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RESEARCH ARTICLE

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Population decline in California spotted owls near their southern range boundary

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Abstract

Species worldwide have begun to shift their range boundaries in response to climate change and other anthropogenic causes, with population declines at the trailing edge of a species' range often foreshadowing future changes in core parts of the range. Therefore, we analyzed a 30-year (1991–2019) data set for the California spotted owl (*Strix occidentalis occidentalis*) near its southern range boundary in southern California, USA, that included the largest regional population (San Bernardino Mountains) to estimate trends in territory occupancy and reproduction. We then assessed how these demographic rates were affected by habitat, wildfire, fuel treatments, and climate. Mean occupancy declined from 0.82 to 0.39 during our study, whereas reproductive output showed no temporal trends ($\bar{x}$ = 0.65 young/occupied territory). Territory extinction (extirpation) rates were relatively low in territories with more large trees (≥50 cm dbh), and colonization increased strongly with large tree density for low-elevation territories within the shrub-woodland ecotype but not for higher-elevation territories within mixed-conifer forest. High-severity wildfire had an adverse effect on occupancy: territory extinction rates steadily increased with the amount of high-severity fire within an owl territory during the previous 10 years, while colonization declined to nearly zero when ≥40% of a territory burned at high-severity during the previous 10 years. The effects of high-severity fire were unlikely to be confounded with post-fire fuel treatments, which primarily consisted of the removal, burning,

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or scattering of brush and small trees and snags (<40.6 cm dbh) and affected much smaller areas than high-severity fire. Of the 40 territories that received fuel treatments within 10 years of a fire, only 3 of them had post-fire fuel treatments that affected >5% of the territory, whereas average area burned at high severity for all 40 territories was 17%. Fuel treatments intended to modify fire behavior and reduce the likelihood of large, high-severity fires led to increases in territory extinction and colonization such that their net effect on occupancy was minimal. Our simulations of occupancy dynamics indicated that high-severity fire accounted for 9.6% of the observed decline in occupancy, whereas fuel treatments effectively accounted for none of the decline. Spotted owl reproductive output was lower at territories where fuel treatments occurred, but low- to moderate-severity fire resulted in much larger, population-level reductions in reproductive output (141 fewer young) from 2006–2019 than treatments (19 fewer young). Thus, the benefits of fuel treatments that reduce fire occurrence and severity appear to outweigh potential short-term costs to spotted owls and their habitat. Because high-severity fire only explained a modest amount of the long-term occupancy decline and much of the decline occurred in the 1990s before large fires occurred, additional factors are likely adversely affecting the owl population and merit further study. Nevertheless, the large observed population decline, limited evidence of owl dispersal among mountain ranges in the southern California metapopulation, and negative effects of increasingly large and severe fire suggest that California spotted owls at their southern range boundary are vulnerable to extirpation. In an era of climate change, owls in the core part of the range will likely become increasingly susceptible to warmer temperatures and increased severe fire activity in the future. Thus, the restoration of historical, low-severity fire regimes through fuels management while maintaining large trees is important to improving owl persistence.

KEYWORDS

climate change, fuel treatment, reproduction, site occupancy, southern California, spotted owl, *Strix occidentalis occidentalis*, wildfire

Species globally have begun range shifts in response to climate change, but many species still face increased extinction risk if they cannot adjust their ranges quickly enough or respond with adaptive evolution or phenotypic plasticity (Chen et al. 2011, Vedder et al. 2013). Furthermore, risks posed by climate change are compounded by additional stressors such as habitat degradation, overexploitation, and invasive species (Brook et al. 2008, Srinivasan and Wilcove 2021). Consequently, the interaction between climate change and other anthropogenic stressors poses one of the greatest risks to species in evolutionary history. These risks may be most apparent at a species' trailing-edge range boundary (i.e., the southern edge in the northern hemisphere). Here, population fragmentation and genetic drift present unique challenges for species conservation (Hampe and Petit 2005), especially given that habitat disturbance can strongly affect remaining populations (Slaton 2015). Trailing-edge populations may also experience reduced individual fitness from physiological responses to stressful environmental conditions (Hoy et al. 2018). In addition, species adapted to montane ecosystems may be limited by a lack of suitable habitat at higher elevations because the vegetative component of their habitat does not respond rapidly enough to climate change (Anderson et al. 2009, Yandow et al. 2015).

Trailing-edge populations of long-lived organisms might respond even more slowly to environmental changes than populations in the core part of the range because of lagged extinction processes (Hampe and Petit 2005), so observations of population shifts or declines could indicate that important changes are well underway. The California spotted owl (*Strix occidentalis occidentalis*) is a long-lived raptor that is restricted to isolated mountain ranges at its southern range limit in southern California, USA, where suitable habitat is limited by microclimate and altitudinal variation (Gutiérrez et al. 2017). Owls here are threatened by hotter, drier conditions under climate change owing to their narrow thermal niche, and from habitat loss and reduced connectivity among populations because of development (Gutiérrez et al. 2017, Conlisk et al. 2021). Spotted owls are also biologically vulnerable to climate (and other environmental) change because of their low reproductive output, habitat specialization, and small population sizes (Hoffmann and Sgrò 2011, Razgour et al. 2018). For these reasons, quantifying population trends at the trailing edge of the California spotted owl range may be particularly important for predicting future responses by populations within the species' core range.

One of the most impactful broad-scale environmental trends across the range of the spotted owl is the emergence of megafires (Stephens et al. 2014; Jones et al. 2016*a*; Wan et al. 2018, 2019*a*). These large, stand-replacing wildfires can negatively affect spotted owls (Lee et al. 2013; Jones et al. 2016*a*, 2020; Rockweit et al. 2017) and have increased in frequency because of unnaturally high fuel loads after decades of fire suppression, increased human ignitions, and the warmer, drier conditions associated with climate change (Syphard et al. 2007, Steel et al. 2015, Abatzoglou and Williams 2016, Westerling 2016, Stevens et al. 2017). Conversely, historical fire regimes in seasonal dry forests throughout the spotted owl's range consisted of frequent fires that burned primarily at low and moderate severity with smaller patches of high-severity fire (Stephens and Collins 2004, Safford and Stevens 2017). Consequently, owls appear to be well-adapted to these regimes (Bond et al. 2002, 2009; Jones et al. 2020; Schofield et al. 2020; Kramer et al. 2021). To address the increasing threat of megafires, forest managers have implemented fuel-reduction projects that employ techniques such as tree thinning, understory removal, and prescribed fire (Collins et al. 2010, 2013). These treatments and post-fire salvage logging can potentially have negative impacts on spotted owl habitat (Lee et al. 2013, Tempel et al. 2015, Gallagher et al. 2019, Jones et al. 2020). Further investigation of the effects of wildfire and fuel treatments on owls is thus needed to resolve the uncertainty surrounding their relative impacts on owl population dynamics.

The California spotted owl is the only spotted owl subspecies not protected under the Endangered Species Act (ESA). Owl population trends in southern California have not been recently assessed, although prior research demonstrated that the largest population in southern California in the San Bernardino Mountains decreased during the 1990s (Franklin et al. 2004, LaHaye et al. 2004). Since then, temperatures in the region have risen and high-severity fire has increased in area and patch size (Nigro and Molinari 2019), which may have negatively affected these spotted owl populations at the trailing edge of their range. Therefore, we assessed owl demographic trends and the environmental factors that might be affecting these trends to help with conservation decision-making, forest management, and future ESA listing decisions.

We used a 30-year spotted owl data set in southern California to estimate trends in territory occupancy and reproduction and to understand how environmental factors and management actions, such as climate, wildfire, and fuel treatments, have shaped these demographic rates. We predicted that owl occupancy and reproduction were negatively affected by large areas of high-severity fire within their territories, and to a lesser degree, by fuel treatments. We also expected that owls fared better at high elevations than low elevations because of cooler temperatures and more extensive forest cover.

STUDY AREA

Our study area was located within the San Bernardino and Angeles national forests approximately 100–150 km northeast of Los Angeles, California, from 1991–2019. It encompassed the San Bernardino Mountains, San Jacinto Mountains, and eastern extreme of the San Gabriel Mountains (Figure 1) with a total area of approximately 9,000 km^2. These mountain ranges are surrounded by unsuitable landscapes for California spotted owls (e.g., desert, chaparral, urban areas) and movement of owls between the ranges has not been documented (Gutiérrez et al. 2017). Elevations ranged from approximately 500 m to 3,500 m. The climate was Mediterranean, and most precipitation occurred from December–February (winter) as rain or snow. Annual precipitation ranged from 250 mm to 1,000 mm and varied greatly with location, elevation, and topography (Minnich et al. 1995). Vegetation communities transitioned from Mojave Desert scrub and southern coastal scrub at lower elevations to alpine at the highest elevations (Minnich et al. 1995). Great horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*),

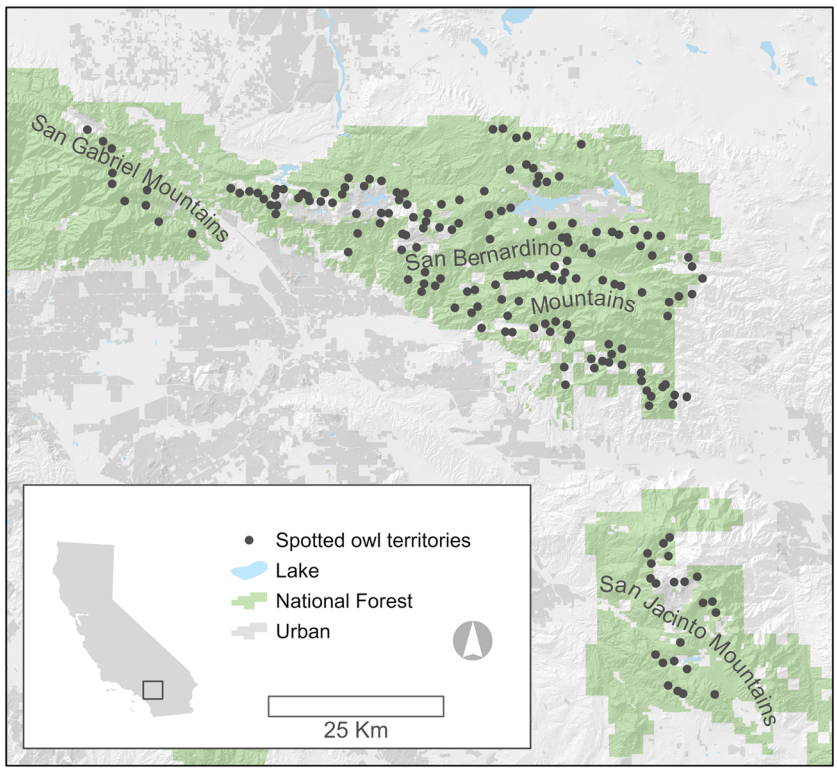

FIGURE 1 Study area in the San Bernardino and Angeles national forests in California, USA, with the locations of California spotted owl territories, 1991–2019

and red-tailed hawks (*Buteo jamaicensis*) were the main predators of spotted owls (Gutiérrez et al. 1995). The dusky-footed woodrat (*Neotoma fuscipes*), Botta's pocket gopher (*Thomomys bottae*), and northern flying squirrel (*Glaucomys sabrinus*) were the primary prey species (Smith et al. 1999). At lower elevations, owl nesting and roosting habitat was restricted to drainages that contained large big-cone Douglas-fir (*Pseudotsuga macrocarpa*) and canyon live oak (*Quercus chrysolepis*) trees and was surrounded by large expanses of shrubs. At higher elevations, mixed-conifer forests were dominated by white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and California black oak (*Q. kelloggii*; LaHaye et al. 2004).

