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Forest structure and pattern vary by climate and landform across active-fire landscapes in the montane Sierra Nevada

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ABSTRACT

Restoration of fire-dependent forests is often guided by reference conditions from forests with an active fire regime, thought to be resilient to current and future disturbances and stresses. Reference conditions are usually based on historical data or reconstruction, which greatly limits the scale and completeness of data that can be collected. In the Sierra Nevada of California, large areas with reintroduced active fire regimes coupled with extensive lidar data coverage provide the unique opportunity to develop a contemporary regional reference condition dataset across a wide gradient of biophysical conditions. We developed this dataset with a focus on three questions: (1) What is the geographic and environmental distribution of restored active-fire forest areas in the Sierra Nevada mixed-conifer zone? (2) What are the ranges of variation in forest structure and spatial patterns across reference areas? And (3) How do stand density, tree clumping, and canopy opening patterns vary by topography and climate in reference areas? We analyzed fire history and environmental conditions over 10.8 million ha, including 3.9 million ha in the Sierra Nevada mixed-conifer zone, and found 30,377 ha of restored active-fire areas. Although reference areas were distributed throughout the Sierra Nevada they were more abundant on National Park lands (81% of reference areas) than National Forest lands and were associated with higher lightning strike density. Lidar-measured ranges of variation in reference condition structure were broad, with tree densities of 6–320 trees ha^{-1} (median 107 trees ha^{-1}), basal area of 0.01–113 $\text{m}^2\ \text{ha}^{-1}$ (median 21 $\text{m}^2\ \text{ha}^{-1}$), average size of closely associated clumps of trees from > 1 to 207 trees (median 3.1 trees), and average percent of stand area > 6 m from the nearest canopy ranging from 0% to 100% (median 5.1%). These ranges correspond well with past studies reporting density and spatial patterns of contemporary and historical active-fire reference stands in the Sierra Nevada, except this study observed greater total variation due to the much greater spatial extent of sampling. Within the montane forest zone, reference areas at middle elevations had lower density (86 vs. 121 trees ha^{-1}), basal area, (13.7 vs. 31 $\text{m}^2\ \text{ha}^{-1}$), and mean clump size (2.7 vs. 4.0 trees) compared to lower- and higher-elevation reference areas, while ridgetops had lower density (101 vs. 115 trees ha^{-1}), basal area (19.6 vs. 24.1 $\text{m}^2\ \text{ha}^{-1}$), and mean clump size (3.0 vs. 3.3 trees) and more open space (7.4% vs. 5.1%) than other landforms. Many of the relationships between physiography and reference structure were context-dependent, suggesting that management practices should create heterogeneous forest structure congruent with local climatic and topographic factors influencing stand conditions.

1. Introduction

Restoration of forest resilience – the ability of an ecosystem to maintain or quickly recover function after disturbance – is an important goal in contemporary forest management, especially in fire-dependent forests of the western United States (North et al., 2009; Churchill et al., 2013; Hessburg et al., 2013; DeRose and Long, 2014; Hessburg et al., 2015; Seidl et al., 2015; Johnstone et al., 2016; Stephens et al., 2016). Reference conditions describing characteristics of ecosystems that portray or embody desired functional outcomes can provide a quantifiable link between structure, composition, and desired function (Churchill et al., 2013). Reference conditions can serve as both waypoints to inform restoration targets (Kaufmann et al., 1998; Moore et al., 1999) and benchmarks for evaluating restoration progress (Christensen et al., 1996; Larson and Churchill, 2012). In either case, reference conditions use a desirable ecosystem as an example for relating function to measurable aspects of structure and composition.

Reference conditions in fire-dependent forests are often drawn from historical data, including recovered historical inventories (Leiburg, 1900; Langille, 1903; Munger, 1912; Collins et al., 2011; Hagmann et al., 2013; Lydersen et al., 2013; Hagmann et al., 2014) as well as reconstructed forest conditions (Fulé et al., 1997; Hessburg et al., 1999; Scholl and Taylor, 2010; Churchill et al., 2013; Barth et al., 2015; Schneider et al., 2015; Clyatt et al., 2016; Churchill et al., 2017). Historical references represent conditions that existed before Euro-American settlement when linkages between process and pattern remained

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within the bounds of their evolutionary environment (Moore et al., 1999; Hessburg et al., 2005; Larson and Churchill, 2012), recognizing that Native American influences constituted a part of that environment (Vale, 2013). However, primary historical data suitable for defining reference conditions are rare and often limited in spatial extent and data quality (Stephens et al., 2015). Reconstructed forest conditions based on analysis of remnant structures (e.g., live trees, snags, and logs) can be quite uncertain for smaller trees, and the uncertainty increases as reconstructions reach farther back in time (Barth et al., 2015). Due to the amount of labor involved, reconstruction studies are also limited in their spatial extent. Thus, they are able to characterize stand-level structure adequately but may not capture variation across wide biophysical gradients within landscapes (Hessburg et al., 1999; Dickinson, 2014), an important aspect of restoration planning (Hessburg et al., 2015). Also, climates have been and are changing, limiting historical reference data because it describes forest conditions under a climate different than today (Millar and Woolfenden, 1999; Stephens et al., 2010; Heyerdahl et al., 2014; Hanberry et al., 2015; Hart et al., 2015; Johnstone et al., 2016).

Reference conditions can also be drawn from contemporary forests in areas where characteristic disturbance regimes have been maintained or reintroduced and modern anthropogenic disturbances like logging, mining, and grazing have been minimal (Taylor, 2010; Collins et al., 2016). In the western United States, fire is the primary process that structures dry forests (Brown et al., 2004; Hessburg et al., 2005), maintaining stands characterized by a fine-scale mosaic of tree clumps and canopy openings (Larson and Churchill, 2012; Churchill et al., 2013). Since the late 1960s, after about 60 years of fire suppression, forest managers in the Sierra Nevada region have been making a concerted effort to reintroduce frequent lower-severity fire to mixed-conifer forests, especially in National Parks (Parsons and Botti, 1996; van Wagtendonk, 2007). However, there has been no critical assessment of where fire regimes have begun to be restored in the Sierra Nevada nor how much of the region could be considered a reference condition. Defining contemporary reference conditions for the Sierra Nevada would supplement existing historical references in three important ways. First, contemporary measurements are precise with respect to sizes and locations of trees across the diameter distribution. Second, contemporary reference conditions inherently incorporate the effects of recent changes in climate. And third, remote sensing allows quantification of large reference landscapes.

The structural conditions associated with resilient forest ecosystems vary with fine-scale changes in topography and environment (Lydersen and North, 2012; Kane et al., 2015b; Churchill et al., 2017). Thus, a regional reference condition dataset should have a wide range of variation reflecting the diversity of physiographic and climatic conditions across the region. Reference conditions used for a given area should be drawn from an environmentally and climatically similar reference site to ensure that resilient conditions in one location will translate to another. This concept is derived from climate analogs (*sensu* Churchill et al., 2013), and we refer to it in a broadened sense as biophysical analogs.

Our objective was to identify and describe contemporary active-fire reference areas for different biophysical settings within the Sierra Nevada mixed-conifer zone to support planning, implementing, and monitoring restoration treatments. We sought to quantify how structure and spatial pattern vary with topography and climate. We conceptualized spatial pattern as a fine-scale mosaic of widely space individual trees, clumps of trees closely aggregated in space, and open space between tree crowns (Churchill et al., 2013).

Our research questions were:

(1) What is the geographic and environmental distribution of restored active-fire forest areas in the Sierra Nevada mixed-conifer zone?
(2) What are the ranges of variation in structure and spatial patterns across reference areas?

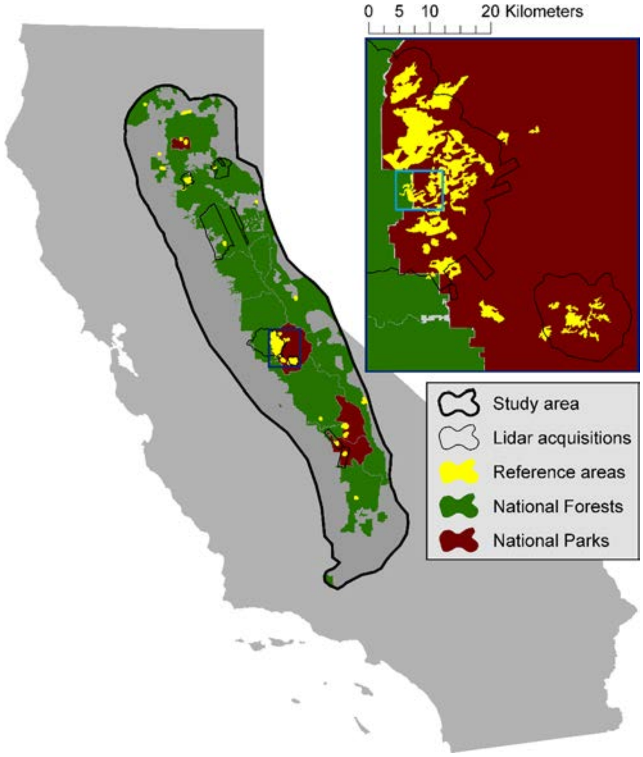

Fig. 1. Map of study area showing reference areas across the Sierra Nevada, federal ownership, and lidar acquisitions. Inset shows detail of area with high reference area density in western Yosemite. Light blue box indicates location shown in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(3) How do density, tree clumping, and canopy opening patterns vary by topography and climate in reference areas?

2. Methods

2.1. Classifying the biophysical environment

2.1.1. Climate classes

We began by defining climate classes across the Sierra Nevada (Fig. 1) to delineate the mixed-conifer zone and to provide the biophysical context for analyzing variation in reference condition structure.

We defined climate classes using the grain size of catchment basins. Catchment basins form ecologically relevant units (a connected watershed) that are familiar to forest managers and are operationally practical for mechanical (e.g., road building and yarding) and fire treatments (e.g., placement of fire line). We used basin data from the National Hydrography Dataset (EPA and USGS, 2018), with catchment sizes ranging from 7 to 1013 ha. We combined any catchments smaller than 100 ha with their immediate neighbors until a minimum size of 100 ha was reached; the smallest catchment after consolidation was 109.3 ha. For climate classification variables we focused on metrics integrating the biophysical conditions experienced by vegetation (Stephenson, 1998). Following the definition of climate analogs by Churchill et al. (2013), we selected actual evapotranspiration (AET) and climatic water deficit (Deficit) which are integrated measures of productivity and moisture stress, respectively (Lutz et al., 2010). We supplemented these with January minimum temperature (T_{min}), which can help to pinpoint limitations on regeneration and growth (Lutz et al., 2010; Dobrowski et al., 2013). We gathered annual AET, Deficit, and T_{min} data averaged over the 1981–2010 period from the Basin Characterization Model dataset (Flint et al., 2013, 2014) at a 270 m pixel

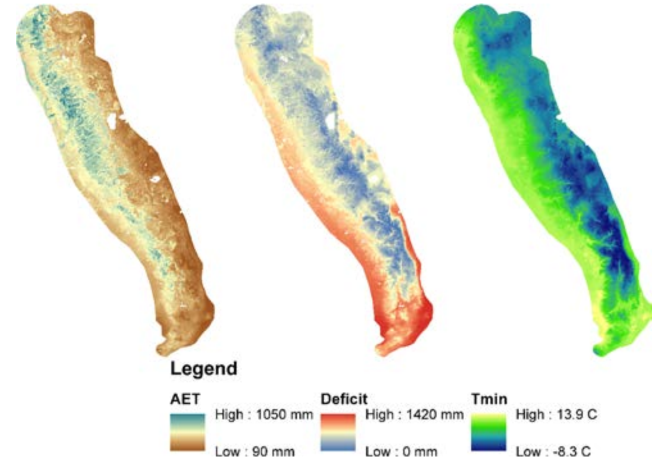

Fig. 2. Map of layers used to classify climate – annual actual evapotranspiration (AET), climatic water deficit (Deficit), and January minimum temperature (T_{min}) – across the study area. Data from Flint et al. (2014).

resolution. We calculated the 25th and 75th percentile from the values for each metric distributed throughout each catchment (Fig. 2).

We used the six resultant variables for each catchment (25th and 75th percentile values for each of AET, Deficit, and T_{min}) – normalized by global maxima – in a hierarchical classification with Euclidean distances and a complete linkage method, and implemented using the hclust function in R (R Core Team, 2016). We chose to use 20 classes by inspecting the dendrogram (Fig. A.1) and scree plot as well as by inspecting the classification results for cuts at 4, 8, 12, 16, 20, 24, 28, and 32 classes. We assigned descriptive names to each class based on inspection of the dendrogram and boxplots of class-wise distributions of AET, Deficit, and T_{min} (Table 1, Fig. A.2).

We validated the climate classes by testing their ability to discriminate between forest composition using Sierra Nevada data from USFS Forest Inventory and Analysis (FIA) plots (Bechtold and Patterson, 2005). We selected 3217 plots that represent native forested communities using the following criteria: (1) minimum 10% forest cover, (2) natural stand origin, and (3) no artificial regeneration. We summarized composition on each plot by calculating proportions of live tree basal area by species and assigned each plot a climate class based on its publicly available fuzzed location (within 1.6 km of the true location).

We used PERMANOVA (McCune et al., 2002) to test whether composition varied by climate class. With the adonis function in the R package vegan (Oksanen et al., 2016), we compared proportionate live basal area by species across climate classes using the Bray-Curtis dissimilarity measure (Bray and Curtis, 1957) and assessed significance with 1000 permutations of climate class labels.

To provide a more specific idea of how composition varied by climate class we took two approaches to associating tree species with each climate class. First, we created lists for each class giving the species that are dominant by basal area on at least 5% of FIA plots, in decreasing order of dominance frequency.

Second, we performed an indicator species analysis (ISA) (McCune et al., 2002) to determine the most characteristic indicator species for each class. The ISA calculates indicator values (IVs) for each species in each class representing how faithful and how exclusive the species is to that class (McCune et al., 2002). We assessed significance of IVs using a permutation test, randomly shuffling the climate classes 1000 times. We assigned an indicator species to each class by taking the species with the highest IV that was also significant under the permutation test ($p < 0.05$). When two climate classes had the same indicator species we differentiated them by also considering the species with the second highest significant IV. For pairs of classes where the primary and secondary indicator species were both the same, we tested for differences in composition with PERMANOVA using the adonis function, Bray-Curtis dissimilarities, and 1000 permutations to assess significance.

We used the results of these two composition analyses to make associations between climate classes and the ecological zones and forest types defined by van Wagtendonk et al. (2018). We also associated the climate classes into five major groups: Foothills, Low Montane, Mid-Montane, Upper Montane, and High Sierra.

2.1.2. *Landscape management units*

We subdivided catchments by topographic position to capture localized patterns of change in solar demand, soil depth, and water availability that can influence the biophysical environment and reference conditions at fine scales (Wiggins, 2017). We classified areas in terms of landscape management unit (LMU, *sensu* Underwood et al., 2010) using the Landscape Management Unit Tool version 2 (Boynton et al., 2015). This tool operates by classifying a digital elevation model (DEM) by topographic position. We used the simplified output from the tool and created the following classes based on a 30 m resolution DEM and default parameters: ridge, valley, SW slope (135–225° aspect), and NE slope (0–135° and 225–360° aspect). The resultant LMU sizes ranged from 0.1 to 56.6 ha and averaged 12.0 ha. We did not perform validation on the LMU classes since the nature of LMUs has already been described for California (Underwood et al., 2010; Lydersen and North, 2012; Wiggins, 2017).

2.2. *Locating reference areas*

We selected study areas in the Sierra Nevada mixed-conifer zone, where forests are dominated by a variable mix of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), red fir (*A. magnifica*), and incense cedar (*Calocedrus decurrens*). This corresponds with the lower-montane and upper montane forest zones of van Wagtendonk et al. (2018) (Table 1). This zone is the center of most contemporary forest management in the Sierra Nevada and has a greater restoration need than other forest types due to its greater departure from characteristic fire return intervals (25–40 years greater departure than other Sierra Nevada forest zones) (Safford and Van de Water, 2014).

We defined reference areas across the Sierra Nevada based on management and fire history. We restricted the study to federal lands so that we had access to records of past management. This included all or part of 13 National Forests and three National Parks (Fig. 1). We created a raster layer at a 30 m resolution where pixel values were scored as integers from 0 to 5 representing how restored the fire regime of that pixel was (Fig. 3). One point was scored for each of the following criteria:

1. No records existed of past timber management (planting, harvest, thinning, etc.);
2. The pixel had experienced at least two fires in the last 60 years, so that a "regime" was beginning to be defined (Taylor, 2010; Lydersen and North, 2012; van Wagtendonk et al., 2012);
3. At least one of these fires occurred within the last 30 years, so that the results of reintroduced fire were still extant (Lydersen and North, 2012);
4. At least one of these fires had moderate severity effects on the pixels, because moderate severity fire kills more trees in lower canopy strata than low severity fire, thereby doing more work to return a fire-excluded stand to resilient conditions (Collins et al., 2011; Becker and Lutz, 2016); and
5. The pixel had not experienced high severity effects, because high amounts of mortality indicate low fire resistance (North et al., 2012; Stephens et al., 2013).

Timber management history data were retrieved from the Forest Service national geodata clearinghouse (USDA Forest Service, 2018), supplemented by manual inspection of aerial imagery for signs of

Table 1
Climate class characteristics in terms of climate variables, species composition, and forest type. Values shown here are descriptive; they are not the input values used for classification. AET = actual evapotranspiration, T_{min} = annual minimum temperature. Species codes are given in Table A.1. Ecological zones, forest types, and historical fire return intervals are as defined by van Wagtendonk et al. (2018).

Class	Reference area (area with lidar) (ha)	Median Values				Species dominant by BA in at least 5% of plots	Indicator species
		Elevation (m)	AET (mm)	Deficit (mm)	T_{min} (° C)		
Dry Foothills	–	270	386	903	9.5	QUDO, QUWI, PISA, QUCH	QUDO, QUWI
Hot Southern Foothills	–	240	276	1145	9.8	QUDO, QUWI, QUCH, AECA	QUDO, AECA
Warm Southern Foothills	–	1280	241	1057	7.4	QUDO, QUCH, QUWI, QUKE, PIMO	JUCA
Foothill Valleys	–	390	553	640	9.4	PIPO, PSME, LIDE, QUWI, QUDO	PSME, PIPO
Foothill-Low Montane Transition	–	770	452	755	7.7	QUCH, PIPO, QUWI, QUKE, QUDO, PSME, CADE	QUKE
Very Hot Low Montane	–	770	545	617	7.6	PSME, PIPO, QUKE, CADE	PSME, QUKE
Hot Low Montane	–	1010	611	482	5.7	PIPO, CADE, PSME, LIDE, QUKE, QUCH, ABCO	LIDE
South Sierra Low Montane	933 (0)	1740	160	927	3.9	QUCH, PIMO, PIJE, ABCO, QUWI, QUKE, CADE	PIMO
Warm Dry Low Montane	2121 (1505)	1310	485	573	5.2	PSME, ABCO, PIPO, QUKE, CADE, QUCH	PSME, QUKE
Warm Mesic Low Montane	10,221 (9379)	1670	376	620	3.5	ABCO, CADE, PSME, PIPO, PILA, PIJE	CADE
Xeric Mid Montane	1713 (1150)	1470	229	756	1.9	PIJE, JUOC, ABCO, CADE, QUCH, PIPO, PISA	PIJE, JUOC
Warm Mesic Mid Montane	0 (0)	1470	507	416	2.7	ABCO, PSME, CADE, PIPO	ABCO, CADE
Cool Dry Mid Montane	10,119 (7978)	1810	359	517	1.5	ABCO, ABMA, CADE, PSME, PIPO, PIJE	ABCO, ABMA
Xeric High Montane	2566 (1695)	1850	220	628	0.1	PIJE, ABCO, JUOC, PIPO, ABMA, CADE	PIJE, JUOC
Cool Mesic High Montane	524 (0)	2170	443	321	0.0	ABMA, ABCO, PICO, PIMO2, PIJE, TSME	ABMA, ABCO
Cool Dry High Montane	2180 (1050)	2110	298	465	−0.8	ABCO, ABMA, PICO, PIJE, PIPO	ABMA, PICO
Cold Dry High Montane	–	2330	224	523	−2	PIJE, PICO, ABMA, ABCO, JUOC	PIJE, PICO
High Sierra	–	2950	224	353	−3.5	PICO, PIAL, ABMA, PIBA	PICO
High Valleys and Meadows	–	2880	379	155	−3.8	PIBA	PIBA
Subalpine	–	3400	201	252	−5.1	PIAL, PICO, PIBA, TSME	PIAL

Class	Ecological zone	Common forest type(s)	Historical fire return interval
Dry Foothills	Foothill shrubland and woodland	QUDO woodland, PISA-QUWI woodland	Short
Hot Southern Foothills	Foothill shrubland and woodland	QUDO woodland, mixed hardwood woodland	Short
Warm Southern Foothills	Foothill shrubland and woodland	QUDO woodland, mixed hardwood woodland	Short-Medium
Foothill Valleys	Foothill shrubland and woodland/Lower-montane forest transition zone	QUDO woodland, PISA-QUWI woodland, riparian forest	Medium
Foothill-Low Montane Transition	Foothill shrubland and woodland/Lower-montane forest transition zone	Mixed hardwood woodland, QUDO woodland, mixed evergreen	Short-Medium
Very Hot Low Montane	Lower-montane forest	QUKE-PIPO-ABCO-PSME forest, mixed evergreen	Short
Hot Low Montane	Lower-montane forest	QUKE-PIPO-ABCO-PSME forest, mixed evergreen	Short-Medium
South Sierra Low Montane	Lower-montane forest	QUKE-PIPO-ABCO-PSME forest, mixed conifer	Short
Warm Dry Low Montane	Lower-montane forest	Mixed evergreen, mixed conifer	Short
Warm Mesic Low Montane	Lower-montane forest	Mixed conifer	Short
Xeric Mid Montane	Lower-montane forest/Upper montane forest transition zone	PIJE woodland, JUOC woodland, mixed evergreen	Short
Warm Mesic Mid Montane	Lower-montane forest/Upper montane forest transition zone	Mixed conifer	Short
Cool Dry Mid Montane	Lower-montane forest/Upper montane forest transition zone	Mixed conifer, PIJE woodland	Short-Medium
Xeric High Montane	Upper montane forest	PIJE woodland, mixed conifer, JUOC woodland	Medium
Cool Mesic High Montane	Upper montane forest	ABMA forest, PIMO2 forest, PIJE woodland	Medium
Cool Dry High Montane	Upper montane forest	ABMA forest, PICO forest, PIJE woodland	Medium-Long
Cold Dry High Montane	Upper montane forest	PIJE woodland, PICO forest, ABMA forest, JUOC woodland	Medium-Long
High Sierra	Upper montane forest/Subalpine forest transition zone	PICO forest, PIAL woodland, ABMA forest, PIBA woodland	Long
High Valleys and Meadows	Subalpine forest	PIBA woodland	Long
Subalpine	Subalpine forest	PIAL woodland, PICO forest, PIBA woodland, TSME forest	Long

mechanical treatment in potential reference areas. Low-intensity historical logging may have been missed in this procedure. We did not consider management history for National Parks aside from prescribed burning, since mechanical treatments have seldom been used in park management. Fire history was drawn from the FRAP fire atlas (Cal Fire, 2018) for years 1957–1983 and Monitoring Trends in Burn Severity (Eidenshink et al., 2007) for years 1984–2014. The Cal Fire (2018) data did not include spatially explicit burn severities, so we treated all management ignitions as low severity fires throughout. Fires started by lightning and accidental human ignition were assumed to be low severity when they were small (< 400 ha) and successfully suppressed within a 3 days. Larger fire areas from 1957 to 1983 with unknown severity were excluded from the analysis.

Using the defined raster layer, we drew polygons around areas with high scores (at least four, mostly five), following natural boundaries of fire history and topography to separate areas (Fig. 3). We enforced the following criteria for each area:

1. Patch size was at least 100 ha, to provide a meaningful sample of fire effects within each one;
2. Any high-severity patches incorporated into the reference area were no larger than 10 ha, since the majority of high-severity patches

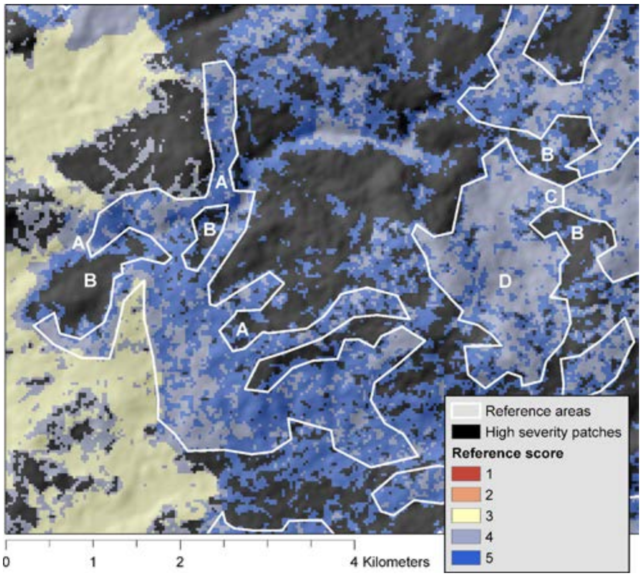

Fig. 3. Illustration of reference patch delineation, showing some key elements of the manual delineation methods. The background reference score (Landsat pixel size of 30 m) ranges from one to five depending on fire history (section 2.2). Constraints applied in patch delineation: (A) Stringers were cut off at a 100 m width threshold. (B) High-severity patches greater than 10 ha in size were excluded. This resulted in “donut holes” when the 100 m width threshold allowed. (C) Contiguous patches were split apart on catchment divides (pictured) and fire perimeters. (D) Areas scoring mostly five were favored but areas scoring mostly four were allowed when the only criterion not met was “at least one moderate severity fire” and the number of fires was greater than two.

found historically were no more than a few hectares in size (Kilgore, 1973; Skinner and Chang, 1996; Keeley and Stephenson, 2000);

3. No more than 10% of the polygon had burned at high severity, which is near the high end of the range of variation in historical high severity proportions (Mallek et al., 2013 and references therein; Stephens et al., 2015);
4. The average number of fires in the polygon was ≥ 2, to ensure that the area has, on the whole, experienced multiple fires; and
5. The average number of recent fires (< 30 yr. old) in the polygon was ≥ 1, to ensure that the area has, on the whole, burned recently.

These criteria ensured that polygons represent patches with a variety of patterns, mainly characterized by pixels with a score of five (Fig. 4). The criteria allowed for flexibility in several ways. First, even though high-severity pixels were not favored in the pixel criteria, we recognized that some amount of high severity fire is expected to occur in reference areas (Collins and Stephens, 2010; Mallek et al., 2013) and so some high-severity patches were included. We chose to make the limits for high severity inclusion within these areas liberal relative to published historical conditions because (1) studies capturing historical conditions likely missed some of the largest patches and, (2) these reference stands have had several fires recently but are still recovering from decades of fire suppression, so we did not expect them to fully match historical conditions. The criteria also allowed for unburned patches to be incorporated within the matrix of burned lands. This is intentional, since unburned refugia are critical elements of resilience in post-fire landscapes (Kolden et al., 2015; Meddens et al., 2018; Meigs and Krawchuk, 2018). In contrast, we did not allow any mechanical treatment activity within the reference areas.

We visited 11 of the 85 identified reference areas, focusing on northwestern Yosemite. We walked through the areas in an informal survey guided by aerial photos and the lidar canopy models with the goal of seeing as many different kinds of conditions as possible. We collected notes and photographs characterizing forest structure over a total path length of about 200 km. We used the qualitative data collected in these visits to improve our interpretation of fire history data and modified reference area boundaries in light of what we learned. Specifically, we redrew boundaries to more closely follow topographic features, we became stricter with excluding high severity areas, and we decided to allow patches that had only burned at low severity when they had burned three or more times.

2.3. *Quantifying reference area structure*

We used lidar data to characterize the forest structure of the reference areas and provide a set of quantitative reference conditions. Lidar data provides measurements of structure at a resolution of several data points per square meter across areas tens to hundreds of thousands of hectares in size, and so allowed us to quantify structural variation across entire reference areas. We characterized structure using lidar-identified tree-approximate objects (TAOs) (North et al., 2017; Jeronimo et al., 2018). TAOs are an ecologically meaningful unit of measurement representing a canopy tree that was detected by the lidar along with subordinate trees that cannot be individually resolved. The canopy tree may be an individual with no subordinates or may be associated with a small number of understory trees (mean 1.5 [sd 1.2] undetected trees per TAO; S. Jeronimo, *unpublished data*). Using TAOs allows for a consistent unit of analysis even while tree detection accuracy changes with forest structure (Jeronimo et al., 2018). Since large trees, which are more visible to lidar, dominate basal area and spatial heterogeneity (Lutz et al., 2012, 2013, 2018), directly measuring patterns of TAOs maintains much of the useful information that would be gathered in a traditional tree-based survey. By necessity, this portion of the analysis was limited to areas with available lidar data (Fig. 1; Table 2). This included 76% of the identified reference areas, or 23,088 ha.

Across each lidar acquisition area we created ground-normalized canopy height models using a 0.75 m resolution and a 3 × 3 pixel smoothing window (Jeronimo et al., 2018) and segmented the canopy height model into TAOs using the TreeSeg tool in the FUSION Lidar Toolkit (McGaughey, 2018). The TreeSeg tool associates each TAO with a location and a height. We additionally modeled dbh for each TAO using regressions developed from the 3217 FIA plots described above. We used the following regression model form:

$$\text{dbh} = b_0 \text{height}^{b_1}, \tag{1}$$

fitting a separate set of coefficients for each climate class (Table A.2).

We split reference areas into polygons by LMU, and for each polygon calculated summary metrics quantifying conditions in terms of TAO size distributions, stocking, and spatial pattern. We did not attempt to separate TAOs dominated by a live tree from TAOs dominated by a snag. Size distributions were quantified in terms of modeled dbh distributions. Stocking was quantified by TAO density and basal area based on modeled dbh. Spatial pattern metrics followed the Individuals, Clumps, and Openings method (ICO) (Churchill et al., 2013). TAOs were considered members of the same clump if their high points were within 6 m of one another, and TAOs with no neighbors within 6 m were considered individuals. This limiting distance was chosen to represent the average crown width of a mature conifer and was validated using plot data from Yosemite (n = 97 trees, data not shown). Clump size distributions were reported as proportions of TAOs in clumps of different sizes: individuals, small clumps (2–4 TAOs), medium clumps (5–9 TAOs), large clumps (10–14 TAOs), super clumps (15–30 TAOs), and mega clumps (> 30 TAOs). Any area with no vegetation taller than 2 m in the canopy height model was considered open space. We created open space distributions to describe the amount of area at varying distances from the nearest canopy: 0–10 m in 2 m bins, 10–20 m, and > 20 m (Churchill et al., 2017). We delineated canopy gaps with methods from Lydersen et al. (2013), which uses image morphology

Fig. 4. Photos exemplifying conditions in reference areas. (a) shows a hillslope view exhibiting a complex patch mosaic. (b), (c), and (d) show open, fire-resistant conditions with scattered large trees and very little understory. (e) and (f) show sites that have burned fewer times or at lower severity, where stem density appears high but most small trees are dead and surface fuel loads are low.

operations to identify gaps at least 60 m^2 in size and cut off long meandering gaps at ecologically relevant thresholds. Gaps were summarized in terms of gap density and gap size distributions. Clumps, open space, and gaps were all quantified across entire reference areas before being subdivided by LMU to avoid edge effects.

Table 2
Lidar acquisitions used in this study and their key technical specifications. Vendor abbreviations: WSI = Watershed Sciences, Inc. (today Quantum Spatial), NCALM = National Center for Airborne Laser Mapping, CIS = Carnegie Institution for Science. CAO = Carnegie Airborne Observatory (Asner et al., 2007).

Acquisition	Illilouette Basin	Rim Fire	Sequoia National Park	Storrie Fire	Moonlight Fire	Tahoe National Forest
Mo./yr. acquired	Aug. 2011	Nov. 2013	Aug. 2015	Aug. 2009	Aug. 2013	Jun. 2013
Collected by	WSI	NCALM	CIS	WSI	WSI	NCALM
Instrument	Dual Leica ALS50 ii	Optech Gemini ALTM	CAO	Dual Leica ALS50 ii	Dual Leica ALS50 ii	Optech Gemini ALTM
Max. returns per pulse	4	4	4	4	4	4
Average pulse density (# m^{-2})	12	12	14	7	11	8.5
Laser pulse frequency (kHz)	83	125	100	90	90	100
Field of view (°)	± 14	± 14	± 17	± 14	± 14	± 18

2.4. Differences in reference structure across biophysical environments

To assess how structure of reference areas changes across different biophysical environments we tested for differences in forest structure and pattern between climate and LMU classes, including an interaction term, using analysis of variance (ANOVA) and structural indices. We used data from the six climate classes that had at least 100 ha of reference areas with lidar coverage (Warm Dry Low Montane, Warm Mesic Low Montane, Xeric Mid Montane, Cool Dry Mid Montane, Xeric High Montane, and Cold Dry High Montane). The structure and pattern indices were TAO density, TAO basal area, mean clump size, and proportion of open space $>$ 6 m from the nearest canopy. These metrics are a good summary of stocking and pattern (Churchill et al., 2013). The indices were calculated based on LMUs within each reference area. We confirmed that the distributions of the indices met the assumptions of ANOVA, which required log-transforming the clump and opening indices. We then tested for significant differences between climate and LMU classes for each of these metrics in separate univariate two-way ANOVAs. For any tests that gave significant results we used a Tukey HSD post-hoc test to find significant differences between pairs of classes.

3. Results

3.1. Climate classes

The 20 climate classes identified across the Sierra Nevada were distinctly different in terms of AET, Deficit, T_{min}, and species composition (Fig. A.2). The warmest, driest class, Dry Foothills, had a median AET of 386 mm (range 229–856 mm, mean 396 mm), a median Deficit of 903 mm (range 317–1202 mm, mean 893 mm), and a median T_{min} of 9.5 °C (range 2.1–12.5 °C, mean 9.4 °C). In contrast, the coldest, wettest class, Subalpine, had a similar median AET of 379 mm (range 100–483 mm, mean 207 mm), a much lower median Deficit of 155 mm (range 12–767, mean 255 mm), and a median T_{min} of -3.8 °C (range –8.3 to 0.9 °C, mean –5.2 °C) (Table 1). Five classes fell into the Foothills category, five were Low Montane, three were Mid-Montane, four were Upper Montane, and three were High Sierra. Geographically, climate class groupings followed two major gradients: latitude and elevation. A noticeable break in classification occurred around 38°N latitude, with some higher-Deficit classes introduced south of that line. The elevation gradient is clear, and is expressed in roughly parallel bands running north-south along the range (Fig. 5).

Composition of FIA plots was different among climate classes ($p < 0.01$). Classes in the Foothills group were dominated by oaks (*Quercus* spp.) and gray pine (*Pinus sabiniana*), with California buckeye (*Aesculus californica*) and single-leaf pinyon (*P. monophylla*) in the Southern Foothills. Ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and tanoak (*Lithocarpus densiflorus*) occurred in Foothill Valleys and incense-cedar additionally occurred in the Foothills-Low Montane Transition zone. Low Montane classes were dominated by Douglas-fir, white fir, sugar pine, incense cedar, and ponderosa pine, but red fir was notably absent. California black oak (*Q. kelloggii*) was also common and canyon live oak (*Q. chrysolepis*) was present. Sugar pine was most dominant in the Warm Mesic Low Montane class. Mid-Montane classes had a similar species assemblage but also included red fir, and Jeffrey pine was dominant in the Xeric Mid Montane class. High Montane classes were dominated by red fir, Jeffrey pine, and white fir, with some of the other pines still present. Lastly, the High Sierra group was dominated by high-altitude pines (*P. contorta*, *P. albicaulis*, and *P. balfouriana*) with some red fir and mountain hemlock (*Tsuga mertensiana*) (Table 1).

The indicator species analysis (ISA) yielded significant results for all climate classes. Within the Montane classes Douglas-fir and California black oak were indicators for warmer, drier classes (high AET and high Deficit) while incense cedar indicated cooler classes (lower T_{min}). Edaphically xeric classes (low AET with high Deficit) were indicated by Jeffrey pine and western juniper (*Juniperus occidentalis*). Red fir and lodgepole pine (*P. contorta*) indicated classes with T_{min} values at or below 0 °C (Table 1).

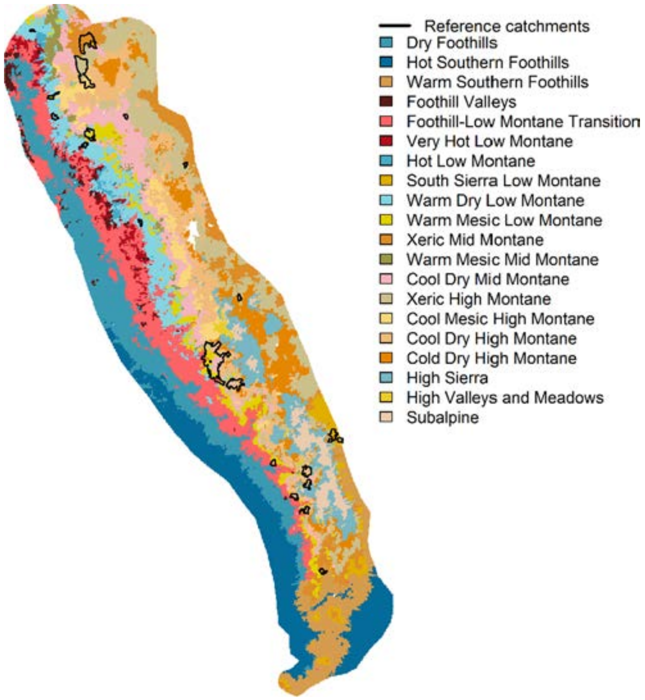

Fig. 5. Map of climate classes. Catchments containing at least one reference area indicated to illustrate the environmental distribution of reference areas.

There were two cases when pairs of classes shared the same primary and secondary indicator species. The Very Hot Low Montane class and the Warm Dry Low Montane class both had Douglas-fir and California black oak as indicators, and the Xeric Mid Montane and Xeric High Montane classes shared Jeffrey pine and western juniper. In both cases PERMANOVA tests with pairwise contrasts showed significant differences in FIA plot composition ($p < 0.01$).

3.2. Reference areas

We identified a total of 30,377 ha of reference areas across the Sierra Nevada mixed-conifer zone (Table 1). Median contiguous patch size was 260 ha and the maximum was 5500 ha. Reference areas were distributed across the latitudinal and altitudinal ranges of our study area, mostly on the west slope of the Sierra Nevada (Fig. 1). By far the majority of reference area was in the central and southern Sierra (25,663 ha), concentrated in Yosemite National Park (19,990 ha) and Sequoia-Kings Canyon National Park (3927 ha), along with 1380 ha on the Sierra, Sequoia, and Inyo National Forests. The majority of reference areas in the northern Sierra were on the Plumas and Lassen National Forests (3532 ha) and Lassen National Park (701 ha).

3.3. Reference conditions

The envelope of reference area structure was broad and variable (Figs. 4, 6). TAO density varied from 6 to 320 TAOs ha^{-1} distributed widely across diameter classes (Fig. 6b). Typical LMUs had up to 42.9 TAOs ha^{-1} $<$ 20 cm dbh, up to 29.2 TAOs ha^{-1} 20–40 cm dbh, up to 26.0 TAOs ha^{-1} 40–60 cm, up to 21.6 TAOs ha^{-1} 60–80 cm, up to 15.3 TAOs ha^{-1} 80–100 cm, and up to 7.4 TAOs ha^{-1} 100–120 cm dbh (all values given are 75th percentile values) (Fig. 6a). Overall density was normally distributed (Fig. 6b) with a mean of 111 TAOs ha^{-1} and a standard deviation of 40 TAOs ha^{-1}. Basal area was distributed with a

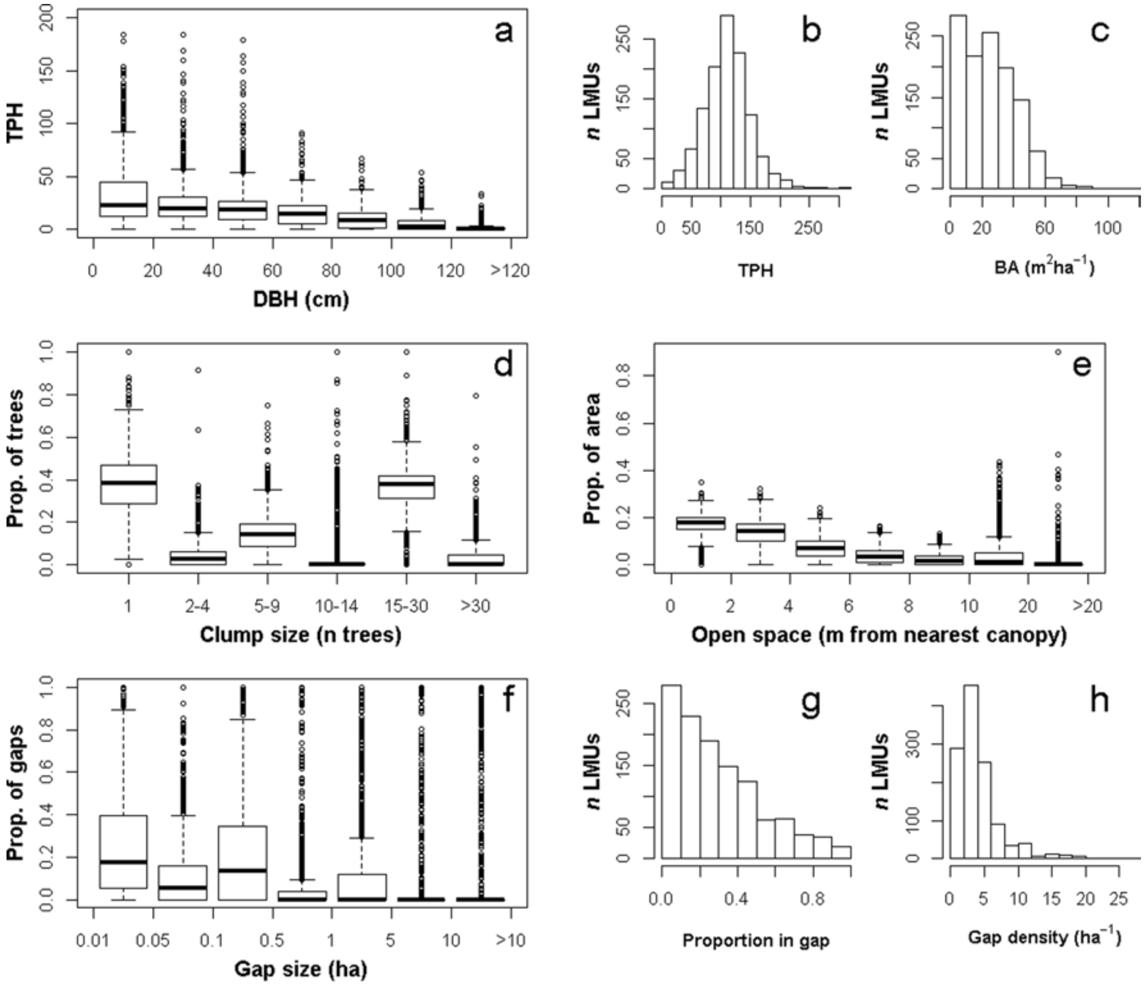

Fig. 6. Ranges of variation in reference condition structure across all reference areas with available lidar data. Each data point represents one landscape management unit. TPH = TAOs per hectare, DBH = diameter at breast height, BA = basal area. Horizontal axes for panels a, e, and f show break points between bins.

mode at 25 m^2 ha^{-1} (standard deviation 17 m^2 ha^{-1}) and a right skew. The majority of LMUs had less than 10 m^2 ha^{-1} of basal area, but only five percent had less than 2 m^2 ha^{-1} (Fig. 6c).

Spatial patterns of TAOs in reference areas had some consistent patterns of variation. TAOs were most commonly arranged as individuals with no close neighbors and in clumps of 15–30 (both median 38% of TAOs per LMU). LMUs with many clumps of 2–14 or $>$ 30 TAOs were less common (Fig. 6d). Between 25% and 40% of stand area was usually situated in openings $<$ 4 m from the nearest canopy, whereas less than 15% was usually $>$ 6 m from the nearest canopy. However, as is evident in the basal area distribution, some LMUs were very open and it was not uncommon for 10–20% of the LMU area to be located $>$ 10 m from the nearest canopy (Fig. 6e). Delineated gaps at least 12 m in diameter were present on 94% of LMUs, usually representing $<$ 50% of LMU area. On most LMUs the majority of gaps were under 0.5 ha in size (median 72%), with 25% under 0.05 ha (Fig. 6f). However, larger gaps were often present including commonly up to 13% of gaps in the 1–5 ha size class, and 94% of total gap area across reference areas was accounted for by gaps $\geq$ 1 ha. Most LMUs had 0–10% of area in gaps (Fig. 6g) at a density of 2–5 gaps ha^{-1}, and up to 8 gaps ha^{-1} was common (Fig. 6h). The highest observed gap density was 26 ha^{-1}.

3.4. Variation in reference structure across biophysical environments

All of the stocking and spatial pattern indices we tested varied significantly by climate class and LMU. Density and mean clump size also had significant climate class-LMU interaction terms (Fig. 7). Of the six climate classes analyzed the lowest- and highest-elevation classes had the highest densities (median 121 TAOs ha^{-1}), following a roughly U-shaped distribution across the elevation gradient. The Xeric Mid Montane class had significantly lower density than any other class (median 86 TAOs ha^{-1}). Density was also significantly lower on ridges compared to valleys, but the absolute difference was not large (medians 101 vs. 115 TAOs ha^{-1}). Ridges and valleys diverged from the general U-shaped distribution in the highest elevation class, Cold Dry High Montane, where densities were almost as low as for the Xeric Mid Montane class (Fig. 7). Basal area followed density in its response to topography (slightly lower on ridges), but its relationship with climate was more complex. The two edaphically xeric classes had lower basal area (median 3.7 and 22 m^2 ha^{-1}) as did the Warm Mesic Low Montane class (median 13.7 m^2 ha^{-1}). However, the Cool Dry Mid Montane class, which had relatively low density, had the highest basal area (median 31 m^2 ha^{-1}). There was no significant climate class-LMU interaction for basal area.

Mean clump size was indistinguishable among five of the six tested climate classes (Fig. 7). The Cool Dry Mid Montane class had a lower mean clump size than the rest (median 2.7 vs. 4.0 trees). Mean clump size differed between ridges (median 3.0 trees) and other landforms (median 3.3 trees). More pronounced was the interactive effect of climate class and LMU on mean clump size. Clump sizes were larger in valleys compared to other landforms in the Warm Dry Low Montane, Xeric Mid Montane, and Xeric High Montane climate classes (Fig. 7). Southwest-facing slopes also had higher mean clump sizes in the Xeric

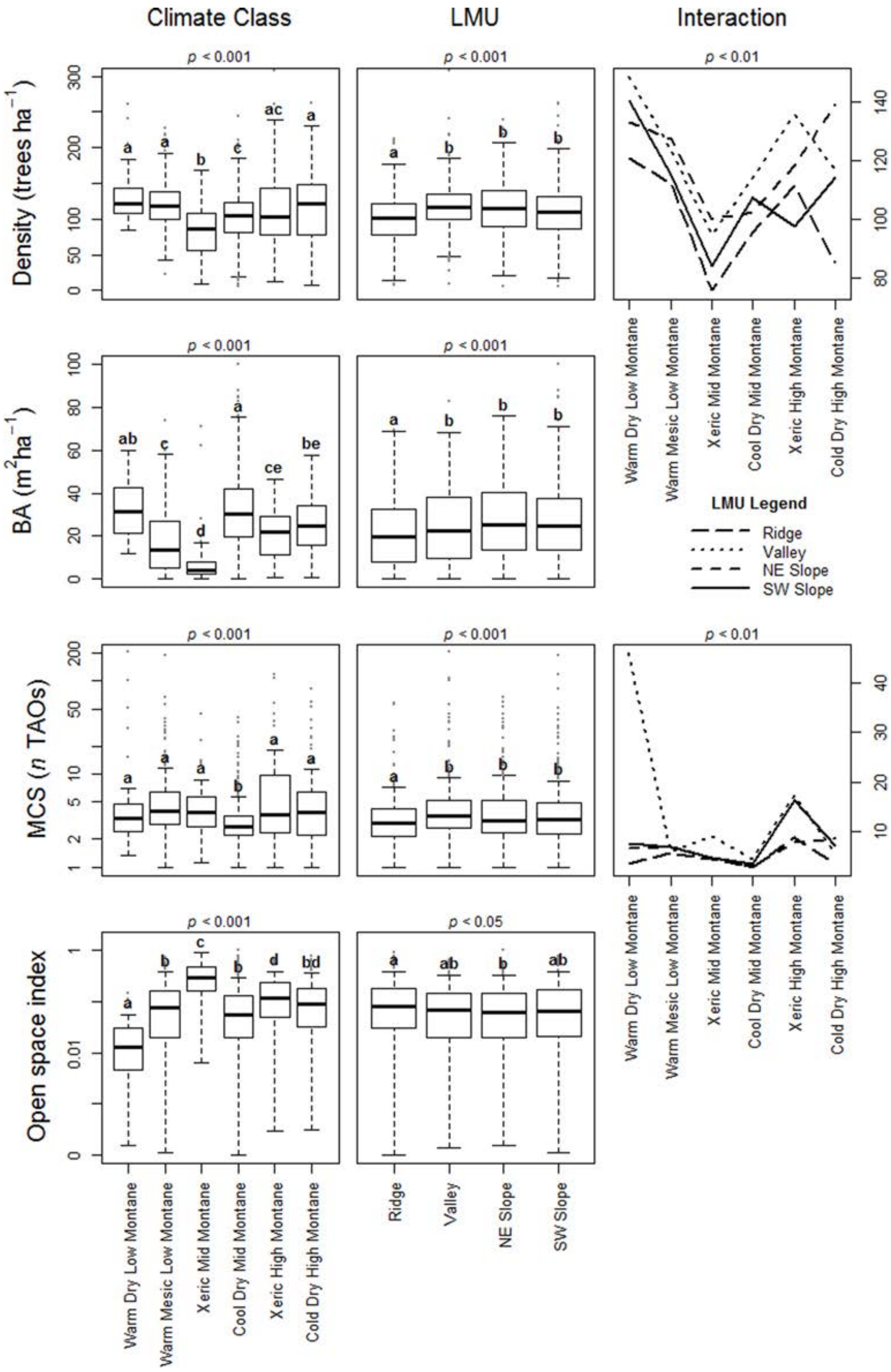

Fig. 7. Structure and pattern indices varying by climate class and landscape management unit (LMU). Interaction terms are shown where significant. Letters above box plots indicate statistically distinct groupings based on Tukey tests. Open space index refers to the proportion of area > 6 m from the nearest canopy. BA = basal area, MCS = mean clump size, TAO = tree-approximate object.

High Montane climate class. The open space index, measuring the proportion of stand area greater than 6 m from the nearest canopy edge, varied across climate classes and LMUs almost as a mirror image of basal area when plotted on a log scale (Fig. 7). The open space index was lowest in the Warm Dry Low Montane class (median 0.01) and highest in the Xeric Mid Montane class (median 0.29). Open space was higher on ridges (median 0.074) and lower on NE-facing slopes (median 0.046), while valleys and SW slopes were transitional (median 0.056).

4. Discussion

We found that contemporary fire-dependent forests, often used to inform restoration targets, vary by climate and topographic position, producing an array of structural conditions that are highly variable at landscape scales. Our results reaffirm the importance of managing for wide and flexible ranges of variation at multiple scales rather than managing for one specific condition at any one scale (Larson and Churchill, 2012; Hessburg et al., 2015; Collins et al., 2016). Given the complex relationship between environmental setting and reference condition structure, it is valuable to use the most biophysically analogous data available for evaluating departure from reference conditions (Churchill et al., 2013). We found that climate classes at coarse scales and LMUs at fine scales provided a meaningful biophysical template for forest structure and spatial pattern. Using this framework, management objectives for a departed landscape could be defined to produce a range of stand structures congruent with climatic and physiographic factors that may improve forest resilience to increasing severity and frequency of fire and drought stresses.

4.1. Geographic and environmental distribution of reference areas

The geographic distribution of reference areas was most obviously due to management practices associated with different land ownerships. We required that reference areas had no history of active forest management such as planting, thinning, or logging. Timber management has been widespread across National Forests of the Sierra Nevada since the early 1900s (Laudenslayer and Darr, 1990), but has generally not occurred in the National Parks which were protected from most resource extraction starting in 1890 (Yosemite and Sequoia-Kings Canyon) and 1907 (Lassen) (Parsons and van Wagtendonk, 1996). Logging that did occur before the parks were protected was mostly opportunistic and small-scale (Laudenslayer and Darr, 1990). Second, fire policy has been very different between National Forests versus National Parks in the Sierra Nevada, especially since the early 1970s when the parks began phasing out full suppression policies and adopting instead active prescribed fire and managed wildfire programs (Parsons and Botti, 1996; van Wagtendonk, 2007; van Wagtendonk and Lutz, 2007). In contrast, National Forests started using prescribed burning more recently and have adopted managed wildfire primarily in designated wilderness (Stephens and Ruth, 2005). This in large part accounts for the fact that 81% of the reference area in the Sierra Nevada mixed-conifer zone is in National Parks, even while the parks represent less than 13% of the federal land base in the Sierra Nevada.

Some part of the distribution of reference areas can also be attributed to environmental conditions, in particular, lightning strikes. Lightning ignitions are an important environmental factor in Sierra Nevada fire regimes, since essentially all of the montane forest is dry enough to burn during the annual summer drought (Lutz et al., 2009). Lightning strike density varies with elevation across the Sierra, peaking in the 1800–2400 m elevation band (van Wagtendonk, 1994; van Wagtendonk and Cayan, 2008). This may explain why there were no reference areas in the two lowest-altitude montane climate classes (Very Hot Low Montane, Hot Low Montane). The elevation band that these classes primarily occupy, 600–1200 m, receives less than half as many lightning strikes of any of the other montane classes, and less than a quarter as many strikes as the three highest-elevation montane classes (van Wagtendonk and Cayan, 2008). Another explanation may be the tendency of forests in this elevation band to burn in human-caused fires with large high-severity patches.

A final factor that influenced the distribution of reference areas was the 2013 Rim fire. The Rim fire burned 31,519 ha of western Yosemite (Lydersen et al., 2014), reburning a series of fires from the 1980s to 2000s that had substantial lower-severity components. This initial series of fires primed western Yosemite for a subsequent lower-severity burn. Although the Rim fire burned at high severity on the adjacent Stanislaus National Forest, severity in Yosemite was much more mixed in part because of the previous fire history (Lydersen et al., 2014; Kane et al., 2015a; Lydersen et al., 2017). Over half of the reference areas in Yosemite only met our criteria after being burned by the Rim fire.

4.2. Ranges of variation in reference stand structure and pattern

The ranges of variation in density that we measured in reference areas generally matched ranges reported by past studies quantifying active-fire Sierra Nevada forest structure. For example, several reconstructed and historical datasets report mean densities ranging from 60 to 314 TAOs ha^{-1}, with total density ranges from 16 to 650 TAOs ha^{-1} (minimum dbh values varied from 5 to 15.2 cm) (North et al., 2007; Scholl and Taylor, 2010; Collins et al., 2011; Van de Water and North, 2011; Knapp et al., 2013; Barth et al., 2015; Stephens et al., 2015). This matches well with our measured mean density of 111 TAOs ha^{-1} (range 6–320), even when considering that each TAO may represent both the identified overstory tree and up to several subordinate trees. These same studies report mean basal area between 21 and 54 m^2 ha^{-1} with a range of 0.3–89 m^2 ha^{-1}, compared to our mean basal area of 25 m^2 ha^{-1} (range 0.01–113). This alignment indicates that the reference areas we identified exhibit some of the key structural features associated with historically resilient stands, namely, lower densities than contemporary fire-suppressed forests and dominance by large trees (North et al., 2009; Stephens et al., 2015; Safford and Stevens, 2017). However, dominance by large trees was not observed in every reference area. In particular, small old trees (often 10–20 cm dbh observed during field visits) dominated the Xeric Mid-Montane climate class, which is characterized by shallow, gravelly soils with very sparse forest cover and stringers of denser cover in patches of convergent topography.

In contrast, correspondence between our measurements of spatial pattern and reported measurements for historical Sierra Nevada forests was mixed. We are aware of only one study using spatially-explicit data to describe historical spatial patterns in the Sierra Nevada: Lydersen et al. (2013) used 1929 stem map data from the “Methods of Cutting” experiment on the Stanislaus-Tuolumne Experimental Forest to quantify tree clumps and canopy opening patterns. Our measurements of TAO clumps did not directly align with their measurements of tree clumps. Specifically, we measured a higher proportion of individuals (38% vs. 5.6%) and a lower proportion of small clumps of 2–4 trees/TAOs (4.2% vs. 13.4%). This is probably because many TAOs counted as individuals actually represent two or three trees. In this sense our data and the data from Lydersen et al. (2013) are not directly comparable. However, measurements of open space do not rely on tree counts and so can be directly compared. Our average measurements were similar to the Methods of Cutting plots. Lydersen et al. (2013) found 40% of plot area was in open space < 3 m from the nearest canopy compared to our finding of 25–40% within 4 m. The Methods of Cutting plots averaged 5.2 delineated gaps ha^{-1} compared to our 4.1 ha^{-1}, and the distributions of gap sizes were also comparable. We additionally identified many large gaps (> 10 ha) that were not possible to detect with the 4 ha plots used by Lydersen et al. (2013).

Contemporary measurements of spatial pattern in the active-fire Sierra San Pedro Martir in northern Baja California, Mexico provide another point of reference. Fry et al. (2014) found that 10–14% of trees in Jeffrey pine-mixed conifer stands were individuals with no close neighbors, while 20–25% of trees were in small clumps and 18–24% of trees were in medium clumps of 5–9 trees. These proportions represent a somewhat less clumped stand than the Lydersen et al. (2013) data (more individuals and small clumps, fewer large clumps), but compare to our findings similarly. That is, we found higher proportions of individuals and lower proportions of small clumps overall.

