicable, as procedure is based on temperature only. ΔT_g is derived from published values simulated by the used GCM(s)	Not derivable
f	Cases where upscaling is not possible because regional temperature changes are out of range of the GCM patterns available	Estimated from maps in Meehl et al. (2007) relating local and global temperature change	Not derivable
g	As c or e but GCM output comes from 3 or more different GCM models	Mean of values as simulated by the used GCM(s)	Range derived from published values simulated by the used GCM(s)
h	Cases where the key variable is sea surface temperature	Estimated from maps in Meehl et al. (2007) relating local surface air temperature over the sea to ΔT_g, since maps of SST were not readily available, and increases in surface air temperature over the ocean were assumed to approximate increases in SST	Not derivable

temperature increase corresponding to CO_2 doubling, taking into account the control CO_2 concentration as necessary.

2.3 Dynamics

Many reviewed studies do not consider a temporal dimension. There are two issues here (1) whether the climate scenario a study considers relates to transient or equilibrium climate change and (2) whether the projected ecological response is considered a steady state. Studies in class b project impacts without distinguishing between transient and equilibrium temperature change. However, most studies use models, which project the future long-term ecological response to a changed climate (i.e. a new steady state) while the climate scenario is a transient one: studies in classes c and e are typically based on transient climate change scenarios produced by GCMs, although there are a few which also include equilibrium temperature change scenarios. Hence, the ecological projections are *not* mere snapshots of a transient climate change and its concomitant response, rather do these studies artificially hold the transient climate constant and assume the ecosystem response to equilibrate, regardless of the time the system may need to actually reach such an equilibrium. Thus an important question is the time lag between the forcing temperature change, be it transient or equilibrium, and the ecosystem response (see Section 4). The upscaling procedure described below is based on transient GCM scenario outputs throughout.

2.4 Upscaling procedure

The upscaling procedure involved the use of 0.5 × 0.5° resolution outputs produced from original 5 × 5° resolution outputs of five GCM models HadCM3, ECHAM4, CSIRO2, PCM, and CGCM2, by using pattern scaling and downscaling methods (Christensen et al. 2007). These climate projections based on transient GCM outputs were available for the entire global land area at a resolution of 0.5 × 0.5°. They were produced from up to four IPCC SRES emission scenarios (Nakicenovic et al. 2000) providing 13 different GCM patterns on which to base the upscaling (available at http://ipcc-ddc.cru.uea.ac.uk). In each 0.5 × 0.5° grid cell, 13 alternative twenty-first century time series of regional annual (or if required seasonal) temperature were thus available, each one expressed as the running 30-year mean temperature increase since 1961–1990 mean climate, to smooth inter-annual variability.

For each study in Table 1 of type b or c, the location was then related to a grid cell or to grid cells depending on how large an area the study covered. For each grid cell, all 13 upscaling calculations were carried out, to encompass the full range of inter-GCM and inter-scenario pattern variability as an uncertainty surrogate. The upscaling calculation was simply performed by examining any one of the 13 time series for a grid cell. A computer program calculated the date at which the regional temperature reached the temperature threshold which is referred to in the study of type b or c and therein associated with some particular impact on an ecological system. The program then used this derived date to identify the associated global temperature rise ΔT_g in the transient GCM runs, matching this same date, using if available the global temperature time series from the exact same GCM scenario as

Table 2 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: range losses for species, habitats or whole ecosystems

No.	ΔT_g above pre-ind °C	ΔT_g (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
1	1.3	1.1–1.6	1	8% loss freshwater fish habitat, 15% loss in Rocky Mountains, 9% loss of salmon	N America	Fish	13
2	1.6			Bioclimatic envelopes eventually exceeded leading to 10% transformation of global ecosystems; loss of 47% wooded tundra, 23% cool conifer forest, 21% scrubland, 15% grassland/steppe, 14% savannah, 13% tundra and 12% temperate deciduous forest. Ecosystems variously lose 2–47% areal extent	Globe		6
3	1.6	1.1–2.1	1	Suitable climates for 25% of eucalypts exceeded	Australia	Plants	12
4	1.7	1.3–2.4	2	16% freshwater fish habitat loss, 28% loss in Rocky Mountains, 18% loss of salmon	N America	Fish	13
5	1.8			Mean latitude of range of *Aloe dichotoma* shifts S by 1.1° of latitude causing range loss	Namibia	Plants	68
6	<1.9	<1.6–2.4	<1	Range loss begins for Golden Bowerbird	Australia	Birds	4
7	1.9	1.6–2.4	1	Range loss of 40–60% for Golden Bowerbird	Australia	Birds	4
8	2.1			Without dispersal 17 common European deciduous trees variously lose 1–100% of their range (2 sp. lose 100%); whilst full dispersal could reduce this to 11 losing between 1–99% (2 sp. lose 99%) and 6 increasing their range by 42–303%	Europe	Plants	67
9	2.3	1.6–3.2	3	24% loss freshwater fish habitat, 40% loss in Rocky Mountains, 27% loss of salmon	N America	Fish	13
10	2.4			63 of 165 rivers studied lose >10% of their fish species	Globe	Fish	19
11	2.5	1.9–4.3		42% of UK land area with bioclimate unlike any currently found there; in Hampshire, declines in climate suitability space for curlew and hawfinch and gain for yellow-necked mouse; loss of montane habitat in Scotland; potential bracken invasion of Snowdonia montane areas	UK, Europe	Birds, mammals, plants	57
12	2.5			20–70% loss (mean 44%) of coastal bird habitat at 4 sites	USA	Birds	29

13	2.5	1.9–3.5		20% loss of coastal migratory bird habitat	Delaware, USA	Birds	36
14	2.7			32–70% of 111 European mammals studied lose >30% of current distribution whilst 24–35% undergo range expansions	Europe	Mammals	71
15	2.7			Bioclimatic envelopes exceeded leading to eventual transformation of 16% of global ecosystems: loss of 58% wooded tundra, 31% cool conifer forest, 25% scrubland, 20% grassland/steppe, 21% tundra, 21% temperate deciduous forest, 19% savanna. Ecosystems variously lose 5–66% of their areal extent	Globe		6
16	2.8	2.3–4.6	2.1–2.5	Cloud forest regions lose hundreds of metres of elevational extent, potential extinctions ΔT_{reg} 2.1°C for C America and ΔT_{reg} 2.5°C for Africa	C. America, Tropical Africa, Indonesia		17
17	2.8	2.1–3.1	3	Eventual loss of 9–62% of the mammal species from Great Basin montane areas	USA	Mammals	32
18	2.8			Most European bird distributions are reduced in area by 81% and displaced from 38–53% of their present location; 25% have ranges reduced by > = 90%. Avian species richness reduced by 9–60% depending on dispersal assumptions	Europe	Birds	65
19	2.8	1.9–3.8	3	38–54% loss of waterfowl habitat in prairie pothole region	USA	Birds	37, 38
20	2.9		3.2–6.6	50% loss existing tundra offset by only 5% eventual gain; millions of Arctic nesting shorebirds species variously lose up to 5–57% of breeding area; high Arctic species most at risk; geese species variously lose 5–56% of breeding area	Arctic	Birds	14
21	2.9			Lat. of N forest limits shifts N by 0.5° latitude in W Europe, 1.5° in Alaska, 2.5° in Chukotka and 4° in Greenland	Arctic	Plants	40
22	2.9			Substantial loss of boreal forest	China	Plants	15
23	3.0			66 of 165 rivers studied lose >10% of their fish species	Globe	Fish	19

Table 2 (continued)

No.	ΔT_g above pre-ind °C	ΔT_g (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
24	2.4–4.0			431 bird species lose on average 76–89% of their present range, with new potential ranges overlapping original ones by 31–47% so that species richness declines locally by a mean of 9–56% depending on dispersal assumptions	Europe	Birds	73
25	3.3	2.3–3.9	2.6–2.9	Substantial loss of alpine zone, and its assoc. flora and fauna (e.g., alpine sky lily, and mountain pygmy possum)	Australia	Plants, marsupials	45
26	3.4			6–22% loss of coastal wetlands; large loss migratory bird habitat particularly in USA, Baltic and Mediterranean	Globe	Birds	35, 36
27	3.5	2.3–4.1	2.5–3.5	Loss of temperate forest wintering habitat of Monarch butterfly	Mexico	Insects	28
28	3.6	2.6–4.3	3	Bioclimatic limits of 50% of eucalypts exceeded	Australia	Plants	12
29	3.6	3.0–3.9		Parts of the USA lose 30–57% neotropical migratory bird species richness	USA	Birds	43
30	3.7			Bioclimatic envelopes exceeded leading to eventual transformation of 22% of global ecosystems; loss of 68% wooded tundra, 44% cool conifer forest, 34% scrubland, 28% grassland/steppe, 27% savannah, 38% tundra and 26% temperate deciduous forest. Ecosystems variously lose 7–74% areal extent	Globe		6
31	3.7	2.6–4.8	3	Up to 60% loss in upland stream macro-invertebrate abundance; local extinction of 4 taxa; 25% of mean species richness at risk of local extinction	UK	Invertebrates	62

32	4.0	3.3	47–78% of 111 European mammals studied lose >30% of current distribution whilst 13–33% undergo range expansions	Europe	Mammals	71
33	>>4.0	5	Bioclimatic limits of 73% of eucalypts exceeded	Australia	Plants	12
34	4.9		Without dispersal 17 common European deciduous tree species variously lose 15–100% of their range; full instantaneous dispersal could reduce this to 11 losing between 13% and 100% and 6 increasing their range by 3–320%	Europe	Plants	67
35	5.0		92–97% of 100 *Banksia* species studied experience range contraction, 9% expand	W Australia	Plants	74
36	5.2		62–100% loss of bird habitat at 4 major coastal sites	USA	Birds	29

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)

Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

Table 3 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: extinction risks

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
37	0.6			Amphibian extinctions/extinction risks on mountains due to climate-change induced disease outbreaks	Costa Rica, Spain, Australia	Amphibians	52, 54
38	1.6	1.2–2.0	0.7–1.5	9–31% (mean 18%) of species committed to extinction	Globe (20% terrestrial surface)	Plants, vertebrates and insects	1
39[a]	1.6			23–25% of bird species at risk of extinction, and 1–2% projected extinct	Western Hemisphere	Birds	70
40	1.7	1.2–2.6		38–45% of the plants in the Cerrado committed to extinction	Brazil	Plants	1, 44
41	1.7	1.3–3		2–18% of the mammals, 2–8% of the birds and 1–11% of the butterflies committed to extinction	Mexico	Mammals, birds, insects	1, 26
42	1.75	1.5–2.0		2–4% loss of global vascular plant diversity	Globe	Plants	64
43	1.9	1.6–2.4	1	7–14% of reptiles, 8–18% of frogs, 7–10% of birds, and 10–15% of mammals committed to extinction as 47% of appropriate habitat in Queensland lost	Australia	Reptiles, amphibians, birds, mammals	1, 7
44	2.1			41–51% loss in plant endemic species richness	S Africa, Namibia	Plants	39
45	2.1		1.4–2.6	13–23% of butterflies committed to extinction	Australia	Insects	1, 30
46	2.1	1.4–2.6		Bioclimatic envelopes of 2–10% plants exceeded leading to endangerment or extinction; mean species turnover of 48% (spatial range 17–75%); mean species loss of 27% (spatial range 1–68%)	Europe	Plants	22

47	2.2			3–16% of plants committed to extinction	Europe	Plants	1
48	2.2	2.1–2.3	1.6–1.8	15–37% (mean 24%) of species committed to extinction	Globe (20% terrestrial surface)	Plants, vertebrates and insects	1
49	2.2	1.7–3.2		8–12% of 277 medium/large mammals in 141 national parks critically endangered or extinct; 22–25% endangered	Africa	Mammals	23
50	2.3	1.5–2.7	2°C SST	Loss of Antarctic bivalves and limpets	Southern Ocean	Molluscs	51
51	2.3	1.5–2.7	2.5–3.0	Extinctions (100% potential range loss) of 10% endemics; 51–65% loss of Fynbos; including 21–40% of *Proteaceae* committed to extinction; Succulent Karoo area reduced by 80%, threatening 2800 plant species with extinction; 5 parks lose >40% of plant species	S Africa	Plants	1, 5, 24, 25
52	2.3	2.3–4.0	2.5–3.0	24–59% of mammals, 28–40% of birds, 13–70% of butterflies, 18–80% of other invertebrates, 21–45% of reptiles committed to extinction; 66% of animal species potentially lost from Kruger National Park	S Africa	Mammals, birds, reptiles, insects, other invertebrates	1, 27
53	2.3	2.2–4.0		2–20% of mammals, 3–8% of birds and 3–15% of butterflies committed to extinction	Mexico	Mammals, birds, insects	1, 26
54	2.3	1.6–3.2		48–57% of Cerrado plants committed to extinction	Brazil	Plants	1
55[a]	2.3			27–28% of bird species at risk of extinction, and 2–3% projected extinct	Western Hemisphere	Birds	70
56	2.3			Changes in ecosystem composition, 32% of plants move from 44% of area with potential extinction of endemics	Europe		16

Table 3 (continued)

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
57	2.4			Bioclimatic range of 25–57% (full dispersal) or 34–76% (no dispersal) of 5,197 plant species exceeded leading to extinction risks	Subsaharan Africa		60
58	2.5		2°C SST	Functional extinction of coral reef ecosystems (overgrown by algae)	Indian Ocean	Corals, fish	9
59	2.6			4–21% of plants committed to extinction	Europe	Plants	1
60	2.7			1–6 rodent species (1–5% of 111 mammals studied) committed to extinction	Europe	Mammals	71
61	2.8	2.5–3.0		Multimodel mean 62% (range 40–100%) loss Arctic summer ice extent, high risk of extinction of polar bears, walrus, seals; Arctic ecosystem stressed	Arctic	Mammals	11, 53
62	2.8			65 species at increased risk of extinction with high risk for endemic Scottish Crossbill, Imperial Eagle and Marmora's warbler	Europe	Birds	65
63	2.9		2.1–3.9	21–36% of butterflies committed to extinction; >50% range loss for 83% of 24 lat. restricted species	Australia	Insects	1, 30
64	2.9	2.6–3.3	2.1–2.8	21–52% (mean 35%) of species committed to extinction	Globe (20% terrestrial surface)	Plants, vertebrates and insects	1
65	3.1	2.3–3.7	2°C SST	Functional extinction of remaining coral reef ecosystems (overgrown by algae)	Globe	Corals, fish	2
66	3.1	2.5–4.0	2	High risk of extinction of Golden Bowerbird as habitat reduced by 90%	Australia	Birds	4

67	3.1	1.8–4.2	3–4	Risk of extinction of Alpine species	Europe	Plants	41
68	2.4–4.0			Of 40 endemic/near endemic species studied, 5–8 are threatened with extinction losing 90–100% of their original range	Europe	Birds	73
69	3.3	2.8–3.8	2	Risk of extinction of Hawaiian honeycreepers as suitable habitat reduced by 62–89%	Hawaii	Birds	18
70	3.3		3.7	4–38% of birds committed to extinction	Europe	Birds	1
71[a]	3.3			32–34% of bird species at risk of extinction, and 6–8% projected extinct	Western Hemisphere	Birds	70
72	3.5	2.0–5.5		Projected extinction of 15–40% endemic species in global biodiversity hotspots (narrow specificity)	Globe		50
73	3.6	2.6–3.7		30–40% of 277 mammals in 141 parks critically endangered/extinct; 15–20% endangered	Africa	Mammals	23
74	3.9			4–24% plants critically endangered/extinct; mean species turnover of 63% (spatial range 22–90%); mean species loss of 42% (spatial range 2.5–86%)	Europe	Plants	22
75	4.0	3.0–5.1	3	Likely extinctions of 200–300 species (32–63%) of alpine flora	New Zealand	Plants	33
76	4.0			1–10 species (1–9.% of 111 mammals studied) committed to extinction	Europe	Mammals	71
77	>4.0		3.5	38–67% of frogs, 48–80% of mammals, 43–64% of reptiles and 49–72% of birds committed to extinction in Queensland as 85–90% of suitable habitat lost	Australia	Reptiles, amphibians, birds, mammals	1, 7
78[a]	4.5			39–42% of bird species at risk of extinction, and 10–15% projected extinct	Western Hemisphere	Birds	70
79	>>4.0		5	57 endemic frogs/mammals eventually extinct, 8 endangered	Australia	Amphibians, mammals	7

Table 3 (continued)

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
80	>>4.0		7	Eventual total extinction of all endemic species of Queensland rainforest	Australia	Reptiles, amphibians, birds, mammals	7
81	5.0			22–24% of 100 *Banksia* species studied projected extinct	W. Australia	Plants	74
82[a]	6.9			50–57% of bird species at risk of extinction, and 19–30% projected extinct	Western Hemisphere	Birds	70

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)

Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

[a] Uniquely in this table, these five entries originate from a study which considers impacts by 2100 through a combination of climate change and land use change

Table 4 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: large-scale ecosystem collapse

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
83	2.5		2°C SST	Functional extinction of coral reef ecosystems (overgrown by algae)	Indian Ocean	Corals, fish	9
84	2.5	2.0–3.0		Major loss of Amazon rainforest with large losses of biodiversity	S America, Globe		21, 46
85	>2.5			Sink service of terrestrial biosphere saturates and begins turning into a net carbon source	Globe	Land ecosystems	58, 59
86	3.1	2.3–3.7	2°C SST	Functional extinction of remaining coral reef ecosystems (overgrown by algae)	Globe	Corals, fish	2
87	3.7			Few ecosystems can adapt	Globe		6
88	3.7			50% of nature reserves cannot fulfil conservation objectives	Globe		6

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)

Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

Table 5 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: miscellaneous impacts

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
89	0.6			Increased coral bleaching	Caribbean, Indian Ocean, Great Barrier Reef	Corals	2
90	<1			Marine ecosystems affected by continued reductions in krill possibly impacting Adelie and chinstrap penguin populations; Arctic ecosystems increasingly damaged	Antarctica, Arctic	Crustaceans	42, 11, 14
91	1.7	1–2.3	1°C SST	All coral reefs bleached	Great Barrier Reef, SE Asia, Caribbean	Corals	2
92	1.9	1.0–2.8		Most areas experience 8–20% increase in number ≥7 day periods with Forest Fire Weather Index > 45: increased fire frequency converts forest and Macquis to scrub, leads to more pest outbreaks	Mediterranean		34
93	2.0	1.3–2.3	1	21% decline in spring macro-invertebrate abundance in upland streams	UK	Invertebrates	62
94	2.1	1.0–3.2	1–2	Alpine systems in Alps can tolerate local temperature rise of 1–2°C, tolerance likely negated by land use change	Europe		8
95	2.2	–		Net primary production rises from 45–60 (pre-industrial) to 60–75 Pg C/year; net ecosystem production from zero (pre-industrial) to 2.5–7.5 Pg C/year	Globe		69
96	2.3	2.0–2.5		Fish populations decline, wetland ecosystems dry and disappear	Malawi (Africa), Great Lakes	Fish	20
97	2.4	2.0–3.5		4–20% of the earth's terrestrial surface experiences novel climate; 4–20% experiences disappearing climate	Globe		61
98	2.4	1.8–3.2	3	Extreme levels of mortality in loggerhead sea turtle	Southern US	Reptiles	63
99	2.6	1.6–3.5		Most areas experience 20–34% increase in number ≥7 day periods with Forest Fire Weather Index > 45: increased fire frequency converts forest and Macquis to scrub, causes more pest outbreaks	Mediterranean		34

100	2.8	1.2–4.5	1–3	Extensive loss/conversion of habitat in Kakadu wetland due to sea level rise and saltwater intrusion	Australia		10
101	2.8	2.5–3.0		Multimodel mean 62% (range 40–100%) loss Arctic summer ice extent, high risk of extinction of polar bears, walrus, seals; Arctic ecosystem stressed	Arctic	Mammals	11, 53
102	2.9	1.6–4.1		Threat of marine ecosystem disruption through loss of aragonitic pteropods	S Ocean	Crustaceans	49
103	2.9	1.6–4.1		70% reduction in deep-sea cold-water aragonitic corals	Ocean Basins	Corals	48
104	3.0			In a study of 1420 pollinator species feeding on 429 plant species, 17–50% experience disruption in food supply	Illinois, USA	Plants, insects	72
105	3.1	1.9–4.1	3–4	Alpine systems in Alps degraded	Europe		8
106	3.2	–		Net primary production rises from 45–60 (pre-industrial) to 72–93 Pg C/year; net ecosystem production from zero (pre-industrial) to 0–7 Pg C/year	Globe		69
107	3.3	2.0–4.5		Reduced growth in warm water aragonitic corals by 20–60%; 5% decrease in global phytoplankton productivity	Globe	Corals	2, 47, 48
108	4.0	2.5–4.5		12–39% earth's surface experiencing novel climate; 10–48% disappearing climate	Globe		61

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)

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used originally by the study to assess the impact. The process was repeated (1) for the other 12 GCM/emission scenarios and (2) for eight surrounding adjacent grid cells to test the sensitivity of the results in terms of spatial coherence when using a group of grid cells versus a single grid cell. For each GCM scenario, the average ΔT for the nine (central plus eight adjacent) grid cells was computed. The resultant collection of up to 13 global ΔT values gave the range of global annual mean temperature rise as listed in Tables 2, 3, 4 and 5. In cases where a study has referred to an area larger than a group of nine grid cells, either a cluster of disjunct groups or contiguous orographic features, such as a mountain range or a plain, were aggregated into several clusters of grid cell groups across the region. The entries in the tables reflect also the average and range of outputs over the appropriate clusters of groups of grid cells.

Large local temperature increases can lie outside the range of the outputs of the GCMs held in the database. If this was the case, the study was not included in the upscaling calculations. GCMs with temperature changes that were too low to reach the study value(s) were excluded. Table 6 in the Appendix details which GCMs were used in the upscaling. If more than two GCMs were thus out of range, we assumed case f (Table 1) to avoid underestimating ΔT_g. Note that the GCM time series for ΔT_g are provided with respect to an observed mean over the period 1961–1990, ensuring that correct temperature reference points were maintained in all upscaling.

3 Results

Tables 2, 3, 4 and 5 provide the resultant summary of key impacts on various ecological systems, ranging from the global level to that of individual, endemic species. The supplementary information in Table 6 in the Appendix provides for each entry from Table 2a–d information on the GCM runs used in upscaling, the climate variables considered by the impact study, and the category of the upscaling method we applied (a–h, see Table 1). 71 studies were found to provide sufficient quantitative climatic and ecological information for inclusion in Table 2a–d. Projected impacts were found for all major world regions, but only one study focused on Asia. Most studies were on terrestrial systems, whilst relatively few covered changes in the marine environment. Range losses and extinctions (Tables 2 and 3) were projected for many important taxa with vascular plants, birds, and mammals being particularly well represented. A significant number of studies also projected impacts on amphibians, reptiles, fish, butterflies, and freshwater or marine invertebrates. Table 2 also shows many projections for major losses of regional ecosystems as climate changes. Table 4 shows projections for large scale collapse in ecosystems, i.e. thresholds at which major components of the world's ecosystems become irreversibly damaged, positive feedbacks emerge, or their functioning, collapse. As global temperatures rise, many of these thresholds start to be crossed at around $\Delta T_g = 2.5°C$ above the pre-industrial level.

A key finding is that some significant negative impacts for range losses and extinctions (Tables 2 and 3), and also damages to marine ecosystems (Table 4), were projected to occur for values of ΔT_g below 2°C, especially in some biodiversity hotspots, and also globally for the diversity rich coral reef ecosystems ($\Delta T_g = 1.7°C$). However, it is also noticeable that, given the analyzed literature, projected impacts increase in magnitude, numbers and geographic spread once a 2°C rise in global mean temperature is reached. Beyond this temperature rise the level of impacts and the transformation of the Earth's ecosystems become steadily more severe, with the potential collapse of some entire ecosystems, and extinction risks accelerating and becoming widespread. Additional positive feed-backs emerge causing land ecosystems to transition from their current status as a net carbon sink to a net carbon source.

4 Discussion

4.1 General

A large body of literature exists discussing the potential future impacts of climate change upon ecosystems, as reviewed in Fischlin et al. (2007). Much of this literature does contain only qualitative or no directly comparable quantitative projections of change or does not relate any quantitative estimates of change to quantitative changes in global climate. Previous integrating summaries of climate change impacts on wild species and ecosystems have suggested substantial ecosystem disruption with projected anthropogenic climate changes, and particularly the increased risk of species extinction (e.g. Thomas et al. 2004a, b). Such findings have been criticised partly because they did not reference the projected impacts to a consistent measure of climate change. In order to provide robust findings in a policy relevant manner, it is critical to reduce the uncertainty created by this lack of a common reference. Hence Warren (2006) and Hare (2006) both took steps to do so. The results reported here, through use of a common temperature reference point, confirm the likelihood of significant negative impacts of climate change first mooted in studies such as Thomas et al. (2004a, b), but provide a far clearer picture of the likely increase in scale of impacts with increasing levels of climate change, together with an indication of uncertainty associated with ΔT_g.

With our common referencing system, we can also address the question as to what extent the literature has sampled the range of climate change forcings of the next few centuries adequately for the observations made by this study to be valid. The likely range of temperature increase in 2100 is 1.1°C to 6.4°C above the 1980–1999 average (i.e. 1.6°C to 6.9°C above the pre-industrial level), showing that the literature currently does not sample the upper end of this range, with most studies considering only the range between 1.5°C and 4°C above pre-industrial). Within these limits however, a broad range of global annual mean temperature rises is sampled, owing to the many different scenarios and GCMs used. This is the case for those studies that are based on GCM scenario outputs as well as the many other regional scenarios based only upon potential local, non-GCM-scenario based climate changes. A small subset of the studies considers the effects of doubling CO_2 concentrations, whilst another subset is based on transient climate change simulations. Because different GCMs are used in these subsets, the resultant global mean temperature, and concomitantly precipitation, values vary considerably among climate models, in particular in cases where regional scenarios of climate change were derived. We believe the small subset of table entries referring only to CO_2 concentration doubling has not introduced a bias. Owing to a sampling of a relatively comprehensive temperature range similar to that covered by many scenarios (0.3–6.4°C, IPCC 2007), the overall interpretation of the results is not biased by any artificial clustering of data around a particular global mean temperature rise.

The majority of the impacts found in the literature are negative, with the exception of those projecting increases in primary production. Whilst a higher productivity may indeed increase vegetation growth, this in itself can disrupt species assemblages and thereby degrade ecosystems. For example, in tropical forests increased concentrations of CO_2 are stimulating rapid growth by vines (Granados and Körner 2002), which can strangle large trees (Phillips et al. 2002); and increasing growth rate and turnover of trees could even result in lower carbon storage rates, thus reducing the forest's service as a carbon sink (Feeley et al. 2007). Hence, with the exception of enhanced growth at moderate climate change we have rarely identified definitively positive impacts of climate change upon ecosystems. Whilst some authors consider transitions from desert to grassland or grassland to forest as "positive" in terms of gains in net primary production, this often neglects the issue of transient dynamics between previous and new equilibrium, and threats to endemic and specialist organisms of the replaced environments. Some studies indicate transitionally an even lower productivity (e.g., Fischlin and Gyalistras 1997).

4.2 Uncertainties in the analysis

This study has considered the role of uncertainty only in a limited manner, as it is difficult to quantify. The uncertainty analysis carried out is limited by its dependency on downscaling and upscaling of pattern-scaled transient temperature outputs of GCMs, and thus is contingent on the assumptions of pattern regularity as assumed in most down-scaling procedures (e.g., Gyalistras et al. 1994), in particular that the patterns are constant over a particular temperature range. It is also assumed that the patterns are independent of the history of greenhouse gas forcing, whereas in actuality an equilibrium climate change pattern may differ from transient ones. Equilibrium patterns were not available for this analysis, but would be more suitable for use with studies of type b, or studies of type c or d which actually use outputs of equilibrium runs of GCMs. The uncertainty analysis also reflects only the different relationships between global and local temperature displayed by various GCMs, and not the relationship between global temperature and local precipitation changes. In some cases where impacts are strongly driven by precipitation and models differ widely for the location in question, for example entry 41, the loss of forest cover in the Amazon basin (Cox et al. 2004), this could be important.

Much of the literature reviewed here is based on a biogeographical or bioclimatic approach. Whilst this approach has been criticised for its shortcomings in largely ignoring some mechanisms such as physiological responses, the treatment of species–species interactions, the limited accounting for population processes or migration (Pearson and Dawson 2003; Pearson 2006), or the common assumption that current species distributions are in equilibrium with current climate, the approach has nevertheless proved capable of simulating known species range shifts in the distant and the recent past (Martinez-Meyer et al. 2004, Araujo et al. 2005), and furthermore, is generally corroborated by the observed responses of many species to recent climatic changes (e.g. Walther et al. 2002; Root et al. 2003; Rosenzweig et al. 2007) and climate-change induced changes in geographical species ranges, which are starting to be reported (Thomas et al. 2006; Foden et al. 2007). However the approach remains nevertheless to be comprehensively and explicitly tested against the observational record (Midgley and Thuiller 2005), an opportunity that should be taken as soon as possible. Most of the studies reported in Tables 2 and 3 result from detailed analysis of well-studied species and ecosystems in a given locality. In the case of the global extinction rate estimates (Thomas et al. 2004a) there has been a debate as to the validity of the particular species–area relationship used to estimate extinction rates (Thuiller et al. 2004; Thomas et al. 2004b; Buckley and Roughgarden 2004; Harte et al. 2004; Lewis 2006). Whilst these estimates are based on extrapolation of studies of endemics, Thomas et al. (2004b) argue that this creates only a small bias because such a large percentage of global species are in fact endemics. The study of Malcolm et al. (2006) provides an overall estimate of extinctions of endemics in biodiversity hotspots that does not rely on bioclimatic modelling of individual species, and generally supports the findings of Thomas et al. (2004a), though the use of endemic–area relationships rather than simple species–area relationships indicates some reduced impacts.

Responses of species to changing climate will also be affected by biotic interactions, which affect the levels of space occupancy and dispersal; e.g. in alpine plant communities, mutualists are expected to be able to tolerate greater climate change than competitors at slow rates of climate change, whereas at faster rates they may be excluded by competitors if these can easily disperse into newly climatically suitable areas (Brooker et al. 2007).

4.3 Factors omitted or partly considered in this study and the underlying literature

4.3.1 Direct effects from raising atmospheric CO_2 concentrations

In Tables 2, 3, 4 and 5, the temperature column is essentially used as a proxy for the accompanying other changes, which will occur concurrently, such as precipitation change or elevated CO_2 concentrations. However, only a limited number of studies that project climate change impacts upon ecosystems consider concurrent changes such as the direct effects of elevated ambient CO_2 concentrations associated with local or global scenarios of temperature rise. This is particularly true of studies based on bioclimatic modeling, or niche-based modelling techniques that simulate species geographic range shifts. Despite increasing evidence that CO_2 fertilization effects on crop species have been somewhat overestimated in the past (Fischlin et al. 2007), those on wild plant species and particularly trees are corroborated by strong evidence (e.g., Ainsworth and Long 2005). This may remain a significant omission in the modeling of some ecosystem types. For example, CO_2 fertilization may differentially affect woody and herbaceous species, affecting the dynamics of forest–savanna–grassland conversions with major implications for biodiversity (Bond et al. 2003). Whilst a small number of entries in the tables derive from consideration of ocean acidification, the literature in this area is in its infancy. As oceans continue to acidify as atmospheric CO_2 concentrations rise concurrently with warming, there is significant potential for changes in marine food webs and hence the valuable ecosystem services that the oceans provide for humankind (Orr et al. 2005; Haugan et al. 2006).

4.3.2 Indirect effects of climate change

Tables 2, 3, 4 and 5, and the literature upon which they are based, largely document only the projected impacts on ecological systems resulting directly from climate changes such as changes in temperature and precipitation, the most commonly considered variables. However, there are a number of other impacts on ecosystems to be expected, that result from non climatic causes or indirectly via climatic changes. For example (1) wildfires and certain defoliating insects are projected to increase with warming (for example in boreal forests and the Mediterranean, e.g., Fischlin et al. 2007; Kurz et al. 2008), and decomposition rates will change by large percentages as rainfall changes (for example in deciduous forests in the USA, e.g. Lensing and Wise 2007) both of which is likely to have further impacts on forest and grassland ecosystems as well as causing substantive biotic feedbacks to the climate system; (2) secondary succession may last several centuries (Fischlin and Gyalistras 1997), thus delaying actual impacts and causing additional effects in other communities; (3) surprising ecological changes may also occur in marine and terrestrial communities with climate change if predators and prey become decoupled, or newly engage with each other, which could occur if they have differing phenological, geographical, and/or physiological responses to climate change (Price 2002; Burkett et al. 2005); (4) indirect impacts from sea ice melting, for example reductions in sea ice in the Antarctic are likely to have contributed to the dramatic 80% declines in krill observed since 1970 (Atkinson et al. 2004) with penguin populations already affected, and particularly if climate change shifts the Antarctic Circumpolar Current, krill could suffer further and the ecosystem could be severely impacted; (5) climate change is also projected to cause deglaciations, e.g. of the Himalayan region, which would adversely affect the hydrology of the downstream regions, e.g. of the Indian region including its ecosystems; (6) increases in the magnitude and/frequency of (intra-annual) extreme weather events are projected with climate change as climate variability increases (e.g. Schär et al. 2004; Meehl et al. 2007), all of which have a significant potential to affect ecosystems further (e.g. Fuhrer et al. 2006). Many impact models consider such effects only in a limited manner, e.g. because of a too coarse temporal resolution; (7) climate change may affect major modes of inter-annual cyclic variability such as El Nino, the North Atlantic Oscillation, or the Pacific Decadal Oscillation. GCMs do not capture such changes to a realistic extent and many impact models have only captured such climate variability effects to a limited extent if at all. Changes to these cycles are likely to affect ecosystems through for example, changed rainfall patterns and/or drought and fire incidence (e.g. Holmgren et al. 2001).

4.3.3 Land-use change

This meta-analysis focuses on the impacts of climate change and does not account for the effects of land-use change. More realistic impacts, notably those of species extinctions in 2100 and beyond, are likely to be greater than Tables 2, 3, 4 and 5 indicate, since land-use change is included in only one study (Sekercioglu et al. 2008), and is known to negatively impact biodiversity. These additional negative impacts from land-use change would only be avoided if effective stringent policies would soon be put into place that avoid further conversion of natural and semi-natural ecosystems to agriculture, landscape fragmentation, and/or other degradations within a given type of land use as for instance also caused by intensification of agricultural practices. Owing to the development of human systems and their adaptation to climate change, including the potential use of biofuels as a mitigation measure, both of which may force new areas into cultivation, and the projected increases in global human populations, there are in fact rather to be expected increased pressures on extant land uses than the reverse. Some scenarios of future land uses have been developed for and reviewed in the Millennium Ecosystem Assessment (2005) and evince this overall trend.

Since land-use change is well known to be of critical relevance for biodiversity conservation, Lewis (2006) raised the concern that recent literature on potential extinctions due to climate change could distract conservationist's efforts in preventing land-use change in existing ecosystems, in particular with respect to avoiding deforestation. Jetz et al. (2008) projects losses of current ranges for 21–26% of the world's approximately 8,750 bird species by 2050, and for 29–35% by 2100, due to the combination of climate change scenarios from Solomon et al. (2007) and land-use change scenarios from the Millennium Ecosystem Assessment (MEA 2005). The need to provide for species to disperse successfully to reach areas that become newly climatically suitable increases the need for protecting existing ecosystems from land-use change. These findings suggest that avoided deforestation policies offer a crucial double benefit of reducing both climate change and land-use change impacts upon biodiversity. Thus, for these reasons we consider evidence that climate change can have severe impacts on biodiversity as presented in this analysis rather to provide an additional strong incentive for preserving existing ecosystems, including their protection from land-use changes, than an invitation to neglect conservation policies.

4.3.4 Dynamics

There are very few studies in the literature, which take into account the effect that the rate of climate change exerts upon ecosystems. This is also likely to be a key factor, since the slower the rate of change the greater is the potential for adaptation by dispersal or through natural selection for physical or behavioural characteristics better suited to a changed climate (for a recent review see Fischlin et al. 2007, notably Section 4.4.5). For very small amounts of warming there may be benefits in terms of increased productivity in ecosystems which are below their thermal optimum, for example in boreal forests. However, as temperature increases further the thermal optimum is passed, and the ecosystem begins to decline. It is the passing of such thresholds or "tipping points", the onset of negative impacts, which are the focus of the literature underlying this paper.

Some such "tipping points" are breached when a certain magnitude of climate change is reached. Regional features of the earth's climate system might also be disrupted, with concurrent un-quantified impacts upon ecosystems. For example, the Indian Monsoon might be disrupted (Zickfield et al. 2005). At the Earth system scale, as temperature continues to rise, additional positive feedback mechanisms may be activated. Examples are the saturation of the net carbon sink land ecosystems currently provide, the transition to a net source (Fischlin et al. 2007, Fig. 4.2), or the risk for the potential release of methane from tundra yedoma and permafrost (Fischlin et al. 2007) and perhaps beyond 2100 even clathrates from shallow seas. The weakening of the land sink, let alone the turning into a source, as well as a release of substantive amounts of methane would cause a strong amplification of the greenhouse effect, greatly exacerbating the ongoing climate change.

Some such "tipping points" are breached when a certain rate of climate change surpasses the rate by which ecosystems can adapt naturally. During past phases of large climate changes, species have typically responded by shifting range rather than by evolving in situ (Davis and Shaw 2001). Ecosystems have been estimated to be able to withstand a temperature increase of only 0.05–0.1°C/decade (van Vliet and Leemans 2006), much slower than the current rate of 0.13°C/decade (Solomon et al. 2007) and hugely slower than the current rate near the poles of 0.46°C/decade, considered sufficient to cause serious ecosystem disruption. Foden et al. (2007) show how the currently observed migration rate of *Aloe dichotoma* (quiver tree), a Namib desert plant, in response to observed climate change, would be insufficient to keep pace with a moderate climate change scenario for 2050. Based on a comprehensive review of these issues Fischlin et al. (2007) concluded that "The resilience of many ecosystems is likely to be exceeded this century" for business-as-usual emissions scenarios (e.g. IS92a, A1FI, A2). Resilience is here understood as the capacity of ecosystems to adapt naturally and sufficiently fast to their changing environment without altering their mode of operation entirely.

This meta-analysis is based on impact studies that assume in many cases a new hypothetical equilibrium between the projected climate change and the impacted ecosystems. Typically the forcing climate change is then assumed to have remained constant indefinitely at the ΔT_g for which the impact was assessed and that the ecosystems are given sufficient time to adapt till the new estimated equilibrium has been reached. Most of the literature used in this analysis does not explicitly discuss the time dimension, but it can nevertheless be assumed in most cases that the ecosystem impacts in Table 5 might also occur if the temperature thresholds are breached transiently (i.e. local or regional temperature "overshoots") as simulated in various studies of the dynamics of climate change (O'Neill and Oppenheimer 2004).

Den Elzen and Meinshausen (2006) show that transient probabilities of exceeding various temperature thresholds might either be higher, or lower, than the equilibrium probabilities of exceedance of that threshold. Similarly Mastrandrea and Schneider (2006) show how probability of exceedance of temperature thresholds in stabilisation scenarios is a strong function of the pathway to stabilisation. Thus, one may argue that our assessment may indeed be questioned as the evolution of temperature and other concomitant climate change variables differ. However, the advantage of our approach is that the ranking of the impacts relative to the temperature increase as an indicator of climate change is unlikely to be affected even if the absolute values might have to be corrected as our understanding of these relationships progresses. In this respect our results can be viewed as being quite robust and conservative.

The question remains whether the impact models used have realistic sensitivities. Otherwise overestimations or underestimations of the impacts would have to be expected. The majority of the impact models we used here have considered changes in temperature as well as precipitation and many have also considered the beneficial effects from CO_2 fertilisation, in particular at the global level. This makes the models more likely to exhibit realistic responses to climate change than this was the case for many earlier studies, which followed less integrative approaches.

Nevertheless, the particular approach that many current state-of-the-art impact models follow may lead to biases. First in cases where the climate change was assumed to remain constant after having reached ΔT_g, the impact models that have not yet reached the new equilibrium tend to underestimate the impacts. Secondly, if the magnitude of climate change exceeds rapidly certain tolerances, i.e. the fundamental niches, of impacted species, even long-lived species such as trees are likely to suffer mortalities before they are replaced by newly arriving, other species for which the new, climatic situations are more benevolent. Thus, in general the more rapid climate change, the more likely such transient ecosystem degradations become. Indeed, the modelling approaches generally followed do incompletely mimic such effects and for these reasons tend to rather underestimate than overestimate impacts. Finally, for other processes such as coral bleaching and local extinction of sensitive species, which can occur within a relatively short time span of a few years, transient temperature peaks might be very critical. If emissions are reduced in a manner such that there is transient overshooting of the final equilibrium temperature, impacts may then be considerably greater than indicated in Tables 2, 3, 4 and 5.

Therefore we consider the results from our meta-analysis to be in general rather conservative and it appears to be unlikely that they are biased towards overestimating the severity of the consequences of climate change for ecosystems. However, critical uncertainties remain, in particular because most impact models depend to a large extent on knowledge about the realized niches only. Should fundamental niches be significantly larger than the realized ones, overestimations of climate change impacts are bound to result. Indeed, the difficulties to assess the true fundamental niches of most species remain a relevant source of uncertainty (Kirschbaum and Fischlin 1996), a fact that still significantly constrains the ability of most currently used kinds of ecological models to assess climate change impacts.