The historical fire regime within the mixed-conifer forest at higher elevations on our study area largely consisted of frequent, low- and moderate-intensity fires, but modern fire suppression has resulted in increased tree densities with fewer fire-resistant large trees (Minnich et al. 1995). Within the big-cone fir-live oak stands at lower elevations, historical fires occurred less frequently with a mean fire return interval of approximately 30 years (Lombardo et al. 2009). Traditional timber harvest on our study area (i.e., with the removal of larger, commercially valuable trees) ended in the early 1980s when most mills in southern California closed (I. E. Turner, U.S. Forest Service [USFS], personal communication). During our study period, forest management consisted mainly of forest restoration and fuel reduction projects to remove smaller trees (<40.6 cm dbh) and understory fuels (USFS 2005), which we collectively refer to as fuel treatments. Major disturbances during our study included the 2003 Old Fire complex, 2007 Butler and Slide fires, 2015 Lake Fire, and a pulse of tree mortality from 2002–2004 in response to drought and bark beetles (*Dendroctonus* spp.). Commercial timber harvest on private lands within our study area was rare (8 records, 140 ha; https://gis.data.ca.gov/, accessed 13 Jul 2020).

METHODS

Spotted owl surveys

We conducted surveys at 181 historical spotted owl territories, whose locations had been previously established during surveys by researchers, consultants, and USFS personnel. Survey effort varied each year depending on available funding, so that not all territories were surveyed every year. We surveyed owl territories from March to September 1991–2019 except for 2001, 2002, and 2014 when a lack of funding precluded any surveys. From 1991–2000, we conducted surveys within the San Bernardino Mountains for a demographic study using mark-recapture methods (LaHaye et al. 2004, Zimmerman et al. 2007). From 2003–2019, we conducted surveys in all 3 mountain ranges strictly to assess occupancy and reproduction (i.e., we did not capture or band birds). We detected owls at night by imitating owl vocalizations at call stations and along survey routes within owl territories (LaHaye et al. 2004). We then conducted diurnal walk-in surveys at territories with recent detections to assess occupancy and reproduction, and to capture and resight birds during the demographic study.

We estimated spotted owl reproduction by feeding live mice to owls and observing the owls' behavior after taking mice. We inferred non-reproduction if an owl ate or cached ≥4 mice or if we observed a roosting female for ≥45 minutes prior to 15 May. Once a pair was known to be nesting, we visited the site after 1 June to visually count fledglings (or band them during the demographic study).

Model covariates and multi-scale framework

We first identified covariates related to vegetation, disturbance, topography, and climate that could affect spotted owl site occupancy and reproduction (Table 1). When estimating covariate values, we created a circle around the territory center with a radius equal to the specified spatial scale and computed the covariate value within the

THE WILDLIFE SOCIETY
THE JOURNAL OF WILDLIFE MANAGEMENT

TABLE 1 Covariates along with their predicted effects and optimal spatial scale for California spotted owl territory extinction (ε), territory colonization (γ), and reproductive output (*R*) in the Angeles and San Bernardino national forests in California, USA, 1991–2019. Predicted effects of each covariate on a parameter could be positive (+), negative (−), or no specific prediction (n/a)

			Predicted effect			Optimal scale (m)		
Covariate	**Description**	**Type**	**ε**	**γ**	***R***	**ε**	**γ**	***R***
LowCC	Annual proportion of territory with canopy cover >30%	Vegetation	−	+	+	3,000	3,000	600
MedCC	Annual proportion of territory with canopy cover >50%	Vegetation	−	+	+	3,000	1,000	600
HighCC	Annual proportion of territory with canopy cover >70%	Vegetation	−	+	+	2,200	1,000	600
Tree	Annual average density of large trees ≥50 cm dbh (tree/ha)	Vegetation	−	+	+	3,000	2,600	2,200
Conifer	Proportion of territory containing montane conifer forest or subalpine forest ecotype	Vegetation	−	+	+	600	3,000	3,000
Hardwood	Annual proportion of hardwoods among all live trees within territory	Vegetation	−	+	+	3,000	2,200	600
Range	Mountain range (0 = San Jacinto or San Gabriel, 1 = San Bernardino, predicted effect for San Bernardino)	Topographic	−	+	+	n/a	n/a	n/a
Elevation	Average elevation (m) within territory	Topographic	−	+	+	600	600	1,800
LMU	Proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW (predicted effect for canyon and midslope NE)	Topographic	−	+	+	1,800	1,000	1,000
Pnest	Average precipitation within territory during the nesting period (Mar–May)	Climate	n/a	n/a	−	n/a	n/a	1,000
Pwinter	Average winter (Dec–Feb) precipitation within territory	Climate	+	−	+	600	3,000	1,800
Tnest	Average minimum temperature within territory during the nesting period (Mar–May)	Climate	n/a	n/a	−	n/a	n/a	1,000
LSfire	Proportion of territory burned by low- or moderate-severity wildfire[a]	Disturbance	−	+	+	1,000	3,000	600
HSfire	Proportion of territory burned by high-severity wildfire[b]	Disturbance	+	−	−	600	600	600

TABLE 1 (Continued)

Covariate	Description	Type	Predicted effect			Optimal scale (m)		
			ε	γ	*R*	ε	γ	*R*
HSpatch	Maximum patch size of high-severity fire within territory[b]	Disturbance	+	−	−	1,000	600	600
WUI	Proportion of territory containing wildland-urban interface	Disturbance	+	−	−	3,000	1,400	2,200
Fuel all	Proportion of territory with possible fuel reduction treatments (all treatments in FACTS database)[c]	Disturbance	+	−	−	1,000	600	1,000
Fuel NAIP	Proportion of territory with confirmed fuel reduction treatments (using aerial photos)[c]	Disturbance	+	−	−	600	600	600
Post-fire	Proportion of territory with post-fire fuel reduction treatments[c]	Disturbance	+	−	−	1,000	1,000	1,000
Mortality	Total % tree mortality within territory from 2001–2005 that was unrelated to fuel treatments or wildfire	Disturbance	+	−	−	1,000	1,000	1,000

[a]Evaluated at 2 time scales: within the previous year and previous 5 years.

[b]Evaluated at 3 time scales: within the previous year, previous 5 years, and previous 10 years.

[c]Evaluated at 2 time scales: within the previous year and previous 3 years.

THE JOURNAL OF WILDLIFE MANAGEMENT
THE WILDLIFE SOCIETY

defined area. We determined the territory center using the following hierarchy of information: the average coordinates of all nest locations, the average coordinates of all roost locations, or the centroid of the protected activity center designated by the USFS. We computed covariate values at 7 spatial scales (600–3,000 m using 400-m increments) and determined the optimal scale for each covariate independently (Statistical analyses—model selection).

Vegetation covariates

California spotted owls depend upon large trees for nest sites that are typically located in forests with high canopy cover (LaHaye et al. 1997, Roberts 2017). Blakesley et al. (2005) reported that site occupancy was positively related to the amount of forest with large trees (>61 cm dbh) and high canopy cover (>70%) in the nest area (203 ha). Other researchers reported a positive association between site occupancy in the Sierra Nevada and forests with high canopy cover that contain medium-sized (30.4–61 cm dbh) or large trees (Seamans and Gutiérrez 2007*a*, Tempel et al. 2014), or with forests that have medium (40–70%) or high canopy cover (Tempel et al. 2016). These studies were all conducted at a spatial scale equal to half the mean nearest neighbor distance among territories. California spotted owls also select forest stands with medium to large trees and high canopy cover for nesting (LaHaye et al. 1997, Moen and Gutiérrez 1997, Blakesley et al. 2005); therefore, reproduction may also be positively associated with larger trees and higher canopy cover. Using the same criteria for tree size and canopy cover as above, we originally defined 4 categories of owl habitat: large trees, high canopy cover; large trees, medium canopy cover; medium trees, high canopy cover; and medium trees, medium canopy cover. The resulting habitat maps showed that most owl territories on our study area contained little habitat in either large tree category, particularly with high canopy cover. This finding was likely the result of differences between southern California and the Sierra Nevada in climate, vegetation types, and growing conditions that led to sparser tree cover in southern California. These differences could also affect the optimal tree size and canopy cover for owl habitat selection in southern California. Therefore, we instead defined independent covariates for 3 categories of canopy cover (>30%, >50%, >70%) and the average density of large trees (≥50 cm dbh) within owl territories. The canopy cover categories were nested, which allowed us to assess the importance of specific ranges of canopy cover. For example, if a model with >50% canopy cover was a better predictor than a model with >30% canopy cover, then forests with canopy cover between 30–50% would be relatively less important than forests with canopy cover >50%.

Territory density and nest productivity (number of young per successful nest) in the San Bernardino Mountains is greater in coniferous forests containing more oak trees (e.g., big-cone Douglas-fir–canyon live oak forest; LaHaye et al. 1997, Smith et al. 2002). Forests on our study area with a significant oak component likely support a higher density of dusky-footed woodrats than forests with fewer oaks because acorns are an important food source for the woodrats (Horton and Wright 1944, Innes et al. 2007), and woodrats in turn are the most important prey item for spotted owls on our study area (Smith et al. 1999). Owls that consume more woodrats have greater reproductive success in this area (Smith et al. 1999). Thus, we included the proportion of hardwoods within forested areas as a covariate.

Vegetation mapping

We used gradient nearest neighbor (GNN) forest maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group at Oregon State University (https://lemma.forestry.oregonstate.edu/, accessed 14 Oct 2020) to estimate vegetation covariate values within owl territories. The GNN applied direct gradient analysis and nearest-neighbor imputation to regional field plot data, mapped environmental data, and Landsat imagery to generate predictive maps of forest structure and composition (Ohmann and Gregory 2002). The GNN

maps had a 30 × 30-m spatial resolution and were available annually for our study area. We used these maps to estimate each year the proportion of each territory containing the 3 canopy cover classes and the average large tree density within each territory. Finally, we estimated the proportion of hardwoods as the basal area of live hardwoods ≥2.5 cm dbh divided by the basal area of all live trees (hardwood and conifer) ≥2.5 cm dbh.

We also obtained Level IV ecosystem maps produced by the Environmental Protection Agency (https://www.epa.gov/eco-research/ecoregions, accessed 13 Jul 2020). These ecosystem maps were last updated in 2013. Four ecosystem types were present on our study area: montane conifer, subalpine-alpine, lower montane shrub-woodland, and arid montane. We combined montane conifer with subalpine-alpine and lower montane shrub-woodland with arid montane because only a few owl territory centers were located within the subalpine-alpine and arid montane zones. We were particularly interested in models that included an interaction between the proportion of montane conifer forest and hardwoods because conifer forests with more oak trees may contain more woodrats (Innes et al. 2007). Because territories containing more montane conifer forest may have been more likely to persist during our study period, we also included an interaction between montane conifer forest and a linear time trend.

Topographic and climate covariates

Higher elevations may offer refugia to owls faced with warming temperatures from climate change (Jones et al. 2016*b*), and reproductive success on our study area has a strong positive association with elevation (Smith et al. 1999). Because higher-elevation territories having more forest and cooler temperatures may have been more likely to retain owls over the course of our study, we also included a model with an interaction between elevation and a linear time trend. The San Bernardino Mountains harbor the largest population of spotted owls and greatest extent of suitable habitat in southern California (Gutiérrez et al. 2017), so we included a covariate for mountain range (San Bernardino vs. San Jacinto or San Gabriel). Territories located on north-facing slopes and in riparian areas may provide more favorable microclimates for spotted owls and their prey (Gutiérrez et al. 2017, Hobart et al. 2019*b*), so we included a covariate for land management unit (LMU; North et al. 2012). We used this covariate to classify 4 categories of topography and aspect: ridge, canyon or drainage, midslope with northeast aspect (316° to 135°), and midslope with southwest aspect (136° to 315°).