4.3. Variation in reference structure across biophysical environments

Patterns of variation in active-fire forest structure are very complex, driven by multiple interactions between fire, topography, and moisture (Kane et al., 2013, 2015a; Collins et al., 2016). Some of this variation can be explained by elevation, water balance, and topographic position. For example, Collins et al. (2015) found that elevation and AET strongly differentiated between different classes of tree size and stand basal

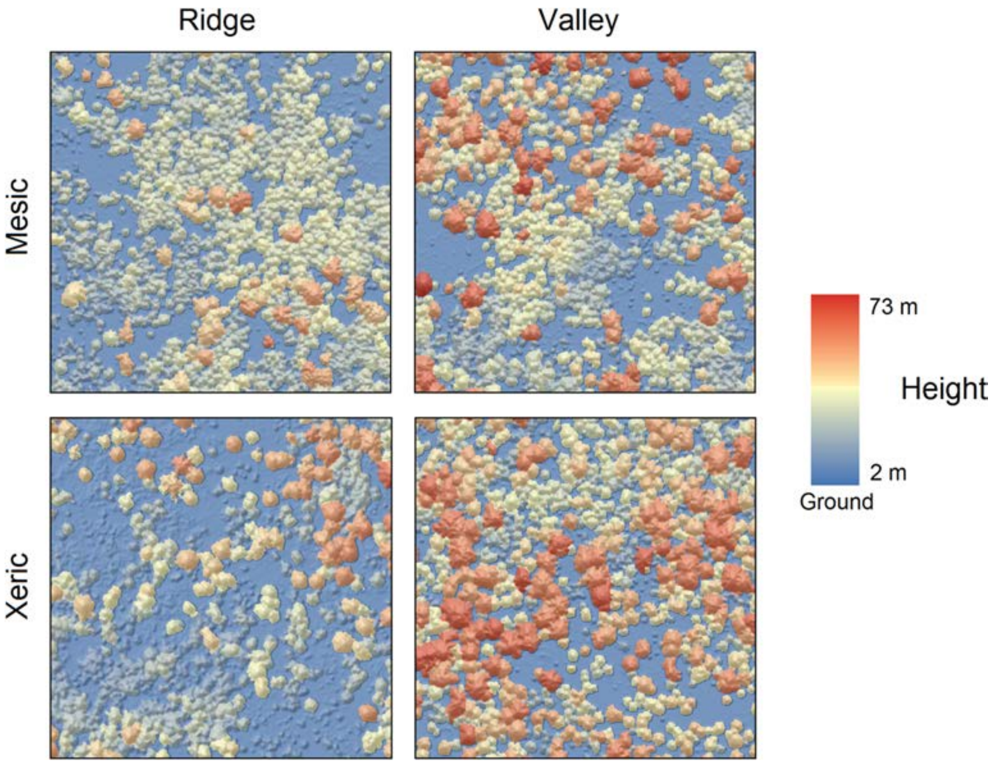

Fig. 8. Example illustrating context-dependent relationships of climate and landform driving structure and pattern in reference areas, as is quantitatively shown in Fig. 7. In mesic conditions, density and spatial patterns are similar between ridges and valleys; only the sizes of trees differ. In xeric conditions trees are still larger in valleys than on ridges, but density and mean clump size are also higher in valleys.

area. Kane et al. (2015b) found that AET and Deficit, along with slope and topographic position, were good predictors of canopy cover and tree height in twice-burned stands. Lydersen and North (2012) found gradients of tree size and density associated with slope position, which differentiated between structural conditions better than aspect did. However, there was residual variation around these patterns in all cases. Our results suggest that the way the biophysical environment drives structure in active-fire landscapes is context-dependent, which may partially account for high amounts of unexplained variation in earlier research. This agrees with findings of Abella et al. (2015) from the Spring Mountains of Nevada. Here we provide examples illustrating the complex context dependency in relationships between the biophysical environment and structure (Fig. 8).

We found that ridgetops had lower density, lower basal area, smaller tree clumps, and more open space than other landforms (Fig. 7). This matches descriptions by Lydersen and North (2012), who suggest that ridges uniquely combine lower productivity with more severe fire effects (i.e., more fire mortality) to result in a fundamentally different growing environment than other landforms. However, climate conditions can alter or enhance this relationship. For instance, the basic relationship between landform and density is reversed in the Xeric High Montane climate class, where ridges are similar to NE slopes while SW slopes have the lowest density (Fig. 7). One possible explanation is that this climate class is characterized by shallow, rocky soils throughout, so ridgetop soil conditions are not very different from other landforms. This normalization of landform effects may allow the (usually less important) effect of aspect on insolation to be expressed in the form of reduced density on SW slopes. In contrast, the relationship between landform and density is enhanced in the Cold Dry High Montane class, where ridgetop density was lower than density on other landforms by a much greater margin than in any other climate class (Fig. 7). One possible explanation for this pattern is that ridges in this climate class, which was the only sampled climate class with average T_{min} values below 0 °C (Fig. A.2), experience strong winds carrying damaging ice crystals more commonly than warmer classes, and so the uniquely difficult growing environment found on ridges is made even more difficult relative to other climate classes.

A strongly context-dependent relationship was observed between landform and mean clump size. Overall, clump sizes in valleys were not significantly different than for any other landform; however, in the warmest and driest climate classes, valleys had significantly larger clumps on average. For the Xeric Mid Montane and Xeric High Montane classes the difference was approximately a factor of 2, while the Warm Dry Low Montane class, the hottest class sampled, the difference was a factor of over 100 (Fig. 7). This pattern, along with the patterns related to ridgetops discussed above, suggests that while broad conclusions about structural variation across elevation, water balance, and topography may be helpful guideposts, the signs and magnitudes of relationships between these factors and structure are not consistent across biophysical space.

The U-shaped distribution of density and basal area with increasing elevation within the six montane classes under study (Fig. 7) runs counter to the expectation that stand density should increase approximately monotonically with elevation due to the combination of orographic precipitation and longer fire return intervals (van Wagtendonk et al., 2018). This can be explained by considering actual evapotranspiration – a surrogate for productivity (Stephenson, 1998) – instead of precipitation. Actual evapotranspiration was negatively correlated with elevation for the montane climate classes ($r = -0.33$, Table 1), suggesting that lower densities in the mid-montane classes may be due to lower productivity coupled with similarly frequent fire compared to the low-montane classes. This effect was clearer than the effect of recent fire regimes. We were not able to find any statistical relationships between recent fire severity and climate classes, and fire regimes have not been reestablished long enough to test for effects of fire frequency.

One limitation to the model discussed in this section is that our study design did not fully address potential spatial autocorrelation of LMUs. Adjacent LMUs within the same or adjacent reference areas are more likely to have similar fire history, be structurally similar, and be in the same climate class. Although we did not sample enough sites to control for this factor, we suggest that, at least from a management perspective, LMUs can be considered independently.

4.4. Using reference condition data in forest management

The structural data for Sierra Nevada reference areas presented here are intended to be applied to forest restoration planning and treatments. The envelopes of forest structure indices (Fig. 6) can provide quantitative waypoints for interpreting current conditions and planning restoration treatments or comparing to post-treatment conditions for monitoring. Further research formalizing the inclusion of lidar-measured structure and spatial pattern into forest restoration planning is currently underway.

Evaluating departure from the reference conditions presented here is more straightforward if lidar data are available for the departed area under analysis. This allows for consistent data processing and direct comparisons between two TAO-based sets of metrics. However, the reference conditions we report can also be compared to ground-based measurements (i.e., tree lists) as long as the limitations of lidar measurements are accounted for. Specifically, each TAO may represent between one and several trees, and so measures of TAO density and clump sizes will be smaller than measures of tree density and clump sizes. For these measures our results can be taken as a lower range estimate. On the other hand, our results for basal area should be close to the actual values, since lidar accurately captures the larger trees that constitute most of the basal area (Lutz et al., 2012; Jeronimo et al., 2018). Similarly, since lidar is very effective at measuring canopy gaps our results for the open space index should be very similar to results from a field-measured stem map (Koukoulas and Blackburn, 2004).

Our results indicate that fire use has been an effective restoration tool where implemented, since the reference areas we identified are apparently set to continue burning at lower severity and are structurally similar to historical forest conditions that are thought to be resilient. Nevertheless, Sierra Nevada forest managers have been conservative in fire reintroduction and the rate of restoration lags behind regional targets (North et al., 2015; Stephens et al., 2016). This research provides strong support for increasing the use of restorative fire in the Sierra Nevada.

4.5. Limitations

An important drawback to using lidar measurements as the sole data source is that there are no composition data to go along with the structural measurements. Composition data must come from other sources such as modeling or imputation from structure, Landsat or other spectral data sources, or field surveys (Jeronimo et al., 2018). Lidar is also only able to characterize the shrub layer in general terms (Martinuzzi et al., 2009), which can be a problem since shrubs, as angiosperms, are a key element of mammal and bird diets in the Sierra Nevada (Lutz et al., 2014, 2017). However, the reference conditions we provide here are associated with species assemblages (Table 1). Since restoration treatments typically favor fire- and drought-tolerant species it should be clear which species will be expected for retention in a given climate class. Nevertheless, field visits and silvicultural knowledge will still be necessary to set realistic composition targets.

Another limitation of lidar is a difficulty differentiating live trees from dead trees. Some studies have used return intensity data to estimate dead tree parameters (e.g., Kim et al., 2009), but no method has yet been widely accepted and no study has been done at the TAO or equivalent scale. For these reasons we chose not to separate TAOs dominated by a live tree from TAOs dominated by a dead tree in our analyses. This may be consequential for some reference areas. For example, lidar data for areas within the Rim Fire were collected only 8–12 weeks after initial burning, probably before much of the mortality from that fire was actually discernible from lidar. We justify our inclusion of these data in two ways. Since we focused on areas that burned at low and moderate severities (1) we expect that much of the mortality was concentrated in smaller size classes, not in the larger trees that dominate TAOs, and (2) even when the measurements we report represent something closer to pre-fire structure than post-fire structure, that structure led to low and moderate severity burning and thus can be considered a desirable condition.

While the reference areas we present have experienced some fire reintroduction, they also previously experienced decades of fire suppression and other anthropogenic disturbances (e.g., grazing). We do not claim that these forests are fully restored nor that they are in the most resilient condition possible. Nevertheless, these areas have burned multiple times and are still forested with a degree of heterogeneity comparable to historical measurements. They are the best extant examples of Sierra Nevada mixed-conifer forests under an active fire regime.

In this study we have analyzed and presented results representing ranges of structure at scales of topographic facets with areas mostly around 2–20 ha. However, spatial heterogeneity in forest structure also occurs across broader scales: landscape conditions are a mix of a tree clump and canopy opening patch mosaic, shrubland and herbland covering dozens of hectares of potential forest sites, and some large aggregations of closed-canopy forest (Hessburg et al., 2005; Kane et al., 2014). Analyzing these reference areas in terms of landscape patches (e.g. seral stages *sensu* Gärtner et al., 2008) would be a valuable complement to the finer-scale data we have presented here.

5. Conclusions

Forest structure in active-fire landscapes is highly variable at multiple scales (Fry et al., 2014; Belote et al., 2015; Collins et al., 2016). Measuring reference conditions across contemporary active-fire landscapes using lidar affords some key advantages over historical reference conditions and field-based sampling. The Sierra Nevada region may be unique in having broad lidar coverage coupled with large areas of reintroduced fire. This allowed us to quantify landscape features over reference areas on the scale of hundreds to thousands of hectares that would not have been practically measurable with reconstruction techniques or using ground-based surveys. We captured the full range of structural variability present in the reference areas, including dense aggregations of hundreds of trees as well as large meandering openings snaking across dozens of hectares. While our novel techniques provided some new insights into forest structure under active fire conditions, our findings also confirmed past research indicating that frequent lower-severity fire leads to highly variable landscapes patterned after climatic and topographic gradients.

Conflict of interest

None.

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Appendix A:. Additional tables and figures

See Tables A1 and A2.

Table A1
Species codes, Latin names, and common names key for Table 1.

Species code	Latin name	Common name
ABCO	*Abies concolor*	White fir
ABMA	*Abies magnifica*	Red fir
AECA	*Aesculus californica*	California buckeye
CADE	*Calocedrus decurrens*	Incense-cedar
JUCA	*Juniperus californica*	California juniper
JUOC	*Juniperus occidentalis*	Western juniper
LIDE	*Lithocarpus densiflorus*	Tanoak
PIAL	*Pinus ablicaulis*	Whitebark pine
PIBA	*Pinus baulforiana*	Foxtail pine
PICO	*Pinus contorta*	Lodgepole pine
PIJE	*Pinus jeffreyi*	Jeffrey pine
PILA	*Pinus lambertiana*	Sugar pine
PIMO	*Pinus monophylla*	Single-leaf pinyon
PIMO2	*Pinus monticola*	Western white pine
PIPO	*Pinus ponderosa*	Ponderosa pine
PISA	*Pinus sabiniana*	Gray pine
PSME	*Pseudotsuga menziesii*	Douglas-fir
QUCH	*Quercus chrysolepis*	Canyon live oak
QUDO	*Quercus douglasii*	Blue oak
QUKE	*Quercus kelloggii*	Black oak
QUWI	*Quercus wislizeni*	Interior live oak
TSME	*Tsuga mertensiana*	Mountain hemlock

Table A2
Model coefficients and statistics for height-diameter regressions on forest inventory and analysis plots within each climate class (total number of plots = 3217). Model form is dbh = $b_0$height^{b_1}, with dbh in cm and height in m.

					Data used to build model					
Class	b_0	b_1	r^2	RMSE (cm)	N plots	N trees	DBH min (cm)	DBH max (cm)	Height min (m)	Height max (m)
1	1.53856	1.14648	0.64	3.99	216	3179	2.5	121.2	1.2	45.1
2	2.72283	1.02325	0.61	3.38	31	304	3.6	101.3	2.7	30.5
3	2.05648	1.15830	0.70	4.29	69	1310	2.5	115.1	0.9	34.4
4	1.14798	1.12029	0.86	5.09	21	654	2.5	149.6	2.7	64.6
5	1.37670	1.10943	0.79	4.73	460	13,524	2.5	209.0	1.8	68.9
6	1.19206	1.12831	0.86	5.06	88	3311	2.5	182.6	1.8	68.9
7	1.07742	1.16068	0.84	5.16	27	1091	2.5	161.0	2.1	60.4
8	3.03182	0.95797	0.64	5.64	30	723	2.5	158.2	1.5	46.3
9	1.44673	1.08746	0.86	4.74	335	13,501	2.5	203.2	0.9	70.1
10	1.69328	1.05785	0.86	5.10	224	8712	2.5	245.6	1.5	75.6
11	2.31671	1.00310	0.81	5.60	113	2251	2.5	157.5	1.2	51.8
12	1.40413	1.10804	0.86	4.78	62	2414	2.5	177.8	1.8	60.7
13	1.78311	1.04917	0.85	5.32	356	13,568	2.5	216.7	0.6	80.5
14	2.82546	0.92227	0.75	5.58	312	8589	2.5	164.6	0.3	59.4
15	1.93072	1.04232	0.84	5.77	127	4231	2.5	201.4	0.9	59.4
16	1.91499	1.06052	0.83	6.33	328	10,398	2.5	261.9	0.6	59.4
17	2.05270	1.06432	0.79	6.15	233	6498	2.5	176.8	0.9	67.1
18	2.58053	1.00908	0.74	7.68	164	5082	2.5	196.3	1.2	57.9
19	15.64717	0.67221	0.44	5.68	1	34	56.4	127.3	8.2	17.4
20	2.96029	1.02971	0.72	8.15	44	990	2.5	154.2	1.5	33.2

See Figs. A1 and A2.

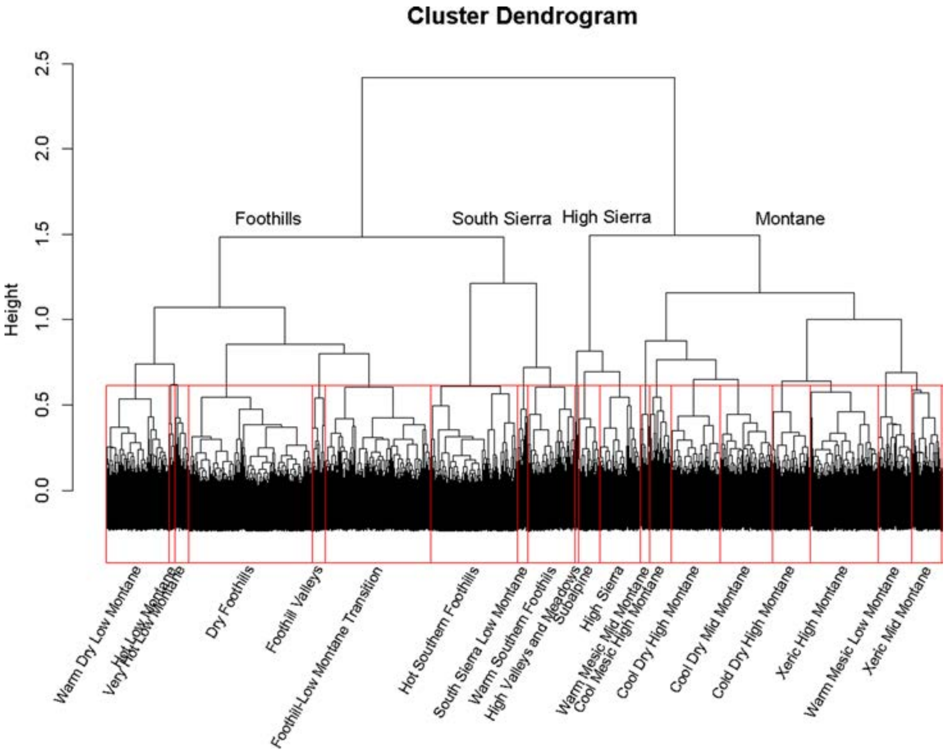

Fig. A1. Cluster dendrogram for climate classes. The labels at the second split indicate broad climate zones. Labels along the bottom are names of the 20 final climate classes (red boxes), interpreted by inspecting this graphic as well as Fig. A.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

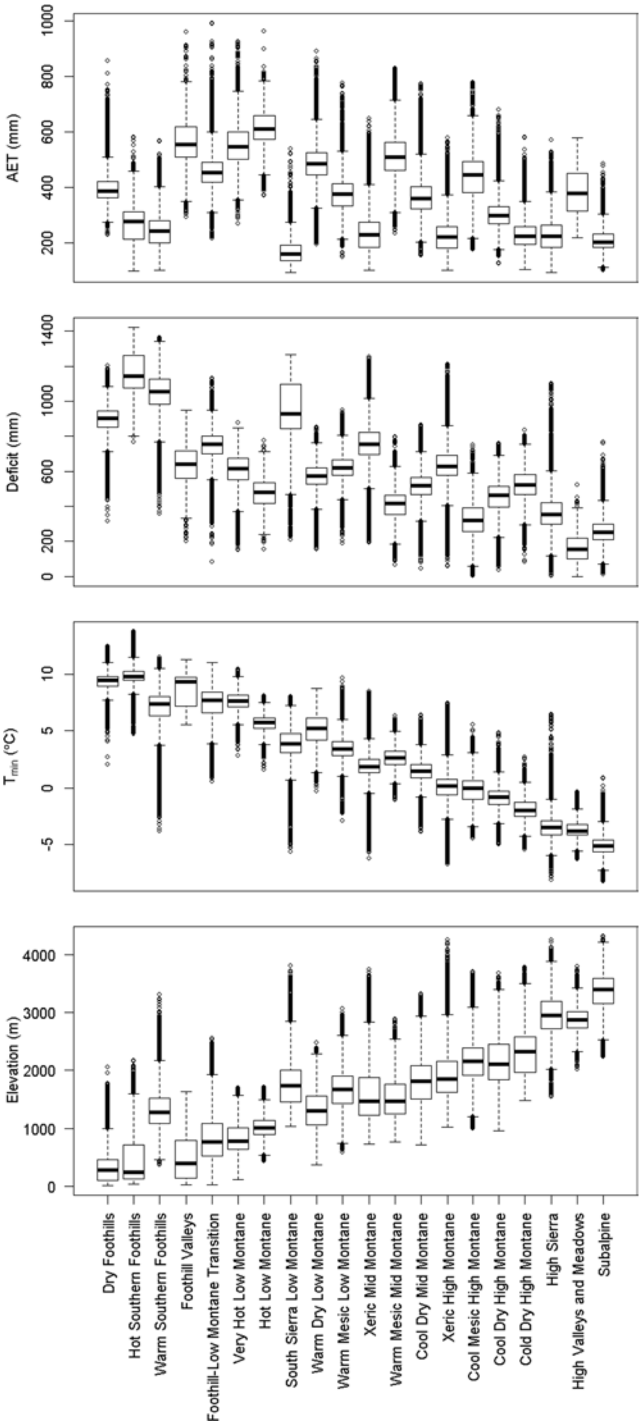

Fig. A2. Characteristics of the 20 climate classes in terms of actual evapotranspiration (AET), climatic water deficit (Deficit) and January minimum temperature (T_{min}), which were the input variables for the classification, as well as elevation, for reference. See Table 1 for class descriptions.

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.01.033.

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BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Declining old-forest species as a legacy of large trees lost

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Abstract

Aim: Global declines in large old trees from selective logging have degraded old-forest ecosystems, which could lead to delayed declines or losses of old-forest-associated wildlife populations (i.e., extinction debt). We applied the declining population paradigm and explored potential evidence for extinction debt in an old-forest dependent species across landscapes with different histories of large tree logging.

Location: Montane forests of the Sierra Nevada, California, USA.

Methods: We tested hypotheses about the influence of forest structure on territory extinction dynamics of the spotted owl (*Strix occidentalis*) using detection/non-detection data from 1993 to 2011 across two land tenures: national forests, which experienced extensive large tree logging over the past century, and national parks, which did not.

Results: Large tree/high canopy cover forest was the best predictor of extinction rates and explained 26%–77% of model deviance. Owl territories with more large tree/high canopy cover forest had lower extinction rates, and this forest type was ~4 times more prevalent within owl territories in national parks ($\bar{x}$ = 19% of territory) than national forests ($\bar{x}$ = 4% of territory). As such, predicted extinction probability for an average owl territory was ~2.5 times greater in national forests than national parks, where occupancy was declining ($\hat{\bar{\lambda}} < 1$) and stable ($\hat{\bar{\lambda}} = 1$), respectively. Large tree/high canopy cover forest remained consistently low, but did not decline, during the study period on national forests while owl declines were ongoing—an observation consistent with an extinction debt.

Main conclusions: In identifying a linkage between large trees and spotted owl dynamics at a regional scale, we provide evidence suggesting past logging of large old trees may have contributed to contemporary declines in an old-forest species. Strengthening protections for remaining large old trees and promoting their recruitment in the future will be critical for biodiversity conservation in the world's forests.

KEYWORDS
declining population paradigm, forest management, forest restoration, logging, occupancy modelling, spotted owl

1 | INTRODUCTION

Large old trees have declined across nearly all global ecosystems, in part because their high commercial value has led to logging pressure that outpaces sometimes centuries-long recruitment and development (Lindenmayer, Laurance, & Franklin, 2012). Agriculture (Laurance, Sayer, & Cassman, 2014), fire (Jones, Gutiérrez, Tempel, Whitmore et al., 2016; Westerling, 2016) and disproportionate drought susceptibility (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015) also increasingly threaten large old trees and conservation of old-forest ecosystems (Lindenmayer & Laurance, 2017). Loss of large old trees is a major contributor to habitat loss for many globally endangered old-forest-dependent (hereafter "old-forest") species such as the orangutan (*Pongo spp.*) in South-East Asia (Wich et al., 2003), the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) in western North America (Noon & Blakesley, 2006; Raphael, 2006), the Leadbeater's possum (*Gymnobelideus leadbeateri*) in south-east Australia (Lindenmayer et al., 2013) and the Blakiston's fish owl (*Bubo blakistoni*) in the Russian Far East and Japan (Slaght, Surmach, & Gutiérrez, 2013).

Like large old trees, many old-forest species have "slow" life histories with long generation times and high adult survival, which increases vulnerability when environments change rapidly (Webb, Brook, & Shine, 2002). Long-lived individuals may persist for many years in marginal or degraded forests long after critical breeding habitat elements such as large old trees are lost or substantially reduced, but gradually these individuals die off and may not be replaced. Delayed population declines or local extinctions resulting from prior habitat loss or degradation is termed "extinction debt," which can be assessed across different levels of organization (e.g., individual species vs. community) and may be evaluated at spatial scales ranging from local extirpation within a habitat patch to regional or global extinction of a species. Extinction debt challenges the ability of scientists to establish causal links between habitat loss and population declines of individual species (Kuussaari et al., 2009). Uncertainty about population status or causes of decline, then, could delay implementing conservation measures for old-forest species and the restoration of degraded old-forest ecosystems. Moreover, this uncertainty creates political opportunities to undermine governmental or social responses to make corrective changes (Oreskes & Conway, 2010).

Global challenges facing the conservation of large old trees and old-forest-associated species (Lindenmayer & Laurance, 2016) have led some to propose new and more rigorous policies for ensuring their protection and improving conservation outcomes (Lindenmayer et al., 2014). Nevertheless, if an extinction debt has already been created, population declines of old-forest species may continue to occur long after policies protecting large old trees are put into place. Here, we studied the potential long-term (multi-generational) impacts of large tree loss on an old-forest species, the spotted owl (*S. occidentalis*), across a large mountain ecosystem by comparing forest conditions and population dynamics between national parks (long-established protected areas) and national forests (areas that experienced widespread large tree logging but more recent protections). Following a century of extensive, intensive and selective logging of very large trees on national forests (Laudenslayer & Darr, 1990; Stephens, Lydersen, Collins, Fry, & Meyer, 2015), forest policy was enacted immediately prior to our study to conserve remaining old-forest elements such as large trees and multilayered canopy around spotted owl activity centres (Verner et al., 1992).

Despite these recent protections, we hypothesized that this historical loss of large trees on national forests could be associated with contemporary population declines, or an extinction debt, for spotted owls. In testing this hypothesis, we treated protected areas (national parks) as "contemporary reference landscapes" (Collins et al., 2016; Meyer, 2015; Miller et al., 2016), because prohibition of logging within national park boundaries over the past century has largely preserved historical forest structure and prevalence of very large and old trees (Beesley, 1996; Lydersen & North, 2012). Thus, in principle, contemporary forests characteristics in spotted owl territories on national parks (e.g., large trees) might more closely represent forests characteristics that might have existed on national forests if protections for large trees had been established long ago.

Comparing spotted owl populations on national forests and national parks, then, allowed us to diagnose causes of decline (Caughley, 1994; Green, 1995; Peery, Beissinger, Newman, Burkett, & Williams, 2004) for a species considered to be a barometer of old-forest wildlife community health in western North America (Simberloff, 1998). Despite the fact that the spotted owl is one of the most intensively studied species in the world with 40 years of demographic and ecological research across its range, no definitive causal link between ongoing owl declines and changes in habitat has been established. Here, we offer insight into this elusive question by applying the concept of extinction debt and provide an unprecedented case study about the potential ecological legacies of large tree loss on increasingly rare global old-forest species and ecosystems (Lindenmayer et al., 2012, 2014).

2 | METHODS

2.1 | Study areas and logging histories

Four spotted owl study areas—Lassen (LAS), Eldorado (ELD), Sierra (SIE) and Sequoia-Kings Canyon (SKC)—span nearly the entire latitudinal range of California's Sierra Nevada (Figure 1). Elevations range

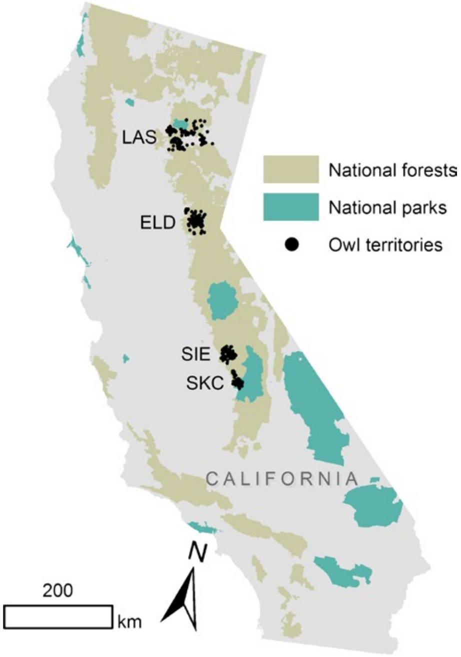

FIGURE 1 Locations of owl territories across the four spotted owl study areas in the Sierra Nevada, California, USA. [Colour figure can be viewed at wileyonlinelibrary.com]

from 300 to 3,050 m across the four study areas, and the climate is Mediterranean (Tempel et al., 2016). LAS, ELD and SIE study areas are primarily located within national forests (with intermixed private land), whereas SKC occurs within two national parks of the same name. While Sierran mixed-conifer montane forest is the primary vegetation type within owl territories across all study areas (Tempel et al., 2016), contemporary structure of these forests has been strongly affected by different management legacies across the two land tenures (i.e., national forests vs. national parks).

Very large (e.g., >125 cm dbh) old trees were not uncommon throughout the Sierra Nevada at the turn of the twentieth century (McKelvey & Johnston, 1992; Safford & Stevens, 2016). Several national parks including Sequoia (of SKC) were established in 1890 (Kings Canyon National Park adjoined in 1940), and the prohibition of logging within park boundaries over the following century largely acted to preserve historical forest structure and prevalence of very large and old trees (Beesley, 1996; Lydersen & North, 2012). In contrast, logging activities on what would eventually become Sierra Nevada national forest lands were well underway by 1900 (Beesley, 1996; Thomas, 2008). Commercial logging (i.e., selective removal of very large trees) on Sierra Nevada national forests increased from ~470,000 cubic metres (m^3) $year^{-1}$ in the 1870s to its peak during the 1940s when timber production reached 4.5 million m^3 $year^{-1}$. Timber production remained reasonably high thereafter (generally between 2.8 and 3.8 million m^3 $year^{-1}$) for several decades before a near-historic peak in timber production in 1990 when production again neared 4.5 million m^3 $year^{-1}$ (McKelvey & Johnston, 1992).

Concern about the continued and cumulative loss of large trees required by spotted owls reached a highpoint around the same time and as a result, in 1992, logging of ≥76 cm dbh trees on national forests was restricted (with some allowable exceptions for equipment operability), as was almost all logging within 121 ha areas around known owl nest and roost sites (USFS, 2004; Verner et al., 1992). Our study on spotted owls began in 1993, immediately following near-peak logging activity and subsequent restrictions. Recent work has established that national forest lands indeed contain greater prevalence of younger trees that are smaller in diameter and height (Laudenslayer & Darr, 1990; Stephens et al., 2015) and significantly fewer trees in the largest size classes compared to historical baselines (Collins, Fry, Lydersen, Everett, & Stephens, in press; McIntyre et al., 2015; Safford & Stevens, 2016; Stephens et al., 2015). Given that SKC did not experience the same history of selective logging and forest structural change as the three study areas on national forests, we treated it as a contemporary reference landscape for evaluating differences in forest structure and owl population dynamics between land tenures.

2.2 | Owl surveys

As part of prior work, we have established that temporal changes in occupancy rates of spotted owl territories (i.e., based on detection/non-detection data) can provide inferences regarding overall population trends that are comparably reliable to estimates of overall population trends based on changes in abundance (Conner, Keane, Gallagher, Munton, & Shaklee, 2016; Tempel & Gutiérrez, 2013; Tempel, Peery, & Gutiérrez, 2014). As such, we conducted detection/non-detection surveys for spotted owls at 275 owl territories located during breeding seasons (Apr–Aug on LAS and ELD; Mar-Sept on SIE and SKC) across the four study areas over a 19-year period (1993–2011). All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e., both the areas containing owl territories and all areas not containing known owl territories within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (LAS) or as individual "satellite" territories (i.e., adjacent to, but not part of, the core area) to increase owl sample sizes for demographic analysis (LAS and ELD), and we dropped a portion of SKC in 2006 (Tempel et al., 2016). We surveyed all satellite territories used in our occupancy analyses for a minimum of 3 years; most territories in the core areas were surveyed for ≥15 years.

We located spotted owls by imitating their vocalizations (vocal lure) for 10 min at a survey station or used vocal lures while walking along a survey route. We then considered sites to be a territory where owls responded to vocal lures and were subsequently observed either roosting or nesting during diurnal hours. Some surveys occurred prior to 1993 but previous analyses have determined that survey coverage and effort required for population analyses (such as ours presented here) became adequate beginning in 1993 (Tempel & Gutiérrez, 2013; Tempel et al., 2016). We did not survey all territories in all years of the study. However, of the 275 owl territories used in the study, ≥205 were surveyed in all but the first year of the study (in 1993, 187 owl territories were surveyed). The average number of owl territories surveyed annually was 239 (87% of all known territories; standard error = 21 territories), with a maximum of 263 territories surveyed in 2008 (95.6% of all known territories). Moreover, while most intervening area between territories was intensively surveyed each year, spotted owls on our study areas rarely established new territories outside of territories located in the early stages of the study. For example, the most recently located territory on the ELD was found in 1997. We included all surveys in our analyses but excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique colour legbands as part of a concomitant mark-recapture study) that occurred outside of a delineated territory boundary (see below for information on owl territories) using a Geographic Information System (GIS) to eliminate potential spurious positive detections of owls not occupying the nominal territories. A survey in which no owls were detected needed a total duration of ≥30 min to be included as an absence record. Extensive details about each study area and additional survey details can be found in Tempel et al. (2016).

2.3 | Sampling units and vegetation covariates

We treated owl territories as sampling units, where a territory had at least one owl detection during diurnal hours in ≥3 years. For quantifying habitat covariates within spotted owl territories, we first calculated the geometric centre of each territory as the average spatial coordinates of all nest and roost locations across all years in the territory.

We then calculated the mean nearest neighbour distance among territory centres for each study area as the average distance between each territory centre and the centre of its nearest neighbouring territory. Thus, the location of owl territories was assumed to remain the same throughout the study period, and territories in each study area were assumed to be of equal size based on the nearest neighbour distance. In a recent meta-analysis (Tempel et al., 2016), we defined the spatial extent of a territory as a circle around each territory centre with a radius equal to half of the mean nearest neighbour distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius) and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. In the present study, we defined territories as hexagons instead of circles with areas and geometric centres equal to those determined by Tempel et al. (2016) to facilitate integration into concurrent projects using spatial population models (e.g., HexSim; Schumaker, 2015).

We defined site-specific covariates based on two vegetation variables within owl territories using the "GNN" (Gradient Nearest Neighbour) forest structural maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group (Oregon State University, Corvallis, OR, USA). GNN is an imputation method used by LEMMA that integrates regional forest inventory plots with Landsat imagery to produce fine-scale (30-m resolution) and large-domain (currently the entire land area for the U.S. states of Washington, Oregon and California) vegetation structure and species composition maps. The GNN approach is one variation of nearest neighbour imputation methods that use (1) a neighbourhood value of $k = 1$ as the number of neighbours imputed to each cell and (2) direct gradient analysis as the "distance" metric (see https://lemma.forestry.oregonstate.edu/methods). The first variable was the quadratic mean diameter of dominant and codominant trees in each 30 × 30 m pixel ("QMD_DOM"). Quadratic mean diameter (QMD) is a commonly used metric in forestry that more strongly reflects the influence of large trees on stand tree size classifications than arithmetic mean (Curtis & Marshall, 2000). The second variable was the per cent canopy cover of live trees in each pixel ("CANCOV").

Large trees are a key feature of spotted owl nest sites (Gutiérrez et al., 1992), and owl site occupancy has been positively correlated with large trees (>61 cm dbh) and high canopy cover (>70%) at nest areas (Blakesley, Noon, & Anderson, 2005). However, forests with intermediate canopy cover (40%–70%) can constitute spotted owl nesting or roosting habitat if large, remnant trees are present (Hunter & Bond, 2001; Moen & Gutiérrez, 1997), and recent work found that both medium and high canopy cover were associated with spotted owl occupancy in the Sierra Nevada (Jones, Gutiérrez, Tempel, Zuckerberg, & Peery, 2016; Tempel, Gutiérrez, et al., 2014; Tempel et al., 2016). Thus, we estimated the proportion of each owl territory containing the following five covariates: large trees (QMD > 61 cm) regardless of canopy cover class; high canopy cover (>70% cover) regardless of tree size class; as well as the spatial intersection (∩; see Figure 2) of large trees and high canopy cover, large trees and medium canopy cover (40%–70% cover), and medium trees (QMD = 30–61 cm) and high canopy cover. These proportions were calculated by dividing the number of 30 × 30 m pixels in the territory for a particular variable by the total number of 30 × 30 m pixels in the territory. Several of the predictor variables were highly collinear (e.g., $r = .7–.9$), so we developed

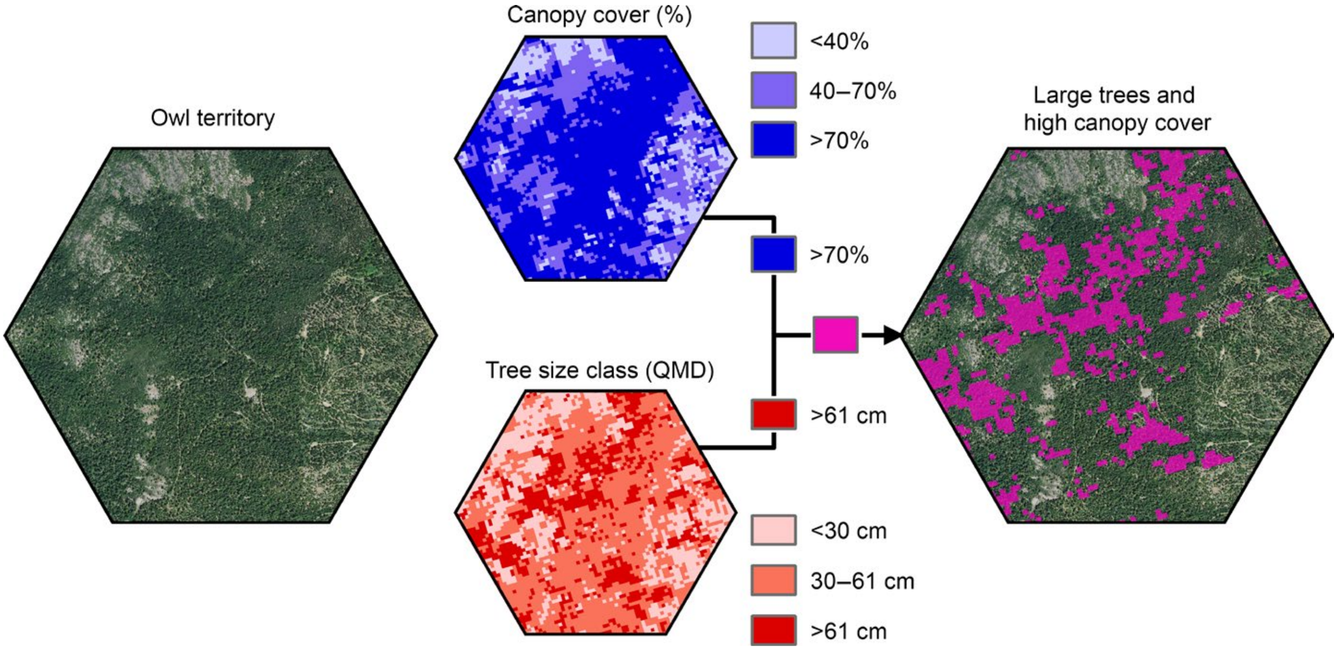

FIGURE 2 An example showing how we produced covariates representing spatial intersections between GNN-derived canopy cover and tree size classes by overlaying classified pixels using a GIS. Here, we see the high canopy cover class (>70% canopy cover) and the large tree size class (>61 cm dbh) combining in a spatial intersection (∩) to produce a covariate called "large trees and high canopy cover" for an example spotted owl territory. [Colour figure can be viewed at wileyonlinelibrary.com]

models that contained a single predictor variable and used AIC to identify which predictor variables best explained owl extinction dynamics (see below).

We adopted the above tree size classes because they are commonly used by foresters (Blakesley et al., 2005; Verner et al., 1992), although the large old trees used by owls for nesting are typically larger than 61 cm dbh (e.g., mean 157 cm dbh; North et al., 2000). Median QMD in the >61 cm dbh size class was 75.5 cm and reached a maximum of 279 cm (Fig. S1). Finally, for each forest structure variable listed above, we averaged the within-territory covariate values across all years (1993–2011) to produce a single, static territory-level covariate that varied across space (but was averaged over time), because nearly all variation in the covariates was spatial rather than temporal (large among-territory differences). Ranges of covariate values for each study area are provided in Table 1.

2.4 | Statistical analysis and model selection

We used multi-season occupancy models to assess territory occupancy dynamics on each study area separately (Tempel et al., 2016) using program PRESENCE 11.5. The models contained parameters for initial occupancy (ψ_1), local extinction (ε_t), local colonization (γ_t) and detection probability ($p_{t,j}$) (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Our primary sampling periods (t) were breeding seasons (i.e., years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (April 1–15, April 16–30, etc.). No surveys were conducted on SKC in 2005 so we fixed p, ε and γ for that year to zero. We allowed colonization to vary as a year-specific effect rather than a function of covariates because (1) colonization may be related more to site availability than site conditions, and (2) we were interested in factors associated with elevated extinction rates.

We used multi-stage modelling (Tempel et al., 2016). At each stage, we ranked models using AIC (Burnham & Anderson, 2002) to select the base model for the next stage. We first modelled p as a function of the above forest structure covariates and within- and among-year temporal trends (i.e., linear, log-linear or quadratic trends in p) while γ and ε varied by year. We then examined linear, logarithmic and quadratic forms of covariates on ψ_1 while γ and ε varied by year. Finally, we examined the potential effects of covariates on ε while γ varied by year, again considering linear, logarithmic and quadratic covariate forms because previous owl studies showed evidence of non-linear relationships (Dugger, Wagner, Anthony, & Olson, 2005; Forsman et al., 2011). We used analysis of deviance to assess the amount of variation explained by model covariates. This approach compares deviance explained by the covariates in a model with the amount of deviance not explained by these covariates, thus providing an estimate of r^2 for the model (Skalski, Hoffman, & Smith, 1993). The global model for the analysis of deviance consisted of the top-ranked model for the given study area with additional annual effects for ε, and the constant model consisted of the best detection structure with only and intercept for ε (Tempel et al., 2016).

We used the best p model from the first stage with year-specific γ and ε to obtain derived estimates of ψ_t which we used to calculate the geometric mean of the rate of change in occupancy ($\hat{\hat{\lambda}}$) and estimated the realized change in occupancy (Δ_k) for each study area. We calculated variance for $\hat{\hat{\lambda}}$ and Δ_k using the delta method (Powell, 2007).

3 | RESULTS

We found that local extinction rates were higher when owl territories contained less forest characterized by large trees (>61 cm dbh) and high canopy cover (>70%), and extinction rates declined as this forest type increased (Figure 3). Indeed, local extinction was best explained by the proportion of an owl territory containing large tree/high canopy cover forest, as evidenced by the presence of this covariate in the top models on three of the four study areas (ELD, SIE, SKC) having nearly all (88%–97%) of AIC weight (Table S1). The top three models for the fourth study area (LAS) were closely competing (within 1 AIC), containing parameters for large trees only, large trees and high canopy

TABLE 1 Median (*SD*) proportion of a spotted owl territory[a] containing GNN structure variables used to assess local extinction dynamics on four study areas[b] in the Sierra Nevada, CA, USA. The number of spotted owl territories identified on each study area is shown in the bottom row of the table

	Study area			
Variable	LAS	ELD	SIE	SKC
Large trees[c]	0.07 (0.05)	0.11 (0.06)	0.13 (0.11)	0.33 (0.19)
High canopy cover[d]	0.46 (0.16)	0.54 (0.14)	0.25 (0.16)	0.48 (0.16)
Large trees and high canopy cover	0.03 (0.05)	0.06 (0.05)	0.04 (0.08)	0.19 (0.14)
Large trees and medium canopy cover	0.02 (0.02)	0.02 (0.03)	0.05 (0.06)	0.10 (0.08)
Medium trees and high canopy cover	0.28 (0.12)	0.32 (0.09)	0.15 (0.10)	0.18 (0.12)
	n = 90	*n* = 74	*n* = 66	*n* = 45

[a] Territory areas (ha) for each study area were as follows: LAS (639.4), ELD (399.5), SIE (301.6) and SKC (254.3) (Tempel et al., 2016).

[b] Study area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon.

[c] Summed across all canopy cover classes.

[d] Summed across all tree size classes.

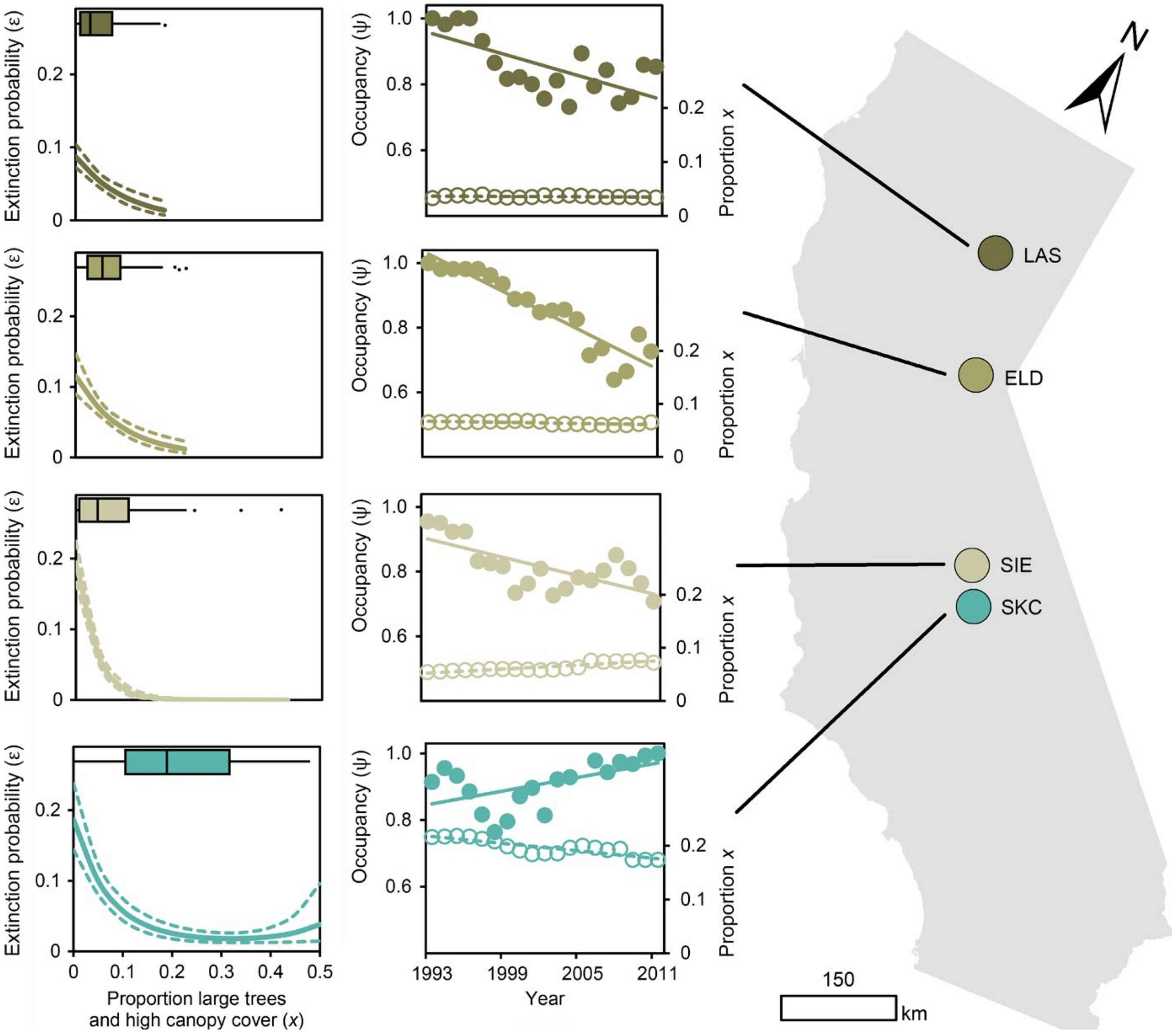

FIGURE 3 The relationship between large tree/high canopy cover forest and spotted owl occupancy dynamics. The left column of panels shows (1) the modelled relationship between spotted owl territory extinction probability and the proportion of an owl territory containing forests with large trees and high canopy cover (*x*), where the solid coloured lines represent the modelled relationship and the dashed lines represent ±1 *SE*, plotted over the range of observed values, and (2) the distribution of values for *x* present on each study area, which are represented by horizontal boxplots (corresponding to the *x*-axis). The right column of panels shows (1) annual estimates of derived occupancy (solid circles) from a fully time-varying model (see Methods) on the primary (left) axis, where the solid line represents a linear trend to emphasize population trajectories (see Table 2) over the 19-year study period, and (2) the median annual proportion of large tree/high canopy cover forest (*x*; open circles) on the secondary (right) axis, where the dashed line represents a linear trend to emphasize that this variable did not decline on national forests (three northernmost study areas, colored brown) over the 1993–2011 study period (also see Fig. S2). [Colour figure can be viewed at wileyonlinelibrary.com]

cover, and high canopy cover only, respectively (Table S1), although the coefficient estimate for the high canopy cover only model was imprecise (Table S2).

No other models were competitive with the large tree/high canopy cover model for any study area (all >5 AIC from top model; Tables S1 and S3). However, models containing other forest structural covariates such as high canopy cover, medium trees and high canopy cover, and large trees and medium canopy cover sometimes outperformed the null model and yielded coefficient estimates with 95% confidence intervals that did not overlap zero (Table S2), suggesting they may be biologically meaningful. Analysis of deviance showed that the covariate for large tree/high canopy cover forest explained 28%, 26%, 77% and 53% of the variation in local extinction rates on LAS, ELD, SIE and SKC, respectively.

The median proportion of an owl site containing large tree/high canopy cover forest on national forests (LAS, ELD, SIE) was similar, ranging from 0.03 to 0.06 (Table 1). These values corresponded with higher predicted rates of local extinction ($\varepsilon = 0.06–0.074$) and ongoing

TABLE 2 Estimates[a] of model parameters[b] and occupancy trends[c] for California spotted owls on four study areas in the Sierra Nevada, CA, USA

Study area	α	β_x	β_x^2	$\hat{\hat{\lambda}}$	Δ_k
LAS	−2.35 [−2.74, −1.96]	−10.58 [−18.68, −2.48]	—	0.991 [0.9827, 0.9997]	0.853 [0.720, 0.987]†
ELD	−2.04 [−2.58, −1.50]	−11.84 [−20.25, −3.43][d]	—	0.983 [0.9733, 0.9918]	0.728 [0.601, 0.855]†
SIE	−1.45 [−1.82, −1.08]	−26.24 [−36.28, −16.19]	—	0.981 [0.9717, 0.9904]	0.709 [0.583, 0.834]†
SKC	−1.47 [−2.08, −0.87]	−15.66 [−24.85, −6.47]	24.30 [1.86, 46.74]	1.005 [0.9997, 1.0105]	1.096 [0.990, 1.202]*

[a] Numbers in square brackets represent the lower and upper boundaries of 95% confidence intervals for the point estimate, which precedes the square brackets.

[b] α = intercept, β_x = model coefficients for the variable (x) representing the proportion of a spotted owl territory containing large trees and high canopy cover.

[c] $\hat{\hat{\lambda}}$ = geometric mean of the annual rate of change in occupancy, Δ_k = realized change in occupancy (ψ_k/ψ_1) where k is the number of years in the study. Symbols († and *) following estimates and confidence intervals for Δ_k indicate groups resulting from pairwise comparisons where estimates that share the same symbol had Δ_k estimates that were not statistically different from one another at the α = 0.05 level.

[d] $\beta_{\ln(x)}$.

occupancy declines according to estimates of the geometric mean rate of change in occupancy ($\hat{\hat{\lambda}} < 1$) and realized change in occupancy ($\Delta_k < 1$) over the period 1993–2011 (Table 2). By contrast, the median proportion of large tree/high canopy cover forest within owl territories on national parks (SKC) was 0.19 (Table 1), which was associated with much lower predicted extinction rates (ε = 0.027) and stable occupancy ($\hat{\hat{\lambda}} = 1$, $\Delta_k = 1$) (Figure 3, Table 2). Thus, extinction probability at a "typical" owl territory was ~2.5 higher on average in national forests (LAS, ELD, SIE) than national parks (SKC). A post-hoc comparison showed that estimates of realized change in occupancy (Δ_k) for LAS, ELD and SIE were not statistically different from one another, but all were significantly lower than SKC (Table 2).

The extent of large trees/high canopy cover forest within owl territories differed among study areas ($F_{3,271}$ = 38.3, p < .01) and was ~4 times greater in national parks than in national forests on average (Table 1). Furthermore, this forest type did not appear to decline within owl territories on national forests over the study period (Figures 3 and S2), suggesting the considerable deficit of large tree/high canopy cover forest on national forests may have resulted from historical (as opposed to more recent) logging activities that selectively removed very large old trees (Collins et al., in press; Laudenslayer & Darr, 1990; McKelvey & Johnston, 1992; Stephens et al., 2015).

4 | DISCUSSION

4.1 | Extinction debt and restoration opportunities

Our work presents several key inferences suggesting ongoing declines in spotted owl populations on national forests are consistent with an extinction debt, or a legacy effect, resulting from logging of large trees prior to the initiation of our study. First, we found that local extinction rates were consistently higher across a large bioregion (the Sierra Nevada) when large tree/high canopy cover forest was less common in owl territories. Second, large tree/high canopy cover forest was far more common in owl territories on national parks (SKC), where large trees have not been logged. Third, owl populations are declining on all national forest study areas, which contain far less large tree/high canopy cover forest in owl territories than national parks where the owl population is stable. Fourth, although logging activities prior to our study led to a deficit of large tree/high canopy forest on national forests, no further declines in this forest type were observed from 1993 to 2011 (Fig. S2) while owl populations experienced long-term declines over the same period. Together, these inferences suggest that past large tree logging on national forests, which removed key habitat elements for spotted owls, may have created an extinction debt that led to contemporary owl declines long after policies were enacted to protect large trees (Figure 3).

We note that other emerging threats to the spotted owl, such as large, severe wildfires (Jones, Gutiérrez, Tempel, Whitmore et al., 2016) and invasive barred owls (*S. varia*) (Wiens, Anthony, & Forsman, 2014) did not contribute to observed declines given that our study areas did not experience significant severe fire or appreciable numbers of barred owls during the study period (Keane, 2017). Secondary ingestion of anticoagulant rodenticides used to kill rodents on illegal marijuana (*Cannabis* sp.) cultivations has been documented in fishers (*Pekania pennanti*) and barred owls in the Sierra Nevada and northwestern California (Gabriel et al., 2012; Keane, 2017). However, we know of no documented cases of exposure in spotted owls, and it is currently unknown to what extent this stressor has contributed to observed changes in spotted owl populations.

The concept of extinction debt is defined by the idea that individuals, populations or species can initially survive habitat change but later become locally extirpated or experience declines without any further habitat modification (Kuussaari et al., 2009). As such, it is important to note that by identifying the potential presence of an extinction debt in owl populations on national forests, our inferences do not suggest that total population extinction is a foregone conclusion. On the contrary, it is possible (or even likely) that spotted owl occupancy on national forests will eventually reach a new, lower equilibrium once the extinction debt is paid (Hylander & Ehrlén, 2013). In the present study, we did not explore when the extinction debt might be paid off (i.e., when the population will stop declining and persist at its new lower equilibrium level), nor did we attempt to identify an empirical extinction threshold (i.e., the minimum amount of habitat required in a territory for individuals to persist). Rather, we focused on identifying potential mechanisms of extinction debt to guide more targeted conservation action (Hylander & Ehrlén, 2013).

An emerging conservation paradigm for degraded old-forest ecosystems, and the many endangered species that inhabit them, centres on restoring forest structure and function (Chazdon, 2008) thereby increasing forest resilience to disturbance from fire, disease, and drought (Millar & Stephenson, 2015) and conserving wildlife habitat over the long term (Tempel et al., 2015). The consistent relationship we identified between spotted owl extinction rates and large tree/high canopy cover forest across the latitudinal range of the Sierra Nevada has significant implications for developing meaningful ecosystem restoration targets at bioregional scales (Peery et al., 2017). In particular, high canopy cover is thought to increase severe fire risk and spread by creating fuel continuity, yet appears to be relatively more prevalent (when co-occurring with large trees) within owl territories in national parks (SKC) that have been subjected to restored, lower-severity frequent-fire regimes for nearly half a century (van Wagtendonk, 2007). This indicates the potential that increased prevalence of large tree/high canopy cover forest types within owl territories in national forests may not be incompatible with fire resistance/resilience while at the same time providing conservation benefits to spotted owls.

The potential direct benefits to owls of increasing this forest type may be considerable. Employing our models, increasing large tree/high canopy cover forest from the median within-territory value of 0.03–0.06 to 0.10 (30–64 ha) on national forests reduced predicted local extinction rates by 36%–79%. Increasing the median within-territory value further to 0.20 (60–127 ha), similar to the median value at SKC (0.19), reduced predicted extinction rates by 80%–98%. Furthermore, because they are cornerstones of old-forest ecosystem stability, greater prevalence of large trees within owl territories and across the broader landscape probably would provide direct benefits to both spotted owls and increase resilience of old-forest ecosystems to emerging stressors.

Forests in national parks representing contemporary reference landscapes generally contain less canopy cover and lower tree densities than fire-suppressed forests on average (Lydersen & North, 2012). Why then do owl territories on national parks appear to contain considerably more large tree/high canopy cover forest than their counterparts on national forests? First, although national forests may contain higher densities of trees of all sizes, they contain significantly lower densities of trees in the largest diameter (i.e., >91 cm dbh) (Collins et al., in press) and height classes (>48 m) (North et al., 2017). Second, forest patches characterized by both large trees and higher canopy cover are not a product of fire suppression, but occurred historically throughout Sierra Nevada forests within a diverse mosaic of forest types in systems maintained by mixed-severity fire regimes (Hessburg et al., 2016). Spotted owl territories likely contained disproportionately more large trees and higher canopy cover than the broader forested landscape because owls are known to select for these specific features (Lahaye, Gutiérrez, & Call, 1997; Moen & Gutiérrez, 1997; North et al., 2017).

While areas managed for multiple uses including resource extraction (i.e., national forests) and protected areas serve different societal purposes and, for this reason and others, are unlikely to have convergent forest structure and function, we can still learn important lessons when protected areas contain stable populations of species of conservation concern. For example, protected areas often form refuges for ecosystems containing distinctive biological features such as large old trees (Miller et al., 2016) and, therefore, they can act as blueprints for ecological restoration (Boisramé, Thompson, Collins, & Stephens, 2017). Furthermore, protected areas may contain tree sizes, age structure and intact disturbance regimes (Lydersen & North, 2012) characteristic of ecologically resilient landscapes (i.e., landscapes that have the capacity to recover their ecological functioning following a disturbance) and that more closely reflect species' evolutionary environments (Moore, Covington, & Fulé, 1999). Thus, in certain cases, protected areas might act as contemporary reference landscapes (Collins et al., 2016; Meyer, 2015) to provide a frame of reference for the goals of ecological restoration (White & Walker, 1997) for large old trees and recovery of old-forest-associated species across different land tenures.

Care should be taken, however, to acknowledge the potential limitations of using national parks and other protected areas as contemporary reference landscapes to inform conservation action at broader spatial scales. For example, protected areas do not necessarily represent a random sampling of area on the landscape, but instead are often biased towards places that are less likely to face land conversion pressures—areas characterized by higher elevations, steeper slopes and greater distances to roads and cities (Joppa & Pfaff, 2009). In our study, we treat Sequoia and Kings Canyon national parks (SKC) as a contemporary reference landscape, yet it is also most southerly of all study areas examined (Figure 3). This raises the question of whether SKC can truly act as a reference, or if other fundamental differences related to differences in latitude (e.g., climate or vegetation types) could play a stronger role than past forest management on observed dynamics of spotted owls.

While this is a possibility, we present several lines of evidence to support our use of SKC as a contemporary reference landscape. First, average temperatures and annual precipitation in SKC fell within the range experienced by the other three more northerly studies (Franklin et al., 2004). Second, mixed-conifer forests characterized primarily by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*) and incense cedar (*Calocedrus decurrens*) were the dominant vegetation type on all four study areas. While SKC did contain ten groves of giant sequoia (*Sequoiadendron giganteum*), these covered only 7% of the study area (Tempel et al., 2016). Third, the two most southerly study areas, SIE and SKC, occur immediately adjacent to one another in the southern Sierra Nevada in a paired study design. Yet these two study areas exhibit the largest differences in population trends according to estimates of $\hat{\hat{\lambda}}$ and Δ_k (Table 2), suggesting differences in trajectory may be unrelated to underlying differences in climate or potential vegetation type.

4.2 | Global conservation of large trees and forest policy

The case study presented here demonstrates globally informative principles for old-forest species and large tree conservation. Notably, our results are consistent with an extinction debt resulting from historical logging of large trees that yielded long-term declines in old-forest species populations even after policies protecting large trees were enacted, highlighting an urgent need to protect existing old-forest habitat and potential large tree refugia (Lindenmayer et al., 2014). Indeed, national and international environmental legislation often do not emphasize the protection of large trees and old-forest ecosystems (e.g., the European Union Habitats Directive; EU, 1992).