5 Conclusions

A literature-based integrated assessment of the effects of climate change upon a wide range of ecological systems has shown that the negative impacts accrue as annual global mean temperature rise as little as 1.6°C (low end of the likely range of IPCC scenarios,[1] IPCC 2007) above the pre-industrial level, already with several examples of projected severe damages, range losses, and extinctions. As global temperatures reach and exceed 2°C above pre-industrial levels, negative impacts rapidly increase. This includes increases in range losses and extinctions and increasing damage to some critical ecosystem structure and functioning. As global temperatures increase further beyond 2°C above pre-industrial, the literature and models increasingly project impacts accruing to entire systems and becoming more widespread across a range of different species groups and regions. Several critical aspects of ecosystem functioning are projected to begin to collapse at a temperature of 2.5°C (Table 4). These represent either the potential collapse of entire ecosystems e.g. wide-spread impoverishment of coral reefs, or comprise impacts, which are in our judgement dangerous, because they likely imply irreversible damages, such as extinctions of key species, or the onset of positive feedbacks, such as CO_2 emissions, accelerating climate change. In our judgement, risking the widespread collapse of multiple global

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[1] This value considers the multi-model projected lower end of the likely range of the IPCC SRES B1 scenario (IPCC 2007, Table SPM.3) of +1.1°C warming by 2100 relative to 1980–1999 and adding +0.5°C already realized global warming for period 1980–1999 relative to preindustrial climate.

ecosystems (Table 4) represents “dangerous anthropogenic interference” and would comprise a breach of compliance with Article 2 of the United Nations Framework Convention on Climate Change.

This meta-analysis confirms and expands upon the results of other assessments (Houghton et al. 2001; Hare 2006; Warren 2006; Fischlin et al. 2007), which have shown that climate change is a threat to ecosystems and species worldwide, with coral reef, Arctic, Mediterranean, and mountain ecosystems including many biodiversity hotspots being particularly at risk. Hare (2006) also identified substantial increases in risks to ecosystems and species beyond the EU 2°C target using “burning ember” diagrams. We consider that our study, with a more extensive literature review, using a tabular approach and including some uncertainty analysis, provides further strong justification for policies constraining annual global mean temperature change relative to preindustrial climate to no more than 2°C—at least from an ecosystem preservation point of view. This temperature would avoid the projected breaching of the aforementioned large-scale ecosystem collapses, as well as a large proportion of the onset of many of the projected negative impacts such as range losses, extinctions, ecosystem damages including disruptions of their structure and functioning. Since we identified some significant impacts in biodiversity hotspots such as amphibian extinctions in tropical forests and wide spread coral bleaching in reefs below a 2°C warming, protection of the majority of ecosystems would however require a more stringent target, as argued by Rosentrater (2005) for the Arctic.

Many of the impacts tabulated here appear to be clearly in conflict with Article 2 of the United Nations Framework Convention on Climate Change in not allowing ecosystems to adapt naturally. Minimising the rate of climate change is expected to also reduce the risks of climate change for ecosystems, although this aspect can not yet be well analysed with current techniques available to assess impacts. According to the precautionary principle it appears that a reduction in current and future land use change will give ecosystems and species the best chance to adapt to the climate changes that are projected to occur in the twenty-first century even under stringent mitigation policy. In particular, avoided deforestation is a policy which meets both these goals, although alone this policy is of course not sufficient to constrain climate change to 2°C above pre-industrial levels. Further analyses of many of the findings from this study made in an even broader context of climate change impacts on ecosystems can be found in Fischlin et al. (2007).

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Appendix

The Table 6 below contains detailed information concerning the underlying studies used in each entry of Tables 2–5, where column 1 is identical to column 1 of Tables 2–5, and the following abbreviations are used: **E** indicates an empirical derivation, **M** indicates a modelling study, a **number** refers to how many GCMs were used in the original literature. Other codes indicate if model projections included precipitation (**P**), ocean acidification (**pH**), sea ice (**SI**), sea level rise (**SLR**), sea surface temperature (**SST**) or anthropogenic water use (**W**); dispersal assumptions from the literature. **D**—estimate assumes dispersal; **ND**—estimate assumes no dispersal; **NR**—not relevant since species/ecosystem has nowhere to disperse to in order to escape warming (e.g. habitat is at top of isolated mountain or at southern extremity of austral landmass). **IMAGE**, **BIOME4**, **LPJ**, **MAPSS** refer to specific models as used in the study, to assess climate change impacts, e.g. LPJ denotes the Lund–Potsdam–Jena dynamic global vegetation model (Sitch et al. 2003). **DVGM** refers to dynamic global vegetation model. GCM abbreviations used here: **H2**—HadCM2, **H3**—HadCM3, **GF**—GFDL, **EC**—ECHAM4, **CS**—CSIRO, **CG**—CG, **PCM**—NCAR PCM. Lower case a–h refers to how the literature was addressed in terms of up/downscaling and these are defined in Table 1. The GCM outputs used in the upscaling calculations are those used in the IPCC Third Assessment Report (TAR IPCC 2001) and are at 5° resolution: HadCM3 A1FI, A2, B1, B2 where A2 is an ensemble of 3 runs and B2 is an ensemble of 2 runs; ECHAM4 A2 and B2 (not ensemble runs); CSIRO mark 2 A2, B1, B2; NCAR PCM A2 B2; CGCM2 A2 B2 (each an ensemble of 2 runs). Where GCM scenario names only were provided further details were taken from: HadCM2/3 (Mitchell et al. 1995; Hulme et al. 1999; Arnell et al. 2004), http://ipcc-ddc.cru.uea.ac.uk.

Table 6 Supplementary to Tables 2, 3, 4 and 5: the table below contains detailed information on models and how the upscaling and downscaling were performed for each entry in Tables 2, 3, 4 and 5 and uses the same numbering scheme

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
2	1, 4, 9	M, 5, ND, c; ref. quotes 13.8% loss in Rocky Mountains for each 1°C rise in JJA temperature, upscaled with CS, PCM, CG
2	2, 15	M, 5, IMAGE, a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990
2	3	M, D, b; no GCM used in ref.; upscaled with H3, EC, CS, PCM, CG
2	14, 32	M, P, GDD, D&ND, a; ref uses B1 and A2 of H3 with ΔT rise of 2.4°C and 3.7°C respectively compared to the 1961–1990 mean
2	6, 7	M, P, NR, e; upscaled at several sites using H3, EC, CS, PCM, CG
2	5	M, H3, E4, P, D&ND, a; GFDL based estimates omitted due to lack of access to global temperature time series
2	10	M, H3, W, a; ref. uses B2 of H3 in 2070 that has a ΔT rise of 2.1°C with respect to the 1961–1990 mean
2	11	M, P, D, d; UKCIP02 high emission scenario used as central value; upscaled for Hampshire from UKCIP02 (Hulme et al. 2002) regional maps using H3, EC, CS
2	12	M, SLR, a; analysis based on transient 50% probability of sea level rise using the US EPA scenarios for ΔT of 2°C above 1990 baseline

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
2	13	M, H3, SLR, a; IS92a median ΔT 2.0°C above 1990 (Kattenberg et al. 1996, Fig. 6.20) and range 1.4–3.0°C
2	16	M, GE, P, NR, d; GENESIS GCM with 2.5°C rise for CO_2 doubling from 345 to 690ppm, 345 ppm corresponds quite closely to the 1961–1990 mean; upscaling then gives the range; across locations variously used H3, EC, CS, CG
2	17	M, NR, b; upscaled with H3, EC, CS, and CG
2	18	M, P, D, HadCM3, ECHAM4, GFDL, a; Huntley et al. (2006) give 2.5°C relative to 1961–1990 mean
2	19	M, 2, P, d, g; range is due to importance of ΔP, GFDL CO_2 doubling is from 300 ppm which is close to 1900 climate sensitivity in ref of 3.7; UKMO in 2050 is 1.6°C above 1961–1990 mean, 1.9°C above preindustrial
2	20, 21	M, H2, BIOME4, P, NR, c; A1 scenario of H2GS has ΔT of 2.6°C relative to 1961–1990 mean
2	22	M, BIOME3, P, d, f; H2 2080s has global ΔT of 2.6°C above 1961–1990 mean
2	23	M, H3, W, a; ref. uses A2 of H3 in 2070 that has a ΔT of 2.7°C with respect to the 1961–1990 mean and hence 2.5°C with respect to 1990
2	24	M, H3, GF, EC, P, D&ND, a
2	25	M, CS, P, d; upscaled with H3, EC, CS, CG
2	26	M, H2, SLR, NR, a; H2 2080s without aerosols has global ΔT of 3.4°C above pre-industrial (Hulme et al. 1999)
2	27	M, 2, P, D, d; study used CO_2 doubling scenarios—CCC ΔT at doubling is 3.5°C relative to 1900 whilst GFDL R30 is 3.3°C relative to 1900; upscaling gives range H3, EC, CG
2	28	M, D, b; upscaled with H3, EC, CS
2	29	M, CCC, P, D, d; CO_2 equilibrium doubling scenario has ΔT of 3.5°C relative to 1900; downscaled with CGCM and upscaled with H3, EC, CS, CG
2	30	M, 5, IMAGE, P,a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990
2	31	M, P, D (based on empirical calibration), d; upscaled with H3, EC, CS, PCM, CG
2	33	M, D, f; Meehl et al. (2007), Fig. 10.3.5 shows this occurs for $\Delta T \geq 3.5°C$ above 1990
2	12, 34	M, D&ND, P, HadCM3, a; Ohlemüller et al. (2006) use HadCM3 projections quoted as ‘2.0, 4.8°C above 1931–1960 mean for entries 12, 34 respectively, add 0.1°C to convert to pre-industrial

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
2	35	M, 3, P, a
2	36	M, SLR, a; US EPA scenario of 4.7°C above 1990.
3	37	E
3	38	M, D&ND, a; 18% matches minimum expected climate change scenarios which Table 3 of Thomas et al. (2004a) lists as ΔT of 0.9°–1.7°C (mean 1.3°C) above 1961–1990 mean; 8 of 9 sub-studies used H2
3	39, 55, 71, 78, 82	M, D, a;
3	40	M, H2, P, ND, d; table 3 of Thomas et al. (2004a) gives global ΔT of 1.35°C above 1961–1990; HHGSDX of H3; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	41	M, H2, P, D&ND, d; Beaumont and Hughes (2002) give global mean temperature rise of 1.8°C relative to the 1961–1990 mean
3	42	M, D, P, a
3	43	M, D, b; upscaled using H3, EC, CS, PCM, CG
3	44	M, H3, P, D, d; H3 2050 SRES mean
3	45	M, H2, P, D, d, g; table 3 of Thomas et al. (2004a) gives global ΔT of 1.35°C above 1961–1990; upscaled with H3, EC, CS, PCM, CG; uses a local ΔT range across Australia
3	46	M, H3, P, D&ND, d; ref. uses B1 of H3 in 2050 with a ΔT of 1.8°C above the 1961–1990 baseline; downscaled with H3 and then upscaled with H3, EC, CG
3	47	M, H2, P, D&ND, d; studies used global annual mean ΔT of 1.7–2.0°C above 1961–1990 mean
3	48	M, P, D&ND, a; table 3 of Thomas et al. (2004a) mid-range climate scenarios have a mean ΔT of 1.9°C above 1961–1990
3	49	M, H2, P, D&ND, d; ref. refers to A2 of H3 in 2050 that has a ΔT of gives as 1.9°C above 1961–1990 (Arnell et al. 2004); downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	50	H; upscaled using maps from WGI, chapter 10
3	51	M, 2, P, NR, d; scenarios on CRU website used with ΔT of 2.0°C above 1961–1990, agrees with Table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	52	M, H2, P, D, d; the 66% is from a suite of 179 representative species, table 3 of Thomas et al. (2004a) lists global ΔT of 2.0°C above 1961–1990 mean, upscaled with H3, EC, CS, CG
3	53	M, H2, P, D&ND, d; table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean using HHGGAX; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
3	54	M, H2, P, ND, d; table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean using HHGGAX; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	56	M, IMAGE, P, D&ND; Bakkenes et al. (2002) gives the global temperature change relative to 1990
3	57	M, P, D&ND; ref. uses B1 in H3 in 2080s from (Arnell et al. 2004)
3	58	M, SST, h
3	59	M, H2, D&ND, d; ref. uses global ΔT of 2.3°C above 1961–1990 mean; downscaled with H3 and upscaled with H3, EC, CG
3	60, 76	M, P, D & ND, a
3	61	M, 15, SI, a; Arzel et al. (2006) uses 15 GCMs with A1B for 2080s, ΔT A1B 2080s multi-model from WGI, chapter 10, Fig. 10.3.2 is 2.5°C above 1990; ACIA uses 4 GCMs with B2, multi-model ΔT is 2.2°C over 1961–1990 or 2.0°C above 1990
3	62	M, P, D, HadCM3, ECHAM4, GFDL, a; Huntley et al. (2006) give 2.5°C relative to 1961–1990 mean
3	63	M, 10, P, D, d, g; Beaumont and Hughes (2002) give global mean temperature rise of 2.6°C relative to the 1961–1990 mean
3	64	M, P, D, ND, a; Table 3 of Thomas et al. (2004a) maximum climate scenarios have a mean ΔT of 2.6°C above 1961–1990 or 2.3°C above 1990
3	65	M, SST, h
3	66	M, P, NR, e; upscaled for several sites taken from maps in ref., using H3, EC, CS, CG
3	67	M, NR
3	68	M, 3, a, P, cloudiness, D & ND
3	69	M, NR, b; % derived from Table 1 in Benning et al. (2002) for all forest areas combined on the 3 islands studied; upscaling considers changes averaged over 3 islands and uses H3, EC, CS, CG
3	70	M, H3, P, D&ND, d, f; table 3 of Benning et al. (2002) lists global ΔT of 3°C above 1961–1990 mean
3	72	M, 7, BIOME3, MAPSS, P, D&ND, a; uses CO_2 doubling scenarios from Neilson and Drapek (1998) Table 2; control concentrations were obtained directly from modellers; thus deduced mean global mean ΔT for this study
3	73	M, H3, P, D&ND, d; ref. uses A2 in H3 in 2080 that has a ΔT of 3.3°C above 1961–1990 (Arnell et al. 2004)
3	74	M, H3, P, D, d, f; ref. lists ΔT of 3.6°C for A1 in H3 in 2080 relative to 1961–1990, downscaled with H3 and upscaled with H3, EC, CG

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
3	75	M, NR, b; upscaled with H3, EC, CG
3	77	M, NR, b, f; Meehl et al. (2007), Figs. 10.3.5 and 10.3.2 suggest global ΔT of 3.5°C relative to 1990
3	79	M, NR, b, f; Meehl et al. (2007), Fig. 10.3.5 shows this occurs for ΔT ≥3.5°C above 1990
3	80	M, NR, b, f
3	81	M, 3, P, a
4	83	M, SST, h
4	84	M, a
4	85	M, 2, P, LPJ; upscaled with H3, EC5
4	86	M, SST, h
4	87, 88	M, 5, IMAGE, a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990
5	89	M, 4, SST
5	90	E, SI
5	91	M, SST, h
5	92	M, P, NR, d; HadRM3PA2 in 2050, Fig. 13 in Moriondo et al. (2006) shows ΔT matching B2 of H3 of 1.6°C above 1961–1990 mean; downscaled with H3 and upscaled with H3, EC, CS, PCM, CG
5	93	M, P, D (based on empirical calibration), d, upscaled with H3, EC, CS, PCM, CG
5	94	E, P, D, b; upscaled using H3, EC, CS, PCM, CG
5	95	M, H2 with aerosols in 2050, a, 6 DVGMs, global temperature taken from Raper et al. (2001).
5	96	E, P, NR, a
5	97	M, a; Williams et al. (2007) use the B1 scenario from a mean of 9 GCM simulations used in IPCC (2007) which have a global temperature increase of 1–2.5°C averaging approximately 1.9°C above 1990 (hence 2.4 above pre-industrial)
5	98	M, d; upscaled using H3, EC, CS, PCM, CG
5	99	M, P, NR, d; HadRM3PA2 in 2050, taken from Fig. 13 of Moriondo et al. (2006)
5	100	M, CS, b; upscaled with H3, EC, CS, PCM, CG
5	101	M, 15, SI, a; Arzel et al. (2006) uses 15 GCMs with A1B for 2080s, ΔT A1B 2080s multi-model from WGI, chapter 10, Fig. 10.3.2 is 2.5°C above 1990; ACIA uses 4 GCMs with B2, multi-model ΔT is 2.2°C over 1961–1990 or 2.0°C above 1990
5	102, 103	pH, g; IS92a in 2100 has 788 ppm CO_2 and ΔT of 1.1–3.6°C above 1990
5	104	M, a;
5	105	E, P, D, e; upscaled with H3, EC, CS
5	106	M, H2 with aerosols in 2100, a, 6 DVGMs, global temperature taken from Raper et al. (2001)

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
5	107	pH, a; impact is at CO_2 doubling, T range given by IPCC (2007) for equilibrium climate sensitivity
5	108	M, a; Williams et al. (2007) use the A2 scenario from a mean of 9 GCM simulations used in IPCC (2007) which have a global temperature increase of 2–4°C averaging approximately 3.5°C above 1990 (hence 4°C above pre-industrial)

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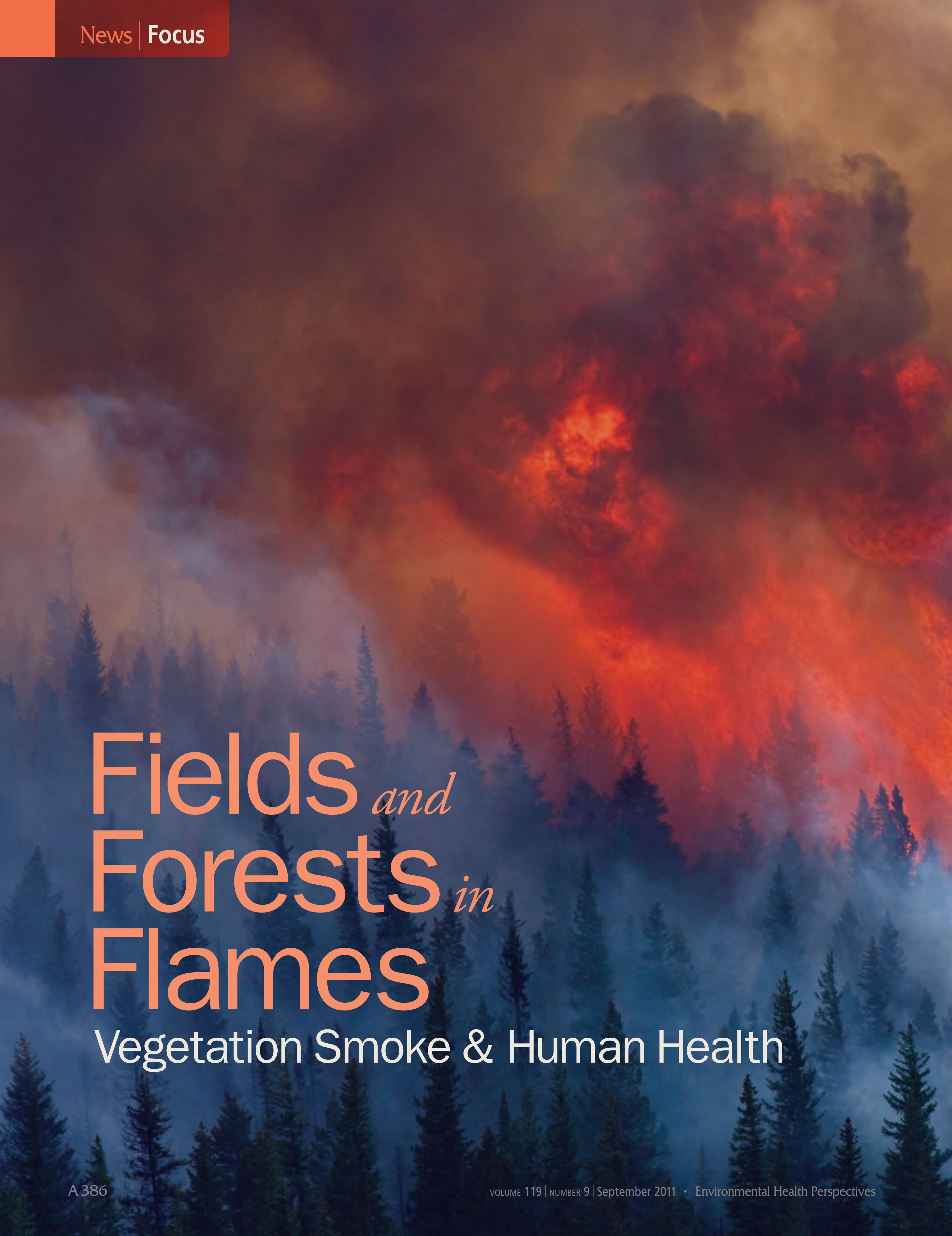

Fields *and* Forests *in* Flames

Vegetation Smoke & Human Health

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The Red Eagle Fire of 2006 burned more than 34,000 acres across Glacier National Park and adjacent Blackfeet Tribal Land.

Author Bob Weinhold lived this article this summer as the area where he lives was regularly swathed in smoke from wildfires nearby and in New Mexico and Arizona, each of which had the largest wildfire in its history. The smell of the fumes reminded him of his days fighting and patrolling for wildfires while working for the U.S. Forest Service in Oregon.

People have lived for tens of thousands of years in the presence of smoke from fires. That long period of adaptation tends to allow healthy younger adults in today's environments to be generally resistant to serious adverse health effects from smoke from sources such as wildfires, prescribed forest burns, agricultural field burns, and peat bog fires, says Wayne Cascio, director of the U.S. Environmental Protection Agency (EPA) Environmental Public Health Division.

But a high percentage of people aren't young, healthy adults. In the United States, nearly half the population suffers from at least one chronic illness,[1] potentially placing them at risk for adverse effects from exposure to fire smoke. Children and older adults also are considered more vulnerable to smoke's effects.[2] The limited health research that's been done on smoke from large-scale fires has provided some refinements to these general categories of vulnerable people, and new information occasionally emerges. There also has been a trickle of information identifying the toxic substances that characterize smoke from various kinds of fires, and pinning down the specific body systems that are vulnerable and the pathways through which damage occurs.

But much remains unknown about the varying toxicity of emissions from different types of vegetation fires and the vulnerability of specific groups of people, although a good deal of research has examined the adverse health effects of smoke related to heating and cooking with wood.[3] Filling these voids is essential, Cascio says. "It is critically important to define who is at highest risk so that individual and community-based intervention strategies can be developed to specifically mitigate the health risks associated with smoke exposure," he says. "The goal, of course, is to provide education or intervention to the most sensitive individuals in the most cost-effective way without needlessly worrying or interfering with the daily activities of [others]."

Such information can also help organizations and individuals who deal with fire threats as they work to integrate health concerns with many other factors, such as land management practices and programs, cultural mores, political influences, and funding.

Conflagrations in the Woods

In the United States there has been an irregular but generally upward trend in the occurrence and severity of forest wildfires in the last 50 years. Each year between 1960 and 2010, some 1.1–9.9 million acres burned, with the highest acreage burned in 2006.[4] At least 7 million acres burned in each of 7 of those 50 years; 6 such years occurred in the period 2000–2010.[4] At least 5 million acres burned in each of 14 years, 10 of which fell in the period 1996–2010.

The annual acreage burned is expected to increase to about 10–12 million acres within just a few years.[5] One of the forces expected to drive this projected increase in fires is climate change, which is expected to usher in increased drought, spreads in insect damage, and longer fire seasons, according to the U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, Bureau of Indian Affairs, and National Association of State Foresters, and a growing body of independent studies.[5,6,7] Among the areas expected to face the greatest increase in fire threats are the Southeast, Southwest, and West, although the Midwest and East also are expected to experience some increases.

However, some experts remain cautious, saying the science on wildfires and future impacts of climate change is still a work in progress. Brian Schwind, director of the U.S. Forest Service's Remote Sensing Applications Center, says, "It's a really complicated picture with a lot of variables. We're early in the analytical phases. Sometimes we jump to conclusions a little fast."

Clockwise from top left: The Station Fire burns north of Los Angeles, California, 30 August 2009. A wall of smoke from the fire rises over the city that same day; by the next day the Los Angeles skyline was obscured. The Station Fire was considered a "megafire," meaning it could not be extinguished without the aid of natural forces such as rain.

Clockwise from top left: © Gene Blevins/Reuters; © AP Photo/Jon Vidar; © Fred Prouser/Reuters

Historically, people have caused most wildfires. Of the 63,591–96,386 fires that occurred each year from 2001 to 2010, 80–90% were human-caused in any given year.[8] For acreage burned, lightning often plays a much bigger role—when lightning fires strike backcountry areas, they are more often allowed to burn. But people still were the ignition source for 12–65% of the acreage burned in any of those years.[8] Among the human causes of fires are arson, accidents, carelessness, and intentional prescribed fires designed to reduce acute threats or remove vegetation for planting, wildlife management, or other purposes.

More people have the opportunity to accidentally or intentionally start a fire as they increasingly move into the so-called wildland–urban interface, where residential areas butt up against and mingle with forests.[5] That settlement pattern puts more people into close proximity to major fire sources, increasing the odds they'll receive significant smoke exposures. It also results in an increase in man-made structures being burned by forest fires, says Stephen Mueller, a senior specialist in atmospheric science for the Tennessee Valley Authority. "Buildings and other structures usually contain plastic materials and various stored chemicals—pesticides, insecticides, paint, solvents, cleaning solutions, etc.—that release extremely toxic substances when burned," he says. "This can represent a significant source of toxic air pollutants in certain areas."

Globally, forest wildfire statistics are very scarce, says Pieter van Lierop, forestry officer with the Food and Agriculture Organization (FAO) of the United Nations. In 2010 hard data were available for less than half the world's countries and only about three-fourths of the world's forests.[9] Inconsistent methods and reporting make it impossible to determine realistic total numbers of fires and acreage burned for any given year, or to detect trends. But it's clear from global satellite images that significant fires in all types of vegetation occur multiple times every year on all continents except Antarctica.[10] The percentage of these fires that are caused by humans is considered to be roughly 90–95%, van Lierop says.

Although hard global data aren't available, researchers have used models and satellite images to calculate that fires in grasslands and savannas account for 44% of fire-derived carbon emissions, with 20% from tropical deforestation and degradation fires, 16% from tropical woodland fires, 15% from fires in forests outside the tropics, 3% from agricultural field burning, and 2% from peat fires.[11] These estimates don't necessarily reflect emissions of toxic substances, though, because emissions vary according to factors such as the type of vegetation burned, moisture content, fire temperature, wind conditions, how "aged" the smoke is, and time of year.

A global picture is also emerging for what are being termed "megafires," according to a report sponsored by the FAO.[12] The authors say the megafire label applies when a burn can't be controlled by people without the help of natural forces such as rain, and it causes significant, long-lasting effects on an area's environment and social and economic structure. Prime examples covered in some detail in the report include fires in Australia (2009), Botswana (2008), Brazil (1998), Greece (2007), Indonesia (1997/1998), Israel (2010), Russia (2010), and the United States (2003).

Other megafires have occurred in other years in some of these countries as well as in countries such as Canada, China, South Africa, Portugal, Spain, and Turkey. All were fueled in part by overzealous fire suppression or land practices that substantially altered the more fire-resistant natural vegetation mosaic and allowed fuels[13] to accumulate.[12] Drought and "extreme fire weather" (i.e., low humidity and high temperature combined with high winds) increased the hazard, and people almost always were the final straw, acting as the match in one way or another. Should these preventable fires increase as projected,[9] their size and inability to be controlled will escalate the number of people exposed to toxic smoke and the length of time they are at risk.

Who's Affected by Wildfire Smoke?

The general health threat posed by smoke close to a fire has been widely recognized in the past decade by organizations such as the EPA,[14] the U.S. Centers for Disease Control and Prevention,[2] the California Department of Public Health,[15] and the Pediatric Environmental Health Specialty Units, a network of academically based children's environmental health experts.[16] But people some distance away also are exposed. For instance, on many days in June 2011 the smoke plume from Arizona and New Mexico's Wallow Fire extended as far as 1,000 miles.[17]

However, one of the large deficits in knowledge about the toxicity of smoke is the distance from a fire at which the smoke still poses a significant health threat, according to many experts. "Smoke changes as it travels, and the PM [particulate matter] might pose greater risk when it is closer to the source," says Sarah Henderson, an environmental epidemiologist at the British Columbia Centre for Disease Control. However, she adds, "Anytime that smoke results in elevated PM, it has health effects."

Smoke can contain thousands of individual compounds, in categories such as PM, hydrocarbons and other organic chemicals, nitrogen oxides, trace minerals, carbon monoxide, carbon dioxide, and water vapor.[15] As just one example of elements in a complex mix, a 2009 fire in a mixed-evergreen forest in central Portugal generated emissions that included degradation products from biopolymers (such as levoglucosan from cellulose and methoxyphenols from lignin), *n*-alkanes, *n*-alkenes, *n*-alkanoic acids, *n*-alkanols, monosaccharide derivatives from cellulose, steroid and terpenoid biomarkers, polycyclic aromatic hydrocarbons (with retene being the most abundant), and even-carbon-number homologs of monoglycerides (which the authors say were identified for the first time as biomarkers in biomass burning aerosols).[18]

The health effects widely considered to be linked with wildfire smoke include exacerbation of preexisting respiratory conditions such as asthma and chronic obstructive pulmonary disease (COPD), reduced lung function, chest pain, and general symptoms such as eye irritation, fatigue, headache, dizziness, and stress.[15] Woodsmoke exposure may depress the respiratory immune defenses[19] and has been linked with emergency department visits for upper and lower respiratory effects.[20] The evidence regarding cardiovascular effects has been mixed, but recent research is reinforcing these health issues as a possible area of concern, though sometimes only for certain categories of people in any given study.[21,22,23,24,25,26]

Based on the limited research conducted so far, public health officials generally consider children, older people, pregnant women, smokers, and people with chronic respiratory problems to be especially vulnerable to health effects from outdoor fires.[2,15,16] Cascio says other populations that might be vulnerable and deserve greater study include diabetics, fetuses, people with cystic fibrosis and primary pulmonary hypertension, and those carrying certain genetic polymorphisms.

Refinements to this information are surfacing as studies trickle out. For instance, a study of bushfires in the Darwin, Australia, area in 2000, 2004, and 2005 found indigenous people were significantly more vulnerable to a range of respiratory disorders and had a statistically significant increase in hospital emissions for ischemic heart disease 3 days after initial exposure to smoke in relation to each 10-$\mu g/m^3$ increase in PM_{10}.[22] The patients may have been at greater risk than others in the area because of greater underlying cardiorespiratory problems, the authors say.

This finding may be broadly applicable around the world. "Many other indigenous populations have a similar spectrum of social disadvantage and ill health as those from Australia, so the higher risk we saw in indigenous Australians is likely to be similar for those groups," says Fay Johnston, lead author of the study and a public health physician and research fellow at the University of Tasmania's Menzies Research Institute. This kind of knowledge can help refine local responses

Top to bottom: **The Las Conchas Fire burns in the Jemez Mountains of New Mexico southwest of Los Alamos National Laboratory, June 2011. If the fire had reached the nuclear waste stored at the laboratory, the result could have been a plume of radioactive smoke; extensive thinning around the facility reportedly averted such a disaster. October 2003 wildfires in San Diego County, California, destroyed more than 900 homes. The burning of buildings, vehicles, and other trappings of human society can add more toxic substances to wildfire smoke.**

Top to bottom: NASA; © Mark Avery/Orange County Register/Corbis

to fires. "If a severe smoke pollution event were to affect an indigenous community," Johnston says, "the health outcomes are likely to be more serious, and public health officials would need to consider this when planning their responses."

Another line of research involves the toxicologic differences between wildfire smoke and other types of particulate pollution. In an investigation of wildfires in central and northern California in 2008, researchers found that PM collected in the city of Tracy over 2 days at the peak of the fires was about 10 times more damaging to alveolar macrophages than ambient PM collected in the area under normal conditions, on an equal-dose basis.[27] In California's Central Valley, another team of researchers investigated differences between air in an urban area, Fresno, and near a wildfire about 100 miles to the northwest near Escalon.[28] PM from each area induced very different inflammatory, oxidative stress, and xenobiotic responses in human bronchial epithelial cells, providing further evidence that it's probably inappropriate to simply extrapolate findings on urban pollution to wildfire pollution.

However, urban air and wildfire smoke can have one thing in common—isocyanic acid, which was recently identified for the first time in outdoor air in each of these settings.[26] The limited information available indicates the acid could plausibly contribute to cardiovascular problems and inflammation, although effects at the concentrations present in wildfire smoke have yet to be observed.

Much more is generally known about the health risks posed by ground-level ozone, and a recent study indicates wildfires in the western United States can help spark the formation of the toxic substance, increasing ambient ozone by up to 50 ppb for a short period of time and potentially traveling long distances.[29] Such bursts of ozone could cause affected areas to exceed the current federal 8-hour ozone standard of 75 ppb.[30]

In addition to polluting the air, wildfires can affect soil and water quality. In a study following fires in 2005 and 2006 in three watersheds in Southern California, researchers found organic or particulate-bound mercury in surface soils can be more readily deposited in waterways after a fire.[31] Awareness of that tendency could lead to actions such as better testing of fish in affected waterways or improved sampling for water quality if the waterways are a drinking water source. However, it appears this phenomenon may depend on local soils, vegetation, waterways, and weather, because an analysis of 146 sites in Minnesota that had burned some time between 1759 and 2004 found intense fires had reduced soil mercury concentrations for tens, even hundreds, of years.[32] In contrast, such reductions lasted only a year or so in the California settings.[31]

Prescriptions for Fires

Wildfires are not the only large-scale fires humans encounter; in many areas around the world, people are exposed for substantial periods of time each year to smoke from prescribed (or controlled) fires, which are commonly used to preclude out-of-control wildfire threats. Experts attempt to do these on days with suitable weather (i.e., higher humidity, lower temperature, and low wind), when atmospheric conditions allow optimal smoke dispersion. They also try to restrict how the fire will spread, for instance by scraping out a perimeter line or setting fires from an outside boundary where terrain or winds will force the burn inward. But such fires still generate considerable smoke of varying compositions. In addition, they occasionally escape their intended boundaries and turn into wildfires.

U.S. federal, state, and other agencies have conducted prescribed burns on about 2.2 million acres per year in the past decade.[33] Prescribed fires also are widely used globally, though hard data is scant.

Research on the health effects of prescribed burns is very limited. In a study of South Carolina prescribed fires, researchers found that plots in which the vegetation had been mechanically chipped in advance of burning emitted significantly less PM and carbon monoxide than nonchipped plots.[34] The authors say this has implications for both firefighters and nearby communities. In Georgia, another team found emissions of most volatile organic compounds were much higher during the smoldering phase of prescribed fires in pine forests compared with the flaming phase.[35] They also found emissions of several pinene compounds from prescribed fires were much higher than those from fireplace wood burning.

A study of prescribed burns in Arizona ponderosa pine forests found the emissions, which included PM, polycyclic aromatic hydrocarbons, organic carbon, elemental carbon, potassium, chlorine, sulfur, and silicon, were characteristic of smoldering, low-intensity burns.[36] On the basis of the information in this and other studies, Marin Robinson, chairwoman of the Department of Chemistry and Biochemistry at Northern Arizona University, says, “I would argue that the biggest health effects associated with prescribed burns are short-term and involve susceptible individuals living in neighboring communities.”

Problems could be significant in some settings, though. In another study of the Darwin, Australia, area, researchers found that when PM$_{10}$ from fires (many of which were prescribed burns) exceeded 40 µg/m^3, emergency department admissions for asthma increased sharply.[37] That concentration is far below the current 24-hour standard of 150 µg/m^3 established by the U.S. EPA[38] and even the level of 65–75 µg/m^3 recommended in September 2010 by the agency’s Clean Air Scientific Advisory Committee.[39] Other researchers report that smoke from prescribed fires in Australian bushlands contained acrolein, formaldehyde, and carbon monoxide at levels of concern.[40]

Other Types of Fires: Bogs and Cropland

Although wildfires in peat bogs are the source of just a small fraction of the world’s smoke emissions, they can have a major impact on air quality in the areas where they burn. For instance, they were an important fuel in the megafires in Russia and Indonesia, and they occur widely in boreal forests. Since they become more flammable in normally moist areas that are undergoing extended drought, they could become an increasingly important smoke source if drought becomes more common in some areas.

A large June 2008 peat bog fire in North Carolina that burned about 6 weeks generated smoke affecting significant portions of the state. The fire, smoldering in peat 3–15 ft deep, had a poor oxygen supply and generated extensive smoke due to incomplete combustion. There were periods of PM$_{2.5}$ concentration greater than 200 µg/m^3 at ground-based monitors 200 km from the fire.[21] The composition of peat fire emissions is known to differ substantially from forest fires, but the relative toxicity of these emissions is unknown. However, Mueller points out that low-temperature or smoldering combustion such as that associated with peat fires (and fireplaces) is notorious for emitting high amounts of carbon monoxide.

Whatever the specific toxic substances were, researchers studying cardiopulmonary-related emergency department visits associated with the 2008 peat bog fire found a 37% relative increase in heart failure (traits of the population studied, such as low income and high prevalence of health problems such as hypertension, diabetes, ischemic heart disease, and heart failure, may have contributed to susceptibility).[21] They also reported increases in emergency department visits for COPD (73% increase), asthma (65% increase), and pneumonia and acute bronchitis (59% increase).[21] Major peat fires were burning once again in North Carolina throughout late spring and summer of 2011.[41,42,43]

In agricultural fields, burning residue is a common practice worldwide. It’s done to kill pests, improve fertilization (by increasing nitrogen availability), and make planting easier, often at a lower cost than some other options such as mechanical tilling. As with forest wildfires, global data on field burning is limited. However, an analysis of satellite images from 2001 through 2003 indicated that about 1.5–1.6 million agricultural field burns occurred each year, accounting for an average 8–11% of annual global fire activity.[44] Regions with the highest activity included the Russian Federation, Eastern Europe, and Central Asia.

In the United States, field burning averaged 43% of the equivalent area burned by wildfires from 2003 to 2007 and peaked at 79% of the equivalent area in 2003.[45] Field burning is a source of pollutants such as fine and coarse PM, nitrogen dioxide, sulfur dioxide, carbon monoxide, and methane.[46] The states with the highest emissions (largely from sugarcane, wheat, rice, and bluegrass fields) are Arkansas, California, Florida, Idaho, Texas, and Washington. In those six states alone, about 15.5 million people live in “source” counties (that is, counties with crop burning

Moscow, Russia, during wildfires of the summer of 2010. Record-breaking high temperatures and drought conditions across Russia set the stage for these 2010 fires. These “extreme fire weather” factors are expected to occur more frequently in more locales in coming years.

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areas), although it's uncertain how many had significant smoke exposures.[46] The percentage of a state's population that lives in source counties can be quite high, such as 47% in Idaho and 25% in Arkansas.[46]

Field burning can occur for extended periods of time in any given area, leading to chronic exposures to the emissions.[46] Smoke can readily waft beyond the source counties, although as with forest fires, the distance at which toxic effects occur remains largely unknown.

The limited research on health effects of field burning has found some significant respiratory and cardiopulmonary problems, says Jessica McCarty, a research scientist at Michigan Tech Research Institute. "The threat is highly variable, based on [local farming] laws, air quality laws, crop type, and cultural practices of burning," she says.

Few Studies, Many Possibilities

All together, there have been several dozen studies of health effects related to wildfires, prescribed forest burns, peat bog fires, and agricultural field burning. That's a relatively small number given the huge variation in source material that can burn, the various underlying conditions of people who can be affected, and other variables (by comparison, more than 1,700 health studies have been conducted for ground-level ozone). One reason for that dearth is that the research is hard to do.

Johnston explains that fires often are short-term events, and appropriate individual health data are often lacking, as are data on possible confounders. Sometimes the available study population isn't large enough to generate clear associations. Another major limitation is the lack of monitoring data in burn areas. More recent studies are beginning to circumvent this issue by using tools such as pollution models and satellite data. But those approaches still have limitations that often don't allow them the precision of ground monitors.

Despite the difficulties, "it is clear that more research must be done to fully characterize the chemical composition of the particulate matter arising from these various sources," Cascio says. Ralph Delfino, vice chair for research and graduate studies at the University of California, Irvine, Department of Epidemiology, says more information is needed about the mechanisms through which fire emissions cause harm. "It would also be useful from a public health perspective to have better information for health advisories such as data to forecast the locations of smoke plumes and data on the clinical characteristics of potentially susceptible populations to enable targeted alerts. There is sufficient evidence to warn people with persistent asthma who may benefit from the use of preventive antiinflammatory medications," he says. He adds that improved application of satellite imagery plus ground-level air monitoring could help in forecasting smoke movements.

Despite the potential public health benefits to be had from these types of studies, Delfino says he has repeatedly found little support for this kind of research, possibly because decision makers and funders are rarely exposed to significant smoke. "People change their minds when they are in the middle of it, though," he says.

The Pains Bay peat fire in Dare County, North Carolina, was started 5 May 2011 by a lightning strike. The peat that feeds smoldering fires like this one can extend more than a dozen feet underground. These fires are notoriously hard to extinguish.

North Carolina Forest Service

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Clockwise from top left: a sweet potato field in Indonesia; a sugarcane field in Cuba; a bluegrass field in Rathdrum, Idaho. Agricultural field burning is practiced around the world as a relatively inexpensive way to prepare fields for crops. Some jurisdictions around the world require permits prior to an agricultural burn, addressing issues such as extent and timing, in an effort to reduce health risks to area residents.