Climatic conditions (temp, precipitation) and the age of breeding females affect reproductive output in spotted owls (LaHaye et al. 2004, Seamans and Gutiérrez 2007*b*). We lacked information on the age and identity of territorial birds after the demographic study ended in 2000, but we obtained monthly temperature and precipitation data with a 4-km × 4-km spatial resolution from the PRISM Climate Group at Oregon State University (https://prism.oregonstate.edu/, accessed 18 Sep 2020). LaHaye et al. (2004) reported that reproductive output on our study area was positively associated with drier conditions during the nesting period and wetter conditions during the preceding winter. Cold weather during the nesting period can also reduce reproductive output in spotted owls (Seamans and Gutiérrez 2007*b*). Therefore, we estimated the annual average precipitation within spotted owl territories during the nesting period (Mar–May) and previous winter (Dec–Feb), and the annual average minimum temperature during nesting. We did not include the nesting season covariates in the occupancy models.

Disturbance covariates

We included 3 covariates that reflected wildfire history within owl territories: proportion of an owl territory that burned at low- or moderate-severity (low-moderate severity), proportion of an owl territory that burned at high-severity, and maximum patch size of high-severity fire within an owl territory. We defined high-severity fire as fire that resulted in >75% overstory mortality, then we classified all other fire as low-moderate severity. We used a

combination of 2 data sources to assess burned area and fire severity. The first was the Monitoring Trends in Burn Severity database (MTBS; http://www.mtbs.gov/, accessed 2 Jul 2020), which accounted for severity in all fires in our study area >405 ha in size (Eidenshink et al. 2007). We supplemented this dataset with fire perimeters for fires <405 ha in size from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP; https://frap.fire.ca.gov/, accessed 22 Sep 2020), which included all wildland fires that burned >40.5 ha but did not include an assessment of severity. Because smaller fires are often of lower severity, however, we included these areas in the low-moderate severity category. If this assumption was incorrect, we expected it to have little effect on our analyses because only 6.5% of the burned area during our study was from fires <405 ha. We hypothesized that low- to moderate-severity fire would have a positive or no effect on spotted owl occupancy and reproduction (Bond et al. 2002, 2009, 2016; Schofield et al. 2020; Kramer et al. 2021) but that high-severity fire (extent and patch size) would have a negative effect (Lee et al. 2013; Jones et al. 2016*a*, 2020; Rockweit et al. 2017). Because fire can affect spotted owl habitat for extended time periods, we estimated these covariates at 2 temporal scales: within the previous year and within the previous 5 years. We expected the effects of high-severity fire, particularly large patches, to persist longer than low- to moderate-severity fire (Jones et al. 2021), so for high-severity fire extent and patch size we also included the amount that occurred within the previous 10 years.

To estimate the proportion of an owl territory affected by fuel treatments, we obtained fuel treatment data on our study area from the USFS Activity and Tracking System (FACTS; https://data.fs.usda.gov/geodata/, accessed 13 Jul 2020). When estimating fuel treatment covariates, we used all treatments in the FACTS database regardless of the activity type. Spatially explicit data were only available from 2003 onwards, so we estimated the fuel treatment covariates at a 1-year and 3-year time scale to use as much of the owl data as possible. We then conducted separate analyses of fuel treatments using a subset of the spotted owl data (2006–2019). We considered 2 spatial scales (600 m and 1,000 m) for all fuel treatment covariates. To assess the accuracy of the FACTS data, we compared the treatment boundaries to National Agriculture Imagery Program (NAIP) aerial imagery from 2002, 2005, 2009, 2010, 2012, 2014, 2016, and 2018. We specified 2 categories for treatments in the FACTS database: those that we confirmed from aerial imagery (i.e., we saw clear evidence of tree or shrub removal) and those that we could not confirm (i.e., no clear evidence from imagery). Unconfirmed treatments may have been the result of errors in the database (i.e., planned projects that were never completed) or may have been undetectable from aerial photos (i.e., understory removal obscured by overstory trees).

To reflect our uncertainty in these data, we created 2 fuel treatment covariates: one that included all treatments in the FACTS database and one that included only confirmed fuel treatments. The effect of salvage logging in the Sierra Nevada on owls has been variable (Lee et al. 2013; Jones et al. 2016*a*, 2020), and while there is not a direct equivalent to salvage logging in southern California, we included post-fire fuel treatments as a proxy. We defined post-fire fuel treatments as those that occurred up to 10 years after a fire and within the fire perimeter.

In addition, many treatments were performed between 2003–2010 in forests with recent tree mortality from drought and bark beetles (I. E. Turner, USFS, personal communication). Because fuel treatment effects on owls at these locations may have been confounded with prior tree mortality, we included a covariate for cumulative tree mortality unrelated to fuel treatments or wildfire that occurred from 2001–2005. We obtained tree mortality information at 30-m resolution from the Ecosystem Disturbance and Recovery Tracker (eDaRT), an image analysis system that processes historical Landsat imagery to detect disturbances as compared to a recent historical baseline (Koltunov et al. 2020; complete details available online in Supporting Information). We excluded areas with fuel treatments and wildfire during the year that these tree mortality disturbances occurred and the following year, except for high-severity fire where we excluded these areas for the following 4 years.

Finally, several communities and private developments were interspersed throughout our study area, creating areas of wildland urban interface (WUI). The WUI can negatively affect wildlife through habitat loss, fragmentation, and associated human activities such as recreation (Theobald et al. 1997, Bar-Massada et al. 2014). For public safety purposes, many fuel-reduction treatments were also located within or in proximity to the WUI. We acquired

WUI data for 1990, 2000, and 2010 from the Spatial Analysis for Conservation and Sustainability lab at the University of Wisconsin (http://silvis.forest.wisc.edu/, accessed 10 Sep 2020). We estimated the proportion of an owl territory containing WUI using the combined amount of the interface and intermix categories (Bar-Massada et al. 2014, Radeloff et al. 2018).

Statistical analyses

Territory occupancy

We used a dynamic occupancy model that contained parameters for initial occupancy (ψ_1), territory extinction (ε_t), territory colonization (γ_t), and detection probability ($p_{t,j}$; MacKenzie et al. 2003). Our primary sampling periods (t) were years, and our secondary sampling periods (j) were survey occasions within years. We used the program PRESENCE (version 12.12) to perform the analyses (Hines 2006). We initially attempted to use multi-state models (MacKenzie et al. 2009) with 3 states (unoccupied, occupied without reproduction, occupied with reproduction), but the large number of parameters in many of the multi-state models resulted in a failure to converge and precluded a robust analysis. We included only diurnal detections in our detection histories to avoid false positive responses from non-territorial floaters or birds in neighboring territories (Berigan et al. 2019). To be included in the detection histories, surveys had to be ≥3 days apart, and the duration of surveys with no detection had to exceed 15 minutes. Because some territories were visited up to 10 times in some years to assess reproduction or resight color bands, we truncated detection histories at 6 survey occasions per year to reduce the number of missing values in the detection data.

Reproductive output

We used mixed-model analysis of variance (PROC MIXED in SAS 9.4; Littell et al. 2006) to model covariate effects on reproductive output, which we defined as the number of young fledged at an occupied territory. We treated our covariates as fixed effects, and territory and year as random effects. We considered territory to be a random effect because reproduction within a territory may not be independent among years. We treated reproductive output as a normally distributed variable because normal regression models perform well in analyses of spotted owl reproductive data (McDonald and White 2010). We used restricted maximum likelihood estimation to assess the following variance-covariance structures for repeated observations within territories: compound symmetric, first-order autoregressive, heterogeneous first-order autoregressive, and log-linear (Littell et al. 2006). After identifying the best variance–covariance structure, we used full maximum likelihood estimation to model covariate effects on reproductive output.

Model selection

For both occupancy and reproductive output, we first determined the optimal spatial scale and functional form for each covariate by fitting univariate models (using linear and quadratic forms) at all scales and finding the univariate model with the lowest Akaike's Information Criterion (AIC) value (Burnham and Anderson 2002, Wan et al. 2019*b*). We centered all covariate values to improve the interpretability of regression coefficients in quadratic models (Schielzeth 2010). For occupancy, we identified a separate optimal scale and functional form for each parameter (ψ_1, ε, and γ) using models with a constant value for the non-target parameters (Morin et al. 2020). For all analyses, we did not include highly correlated covariates in the same model (Spearman's rank coefficient, $r_s > 0.6$). Elevation,

for example, could not be included in models with many of the vegetation and climate covariates because of high correlations.

For the occupancy modeling, we used a multi-stage model selection strategy referred to as a secondary candidate set strategy, which can efficiently identify important covariates for models containing multiple parameters (Bromaghin et al. 2013, Morin et al. 2020). We initially determined the best structure for p, which we used in all subsequent modeling. For within-year p, we included a covariate for reproductive status (breeding vs. non-breeding owls; Tempel et al. 2014). For annual p, we used covariates for the survey objectives (1991–2000 demographic study vs. 2003–2019 occupancy surveys), a year effect, and 3 different temporal trends (linear, log-linear, and quadratic). In the first stage, we independently modeled covariate effects at their optimal scale on each parameter (ψ_1, ε, and γ [i.e., a sub-model]). In addition to sub-models with covariate effects, we included a constant (i.e., null) sub-model and a sub-model with year effects for the target parameter. We again held the non-target parameters constant to allow for the investigation of more complex sub-model structures and avoid potential convergence issues (Morin et al. 2020). For each parameter, we then carried forward into the final stage all sub-models within 5 AIC units of the top-ranked sub-model that did not contain uninformative parameters; when an additional parameter was added to the top-ranked model but did not provide a net reduction in AIC, we considered the parameter to be uninformative (Arnold 2010). In the final stage, we fit all combinations of sub-models and ranked this final model set using AIC values.

To assess the effects of fuel treatments and tree mortality on occupancy and reproductive output, we conducted separate analyses using a subset of the owl survey data (2006–2019) because we lacked spatially explicit fuel treatment information prior to 2003 and calculated some covariates on a 3-year time scale. We used the top-ranked model from the 1991–2019 data analyses as a baseline model and added fuel treatment and tree mortality covariates at 2 spatial scales (600 m and 1,000 m) to this model. We used the same model selection strategies discussed above, except that we carried forward into the final stage all sub-models within 2 AIC units of the top-ranked sub-model. For initial occupancy, we ran additional models where we replaced low-severity fire (from the baseline model) with the amount of high-severity fire in the previous 10 years because major fires occurred in 2003. Initial occupancy models with the low- or moderate-severity fire covariate had lower AIC values than models with the high-severity fire covariate, so we retained the baseline model from the 1991–2019 data analyses.

Population impact analyses

We conducted territory-based simulations to assess the degree to which wildfire and fuel treatments affected occupancy and reproductive output over the study period. We simulated occupancy histories from 1991–2019 at each territory using annual colonization and extinction probabilities calculated using beta coefficients from the top-ranked model and territory-specific covariate values. We assigned each territory an initial occupancy state (0 or 1) based on its occupancy status in the first year that we surveyed it during our study, and thereafter we iteratively simulated the annual occupancy state using the following equation (MacKenzie et al. 2003):

$$\psi_t = \psi_{t-1}(1 - \varepsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}.$$

An occupied territory became unoccupied if a random number between 0 and 1 was less than ε_t, and an unoccupied territory became occupied if the random number was less than γ_t. Otherwise, the territory state remained unchanged. We also calculated turnover at each territory, which occurred when a territory changed its occupancy state from the previous year. Finally, we calculated reproductive output for each territory using coefficients from the top-ranked reproductive output model and territory-specific covariate values. If a territory was occupied during a given year, we assigned it the expected reproductive output for that year. If a territory was unoccupied during a given year, reproductive output was zero.