Regional-scale plans to protect and restore old-forest ecosystems allow exceptions to rules limiting removal of large old trees to meet needs for equipment operability in forest restoration projects (e.g., USFS, 2004), and the sale of larger trees is necessary to offset operational costs of ecological restoration activities in heavily managed or degraded forests ecosystems (North et al., 2015). Therefore, alternative approaches for funding restoration may be required to prevent further large tree loss, which may lead to ecosystem collapse in landscapes with significant legacies of exploitive land use (Burns et al., 2015; Lindenmayer, Messier, & Sato, 2016). Despite these global challenges and conservation gaps, an emerging paradigm is to emphasize highly targeted and fine-scale conservation of large old trees as small (or sometimes individual) natural features (Lindenmayer, 2017). Policies that emphasize the protection as well as the social and ecological value of individual large old trees will offer a new hope for the perpetuity of old-forest ecosystems and the increasingly rare biodiversity that depends on them.

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BIOSKETCH

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REVIEW ARTICLE

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Pyrodiversity and biodiversity: A history, synthesis, and outlook

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Abstract

Aim: Pyrodiversity is the spatial or temporal variability in fire effects across a landscape. Multiple ecological hypotheses, when applied to the context of post-fire systems, suggest that high pyrodiversity will lead to high biodiversity. This resultant "pyrodiversity–biodiversity" hypothesis has grown popular but has received mixed support by recent empirical research. In this paper, we sought to review the existing pyrodiversity literature, appraise support for the pyrodiversity–biodiversity hypothesis, examine potential mechanisms underlying the hypothesis and identify outstanding questions about pyrodiversity and future research needs.

Location: Global terrestrial ecosystems.

Methods: We performed a systematic literature review of research related to pyrodiversity and the pyrodiversity–biodiversity hypothesis. We also examined how two individual species with distinct relationships with fire (spotted owl *Strix occidentalis* and black-backed woodpecker *Picoides arcticus*) respond to pyrodiversity as case studies to illustrate underlying mechanisms.

Results: We identified 41 tests of the pyrodiversity–biodiversity hypothesis reported from 33 studies; 18 (44%) presented evidence in support of the pyrodiversity–biodiversity hypothesis, while 23 (56%) did not. Our literature review suggested that support for the pyrodiversity–biodiversity hypothesis varies considerably with no consistent patterns across taxonomic groups and ecosystem types. Studies examining the pyrodiversity–biodiversity hypothesis often define pyrodiversity in different ways, examine effects at different scales and are conducted in ecosystems with different natural fire regimes, baseline levels of biodiversity, and evolutionary histories. We suggest these factors independently and jointly have led to widely varying support for the pyrodiversity–biodiversity hypothesis.

Main Conclusions: Clarifying the pyrodiversity–biodiversity hypothesis will be facilitated by stronger development of the different potential mechanisms underlying pyrodiversity–biodiversity relationships, which can be aided by examining how individual species respond to pyrodiversity. Future research would benefit from a closer examination of the role of scale (e.g. scale dependence) in pyrodiversity–biodiversity relationships, standardization of pyrodiversity metrics, broad-scale mapping of pyrodiversity, and macroecological study of pyrodiversity–biodiversity relationships.

KEYWORDS
ecological mechanisms, fire management, fire mosaic, megafires, pyrodiversity, pyrodiversity–biodiversity hypothesis, scale

1 | A CONCEPTUAL HISTORY AND EVOLUTION OF PYRODIVERSITY

Pyrodiversity describes the degree of variation in post-fire landscape characteristics within or among fires. While at its core pyrodiversity is a technical descriptor of the properties of burned areas, its conceptual roots are biological and tightly linked to community ecology, niche theory and biodiversity conservation. The term was formally introduced by Martin and Sapsis (1992), who described pyrodiversity as an agent of biodiversity, whereby “pyrodiversity begets biodiversity.” The authors hypothesized that the degree of variation contained within different dimensions of a fire regime, such as fire return interval, seasonality, size or intensity, will result in an associated mosaic of successional stages and structure that would define the breadth of niche space for different species to occupy. Thus, pyrodiversity is a composite characteristic of a fire regime: certain fire regimes will have higher or lower pyrodiversity, which will in turn lead to higher or lower biodiversity, respectively.

A central concern in the contemporary pyrodiversity literature is that a variety of anthropogenic factors may be decreasing pyrodiversity across landscapes, potentially leading to biodiversity losses. Indeed, a central element of Martin and Sapsis’ work was pointing out that pyrodiversity was likely decreasing because of recent human activities—in particular, the loss of indigenous fire, which had created or sustained pyrodiversity. Supporting this claim, there is now widespread historical and contemporary evidence of people promoting pyrodiversity across large landscapes (Bird et al., 2008; Taylor et al., 2016; Trauernicht et al., 2015), which is likely to influence how contemporary biotic communities respond to pyrodiversity. Whether real or hypothesized, temporal trends in pyrodiversity have the potential to reshape biodiversity patterns across ecosystems.

Yet, complicating our study of such trends is that there is no single operational definition of pyrodiversity. Martin and Sapsis’ proposition nearly three decades ago provided a strong conceptual foundation for the study of the pyrodiversity–biodiversity hypothesis, but their original definition of pyrodiversity was broad and operationally vague. How could pyrodiversity be measured and the pyrodiversity–biodiversity hypothesis be tested in practice? Since its conceptual introduction, pyrodiversity has been defined in many ways by researchers attempting to test the pyrodiversity–biodiversity hypothesis—each describing a different dimension or “axis of variability” in fire regime characteristics (Appendix 1). In addition, pyrodiversity is etymologically related to other concepts in fire ecology (Box 1), and so, the pyrodiversity–biodiversity hypothesis has—in essence—also been tested under other names (e.g. “patch-mosaic burning hypothesis”).

What constitutes a test of the pyrodiversity–biodiversity hypothesis? Most attempts to define pyrodiversity involve selecting a single fire dimension, such as fire age, and quantifying the spatial variation in that characteristic within each sampling unit (e.g. Taylor et al., 2012). The variability in that characteristic for each sampling unit can then be linked to species diversity within that sampling unit, enabling an explicit test of the hypothesis that increased pyrodiversity correlates with increased biodiversity (typically alpha diversity, but also see studies examining pyrodiversity relationships with beta diversity, e.g. Farnsworth et al., 2014; Leavesley & Cary, 2013; McGranahan et al., 2018; Pastro et al., 2011). Yet, the broad original definition of pyrodiversity has led to some relatively permissive interpretations of the concept, as well as confusion regarding what exactly does, and does not, constitute a study of pyrodiversity and a test of the pyrodiversity–biodiversity hypothesis. In our view, a test of the pyrodiversity–biodiversity hypothesis should meet a defined set of criteria (Box 2). While there exists a vast literature on how fire and fire regimes affect various aspects of biodiversity (e.g. how fire frequency influences plant richness)—and other recent syntheses have focused on these broad questions (Kelly et al., 2020)—relatively few studies explicitly examine the pyrodiversity–biodiversity hypothesis (Box 2).

The lack of a single definition of pyrodiversity has also led to considerable innovation in how pyrodiversity can be measured. Some researchers have explored empirical support for the pyrodiversity–biodiversity hypothesis using multiple independent measures of pyrodiversity (e.g. Farnsworth et al., 2014), while others have developed integrated multi-axis metrics of pyrodiversity (e.g. Ponisio et al., 2016; Steel et al., 2021). More recently, technological advances have permitted an expansion of how pyrodiversity can be defined, particularly incorporating fine-scale heterogeneity. For example, remote sensing tools such as Landsat allow researchers to define pyrodiversity as the variability in burn severity in forest systems (e.g. variation in tree basal area or canopy mortality) following fire in each sampling area (e.g. Tingley et al., 2016). In an interesting deviation from traditional inquiry, Bowman et al. (2016) defined pyrodiversity as “the coupling of biodiversity and fire regimes in food webs” focusing on trophic feedbacks and critiquing “simple, one-way statistical linkages between biodiversity surrogates and fire regimes…” that have characterized pyrodiversity–biodiversity research to date. Bowman et al. (2016)’s renewed focus on mechanism and ecosystem processes that shape and underly the pyrodiversity–biodiversity relationship is useful, and we discuss below the importance of future research focusing on mechanisms. The variety of approaches for defining and quantifying pyrodiversity have their own strengths and weaknesses, but each is also consistent with the breadth of Martin and Sapsis’ pyrodiversity–biodiversity hypothesis. In the absence of any critical evaluation of different metrics, there has been no

BOX 1 Pyrodiversity and related ecological concepts

The term pyrodiversity is related to several other ecological concepts. All of the below concepts are themes in landscape ecology and relate in some way to the measurement of variability but have subtly different histories of use and interpretations. Here, we define several of these concepts and describe how they are intertwined with pyrodiversity.

Patch-mosaic burning is a fire management approach originally applied in some South African national parks (e.g. Kruger and Pilanesberg) in the early 1990s (Van Wilgen et al., 1998). Application of the approach has since expanded and is more or less synonymous with the term pyrodiversity. The goal of patch-mosaic burning was to establish a mosaic of vegetation structural types through prescribed burning that would allow "efficient means of conserving biodiversity" (Van Wilgen et al., 1998). Under this fire management paradigm, prescribed burns are initiated at random locations throughout the project area and allowed to burn out by themselves until an established quota of burned area is reached. The result is a heterogeneous mosaic of burn conditions that vary in extent, seasonality and other characteristics. The emergence of the patch-mosaic burning paradigm paralleled the broader cultural shift away from equilibrium thinking to recognizing the importance of non-equilibrium processes in ecology (Parr & Brockett, 1999; Pickett & White, 1985). Related concepts/terminology include vegetation mosaic, fire mosaic and successional mosaic.

Mixed-severity fire is a term commonly used to describe fires that contain a broad gradient of post-fire tree basal area or canopy mortality (i.e. severity) with some mixture of low-, moderate- and high-severity effects. Mixed-severity fire is most commonly defined as containing between 20% and 70% tree mortality (or "high-severity fire") across a fire area (Agee, 1993) although some definitions include an even broader range (e.g. 5%–70%). Such fires could almost certainly be characterized as containing a relatively high degree of pyrodiversity in most circumstances, although the spatial pattern of burn severity and the scale at which pyrodiversity is summarized may influence this generalization. Many fire regimes, particularly those in western North America, have widely been characterized as having mixed-severity fire regimes (e.g. DellaSala & Hanson, 2015). However, Collins et al., (2017) pointed out that the term mixed-severity fire is so broad that it carries little meaning, because nearly all forest fires experience between 20% and 70% high-severity fire, and moreover, this definition ignores the role of spatial patterns of burn severity. Pyrodiversity may face a similar issue related to how it is defined and interpreted (e.g. at what point is a fire, or a landscape, considered "pyrodiverse") and reinforces the need to consider how pyrodiversity and associated ecological effects may vary as a function of scale.

Fire regime is the typical frequency, size, seasonality, intensity, pattern and other attributes of burned areas that have been typical for a given ecosystem over a long period of time (Agee, 1993; Gill, 1975; Kilgore, 1981). Different ecosystems are characterized by different fire regimes because of broad-scale variation in climate, vegetation type and ignition frequency (Pyne et al., 1996). Pyrodiversity thus might be considered one component of fire regimes (which itself is comprised of one or more components), where fire regimes are characterized by a typical (or range of) within- or among-fire pyrodiversity. For example, frequent-fire regimes in seasonally dry forests might be characterized by relatively high pyrodiversity (i.e. they contain a more dynamic mosaic of successional stages). In contrast, infrequent-fire regimes in more mesic and high-elevation forest types might be characterized by relatively low pyrodiversity (i.e. having larger, more homogeneous fires and even-aged forest conditions). However, this dichotomy depends in part on the spatial and temporal scales being used to characterize fire regimes. Martin and Sapsis (1992) noted that fire suppression has altered fire regimes and has thereby likely reduced pyrodiversity (i.e. made fires more homogeneous), particularly at larger spatial scales, in some systems such as parts of the Pacific Northwest of the United States. Indeed, recent empirical work has confirmed that fires in California, USA, are increasingly becoming more homogenously severe (Stevens et al., 2017; Steel et al., 2018).

*The **intermediate disturbance hypothesis (IDH)*** posits that too much or too little disturbance will favour lower species richness, but moderate levels of disturbance will maximize species richness (Connell, 1978; Karr & Freemark, 1985). For example, if disturbances that reset successional dynamics are very frequent, the community will by dominated by a smaller number of *r*-selected dispersal-adapted species and colonizers. If disturbances are too infrequent, late-successional characteristics will dominate and the community will be characterized by a smaller number of *K*-selected species and old-growth specialists. However, if disturbances are moderately frequent, the community will represent a highly dynamic mixture of *r*- and *K*-selected species that will lead to higher species richness. Fire regimes characterized by higher pyrodiversity may reflect "intermediate" levels of disturbance because low pyrodiversity could reflect either too much or too little disturbance, depending on how pyrodiversity is quantified. Thus, there is a natural connection between the IDH and the pyrodiversity–biodiversity hypothesis. Like pyrodiversity, the IDH is likely to show high sensitivity to the spatial and temporal scales at which disturbance is quantified.

Natural range of variability *(NRV)*, also called historical range of variability (HRV), describes the range of ecological conditions that are typical of a given ecosystem or region, often prior to widespread modification by Western human society. Fire regime is thus an approach for characterizing the NRV of fire in a system. Because pyrodiversity is a metric that characterizes variation in fire conditions, there is therefore a natural linkage between these two concepts: historical patterns of pyrodiversity characterized

BOX 1 (Continued)

one axis of the natural range of variability in fire characteristics. NRV is often invoked in ecosystem restoration, where it is used to guide management and restoration targets to approximate historical and ecologically appropriate landscape conditions (Safford & Stevens, 2017; Swanson et al., 1994).

Patchiness is a concept with roots in landscape ecology that describes the degree of variability in discrete land cover or habitat classes (e.g. vegetation types) in a landscape. Patchiness can be formally quantified in a wide variety of ways, including patch density (number of patches of a given type), mean patch size, patch richness (number of different patch types) or other metrics that characterize patches in terms of their shape (e.g. fractal dimension, perimeter-to-area ratio). Fires can be characterized in terms of their patchiness (e.g. size or shape of different burn severity classes or fire age classes), and thus, there might be some predictable relationships between patchiness and pyrodiversity. For example, landscapes with high patch richness (e.g. many different burn severity or fire age classes) would be more pyrodiverse. Some studies investigating ecological effects of pyrodiversity used fire “patchiness” as a synonym for pyrodiversity (e.g. Lawes et al., 2015; McGranahan et al., 2018; Menges & Quintana-Ascencio, 2004). Patches of different fire severities or ages also imply the existence of edges between patch types, and pyrodiversity characterized at finer spatial scales will be higher at these interfaces between patches than within a given patch.

single “correct” or “best” way to define pyrodiversity, and different researchers have unsurprisingly defined pyrodiversity in different ways according to the objectives and ecological context of their studies.

One consequence of the wide variety of approaches for quantifying pyrodiversity is that different researchers have seldom asked the same question of the pyrodiversity–biodiversity hypothesis. Directly comparing support for the hypothesis among studies that apply different operational definitions of pyrodiversity might seem questionable, because the lack of a consistent definition may make broad generalizations and synthesis across studies challenging. However, this variability may also hold unexpected benefits because different approaches for quantifying pyrodiversity may allow researchers to test different ecological mechanisms underlying the pyrodiversity–biodiversity hypothesis. Among studies, pyrodiversity is not only quantified in different ways, and tests applied to different taxa in different ecosystems, but it is also quantified at different spatial and temporal scales. As is the case for all ecological phenomena (Levin, 1992; Wiens, 1989), pyrodiversity–biodiversity relationships are likely to be scale-dependent. Thus, the scale (e.g. spatial grain or extent, or temporal window) selected by the researcher will influence whether the hypothesis is supported because different scales may test different mechanisms and may be more or less relevant for different taxa.

Here, we attempt to summarize and synthesize the existing state of knowledge on the pyrodiversity–biodiversity hypothesis, provide clarity on proposed mechanisms, and search for any consistent rules or results. Additionally, we present case studies of two focal species of conservation concern in western North America for which emerging research is demonstrating that pyrodiversity plays a role in the species’ ecology, providing intriguing evidence for underappreciated mechanisms that could underlie the pyrodiversity–biodiversity hypothesis. We then identify major unanswered questions and identify research gaps in the study of pyrodiversity and the pyrodiversity–biodiversity hypothesis. In sum, we conclude that, while much research has been conducted on pyrodiversity, rich opportunities remain to rapidly advance pyrodiversity research in the era of megafires.

2 | SYNTHESIS OF EXISTING TESTS OF THE PYRODIVERSITY–BIODIVERSITY HYPOTHESIS

We performed a systematic literature review of pyrodiversity research via Web of Science using the workflow outlined in Grames et al. (2019) and the associated R package litsearchr version 1.0.0. First, we conducted a naive search using the search string (“pyrodiversity” AND “biodiversity”) across three databases: Biological Abstracts, BIOSIS Citation Index and Zoological Record. Then, we used the litsearchr package to consolidate and de-duplicate records from the naive search results and build a keyword co-occurrence network to capture themes related to, but not included in, our original search string. We manually reviewed keywords and generated an expanded Boolean search for a refined literature review. The final search string was ((pyrodivers* OR "fire* mosaic*" OR "burn* pattern*" OR "mosaic* burn*" OR "patch* mosaic*" OR "pyrodivers* landscap*") AND (biodivers* OR "beta* divers*" OR "communiti* composit*" OR "speci* composit*" OR "speci* divers*" OR "speci* rich*" OR "alpha* divers*" OR "communiti* divers*" OR "disturb* hypothesi*" OR "intermedi* disturb*")). We conducted this refined search across the three above-mentioned databases and assembled a final de-duplicated database on 5 October 2020.

Here, we summarize the results of the literature search. The search returned 176 results, 95 of which we determined to be relevant to the present paper (other studies were largely unrelated to fire and biodiversity). In addition, we searched through references of two recent fire-related review papers (He et al., 2019; Kelly et al., 2017) to identify papers that our literature search might have missed; this yielded an additional three papers that clearly examined

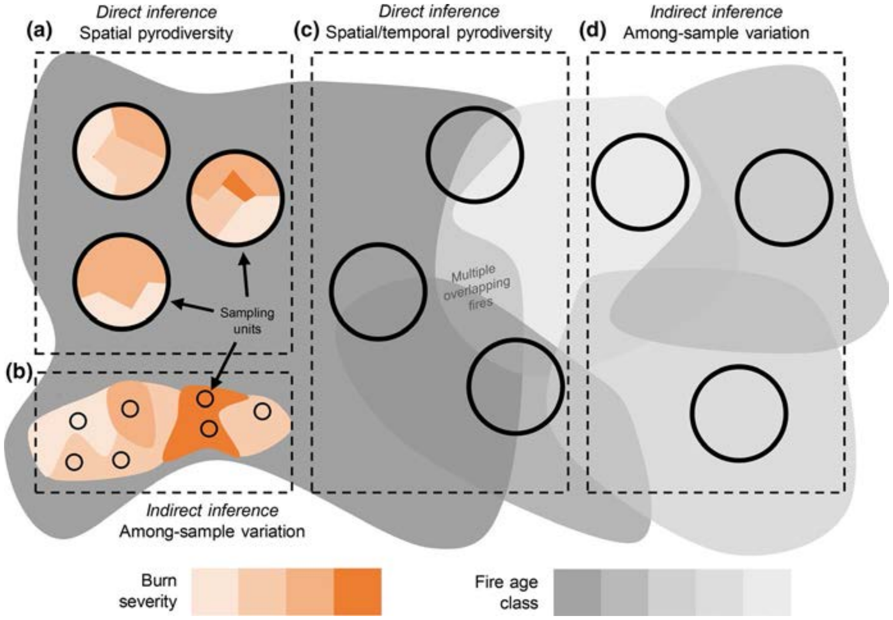
BOX 2 Testing the pyrodiversity–biodiversity hypothesis

Pyrodiversity was originally conceived as an inherently spatio-temporal concept. Martin and Sapsis (1992) described pyrodiversity as "variety in interval between fires, seasonality, dimensions, and fire characteristics, producing biological diversity at the micro-site, stand, and landscape level." This broad (and somewhat vague) definition has led to a proliferation of approaches for testing the pyrodiversity–biodiversity hypothesis in practice. Yet, in our view, simply examining how biodiversity responds to a chosen element of a fire regime does not provide the required elements for a direct test of the pyrodiversity–biodiversity hypothesis.

We propose that a direct test of the pyrodiversity–biodiversity hypothesis should include a metric of variation (e.g. coefficient of variation, Shannon diversity index) to be quantified on a fire characteristic (e.g. fire age, burn severity) *within* spatially replicated sampling units or a buffered area surrounding each sampling unit (insets a and c below). Variation should occur *within* sampling units, not strictly *among* sampling units. The *within*-sample variation in fire characteristics (i.e. pyrodiversity) is then linked to a *within*-sample measure of biodiversity (e.g. alpha diversity), and standard procedures such as regression or other models can be used to determine whether a linear or nonlinear relationship between the two variables exists (e.g. Tingley, et al., 2016).

The pyrodiversity–biodiversity hypothesis is sometimes examined in indirect ways as well. This situation often arises when variation in fire characteristics (e.g. time since fire, fire severity) occur *among* sampling units (see insets b and d below), and variation in species richness or community composition is then linked to *among*-sample variation in fire characteristics. Often, studies taking this approach will then infer that because different species are associated with different fire characteristics, it follows that landscape variation in these characteristics will support higher biodiversity (e.g. Taillie et al., 2018). We refer to this situation as an indirect inference about the pyrodiversity–biodiversity hypothesis. Indirect approaches may also go one step further by using optimization analyses of among-sample variation to more formally assess combinations of fire characteristics expected to promote biodiversity (e.g. Kelly et al., 2015).

Individual studies testing the pyrodiversity-biodiversity hypothesis may quantify either *spatial* or *temporal* components of pyrodiversity, or a combination of both (see below figure). Spatial pyrodiversity is the spatial variation in a fire characteristic (e.g. burn severity) within a sampling unit (see inset a). Temporal pyrodiversity is the spatial variation in a temporal fire characteristic (e.g. fire age/successional stage) within a sample unit (see inset c), which we note is inherently spatio-temporal. If no variation occurs within sampling units (insets b and d), then pyrodiversity has not been measured and a direct test of the pyrodiversity–biodiversity hypothesis is not possible. For example, sampling in inset b would simply yield a test of how biodiversity responds to burn severity, and inset d would test how biodiversity was affected by time since fire; neither would be considered a direct test of the pyrodiversity–biodiversity hypothesis.



the pyrodiversity–biodiversity hypothesis. We reviewed all 98 papers and noted the publication date, geographic location, ecosystem type, taxa studied, whether a test of the pyrodiversity–biodiversity hypothesis appeared to have been performed and whether support for the hypothesis was inferred by the authors, how pyrodiversity was defined or conceptualized, and other key points and conclusions

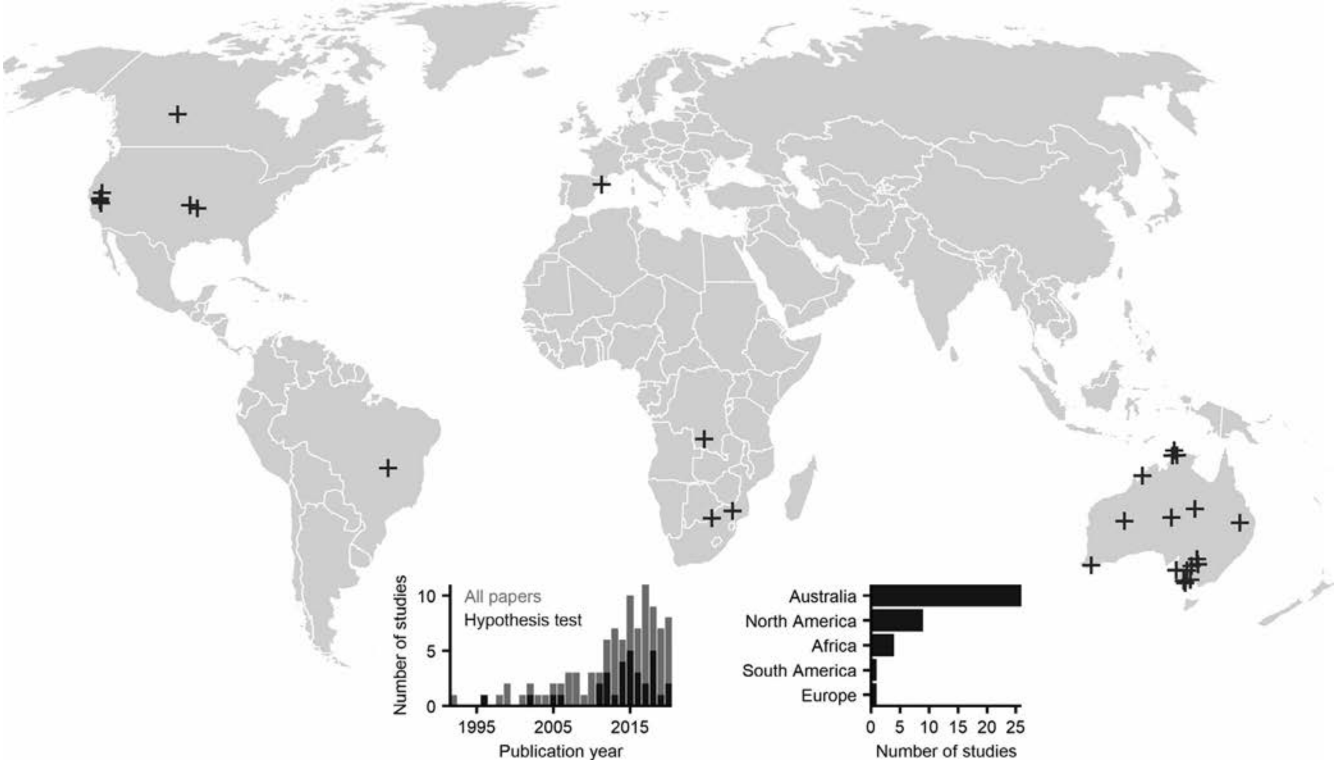


FIGURE 1 Global distribution of pyrodiversity–biodiversity research. Each grey "+" represents the approximate spatial location of studies that tested the pyrodiversity–biodiversity hypothesis (or, for broader-scale studies, the "+" shows the approximate geographic centre of the study area). The inset bar graph on the left shows trends in pyrodiversity-related research over the period 1992–2020; dark grey bars represent studies that tested the pyrodiversity–biodiversity hypothesis, while light grey bars show the total number of relevant studies from our literature search. The inset bar graph on the right shows the number of studies per continent. Our literature search did not reveal existing pyrodiversity–biodiversity research in Asia (there are no wildfires in Antarctica)

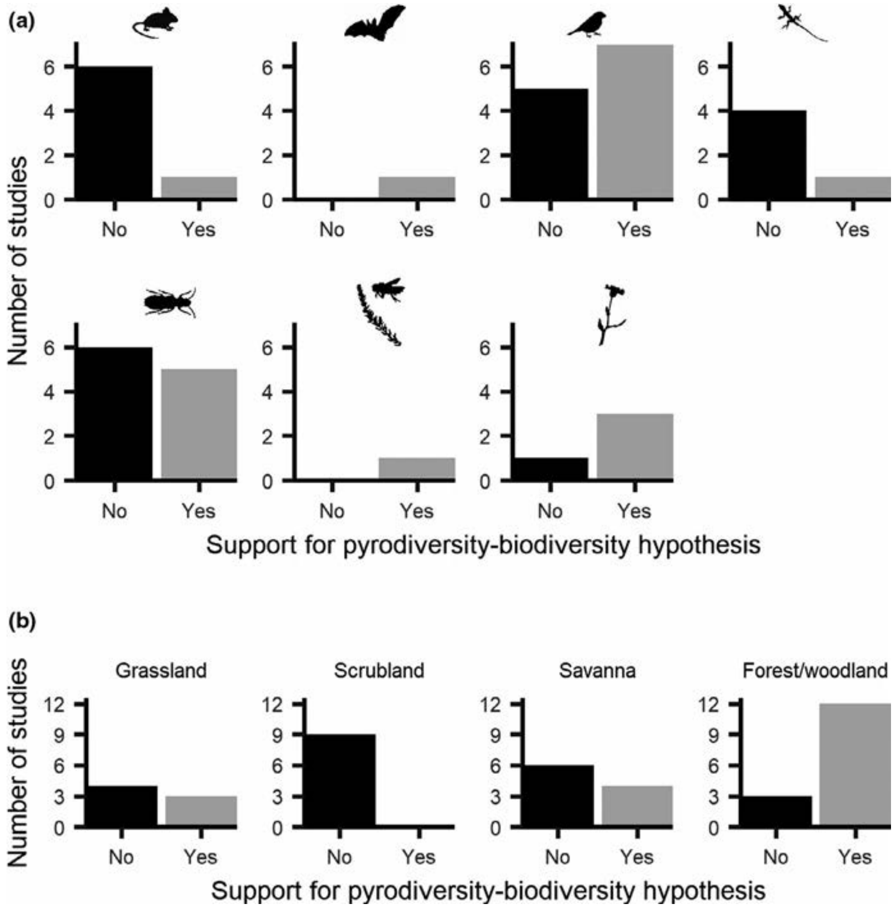
reached by the authors. Thirty-three studies appeared to have performed a test of the pyrodiversity–biodiversity hypothesis, and five of those studies reported effects across more than one broad taxonomic group (for a total of 41 study–taxa combinations that we treat as independent units) (see Appendix 1). We identified a distinction between *direct* and *indirect* inferences about the pyrodiversity–biodiversity hypothesis, which relates to whether the selected fire characteristic varied *within* or *among* sampling units, respectively (Box 2, Appendix 1).

Because of high variability in study design and how pyrodiversity was defined, we did not feel there was enough consistent information to compute standardized effect sizes in a meta-analytic framework. Therefore, effects from studies were tallied using a simplified "vote-counting" approach (Bushman, 1994). Vote-counting approaches have noted shortcomings, including but not limited to failing to account for sample and effect sizes. Moreover, tallying of studies in the "vote-counting" approach may be more likely to mask different kinds of pyrodiversity–biodiversity relationships, such as nonlinear (or "hump-shaped") relationships (e.g., Steel et al., 2021). We acknowledge these caveats and point out that here our aim is to provide a broad summary of the pyrodiversity–biodiversity literature, with a focus on support for positive associations between pyrodiversity and biodiversity. However, there are many ways that spatio-temporal variation in fire regimes can shape biodiversity. As further evidence accumulates and studies of pyrodiversity–biodiversity relationships become more standardized (see "Synthesis and research gaps," as well as Box 2), additional types of evidence synthesis may be possible.

Studies examining the pyrodiversity–biodiversity hypothesis have been conducted on four continents with the majority of studies occurring in Australia (26 studies), followed by North America (9), Africa (4), South America (1) and Europe (1) (Figure 1). We observed a recent increase in research on the pyrodiversity–biodiversity hypothesis, with an initial increase beginning in 2006 (perhaps motivated by the seminal work by Parr & Andersen in 2006 that popularized and critiqued the hypothesis) followed by a rise in tests of the hypothesis after 2011 (Figure 1). The pyrodiversity–biodiversity hypothesis has been examined in birds (12 studies), invertebrates (11), mammals (7), reptiles (5), plants (4), plant–pollinator interactions (1) and bats (1) (Figure 2a). These studies have occurred in grasslands (7 studies), scrub/shrublands (9), savannas (10) and forests/woodlands (15) (Figure 2b).

Our literature review suggests that support for the pyrodiversity–biodiversity hypothesis varies considerably across taxonomic groups and ecosystem types. Of the 41 tests reported from 33 studies, 18 presented evidence in support of the pyrodiversity–biodiversity hypothesis, while 23 did not indicate support for the hypothesis. All taxonomic groups containing more than one study examining the

FIGURE 2 Summary of studies examining the pyrodiversity–biodiversity hypothesis grouped by broad taxonomic group and ecosystem type. (a) Support for the pyrodiversity–biodiversity hypothesis (from top left) terrestrial mammals, bats, birds, reptiles, invertebrates, plant–pollinator interactions, and pollinators (b) Support for the pyrodiversity–biodiversity hypothesis among four broad ecosystem types



pyrodiversity–biodiversity hypothesis showed mixed support: different studies suggested support either for or against the hypothesis (Figure 2a). The same pattern of mixed support was apparent when results were grouped by ecosystem type, except for scrub/shrubland ecosystems in which all existing studies have reported no support for the pyrodiversity–biodiversity hypothesis. Therefore, it does not appear that the pyrodiversity–biodiversity hypothesis is consistently supported or not supported within particular taxonomic groups or ecosystem types, suggesting that variation in the literature may be due to other factors. Thus, we must consider what factors may influence whether the pyrodiversity–biodiversity hypothesis is supported in empirical study.

We suggest that there are at least three interacting factors that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies: mechanism, history, and scale. In this context, mechanism refers to different studies asking different questions of the pyrodiversity–biodiversity hypothesis by defining pyrodiversity in different ways (see Appendix 1). As an example, examining how species richness is affected by the diversity of fire age classes across a landscape is asking a question related inherently to temporal processes—how different species accumulate and replace one another through time across different successional stages initiated by fire (e.g. Nimmo et al., 2013). In contrast, examining how species richness is affected by diversity in burn severity is asking a question inherently about spatial processes—how species accumulate and partition resources across space based on structural heterogeneity produced by a single fire event (e.g. Steel et al., 2019). Questions related to the pyrodiversity–biodiversity hypothesis can thus vary in terms of exploring temporal versus spatial mechanisms, but spatial and temporal processes can also interact to influence strength of a pyrodiversity–biodiversity effect (e.g. Tingley et al., 2016).

Many specific spatial and temporal mechanisms grounded in ecological theory have been proposed (He et al., 2019; Kelly et al., 2017). For example, Kelly et al. (2017) discuss several hypotheses based on ecological mechanisms that may give rise to observed pyrodiversity–biodiversity relationships, including habitat complementation (spatial variation in fire effects fulfils multiple habitat needs of an individual species), habitat heterogeneity (spatial variation in fire effects enhances multispecies coexistence through creation of diverse habitats), habitat refuge (spatial variation in fire effects produces refuges and alters predator–prey interactions) and fire season (temporal variation in fire seasonality influences fire effects and alters multispecies coexistence). Different approaches for quantifying pyrodiversity may allow the above hypotheses to be further parsed. Studies examining these mechanisms and other spatial and temporal mechanisms in different systems should not necessarily be expected to arrive at the same conclusions about the pyrodiversity–biodiversity hypothesis when quantifying pyrodiversity in different ways.

The second factor that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies is history. In this context, history refers to the evolutionary environment and ecological regimes that have characterized different systems over time, and which may constrain the development of pyrodiversity–biodiversity relationships. For example, we may not expect the pyrodiversity–biodiversity relationship to look the same in boreal forests as in temperate or tropical forests. These ecosystems vary greatly in their overall species diversity (generally increasing from boreal to temperate to tropical) (Gaston, 2000) and limiting factors that influence fire ignitions and behaviour (ranging from fuel-limited dry ecosystems to climate-limited wet ecosystems) (Krawchuk & Moritz, 2011).

Fire regimes are a significant evolutionary force in both plants and animals (Bond & Keeley, 2005; Pausas & Parr, 2018). As such, there is an interplay between fire regimes over evolutionary time and accumulation of adaptive traits by species to those fire regimes. For example, conifer species associated with frequent-fire regimes have thick bark, tall crowns and flammable litter, while species associated with infrequent-fire regimes have thin bark, shorter crowns and less flammable litter (Stevens et al., 2020). These adaptations then produce stabilizing feedbacks that reinforce the fire regime (He et al., 2019). Because fire can reset community dynamics (He et al., 2019), there may be an expectation that ecosystems with more frequent-fire and low- to moderate-severity regimes might support more opportunities for evolutionary forces to rapidly give rise to biodiversity. In contrast, infrequent-fire systems might more often be characterized by climax communities dominated by a smaller number of species, and fewer opportunities for fire-related disturbances to open evolutionary pathways. Thus, the same degree of pyrodiversity (however defined) may never be observed in frequent- versus infrequent-fire systems; even if it was, the same degree of pyrodiversity might be associated with different levels of biodiversity and thus a different expected "shape" to the pyrodiversity–biodiversity relationship (e.g., Steel et al., 2021).

The third factor that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies is scale. In this context, scale may refer to several components of a given study, but we are referring to the spatial and temporal extent and grain of the analysis and to what extent these scales relate to relevant ecological scales for the organism(s) or taxa under study. For example, pyrodiversity at larger scales (e.g. larger spatial extent and grain) may be more relevant for larger-bodied mammalian assemblages than for terrestrial invertebrates because often the scale of effect varies positively with characteristics such as body size and dispersal ability (Jackson & Fahrig, 2012). Thus, relevant spatial scales for studying pyrodiversity–biodiversity relationships might scale with body size or other traits. Larger spatial and temporal scales of measurement may also be required to capture sufficient variability to detect a pyrodiversity–biodiversity relationship in infrequent-fire systems in comparison with frequent-fire systems.

In general, our review revealed that little attention is paid to the problem of scale in the study of pyrodiversity–biodiversity relationships, with some exceptions. For example, while studying avian communities in dry mixed-conifer forests of California, Tingley et al. (2016) explored whether support for the pyrodiversity–biodiversity relationship was scale-dependent (e.g. pyrodiversity measured at the plot level or fire level). In this case, the authors found support for this relationship at both spatial scales—although slightly stronger at the larger scale—and similar support for this relationship being time-dependent (and thus scale-dependent in the temporal sense). In general, we advocate for future research to explicitly consider a multi-scale perspective in which support for the pyrodiversity–biodiversity hypothesis is tested at multiple spatial and temporal scales when possible, avoiding assumptions about the correct scale of effect (McGarigal et al., 2016).

In addition to operating independently on apparent pyrodiversity–biodiversity relationships, these three factors are also likely to interact with one another in complex ways. Certain definitions of pyrodiversity may represent mechanisms that more naturally operate at certain spatial or temporal scales, whose relative importance could vary based on the ecological and evolutionary history of the system under study. For example, consider defining pyrodiversity as the spatial variability in burn severity (e.g. Steel et al., 2019). This definition—which provides a mechanism for how species accumulate and partition resources across space based on structural heterogeneity produced by fire—might be more relevant in systems where stronger spatial gradients in burn severity exist because of higher spatial variation in fuel conditions (e.g. fuel-limited dry forest ecosystems). Within-fire variation in burn severity inherently occurs at finer spatial scales than any among-fire measures of pyrodiversity, and therefore might be more relevant for smaller-bodied organisms because of scaling of effects with body size as discussed above. In summary, all three of these factors—mechanism, history and scale—should be considered together when designing and interpreting studies that examine the pyrodiversity–biodiversity hypothesis.

3 | MECHANISMS UNDERLYING A DIVERSE RESPONSE TO PYRODIVERSITY

The high degree of variability in studies testing diversity responses to pyrodiversity gives rise to numerous questions about the mechanisms underlying such a phenomenon and whether a pyrodiversity–biodiversity effect is real. At the same time, there is widespread evidence that environmental heterogeneity broadly drives variation in species richness (Stein et al., 2014) and that this is a consequence of heterogeneity in species' responses to environmental variation. This diversity in species' environmental affinities is the foundational mechanism proposed for why biodiversity should respond positively to pyrodiversity (He et al., 2019; Kelly & Brotons, 2017).

Although beyond the scope of our review, a large and growing literature demonstrates support for species-specific responses to the heterogeneity of habitats and conditions that exist following fire. This literature is much older than the newer phenomenon of explicitly testing pyrodiversity–biodiversity (Figure 1) and has roots in the classic "habitat heterogeneity hypothesis" (Lack, 1969; MacArthur & Wilson, 1967; Simpson, 1949). Given how long this question has captivated ecologists, there now exists a wide variety of studies that convincingly demonstrate that species-specific responses to post-fire conditions exist, at least, in bats (Blakey, Webb, et al., 2019; Buchalski et al., 2013) and other mammals (Bliege Bird et al., 2018), birds (Hutto, 2008; Smucker et al., 2005), herptiles (Rochester et al., 2010; Russell et al., 1999), pollinators (Carbone et al., 2019) and plants (Pausas & Ribeiro, 2017). Moreover, this species-specific variation arises from how different species' traits benefit or hinder establishment along the spectrum of post-fire environments (Blakey, Webb, et al., 2019; Pausas & Keeley, 2014; Pausas & Lavorel, 2003).

Given the preponderance of evidence that species broadly show heterogeneity in response to post-fire ecosystems and that pyrodiversity increases heterogeneity in post-fire landscapes, it is perhaps surprising that direct evidence for a pyrodiversity–biodiversity relationship is so limited and equivocal (Figure 2). In addition to the reasons discussed in the previous section, a challenge in interpreting empirical research to date is that fire is very difficult to experimentally reproduce, lending limited opportunities for mechanism testing. Until many more pyrodiversity–biodiversity studies can be replicated across landscapes, taxa and dimensions of fire variability, such phenomenological studies of species assemblages will likely remain inherently ambiguous in their overall conclusions. In addition, some species might successfully occupy landscapes across a gradient from low to high pyrodiversity but may vary greatly in their abundance across that same gradient. Therefore, there exists the possibility that studies based on presence/absence measures (i.e. species richness) could underestimate the effects of pyrodiversity on generating patterns in biodiversity.

But another approach to learning about the mechanisms underlying pyrodiversity–biodiversity is to decompose the effect from an aggregate impact on biodiversity, to a component effect on individual species. We can thus ask does pyrodiversity benefit individual species? Alternatively, does pyrodiversity harm or inhibit individual species? Depending on the frequency with which species fall into one category or another, we can assemble a bottom-up picture of how pyrodiversity impacts communities. To this end, single-species studies on pyrodiversity impacts can contribute positively to our developing understanding of its effects on biodiversity.

One way to investigate whether there are species that benefit from—or, alternatively, are hindered by—pyrodiversity is to examine species that seemingly exist at opposite ends of the spectrum of affinity for disturbance. Put another way, we should pick a "fire-reliant" species that is attracted to recent patches of severely burned habitat and compare its relationship with pyrodiversity (in this case, spatial variation in burn severity) relative to a species that is known to be intolerant of disturbance, such as an "old-growth" forest indicator. To be clear, neither type of species is expected to respond positively to pyrodiversity: the old-growth species eschews large-scale disturbance of any kind, while the fire-reliant species benefits from recent, severe fire, but not necessarily a diversity of fire characteristics. With no strong expectations of affinity for pyrodiversity from either species, any such discovery to the opposite would effectively change our perceptions of the range of mechanisms underlying a proposed pyrodiversity–biodiversity effect.

4 | CASE STUDY OF AN "OLD-GROWTH" SPECIES, THE SPOTTED OWL

We begin this thought experiment by highlighting recent research conducted on the spotted owl (*Strix occidentalis*), a flagship "old-growth" species of far western North America. We here focus specifically on the California spotted owl (*S. o. occidentalis*), and so, hereafter reference to the "spotted owl" refers to this subspecies. The spotted owl primarily occurs in mid-elevation mixed-conifer montane forest, and many studies and syntheses have demonstrated the species' reliance on late-seral forests characterized by large trees and a relatively closed overstorey canopy (Jones et al., 2018; North et al., 2017; Tempel et al., 2016). Conservation strategies focused on spotted owls have therefore suggested delineating large blocks of undisturbed habitat to meet the needs of the species (Verner et al., 1992). While "old-growth" conditions are considered important for supporting nesting, roosting and foraging activities, spotted owls are known to use a broader range of forest conditions for foraging (Blakey, Siegel, et al., 2019; Roberts, 2017). However, because nesting habitat is considered to be more limited in landscape availability, human and natural disturbances that significantly alter forest structure such as clear-cutting and large, severe fires have long been considered a threat to owl habitat and long-term population persistence (Peery et al., 2017; Verner et al., 1992).

Recent research has indeed shown that large, severe fires are detrimental to spotted owls and their habitat (e.g. Jones et al., 2016), but has also uncovered significant nuance in how spotted owls respond to a range of post-fire conditions and has shed light on potential mechanisms that may underlie owls' response to pyrodiversity. Within fires, spotted owls continue to occupy and reproduce in territories that have experienced relatively high pyrodiversity—as characterized by a mixture of unburned, and low- and moderate-severity fire, with smaller patches of high-severity fire (Jones et al., 2016; Schofield et al., 2020). Over the short term, spotted owls may even continue to occupy and nest in territories that burned extensively at high-severity as long as there is sufficient residual late-seral habitat (e.g. in riparian areas) (Lee & Bond, 2015), but it is unclear how persistent these apparent neutral effects may be. Demographic analysis has suggested that although some spotted owls may continue to occupy territories that have experienced extensive severe fire, these territories show lower survival and increased recruitment rates suggesting that occupied territories within severe fire represent population "sinks" (Rockweit et al., 2017).

Studies of the movement and foraging ecology of owls that persist in burned landscapes have perhaps revealed the most about how pyrodiversity may shape spotted owl habitat. It has long been known that spotted owls will forage in forest habitat that has experienced different burn severities and may even prefer foraging in severely burned forest (Bond et al., 2009). Two recent papers (Jones et al., 2020; Kramer et al., 2021) together suggest that a complex interplay between forest heterogeneity, pyrodiversity, and severe fire patch size may better explain how and why spotted owls use burned landscapes the way that they do. Owl use of severely burned forest appears to be mediated by severe fire patch size. In general, spotted owls select smaller patches of severely burned forest for foraging activities, avoid larger patches (Jones et al., 2020; Kramer et al., 2021) and tend to stay within 100m of "green" forest when foraging in severely burned areas (Jones et al., 2020). Both Jones et al., (2020) and Kramer et al., (2021) tested whether owls selected or avoided areas with higher pyrodiversity (in this case, defined as the Shannon diversity of burn severity classes), and the two studies reached opposite conclusions. Jones et al. (2020) provided some evidence that owls *selected* more pyrodiverse areas for foraging, while Kramer et al., (2021) suggested they *avoid* more pyrodiverse areas.

This apparent contrasting result makes more sense when overlaid on the two study landscapes: Jones et al. (2020) found that owls used more pyrodiverse areas within the context of a broadly homogeneous, fire-suppressed landscape (i.e. U.S. National Forests, a mixed-use landscape); Kramer et al., (2021) found owls avoided more pyrodiverse areas within the context of an already structurally heterogeneous landscape with a long history of managed and prescribed fire use (i.e. U.S. National Parks, a preservation-based landscape). Thus, the relative importance of pyrodiversity in creating owl foraging habitat may depend on the existing degree of surrounding landscape heterogeneity in forest structure. It is clear that spotted owls use more heterogeneous landscapes for foraging activities (Atuo et al., 2019), and in some cases (e.g. in homogeneous fire-suppressed forests), pyrodiversity may introduce some of that important variability to the benefit of spotted owls. Moreover, this observation suggests that in single-species studies, the effect of pyrodiversity on behaviour or vital rates may be related to pyrodiversity creating some minimum, or threshold level of structural diversity in otherwise homogeneous landscapes that provides required resources for the species. Thus, the effects of pyrodiversity on the ecology of single species could be highly nonlinear.

As for the driver of this pyrodiversity relationship, there is some evidence that cross-trophic interactions are the mechanism underlying spotted owls' preference for the structural heterogeneity that can be introduced through pyrodiversity. In the Sierra Nevada of California, spotted owl territories are less likely to go extinct when owls occupying those territories consume more woodrats and fewer flying squirrels (Hobart et al., 2019). Woodrats tend to be associated with open, early-seral forest, while flying squirrels tend to be associated with late-seral, closed-canopy forest (Roberts et al., 2015). Therefore, in fire-suppressed forests, pyrodiverse areas characterized by smaller patches of severely burned forest may introduce forest conditions that either recruit woodrats or increase local densities of flying squirrels (Sollmann et al., 2016), and both outcomes could improve spotted owl hunting efficiency (Hobart et al., 2021). Pyrodiverse areas may also give owls access to "open" forest patches for hunting while maintaining concealment in surrounding green forest from predators such as great horned owls (Gutiérrez et al., 1995; Johnson, 1992).

5 | CASE STUDY OF A "FIRE-RELIANT" SPECIES, THE BLACK-BACKED WOODPECKER

As a counterexample to the spotted owl, we highlight the black-backed woodpecker (*Picoides arcticus*), a species that is emblematic of burned forests in western North America. The black-backed woodpecker occurs broadly across North America, from its southernmost range in the Sierra Nevada of California, eastward across the boreal belt to Québec and the Adirondack and White Mountains of New England and the Maritimes. Everywhere, it is associated with dense pockets of disturbed conifer trees, particularly those killed by fire (Tremblay et al., 2016). The black-backed woodpecker is frequently described as the most fire-associated species of bird in North America, possibly the world (Hutto, 2008). It is also closely associated with recent fires, often colonizing forests within the first year since burning, and declining in density 4–5 years after fire (Tingley et al., 2020). The reason for its strong post-fire affinity derives from its natural history. Black-backed woodpeckers excavate their nests preferentially in recently killed, undecayed snags (i.e. standing dead trees: Saab et al., 2009; Seavy et al., 2012). Foraging also occurs nearly exclusively on dead or dying trees, from which beetle larvae—particularly that of woodboring beetles (e.g. Cerambycidae)—are extracted. As the woodboring beetles primarily lay their eggs in the undecayed wood of recently killed trees (Powell, 2000), the primary food source, and thus the woodpecker itself, is tightly constrained to recent post-fire areas.

The literature surrounding black-backed woodpeckers' post-fire affinity describes a species that should greatly benefit from large, extensive areas of forest burned at high severity (Hutto, 2008). Nest sites are preferentially located in the highest density stands of small- to medium-sized conifer snags (Saab & Dudley, 1998; Seavy et al., 2012). Of North American woodpeckers found in the east, black-backed woodpeckers are considered the most specialized for foraging on dead wood (Nappi et al., 2015), and home range size (as a proxy for resource availability) scales inversely with the density of fire-killed snags within a home range (Tingley et al., 2014). Broadly, black-backed woodpeckers are more likely to be found closer to high-severity burned patches with high snag densities and farther from the fire perimeter (Saracco et al., 2011; Tingley et al., 2020; White et al., 2019).

Yet, new research is highlighting the potentially critical role that pyrodiversity—specifically, spatial heterogeneity in burn severity—plays in structuring the habitat use and selection of black-backed woodpeckers. A critical first observation has come from studies following recent "megafires" in California, where exceptionally large forested areas burned quickly over a matter of days, leaving large expanses of high-severity burned forest (e.g. Coen et al., 2018). Such fires were expected to be ideal breeding grounds for black-backed woodpeckers, yet surveys found surprisingly few individuals (White et al., 2019) and models overpredicted observed abundances (Tingley, Wilkerson, et al., 2016). Tracking studies have helped clarify the reasons behind this discrepancy. In one study following black-backed woodpeckers in six fires of northern California, adult woodpeckers chose to forage in areas of medium and high burn severity, but that were proximal to low-severity or unburned forest (Stillman et al., 2019). Similarly, in the choice of nest location, black-backed woodpeckers were very unlikely to choose to build a nest in a tree that was >500 m from the closest patch of live forest (Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019). In both cases—foraging and nest site placement—adult black-backed woodpeckers selected areas with higher heterogeneity in burn severity (i.e. greater pyrodiversity; Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019).

The mechanism underlying this surprising pyrodiversity affinity in black-backed woodpeckers appears to be predation risk of juveniles. Tracking observations revealed that juveniles—particularly recent fledglings—equally prefer live trees to snags and spend significantly more time in low-severity and unburned forest than adults (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). As juvenile black-backed woodpeckers are often dependent on parents for provisioning for approximately 35 days after fledging, juveniles and adults concentrated in edge areas where live forest abutted high-severity patches with large concentrations of snags (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). The dangers to juvenile black-backed woodpeckers of entering the high-severity burned areas were significant—survival of that 35-day window is only 13% for fledglings in a high-severity patch, but rises to 53% for fledglings in unburned to medium-severity patches (Stillman et al., 2021). Juvenile mortality was primarily due to predation by raptors—hunters that find prey primarily through visual cues. As a result, an age-specific trade-off between predation and starvation (Houston et al., 1993) may drive a species-level habitat affinity for areas with greater pyrodiversity.

6 | SYNTHESIS AND RESEARCH GAPS

The extent to which the pyrodiversity–biodiversity hypothesis is supported depends on a variety of factors, indicating a highly context-specific phenomenon. The strength of the pyrodiversity–biodiversity relationship has been shown to vary by taxa, spatial scale, temporal scale, geographic region and biome (Figure 2). Critically, the strength of the relationship also varies by how pyrodiversity itself has been measured and defined, which widely varies in the literature. Despite more than 40 published examples to date that explicitly test the pyrodiversity–biodiversity hypothesis (Figure 2), the extreme heterogeneity in design, approach, and scale of these studies complicates evidence synthesis. Plainly, we still know far too little about how pyrodiversity impacts biodiversity in most systems in most parts of the world.

Yet, the spotted owl and black-backed woodpecker case studies present an intriguing, alternative path to gaining ecological understanding of pyrodiversity. Here are two iconic species co-occurring in western North American conifer forests that have long been seen to occupy distinct and largely non-overlapping habitats within the same landscape. As scientists dig deeper into how heterogeneity in fire impacts these two species, we learn that the "old-growth specialist" owl can benefit from diverse post-fire landscapes, while the "fire-reliant" woodpecker selects for burned forest patches that are close to living, green forest. The mechanisms underlying these two single-species pyrodiversity–biodiversity relationships seem convergent: severe fire brings a boon of resources (nesting for the woodpecker, food for both the owl and woodpecker), but severe fire also brings danger (predation risk for the woodpecker and possibly the owl, and loss of limiting nesting habitat for the owl). Consequently, a pyrodiverse forest presents sufficient areas with elevated resources that are also adjacent to locations for protection and cover. Pyrodiversity, thus, stands to facilitate the creation of patch diversity that satisfies predictions from predation foraging risk optimization theory (Brown, 1999; Brown et al., 1999).

The amalgam of mixed global support for pyrodiversity–biodiversity relationships, combined with emerging mechanism-based support within individual species, assists in clarifying the existing gaps in our composite understanding of the pyrodiversity–biodiversity hypothesis. To best move forward in testing this hypothesis, we present the following six key research gaps:

1. *Stronger development of the different potential mechanisms underlying the pyrodiversity–biodiversity relationship*. Mechanistic understanding, to date, has been weak to non-existent and was vague in the original conceptualization. Evidence suggests that multiple, non-exclusive mechanisms may impact pyrodiversity–biodiversity relationships (e.g. Kelly et al., 2017), and a stronger inferential approach in the future will result in specific studies designed to test for particular mechanisms within the composite framework.
2. *Testing for sensitivity to different pyrodiversity metrics and scale dependence*. Examining whether the pyrodiversity–biodiversity relationship is sensitive to different approaches for quantifying pyrodiversity (Appendix 1) could illuminate underlying mechanisms and help explain why some studies do not find support to the relationship. Moreover, the pyrodiversity–biodiversity relationship is likely to be scale-dependent, but general rules for such scale dependence are unknown.
3. *Standardization of metrics for pyrodiversity*. Pyrodiversity has been measured in many different ways, even when describing diversity within a single axis of fire regimes (e.g. variation in burn severity). A strong mechanism-based foundation and further empirical research (examining the relative importance of different pyrodiversity metrics; see #2 above) will help provide a foundation for the superiority of certain metrics over others, while still recognizing that definitions may require adjustments based on data availability or study objectives. Broad adoption of particular metrics

among researchers (and testing of multiple independent metrics) could aid future synthesis and meta-analysis.

4. *Bridging from species to communities*. Biodiversity responses to pyrodiversity have been measured broadly at the aggregate level—for example tallies of species richness—yet biodiversity is composed of many species, each with their own traits and preferences. With evidence that individual species may benefit from pyrodiversity, it is important to know how widespread this phenomenon is, and whether other species (and how many) show opposite responses. Analysis of functional traits and phylogeny may help build generalizable predictions of pyrodiversity–biodiversity strength that can be translated into less data-rich systems.
5. *Broad-scale spatial and temporal mapping of pyrodiversity*. Pyrodiversity has been assumed to have decreased because of human landscape modification and fire suppression (Martin & Sapsis, 1992). However, little empirical work has explored how pyrodiversity has changed through time across global ecosystems. Quantifying pyrodiversity across large (regional, global) spatial extents (e.g. Hempson et al., 2018; Steel et al., 2021), spatial scaling of pyrodiversity, and evaluating consistency of these patterns using different definitions of pyrodiversity will go a long way in understanding its fundamental ecological role across ecosystems.
6. *Macroecological studies of pyrodiversity–biodiversity relationships*. Most studies of pyrodiversity–biodiversity relationships have focused on study areas with a relatively small spatial extent. Large-scale mapping of pyrodiversity (see #5 above) will facilitate linking measures of pyrodiversity to regional, continental, or global biodiversity datasets that could facilitate a valuable macroecological perspective of pyrodiversity–biodiversity relationships.

Research that focuses on the above needs will improve our understanding of pyrodiversity and the pyrodiversity–biodiversity hypothesis. In an era of unprecedented changes to fire regimes because of climate change and past land use, a better understanding of pyrodiversity–biodiversity relationships across global ecosystems could improve forecasts of biodiversity change and bolster conservation and fire management planning. In some systems and at certain scales, a pyrodiversity paradigm may help maintain biodiversity, promote conservation of focal species with different life histories and permit flexibility and creativity in the implementation of fire management. However, the current literature does not illuminate those relevant systems and scales. Additional research and syntheses are urgently needed in this era of megafires.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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BIOSKETCHES

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APPENDIX 1

Summary of studies that examined the pyrodiversity–biodiversity hypothesis (PBH). Each row corresponds to a study–taxa combination because some studies examined support for the hypothesis across multiple taxonomic groups.