Clockwise from top left: © Rob Huibers/Panos Pictures; © Chris de Bode/Panos Pictures; © Jerome A. Pollos/AP Photo

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RESEARCH ARTICLE

Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species

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Abstract

Current climate change may be a major threat to global biodiversity, but the extent of species loss will depend on the details of how species respond to changing climates. For example, if most species can undergo rapid change in their climatic niches, then extinctions may be limited. Numerous studies have now documented shifts in the geographic ranges of species that were inferred to be related to climate change, especially shifts towards higher mean elevations and latitudes. Many of these studies contain valuable data on extinctions of local populations that have not yet been thoroughly explored. Specifically, overall range shifts can include range contractions at the "warm edges" of species' ranges (i.e., lower latitudes and elevations), contractions which occur through local extinctions. Here, data on climate-related range shifts were used to test the frequency of local extinctions related to recent climate change. The results show that climate-related local extinctions have already occurred in hundreds of species, including 47% of the 976 species surveyed. This frequency of local extinctions was broadly similar across climatic zones, clades, and habitats but was significantly higher in tropical species than in temperate species (55% versus 39%), in animals than in plants (50% versus 39%), and in freshwater habitats relative to terrestrial and marine habitats (74% versus 46% versus 51%). Overall, these results suggest that local extinctions related to climate change are already widespread, even though levels of climate change so far are modest relative to those predicted in the next 100 years. These extinctions will presumably become much more prevalent as global warming increases further by roughly 2-fold to 5-fold over the coming decades.

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Abbreviations: GLM, general linear model; GLMM, general linear mixed model.

Author Summary

Climate change is an important threat to the world's plant and animal species, including species on which humans depend. However, predicting how species will respond to future climate change is very difficult. In this study, I analyze the extinctions caused by the climate change that has already occurred. Numerous studies find that species are shifting their geographic ranges in response to climate change, typically moving to higher elevations and latitudes. These studies also contain valuable data on local extinctions, as they document the loss of populations at the "warm edge" of species' ranges (lower elevations and latitudes). Here, I use these data to show that recent local extinctions related to climate change have already occurred in hundreds of species around the world. Specifically, among 976 species surveyed, local extinctions occurred in 47%. These extinctions are common across climatic zones, habitats, and groups of organisms but are especially common in tropical regions (which contain most of Earth's species), in animals (relative to plants), and in freshwater habitats. In summary, this study reveals local extinctions in hundreds of species related to the limited global warming that has already occurred. These extinctions will almost certainly increase as global climate continues to warm in the coming decades.

Introduction

Anthropogenic climate change may be a major driver of biodiversity loss in the next 100 years, but the possible impacts of climate change on species survival remain highly uncertain [1–3]. Global mean annual temperatures increased by ~0.85°C between 1880 and 2012 and are likely to rise by an additional 1°C to 4°C by 2100 [4]. Modeling studies have predicted that various levels of species loss will result from this future climate change, ranging from 0% to >50% of all species currently known [3]. This uncertainty has many sources (e.g., different climate models and different hypotheses about species dispersal). One of the most important sources of uncertainty hinges on the details of how species respond to climate change. For example, if species can evolve rapidly enough in response to changing climate, then species extinctions due to climate change might actually be limited [5,6].

Species can potentially respond to climate change in several ways. The most important case to consider may be that when the species' present-day (realized) climatic niche no longer occurs within the species' current geographic range (because of the potential for global extinction of the species under these conditions). In this case, the possible responses of the species include the following: (i) undergoing niche shifts, such that the species' realized niche changes to incorporate these new climatic conditions (e.g., through plastic changes and/or by evolutionary adaptation to the modified abiotic and/or biotic conditions), (ii) dispersing to track the original climatic conditions over space (e.g., moving to higher latitudes or elevations), and (iii) going extinct [5–8]. While each of these responses has been shown in some cases (at least in local populations), the relative frequency of each is still unclear [7,8]. However, changes in species' geographic ranges have been especially well documented [9–11].

These data on geographic range shifts contain important but underutilized information on how species respond to climate change. Range shifts observed under climate change typically involve an overall shift towards higher latitudes and higher elevations [9–11]. These shifts can be composed of one (or both) of two types of changes (Fig 1): (i) range expansions at the cool edge of the species range (higher latitudes and elevations) and (ii) range contractions at the warm edge (lower latitudes and elevations). The presence of warm-edge contractions is critically important. A warm-edge contraction occurs when populations from one or more localities at the lowest latitudes or elevations of a species' regional distribution disappear (i.e., are inferred to no longer occur at those localities), leading to an overall shift in the species range towards higher latitudes or elevations. These contractions indicate that species are failing to shift their niches sufficiently to tolerate these new conditions and that these populations are instead going extinct (referred to as "local extinction" hereafter). This must be true regardless of the specific mechanism of local extinction (e.g., elevated death rates, increased emigration, or declining recruitment). The many papers that have assessed range shifts and that have included surveys of warm-edge populations can therefore provide a wealth of data about

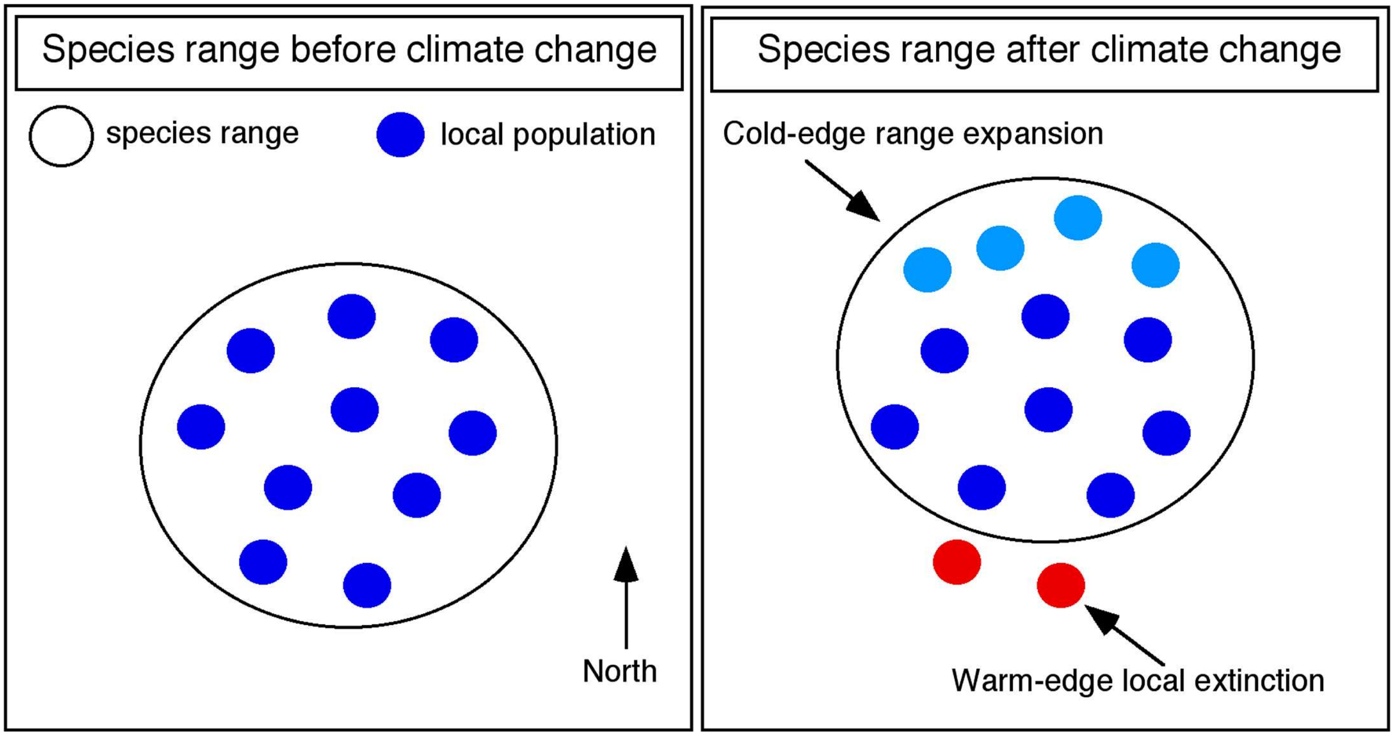

Fig 1. Hypothetical example illustrating the two components of a geographic range shift associated with climate change. The large open circle indicates the species' overall geographic range. Small dark blue circles indicate populations before climate change. After climate change, the overall geographic range is shifted northward (large open circle), both through the range expansion (new populations; small light blue circles) added at the northern, "cold" edge of the species range and range contraction (local extinction of original populations; small red circles) at the southern, "warm" edge of the species range. Similar patterns occur for range shifts along an elevational gradient. Modified from Cahill et al. [12].

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which species have (and have not) undergone local extinctions potentially related to climate change. These data are particularly useful because published papers on range shifts need not be strongly biased towards documenting warm-edge contractions, given that many studies that included data on warm edges also surveyed the cool edge. Thus, even though studies that failed to find any range shifts might go unpublished (a potential source of bias), studies that documented an overall range shift need not show a warm-edge contraction.

Here, I analyze the extensive data on range shifts to examine the prevalence of local extinctions related to modern climate change. I also provide a synthesis of inferred local extinction across habitats, climatic zones, and taxonomic groups. I systematically searched the literature for studies that examined shifts in species' ranges at their warm edges, shifts that were considered (in the original studies) to be related to current climate change. Hundreds of examples of local extinctions were found across diverse climatic zones, habitats, and taxonomic groups. Not all species exhibiting range shifts showed warm-edge contractions, but ~50% of the species surveyed had local extinctions inferred to be related to climate change. These results suggest that even the relatively small changes in climate that have already occurred are sufficient to cause widespread local extinctions and that many species may be unable respond to climate change fast enough to avoid extinction as global climate warms even further.

Results

The Web of Science was searched repeatedly between December 2014 and March 2016 using keywords related to climate change, range shifts, and local extinctions (see Materials and

Methods). All studies that monitored the warm edge of at least one species' range and that tied their results to climate change with explicit statistical analyses were included. Importantly, studies can document overall range shifts but need not find that the warm-edge populations that they examined had local extinctions.

A total of 27 studies (Table 1; [13–39]) met all the necessary criteria to address potential climate-associated warm-edge range shifts (see Materials and Methods). The sampled species were broadly distributed across clades (e.g., animals = 716; plants = 260) and regions (e.g., Asia = 332; Europe = 268; Madagascar = 30; Oceania = 58; North America = 233; South America = 55). Among the 976 unique species surveyed, 460 species had warm-edge contractions, and 516 did not (S1 Appendix). Therefore, local extinctions related to climate change are already very common (47.1% of species examined), even given the relatively modest rise in global temperatures that has occurred so far (less than 1°C increase in global mean annual temperature; [4]).

These 976 species spanned many clades, habitats, and regions (Table 1; S1 Appendix). Comparison between those species that showed warm-edge contractions and those that did not provides potential insights into which species may be most sensitive to climate change, in terms of the climatic zones and habitats that they occur in and the clades that they belong to. Furthermore, there is no evidence that there were more species with local extinctions in studies that ended more recently, were of longer duration, or began earlier (based on midpoints for ranges of values; Table 1). Specifically, regression analyses of the proportion of species with local extinctions against (i) the study end date, (ii) the duration of the study, and (iii) the study start date all yielded nonsignificant results (end date: $r^2 = 0.001$, $p = 0.8910$; duration: $r^2 = 0.045$, $p = 0.2896$; start date $r^2 = 0.047$, $p = 0.2788$; after removing nine studies with four or fewer species: end date: $r^2 = 0.146$, $p = 0.1181$; duration: $r^2 = 0.132$, $p = 0.1376$, but unexpectedly trending towards fewer extinctions in studies with longer durations; start date $r^2 = 0.177$, $p = 0.0821$, with more extinctions in studies beginning more recently, not earlier). Therefore, the frequency of local extinctions was initially compared across species in different studies, regardless of differences in the duration, beginning, or end date of the study in which they were surveyed.

Overall, the frequency of local extinctions was similar (close to 50%) across most climatic zones, habitats, gradients, and clades. Nevertheless, there were some significant differences. First, local extinctions were significantly more common in species from tropical and subtropical regions (combined and referred to as tropical hereafter for brevity) than in those from temperate regions ($p < 0.0001$; Chi-squared test, testing the assumption of equal frequencies of local extinction among species between regions; subsequent p-values are also from Chi-squared tests). Specifically, 54.6% of the 504 included tropical species had local extinctions, whereas only 39.2% of the 472 temperate species did (Fig 2A). The pattern was even stronger when only considering terrestrial species on elevational gradients (54.6% of 504 tropical species versus 28.2% of 301 temperate species), which applied to all plants and most animals. In part, this pattern of more frequent tropical extinction arose from a much lower frequency of extinctions for temperate plants (59.4% of 155 tropical species versus 8.6% of 105 temperate species; $p < 0.0001$). The very low frequency of temperate extinctions in plants was based on a single study from very high latitudes [19]. Nevertheless, there were also significantly more local extinctions in tropical animals (52.4% of 349 tropical species versus 38.8% of 196 temperate species; $p = 0.0022$), if one compares terrestrial species on elevational gradients. This restriction also made them more comparable to the sampled plants (all from terrestrial, elevational gradients) and still encompassed most sampled animal species (76.1%; 545 of 716 species). Across all animals, the difference was not significant ($p = 0.2309$), possibly because of the influence of temperate marine and freshwater species (see below). Among the most well-

Table 1. Summary information on the 27 range-shift studies used to document local extinctions related to climate change. Studies are listed alphabetically by first author. The major taxonomic group surveyed is given (Taxon, all groups are animals except for "Plant"), along with the total number of species surveyed (Total Species), the percentage of those species with one or more local extinctions (% Local Extinction), the general habitat type (Habitat; including terrestrial, freshwater, and marine), the climatic region (tropical-subtropical versus temperate), the geographic region where the study was conducted (note that North America here extends to Central America), the type of range shift (latitudinal, elevational), the dates of the initial survey and the resurvey, and the duration in between (for surveys and/or resurveys spanning multiple years, the midpoint of each was used to calculate the duration).

Reference	Taxon	Total Species	% Local Extinction	Habitat	Climatic Region	Geographic Region	Range Shift	Initial Survey	Resurvey Date	Duration
Angelo and Daehler [13]	Plant	4	50	Terrestrial	Tropical	Oceania (Hawaii)	Elevational	1966–1967	2008	41.5
Beever et al. [14]	Mammal	1	100	Terrestrial	Temperate	North America	Elevational	1898–1956	2003–2006	77.5
Brusca et al. [15]	Plant	27	56	Terrestrial	Tropical	North America	Elevational	1963	2011	48
Chen et al. [16]	Insect	208	56	Terrestrial	Tropical	Asia	Elevational	1965	2007	42
Comte and Grenouillet [17]	Fish	31	74	Fresh.	Temperate	Europe	Elevational	1980–1992	2003–2009	20
Dieker et al. [18]	Insect	2	50	Terrestrial	Temperate	Europe	Elevational	1958–1986	2008–2009	36.5
Felde et al. [19]	Plant	105	9	Terrestrial	Temperate	Europe	Elevational	1900	2008	108
Forero-Medina et al. [20]	Bird	55	29	Terrestrial	Tropical	South America	Elevational	1969	2010	41
Franco et al. [21]	Insect	3	100	Terrestrial	Temperate	Europe	Latitudinal	1970–1999	2004–2005	20
Freeman and Freeman [22]	Bird	54	74	Terrestrial	Tropical	Oceania (New Guinea)	Elevational	1965	2012	47
Hiddick et al. [23]	Marine invertebrates	65	55	Marine	Temperate	Europe	Latitudinal	1986	2000	14
Hitch and Leberg [24]	Bird	1	100	Terrestrial	Temperate	North America	Latitudinal	1967–1971	1998–2002	31
Menendez et al. [25]	Insect	39	54	Terrestrial	Temperate	Europe	Elevational	1981–1993	2006–2007	24
Moritz et al. [26]	Mammal	27	41	Terrestrial	Temperate	North America	Elevational	1914–1920	2003–2006	87.5
Myers et al. [27]	Mammal	8	12	Terrestrial	Temperate	North America	Latitudinal	1883–1980	1981–2006	62
Nye et al. [28]	Fish	28	50	Marine	Temperate	North America	Latitudinal	1968	2008	40
Perry et al. [29]	Fish	10	40	Marine	Temperate	North America	Latitudinal	1997	2001	24
Ploquin et al. [30]	Insect	16	69	Terrestrial	Temperate	Europe	Elevational	1988–1989	2007–2009	19.5
Pomara et al. [31]	Squamate	1	100	Terrestrial	Temperate	North America	Elevational	1965	2008	43
Raxworthy et al. [32]	Amphibian-Squamate	30	37	Terrestrial	Tropical	Madagascar	Elevational	1993	2003	10
Rowe et al. [33]	Mammal	4	25	Terrestrial	Temperate	North America	Elevational	1927–1929	2006–2008	79
Rubal et al. [34]	Mollusca	7	29	Marine	Temperate	Europe	Latitudinal	1917, 1940	2011	94
Sheldon [35]	Insect	1	0	Terrestrial	Temperate	North America	Elevational	1977–1978	2006	28.5
Telwala et al. [36]	Plant	124	60	Terrestrial	Tropical	Asia	Elevational	1849–1850	2007–2010	159
Tingley et al. [37]	Bird	92	25	Terrestrial	Temperate	North America	Elevational	1900–1930	1980–2006	78
Warren and Chick [38]	Insect	2	0	Terrestrial	Tropical	North America	Elevational	1973–1974	2012	38.5

(*Continued*)

Table 1. (*Continued*)

Reference	Taxon	Total Species	% Local Extinction	Habitat	Climatic Region	Geographic Region	Range Shift	Initial Survey	Resurvey Date	Duration
Zuckerberg et al. [39]	Bird	31	71	Terrestrial	Temperate	North America	Both	1980–1985	2000–2005	20

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sampled groups of animals, tropical extinction was significantly more common in birds (51.4% of 109 tropical species versus 37.1% of 124 temperate species; $p = 0.0284$), but not in insects (local extinctions in 55.2% of 210 tropical species versus 59.0% of 61 temperate species; $p = 0.6007$). For other animal groups, the species sampled here were either predominantly temperate (mammals, fish, and marine invertebrates) or tropical (squamate reptiles and amphibians), and so did not allow for similar within-clade comparisons.

Overall, the frequency of climate-related local extinctions (Fig 2B) was similar in terrestrial (45.6% of 835 species) and marine environments (50.9% of 110; $p = 0.2964$). In contrast, the frequency in freshwater species was substantially higher (74.2% of 31; $p = 0.0053$ across all three habitats). However, the estimate for freshwater species was based on a single study of European fishes [17]. Comparing fish only (all temperate) also supported a significantly higher frequency of extinction in freshwater environments relative to marine environments ($p = 0.0240$; local extinctions in 47.4% of 38 marine species versus 74.2% of 31 freshwater species). All marine species included here were temperate animals, but there was no significant difference in extinction frequencies between marine and terrestrial environments when only temperate animals were compared ($p = 0.1676$; marine: 50.9% of 110 species, terrestrial: 42.9% of 226 species). Terrestrial and freshwater species remained significantly different in this more restricted comparison ($p = 0.0011$).

The frequency of local extinctions (Fig 2C) was somewhat lower for species surveyed along elevational gradients relative to those on latitudinal gradients (elevational: 45.8% of 836 species; latitudinal: 55.0% of 140 species; $p = 0.0439$). Most (78.6%) species measured along latitudinal gradients were marine (and all marine studies focused on latitudinal gradients), and all were temperate. Again, most species included here were based on studies of elevational gradients in terrestrial environments.

Local extinctions were also broadly similar in frequency across taxonomic groups (Fig 3). Nevertheless, local extinctions were significantly more common ($p = 0.0018$) in animals (50.1% of 716) than plants (38.8% of 260). This difference was reduced when comparing only animals and plants on terrestrial, elevational gradients (47.3% of 556 animal species versus 38.8% of 260 plant species; $p = 0.0236$). Among these latter species, the plant–animal difference was nonsignificant for tropical species (and was actually reversed: local extinctions in 52.4% of 349 tropical animal species versus 59.4% of 155 tropical plants; $p = 0.1500$) but was strong for temperate species (38.6% of 207 temperate animal species versus 8.6% of 105 temperate plants; $p < 0.0001$).

The frequencies of local extinctions across different animal groups (Fig 3) were broadly similar to the overall value for animals (50.1%), but with higher values in insects (56.1% of 271 species; based on six studies; Table 1) and fish (59.4% of 69 species; three studies) relative to mammals (35.0% of 40 species; four studies), birds (43.8% of 233 species; five studies), amphibians (36.8% of 19 species; one study), and squamate reptiles (lizards and snakes; 41.7% of 12 species; two studies). Local extinctions were also broadly similar in frequency in various groups of marine invertebrates, including crustaceans (46.7% of 15; one study), annelids (64.5% of 31; one study), and molluscs (45.4% of 22; two studies). The frequency in echinoderms was lower (25.0%; one study) but was based on a very small sample size (4 species).

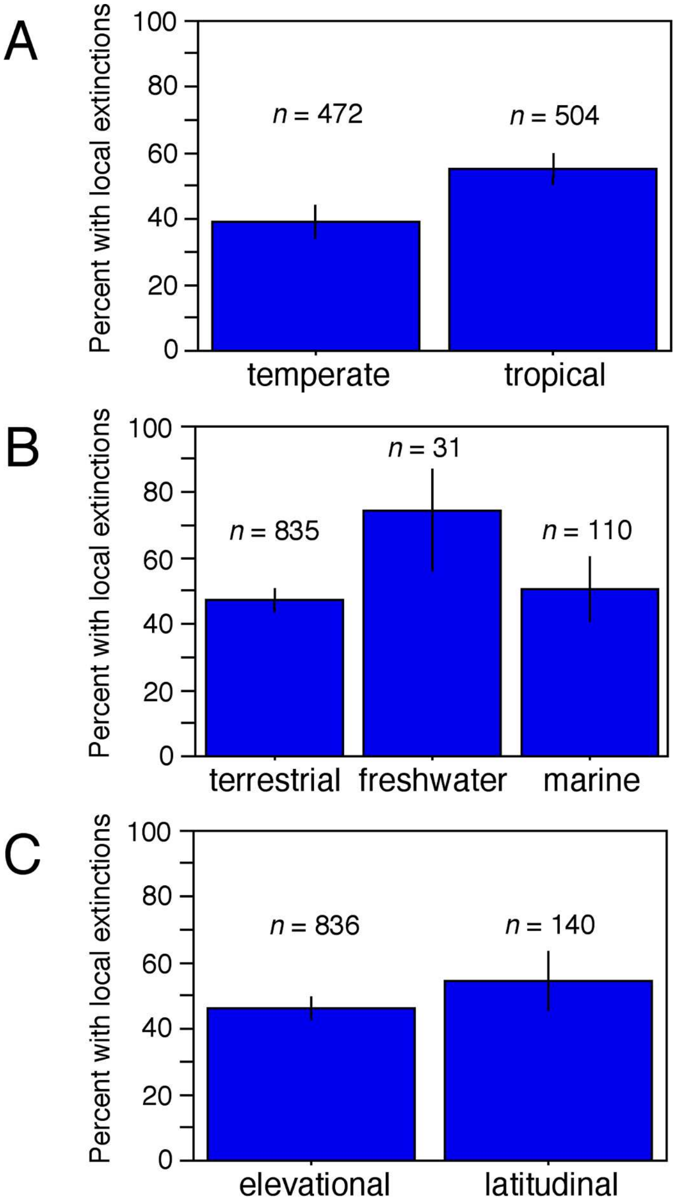

Fig 2. The frequency of local extinctions related to climate change across different climatic regions, habitats, and gradients. (A) Species are categorized as temperate or tropical (based on the location of the study), and the percentage of species with one or more local extinctions is shown, along with the sample sizes of species in each region. (B) Species are categorized as terrestrial, freshwater, or marine, and the frequency of species with local extinctions is shown (along with total species per habitat). (C) Species are categorized based on whether they were surveyed along elevational or latitudinal transects. Vertical lines indicate 95% confidence intervals on the estimated frequency of species with local extinctions.

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Results were generally similar using both general linear models (GLMs; see below) and general linear mixed models (GLMMs; see next paragraph). GLM results are given in full in S2 Appendix and are summarized here. Simultaneously including all 976 species and most variables (habitat [terrestrial versus freshwater versus marine], climatic regions [tropical versus temperate], taxonomic group [plants versus animals], survey type [latitudinal versus elevational], and study dates [start date, end date, and duration in between]) showed that most

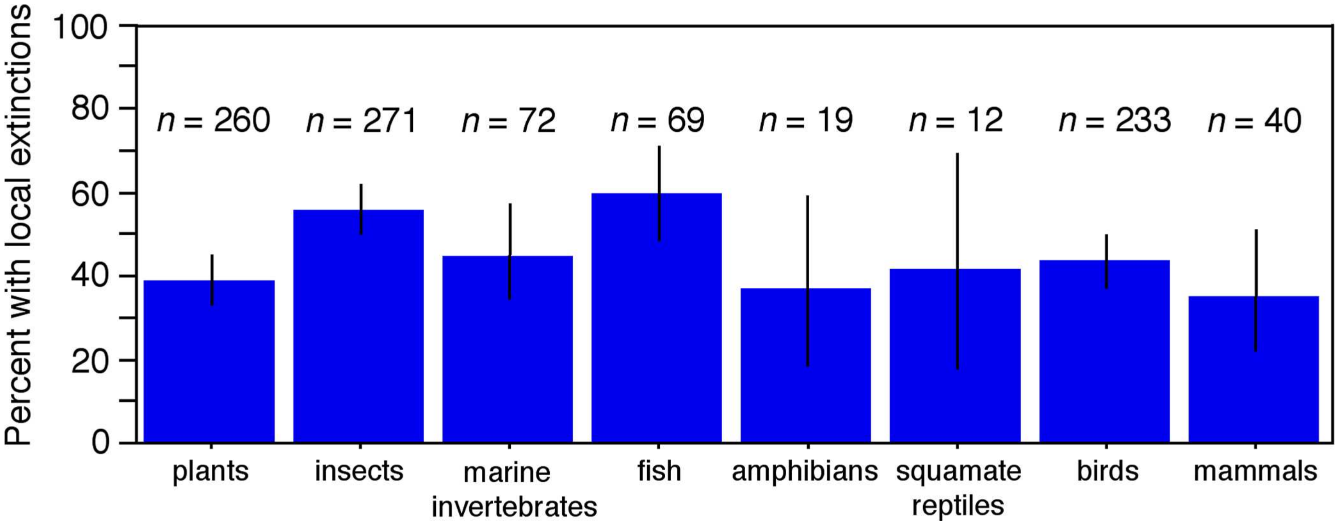

Fig 3. The frequency of local extinctions related to climate change across different taxonomic groups. The percentage of species with one or more local extinctions in each taxonomic group is shown, along with the total sample size of species surveyed in that group. For ease of presentation, four different groups of marine invertebrates (annelids, crustaceans, molluscs, and echinoderms) are shown together. Frequencies for these four groups were averaged to obtain a single value, and sample sizes of species across groups were summed. Squamate reptiles include lizards and snakes. Vertical lines indicate 95% confidence intervals on the estimated frequency of species with local extinctions.

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variables had significant effects on the frequency of extinction, except for the study dates. There were strong effects of habitat and climate ($p < 0.00001$) but weaker effects of taxonomic group ($p = 0.0246$). Results were similar when excluding study dates and taxonomic group. Including geographic regions showed that most regions had no significant effect (except for Madagascar and South America). Given that Madagascar and South America were represented by one study each, these region effects were not considered further. Furthermore, the effects of climatic region, habitat, taxonomic group, and survey type remained significant when geographic regions were included. Comparing species only on terrestrial elevational gradients (805 species in total) further confirmed the significant effects of climate and taxonomic group. Similarly, considering plants only (260 species) also confirmed the significant effects of climatic region. Considering only terrestrial animals on elevational gradients (545 species) showed a significant effect of climate ($p = 0.0023$) after removing study dates, which had no significant effect. Considering birds alone (233 species) and including climatic region, survey type, and study dates showed that climatic region, survey type, start date, and end date had significant effects. For insects (271 species), when including climatic region, study dates, and survey type, no variables were significant. For fish (69 species), a model including habitat (freshwater versus marine), study dates, and survey type showed that no variables were significant. However, habitat was significant if other variables were removed. Similarly, for temperate animals (367 species), a model including habitat, survey type, and study dates showed that only habitat and survey type were significant. Comparison of plants and animals on terrestrial elevational gradients (including study dates) showed that extinction is significantly different between temperate plants and animals (more common in animals), but not between tropical ones. Across animals, the effects of taxonomic group were limited and depended on the other variables included. If only taxonomic groups and study dates were included, then annelids, fish, and insects showed significantly more extinction ($p = 0.03$–0.05). Including habitat and survey type (and removing study dates) showed stronger effects in fish and annelids (as well as in crustaceans and molluscs), but not in insects.

Results were also broadly similar using GLMMs, with study identity included as a random effect. Results are summarized below and given in full in S3 Appendix. The impacts of study dates were somewhat counterintuitive (and rarely significant), and analyses including them sometimes failed. When most variables were included (habitat, climatic region, taxonomic group [plant versus animal], survey type, and study dates), all variables were significant except for study dates and taxonomic group, with strong effects of habitat, climatic region, and survey type. When study dates were removed, only habitat and survey type were significant. When geographic regions were included (and study dates excluded), only South America had a significant effect, and habitat, taxonomic group, and climatic region were significant or marginally significant. Comparing tropical and temperate species on terrestrial, elevational gradients showed significant effects of climatic region ($p = 0.0017$) and taxonomic group ($p = 0.0119$), but not of study dates. When study dates were removed, no variables were significant. Plants alone showed a significant effect of climatic region ($p < 0.0001$), but analyses failed if study dates were included. Animals on terrestrial, elevational gradients showed no significant effect of climatic region (again, study dates had to be excluded). Considering birds alone showed no significant effect of climate but a significant effect of survey type (excluding study dates). Insects showed no significant effects of climate or survey type, regardless of whether study dates were included. Analyses of fish failed unless study dates and survey type were excluded, but habitat alone (marine versus freshwater) had a significant effect ($p = 0.0265$). Analyses of temperate animals (367 species) including habitat, survey type, and study dates showed only habitat type as significant ($p = 0.0307$), but excluding study dates showed significant effects of habitat and survey type. Comparing only temperate plants and animals showed a significant effect of taxonomic group, when study dates were included ($p = 0.0116$) or excluded ($p = 0.0005$; study dates had no significant effect). In contrast, there was no significant effect of taxonomic group when comparing tropical plants and animals (504 species total; excluding study dates). Analyses of animals alone showed no significant effect of taxonomic group.

In summary, several patterns emerged as significant across all (or most) analyses. First, there were significant effects of climatic region overall, with extinction more common in tropical regions. This was present in plants across all analyses and generally present in animals. Animals showed significantly more extinction than plants overall and when comparing temperate, but not tropical, species. There were significant effects of habitat on animals overall (higher extinction in freshwater), even when considering fish alone. Finally, GLM analyses showed some effects of taxonomic groups across animals (with higher extinction in fish and annelids) and possibly in insects, molluscs, and crustaceans. The GLMM analyses did not show these group effects, possibly because many animal groups are included based on a single study.

Discussion

The results of this study show that local extinctions (inferred to be related to climate change) are already widespread and have occurred in hundreds of species. Roughly half of the 976 species that were surveyed for range shifts showed evidence of local extinctions (47%). This proportion was surprisingly similar across diverse climatic regions, habitats, and taxonomic groups. The results here suggest that even the modest changes in climate that have occurred so far are enough to drive local populations in many species to extinction. The results here also suggest that local populations in many species cannot shift their climatic niches rapidly enough to prevent extinction. This pattern of widespread local extinction seems likely to become even more prevalent as the global climate warms further (by roughly 2 to 5-fold [4]) in the next several decades.

The results here showed generally similar patterns of local extinction across climatic zones, habitats, and clades. Nevertheless, most analyses showed that local extinctions were significantly more common in tropical species (Fig 2A), in freshwater species (Fig 2B), and in animals. A greater impact of climate change on tropical species has been predicted by several authors (e.g., [40–42]). This prediction is related to the narrower climatic niche widths for temperature-related variables in tropical species that are associated with reduced temperature seasonality in the tropics (e.g., [43,44]) and lower rates of temperature-related climatic niche change in tropical species (e.g., [42]). The results here provide support for this prediction based on documented local extinctions that have already occurred: species in tropical regions had local extinctions more frequently than those in temperate regions (54.6% versus 39.2%), especially when species were compared on terrestrial, elevational gradients (54.6% versus 28.2%). This pattern was strongest in plants and when animals were compared on terrestrial elevational gradients. Overall, these results further support the idea that the negative impacts of climate change on biodiversity are more frequent (per species) in tropical regions [40–42], where biodiversity is highest.

Climate-related local extinctions were also similar in frequency in marine and terrestrial species (Fig 2B) but were more common in freshwater species (although freshwater habitats were represented by a single study). Freshwater species may be especially susceptible to changes in precipitation patterns (e.g., drought), which can substantially alter or eliminate their habitats (e.g., [45]), quickly resulting in local extinction. In contrast, marine species may experience less impact from changes in precipitation. Furthermore, they may be buffered from temperature changes because they can potentially adjust the temperatures that they experience by movement within the water column (more so than is possible for most freshwater species; [46,47]).

The frequency of local extinctions was also broadly similar across diverse taxonomic groups (~35%–60%; Fig 3), including plants, insects, fish, amphibians, squamate reptiles, endothermic vertebrates (birds and mammals), and many marine invertebrates (annelids, crustaceans, and molluscs). However, local extinctions were significantly more common in animals than plants (and animals are far more species-rich than plants). They were also relatively common in insects (the most species-rich group of animals) and fish (the most species-rich group of vertebrates). Local extinctions were not particularly common in amphibians (36.7%) or squamate reptiles (41.7%), although both groups were included here based primarily on one study [32]. Nevertheless, both groups appear to have been strongly impacted by climate change overall. For example, many amphibian species have undergone sharp declines and global extinctions, many of which are thought to be caused by an interaction between climate change and an infectious disease (chytrid fungus; [48]). However, these chytrid studies were not included here because they were not focused on surveying warm-edge populations over time. Similarly, local extinctions related to climate change have been documented in many lizard species [49]. Again, these were not included here because they were not based on a systematic survey of warm-edge populations. Nevertheless, if the species studied by Sinervo et al. [49] were included here, the frequency of local extinctions in squamates would go from 41.7% (of 12 species) to 77.4% (of 124 species), but with the caveat that their study focused on documenting local extinctions and so might overestimate this frequency. It should also be noted that the well-publicized declines in amphibian populations globally are not necessarily inconsistent with the frequency of local extinction observed here. For example, a global assessment of amphibian populations [50] noted declines in 43% of amphibian species (compare to the 47% of all species here with local extinctions and the 37% for amphibians), but these declines also included those unrelated to climate change (e.g., habitat destruction and overexploitation). Thus, the frequency of climate-related declines here is not necessarily an underestimation relative to the declines documented by the global amphibian assessment [50].

A major conclusion of this study is that populations of many species are already unable to undergo niche shifts that are fast enough to prevent local extinction from climate change. The rate is emphasized here because even if the absolute amount of niche change needed to avoid extinction might be attainable, it might require more time to achieve than is allowed by the rapid pace of anthropogenic climate change. Given this result, and that climate is predicted to change even further in the near future, the persistence of many species might depend largely on their ability to successfully shift their geographic ranges to higher latitudes or elevations and remain within their original climatic niche. Indeed, the summary here shows numerous instances of cool-edge expansions (in 367 of 904 species, with cool edges that were stable in 371 others and contracted in 166 others).

Unfortunately, these movements may be impeded for many species by one or more factors. First, human impacts may prevent species from successfully dispersing (including agriculture, roads, and urbanization), or these human impacts may simply leave them no habitat to disperse to (e.g., [51,52]). Second, many species are already confined to islands, peninsulas, and mountaintops, where dispersal to higher latitudes or elevations may not be possible (e.g., [53]). Third, even if dispersal is unimpeded by human or natural barriers, it may simply occur too slowly to allow species to remain within their climatic niche (e.g., [54,55]).

The combination of these potential limits to dispersal and the widespread local extinctions documented here is troubling. However, the results here do not rule out the possibility that rapid niche shifts will occur in some populations of many species in the future, preventing global extinctions. Indeed, roughly half of the species surveyed showed no local extinctions, and most species had some populations that persisted locally (but again, this is under the limited climate change that has already occurred). The future persistence of species will depend on many factors [6,8], including rates and patterns of climate change at each location, dispersal, niche shifts, local climatic microrefugia [56], and the contribution of population-level niche width to species-level niche width (e.g., whether species are broadly tolerant or locally specialized to different climatic conditions across their ranges [44]). Most importantly, I suggest that the patterns of present-day local extinctions obtained from range-shift studies should be part of the evidence used to predict species persistence in the future.

There are several potential sources of bias that may have influenced some aspects of these results but should not overturn the major conclusions. First, “local extinction” means that individuals of a given species are entirely absent from a location that they previously occupied. However, it can be difficult to distinguish between extinction and a substantial decline in abundance that causes the species to go undetected at a given location (e.g., [57]), and studies did not necessarily provide statistical evidence for the absence of a species at a site. Here, the estimates of previous researchers were used, and it was assumed that they adequately documented local absences (otherwise, their estimates of range shifts would also be erroneous). Furthermore, strong declines that make a species undetectable at a given site might soon lead to local extinction. Second, there may be a bias in terms of unpublished results. Specifically, some researchers who monitored the warm edge of a population but failed to find any changes associated with climate change may not have published their negative results. Such a reporting bias would lead to overestimating the proportion of species experiencing local extinction in this study. Nevertheless, local extinctions were still documented in hundreds of species across regions and clades, even if there are hundreds of additional species in which these local extinctions did not occur. Additionally, numerous species ($n = 171$) showed evidence of a cool-edge expansion without a corresponding contraction in the warm edge. Thus, a species can undergo a range shift but without local extinction, which should limit this source of publication bias. Third, it was assumed that previous researchers correctly associated the patterns that they observed with climate change. In theory, other factors such as overharvesting or habitat destruction may have contributed to the observed local extinctions in some cases (e.g., [21]).

Again, the analyses here primarily assume that the main conclusions of these previous studies were not erroneous.

Finally, despite the widespread pattern of warm-edge contractions and local extinctions, 521 species showed no local extinctions at the warm edge, indicating that they have successfully persisted in the face of the climate change that has occurred so far. However, even these species might still go globally extinct when global climate changes further. Additionally, contrary to the overall trend, 54 species were documented here as having expansions at both their warm edge and their cool edge (6.0% of 904 species with data on both cool and warm edges). One scenario by which this may occur is if cool-edge limits are set by colder temperatures (allowing expansion as global climate warms) and warm-edge limits are set by low precipitation (allowing warm-edge expansion), given that precipitation may increase in some areas because of climate change [4]. Indeed, some studies have found evidence for warm-edge expansions through this mechanism [58]. It is also important to note that local extinctions related to climate change need not be confined to the warm edge of the species range and so might actually be underestimated here. For example, there could be climate-related local extinctions far from the warm edge that are associated with certain microclimates (e.g., equatorially facing slopes at the cool edge of a species range; [59]).

In summary, the results here show that widespread local extinctions (seemingly related to climate change) have already occurred in hundreds of species, with broadly similar patterns of extinction across diverse clades, habitats, and climatic regions. Importantly, levels of climate change so far are limited relative to those generally predicted for the next 100 years [4]. The results here suggest that many species are unable to shift their niches rapidly enough to prevent local extinction. This inference of climate change outpacing niche change supports predictions from other sources, including transplant experiments in plants [60], phylogenetic analyses of rates of niche change in plants and animals [42,61,62], and projections based on selection, heritability, and temperature tolerances in lizards [49]. Local extinctions from climate change might also impact species that many human populations depend on for food, such as grasses (e.g., wheat, rice, and corn [62]). More generally, this study demonstrates that analyses of range shifts can provide extensive data on local extinctions related to climate change that have already occurred. These local extinctions offer a potentially important but underutilized source of information for the challenging task of predicting patterns of species survival and extinction in the future.

Materials and Methods

Selection of Studies

Web of Science searches were initially conducted from December 2014 to April 2015 using the Boolean search terms Topic = (global warming OR climate change) AND Topic = (local extinction OR range contraction OR range shift). A second Web of Science search was conducted between April 2015 and May 2015 to identify additional studies potentially missed by the first set of keywords, using the search terms TS = (global warm* OR climate change) AND TS = (extinction* OR contraction* OR range shift*), excluding results from TS = (global warming OR climate change) AND TS = (local extinction OR range contraction OR range shift). Each set of Web of Science results was sorted by relevance and then binned into subsets of 50. Searching was ceased when less than 1 in 50 studies per subset was relevant (see below for criteria). Finally, a third Web of Science search was performed on 1 March 2016 to find more recently published studies. This third search used the keywords TS = (global warm* OR climate change) AND TS = (extinction* OR contraction* OR range shift*). A total of 1,530 results were found in this third search. Results were sorted by relevance, and the first 300 (~20%) were examined. The last 40 of these 300 included no relevant studies.

Some additional studies were also found that were listed as references in the papers identified by these initial Web of Science searches. The reference list was also checked against a recent review study [11], which also conducted thorough searches of the literature on climate-related range shifts. Three studies were added from that survey which were not initially included here. Finally, several relevant studies were also found in the survey of Gibson-Reinemer et al. [63], which had similar rules for inclusion of studies. Although those authors did not conduct a systematic search of the literature (as done here), they nevertheless included five studies not found in the searches described above. These were also added here.

In theory, the fact that "extinction" and "contraction" were included as keywords might have biased the results to include more papers documenting local extinctions and range contractions than would be obtained from a search of range-shift studies that excluded these as keywords (possibly leading to overestimation of the frequency of local extinctions). However, this seems unlikely in practice. First, these were included as "or" keywords, along with "range shifts." Examining the keywords and titles of the 27 selected papers showed that most were focused on overall range shifts, with no mention of local extinction (extinction or extirpation are mentioned in the titles of only 4 of 27 studies and as keywords in only 4 of the 21 studies with keywords; "contraction" is mentioned in only 1). Furthermore, the fact that the survey results here were checked against another recent review on range shifts [11], and that three missing studies were added, also makes this potential bias seem unlikely. In other words, if many range-shift studies were missed because of this bias, they should have been added at that point.