We ran 10,000 simulations of occupancy and reproduction dynamics under 2 scenarios: a baseline scenario that used the actual, centered covariate values from our study and a no-fire scenario that used actual covariate values except for wildfire, which was assigned zero values for all years (i.e., these values were slightly negative because we centered all covariates in our analyses). To determine the impacts of wildfire and fuel treatments from 2006–2019, we repeated these simulations under 3 scenarios: a baseline scenario that used the actual covariate values, a no-fire scenario, and a no-treatment scenario. We conducted these analyses with Microsoft Excel (Microsoft Corporation, Redmond, WA, USA) and @Risk (Palisade Software, Ithaca, NY, USA).

RESULTS

We conducted 12,965 owl surveys during our study. In years that we conducted surveys, the average number of territories surveyed was 114.0 (range = 7–179). The average number of years that a territory was surveyed was 16.3 (range = 3–25).

Occupancy

Primary analyses

Detection probability for owls was best explained by reproductive status and year with breeding owls more likely to be detected than non-breeders ($\beta = 0.95 \pm 0.07$ [SE]). With our primary analyses using data from all years, the optimal spatial scale of covariates for territory extinction and colonization was predominantly at either the smaller 2 or largest scales. Fifty percent of the covariates had an optimal scale of 600 m or 1,000 m and 33.3% had an optimal scale of 3,000 m (Table 1). We carried forward 4 sub-models for initial occupancy, 2 sub-models for colonization, and 8 sub-models for territory extinction to the final modeling stage (Tables S1–S3; available online in Supporting Information). Mountain range was a covariate in 3 of the initial occupancy sub-models, but in the final stage the beta coefficient for range could not be estimated. Thus, we removed range as a covariate from ψ_1 sub-models in the final modeling stage. In the final stage, 18 models were within 2 AIC units of the top model (Table 2), which suggested substantial uncertainty. These models contained many of the same covariates (Table 2), and the beta coefficients for territory colonization and extinction were very similar among the different models for common covariates. For example, all competing models indicated a quadratic relationship between colonization and either high-severity fire (10-yr time scale) or high-severity patch size (10-yr time scale). In addition, all models showed an effect of high-severity fire on territory extinction, either a linear relationship at the 10-year time scale or a quadratic relationship at the 5-year time scale. All models also included a quadratic relationship between large tree density and both territory colonization and extinction.

The top-ranked model contained a term for high-severity fire patch size on colonization, but the total amount of high-severity fire had a similar functional relationship with colonization and was in a closely competing model (ΔAIC = 0.37; Table 2). When high-severity fire burned >40% of a territory at the 600-m scale, colonization declined to nearly zero, while extinction continued to increase with more high-severity fire (Figure 2A). Similarly, colonization declined to nearly zero when the maximum patch size of high-severity fire was >25% of a territory at the 600-m scale. The most significant fire year was 2003 when 32 territories were affected by high-severity fire at the 600-m spatial scale (Figure 3A), and the average proportion of these territories burned by high-severity fire was 0.28 (range = 0.01–0.73). Although historical fire regimes differed between low-elevation and high-elevation vegetation types, fire occurrence during our study was similar for the shrub-woodland and conifer ecotypes. Fire burned 46% of the shrub-woodland ecotype and 43% of the conifer ecotype, with nearly identical proportions of low-moderate and high-severity fire occurring in each ecotype.

TABLE 2 Top-ranked models for dynamic occupancy analysis of California spotted owl territories in the San Bernardino and Angeles national forests in California, USA, 1991–2019. Detection probability (p) varied with year and the reproductive status of territorial birds. Other model terms are initial occupancy (ψ_1), territory colonization (γ), and territory extinction (ε). All models with difference in Akaike's Information Criterion (ΔAIC) < 2.0 are included, K = number of parameters, and $\log\mathscr{L}$ = log likelihood. Quadratic relationships are indicated by covariate^2

Sub-models[a]	ΔAIC	AIC	AIC weight	*K*	$-2\log\mathscr{L}$
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2)	0.00	8,975.48	0.056	54	8,867.48
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, LMU, WUI^2)	0.08	8,975.56	0.054	57	8,861.56
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2)	0.37	8,975.85	0.046	54	8,867.85
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, LMU, WUI^2)	0.65	8,976.13	0.040	57	8,862.13
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, LMU, WUI^2)	0.70	8,976.18	0.039	58	8,860.18
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, WUI^2, HighCC^2)	0.80	8,976.28	0.037	57	8,862.28
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2, HighCC^2)	0.84	8,976.32	0.037	56	8,864.32
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, WUI^2)	0.88	8,976.36	0.036	55	8,866.36
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, WUI^2)	0.88	8,976.36	0.036	55	8,866.36
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, LMU, WUI^2)	1.01	8,976.49	0.034	58	8,860.49
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, WUI^2, HighCC^2)	1.06	8,976.54	0.033	57	8,862.54
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2, MedCC)	1.39	8,976.87	0.028	55	8,866.87
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2, HighCC^2)	1.40	8,976.88	0.028	56	8,864.88
ψ_1(LMU, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2)	1.48	8,976.96	0.027	53	8,870.96
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, WUI^2, MedCC)	1.56	8,977.04	0.026	56	8,865.04
ψ_1(LMU, LSfire1), γ(tree^2, range, HSpatch10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, LMU, WUI^2)	1.62	8,977.10	0.025	56	8,865.10

TABLE 2 (Continued)

Sub-models[a]	ΔAIC	AIC	AIC weight	*K*	−2log$\mathscr{L}$
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire5^2, WUI^2, MedCC)	1.80	8,977.28	0.023	56	8,865.28
ψ_1(LMU, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2)	1.82	8,977.30	0.023	53	8,871.30
ψ_1(LMU, WUI, LSfire1), γ(tree^2, range, HSfire10^2, LMU, WUI, Pwinter), ε(tree^2, range, HSfire10, WUI^2, MedCC)	1.92	8,977.40	0.021	55	8,867.40

[a]The covariates are defined as tree = annual average density of large trees ≥50 cm dbh (trees/ha); MedCC = annual proportion of territory with canopy cover >50%; HighCC = annual proportion of territory with canopy cover >70%; range = mountain range (0 = San Jacinto or San Gabriel, 1 = San Bernardino); Pwinter = average winter (Dec–Feb) precipitation within territory; LMU = proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW; LSfire1 = proportion of territory burned by low- or moderate-severity wildfire in previous year; HSfire5 = proportion of territory burned by high-severity wildfire within previous 5 years; HSfire10 = proportion of territory burned by high-severity wildfire within previous 10 years; HSpatch10 = maximum patch size of high-severity fire within territory within previous 10 years; WUI = proportion of territory containing wildland-urban interface.

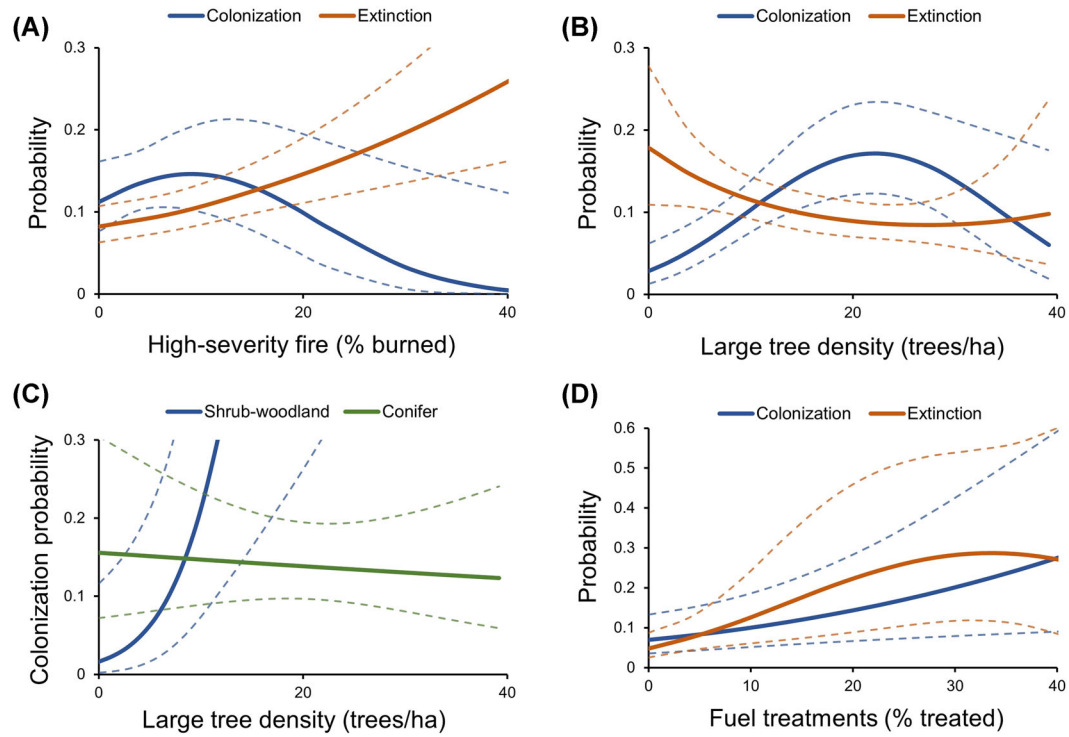

FIGURE 2 Selected covariate relationships with site colonization and extinction for California spotted owl territories in the San Bernardino and Angeles national forests in California, USA. The dashed lines indicate 95% confidence intervals. A) The effect of high-severity fire in the previous 10 years on territory colonization and extinction, 1991–2019. B) The effect of large tree density on colonization and extinction for all spotted owl territories, 1991–2019. C) The effect of large tree density on colonization for spotted owl territories within the shrub-woodland and conifer ecotypes, 1991–2019. D) The effect of fuel treatments in the previous 3 years on territory colonization and extinction, 2006–2019

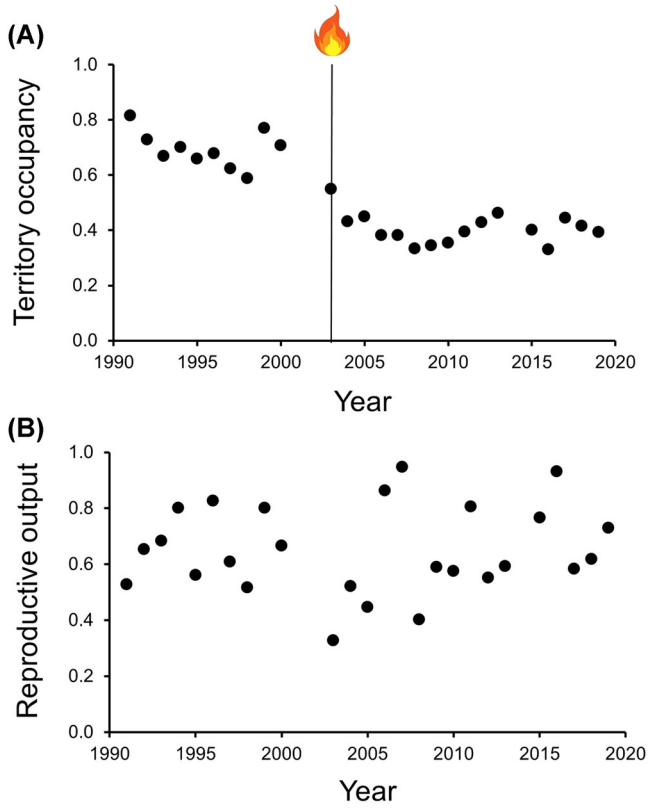

FIGURE 3 A) Mean site occupancy at California spotted owl territories (n = 181) in the San Bernardino and Angeles national forests in California, USA, 1991–2019. Mean occupancy was estimated from conditional occupancy probabilities at each territory provided by program PRESENCE. The 2003 fire season is indicated by the vertical bar and flame symbol. B) Mean reproductive output (number of young fledged) per occupied spotted owl territory, 1991–2019