Reference	Support inferred for PBH	Direct test or indirect inference	How "pyrodiversity" was defined or conceptualized	Variation within or among sampling units	Continent	Ecosystem	Taxa
Masters (1996)	Yes	Indirect	"Fire mosaic"; variation in time since fire	Among	Australia	Grasslands	Reptiles
Stuart-Smith et al. (2002)	Yes	Direct	"Patchy mosaic"; implicit structural heterogeneity within burned plots	Within[a]	North America	Forest/woodland	Birds
Brotons et al. (2005)	Yes	Direct	Variation in habitat type composition and configuration created by fire	Within	Europe	Forest/woodland	Birds
Cook and Holt (2006)	No	Direct	"Mosaic burning"; vegetation heterogeneity	Within	North America	Grasslands	Beetles
Pastro et al. (2011)	No	Direct	Mixture of successional stages; implicit structural heterogeneity within prescribed burn plots	Within[a]	Australia	Grasslands	Plants
Pastro et al. (2011)	No	Direct	Same as above	Within[a]	Australia	Grasslands	Reptiles
Pastro et al. (2011)	No	Direct	Same as above	Within[a]	Australia	Grasslands	Mammals
Andersen and Hoffmann (2011)	No	Direct	Implicit successional heterogeneity present in frequent-fire versus long-unburned areas	Within[a]	Australia	Savanna	Ants
Langlands et al. (2012)	Yes	Indirect	Variation in post-fire ages, scale or intensity of fire	Among	Australia	Grasslands	Spiders
Davies et al. (2012)	No	Indirect	Variation in seasonality and frequency of fire	Among	Africa	Savanna	Termites
Kelly et al. (2012)	No	Direct	Shannon diversity of fire age classes	Within	Australia	Scrubland	Mammals
Taylor et al. (2012)	No	Direct	Shannon diversity index of fire age classes within sampling units	Within	Australia	Scrubland	Birds
Nimmo et al. (2013)	No	Direct	Shannon diversity index of the proportional cover of three fire age classes	Within	Australia	Scrubland	Reptiles
Maravalhas and Vasconcelos (2014)	Yes	Indirect	Variation in fire frequency and timing	Among	South America	Savanna	Ants
Andersen et al. (2014)	No	Indirect	Variation in fire frequency and seasonality	Among	Australia	Savanna	Ants
Farnsworth et al. (2014)	No	Direct	Shannon diversity index of fire age classes	Within	Australia	Scrubland	Reptiles
Sitters et al. (2014)	Yes	Direct	Variation in age class diversity and configuration	Within	Australia	Forest/woodland	Birds
Avitabile et al. (2015)	No	Direct	Shannon diversity index of fire age classes	Within	Australia	Scrubland	Termites
Cohn et al. (2015)	Yes	Direct	Number of fire age classes in a sampling unit	Within	Australia	Forest/woodlands	Plants
Radford et al. (2015)	No	Direct	Number of fire age classes in a sampling unit	Within	Australia	Savanna	Mammals
Kelly et al. (2015)	No	Indirect	Variation in time since fire; optimization of a mixture of successional stages	Among	Australia	Scrubland	Birds
Kelly et al. (2015)	No	Indirect	Same as above	Among	Australia	Scrubland	Reptiles

APPENDIX 1 (Continued)

Reference	Support inferred for PBH	Direct test or indirect inference	How "pyrodiversity" was defined or conceptualized	Variation within or among sampling units	Continent	Ecosystem	Taxa
Kelly et al. (2015)	No	Indirect	Same as above	Among	Australia	Scrublund	Mammals
Lawes et al. (2015)	No	Direct	"Patchiness"; average distance to unburned area over the sampling unit	Within	Australia	Savanna	Mammals
Burgess and Maron (2016)	No	Direct	Simpson diversity index of fire-mediated patch types	Within	Australia	Forest/ woodlands	Birds
Tingley et al., (2016)	Yes	Direct	Standard deviation of continuous burn severity (per cent canopy mortality) in a sampling unit	Within	North America	Forest/ woodlands	Birds
Ponisio et al. (2016)	Yes	Direct	Simpson's diversity of unique fire history classes	Within	North America	Forest/ woodlands	Bees
Ponisio et al. (2016)	Yes	Direct	Same as above	Within	North America	Forest/ woodlands	Flowering plants
Ponisio et al. (2016)	Yes	Direct	Same as above	Within	North America	Forest/ woodlands	Plant:pollinator inxn
Prowse et al. (2017)	No	Indirect	Variation in time since fire	Among	Australia	Forest/ woodlands	Birds
Brown and York (2017)	Yes	Direct	Variation in post-fire age classes and number of fires	Within	Australia	Forest/ woodlands	Flies
Brown and York (2017)	Yes	Direct	Same as above	Within	Australia	Forest/ woodlands	Wasps
Taillie et al. (2018)	Yes	Indirect	Variation in burn severity, time since fire and their interaction	Among	North America	Forest/ woodlands	Birds
McGranahan et al. (2018)	Yes	Direct	Variation in number of patches in a sampling unit, fire return interval and burn season	Within	North America	Grasslands	Prairie plants
Davies et al. (2018)	No	Indirect	Variation in fire frequency	Among	Australia	Savanna	Mammals
Davis et al. (2018)	No	Direct	Shannon diversity index of fire age classes within sampling unit	Within	Australia	Scrublund	Termites
Beale et al. (2018)	Yes	Direct	Volume of the minimum convex hull of the four-dimensional space described by all the fires within a sampling unit	Within	Africa	Savanna	Birds
Beale et al. (2018)	Yes	Direct	Same as above	Within	Africa	Savanna	Mammals
Bliege Bird et al. (2018)	Yes	Indirect	Shannon diversity of successional stages within sampling units	Within	Australia	Scrublund	Mammals (and one species of Reptile)
Steel et al. (2019)	Yes	Direct	Heterogeneity in burn severity within a sampling unit, corrected for mean severity	Within	North America	Forest/ woodlands	Bats
Docherty et al. (2020)	Yes	Direct	Multiple measures including Shannon diversity in age class, shape complexity, edge contrast index and fire frequency	Within	Africa	Savanna	Birds
Wills et al. (2020)	No	Direct	Variation in fire age class/vegetation succession	Within	Australia	Forest/ woodlands	Birds

[a] Study inferred pyrodiversity effects from assumed (unmeasured) heterogeneity within sampling units experiencing certain fire regimes.

Megafires: an emerging threat to old-forest species

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Increasingly frequent "megafires" in North America's dry forests have prompted proposals to restore historical fire regimes and ecosystem resilience. Restoration efforts that reduce tree densities (eg via logging) could have collateral impacts on declining old-forest species, but whether these risks outweigh the potential effects of large, severe fires remains uncertain. We demonstrate the effects of a 2014 California megafire on an iconic old-forest species, the spotted owl (*Strix occidentalis*). The probability of owl site extirpation was seven times higher after the fire (0.88) than before the fire (0.12) at severely burned sites, contributing to the greatest annual population decline observed during our 23-year study. The fire also rendered large areas of forest unsuitable for owl foraging one year post-fire. Our study suggests that megafires pose a threat to old-forest species, and we conclude that restoring historical fire regimes could benefit both old-forest species and the dry forest ecosystems they inhabit in this era of climate change.

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The frequency and severity of "megafires" (ie large wildfires >10,000 ha in extent [Stephens *et al*. 2014b]) in the dry forests of North America has increased after a century of fire suppression and climate warming (Westerling *et al*. 2006; Miller *et al*. 2009b), incurring considerable societal and economic costs by destroying homes, human infrastructure, and timber resources, in addition to necessitating increased taxpayer-funded support for fire-fighting (Stephens *et al*. 2013, 2014b). In the western US, major reforms in forest fire management have been proposed to restore low- and moderate-severity fire regimes through forest tree thinning (North *et al*. 2015). However, the vision of restoring "pre-European" fire regimes, as well as forest structure and composition, is constrained by concerns over fuels-reduction treatments that simplify the structurally and floristically diverse forests inhabited by old-forest species (ie species that inhabit forests characterized by large, old trees, closed overstory canopy, and complex vertical structure) (Pilliod *et al*. 2006). Potential short-term consequences of fuels-reduction and restoration treatments may be outweighed by long-term benefits of forest restoration if large, high-severity fires negatively affect old-forest species (Sweitzer *et al*. 2015; Tempel *et al*. 2015). However, research suggests that severe fires may have neutral or beneficial effects on biodiversity, including old-forest species (Hutto 2008; Swanson *et al*. 2011; DellaSala and Hanson 2015; Lee and Bond 2015), which seemingly increases the perceived divide between forest restoration and species conservation objectives. Nevertheless, the ecological effects of high-severity fire likely depend in part on the size, distribution, and configuration of burned patches (Fontaine and Kennedy 2012), and the impacts of large, severe fires on old-forest species remain a source of considerable uncertainty.

Here, we demonstrate the negative short-term impacts of a California megafire on a model old-forest species, the spotted owl (*Strix occidentalis*; Figure 1), by taking advantage of a natural before–after control–impact (BACI) experimental design on our long-term (23-year) demographic study area. In September and October 2014, the human-ignited "King Fire" burned 39,545 ha and was one of the largest and most severe forest fires recorded in California history (Figure 2), with high-severity fire (75–100% canopy mortality) occurring on 19,854 ha (50% of the area burned), with one continuous 13,683-ha high-severity burned patch. The King Fire affected 15,594 ha (44%) of our 35,500 ha study area and overlapped 30 of 45 spotted owl sites we have monitored continuously since 1993 (Tempel *et al*. 2014b). Of the 15,594 ha that burned within our study area, 64% burned at high-severity (WebTable 1). The extreme nature of the fire, more than two decades of pre-fire site occupancy data, and location information on owls – outfitted with Global Positioning System (GPS) receivers and tagged with colored leg bands for identification of individual birds – allowed us to draw strong inferences regarding the effect of severe fire on a species considered to be a barometer of old-forest wildlife community health (Simberloff 1998). Our results suggest that (1) reducing the frequency of large, severe fires could benefit spotted owls and, by extension, other old-forest species, and (2) forest restoration and old-forest species conservation objectives may be more compatible than previously believed.

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SA Whitmore

Figure 1. *A female California spotted owl (*Strix occidentalis occidentalis*) within the Eldorado Density Study Area in the central Sierra Nevada, California.*

Methods

Study area and spotted owl surveys

We conducted our study on the contiguous 35,500-ha Eldorado Density Study Area (EDSA) within the Eldorado National Forest in the central Sierra Nevada, California. The EDSA has been the site of a long-term mark–recapture demographic study of California spotted owls (Tempel and Gutiérrez 2013), and forms the primary part of a larger study area containing a greater number of owl sites (Tempel *et al.* 2014a). We used data from owl sites only within the EDSA because some sites outside of this area experienced a complex history of fire and post-fire management that could have confounded the natural BACI design within the EDSA. Moreover, sites outside of the EDSA were added at various times during the study, potentially complicating our evaluation of the effect of the King Fire on long-term spotted owl population trends.

Approximately 60% of the EDSA was public lands managed by the US Forest Service (USFS) and 40% was private land managed by timber companies. The primary vegetation type within the EDSA was mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Forests within the EDSA have a complex history of management, logging, and fire suppression dating back at least 100 years. Early timber harvesting generally involved the selective removal of large, commercially valuable trees, with a more recent emphasis on clear-cutting on private lands and "diameter-limited thinning from below" on public lands. Prior to fire suppression, the ingrowth of shade-tolerant trees, and the removal of large trees, historical fire regimes consisted mainly of frequent low- to moderate-severity fire occurring in 5–15-year intervals (Stephens and Collins 2004). Elevation within the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

We surveyed the entire area each year for territorial spotted owls during the breeding season (1 Apr to 31 Aug) without regard to land cover, topography, access, or land ownership, and for this analysis we used survey data from 1993–2015. Spotted owls (usually mated pairs, but sometimes single birds) occupy and defend sites (ie "territories"), the locations of which remain reasonably stable across years. We considered a site to be occupied in a given year when at least one owl was detected. Additional survey details can be found elsewhere (Tempel and Gutiérrez 2013; Tempel *et al.* 2014b).

BACI analysis

We evaluated the potential impact of high-severity fire on spotted owls using a BACI design with multi-season site occupancy data (MacKenzie *et al.* 2003; Popescu *et al.* 2012). We carried out parallel continuous and categorical BACI analyses, where the proportion of a spotted owl site (a circle with radius equal to one-half the mean nearest-neighbor distance across years = ~1100 m; Tempel *et al.* 2014a) affected by high-severity fire was the impact covariate (ie "treatment"). We defined "high-severity" as forests that experienced 75–100% canopy mortality (Lee and Bond 2015), corresponding to a relative differenced Normalized Burn Ratio (RdNBR) threshold of >572 (Miller *et al.* 2009a). The continuous BACI analysis contained two groups: sites that were unburned (n = 15) and sites that overlapped with the King Fire and thus experienced some degree of burn (n = 30). The categorical BACI analysis contained three groups: sites that were unburned (n = 15), sites that experienced <50% high-severity fire (n = 16), and sites that experienced >50% high-severity fire (n = 14). For both continuous and categorical BACI analyses, we followed a hierarchical modeling procedure by first modeling within-season detection probability as a function of covariates (WebTable 2). We then modeled the potential effects of high-severity fire on colonization (γ) and extinction (ε) rates separately using Akaike's information criterion (AIC) to select between competing models (WebTable 3), while allowing the non-focal parameter to vary by year (Tempel *et al.* 2014a).

Previous attempts to test for the effects of wildfire on spotted owls have been hindered by the potential confounding effect of post-fire salvage logging (Lee *et al.* 2012; Clark *et al.* 2013). However, in our study, all surveys used to estimate occupancy metrics were completed before the implementation of proposed post-fire salvage logging on public lands (USFS 2015), which comprised a median of 89% of the area that occurred within burned owl sites (versus ~11% on private lands). We also evaluated the potential effects of post-fire salvage logging on private lands in the continuous site occupancy analysis. Specifically, when fire effects were supported, we introduced a covariate representing the proportion of spotted owl sites that experienced salvage logging. The continuous variables – high-severity fire and salvage logging – were not strongly associated at fire-affected sites ($R^2 = 0.10$).

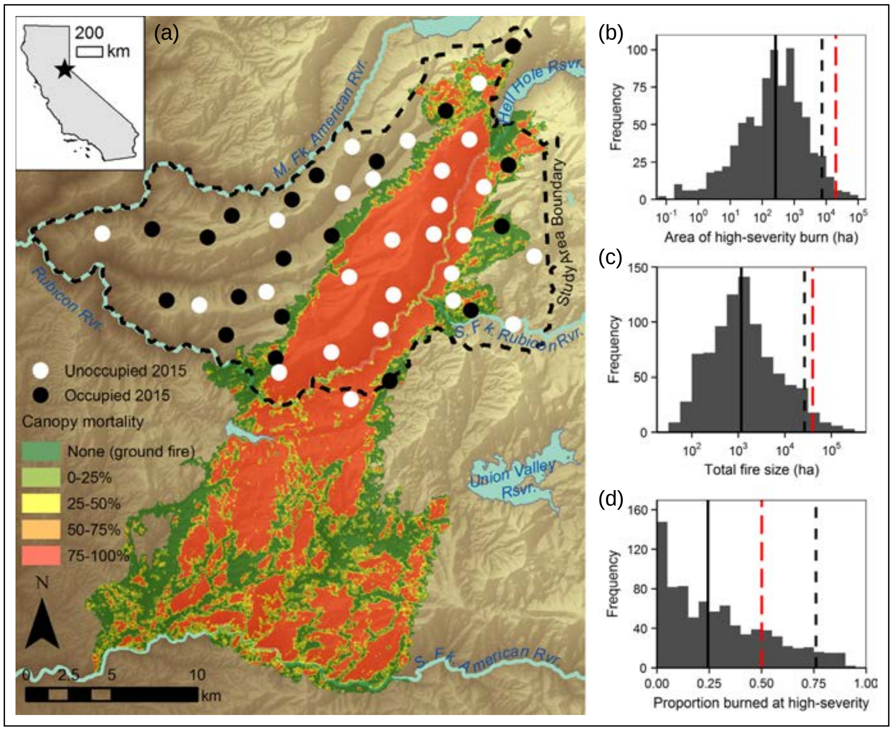

Figure 2. *The geography and historical context of the 2014 King megafire. (a) The distribution of occupied and unoccupied spotted owl sites in 2015 within our 23-year demographic study area, which was located ~20 km west of Lake Tahoe, California. Elevation is represented by brown shading (darker brown = low elevation, lighter brown = high elevation) and ranges from approximately 150 to 3000 m. (b–d) A comparison of the King Fire to all California fires since 1984 in terms of area of high-severity burn (b), total fire size (c), and proportion burned at high-severity (d); the solid black lines represent the 50th percentile, the dashed black lines represent the 95th percentile, and the dashed red lines represent the 2014 King Fire.*

Population trend analysis

We fit a fully time-varying dynamic occupancy model to our 23-year detection/non-detection data to obtain unconstrained annual estimates of occupancy (ψ_t) and rate of change in occupancy (λ_t) for the study area (MacKenzie *et al.* 2003). Our statistical model directly estimated initial occupancy (ψ_1), annual estimates of extinction (ε_t), and annual estimates of colonization (γ_t), so we used the recursive equation

$$\psi_t = \psi_{t-1}(1-\varepsilon_{t-1}) + (1-\psi_{t-1})\gamma_{t-1} \qquad \text{(Eq 1)}$$

to estimate occupancy (ψ_t) for each year of the study period. Then, using the estimates of ψ_t, we calculated λ_t for each year using the equation:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t} \qquad \text{(Eq 2).}$$

This analysis allowed us to consider occupancy and rate of change in occupancy after the King Fire within the context of a long-term decline in our study population (Tempel and Gutiérrez 2013). We fit several linear models to annual estimates of occupancy ψ_t and used AIC to evaluate relative support for different time trends (linear, log-linear, quadratic) and a segmented (ie "breakpoint") model over the pre-fire years 1993–2014 (WebTable 4). We used the segmented model to evaluate support for an initial decline followed by a period of apparent population stability prior to the King Fire.

Habitat use and selection analysis

We collected post-fire foraging locations from nine spotted owls during the 2015 breeding season using backpacks equipped with a Lotek Pinpoint 100 mini-GPS archival tag and a VHF radio transmitter. GPS tags recorded 1–2 locations at random times between dusk and dawn each night, May–August, to characterize nocturnal habitat use during the breeding season. We collected 1085 locations but discarded ~11 locations per owl with suboptimal measures of precision (dilution of precision [DOP] ≥ 5). Using burn severity maps produced by the USFS, we performed a compositional analysis of habitat use (Aebischer *et al.* 1993) and derived Manly's selection ratios (ω_i; Manly *et al.* 2002)

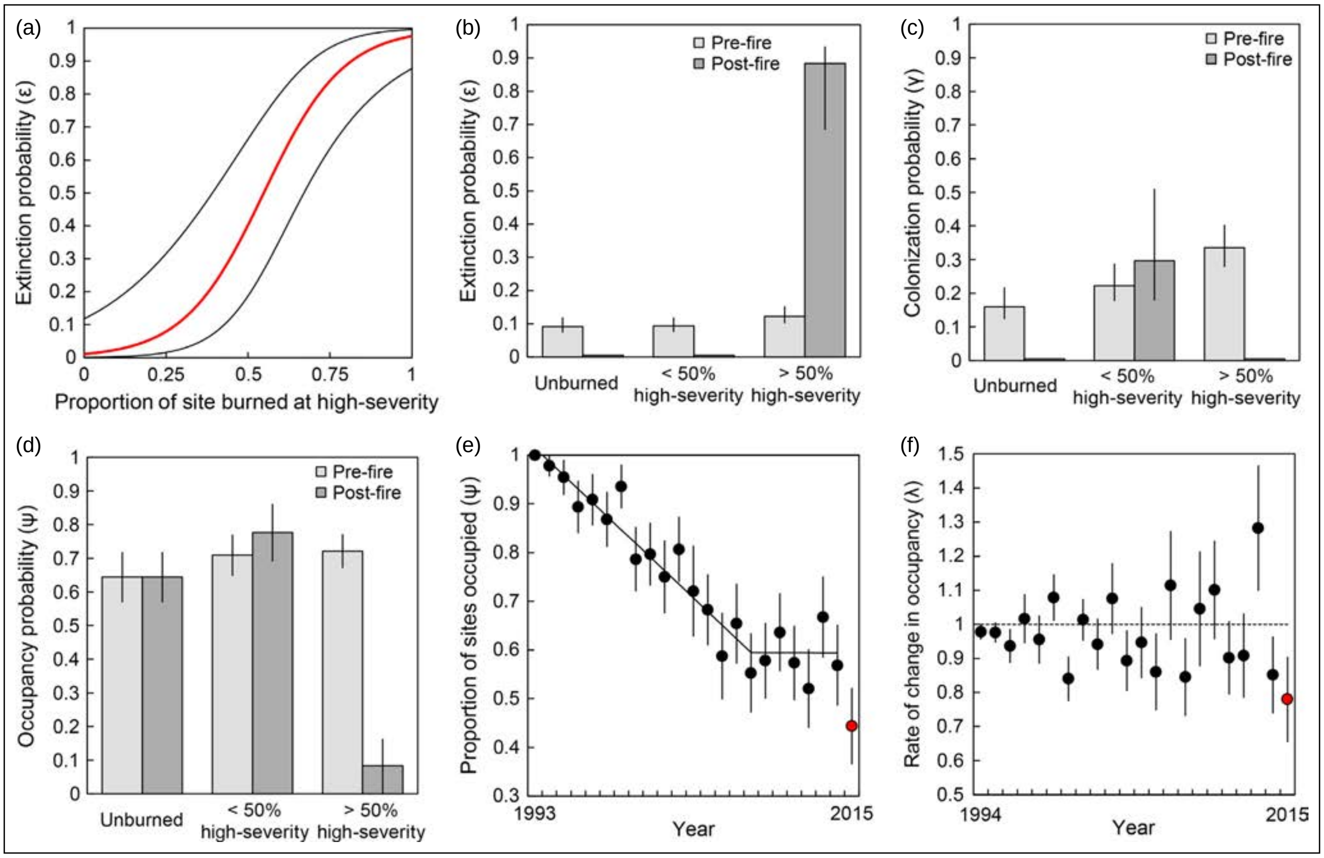

Figure 3. *Before–after control–impact and population analyses. (a) The continuous relationship between the proportion of an owl site that burned at high-severity and the probability of site extinction. (b–d) Colonization (b), extinction (c), and occupancy (d) probabilities for owl sites that experienced different degrees of high-severity burn both pre- and post-fire. (e) Annual estimates of occupancy (ψ) over the study period, where the black line represents a segmented regression function fitted to the mean occupancy for years 1993–2014 (WebTable 4) demonstrating the periods of decline and subsequent stability before the 2014 King Fire (solid red circle). (f) Annual estimates of rate of change in occupancy (λ) over the study period, where the dashed black line at* y = 1 *indicates a stable rate of change, and the solid red circle indicates the rate of change after the 2014 King Fire. The black curved lines in (a) and all error bars in (b–f) represent ± 1 SE of the mean.*

for third-order habitat selection to assess selection or avoidance of forests in different burn classes (unburned, low-severity, high-severity).

We defined available habitat area for each owl using a circle with the center equal to the geometric mean of 2015 nest tree, roosts, and daytime capture locations (ie "activity center") and a radius equal to the 95th percentile of linear foraging distances from the activity center (similar to Bond *et al*. 2009). We used the 95th (not 100th) percentile so that distant areas rarely visited by owls in foraging bouts (Bond *et al*. 2009) were not counted as "available" habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies (WebFigure 2). We used a circle instead of a minimum convex polygon (MCP) to define available habitat because MCPs often failed to include the large, high-severity patch as "available" although it was generally within the foraging radius of owls (WebFigure 3). We performed habitat selection analyses using the R package "adehabitatHS" (Calenge 2006).

Results and discussion

The BACI analysis indicated that high-severity fire had a strong negative impact on spotted owls. The probability of site extinction (ε) increased from 0.01 to 0.98 as the proportion of high-severity fire at a spotted owl site increased from 0 to 1 (Figure 3a). Moreover, extinction rates at severely burned sites (>50% of site area burned at high-severity) increased sevenfold following the King Fire ($\hat{\varepsilon}_{1993–2014}$ = 0.12, 95% confidence interval [CI] = 0.08–0.18; $\hat{\varepsilon}_{2015}$ = 0.88, CI = 0.49–0.98), whereas post-fire extinction rates were estimated to be zero at less severely burned and unburned sites (Figure 3b). Sites that burned <50% at high-severity were more likely to be colonized after the fire ($\hat{\gamma}_{<50\%\ \text{High-severity}}$ = 0.30, 95% CI = 0.07–0.72) than unburned sites and sites that burned >50% at high-severity ($\hat{\gamma}_{\text{Unburned}}$ and $\hat{\gamma}_{>50\%\ \text{High-severity}}$ = 0; Figure 3c). Colonization of sites after the fire was largely the result of individuals moving to less burned sites after abandoning their original sites that burned at >50% high-severity (WebFigure 4). Predicted occupancy rates ($\hat{\psi}$) at sites that burned >50% at high-severity declined by almost ninefold from their pre-fire value ($\hat{\psi}_{\text{Pre-fire}}$ = 0.72, 95% CI = 0.62–0.82; $\hat{\psi}_{\text{Post-fire}}$ = 0.08, 95% CI = 0.00–0.24), based on a model that combined top colonization and extinction covariate structures in the categorical analysis (Figure 3d).

Using spatially explicit data obtained from privately owned natural resource companies (Sierra Pacific Industries and Mason, Bruce & Girard Inc) that managed timberlands in our study area, we estimated that post-fire salvage logging on private lands constituted a median of only 2% of the area within owl sites. The extent of high-severity fire was large relative to the extent of salvage logging within owl territories (WebFigure 1), strengthening potential inferences because this ratio reduced the confounding effects of high-severity fire and post-fire salvage logging on spotted owls. In addition, the term for salvage logging appeared as an uninformative parameter in the modeling procedure (Arnold 2010), also suggesting that post-fire salvage logging operations did not confound associations between occupancy metrics and high-severity fire (WebTable 3; WebFigures 1 and 5).

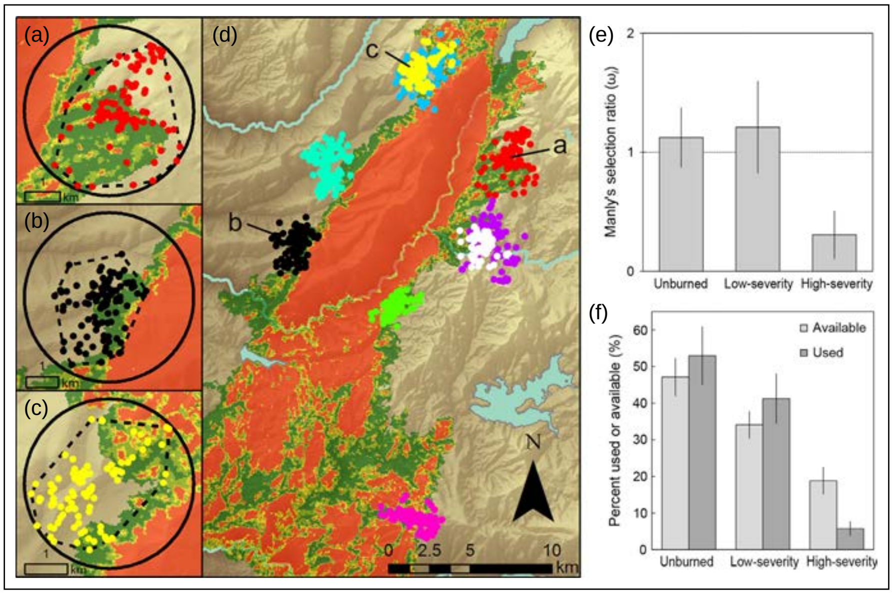

Figure 4. *Distribution of spotted owl foraging locations following a megafire developed from 985 GPS locations from nine owls (individuals represented by different colors) during the 2015 breeding season in relation to the 2014 King Fire (d). Inset examples (a–c) of foraging locations for three owls (small solid-colored circles) and the area defined as available habitat (large open black circles) compared to a minimum convex polygon (black dashed polygon) demonstrate the owls' apparent avoidance of the high-severity burned area. Burn severity for the King Fire is displayed in 25% classes as in Figure 2a. (e) Manly's selection ratios ($\hat{\omega}$) ± 1.96*SE, where a selection ratio $\hat{\omega} > 1$ indicates habitat preference, $\hat{\omega} < 1$ indicates habitat avoidance, and $\hat{\omega} = 1$ indicates neither preference nor avoidance. (f) Mean (± SE) availability and use among nine owls for unburned forests, forests that experienced 0–75% canopy mortality (low-severity), and forests that experienced 75–100% canopy mortality (high-severity).*

The King Fire exacerbated a longer-term decline in spotted owl occupancy within our study area. The proportion of occupied spotted owl sites declined by 43% over a 22-year period leading up to the 2014 King Fire ($\hat{\psi}_{1993}$ = 1.0, standard error of the mean [SE] = 0.0; $\hat{\psi}_{2014}$ = 0.57, 95% CI = 0.41–0.73) (Figure 3e). After the King Fire, occupancy dropped from 0.57 to 0.44 ($\hat{\psi}_{2014}$ = 0.57, 95% CI = 0.41–0.73; $\hat{\psi}_{2015}$ = 0.44, 95% CI = 0.29–0.60) following ~7 years of relatively stable occupancy (Figure 3e). The 22% decline in site occupancy after the fire ($\hat{\lambda}_{2015}$ = 0.78, 95% CI = 0.53–1.03) was the greatest single-year decline recorded over our 23-year study period (Figure 3f).

Analyses of spotted owl foraging locations along the perimeter of the King Fire (no owls were present in the interior of the large patch that burned at high-severity; Figure 3, a–d) indicated that spotted owls foraged non-randomly (Wilks's lambda Λ = 0.40, P = 0.017) by avoiding foraging in areas that burned at high-severity ($\hat{\omega}_{\text{High-severity}}$ = 0.31, 95% CI = 0.10–0.51) (Figure 4, e and f). Forests that burned at low-severity and unburned forests were used in proportion to their availability on the landscape ($\hat{\omega}_{\text{Low-severity}}$ = 1.21, 95% CI = 0.82–1.60; $\hat{\omega}_{\text{Unburned}}$ = 1.12, 95% CI = 0.87–1.38) (Figure 4, e and f).

The observation that lower-severity fire is benign, and perhaps even moderately beneficial, to spotted owls is consistent with previous studies (Roberts *et al.* 2011; Lee *et al.* 2012) and is not surprising given that, within dry mixed-conifer forests, the spotted owl and other old-forest species evolved in association with such fire regimes (Noss *et al.* 2006; North *et al.* 2009). However, we provide the first definitive evidence that a large, high-severity fire (ie a megafire) had strong negative population impacts on an old-forest species and that areas burned at high-severity were avoided by individuals of that species. These findings contrast with a recent spotted owl population study that reported high site occupancy after another megafire (the "Rim Fire"; Lee and Bond 2015). The Rim and King fires could have affected owls differently because of differences in the patterns of patches that burned at high-severity and the resulting distribution of remnant habitat. The largest high-severity patch in the Rim Fire (21,426 ha) was 1.5 times larger than the largest high-severity patch in the King Fire (13,683 ha), but made up a smaller percentage of the total area burned (21% versus 36% for the Rim and King fires, respectively) and, despite its larger area, had an edge-to-area ratio 1.5 times greater than that of the King Fire. The relatively high spatial complexity and heterogeneity in high-severity burn patterns in the Rim Fire may have resulted in a wider range of vegetation conditions and more remnant live trees suitable for owls (Lee and Bond 2015) as compared with the King Fire, where the largest patch of high-severity fire was more homogeneously severe and overlapped a greater density of owl sites (Figure 2; see WebFigure 6). Alternatively, because owls were not individually marked in the Rim Fire study, some detections at "occupied" sites may have involved individuals from neighboring territories or non-territorial "floaters" (Lee and Bond 2015), both of which may have contributed to inflated estimates of territory occupancy. Regardless, our study demonstrates that megafires can have strong negative effects on spotted owls, particularly when severely burned areas occur as large homogenous patches that leave little or no interspersed remnant habitat.

While we used only one year of post-fire data, the substantial decline in occupancy at severely burned sites is unlikely to reflect a temporary loss of individuals that will soon be replaced by colonization, but rather represents a direct loss of suitable nesting and roosting habitat that will likely not be replaced for many decades. Moreover, we found the scorched remains of one adult spotted owl from a severely burned site (WebFigure 7), indicating that, in some instances, this highly vagile species was unable to avoid the rapidly moving fire. It is not unreasonable to suspect that less mobile old-forest specialists will be equally – and perhaps more – affected by megafires like the King Fire. Collectively, these findings suggest that megafires constitute an additional mechanism by which climate change will threaten old-forest species, along with previously recognized climate-associated stressors such as habitat shifts, physiological impacts, and changes in community interactions (Dawson *et al*. 2011).

Conclusions

Our study demonstrates that increasingly frequent megafires pose a threat to spotted owls and likely other old-forest species and, as a result, suggests that forest ecosystem restoration and old-forest species conservation may be more compatible than previously believed. Restoration practices that can demonstrably reduce the frequency of large, high-severity fires and reintroduce low- to moderate-severity fire as the dominant disturbance regime will likely benefit both dry-forest ecosystems and old-forest species such as spotted owls. Yet forest restoration efforts that remove key habitat elements and areas of currently suitable habitat could exacerbate the risk of extirpation in the short term before the long-term benefits of restored fire regimes are realized, particularly in light of the present deficit in large and old trees in natural landscapes (Tempel *et al*. 2015). Rather, implementing fuels and restoration treatments outside of key habitats (eg nesting and denning areas) is more likely to minimize short-term impacts and ensure that old-forest species persist until forest resiliency objectives are achieved (Stephens *et al.* 2014a). However, the calculus behind these trade-offs is complex and depends on several considerations that merit additional research, such as the magnitude of short-term impacts that treatments impose on old-forest species, the relative increase in the frequency of severe fire as a function of climate change, and the efficacy of forest restoration for reducing both severe fires and tree mortality from drought and insects (Asner *et al*. 2015). Managers and policy makers will be faced with challenging decisions regarding the pace and scale of forest restoration efforts in light of scientific uncertainty and conflict among stakeholders (Redpath *et al*. 2013). We suggest, however, that old-forest species should not be viewed as an impediment to forest restoration objectives; rather, ensuring the persistence of old-forest species including the spotted owl, northern goshawk (*Accipiter gentilis*), pileated woodpecker (*Dryocopus pileatus*), Pacific fisher (*Pekania pennanti*), and American marten (*Martes americana*) can serve as a barometer for the successful restoration of the ecosystems they inhabit.

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Supporting Information

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RESEARCH ARTICLE

Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes

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Abstract

Context Climate and land-use change have led to disturbance regimes in many ecosystems without a historical analog, leading to uncertainty about how species adapted to past conditions will respond to novel post-disturbance landscapes.

Objectives We examined habitat selection by spotted owls in a post-fire landscape. We tested whether selection or avoidance of severely burned areas could be explained by patch size or configuration, and whether variation in selection among individuals could be explained by differences in habitat availability.

Methods We applied mixed-effects models to GPS data from 20 spotted owls in the Sierra Nevada, California, USA, with individual owls occupying home ranges spanning a broad range of post-fire conditions after the 2014 King Fire.

Results Individual spotted owls whose home ranges experienced less severe fire ($< 5\%$ of home range severely burned) tended to select severely burned forest, but owls avoided severely burned forest when more of their home range was affected ($\sim$ 5–40%). Owls also tended to select severe fire patches that were smaller in size and more complex in shape, and rarely traveled $>$ 100-m into severe fire patches. Spotted owls avoided areas that had experienced post-fire salvage logging but the interpretation of this effect was nuanced. Owls also avoided areas that were classified as open and/or young forest prior to the fire.

Conclusions Our results support the hypothesis that spotted owls are adapted to historical fire regimes characterized by small severe fire patches in this region. Shifts in disturbance regimes that produce novel landscape patterns characterized by large, homogeneous patches of high-severity fire may negatively affect this species.

Keywords California spotted owl · Disturbance · Functional response · Individual variation · Resource selection · Salvage logging · *Strix occidentalis* · Wildfire

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Introduction

Disturbance regimes create and maintain the characteristic vegetation patterns and dynamics to which animals are adapted in ecological systems (Lytle 2001; Betts et al. 2019). Climate and human land use change have led to modern disturbance regimes in many ecosystems that do not have a historical analog (Seidl et al. 2016), giving rise to novel post-disturbance landscape mosaics and altered regeneration pathways (Johnstone et al. 2016). Landscapes experiencing novel disturbance regimes are often characterized by changes in vegetation composition, patch size, and configuration that are expected to change selection pressures, which can affect the behavior and fitness of individual organisms (Karr and Freemark 1985). Responses to changing disturbance regimes vary among taxa (Elmqvist et al. 2003), but are likely to depend on the species' degree of habitat specialization as well as the extent to which these novel disturbances affect resources that limit individuals and populations (e.g., nesting or denning sites, primary prey/food) (Clavero et al. 2011). Therefore, the way in which individuals and populations select or avoid conditions in novel post-disturbance landscapes may offer insights into the ability of species to persist in landscapes experiencing changing disturbance regimes.

Wildfire is an important disturbance regime that is changing worldwide (Turner 2010; Seidl et al. 2017), and is considered to be a significant evolutionary force (Bond and Keeley 2005; Pausas and Parr 2018; Foster et al. 2020). The dry forests of western North America appear to be experiencing changes from a historically frequent-fire regime that consisted of predominately lower-severity fire with a relatively small component of high-severity fire by comparison (Stephens and Collins 2004; Steel et al. 2015; Safford and Stevens 2017), to one where fires have become larger and more severe (Steel et al. 2015; Abatzoglou and Williams 2016; Westerling 2016). More frequent 'megafires' in western dry forests are generally thought to be the consequence of a century of fire suppression, which increased landscape fuels (Stephens et al. 2014; Collins et al. 2017a), and anthropogenic climate change, which produced conditions enhancing fire risk (Diffenbaugh et al. 2015). As a consequence, the patch structure in post-fire landscapes is increasingly characterized by homogeneous large patches of severely burned areas (Collins et al. 2017b; Stevens et al. 2017). Decreased heterogeneity in post-fire conditions (i.e., more homogeneously severe burned areas) may influence the behavior and space use of species that have evolved to exploit more heterogeneous environments and ultimately reduce individual fitness and population abundance.

Forest-dependent species inhabiting dry forests in western North America evolved under a frequent-fire regime that created diverse mosaics of post-fire conditions and thus have developed life history strategies to accommodate the structural and landscape heterogeneity created by fire. One of the more well-known of these species is the spotted owl (*Strix occidentalis*), an older-forest associated raptor that inhabits dry forests in portions of its geographical range that has been the focus of forest management conflict in the western United States for several decades (Simberloff 1987; Redpath et al. 2013; Gutiérrez et al. 2015). Recently, this conflict has shifted from "owls versus jobs" to "owls versus forest restoration"—a seemingly intractable conflict between efforts to increase resilience of seasonal dry forests and the conservation of spotted owl habitat (Peery et al. 2019; Stephens et al. 2019). A key feature of the current conflict involves the potential effects of large, severe wildfires on spotted owls. If such fires render forests unusable by spotted owls and thereby adversely affect owl populations, then fuels reduction activities (e.g., mechanical removal of small and medium trees, prescribed fire, and managed fire) might benefit this species by reducing severe fire impacts, if fuels reduction activities have minimal negative effects to owls (Peery et al. 2017). However, there is considerable disagreement in the literature regarding these tradeoffs and this has led to uncertainty about how to manage forests (Ganey et al. 2017; Lee 2018).

Uncertainties about how spotted owls respond to severe fire may resolved, in part, by (*i*) distinguishing between the mean, population-level response and variation in responses by individual owls that experience a range of post-fire conditions, and (*ii*) explicitly incorporating the role of the spatial configuration of severe fire (e.g., patch size and shape), which has not been the focus of previous studies (Ganey et al. 2017). Resource selection functions (RSFs) offer an analytical method for characterizing selection or avoidance of resources (hereafter 'habitat'; i.e., cover types) that are available to individuals or populations

(Manly et al. 2002). It is often assumed when using RSFs that individuals will select (or avoid) habitats in the same way (i.e., habitat selection is a constant function of habitat availability; Mysterud and Ims 1998). However, the strength of habitat selection or avoidance can vary strongly in both direction and magnitude among individuals within a population, so accounting for individual variation in selection patterns is important for statistically rigorous testing of population-level selection (Duchesne et al. 2010). Individual-specific habitat selection may vary as a function of habitat availability, a phenomenon known as a "functional response" in habitat selection (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Matthiopoulos et al. 2011; Aarts et al. 2013). Testing for functional responses may give insights into how individuals respond across a gradient of habitat conditions—including novel landscape conditions and configurations—and allow explicit testing of hypotheses about the effects of increasing novelty caused by either climate change or human impacts on habitat selection.

We used mixed-effects RSFs to examine both individual- and population-level habitat selection (Muff et al. 2020) in GPS-tagged California spotted owls (*S. o. occidentalis*) occupying home ranges containing a wide range of high-severity fire effects following a recent California megafire (2014 King Fire; Jones et al. 2016). We examined the potential effects of fire characteristics (fire severity, pyrodiversity, and severe fire patch size and configuration) on owls while controlling for potential confounding factors (pre-fire forest cover), post-fire salvage logging, and the central-place foraging behavior exhibited by spotted owls (Carey and Peeler 1995; Rosenberg and McKelvey 1999). Because spotted owls have presumably adapted to frequent-fire regimes dominated by lower-severity effects (Ganey et al. 2017; Rockweit et al. 2017), we predicted that individual owls would avoid severely burned forests when these areas comprised a large portion of the home range or occurred in large patches. We also predicted that spotted owls would select burned areas with greater pyrodiversity, which would be expected to create structural and landscape heterogeneity preferred by owls (Gutiérrez et al. 1995; Franklin et al. 2000). In addition, we tested for the potential effects of salvage logging in burned forests on habitat use because previous studies have found that spotted owls tend to avoid foraging in logged, post-fire landscapes (Comfort et al. 2016). We tested whether spotted owls exhibited functional responses to novel habitat conditions by assessing support for interaction terms within the RSF.

Methods

Study area

The study was conducted in the central Sierra Nevada, California, USA, as part of a longer-term spotted owl demographic study on the Eldorado and Tahoe national forests (Tempel et al. 2016; Jones et al. 2018). The study area was ~ 50,000-ha in size and consisted of mixed-use publicly-owned lands (~ 54%) managed by the U.S. Forest Service and privately-owned lands (~ 46%) managed primarily for timber resources. Elevations ranged from 590 to 2200 m, the climate was Mediterranean with warm, dry summers and cool, wet winters, and the dominant vegetation type was Sierran mixed-conifer montane forest. The elevational range, climate, and species composition of these forests historically resulted in frequent fires (mean return interval = 11 years; range = 5–50 years) of generally lower severity (5–15% area burned at high-severity), with some inclusion of smaller (< 10–100 ha) patches of high-severity fire (Stephens and Collins 2004; Safford and Stevens 2017).

In September and October 2014, the King Fire burned ~ 40,000 ha of primarily forested land in the central Sierra Nevada (Jones et al. 2016). Approximately half (~ 20,000 ha) of the King Fire burned at high-severity (> 75% canopy mortality), including very large contiguous patches, making the King Fire one of the largest and most uniformly severe fires in recent California history (Stevens et al. 2017). Areas along the fire boundary and in the southern portion of the King Fire experienced greater "mixed-severity" fire effects, characterized by a mosaic of low, moderate, and high-severity fire. Post-fire salvage logging occurred in portions of the burned area (Fig. 1) and the majority of salvage-logged areas (89%) occurred on private lands.

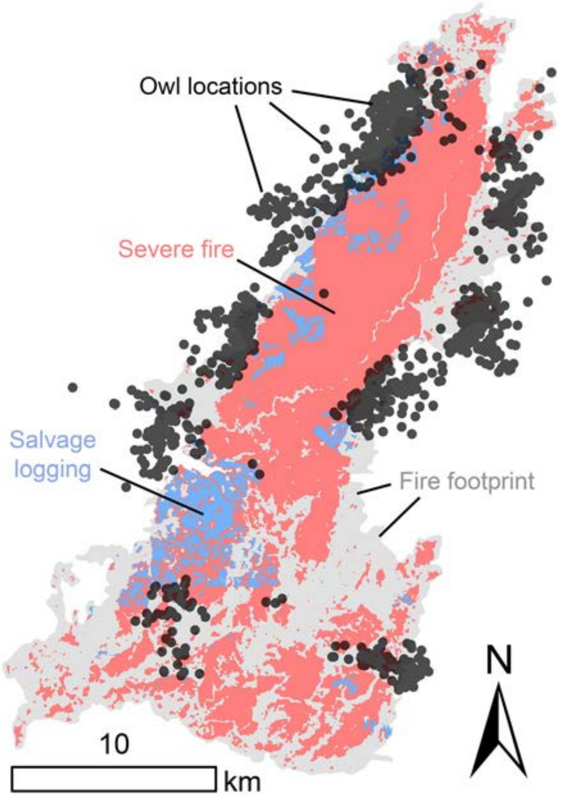

Fig. 1 King fire study area, showing the extent of the fire, severe fire, salvage logging, and locations used by owls

Global positioning system (GPS) data

In 2015–2017, we captured adult spotted owls occupying forests within and near the King Fire perimeter (Fig. 1) and fitted them with 7–10 g backpack-mounted dual GPS/VHF units (hereafter "GPS tags") (Biotrack Ltd., Wareham, UK). We exhaustively searched the study area to locate owls during daytime and nocturnal walk-in surveys, and once located we captured owls using snare poles, hand-grabs, or bal-chatri traps. All relevant state and federal permits were obtained prior to capture and handling. In 2015, 2016, and 2017, we deployed 12, 10, and 4 GPS tags, respectively (total $n = 26$). There were no owls available for GPS tagging within the large, severely burned patch in the center of the study area (Fig. 1) because owl territories in that patch went extinct immediately after the fire (Jones et al. 2016) and were not re-colonized during the course of the study (G.M. Jones, unpublished data). Three individual spotted owls with GPS tags dispersed before data could be retrieved (two in 2015, one in 2016), so our final sample size was 23. Of the 23 owls sampled, three individuals were sampled in consecutive years, which we accounted for by specifying a random effect for individual owl. GPS tags were deployed each year in May and early June and recorded 100–150 locations during nocturnal hours (1–3 per night; mean = 1.33/night/owl), and were retrieved in July and August. When multiple locations were recorded in a single night, they were pre-programmed to be separated by at least two hours to reduce spatial autocorrelation. GPS tags had a median location error of approximately ± 20-m when data were filtered to include only those points recorded with ≥ 5 satellites and a dilution of precision (DOP) ≤ 3 (HA Kramer, *unpublished data*), so we used only these data in analyses.

Habitat selection analysis

We analyzed our data using mixed-effects RSFs (logistic regression) with intercepts and slopes that varied by individual (Duchesne et al. 2010; Muff et al. 2020). Including coefficients that vary by individual enables explicit modeling of functional responses (Mysterud and Ims 1998) and reduces biases in estimated population-level (fixed) effects (Duchesne et al. 2010; Harrison et al. 2018). Available points were assigned weight $W = 1000$ to facilitate approximate convergence to the inhomogeneous Poisson process likelihood, and we fixed the variance term for individual-specific intercepts to a large value ($\sigma^2 = 1000$) to avoid shrinkage toward zero (Muff et al. 2020). Available area for each individual owl was defined as a circle with radius equal to the furthest Euclidean GPS distance from the activity center (minimum radius = 1654.8 m; maximum = 5165.5 m; mean = 3437.6 m), where the activity center was the geometric mean of annual daytime nest and roost locations obtained from walk-in surveys. We generated 10 times as many available points as used points for each owl (Hooten et al. 2017). Available points were distributed uniformly with respect to distance to the activity center (i.e., all distances had equivalent point densities).

There were three types of inferences we were interested in drawing from mixed-effects RSF models. First, we were interested in understanding how spotted owl habitat selection was explained by a suite of environmental predictor variables including pre-fire forest conditions, fire conditions including whether or not areas burned at high-severity and the diversity of fire effects (pyrodiversity), and post-fire management (salvage logging). Second, we were interested in whether spotted owl use (or non-use) of areas that burned at high-severity could be explained by spatial characteristics of those areas, such as severe fire patch size and configuration. Finally, we wanted to examine whether there was evidence for functional responses in habitat selection. With respect to severe fire effects, these inferences can be viewed as a set of three sequential or hierarchical questions: do owls select or avoid severely burned areas; is that selection (or avoidance) mediated by spatial characteristics of severely burned areas; are these patterns driven by variation in the availability of severe fire within individual home ranges? We therefore examined these questions in three stages, constructing models in each stage that allowed us to test the underlying hypothesis related to each question in sequence.

In the first stage, we fitted a single model containing covariate effects for distance to activity center, pre-fire forest cover (sparse/open forest and young forest), and disturbance-related covariates (severe fire, pyrodiversity, and post-fire salvage logging) (Table 1). Each covariate effect was specified as having a fixed component (population-level coefficient that was constant across individuals) and a random component (coefficient varying by individual) following Muff et al. (2020). The model intercept varied by individual owl. We expected distance to activity center and pre-fire forest cover covariates to be important in explaining space use patterns in spotted owls, but they were not the central focus of this analysis; we included them to control for their potential effects. Distance to activity center was the Euclidean distance (m) between a given GPS location and the individual's geographic activity center. Including distance to activity center as a model covariate in RSFs of central place foragers reduces the potential for a positive bias of selection for habitat types near the central place as well as a negative bias for habitat types more distant from the central place (Rosenberg and McKelvey 1999). Preliminary analyses supported the use of a quadratic (distance + distance^2) form, which we used in all subsequent models. Pre-fire sparse/open forest cover was defined as 30 × 30-m pixels with $< 40\%$ canopy cover in the year prior to the King Fire (2014)

Table 1 Model covariates for habitat selection function (RSF) analysis including the variable description, group, type and range of values

Variable	Description	Group	Type	Range of used values
Distance to activity center	The Euclidean distance between a point and the annual activity center	–	Continuous	0–5165 m
Pre-fire sparse/open forest	Areas with $< 40\%$ canopy cover prior to the King Fire	Pre-fire	Categorical	0 or 1
Pre-fire young forest	Areas with $> 40\%$ canopy cover but smaller (< 25 cm QMD) average tree size	Pre-fire	Categorical	0 or 1
Severe fire	Areas that experienced $> 75\%$ canopy mortality following the King Fire and were *not* salvage-logged	Disturbance	Categorical	0 or 1
Pyrodiversity	Shannon Diversity Index of burn severity classes	Disturbance	Continuous	0–1.38 unitless
Salvage logging	Areas that experienced post-fire management that removed standing and downed trees	Disturbance	Categorical	0 or 1
Patch size	The area of a contiguous grouping of severely burned forest	Patch-based	Continuous	0–88.2 km^2
Patch complexity	The perimeter-to-area ratio of a severe fire patch	Patch-based	Continuous	0–0.066 m/m^2
Permeation distance	The distance traveled into a severely burned patch	Patch-based	Continuous	0–356.3 m

All continuous variables were scaled to a range of 0–1 for model fitting as determined using the VEGCLASS variable classes 1 and 2 in the Gradient Nearest Neighbor (GNN) forest structure dataset for our study area (LEMMA Lab, Oregon State University, Corvallis, OR; lemma.forestry.oregonstate.edu) (Ohmann and Gregory 2002). Pre-fire young forest was also calculated using the VEGCLASS category of the GNN dataset (classes 3, 5, and 8), defined as 30 × 30-m pixels with $> 40\%$ canopy cover but with smaller trees (quadratic mean diameter < 25 cm). Including pre-fire sparse/open/young forest vegetation covariates controlled for potential bias toward avoidance of these forest types, independent of the post-fire vegetation patterns created by the King Fire. We assigned the pre-fire sparse/open or young forest class to used/available points when these cover types were the majority class within a 100-m buffer around a given point location.

Disturbance covariates were severe fire, pyrodiversity, and post-fire salvage logging (Table 1). We defined severe fire as areas that experienced $> 75\%$ overstory mortality resulting from the King Fire. We used the 75% overstory mortality threshold to define high-severity because it increases our capacity to compare our results to previous studies (Bond et al. 2009, 2016; Eyes et al. 2017), while acknowledging that more notable ecological effects may correspond with a higher (e.g. 90%) threshold (Miller and Quayle 2015; Jones 2019). We treated this covariate as a categorical effect, such that $x_{ij} = 1$ if the GPS location for individual $i = 1, \ldots, I$ at location $j = 1, \ldots, J_i$ occurred in severely burned forest and $x_{ij} = 0$ otherwise. If a point fell within a severely burned area that was also salvage-logged (see below), we set the categorical effect for severe fire to $x_{ij} = 0$ and the effect for salvage logging to $x_{ij} = 1$. Thus, within our model the 'severe fire' effect can be interpreted as the selection coefficient for 'unlogged snag forest'. We obtained burn severity data from the Monitoring Trends in Burn Severity (MTBS) project (www.mtbs.gov). We did not investigate potential selection patterns related to forests that burned at low- and moderate-severity because (i) we wanted to limit the number of candidate variables to reflect key hypotheses of interest and (ii) previous work has shown that either they do not affect spotted owls or owls generally use these types of burned forest in proportion to their availability during nocturnal hours (Bond et al. 2009, 2016; Jones et al. 2016; Eyes et al. 2017). Thus, low and moderate burn severities, as well as unburned forests, were effectively grouped together in the reference class of our models. However, we did more explicitly consider low and moderate fire severity in the context of pyrodiversity, which was defined as the Shannon Diversity Index of unburned or unchanged (under 5% site area burned), low severity (up to 25% overstory mortality), moderate severity (25–75% overstory mortality), and high-severity (over 75% overstory mortality) classes within a 100-m buffer of point locations. Based on Google Earth aerial imagery, we determined that the majority of salvage operations that occurred within owl home ranges were completed in late 2014 and early 2015 prior to the initiation of this study (2015), so we hand-digitized areas that had been post-fire salvage logged from the National Agriculture Imagery Program (NAIP) aerial imagery from July 2016. We delineated polygons containing visible heavy disturbance (including areas where logging roads had been created, presumably in preparation for salvage logging) in areas that burned in the King Fire, and that had forest present before the fire. While our delineation of salvage logging was limited to areas visibly discernable on NAIP imagery, territory-scale estimates of salvage were highly correlated (r = 0.88) with estimates obtained from timber companies conducting salvage operations within our study area (HA Kramer, unpublished data). We erased pre-fire sparse/open forest (GNN) and areas classified as unburned or outside the fire perimeter so that the salvage layer only included areas that were forested pre-fire and disturbed by dense road networks or logging post-fire. Approximately 80% of salvage logging occurred in areas that experienced high-severity fire.

In the second stage, we explored whether severe fire patch characteristics affected spotted owl habitat selection: patch size, patch complexity, and permeation distance (distance an owl traveled into a severely burned patch) (Table 1). We did so adding covariate effects for each of the above variables to the stage one model, and likewise allowed coefficients to vary by individual owl. Stage two variables were moderately- to highly-collinear with each other and therefore were not included in the same model; thus stage two consisted of three separate RSF models. Patch size was the total area (m^2) of a severe fire patch delineated with the four-neighbor rule (Turner et al. 2001). Patch complexity was calculated as the perimeter-to-area ratio of a severe fire patch. Permeation distance was the minimum Euclidean distance (m) from a used or available point occurring within a severe fire patch to the patch edge (all points outside of severe fire patches were assigned $x = 0$). We transformed stage two variables using the natural logarithm (ln).

In the third stage, we tested for evidence of functional responses by including an interaction term between habitat availability at the level of the individual owl (the mean covariate value in an individual's home range for available points) and the corresponding habitat covariate (sensu Matthiopoulos et al. 2011; Aarts et al. 2013). For example, to test for a functional response related to high-severity fire, we included: (i) a covariate for whether a used/available point occurred in severely burned forest (0/1; Table 1), (ii) a covariate that represented the proportion of an owl's home range that burned severely (i.e., this covariate had a constant value for each individual), and (iii) an interaction between these two covariates. If the interaction term (slope) was statistically different from zero, we interpreted this as evidence in support of a functional response in habitat selection. We transformed habitat availability using the natural logarithm because functional responses are assumed to be nonlinear (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Beyer et al. 2010). We conducted tests for functional responses among disturbance and patch-level covariates when individual coefficients (i.e. random slope variance) improved model fit according to likelihood ratio tests (see below) from stages one and two to minimize the potential for spurious inferences. We note that while using the mean habitat value within an individual's home range is commonplace in the literature when computing functional response (Gillies et al. 2006; Hebblewhite and Merrill 2008; Aarts et al. 2013), the underlying assumption is that the average value sufficiently describes availability. Such an assumption could mask differences among individuals if the average availability does not reflect the encounter rate of different habitats across the landscape (Beyer et al. 2010).

We made inferences about the statistical importance of fixed effects from their direction (positive/negative), effect size (magnitude), and uncertainty (95% confidence intervals), but avoided interpreting the "significance" of estimates using arbitrary p-value thresholds when possible (Amrhein et al. 2019). We determined whether the variance terms for the random slopes improved model fit (test of H_0: $\sigma^2 = 0$) by performing likelihood ratio tests (LRT) using restricted maximum likelihood (REML) estimation, correcting for the 'testing on the boundary' problem using $p = 0.5 \times (\chi_1^2 + \chi_2^2)$ (Zuur et al. 2009). All mixed-effects models were fitted using REML (Zuur et al. 2009). We rescaled all continuous covariates to range from 0 to 1. We used the R packages glmmTMB v. 0.2.3 to fit models. All analyses were conducted in program R version 3.6.0.

Results

Variables describing the central place foraging behavior of owls, pre-fire forest cover, and disturbance effects were all associated with spotted owl habitat selection. Population-level (fixed) effects from the stage one model indicated overall selection for areas closer to the activity center ($\beta_{distance} = 1.6$, 95% confidence interval [-0.19, 3.43]; $\beta_{distance^2} = -8.25$ [-11.44, -5.06]). The model also indicated avoidance of pre-fire sparse/open forest ($\beta_{sparse/open} = -1.00$ [-1.41, -0.59]), young forest ($\beta_{young} = -0.32$ [-0.63, -0.001]), and salvage-logged areas ($\beta_{salvage} = -1.07$ [-1.88, -0.26]) (Fig. 2a). The estimated coefficient for pyrodiversity was in the hypothesized direction (positive) but slightly overlapped zero ($\beta_{pyrodiversity} = 0.49$ [-0.12, 1.09]) (Fig. 2a). Similarly, the coefficient for the effect of severe fire (binary effect disregarding patch characteristics) was in the hypothesized direction (negative) but with confidence intervals that overlapped zero ($\beta_{severe} = -0.35$ [-1.07, 0.37]) (Fig. 2a). While estimated coefficients for pyrodiversity and severe fire overlapped zero when considered at the population-level (i.e., effect fixed across individuals), individual-specific coefficients showed a high degree of variability (Fig. 2b) that improved model fit (likelihood ratio tests; $p < 0.001$). Thus, while the mean effect of pyrodiversity at the population level was 0.49, the deviation from that effect varied significantly across individuals with an estimated variance of $\sigma^2 = 1.92$ (individual coefficients ranged from -1.2 to 2.9) (Fig. 2b). Likewise, while the mean effect of severe fire at the population-level was -0.35, individual-specific deviations from that effect were considerable ($\sigma^2 = 2.49$; individual coefficients ranged from -3.4 to 2.8) (Fig. 2b).

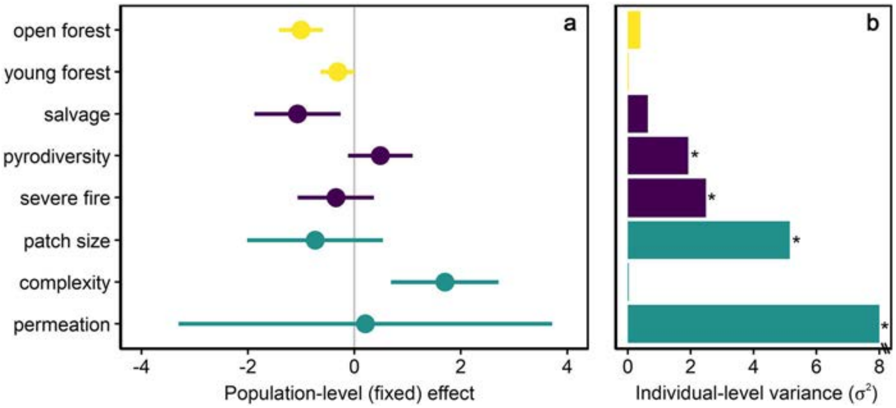

Fig. 2 Coefficient estimates from mixed-effects habitat selection functions. **a** Mean fixed-effects coefficients and their associated 95% confidence intervals. **b** The variance estimates for the individual slope coefficients (random effects), with effects that improved model fit (using likelihood ratio tests) indicated with an asterisk (*). the x-axis of b is truncated to a smaller range (0–8) for visualization, but note that the variance term for permeation distance was 58.9. Colors correspond with different covariate groups (see Table 1); yellow = pre-fire forest cover, dark blue = disturbance variables, turquoise = severe fire patch variables. (Color figure online)

Selection/avoidance of severely-burned areas by spotted owls appeared to be mediated by spatial characteristics of severe fire patches (stage two). Population-level (fixed) effects for patch size was negative ($\beta_{\text{patchSize}} = -0.74$ [-2.01, 0.54]) indicating spotted owls selected smaller patches of severely-burned forest, but the 95% confidence interval overlapped zero (Fig. 2a). Spotted owls selected severe fire patches with greater spatial complexity (higher perimeter-area ratio; $\beta_{\text{complexity}} = 1.70$ [0.69, 2.71]) (Fig. 2a). The population-level effect of permeation distance was slightly positive ($\beta_{\text{permeation}} = 0.21$ [-3.30, 3.72]) but confidence intervals widely overlapped zero (Fig. 2a). While their population-level coefficient estimates overlapped zero, both patch size and permeation distance showed significant variation among individuals; individual-specific coefficients improved model fit (likelihood ratio tests; $p < 0.001$). While the mean effect of severe fire patch size at the population level was -0.74, the deviation from that effect varied significantly across individuals with an estimated variance of $\sigma^2 = 5.15$ (individual coefficients ranged from -4.22 to 5.4) (Fig. 2b). Likewise, while the mean effect of permeation distance (distance traveled into severe fire patch) at the population-level was 0.21, individual-specific deviations from that effect were considerable ($\sigma^2 = 8.0$; individual coefficients ranged from -5.3 to 28) (Fig. 2b).