Overall, these searches were extensive but may not be truly exhaustive. Regardless, many studies were found that documented local extinctions, and finding more studies that did so would not overturn this main conclusion.

Studies were included that monitored one or more populations at the warm edge of a species' range (the edge that is lower in elevation or closer to the equator) over a relatively long time span. Studies were only included that spanned an interval of at least 10 years. The mean study duration was ~50 years (range = 14 to 159; Table 1). Studies were included that related their findings on range shifts to climate change through an explicit statistical analysis (but noting that these inferences could still be incorrect, for example, if other factors instead of climate change caused local extinctions of a particular species). The included studies all documented populations along elevational or latitudinal transects at two or more discrete time points.

Some recent studies have inferred climate-related range shifts based on overall trends in latitudinal and elevational distributions across a large number of localities over time, rather than systematically resurveying specific localities at different time points (e.g., [64]). These studies are valuable for documenting range shifts in general but were excluded here, since they do not unambiguously represent local extinctions (because the overall patterns described might be driven solely by range expansions instead).

Categorizing Species

Studies that documented warm-edge range contractions (and that were linked to climate change by the authors of the original studies) were considered evidence of climate-associated local extinction, regardless of changes at the cool edge. Studies differed in whether they reported changes at the population level (e.g., [28,37]) or species level (e.g., [33]). The analysis here was conducted at the species level. Therefore, if populations of the same species differed in the pattern of their range shifts, the species was categorized as showing evidence of local extinction if at least one population did so.

Most species were included in only one study. However, the plant species *Anthoxanthum odoratum* was included by both Angelo and Daehler [13] (in Hawaii) and Felde et al. [19] (in

Europe). However, since this species is not native to Hawaii, it was excluded from the dataset of Angelo and Daehler [13], along with all other nonnative species in that study.

For each study, it was noted whether the range shifts were elevational or latitudinal, as well as the general habitat of the organisms (i.e., terrestrial, freshwater, or marine), the higher taxa to which they belonged, the specific geographic location of the study, and whether the species occurred in a tropical or subtropical region (arbitrarily defined as within 35° of the equator) or in a temperate region (>35°). Species were assigned to these climatic regions based solely on the location where they were surveyed, rather than on their overall geographic range. Species were also assigned to taxonomic categories, including plants, insects, fish, amphibians, birds, mammals, and squamate reptiles (i.e., lizards and snakes), as well as marine annelids, crustaceans, echinoderms, and molluscs. The beginning and end dates of the study were also noted (e.g., the date of the initial survey and the subsequent resurvey) and were used to estimate the duration of the study. Some studies provided a range of dates for the start and/or end date. In these cases, the midpoint of each range of dates was used to estimate the start, end, and duration (Table 1). Data for all species are provided in S1 Appendix.

The studies included (Table 1) spanned many geographic regions (e.g., North America, South America, Europe, Asia, and Oceania). Many studies were conducted in North America (n = 13; here extending to Central America) and Europe (n = 8), but the actual number of species sampled was more broadly distributed among regions (e.g., Asia = 332; Europe = 268; Madagascar = 30; Oceania = 58; North America = 233; and South America = 55). Africa and Australia were not represented, although nearby Madagascar and New Guinea were. The numbers of temperate and tropical species included were nearly equal. Further, there was no clear hypothesis for why particular continents alone should be an important factor influencing the frequency of local extinctions (e.g., separate from temperate versus tropical effects).

Statistical Analyses

Chi-squared analyses were initially used to compare the proportion of climate-associated local extinctions across some categories (i.e., tropical versus temperate; freshwater versus marine versus terrestrial; and latitudinal versus elevational gradients), testing the null hypothesis that frequencies of local extinction were equal between these categories. A series of analyses were conducted to assess whether frequencies of local extinction were higher in tropical regions relative to temperate regions, after accounting for the potential influence of different habitats, gradients, and clades (see Results). Similar analyses were conducted to assess the impacts of different habitats and clades (i.e., plants versus animals). However, potential analyses were restricted by the available data. For example, it was not possible to compare the effect of tropical versus temperate climates on marine or freshwater organisms, since only temperate marine and freshwater species were included here. For this reason, different sets of analyses were conducted for each question.

These analyses were then repeated using GLMs and GLMMs, both in R. These analyses were implemented treating the presence of warm-edge local extinction in a species as the binomial, dependent variable. GLMM analyses were conducted using the R package *lme4* [65]. GLMM analyses treated the study (from which the species data were obtained) as the random variable and the other variables as the fixed variables. GLM and GLMM analyses initially included all species and all or most variables and were then restricted to smaller sets of species (and variables) to test additional hypotheses and reduce potentially confounding effects (as in the Chi-squared analyses).

Phylogenetic information was not incorporated here, since phylogenies and comparable branch lengths spanning all the included species were not available (especially species-level phylogenies for fish, insects, plants, and marine invertebrates). Nevertheless, some analyses were conducted to assess patterns within and between clades (see Results).

Supporting Information

S1 Appendix. Data for the 976 species used in this study.
(XLSX)

S2 Appendix. Results of GLM analyses, showing variable coefficients.
(DOC)

S3 Appendix. Results of GLMM analyses, showing variable coefficients.
(DOC)

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BEFORE THE CALIFORNIA FISH AND GAME COMMISSION

A Petition to List the Southern California/Central Coast Evolutionarily Significant Unit (ESU) of Mountain Lions as Threatened under the California Endangered Species Act (CESA)


A Mountain Lion in the Verdugo Mountains with Glendale and Los Angeles in the background.
Photo: NPS

Center for Biological Diversity and the Mountain Lion Foundation
June 25, 2019

Notice of Petition

For action pursuant to Section 670.1, Title 14, California Code of Regulations (CCR) and Division 3, Chapter 1.5, Article 2 of the California Fish and Game Code (Sections 2070 *et seq*.) relating to listing and delisting endangered and threatened species of plants and animals.

I. SPECIES BEING PETITIONED:

Species Name: Mountain Lion (*Puma concolor*). Southern California/Central Coast Evolutionarily Significant Unit (ESU)

II. RECOMMENDED ACTION: Listing as Threatened or Endangered

The Center for Biological Diversity and the Mountain Lion Foundation submit this petition to list mountain lions (*Puma concolor*) in Southern and Central California as Threatened or Endangered pursuant to the California Endangered Species Act (California Fish and Game Code §§ 2050 et seq., "CESA"). This petition demonstrates that Southern and Central California mountain lions are eligible for and warrant listing under CESA based on the factors specified in the statute and implementing regulations. Specifically, petitioners request listing as Threatened an Evolutionarily Significant Unit (ESU) comprised of the following recognized mountain lion subpopulations:

1. Santa Ana Mountains
2. Eastern Peninsular Range
3. San Gabriel/San Bernardino Mountains
4. Central Coast South (Santa Monica Mountains)
5. Central Coast North (Santa Cruz Mountains)
6. Central Coast Central

Alternatively, as detailed in the petition, in the event the Commission determines that these six populations collectively either do not comprise a single Southern California/Central Coast ESU or otherwise do not meet the criteria for listing as Threatened, petitioners request the Commission consider whether any of these populations, singularly or in combination, comprise one or more ESUs and meet the criteria for listing as Threatened or Endangered pursuant to CESA.

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I hereby certify that, to the best of my knowledge, all statements made in this petition are true and complete.

Signature: ____________________ Date: 6/25/19

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Executive Summary

The Center for Biological Diversity and the Mountain Lion Foundation submit this petition to list mountain lions (*Puma concolor;* cougar, puma) in Southern and Central Coastal California as "threatened" or "endangered" pursuant to the California Endangered Species Act (CESA) (California Fish and Game Code §§ 2050 et seq.). Following Section 670.1, Title 14, California Code of Regulations, petitioners present scientific information regarding life history, population trend, range, distribution, abundance, kind of habitat necessary for survival, factors affecting the ability to survive and reproduce, degree and immediacy of threat, impact of existing management efforts, suggestions for future management, availability of sources and information, and a detailed distribution map.

Specifically, petitioners request listing as a "threatened species" an evolutionarily significant unit (ESU) comprised of the following recognized mountain lion subpopulations:

1. Santa Ana Mountains
2. Eastern Peninsular Range
3. San Gabriel/San Bernardino Mountains
4. Central Coast South (Santa Monica Mountains)
5. Central Coast North (Santa Cruz Mountains)
6. Central Coast Central

As demonstrated in this petition, mountain lions in these areas comprise an ESU (referred to as the "Southern California/Central Coast ESU") and meet the statutory definition of a "threatened species."

The California Fish and Game Commission has long recognized that ESUs can be designated and listed under CESA, and this interpretation of CESA has been upheld by the courts. *See California Forestry Assn. v. California Fish & Game Com.* (2007) 156 Cal.App.4th 1535, 1540 ("Consistent with the policy of the CESA, we will hold that the term 'species or subspecies' includes evolutionarily significant units"); *Central Coast Forest Assn. v. Fish & Game Com.* (2018) 18 Cal.App.5th 1191, 1197, fn. 4 [*"CCFA II*"] ("An ESU is included within the term 'species or subspecies' in sections 2062 and 2067."). While the ESU concept has primarily been applied to fish, the Commission recently listed an ESU of a mammal, the Pacific Fisher, as a "threatened species." *See* 14 C.C.R. 670.5(b)(6)(J) ("Fisher (*Pekania pennant*) Southern Sierra Nevada Evolutionarily Significant Unit").

Under CESA, a "threatened species" is "a native species or subspecies of a … mammal… that, although not presently threatened with extinction, is likely to become an endangered species in the foreseeable future in the absence of the special protection and management efforts . . . ." Cal. Fish & Game Code § 2067. An animal is an "endangered species" when it is "in serious danger of becoming extinct throughout all, or a significant portion, of its range due to one or more causes, including loss of habitat, change in habitat, overexploitation, predation, competition, or disease." Cal. Fish & Game § 2062.

Certain populations of the Southern California/Central Coast mountain lion ESU are already "in serious danger of becoming extinct" (*e.g*. Santa Ana and Santa Monica mountains), and if assessed separately, would individually meet the definition of an "endangered species." When considered as a whole, the Southern California/Central Coast ESU is not at imminent risk of extinction but still faces significant and growing threats that ultimately threaten the viability of the entire ESU; it consequently meets the definition of a "threatened species."

Currently, there is no reliable estimate of mountain lion abundance in California. In 1984 the California Department of Fish and Wildlife (CDFW) estimated between 4,000-6,000 adult mountain lions in the state (Mansfield and Weaver 1984). However, CDFW acknowledges that this estimate is outdated and likely overestimates mountain lion abundance. CDFW is currently undertaking a large-scale research effort to estimate mountain lion numbers throughout California.

While reliable absolute abundance estimates are unavailable, recent genetic research has led to estimates of effective population size for California mountain lion populations.[1] These estimates highlight the genetic isolation among California mountain lion populations and raise significant concerns for the continued viability of mountain lions in Southern California and along the Central Coast.

Researchers have recently identified 10 genetically distinct mountain lion populations in California (Figure ES-1) (derived from Gustafson et al. 2018). Nine of these populations occur almost exclusively in California, while one is centered in Nevada but extends into the northeastern corner of California.

The abundance of mountain lions in the North Coast and inland populations (Western Sierra Nevada, Eastern Sierra Nevada, and the genetic cluster centered in the state of Nevada) is not well established; however, these populations are better connected than Southern California and Central Coast mountain lions, and they show relatively high levels of genetic diversity. Gustafson et al. (2018) suggest that these four populations may comprise an ESU. While these populations should be monitored and managed to ensure their continued viability, petitioners do not seek protection of these populations as an ESU under CESA at this time.

Considering the genetic source-sink dynamics among the remaining six populations, petitioners demonstrate that the populations along the Central Coast and in Southern California collectively comprise an ESU that warrants protection under CESA.[2] The Southern California/Central Coast ESU is comprised of six genetically distinct mountain lion populations: Central Coast North (CC-N, which includes mountain lions in the Santa Cruz Mountains and East Bay), Central Coast

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[1] At its simplest, effective population size is the number of animals contributing offspring to the next generation. It is an important measure of the genetic health of a population.

[2] As explained *infra* at Section 3.0, these remaining populations can be grouped into one or several potential ESUs. Petitioners believe that for purposes of listing under CESA, treating them as a single ESU is supported by the best available science. Moreover, a single ESU also is the most pragmatic from a management perspective, as recovery of the individual populations ultimately depends upon maintaining and/or reestablishing connectivity between them. *See CCFA II,* 18 Cal.App.5th 1191, 1237 ("[T]he nature of the ESU designation is such that genetics alone are not determinative: One must look beyond genetics to questions of policy to determine which populations to include in an ESU.")(quotations omitted).

Central (CC-C), Central Coast South (CC-S, which includes the mountain lions in the Santa Monica Mountains), San Gabriel/San Bernardino Mountains (SGSB), Santa Ana Mountains (SAM), and Eastern Peninsular Range (EPR) (Gustafson et al. 2018).

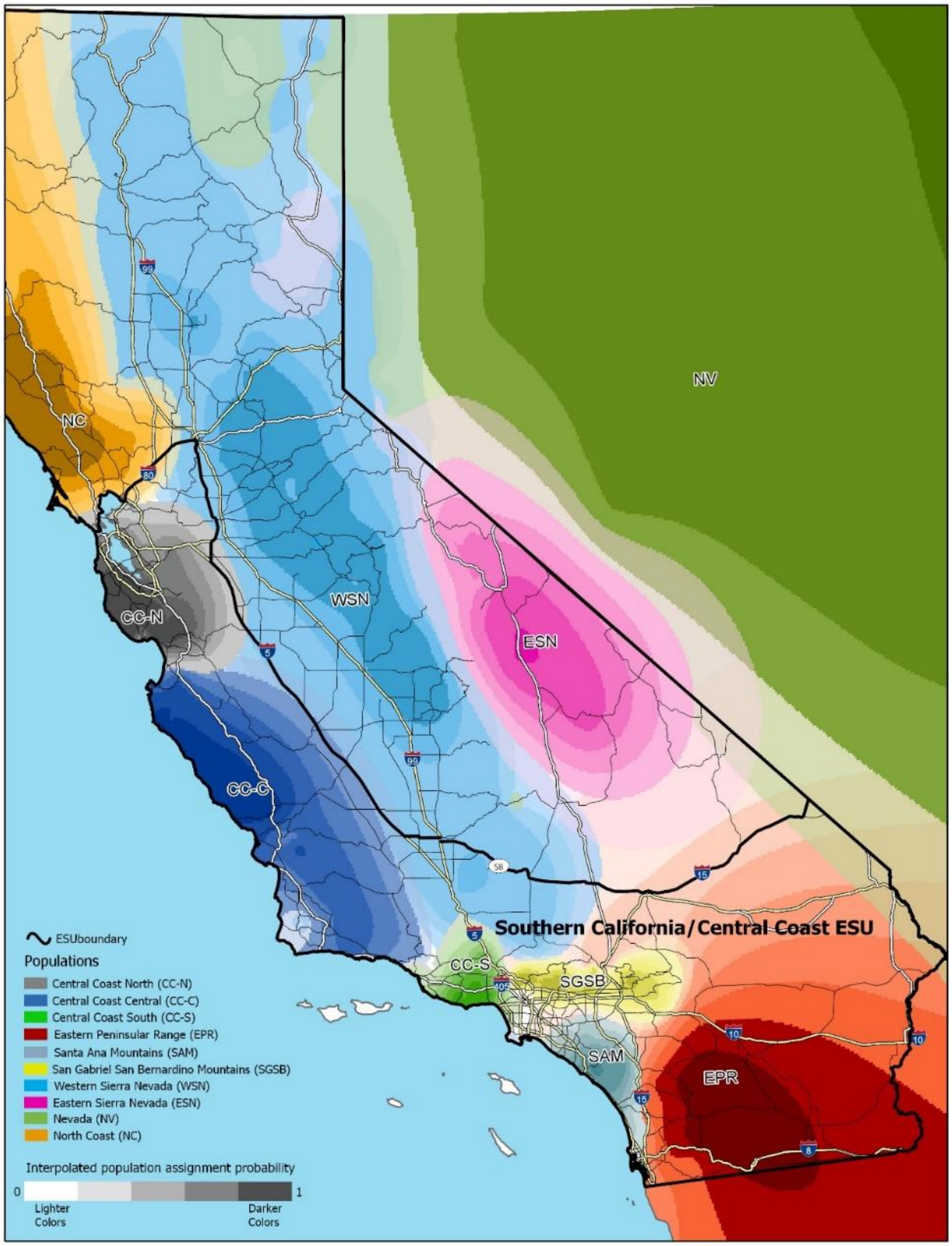

Figure ES-1. Map of genetically distinct mountain lion populations and major roadways in California based on data collected from 1992-2016 (the division and status of these populations could change over time and with further research). The black lines show the proposed Southern California/Central Coast ESU boundary. Derived from Gustafson et al. (2018). Genetics data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie. Roads data source: ESRI.

The boundary of the Southern California/Central Coast ESU is proposed in Figure ES-1, and includes mountain lions that occur south of the San Francisco Bay and I-80, west of I-5 to the intersection of I-5 and SR-58, south of SR-58 to I-15, south of the I-15 from the SR-58 intersection to the California-Nevada border, and, for the purposes of CESA, as far south as the California-Mexico border. These boundaries are recommended as they include virtually all mountain lions associated with the six populations comprising the ESU and are also unambiguous and readily discernable for purposes of management. We recommend including mountain lions in the Tehachapi and Sierra Pelona Mountains south of SR-58 in this ESU. While most mountain lions sampled from this region share some genetic affinities with Western Sierra Nevada (WSN) animals, many also show genetic connections with CC-S, SAM, EPR and SGSB mountain lions. This area serves not just as a connecting link between mountain lion populations comprising the Southern California/Central Coast ESU, but also between this ESU and all other California mountain lions and is therefore essential for the overall genetic health of mountain lions in the state.

While Southern California and Central Coast mountain lions face a multitude of threats, the greatest challenges stem from habitat loss and fragmentation and the consequent impact on their genetic health. Most of the populations comprising the ESU have low genetic diversity and effective population sizes, which puts them at increased risk of extinction (Ernest et al. 2003; Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016; Gustafson et al. 2018; Benson et al. 2019). The populations most at risk are the SAM, CC-S, SGSB, and CC-N populations. Due to extreme isolation caused by roads and development, the SAM and CC-S, populations exhibit high levels of inbreeding, and, with the exception of the endangered Florida panther, have the lowest genetic diversity observed for the species globally (Ernest et al. 2014; Riley et al. 2014; Gustafson et al. 2018; Benson et al. 2019). The SGSB and CC-N similarly have low observed genetic diversity and effective population sizes, and they reside in areas of significant isolation and habitat fragmentation, which also puts them at increased risk (Gustafson et al. 2018). And although the CC-C and EPR populations have slightly higher levels of genetic diversity and effective population sizes, high rates of development, habitat loss and fragmentation, and human-caused mortalities in both areas could lead to a similar fate of isolation, genetic drift, low effective population size, and increased risk of extinction in the foreseeable future.

Although minimum viable effective population size has been found to vary depending on the species (Frankham 1995; Traill et al. 2010), general conservation management practice over the past few decades has followed a 50/500 rule, under which an effective population size of 50 is assumed sufficient to prevent inbreeding depression in the short term (over the duration of five generations) and an effective population size of 500 is sufficient to retain evolutionary potential in perpetuity (Traill et al. 2010; Frankham et al. 2014). It is clear that Central Coast and Southern California mountain lion populations are genetically compromised and face significant risk of extinction in both the short- and long-term. Five of the six populations have effective population sizes well below 50 (from lowest to highest: CC-S, SGSB, SAM, CC-N, EPR), and one population (CC-C) is just barely above that threshold at $N_e = 56.6$ (Table ES-1) (Gustafson et al. 2018).

Table ES-1. Effective population size from Gustafson et al. (2018) and estimated total adult population of Central Coast and Southern California Mountain Lion Populations.

Population	Effective Population Size (N_e)	Estimated Total (Adult) Population (N)[1]
Central Coast North (CC-N)	16.6	33-66
Central Coast Central (CC-C)	56.6	113-226
Central Coast South (CC-S)	2.7[2]	5-10
Santa Ana Mountains (SAM)	15.6[3]	31-62
San Gabriel/ San Bernardino Mountains (SGSB)	5	10-20
Eastern Peninsular Range (EPR)	31.6	63-126
Total		255-510

[1] Calculations are based on the estimated ratio of effective to total adult population size (N_e/N) of Florida panthers being 0.25 to 0.5 (Ballou et al. 1989). This ratio was used in the USFWS Florida Panther Recovery Plan (USFWS 2008). Petitioners recognize that these derived population estimates, while informative, are not definitive and will likely be superseded by new population estimates being developed by CDFW.

[2] Benson et al. (2019) calculated an N_e of 4 for the Santa Monica Mountains population within the CC-S. Applying the Ballou et al. (1989) factors would lead to an estimate of 8-16 mountain lions in this area, which is roughly consistent with current estimates of this well-monitored population.

[3] Several studies provide N_e calculation for the SAM population. Ernest et al. (2014) calculated an N_e of 5.1 and Benson et al. (2019) calculated an N_e of 6. Applying the Ballou et al. (1989) factors to the most recent calculation would lead to an estimate of 12-24 mountain lions in the SAM, which is roughly consistent with current estimates.

Although low effective population sizes standing alone are cause for conservation concern for Southern California and Central Coast mountain lion populations, there are other human-caused factors that further limit their long-term persistence. Habitat loss and fragmentation due to roads and development have led to extreme levels of isolation and high mortality rates. With low genetic diversity and high risk of inbreeding depression due to genetic isolation, vehicle strikes on roads, increased conflicts with humans that lead to depredation kills, high levels of intraspecific strife likely due to limited space and lack of connectivity, rodenticide and other environmental toxicant poisoning, and impacts of more frequent human-caused wildfires and climate change, the small isolated mountain lion populations of Southern California and the Central Coast will likely not persist without the restoration and enhancement of functional connectivity between populations and large blocks of heterogeneous habitats.

Loss of mountain lions in Southern California and the Central Coast would be devastating not just for the mountain lions themselves but also the many species that directly and indirectly rely on them. These top predators are important ecosystem engineers that facilitate healthy ecosystems and allow biodiversity to thrive (Ripple and Beschta 2006; Ripple and Beschta 2008;

Ripple et al. 2014; Ruth and Elbroch 2014; Barry et al. 2019; Elbroch and Quigley 2019). As keystone species mountain lions help support plant recruitment in riparian areas, stabilize stream banks, and sustain healthy habitats for a myriad of aquatic and terrestrial species, including plants, invertebrates, fish, amphibians, reptiles, birds, and mammals (Ripple and Beschta 2006; Ripple and Beschta 2008; Ripple et al. 2014). Their kills are also an important source of food for multiple terrestrial and avian scavengers (Ruth and Elbroch 2014; Barry et al. 2019; Elbroch and Quigley 2019).

Existing laws and regulations have proven to be inadequate to protect Southern California and Central Coast mountain lions. Although the California Wildlife Protection Act of 1990 (Proposition 117) prohibits hunting of mountain lions and has funded the acquisition of important habitat for preservation, the Act alone does not ensure that core habitats and connectivity are protected from development, highways, or other threats. Moreover, numerous mountain lions are killed each year pursuant to depredation authorizations issued under this regime, and there is no limit to the number of depredation permits a property owner can request or any limit to the number of depredation permits which can be issued for any population. And while CDFW has proactively issued a bulletin detailing a new depredation policy for mountain lions in the CC-S and SAM that requires property owners to first implement non-lethal measures prior to being issued a kill permit, this policy does not apply to other vulnerable populations.

Other environmental laws also are insufficient. State and local agencies continue to interpret the California Environmental Quality Act (CEQA) as allowing for the construction of highways and other development in mountain lion habitat and essential corridor areas without adequate mitigation despite severe impacts of such projects on mountain lions. Agencies likewise have generally interpreted CEQA and the federal National Environmental Policy Act as not requiring implementation of connectivity measures when projects fragment or destroy mountain lion habitat. And perhaps most importantly, Caltrans lacks a clear affirmative mandate to design, build, or improve crossings for mountain lions on existing highways, despite the undisputed role of transportation infrastructure in preventing connectivity and gene flow.

Future human population growth and associated development will further diminish and fragment remaining mountain lion habitat, driving Southern California and Central Coast mountain lions closer to extinction and undermining any chance of recovery. Should state and local agencies continue to build and expand roads and highways and permit construction in wildlife habitat and corridors without ensuring adequate habitat connectivity, the genetic health of mountain lion populations will continue to decline while the number of mountain lions killed by vehicle strikes and other human activity will increase.

Ultimately, without a reversal of these trends, mountain lions will disappear from Southern and Central Coastal California in the coming decades, representing a loss of the species from a significant portion of its range in the state. Nevertheless, most of the threats facing mountain lions can be halted or sufficiently reduced if CDFW is provided with adequate resources and all relevant state and local agencies sufficiently prioritize mountain lion conservation in their decision-making. Legal protection of mountain lions under CESA, along with the attention and resources that such listing will generate, can help ensure the long-term survival of this iconic and ecologically significant species in Southern and Central Coastal California.

The Southern California/Central Coast Evolutionarily Significant Unit (ESU) of Mountain Lions Warrants Listing as Threatened under the California Endangered Species Act (CESA)

1 Introduction

This petition summarizes available scientific information regarding the natural history of mountain lions, their distribution and abundance in California, population trends and threats, describes the proposed ESU, and discusses the limitations of existing management measures in protecting the species. As demonstrated below, mountain lions in Southern California and along the Central Coast meet the criteria for protection as a threatened species under the California Endangered Species Act (CESA), and would benefit greatly from such protection.

2 Life History

2.1 Species Description

Adult female mountain lion (left) and kittens (right). Photos: NPS.

The mountain lion (*Puma concolor*) is also commonly called a puma (from the Inca language Quechua) or cougar (corrupted from cuguacuarana from the indigenous Guarani people in Paraguay, Argentina, Bolivia, and Brazil). Adults are large, slender cats with short, muscular limbs and a long tail that is about one third of the animal’s total length. Their hind limbs are longer than their fore limbs, which makes them highly adapted for jumping through rugged terrain or pouncing on their prey. They have tawny pelage that can be lighter/whitish on their belly and the undersides of their legs and they have areas of white around the muzzle, throat and chest. They have black fur on the backs of their rounded ears, the tip of their tail, and outlining their muzzle. Their eyes are a grayish brown to golden color, and the nose is pink with a black outline.

Adult body size and weight can vary depending on the geographic range (Iriarte et al. 1990). Mountain lions are smaller and weigh less near the equator and are larger and heavier towards the poles, which likely reflects the size of available prey and the presence of sympatric carnivores (Iriarte et al. 1990). Males are typically larger than females. Males generally weigh 55-65kg with a length of 2.2-2.3m from the nose to the tip of the tail, and females generally weigh 35-45kg with a length of 2.0-2.1m (Currier 1983).

Mountain lion kittens are born weighing approximately 400g, and their eyes and ear canals remain closed for one to two weeks after birth (Currier 1983). They have light coats with dark spots and a white muzzle, chest, and belly. Like the adults, they have black fur on the backs of their rounded ears, the tip of their tail, and outlining their muzzle. Their eyes are initially blue, change to mostly brown within four months, and then change to a golden color at around nine months (Currier 1983). The dark spots on their coat start to fade at 12-14 weeks of age, presumably when a kitten starts to accompany its mother on hunts, but the spots are still distinguishable until the animal is about one year old (Currier 1983). Adult weight is typically reached between the second and fourth year.

2.2 Taxonomy and Population Genetics

The mountain lion is in the order Carnivora and is a member of the cat family Felidae. Unlike the large, roaring cats of the subfamily Pantherinae (*e.g.*, lions, tigers, and leopards), mountain lions are categorized with small, purring cats in the subfamily Felinae (*e.g.*, bobcats, lynxes, ocelots, cheetahs, and jaguarundi). Their scientific name is *Puma concolor*, formerly called *Felis concolor*. Based on molecular and morphological features, it is thought that mountain lions share a common ancestor with cheetahs (*Acinonyx jubatus*) and jaguarundi (*Puma yaguaroundi*).

Mountain lion fossil records in North America date back 300,000 years (Pierce and Bleich 2003); however, they were likely extirpated during a massive extinction event at the end of the Pleistocene, which eliminated about 80% of large vertebrates in North America (Culver et al. 2000; Caragiulo et al. 2013). Genetic studies suggest that after this extinction event, a small number of Central and South American mountain lions migrated north and repopulated North America (Culver et al. 2000; Caragiulo et al. 2013). As a result, existing North American mountain lions exhibit founder effects and have less genetic diversity compared to mountain lions in Central and South America (Culver et al. 2000; Caragiulo et al. 2013).

There is some debate regarding the number of subspecies of mountain lions. Two subspecies are “tentatively” recognized by the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Cat Specialist Group: *Puma concolor concolor* (Linnaeus, 1771) in South America and *Puma concolor couguar* (Kerr, 1792) in North and Central America and possibly northern South America west of the Andes Mountains (Kitchener et al. 2017). However, there are various studies that suggest the divergence of multiple subspecies of mountain lions. About 30 subspecies of mountain lions throughout the Americas have been referenced in the literature, with about 15 subspecies in North America (Young and Goldman 1946; Currier 1983; Pierce and Bleich 2003).

Based on more recent genetic analyses of mitochondrial DNA (mtDNA) from mountain lions throughout the Americas, Caragiulo et al. (2013) found that the mountain lions they sampled could be separated into three broad groupings: North America, Central America, and South America, with North American mountain lions having the least variation in mtDNA compared to populations in Central and South America. Although that study genotyped 601 specimens, the distribution of sampling within the broad geographic range was limited compared to a study conducted by Culver et al. (2000), which analyzed mtDNA from 315 mountain lions sampled from more locations throughout the species' geographic distribution. Culver et al. (2000) found six phylogeographic groupings or subspecies throughout the Americas.

Despite this ongoing debate, the United States Fish and Wildlife Services (USFWS) has long recognized mountain lion subspecies under the federal Endangered Species Act (ESA). Two of these subspecies have been protected under the ESA due to low population sizes: the eastern cougar (*Puma concolor couguar*), which was listed as endangered and is now thought to be extinct, with the last recorded occurrence in 1938 (USFWS 2018), and the endangered Florida panther (*Puma concolor coryi*), which is an isolated population that is now restricted primarily to the cypress swamps of southern Florida. In addition, the California mountain lion (*Puma concolor californica*) was recognized by USFWS in response to a 1994 petition by the Mountain Lion Foundation to list the population of California mountain lions in the Santa Ana Mountains as endangered, as those populations that occur within most of California, southern Oregon, western Nevada, and northern Baja California, Mexico (USFWS 1994). Additionally, the California Department of Fish and Wildlife (CDFW) recognizes the Yuma Puma (*Puma concolor browni*) as a (sub)species of special concern that occurs in the desert plains and low mountains along the Colorado River in southeastern California, southwestern Arizona, northeastern Baja California, Mexico, and northwestern Sonora, Mexico (CDFW 1990).

In California, researchers have recently identified 10 genetically distinct mountain lion populations in California and Nevada, nine of which have core areas in California (Figure 1) (Gustafson et al. 2018). In the study, 992 mountain lions from throughout California and Nevada were genotyped using 42 microsatellite loci to identify regional populations and evaluate functional connectedness between the populations (Gustafson et al. 2018). The divergence of these populations is likely the result of habitat fragmentation caused by roads and development (Ernest et al. 2003; Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). According to Gustafson et al. (2018), mountain lions in the North Coast and inland populations (Nevada, Eastern Sierra Nevada, Western Sierra Nevada) appear to be better-connected than those in the south and along the central coast, with relatively larger effective population sizes and higher levels of genetic diversity. The authors suggest that these populations may comprise an evolutionarily significant unit (ESU). Considering the genetic source-sink dynamics among the remaining populations (Gustafson et al. 2018), petitioners demonstrate that the populations in Southern California and along the Central Coast collectively comprise an ESU (referred to as the "Southern California/Central Coast ESU"). See *Section 3.0 Southern California and Central Coast Mountain Lions Comprise and Evolutionarily Significant Unit* for more discussion.

The Southern California/Central Coast ESU is comprised of six genetically distinct mountain lion populations: Central Coast North (CC-N, which includes mountain lions in the Santa Cruz Mountains), Central Coast Central (CC-C), Central Coast South (CC-S, which includes mountain lions in the Santa Monica Mountains), San Gabriel/San Bernardino Mountains (SGSB), Santa Ana Mountains (SAM), and Eastern Peninsular Range (EPR) (Figure 1) (Gustafson et al. 2018). Most of these populations appear to be struggling with low genetic diversity and effective population sizes, which puts them at increased risk of extinction (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2018;

Benson et al. 2019). The populations struggling the most include the SAM, CC-S, SGSB, and CC-N populations. Although the CC-C and EPR have slightly higher levels of genetic diversity and effective population sizes, high rates of development in both areas could lead to a similar fate of isolation, genetic drift, low effective population size, and increased risk of extinction in the foreseeable future.

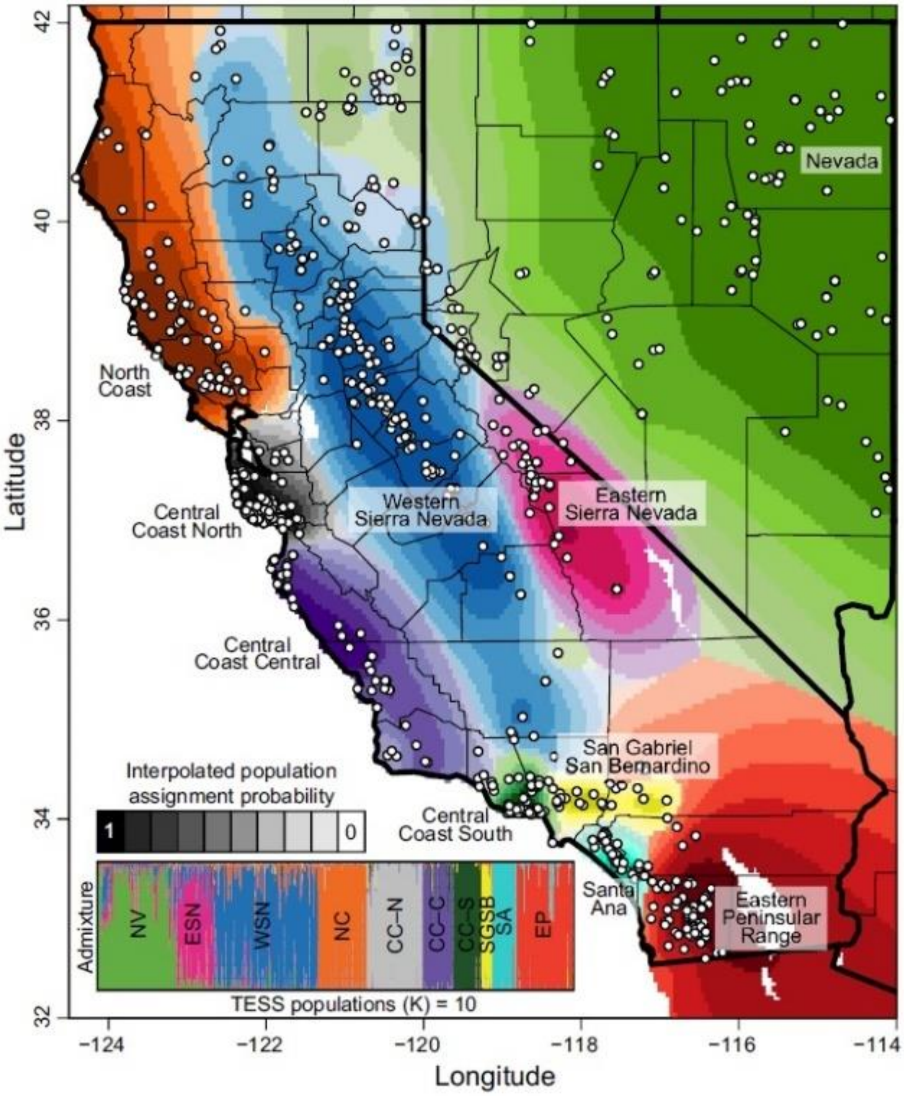

Figure 1. Map of genetically distinct mountain lion populations in California. The Central Coast North (CC-N), Central Coast Central (CC-C), Central Coast South (CC-S), San Gabriel/San Bernardino (SGSB), Santa Ana Mountains (SAM), and Eastern Peninsular Range (EPR) mountain lion populations should be considered an evolutionarily significant unit (ESU). Each color represents a genetically distinct mountain lion population. White dots are individual animals sampled. Source: Gustafson et al. (2018).

Although discrete populations have been identified in Southern California mountain ranges, other mountain lions have been regularly observed outside of the CC-S, SAM, SGSB, and EPR core areas, including transient and resident mountain lions in the Mojave and Colorado deserts and along the Lower Colorado River (*i.e*., Yuma mountain lion [*Puma concolor browni*], a recognized subspecies of special concern). These populations presumably occur in low densities due to limited resources, such as lower prey abundance/vulnerability or less suitable habitat. In fact, Kucera (1998) states that habitat within the Yuma mountain lion range is generally considered to be of low or no suitability for mountain lions. Relatively low density populations are inferred by the larger ranges of mountain lions in desert environments; four individual Yuma mountain lions had home ranges of 389km^2 to 1621km^2, which is much larger than other California mountain lion home ranges (Grigione et al. 2002; Riley et al. 2014; Zeller et al. 2017; see *Section 2.5 Habitat Requirements* for more details) but similar to those estimated for other desert mountain lions (Kucera 1998). This petition considers these low-density transients and resident lions as included within the Southern California/Central Coast ESU.

2.2.1 Effective Population Size and Extinction Risk

It has been established that genetic factors play a critical role in extinction risk. Inbreeding depression, loss of genetic diversity, and accumulation of deleterious mutations can lead to elevated extinction risk due to reduced reproductive fitness and evolutionary potential (*i.e*., the ability to adapt to change) (Spielman et al. 2004; Frankham 2005; Traill et al. 2010). Effective population size (N_e) is a key metric used to assess a population's genetic viability and its chances of long-term persistence. Effective population size is an estimate of the size of an idealized population that would lose heterozygosity (*i.e*., genetic diversity) at the same rate as the observed population; it indicates a population's rates of inbreeding and genetic drift (changes in allele frequencies over generations based purely on chance). A lower effective population size indicates a higher risk of inbreeding depression. Factors that affect effective population size include census population size (*i.e*., the total number of individuals within a population), breeding sex ratio, variance in reproductive success, and population density. Several characteristics of these mountain lion populations, including small census population size, low density, female-biased sex ratios, and skewed male reproductive success, reduce effective population size, which suggests that these populations have an increased risk of inbreeding depression and extinction (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019).

The minimum effective population size for a population to persist has been debated (*e.g*., Jamieson and Allendorf 2012; Frankham et al. 2014). Although minimum viable effective population size has been found to vary depending on the species (Frankham 1995), general conservation management practice over the past few decades has followed a 50/500 rule, which purports that an effective population size of 50 is sufficient to prevent inbreeding depression in the short term (over the duration of five generations) and an effective population size of 500 is sufficient to retain evolutionary potential in perpetuity (Frankham et al. 2014). In a 2012 review, Jamieson and Allendorf (2012) concluded that the 50/500 rule is a useful guiding principle in conservation management when genetic concerns are likely to affect the short- and long-term viability of populations. However, Frankham et al. (2014) later revised the 50/500 rule and recommended an effective population size of 100 to limit the loss of total fitness to <10% in the short-term and an effective population size of 1,000 to retain evolutionary potential for fitness in perpetuity, while recognizing that fragmented populations should be evaluated on a case-by-case basis.

Whether the 50/500 or 100/1,000 rule is considered, it is clear that Central Coast and Southern California mountain lion populations are genetically imperiled and face extinction in both the short- and long-term. Five of the six populations have effective population sizes well below 50 (from lowest to highest, according to Gustafson et al. 2018: CC-S, SGSB, SAM, CC-N, EPR), and the remaining population (CC-C) is just barely above that threshold at $N_e = 56.6$ (Table 1) (Ernest et al. 2014; Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). Although the ratio of effective to total adult population size (N_e/N) varies by species, the effective population size is often much lower than the total adult population size (Frankham 1995). Several studies indicate that the N_e/N in wild vertebrate populations ranges from 0.2 to 0.5 (Ballou et al. 1989; Mace and Lande 1991; Spong et al. 2000; Laundré and Clark 2003). Ballou et al. (1989) estimated the N_e/N to be 0.25-0.5 in their population viability assessment of the Florida Panther, which aligns with other studies on big cats (Frankham 1995; Spong et al. 2000). This range was used in the USFWS's Florida Panther Recovery Plan (USFWS 2008), and, if applied to the Central Coast and Southern California mountain lion populations, the total number of mountain lions in the areas combined would be 255 to 510 individuals (Table 1). This is well below the recommended minimum viable population size of at least 5,000 adult individuals for the long-term persistence of a population (Frankham 1995; Reed et al. 2003; Traill et al. 2010).

Table 1. Effective population size and estimated total adult population of Central Coast and Southern California Mountain Lion Populations from Gustafson et al. (2018).

Population	**Effective Population Size (N_e)**	**Estimated Total (Adult) Population (N)**[1]
Central Coast North (CC-N)	16.6	33-66
Central Coast Central (CC-C)	56.6	113-226
Central Coast South (CC-S)	2.7[2]	5-10
Santa Ana Mountains (SAM)	15.6[3]	31-62
San Gabriel/ San Bernardino Mountains (SGSB)	5	10-20
Eastern Peninsular Range (EPR)	31.6	63-126
Total		255-510

[1] Calculations are based on the estimated ratio of effective to total adult population size (N_e/N) of Florida panthers being 0.25 to 0.5 (Ballou et al. 1989). This ratio was used in the USFWS Florida Panther Recovery Plan (USFWS 2008). Petitioners recognize that these derived population estimates, while informative, are not definitive and will likely be superseded by new population estimates being developed by CDFW.