Territory colonization increased as large tree density increased to about 20 trees/ha then declined with greater density, whereas territory extinction declined by half as tree density increased to approximately 20 trees/ha before leveling off (Figure 2B; Table 3). This quadratic relationship between large trees and colonization was apparently largely driven by the difference between lower-elevation territories in the shrub-woodland ecotype and higher-elevation territories in the conifer ecotype. Therefore, we compared parameter estimates for the linear effect of large trees on colonization from models using data from territories completely within the shrub-woodland ecotype at the 600-m scale (n = 42), and data from territories completely within the conifer ecotype (n = 112) at the 600-m scale. We observed a strong, positive relationship between colonization and large tree density for shrub-woodland territories, and a weak, negative relationship for conifer territories (Figure 2C). Furthermore, 95% of shrub-woodland territories had large tree densities <10 trees/ha, whereas 90% of conifer territories had densities >10 trees/ha. We then conducted a *post hoc* model using the full data set that contained an interaction between large tree density and the proportion of conifer forest. Although this model had ΔAIC = 3.89, the beta coefficients for colonization indicated a negative interaction between large trees and conifer forest ($\beta_{tree} = 1.55 \pm 0.79$; $\beta_{conifer} = -0.25 \pm 0.59$; $\beta_{tree \times conifer} = -4.74 \pm 2.14$). This suggested that the quadratic relationship between colonization and large tree density for all territories was influenced by the dichotomy between ecotypes.

TABLE 3 Beta coefficients (SE) for covariate effects from the top-ranked models for dynamic occupancy and reproductive output (*R*) at California spotted owl territories in the Angeles and San Bernardino national forests in California, USA, 1991–2019. The model parameters for dynamic occupancy are initial occupancy (ψ_1), territory extinction (ε), and territory colonization (γ). An asterisk (*) indicates that the 95% confidence interval did not overlap zero. The beta coefficients for fuel treatment and tree mortality covariates were estimated from models using 2006–2019 data

Covariate[a]	ψ_1	ε	γ	*R*
Tree		−1.06 (0.41)*	2.15 (0.60)*	
Tree^2		1.64 (1.51)	−5.61 (1.92)*	
HighCC				0.29 (0.12)*
Range		−0.61 (0.31)*	0.56 (0.32)	
Pwinter			−2.66 (0.93)*	
Tnest				0.17 (0.11)
LMU: NE slope	−0.08 (4.83)		−4.27 (1.50)*	−0.11 (0.30)
LMU: ridge	−6.78 (8.39)		−4.22 (2.75)*	−0.92 (0.52)
LMU: SW slope	−9.86 (5.90)		−5.36 (1.72)*	−0.61 (0.35)
LSfire1	−1,269.95 (448.93)*			
LSfire5				−0.46 (0.21)*
HSfire10		3.38 (0.83)*		
HSpatch10			2.11 (4.04)	
HSpatch10^2			−105.93 (52.46)*	
WUI	6.59 (4.08)	−2.95 (1.11)*	2.46 (0.97)*	
WUI^2		9.17 (2.67)*		
Fuel all3	−26.49 (16.91)	10.86 (4.95)*	3.93 (1.60)*	−0.87 (0.49)
Fuel all3^2	113.12 (74.12)	−17.27 (14.05)		
Mortality	0.23 (0.06)*	−0.21 (0.05)*		
Mortality^2	−0.03 (0.01)*	0.03 (0.01)*		

[a]The covariates are defined as tree = annual average density of large trees ≥50 cm dbh (trees/ha); HighCC = annual proportion of territory with canopy cover >70%; range = mountain range (0 = San Jacinto or San Gabriel, 1 = San Bernardino); Pwinter = average winter (Dec–Feb) precipitation within territory; Tnest = average minimum temperature within territory during the nesting period (Mar–May); LMU = proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW; LSfire1 = proportion of territory burned by low- or moderate-severity wildfire in previous year; LSfire5 = proportion of territory burned by low- or moderate-severity wildfire within previous 5 years; HSfire10 = proportion of territory burned by high-severity wildfire within previous 10 years; HSpatch10 = maximum patch size of high-severity fire within territory within previous 10 years; WUI = proportion of territory containing wildland-urban interface; Fuel all3 = proportion of territory with possible fuel reduction treatments (all treatments in FACTS database) within previous 3 years; mortality = total % tree mortality within territory from 2001–2005 that was unrelated to fuel treatments or wildfire.

Other beta coefficients from the top-ranked model indicated higher colonization and lower extinction rates in the San Bernardino Mountains compared to the San Jacinto and San Gabriel Mountains, which resulted in higher occupancy rates in the San Bernardino Mountains (Table 3; Figure S1 in Supporting Information). Colonization probabilities were higher in territories that contained a greater proportion of canyon drainages relative to the other landscape types (ridges and slopes; Table 3). For example, the odds ratio indicated that a territory located entirely

on a ridge was 68 times more likely not to be colonized than a territory located entirely within a drainage (i.e., a 1-unit increase in the amount of ridge because the LMU covariates were expressed as the proportion of a territory in each category). Also, the WUI was positively related to colonization and had a quadratic relationship with extinction, which was lowest at intermediate amounts of WUI within territories (Table 3). Finally, colonization was lower in territories with more winter precipitation (Table 3). For example, the odds ratio indicated that a territory with twice the precipitation as another territory was 7.1 times more likely not to be colonized.

We used the conditional occupancy probabilities at each territory from the PRESENCE output for the top-ranked model to find the annual mean territory occupancy, and we estimated the variance of annual mean occupancy using the delta method (Powell 2007). Conditional occupancy is derived from the survey history at a territory (Hines 2006). If there is ≥1 detection, the territory is considered occupied with no error. If there are no detections, the occupancy probability and standard error are estimated from the number of surveys and p for each survey. The mean occupancy declined from 0.82 ± 0.01 in 1991 to 0.39 ± 0.00 in 2019, which was a proportional decline of 52.4% (Figure 3A).

Secondary analyses of fuel treatments

We confirmed that 55.8% of the fuel treatments in the FACTS database were visible in NAIP imagery. The remaining treatments may have occurred but were undetectable from the imagery (e.g., consisted of understory removal that was obscured by the tree canopy). In our initial secondary analyses using data from 2006–2019, we observed an extreme quadratic relationship between post-fire fuel treatments and territory extinction, where extinction was high at intermediate values of post-fire treated area within a territory and nearly zero for low and high values of post-fire treated area. Upon further investigation, we noted that only 40 territories received post-fire fuel treatments, and 24 of these territories had treatments that affected <0.05 of the territory. In addition, only 3 territories with >0.05 treated area were occupied prior to treatment, and thus had the potential to become locally extinct. This resulted in erratic model behavior, which dictated that we remove the post-fire fuel treatment covariate from the analyses (Appendix A). We carried forward 5 sub-models for initial occupancy, 2 sub-models for territory colonization, and 1 sub-model for territory extinction to the final modeling stage (Tables S4–S6; available online in Supporting Information). In the final stage, there were 6 models with $\Delta AIC < 2.0$ (Table S7); however, these models were similar in that the amount of all fuel treatments in the FACTS database within the previous 3 years was a covariate for both territory colonization and extinction and tree mortality from drought and bark beetles from 2001–2005 was a covariate for territory extinction.

In the top-ranked model, territory colonization increased with the amount of fuel treatments in the previous 3 years (Table 3). Fuel treatments had a quadratic relationship with territory extinction where extinction increased with the amount of fuel treatments before declining slightly at higher values (Table 3). These relationships with territory colonization and extinction offset each other, so the net effect on territory occupancy was largely neutral (Figure 2D). The amount of tree mortality caused by drought and bark beetles from 2001–2005 also had a quadratic relationship with territory extinction, which was lowest at intermediate values of tree mortality (Table 3).

Reproductive output

Our primary analyses using data from all years showed that the optimal spatial scale of covariates for reproductive output (number of young fledged at an occupied territory) was predominantly at the 2 smallest scales; 70% of the covariates had an optimal scale of 600 m or 1,000 m (Table 1). Similar to occupancy, 11

models had ΔAIC < 2.0, but these models contained many of the same covariates (Table 4). In this case, the primary difference was whether the model contained a canopy cover covariate for medium or higher (>50%) or high (>70%) canopy cover within a territory with the beta coefficients for these 2 covariates always positive and of similar value.

The top-ranked model indicated that high canopy cover forest had a positive linear relationship with reproductive output (Table 3); for every 10% increase in the proportion of high canopy cover forest within a territory, reproductive output each year increased by 0.03 young fledged. In addition, territories located proportionally more within drainages or on northeast-facing slopes had greater reproductive output (Table 3). For example, a 10% increase in the proportion of drainages within a territory and a 10% decrease in the proportion of ridges resulted in 0.09 more young fledged each year. Reproduction was also positively correlated with the average minimum temperature during the nesting season (Table 3); for every 1°C increase in minimum temperature, reproductive output increased by 0.17 young fledged. Finally, reproduction was negatively correlated with the amount of low- to moderate-severity fire during the previous 5 years (Table 3); every 10% increase in the proportion of low- to moderate-severity fire within a territory resulted in 0.05 fewer young fledged each year. Mean reproductive output showed no evidence of a temporal trend over the duration of our study (Figure 3B). The average reproductive output for all years was 0.65 ± 0.16 and ranged from 0.33–0.95.

In our secondary analyses using data from 2006–2019, the top-ranked model contained a covariate for all fuel treatments in the FACTS database during the previous 3 years. A closely competing model (ΔAIC = 0.50; Table S8 in Supporting Information) contained a covariate for confirmed fuel treatments in the previous 3 years. In both cases, fuel treatments were negatively correlated with reproductive output (Table 3). For example, every 10% increase in the proportion of a territory containing any fuel treatment in the FACTS database resulted in 0.09 fewer young fledged each year.

TABLE 4 Top-ranked models for reproductive output of territorial California spotted owls in the San Bernardino and Angeles national forests in California, 1991–2019. All models with difference in corrected Akaike's Information Criterion (ΔAIC_c) < 2.0 are included, K = number of parameters, and $\log\mathscr{L}$ = log likelihood

Model covariates[a]	ΔAIC_c	AIC_c	AIC_c weight	K	$-2\log\mathscr{L}$
HighCC, LMU, LSfire5, Tnest	0.00	3,207.98	0.077	10	3,187.8
HighCC, LMU, LSfire5	0.37	3,208.34	0.064	9	3,190.2
MedCC, LMU, LSfire5, Tnest	0.60	3,208.58	0.057	10	3,188.4
MedCC, LMU, LSfire5	0.97	3,208.94	0.047	9	3,190.8
HighCC, elevation, LMU, LSfire5	1.00	3,208.98	0.047	10	3,188.8
HighCC, LMU, LSfire5, Pwinter, Tnest	1.64	3,209.61	0.034	11	3,187.4
HighCC, LMU, LSfire5, Pnest, Tnest	1.74	3,209.71	0.032	11	3,187.5
MedCC, LMU	1.74	3,209.72	0.032	8	3,193.6
HighCC, LMU, LSfire5, Pnest, Tnest	1.84	3,209.81	0.031	11	3,187.6
HighCC, LMU, LSfire5, Pwinter	2.00	3,209.98	0.028	10	3,189.8
MedCC, elevation, LMU, LSfire5	2.00	3,209.98	0.028	10	3,189.8

[a]The covariates are defined as MedCC = annual proportion of territory with canopy cover >50%; HighCC = annual proportion of territory with canopy cover >70%; elevation = average elevation (m) within territory; Pnest = average precipitation within territory during the nesting period (Mar-May); Pwinter = average winter (Dec-Feb) precipitation within territory; Tnest = average minimum temperature within territory during the nesting period (Mar-May); LMU = proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW; LSfire5 = proportion of territory burned by low- or moderate-severity wildfire within previous 5 years.