The large variation in habitat selection coefficients among individual owls for severe fire (stage one), severe fire patch size (stage two), and permeation distance (stage two) was partially explained by differences in individual-level habitat availability, indicating an apparent functional response (FR). Habitat × availability interaction coefficients and 95% confidence intervals for these three variables did not overlap zero in stage three models testing for functional responses. Moreover, functional response curves identified thresholds in habitat availability at which point predicted individual coefficients changed sign from positive to negative (the point at which the fitted curve crosses zero; Fig. 3a–c). Individual spotted owls tended to select severely burned forest only when it represented a small proportion of their home range (< 0.05), but avoided severely burned forest when it was more prevalent ($\beta_{\text{severe-FR}} = -0.76$ [-1.33, -0.19]) (Fig. 3a). Individual owls tended to select larger patches of severe fire when the area-weighted average patch size in their home range was smaller than ~ 115 ha, but selected smaller patches of severe fire when their home ranges were characterized by larger patches ($\beta_{\text{patch-FR}} = -9.39$ [-13.78, -5.00]) (Fig. 3b). Owls also avoided making deep forays into severe fire patches when the average permeation distance in their home range exceeded 47 m, corresponding with larger patches on average ($\beta_{\text{permeation-FR}} = -28.17$ [-43.67, -12.68]) (Fig. 3c). Figure 4 provides examples of spotted owls

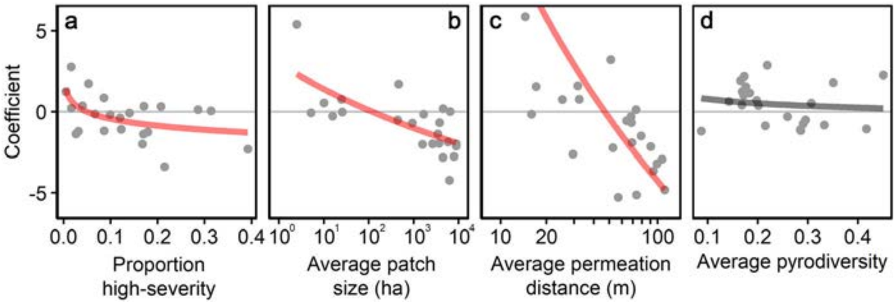

Fig. 3 Functional responses in habitat selection. **a** Severe fire, **b** patch size, **c** permeation distance, **d** pyrodiversity. The y-axes represent slope coefficient estimates for individual owls, and the x-axis represents average covariate conditions within an individual owl's home range (**b**, **c** represent area-weighted means for patch-based covariates). Functional responses with 95% confidence intervals that did not overlap zero are depicted in red (**a**–**c**). Note that the y-axis is truncated in panel **c** for better visualization; there is one additional data point located at x = 11.1, y = 27.98. (Color figure online)

selecting smaller patches of severe fire (Fig. 4a, b), avoiding larger patches of severe fire (Fig. 4b, c), and using a large severe fire patch (unlogged snag forest) but only making short forays into it (Fig. 4c). There was no evidence for a functional response in habitat selection for pyrodiversity ($\beta_{\text{permeation-FR}} = -0.48$ [-2.15, 1.20]) (Fig. 3d).

Discussion

There is a natural hierarchical response by species that can be estimated following disturbance: a primary response and a secondary response. The *primary response* is whether an individual either survives or is able to remain (i.e., occupy) in the affected area following a disturbance event. The *secondary response* is conditional on the primary response (i.e., continued occupancy) and may represent shifts in movement, foraging, or reproductive behavior by persisting individuals that are induced by the disturbance. Key uncertainties exist regarding both primary and secondary responses by spotted owls to fire. With respect to primary responses, the 2014 King Fire displaced a significant portion of the population that experienced extensive severe fire and at least one apparent direct mortality (Jones et al. 2016), but other researchers reported no negative effects in a different population of owls that experienced a large, severe fire (Lee and Bond 2015, but see Berigan et al. 2019). With respect to secondary responses, different studies have revealed that GPS- or VHF-tagged owls avoided (Jones et al. 2016; Eyes et al. 2017), preferentially selected (Bond et al. 2009), or used severely burned forests in proportion to their availability (Bond et al. 2016) when foraging. The analytical approaches used in these studies were similar, raising the question of why owls apparently responded in different ways. We posit one of the reasons may be that these studies have lacked an explicit landscape perspective (i.e., role of spatial patterns of severe fire), which precluded the ability to disentangle different factors that might have led to these conflicting results. While previous work has advanced our understanding of the importance of edges between fire severity classes as a predictor of spotted owl habitat selection (Bond et al. 2009, 2016; Eyes et al. 2017) and the role of these edges across scales (Comfort et al. 2016), they did not explicitly consider the role of severe fire patch size, configuration, permeation distance, or how responses may be conditional on individual variation in habitat availability (i.e., functional response).

Owl response to high-severity fire

Landscape structure and composition following fires appear to affect habitat selection by spotted owls in a more nuanced way than previously reported. Although severe fire was not clearly avoided nor selected at the population level, individuals showed avoidance of severely burned forests (i.e., expected individual coefficients became negative) when $> 5\%$ of their home range burned at high-severity (Fig. 3a). Thus, for those owls not displaced or killed, severe fire appeared to be, on average, benign or beneficial below this threshold, yet appeared to affect owl movements above this threshold. Therefore, spotted owls continued to occupy home ranges in the short term when

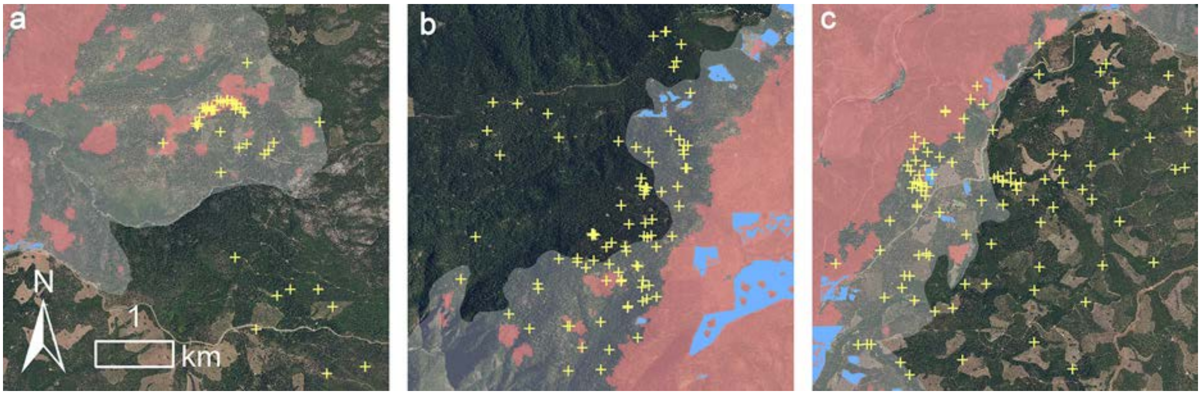

Fig. 4 Examples of owl locations that show selection preferences across different availabilities of severe fire and patch sizes. **a** Selection for a small patch of severe fire; **b**, **c** avoidance of a large patch of severe fire; **c** also shows short (< 100 m) forays into a large severe fire patch. The fire area is shown in semitransparent white, high-severity fire with no salvage logging in red, salvage logging in blue, and owl locations as yellow "+" signs. (Color figure online)

their home ranges were burned by up to 40% severe fire (the maximum extent experienced by GPS-tagged owls in this study), perhaps via behavioral plasticity including the shifting of foraging sites. However, previous work has shown that habitat loss related to severe fire occurring over > 50% of an owl territory led to territory abandonment and mortality (Jones et al. 2016). These thresholds could serve as benchmarks for understanding severe fire effects on spotted owls when detailed site occupancy and tagging information are not available, but we hypothesize that wildfires with different severe fire spatial patterns may result in different responses by owls than we report here. We observed similar functional responses for severe fire patch size and permeation distance; owls avoided using larger patches of severe fire and avoided making deeper forays into severely burned areas when their home ranges were characterized by a larger severe fire component. Had we used a more traditional analysis that did not account for individual variation and spatial configuration, and simply made inference about population-level effects, we would likely have concluded that owls use severely burned forests in proportion to its availability (i.e., the model from stage one). Instead, we gained a more nuanced understanding that patch size and the spatial extent and configuration of severely burned forests within individual spotted owl home ranges strongly mediated the effect of severe fire.

The specific thresholds at which we observed that spotted owls began to avoid severely burned forest appear to align closely with the best available estimates of historical severe fire extent and patch sizes within dry mixed-conifer forests (Safford and Stevens 2017). Specifically, fires that historically burned in yellow pine mixed-conifer forests in the Sierra Nevada contained 5–15% severe fire effects (Safford and Stevens 2017); our study suggested owls tended to avoid severely burned forest when more than 5% of their home range was affected. Moreover, historical severe fire patch sizes in yellow pine mixed-conifer forests in the Sierra Nevada typically ranged from 10 to 100 ha in size (Safford and Stevens 2017); we showed that spotted owls tended to avoid larger severe fire patches when the average patch size in their home range exceeded $\sim$ 115 ha in size. In addition, the spatial complexity of severe fire patches has been decreasing in recent decades (Stevens et al. 2017); we showed that owls select more complex severe fire patches. We suggest these results provide evidence that owls are responding to severe fire in a way that reflects adaptation to historical fire regimes under which this species evolved. Our work suggests that increasingly novel fire conditions within this system—i.e., more severe fire characterized by patches that are larger and less complex—will negatively affect spotted owls.

There are several possible reasons why spotted owls avoided large patches of unlogged, severely burned forest. First, severe fire in the King Fire likely altered spotted owls' prey communities either (i) indirectly by eliminating the understory and coarse woody debris important for key small mammal prey species such as woodrats (*Neotoma* spp.; Roberts 2017) in the short term, or (ii) directly through fire-related mortality. Although some dense brush cover regenerated within many severely burned patches 1–2 years post-fire that could potentially provide prey habitat, owls appeared to avoid large, severely burned patches throughout the three-year study, suggesting prey populations had not yet recovered. Second, perching structures in large tracts of severely burned forest may not provide adequate concealment for this "sit and wait" predator relative to forests with live trees and foliage structure (Gutiérrez et al. 1995; Ganey et al. 2017). Third, and related to the second reason, large fires create extensive open areas that provide habitat for avian predators of spotted owls such as great-horned owls (*Bubo virginianus*; Gutiérrez et al. 1995), which increases predation risk (Johnson 1992). Discriminating among these hypotheses will be challenging and require both small mammal and predator sampling. There is a fourth explanation for why spotted owls avoided large tracts of severely burned forest: severely burned forest contains a limiting resource (e.g., food) that is preferentially selected when it is scarce, but is relatively less important (and its use/availability ratio decreases) when it is abundant (Beyer et al. 2010; Aarts et al. 2013). Given our three above hypothesized mechanisms for avoidance of large severely burned areas we think this is relatively unlikely because rather than containing abundant resources, large severe fire patches appear to contain fewer food resources and more risks to owls.

Owl response to salvage logging

Salvage logging is a management practice that removes fire-killed or fire-affected trees with the primary intention of recouping economic value and reducing safety hazards in multi-use forests (Lindenmayer and Noss 2006). Salvage logging can affect post-fire forest conditions and ecosystem processes by altering post-fire biological communities (Thorn et al. 2018), increasing fire risk by leaving behind fine and coarse woody fuels (Donato et al. 2006), and reducing natural vegetative recovery (Lindenmayer et al. 2008). However, salvage logging is also being used as a tool for improving post-fire reforestation success in dry forest types of the western US (North et al. 2019) that face an increased risk of natural regeneration failure and conversion to non-forest ecosystems following large, high-severity fires (Welch et al. 2016; Shive et al. 2018; Wood and Jones 2019). Thus, there is strong practical interest among land managers to understand ways to reduce negative effects of salvage logging on species and communities of conservation concern, particularly the spotted owl (Peery et al. 2017).

Our results suggest that spotted owls tended to avoid areas that experienced salvage logging. However, interpreting the significant negative statistical effect of salvage was challenged by several considerations. First, 95% confidence intervals for the population-level severe fire effect (i.e., unlogged snag forest) overlapped the 95% confidence intervals for the salvage effect (Fig. 2)—suggesting that salvage and severe fire effects at the population level may have been similar. Second, salvage logging was often embedded within the very large patch of severely burned forest in the northern part of the King Fire that owls strongly avoided (e.g., Figs. 1, 4b, c) such that owls may have been predisposed to avoiding some salvage-logged areas. Third, salvage-logged areas were relatively rare within owl home ranges (average 3.4% of owl home range) compared to severely burned areas (14.5%), and rare cover types are subject to false negative error (Frair et al. 2010).

Nevertheless, our study may provide some important insights into the relative effects of salvage logging and severe fire on spotted owl habitat selection. While the population-level (fixed) effect of salvage logging was negative and numerically more negative than population-level effect of severe fire, the variance among individual-level effects for salvage logging was narrow ($\sigma^2 = 0.64$) and not statistically different from zero, compared to the significant variance among individual-level effects for severe fire ($\sigma^2 = 2.49$). These variances resulted in a narrow range of individual coefficients (ranging from − 1.6 to − 0.2) for salvage logging, compared to a wider range for severe fire individual coefficients (ranging from − 3.4 to 2.8) (Fig. 5). Thus, it appears that individual owls with relatively large high-severity burned areas within their home range tended to avoid these areas more strongly than any owls avoided salvage-logged areas (Fig. 3a). Conversely, owls with smaller areas of high-severity burned areas in their home ranges tended to select severely burned areas but still tended to avoid salvaged areas, notwithstanding the considerations discussed above.

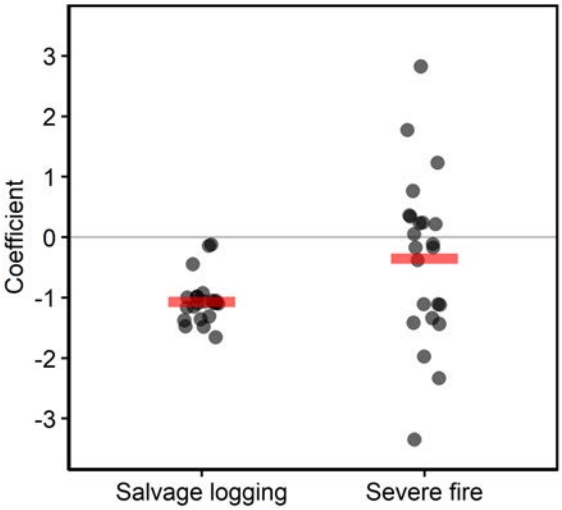

Fig. 5 Comparison of the population-level (red line) and individual-level (black dots) coefficients for salvage logging and severe fire (unlogged snag forest). (Color figure online)

Despite these uncertainties, our findings also have novel implications for post-fire forest management as it relates to species conservation. Specifically, the owls' tendency to avoid large, but not necessarily small patches of severely burned forest and also avoid traversing into interior portions of larger patches (Figs. 3, 4) suggests that salvage logging within interior portions of larger patches may be less likely to affect spotted owls than salvage logging within small patches of severely burned forest. For example, of all spotted owl GPS locations, only 0.6% occurred further than 100 m into a severe fire patch. Stillman et al. (2019) showed that black-backed woodpeckers (*Picoides arcticus*), another focal management species in post-fire landscapes in the Sierra Nevada, tended to use areas of severely burned forest that were closer to patch edges and rarely traveled further than > 500-m into severe fire patches. Thus, salvage operations within the interior of large patches of severely burned patches may be less likely to impact both of these focal species. However, most (89%) of salvage logging within the King Fire perimeter occurred on private lands that often involved higher proportions of harvesting than is typical on national forests (i.e., patches of unlogged snag forest were often left intact within salvage-logged areas on national forests). This limited the inferences we could make about the effects of salvage logging on public lands. Nevertheless, retaining perch sites and snags, and/or creating habitats that promote the preferred prey species of spotted owls in areas that are salvage-logged (e.g., slash piles for woodrats; Innes et al. 2007), might encourage use of these areas by owls in the future.

Implications for dry forest restoration

The tendency of spotted owls to avoid large areas within their home ranges that burned at high-severity has implications for the management of seasonal dry forests within the range of this species. Our findings of avoidance by spotted owls of forests extensively modified by severe fire suggests that the reduction of large, severe fires ("megafires"; Stephens et al. 2014) such as the King Fire by restoring frequent fire regimes characterized by small patches of severe fire is likely to benefit both spotted owl populations and increase forest resilience. This comes with the caveat also supported by our results that salvage logging be judiciously applied particularly in areas where fires burn heterogeneously within occupied spotted owl home ranges, because owls tend to use smaller patches of severely burned forests and forage along edges of larger patches. Our study (i) supports the general premise that species conservation and forest ecosystem restoration objectives in the Sierra Nevada can be compatible (Scheller et al. 2011; Tempel et al. 2015; Jones et al. 2016; Jones 2019) and (ii) could help reconcile a conservation conflict pitting those promoting restoration of seasonal dry forests in parts of western North America against those interested in preserving old-growth trees and habitat for spotted owls (Redpath et al. 2013; Gutiérrez et al. 2017).

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Megafire causes persistent loss of an old-forest species

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Abstract

Climate change and a long legacy of fire suppression are leading to an increased prevalence of 'mega-disturbances' such as drought and wildfire in terrestrial ecosystems. Evidence for the immediate effects of these novel disturbances on wildlife is accumulating, but little information exists on longer term impacts to species and ecosystems. We studied the occurrence dynamics of an iconic old-forest species, the spotted owl (*Strix occidentalis*), on a long-term study area in the Sierra Nevada, CA, USA from 1989 to 2020 to evaluate their multi-scale population response following a 2014 megafire (the 'King' Fire) that affected a portion of our study area. We found that extensive severe fire within spotted owl sites resulted in both immediate site abandonment and prolonged lack of re-colonization by owls six years post-fire. Sites that experienced high pyrodiversity – a mosaic of burn severities – were more likely to persist after the fire, but this effect was only apparent at finer spatial scales. A potentially confounding factor, post-fire salvage logging, did not explain variability in the probability of either owls persisting at sites or sites becoming re-colonized; effects could be attributed only to severe fire extent and pyrodiversity. Our study demonstrates the prolonged effects of severe fire on the occupancy of this forest-dependent species, suggesting that forest restoration that reduces megafires could benefit spotted owls. Our work emphasizes that long-term monitoring can offer surprising learning opportunities and provide unparalleled value for understanding and addressing emerging environmental concerns.

Introduction

Disturbance regimes are changing across global forest ecosystems because of past land use (e.g., fire suppression) and climate change (Seidl et al., 2017). A new era of mega-disturbances catalyzed by a changing climate may lead to large-scale transformation of ecosystems as we know them (Millar & Stephenson, 2015; Westerling et al., 2011). Large-scale droughts and 'megafires' not only threaten the persistence of forest ecosystems, they also threaten the species that inhabit them and the services those ecosystems provide to people (Hurteau et al., 2014; Wood & Jones, 2019). Consequently, in some forest ecosystems, forest managers and policymakers are faced with either the challenges of managing these vital forests for restoration and persistence or allowing their transition to novel non-forest ecosystems (Rissman et al., 2018) with resulting implications for biodiversity and ecosystem services.

Recent extreme global fire years (e.g., 2019–2020) have hastened efforts to quantify potential impacts of megafires on biodiversity. For example, the 2019–2020 Australia bushfires likely resulted in significant (>30%) habitat loss to 70 taxa including 21 already threatened with extinction (Ward et al., 2020). An analysis of the 2019 Amazon fires suggested that most species experienced habitat losses across 20–30% of their range (Mortara et al., 2020). Rapidly changing fire regimes, especially when considered alongside synergies from other pressures (e.g., land-use change, invasive species) threaten the habitat and persistence of at least 4400 taxa globally (Kelly et al., 2020). Forest-dependent taxa, in particular, can experience rapid habitat loss following severe, stand-replacing fires (e.g., bats: Ancillotto et al., 2020; Bosso et al., 2018), but less is understood about longer term dynamics. The emergence of the era of megafires has led scientists and managers to consider what can be done to avoid repeat events of large-scale loss of habitat (Wintle, Legge, & Woinarski, 2020).

Can proactive land management prevent or mitigate large-scale fire events that threaten biodiversity? The answer likely varies across ecosystem types (Halofsky et al., 2018; Krawchuk & Moritz, 2011). In seasonally dry forest ecosystems, notably those in western North America, wildfires are now burning larger, longer and at higher severity than they did historically (Singleton et al., 2018; Steel, Safford, & Viers, 2015; Westerling, 2016). In these forests, large-scale restoration approaches such as prescribed fire, managed wildfire and tree thinning have been proposed to enhance ecosystem resilience to wildfire and drought (Stephens et al., 2020). Abundant empirical observations now demonstrate that these restoration activities alter fire behavior in dry forests by reducing tree densities and fuel loads (Tubbesing et al., 2019), reduce drought-related tree mortality (Bradford & Bell, 2016) and promote structural variability that is expected to increase forest resilience to disturbance (Koontz et al., 2020).

Yet large-scale restoration may also result in short-term negative effects to sensitive wildlife populations by removing or altering key habitat elements (e.g., complex understory and horizontal canopy cover). Recent research has sought to understand trade-offs between these potential short-term negative effects of restoration and longer term benefits of mitigating habitat loss from large, stand-replacing fires (e.g., Scheller et al., 2011; Tempel et al., 2015). Whether short-term negative effects of forest restoration are outweighed by longer term benefits of reducing habitat loss to mega-disturbances hinges on the degree to which restoration alters habitat as well as the magnitude of megafire effects on wildlife. So, for example, if large, severe fires are clearly detrimental to sensitive wildlife populations, then the potential short-term impacts of forest restoration to these species' habitats are likely to be outweighed by longer term benefits – assuming some retention of key elements of the species' habitat can be maintained to support landscape scale occupancy while benefits accrue (e.g., Jones et al. 2018). The potential benefits of restoration further increase if habitat loss from large, severe fires is persistent (i.e., will not regenerate for long time periods).

We studied the empirical short- and longer term effects of a large megafire on a declining population of spotted owls (*Strix occidentalis*) that has been monitored annually since the late 1980s. The King Fire, which burned 97 717 acres of predominately forested land in the central Sierra Nevada, CA, USA in September and October 2014, impacted approximately one half of our study area while leaving the remaining portion unburned (Fig. 1). This event, therefore, allowed the use of a natural Before–After Control-Impact experimental design to examine the effects of this fire on our study population. Whereas we have previously reported the immediate impact of the fire on owls (Jones et al., 2016), here we sought to characterize the population response to the King Fire over a 6-year post-fire period. As a result, this study answers a criticism of such short-term studies that owls and other old-forest species may simply return after a brief displacement by a fire event. In addition, we (i) conducted our population analysis at multiple spatial scales to assess whether and to what extent fire effects are scale-dependent (McGarigal et al., 2016; Wan, Cushman, & Ganey, 2020), (ii) included survey data from additional spotted owl territories in our study area to strengthen inferences about fire effects, (iii) applied a novel data filtering approach of detection/non-detection data to improve biological meaning of effects (Berigan et al., 2019) and (iv) explored the potential role of pyrodiversity (variation in burn severity) in mediating population response to fire (Jones and Tingley, in press).

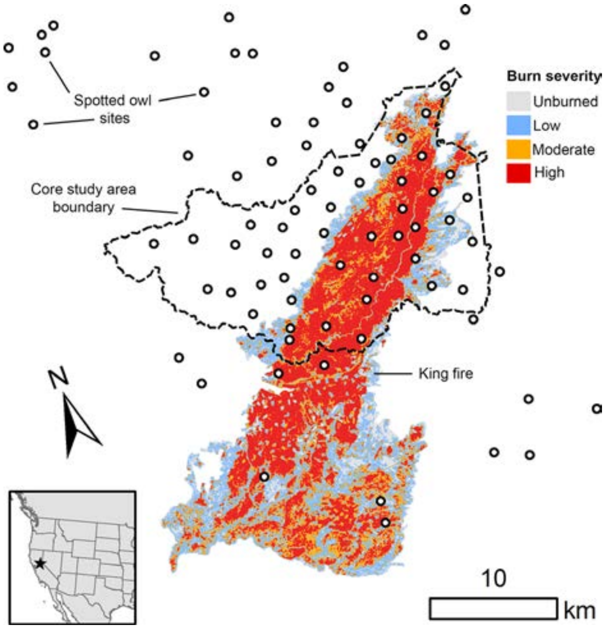

Figure 1 Study area map showing the distribution of spotted owl sites in relation to the 2014 King Fire. The Before–After Control-Impact natural experiment was made possible because a portion of sites was unburned (those outside the King Fire) while other sites experienced a gradient of burn severity. The core study area is outlined with a dashed line; sites outside this boundary were "satellite" territories that were added after initiation of the study (see Methods)

We hypothesized that because spotted owls evolved in a frequent, low-severity fire regime, they are poorly adapted to persist in novel conditions after a large, severe fire (Jones et al., 2020). We developed two predictions that would indicate support for this hypothesis. We predicted that (i) post-fire persistence and colonization rates would decrease in areas with extensive severe fire via loss of larger trees that provide suitable nest sites (e.g., Jones et al., 2016) and (ii) post-fire persistence and colonization would increase in areas with higher pyrodiversity, which may more closely reflect historical post-fire conditions, as well as maintain nest structures and produce diverse prey habitat and hunting cover (e.g., Hobart et al., 2021). We also hypothesized that post-fire owl dynamics were driven by the fire itself, rather than post-fire management. Therefore, we predicted that variation in post-fire persistence and colonization would be associated with high-severity fire and pyrodiversity, rather than post-fire salvage logging.

Materials and methods

Study area and data collection

Our study area encompassed ~800 km^2 of the Eldorado and Tahoe National Forests in the central Sierra Nevada, California, USA. The study area consisted primarily (~63%) of public land managed by the USDA Forest Service, but contained inholdings of private land (~37%). Elevation on the study area ranged between 300 and 2500 m. Summers were hot and dry, and most precipitation fell as rain or snow during the winter and early spring (Franklin et al., 2004). The primary vegetation type was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*) and Douglas-fir (*Pseudotsuga menziesii*). Common understory species were California black oak (*Quercus kelloggii*), tanoak (*Notholithocarpus densiflorus*), canyon live oak (*Q. chrysolepis*) and bigleaf maple (*Acer macrophyllum*). At higher elevations, vegetation transitioned to red fir (*A. magnifica*) and lodgepole pine (*P. contorta*). Barred owls (*S. varia*) were not present on our study area until the last decade but have remained extremely rare once they invaded this area (Keane, 2017). Thus, we remain confident that our inferences about the effects of severe fire on spotted owls were not influenced by the presence of barred owls.

In the midst of a significant multi-year drought (Asner et al., 2015), the King Fire burned across ~39 545 ha (97 717 acres) of predominately forested land in the central Sierra Nevada in September and October of 2014 (Coen, Stavros, & Fites-Kaufman, 2018). Nearly half of the total area burned experienced stand-replacing fire (>75% canopy mortality), making the King Fire one of the most uniformly severe and homogenous megafires in recent California history (Stevens et al., 2017). The King Fire burned ~44% of our core study area and affected 34 of 83 owl sites (at the 1500-m scale; Table 1), most of which have been consistently monitored since the early 1990s (Fig. 1). Of the portion of our study area that burned, most (64%) of that area burned at high severity (Jones et al., 2016). Because the King Fire affected a contiguous portion of our study area and we had over two decades of pre-fire monitoring data (see below), we were afforded an opportunity to study the effects of fire on spotted owls within a natural Before–After Control-Impact (BACI) experimental design framework (Popescu et al., 2012). Since 2014, California has experienced numerous fires that have matched or exceeded the size and severity of the King Fire (e.g., 2020 Creek Fire and 2020 North Complex). Thus, understanding King Fire effects may foreshadow potential effects of more recent megafires on spotted owls.

We conducted spotted owl surveys annually across the study area from 1989 to 2020. We conducted detection/non-detection surveys from April through August each year, which corresponds with the breeding season for spotted owls. Our study area consisted of a core area that was completely surveyed annually, and additional "satellite" survey areas, approximating the size of a spotted owl home range, surrounding the core area that were added over time to increase sample sizes for demographic analyses. Most satellite survey areas were added to annual survey efforts in 1996 and 1997, and thus have been consistently surveyed for close to 25 years. Several additional satellite survey areas were added to annual surveys in 2005 and 2006. Sampling protocols at satellite survey areas were identical to those conducted in the core area and different only in their start year. The original analyses presented in Jones et al. (2016) used owl data only from the core area, but here we expand the analysis to include these satellite survey areas as well (Fig. 1), which includes several additional unburned sites, sites burned by the King Fire and sites burned by other smaller fires earlier in the study period. For the purposes of this analysis, we considered fire effects attributable to the King Fire only, and thus our estimates of fire effects may be conservative because potential variation explained by other fires on the study area was absorbed into other controlling variables in the statistical model (see below). Three smaller fires (2001 Star Fire, 2006 Ralston Fire, 2013 American Fire) occurred on the study area since the year 2000 and resulted in predominately low-severity effects. The 2001 Star Fire likely resulted in reduced post-fire colonization rates at 1–2 territories that experienced moderate amounts of high-severity fire (Tempel et al., 2014). The 2006 Ralston and 2013 American Fires burned ~5 owl territories, but only one territory occurred adjacent to a larger severely burned patch.

We surveyed for spotted owl presence by imitating owl vocalizations at designated survey stations or while walking along routes through historical owl territories or between survey stations (Franklin et al., 1996). When owls were detected through a response vocalization, we determined the sex of the owl by the call pitch, because females have a higher pitched call than males (Forsman, Meslow, & Wight, 1984). Owl surveys were primarily conducted at night, and when owls were detected at night, we conducted follow-up crepuscular and daytime surveys to locate roost and nest locations, assess reproductive status and to capture and band unmarked owls (Franklin et al., 1996). Recent work has

Table 1 Summary of model covariates for burned sites as calculated across the four selected spatial scales of analysis: nest site scale (300 m), protected activity center (PAC) scale (700 m), territory scale (1100 m) and home-range scale (1500 m)

	Spatial scale			
Variable	Nest site 300 m	PAC 700 m	Territory 1100 m	Home range 1500 m
Sites affected by King Fire (*n*)	27	29	32	34
Proportion burned at high severity	0.53 (0.44)	0.49 (0.39)	0.41 (0.35)	0.38 (0.33)
Pyrodiversity	0.56 (0.47)	0.71 (0.41)	0.77 (0.39)	0.81 (0.37)
Proportion salvage logged	0.03 (0.10)	0.06 (0.10)	0.07 (0.10)	0.08 (0.10)

Values represent covariate means with standard deviation in parentheses evaluated at *n* burned sites.

shown that including detections from nocturnal surveys when colored leg bands (used to identify individuals) were not able to be observed likely results in an overestimation of territorial occupancy owing to wide-ranging, extraterritorial movements by owls (Berigan et al., 2019). Therefore, in this present analysis, we included in our detection history only detections recorded during daytime and twilight, or otherwise detections of individuals within their 'home' territories as determined by resighting of uniquely colored leg bands.

Statistical analysis

We used a Bayesian formulation of a dynamic occupancy model (MacKenzie et al., 2003; Royle & Kéry, 2007; Siegel et al., 2019) to assess patterns and correlates of site occupancy on our study area. The model contained parameters for initial occupancy ($\psi_{i,1}$), colonization ($\gamma_{i,t}$), persistence ($\phi_{i,t}$, which is the complement of extinction, $\epsilon_{i,t}$) and detection probability ($p_{i,j,t}$). The primary sampling periods (*t*) were breeding seasons (i.e., April–August) and the secondary sampling periods (*j*) were 2-week periods within each breeding season (April 1–15, April 16–30, May 1–15, etc.). Sometimes, multiple surveys within a given site (*i*) were conducted within a secondary sampling period, in which case a "1" was assigned if owls were detected in any survey during that period, and "0" otherwise. We considered sites where at least one owl was detected during diurnal hours in at least 2 survey years to constitute a bona fide owl territory. Previous research reported one-half the average nearest-neighbor distance between territory centers on our study area to be 1128 m, resulting in ~400-ha circular territories, which approximates an area predicted to be defended by owls (Berigan et al., 2019; Jones et al., 2018; Tempel et al., 2014, 2016).

We calculated a suite of covariates to model the potential effects of the King Fire on local colonization and persistence dynamics of spotted owl territories. We used four spatial scales (varying radii extending from a mapped activity center) to approximate ecologically and/or administratively relevant scales for spotted owls: nest site scale (300 m), protected activity center (PAC) scale (700 m), territory scale (1100 m) and home-range scale (1500 m) (Berigan, Gutiérrez, & Tempel, 2012; Peery et al., 2017; Tempel et al., 2014). We took a multi-scale approach to examine whether and to what extent fire effects were scale dependent (Jackson & Fahrig, 2015; McGarigal et al., 2016; Wan, Cushman, & Ganey, 2020). At each scale, we calculated (i) the proportion of the area that experienced stand-replacing fire (>75% canopy mortality), (ii) the variation in burn severity classes, or pyrodiversity and (iii) the proportion of the area that experienced post-fire salvage logging (Table 1). Fire boundary and severity data were obtained from the Monitoring Trends in Burn Severity project (http://www.mtbs.gov). Pyrodiversity was calculated as the Shannon diversity index of five burn categories: unburned (outside fire perimeter), burned but unchanged canopy structure (within fire perimeter), low severity (<25% canopy mortality), moderate severity (25–75% canopy mortality) and high severity (>75% canopy mortality) (Kramer et al., 2021). Salvage logging was inferred from annual post-fire imagery from the National Agricultural Imagery Program (NAIP) and spatial layers were hand-digitized by one of the authors (HAK) and verified by a second author (WJB). Only areas that had forest cover prior to the fire were considered in salvage digitization; we ensured pre-fire clear-cuts and other non-forested areas were not included in our salvage estimation. Hand-digitized layers were combined with layers indicating that post-fire salvage had occurred in the USDA Forest Service's Forest Activity Tracking System (FACTS) database.

We constructed a model to describe territory occupancy dynamics and the King Fire's effects to the spotted owl population. We modeled detection probability *p* as a logit-linear function of the following covariates:

$$\mathrm{log}it(p_{i,t}) = a_0 + a_1 repro_{i,t} + a_t$$

where a_0 was the intercept, $a_1$was the effect of reproductive status on detection probability where $repro_{it}$ took the value of 0 for non-reproductive territories and 1 for territories that produced young observed on the nest, and a_t was a random year effect to control for unmodeled temporal heterogeneity in *p*.

We modeled initial occupancy during the first year of our study (1989) at each territory $\psi_{i,1}$ using the following logit-linear function:

$$\mathrm{log}it(\psi_{i,1}) = b_0 + b_1 kf_i$$

where kf_i was an indicator variable for territories that intersected with the King Fire footprint. The kf_i covariate helped control for background differences in occupancy rates at owl sites that were affected by the King Fire and those that were not. For the subsequent years ($t > 1$), we modeled annual occupancy as a process dependent on the true occupancy status ($z_{i,t}$) and affected by the probability that a vacant territory would become colonized ($\gamma_{i,t}$) or that an occupied territory would persist ($\phi_{i,t}$):

$$\psi_{i,t} = \gamma_{i,t-1}(1 - z_{i,t-1}) + \phi_{i,t-1} z_{i,t-1}$$

where colonization and persistence patterns were altered through the effects of site- and time-varying covariates constructed to detect pre- and post-fire effects on site occupanc

$$\begin{aligned}\mathrm{log}it(\gamma_{i,t-1}) &= c_0 + c_1 kf_i + c_2 after_t + c_3 kf_i after_t + c_4 kf_i after_t pSev_i \\ &+ c_5 kf_i after_t pyro_i + c_6 kf_i after_t pSalvage_{i,t} + c.year_t\end{aligned}$$

and

$$\begin{aligned}\mathrm{log}it(\phi_{i,t-1}) &= d_0 + d_1 kf_i + d_2 after_t + d_3 kf_i after_t + d_4 kf_i after_t pSev_i \\ &+ d_5 kf_i after_t pyro_i + d_6 kf_i after_t pSalvage_{i,t} + d.year_t\end{aligned}$$

where kf_i was an indicator variable for fire-affected territories as described above, $after_t$ was an indicator variable for post-fire survey years, $pSev_i$ was a continuous variable representing the proportion of the territory that was affected by stand-replacing fire, $pyro_i$ was a continuous variable describing pyrodiversity and $pSalvage_{i,t}$ was a time-varying site covariate describing the cumulative proportion of the owl site that had experienced post-fire salvage logging. We modeled salvage logging as a time-varying covariate because most salvage logging within owl sites occurred immediately after the fire (in 2015), but some additional logging occurred in subsequent years. The terms $c.year_t$ and $d.year_t$ were annual, normally distributed random effects that allowed annual unmodeled heterogeneity in colonization and extinction parameters.

We fit the above model at each of the four covariate scales (300, 700, 1100 and 1500 m) to the data using JAGS (Plummer, 2003) in the R statistical programming environment. All coefficients were assigned uninformative Gaussian priors with $\mu = 0$ and $\sigma = 2$ as recommended by Northrup & Gerber (2018). Although on the logit scale this prior appears informative, it is approximately flat when back-transformed to the probability scale (Northrup & Gerber, 2018). We ran three chains of 10 000 iterations, an adaptation phase of 1500 and a thin rate of 10 yielding 3000 posterior samples for each parameter across all chains. We assessed convergence using the Gelman–Rubin statistic (all values <1.1). We made inference about parameters by examining the direction and magnitude of mean effects, the extent to which posterior distributions overlapped zero, computation of odds ratios following Jones & Peery (2019), and by graphical visualization of derived annual rates of occupancy, colonization and persistence.

Results

Following the King Fire, spotted owl sites were less likely to persist when they experienced more stand-replacing fire (>75% canopy mortality) across all spatial scales examined (Fig. 2a). The strongest effect of severe fire on persistence was found at the 1100 m (territory) scale, where the mean odds of persistence decreased by 7.8% for every 10-ha increase in severely burned area (logit coefficient $d_4 = -3.12$, 95% Bayesian credible interval [−5.05, −1.23]). In contrast, the effect of pyrodiversity on spotted owl site persistence was scale-dependent (Fig. 2a). At the nest area (300 m) and PAC (700 m) scales, increased pyrodiversity led to increased persistence probability ($d_5 = 1.30$ [−0.35, 2.94] and $d_5 = 1.19$ [−0.25, 2.73]), respectively (posterior densities were 93 and 94% positive; Table S1 in Appendix). Whereas at the territory (1100 m) and home-range (1500 m) scales, the pyrodiversity effect weakened and the CRIs widely overlapped zero. Salvage logging had no effect on persistence probability; posterior means were near zero and credible intervals widely overlapped zero across all scales (Fig. 2a). Thus, we considered salvage logging to be an uninformative parameter for spotted owl site persistence.

Like site persistence, more extensive severe fire reduced the probability of site colonization at all spatial scales examined (Fig. 2b). The effect of severe fire was strongest at the territory (1100 m) scale, where the mean odds of colonization decreased by 8.3% for every 10-ha increase in severely burned area ($c_4 = -3.28$ [−5.26, −1.52]). Unlike site persistence, pyrodiversity did not appear to influence site colonization probability, regardless of spatial scale (Fig. 2b). Neither pyrodiversity nor salvage logging had any apparent effects on site colonization probability; posterior means were near zero and credible intervals widely overlapped zero (Fig. 2b). Posterior distributions for all model coefficients for persistence and colonization sub-models, as well as detection and initial occupancy, are available in the Table S1 in Appendix.

Derived estimates of annual occupancy showed a gradual decline in occupancy over a 25-year pre-fire period for all owl sites, followed by the largest single-year occupancy decline over the study period (−0.08; declining from 0.54 to 0.46) in the year following the King Fire. However, when sites were grouped by broad classes of exposure to severe fire at the home-range (1500 m) scale (unburned, <50% high-severity, >50% high-severity), a distinctive “hockey stick” post-fire trajectory for the most severely burned sites was apparent (Fig. 3). The probability that sites that experienced >50% severe fire (at the 1500-m scale) remained occupied dropped sharply from 0.62 in the year prior to the fire (2014) to 0.23 following the fire (2015). Then in 2016, the probability of site occupancy for this severely burned group dropped to 0.039 and remained near zero through the remainder of the study period. Sites that burned less severely (<50% high severity) experienced a relatively smaller apparent decline in occupancy probability after the fire (from 0.59 in 2014 to 0.40 in 2015), but then remained between 0.42 and 0.55 over the period 2016–2020 (Fig. 3). The probability of occupancy for unburned sites appeared to remain stable or slightly increase following the King Fire (Fig. 3).

Discussion

We have shown that a large, severe “megafire” of a type that is becoming more frequent in some forest ecosystems can lead to dramatic and persistent local population declines. Following the 2014 King Fire in the central Sierra Nevada, CA, spotted owls at severely burned sites went locally extinct and did not re-colonize them over a 6-year period following the fire (Fig. 3). These findings support our hypothesis that spotted owls are poorly adapted to survive in post-fire landscapes characterized by extensive severe fire. These results also indicate that initial short-term impacts (1-year post-fire) reported by Jones et al. (2016) have persisted and thus do not represent an ephemeral effect. Hence, this megafire event caused a persistent loss of spotted owl nesting habitat, which is a primary factor limiting populations of this species across its range (Ganey et al., 2017). For this reason, we reject the notion that owls experiencing large, severe fires within their territories may simply show an initial abandonment of sites but return shortly thereafter.

Rapidly changing fire regimes could pose an existential threat to spotted owls and other forest-dependent species as ecosystems cross ‘tipping points’ and experience type conversion (van Nes et al., 2016). Altered fire regimes, in combination with other stressors such as climate change and logging, can lead to ecosystem collapse (Lindenmayer, Messier, & Sato, 2016) and has led to long-term declines in tree-cavity-dependent species in Mountain Ash forests in Australia (Lindenmayer & Sato, 2018). Recent fires in

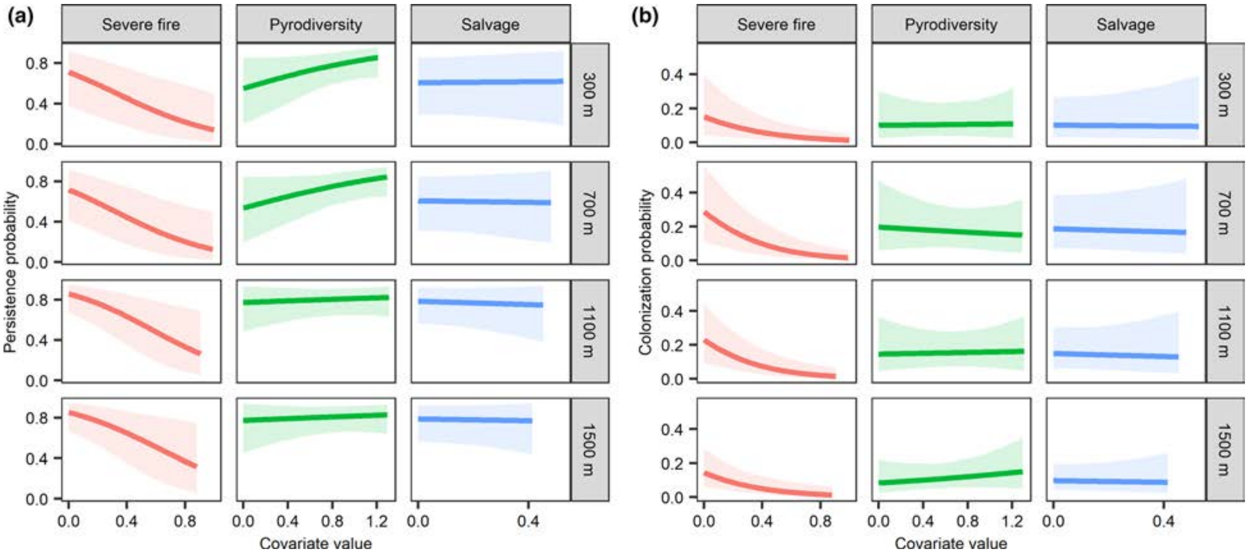

Figure 2 Predicted relationships between covariates (severe fire, pyrodiversity and salvage logging) and dynamic occupancy rates (persistence in panel a; colonization in panel b) across the four scales of analysis (nest area, 300 m; PAC, 700 m; territory, 1100 m and home range, 1500m). The thick colored lines represent the prediction at the posterior mean, while shaded range represents the upper and lower 95% Bayesian credible intervals. Coefficient estimates used to produce figures can be found in the Table S1 in Appendix

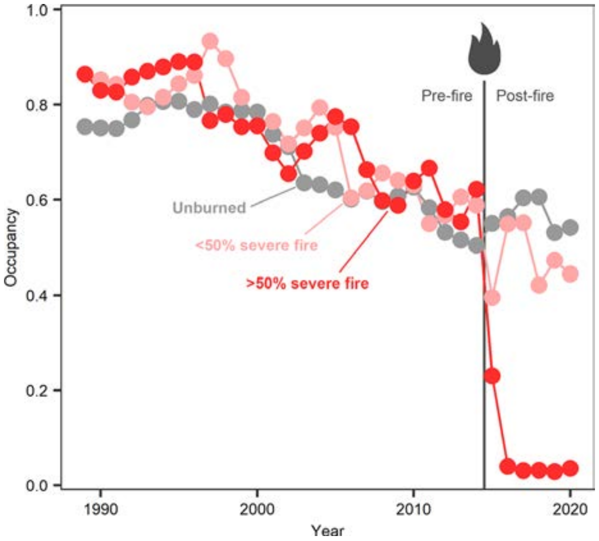

Figure 3 Derived annual occupancy from 1989 to 2020 for spotted owl sites grouped by the percentage of the home-range (1500 m) that experienced severe fire (unburned, <50% severe, >50% severe). The grey vertical line on the x-axis between years 2014 and 2015 indicates the timing of the 2014 King Fire and therefore divides pre- and post-fire occupancy trajectories

California, USA have eclipsed the 2014 King Fire in terms of size and severity (e.g., 2020 Creek fire) and these types of fires could contribute to collapse of dry forest ecosystems through regeneration failure and persistent type conversion (Davis et al., 2019; Stevens et al., 2017). If owl populations are responding similarly to more recent and widespread fire events, landscape-scale population viability over the coming decades could be threatened. Therefore, our results suggest that forest restoration intended to reduce megafires and increase long-term forest resilience are likely to provide co-benefits for this species, forest ecosystems and the people that depend on long-term sustainability of forest ecosystem services (Stephens et al., 2020; Wood & Jones, 2019), so long as keystone structural features of these ecosystems are retained (Jones, 2019; Jones et al., 2018; Tempel et al., 2014).

Many terrestrial vertebrates may respond positively to forest restoration. Mechanical thinning and fire mosaics produced through prescribed and managed fire (i.e., pyrodiversity) can increase structural diversity in homogenized forests, which could result in increased biodiversity (Fontaine & Kennedy, 2012; Steel et al., 2019; Tingley et al., 2016). It has generally been assumed, however, that spotted owls and other sensitive old-forest species will respond negatively to restoration treatments because these species tend to be associated with ‘dense’ and fire-prone forests. Yet for spotted owls, empirical evidence for negative effects of restoration treatments is sparse. Studies that have inferred or are often cited as evidence for negative treatment effects to owls have demonstrated weak effect sizes (Tempel et al., 2014) or did not distinguish between fire and treatment effects (Seamans & Gutiérrez, 2007). Observed owl declines following restoration treatments in another study occurred alongside declines in control groups, such that effects could not be attributed to treatments themselves (Stephens et al., 2014). Still, other studies have found no measurable effects of treatment, or otherwise weak positive (beneficial) effects (Tempel et al., 2016). Indeed, restoration that increases landscape-scale heterogeneity in otherwise fire-suppressed, homogenized forests could directly benefit owls by promoting diverse prey habitat and population stability (Hobart et al., 2019). Moreover, restoration that increases the scale of low-severity fire effects through prescribed fire is likely to recruit preferred owl foraging habitat in the short term (Kramer et al., 2021). Therefore, it is likely that although restoration treatments could in some contexts result in weak negative effects, these effects are substantially exceeded by negative effects of megafires over the long term (Jones, 2019; Tempel et al., 2015).

Observations of ecological phenomena are scale dependent (Levin, 1992; Wiens, 1989), which has led to adoption of multi-scale perspectives in ecological analyses (Jackson & Fahrig, 2015; McGarigal et al., 2016). Scale dependence is also apparent in analyses of the effects of ecological disturbances on biodiversity (Hamer & Hill, 2000; Wan, Cushman, & Ganey, 2020). Using four biologically relevant spatial scales (nest area, activity center, territory and home range), we determined that while some disturbance effects were scale invariant, others were scale dependent. The effect of severe fire on both site colonization and persistence was scale invariant; severe fire had clear negative effects on both parameters across all scales examined, with very little variation in effect size or uncertainty (Fig. 2, also see Table S1 in Appendix). This observation may be related to the patterns of severely burned forest within the King Fire where extremely high spatial contagion (Stevens et al., 2017) rendered homogenous severe fire effects across scales. In contrast, higher pyrodiversity has led to increased persistence at finer spatial scales but not at broader spatial scales. Consequently, pyrodiversity at finer scales may result in greater likelihood of nest stand structure preservation or lead to increased diversity of prey habitat near the nest stand (Hobart et al., 2021). The effect of pyrodiversity may diminish at broader scales because these larger scales are more associated with foraging habitat and foray behaviors (Blakey et al., 2019), the former of which is more flexible for spotted owls than is their choice of roosting and nesting habitats (Atuo et al., 2019; Call, Gutiérrez, & Verner, 1992; Williams et al., 2011). This result suggests a potential benefit to increased use of prescribed and managed fire resulting in diverse post-fire conditions in spotted owl core areas and at the scale of protected activity centers (Kramer et al., 2021). Moreover, this result has broader implications for pyrodiversity research, as little existing work has explored the role of scale in mediating pyrodiversity effects on wildlife and the pyrodiversity–biodiversity hypothesis (Jones and Tingley, in press).

Following large disturbance events such as megafires, windstorms and droughts, land managers will often engage in post-fire management such as salvage logging and reforestation to recover some economic loss and attempt to rebuild resilient forest ecosystems (North et al., 2019). Salvage logging, in particular, is a controversial practice because of its negative effects on certain taxa and ecosystem processes (Lindenmayer et al., 2008; Thorn et al., 2018). In some cases, scientists have debated whether it is the disturbance itself (e.g., fire) or the subsequent management activities (e.g., salvage logging) that has caused estimated effects on sensitive wildlife species such as spotted owls (Hanson, Bond, & Lee, 2018; Jones et al., 2019). It is often the case that fire and salvage effects are confounded and thus cannot easily be separated (Clark, Anthony, & Andrews, 2013; Lee, Bond, & Siegel, 2012). In our study, we were able to separate these two effects and we unequivocally determined that severe fire, and not salvage logging, was correlated with the observed local declines in spotted owl site occupancy. We, thus, reject the hypothesis that salvage logging drove or even contributed to the observed post-fire decline. Given that both severe fire and salvage logging were included as competing covariates, the salvage effects were uninformative across all scales (Fig. 2).

The relative effects of fire and post-fire management on wildlife may, in part, depend on their relative spatial extent. In our study landscape, the spatial extent of severe fire effects not only eclipsed that of salvage logging, but often did so by an order of magnitude (Fig. 4, Table 1). Sites that experienced extensive severe fire (>50%) but very little salvage logging (many close to 0%) remained unoccupied

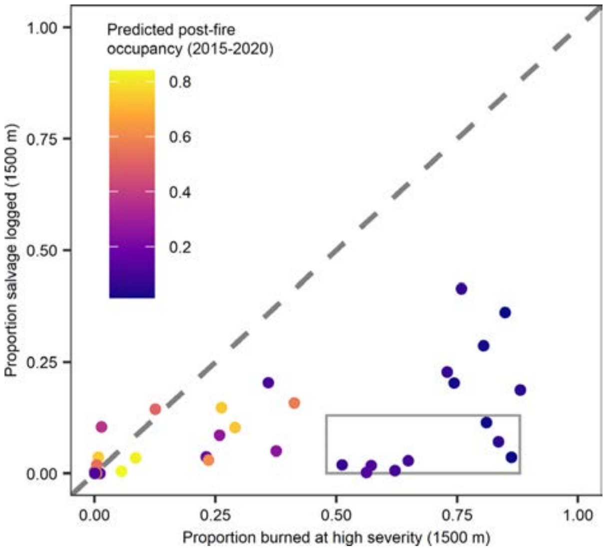

Figure 4 Comparison of the relative extent of salvage logging (y-axis) and severe fire (x-axis) at the home-range (1500 m) scale, where each point represents one spotted owl site. Points are colored by the predicted post-fire (2015–2020) occupancy at each spotted owl site. Points above the grey dashed diagonal 1:1 line indicate sites with a greater extent of salvage logging than high-severity fire; points below the 1:1 line indicate site with more high-severity fire than salvage logging. The grey rectangle in the bottom right surrounds a group of sites that experienced relatively large amounts of severe fire (>50% of home range affected) and relatively little salvage logging (0–12% of home range), highlighting the effect of severe fire on owl occupancy independent of post-fire salvage logging

6 years post-fire, which further indicated that severe fire was more likely of these two forces driving local extirpation and lack of re-colonization (Fig. 4). In some cases, sites that experienced greater salvage logging had higher post-fire occupancy than sites that had experienced less salvage logging, with differences in occupancy instead being clearly linked to variation in severe fire extent and pyrodiversity, not salvage (Fig. 5). Thus, while it is well known that salvage logging can have negative consequences for spotted owls (Lee et al., 2013; Jones et al., 2020) and biodiversity more broadly (Lindenmayer & Noss, 2006; Thorn et al., 2018), the pattern and extent of salvage logging had no measurable effects on spotted owl occupancy dynamics in this study and was transcended by the extreme nature of the King Fire. It is likely that in other cases where post-fire management (such as salvage logging) is more spatially extensive, determining whether fire or post-fire management caused declines would be challenged because the effects would be confounded.

Long-term monitoring programs offer unmatched value for understanding ecosystem change over prolonged time periods (Hughes et al., 2017; Lindenmayer et al., 2012). Our ability to measure a clear and immediate effect of a random event (the King Fire) on spotted owls was only made possible because of the intersection of this fire on a long-term population study, even though the original purpose of owl monitoring was to detect population trends, not to detect the effects of disturbance. Our continuing post-fire monitoring of this population has reinforced initial results (Jones et al., 2016), allowed for further accumulation of evidence (Nichols, Kendall, & Boomer, 2019) and expanded understanding of prolonged effects and mechanisms underlying species response. Thus, we emphasize that long-term monitoring can offer surprising and unparalleled opportunities for learning, which allow monitoring programs to provide unexpected value for addressing emerging environmental concerns (Lindenmayer & Likens, 2009). The before–after control-impact natural experimental design – one of the most powerful designs in ecological field studies (Popescu et al., 2012) – is often only possible in the context of long-term monitoring and unexpected environmental changes. In an era of rapid ecological changes and shifting disturbance regimes in ecosystems, the relative value of long-term monitoring programs may increase through time because they will allow researchers to estimate effects of novel changes in ways

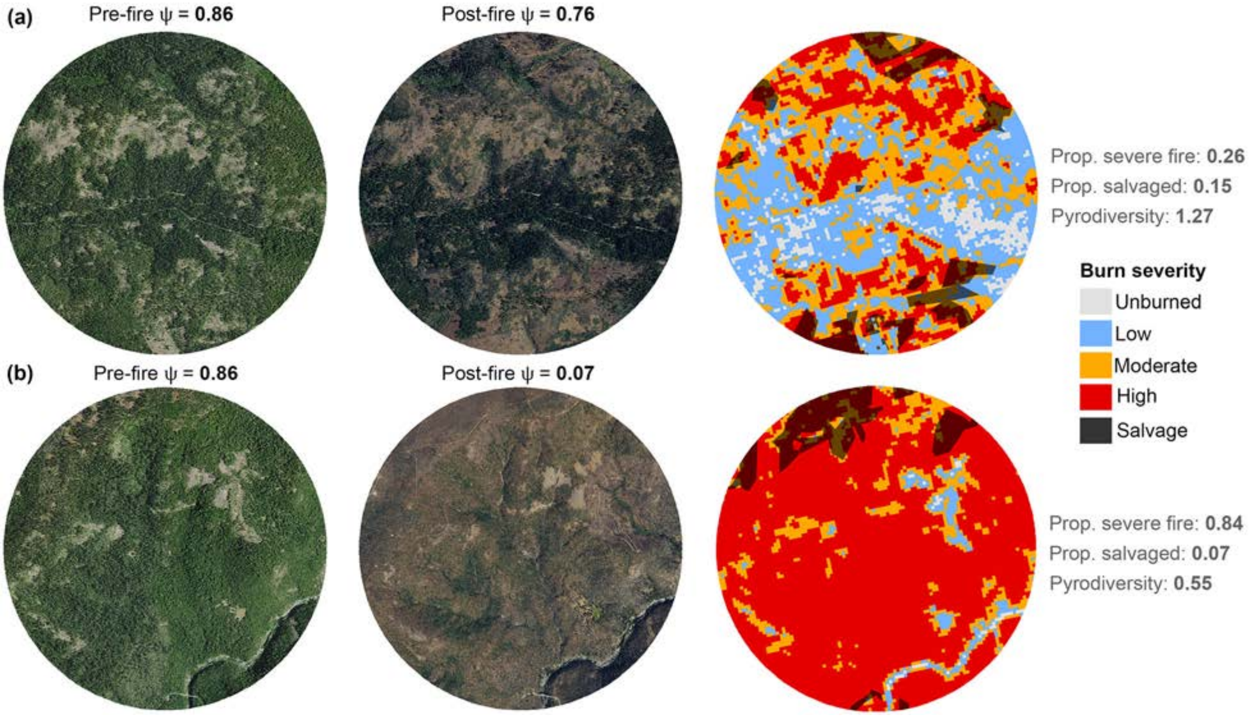

Figure 5 Two selected spotted owl sites (shown at the home-range scale, 1500 m) illustrating the effects of fire severity, pyrodiversity and salvage logging on site occupancy. The owl site in the top row (a; "site A") and bottom row (b; "site B") had the same predicted pre-fire occupancy probability ($\psi = 0.86$). After the fire, predicted occupancy declined slightly for site A (0.10 decline) and dramatically for site B (0.79 decline). These different post-fire trajectories can be attributed to differences in high-severity fire exposure and pyrodiversity. Site A experienced relatively little high-severity fire (proportion of home range affected = 0.26) and relatively high pyrodiversity (index = 1.27). Site B experienced extensive high-severity fire (proportion = 0.84) and low pyrodiversity (index = 0.55). Both sites experienced small amounts of salvage logging, with site A experiencing ~2× as much salvage as site B (15% and 7%, respectively). However, salvage logging was an uninformative parameter, so it had no effect on predicted post-fire occupancy. Aerial photos shown in the left and middle columns represent 2014 (pre-fire) and 2018 (post-fire) NAIP imagery. Pre- and post-fire predicted site occupancy was estimated for a 6-year pre-fire period and 6-year post-fire period, respectively

that more "reactive" research or monitoring may not be able to provide.

Our work offers evidence that the negative effects of novel 'mega-disturbances' in some ecosystems may be permanent, not ephemeral, reinforcing the need to re-think the status quo in forest ecosystem conservation (North et al., 2015; Stephens et al., 2019, 2020; Wintle, Legge, & Woinarski, 2020; Wood & Jones, 2019). In this study, there was no evidence of re-colonization of sites by owls that burned at >50% high severity even 6 years after the fire. This is not surprising, given that in the Sierra Nevada, the regeneration time for old-forest conditions required by spotted owls exceeds 100 years. However, even a 100+ years hypothesized timeline of habitat regeneration relies on the now questionable assumption that forests will have the capacity to regenerate naturally under climate change and increasing frequency of high-severity fire (Davis et al., 2019; Shive et al., 2018; Stevens et al., 2017). Thus, active management to mitigate disturbance effects, increase forest resilience and/or restore disturbed areas may be required to avoid permanent loss of owl habitat in many areas (North et al., 2019). Forest restoration that increases landscape heterogeneity of forest structure and fuels may increase resilience to disturbances (Koontz et al., 2020). Post-fire reforestation strategies could also increase ecosystem resilience and long-term persistence of seasonally dry forests (North et al., 2019) and the ecosystem services they provide to people (Hurteau et al., 2014; Wood & Jones, 2019). The accumulating evidence, including the evidence provided in this paper, suggests that the conservation of spotted owls, and likely other sensitive wildlife species, and dry forest ecosystem restoration are not in conflict. Therefore, we suggest that sensitive species conservation and forest ecosystem restoration can be mutually reinforcing objectives in bioregional-scale forest management.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Full model results for Bayesian dynamic occupancy models at the four spatial scales examined

Fire, forest restoration, and spotted owl conservation in the Sierra Nevada, CA

by

Gavin M. Jones

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Dedication

To my children, Miri and Hugo.