[2] Benson et al. (2019) calculate an N_e of 4 for the Santa Monica Mountains population within the CC-S. Applying the Ballou et al. (1989) factors would lead to an estimate of 8-16 mountain lions in this area, which is roughly consistent with current estimates of this well-monitored population.

[3] Several studies provide N_e calculation for the SAM population. Ernest et al. (2014) calculated an N_e of 5.1 and Benson et al. (2019) calculated an N_e of 6. Applying the Ballou et al. (1989) factors to the most recent calculation would lead to an estimate of 12-24 mountain lions in the SAM, which is roughly consistent with current estimates

Habitat loss and fragmentation due to roads and development have led to extreme levels of isolation in these populations, which have lowered their effective population sizes and, ultimately, their ability to survive and reproduce with a diverse gene pool (Ernest et al. 2014; Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). However, re-establishing gene flow among isolated subpopulations of a species can increase effective population size and reduce extinction risk (Frankham et al. 2014). Thus, the implementation of wildlife crossing infrastructure at existing barriers along with the preservation of intact, heterogeneous habitats would facilitate connectivity among Central Coast and Southern California mountain lion populations and significantly improve their chances of long-term survival.

2.2.2 Central Coast North (CC-N) Mountain Lion Population

In a statewide study, Gustafson et al. (2018) found that the CC-N population clustered genetically with the CC-C and CC-S populations. The population exhibited evidence of a previous genetic bottleneck and was found to have low genetic diversity and a low effective population size ($N_e = 16.6$). There is some evidence, though weak, that suggests the CC-N population is a source population, with limited gene flow with the other Central Coast populations and the Western and Eastern Sierra Nevada populations (Gustafson et al. 2018). CDFW has identified that the Santa Cruz Mountains population, which occurs within the CC-N area, is struggling due to fragmentation from roads and development as well as lack of protected habitat (Dellinger 2019). The low genetic diversity and effective population size threaten both the short- and long-term survival of the CC-N population.

2.2.3 Central Coast Central (CC-C) Mountain Lion Population

The CC-C mountain lion population has been found to exhibit a previous genetic bottleneck (Gustafson et al. 2018). It has intermediate levels of genetic diversity and the highest effective population size ($N_e = 56.6$) among the Central Coast and Southern California populations (Gustafson et al. 2018). Although this effective population size exceeds the older standard of 50 to prevent in-breeding depression in the short-term, it falls well below the recommended newer standard of 100 and is insufficient for the long-term persistence of the population. This population was found to be clustered genetically with the CC-N and CC-S populations and identified as a source population with limited gene flow with other Central Coast populations, the Western and Eastern Sierra Nevada populations, and the SGSB population (Gustafson et al. 2018). Although the CC-C population appears to be the healthiest population in the Central Coast and Southern California, the lack of sufficient protected lands and high rates of development and habitat fragmentation in the area threaten the persistence of this population (Dellinger 2019).

2.2.4 Central Coast South (CC-S) Mountain Lion Population

The CC-S mountain lion population has been found to exhibit a prior genetic bottleneck, with low genetic diversity and an extremely low effective population size ($N_e = 2.7$ to 4) (Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). This population was found to be clustered genetically with the CC-N and CC-C populations and identified as a genetic sink population, with limited gene flow from mountain lions along the Central Coast and in the Sierra Nevada (Gustafson et al. 2018).

A recent population viability analysis focused on the Santa Monica Mountains population, a subpopulation within the CC-S that has been severely isolated due to roads and development, found that if the population remains isolated with little or no immigration (similar to what is currently being observed in the area), the population could experience high levels of genetic erosion, with 40-57% loss of predicted heterozygosity within 50 years (Benson et al. 2016a). When considering just demographic processes with little or no immigration and no inbreeding depression, the population was predicted to have a 15-22% chance of extinction within 50 years (Benson et al. 2016a; Benson et al. 2019). However, if inbreeding depression occurs, which is a strong possibility given the predicted substantial loss of genetic diversity and the documentation of father-daughter, grandfather-granddaughter, and grandmother-grandson inbreeding within the population (*e.g.*, Riley et al. 2014)[3], population growth will likely decline and chances of extinction within 50 years is predicted to be 99.7%, with a median time to extinction of 15.1 years (Benson et al. 2016a; Benson et al. 2019).

2.2.5 Santa Ana Mountains (SAM) Mountain Lion Population

The SAM mountain lion population has been found to have the lowest genetic diversity of all populations in California, with levels nearly as low as the endangered Florida panther (Ernest et al. 2014; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). This population is also estimated to have a low effective population size (N_e = 5.1 to 15.6) and high levels of relatedness and inbreeding (Ernest et al. 2014; Gustafson et al. 2018; Benson et al. 2019). The SAM population was found to be a genetic sink population, with limited gene flow with the EPR population (Gustafson et al. 2018). In a 16-year study (2001-2016) seven migrants (out of 146 sampled animals), were detected via genetics and GPS collar tracking to have crossed the I-15 between the EPR and SAM (three males from the EPR to SAM, four males from the SAM to the EPR); only one migrant is known to have reproduced (Gustafson et al. 2017). Low genetic diversity and effective population size in the SAM are indicative of a genetic bottleneck that is estimated to have occurred 40-80 years ago, around the time when urban development and multi-lane highway construction boomed in Southern California (Ernest et al. 2014; Gustafson et al. 2018). This population was also found to be largely disconnected from all the other California populations, along with the EPR population.

A recent population viability analysis found that if the population remains isolated with little or no immigration (similar to what is currently being observed in the area), the population could experience further genetic erosion, with 28-49% loss of predicted heterozygosity within 50 years (Benson et al. 2019). When considering just demographic processes with little or no immigration and no inbreeding depression, the population was predicted to have a 16-21% chance of extinction within 50 years. However, to avoid inbreeding depression in wild populations, loss in heterozygosity should be less than 5-10% over 100-200 years (Soule et al. 1986; Benson et al. 2016a), which suggests that inbreeding depression in the SAM population is

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[3] Inbreeding has been documented in the SMM population in Riley et al. 2014 and in ongoing studies by the NPS. More information from the NPS is available here: https://www.nps.gov/samo/learn/nature/puma-profiles.htm

a strong possibility. In addition, evidence of potential inbreeding depression has been observed in the population (*e.g.*, kinked tails coupled with low genetic diversity, Figure 2, Ernest et al. 2014). When inbreeding depression was considered in the population viability analysis, population growth will likely decline and chances of extinction within 50 years is predicted to be 100%, with a median time to extinction of 11.7 years (Benson et al. 2019).

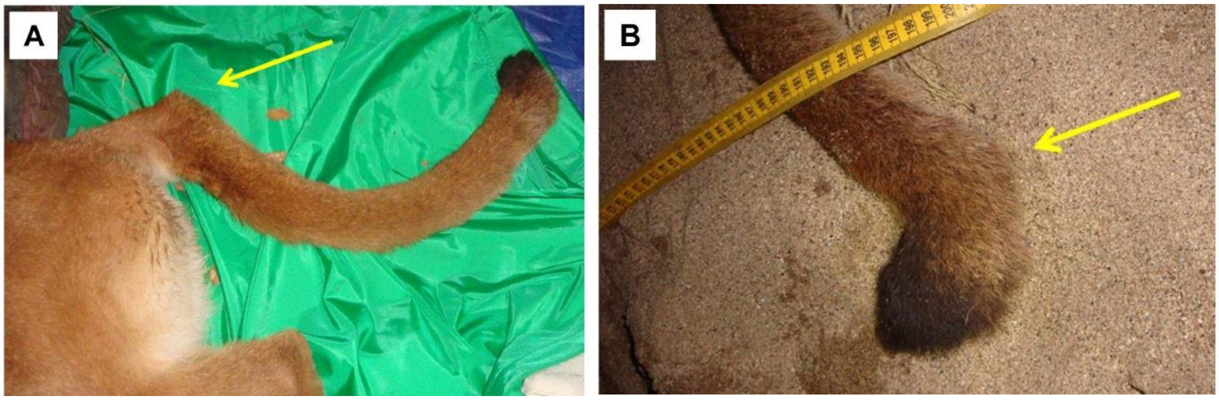

Figure 2. Two SAM mountain lions with a kink at the base of the tail (A) and near the tip of the tail (B). These individuals had among the lowest genetic diversity measured in the study. Source: Ernest et al. 2014.

2.2.6 San Gabriel/San Bernardino Mountains (SGSB) Mountain Lion Population

According to Gustafson et al. (2018), the SGSB mountain lion population exhibits extremely low genetic diversity and effective population size ($N_e = 5$), though the sample size from SGSB was low. They were also found to be a sink population, with limited gene flow with populations in the Western Sierra Nevada, CC-C, and the EPR (Gustafson et al. 2018). Although genetic studies on this population are limited, patterns of isolation, loss of genetic diversity, and low effective population size are similar to those of the SAM and CC-S populations and likely indicate a high risk of extinction. Not only is the population's long-term survival at stake, but the geographic location of the SGSB population is paramount. Despite only limited gene flow between the SGSB population and the Western Sierra Nevada, CC-C, and EPR, this population represents a critical linkage between mountain lion populations in the northern, central coast, and southern mountain ranges of California (Gustafson et al. 2018). Restoration and enhancement of connectivity is key for the continued survival of the SGSB population as well as the Central Coast and Southern California mountain lion populations.

2.2.7 Eastern Peninsular Range (EPR) Mountain Lion Population

Gustafson et al. (2018) found that the EPR population exhibits a prior genetic bottleneck. Although the population was found to have a higher effective population size than the other Southern California mountain lion populations ($N_e = 31.6$), this is still well below the older standard of 50 to prevent in-breeding depression in the short-term and is insufficient for the long-term persistence of the population. In addition, the EPR population was found to be largely disconnected from all the other California populations, with limited gene flow and low connectivity with the SAM and SGSB populations (Gustafson et al. 2018). With continued development in San Diego, Riverside, and Imperial Counties, the EPR population could have a similar fate of isolation, genetic drift and inbreeding, and risk of extinction as the other Central Coast and Southern California populations.

As mentioned previously, there are records for mountain lions outside of the core mountain ranges in Southern California, which are likely transients or residents of smaller populations. For example, the Yuma mountain lion has been recognized by CDFW as a subspecies of special concern, and likely occurs in low density in the desert plains and low mountains of the Colorado River Valley. Genetic studies on the Yuma mountain lion are limited, and no samples were obtained from that area for the study conducted by Gustafson et al. (2018). However, the low densities of transients and smaller populations in areas where roads and development threaten connectivity make them part of the EPR and larger Southern California population, and as such, they are considered a conservation concern and are included in this petition.

2.3 Reproduction and Growth

Dens are often in rocky outcrops (left) or in dense vegetation (right). Photos: NPS.

Mountain lions are polygamous breeders, and mates likely locate each other with auditory and olfactory signals (Currier 1983). They may reproduce at any time of year, though seasonal pulses have been documented and the timing of reproduction may be affected by prey abundance or climate (Pierce and Bleich 2003). In North America, kitten births are most common between April and September (Currier 1983; Beier 1995; Pierce and Bleich 2003).

Pairs generally mate for about 2-5 days (Beier et al. 1995), though there are instances in which pairs have been recorded traveling together for up to 16 days (Seidensticker et al. 1973). During this time they vocalize frequently, travel little, will sometimes share a kill, and copulate up to 70 times per day (Seidensticker et al. 1973; Beier et al. 1995; Pierce and Bleich 2003). Female estrous cycles last an estimated 4-12 days, and it is hypothesized that numerous acts of copulation stimulate ovulation and improve chances of successful fertilization (Pierce and Bleich 2003, Kitchener 1991). If the litter is born dead or removed within 24 hours of birth, females will go into estrous within a few weeks (Currier 1983). In addition, competing males have been known to commit infanticide[4], presumably to trigger estrous in females, though scientists are still investigating what drives this behavior.

Gestation lasts 82-96 days (Young and Goldman 1946; Currier 1983). Litter size ranges from 1-6, though 2-4 kittens per litter are typical (Pierce and Bleich 2003; Beier et al 2010; Riley et al. 2014). Females average larger litters during their first year of reproduction and tend towards smaller litters when they are older (Pierce and Bleich 2003). The sex ratio of litters has generally been found to be equal (Pierce and Bleich 2003). Females keep their kittens in dens located in rocky terrain or in dense vegetation that provide cover (Young and Goldman 1946), and they may move their young to several different dens until the young are weaned at about 2-3 months old (Pierce and Bleich 2003). Denning mountain lions have been found to avoid roads and stay at a distance from human disturbance four times greater (~600m) than non-reproductive mountain lions (~150m) (Wilmers et al. 2013).

Females care for their young for 1-2 years, at which point the mother comes into estrous and either abandons the cubs or acts aggressively towards them to prevent them from following her, as older males will kill cubs (Young and Goldman 1946; Seidensticker et al. 1973; Currier 1983; Beier 1995; Pierce and Bleich 2003). Newly independent young have been found to stay in the area where the mother leaves them for 2-3 weeks, and then disperse away from the direction their mother left (Beier 1995). Typically 50% of females stay in their natal range and 50% disperse while all males disperse, and siblings sometimes travel for a short time together (Pierce and Bleich 2003; Logan and Sweanor 2010). Subadult mountain lions may disperse up to 500km from their natal home ranges as they explore and establish their own territories (Pierce and Bleich 2003).

Mountain lions reach sexual maturity at 2-4 years of age. Although they are rarely known to mate until they have an established home range, transient males may occasionally breed with resident females (Hornocker 1970; Seidensticker et al. 1973; Currier 1983).

2.4 Diet and Foraging Ecology

Mountain lion cub feasting on a deer kill in the Santa Monica Mountains. Photo: NPS.

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[4] Infanticide has been documented in the Santa Monica Mountains mountain lion population. More information from the NPS is available here: https://www.nps.gov/samo/learn/nature/puma-profiles.htm

Large ungulates, especially deer, are the preferred prey of mountain lions, making up about 70% of their diet (Currier 1983; Iriarte et al. 1990). Hornocker (1970) estimated that the average adult mountain lion consumes 860-1,300kg of large prey annually. However, mountain lions are opportunistic predators, and they have been documented eating a wide variety of other large and smaller prey, including moose, elk, wild horses, burros, pronghorn, bighorn sheep, mountain goats, wild hogs, coyotes, bobcats, porcupines, badgers, rabbits, raccoons, rodents, turkeys, and livestock (Currier 1983; Iriarte et al. 1990; Garcelon unpublished data).

Their diet can vary by prey availability, prey vulnerability, the presence of sympatric carnivores, the season, and the age and sex of the mountain lion (Currier 1983; Iriarte et al. 1990; Knopff et al. 2010; Allen et al. 2014a). For example, deer have been found to make up >90% of the diet in mountain lions in the Santa Monica Mountains and in Northern California (Allen et al. 2014a; Riley et al. 2014), while in Florida wild hogs were found to be the most common prey (Maehr et al. 1990), and in northwestern Sonora, Mexico bighorn sheep were found to be the primary prey (Rosas-Rosas et al. 2003). These observed patterns were likely due to the availability of different prey in different geographic regions. A study conducted in Alberta, Canada, Knopff et al. (2010) found that while adult females were more likely to kill small ungulates (*e.g*., deer), adult males were more likely to kill larger ungulates (*e.g*., elk), and subadults relied on both small ungulates and nonungulate prey (*e.g*., beavers, snow hares). A similar pattern was found in a mountain lion population in the Greater Yellowstone Ecosystem, in which older, larger individuals hunted larger prey and younger, smaller individuals hunted smaller prey (Elbroch and Quigley 2019). In addition, mountain lions were found to prey upon female ungulates in the spring before and during the birthing period, and they would more often prey upon male ungulates in the fall during the rut, highlighting that prey vulnerability may play a role in mountain lion predation (Knopff et al. 2010).

Mountain lion preying on a coyote in Joshua Tree, California. Photo: Brendan Cummings

Mountain lions roam through expansive home ranges in search of prey, often hunting between dusk and dawn. Although they are generally most active at dusk and dawn, their peak activities have been observed to shift to more nocturnal patterns when they are closer to human disturbance (Van Dyke et al. 1986). Mountain lions are primarily solitary animals and will repeatedly move and wait as they stalk and ambush their prey (Beier et al. 1995). Once within close proximity, mountain lions will lunge at their prey and kill the animal by crushing the trachea and suffocating it or by breaking its neck at the base of the skull with a bite (Currier 1983; Pierce and Bleich 2003). Instead of eating their kill right away, mountain lions drag their kill to a secluded spot to feed. They cover it with brush and other debris and return to feed at night for up to five days (Currier 1983; Beier et al. 1995). However, the presence or perceived presence of humans has been found to reduce overall feeding time (Smith et al. 2015; Smith et al. 2017).

Deer kill rates vary depending on the sex of the mountain lion, whether or not the female has cubs, and surrounding human land use. Male kill rates have been found to range from 35 to 47 ungulates per year, regardless of housing density (Anderson , Jr . and Lindzey 2003; Cooley et al. 2008; Knopff et al. 2010; Smith et al. 2015). However, kill rates for females differ depending on human disturbance. In lower density housing areas, kill rates of solitary females and females with kittens have been found to be 52-60 and 57-68 ungulates per year, respectively, while females in high density housing areas were found to have a kill rate of 81 ungulates per year (Anderson , Jr . and Lindzey 2003; Cooley et al. 2008; Knopff et al. 2010; Smith et al. 2015). This pattern could be driven by reduced time spent at kill sites in more developed areas, indicating that females are not consuming as much of each carcass and therefore need to kill more prey (Smith et al. 2015). This may reflect a trade-off made by females to choose feeding sites closer to human-disturbed areas and expend more energy killing prey in order to reduce potential encounters with males that pose a threat to themselves or their kittens (Benson et al. 2016b). Another factor that may be contributing to higher kill rates in developed areas is that mountain lions expend more energy traveling faster and farther in human-dominated landscapes and therefore require increased caloric intake compared to mountain lions away from developed areas (Wang et al. 2017).

2.5 Habitat Requirements

Mountain lions are primarily solitary (except in certain situations, such as when breeding, when females are rearing cubs, or when dispersing with siblings), territorial cats that occur in low density. They require large areas of relatively undisturbed habitats with adequate connectivity to allow for dispersal and gene flow. They have large home ranges that include heterogenous habitats. In the United States these often consist of pine forests, riparian and oak woodlands, streams, chaparral, and grasslands, though they are also known to occur in desert habitats (*e.g.*, Figure 3).

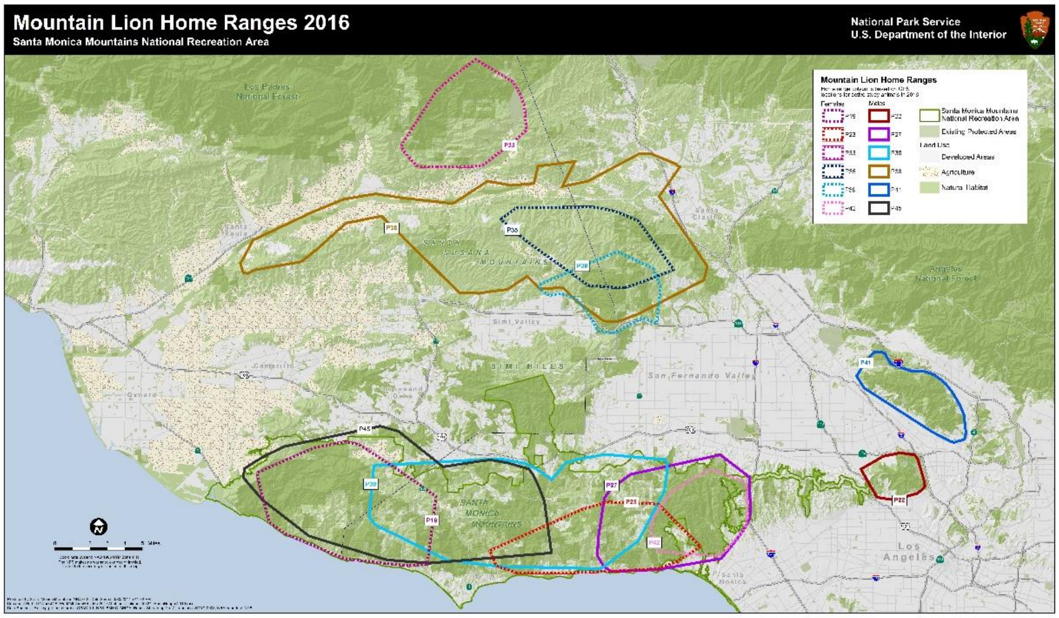

Figure 3. Home ranges of mountain lions being actively studied in 2016 by NPS in and near the Santa Monica Mountains. Source: NPS.

Mountain lions have been found to utilize different habitats within a 24-hour period (Dickson and Beier 2002; Dickson et al. 2005; Dickson and Beier 2006; Kertson et al. 2011; Zeller et al. 2017). Riparian habitats were found to be preferred over grasslands and human-disturbed areas during the day, which likely represents the animals resting in areas with understory vegetation for cover (Dickson and Beier 2002; Dickson et al. 2005). However, nocturnal movement patterns showed that mountain lions utilize a broad range of habitats as they travel through their home ranges and hunt (Dickson et al. 2005). Although riparian vegetation was the highest ranked habitat for nocturnal use, usage of riparian areas was not statistically different from the use of scrub, chaparral, grasslands, or woodlands (Dickson et al. 2005).

Nocturnal patterns of movement and stasis suggest that mountain lions generally avoid areas with human disturbance (*i.e.*, residential developments and two-lane paved roads) and use a variety of habitats to stalk and pursue their prey (Dickson and Beier 2002; Dickson et al. 2005). In addition, Dickson and Beier (2006) found that when mountain lions were traveling or hunting, they preferred canyon bottoms and gentle slopes and used steeper slopes and ridgelines to a lesser extent. And Benson et al. (2016b) found that mountain lions tend to choose feeding sites on steeper slopes in habitats with dense understory vegetation, such as chaparral, scrub, and upland forest. Although mountain lions will use moderately disturbed areas as they travel and hunt (Wilmers et al. 2013; Gray et al. 2016), occupancy is lower in developed areas and they are more likely to use developed areas if they border open spaces (Wang et al. 2015). Thus, mountain lions require a habitat mosaic that provides sufficient room to roam away from human-disturbed areas and connected to expansive, intact, heterogeneous habitats (Beier 1995; Dickson and Beier 2002; Dickson et al. 2005; Kertson et al. 2011; Zeller et al. 2017).

Home range size can vary depending on geographic area, season, sex, reproductive status, and prey density (Currier 1983; Grigione et al. 2002; Riley et al. 2014). Males generally have much larger home ranges than females, and females with cubs tend to have even smaller home ranges (Beier et al. 1995; Grigione et al. 2002). Male home ranges tend to include partially or entirely overlapping female home ranges, and to a limited extent, they may partially overlap with other male home ranges (Figure 3) (Seidensticker et al. 1973; Currier 1983; Pierce and Bleich 2003). Mountain lions mark their home ranges with scrapings in the ground, often containing urine or feces (Seidensticker et al. 1973). Males make scrapings more often than females (Allen et al. 2014b), and females may only make scrapings when they are in estrous (Seidensticker et al. 1973; Currier 1983; Pierce and Bleich 2003).

Seasonal variation in home range size can differ depending on geographic area. Grigione et al. (2002), found strong influences of seasonality in average mountain lion home ranges in the Sierra Nevada mountains, with much larger home ranges in the summer (541km^2 for females, 723km^2 for males) compared to those in the winter (349km^2 for females, 569km^2 for males). These patterns likely reflect the abundance and distribution of deer – during the winter deer would be concentrated at lower elevations, which allowed mountain lions to reduce their home ranges, while in the summer deer could disperse to higher elevations and the mountain lions would expand their ranges accordingly (Grigione et al. 2002). However, seasonal variation was not as pronounced and had the reverse trend in Coastal California mountain ranges, including in the SAM, where the average area of winter home ranges was slightly larger (100km^2 for females, 350km^2 for males) than summer home ranges (90km^2 for females, 300km^2 for males) (Grigione et al. 2002). These differences were not statistically significant, and this pattern is likely due to the moderate year-round climate in the coastal ranges, where prey abundance and distribution does not exhibit as extreme shifts as those in the Sierra Nevada (Grigione et al. 2002). This generally aligns with Zeller et al. (2017), who found that mountain lion home ranges in the SAM and EPR ranged from 41-497 km^2, with mean home range sizes of 188km^2 for females and 316 km^2 for males. And Riley et al. (2014) found that CC-S mountain lions had home ranges similar in size to the SAM and EPR mountain lions, with female home ranges being 100-200km^2 and male home ranges being 300-500 km^2. According to the Santa Cruz Puma Project, in the Santa Cruz Mountains female home ranges are on average about 100 km^2 and male home ranges are about 230 km^2 (Santa Cruz Puma Project 2015). Although studies are limited regarding the home range size of the CC-C and SGSB mountain lions, given their close proximity and similar seasonality to other Central Coast and Southern California populations, they are likely similar.

2.6 Survivorship and Mortality

According to the National Park Service (NPS), mountain lions can live up to 13 years in the wild. As a top carnivore with no natural predators, conspecifics and humans are the main drivers of mountain lion survivorship and mortality. Although studies regarding kitten (<18 months), subadult (18-30 months), and adult (>30 months) survivorship are limited, some long-term studies of radio-collared mountain lions on the CC-S, SAM, and EPR provide valuable insights for these Central Coast and Southern California populations (Beier and Barrett 1993; Riley et al. 2014; Vickers et al. 2015).

In a study conducted in the CC-S area (which encompasses the Santa Monica Mountains, Simi Hills, and Santa Susana Mountains) that included 42 mountain lions from 2002 to 2012, Riley et al. (2014) found an annual adult survival of ≥ 75%, though Benson et al. (2016a) found lower subadult survival rates. Although adult survival in the CC-S is similar to previous studies conducted in California and the southwestern US (Beier 1993; Logan and Sweanor 2001), it is higher than what was found in the SAM and EPR populations during the same time period. From following 74 radio-collared mountain lions from 2001 to 2013, Vickers et al. (2015) found an annual survival rate across all age groups of 56.5% and 55.4% in the SAM and EPR, respectively.

In the Santa Monica Mountains: Female mountain lion P-23 hunted down a deer on Mulholland Drive (left). In 2018 she was killed by a vehicle strike on Malibu Canyon Road. An uncollared mountain lion killed by a vehicle strike on Malibu Canyon Road in 2004 (right). Photos: NPS

Vehicle strikes, depredation kills, and intraspecific strife (including male aggression towards conspecifics and infanticide) are the primary causes of mortality in the Central Coast and Southern California populations (Beier 1993; Riley et al. 2014; Vickers et al. 2015). Other known causes of death in California mountain lion populations include rodenticide poisoning, disease, poaching/illegally killing, starvation/abandonment, public safety removal, and human-caused wildfires (Beier 1993; Riley et al. 2014; Vickers et al. 2015). Causes of mortality will be discussed more in depth in *Section 5.0 Abundance and Population Trends* and *Section 6.0 Factors Affecting Ability to Survive and Reproduce*.

3 Southern California and Central Coast Mountain Lions Comprise an Evolutionarily Significant Unit

3.1 CESA Provides for Listing of ESUs

CESA defines an “endangered species” as a species or subspecies of animal or plant that is in serious danger of becoming extinct through either all or “a significant portion” of its range. (Cal. Fish & Game Code § 2062.) A “threatened species” is likely to become an endangered species in the foreseeable future in the absence of special protection and management efforts. (Cal. Fish & Game Code § 2067.) CDFW has concluded—and appellate courts have upheld—that the term “range” is construed to refer to the range of a species or subspecies *within* California, not the worldwide range of the species or subspecies. (*California Forestry Assn. v. California Fish & Game Com.* (2007) 156 Cal.App.4th 1535, 1550-551.) This means that a species or subspecies which may not be endangered in other states or countries may still be endangered within California. Courts also have confirmed that the phrase “significant portion” of a range authorizes CDFW to designate certain populations of a species or subspecies as "evolutionarily significant units" or "ESUs" and list such populations as endangered under CESA. (*Id.* at 1549; *Central Coast Forest Assn. v. Fish & Game Com.* (2018) 18 Cal.App.5th 1191, 1236-37 [*"CCFA II*"].) In other words, ESUs are a population of a species or subspecies "that is considered distinct for purposes of conservation." (*Central Coast Forest Assn. v. Fish & Game Com*. (2012) 211 Cal.App.4th 1433, 1439 fn 5 [depublished] ["*CCFA I*"].)

CDFW has confirmed that the use of ESUs to evaluate the status of species pursuant to CESA is appropriate.[5] In the *Status Review of Fisher*, CDFW designated fishers in northern California and the southern Sierra Nevada as two separate ESUs based upon the reproductive isolation of these fisher populations and the degree of genetic differentiation between them. In designating these ESUs, CDFW highlighted the need to maintain "geographically widespread and genetically diverse" populations of the species.

3.2 Southern California and Central Coast Mountain Lions are Significantly Reproductively Isolated from Other Populations and Form an ESU

Southern California and Central Coast mountain lion populations could be grouped into one or several potential ESUs. However, petitioners believe that for purposes of listing under CESA, treating the CC-N, CC-C, CC-S, SAM, SGSB, and EPR populations as a single Southern California/Central Coast ESU is both supported by the best available science and makes sense from a management perspective. Gustafson et al. (2018) suggest that the North Coast and inland populations (Nevada, Eastern Sierra Nevada, and Western Sierra Nevada) may form an ESU (hereinafter "North Coast/Inland ESU") given that they were found to be genetically diverse and well-connected. Due to extreme isolation and high levels of human-caused mortalities, functional connectivity between Southern California and Central Coast mountain lion populations and the healthier North Coast/Inland ESU has become severely impaired (Gustafson et al. 2018, see further discussion in *Section 2.2 Taxonomy and Population Genetics* and *Section 6.0 Factors Affecting Ability to Survive and Reproduce*). There is a tenuous link made up of small mountain ranges (*i.e*., Tehachapi and Sierra Pelona Mountains) that connect the North Coast/Inland ESU with the proposed Southern California/Central Coast ESU. Thus, although there is some (limited) connectivity between the North Coast/Inland ESU and the proposed ESU, as a practical matter under current management the two ESUs are functionally isolated.

Southern California and Central Coast populations have lower levels of genetic diversity and are relatively disconnected from each other compared to North Coast and inland populations. The Central Coast populations form a genetic cluster while the SAM and EPR populations form a second, less connected genetic cluster (Figure 4) (Gustafson et al. 2018). The SGSB population, though isolated, is most genetically similar to the Western Sierra Nevada, CC-C, and EPR populations, which indicates that it is an important intersection for statewide genetic connectivity (Figure 4) (Gustafson et al. 2018).

Genetic source-sink dynamics are informative in determining gene flow among the populations and how they are connected. Five genetic source populations were identified: the

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[5] California Department of Fish and Wildlife, *Status Review of Fisher* (June 10, 2015), available at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=101470.

Eastern and Western Sierra Nevada populations, CC-N, CC-C, and EPR (Gustafson et al. 2018). The Sierra Nevada populations were the greatest genetic source populations and the CC-N population had only weak evidence of being a source population (Gustafson et al. 2018). The CC-S, SGSB, and SAM were identified as genetic sink populations with limited connectivity to source populations (Figure 4) (Gustafson et al. 2018). Maintaining and reestablishing genetic connectivity with source populations like the CC-C, EPR, and Western Sierra Nevada populations are important for the long-term viability of Southern California and Central Coast populations (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gray et al. 2016; Gustafson et al. 2017). This underscores the importance of the Tehachapi and Sierra Pelona Mountains as the key remaining linkage, though tenuous, for statewide genetic connectivity.

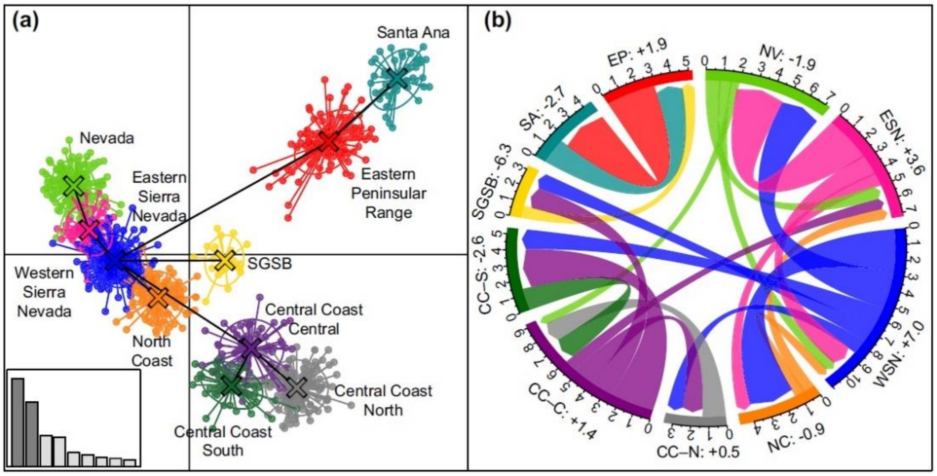

Figure 4. Functional connectedness of California mountain lion populations. Each color represents a genetically distinct population. In (a), the results of the discriminant analysis of principal components shows connectivity among California mountain lions. The x-axis represents latitude with north to the left and south to the right. The y-axis represents longitude, separating the Central Coast populations from Southern California populations. In (b), estimated migration rates between populations are shown. Source-sink dynamics are indicated by positive (source) or negative (sink) net migration rates. Source: Gustafson et al. (2018).

While genetics as currently understood could support several different ESU formulations, petitioners believe a single Southern California/Central Coast ESU is the most pragmatic from a management perspective, as recovery of the individual subpopulations ultimately depends upon maintaining and/or reestablishing connectivity between them. *See CCFA II,* 18 Cal.App.5th 1191, 1237 ("[T]he nature of the ESU designation is such that genetics alone are not determinative: One must look beyond genetics to questions of policy to determine which populations to include in an ESU.") (quotations omitted). Designating Southern California and Central Coast mountain lions as an ESU would help ensure "geographically widespread and genetically diverse" populations of mountain lions in California.

While petitioners believe that listing of a single Southern California/Central Coast ESU as threatened is both a permissible and prudent course of action for the Commission, petitioners also request that as additional data become available over the course of CDFW conducting its status review that the agency also assess other possible ESU formulations for Southern California and Central Coast mountain lions. One such formulation would be to group all three Central Coast populations (CC-N, CC-C and CC-S) into one ESU, with the remaining three populations placed into a second ESU (SAM, EPR and SGSB). Alternatively, the Central Coast populations could be treated as one ESU, SAM and EPR as a second ESU, and SGSB separately listed as a third ESU. Petitioners believe the genetic data in Gustafson et al. (2018) could support each of these alternative formulations. Lastly, given each of the six populations at issue are themselves already genetically distinguishable and occupy significant portions of the range of mountain lions in California, each could be separately treated as an ESU. Under this formulation, the SAM and CC-S populations would clearly warrant endangered listing, the CC-C and EPR populations would warrant threatened listing, and the CC-N and SGSB populations would warrant at least threatened and likely endangered listing.

3.3 Proposed Boundary of the Southern California/Central Coast ESU

We propose the Southern California/Central Coast ESU to include mountain lions that occur in areas east of the Pacific Ocean, south of the San Francisco Bay Area waters and I-80, west of I-5 to the intersection of I-5 and SR-58 at Bowerbank/Buttonwillow, south of SR-58 to I-15, south of the I-15 from the SR-58 intersection to the California-Nevada border, and, for the purposes of CESA, north of the California-Mexico border (Figure 5). These boundaries are recommended as they include virtually all mountain lions associated with the six populations comprising the ESU and are also unambiguous and readily discernable for purposes of management.[6]

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[6] In the event the Commission determines that the proposed ESU should instead be treated as separate Southern California (SAM, EPR, SGSB) and Central Coast (CS-N, CS-C, CS-S) ESUs, we propose the boundary between them to be delimited by I-5 and I-710.

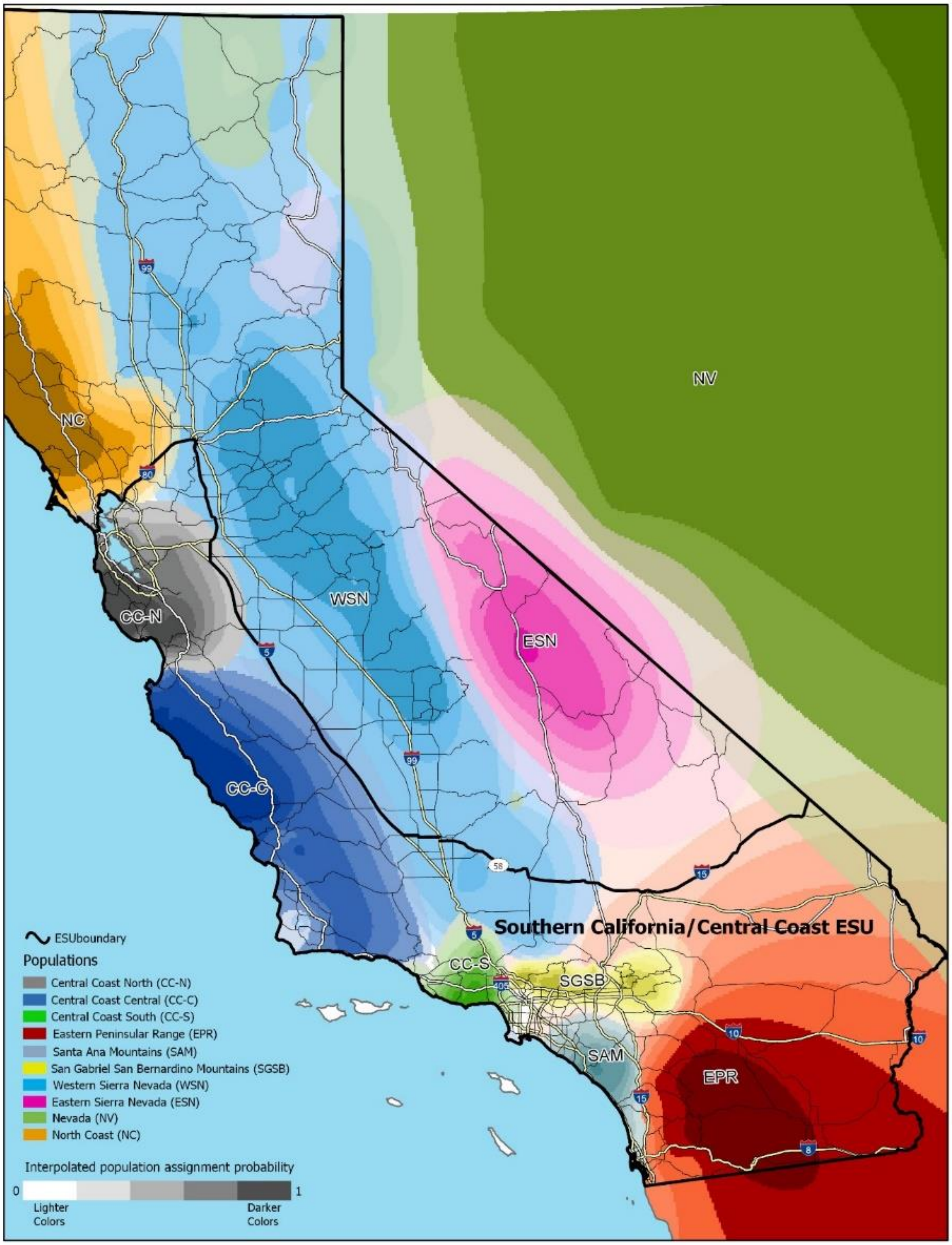

Figure 5. Map of the Southern California/Central Coast ESU boundary. Derived from Gustafson et al. (2018). Genetics data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie. Roads data source: ESRI.

We recommend including mountain lions in the Tehachapi and Sierra Pelona Mountains south of SR-58 in the Southern California/Central Coast ESU. While most mountain lions sampled from this region share some genetic affinities with Western Sierra Nevada (WSN) animals, individuals sampled in the Tehachapi Mountains and surrounding areas, including the Sierra Pelona Mountains in the Angeles National Forest and the Los Padres National Forest, had genetic structures made up of multiple genetic populations from the northern, central coastal, and southern populations (Figure 6). This area serves not just as a connecting link between mountain lion populations comprising the Southern California/Central Coast ESU, but also between this ESU and all other California mountain lions. The Tehachapi and Sierra Pelona Mountains are the last remaining linkages for statewide genetic connectivity and are critical for the overall genetic health of Southern California and Central Coast mountain lions. Consequently, mountain lions in these areas should be considered part of the listed entity.