Population impact analyses

Territory occupancy declined from 75.0% in 1991 to 42.7% in 2019 under the baseline scenario, which was similar to our empirical analyses (Table 5). In the no-fire scenario, the mean territory occupancy in 2019 was 45.8%. Thus, high-severity fire accounted for 9.6% (3.1/32.3) of the overall decline in occupancy during our study period. This translates to about 6 territories that became unoccupied as the result of high-severity fire (0.031 × 181). Mean turnover at territories (i.e., change in occupancy status from the previous year) was 10.5% under both scenarios (Table 5). Total reproductive output was higher under the no-fire scenario than the baseline scenario (1,531 vs. 1,423; Table 5).

Territory occupancy increased slightly from 36.8% in 2006 to 37.9% in 2019 under the baseline scenario and 38.2% under the no-treatment scenario (Table 5). In contrast, territory occupancy in 2019 was 44.3% for the no-fire scenario, which translates to about 12 territories that became unoccupied as the result of high-severity fire (0.064 × 181). There was an even greater effect of high-severity fire on occupancy for the 2006–2019 simulations because most of the high-severity fire on our study area occurred from 2003 onwards. Compared to high-severity fire, fuel treatments had relatively little effect on occupancy. Mean turnover at territories was slightly lower for the no-treatment scenario (7.2%) than for the baseline (7.8%) and no-fire (8.1%) scenarios (Table 5). Total reproductive output was higher for the no-fire scenario (840) than the no-treatment (718) and baseline scenarios (699; Table 5).

DISCUSSION

California spotted owl territory occupancy on our study area in southern California declined by 52.4% from 1991 to 2019, which predicts actual changes in population size (Tempel and Gutiérrez 2013). This population decline near the subspecies' southern range boundary is even more precipitous than in the core part of its range in the Sierra Nevada, where occupancy declined by 15–30% on 3 study areas outside of national parks between 1993–2011 (Tempel et al. 2016). Within our study area, the San Bernardino Mountains had higher occupancy rates than the San Jacinto and San Gabriel Mountains. Owls in other mountain ranges in southern California may also have experienced greater population

TABLE 5 Results of population impact analyses for territorial California spotted owls in the San Bernardino and Angeles national forests in California, USA, 1991–2019. We ran 10,000 simulations of occupancy dynamics and reproductive output at each territory under the following scenarios: baseline where we used actual covariate values at each territory, and no fire where we assigned zero values for all fire covariates. Because we lacked fuel treatment data for part of the study period, we repeated the simulations from 2006–2019 for the following scenarios: baseline, no fire, and no treatments where we assigned zero values for all fuel treatment covariates. We provide mean values and SD for occupancy rate in 2019, turnover rate, and total reproductive output

	Occupancy 2019 (%)		Turnover (%)		Total reproduction	
Scenario	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1991–2019:						
Baseline	42.7	3.5	10.5	0.5	1,423	50
No fire	45.8	3.5	10.5	0.5	1,531	53
2006–2019:						
Baseline	37.9	3.2	7.8	0.5	699	36
No fire	44.3	3.3	8.1	0.6	840	40
No treatments	38.2	3.2	7.2	0.5	718	37

declines than the San Bernardino Mountains. Naive occupancy rates (i.e., not accounting for imperfect detection) within the Cleveland National Forest have declined from 0.52 in 1991 to 0.11 in 2020, and fires in 2003 and 2007 may have contributed to this decline (K. J. Winter, Cleveland National Forest, unpublished data). In general, smaller populations in the region appear to be at risk of local extirpation owing to small population size, population isolation, and limited dispersal among populations (Gutiérrez et al. 2017). Combined with the potential loss of suitable habitat to climate change in coming decades (Conlisk et al. 2021), these results suggest that California spotted owl populations near the species' southern range boundary may be vulnerable to local extinction. This steep population decline near their trailing-edge range boundary may also indicate that owls in the core part of the range in the Sierra Nevada will become increasingly susceptible to warming temperatures and changing fire regimes. As with our study area, stand-replacing patches of fire in the Sierra Nevada from 1984–2015 became larger and more regularly shaped (Stevens et al. 2017). In addition, future increases in burned area within this subspecies' range are projected to be similar for southern California and the Sierra Nevada (Wan et al. 2019*a*).

High-severity fire contributed to the decline in our study population, but its deleterious effects on occupancy occurred at higher values of high-severity patch size and total area burned within the territory. These effects were also independent of post-fire fuel treatments because most territories that burned were not treated and post-fire fuel treatments were small relative to the amount of burned area. Our results corroborate several previous studies from the Sierra Nevada and southern California that revealed negative effects on owl occupancy (Lee et al. 2013; Jones et al. 2016*a*, 2021) and habitat use (Eyes et al. 2017, Jones et al. 2020, Schofield et al. 2020, Kramer et al. 2021) when high-severity fire occurred in larger patches or burned a higher proportion of a spotted owl territory. We specifically observed that colonization approached zero when approximately 40% of a territory burned at high-severity, which suggested that it may take decades for these areas to become suitable owl habitat. Our simulations suggested that high-severity fire accounted for 9.6% of the long-term decline in occupancy. This effect size can be significant for an already declining population, even though much of the decline occurred during the 1990s before high-severity fire had affected much of our study area. Therefore, additional research will be required to assess other potential causes for the decline, such as changes in forest structure during the decades prior to our study (Minnich et al. 1995) or long-term shifts in owl diet owing to land use and management (Hobart et al. 2019*a*).

Low- to moderate-severity fire had a negative impact on the initial probability of occupancy and on reproductive output. These results were opposite of our predictions because previous research has not found a negative effect of low- or moderate-severity fire on spotted owl habitat selection or demographic traits (Bond et al. 2009, 2016; Jones et al. 2020; Schofield et al. 2020; Kramer et al. 2021). With respect to initial occupancy, a *post hoc* examination showed that only 6 territories experienced any low- to moderate-severity fire in the year prior to being surveyed for the first time, and 5 of these sites were initially unoccupied. Thus, the relationship between initial occupancy and low- to moderate-severity fire was derived from a small sample size. With respect to reproduction, we hypothesize that adverse effects of low- to moderate-severity fire would be mediated by changes in prey abundance or access. In the Sierra Nevada, for example, spotted owl diet has been strongly affected by fire history, in terms of extent and frequency (Hobart et al. 2021). In addition, prey may show functional responses in our study area that are different from prey populations in spotted owl ranges where previous owl-fire studies have occurred. Low- to moderate-severity fire could affect small-mammal populations if it reduces important habitat elements such as shrub cover, grass cover, or coarse woody debris (Lee and Tietje 2005, Innes et al. 2007), but impacts of fire on small-mammal abundance can vary by species and location. Some researchers reported an increase in rodent biomass after fire in Mexican spotted owl (*S. o. lucida*) habitat (Converse et al. 2006, Ganey et al. 2014). In contrast, abundance was lower for several species, including the desert woodrat (*N. lepida*), in burned areas within southern California chaparral and woodlands (Brehme et al. 2011).

Fuel-reduction treatments can reduce the future risk of high-severity fire, but these treatments may have short-term negative effects on spotted owls (Lee et al. 2013, Tempel et al. 2015, Gallagher et al. 2019, Jones et al. 2022). Fuel treatments, though not expressly intended to reduce the risk of drought-induced insect mortality, have also been reported to reduce drought effects by reducing water competition among surviving trees (Knapp et al. 2021,

Steel et al. 2021). Tree mortality in California caused by drought and insect outbreaks has increased in recent decades and is forecast to accelerate because of climate change (Preisler et al. 2017, Fettig et al. 2019, Madakumbura et al. 2020). Thus, more extensive tree mortality could necessitate continued fuel treatments, both to mitigate mortality and to reduce the risk of megafires. Fuel treatments were correlated with increased territory extinction and reduced reproductive output, but treatments increased the probability of colonization. In this case, fuel treatment effects on territory colonization and extinction offset so that occupancy was largely unaffected. Our population impact analyses indicated that fuel treatments may have caused small declines in occupancy and total reproductive output, but these effects were minor compared to the effects of fire on occupancy and reproduction. The adverse effects of fire on total reproductive output resulted from a reduction in the number of occupied territories and from the impact of low- to moderate-severity fire on reproduction. Higher extinction and higher colonization rates following treatments suggested greater turnover (change in occupancy status) at treated territories, but the population impact analyses revealed that mean turnover rates between the baseline and no-treatment scenarios were similar.

Several other factors appeared to affect occupancy dynamics during our study. First, large trees were the most important habitat element, which has been a consistent finding among spotted owl habitat studies (Roberts 2017). Territory extinction declined as large tree density increased, which has also been reported previously for 4 study areas in the Sierra Nevada (Jones et al. 2018). We observed a quadratic relationship between large tree density and colonization where colonization was highest at intermediate densities. Although this could indicate that some level of habitat heterogeneity within a territory is optimal for owls (Franklin et al. 2000), our *post hoc* analysis suggested that differences between low-elevation, shrub-woodland territories and high-elevation, conifer forest territories were important in accounting for this relationship. Most territories in the shrub-woodland ecotype had few large trees, and a strong positive relationship with large tree density existed at these sites. Second, territories located predominantly within drainages were more likely to be colonized, less likely to go locally extinct, and had higher reproductive output. Sites in drainages may provide a favorable microclimate for spotted owls that are prone to heat stress (Barrows 1981). Finally, we observed an unexpected positive association between occupancy and the proportion of WUI within a territory, even though many fuel reduction treatments were located within or near WUIs. We speculate that WUIs may support a greater abundance of rodents than the surrounding wildlands, although we found no evidence in the literature to support this conjecture. Alternatively, WUIs on our study area simply may have been associated with other unknown factors that supported spotted owl territories.

The optimal spatial scales for our covariates were predominantly 600 m, 1,000 m, or 3,000 m. Ecological processes have been recognized to operate in a scale-dependent manner (Wiens 1989, Mayor et al. 2009), so studies that incorporate multiple scales should provide a more accurate assessment of how environmental factors affect wildlife populations. Most previous spotted owl studies have defined the territory using a single spatial scale based on nearest-neighbor distances or typical home-range sizes and may have missed important ecological relationships at a different spatial scale (Jackson and Fahrig 2015, Moraga et al. 2019). Previous spotted owl researchers that did incorporate multiple spatial scales have also reported that optimal scales can vary widely among covariates (Timm et al. 2016, Wan et al. 2019*b*). Our 1,000-m scale roughly corresponds to home-range size estimates from our study area (Zimmerman et al. 2001), but the importance of other scales in our analyses suggests that future studies should consider the use of multiple spatial scales and attempt to evaluate the underlying ecological mechanisms at optimal spatial scales. In addition, we encourage future research on the connectivity and demographic status of other local populations in southern California to address current information gaps.