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Dissertation abstract

Fire suppression and climate change have produced disturbance regimes in the Sierra Nevada, California, USA that are increasingly characterized by large, severe fires. Landscape-scale fuel reduction and forest restoration treatments (e.g., thinning and prescribed fire) have the potential to restore more “natural” disturbance regimes to dry forest ecosystems and increase forest ecosystem resilience under climate change. However, treatments that alter forest structure could exacerbate ongoing declines in populations of spotted owls (*Strix occidentalis*) as well as other old-forest species that inhabit dense, fire-suppressed forests. Potential short-term negative effects of treatments might be outweighed by longer-term benefits if treatments are able to mitigate disturbance-induced habitat loss. However, there are key uncertainties concerning the absolute and relative effects of treatment and severe fire on spotted owl populations.

This dissertation seeks to reduce these key uncertainties to facilitate science-based management of dry forest ecosystems and spotted owl populations in the Sierra Nevada. Chapter 1 documents the empirical effect of a large, severe fire (the 2014 King Fire) on a population of spotted owls in the central Sierra Nevada via a natural before-after control-impact experiment. Chapter 2 draws on monitoring data from four long-term spotted owl study areas spanning the latitudinal range of the Sierra Nevada to quantify empirical associations of forest structure (e.g., tree size and canopy cover) on local territory extinction dynamics. The empirical relationships between severe fire, forest structure, and spotted owl occupancy dynamics derived in Chapters 1 and 2 come together in Chapter 3, which projects spotted owl occupancy dynamics as a function of simulated fuel treatment and severe fire occurrence under climate change.

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CHAPTER 3 - BIOREGIONAL-SCALE FOREST RESTORATION LIMITS MEGAFIRES AND SUPPORTS RARE SPECIES CONSERVATION IN A CHANGING CLIMATE 83

Chapter 1 - Megafires: an emerging threat to old-forest species

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Abstract

Increasingly frequent “megafires” in North America’s dry forests have prompted proposals to restore historical fire regimes and ecosystem resilience. Restoration efforts that reduce tree densities (e.g., via logging) could have collateral impacts on declining old-forest species, but whether these risks outweigh the potential effects of large, severe fires remains uncertain. We demonstrate the effects of a 2014 California megafire on an iconic old-forest species, the spotted owl (*Strix occidentalis*). The probability of owl site extirpation was seven times higher after the fire (0.88) than before the fire (0.12) at severely burned sites, contributing to the greatest annual population decline observed during our 23-year study. The fire also rendered large areas of forest unsuitable for owl foraging one year post-fire. Our study suggests that megafires pose a threat to old-forest species, and we conclude that restoring historical fire regimes could benefit both old-forest species and the dry forest ecosystems they inhabit in this era of climate change.

Introduction

The frequency and severity of "megafires" (i.e., large wildfires > 10,000 ha in extent [Stephens *et al.* 2014b]) in the dry forests of North America has increased following a century of fire suppression and climate warming (Westerling et al. 2006, Miller et al. 2009b), incurring considerable societal and economic costs by destroying homes, human infrastructure, timber resources, and elevating taxpayer support for fire-fighting (Stephens et al. 2013, 2014c). In the western United States, major reforms in forest fire management have been proposed to restore low- and moderate-severity fire regimes through forest tree thinning (North et al. 2015b). However, the vision of restoring "pre-European" fire regimes, as well as forest structure and composition, is constrained by concern over fuels-reduction treatments that simplify the structurally and floristically diverse forests inhabited by old-forest species (Pilliod et al. 2006). Potential short-term consequences of fuels-reduction and restoration treatments may be outweighed by long-term benefits of forest restoration if large, high-severity fires negatively impact old-forest species (Sweitzer et al. 2015, Tempel et al. 2015a). However, recent work suggests that severe fires may have neutral or beneficial effects on biodiversity including old-forest species (Hutto 2008, Swanson et al. 2011, DellaSala and Hanson 2015, Lee and Bond 2015), which seemingly exacerbates the perceived divide between forest restoration and species conservation objectives. Nevertheless, the ecological effects of high-severity fire likely depend, in part, on the size, distribution, and configuration of burned patches (Fontaine and Kennedy 2012), and the impacts of large, severe fires remain a source of considerable uncertainty.

Here, we demonstrate the definitive negative short-term impacts of a California megafire on a model old-forest species, the spotted owl (*Strix occidentalis*; Figure 1), by taking advantage of a natural Before-After-Control-Impact experimental design on our long-term (23-year) demographic study area. The human-ignited "King Fire" burned 39,545 ha and was one of the largest and most severe forest fires recorded in California history (Figure 2), with high-severity fire (75-100% canopy mortality) occurring on 19,854 ha (50% of the area burned), with one continuous 13,683 ha high-severity burned patch. The King Fire affected 15,594 ha (44%) of our 35,500 ha study area and overlapped 30 of 45 spotted owl sites we continuously monitored since 1993 (Tempel et al. 2014b). Of the 15,594 ha that burned within our study area, 64% burned at high-severity (Supplementary Table 1). The extreme nature of the fire, more than two decades of pre-fire site occupancy data, and location information on banded and GPS-tagged owls allowed us to draw strong inference regarding the effect of severe fire on a species considered to be a barometer of old-forest wildlife community health (Simberloff 1998). Our results suggest that (*i*) reducing the frequency of large, severe fires could benefit spotted owls and, by extension, other less vagile old-forest species for which we have little information on their response to megafires, and (*ii*) forest restoration and old-forest species conservation objectives may be more compatible than previously believed.

Methods

Study area and spotted owl surveys

We conducted our study on the contiguous 35,500-ha Eldorado Density Study Area (EDSA) on the Eldorado National Forest in the central Sierra Nevada, California. The EDSA has been the site of a long-term mark-recapture demographic study of California spotted owls (Tempel and Gutiérrez 2013), and forms the primary part of a larger study area containing a greater number of owl sites (Tempel et al. 2014a). We only used data from owl sites within the EDSA because some sites outside of the EDSA experienced a complex history of fire and post-fire management that could have confounded the natural BACI design within the EDSA. Moreover, sites outside of the EDSA were added at various times during the study, potentially complicating our evaluation of the effect of the King Fire on long-term spotted owl population trends.

Approximately 60% of the EDSA was public lands managed by the USFS and 40% was private land managed by timber companies. The primary vegetation type on the EDSA was mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Forests on the EDSA have a complex history of management, logging, and fire suppression dating back at least 100 years. Early timber harvesting generally involved the selective removal of large, commercially valuable trees, with a more recent emphasis on clear-cutting on private lands and "diameter-limited thinning from below" on public lands. Prior to fire suppression, the ingrowth of shade-tolerant trees, and the removal of large trees, historic fire regimes consisted mainly of frequent low- to moderate-severity fire occurring in 5-15 year intervals (Stephens and Collins 2004). Elevation on the EDSA ranged from 360 to 2400m, and the climate was characterized by cool, wet winters and warm, dry summers.

We surveyed the entire area each year for territorial spotted owls during the breeding season (1 April to 31 August) without regard to land cover, topography, access, or land ownership, and we used survey data from 1993–2015. Spotted owls (usually mated pairs, but sometimes single birds) occupy and defend sites (i.e. "territories"), the locations of which remain reasonably stable across years. We considered a site to be occupied in a given year when at least one owl was detected. Additional survey details can be found elsewhere (Tempel and Gutiérrez 2013, Tempel et al. 2014b).

Before-After Control-Impact analysis

We evaluated the potential impact of high-severity fire on spotted owls using a Before-After Control-Impact (BACI) design with multi-season site occupancy data (MacKenzie et al. 2003, Popescu et al. 2012). We carried out parallel continuous and categorical BACI analyses, where the proportion of a spotted owl site (a circle with radius equal to one-half the mean nearest-neighbor distance across years = ~1,100m; Tempel *et al.* 2014a) affected by high-severity fire was the impact covariate (i.e., "treatment"). We defined "high-severity" as forests that experienced 75-100% canopy mortality (Lee and Bond 2015), corresponding to a relative differenced Normalized Burn Ratio (RdNBR) threshold of >572 (Miller et al. 2009a). The continuous BACI analysis contained two groups: sites that were unburned (n = 15) and sites that overlapped with the King Fire and thus experienced some degree of burn (n = 30). The categorical BACI analysis contained three groups: sites that were unburned (n = 15), sites that experienced <50% high-severity fire (n = 16), and sites that experienced > 50% high-severity fire (n = 14). For both continuous and categorical BACI analyses, we followed a hierarchical modeling procedure by first modelling within-season detection probability as a function of covariates (Supplementary Table 2). We then modeled the potential effects of high-severity fire on colonization (γ) and extinction (ε) rates separately using AIC to select between competing models (Supplementary Table 3), while allowing the non-focal parameter to vary by year (Tempel et al. 2014a).

Previous attempts to test for the effects of wildfire on spotted owls have been hindered by the potential confounding effect of post-fire salvage logging (Lee et al. 2012, Clark et al. 2013). However, in our study, all surveys used to estimate occupancy metrics were completed prior to the implementation of proposed post-fire salvage logging on public lands (USFS 2015), which comprised a median of 89% of the area that occurred within burned owl sites (versus ~11% on private lands). We also evaluated the potential effects of post-fire salvage logging on private lands in the continuous site occupancy analysis. Specifically, when fire effects were supported, we introduced a covariate representing the proportion of spotted owl sites that experienced salvage logging. The continuous variables, high-severity fire and salvage logging, were not strongly associated at fire-affected sites ($R^2 = 0.10$).

Population trend analysis

We fit a fully time-varying dynamic occupancy model to our 23-year detection/non-detection data to obtain unconstrained annual estimates of occupancy (ψ_t) and rate of change in occupancy (λ_t) for the study area (MacKenzie et al. 2003). Our statistical model directly estimated initial occupancy (ψ_1), annual estimates of extinction (ε_t), and annual estimates of colonization (γ_t), so we used the recursive equation

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

to estimate occupancy (ψ_t) for each year of the study period. Then, using the estimates of ψ_t, we calculated the rate of change in occupancy (λ_t) for each year using the equation:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}$$

This analysis allowed us to consider occupancy and rate of change in occupancy following the King Fire within the context of a long-term decline in our study population (Tempel and Gutiérrez 2013). We fit several linear models to annual estimates of occupancy ψ_t and used AIC to evaluate relative support for different time trends (linear, log-linear, quadratic) and a segmented (i.e., “break-point”) model over the pre-fire years 1993-2014 (Supplementary Table 4). We used the segmented model to evaluate support for an initial decline followed by a period of apparent population stability prior to the King Fire.

Habitat use and selection analysis

We collected post-fire foraging locations from nine spotted owls during the 2015 breeding season using backpacks having a Lotek Pinpoint 100 mini-GPS archival tag and a VHF radio transmitter. GPS tags recorded 1-2 locations at random times between dusk and dawn each night May–August to characterize breeding season nocturnal habitat use. We collected 1085 locations but discarded ~11 locations/owl with suboptimal measures of precision (dilution of precision; DOP ≥ 5). Using burn severity maps produced by the United States Forest Service, we performed a compositional analysis of habitat use (Aebischer et al. 1993) and derived Manly's selection ratios (w_i; Manly *et al.* 2002) for third-order habitat selection to assess selection or avoidance of forests in different burn classes (unburned, low-severity, high-severity).

We defined available habitat area for each owl using a circle with the center equal to the geometric mean of 2015 nest tree, roosts, and daytime capture locations (i.e., "activity center") and a radius equal to the 95th percentile of linear foraging distances from the activity center (similar to Bond *et al.* 2009). We used the 95th (not 100th) percentile so that distant areas rarely visited by owls in foraging bouts (Bond et al. 2009) were not counted as "available" habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies (Supplementary Figure 2). We used a circle instead of a minimum convex polygon (MCP) to define available habitat because MCPs often failed to include the large, high-severity patch as "available" although it was generally within the foraging radius of owls (Supplementary Figure 3). We performed habitat selection analyses using the R package 'adehabitatHS' (Calenge 2006).

Results and Discussion

The BACI analysis indicated that high-severity fire had a strong negative impact on spotted owls. The probability of site extinction (ε) increased from 0.01 to 0.98 as the proportion of high-severity fire at a spotted owl site increased from 0 to 1 (Figure 3a). Moreover, extinction rates at severely burned sites (>50% of site area burned at high severity) increased sevenfold following the King Fire ($\hat{\varepsilon}_{1993\text{-}2014} = 0.12$, 95% confidence interval [CI] = 0.08–0.18; $\hat{\varepsilon}_{2015} = 0.88$, CI = 0.49–0.98), whereas post-fire extinction rates were estimated to be zero at less severely burned and unburned sites (Figure 3b). Sites that burned <50% at high-severity were more likely to be colonized after the fire ($\hat{\gamma}_{<50\%\text{ High-severity}} = 0.30$, 95% CI = 0.07–0.72) than unburned sites and sites that burned >50% at high-severity ($\hat{\gamma}_{\text{Unburned}}$ and $\hat{\gamma}_{>50\%\text{ High-severity}} = 0$; Figure 3c). Colonization of sites after the fire was largely the result of individuals moving to less burned sites after abandoning their original sites that burned at >50% high-severity (Supplementary Figure 4). Predicted occupancy rates ($\hat{\psi}$) at sites that burned >50% at high-severity declined by almost nine-fold from their pre-fire value ($\hat{\psi}_{2014} = 0.72$, 95% CI = 0.62–0.82; $\hat{\psi}_{2015} = 0.08$, 95% CI = 0.00–0.24), based on a model that combined top colonization and extinction covariate structures in the categorical analysis (Figure 3d).

Post-fire salvage logging on private lands constituted a median of only 2% of the area within owl sites based on spatially explicit data obtained from privately-owned natural resource companies managing timberlands on our study area (Sierra Pacific Industries and Mason, Bruce & Girard, Inc.). The extent of high-severity fire was large relative to the extent of salvage logging within owl territories (Supplementary Figure 1), strengthening potential inferences because this ratio reduced the confounding effects of high-severity fire and post-fire salvage logging on spotted owls. In addition, the term for salvage logging appeared as an uninformative parameter in the modeling procedure (Arnold 2010), also suggesting that post-fire salvage logging operations did not confound associations between occupancy metrics and high-severity fire (Supplementary Table 3, Supplementary Figures 1 and 5).

The King Fire exacerbated a longer-term decline in spotted owl occupancy within our study area. The proportion of occupied spotted owl sites declined by 43% over a 22-year period leading up to the 2014 King Fire ($\hat{\psi}_{1993} = 1.0$, SE = 0.0; $\hat{\psi}_{2014} = 0.57$, 95% CI = 0.41–0.73) (Figure 3e). After the King Fire, occupancy dropped from 0.57 to 0.44 ($\hat{\psi}_{2014} = 0.57$, 95% CI = 0.41–0.73; $\hat{\psi}_{2015} = 0.44$, 95% CI = 0.29–0.60) following ~7 years of relatively stable occupancy (Figure 3e). The 22% decline in site occupancy after the fire ($\hat{\lambda}_{2015} = 0.78$, 95% CI = 0.53–1.03) was the greatest single-year decline recorded over our 23-year study period (Figure 3f).

Analyses of spotted owl foraging locations along the perimeter of the King Fire (no owls were present in the interior of the large patch that burned at high-severity; Figure 4a-d) indicated that spotted owls foraged non-randomly (Wilks's lambda $\Lambda = 0.40$, $P = 0.017$) by avoiding foraging in areas that burned at high-severity ($\hat{w}_{\text{High-severity}} = 0.31$, 95% CI = 0.10–0.51) (Figure 4e-f). Forests that burned at low severity and unburned forests were used in proportion to their availability on the landscape ($\hat{w}_{\text{Low-severity}} = 1.21$, 95% CI = 0.82–1.60; $\hat{w}_{\text{Unburned}} = 1.12$, 95% CI = 0.87–1.38) (Figure 4e-f).

The observation that lower-severity fire is benign, and perhaps even moderately beneficial, to spotted owls is consistent with previous studies (Roberts et al. 2011, Lee et al. 2012) and is not surprising given that, within dry mixed-conifer forests, the spotted owl and other old-forest species evolved in association with such fire regimes (Noss et al. 2006, North et al. 2009). However, we provide the first definitive evidence that a large, high-severity fire (i.e., a megafire) had strong negative population impacts on an old-forest species and that areas burned at high severity were avoided by individuals. These findings contrast with a recent study of a population of spotted owls which reported high site occupancy after another megafire (the “Rim Fire”) (Lee and Bond 2015). The Rim and King Fires could have impacted owls differently because of differences in the patterns of patches that burned at high-severity and the resulting distribution of remnant habitat. The largest high-severity patch in the Rim Fire (21,426 ha) was 1.5× larger than that of the largest high-severity patch in the King Fire (13,683 ha), but made up a smaller percentage of the total area burned (21% vs. 36% for the Rim and King fires, respectively) and, despite its larger area, had an edge-to-area ratio 1.5× greater than that of the King Fire. The relatively high spatial complexity and heterogeneity in high-severity burn patterns in the Rim Fire may have resulted in a wider range of vegetation conditions and more remnant live trees suitable for owls (Lee and Bond 2015) compared to the King Fire, where the largest patch of high-severity fire was more homogeneously severe and overlapped a greater density of owl sites (Figure 2; see Supplementary Figure 6). Alternatively, because owls were not individually marked in the Rim Fire study, some detections at “occupied” sites may have involved individuals from neighboring territories or non-territorial “floaters” (Lee and Bond 2015), both of which may have contributed to inflated estimates of territory occupancy. Regardless, our study demonstrates that megafires can have strong negative effects on spotted owls, particularly when severely burned areas occur as large homogenous patches that leave little or no interspersed remnant habitat.

While we only used one year of post-fire data, the substantial decline in occupancy at severely burned sites is unlikely to reflect a temporary loss of individuals that will soon be replaced by colonization, but rather reflects a direct loss of suitable habitat that will likely not be replaced for many decades. Moreover, we found the scorched remains of one adult spotted owl from a severely burned site (Supplementary Figure 7), indicating that, in some instances, this highly vagile species was unable to avoid this rapidly moving fire. It is not unreasonable to suspect that less vagile old-forest specialists will be equally—and perhaps more—impacted by megafires like the King Fire. Collectively, these findings suggest that megafires constitute an additional mechanism by which climate change will threaten old-forest species, along with previously recognized climate-associated stressors such habitat shifts, physiological impacts, and changes in community interactions (Dawson et al. 2011).

Conclusions

Our study demonstrated that increasingly frequent megafires pose a threat to spotted owls and likely other old-forest species and, as a result, suggests that forest ecosystem restoration and old-forest species conservation may be more compatible than previously believed. Restoration practices that can demonstrably reduce the frequency of large, high-severity fires and reintroduce low- to moderate-severity fire as the dominant disturbance regime will likely benefit both dry-forest ecosystems and old-forest species such as spotted owls. However, forest restoration efforts that remove key habitat elements and areas of currently suitable habitat could exacerbate the risk of extirpation in the short-term before the long-term benefits of restored fire regimes are realized, particularly in light of the present deficit in large and old trees in natural landscapes (Tempel et al. 2015a). Rather, implementing fuels and restoration treatments outside of key habitats (e.g., nesting and denning areas) is more likely to minimize short-term impacts and ensure that old-forest species persist until forest resiliency objectives are achieved (Stephens et al. 2014a). The calculus behind these trade-offs, however, is complex and depends on several considerations that merit additional research such as the magnitude of short-term impacts that treatments impose on old-forest species, the relative increase in the frequency of severe fire as a function of climate change, and the efficacy of forest restoration for reducing both severe fires and tree mortality from drought and insects (Asner et al. 2015a). Managers and policy-makers will be faced with challenging decisions regarding the pace and scale of forest restoration efforts in light of scientific uncertainty and conflict among stakeholders (Redpath et al. 2013). We suggest, however, that old-forest species should not be viewed as an impediment to forest restoration objectives; rather, ensuring the persistence of old-forest species such as spotted owls, northern goshawks (*Accipiter gentilis*), pileated woodpeckers (*Dryocopus pileatus*), Pacific fisher (*Pekania pennanti*), American marten (*Martes americana*), and other species can serve as a barometer for the successful restoration of the ecosystems they inhabit.

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Figure legends

Figure 1. A female California spotted owl (*Strix occidentalis occidentalis*) within the Eldorado Density Study Area in the central Sierra Nevada, California.

Figure 2. The geography and historical context of the 2014 King megafire. (a) The distribution of occupied and unoccupied spotted owl sites in 2015 within our 23-year demographic study area, which was located ~20 km west of Lake Tahoe, California. Elevation is represented by brown shading (darker brown = low elevation, lighter brown = high elevation) and ranges from approximately 150 to 3000 m. (b–d) A comparison of the King Fire to all California fires since 1984 in terms of area of high-severity burn (b), total fire size (c), and proportion burned at high-severity (d); the solid black lines represent the 50th percentile, the dashed black lines represent the 95th percentile, and the dashed red lines represent the 2014 King Fire.

Figure 3. Before–after control–impact and population analyses. (a) The continuous relationship between the proportion of an owl site that burned at high-severity and the probability of site extinction. (b–d) Colonization (b), extinction (c), and occupancy (d) probabilities for owl sites that experienced different degrees of high-severity burn both pre- and post-fire. (e) Annual estimates of occupancy (ψ) over the study period, where the black line represents a segmented regression function fitted to the mean occupancy for years 1993–2014 (Supplemental Figure 4) demonstrating the periods of decline and subsequent stability before the 2014 King Fire (solid red circle). (f) Annual estimates of rate of change in occupancy (λ) over the study period, where the dashed black line at $y = 1$ indicates a stable rate of change, and the solid red circle indicates

the rate of change after the 2014 King Fire. The black curved lines in (a) and all error bars in (b–f) represent ± 1 SE of the mean.

Figure 4. Distribution of spotted owl foraging locations following a megafire developed from 985 GPS locations from nine owls (individuals represented by different colors) during the 2015 breeding season in relation to the 2014 King Fire (d). Inset examples (a–c) of foraging locations for three owls (small solid-colored circles) and the area defined as available habitat (large open black circles) compared to a minimum convex polygon (black dashed polygon) demonstrate the owls' apparent avoidance of the high-severity burned area. Burn severity for the King Fire is displayed in 25% classes as in Figure 2a. (e) Manly's selection ratios ($\hat{w}$) ± 1.96*SE, where a selection ratio $\hat{w} > 1$ indicates habitat preference, $\hat{w} < 1$ indicates habitat avoidance, and $\hat{w} = 1$ indicates neither preference nor avoidance. (f) Mean (± SE) availability and use among nine owls for unburned forests, forests that experienced 0–75% canopy mortality (low-severity), and forests that experienced 75–100% canopy mortality (high-severity).

Figure 1.

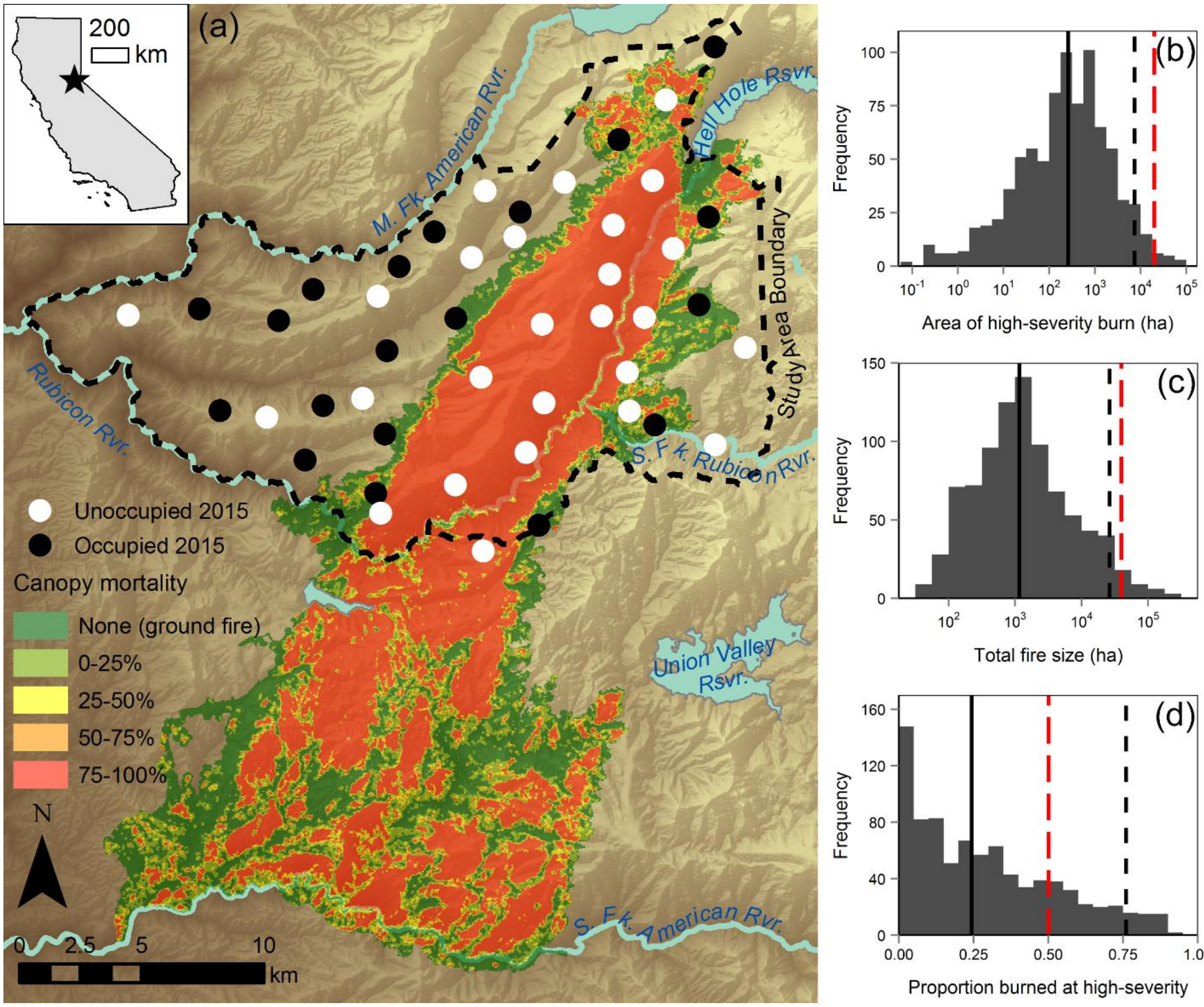

(a)
200
km
M. Fk. American Rvr.
Hell Hole Rsvr.
Study Area Boundary
Rubicon Rvr.
S. Fk. Rubicon Rvr.
Union Valley Rsvr.
S. Fk. American Rvr.
Unoccupied 2015
Occupied 2015
Canopy mortality
None (ground fire)
0-25%
25-50%
50-75%
75-100%
N
0
2.5
5
10
km
(b)
Frequency
0
25
50
75
100
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
10^{4}
10^{5}
Area of high-severity burn (ha)
(c)
Frequency
0
50
100
150
10^{2}
10^{3}
10^{4}
10^{5}
Total fire size (ha)
(d)
Frequency
0
40
80
120
160
0.00
0.25
0.50
0.75
1.00
Proportion burned at high-severity

Figure 2.

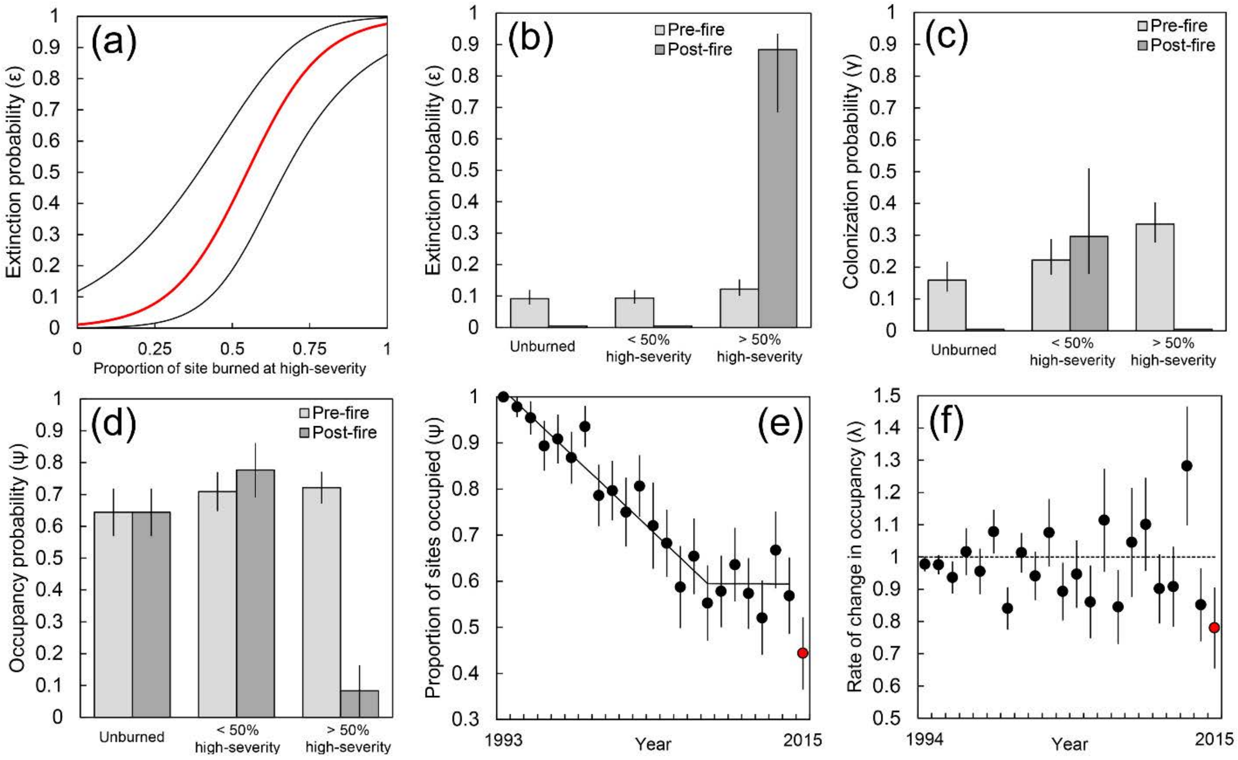

(a)
Extinction probability (ε)
Proportion of site burned at high-severity
0
0.25
0.5
0.75
1
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
(b)
Extinction probability (ε)
Pre-fire
Post-fire
Unburned
< 50% high-severity
> 50% high-severity
(c)
Colonization probability (γ)
Pre-fire
Post-fire
Unburned
< 50% high-severity
> 50% high-severity
(d)
Occupancy probability (ψ)
Pre-fire
Post-fire
Unburned
< 50% high-severity
> 50% high-severity
(e)
Proportion of sites occupied (ψ)
Year
1993
2015
0.3
(f)
Rate of change in occupancy (λ)
Year
1994
2015
1.1
1.2
1.3
1.4
1.5

Figure 3.

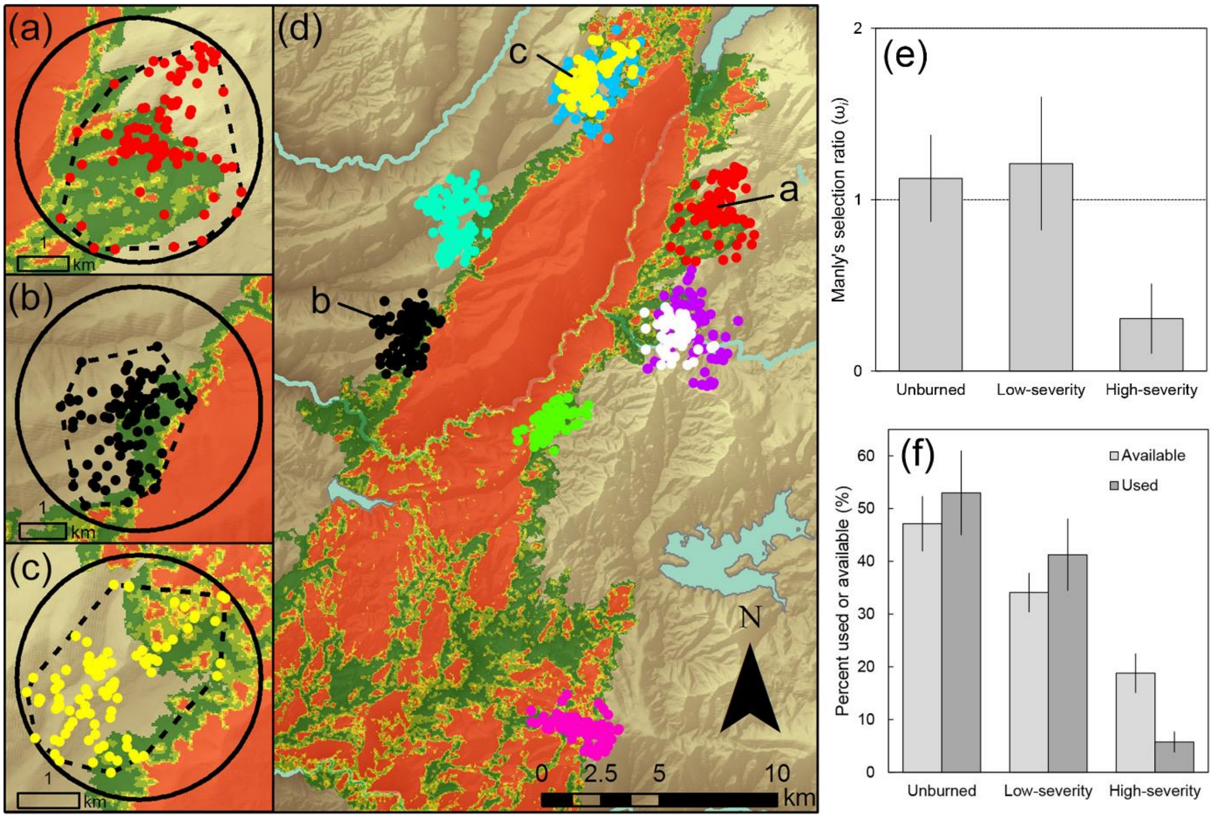

(a)
1
km
(b)
1
km
(c)
1
km
(d)
c
a
b
N
0
2.5
5
10
km
(e)
2
1
0
Manly's selection ratio (ω_i)
Unburned
Low-severity
High-severity
(f)
60
50
40
30
20
10
0
Percent used or available (%)
Available
Used
Unburned
Low-severity
High-severity

Figure 4.

Supplementary materials

Supplementary Table 1. Distribution of burn severities classes (% overstory canopy mortality) within the spotted owl demographic study area.

	None (ground fire)	> 0 to ≤ 25	> 25 to ≤ 50	> 50 to ≤ 75	> 75 to ≤ 100
Area (ha)	2969.35	1646.5	579.6	471.7	9926.7
Proportion	0.19	0.11	0.04	0.03	0.64

Supplementary Table 2. Model selection results for within-season detection probability (*p*) for spotted owls on the Eldorado Density Study Area in the central Sierra Nevada, California.

Model	*AIC*	Δ*AIC*	*w*	*K*
init + repro	3948.47	0	1	70
EL + repro	4044.74	96.27	0	70
T + repro	4047.04	98.57	0	70
lnT + repro	4047.34	98.87	0	70
TT + repro	4048.92	100.45	0	71
repro	4049.56	101.09	0	69
init	4064.01	115.54	0	69
EL	4159.52	211.05	0	69
T	4162.88	214.41	0	69
lnT	4163.72	215.25	0	69
TT	4164.86	216.39	0	70
(.)	4167.14	218.67	0	68

Notes: AIC, Akaike's information criterion; ΔAIC, difference in AIC compared to the model with the lowest AIC value; *w*, Akaike weight; *K*, number of parameters in the model. *Symbol definitions*: an early-late season covariate (EL) where detection probability (*p*) for the first five survey periods was different from *p* for the second five survey periods; an initial detection covariate (init) where *p* was different for all surveys following the initial detection; a reproductive status covariate (repro) where *p* was different for owls that had produced offspring in a given year compared to owls that had not produced offspring; as well as linear (T), quadratic (TT), and log-linear (lnT) within-season time trends. We modeled within-season *p* with covariates but allowed *p* to vary by year.

Supplementary Table 3. Model selection results from continuous and categorical colonization and extinction BACI analyses.

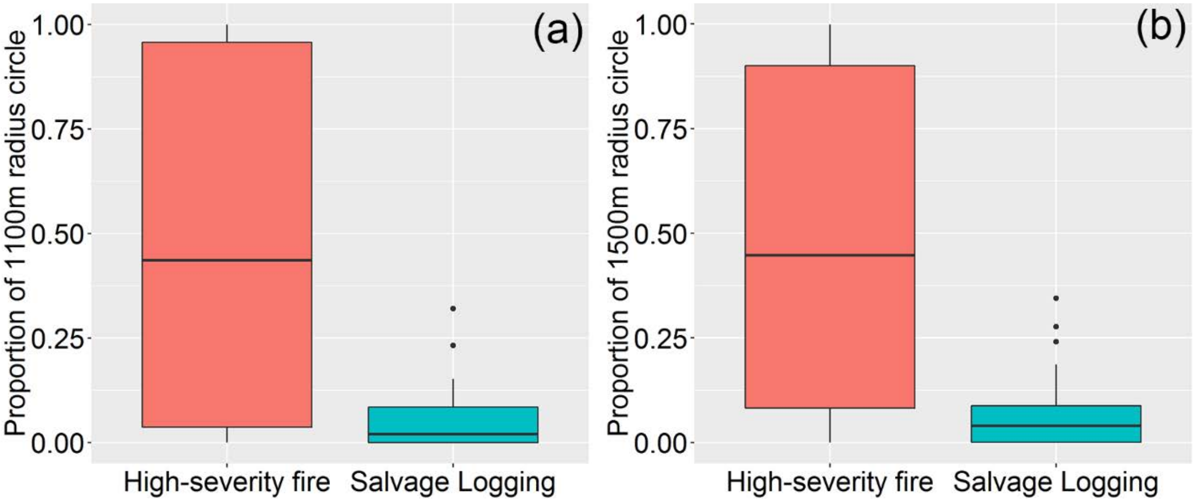
Colonization (γ)				
Continuous analysis	*AIC*	*ΔAIC*	*w*	*K*
SiteTreat + SeasonBA	3925.49	0	0.5205	51
SiteTreat + SeasonBA + SeasonSiteTreat	3926.61	1.12	0.2973	52
Intercept-only (.)	3927.59	2.10	0.1822	49
Categorical analysis	*AIC*	*ΔAIC*	*w*	*K*
SiteTreat1 + SiteTreat2 + SeasonBA + SeasonSiteTreat1	3924.65	0	0.4207	53
SiteTreat1 + SiteTreat2 + SeasonBA + SeasonSiteTreat2	3926.51	1.86	0.1660	53
SiteTreat1 + SiteTreat2 + SeasonBA	3926.56	1.91	0.1619	52
SiteTreat1 + SiteTreat2 + SeasonBA + SeasonSiteTreat1 + SeasonSiteTreat2	3926.65	2.00	0.1548	54
Intercept-only (.)	3927.59	2.94	0.0967	49
Extinction (ε)				
Continuous analysis	*AIC*	*ΔAIC*	*w*	*K*
SiteTreat + SeasonBA + SeasonSiteTreat	3915.25	0	0.7249	52
SiteTreat + SeasonBA + SeasonSiteTreat + SalvageLogging	3917.19	1.94	0.2748	53
SiteTreat + SeasonBA	3931.40	16.15	0.0002	51
Intercept-only (.)	3934.41	19.16	0.0001	49
Categorical analysis	*AIC*	*ΔAIC*	*w*	*K*
SiteTreat1 + SiteTreat2 + SeasonBA + SeasonSiteTreat2	3915.86	0	0.7298	53
SiteTreat1 + SiteTreat2 + SeasonBA + SeasonSiteTreat1 + SeasonSiteTreat2	3917.86	2.00	0.2685	54
SiteTreat1 + SiteTreat2 + SeasonBA + SeasonSiteTreat1	3929.34	13.48	0.0009	53
SiteTreat1 + SiteTreat2 + SeasonBA	3929.36	13.50	0.0009	52
Intercept-only (.)	3934.41	18.55	0.0001	49

Notes: AIC, Akaike's information criterion; ΔAIC, difference in AIC compared to the model with the lowest AIC value; *w*, Akaike weight; *K*, number of parameters in the model. *SiteTreat*: a "group" effect, which was a dummy variable that indicated whether a site was a control or impact site that accounted for background differences in occupancy rates at these sites; *SeasonBA*: a "time" effect, which was a dummy variable coding for before and after the fire, which accounted for differences in occupancy rates due to time and not the fire-related impact; *SeasonSiteTreat*: an "after-impact" effect, we included a term that represented impact sites after the fire occurred equivalent to a SiteTreat × SeasonBA interaction. We compared models with the SeasonSiteTreat term to models without the SeasonSiteTreat term to evaluate support for an effect of high-severity fire on occupancy rates (Popescu et al. 2012)

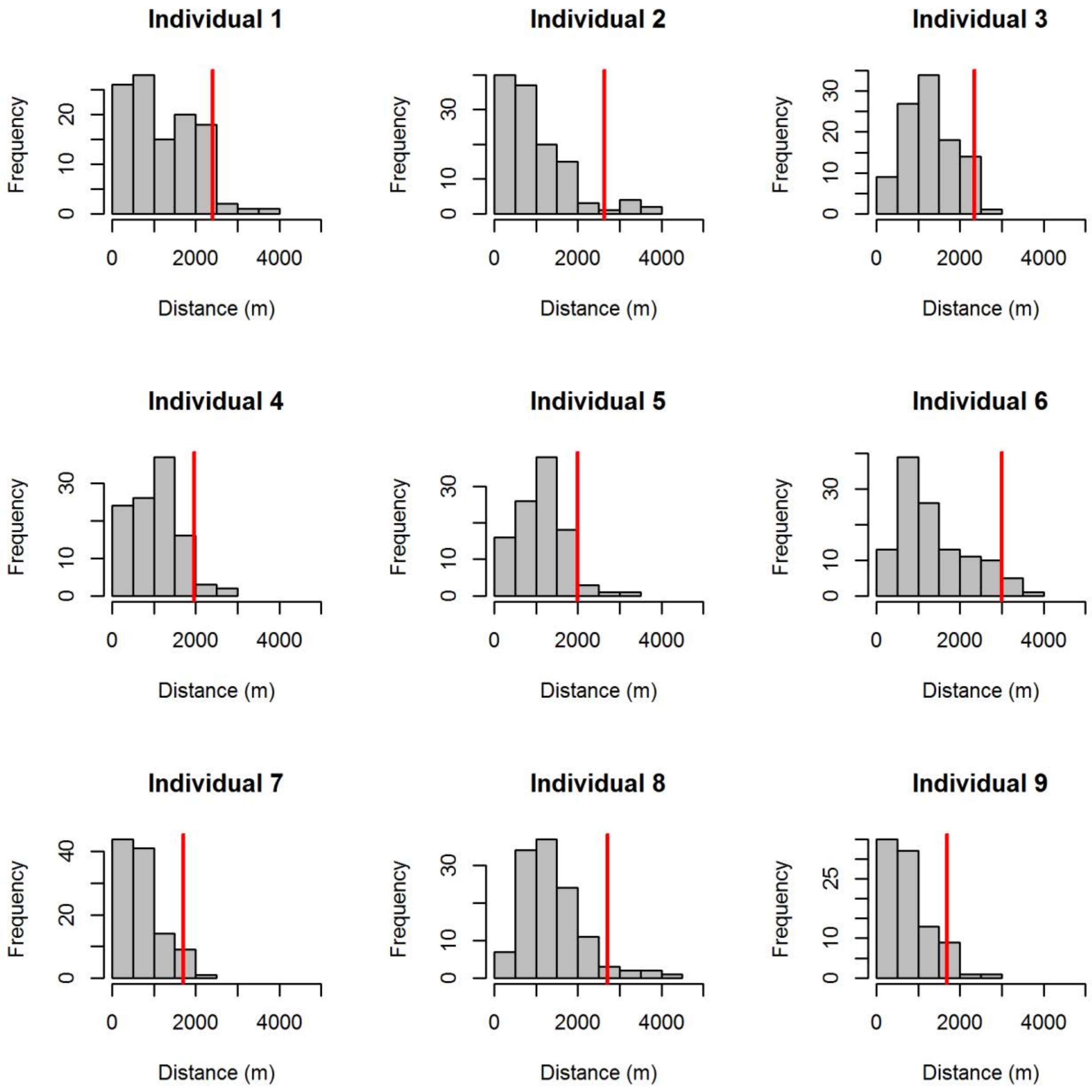
Supplementary Table 4. Model selection results from the annual occupancy trend analysis over the pre-fire years 1993-2014.

Model	*AIC*	Δ*AIC*	*K*	*RSS*	*n*
Segmented	−132.58	0.00	4	0.04	22
Quadratic	−126.62	5.95	4	0.05	22
Linear	−123.62	8.95	3	0.06	22
Log-linear	−114.60	17.97	3	0.09	22

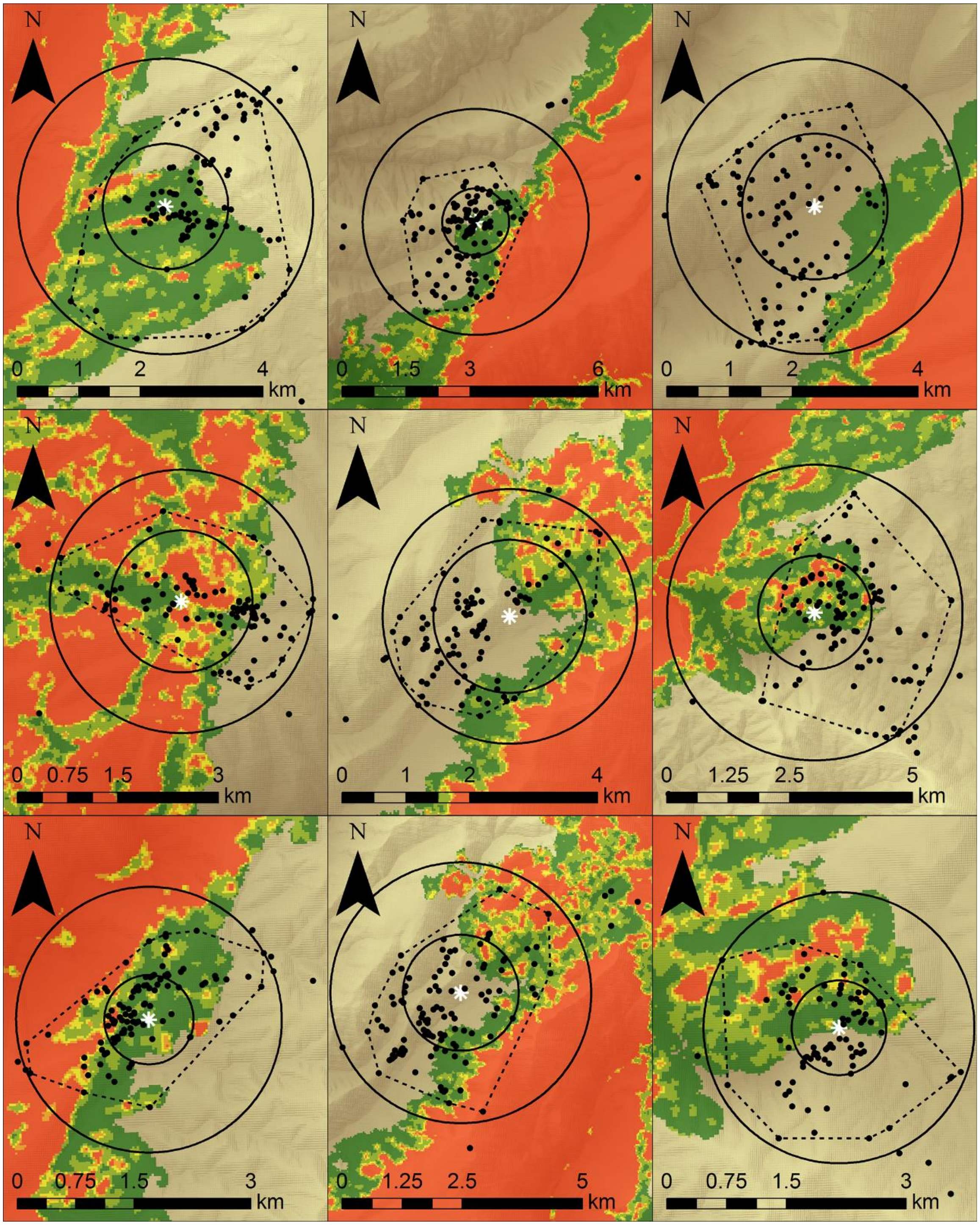
Notes: AIC, Akaike's information criterion; ΔAIC, difference in AIC compared to the model with the lowest AIC value; *K*, number of parameters in the model; *RSS*, residual sum of squares; *n*, number of data points (years) to which linear models were fitted. AIC was calculated manually using the residual sum of squares from each fitted model (Burnham and Anderson 2002).



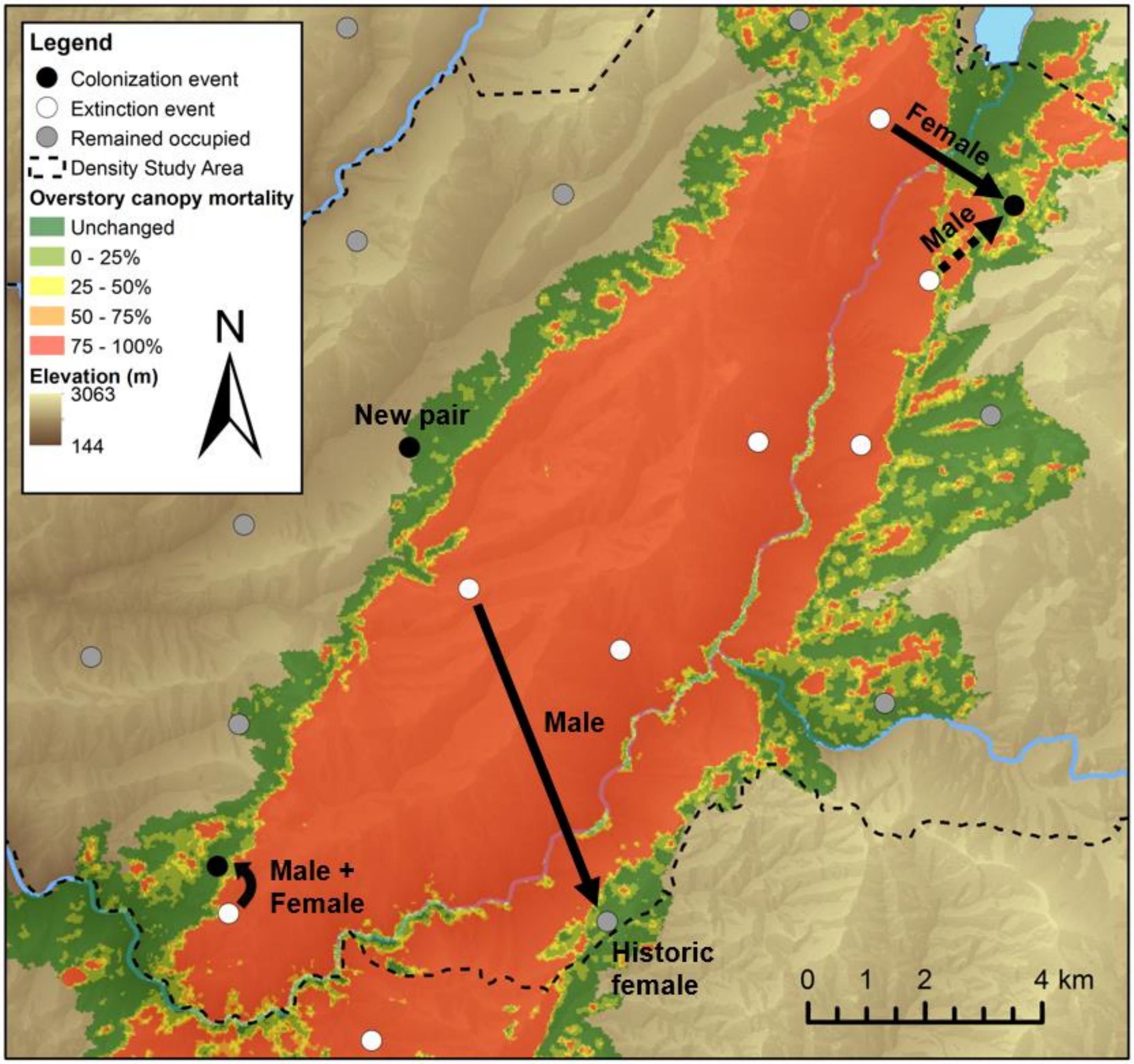
Supplementary Figure 1. Comparison of the extent of high-severity fire and salvage logging within 1100m (a) and 1500m (b) radius circles drawn around spotted owl site centers (long-term average of site nesting and roosting locations)). The circle with an 1100m radius represented the size of an actively defended spotted owl territory, equal to approximately one-half the mean nearest neighbor distance between owl territory centers on the Eldorado Density Study Area (Tempel et al. 2014a); the circle with a 1500m radius represented a larger home range that may support additional habitat use such as foraging activities (Bond et al. 2009, Lee and Bond 2015). We carried out our analysis of the effects on spotted owl site occupancy at the 1100m scale. Note that at both scales, high-severity fire affected a large proportion of territories relative to the proportion of territories affected by salvage activities. This, along with no empirical support for an effect of salvage logging on spotted owl site occupancy, supports the inference that high-severity fire—not post-fire salvage logging—appeared to drive declines in site occupancy.



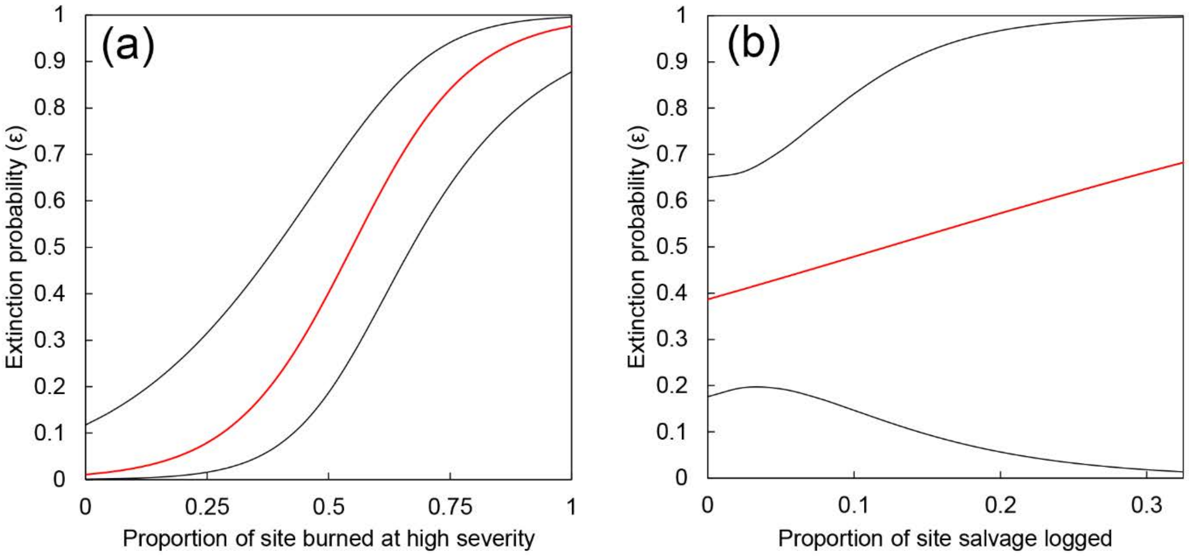
Supplementary Figure 2. Frequency distributions of foraging distance from activity center (i.e. geometric mean of 2015 roosting, nesting, and daytime capture locations) of nine GPS-tracked spotted owls. The red solid line on each graph represents the 95th percentile of foraging distances, which we used as the radius of a circle that defined available habitat for each owl in our habitat selection analysis.



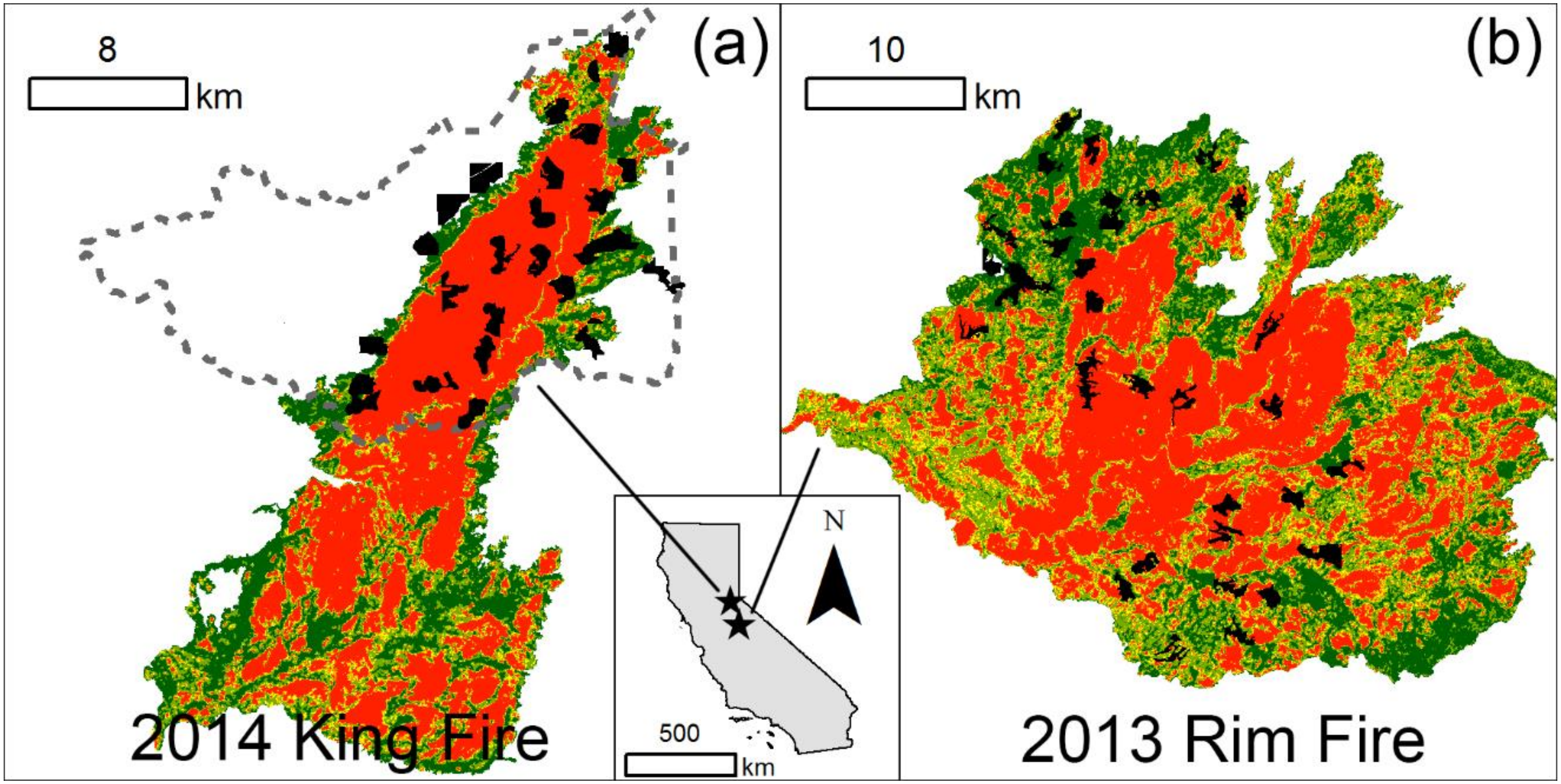
Supplementary Figure 3. Foraging locations for nine GPS-marked spotted owls following the 2014 King Fire (black dots). The largest black circle in each panel represents "available" habitat considered in our habitat selection analysis (i.e. a circle with a radius equal to the 95th percentile of foraging distances for each bird). The smallest black circle in each panel represents a circle with a radius equal to the 50th percentile of foraging distances (for illustrative purposes only). The black dashed polygon in each panel represents a minimum convex polygon fitted to all foraging locations within the 95th percentile of foraging distances.