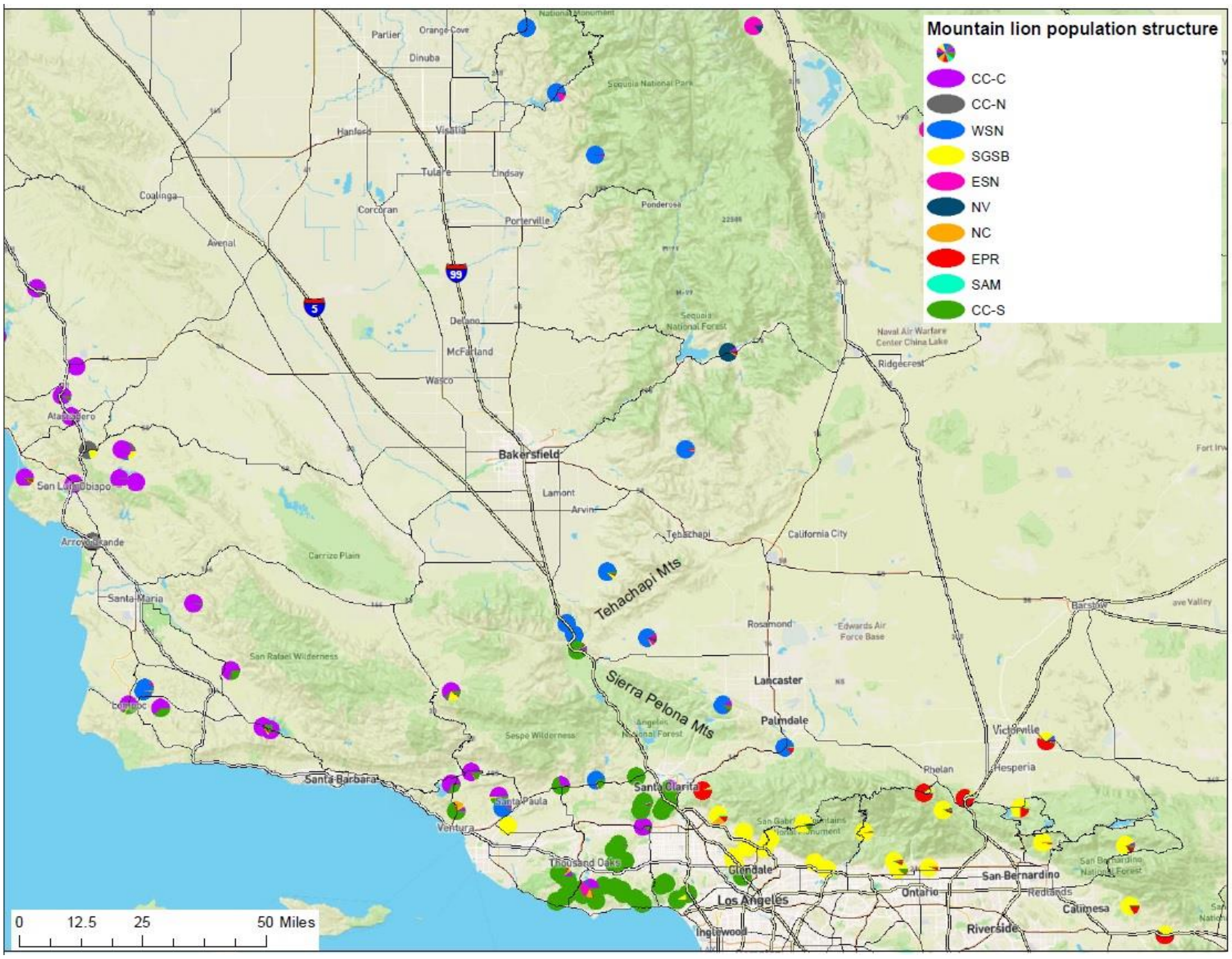

Figure 6. Map of mountain lion genetic structure in and surrounding the Tehachapi and Sierra Pelona Mountains, the last remaining linkage between the coastal, southern, and northern populations. Data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie.

3.4 Southern California and Central Coast Mountains Lions are Essential to the Region's Biodiversity

Additional support for designation of a Southern California/Central Coast ESU is provided by the fact that mountain lions are a keystone species critical to maintaining biodiversity in coastal California's ecosystems. The loss of these mountain lions—which are the only remaining large predator in the region—would lead to a trophic cascade wherein deer populations would increase and overgraze vegetation due to the lack of predation and lack of risk of predation, causing other repercussions to other species and habitats (Ripple and Beschta 2006; Ripple and Beschta 2008; Ripple et al. 2014). In addition, their kills are an important source of food for multiple terrestrial and avian scavengers (Ruth and Elbroch 2014; Elbroch et al. 2017; Barry et al. 2019).

Ripple and Beschta (2006) highlighted the critical role of mountain lions in western ecosystems by comparing habitat quality and the levels of biodiversity in two separate areas of Zion National Park – Zion Canyon, which mountain lions generally avoid due to high human presence, and North Creek, which mountain lions inhabit due to less human presence. The sustained lack of mountain lions in Zion Canyon has led to an unnaturally high density of deer, which has had profound impacts on Zion Canyon ecosystems. Ripple and Beschta (2006) observed Zion Canyon had low numbers of hydrophytic plants, wildflowers, amphibians, lizards, and butterflies while North Creek had significantly higher numbers in each of these categories.

North Creek riparian areas had well vegetated and stable banks while Zion Canyon lacked bank vegetation and its banks were continuing to erode (Ripple and Beschta 2006). The study noted that such geomorphic transformation of stream channels where mountain lions were absent were caused by plant loss on stream banks, which led to high levels of erosion and sedimentation, less shading and higher water temperatures, a larger width:depth ratio in streams, loss of hydrologic connectivity with historical floodplains, and loss of a wide variety of species, including native plants, benthic invertebrates, butterflies, fish, amphibians, and reptiles (Ripple and Beschta 2006).

The study concluded that removing a large carnivore from an ecosystem "appears to have [] profound effects on lower trophic levels, as well as multiple indicators of ecosystem status and native species abundance." (Ripple and Beschta 2006.) A similar study found that in Yosemite Valley—where mountain lions are largely absent due to high human presence—deer populations have expanded leading to a lack of oak recruitment and a decrease in biodiversity (Ripple and Beschta 2008). And their kills support disproportionately high levels of mammal, bird, and invertebrate diversity (Ruth and Elbroch 2014; Elbroch et al. 2017; Barry et al. 2019) and may even play a role in tree and other vegetation growth (Ruth and Elbroch 2014). In sum, extinction of Southern California and Central Coast mountain lions would result in degraded habitats and reduced abundance and diversity of other species, likely undermining the biological diversity, ecosystem function, and resilience of California's coastal regions.

3.5 Californians Derive Aesthetic, Recreational, and Economic Value from Southern California and Central Coast Mountain Lions

The people of California derive aesthetic, recreational, economic, spiritual, scientific, educational, and emotional value from Southern California and Central Coast mountain lions. For instance, the City of Los Angeles has designated October 22 as "P-22 day" to honor a young (and mate-less) male mountain lion that lives in Griffith Park and to acknowledge the importance of Southern California mountain lions to the region. Many people view mountain lions as a symbol of wildness and cherish landscapes that still are home to these predators. People from within and beyond the region choose to recreate, hike, bike, camp, fish, and hunt in California's wildlands in part because they enjoy exploring and sharing landscapes with mountain lions. And these activities are a significant economic driver for the state: A report commissioned for California State Parks found that direct outdoor recreation expenditures for Los Angeles, Southern California, the Central Coast and the San Francisco Bay Area totaled nearly $15 billion per year.[7] The Outdoor Industry Association concluded that outdoor recreation in California generates $92 billion of consumer spending annually and directly employs 691,000 Californians—more jobs than the wine and television industry combined.[8]

Mountain lions also provide an economic and social benefit because, by controlling deer populations, they reduce collisions between deer and automobiles. There are 1.2 million deer-vehicle collisions in the United States per year, incurring an estimated $1.66 billion in damages, 29,000 injuries, and 200 deaths (Gilbert et al. 2016). Impacts of deer-vehicle collisions are particularly severe in the eastern United States where white-tailed deer are overabundant. Gilbert et al. (2016) determined that if mountain lions recolonized the eastern United States, their presence would result in a 22 percent decline in deer-vehicle collisions over thirty years.

It is estimated that 7,000 to 23,000 wildlife vehicle collisions have occurred annually on California roads (Shilling et al. 2017; Shilling et al. 2018; State Farm Insurance Company 2016, 2018). These crashes result in human loss of life, injuries, emotional trauma, and property damages that can add up to $300-600 million per year (Shilling et al. 2018). If Southern California and Central Coast mountain lions became extinct, there would likely be a significant increase in deer-vehicle collisions in the region, along with associated human fatalities, injuries, and property damage.

An overabundance of deer in the eastern United States is also linked to an increase in ticks, which has led to increased incidences of Lyme disease among humans (Telford 2017; Côté et al. 2004). Lyme disease is now the most common vector-borne illness in the United States, with over 30,000 cases per year, primarily in the eastern United States.[9] Increases in deer abundance and attendant increases in ticks and tick-borne disease among humans would be

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[7] BBC Research & Consulting, *California Outdoor Recreation Economic Study: Statewide Contribution and Benefits* (2010), available at https://www.parks.ca.gov/pages/795/files/ca%20outdoor%20rec%20econ%20study-statewide%2011-10-11%20for%20posting.pdf.

[8] Outdoor Industry Association, *California Recreation Report*, available at https://outdoorindustry.org/wp-content/uploads/2017/07/OIA_RecEcoState_CA.pdf.

[9] Centers for Disease Control and Prevention, *Lyme Disease Data and Surveillance*, available at https://www.cdc.gov/lyme/datasurveillance/index.html?CDC_AA_refVal=https%3A%2F%2Fwww.cdc.gov%2Flyme%2Fstats%2Findex.html.

expected if Southern California and Central Coast mountain lions became extinct. Loss of Southern California and Central Coast mountain lions would have far-reaching effects not only on California's ecology, but also on public health and the region's economy.

Protection of Southern California and Central Coast mountain lions under CESA would confirm that this species is a vital member of our ecosystems which is worthy of protection. Conservation of these mountain lions would provide compelling evidence that large carnivores and abundant human populations can co-exist, even in densely populated landscapes (Benson et al. 2019).

4 Historical and Current Distribution

Mountain lions once had the most expansive range of any New World terrestrial mammal (Seidensticker 1991). They roamed most of the Americas (excluding most of Alaska and the northern areas of Canada) from approximately 50º N to 50ºS latitude and could be found from sea level to about 4,000m elevation (Young and Goldman 1946, Pierce and Bleich 2003) in habitats varying from dense forests, to dry deserts, savannahs, and swamp lands.

Due to habitat loss and hunting after the arrival of European colonists, the mountain lion's current range has been reduced to one third of its historical range in North America (Figure 7) (Culver et al. 2000; Pierce and Bleich 2003). In the United States, the species' range has been reduced to 15 western states and a small remnant population in Florida (endangered Florida panthers [*Puma concolor coryi*]), with isolated animals occasionally appearing in additional states. Continued hunting pressure and changes in land management practices have pushed most populations into mountainous, relatively unpopulated areas, though isolated populations are known to occur in more urban areas (Currier 1983; Gustafson et al. 2018).

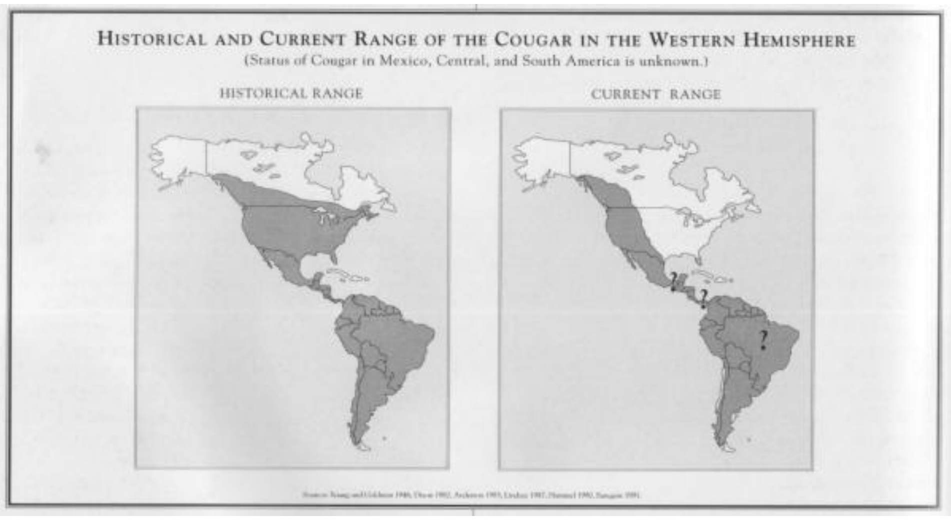

Figure 7. Historical and current range of mountain lions. Source: Hansen 1992.

In California, habitat fragmentation from roads and development has led to highly fragmented, divergent populations (Ernest et al. 2003; Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Gustafson et al. 2018). As mentioned in *Section 2.2 Taxonomy and Population Genetics*, nine genetically distinct populations have been identified within California

(Gustafson et al. 2018), with Southern California and Central Coast populations being the most constrained populations (and a tenth population centered in Nevada but extending slightly into California). Those located in highly urbanized areas of Southern California coastal mountain ranges, including the CC-S, SAM, and SGSB populations are especially restricted (Figure 8) (Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019).

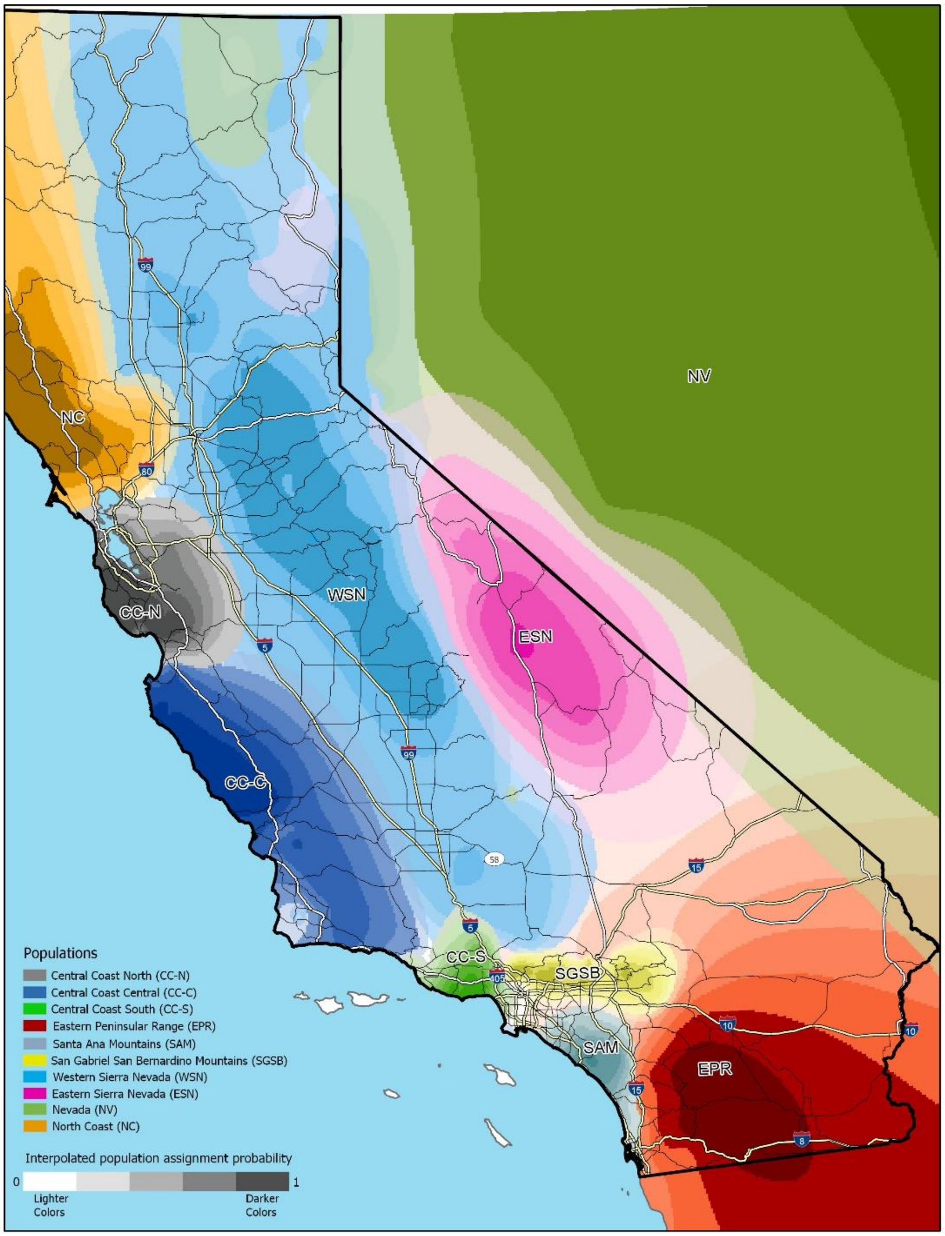

Figure 8. Map of genetically distinct mountain lion populations and major roads in California. The CC-S (which includes the Santa Monica Mountains), SGSB, and SAM populations are exceptionally constrained. The map is based on data collected from 1992-2016 (the division and status of these populations could change over time and with further research. Derived from Gustafson et al. (2018). Genetics data source: Kyle Gustafson, PhD, Department of Biology and Environmental Health, Missouri Southern State University, and Holly Ernest, DVM, PhD, Department of Veterinary Sciences, Program in Ecology, University of Wyoming, Laramie. Roads data source: ESRI.

4.1 Central Coast North (CC-N) Mountain Lion Population

The CC-N mountain lion population occurs mostly within the counties of Alameda, Contra Costa, San Mateo, Santa Clara, and Santa Cruz (Figure 8). The area is almost divided into two portions: an eastern half and a western half. The Santa Cruz Mountains make up the core area of the CC-N, bound by the Pacific Coast to the west, development lining the San Francisco Bay to the north and north west, and Highway 101 to the south. The eastern portion of the CC-N consists of various open space and nature preserves in the Berkeley Hills and Diablo Range bound by development lining the San Francisco Bay and Highway 101 and associated developments to the west, San Pablo Bay and Suisun Bay and associated developments to the north, I-5 to the east, and State Route 130 (SR-130) to the south. Interestingly, the CC-N seems almost bisected by the San Francisco Bay and Highway 101 and associated developments.

4.2 Central Coast Central (CC-C) Mountain Lion Population

The CC-C mountain lion population occurs mostly within the counties of Monterey, San Benito, San Luis Obispo, and Santa Barbara. The area encompasses the central and southern portions of the Southern Coast Ranges, including the Santa Lucia Range, Sierra de Salinas, the Temblor Range, and the Sierra Madre Mountains. It is bound by the Pacific Ocean to the west, Highway 101 and SR-156 and associated development to the north, the I-5 and San Joaquin Valley to the east, and SR-126 and associated developments to the south (Figure 8).

4.3 Central Coast South (CC-S) Mountain Lion Population

The CC-S mountain lion population is limited to the Santa Monica Mountains, Simi Hills, and the Santa Susana Mountains in Ventura and Los Angeles Counties (Figure 8). The Santa Monica Mountains population has the isolated area with about 660 km^2 within the Santa Monica Mountains National Recreation Area (Riley et al. 2014). The Pacific Ocean lies to the south while the cities of Oxnard, Thousand Oaks, San Fernando Valley, Los Angeles, and Santa Monica and major freeways including Highway 101, Interstate 5 (I-5) and Interstate 405 surround the area and create major movement barriers.

The Simi Hills is a smaller area of open space located north of the Santa Monica Mountains; the areas are bisected by Highway 101. This open space is mostly surrounded by development, including Simi Valley to the northwest, Thousand Oaks to the west, Agoura Hills to the southwest, Calabasas to the southeast, and Woodland Hills, Canoga Park, and Chatsworth to the east.

The Santa Susana Mountains are located north of the Santa Monica Mountains and Simi Hills. The area is generally bordered by freeways and the edges of development and agriculture. SR-118 borders the south and southwest, SR-126 borders the north and northwest, and I-5 borders the east.

4.4 San Gabriel/San Bernardino Mountains (SGSB) Mountain Lion Population

The SGSB mountain lion population occurs within the Transverse Ranges located northwest of the City of Los Angeles within Los Angeles, Kern, and San Bernardino Counties (Figure 8). The western and southern boundaries of the San Gabriel and San Bernardino Mountains are lined with urban developments and major freeways, including the San Fernando Valley, cities of San Bernardino, Rancho Cucamonga, and West Covina, and the I-5, I-210, and I-10 freeways. The northern and eastern boundaries of the area are abutted by agriculture, suburban development, high desert, and roads.

4.5 Santa Ana Mountains (SAM) Mountain Lion Population

The SAM mountain lion population inhabits about 1,533km^2 of undeveloped areas of the SAM within Orange, Riverside, and San Diego Counties (Beier and Barrett 1993; Benson et al. 2019). The area is mostly bound by major freeways and development (Figure 8). SR-241 creates the western boundary, SR-91 borders the northwest boundary, I-5 creates the eastern boundary, and agriculture and development border the southern extent. The closest intact habitat known to be used by other mountain lions is to the east/southeast, in the Peninsular Ranges.

4.6 Eastern Peninsular Range (EPR) Mountain Lion Population

The EPR mountain lion population occurs in mountain ranges east of the SAM and south of the San Bernardino Mountains. The EPR is a predominantly north to south range that runs through San Diego, Riverside, and Imperial Counties and the California-Mexico border. They include the San Jacinto, Laguna, and San Ysidro Mountains in California and continue south into the mountain ranges of Baja California, Mexico. The western boundary of the EPR population is lined with roads and urban development, including areas around the cities of Escondido, San Diego, and Chula Vista. Studies regarding the northern, southern, and eastern extent of the population are limited; however, movement patterns documented by Vickers et al. (2015) and Vickers et al. (2017) between 2001 and 2016 suggest that EPR mountain lions generally stay north of the U.S. – Mexico border, along the edges of the desert that borders the east side of the EPR, and south of I-10. Although the EPR population has been found to be largely disconnected from all other California populations, some mountain lion movement was documented traversing between the EPR and SGSB (Vickers et al. 2015), which would have occurred at the northern boundary of the EPR, and there is evidence of limited genetic exchange between the two populations (Gustafson et al. 2018). In addition, one young male mountain lion was documented to the south using the Parque-to-Park Linkage to cross the US-Mexico border several times (where the terrain is too rugged to install a border wall), but he was eventually killed in Mexico in a collision with a vehicle (Vickers et al. 2015; W. Vickers *unpublished data*). Little is known about the mountain lions south of the border, but the movement patterns of EPR mountain lions suggest that they may form a discrete population within the EPR north of the US-Mexico border (Vickers et al. 2015; Vickers et al. 2017).

5 Abundance and Population Trends

According to the International Union for Conservation of Nature (IUCN), mountain lion populations are decreasing throughout their remaining range (Nielsen et al. 2015). Mountain lion population densities are generally low, which may be driven by prey density, competition between males for access to females, and mutual avoidance (Pierce and Bleich 2003). In the United States, population densities for mountain lions have been found to range from 0.4 to 4.3 resident adults per 100km^2 and 0.4 to 7.1 total mountain lions per 100km^2, though it varies by population and the presence of human-induced pressures (*e.g.*, hunting) (Pierce and Bleich 2003). In California, where hunting has been outlawed but other anthropogenic pressures such as roads and development are present, resident adult and total population densities have been found to be 1.1 and 3.6 per 100 km^2, respectively (Pierce and Bleich 2003). Adult sex ratio has been reported to be about 2-3:1 in favor of females (Hornocker 1970; Seidensticker et al. 1973; Beier 1993; Santa Cruz Puma Project 2015). These low population densities and female-biased sex ratios further highlight the species' need for expansive, connected, heterogeneous habitats to support viable populations.

It has been estimated that 4,000 to 6,000 adult mountain lions roam California (Mansfield and Weaver 1989). However, CDFW acknowledges that this estimate from 1984 is outdated and relied on density estimates from regional studies to derive a statewide abundance. The agency has since declared that the number of mountain lions throughout the state is unknown, and they have embarked on an intensive statewide research project to better understand mountain lion numbers regionally and throughout the state.[10] Working with other agencies, academic institutions, and non-profits, CDFW plans to have statewide and region-specific mountain lion population estimates by 2022 (Vaughan 2018).

As mentioned in *Section 2.2 Taxonomy and Population Genetics*, one way in which the abundance of mountain lions can be estimated is with the ratio of effective to total adult population size (N_e/N) of 0.25 to 0.5, as was used by USFWS to generate an abundance estimate for the endangered Florida panther (Ballou et al. 1989; USFWS 2008). Using this method with the estimated effective population sizes of the nine genetically distinct mountain lion populations centered in California from Gustafson et al. (2018) and Benson et al. (2019), the statewide total population would be 818 to 1,634 individuals (255 to 510 in the Central Coast and Southern California populations [Table 1], and 563 to 1,124 in the remaining Eastern Sierra Nevada, Western Sierra Nevada, and North Coast populations), which is much lower than the 4,000 to 6,000 estimate. This is also well below the recommended minimum viable population size of at least 5,000 adult individuals for the long-term persistence of a population (Frankham 1995; Reed et al. 2003; Traill et al. 2010). Petitioners recognize that the N_e/N methodology has limitations and is but one method of generating an overall abundance estimate. More studies are needed to determine regional and statewide mountain lion abundance, including CDFW's ongoing efforts which should produce a more scientifically robust statewide abundance estimate.

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[10] CDFW 2018 - Commonly Asked Questions About Mountain Lions. Accessed on 11 April 2019 at: https://www.wildlife.ca.gov/Conservation/Mammals/Mountain-Lion/FAQ#359951241-how-many-mountain-lions-are-in-california

Despite unknown statewide population estimates, researchers have been closely tracking several of the Central Coast and Southern California populations. Through their published studies and reports they provide some insights regarding abundance and population trends for these populations.

5.1 Central Coast North (CC-N) Mountain Lion Population

Studies on the CC-N mountain lion population are limited, and abundance and population trends are unknown. However, with an effective population size of 16.6 (Gustafson et al. 2018), and an N_e/N of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 33 to 66 individuals (see Table 1). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, these numbers are grossly insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014).

Gustafson et al. (2018) found that this population has low genetic diversity and a low effective population size, which suggests that it is at increased risk of inbreeding depression within five generations and eventual extinction. Ongoing studies in the Santa Cruz Mountains highlight high levels of human-caused mortalities. Depredation kills are the leading cause of death in collared mountain lions in the Santa Cruz Mountains (Wang et al. 2017), and CDFW reported 34 depredation kills between 2010 and 2016 in the CC-N counties of Alameda, Contra Costa, San Mateo, Santa Clara, and Santa Cruz (see Appendix A[11]). In addition, at least six mountain lions have been killed by vehicle strikes on Highway 17 in the Santa Cruz Mountains between 2008 and 2018 (Midpensinsula Regional Open Space 2017; Slade 2018) and news outlets reported at least three mountain lions killed by vehicle strikes on the I-280 in San Mateo County between 2014 and 2016 (Wilmers 2014, CBS SF 2015, Kamala 2016). The poor genetic health of the CC-N population is likely due to habitat fragmentation and isolation caused by roads and development combined with high levels of human-caused mortalities. CDFW has identified the Santa Cruz Mountains population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019). Poor connectivity and continued development in the CC-N will likely lead to further isolation, increased human-caused mortalities, decreased genetic diversity, and increased risk of extinction in the foreseeable future.

5.2 Central Coast Central (CC-C) Mountain Lion Population

Studies on the CC-C mountain lion population are limited, and abundance and population trends are unknown. However, with an effective population size of 56.6 (Gustafson et al. 2018), and an N_e/N of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 113 to 226 individuals (see Table 1).

Although Gustafson et al. (2018) found that this population has intermediate levels of genetic diversity and the highest effective population size among the Central Coast and Southern

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[11] These data were downloaded from the CDFW website; however, they no longer appear to be available online. These numbers have been shown to be low by a factor of two in some areas, likely due to incomplete reporting, and therefore should be considered absolute minimums (W. Vickers, *pers comm*).

California mountain lion populations, with an effective population size of 56.6, it just barely exceeds the older standard of 50 to prevent inbreeding depression in the short-term (Frankham et al. 2014; Gustafson et al. 2018). In addition, it falls well below the recommended newer standard of 100 and is insufficient for the long-term viability of the population (Frankham et al. 2014). And the lack of sufficient protected lands and high rates of development in the area threaten the persistence of this population (Dellinger 2019). Thus, although the CC-C population appears to be the healthiest population in the Central Coast and Southern California, it is still at increased risk of inbreeding depression and extinction, and connectivity to smaller adjacent areas should be improved (Dellinger 2019).

5.3 Central Coast South (CC-S) Mountain Lion Population

The NPS has been studying the CC-S population since 2002, though most studies regarding population dynamics focus on the Santa Monica Mountains mountain lions (Riley et al. 2014; Benson et al. 2019). Since 2002, NPS has collected data from 55 mountain lions within the Santa Monica Mountains and 19 mountain lions from the Simi Hills and Santa Susana Mountains.[12] There are currently 20-25 live mountain lions being tracked in the Santa Monica Mountains, 7-12 of which are adults (born in 2014 or earlier, the status of 5 adults are unknown) and 13 of which are juveniles or subadults (born in 2015 or later).[13] Given that the Santa Monica Mountains area is relatively small, adult survival rate is high (≥ 75%), and juvenile/subadult survival is low due to intraspecific strife and the inability to disperse, the Santa Monica Mountains population is likely space-limited and these numbers may represent the Santa Monica Mountains' carrying capacity (Riley et al. 2014; Benson et al. 2019). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, the extremely low effective population size and total adult population size are grossly insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014). And CDFW has identified the CC-S population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019).

The long-term survival of the Santa Monica Mountains population is severely threatened due to extreme habitat fragmentation and isolation caused by surrounding roads and development that impede movement in or out of the area (Riley et al. 2014). Limited space and lack of connectivity with suitable mountain lion habitat inhibit dispersal for subadults and likely drive unusually high levels of intraspecific strife, which is the most common cause of mortalities in the

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[12] The NPS provides puma profiles (last updated August-November 2018) of the marked animals (*i.e.*, tagged or radio-collared) they have been studying in the CC-S, which includes those studied in Riley et al. (2014). Some data presented in this section take these data into account. Accessed on 3 April 2019 at: https://www.nps.gov/samo/learn/nature/puma-profiles.htm.

[13] The adult population in the Santa Monica Mountains is generally consistent with the estimated 0.25 to 0.5 N_e/N; the Santa Monica Mountains was estimated to have an effective population size of four (Benson et al. 2019), which would suggest a total adult population size of 8 to 16. Interestingly, Gustafson et al. (2018) estimated an effective population size of 2.7 for the greater CC-S population, which would indicate a total adult population of 5 to 10 individuals throughout the Santa Monica Mountains, Simi Hills, and Santa Susana Mountains (see Table 1). There are currently 10 to 17 adult mountain lions being tracked throughout the CC-S area, which would put their N_e/N ratio at 0.16 to 0.27, which is still within the range of other species' N_e/N ratios (Frankham et al. 1995; Ballou et al. 1989; Mace and Lande 1991; Spong et al. 2000; Laundré and Clark 2003).

area (Riley et al. 2014). Although intraspecific strife is known to occur among mountain lions, there have been multiple cases of aggressive adult males killing their siblings, female offspring, and previous mates documented in the Santa Monica Mountains population, and researchers noted that "clearly this is rarely a sound evolutionary strategy as the survivorship of offspring or siblings is traded against the probability of future reproduction" (Riley et al. 2014). For 23 radio-collared individuals within the Santa Monica Mountains for which the cause of death is known, nine deaths were the result of instraspecific strife. Eight of the nine deaths (89%) were of animals less than four years old. In addition, three uncollared mountain lions in the Santa Monica Mountains less than four years old were found dead by intraspecific strife, which brings the total to 12 deaths by intraspecific strife documented in the Santa Monica Mountains between 2002 and 2018.

Although all subadult males and half of subadult females typically disperse from their natal areas (Logan and Sweanor 2010), only one subadult successfully dispersed from the Santa Monica Mountains between 2002 to 2012 – P-22, the famous male mountain lion who successfully crossed Highway 101 and I-405 freeways and established his home range in Griffith Park (Riley et al. 2014). Unfortunately, P-22 is extremely isolated with the smallest home range ever reported for an adult male ($26km^2$), and he has not had any opportunities to mate (Riley et al. 2014). In addition, vehicle strikes account for 17% (4/23) of known radio-collared mountain lion deaths in the Santa Monica Mountains. According to the NPS, most males in the Santa Monica Mountains do not live past the age of two. Thus, many healthy, young animals are not able to disperse from the Santa Monica Mountains, establish their own home ranges, and successfully reproduce.

Conversely, lack of connectivity also inhibits migrants coming from outside the Santa Monica Mountains and contributing to the population's gene pool. Only two outside mountain lions have been known to immigrate into the Santa Monica Mountains since 2002: P12 (from Simi Hills, alive as of August 2018, age 12) and P45 (from north of Highway 101, status unknown, age would be 6-7 if alive). While there has been no sign of P-45 since February, 2019 and no offspring from him have been detected, P-12 has been fairly prolific in the Santa Monica Mountains, fathering at least eight litters. Although P-12's appearance initially improved genetic diversity in the Santa Monica Mountains population, consistent immigration in small populations is needed so that the genetic diversity gains of immigrant mountain lions are not lost (Riley et al. 2014; Benson et al. 2016a; Benson et al. 2019). Subsequent inbreeding by P-12 with his daughters and granddaughters and inbreeding already occurring with other breeding adults in the Santa Monica Mountains have led to dangerously low genetic diversity (Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). With continued isolation, inbreeding, and loss of genetic diversity, there is increasing risk of inbreeding depression and extinction. With inbreeding depression, the probability of extinction within 50 years is predicted to be 99.7 %, with a median time to extinction of 15.1 years (Benson et al. 2016a; Benson et al. 2019).

5.4 Santa Ana Mountains (SAM) Population

Restricted habitat availability and high mortality rates in the SAM likely limits population size, and Benson et al. (2019) estimated that the SAM population is likely comprised of 16 adults and 13 juveniles (kittens and subadults). These numbers are slightly lower than the 31 to 62 adult mountain lions estimated from the SAM population's effective population size of 15.6 (Gustafson et al. 2018) (see Table 1). According to (Benson et al. 2019), high levels of human-caused adult mortalities may limit growth potential in the SAM, and it is uncertain if the population could be larger without as many anthropogenic pressures. In fact, although hunting is illegal in California, mountain lions in Southern California have a lower annual survival than many hunted populations (Vickers 2014). Interestingly, other studies calculated a much lower effective population size of 5.1 (Ernest et al. 2014) and four (Benson et al. 2019), which would align with the suggested carrying capacity. Regardless of which effective population size is used, they are all well below the frequently-used threshold of 50 and insufficient to prevent inbreeding depression in the short-term.

Although population trends are unclear, two long-term studies on radio-collared mountain lions in the SAM provide some insight (Beier 1993; Vickers et al. 2015). In a study that consisted of 32 radio-collared animals in the SAM from 1988 to 1993, researchers found a 75% adult survival rate (Beier and Barrett 1993), which is similar to adult survival rates in other populations, like the CC-S population (Riley et al. 2014). However, in a second, more recent study conducted in the area consisting of 31 marked mountain lions from 2001 to 2013, researchers found a 56.5% survival rate across all sexes and age groups (Vickers et al. 2015). The marked decrease in adult survival rate between the two studies coincides with an increase in the proportion of mortalities caused by vehicle strikes, with the 1988-1993 and the 2001-2013 studies resulting in 32% (10/31) and 46% (6/13) of deaths caused by vehicle strikes, respectively (Beier 1993; Vickers et al. 2015). It also parallels an upward trend of mountain lion mortalities caused by vehicle strikes throughout Southern California over time (Vickers et al. 2015). Other causes of death in the SAM population included depredation kills, illegal killing, disease, intraspecific strife, and human-caused wildfires (Beier and Barrett 1993; Vickers et al. 2015). Depredation kills were found to be 3.4 times more likely with males compared to females (Vickers et al. 2015).

The SAM mountain lion population's high adult mortality rates combined with isolation, small size, low genetic diversity, low effective population size, and limited immigration of new individuals cause demographic instability and put the population at high risk of extinction (Beier 1993; Beier and Barrett 1993; Ernest et al. 2014; Vickers et al. 2015; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, the extremely low effective population size and total adult population size are insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014). Roads and development prevent dispersal and sustained immigration in the SAM, and lack of consistent gene flow has led to high levels of inter-relatedness and inbreeding (Ernest et al. 2014; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). Further genetic erosion is likely without improved connectivity to facilitate immigration (Benson et al. 2019). CDFW has identified the SAM population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019). If inbreeding depression occurs within this population, population growth will likely decline and the probability of extinction within 50 years is predicted to be 100%, with a median time to extinction of 11.7 years (Benson et al. 2019).

In 13 years, only one radio-collared individual crossed I-15, the major barrier between the SAM and the EPR, and that animal was killed 25 days after his crossing for depredating domestic sheep (Vickers et al. 2015). And although Gustafson et al. (2017) documented three males immigrating into the SAM from the EPR and four males emigrating from the SAM to the EPR over a 15-year period, only one of the males (M86, an immigrant to the SAM) is known to have successfully bred. While M86 improved the SAM population's genetic diversity (Gustafson et al. 2017), high levels of mortalities due to vehicle strikes and depredation/illegal killings likely reduce the number of immigrants that can successfully establish as breeding adults (Vickers et al. 2015). With high levels of adult mortalities due to vehicle strikes, depredation kills affecting 3.4 times more males than females, and a small population with a female-biased adult sex ratio, there is potential for occasional male extinction in the SAM, which could severely limit the short- and long-term viability of the population (Beier and Barrett 1993; Benson et al. 2019).

5.5 San Gabriel/San Bernardino Mountains (SGSB) Population

Studies on the SGSB mountain lion population are limited, and the abundance and population trends are unknown. However, with an effective population size of 5 (Gustafson et al. 2018), and an N_e/N of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 10 to 20 individuals (see Table 1). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, these numbers are grossly insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014). And CDFW has identified the SGSB population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019).

Although a population viability study has not been conducted for the SGSB population, given its low genetic diversity, low effective population size, and patterns of isolation due to roads and development creating movement barriers (Gustafson et al. 2018), the SGSB mountain lion population likely has high risk of inbreeding depression and extinction. The loss of this population could undermine genetic connectivity for mountain lions statewide because the SGSB population, along with the Tehachapi and Sierra Pelona Mountains, represents a critical linkage between mountain lion populations in the northern and southern mountain ranges of California (Gustafson et al. 2018). Restoration and enhancement of connectivity in the SGSB and surrounding mountain ranges are key for the continued survival of the SGSB population as well as all of the Central Coast and Southern California mountain lion populations.

5.6 Eastern Peninsular Range (EPR) Population

Studies on the EPR mountain lion population are limited and the abundance and population trends are unknown. However, with an effective population size of 31.6 (Benson et al. 2019), and an N_e/N of 0.25 to 0.5 (Ballou et al. 1989; USFWS 2008), the estimated total adult population would be 63 to 126 individuals (see Table 1). As mentioned previously in *Section 2.2 Taxonomy and Population Genetics*, these numbers are insufficient to prevent inbreeding depression in the short term or maintain evolutionary potential in the long term (Jamieson and Allendorf 2012; Frankham et al. 2014).

Vickers et al. (2015) followed 43 marked mountain lions in the EPR from 2001 to 2013, and their study provides some insight regarding survival rate and causes of mortality. Annual survival rate was found to be 55.4% in the EPR, which is similar to the SAM population (Vickers et al. 2015). The primary causes of death of marked mountain lions were depredation kills (26% [6/23]) and vehicle strikes (17% [4/23]). When assessing mountain lion death data from CDFW from 1981 to 2013, depredation and vehicle strikes accounted for about 70% of mountain lion deaths in the EPR: 40% (62/154) by depredation kills and 30% (46/154) by vehicle strikes (Vickers et al. 2015).

Although the EPR population was found to have the highest genetic diversity and effective population size among the Southern California mountain lion populations (Gustafson et al. 2018), movement and genetic studies have shown that the EPR population is largely disconnected from all other California populations (Ernest et al. 2014; Vickers et al. 2015; Vickers et al. 2017; Gustafson et al. 2018). And CDFW has identified the EPR population as at risk due to current habitat and genetic concerns, at-risk internal habitat and connectivity, limited external connectivity, and lack of protected habitat (Dellinger 2019). Thus, high human-caused mortality rates combined with continued development in San Diego, Riverside, and Imperial Counties could lead to further isolation, decreased genetic diversity, increased inbreeding depression, and increased risk of extinction.

6 Factors Affecting Ability to Survive and Reproduce

Female mountain lion, P-23, crossing a road in the Santa Monica Mountains. She was struck by a vehicle and found dead near Malibu Canyon Road in January 2018. Photo: NPS

Most, if not all, factors affecting the ability of the Southern California and Central Coast mountain lion populations to survive and reproduce are caused by humans. Lack of wildlife connectivity is the primary driver of their potential demise. Habitat loss and fragmentation due to roads and development have led to extreme levels of isolation and high mortality rates, which are driving these populations towards extinction. Continued development in current suitable mountain lion habitat further threatens these populations. With low genetic diversity and high risk of inbreeding depression due to genetic isolation, vehicle strikes on roads, increased conflicts with humans that lead to depredation kills, high levels of intraspecific strife likely due to limited space and lack of connectivity, rodenticide and other environmental toxicant poisoning, and impacts of more frequent wildfires and climate change, Southern California and Central Coast mountain lions will likely not persist unless there is a concerted effort to restore and enhance functional connectivity between populations and large blocks of heterogeneous habitats.

The populations in Southern California are especially vulnerable to extinction, which is reflected in a 2005 review conducted by the US Forest Service regarding Land Management Plans in the National Forests of Southern California that states the “greatest concern for the long-term health of mountain lion populations on the national forests of southern California is loss of landscape connectivity between mountain ranges and large blocks of open space on private land.”[14] The review emphasizes that continued development along with new and wider roads degrade habitat linkages and create movement barriers, and “[w]ithout the national forests and linkages between the mountain ranges and other large habitat preserves, there is not much long term potential for mountain lions in southern California.”

Ultimately, the persistence of mountain lions in the Central Coast and Southern California requires maintenance and restoration of connectivity between subpopulations and adequate habitat. The extreme isolation, dangerously low genetic diversity, high levels of inbreeding, and high rates of human-caused mortalities (*e.g.*, vehicle strikes, depredation kills, intra-specific strife due to limited space, rodenticide poisoning, etc.) underscore the urgent need for proactive measures to enhance connectivity (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2017; Benson et al. 2019).