MANAGEMENT IMPLICATIONS

Active forest management that includes fuel treatments with the concomitant retention and recruitment of large trees is likely to provide long-term benefits that outweigh any short-term costs for spotted owls. The retention of large trees is likely to be particularly important at low-elevation sites in southern California, which have fewer large

trees than sites at higher elevations and where owl presence is strongly linked to greater large tree densities. When planning fuel treatments, managers could reduce potential impacts to owls by retaining relatively higher canopy cover in drainages while implementing more intensive treatments on ridges and drier sites, thereby still achieving desired fuel-reduction goals across the landscape. Our estimates of population trends and characterization of environmental factors that influence these trends will provide an improved scientific basis for future evaluations of the spotted owls' protected status in southern California.

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CONFLICT OF INTERESTS

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

We ensured proper care and handling of all animals by following procedures that were part of a study plan approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol number 0003A4261).

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REFERENCES

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113:11770–11775.

Anderson, B. J., H. R. Akçakaya, M. B. Araújo, D. A. Fordham, E. Martinez-Meyer, W. Thuiller, and B. W. Brook. 2009. Dynamics of range margins for metapopulations under climate change. Proceedings of the Royal Society B 276: 1415–1420.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bar-Massada, A., V. C. Radeloff, and S. I. Stewart. 2014. Biotic and abiotic effects of human settlements in the wildland-urban interface. BioScience 64:429–437.

Barrows, C. W. 1981. Roost selection by spotted owls: an adaptation to heat stress. Condor 83:302–309.

Berigan, W. J., G. M. Jones, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2019. Cryptic wide-ranging movements lead to upwardly biased occupancy in a territorial species. Journal of Applied Ecology 56:470–480.

Bond, M. L., C. Bradley, and D. E. Lee. 2016. Foraging habitat selection by California spotted owls after fire. Journal of Wildlife Management 80:1290–1300.

Bond, M. L., R. J. Gutiérrez, A. B. Franklin, W. S. LaHaye, C. A. May, and M. E. Seamans. 2002. Short-term effects of wildfires on spotted owl survival, site fidelity, mate fidelity, and reproductive success. Wildlife Society Bulletin 30: 1022–1028.

Bond, M. L., D. E. Lee, R. B. Siegel, and J. P. Ward, Jr. 2009. Habitat use and selection by California spotted owls in a postfire landscape. Journal of Wildlife Management 73:1116–1124.

Blakesley, J. A., B. R. Noon, and D. R. Anderson. 2005. Site occupancy, apparent survival, and reproduction of California spotted owls in relation to forest stand characteristics. Journal of Wildlife Management 69:1554–1564.

Brehme, C. S., D. R. Clark, C. J. Rochester, and R. N. Fisher. 2011. Wildfires alter rodent community structure across four vegetation types in southern California, USA. Fire Ecology 7:81–98.

Bromaghin, J. F., T. L. McDonald, and S. C. Amstrup. 2013. Plausible combinations: an improved method to evaluate the covariate structure of Cormack-Jolly-Seber mark-recapture models. Open Journal of Ecology 3:11–22.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers from global change. Trends in Ecology and Evolution 23:453–460.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Collins, B. M., H. A. Kramer, K. Menning, C. Dillingham, D. Saah, P. A. Stine, and S. L. Stephens. 2013. Modeling hazardous fire potential within a completed fuel treatment network in the northern Sierra Nevada. Forest Ecology and Management 310:156–166.

Collins, B. M., S. L. Stephens, J. J. Moghaddas, and J. Battles. 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. Journal of Forestry 108:24–31.

Conlisk, E., E. Haeuser, A. Flint, R. L. Lewison, and M. K. Jennings. 2021. Pairing functional connectivity with population dynamics to prioritize corridors for Southern California spotted owls. Diversity and Distributions 27:844–856.

Converse, S. J., G. C. White, and W. M. Block. 2006. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forests of the southwestern United States. Journal of Wildlife Management 70:1711–1722.

Eidenshink, J., B. Schwind, K. Brewer, Z.-L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3:3–21.

Eyes, S. A., S. L. Roberts, and M. D. Johnson. 2017. California spotted owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape. Condor: Ornithological Applications 119:375–388.

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecology and Management 432:164–178.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, et al. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. Ornithological Monographs 54:1–54.

Gallagher, C. V., J. J. Keane, P. A. Shaklee, H. A. Kramer, and R. Gerrard. 2019. Spotted owl foraging patterns following fuels treatments, Sierra Nevada, California. Journal of Wildlife Management 83:487–501.

Ganey, J. L., S. C. Kyle, T. A. Rawlinson, D. L. Apprill, and J. P. Ward, Jr. 2014. Relative abundance of small mammals in nest core areas and burned wintering areas of Mexican spotted owls in the Sacramento Mountains, New Mexico. Wilson Journal of Ornithology 126:47–52.

Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted owl (*Strix occidentalis*), version 2.0. Account *in* The birds of North America. A. F. Poole and F. B. Gill, editors. Cornell Lab of Ornithology, Ithaca, New York, USA.

Gutiérrez, R. J., D. J. Tempel, and M. Z. Peery. 2017. The spotted owl in southern and central coastal California. Pages 239–262 *in* The California spotted owl: current state of knowledge. R. J. Gutiérrez, P. N. Manley, and P. A. Stine, technical editors. U.S. Forest Service General Technical Report PSW-GTR-254, Albany, California, USA.

Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8: 461–467.

Hines, J. E. 2006. PRESENCE2—software to estimate patch occupancy and related parameters. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA. http://www.mbr-pwrc.usgs.gov/software/presence.html

Hobart, B. K., G. M. Jones, K. N. Roberts, B. P. Dotters, S. A. Whitmore, W. J. Berigan, M. G. Raphael, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2019*a*. Trophic interactions mediate the response of predator populations to habitat change. Biological Conservation 238:108217.

Hobart, B. K., H. A. Kramer, G. M. Jones, B. P. Dotters, S. A. Whitmore, J. J. Keane, and M. Z. Peery. 2021. Stable isotopes reveal unexpected relationships between fire history and the diet of spotted owls. Ibis 163:253–259.

Hobart, B. K., K. N. Roberts, B. P. Dotters, W. J. Berigan, S. A. Whitmore, M. G. Raphael, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2019*b*. Site occupancy and reproductive dynamics of California spotted owls in a mixed-ownership landscape. Forest Ecology and Management 437:188–200.

Hoffmann, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Horton, J. S., and J. T. Wright. 1944. The wood rat as an ecological factor in southern California watersheds. Ecology 25: 341–351.

Hoy, S. R., R. O. Peterson, and J. A. Vucetich. 2018. Climate warming is associated with smaller body size and shorter lifespans in moose near their southern range limit. Global Change Biology 24:2488–2497.

Innes, R. J., D. H. V. Vuren, D. A. Kelt, M. L. Johnson, J. A. Wilson, and P. A. Stine. 2007. Habitat associations of dusky-footed woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. Journal of Mammalogy 88: 1523–1531.

Jackson, H. B., and L. Fahrig. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63.

Jones, G. M., R. J. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2016*a*. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment 14:300–306.

Jones, G. M., R. J. Gutiérrez, D. J. Tempel, B. Zuckerberg, and M. Z. Peery. 2016*b*. Using dynamic occupancy models to inform climate change adaptation strategies for California spotted owls. Journal of Applied Ecology 53: 895–905.

Jones, G. M., J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2018. Declining old-forest species as a legacy of large trees lost. Biodiversity Research 24:341–351.

Jones, G. M., A. R. Keyser, A. L. Westerling, W. J. Baldwin, J. J. Keane, S. C. Sawyer, J. D. J. Clare, R. J. Gutiérrez, and M. Z. Peery. 2022. Forest restoration limits megafires and supports species conservation under climate change. Frontiers in Ecology and the Environment 20:in press. http://doi.org/10.1002/fee.2450

Jones, G. M., H. A. Kramer, W. J. Berigan, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2021. Megafire causes persistent loss of an old-forest species. Animal Conservation 24:925–936.

Jones, G. M., H. A. Kramer, S. A. Whitmore, W. J. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, T. Erker, F. A. Atuo, N. F. Pietrunti, et al. 2020. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. Landscape Ecology 35:1199–1213.

Knapp, E. E., A. A. Bernal, J. M. Kane, C. J. Fettig, and M. P. North. 2021. Variable thinning and prescribed fire influence tree mortality and growth during and after a severe drought. Forest Ecology and Management 479:118595.

Koltunov, A., C. M. Ramirez, S. L. Ustin, M. Slaton, and E. Haunreiter. 2020. eDaRT: The Ecosystem Disturbance and Recovery Tracker system for monitoring landscape disturbances and their cumulative effects. Remote Sensing of Environment 238:111482.

Kramer, A., G. M. Jones, S. A. Whitmore, J. J. Keane, F. A. Atuo, B. P. Dotters, S. C. Sawyer, S. L. Stock, R. J. Gutiérrez, and M. Z. Peery. 2021. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. Forest Ecology and Management 479:118576.

LaHaye, W. S., R. J. Gutiérrez, and D. R. Call. 1997. Nest-site selection and reproductive success of California spotted owls. Wilson Bulletin 109:42–51.

LaHaye, W. S., G. S. Zimmerman, and R. J. Gutiérrez. 2004. Temporal variation in the vital rates of an insular population of spotted owls (*Strix occidentalis occidentalis*): contrasting effects of weather. Auk 121:1056–1069.

Lee, D. E., M. L. Bond, M. I. Borchert, and R. Tanner. 2013. Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto Mountains of southern California. Journal of Wildlife Management 77:1327–1341.

Lee, D. E., and W. D. Tietje. 2005. Dusky-footed woodrat demography and prescribed fire in a California oak woodland. Journal of Wildlife Management 69:1211–1220.

Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. Second edition. SAS Institute, Cary, North Carolina, USA.

Lombardo, K. J., T. W. Swetnam, C. H. Baisan, and M. I. Borchert. 2009. Using bigcone Douglas-fir fire scars and tree rings to reconstruct interior chaparral fire history. Fire Ecology 5:35–56.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

Madakumbura, G. D., M. L. Goulden, A. Hall, R. Fu, M. A. Moritz, C. D. Koven, L. M. Kueppers, C. A. Norlen, and J. T. Randerson. 2020. Recent California tree mortality portends future increase in drought-driven forest die-off. Environmental Research Letters 15:124040.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Écoscience 16: 238–247.

McDonald, T. L., and G. C. White. 2010. A comparison of regression models for small counts. Journal of Wildlife Management 74:514–521.

Minnich, R. A., M. G. Barbour, J. H. Burk, and R. F. Fernau. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. Conservation Biology 9:902–914.

Moen, C. A., and R. J. Gutiérrez. 1997. California spotted owl habitat selection in the central Sierra Nevada. Journal of Wildlife Management 61:1281–1287.

Moraga, A. D., A. E. Martin, and L. Fahrig. 2019. The scale of effect of landscape context varies with the species' response variable measured. Landscape Ecology 34:703–715.

Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, D. B. Lesmeister, C. K. Nielsen, J. Reid, and E. M. Schauber. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere 11:e02997.

Nigro, K., and N. Molinari. 2019. Status and trends of fire activity in southern California yellow pine and mixed conifer forests. Forest Ecology and Management 441:20–31.

North, M., R. Boynton, P. Stine, K. Shipley, E. Underwood, N. Roth, J. Viers, and J. Quinn. 2012. Geographic information system landscape analysis using GTR 220 concepts. 2012. Pages 107–115 *in* M. North, editor. Managing Sierra Nevada forests. U.S. Forest Service General Technical Report PSW-GTR-237, Albany, California, USA.

Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, U.S.A. Canadian Journal of Forest Research 32:725–741.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:949–954.

Preisler, H. K., N. E. Grulke, Z. Heath, and S. L. Smith. 2017. Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California. Forest Ecology and Management 399:166–178.

Radeloff, V., D. P. Helmers, H. A. Kramer, M. H. Mockrin, P. M. Alexandre, A. Bar-Massada, V. Butsic, T. Hawbaker, S. Martinuzzi, A. D. Syphard, et al. 2018. Rapid growth of the U.S. Wildland Urban Interface increases wildfire risk. Proceedings of the National Academy of Sciences 115:3314–3319.

Razgour, O., J. B. Taggart, S. Manel, J. Juste, C. Ibáñez, H. Rebelo, A. Alberdi, G. Jones, and K. Park. 2018. An integrated framework to identify wildlife populations under threat from climate change. Molecular Ecology Resources 18:18–31.

Roberts, S. L. 2017. California spotted owl habitat characteristics and use. Pages 49–73 *in* The California spotted owl: current state of knowledge. R. J. Gutiérrez, P. N. Manley, and P. A. Stine, technical editors. U.S. Forest Service General Technical Report PSW-GTR-254, Albany, California, USA.

Rockweit, J. T., A. B. Franklin, and P. C. Carlson. 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. Ecology 98:1574–1582.

Safford, H. D., and J. T. Stevens. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. U.S. Forest Service General Technical Report PSW-GTR-256, Albany, California, USA.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schofield, L. N., S. A. Eyes, R. B. Siegel, and S. L. Stock. 2020. Habitat selection by spotted owls after a megafire in Yosemite National Park. Forest Ecology and Management 478:118511.

Seamans, M. E., and R. J. Gutiérrez. 2007*a*. Habitat selection in a changing environment: the relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. Condor 109:566–576.

Seamans, M. E., and R. J. Gutiérrez. 2007*b*. Sources of variability in spotted owl population growth rate: testing predictions using long-term mark-recapture data. Oecologia 152:57–70.

Slaton, M. R. 2015. The roles of disturbance, topography and climate in determining the leading and rear edges of population range limits. Journal of Biogeography 42:255–266.

Smith, R. B., W. S. LaHaye, R. J. Gutiérrez, and G. S. Zimmerman. 2002. Spatial habitat characteristics of an insular spotted owl (*Strix occidentalis*) population in southern California. Pages 137–147 *in* I. Newton, R. Kavanagh, J. Olsen, and I. Taylor, editors. Ecology and conservation of owls. CSIRO Publishing, Collingwood, Victoria, Australia.

Smith, R. B., M. Z. Peery, R. J. Gutiérrez, and W. S. LaHaye. 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. Wilson Bulletin 111:22–29.

Srinivasan, U., and D. S. Wilcove. 2021. Interactive impacts of climate change and land-use change on the demography of montane birds. Ecology 102:e03223.

Steel, Z. L., M. J. Goodwin, M. D. Meyer, G. A. Fricker, H. S. J. Zald, M. D. Hurteau, and M. P. North. 2021. Do forest fuel reduction treatments confer resistance to beetle infestation and drought mortality? Ecosphere 12:e03344.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:8.

Stephens, S. L., N. Burrows, A. Buyantuyev, R. W. Gray, R. E. Keane, R. Kubian, S. Liu, F. Seijo, L. Shu, K. G. Tolhurst, et al. 2014. Temperate and boreal forest mega-fires: characteristics and challenges. Frontiers in Ecology and the Environment 12:115–122.

Stephens, S. L., and B. M. Collins. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. Northwest Science 78:12–23.

Stevens, J. T., B. M. Collins, J. D. Miller, M. P. North, and S. L. Stephens. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management 406:28–36.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. Ecological Applications 17:1388–1402.

Tempel, D. J., and R. J. Gutiérrez. 2013. Relation between occupancy and abundance for a territorial Species, the California spotted owl. Conservation Biology 27:1087–1095.

Tempel, D. J., R. J. Gutiérrez, J. J. Battles, D. L. Fry, Y. Su, Q. Guo, M. J. Reetz, S. A. Whitmore, G. M. Jones, B. M. Collins, et al. 2015. Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. Ecosphere 6:261.

Tempel, D. J., R. J. Gutiérrez, S. A. Whitmore, M. J. Reetz, R. E. Stoelting, W. J. Berigan, M. E. Seamans, and M. Z. Peery. 2014. Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. Ecological Applications 24:2089–2106.

Tempel, D. J., J. J. Keane, R. J. Gutiérrez, J. D. Wolfe, G. M. Jones, A. Koltunov, C. M. Ramirez, W. J. Berigan, C. V. Gallagher, T. E. Munton, et al. 2016. Meta-analysis of California spotted owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: habitat associations and their implications for forest management. Condor: Ornithological Applications 118:747–765.

Theobald, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Timm, B. C., K. McGarigal, S. A. Cushman, and J. L. Ganey. 2016. Multi-scale Mexican spotted owl (*Strix occidentalis lucida*) nest/roost habitat selection in Arizona and a comparison with single-scale modeling results. Landscape Ecology 31: 1209–1225.

U.S. Forest Service. 2005. Land Management Plan—Part 2: San Bernardino National Forest Strategy. Pacific Southwest Region, Vallejo, California, USA.

Vedder, O., S. Bouwhuis, and B. C. Sheldon. 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. PLoS Biology 11:e1001605.

Wan, H. Y., S. A. Cushman, and J. L. Ganey. 2019*a*. Recent and projected future wildfire trends across the ranges of three spotted owl subspecies under climate change. Frontiers in Ecology and Evolution 7:1–12.

Wan, H. Y., S. A. Cushman, and J. L. Ganey. 2019*b*. Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas. Landscape Ecology 34:503–519.

Wan, H. Y., J. L. Ganey, C. D. Vojta, and S. A. Cushman. 2018. Managing emerging threats to spotted owls. Journal of Wildlife Management 82:682–697.

Westerling, A. L. 2016. Increasing western U.S. forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B 371:20150178.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Yandow, L. H., A. D. Chalfoun, and D. F. Doak. 2015. Climate tolerances and habitat requirements jointly shape the elevational distribution of the American pika (*Ochotona princeps*), with implications for climate change effects. PLoS ONE 10:e0131082.

Zimmerman, G. S., R. J. Gutiérrez, and W. S. LaHaye. 2007. Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. Journal of Applied Ecology 44:963–971.

Zimmerman, G. S., W. S. LaHaye, and R. J. Gutiérrez. 2001. Breeding-season home ranges of spotted owls in the San Bernardino Mountains, California. Western Birds 32:83–87.

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SUPPORTING INFORMATION

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APPENDIX A: POST-FIRE FUEL TREATMENTS

In our initial analyses of data from 2006–2019 where we assessed the effects of fuel and post-fire fuel treatments on California spotted owl territory occupancy dynamics, we found an extreme quadratic relationship between post-fire fuel treatments and extinction probability (Figure A1A). Territory extinction probability approached 0.8 when 10% of a territory was subject to post-fire fuel treatment in the previous 3 years, but territory extinction was nearly zero at lower (<1%) and higher (>20%) values of post-fire treated area. In addition, colonization probability was nearly zero after about 3% of a territory received post-fire fuel treatments. These relationships were not biologically realistic, so we investigated the results further. We found 3 factors that affected the relationships between post-fire fuel treatments and both territory colonization and extinction:

1. Post-fire fuel treatments were less common and less spatially extensive than other fuel treatments (i.e., those that did not occur after fire) and high-severity fire. Forty territories received post-fire fuel treatments, but 24 of these territories had <5% of the territory area affected by the treatments (Figure A1A). In contrast, other fuel treatments and high-severity fire affected more territories and affected proportionally more area within territories (Figure A1B).

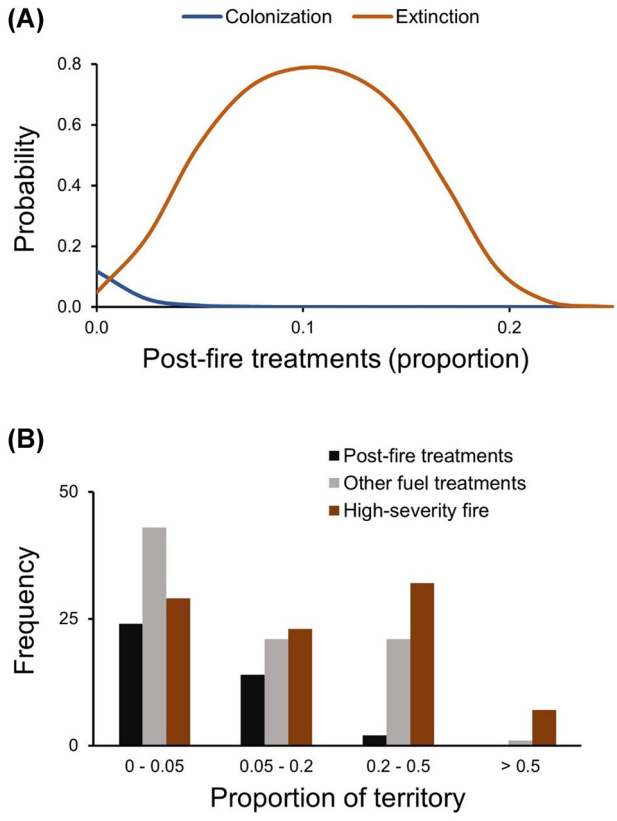

FIGURE A1 A) The effect of post-fire fuel treatments in the previous 3 years on the probabilities of colonization and extinction at California spotted owl territories in the San Bernardino and Angeles national forests in California, USA, 2006–2019. The territory spatial scale is 1,000 m. B) The number of spotted owl territories affected by post-fire fuel treatments, other fuel treatments, and high-severity fire within categories based on the proportion of the territory affected at the 1,000-m spatial scale

2. Only 3 of the territories with post-fire treated area >5% were occupied prior to the post-fire fuel treatment, and thus had the opportunity to go locally extinct. Two territories went extinct in the year following the treatment, and the third remained occupied for 2 years before going extinct. Thus, most of the curve for territory extinction probability (Figure A1A) was based on a sample size of 5 total extinction opportunities. Furthermore, the post-fire fuel treatments occurred the year after the fire at 2 of these territories, and 5 years after the fire at the third territory. So, the territory extinction events at these sites may have been a delayed response to the fire itself, particularly since spotted owls display high site fidelity.
3. Thirty-two of the 40 territories with post-fire fuel treatments were also affected by high-severity fire, including 13 of 16 territories with >5% post-fire treated area. For the 3 territories above with post-fire treated area >5% that were occupied prior to the post-fire fuel treatment, high-severity fire burned 8%, 21%, and 40% of the territories, respectively. For all 40 territories with post-fire fuel treatments, the proportion of high-severity fire within the territory (0.17) was greater than the proportion of post-fire treated area (0.06; one-tailed *t*-test, $P \leq 0.001$). Thus, the effects of post-fire fuel treatments were confounded with the effects of high-severity fire, and this may have affected the relationships between post-fire fuel treatments and both territory colonization and extinction.

These findings suggested that the inclusion of post-fire fuel treatments in our analyses led to erratic model behavior due to extremely low sample size (territory extinction opportunities) and extended or delayed effects of fire. In addition, the significantly greater amount of high-severity burned area compared to treated area within post-fire fuel treatment territories makes it likely that fire effects obscured any potential relationships between occupancy and post-fire fuel treatments. As a result, we removed the post-fire fuel treatment covariate from our analyses.