Supplementary Figure 4. Relocation of marked spotted owls following the 2014 King Fire. Black arrows begin at the site occupied by a given owl in 2014 and end pointing to the site the same owl occupied in 2015. Solid black lines represent confirmed movements (via re-sighting of unique color bands). The single dashed line represents a putative relocation by a male spotted owl that was not confirmed by re-sight, but was thought to be the same male based on behavioral observations.



Supplementary Figure 5. A comparison of the influence of high-severity fire (a; see Fig. 1A in manuscript) and post-fire salvage logging operations (b) on site extinction probability following the 2014 King Fire. The proportion of a spotted owl site that burned at high-severity fire was a strong predictor of site extinction ($\beta_{\text{high-severity}}$ = 8.23, 95% confidence interval [CI] = 0.92 to 15.54), while post-fire salvage logging was an uninformative parameter (see Table S2) with no statistical relationship with site extinction probability (β_{salvage} = 3.77, 95% confidence interval [CI] = −27.85 to 35.39). The plot in panel (a) was generated with coefficients from the extinction model from the continuous extinction analysis with the lowest AIC, while the plot in panel (b) was generated with coefficients from the extinction model from the continuous extinction analysis containing the '*SalvageLogging*' term (second-lowest AIC) while holding the value for high-severity fire at 0.5. Red lines represent the mean point estimate and black lines represent the mean ± 1 SE.



Supplementary Figure 6. A comparison of the 2014 King Fire (a) and the 2013 Rim Fire (b). Burn severity is represented as overstory canopy mortality by the convention of Fig. S1. Black polygons represent ~121 ha spotted owl Protected Activity Centers (PACs) that were coincident with each respective study area (Lee and Bond 2015). Note that the burn pattern of the 2014 King Fire (a; present study) produced one large, contiguous patch of high-severity fire that left little intact habitat for spotted owls occupying severely burned PACs; while the 2013 Rim Fire (b) burned with greater heterogeneity, potentially leaving small, intact patches of suitable habitat for owls that may have occupied adjacent PACs that were severely burned. These differences in burn patchiness could partly explain the apparent differences in owl response to megafires.

Supplementary Figure 7. Fire-scorched tarsometatarsus bones of a California spotted owl and USFWS aluminum locking leg-band recovered from a historic spotted owl territory following the 2014 King Fire. When recovered, the bones were inside of the leg-band. The individual owl that apparently perished in the fire was a male identified as one of the most productive individuals (in terms of total number of offspring fledged) over the 23-year study period (M. Z. Peery, unpublished data). Photo by Sheila Whitmore.

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<u>Chapter 2</u> - Declining old-forest species as a legacy of large trees lost

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Abstract

Global declines in large old trees from selective logging has degraded old-forest ecosystems, which could lead to delayed declines or losses of old-forest associated wildlife populations (i.e. extinction debt). We applied the declining population paradigm and explored potential evidence for extinction debt in an old-forest dependent species across landscapes with different histories of large tree logging. We tested hypotheses about the influence of forest structure on territory extinction dynamics of the spotted owl (*Strix occidentalis*) using detection/non-detection data from 1993-2011 across two land tenures: national forests, which experienced extensive large tree logging over the past century, and national parks, which did not. Our study area was located in montane forests of the Sierra Nevada, California, USA. Large tree/high canopy cover forest was the strongest predictor of extinction rates, and explained 26-77% of model deviance. Owl territories with more large tree/high canopy cover forest had lower extinction rates, and this forest type was ~4 times more prevalent within owl territories in national parks ($\bar{x}$ = 19% of territory) than national forests ($\bar{x}$ = 4% of territory). As such, predicted extinction probability for an average owl territory was ~2.5 times greater in national forests than national parks, where occupancy was declining ($\hat{\bar{\lambda}} < 1$) and stable ($\hat{\bar{\lambda}} = 1$), respectively. Large tree/high canopy cover forest remained consistently low, but did not decline, during the study period on national forests while owl declines were ongoing – an observation consistent with an extinction debt. In identifying a linkage between large trees and spotted owl dynamics at a regional scale, we provide evidence suggesting past logging of large old trees may have contributed to contemporary declines in an old-forest species. Strengthening protections for remaining large old trees and promoting their recruitment in the future will be critical for biodiversity conservation in the world's forests.

Introduction

Large old trees have declined across nearly all global ecosystems, in part because their high commercial value has led to logging pressure that outpaces sometimes centuries-long recruitment and development (Lindenmayer et al. 2012). Agriculture (Laurance et al. 2014), fire (Jones et al. 2016a, Westerling 2016), and disproportionate drought susceptibility (Bennett et al. 2015) also increasingly threaten large old trees and conservation of old-forest ecosystems (Lindenmayer and Laurance 2017). Loss of large old trees is a major contributor to habitat loss for many globally endangered old-forest dependent (hereafter ‘old-forest’) species such as the orangutan (*Pongo spp.*) in southeast Asia (Wich et al. 2003), the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) in western North America (Noon and Blakesley 2006, Raphael 2006), the Leadbeater’s possum (*Gymnobelideus leadbeateri*) in southeast Australia (Lindenmayer et al. 2013), and the Blakiston’s fish owl (*Bubo blakistoni*) in the Russian Far East and Japan (Slaght et al. 2013).

Like large old trees, many old-forest species have “slow” life histories with long generation times and high adult survival, which increases vulnerability when environments change rapidly (Webb et al. 2002). Long-lived individuals may persist for many years in marginal or degraded forests long after critical breeding habitat elements such as large old trees are lost or substantially reduced, but gradually these individuals die off and may not be replaced. Delayed population declines or local extinctions resulting from prior habitat loss or degradation is termed “extinction debt”, which can be assessed across different levels of organization (e.g., individual species vs. community) and may be evaluated at spatial scales ranging from local extirpation within a habitat patch to regional or global extinction of a species. Extinction debt challenges the ability of scientists to establish causal links between habitat loss and population declines of individual species (Kuussaari et al. 2009). Uncertainty about population status or causes of decline, then, could delay implementing conservation measures for old-forest species and the restoration of degraded old-forest ecosystems. Moreover, this uncertainty creates political opportunities to undermine governmental or social responses to make corrective changes (Oreskes and Conway 2010).

Global challenges facing the conservation of large old trees and old-forest associated species (Lindenmayer and Laurance 2016) have led some to propose new and more rigorous policies for ensuring their protection and improving conservation outcomes (Lindenmayer et al. 2014). Nevertheless, if an extinction debt has already been created, population declines of old-forest species may continue to occur long after policies protecting large old trees are put into place. Here, we studied the potential long-term (multi-generational) impacts of large tree loss on an old-forest species, the spotted owl (*S. occidentalis*), across a large mountain ecosystem by comparing forest conditions and population dynamics between national parks (long-established protected areas) and national forests (areas that experienced widespread large tree logging but more recent protections). Following a century of extensive, intensive, and selective logging of very large trees on national forests (e.g., ~90-215 cm dbh; Laudenslayer & Darr, 1990; Stephens et al., 2015), forest policy was enacted immediately prior to our study to conserve remaining old-forest elements such as large trees and multi-layered canopy around spotted owl activity centres (Verner et al. 1992).

Despite these recent protections, we hypothesized that this historical loss of large trees on national forests could be associated with contemporary population declines, or an extinction debt, for spotted owls. In testing this hypothesis, we treated protected areas (national parks) as “contemporary reference landscapes” (Meyer 2015, Collins et al. 2016, Miller et al. 2016), because prohibition of logging within national park boundaries over the past century has largely preserved historical forest structure and prevalence of very large and old trees (Beesley 1996, Lydersen and North 2012). Thus, in principle, contemporary forests characteristics in spotted owl territories on national parks (e.g., large trees) might more closely represent forests characteristics that might have existed on national forests if protections for large trees had been established long ago.

Comparing spotted owl populations on national forests and national parks, then, allowed us to diagnose causes of decline (Caughley 1994, Green 1995, Peery et al. 2004) for a species considered to be a barometer of old-forest wildlife community health in western North America (Simberloff 1998). Despite the fact that the spotted owl is one of the most intensively studied species in the world with 40 years of demographic and ecological research across its range, no definitive causal link between ongoing owl declines and changes in habitat has been established. Here, we offer insight into this elusive question by applying the concept of extinction debt and provide an unprecedented case study about the potential ecological legacies of large tree loss on increasingly rare global old-forest species and ecosystems (Lindenmayer et al. 2012, 2014).

Methods

Study areas and logging histories

Four spotted owl study areas – Lassen (LAS), Eldorado (ELD), Sierra (SIE), and Sequoia-Kings Canyon (SKC) – span nearly the entire latitudinal range of California's Sierra Nevada (Fig. 1). Elevations range from 300–3,050 m across the four study areas, and the climate is Mediterranean (Tempel et al. 2016). LAS, ELD, and SIE study areas are primarily located within national forests (with intermixed private land), whereas SKC occurs within two national parks of the same name. While Sierran mixed-conifer montane forest is the primary vegetation type within owl territories across all study areas (Tempel et al. 2016), contemporary structure of these forests has been strongly affected by different management legacies across the two land tenures (i.e., national forests vs. national parks).

Very large (e.g., >125 cm dbh) old trees were a dominant feature throughout the Sierra Nevada at the turn of the twentieth century (Safford & Stevens, 2017; McKelvey & Johnston, 1992). Several national parks including Sequoia (of SKC) were established in 1890 (Kings Canyon National Park adjoined in 1940), and the prohibition of logging within park boundaries over the following century largely acted to preserve historical forest structure and prevalence of very large and old trees (Beesley 1996, Lydersen and North 2012). In contrast, logging activities on what would eventually become Sierra Nevada national forest lands were well underway by 1900 (Beesley 1996, Thomas 2008). Commercial logging (i.e. selective removal of very large trees) on Sierra Nevada national forests increased from ~470,000 cubic meters (m^3) $year^{-1}$ in the 1870s to its peak during the 1940s when timber production reached 4.5 million m^3 $year^{-1}$. Timber production remained reasonably high thereafter (generally between 2.8 and 3.8 million m^3 $year^{-1}$) for several decades before a near-historic peak in timber production in 1990 when production again neared 4.5 million m^3 $year^{-1}$ (McKelvey and Johnston 1992).

Concern about the continued and cumulative loss of large trees required by spotted owls reached a highpoint around the same time and as a result, in 1992, logging of ≥76 cm dbh trees on national forests was restricted (with some allowable exceptions for equipment operability), as was almost all logging within 121 ha areas around known owl nest and roost sites (Verner et al. 1992, USFS 2004). Our study on spotted owls began in 1993, immediately following near-peak logging activity and subsequent restrictions. Recent work has established that national forest lands indeed contain greater prevalence of younger trees that are smaller in diameter and height (Laudenslayer and Darr 1990, Stephens et al. 2015) and significantly fewer trees in the largest size classes compared to historical baselines (McIntyre et al., 2015; Stephens et al., 2015; Collins et al., 2017; Safford & Stevens, 2017). Given that SKC did not experience the same history of selective logging and forest structural change as the three study areas on national forests, we treated it as a contemporary reference landscape for evaluating differences in forest structure and owl population dynamics between land tenures.

Owl surveys

As part of prior work, we have established that temporal changes in occupancy rates of spotted owl territories (i.e., based on detection/non-detection data) can provide inferences regarding overall population trends that are comparably reliable to estimates of overall population trends based on changes in abundance (Tempel and Gutiérrez 2013, Tempel et al. 2014b, Conner et al. 2016). As such, we conducted detection/non-detection surveys for spotted owls at 275 owl territories located during breeding seasons (Apr-Aug on LAS and ELD; Mar-Sept on SIE and SKC) across the four study areas over a 19-year period (1993-2011). All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e., both the areas containing owl territories and all areas not containing known owl territories within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (LAS) or as individual "satellite" territories (i.e., adjacent to, but not part of, the core area) to increase owl sample sizes for demographic analysis (LAS and ELD), and we dropped a portion of SKC in 2006 (Tempel et al. 2016). We surveyed all satellite territories used in our occupancy analyses for a minimum of 3 years; most territories in the core areas were surveyed for ≥ 15 years.

We located spotted owls by imitating their vocalizations (vocal lure) for 10 minutes at a survey station or used vocal lures while walking along a survey route. We then considered sites to be a territory where owls responded to vocal lures, and were subsequently observed either roosting or nesting during diurnal hours. Some surveys occurred prior to 1993 but previous analyses have determined that survey coverage and effort required for population analyses (such as ours presented here) became adequate beginning in 1993 (Tempel and Gutiérrez 2013, Tempel et al. 2016). We did not survey all territories in all years of the study. However, of the 275 owl territories used in the study, ≥205 were surveyed in all but the first year of the study (in 1993, 187 owl territories were surveyed). The average number of owl territories surveyed annually was 239 (87% of all known territories; standard error = 21 territories), with a maximum of 263 territories surveyed in 2008 (95.6% of all known territories). Moreover, while most intervening area between territories was intensively surveyed each year, spotted owls on our study areas rarely established new territories outside of territories located in the early stages of the study. For example, the most recently located territory on the ELD was found in 1997. We included all surveys in our analyses but excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique colour leg-bands as part of a concomitant mark-recapture study) that occurred outside of a delineated territory boundary (see below for information on owl territories) using a Geographic Information System (GIS) to eliminate potential spurious positive detections of owls not occupying the nominal territories. A survey in which no owls were detected needed a total duration of ≥30 min to be included as an absence record. Extensive details about each study area and additional survey details can be found in Tempel et al. (2016).

Sampling units and vegetation covariates

We treated owl territories as sampling units, where a territory had at least one owl detection during diurnal hours in ≥3 years. For quantifying habitat covariates within spotted owl territories, we first calculated the geometric centre of each territory as the average spatial coordinates of all nest and roost locations across all years in the territory. We then calculated the mean nearest-neighbour distance among territory centres for each study area as the average distance between each territory centre and the centre of its nearest neighbouring territory. Thus, the location of owl territories was assumed to remain the same throughout the study period, and territories in each study area were assumed to be of equal size based on the nearest neighbour distance. In a recent meta-analysis (Tempel et al. 2016) we defined the spatial extent of a territory as a circle around each territory centre with a radius of half of the mean nearest-neighbour distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius), and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. In the present paper, we defined territories as hexagons instead of circles with areas and geometric centres equal to those determined by Tempel et al. (2016) to facilitate integration into concurrent projects using spatial population models (e.g., HexSim; Schumaker, 2015).

We defined site-specific covariates based on two vegetation variables within owl territories using the ‘GNN’ (Gradient Nearest Neighbour) forest structural maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group (Oregon State University, Corvallis, OR, USA). GNN is an imputation method used by LEMMA that integrates regional forest inventory plots with Landsat imagery to produce fine-scale (30-m resolution) and large-domain (currently the entire land area for the U.S. states of Washington, Oregon, and California) vegetation structure and species composition maps. The GNN approach is one variation of nearest neighbour imputation methods that uses (*i*) a neighbourhood value of k=1 as the number of neighbours imputed to each cell and (*ii*) direct gradient analysis as the ‘distance’ metric (see https://lemma.forestry.oregonstate.edu/methods). The first variable was the quadratic mean diameter of dominant and codominant trees in each 30×30 m pixel ("QMD_DOM"). Quadratic mean diameter (QMD) is a commonly used metric in forestry that more strongly reflects the influence of large trees on stand tree size classifications than arithmetic mean (Curtis and Marshall 2000). The second variable was the percent canopy cover of live trees in each pixel ("CANCOV").

Large trees are a key feature of spotted owl nest sites (Gutiérrez et al. 1992), and owl site occupancy has been positively correlated with large trees (> 61 cm dbh) and high canopy cover (> 70%) at nest areas (Blakesley et al. 2005). However, forests with intermediate canopy cover (40-70%) can constitute spotted owl nesting or roosting habitat if large, remnant trees are present (Moen and Gutiérrez 1997, Hunter and Bond 2001), and recent work found that both medium and high canopy cover were associated with spotted owl occupancy in the Sierra Nevada (Tempel et al. 2014a, 2016, Jones et al. 2016b). Thus, we estimated the proportion of each owl territory containing the following five covariates: large trees (QMD ≥ 61 cm) regardless of canopy cover class; high canopy cover (> 70% cover) regardless of tree size class; as well as the spatial intersection (∩; see Fig. 2) of large trees and high canopy cover, large trees and medium canopy cover (40-70% cover), and medium trees (QMD = 30-61 cm) and high canopy cover. These proportions were calculated by dividing the number of 30×30 m pixels in the territory for a particular variable divided by the total number of 30×30 m pixels in the territory. Several of the predictor variables were highly collinear (e.g., $r = 0.7$-0.9), so we developed models that contained a single predictor variable and used AIC to identify which predictor variables had the most explanatory power (see below).

We adopted the above tree size classes because they are commonly used by foresters (Verner et al. 1992, Blakesley et al. 2005), although the large old trees used by owls for nesting are typically larger than 61 cm dbh (e.g., 125-150 cm dbh; North et al., 2000). Median QMD in the ≥ 61 cm dbh size class was 75.5 and reached a maximum of 279 (Fig. S1). Finally, for each forest structure variable listed above, we averaged the within-territory covariate values across all years (1993-2011) to produce a single, static territory-level covariate that varied across space (but was averaged over time), because nearly all variation in the covariates was spatial rather than temporal (large among-territory differences). Ranges of covariate values for each study area are provided in Table 1.

Statistical analysis and model selection

We used multi-season occupancy models to assess territory occupancy dynamics on each study area separately (Tempel et al. 2016) using program PRESENCE 11.5. The models contained parameters for initial occupancy (ψ_1), local extinction (ε_t), local colonization (γ_t), and detection probability ($p_{t,j}$) (MacKenzie et al. 2003). Our primary sampling periods (t) were breeding seasons (i.e., years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (April 1-15, April 16-30, etc.). No surveys were conducted on SKC in 2005 so we fixed p, ε, and γ for that year to zero. We allowed colonization to vary as a year-specific effect rather than a function of covariates because (*i*) colonization may be related more to site availability than site conditions, and (*ii*) we were interested in factors associated with elevated extinction rates.

We used multi-stage modelling (Tempel et al. 2016). At each stage, we ranked models using AIC (Burnham and Anderson 2002) to select the base model for the next stage. We first modelled p as a function of the above forest structure covariates and within- and among-year temporal trends (i.e., linear, log-linear, or quadratic trends in p) while γ and ε varied by year. We then examined linear, logarithmic, and quadratic forms of covariates on ψ_1 while γ and ε varied by year. Finally, we examined the potential effects of covariates on ε while γ varied by year, again considering linear, logarithmic, and quadratic covariate forms because previous owl studies showed evidence of non-linear relationships (Dugger et al. 2005, Forsman et al. 2011). We used analysis of deviance to assess the amount of variation explained by model covariates. This approach compares deviance explained by the covariates in a model with the amount of deviance not explained by these covariates, thus providing an estimate of r^2 for the model (Skalski et al. 1993). The global model for the analysis of deviance consisted of the top-ranked model for the given study area with additional annual effects for ε, and the constant model consisted of the best detection structure with only and intercept for ε (Tempel et al. 2016).

We used the best p model from the first stage with year-specific γ and ε to obtain derived estimates of ψ_t which we used to calculate the geometric mean of the rate of change in occupancy ($\hat{\hat{\lambda}}$) and estimated the realized change in occupancy (Δ_k) for each study area. We calculated variance for $\hat{\hat{\lambda}}$ and Δ_k using the delta method (Powell 2007).

Results

We found that local extinction rates were high when owl territories contained less forest characterized by large trees (≥ 61 cm dbh) and high canopy cover (>70% cover), and extinction rates declined as this forest type increased (Fig. 3). Indeed, local extinction was best explained by the proportion an owl territory containing large trees/high canopy cover forest, as evidenced by the presence of this covariate in the top models on three of the four study areas (ELD, SIE, SKC) having nearly all (88-97%) of AIC weight (Table S1). The top three models for the fourth study area (LAS) were closely competing (within 1 AIC), containing parameters for large trees only, large trees and high canopy cover, and high canopy cover only, respectively (Table S1), although the coefficient estimate for the high canopy cover only model was imprecise (Table S2).

No other models were competitive with the large trees/high canopy cover model for any study area (all >5 AIC from top model; Tables S1 and S3). However, models containing other forest structural covariates such as high canopy cover, medium trees and high canopy cover, and large trees and medium canopy cover sometimes outperformed the null model and yielded coefficient estimates with 95% confidence intervals that did not overlap zero (Table S2), suggesting they may be biologically meaningful. Analysis of deviance showed that the covariate for large trees/high canopy cover explained 28%, 26%, 77%, and 53% of the variation in local extinction rates on LAS, ELD, SIE, and SKC, respectively.

The median proportion of an owl site containing large trees/high canopy cover forest on national forests (LAS, ELD, SIE) was similar, ranging from 0.03-0.06 (Table 1). These values corresponded with higher predicted rates of local extinction ($\varepsilon = 0.06\text{-}0.074$) and ongoing occupancy declines according to estimates of the geometric mean rate of change in occupancy ($\hat{\bar{\lambda}} < 1$) and realized change in occupancy ($\Delta_k < 1$) over the period 1993-2011 (Table 2). By contrast, the median proportion of large trees/high canopy cover forest within owl territories on national parks (SKC) was 0.19 (Table 1), which was associated with much lower predicted extinction rates ($\varepsilon = 0.027$) and stable occupancy ($\hat{\bar{\lambda}} = 1$, $\Delta_k = 1$) (Fig. 3, Table 2). Thus, extinction probability at a “typical” owl territory was ~2.5 higher on average in national forests (LAS, ELD, SIE) than national parks (SKC). A post-hoc comparison showed that estimates of realized change in occupancy (Δ_k) for LAS, ELD, and SIE were not statistically different from one another, but all were significantly lower than SKC (Table 2).

The extent of large trees/high canopy cover forest within owl territories differed among study areas ($F_{3,271} = 38.3$, $P < 0.01$), and was ~4 times greater in national parks than in national forests on average (Table 1). Furthermore, this forest type did not appear to decline within owl territories on national forests over the study period (Fig. 3, Fig. S2), suggesting the considerable deficit of large tree/high canopy cover forest on national forests may have resulted from historical (as opposed to more recent) logging activities that selectively removed very large old trees (Laudenslayer & Darr, 1990; McKelvey & Johnston, 1992; Stephens et al., 2015; Collins et al., 2017).

Discussion

Extinction debt and restoration opportunities

Our work presents several key inferences suggesting ongoing declines in spotted owl populations on national forests are consistent with an extinction debt, or a legacy effect, resulting from logging of large trees prior to the initiation of our study. First, we found that local extinction rates were consistently higher across a large bioregion (the Sierra Nevada) when large tree/high canopy cover forest was less common in owl territories. Second, large tree/high canopy cover forest was far more common in owl territories in the national parks study area (SKC), where large trees have not been logged. Third, owl populations are declining on all national forest study areas, which contain far less large tree/high canopy cover forest in owl territories than national parks where the owl population is stable. Fourth, although logging activities prior to our study led to a deficit of large tree/high canopy forest on national forests, no further declines in this forest type were observed from 1993-2011 (Fig. S2) while owl populations experienced long-term declines over the same period. Together, these inferences suggest that past large tree logging on national forests, which removed key habitat elements for spotted owls, may have created an extinction debt that led to contemporary owl declines long after policies were enacted to protect large trees (Fig. 3).

We note that other emerging threats to the spotted owl, such as large, severe wildfires (Jones et al. 2016a) and invasive barred owls (*S. varia*) (Wiens et al. 2014) did not contribute to observed declines given that our study areas did not experience significant severe fire or appreciable numbers of barred owls during the study period (Keane 2017). Secondary ingestion of anticoagulant rodenticides used to kill rodents on illegal marijuana (*Cannabis* sp.) cultivations has been documented in fishers (*Pekania pennanti*) and barred owls in the Sierra Nevada and north-western California (Gabriel et al. 2012, Keane 2017). However, we know of no documented cases of exposure in spotted owls, and it is currently unknown to what extent this stressor has contributed to observed changes in spotted owl populations.

The concept of extinction debt is defined by the idea that individuals, populations, or species can initially survive habitat change but later become locally extirpated or experience declines without any further habitat modification (Kuussaari et al. 2009). As such, it is important to note that by identifying the potential presence of an extinction debt in owl populations on national forests our inferences do not suggest that total population extinction is a foregone conclusion. On the contrary, it is possible (or even likely) that spotted owl occupancy on national forests will eventually reach a new, lower equilibrium once the extinction debt is paid (Hylander and Ehrlén 2013). In the present study, we did not explore when the extinction debt might be paid off (i.e., when the population will stop declining and persist at its new lower equilibrium level), nor did we attempt to identify an empirical extinction threshold (i.e., the minimum amount of habitat required in a territory for individuals to persist). Rather, we focused on identifying potential mechanisms of extinction debt to guide more targeted conservation action (Hylander and Ehrlén 2013).

An emerging conservation paradigm for degraded old-forest ecosystems and, the many endangered species that inhabit them, centres on restoring forest structure and function (Chazdon 2008) thereby increasing forest resilience to disturbance from fire, disease, and drought (Millar and Stephenson 2015) and conserving wildlife habitat over the long term (Tempel et al. 2015b). The consistent relationship we identified between spotted owl extinction rates and large tree/high canopy cover forest across the latitudinal range of the Sierra Nevada has significant implications for developing meaningful ecosystem restoration targets at bioregional scales (Peery et al. 2017). In particular, high canopy cover is thought to increase severe fire risk and spread by creating fuel continuity, yet appears to be more relatively more prevalent within owl territories in national parks (SKC) that have been subjected to restored, lower-severity frequent-fire regimes for nearly half a century (van Wagtendonk 2007). This indicates the potential that increased prevalence of large tree/high canopy cover forest types within owl territories in national forests may not be incompatible with fire resistance/resilience while at the same time providing conservation benefits to spotted owls.

The potential direct benefits to owls of increasing this forest type may be considerable. Employing our models, increasing this forest type (large trees with high canopy cover) from the median within-territory value of 0.03-0.06 to 0.10 (30-64 ha) on national forests reduced predicted local extinction rates by 36-79%. Increasing the median within-territory value further to 0.20 (60-127 ha), similar to the median value at SKC (0.19), reduced predicted extinction rates by 80-98%. Furthermore, because they are cornerstones of old-forest ecosystem stability, greater prevalence of large trees within owl territories and across the broader landscape probably would provide direct benefits to both spotted owls and increase resilience of old-forest ecosystems to emerging stressors.

Forests in national parks representing contemporary reference landscapes generally contain less canopy cover and lower tree densities than fire-suppressed forests on average (Lydersen and North 2012). Why then do owl territories on national parks appear to contain considerably more large tree/high canopy cover forest than their counterparts on national forests? First, although national forests may contain higher densities of trees of all sizes, they contain significantly lower densities of trees in the largest diameter (i.e., > 91 cm dbh) (Collins et al., 2017) and height classes (> 48 m) (North et al. 2017) . Second, forest patches characterized by both large trees and higher canopy cover are not a product of fire suppression, but occurred historically throughout Sierra Nevada forests within a diverse mosaic of forest types in systems maintained by mixed-severity fire regimes (Hessburg et al. 2016). Spotted owl territories likely contained disproportionately more large trees and higher canopy cover than the broader forested landscape because owls are known to select for these specific features (Lahaye et al. 1997, Moen and Gutiérrez 1997, North et al. 2017).

While areas managed for multiple uses including resource extraction (i.e., national forests) and protected areas serve different societal purposes and, for this reason and others, are unlikely to have convergent forest structure and function, we can still learn important lessons when protected areas contain stable populations of species of conservation concern. For example, protected areas often form refuges for ecosystems containing distinctive biological features such as large old trees (Miller et al. 2016) and, therefore, they can act as blueprints for ecological restoration (Boisramé et al. 2017). Furthermore, protected areas may contain tree sizes, age structure, and intact disturbance regimes (Lydersen and North 2012) characteristic of ecologically resilient landscapes (i.e., landscapes that have the capacity to recover their ecological functioning following a disturbance) and that more closely reflect species' evolutionary environments (Moore et al. 1999). Thus, in certain cases, protected areas might act as contemporary reference landscapes (Meyer 2015, Collins et al. 2016) to provide a frame of reference for the goals of ecological restoration (White and Walker 1997) for large old trees and recovery of old-forest associated species across different land tenures.

Care should be taken, however, to acknowledge the potential limitations of using national parks and other protected areas as contemporary reference landscapes to inform conservation action at broader spatial scales. For example, protected areas do not necessarily represent a random sampling of area on the landscape, but instead are often biased towards places that are less likely to face land conversion pressures – areas characterized by higher elevations, steeper slopes, and greater distances to roads and cities (Joppa and Pfaff 2009). In our study, we treat Sequoia and Kings Canyon national parks (SKC) as a contemporary reference landscape, yet it is also most southerly of all study areas examined (Fig. 3). This raises the question of whether SKC can truly act as a reference, or if other fundamental differences related to differences in latitude (e.g., climate or vegetation types) could play a stronger role than past forest management on observed dynamics of spotted owls.

While this is a possibility, we present several lines of evidence to support our use of SKC as a contemporary reference landscape. First, average temperatures and annual precipitation in SKC fell within the range experienced by the other three more northerly studies (Franklin et al. 2004). Second, mixed-conifer forests characterized primarily by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), and incense cedar (*Calocedrus decurrens*) was the dominant vegetation type on all four study areas. While SKC did contain ten groves of giant sequoia

(*Sequoiadendron giganteum*), these covered only 7% of the study area (Tempel et al. 2016). Third, the two most southerly study areas, SIE and SKC, occur immediately adjacent to one another in the southern Sierra Nevada in a paired study design. Yet these two study areas exhibit the largest differences in population trends among all study areas according to estimates of $\hat{\bar{\lambda}}$ and Δ_k (Table 2), suggesting differences in trajectory may be unrelated to underlying differences in climate or potential vegetation type.

Global conservation of large trees and forest policy

The case study presented here demonstrates globally informative principles for old-forest species and large tree conservation. Notably, our results are consistent with an extinction debt resulting from historical logging of large trees that yielded long-term declines in old-forest species populations even after policies protecting large trees were enacted, highlighting an urgent need to protect existing old-forest habitat and potential large tree refugia (Lindenmayer et al. 2014). Indeed, national and international environmental legislation often do not emphasize the protection of large trees and old-forest ecosystems (e.g., the European Union Habitats Directive; EU, 1992).

Regional-scale plans to protect and restore old-forest ecosystems allow exceptions to rules limiting removal of large old trees to meet needs for equipment operability in forest restoration projects (e.g., USFS, 2004), and the sale of larger trees is necessary to offset operational costs of ecological restoration activities in heavily managed or degraded forests ecosystems (North et al. 2015a). Therefore, alternative approaches for funding restoration may be required to prevent further large tree loss, which may lead to ecosystem collapse in landscapes with significant legacies of exploitive land use (Burns et al. 2015, Lindenmayer et al. 2016). Despite these global challenges and conservation gaps, an emerging paradigm is to emphasize highly targeted and fine-scale conservation of large old trees as small (or sometimes individual) natural features (Lindenmayer 2017). Policies that emphasize the protection as well as the social and ecological value of individual large old trees will offer a new hope for the perpetuity of old-forest ecosystems and the increasingly rare biodiversity that depends on them.

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Tables

Table 1. Median (SD) proportion of a spotted owl territory[a] containing GNN structure variables used to assess local extinction dynamics on four study areas[b] in the Sierra Nevada, CA, USA. The number of spotted owl territories identified on each study area is shown in the bottom row of the table.

Variable	Study area			
	LAS	ELD	SIE	SKC
Large trees[c]	0.07 (0.05)	0.11 (0.06)	0.13 (0.11)	0.33 (0.19)
High canopy cover[d]	0.46 (0.16)	0.54 (0.14)	0.25 (0.16)	0.48 (0.16)
Large trees and high canopy cover	0.03 (0.05)	0.06 (0.05)	0.04 (0.08)	0.19 (0.14)
Large trees and medium canopy cover	0.02 (0.02)	0.02 (0.03)	0.05 (0.06)	0.10 (0.08)
Medium trees and high canopy cover	0.28 (0.12)	0.32 (0.09)	0.15 (0.10)	0.18 (0.12)
	n = 90	*n* = 74	*n* = 66	*n* = 45

[a] territory areas (ha) for each study area were as follows: LAS (639.4), ELD (399.5), SIE (301.6), and SKC (254.3) (Tempel et al., 2016).

[b] study area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon.

[c] summed across all canopy cover classes;

[d] summed across all tree size classes

Table 2. Estimates[a] of model parameters[b] and occupancy trends[c] for California spotted owls on four study areas in the Sierra Nevada, CA, USA.

Study area	α	β_x	β_x^2	$\hat{\bar{\lambda}}$	Δ_k
LAS	−2.35 [−2.74, −1.96]	−10.58 [−18.68, −2.48]	-	0.991 [0.9827, 0.9997]	0.853 [0.720, 0.987] †
ELD	−2.04 [−2.58, −1.50]	−11.84 [−20.25, −3.43][d]	-	0.983 [0.9733, 0.9918]	0.728 [0.601, 0.855] †
SIE	−1.45 [−1.82, −1.08]	−26.24 [−36.28, −16.19]	-	0.981 [0.9717, 0.9904]	0.709 [0.583, 0.834] †
SKC	−1.47 [−2.08, −0.87]	−15.66 [−24.85, −6.47]	24.30 [1.86, 46.74]	1.005 [0.9997, 1.0105]	1.096 [0.990, 1.202] *

[a] numbers square brackets represents the lower and upper boundaries of 95% confidence intervals for the point estimate, which precedes the square brackets.

[b] α = intercept, β_x = model coefficients for the variable (x) representing the proportion of a spotted owl territory containing large trees and high canopy cover

[c] $\hat{\bar{\lambda}}$ = geometric mean of the annual rate of change in occupancy, Δ_k = realized change in occupancy (ψ_k/ψ_1) where k is the number of years in the study. Symbols following estimates and confidence intervals for Δ_k indicate groups resulting from pairwise comparisons where estimates that share the same symbol had Δ_k estimates that were not statistically different from one another at the $\alpha = 0.05$ level.

[d] $\beta_{\ln(x)}$

Figure legends

Figure 1. Locations of owl territories across the four spotted owl study areas in the Sierra Nevada, California, USA.

Figure 2. An example showing how we produced covariates representing spatial intersections between GNN-derived canopy cover and tree size classes by overlaying classified pixels using a GIS. Here, we see the high canopy cover class (>70% canopy cover) and the large tree size class (≥ 61 cm dbh) combining in a spatial intersection (∩) to produce a covariate called "large trees and high canopy cover" for an example spotted owl territory.

Figure 3. The relationship between large tree/high canopy cover forest and spotted owl occupancy dynamics. The left column of panels shows: (*i*) the modelled relationship between spotted owl territory extinction probability and the proportion of an owl territory containing forests with large trees and high canopy cover (x), where the solid coloured lines represents the modelled relationship and the dashed lines represent ± 1 SE, plotted over the range of observed values, and; (*ii*) the distribution of values for x present on each study area, which are represented by horizontal boxplots (corresponding to the x-axis). The right column of panels shows: (*i*) annual estimates of derived occupancy (solid circles) from a fully time-varying model (see Methods) on the primary (left) axis, where the solid line represents a linear trend to emphasize population trajectories (see Table 2) over the 19-year study period, and; (*ii*) the median annual proportion of large trees and high canopy cover (x; open circles) on the secondary (right) axis, where the dashed line represents a linear trend to emphasize that this variable did not decline on national forests over the 1993-2011 study period (also see Fig. S2).

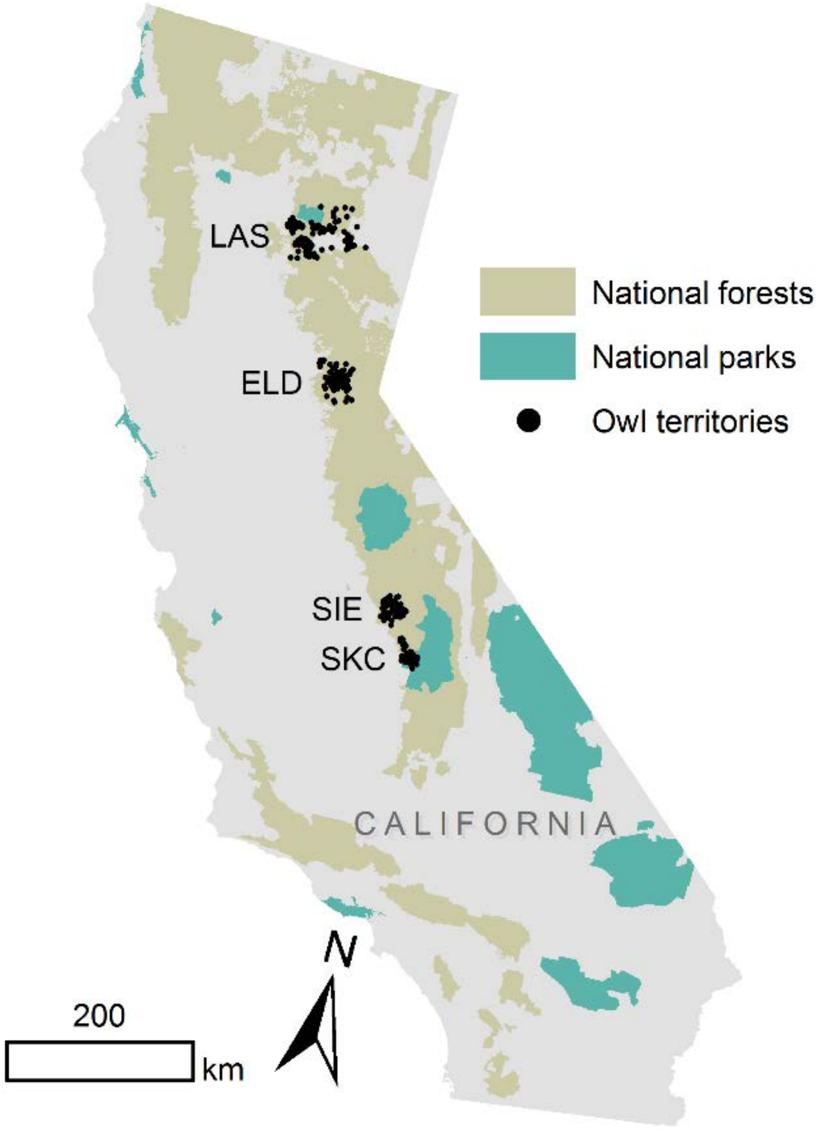
LAS
ELD
SIE
SKC
National forests
National parks
Owl territories
CALIFORNIA
N
200
km

Figure 1

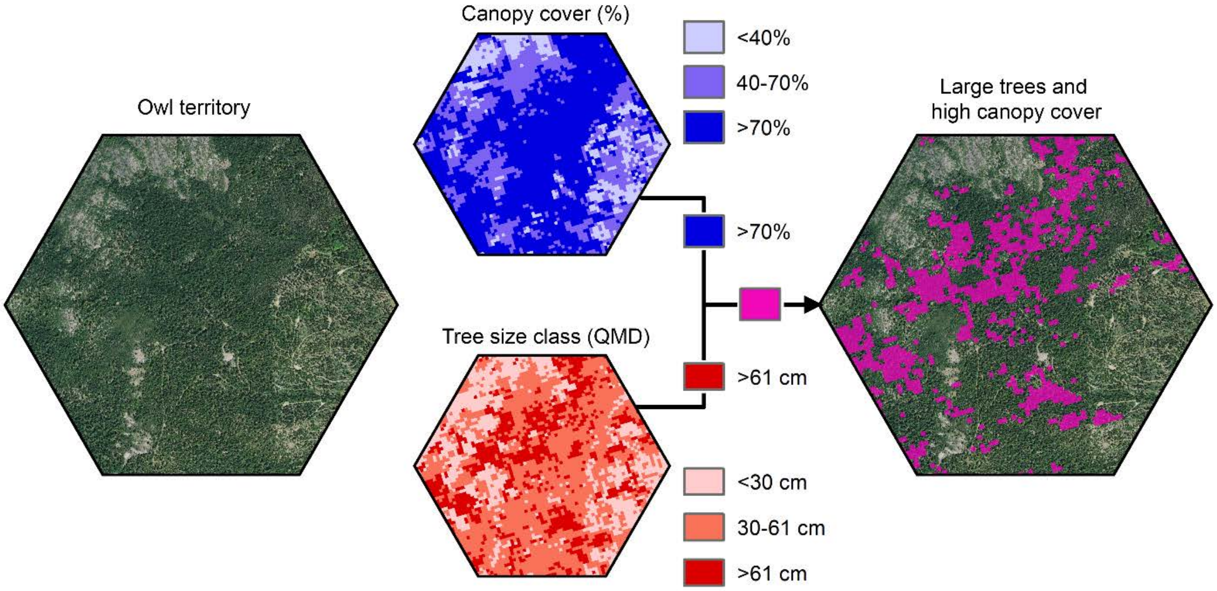
Owl territory
Canopy cover (%)
<40%
40-70%
>70%
>70%
Tree size class (QMD)
>61 cm
<30 cm
30-61 cm
>61 cm
Large trees and
high canopy cover

Figure 2

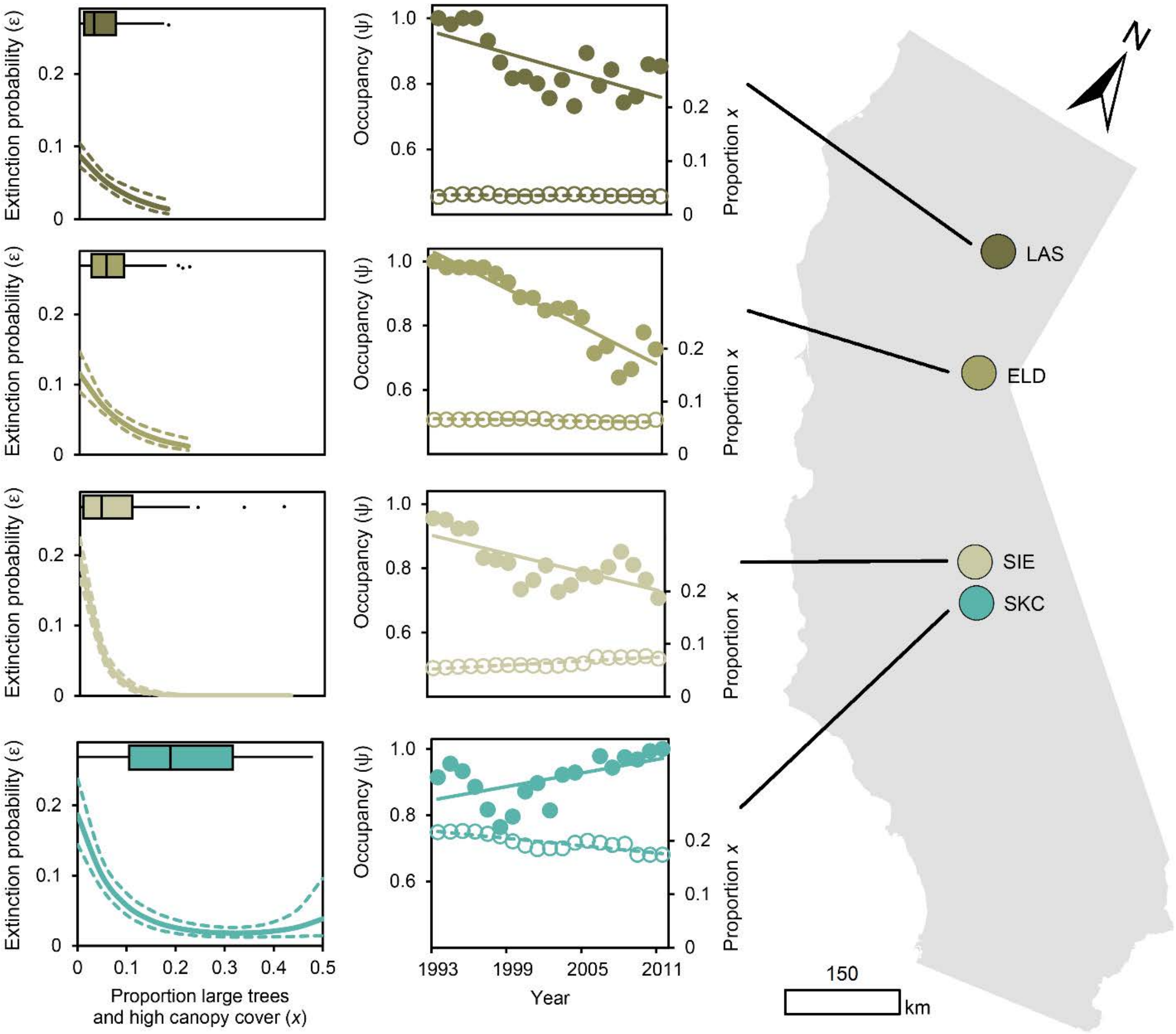
Extinction probability (ε)
0
0.1
0.2
Proportion large trees
and high canopy cover (x)
0
0.1
0.2
0.3
0.4
0.5
Occupancy (ψ)
0.6
0.8
1.0
Proportion x
0
0.1
0.2
Year
1993
1999
2005
2011
LAS
ELD
SIE
SKC
N
150
km

Figure 3

Supplementary materials

Table S1. Models relating tree size and canopy cover classes to California spotted owl territory extinction dynamics from 1993-2011 in the Sierra Nevada, CA, USA. Linear, logarithmic, and quadratic forms of each variable were evaluated; we displayed only the form for each variable that received the most empirical support in preliminary analyses. Study area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon. The symbol "∩" indicates the intersection (spatial co-occurrence) of two variables.

LAS	AIC	ΔAIC	w_i	K
ln[large trees]	6741.75	0.00	0.40	42
large trees ∩ high canopy	6742.41	0.66	0.29	42
quad[high canopy]	6742.49	0.74	0.27	43
medium trees ∩ high canopy	6747.00	5.25	0.03	42
null	6749.08	7.33	0.01	41
large trees ∩ medium canopy	6750.43	8.68	0.01	42
year	6758.08	16.33	0.00	58

ELD	AIC	ΔAIC	w_i	K
ln[large trees ∩ high canopy]	4153.82	0.00	0.88	42
ln[large trees]	4160.21	6.39	0.04	42
high canopy	4160.44	6.62	0.03	42
null	4161.54	7.72	0.02	41
ln[medium trees ∩ high canopy]	4161.94	8.12	0.02	42
quad[large trees ∩ medium canopy]	4162.62	8.80	0.01	43
year	4163.05	9.23	0.01	58

SIE	AIC	ΔAIC	w_i	K
large trees ∩ high canopy	5319.37	0.00	0.97	28
ln[large trees]	5326.53	7.16	0.03	28
high canopy	5342.21	22.84	0.00	28
quad[medium trees ∩ high canopy]	5343.98	24.61	0.00	29
quad[large trees ∩ medium canopy]	5348.72	29.35	0.00	29
null	5368.04	48.67	0.00	27
year	5389.43	70.06	0.00	44

SKC	AIC	ΔAIC	w_i	K
quad[large trees ∩ high canopy]	4161.14	0.00	0.96	46

ln[large trees]	4168.76	7.62	0.02	45
quad[large trees ∩ medium canopy]	4170.25	9.11	0.01	46
high canopy	4171.00	9.86	0.01	45
quad[medium trees ∩ high canopy]	4173.72	12.58	0.00	46
null	4178.20	17.06	0.00	44
year	4189.29	28.15	0.00	61

Notes: AIC, Akaike information criterion; ΔAIC, difference in AIC compared to the model with the lowest AIC value; w_i, Akaike weight; *K*, number of parameters in the model.

Table S2. Coefficient estimates, standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits for the intercept (α) and covariates (β) used to model extinction probability (i.e., the final modeling stage) of spotted owls in the Sierra Nevada, CA. The symbol "∩" indicates the intersection (spatial co-occurrence) of two variables.

	ΔAIC	α				β_x				β_x^2			
Lassen (LAS)		**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**
ln[large trees]	0.00	−2.05	0.26	−2.56	−1.54	−10.95	3.88	−18.55	−3.34	-	-	-	-
large trees ∩ high canopy	0.66	−2.35	0.20	−2.74	−1.96	−10.58	4.13	−18.68	−2.48	-	-	-	-
quad[high canopy]	0.74	−3.86	2.06	−7.89	0.17	9.38	10.92	−12.02	30.79	−14.61	13.61	−41.29	12.07
medium trees ∩ high canopy	5.25	−2.07	0.37	−2.79	−1.34	−2.66	1.40	−5.39	0.08	-	-	-	-
large trees ∩ medium canopy	8.68	−2.62	0.23	−3.08	−2.16	−5.62	7.25	−19.83	8.58	-	-	-	-

	ΔAIC	α				β_x				β_x^2			
Eldorado (ELD)		**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**
ln[large trees ∩ high canopy]	0.00	−2.04	0.28	−2.58	−1.50	−11.84	4.29	−20.25	−3.43	-	-	-	-
ln[large trees]	6.39	−2.17	0.36	−2.87	−1.46	−5.79	3.27	−12.20	0.61	-	-	-	-
high canopy	6.62	−1.77	0.57	−2.89	−0.65	−2.03	1.15	−4.29	0.23	-	-	-	-
ln[medium trees ∩ high canopy]	8.12	−1.94	0.68	−3.27	−0.62	−3.08	2.50	−7.98	1.81	-	-	-	-
quad[large trees ∩ medium canopy]	8.80	−2.50	0.33	−3.15	−1.86	−17.79	14.26	−45.74	10.15	158.65	96.26	−30.02	347.32

	ΔAIC	α				β_x				β_x^2			
Sierra (SIE)		**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**
large trees ∩ high canopy	0.00	−1.45	0.19	−1.82	−1.08	−26.21	5.17	−36.35	−16.07	-	-	-	-
ln[large trees]	7.16	−1.05	0.25	−1.54	−0.57	−13.93	2.54	−18.91	−8.96	-	-	-	-
high canopy	22.84	−1.44	0.23	−1.89	−0.99	−5.30	1.08	−7.41	−3.18	-	-	-	-
ln[medium trees ∩ high canopy]	24.61	−1.55	0.22	−1.98	−1.13	−9.12	1.90	−12.83	−5.40	-	-	-	-
quad[large trees ∩ medium canopy]	29.35	−1.54	0.23	−1.99	−1.08	−30.74	7.31	−45.08	−16.41	104.81	34.30	37.58	172.05

Sequoia-Kings Canyon (SKC)	ΔAIC	**α**				**β_x**				**β_x^2**			
		estimate	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**	**estimate**	**SE**	**LCL**	**UCL**
quad[large trees ∩ high canopy]	0.00	−1.47	0.31	−2.08	−0.87	−15.66	4.69	−24.85	−6.46	24.30	11.45	1.86	46.75
ln[large trees]	7.62	−1.84	0.35	−2.52	−1.16	−4.66	1.37	−7.34	−1.99	-	-	-	-
quad[large trees ∩ medium canopy]	9.11	−1.88	0.34	−2.55	−1.21	−25.08	7.09	−38.96	−11.19	80.40	23.15	35.02	125.77
high canopy	9.86	−1.38	0.51	−2.38	−0.38	−3.89	1.26	−6.37	−1.42	-	-	-	-
quad[medium trees ∩ high canopy]	12.58	−1.58	0.46	−2.49	−0.67	−17.02	5.76	−28.30	−5.74	34.71	13.32	8.61	60.82

Table S3. Full model selection results from the multi-stage modeling procedure. The top model from each stage was advanced to the subsequent stage as the base model. Covariate abbreviations are as follows: lt=large trees (≥61cm dbh), mt=medium trees (30-61cm dbh), dc=dense canopy (≥70%), mc=medium canopy (40-70%), year=annually varying time effect, T=linear time trend, TT=quadratic time trend, lnT=logarithmic time trend, repro=detection is different for reproducing owls, initial=detection is different after the first within-year detection at a site, survey=detection is different for each within-season survey period, (.)=intercept-only. The symbol "∩" indicates the intersection (spatial co-occurrence) of two variables.

Lassen (LAS)							
within-season detection probability (*p*)							
ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+initial	6758.08	0	1	58
(.)	year	year	year, repro+survey	6823.35	65.27	0	66
(.)	year	year	year, repro+TT	6833.84	75.76	0	59
(.)	year	year	year, repro+T	6873.7	115.62	0	58
(.)	year	year	year, repro	6880.33	122.25	0	57
(.)	year	year	year, repro+lnT	6881.06	122.98	0	58
(.)	year	year	year, initial	7014.76	256.68	0	57
(.)	year	year	year, survey	7071.63	313.55	0	65
(.)	year	year	year, T	7123.83	365.75	0	57
(.)	year	year	year, (.)	7131.23	373.15	0	56
(.)	year	year	year, lnT	7131.87	373.79	0	57
among-season detection probability + covariates (*p*)							
ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+initial	6758.08	0	0.9968	58
(.)	year	year	lnT, repro+initial	6770.06	11.98	0.0025	41
(.)	year	year	TT, repro+initial	6773.74	15.66	0.0004	42
(.)	year	year	T, repro+initial	6774.25	16.17	0.0003	41

(.)	year	year	(.), repro+initial	6789.85	31.77	0	40
(.)	year	year	lt, repro+initial	6830.04	71.96	0	41
(.)	year	year	dc, repro+initial	6831.07	72.99	0	41
(.)	year	year	mt∩dc + lt∩mc + lt∩dc, repro+initial	6832.99	74.91	0	43

initial occupancy probability (ψ_1)

ψ_1	γ	ε	p	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+initial	6758.08	0	0.3522	58
ln[lt∩mc]	year	year	year, repro+initial	6760.08	2	0.1296	59
lt∩dc	year	year	year, repro+initial	6760.08	2	0.1296	59
mt∩dc	year	year	year, repro+initial	6760.08	2	0.1296	59
lt	year	year	year, repro+initial	6760.08	2	0.1296	59
dc	year	year	year, repro+initial	6760.08	2	0.1296	59

extinction probability (ε)

ψ_1	γ	ε	p	AIC	ΔAIC	w_i	K
(.)	year	ln[lt]	year, repro+initial	6741.75	0	0.3967	42
(.)	year	lt∩dc	year, repro+initial	6742.41	0.66	0.2852	42
(.)	year	quad[dc]	year, repro+initial	6742.49	0.74	0.274	43
(.)	year	mt∩dc	year, repro+initial	6747	5.25	0.0287	42
(.)	year	(.)	year, repro+initial	6749.08	7.33	0.0102	41
(.)	year	lt∩mc	year, repro+initial	6750.43	8.68	0.0052	42
(.)	year	year	year, repro+initial	6758.08	16.33	0.0001	58

Eldorado (ELD)

within-season detection probability (p)

ψ_1	γ	ε	p	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+initial	4163.05	0.00	1.000	58
(.)	year	year	year, repro+survey	4307.27	144.22	0.000	66
(.)	year	year	year, repro+T	4309.20	146.15	0.000	58
(.)	year	year	year, repro+lnT	4310.45	147.40	0.000	58

(.)	year	year	year, repro+TT	4310.83	147.78	0.000	59
(.)	year	year	year, repro	4326.19	163.14	0.000	57
(.)	year	year	year, initial	4351.89	188.84	0.000	57
(.)	year	year	year, survey	4491.49	328.44	0.000	65
(.)	year	year	year, T	4498.21	335.16	0.000	57
(.)	year	year	year, lnT	4499.84	336.79	0.000	57
(.)	year	year	year, (.)	4516.76	353.71	0.000	56

among-season detection probability + covariates (*p*)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+initial	4163.05	0	0.9418	58.00
(.)	year	year	T, repro+initial	4169.74	6.69	0.0332	41.00
(.)	year	year	TT, repro+initial	4171.15	8.1	0.0164	42.00
(.)	year	year	lnT, repro+initial	4172.44	9.39	0.0086	41.00
(.)	year	year	mt∩dc+lt∩mc+lt∩dc, repro+initial	4191.5	28.45	0	43.00
(.)	year	year	(.), repro+initial	4191.53	28.48	0	40.00
(.)	year	year	dc, repro+initial	4191.86	28.81	0	41.00
(.)	year	year	lt, repro+initial	4193.44	30.39	0	41.00

initial occupancy probability (ψ_1)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+initial	4420.52	0	0.3522	58
lt∩dc	year	year	year, repro+initial	4422.52	2	0.1296	59
lt∩mc	year	year	year, repro+initial	4422.52	2	0.1296	59
mt∩dc	year	year	year, repro+initial	4422.52	2	0.1296	59
lt	year	year	year, repro+initial	4422.52	2	0.1296	59
dc	year	year	year, repro+initial	4422.52	2	0.1296	59

extinction probability (ε)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	ln[lt∩dc]	year, repro+initial	4153.82	0	0.8788	42

(.)	year	ln[lt]	year, repro+initial	4160.21	6.39	0.036	42
(.)	year	dc	year, repro+initial	4160.44	6.62	0.0321	42
(.)	year	(.)	year, repro+initial	4161.54	7.72	0.0185	41
(.)	year	ln[mt∩dc]	year, repro+initial	4161.94	8.12	0.0152	42
(.)	year	quad[lt∩mc]	year, repro+initial	4162.62	8.8	0.0108	43
(.)	year	year	year, repro+initial	4163.05	9.23	0.0087	58

Sierra (SIE)

within-season detection probability (*p*)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+TT	5409.06	0.00	0.997	59
(.)	year	year	year, repro+survey	5420.74	11.68	0.003	70
(.)	year	year	year, repro+T	5433.64	24.58	0.000	58
(.)	year	year	year, repro+lnT	5470.03	60.97	0.000	58
(.)	year	year	year, repro+initial	5537.40	128.34	0.000	58
(.)	year	year	year, repro	5564.66	155.60	0.000	57
(.)	year	year	year, survey	5593.52	184.46	0.000	69
(.)	year	year	year, T	5619.05	209.99	0.000	57
(.)	year	year	year, lnT	5661.57	252.51	0.000	57
(.)	year	year	year, initial	5741.33	332.27	0.000	57
(.)	year	year	year, (.)	5770.69	361.63	0.000	56

among-season detection probability + covariates (*p*)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	dc, repro+TT	5392.88	0	0.6368	42.00
(.)	year	year	mt∩dc + lt∩mc + lt∩dc, repro+TT	5394.04	1.16	0.3565	44.00
(.)	year	year	lt, repro+TT	5402.07	9.19	0.0064	42.00
(.)	year	year	year, repro+TT	5409.06	16.18	0.0002	59.00
(.)	year	year	lnT, repro+TT	5411.52	18.64	0.0001	42.00
(.)	year	year	T, repro+TT	5414.44	21.56	0	42.00
(.)	year	year	TT, repro+TT	5415.83	22.95	0	43.00

(.)	year	year	(.), repro+TT	5433.1	40.22	0	41.00

initial occupancy probability (ψ_1)

ψ_1	γ	ε	p	AIC	ΔAIC	w_i	K
quad[mt∩dc]	year	year	dc, repro+TT	5389.43	0	0.2875	44
quad[dc]	year	year	dc, repro+TT	5389.44	0.01	0.2861	44
quad[lt∩mc]	year	year	dc, repro+TT	5389.44	0.01	0.2861	44
lt∩dc	year	year	dc, repro+TT	5392.47	3.04	0.0629	43
lt	year	year	dc, repro+TT	5392.84	3.41	0.0509	43
(.)	year	year	dc, repro+TT	5392.88	3.45	0.0512	42

extinction probability (ε)

ψ_1	γ	ε	p	AIC	ΔAIC	w_i	K
quad[mt∩dc]	year	lt∩dc	dc, repro+TT	5319.37	0	0.9729	28
quad[mt∩dc]	year	ln[lt]	dc, repro+TT	5326.53	7.16	0.0271	28
quad[mt∩dc]	year	dc	dc, repro+TT	5342.21	22.84	0	28
quad[mt∩dc]	year	quad[mt∩dc]	dc, repro+TT	5343.98	24.61	0	29
quad[mt∩dc]	year	quad[lt∩mc]	dc, repro+TT	5348.72	29.35	0	29
quad[mt∩dc]	year	(.)	dc, repro+TT	5368.04	48.67	0	27
quad[mt∩dc]	year	year	dc, repro+TT	5389.43	70.06	0	44

Sequoia-Kings Canyon (SKC)

within-season detection probability (p)

ψ_1	γ	ε	p	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+TT	4192.14	0.00	0.900	59
(.)	year	year	year, repro+T	4197.16	5.02	0.073	58
(.)	year	year	year, repro+survey	4199.18	7.04	0.027	70
(.)	year	year	year, repro+lnT	4215.99	23.85	0.000	59
(.)	year	year	year, repro+initial	4219.18	27.04	0.000	58
(.)	year	year	year, repro	4250.52	58.38	0.000	57
(.)	year	year	year, T	4365.19	173.05	0.000	57
(.)	year	year	year, survey	4368.48	176.34	0.000	69

(.)	year	year	year, lnT	4384.06	191.92	0.000	58
(.)	year	year	year, initial	4386.10	193.96	0.000	57
(.)	year	year	year, (.)	4423.27	231.13	0.000	56

among-season detection probability + covariates (*p*)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
(.)	year	year	year, repro+TT	4192.14	0	0.7736	59.00
(.)	year	year	mt∩dc + lt∩mc+lt∩dc, repro+TT	4194.72	2.58	0.213	44.00
(.)	year	year	lt, repro+TT	4201.96	9.82	0.0057	42.00
(.)	year	year	dc, repro+TT	4202.11	9.97	0.0053	42.00
(.)	year	year	T, repro+TT	4205.59	13.45	0.0009	42.00
(.)	year	year	(.), repro+TT	4206.67	14.53	0.0005	41.00
(.)	year	year	TT, repro+TT	4206.8	14.66	0.0005	43.00
(.)	year	year	lnT, repro+TT	4207.1	14.96	0.0004	42.00

initial occupancy probability (ψ_1)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
quad[lt∩mc]	year	year	year, repro+TT	4189.29	0	0.5114	61
ln[dc]	year	year	year, repro+TT	4191.58	2.29	0.1628	60
(.)	year	year	year, repro+TT	4192.14	2.85	0.123	59
lt	year	year	year, repro+TT	4193	3.71	0.08	60
lt∩dc	year	year	year, repro+TT	4193.15	3.86	0.0742	60
ln[mt∩dc]	year	year	year, repro+TT	4194	4.71	0.0485	60

extinction probability (ε)

ψ_1	γ	ε	*p*	AIC	ΔAIC	w_i	K
quad[lt∩mc]	year	quad[lt∩dc]	year, repro+TT	4161.14	0	0.9597	46
quad[lt∩mc]	year	ln[lt	year, repro+TT	4168.76	7.62	0.0213	45
quad[lt∩mc]	year	quad[lt∩mc]	year, repro+TT	4170.25	9.11	0.0101	46
quad[lt∩mc]	year	dc	year, repro+TT	4171	9.86	0.0069	45
quad[lt∩mc]	year	quad[mt∩dc]	year, repro+TT	4173.72	12.58	0.0018	46

quad[lt∩mc]	year	(.)	year, repro+TT	4178.2	17.06	0.0002	44
quad[lt∩mc]	year	year	year, repro+TT	4189.29	28.15	0	61

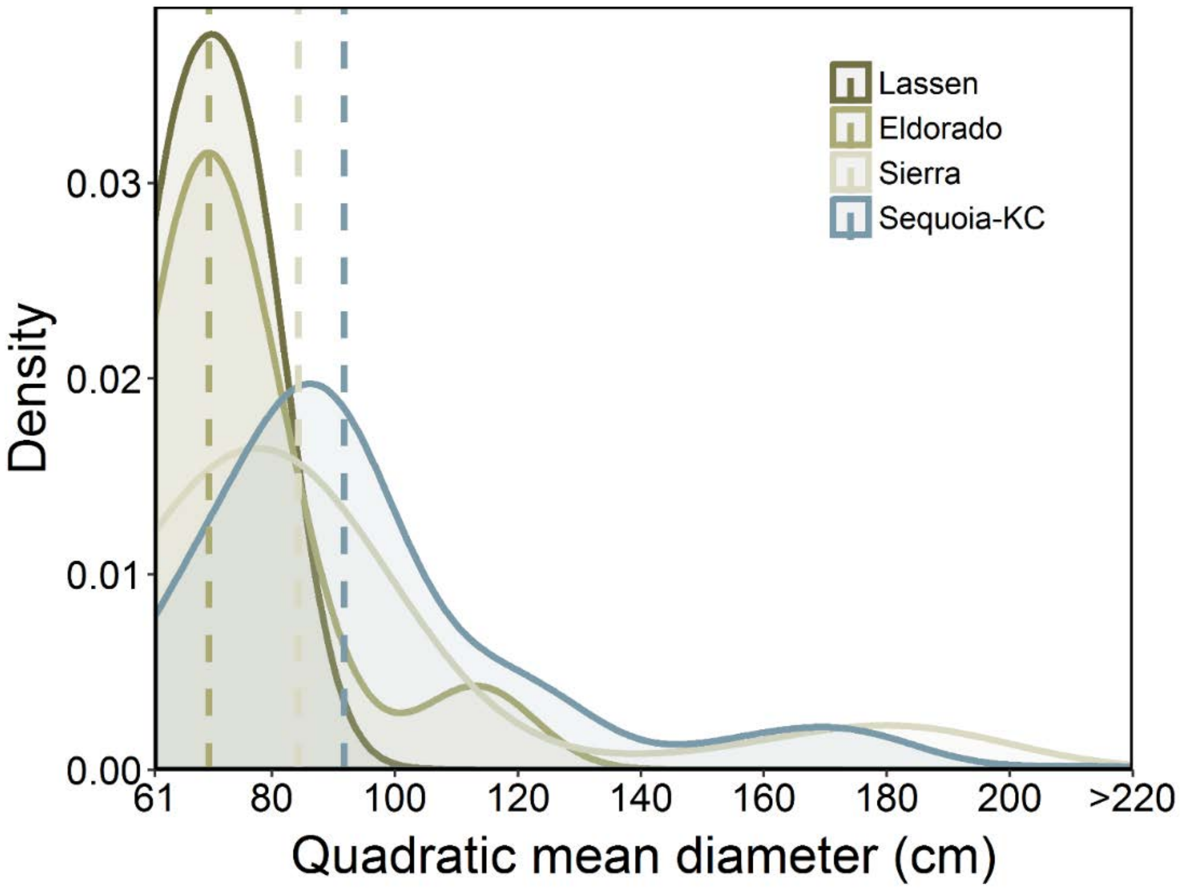

Figure S1. Density plot of quadratic mean diameter (QMD) values in the large tree class (≥ 61 cm) when co-occurring with ≥ 70% canopy cover in spotted owl territories for the year 1993. The median QMD for each study area is represented by the vertical dashed line. QMD exceeded 220 cm in some cases (maximum value 279 cm, occurring on both SIE and SKC), but we truncated the *x*-axis to improve visualization. Units of observation were 30×30 m grid cells.