Male mountain lion M110 in San Diego County was euthanized by a CDFW warden because he was severely injured and for stated public safety concerns (he was found in a neighborhood close to homes). This occurred days after he was illegally shot by a livestock owner (open wound on right flank). Necropsy results indicated he had two broken legs consistent with a vehicle strike and four different compounds of anticoagulant rodenticides in his blood. Had he not been euthanized, he likely would have died from starvation due to his injuries. Source: Vickers (2014).

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[14] Forest Service, U.S. Department of Agriculture, *Final Environmental Impact Statement, Land Management Plans, Angeles National Forest Cleveland National Forest Los Padres National Forest San Bernardino National Forest* (Sept. 2005), available at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5166889.pdf.

Measures to conserve core habitat areas and functional wildlife corridors, like the recently adopted Habitat Connectivity and Wildlife Movement Ordinances in Ventura County,[15] are vital to the preservation of Central Coast and Southern California mountain lion populations, but just protecting land is not enough to ensure their survival. Conserving natural habitats on both sides of freeways and constructing effective crossing infrastructure (*e.g.*, culverts, underpasses, vegetated overpasses, and exclusionary fencing) at existing roads and barriers would facilitate movement and gene flow while reducing mortalities due to vehicle strikes (Riley et al. 2014; Vickers et al. 2015; Benson et al. 2019). Promoting wider implementation of predator-proof enclosures for domestic animals would further reduce human-caused mortalities by limiting opportunities for potential conflict and reducing the use of depredation permits (Vickers et al. 2015). In addition, changes in depredation permit policy could further reduce mortalities. For example, CDFW adopted a new depredation permit policy based on a 2017 bulletin for mountain lions in the CC-S and SAM areas, which requires affirmative non-lethal alternatives and improved husbandry before kill permits are issued when mountain lion depredations occur in those areas (CDFW 2017; see *Section 8.1.1 CDFW Departmental Bulletins*). Expanding these policies in conjunction with enforceable implementation and reporting requirements across the state, or at least into the SGSB, EPR, CC-N, and CC-C, population areas, would reduce mortalities from this source. Prohibiting the use of second-generation anticoagulants, rodenticides, and other environmental toxicants in California (*i.e.*, with AB 1788, sponsored by Assembly Member Richard Bloom in 2019) would even further reduce human-caused mortalities of mountain lions, as toxicants bioaccumulate up the food chain and can kill mountain lions or weaken their immune systems and make them more susceptible to disease or more vulnerable to conspecifics (Riley et al. 2003; Riley et al. 2007; Serieys et al. 2015). A combination of habitat conservation, implementation of effective road/barrier crossing infrastructure, and outreach and education to property owners and owners of domestic animals combined with depredation permit policy change could save these populations from extinction (Vickers et al. 2015).

6.1 Low Genetic Diversity and Inbreeding Depression

As detailed in *Section 2.2 Taxonomy and Population Genetics* and *Section 5.0 Abundance and Population Trends*, inbreeding is a serious threat to the persistence of the Central Coast and Southern California mountain lion populations. Inbreeding depression, loss of genetic diversity, and accumulation of deleterious mutations can lead to elevated extinction risk due to reduced reproductive fitness and evolutionary potential (*i.e.*, the ability to adapt to change) (Spielman et al. 2004; Frankham 2005; Traill et al. 2010). Decades of isolation due to roads and development fragmenting habitat and limiting connectivity has led to low genetic diversity and effective population sizes, high levels of inter-relatedness, and dangerous levels of inbreeding, especially in the CC-S, SAM, SGSB, and CC-N populations (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Gustafson et al. 2017; Gustafson et al. 2018; Benson et al. 2019). Although demographic and environmental stochasticity (*e.g.*, a disease outbreak, wildfire, drought or flooding) can increase risk of extinction, especially in small populations, inbreeding has also been shown to be an indicator of extinction risk and may impact how populations are able to respond to stochastic events (Frankham and Ralls 1998). In addition, endangered species

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[15] More information regarding the Habitat Connectivity and Wildlife Movement Ordinances available at: https://vcrma.org/habitat-connectivity-and-wildlife-movement-corridors

tend to have lower genetic diversity than non-endangered species, which suggests that inbreeding and low genetic variation may have an important role in a species' risk of extinction (Frankham and Ralls 1998). Thus, genetic factors should be considered when assessing the status of these populations.

The CC-S, SAM, SGSB, and CC-N populations have been found to have low genetic diversity, with the SAM population's genetic variation nearly as low as the endangered Florida panther's (*Puma concolor coryi*) (Ernest et al. 2014; Riley et al. 2014; Gustafson et al. 2017). And, as mentioned previously in *Section 2.2 Taxonomy and Population Genetics,* the CC-S, SGSB, SAM, CC-N, and EPR populations have effective population sizes well below the older and less conservative threshold of 50, while the CC-C population's effective population size is just barely above that threshold at $N_e = 56.6$ (Ernest et al. 2014; Riley et al. 2014; Benson et al. 2016a; Gustafson et al. 2018; Benson et al. 2019). These numbers suggest that inbreeding depression could occur within the short-term (over the duration of five generations) and these populations are at increased risk of extinction.

Without improved connectivity, the SAM and Santa Monica Mountains (within the CC-S) populations are predicted to experience continued genetic erosion and losses in heterozygosity of 28-49% and 40-57%, respectively, within 50 years (Benson et al. 2016a; Benson et al. 2019). This could lead to inbreeding depression, which could cause reduced fitness in a variety of ways. In Florida panthers, inbreeding depression led to reproductive issues (*e.g.*, poor sperm quality, low testosterone levels, poor fecundity and recruitment, failure of testes to descend), increased susceptibility to parasites and disease, and physical issues (*e.g.*, atrial septal defect, a deadly congenital heart defect; kinked tails) (Roelke et al. 1993; Johnson et al. 2010). Suffering from shrinking, fragmented habitats, high mortality rates from hunting, and inbreeding depression, the Florida panther population declined to less than 30 individuals, and genetic restoration via the translocation of eight female mountain lions from Texas (*Puma concolor stanleyana*) was needed to prevent their extinction (Johnson et al. 2010).

The SAM and CC-S populations are severely constrained in fragmented habitats with similar numbers as the Florida panther population prior to genetic rescue (Beier and Barrett 1993; Johnson et al. 2010; Riley et al. 2014; Vickers et al. 2015). Although the fragmented populations appear to be stable, high levels of inbreeding have been documented in the Santa Monica Mountains (Riley et al. 2014) and evidence of inbreeding depression (*i.e.*, low genetic diversity and kinked tails) has been observed in the SAM (Ernest et al. 2014). If these populations remain isolated, they will inevitably have the same fate as the Florida panthers. Researchers predict that with inbreeding depression, the SAM and Santa Monica Mountains populations have a 100% and 99.7% chance of becoming extinct within 50 years, with median time to extinction of 11.7 and 15.1 years, respectively (Benson et al. 2019).

The SGSB population was also found to have low genetic diversity and effective population size (Gustafson et al. 2018), which suggests that the population experienced a prior genetic bottleneck and inbreeding is likely. Although genetic studies on this population are limited, it is clear that continued development in and around the SGSB will further isolate the population and lead to more inbreeding and even lower genetic diversity, which will drive the population faster towards extinction. It is important to note that despite only limited gene flow between the SGSB population and the Western Sierra Nevada, CC-C, and the EPR (Gustafson et al. 2018), this population represents a critical linkage between mountain lion populations in the northern and southern mountain ranges of California. Restoration and enhancement of connectivity is key for the continued survival of the SGSB population as well as all of the other the Central Coast and Southern California mountain lion populations.

Gustafson et al. (2018) found that the EPR population also exhibits a prior genetic bottleneck. The EPR population was found to be largely disconnected from all the other California populations, with limited gene flow and low connectivity with the SAM and SGSB populations (Gustafson et al. 2018). Movement patterns and genetics indicate potential isolation from other populations (Vickers et al. 2015; Gustafson et al. 2017; Gustafson et al. 2018), and continued development in these areas will likely lead to further isolation, genetic drift, and risk of extinction similar to what is being observed in the CC-S, SAM, and SGSB populations.

Although genetic studies are limited for the CC-N population, it was found to have low genetic diversity and low effective population size (Gustafson et al. 2018), which forewarns of inbreeding depression and increased risk of extinction. CDFW has identified the Santa Cruz Mountains mountain lion population, which occurs within the CC-N area, as vulnerable to decline and extinction due to fragmentation from roads and development as well as lack of protected habitat (Dellinger 2019).

Studies suggest that one immigrant every 1-2 years would reduce extinction risk in the SAM and Santa Monica Mountains populations (Beier and Barrett 1993; Gustafson et al. 2017; Benson et al. 2019). This may apply to the other populations with low genetic diversity and effective population size (Gustafson et al. 2018). Increasing connectivity throughout the Central Coast and Southern California would address issues of inbreeding by facilitating movement between populations, increasing effective population size, and reducing high mortality rates driven by vehicle strikes and depredation. Thus, proactive measures to effectively restore and enhance connectivity are needed to minimize risk of inbreeding depression and extinction in Central Coast and Southern California populations.

6.2 Vehicle Strikes

In California, an estimated 100 mountain lions are killed every year by vehicle strikes (Pollard 2016). In the Central Coast and Southern California, vehicle strikes represent a significant threat to the persistence of mountain lion populations, though Southern California has more documentation regarding this issue. The number of mortalities caused by vehicle strikes has been increasing in Southern California since the 1980s, and vehicle strikes account for a high proportion of deaths in mountain lions in the SAM, CC-S, and EPR (Beier and Barrett 1993; Riley et al. 2014; Vickers et al. 2015:Vickers et al. 2017). From 1981 to 2013 vehicle strikes accounted for 53% (50/94) of mountain lion deaths in the SAM and 30% of mountain lion deaths in the EPR (46/154) (Vickers et al. 2015). Riley reported that 14% (2/14) of collared mountain lion deaths from 2002 to 2012 were due to vehicle strikes, and the NPS reported that 18 mortalities from vehicle strikes occurred between July 2002 and January 2018 in the CC-S (Figure 9). Although the CC-N population is less studied, there is evidence that vehicle strikes are a significant cause of mortalities in this population; at least six mountain lions have been killed by vehicle strikes on Highway 17 in the Santa Cruz Mountains between 2008 and 2018 (Midpeninsula Regional Open Space 2017; Slade 2018) and news outlets reported at least three vehicle strikes killing mountain lions on the I-280 in San Mateo County between 2014 and 2016 (Wilmers 2014; CBS San Francisco 2015; Kamala 2016). Similarly, in 2018 at least two mountain lions were reported to have been killed by vehicle strikes in San Luis Obispo County in the CC-C (Tanner 2018). Clearly, vehicle strikes are an important cause of mortality for the Central Coast and Southern California mountain lion populations.

Figure 9. Locations of 18 mountain lion vehicle strikes in the Santa Monica Mountains and surrounding areas from July 2002 to January 2018. Source: NPS

High adult mortality rates can have severe consequences, particularly for small populations with female-biased adult sex ratios and low effective population sizes (Beier and Barrett 1993; Benson et al. 2019). Vehicle strikes have been found to affect males and females equally, regardless of age, which can result in relatively high adult male mortalities (Vickers et al. 2015). Low male adult survival increases the risk of extinction, as it could result in occasional extinctions of breeding males and therefore reduced reproductivity (Benson et al. 2019), which has been previously observed in the SAM (Beier and Barrett 1993). In the Santa Monica Mountains, where adult survival is high, vehicle strikes (along with intraspecific strife) make it more difficult for subadults to successfully disperse, which limits breeding opportunities for mountain lions born in the Santa Monica Mountains (Riley et al. 2014; Benson et al. 2019). Freeways and vehicle strikes also limit the ability for immigrants to enter the Santa Monica Mountains and contribute to the population's gene pool (Riley et al. 2014; Benson et al. 2019). These patterns highlight the dire outlook for Central Coast and Southern California mountain lion populations due to lack of connectivity between populations and suitable habitat. The continued construction of roads and development and inaction to enhance connectivity threatens the survival of these struggling populations.

6.3 Depredation and Illegal Kills

Mountain lions killed on depredation permits (and one killed by vehicle strike) in San Diego County in 2015. Source: Vickers et al. (2017).

In 1990 California voters passed The California Wildlife Protection Act (Proposition 117), making the mountain lion a "specially protected species" and outlawing mountain lion sport-hunting in California. However, the law requires CDFW to issue depredation permits that allow people to "take" mountain lions when a mountain lion kills or injures domestic animals such as livestock or pets or damages property. The legal definition of "take" is to "hunt, pursue, catch, capture, or kill, or attempt to hunt, pursue, catch, capture, or kill" (Cal Fish & Game Code, *§86*), and the vast majority of permits to take in the three decades since the passage of Proposition 117 have authorized killing one or more mountain lions. The number of depredation permits issued and the number of reported kills has varied over time, and on average over 40% of permits result in reported kills. Since 1990 there has been an average of 97 reported depredation kills every year; however, these estimates are likely low due to underreporting and incomplete records (W. Vickers, *pers comm*). Depredation kills (along with vehicle strikes) account for the majority of mountain lion mortalities in the SAM and EPR (Vickers et al. 2015; Vickers et al. 2017). Although less is known about depredation kill impacts in the CC-N and CC-C, there is evidence that suggests depredation kills could be a significant source of mortality in these populations. In the Santa Cruz Mountains in the CC-N, depredation kills are the leading cause of death in collared mountain lions (Wang et al. 2017), and CDFW reported 34 depredation kills between 2010 and 2016 in the CC-N counties of Alameda, Contra Costa, San Mateo, Santa Clara, and Santa Cruz (see Appendix A[16]). Although population dynamics are even less studied in the CC-C, between 2010 and 2016 there were 46 reported depredation kills in the counties of Monterey, San Benito, San Luis Obispo, and Santa Barbara (See Appendix A[*Id.*]).

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[16] These data were downloaded from the CDFW website; however, they no longer appear to be available online. These numbers have been shown to be low by a factor of two in some areas, likely due to incomplete reporting, and therefore should be considered absolute minimums (W. Vickers, *pers comm*).

An illegally killed mountain lion in San Mateo County. Photo: Tiffany Yap

Depredation kills result in more deaths in male mountain lions compared to female mountain lions. Statewide, of mountain lions killed for depredation in 2017, 68% were males (CDFW 2018), and from 1981 to 2013, there were 3.4 times more male than female mountain lions killed for depredating in the SAM and EPR (Vickers et al. 2015). The majority of lions reported killed for depredating were of subadult (1-2 years old) and adult mountain lions (>2 years old) (CDFW 2018), many of which were likely dispersers that may have not yet established home ranges. Dispersing lions often come up against roads and development as they search to establish home ranges (Beier 1995, Vickers 2015, Riley 2014). This suggests that even if individuals are able to navigate across roads and freeways without being struck by vehicles, they often come into conflict with humans, which threatens their survival. This was reflected in the EPR, when the only GPS collared immigrant to have crossed I-15 from 2001 to 2013 arrived from the SAM only to be killed on a depredation permit 25 days after his arrival for depredating a sheep (Vickers et al. 2015). Not only do lions killed for depredating diminish the total abundance of these populations, but because males are predominantly killed, the number of animals that are the primary gene dispersers are also greatly reduced, which further inhibits adequate genetic connectivity (Vickers et al. 2017).

Reported depredation kills do not include mountain lions that are illegally poached or killed, many of which likely go undocumented (Beier and Barrett 1993; Vickers et al. 2015). Illegal kills have been observed in the CC-S, SAM, and EPR (Beier and Barrett 1993; Riley et al. 2014; Vickers et al. 2015) as well as in the CC-N (Yap 2018 *pers observation*), and although 80 mountain lions were reported as being killed under depredation permits in 2017, 89 deaths were being investigated (CDFW 2018).

As mentioned in *Section 6.2 Vehicle Strikes*, high levels of mortalities among male breeders or potential male breeders (*i.e.*, dispersers) can have severe impacts on small, isolated mountain lion populations with female-biased adult sex ratios and low effective population sizes (Beier and Barrett 1993; Benson et al. 2019). Low survival of breeding males increases extinction risk, as occasional breeding male extinctions can occur and therefore reduce reproductivity throughout the population (Beier and Barrett 1993; Benson et al. 2019). And low survival of subadults and adults may limit both dispersers and immigrants from successfully breeding and increasing genetic diversity (Vickers et al. 2015; Benson et al. 2019). Thus, depredation and illegal kills in conjunction with lack of connectivity between populations and suitable habitat in the Central Coast and Southern California severely limit the potential for these populations to survive and reproduce. Continued development and lack of connectivity will likely push mountain lions into more conflicts with humans, which could increase depredation and retributory kills and further drive these populations towards extinction.

6.4 *Intraspecific Strife*

Intraspecific strife: a female mountain lion, P-7, was killed by her father, P-1. Photo: NPS

As detailed in *Section 5 Abundance and Population Trends*, intraspecific strife is the leading cause of mortality in the Santa Monica Mountains (Riley et al. 2014). Although intraspecific strife is a common source of mortality in mountain lion populations, (Beier and Barrett 1993; Logan and Sweanor 2001; Allen 2014), unusually high levels of intraspecific strife have been observed in this population (Riley et al. 2014). About 41% (9/22) of deaths in radio-collared mountain lions being tracked from 2002 to 2018 were from intraspecific strife,[17] with multiple cases of aggressive adult males killing their siblings, offspring (male and female), and previous mates (Riley et al. 2014). While males are likely to have larger home ranges to protect food resources and access to females, killing offspring or potential mates has no apparent evolutionary benefit, as it reduces chances of future reproduction (Riley et al. 2014). In addition, infanticide has been documented in the Santa Monica Mountains (Riley et al. 2014), perhaps to trigger the female to come into estrous. These high levels of intraspecific strife are likely due to limited space in the Santa Monica Mountains caused by dispersal barriers (Riley et al. 2014; Benson et al. 2019). As roads and development further encroach on Central Coast and Southern California mountain lion populations, intraspecific strife could become more common; this was

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[17] The NPS provides puma profiles (last updated August-November 2018) of the marked animals (*i.e.*, tagged or radio-collared) they have been studying in the CC-S, which includes those studied in Riley et al. (2014). Some data presented in this section take these data into account. Accessed on 3 April 2019 at: https://www.nps.gov/samo/learn/nature/puma-profiles.htm.

documented in the SAM on two occasions (one GPS-collared, one previously GPS-collared) since the publication of Vickers et al. (2015) (W. Vickers *unpublished data*). Enhanced connectivity between populations and suitable habitat would facilitate dispersal, which would reduce and/or prevent high levels of intraspecific strife (Riley et al. 2014; Benson et al. 2019) and improve the survival and reproduction rates, especially for the most struggling populations.

6.5 Abandonment

Santa Monica Mountains mountain lion kittens P-57 and P-58 were abandoned by their mother, P-42, a first-time mother who left with male P-27 and never returned. Photo: NPS

Abandonment of kittens is fairly common in the Santa Monica Mountains and accounts for about 23% (5/22) of the known causes of death for marked/collared animals.[18] Although this likely occurs in other mountain lion populations, the causes of abandonment are unclear. There are various reasons why females might abandon their cubs. The cubs could be sick, the female may not be able to take care of them, or perhaps the female was initially protecting them from a mature male. Unfortunately, there is a lack of data regarding why and how often cubs get abandoned. Yet this is one of the main causes of death for mountain lions in the Santa Monica Mountains, which likely affects this already-small population.

Mountain lion cubs can also become orphaned if the mother is killed before they have dispersed. If they are too young to fend for themselves, they likely starve to death or are preyed upon by other predators. If the young are more mobile, they may come up against areas where they are more likely to encounter humans as they search for food. This was seen in November 2017, when a mother mountain lion was killed by a vehicle strike in the SAM and two of her cubs were found roaming near human establishments – one in a backyard and the other along a road (Veklerov 2018). Both were too young to survive on their own and were placed in the Oakland Zoo.

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[18] Id.

6.6 Poisoning from Rodenticides and Other Environmental Toxicants

The famous mountain lion of Griffith Park, P-22, suffering from notoedric mange, a parasitic skin disease that has been linked with the ingestion of rodenticide poisoning (left) and mountain lion P-34 found dead on a trail due to rodenticide poisoning (right). Photos: NPS

Although mountain lions are not the primary target of environmental toxicants, such as rodenticides and other pesticides and herbicides, secondary poisoning has been documented in many non-target animals, especially predators (e.g., coyotes (Riley et al. 2003), bobcats (Riley et al. 2007; Serieys et al. 2015), San Joaquin kit fox (McMillin et al. 2008), California fishers (Gabriel et al. 2012), raptors (Lima and Salmon 2010), and many more). Data regarding pesticide poisoning in mountain lions are limited; however, there is evidence that these big cats are likely vulnerable to similar negative impacts that other predators experience, including direct death, weakened immune systems, and vulnerability to predators or conspecifics (Riley et al. 2003; Riley et al. 2007; Serieys et al. 2015; Rudd et al. 2019).

While poisoning can sometimes lead to direct death, rodenticide exposure has also been associated with notoedric mange, a parasitic skin disease that has led to high levels of mortalities, population declines, and even local extirpations in Southern California bobcats (Riley et al. 2007; Serieys et al. 2015). Although the link between rodenticide poisoning and mange is not as clear in mountain lions, since 2002 five mountain lions in the CC-S have been found suffering from mange, and researchers suspect that rodenticide poisoning may have played a role (Reyes-Velarde 2019a). In addition, of four dead mountain lions in the Santa Monica Mountains that were found to have rodenticides in their systems, two died from poisoning and two died from intraspecific strife, and it is possible that indirect effects of poisoning may have prevented the mountain lions from escaping conflict or fighting back (Riley et al. 2007). And rodenticide poisoning is suspected to be the cause of death in mountain lion P-47, who was recently found dead in Santa Monica Mountains (Reyes-Velarde 2019b), and CC-N mountain lion 36m, who was found dead in the Santa Cruz Mountains in 2015 (Wilmers 2015).

The Department of Pesticide Regulation (DPR) analyzed data provided by CDFW and found that 92% (59/64) of tested mountain lions from throughout the state had detectable levels of anticoagulant rodenticides, which indicates alarmingly high exposure rates (DPR 2018). This has been found to be true in the CC-S as well, where researchers have found that 94% (17/18) of mountain lions tested had traces of rodenticides in their systems (Reyes-Velarde 2019a).

Rodenticides have been implicated in mountain lion mortalities in the CC-S, and in the SAM anticoagulant rodenticide residues were detected in the livers of 100% of deceased animals tested, with up to five different compounds being detected in some animals (Riley et al. 2007; Riley et al. 2014; W. Vickers, *pers comm*). And a study conducted by CDFW and the Integral Ecology Research Center (IERC) has found that mountain lions are being exposed to dangerously high levels of illegal pesticides, such as carbofuran, being used on illegal marijuana grow sites, which can also bioaccumulate and cause health issues (Rudd et al. 2019). Furthermore, it is possible that herbicide exposure from deer could be detrimental to mountain lions as well. Although poisoning from environmental toxicants may not constitute a large proportion of direct deaths (that we are aware of), it is possible that high exposure levels influence other causes of mortalities. Any additional mortalities in the small, isolated Central Coast and Southern California populations suffering from other anthropogenic pressures could impact the short- and long-term survival of these mountain lions.

6.7 Wildfires

After the Woolsey Fire, the body of mountain lion P-64, known to use culverts to cross the Hwy-101 and SR-118 freeways a total of 41 times, was found dead with severely burned paws. Photos: NPS

Although fire is a natural disturbance in California ecosystems, sprawl development with low/intermediate densities extending into habitats that are prone to fire have led to more frequent wildfires that burn larger areas (Syphard et al. 2007; Syphard et al. 2009). Most wildfires in California are caused by human ignitions, like power lines, arson, improperly disposed cigarette butts, debris burning, fireworks, campfires, or sparks from cars or equipment (Keeley and Fotheringham 2003; Syphard et al. 2007; Syphard et al. 2012; Bistinas et al. 2013; Balch et al. 2017; Radeloff et al. 2018; Syphard et al. 2019). In fact, human-caused fires account for 95-97% of all fires in California’s Mediterranean habitats (Syphard et al. 2007, Balch et al. 2017). In addition, climate change is leading to hotter, drier conditions that make fires more likely to burn. At least 29 fires throughout California in the last two years were caused by electric power and distribution lines, and transmission lines are suspected to be the cause of last year’s Camp Fire and Woolsey Fire (Atkinson 2018; Chandler 2019).

Increased frequency of wildfires poses a threat to the survival of Central Coast and Southern California mountain lions. Although mountain lions are highly mobile and generally able to move away from wildfires, in severe weather conditions wind-driven fires can spread quickly – they can cover 10,000 hectares in one to two days, as embers are blown ahead of the fires and towards adjacent fuels (*e.g.*, flammable vegetation, structures) (Syphard et al. 2011). If their movement is constrained by roads and development and they are unable to access escape routes, then their chances of surviving wildfires are greatly reduced. Vickers et al. (2015) documented one death of a collared mountain lion in the SAM and one in the EPR due to human-caused wildfires, and the deaths of two collared mountain lions in the CC-S in 2018 have been attributed to the Woolsey Fire.[19] Environmentally stochastic events (*e.g.*, wildfires, flooding) could destabilize small mountain lion populations and make them vulnerable to extinction (Benson et al. 2016a; Benson et al. 2019). In addition, increased frequency of fire ignitions can cause shifts in natural fire regimes, which can lead to large-scale landscape changes, such as vegetation-type conversion or habitat fragmentation, which can impact wide-ranging species like the mountain lion (Jennings 2018).

Increasing landscape connectivity (*e.g.*, by designing corridors, removing barriers, and preserving habitats that are close to each other) is important for resilience to environmentally stochastic events and climate change adaptation (Heller and Zavaleta 2009). Enhanced connectivity that incorporates corridor redundancy (*i.e*. the availability of alternative pathways for movement) would allow for improved functional connectivity and resilience. Compared to a single pathway, multiple connections between habitat patches increase the probability of movement across landscapes by a wider variety of species, and they provide more habitat for low-mobility species while still allowing for their dispersal (Mcrae et al., 2012; Olson & Burnett, 2008; Pinto & Keitt, 2008). In addition, corridor redundancy provides resilience to uncertainty, impacts of climate change, and extreme events, including wildfires, by providing alternate escape routes or refugia for animals seeking safety (Cushman et al., 2013; Mcrae et al., 2008; Mcrae et al., 2012; Olson & Burnett, 2008; Pinto & Keitt, 2008).

6.8 Climate Change

A strong, international scientific consensus has established that human-caused climate change is causing widespread harms to human society and natural systems, and climate change threats are becoming increasingly dangerous. In a 2018 *Special Report on Global Warming of 1.5°C* from the Intergovernmental Panel on Climate Change (IPCC), the leading international scientific body for the assessment of climate change describes the devastating harms that would occur at 2°C warming, highlighting the necessity of limiting warming to 1.5°C to avoid catastrophic impacts to people and life on Earth (IPCC 2018). In addition to warming, many other aspects of global climate are changing. Thousands of studies conducted by researchers around the world have documented changes in surface, atmospheric, and oceanic temperatures; melting glaciers; diminishing snow cover; shrinking sea ice; rising sea levels; ocean acidification; and increasing atmospheric water vapor (USGCRP, 2017).

Climate change is increasing stress on species and ecosystems, causing changes in distribution, phenology, physiology, vital rates, genetics, ecosystem structure and processes, and increasing species extinction risk (Warren et al., 2011). A 2016 analysis found that climate-related local extinctions are already widespread and have occurred in hundreds of species, including almost half of the 976 species surveyed (Wiens 2016). A separate study estimated that nearly half of terrestrial non-flying threatened mammals and nearly one-quarter of threatened

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[19] Id.

birds may have already been negatively impacted by climate change in at least part of their distribution (Pacifici et al. 2017). A 2016 meta-analysis reported that climate change is already impacting 82% of key ecological processes that form the foundation of healthy ecosystems and on which humans depend for basic needs (Scheffers et al. 2016). Genes are changing, species' physiology and physical features such as body size are changing, species are moving to try to keep pace with suitable climate space, species are shifting their timing of breeding and migration, and entire ecosystems are under stress (Cahill et al., 2012; Chen et al., 2011; Maclean & Wilson, 2011; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Warren et al., 2011).

Improving landscape connectivity is a key factor for climate change resilience and adaptation (Heller and Zavaleta 2009). Without functional connectivity that provides multiple pathways for mountain lion movement, isolated Central Coast and Southern California mountain lion populations and the prey they depend on may not be able to shift their ranges as available resources shift. Enhanced connectivity that provides redundant corridors for safe passage between suitable habitats would improve chances of survival and reproduction in the face of climate change by increasing the probability of movement across landscapes by a wider variety of species and providing alternate escape routes or refugia for animals seeking safety (Mcrae et al. 2008; Pinto and Keitt 2008; Mcrae et al. 2012; Cushman et al. 2013; Olson and Burnett 2013).

7 Degree and Immediacy of Threat

As demonstrated in the previous sections, Central Coast and Southern California mountain lions are at risk of extirpation under current conditions. Roads and development have fractured connectivity, which has led to the separation of at least six isolated, genetically distinct populations in the CC-N, CC-C, CC-S, SAM, SGSB, and EPR (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Benson et al. 2019). Due to extreme isolation and high levels of human-caused mortalities, the SAM and CC-S mountain lions have low genetic diversity, low effective population sizes, and high levels of inbreeding (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Benson et al. 2019). Benson et al. (2019) predicted high losses of heterozygosity in the SAM and Santa Monica Mountains populations, which suggests that inbreeding depression is imminent. If inbreeding depression occurs, the SAM and Santa Monica Mountains/CC-S populations will likely go extinct within 50 years, with median times to extinction of 11.7 years and 15.1 years, respectively (Benson et al. 2019). With similarly low genetic diversity and effective population size, the SGSB and CC-N populations likely have a similar fate. And although the CC-C and EPR populations appear to be slightly healthier with more genetic diversity and a higher effective population size, these populations have effective population sizes that are still well below the most recent recommended threshold to prevent inbreeding depression in the short-term (Frankham et al. 2014; Gustafson et al. 2018); continued development in these areas could propel these populations towards extinction more quickly. Clearly, Central Coast and Southern California mountain lion populations are succumbing to anthropogenic pressures, and without immediate action to restore and enhance connectivity between the populations and suitable habitat, they will be lost, potentially within our lifetimes.

Immediate action is critical for the long-term persistence of Central Coast and Southern California mountain lions and the health of Central Coast and Southern California ecosystems. Connectivity between the populations and suitable habitat must be restored and enhanced to facilitate movement and gene flow while reducing human-caused mortalities. Anthropogenic pressures, especially vehicle strikes and depredation kills, should be minimized to help the recovery of these populations. Although translocation of outbred animals has been shown to be effective to increase genetic diversity (Johnson et al. 2010), this would only be a short-term, unsustainable solution given the current level of isolation of these populations (Ernest et al. 2014; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016a; Benson et al. 2019). Strategically-placed road/barrier crossing infrastructure that allows for dispersal and gene flow and reduces mortalities would be a more comprehensive, long-term solution to save these populations in perpetuity. And the preservation of intact linkages, especially the Tehachapi and Sierra Pelona Mountains, is essential to maintain statewide genetic connectivity. Immediate regulatory action under the CESA is needed to enhance connectivity among Central Coast and Southern California mountain lion populations and suitable habitat to ensure the conservation of these iconic big cats.

8 Inadequacy of Existing Regulatory Mechanisms

8.1 State Regulatory Mechanisms

<u>Proposition 117</u>

The California Wildlife Protection Act of 1990 (Proposition 117) declared that the mountain lion is a “specially protected mammal under the laws of this state.” (Cal. Fish & Game Code § 4800(a).) Proposition 117 acknowledged that mountain lion habitat in the Santa Monica Mountains, Santa Ana Mountains, Santa Susana Mountains, and Simi Hills is disappearing rapidly and that “[s]mall and often isolated wildlife populations are forced to depend upon these shrinking habitat areas within the heavily urbanizing areas of this state.” (Cal. Fish & Game Code § 2780(d).) Proposition 117 further found that “[c]orridors of natural habitat must be preserved to maintain the genetic integrity of California’s wildlife.” (*Id*.)

In order to preserve mountain lion populations in California, Proposition 117 mandated that mountain lions are not to be considered a “game mammal,” such that hunting is generally prohibited. (Cal. Fish & Game Code § 3950.1(a).) Subject to certain exceptions, Proposition 117 makes it unlawful to take, injure, possess, transport, import, or sell a mountain lion. (Cal. Fish & Game Code § 4800(b).) Nonetheless, a mountain lion may still be removed or killed if it is “perceived to be an imminent threat to public health or safety” or is perceived by CDFW to be “an imminent threat to the survival of any threatened, endangered, candidate, or fully protected sheep species.” (Cal. Fish & Game Code § 4801.) Mountain lions that have not been designated an “imminent threat to public health or safety” may still be removed via nonlethal means. (Cal. Fish & Game Code § 4801.5(a).)

A person whose livestock or other property has been damaged or destroyed by a mountain lion may request a permit to “take” the mountain lion. (Cal. Fish & Game Code § 4802.) CDFW is required to immediately take action to confirm that there has been a depredation. (Cal. Fish & Game Code § 4803.) If CDFW is satisfied that there has been a depredation, CDFW "shall promptly issue a permit to take the depredating mountain lion." (*Id*.) There is no limit to the number of depredation permits a property owner can request from CDFW. In addition, mountain lions that are encountered while pursuing or inflicting injury on livestock or domestic animals may be taken immediately without the need for a permit. (Cal. Fish & Game Code § 4807.)

While Proposition 117 prohibits all hunting of mountain lions as well as the purposeful killing of mountain lions in most circumstances, it does not contain provisions to ensure that connectivity between core habitats for the Southern California or Central Coast mountain lions will be protected. As discussed above in *Section 6.0 Factors Affecting the Ability to Survive and Reproduce*, the primary threat to Southern California and Central Coast mountain lions is not hunting—it is habitat fragmentation and the lack of crossing infrastructure, which has led to major declines in genetic diversity, high levels of inbreeding, and high levels of human-caused mortalities via vehicle strikes, depredation kills, and intraspecific strife due to limited space and the inability for young mountain lions to disperse.

8.1.1 CDFW Departmental Bulletins

CDFW has issued "Departmental Bulletins" relating to mountain lions. The most recent bulletin was issued in December 2017 and applied specifically to the Santa Monica Mountains and SAM mountain lion populations (the "2017 Bulletin") (CDFW 2017).[20] The 2017 Bulletin acknowledged (1) the lack of genetic diversity in the Santa Monica Mountains and SAM mountain lion populations and (2) that human population growth and anthropogenic barriers are restricting connectivity with other mountain lion populations. In order to reduce unnecessary killings of mountain lions in the Santa Monica Mountains and SAM populations, the 2017 Bulletin provides that any person reporting a depredation (a "reporting party") may be issued a first permit to employ non-lethal measures to deter mountain lions from further depredation, and a second permit to "haze" a depredating mountain lion. In the first instance, the reporting party would institute economically feasible measures designed to reduce the potential for attracting mountain lions such as removing the carcasses of depredated animals, installing or repairing and consistently using enclosures to exclude mountain lions, or employing guardian animals in the immediate vicinity of livestock or other domestic animals. The 2017 Bulletin provides that CDFW would not be required to issue a lethal depredation permit until (1) a third depredation event has occurred, and (2) CDFW has confirmed that the reporting party has already implemented all reasonable preventative measures.

In January of 2018, CDFW adopted the 2017 Bulletin's new depredation permit policy. Although this provides some additional protections and will likely reduce lethal take of mountain lions in the Santa Monica Mountains and the SAM, researchers have documented instances wherein domestic animal owners killed mountain lions in these areas without complying with CDFW instructions under the new policy (W. Vickers, *pers comm*). The 2017 Bulletin does not apply to other vulnerable populations, like the SGSB, EPR, CC-N, and CC-C mountain lions. In

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[20] California Department of Fish and Wildlife, *Human/Wildlife Interactions in California: Mountain Lion Depredation, Public Safety, and Animal Welfare – Amendment to Department Bulletin 2013-02* (Dec. 15, 2017), available at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=153021.

addition, the new policy is not designed to ensure protection of habitat or connectivity necessary for the continued survival of the Santa Monica Mountains and SAM mountain lion populations and is insufficient to ameliorate the anthropogenic mortalities related to potential extirpation.

8.1.2 California Environmental Quality Act

The California Environmental Quality Act ("CEQA") is California's landmark environmental law and establishes a state policy to prevent the "elimination of fish or wildlife species due to man's activities, ensure that fish and wildlife populations do not drop below self-perpetuating levels, and preserve for future generations representations of all plant and animal communities...." (Cal. Pub. Res. Code § 21001(c)). Towards this end, state and local agencies are required to analyze and disclose the impacts of any discretionary decision or activity. CEQA contains a substantive mandate that agencies should not approve projects as proposed if there are feasible alternatives or mitigation measures which would substantially lessen the significant environmental effects of such projects. (Cal. Pub. Res. Code § 21002.)

CEQA requires a "mandatory finding of significance" if a project may "substantially reduce the number or restrict the range of an endangered, rare or threatened species." (Cal. Code Regs., tit. 14, § 15065(a)(1).) CDFW has interpreted this provision to apply to species of special concern, which are species that are "experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State threatened or endangered status."[21] CDFW further provides that species of special concern "should be considered during the environmental review process." (*Id.*; Cal. Code Regs., tit. 14, § 15380.) Thus, a potentially substantial impact on a species of special concern, threatened species, or endangered species could be construed as "per se" significant under CEQA. (*Vineyard Area Citizens for Responsible Growth, Inc. v. City of Rancho Cordova* (2007) 40 Cal.4th 412, 449.) And under CEQA, when an effect is "significant," the lead agency approving the project must make a finding that changes or alterations have been incorporated into the project to avoid or mitigate its significant impacts, or that such changes are within the responsibility of another agency, or that mitigation is infeasible. (Cal. Pub. Res. Code § 21081(a).) These provisions therefore provide some protections to species that are listed as species of special concern, threatened, or endangered.

However, Southern California and Central Coast mountain lions are not listed as a species of special concern or as threatened or endangered, such that a project that has the potential to significantly impact one of these populations would not necessarily qualify as a "significant effect" under a lead agency's interpretation of CEQA. In such case, CEQA's substantive mandate to adopt all feasible alternatives or mitigation measures might not be triggered.

CEQA also requires a "mandatory finding of significance" if a project may "substantially reduce the habitat of a fish or wildlife species; cause a fish or wildlife population to drop below self-sustaining levels; threaten to eliminate a plant or animal community." (Cal. Code Regs., tit. 14, § 15065.) Moreover, CEQA's "Environmental Checklist" in Appendix G of the CEQA

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[21] California Department of Fish and Wildlife, *Species of Special Concern* , available at https://www.wildlife.ca.gov/Conservation/SSC.

Guidelines characterizes a project's effects as "significant" if the project would "interfere substantially with the movement of any native [] wildlife species or with established native resident or migratory wildlife corridors...."

While these provisions might theoretically offer some protection for Southern California or Central Coast mountain lions, in practice they have not provided sufficient protection. Under CEQA, lead agencies have discretion to develop their own thresholds of significance. (*East Sacramento Partnerships for a Livable City v. City of Sacramento* (2016) 5 Cal.App.5th 281, 300; Cal. Code Regs., tit. 14, § 15064(d)). This allows local agencies—who are often under pressure from developers to approve projects—to make significance determinations that are inconsistent with independent scientific analysis, including CDFW's analysis. For instance, in December 2017, the City of Temecula approved a 200-acre mixed use project called the Altair Specific Plan that would allow development in the last remaining viable linkage for the SAM mountain lion population between the Santa Ana Mountains and Peninsular Ranges. The City determined that impacts to mountain lions were not significant despite strong disagreement by CDFW, USFWS, and independent mountain lion experts.[22] CDFW warned the City of Temecula that the SAM population has "extremely low genetic diversity which is attributed to low gene flow between the small Santa Ana Mountains population and the larger population in the Peninsular Ranges" and that development is contributing to this genetic decay. (*Id*.) CDFW concluded that "increased human activity associated with the proposed Civic Site at this sensitive location would [] be detrimental to facilitating the movement of mountain lions across Interstate Highway 15 (I-15) to the Peninsular Range." (*Id*.)

Even when a lead agency acknowledges that an effect is "significant," CEQA allows a lead agency to adopt a "statement of overriding considerations" and approve a project if the agency finds that other factors outweigh the environmental costs of the project or that further mitigation is infeasible. (Cal. Code Regs., tit. 14, § 15093(b); Cal. Pub. Res. Code § 21081.) This means that even if a project may have a significant effect on a "wildlife population" like the CC-S, SAM, SGSB, or EPR mountain lions, an agency could interpret CEQA as still allowing approval of the project. CEQA in practice is therefore inadequate to protect the Southern California and Central Coast mountain lions.

Finally, as noted above, the lack of adequate wildlife connectivity and wildlife crossings is the primary factor driving Southern California and Central Coast mountain lions closer to extinction. Yet, agencies have not interpreted CEQA (or the National Environmental Policy Act, discussed further below) as including a clear legal mechanism for mitigation for impacts on wildlife connectivity. For example, in the Final Environmental Impact Report/Final Environmental Impact Statement for the Northwest 138 Corridor Improvement Project (the "Northwest 138 EIR"), Caltrans and the Los Angeles County Metropolitan Transportation Authority wrote: "The proposed project has the potential to directly or indirectly impact wildlife movement throughout the project limits. However, with the inclusion of the proposed avoidance and minimization measures, impact levels area expected to be relatively low. Exact acres of impacts to wildlife corridors are unable to be quantified, and currently there is no real

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[22] City of Temecula, *Altair Specific Plan Final Environmental Impact Report* (Oct. 2017), available at https://temeculaca.gov/DocumentCenter/View/4513/Altair-Specific-Plan-Final-Environmental-Impact-Report-FEIR.

mechanism for compensatory mitigation for these types of impacts."[23] The Northwest 138 EIR also contained no analysis of the highway's impacts on mountain lions, given that they are not presently listed as threatened or endangered.

Indeed, CDFW has urged lead agencies to consider wildlife connectivity in CEQA planning documents, without success. For instance, the Los Angeles County General Plan Draft EIR concluded that the buildout of the General Plan "will impact regional wildlife linkages" and have a "significant adverse effect on wildlife movement."[24] The Draft EIR concluded that policies proposed in the General Plan "do not provide for mitigation for loss of wildlife movement opportunities. If development impacts regional wildlife linkages and impedes wildlife movement, connectivity will be lost on a regional scale in these vital landscape corridors and linkages. Thus impacts to wildlife movement remain significant at the General Plan level." (*Id*.) In commenting on the Draft EIR, CDFW specifically objected to this conclusion:

> The Department does not concur with the conclusion in the DPEIR that unavoidable loss of wildlife movement opportunities or nursery sites within or outside of an SEA does not warrant mitigation. Without mitigation, the Project and subsequent projects would result in direct and cumulative loss of biological diversity. Mitigation opportunities for wildlife corridors and nursery sites are best established during large scale planning efforts such as this General Plan. Wildlife corridor areas can be delineated and set aside in the General Plan for current and future conservation efforts. An assessment could be placed on development within the Project area to secure the acquisition of these critical linkages and sites, therefore reducing impacts to wildlife corridors and nursery sites and ensuring biological diversity.[25]

In responding to this comment, Los Angeles County refused to implement CDFW's recommendations, claiming "it cannot be assumed that wildlife corridor areas for future conservation that can be set aside because those properties may not become publicly owned." (*Id*.) Los Angeles County's responses to CDFW's recommendations underscore that lead agencies have not interpreted CEQA to include a clear legal mechanism for mitigation for impacts on wildlife connectivity, even though such connectivity is critical to the survival of Southern California and Central Coast mountain lions.

8.1.3 Significant Natural Areas Program

The Significant Natural Areas Program ("SNAP") requires CDFW to develop and maintain a spatial data system that identifies those areas in the state that are most essential for maintaining habitat connectivity, including wildlife corridors and habitat linkages. (Cal. Fish & Game Code § 1932(b).) SNAP also requires CDFW to consult with other government agencies and stakeholders to identify natural areas deemed to be most significant. (Cal. Fish & Game

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[23] State of California Department of Transportation, *Northwest State Route 138 Corridor Improvement Project Final Environmental Impact Report / Environmental Impact State and Section 4(f) Evaluation* (June 2017), available at https://www.metro.net/projects/nw138/nw138-FEIR-FEIS/.

[24] County of Los Angeles, *Los Angeles County General Plan Update Draft Environmental Impact Report* (June 2014), available at http://planning.lacounty.gov/assets/upl/project/gp_2035_deir.pdf.

[25] County of Los Angeles, *Los Angeles County General Plan Update Final Environmental Impact Report* (March 2015), available at http://planning.lacounty.gov/assets/upl/project/gp_2035_lac-gpu-final-eir-final.pdf.

Code § 1932(f).) SNAP further requires CDFW to seek maintenance and perpetuation of the state's most significant natural areas for present and future generations in the most feasible manner. (Cal. Fish & Game Code § 1932(g).)

However, SNAP does not require or authorize any particular land use action or decision. (Cal. Fish & Game Code § 1932.5.) Likewise, SNAP does not change or prevent the change of use of any area identified pursuant to the program. (Cal. Fish & Game Code § 1933.) It therefore does not *require* any particular natural areas to be conserved. Because of this, it is insufficient to protection wildlife connectivity essential to the survival of Southern California and Central Coast mountain lions.

8.1.4 Natural Community Conservation Planning Act

The Natural Community Conservation Planning Act is a voluntary conservation planning mechanism for proposed development projects within a planning area to avoid or minimize impacts to wildlife. (Cal. Fish & Game Code § 2801(f).) The NCCP Act is designed to promote coordination among agencies and landowners to conserve unfragmented habitat areas and multihabitat management. (Cal. Fish & Game Code § 2801(d).)[26]

There are no Natural Community Conservation Plans ("NCCPs") that cover the Santa Monica Mountains or San Gabriel Mountains. There are a few NCCPs that cover portions of the Santa Ana Mountains and Eastern Peninsular Ranges, some of which also act as "habitat conservation plans" or "HCPs" pursuant to the Federal Endangered Species Act (16 U.S.C. § 1539). These include the County of Orange (Central Coastal) NCCP/HCP, the Orange County Transportation Authority NCCP/HCP, Western Riverside County Multiple Species HCP, San Diego Multiple Habitat Conservation Program, San Diego Multiple Species Conservation Program, and the San Diego North County Multiple Species Conservation Plan. There also is an NCCP that covers the Coachella Valley and portions of the San Bernardino Mountains called the Coachella Valley NCCP/HCP.

Of these NCCPs, only four "cover" portions of the Southern California mountain lion populations: (1) Western Riverside County Multiple Species HCP; (2) San Diego Multiple Habitat Conservation Program; (3) San Diego County Multiple Species Conservation Program; and (4) San Diego North County Multiple Species Conservation Plan.[27] Below is a discussion of each as they relate to mountain lions:

(1) The Western Riverside County Multiple Species HCP acknowledges that the SAM mountain lion population is at high risk of extirpation due to demographical instability unless there is a "movement connection between the Santa Ana Mountains

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[26] The NCCP Act also is described on CDFW's website at https://www.wildlife.ca.gov/conservation/planning/NCCP.

[27] California Department of Fish and Wildlife, *Conservation Plans By Species*, available at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=108719&inline. Both San Diego Gas & Electric and San Diego County Water Authority are permittees of HCPs/NCCPs covering mountain lions, but these only apply to activities undertaken by these entities.

and the Palomar Mountains."[28] However, mountain lions are considered to be "adequately conserved."[29] As such, the Western Riverside County Multiple Species HCP offers little protection for the SAM mountain lion population. While this HCP does identify linkages designed to ensure connectivity for mountain lions, the Western Riverside County Regional Conservation Authority has failed to enforce the HCP to protect such linkages when permittees such as the City of Temecula approve development that would severely constrict or impair such linkages.

(2) The San Diego Multiple Habitat Conservation Program is an NCCP and HCP that purportedly covers mountain lions, but the program readily concedes that mountain lions (as well as deer) "were not a major consideration in linkage design."[30] In addition, the EIR/EIS states that "[d]ue to the limited availability of habitat in the study area, implementation of the MHCP is not expected to substantially increase or decrease the population viability of the mountain lion."[31] The EIR/EIS likewise concludes there are no major populations or critical locations for the mountain lion within the plan area, and concludes it is "adequately conserved" under the plan. (*Id*.)

(3) The San Diego Multiple Species Conservation Program is an NCCP and HCP that covers 900 square miles in the southwestern portion of the San Diego. The Program lists mountain lions as "conserved" and states that mountain lions "will be covered by the MSCP because 81% of the core areas (105,000± acres) that support its habitat will be conserved."[32] While the Program generally notes that linkage areas were designed to accommodate "large animal movement," the Program does not identify any linkages designed for mountain lions or any specific measures designed to protect them. Likewise, while the Program states that "[s]pecific design criteria for linkages and road crossings/undercrossings are included in subarea plans," not all subarea plans are complete.

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[28] Western Riverside County Regional Conservation Authority, *Western Riverside County MSHCP Species Accounts*, available at http://wrcrca.conserveriverside.com/wrcrca/Permit_Docs/MSHCP_Docs/volume2/vol2-secb_Mammals.pdf.

[29] Western Riverside County Regional Conservation Authority, *Western Riverside County Multiple Species Habitat Conservation Plan*, available at http://wrcrca.conserveriverside.com/wrcrca/Permit_Docs/MSHCP_Docs/volume1/Vol1-sec2.pdf.

[30] San Diego Association of Governments, *San Diego Multiple Habitat Conservation Program Biological Monitoring and Management Plan (Volume III)* (Mar. 2003), available at https://www.sandag.org/programs/environment/habitat_preservation/mhcp_vol3.pdf.

[31] San Diego Association of Governments, *Final Environmental Impact Statement/Environmental Impact Report for Threatened and Endangered Species Due to Urban Growth within the Multiple Habitat Conservation Program Planning Area* (Mar. 2003), available at https://www.sandag.org/programs/environment/habitat_preservation/mhcp_eir_vol1.pdf.

[32] County of San Diego, *Final Multiple Species Conservation Program* (Aug. 1998), available at https://www.sandiegocounty.gov/content/dam/sdc/pds/mscp/docs/SCMSCP/FinalMSCPProgramPlan.pdf.

(4) The San Diego North County Multiple Species Conservation Plan is one of the "subarea" plans anticipated by San Diego Multiple Species Conservation Program. However, it has not been completed and is still "in development."[33]

(5) The Orange County Transportation Authority NCCP/HCP ("OCTA Plan") lists the mountain lion as a covered species for purposes of the federal HCP, but not for purposes of the NCCP permit. The OCTA Plan acknowledges that despite protection from hunting, annual survival for radio-collared lions is "surprisingly low" at 55.8 percent and that vehicle collisions and depredation permits are primary sources of mortality. The OCTA Plan states that targeted investment in habitat protection is "especially urgent to maintain viability of the Santa Ana Mountains populations."[34] The OCTA Plan does contain four "Species Goals" for mountain lions, including (1) acquiring 1,013 acres of suitable habitat; (2) fencing realignment near the Highway 241 toll road; (3) funding of the North Coal Canyon Restoration Project; and (4) a "wildlife crossing policy" requiring pre-construction surveys to ensure existing crossings "maintain or improve functionality" if modified by new freeway projects. However, despite allowing the expansion of two highways in lion habitat (Projects G and J), the OCTA Plan does not require the construction of any specific wildlife crossings. The OCTA Plan nonetheless claims that impacts on the mountain lion will be offset through these "Species Goals."

There are no NCCPs that cover the Central Coast. In addition, there are no NCCPs that cover portions of the Santa Cruz Mountains except the Santa Clara Valley Habitat Plan. However, this Plan does not cover mountain lions.

8.2 Federal Regulatory Mechanisms

8.2.1 National Environmental Policy Act

The National Environmental Policy Act ("NEPA") is the nation's charter for protection of the environment. (40 C.F.R. § 1500.1(a).) NEPA is designed to ensure that environmental information is available to the public *before* decisions are made or actions taken and to help public officials make decisions based on an understanding of the environmental consequences. (40 C.F.R. § 1500.1(b)-(c).) Federal agencies must prepare an environmental impact statement ("EIS") if it is known that an action will significantly affect the environment, or an environmental assessment ("EA") if the extent of effects are unknown. (42 U.S.C§ 4332; 40 C.F.R. §§ 1502.3 & 1508.9.) NEPA further requires federal agencies to analyze reasonable alternatives to the proposed project. (40 C.F.R. § 1502.14(a)-(c).) NEPA requires the federal agency to consider the degree of adverse effect on a species or its critical habitat designated pursuant to the Federal Endangered Species Act. (*Conservation Cong. v. United States Forest Serv*. (E.D.Cal. 2017) 235 F.Supp.3d 1189, 1207.)

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[33] County of San Diego, *Multiple Species Conservation Program*, available at https://www.sandiegocounty.gov/pds/mscp/.

[34] Orange County Transportation Authority, *Natural Community Conservation Plan/Habitat Conservation Plan* (Nov. 2016), available at https://www.octa.net/pdf/NCCP%20HCP%20FINAL.pdf.

However, agencies have not interpreted NEPA as requiring analysis of impacts to populations that are not currently listed as threatened or endangered, such as the Southern California or Central Coast mountain lions. For instance, Caltrans prepared an Initial Study with Proposed Mitigated Negative Declaration/Environmental Assessment for the State Route 118 Widening Project (the "State Route 118 EA") in October 2017 pursuant to NEPA and CEQA. The State Route 118 EA contains no analysis of whether adding more traffic lanes to State Route 118 will impact mountain lions or degrade wildlife connectivity even though multiple mountain lions have died recently attempting to cross State Route 118.[35]

NEPA also is insufficient to protect Southern California and Central Coast mountain lions because courts have interpreted NEPA as primarily a "procedural" statute. While NEPA does require federal agencies to consider detailed information regarding a project's environmental effects, "NEPA itself does not mandate particular results." (*Winter v. NRDC, Inc.* (2008) 555 U.S. 7, 23.)

8.3 Regional and Local Plans and Policies

8.3.1 Santa Monica Mountains National Recreation Area General Management Plan

The Santa Monica Mountains National Recreation Area General Management Plan ("GMP") was prepared pursuant to NEPA and provides a framework for the management of the Santa Monica Mountains National Recreation Area ("SMMNRA"), which is administered by the National Park Service, California State Parks, and the Santa Monica Mountains Conservancy. The GMP recognizes that the Santa Monica Mountains mountain lion population's ability to survive in the face of large-scale habitat fragmentation and destruction is uncertain.[36] (GMP at 154.) The GMP states that "it is likely that their persistence [] would depend upon their capability of dispersing to and from other habitat areas beyond the Santa Monica Mountains." (GMP at 154; see also GMP at 157.) The GMP identifies the "greatest threat" to natural resource preservation in the SMMNRA as "loss of habitat connectivity from increased development and urban encroachment." (*Id*. at 157.) The GMP concedes that "the situation is especially serious for mountain lions" and lists mountain lions as a "park species of concern." (*Id*. at 157 & 161.) The GMP agrees that improvements to facilitate wildlife movement across freeways or through developments may be necessary, but does not propose or require any specific actions to improve wildlife movement across freeways or through development.

The preferred alternative in the GMP provides for enhancing connectivity of undisturbed habitats in the SMMNRA by creating large expanses of open space. (*Id*. at 292.) In addition, the Las Virgenes Canyon and Liberty Canyon areas are included within the SMMNRA boundary to help provide wildlife connectivity for mountain lions and other large species. (*Id*. at 293.) Even though the GMP recognizes the threats facing the Santa Monica Mountains mountain lion

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[35] National Parks Traveler, *Another Mountain Lion Killed Near Santa Monica Mountains National Recreation Area* (Jan. 27, 2017), available at https://www.nationalparkstraveler.org/2017/01/another-mountain-lion-killed-near-santa-monica-mountains-national-recreation-area.

[36] National Park Service, U.S. Department of Interior, *Santa Monica Mountains National Recreation Area General Management Plan Environmental Impact Statement* (July 2002), available at https://www.nps.gov/samo/learn/management/loader.cfm?csModule=security/getfile&PageID=383979.

population and takes steps to protect this population, the GMP does not apply to lands outside of the SMMNRA and thus is insufficient to address the regional connectivity issues facing the population. Nor does the GMP apply to roads and highways under Caltrans' jurisdiction.

8.3.2 Ventura County Wildlife Connectivity Ordinance

The Ventura County Board of Supervisors adopted an ordinance on March 12, 2019 (the "Connectivity Ordinance") to help facilitate wildlife connectivity and minimize habitat fragmentation for mountain lions, mule deer, California gnatcatchers, bobcats, least bell's vireos, California red-legged frogs, and other species. The Connectivity Ordinance establishes overlay zones called "habitat connectivity and wildlife corridors" ("HCWCs") and "critical wildlife passage areas" ("CWPAs") in which development standards and permitting requirements apply. Development standards include 200-foot setbacks from surface water features such as streams and wetlands, limits on certain wildlife impermeable fencing, encouraging compact siting of development, and prohibiting non-commercial planting of invasive plants. Two of the linkages targeted in the Connectivity Ordinance are the Santa Monica Mountains – Sierra Madre Mountains connection and the Sierra Madre Mountains – Castaic Connection, which connect wildlife habitat in the Santa Monica Mountains, Santa Susana Mountains, Simi Hills, and Los Padres National Forest.

While the Connectivity Ordinance should help allow wildlife to move more easily through private lands between core habitat areas, it would do little to ensure connectivity across major roads and highways because Ventura County does not have jurisdiction over these areas. The ordinance would, however, establish 200-foot setbacks from the exit and entry points of 25 existing road crossings in order to facilitate wildlife movement through the crossings. Caltrans and its road maintenance and improvement activities are not regulated by the Connectivity Ordinance. The Connectivity Ordinance is therefore a step in the right direction but insufficient on its own to address the threats facing the CC-S mountain lion population.

8.3.3 Los Angeles County Significant Ecological Areas Program

Los Angeles County is currently in the process of updating the Significant Ecological Areas ("SEAs") Ordinance. The draft ordinance is intended to protect biodiversity in SEAs from incompatible development and ensure that projects reduce habitat fragmentation and edge effects by providing technical review of impacts and requiring mitigation.[37] Like the Ventura County ordinance, the SEAs designations can lead to compact development and allow wildlife to more easily move across private lands between core habitat areas. However, the SEA ordinance is not specifically designed to protect mountain lions and would not regulate Caltrans and its road maintenance and expansion activities.

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[37] Los Angeles County Department of Regional Planning, *Significant Ecological Areas Ordinance Update, Public Hearing Draft* (Feb. 14, 2019), available at http://planning.lacounty.gov/site/sea/wp-content/uploads/2019/02/EX-C-SEA-Ordinance-Public-hearing-Draft-2-14-2019.pdf

8.4 Future Development Will Further Threaten the Survival of Southern California Mountain Lions

Continued development in Southern California is expected to further impair connectivity between core habitat areas, leading to further decreases in genetic diversity for Southern California mountain lions. In the environmental review for Southern California national forest land management plans, the U.S. Forest Service found that impaired connectivity poses a serious threat to Southern California mountain lions: the "greatest concern for the long-term health of mountain lion populations on the national forests of southern California is loss of landscape connectivity between mountain ranges and large blocks of open space on private land."[38] The review warned that private land development in Southern California is "steadily reducing the habitat linkages that wildlife species need to connect large blocks of national forest land with other public and private natural spaces and habitat reserves." The review observed that the "widening of the existing highway system and new highways" are a threat to mountain lions because they create barriers to movement. The review concluded that "[w]ithout the national forests and linkages between the mountain ranges and other large habitat preserves, *there is not much long term potential for mountain lions in southern California.*" The review noted that maintenance and restoration of corridors between large wildlands is essential to conserving mountain lions in Southern California

As anticipated by the U.S. Forest Service's environmental review, private land development is currently being approved on linkage areas without sufficient mitigation for Southern California mountain lions or wildlife connectivity. For instance, the 1,000-acre Northlake Specific Plan ("Northlake") was approved by the Los Angeles County Board of Supervisors on April 2, 2019. The Santa Monica Mountains Conservancy ("SMMC") formally objected to the Board's approval of Northlake, noting that the development would degrade a known wildlife linkage between the Angeles National Forest and Los Padres National Forest.[39] CDFW raised similar concerns about the development because it would impair a linkage that is "highly suitable for regional wildlife movement and connectivity" for mountain lions and other species.[40] The Board of Supervisors approved Northlake notwithstanding the objections and concerns of SMMC and CDFW.

Likewise, the Los Angeles County Board of Supervisors approved the 12,000-acre Centennial Specific Plan ("Centennial") on April 30, 2019, despite SMMC warning the Board that Centennial "would sever the most optimal five-mile-wide habitat linkage across Highway 138 between I-5 and State Route 14."[41]

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[38] Forest Service, U.S. Department of Agriculture, *Final Environmental Impact Statement, Land Management Plans, Angeles National Forest Cleveland National Forest Los Padres National Forest San Bernardino National Forest* (Sept. 2005), available at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5166889.pdf.

[39] Santa Monica Mountains Conservancy, *Draft Supplemental Environmental Impact Report Comments on Northlake Specific Plan Project,* May 22, 2017.

[40] California Department of Fish and Wildlife, *Draft Supplemental Environmental Impact Report Comments on Northlake Specific Plan*, June 12, 2017.

[41] Santa Monica Mountains Conservancy, *Centennial Project Draft Environmental Impact Report Comments County Project No. 02-232,* July 17, 2017.

In the SAM, key linkage and habitat areas remain unprotected and subject to potential or actual development. The Altair Specific Plan discussed in *Section 8 Inadequacy of Existing Regulatory Mechanisms* exemplifies this trend. Other lands in the Santa Ana-Palomar Mountain linkage have been subject to development proposals such as the Temecula Creek Inn (Vickers 2015). The Orange County Board of Supervisors also approved a 6,000-acre development in the Santa Ana Mountains in the "center of puma habitat" (Vickers 2015).[42]

Development in wildlands and linkages will intensify as Southern California's population increases. The Southern California Association of Governments ("SCAG") Program EIR estimates that between 2016 and 2040 the Southern California region will grow by 3.8 million residents and 1.5 million households.[43] The SCAG Program EIR concludes that transportation projects within the SCAG region such as "mixed flow lane projects" and "grade separation projects" may result in significant impacts on wildlife movement, including direct habitat removal and fragmentation that would disrupt corridor functionality. The SCAG Program EIR also acknowledges that "an increase in wildlife-roadway interactions as a result of the development of new transportation projects may increase wildlife injury and fatalities."

The SCAG Program EIR recognizes that "[b]arriers to wildlife movement exist throughout the SCAG region, including large areas of urban development and multilane freeways that cut off regional movement corridors for large migratory species such as mountain lions (*Puma concolor*)." SCAG Program EIR further notes that "wildlife crossings serve to alleviate these barriers and facilitate wildlife movement through the region" and references the planned Liberty Canyon Crossing. However, the Program EIR does not identify any other planned crossings or identify funding for the Liberty Canyon Crossing.

The SCAG Program EIR also confirms that only portions of the lands in the Santa Monica Mountains, SAM, SGSB, and EPR are designated as "open space and recreation" or "undevelopable and protected." Indeed, much of these lands are designated for single family residential or mixed residential. At this time, there are also "vast areas" in Southern California that are undeveloped but are not designated as open space or are otherwise protected, according to SCAG. In addition, agricultural lands are rapidly being converted to urban development throughout Southern California with an estimated 230,000 acres converted between 1996 and 2004 and up to 700,000 acres may be converted by 2030. In short, SCAG recognizes that wildlife connectivity will become even more impaired in the Southern California region due to anticipated growth, but SCAG does not offer any solutions to address the effects of this impaired connectivity on Southern California mountain lions.

Other studies confirm that much of the remaining mountain lion habitat in Southern California is on unprotected lands and at risk of development. According to Burdett et al. (2010), almost half of suitable mountain lion habitat in Southern California (since 1970) is on private lands, of which 35% will be developed by 2030, and other currently contiguous habitat will

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[42] See also Chris Boucly, "New community coming to South County," *The Orange County Register* (Mar. 24, 2012), available at https://www.ocregister.com/2012/03/24/new-community-coming-to-south-county/

[43] Southern California Association of Governments, *Draft Program Environmental Impact Report* (Dec. 2015), available at http://scagrtpscs.net/Documents/2016/peir/draft/2016dPEIR_Complete.pdf.

become fragmented. Hunter et al. (2003) similarly found that 30% of high suitability mountain lion habitat and 76% of medium suitability mountain lion habitat in Southern California is not protected from development. In addition, Zeller et al. (2017) found that only 35% of resource-use patches and 47% of corridors identified in their study area, which encompassed much of the SAM and EPR, were fully protected. Given the extreme isolation, low genetic diversity, and high adult mortality rates from vehicle strikes and depredation kills, increased efforts to protect the species and their habitat are warranted.

Within Riverside County, which covers a significant portion of the Santa Ana Mountains, population growth is expected to be especially high; the Riverside County General Plan predicts that the County's population and housing stock will increase to 3.6 million people and 1.3 million dwelling units by 2035, which constitutes a 65 percent increase.[44] Within San Bernardino County, which encompasses portions of the San Bernardino and San Gabriel Mountains, more than 630,000 people will be added to the County along with 230,000 homes.[45] As urban development overtakes mountain lion habitat and linkage areas throughout the region, conflict with mountain lions, and consequent killing of lions under depredation permits will likely increase. Similarly, use of anticoagulant rodenticides and other environmental toxicants in these areas will likely increase, leading to increased illness and fatalities to "non-target organisms" such as Southern California mountain lions.

Caltrans and local transportation agencies are expected to continue building and expanding roads and highways in Southern California to accommodate actual and anticipated vehicles and development. Caltrans' 2018 State Transportation Improvement Program ("STIP") lists many large-scale road and highway projects planned for Southern California.[46] These include converting SR-71 to a four- and six-lane freeway as well as adding more lanes to the I-15 Freeway adjacent to the SAM,[47] which already acts as a nearly impenetrable barrier to the SAM and EPR mountain lion populations. As noted in *Section 8 Inadequacy of Existing Regulatory Mechanisms*, Caltrans has certified an EIR/EIS to convert the existing two-lane SR-138 into a four or six-lane highway, which will create major barrier between the Tehachapi Mountains and Angeles National Forest. Caltrans also intends to widen SR-118, which will further impair connectivity between the Santa Monica Mountains and Santa Susana Mountains to the detriment of the Santa Monica Mountains mountain lions. There are numerous other road and highway projects planned for Southern California in the next few years.[48] These projects will be funded in part by SB 1, which will raise approximately $52 billion over 10 years.

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[44] County of Riverside, *Riverside County General Plan Environmental Impact Report No. 521* (March 2014), available at https://planning.rctlma.org/Portals/14/genplan/general_plan_2014/EnvironmentalImpactReport/03-0_ProjectDescription_2014-04-07.pdf.

[45] San Bernardino County, *Countywide Plan Growth Forecast*, available at http://countywideplan.com/wp-content/uploads/2018/08/CWP_OH_GrowthForecast_FINAL_20180809.pdf.

[46] California Department of Transportation, *2018 Report on STIP Balances County and Interregional Shares* (Aug. 1, 2018), available at http://www.catc.ca.gov/programs/stip/2018-stip/2018_ORANGE_BOOK.pdf.

[47] Riverside County Transportation Commission, *I-15 Express Lanes Project Southern Extension*, https://www.rctc.org/i15-express-southern-extension/

[48] Kurt Snibbe, "Here are the major highway improvement projects happening in Southern California through 2023," *Orange County Register* (Jan. 23, 2018), https://www.ocregister.com/2018/01/23/here-are-maps-and-a-list-of-the-major-highway-improvement-projects-in-southern-california/; Jeong Park, "2019 will be a busy year for big road construction projects in Orange County," *Orange County Register* (Dec. 31, 2018),

Along with this expansion in roads and highways will come an increase in automobile use: SCAG predicts that the number of vehicle miles travelled ("VMT") in the region is expected to increase 13.3 percent by 2040 (from 448 million VMT per day to 504 million VMT per day). This significant increase in automobile use will further impair connectivity and lead to more collisions between automobiles and lions.

8.5 Future Development Will Further Threaten the Survival of Central Coast Mountain Lions

Future development and highway expansion in the San Francisco Bay Area and Central Coast is anticipated to further fragment habitat for Central Coast mountain lion populations and will increase threats to their survival.

The Association of Bay Area Governments' Plan Bay Area projects that the population of the San Francisco Bay Area is expected to increase from 7.2 million to 9.3 million by 2040—a 30 percent increase.[49] This includes a 26 percent increase in San Mateo County and a 36 percent increase in Santa Clara County, both of which encompass significant portions of the Santa Cruz Mountains. The Plan Bay Area also envisions a 25 percent increase in housing units in San Mateo County, and a 31 percent increase in Santa Clara County.

The Greenbelt Alliance's "At Risk" Report ("Greenbelt Report") estimates that 22,700 acres in San Mateo County are at medium or high risk for development, significant portions of which are in the Santa Cruz Mountains.[50] The Greenbelt Report shows that only 113,000 acres of the Santa Cruz Mountains are permanently protected and warns that San Mateo County has planned to develop housing in remote areas on the eastern slope of the Santa Cruz Mountains. The Greenbelt Report estimates that Santa Clara County has 54,100 acres at high or medium risk of development, significant portions of which are in the Santa Cruz Mountains and eastern foothills. The Greenbelt Report further shows that while large swaths of the eastern Santa Cruz Mountains are currently at "low risk" for development, only fragmented portions enjoy permanent protection.

Similarly, the EIR for the Plan Bay Area 2040 notes that land use growth footprints overlap with approximately 1,040 acres of "Essential Connectivity Areas" or "ECAs." [51] The EIR claims these growth footprints are in already urbanized corridors that are degraded so that their function as linkages is limited. The EIR acknowledges that development projects may directly encroach on wildlife corridors, but does not provide any plan to address the effects of

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https://www.ocregister.com/2018/12/31/2019-will-be-a-busy-year-for-big-road-construction-projects-in-orange-county/.

[49] Metropolitan Transportation Commission and Association of Bay Area Governments, *Bay Area Plan*: *A Strategy for A Sustainable Region* (July 18, 2013), available at http://files.mtc.ca.gov/pdf/Plan_Bay_Area_FINAL/Plan_Bay_Area.pdf.

[50] Greenbelt Alliance, *At Risk 2017* (May 2017), available at https://www.greenbelt.org/at-risk-2017/.

[51] Metropolitan Transportation Commission and Association of Bay Area Governments, *Draft Environmental Impact Report for Plan Bay Area 2040* (April 2017), available at http://2040.planbayarea.org/cdn/farfuture/JHbwWZgw24OSpVBL0b8cJ5_2KHOdckVexpxYp5McOkI/1499352691/sites/default/files/2017-07/PBA%202040%20DEIR_0_1.pdf.

such encroachment. In addition, Caltrans has a number of highway improvement projects planned in Santa Clara and San Mateo counties.[52]

There also is development pressure on the Pajaro Hills linkage, which is important to the Central Coast North mountain lion population and connects the Santa Cruz Mountains and Gabilan Range.[53] The Land Trust of Santa Cruz County notes that while a few large ranches cover most of the Pajaro Hills, many of the properties are parcelized, creating the potential for development which would fragment the landscape. Only 8 percent of the Pajaro Hills is permanently protected.

Growth is expected to increase in the Monterey Bay Area, leading to further fragmentation of natural habitats by urban or exurban development. The Association of Monterey Bay Area Governments predicts that the population in the Monterey Bay Area will rise from 755,403 in 2015 to 883,300 in 2040.[54] The Land Trust of Santa Cruz County notes that while high rates of conversion of forests, rangeland and farmland has largely been prevented in Santa Cruz County, exurban development, roads and mining are fragmenting wildlife habitat. Vineyard conversion adjacent to Zayante, Beer Creek, and Summit roads is causing habitat fragmentation in one of the largest intact habitat patches connecting Santa Cruz and Santa Clara counties. The Land Trust of Santa Cruz County estimates that only 44 percent of the large patches of intact habitat are protected. The Conservation Lands Network likewise confirms that much of the Santa Cruz Mountains do not currently qualify as protected areas.[55]

In San Luis Obispo County, the population is expected to increase by 41,650 between 2015 and 2045.[56] The sparsely populated North Coast region of San Luis Obispo County is currently characterized by ranchlands, rural development, and open space. However, the San Luis Obispo Council of Governments ("SLOCOG") predicts more population growth in this region as compared to other regions. SLOCOG also predicts significant increases in traffic volumes on Highway 101 throughout San Luis Obispo County. The US 101 Corridor Mobility Master Plan also contains various proposals to expand the Interstate 101 freeway in San Luis Obispo County, including adding more lanes to the freeway.[57] There are also proposals to widen portions of State Route 46, the western portions of which bisect mountain lion habitat. The Caltrans State Route 46 Corridor System Management Plan concedes that widening segments 2 and 3 of State Route 46 "could present additional barriers to animal movements by further

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[52] Caltrans District 4, *Projects By County*, available at http://www.dot.ca.gov/d4/projects_list.htm.

[53] Land Trust of Santa Cruz County, *A Conservation Blueprint* (May 2011), available at https://landtrustsantacruz.org/blueprint/conservation-blueprint_low-res_110522.pdf.

[54] Association of Monterey Bay Area Governments, *2040 Metropolitan Transportation Plan/Sustainable Communities Strategy* (June 2018), available at http://ambag.org/programs/met_transp_plann/documents/Final_2040_MTP_SCS/AMBAG_MTP-SCS_Final_EntireDocument.pdf.

[55] Conservation Lands Network, *1.0 Progress Report* (2014), available at https://www.bayarealands.org/wp-content/uploads/2017/07/CLN-1.0-Progress-Report.pdf.

[56] San Luis Obispo Council of Governments, *2019 Regional Transportation Plan Public Review Draft* (Feb. 2019), available at https://www.dropbox.com/s/6pysudp1g36n4a5/__Public%20Rev%20draft.pdf?dl=0 .

[57] San Luis Obispo County of Governments, *US 101Corridor Mobility Master Plan* (Sept. 2014), available at http://www.dot.ca.gov/hq/tpp/offices/ocp/5_SLOCOG%20101_executive_summary_draft_9%2019%2014.pdf.

dividing large, contiguous wildlife habitat areas."[58] There are numerous other road and highway expansion projects planned for Santa Cruz, Monterey, San Luis Obispo, and Santa Barbara counties.[59] The expansion of existing roads and highways along with increased numbers of automobiles will further impair connectivity in the Central Coast region.

9 CESA Listing for Southern California and Central Coast Mountain Lions Would Supplement Proposition 117's Protections.

9.1 CESA Listing is Consistent with Proposition 117.

CESA protections for Southern California and Central Coast mountain lions are consistent with and supplemental to those established by Proposition 117. Both CESA and Proposition 117 include "take prohibitions"—CESA makes it unlawful for any person or agency to import, export, take, possess, or purchase a listed species. (Cal. Fish & Game Code § 2080.) By the same token, Proposition 117 makes it unlawful to take, injure, possess, transport, import, or sell a mountain lion. (Cal. Fish & Game Code § 4800(b).)

Both CESA and Proposition 117's take prohibitions are subject to certain exceptions. Under CESA, CDFW may authorize that a person, agency, or institution take a listed species "for scientific, educational, or management purposes." (Cal. Fish & Game Code § 2081(a).) CESA defines scientific resources management activities to include "research, census, law enforcement, habitat acquisition, restoration and maintenance, propagation, live trapping, and, transplantation, and, in the extraordinary case where population pressures within a given ecosystem cannot be otherwise relieved, [] regulated taking." (*San Bernardino Valley Audubon Society v. City of Moreno Valley* (1996) 44 Cal.App.4th 593, 604, quoting Cal. Fish & Game Code § 2061.) The regulations implementing CESA also allow for the take of a listed species for management or law enforcement purposes: "Department wildlife management activities. The possession or take of endangered, threatened, or candidate species by employees and agents of the Department for scientific, educational and management purposes, and for law enforcement purposes, is not prohibited." (Cal. Code Regs., tit. 14, § 783.1(c).) As discussed above in *Section 8 Inadequacy of Existing Regulatory Mechanisms*, Proposition 117 also contains exceptions which allow for the take of mountain lions in certain circumstances. These exceptions are sufficiently similar that in most cases take of mountain lions properly authorized by Proposition 117 could be consistent with CESA's exceptions for wildlife management activities or law enforcement purposes. (Cal. Code Regs., tit. 14, § 783.1(c).)

9.2 CESA Listing Would Further the Goals of Proposition 117.

CESA listing would further Proposition 117's goals of protecting and restoring wildlife habitat as human populations increase. (Cal. Fish & Game Code § 2780(a).) CESA listing would also help preserve "corridors of natural habitat [] to maintain the genetic integrity" of mountain lions in the Santa Monica Mountains, Santa Ana Mountains, Santa Susana Mountains, Simi Hills, and Coast Range. (Cal. Fish & Game Code § 2780(a).)

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[58] Caltrans, *State Route 46 Corridor System Management Plan* (June 2009), available at http://www.dot.ca.gov/hq/tpp/corridor-mobility/CSMPs/d5_CSMPs/SR%2046/SR-46%20CSMPo100.pdf.

[59] Caltrans District 5, *Projects By County*, available at http://www.dot.ca.gov/d5/.

Likewise, CESA requires that “reasonable and prudent alternatives” that will not jeopardize the existence of a listed species be developed in coordination with the project proponent and state lead agency consistent with conserving the listed species and maintaining the project purpose to the greatest extent feasible. (Cal. Fish & Game Code § 2053(b).) In the event that such alternatives are infeasible, individual projects may still be approved if appropriate mitigation measures are implemented. (Cal. Fish & Game Code § 2054.) CESA envisions these mandates will be incorporated into the CEQA process. (Cal. Fish & Game Code §§ 2064-2065; Cal. Code Regs., tit. 14, §§ 783.3 & 783.5.)

Consistent with Proposition 117, CESA further provides that it is the policy of the state to conserve and protect listed species and their habitat, including through acquiring lands for habitat. (Cal. Fish & Game Code § 2052.) Towards this end, CESA directs state agencies to utilize their authority to conserve listed species. (Cal. Fish & Game Code § 2055.) If the Southern California and Central Coast mountain lions were listed under CESA, this mandate would apply to, for example, Caltrans, which currently lacks a clear mandate to conserve these lions or habitat connectivity necessary for their continued survival.

CESA authorizes CDFW to develop and implement “nonregulatory recovery plans” for listed species with priority given to species that are or may be “significantly affected by anticipated land use changes, climate change, or changes in aquatic conditions.” (Cal. Fish & Game Code §§ 2079.1(a) & (b).) Given the strong evidence that land use changes will significantly affect (and have already significantly affected) Southern California and Central Coast mountain lions, CDFW could develop and implement a recovery plan for these lions pursuant to this provision.

In sum, CESA listing would build upon the protections in Proposition 117 by establishing an affirmative duty to ensure the survival and recovery of the Southern California and Central Coast mountain lions by, *inter alia,* (1) prohibiting the approval of projects that could jeopardize their continued existence or result in destruction of essential habitat (Cal. Fish & Game Code § 2053(a)); (2) requiring state agencies such as Caltrans to utilize their authority to conserve listed species (Cal. Fish & Game Code § 2055); and (3) requiring appropriate mitigation measures be implemented for projects that could destroy mountain lion habitat or impair connectivity (Cal. Fish & Game Code § 2054).

To the extent there is any tension between the provisions in Proposition 117 and CESA, Proposition 117 is to be “liberally construed to further its purposes.” (Prop. 117 § 9.) Because Proposition 117 and CESA both have similar purposes, Proposition 117 should be construed to be consistent with CESA.

10 Recommended Management and Recovery Actions

Recommendations for the management and recovery of Southern California and Central Coast mountain lion populations are as follows:

1. Design and build crossing infrastructure in strategic locations to improve wildlife connectivity and permeability at existing roads and highways. Crossing infrastructure should include but is not limited to overcrossings, underpasses, culverts, and exclusionary fencing that guides animals to safer crossing areas. The following crossing locations have been identified by mountain lion experts and should be prioritized for the implementation of crossing infrastructure: 1) I-15 Freeway at Temecula Creek Bridge to enhance the Palomar Linkage and connect the Santa Ana and Eastern Peninsular Mountain Ranges (Gustafson et al. 2017; Zeller et al. 2017; Ernest et al. 2014; Riley et al. 2018); 2) I-15 Freeway at "Site 5" as described in Riley et al. (2018); 3) Hwy-101 at West Liberty Canyon. (Riley et al. 2018.)

2. Improve or add large culverts to existing freeways in areas suitable for mountain lion crossing. (Vickers 2015).

3. Dedicate sufficient Wildlife Conservation Board, Habitat Conservation Fund and other state funding sources towards acquiring key mountain lion habitat and for establishment of highway crossing infrastructure.

4. Ensure that suitable habitat exists (through preservation or restoration/enhancement) on both sides of crossing structures and culverts (South Coast Wildlands 2008). Restrict human activity near crossing structures and relocate foot trails away from these structures (South Coast Wildlands 2008).

5. Fully protect mountain lion habitat, including resource-use patches and corridors (Zeller et al. 2017; Vickers et al. 2015). Prohibit large-scale development in primary travel corridors and habitat linkages, such as in and around the last remaining linkage for statewide genetic connectivity in the Tehachapi and Sierra Pelona Mountains (Gustafson et al. 2018) and in corridor areas between the SAM and EPR (Gustafson et al. 2017).

6. Require analysis of region-wide wildlife connectivity in all new development proposals (Gustafson et al. 2018).

7. Reduce depredation conflicts that precipitate mountain lion deaths (Vickers et al. 2015). Develop and implement outreach and education activities to promote use of predator-proof enclosures for domestic animals. (Vickers et al. 2015.) Expand CDFW's new three-step depredation permit policy in the CC-S and SAM areas to include all mountain lions across the state, or at a minimum, within the SGSB, EPR, CC-N, and CC-C population areas. Enhance the policy with enforceable implementation of non-lethal protective measures and reporting requirements.

8. Prohibit the use of second-generation anticoagulant rodenticides ("SGARs"), such as brodifacoum, bromadiolone, difenacoum, and difethialone in Southern California and Central Coast mountain lions' core habitat areas and linkages. Limit the use of other pesticides and herbicides that may have negative effects on mountain lion populations in Southern California and the Central Coast.

9. Identify “priority areas” for establishing wildlife passage features for the Southern California and Central Coast mountain lions using the best available science, including data collected by various agencies, academic institutions, and organizations, including but not limited to the National Park Service, the Karen C. Drayer Wildlife Health Center at UC Davis, the Road Ecology Center at UC Davis, and the Santa Cruz Puma Project at UC Santa Cruz.

10. Require Caltrans to analyze how projects in the State Highway Operation Protection Program and State Transportation Improvement Program can be designed to facilitate wildlife connectivity through wildlife passage features such as culverts, undercrossings, overcrossings, bridges, directional fencing, scuppers, barrier breaks, roadside animal detection systems, etc. Require Caltrans to collect and analyze roadkill data to identify hotspots where mountain lions are killed. Require Caltrans to implement wildlife passage features to the greatest extent feasible and as expeditiously as possible.

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