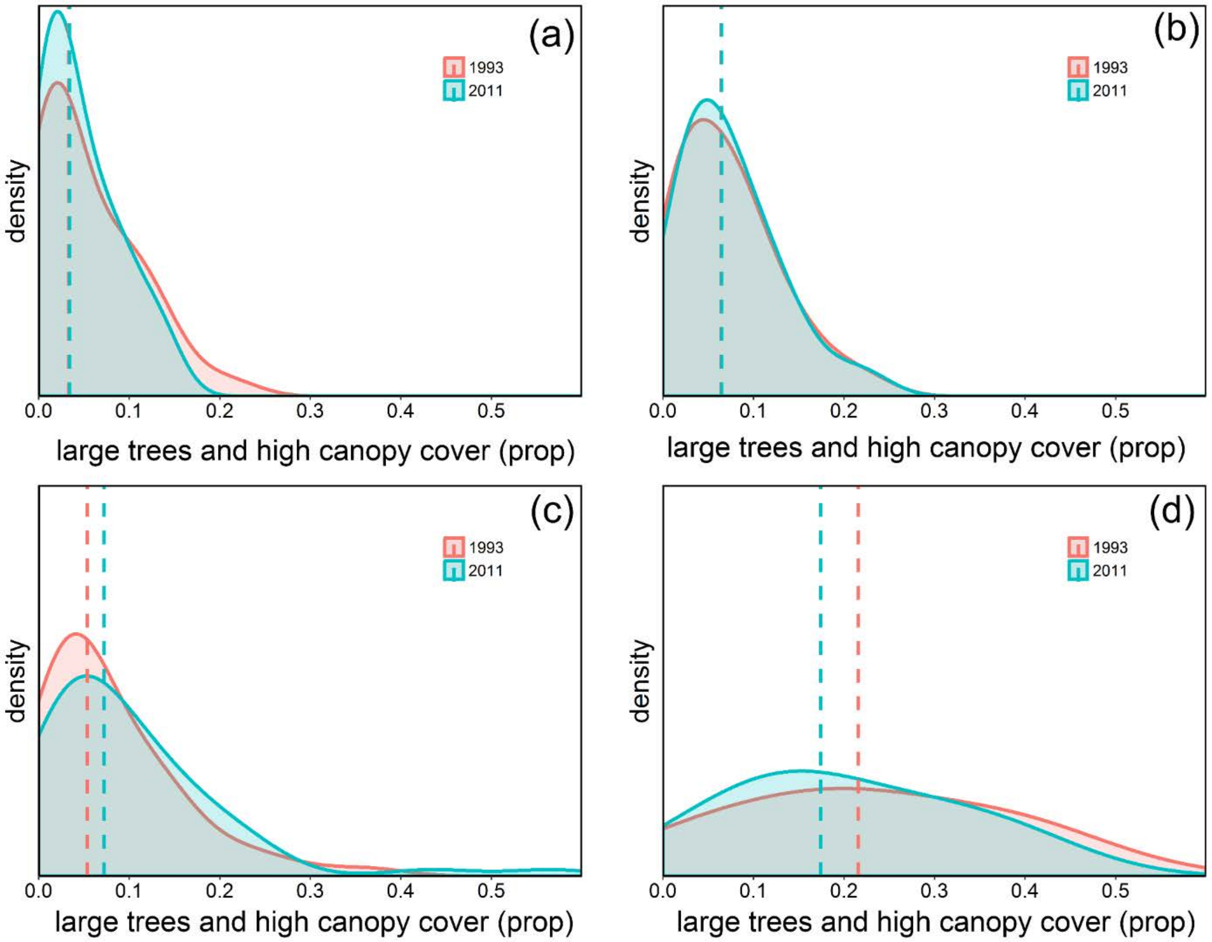

Figure S2. Density plots of the proportion of individual owl territories containing forests with large tree class (≥ 61 cm) and high canopy cover (≥ 70% canopy cover) for the year 1993 and 2011 for (a) LAS, (b) ELD, (c) SIE, and (d) SKC. Dashed vertical lines indicate the median value for each year. In panel (a) and (b), only one dashed line appears because the second line is approximately the same value. Units of observation were individual owl territories.

Chapter 3 - Bioregional-scale forest restoration limits megafires and supports rare species conservation in a changing climate

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Abstract

Climate change and fire suppression have altered disturbance regimes in forest ecosystems worldwide. In western North American dry forests, large-scale ecological restoration efforts may reduce severe fires and increase forest resilience to climate change, but restoration techniques may remove key structural habitat elements used by rare and declining old-forest species. We simulated bioregional-scale effects of forest restoration (i.e., fuel reduction treatments) on (1) future severe fire activity and (2) population dynamics of a focal old-forest species, the spotted owl (*Strix occidentalis*) in the Sierra Nevada, USA. We developed a predictive model of future severe fire coupled with a spatial occupancy model for spotted owls, with behavior of both models linked to fuel treatment location and extent. Our findings suggest restoring historical forest structure may mitigate future severe fire activity in the Sierra Nevada as the climate warms and dries, particularly when fuel treatments occur within spotted owl territories. On average, benefits provided by simulated fuel treatments to spotted owls (reducing severe fire activity) exceeded potential costs (direct habitat alteration) by mid-century at the bioregional scale. However, relative costs and benefits of fuel treatments to owls vary at finer scales, which will help to inform targeted restoration planning. Our study suggests that when large, old trees are maintained, fuel reduction and forest restoration in the Sierra Nevada is likely to benefit both old-forest species and forest ecosystem resilience under climate change.

Introduction

Climate change profoundly affects the distribution, structure, and disturbance regimes of forests worldwide (Seidl et al. 2017). Humans also continue to shape forests globally, such as in the seasonally dry forests of western North America, where a century of fire suppression and large-tree logging has changed forests from historical conditions. Forests that were historically "open", with low tree densities maintained by frequent low- and mixed-severity fire regimes, now have high densities of small and medium-sized trees and a deficit of large trees (Safford and Stevens 2017). Consequently, these forests are at increased risk of high-severity fire and decreased resilience, defined as the capacity of an ecosystem to recover from disturbance while maintaining its characteristic structure and function (Hessburg et al. 2016). These altered forest structures—combined with warmer and drier conditions associated with climate change—have led to larger and more severe fires (Steel et al. 2015, Abatzoglou and Williams 2016, Westerling 2016, Stevens et al. 2017) and widespread drought-related tree mortality (Asner et al. 2015b, Diffenbaugh et al. 2015, Fettig et al. 2019) in western dry forests with substantial impacts both to humans and forests. While frequent low- and mixed-severity fire provides key ecological benefits to these fire-adapted systems, large areas of severe fire pose a significant threat to the persistence of these ecosystems and the species and services they support (Jones et al. 2016a). Post-disturbance forest regeneration may fail when disturbances exceed the natural range of system variability, which could lead to the persistent loss of forest ecosystems in some regions (Johnstone et al. 2016, Stevens et al. 2017, Shive et al. 2018). Both the current state of western North American dry forests and the potential for rapid changes in the near future that will lead to ecological novelty and altered provision of ecosystem goods and services to society are broadly considered to be undesirable (Rissman et al. 2018).

Landscape-scale fuels reduction and forest restoration treatments (Agee and Skinner 2005, Stephens et al. 2012) have the potential to increase dry forest ecosystem resilience (Hessburg et al. 2016). Treatments reduce accumulation and increase heterogeneity of landscape fuels through thinning and prescribed fire (Knapp et al. 2017), and promote the development of large, fire-resistant trees (Agee and Skinner 2005) that reduce risk of severe fire and drought-related tree mortality (Bradford and Bell 2016, Lydersen et al. 2017). However, treatments may simplify forests inhabited by rare and declining old-forest species that depend on large, old trees, high canopy cover, and complex vertical structure (Tempel et al. 2014a) and concern over these species and their habitat has limited the pace and scale of forest restoration efforts. Thus, restoring dry forest ecosystems while safeguarding vulnerable populations of old-forest species presents a conundrum to natural resource agencies: how can treatments occur without jeopardizing rare species that use “departed” forest conditions (Peery et al. 2017)?

A key to solving this conundrum is to first understand whether the potential negative impacts of treatments on old-forest species are outweighed by benefits to these species achieved by reducing habitat loss to future severe wildfires (Scheller et al. 2011, Tempel et al. 2015b, Stephens et al. 2016). Yet, our ability to model these theoretical trade-offs has been challenged by the following factors: existing process-based fire simulation models (e.g., LANDIS-II, FARSITE, FlamMap) are unable to reproduce large patches of severe fire that are becoming more common in western North America (Tempel et al. 2015b, Coen et al. 2018), our empirical understanding of the response of old-forest species to treatments and fire has, until recently, been limited (Tempel et al. 2016), and modeling wildfire and wildlife population dynamics at large spatial extents is computationally intensive (Scheller et al. 2011). To address these limitations, we used extreme value theory and random forests to develop a novel, empirically-based probabilistic fire model (hereafter, "fire model") that generated robust, fine-grain (30-m) predictions of future severe fire activity linked to changing climate and fuels conditions. Then, we modeled potential effects of fuels reduction treatments and future severe wildfire activity on old-forest species by simulating changes to fine-scale forest structure within a sensitivity analysis framework to bracket uncertainty. In doing so, we assessed the following central question: Do large-scale fuels reduction and forest restoration practices support or hinder conservation of declining old-forest species in the Sierra Nevada in a changing climate?

We coupled the fire model with a spatial occupancy model ("population model") (Chandler et al. 2015) to evaluate relative and scale-dependent future effects of treatment and severe fire on an old-forest species, the spotted owl (*Strix occidentalis*), across the Sierra Nevada, USA (~120,000 km^2). We fit the two empirical models independently over the period for which data existed (1984-2015), but we linked them together during forward simulations of treatment- and climate-induced changes in patterns of severe fire and owl population dynamics (through 2064) (Fig. S1). Climate change effects were assessed using two global circulation models, CanESM2 (relatively modest future warming and drying) and CNRM-CM5 (more extreme future warming and drying), to bracket uncertainty. The fire model produced annual spatially-explicit predictions of severe fire occurrence across the Sierra Nevada through mid-century (2064) that we introduced to the population model over the forecasting period; then the behavior of both models was linked to a factorial design that systematically varied fuel treatment total extent and location across the landscape. Fuel treatments were simulated across all landscapes deemed to be "treatable" (i.e., on public lands without significant operational constraints) (North et al. 2015a) with total treatment extent varying by equal intervals (18%, 36%, 54%, 72%, 90%) (Fig. S2). Treatable lands (i.e. 100% of "treatable" area) comprised ~35%

of the entire Sierra Nevada landscape (Fig. S4). A second set of treatment scenarios were then developed in which the same total landscape extent was treated, but treatments were excluded from owl territories (hexagons approximating the area defended by territorial individuals) (Jones et al. 2018) (Figs. S2 and S3). This design allowed us to explore how reducing fuel in owl territories affected future severe fire activity and assess the net costs and benefits of treatment to owls.

Methods

Fuels

Within the fire model, fuels were represented by fire regime current condition class (hereafter, "FRCC") (Schmidt et al. 2002). FRCC describes ecosystem departure from historical conditions in terms of vegetation structure and composition and is an important predictor of fire activity in the region (Keyser and Leroy Westerling 2017, Keyser and Westerling 2019) (Supplemental materials). Although other factors can alter vegetation conditions, fire suppression was the principal driver of forest change in the Sierra Nevada in the past century (Collins et al. 2017). We assumed that fuel reduction treatments, however implemented, would modify FRCC from a departed to non-departed state (Supplemental materials). Fuel treatments were randomly allocated to 30-m pixels in areas of the landscape meeting administrative constraints, with each scenario built sequentially using the previous scenario as a starting point (e.g., the pixels treated in the 18% scenario were nested within the 36% scenario). Within the population model, fuels were represented by canopy continuity of forest vegetation structure variables that strongly predict spotted owl occupancy dynamics (Jones et al. 2018, LEMMA 2018). We assumed that fuels reduction treatments would reduce canopy cover from ≥70% to 40-70% while maintaining large trees, which follows basic principles of restoration treatments (Agee and Skinner 2005, Stephens et al. 2014b). Fuel reduction treatments were introduced in the first year of the forward simulation and altered fuels remained static thereafter. We performed sensitivity analyses by varying the strength of treatment effects on spotted owl habitat (no habitat effects, weak habitat effects, strong habitat effects) to evaluate the degree to which our assumptions might affect inferences. Briefly, ‘no habitat effects’ assumed that treatment in owl territories did not modify large tree/high canopy cover forest; ‘weak habitat effects’ assumed that for each 1-ha treated within an owl territory, 0.25 ha of large tree/high canopy cover forest was changed to large tree/medium canopy forest; ‘strong habitat effects’ assumed that for each 1-ha treated within an owl territory, 1 ha of large tree/high canopy cover forest was changed to large tree/medium canopy forest (Supplemental materials).

Fire model overview

We downloaded fire severity polygons from United States Department of Agriculture Forest Service (USFS) Region 5 that classified burn severity as the percent change in basal area for 1984-2015. We used the 90% basal area (BA90) killed value as our measure of high severity fire occurrence (instead of a lower threshold such as 50% or 75%) for two reasons. First, there was a high certainty that BA90 represented acute ecological change relevant to spotted owls and old-forest ecosystems (JA Fites-Kaufmann, *personal communication*). Second, map accuracy is exceptionally high for BA90 (Miller and Quayle 2015). This fire severity data set was the response variable for both large (LS) and fine scale (FS) fire model development (Fig. S1).

Large scale (LS) fire model

We fit a spatially explicit logistic regression model (LR1) on a 1/16th degree latitude/longitude grid to estimate the monthly probabilities of the occurrence of at least one fire >400-ha as a function of topography, human population, vegetation fraction, and climate using the glm function in R (Westerling 2018) (Supplemental materials, Table S3). Model specifications were compared using AIC to select for parsimonious models despite the presence of spatially auto-correlated variables (Akaike 1974, 1981). Specifications tested here extend models used in (Westerling et al. 2011a) to a finer spatial scale (1/16th degree latitude/longitude grid instead of 1/8th degree). The selected model was validated by applying parameters calculated with the first half of the data (1984-1999) to the full sample, and comparing Spearman's rank correlations over each period with correlations for the model estimated with the full 30-year sample (Westerling 2018).

For each fire >400-ha, the probability of >50-ha burning in BA90 was estimated by fitting a logistic regression (LR2) with climate covariates using the glm function in R. To estimate the conditional extent of BA90 burned area, for each fire with >50-ha BA90 burned, a generalized Pareto distribution (GPD) was fit with climate and FRCC covariates. Large-scale BA90 area burned was simulated for each climate and treatment scenario as follows: first, we repeated random draws from the binomial distribution using probabilities from LR1 to generate large (>400-ha) fire occurrence; second, for each simulated large fire, a random draw from the binomial distribution using probabilities from LR2 was used to generate BA90 occurrence >50-ha; third, for each BA90 occurrence >50-ha, a random draw from the GPD was used to generate total BA90 area.

Fine scale (FS) fire model

We used a presence/absence approach, similar to a species distribution model, to model the probability of high severity fire occurrence across the Sierra Nevada bioregion at 30-m resolution. We chose twenty fires from the fire severity dataset that met our modeling criteria to build the downscaled fire severity model, selecting fires that yielded the most complete coverage of year, ignition month, fire size, and severity (Table S4). Individual pixels were classified as 0 or 1, where 1 represented a pixel that experienced 90% basal area killed (BA90). The training set of fires contained 556,444 pixels: 47.8% had a value of 1, 52.2% had a value of 0.

We used the classification and regression tree model Random Forests to predict occurrence of BA90 pixels on the landscape as a function of topography, vegetation, and fire size. To select the most parsimonious model for BA90 presence, we used the rfUtilities package in R (Murphy et al. 2010, Evans and Murphy 2018). We evaluated model accuracy using Cohen's Kappa and the area under the Receiver Operating Curve (AUC). Using the best-fit model, we produced a set of probability surfaces for seven fire size bins for the Sierra Nevada bioregion (Table S4); each 30-m pixel was assigned a probability of burning at high severity for fires in each fire size bin (Supplemental materials). The inclusion of fire size as a predictor in our classification model necessitated a separate probability surface for each fire size class. The remaining classification variables did not vary temporally so the same set of probability surfaces informed all management and climate change scenarios.

Spatial allocation of fire

The logit and generalized Pareto distribution models, driven by climate and fuel treatment scenarios, produced annual distributions of fire size and severity at the 1/16th degree scale (LS). We developed a spatial allocation algorithm to assign severely-burned pixels to the 30-m landscape surface (FS). Each projected LS fire occurrence was assigned to the appropriate fire size bin and subsequently allocated to the FS landscape using a Monte Carlo simulation drawing from the probability surface for the corresponding fire size bin. Starting with a randomly assigned ignition point within the LS modeling pixel, the algorithm assigned FS pixels as BA90 true/false in an iterative fashion based on the modeled probability surface until the predicted LS fire size was reached. This procedure was repeated 100 times for each unique treatment/climate scenario; each individual simulation was delivered to the spatial occupancy model for spotted owls (see below). We utilized the MERCED high-performance computing cluster at University of California Merced to complete simulations.

To ensure that a BA90 pixel was not assigned to more than one fire each year or assigned a repeat fire in too short an interval, each pixel was deactivated for 9 years before it could burn again (at any severity). Limited information exists on the actual time interval between high-severity fires in the Sierra Nevada, but some research suggested previous fire occurrence limits high-severity fire for at least 9 years (Collins et al. 2009). After each fire was allocated to the landscape, the number of high severity pixels intersecting owl territories was calculated and passed to the population model (see below). See Supplemental materials for full model description, accuracy assessment, and allocation examples.

Owl population model

We modeled owl territory occupancy using a Bayesian dynamic spatial occupancy model (Chandler et al. 2015). The model was fitted using repeated within-season detection/non-detection surveys in *n*=275 spotted owl sites on four demographic study areas spanning the latitudinal range of the Sierra Nevada between 1993-2011 (Fig. S1) (Tempel et al. 2016, Jones et al. 2018). The spatial dependence in the model's structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites that represented nearly all suitable habitat in the Sierra Nevada (Fig. S14). Covariates were selected *a priori* based on published information regarding spotted owl habitat-occupancy associations (Jones et al. 2018). Specifically, site extinction probability was modeled as a function of forest structural variables representing the proportion of each owl site containing large trees (quadratic mean stand diameter ≥61 cm) and high canopy closure (≥70% canopy cover), and large trees and medium canopy closure (40-70% canopy cover), respectively (Fig. S1, Supplemental materials) (Jones et al. 2018). These same covariates were used to model detection probability.

We combined fire forecasts with posterior draws of parameter distributions to project the spotted owl population forward over the period 2012-2064 (Fig. S1; see Supplemental materials). Simulated treatment effects within individual owl territories were modeled by modifying forest structure covariate values (from above) in a manner consistent with expected changes in horizontal canopy structure due to fuel treatments (i.e., reducing fuel continuity by reducing canopy cover). Thus, when simulated fuel treatments occurred within portions of an owl site we re-allocated large tree/high canopy cover forest to large tree/medium canopy cover forest in proportion to the area treated, where the effects to owls were based on statistical associations between each forest cover type and local extinction probabilities (Supplemental materials). Severe fire effects were modeled by the addition of a parameter that represented an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a before-after control-impact natural experiment (Jones et al. 2016a) (Fig. S1). To model potential semi-permanent vacancy of sites that experienced large amounts of severe fire (Jones et al. 2016a), we included a threshold effect in the colonization function that forced all future colonization probabilities to zero when exceeded (Supplemental materials). Simulations were conducted on the high-throughput computing platform HTCondor at the University of Wisconsin-Madison.

Results

Severe fire (>90% tree basal area mortality) was predicted to burn ~23,500-ha/year in the Sierra Nevada by mid-century in the absence of fuel treatments, or >680,000-ha during a 30-year mid-century climate window (2035-2064) (Fig. S5). Landscape-scale fuel reduction treatments strongly reduced severe fire extent in the Sierra Nevada by mid-century. Treatments reduced predicted severe fire area by a minimum of 1.65% (11,200-ha) to a maximum of 30.5% (207,353-ha) from 2035-2064, depending on treatment extent, treatment location, and climate scenario (Fig. 1, Fig. S6, Table S1). More extensive fuel treatments consistently reduced severe fire area across the landscape, and this effect was proportionally larger when treatments were included in owl territories (Fig. 1B). Moreover, higher levels of treatment (e.g., >50% of the treatable landscape) appeared to reduce severe fire activity even in years when climate models produced extreme fire conditions, most notably when treatments were included in owl territories (Fig. S7).

The degree to which owl territories were exposed to extinction-inducing severe fire (Jones et al. 2016a) depended on the spatial extent of our simulated fuel treatments and whether treatments were or were not allowed within owl territories (Figs. S8 and S9). Population projections indicated that fuel treatments have the potential to provide net benefits to spotted owls inhabiting the Sierra Nevada by mid-21st century under all scenarios considered (Fig. 2, Fig. S10). When landscape fuel treatments were excluded from owl territories (Fig. 2A), owl populations experienced net benefits that increased with more treatment but the long-term benefits were generally lower compared to scenarios where owl territories received fuel treatments (Fig. 2B-D). Owls benefited most when fuel treatments occurred within territories but treatments were designed to avoid modifying large tree/high canopy cover forest (Fig. 2B). When fuel treatments occurred inside territories and owl habitat was modified (Fig. 2C-D), a downward pressure was imposed on owl populations over the initial years of the simulation but varied in degree depending on assumptions made about strong versus weak effects of treatment on owl habitat (see also Methods and Supplemental materials). The downward pressure on owl populations eased following the initial years of the simulation, and the net costs of treatment were offset by the cumulative benefits of reduced severe fire exposure by the 2040s and 2050s for all treatment scenarios (Fig. 2C-D).

When averaged across the entire Sierra Nevada, treatment effects on population occupancy were apparent but modest in magnitude (e.g., −0.01 to +0.04) (Fig. 2). However, larger effects that varied considerably in space emerged when outcomes were mapped to individual territories across the Sierra Nevada (e.g., ±0.30) (Fig. 3, Figs. S11 and S12). When treatments were excluded from owl territories, there were relatively uniform benefits to mid-century territory occupancy compared to a no-treatment scenario (e.g., −0.06 to +0.11; range of 99th percentile of values) (Fig. 3A). These benefits grew (e.g., −0.07 to +0.20) when treatments were simulated to occur within owl territories but were designed to avoid modifying large tree/high canopy cover forest (Fig. 3B). When simulated treatments were applied in owl territories and treatment modified owl habitat, strong regional-scale patterns in trade-offs emerged (e.g., −0.11 to +0.22) (Fig. 3C). Owls in the northern Sierra Nevada were predicted to experience larger benefits from treatment in territories across all treatment levels, with mid-century occupancy probability expected to rise by >0.20 for many territories in this region compared to a no-treatment scenario. Owls in a portion of the central Sierra Nevada were also expected to experience net benefits if treatment occurred within territories, but clear benefits tended to accrue only at higher levels of treatment (~50-90%) (Fig. 3C). Owls in the north-central and southern Sierra Nevada were predicted to experience net costs of treatment in territories across all treatment levels when we assumed treatment would have negative habitat effects (Fig. 3C).

Discussion

Severe fires are increasing due to climate change and fuel buildup from historical fire suppression, and have the potential to disrupt forest ecosystems and destroy human communities. Our simulations show that bioregional-scale fuel treatments have the potential to substantially reduce future severe fire extent and therefore increase dry forest resilience to climate change. These treatments also appear to support the conservation of a focal old-forest species, the spotted owl, in the Sierra Nevada, USA. In our simulations, the relative costs and benefits of treatments to owl populations varied across space and through time, particularly when treatments occurred in owl territories (Fig. 3). Owls experienced relatively large benefits from treatment (Fig. 3) in areas where treatments considerably reduced future severe fire (Fig. 1). Conversely, areas where owls experienced net negative treatment effects (Fig. 3) were characterized by lower future exposure to severe fire (Fig. 1), more pronounced direct treatment impacts on predicted territory extinction rates because of regionally-varying treatment effects (Supplemental materials, Table S2), or both. When fuel treatments occurred in owl territories, but were simulated to have no effects on key owl habitat (e.g., because treatment designs that avoided modifying large tree/high canopy forest), benefits were nearly universal and larger than alternative scenarios (Figs. 2B and 3B). Optimal management strategies might entail a mixed approach where treatments are excluded from owl territories, or designed to maintain high-quality owl habitat, in certain regions where negative impacts are greatest, and included elsewhere where costs are less or benefits are predicted to be positive (Fig. 3). Compatibilities may exist between cost-benefit trade-offs to owls and feasibility of treatment in some regions. For example, steeper and more remote terrain in national forest lands of the southern Sierra Nevada make implementation of treatments more difficult (North et al. 2015a), but owls in this region also show strong negative costs of within-territory treatment. In our simulations, we considered an owl territory to be that area surrounding the owl's central activity center (nest, roost), which ranged from ~250-640 ha (Jones et al. 2018).

Mechanistic simulation studies (Moghaddas et al. 2010, Collins et al. 2011) and empirical observations (Safford et al. 2012, Lydersen et al. 2017, Tubbesing et al. 2019) have suggested fuels reduction can significantly reduce severe fire activity in the Sierra Nevada. Our results, obtained using a novel modeling approach that drew on empirical data to reproduce larger severe fire patches, corroborate these general conclusions but did so at a much larger spatial extent than was previously possible. We used 31 years of empirical fire records and a probabilistic forecasting approach to show that restoring Sierra Nevada forest structure to historical conditions reduced predicted severe fire extent by mid-century (Figs. 1 and 2). Although this was an expectation for fuel-limited dry forest ecosystems (Stephens et al. 2013), there is concern that fuels management may be inadequate to alter severe wildfire in a changing climate when extreme fire conditions become more common on an annual basis (Schoennagel et al. 2017). Indeed, we observed some degree of increase in severe fire activity under all treatment scenarios with climate warming (e.g., Fig. S7). However, as more of the landscape was treated, future severe fire extent was reduced (Fig. 1). Importantly, treating more of the landscape also reduced severe fire activity even in years with extreme fire weather, an effect that was particularly notable when larger proportions of landscapes were treated (e.g., >50%, Fig. S7). These results suggested that large-scale forest restoration efforts have the potential to alter severe fire activity and reduce fire-related risk to spotted owls in a changing climate.

The primary mechanism by which severe fire negatively affects spotted owls and other old-forest species is through the elimination of nesting and denning habitat (Scheller et al. 2011, Ganey et al. 2017). The availability of nesting habitat and thermally beneficial roosting sites (large, old trees and high canopy cover) is a limiting factor for spotted owl populations in the Sierra Nevada because of historical selective logging activities that removed large, old trees (Collins et al. 2017, Jones et al. 2018). Moreover, regression analyses suggest that in the next 75 years, the cumulative amount of spotted owl nesting habitat in the Sierra Nevada predicted to experience significant severe fire effects (>50% tree basal area mortality) will exceed the total existing habitat amount (Stephens et al. 2016). Indeed, although we used a more conservative severity threshold (>90% tree basal mortality) (see Methods), loss of nesting habitat to extensive severe fire was the key driver of future population declines within our model (Fig. S13). Moreover, by explicitly linking habitat changes from fire and treatment effects to a demographic model, we were able to rigorously evaluate trade-offs in a population viability context. Previous studies that have applied demographic models to evaluate fuel treatment trade-offs in the Sierra Nevada have also showed that the indirect benefits of treatment (reducing severe fire activity) may outweigh direct costs of habitat manipulation (Scheller et al. 2011, Tempel et al. 2015b). Our results generally support these findings (Fig. 2), while broadening inferences to the entire Sierra Nevada ecosystem and providing insights about how costs and benefits might vary in space across a large bioregion experiencing climate change (Fig. 3, Figs. S19 and S20).

Forest restoration and fuels reduction treatments now occur at levels below those desired by managers (North et al. 2015b) because implementation is constrained by legal, administrative, and financial factors (Collins et al. 2010, North et al. 2015a). So we examined fuel treatment scenarios that ranged from highly feasible (e.g., 18% of the treatable landscape) to relatively less feasible (90% of the treatable landscape) to bracket the hypothetical range of uncertainty regarding fuel treatment effects on fire activity and owl populations. When treatments occurred across much of the landscape (e.g., >50%), future occurrence of severe fire was reduced in the region. However, even low levels of treatment appeared to provide benefits to owls by modifying severe fire area in some regions, even when treatments were restricted from owl territories. Although owl territories made up a small proportion (~10%) of treatable area in the Sierra Nevada (North et al. 2015a), scenarios that permitted within-territory treatment resulted in less severe fire activity than scenarios treating the same total area but outside of owl territories. We think this finding can be explained by two factors. First, the vegetation within owl territories is particularly productive because of soil and moisture conditions and therefore contains large amounts of fuel compared to the broader landscape (Spies et al. 2006, Collins et al. 2010). Second, some areas (e.g., northern and central Sierra Nevada) have relatively high densities of owl territories and therefore treatment restrictions result in relatively large contiguous areas of untreated forest with high risk of severe fire (Figs. S3 and S14). Over the past several decades, treatments have sometimes been implemented within portions of owl territories (~300-600 ha), but generally not in the "core" areas of the territory corresponding with management units called protected activity centers (PACs; ~121 ha) (Peery et al. 2017). Our study treated the entire territory as the management unit (including the smaller PAC) and therefore we did not estimate potential effects of fuels management at the PAC scale alone. However, previous syntheses have recommended lower-intensity fuel treatments at the scale of the activity center (nest, roost) to reduce potential habitat-related negative effects to owls (Peery et al. 2017).

While our model offers a robust starting point for forecasting wildfire and population dynamics across this large bioregion (e.g., Dietze et al., 2018), it has limitations. We assessed the sensitivity of our results to several modeling decisions and assumptions (Supplemental materials), but potential limitations of our study include aspects of our characterization of fuel treatments and fire effects on owls. In both the fire model and spotted owl population model, we only considered how the expected changes in forest structure resulting from treatment interacted with models, not potential effects of the treatment method itself (e.g., prescribed burning, hand-removal of small trees, thinning and/or logging of medium-sized trees). Within the fire model, the effect of treatment on forest structure was represented by simulated changes to fire regime condition class (Schmidt et al. 2002) (see Methods and Supplemental materials), which is a coarse depiction of vegetation change. Within the owl model, treatments reduced canopy cover in some scenarios (Fig. S1), but we were unable to assess how other changes (e.g., understory vegetation or increase in mean tree diameter size) might affect spotted owl occupancy dynamics. We modeled treatment effects to owls by altering a specific habitat type, large tree/high canopy cover forest (Jones et al. 2018), within owl territories (Fig. S1). However, given that large tree/high canopy cover habitat generally makes up a small proportion of each territory (mean = 0.05), it is likely possible to design treatments that avoid canopy reduction in this habitat (Figs. 2B and 3B) even when treatments occur across large portions of the territory and/or landscape. Vegetation and fuels within our models were static, and treatments were introduced once at the beginning of forward simulations. Recent work suggests that temporally dynamic treatments reduce severe fire area in a changing climate more than static treatments (Hurteau et al. 2019), meaning that we may have underestimated the benefits of treatments to owls by using a static approach. Future efforts therefore may benefit from using dynamic treatment models. Whereas treatments were placed randomly across the landscape in our model, strategic placement in areas with high baseline fire risk might make treatments more effective at lower treatment extents in the real world (Tubbesing et al. 2019). We assumed that the probability of spotted owl territory extinction would relate to the proportion of the territory that burned severely, consistent with findings from field studies (Jones et al. 2016a). However, spotted owl response may also depend on either the spatial configuration of severe fire, latitudinal and/or elevational gradients, or specific pre- and post-fire vegetation conditions. Finally, our simulations assumed larger trees (>61 cm dbh) would be retained (not removed intentionally either before or after treatment), although the trees used by owls for nesting are usually much larger (e.g., mean 157 cm dbh) (North et al. 2000, Jones et al. 2018).

Sierra Nevada forests face an increased probability of disturbance-initiated transition to non-forest landscapes without active management to restore ecologically-appropriate forest conditions and reduce accumulated fuels (Stephens et al. 2013, Rissman et al. 2018). Although owls inhabit forests with high tree densities, these conditions also increase the risk of severe fire and drought-related tree mortality (Bradford and Bell 2016, Stephens et al. 2018, Fettig et al. 2019) that results in loss of ancient trees (Jones et al. 2016a). Broadening forest restoration efforts in the Sierra Nevada has the potential to enhance forest resilience and reduce risk of severe fire that negatively impacts forests, carbon storage, water supply, air quality, and local communities as the climate changes. Moreover, our simulations predicted that forest restoration appears to be largely compatible with conservation of an old-forest species. Yet, to minimize the effects of fuel reduction and forest restoration on spotted owls and other old-forest species including the Pacific fisher (*Pekania pennanti*), northern goshawk (*Accipiter gentilis*), and American marten (*Martes americana*), it is essential that large, old trees and core nesting/roosting areas within territories be maintained (Peery et al. 2017, Jones et al. 2018). When large, old trees are maintained and recruited (Hessburg et al. 2016), fuel reduction and forest restoration in the Sierra Nevada can benefit both old-forest species and forest ecosystem resilience under climate change.

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Figure legends

Figure 1. Expected annual changes in severe fire (90% basal area killed) extent from 2035-2064 relative to the baseline no-treatment (0%) scenario. (A) Treatments excluded from owl territories. (B) Treatments included in owl territories. Results are summarized from the large-scale fire model (6-km) (see Methods).

Figure 2. Summary effects of treatment on spotted owls in the Sierra Nevada showing annual range-wide occupancy for each treatment scenario relative to the baseline no-treatment scenario (red line). (A) Occupancy when treatments are excluded from owl territories. (B-D) Occupancy when treatment occurs inside owl territories but vary in their assumptions about how treatments affect owl habitat (no effects, weak effects, strong effects). Trajectories were averaged across 50,000 simulations (Supplemental materials) using the CRNM-CM5 global circulation model (see Supplemental materials for CanESM-2).

Figure 3. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. (A) Occupancy when treatments are excluded from owl territories. (B-D) Occupancy when treatment occurs inside owl territories but vary in their assumptions about how treatments affect owl habitat (no effects or strong effects; see Supplemental materials for weak effects). Averaged across 50,000 simulations (Supplemental materials) using the CRNM-CM5 global circulation model (see Supplemental materials for CanESM-2).

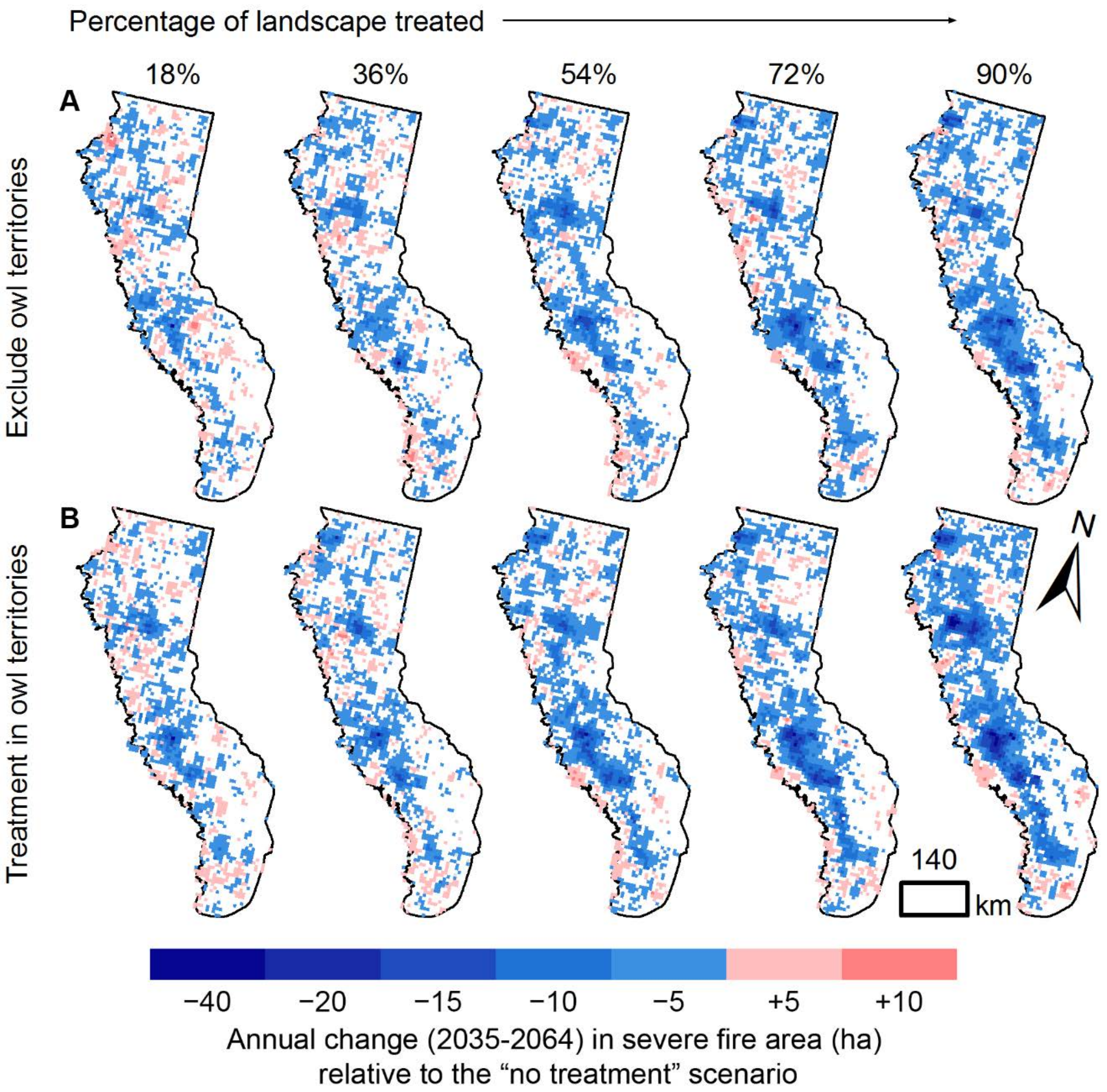
Percentage of landscape treated
18%
36%
54%
72%
90%
A
Exclude owl territories
B
Treatment in owl territories
N
140
km
−40
−20
−15
−10
−5
+5
+10
Annual change (2035-2064) in severe fire area (ha)
relative to the "no treatment" scenario

Figure 1.

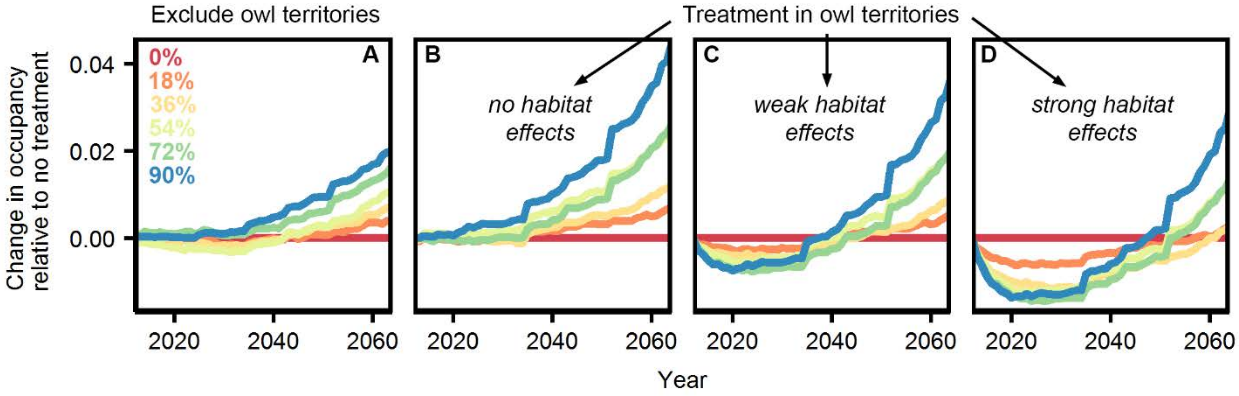
Exclude owl territories
Treatment in owl territories
A
B
C
D
0%
18%
36%
54%
72%
90%
no habitat effects
weak habitat effects
strong habitat effects
Change in occupancy relative to no treatment
0.04
0.02
0.00
2020
2040
2060
Year

Figure 2.

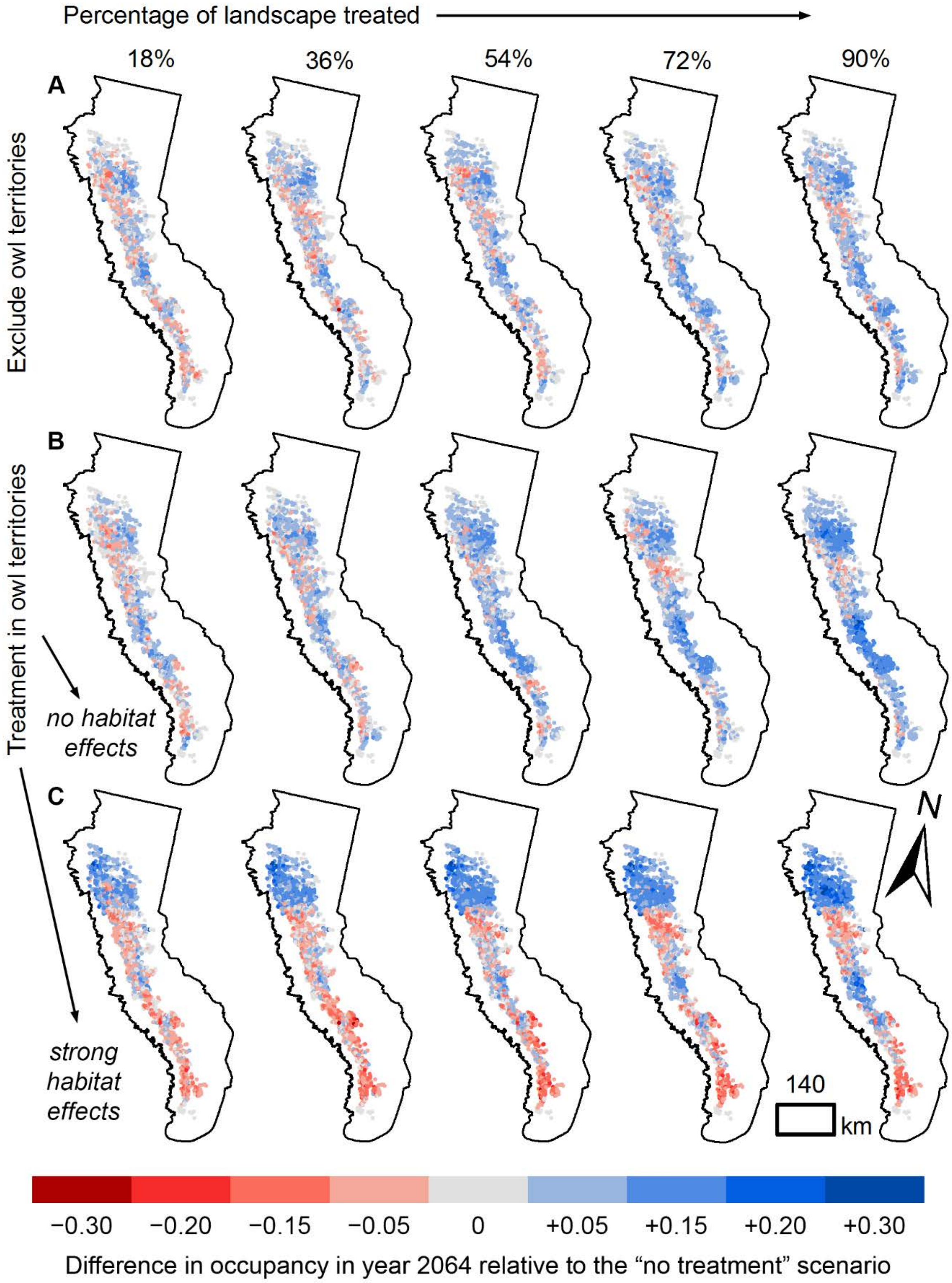
Percentage of landscape treated
18%
36%
54%
72%
90%
A
B
C
Exclude owl territories
Treatment in owl territories
no habitat effects
strong habitat effects
N
140 km
−0.30
−0.20
−0.15
−0.05
0
+0.05
+0.15
+0.20
+0.30
Difference in occupancy in year 2064 relative to the "no treatment" scenario

Figure 3.

Supplementary materials

Fire model

Fuels. Within our fire model, we used fire regime current condition class (FRCC) as a proxy for the effects of fire suppression (i.e., accumulation of fuels and altered stand structure/ composition). We acknowledge that other factors can alter vegetation condition, but fire suppression has been the major driver of vegetation change in the Sierra Nevada over the past century (Collins et al. 2017). FRCC is a metric that characterizes how land management decisions have affected ecosystems (LANDFIRE project; www.landfire.gov). Specifically, FRCC quantifies the degree to which current vegetation differ from the historical range of variability (HRV) under a natural fire regime on a continuous scale of 0–100% (Keyser and Westerling 2019). This continuous departure metric, which refers to changes in vegetation composition, are categorized into three groups: FRCC1, which represents areas within HRV (<33% departure); FRCC2, which represents areas that are moderately departed HRV (33 to 66% departure); and FRCC3, which represents areas that are highly departed and outside HRV (≥67% departure).

We used two sets of FRCC treatments within an existing mask defining areas where mechanical fuel reduction treatments are feasible (Collins et al. 2010) on non-subalpine federal lands in the Sierra Nevada bioregion. A federal ownership administrative mask provided by USDA Forest Service Pacific Southwest Region (PSW) defined the first treatment set. Fuel reduction treatments were simulated by modifying FRCC classes 2 or 3 to class 1 (Westerling 2018). Six treatment layers were produced with 18% increments between treatment extents for our analysis: 0% (i.e., no treatment), 18%, 36%, 54%, 72%, and 90% (Fig. S2). Each treatment layer was nested within the mask of the next highest percentage treatment layer. As an example, the 18% layer was randomly sampled from the 36% layer, not the 90% layer. As noted in the main text, treatment levels (18%, 36%, 54%, 72%, and 90%) refer to the percentage of treatable lands (public lands without significant operational constraints) that are restored to FRCC class 1, which reflect a fraction (~36%) of the entire Sierra Nevada landscape (Fig. S4).

The second treatment set excluded mapped owl territories within the administrative mask, resulting in a 10% reduction in total treatable area. For the treatments excluding owl territories, we started with the 100% administrative treatment layer and masked out all owl territories to create a new maximum potential treatment layer, which represented 90% of the treatable landscape. In order for each scenario to match the total treatment extent from the first treatment set, we used the new out of territory (OOT) 90% treatable layer and sequentially selected 72, 54, 36, and 18% of pixels as treatment pixels. As in the first treatment set, each fractional layer nests within the mask of the next higher percentage treatment layer. We used map algebra to change FRCC values in the treatment mask from FRCC 2 or 3 to 1 from the original FRCC values. With the exclusion of the owl territories, it was not possible to treat the same pixels in the two FRCC treatment sets, but we treated an equivalent number of pixels in the 18-90% treatment layers. The effect of excluding owl territories on the potential area treated is evident at the fine scale (see Fig. S3 for inset images from Fig. S2). In some areas, owl territories made up large proportions (up to 0.8) of large-scale (1/16th degree) modeling pixels (Fig. S15), which strongly limited the potential for treatment to reduce severe fire activity in our model when treatments were excluded from territories.

Fire occurrence data. We downloaded fire severity polygons from USDA Forest Service Region 5 that classified burn severity as percent change in basal area for years 1984-

2015. We used the 90% basal area (BA90) killed value as our measure of high severity fire occurrence (USDA 2017). This dataset was the dependent variable for all fire modeling.

Large scale (LS) model. We fit a spatially explicit logistic regression model (m1; Fig. S1) on a 1/16th degree latitude/longitude grid to estimate the monthly probabilities of the occurrence of at least one fire >400-ha as a function of topography, human population, vegetation fraction, and climate using the glm function in R (Westerling 2018). Human population and vegetation data were obtained from ref. (Sleeter et al. 2017). Climate data were obtained from the Livneh Research Group at the University of Colorado, Boulder (B. et al. 2013). Additional details about LS data can be found in ref. (Westerling 2018). Model specifications were compared using AIC to select for parsimonious models despite the presence of spatially auto-correlated variables (Akaike 1974, 1981). Specifications tested here extend models used in (Westerling et al. 2011a) to a finer spatial scale (1/16th degree latitude/longitude grid instead of 1/8th degree). The selected model was validated by applying parameters calculated with the first half of the data (1984-1999) to the full sample, and comparing Spearman's rank correlations over each period with correlations for the model estimated with the full 30-year sample (Westerling 2018). For each fire >400-ha, the probability of >50-ha burning in BA90 was estimated by fitting a logistic regression (m2; Fig. S1) with climate covariates using the glm function in R. To estimate the conditional extent of BA90 burned area, for each fire with >50-ha BA90 burned, a generalized Pareto distribution (GPD) was fit with climate and FRCC covariates (m3; Fig. S1).

Large-scale BA90 area burned was simulated for each climate and treatment scenario as follows. First, we repeated random draws from the binomial distribution using probabilities from LR1 to generate large (>400-ha) fire occurrence. For each simulated large fire, a random draw from the binomial distribution using probabilities from LR2 was used to generate BA90 occurrence >50-ha. For each BA90 occurrence >50-ha, a random draw from the generalized Pareto distribution using probabilities from the GPD was used to generate total BA90 area.

The logit, defined as $ln(\boldsymbol{p}/(1-\boldsymbol{p}))$, where $\boldsymbol{p}$ refers to the probability of large fire (>400-ha) occurrence, was modeled as follows:

$$\ln\left(\frac{\boldsymbol{p}}{1-\boldsymbol{p}}\right) = \boldsymbol{\beta}_m \times g(AETmu_i, CWDmu_i) + \sum \boldsymbol{\beta}_m \times g(AETmu_i, CWDmu_i)$$

$$\times q_m\left(X_{mij}\right) + \sum \boldsymbol{\beta}_m \times X_{mij}$$

where X_{mij} is the *m*th explanatory variable for location *i* and month *j* (see Table S3 for further description), $g(AETmu_i, CWDmu_i)$ was a semiparametric function *g* of the interaction between long term average evapotranspiration ($AETmu_i$) and long-term average climatic water deficit ($CWDmu_i$), $q_m\left(X_{mij}\right)$ was a parametric or semiparametric function of the *m*th explanatory variable (Hastie et al. 2001), and $\boldsymbol{\beta}$ are estimated parameters (Westerling 2018). Semiparametric functions are splines and thin-plate splines expanded into basis functions that can be used linearly in the regression (Preisler and Westerling 2007). Similar mixed parametric and semiparametric models have been used by for seasonal forecasting and climate change impact assessment (Preisler and Westerling 2007, Preisler et al. 2008, 2011, Westerling et al. 2011b, 2011a). Long-term average climatic water deficit and evapotranspiration best predict the occurrence of coarse vegetation types on the landscape (Stephenson 1998), which in turn shape the frequency, extent and severity of fire in response to shorter term climatic variability (Westerling 2009, Westerling et al. 2009, Krawchuk and Moritz 2011). Prior work has extended this to modeling fire presence/absence using cumulative moisture deficit (Westerling et al. 2011b, 2011a).

The best fit presence/absence model for 50-ha or more of BA90 area conditional on a 400-ha fire being present was a generalized linear model using cumulative monthly climate water deficit (CWD_{ij}), cumulative monthly actual evapotranspiration (AET_{ij}), cumulative water year climate water deficit ($CWD0_{ij}$), and June-July-August (JJA) average temperature ($Tjja_{ij}$). The extent of BA90 area conditional on 50-ha BA90 being present was estimated using a generalized Pareto distribution fit to climate and vegetation characteristics as covariates. Model specifications were assessed using AIC (Akaike 1974, 1981, Burnham and Anderson 2002).

The best fit generalized Pareto distribution for BA90 extent had a constant shape parameter and a scale parameter modeled as a linear function of monthly climate water deficit (CWD_{ij}) and the interaction between cumulative current water year climate deficit and grid cell fraction in fire regime current condition (FRCC) classes 2 and 3 ($CWD0_{ij}$ x $FRCC23_i$), where $FRCC23_i$ was normalized to provide a continuous variable not bounded by [0,1] as:

$$FRCC23_i = log((f23_i)/(1 - f23_i))$$

In order to make this model relevant to spotted owl territories, we developed a framework to downscale our predictions of high severity fire from 1/16th (LS) degree to 30-m resolution fine-scale model (FS) (see below).

We obtained gridded downscaled climate simulations for 1950-2099 from two global climate models using the Representative Concentration Pathway (RCP) 8.5 emissions scenario (see ref. (IPCC AR5 WG1 2013)) via Scripps Institution of Oceanography, including global models from Centre National de Recherches Météorologiques (CNRM-CM5, see ref. (Voldoire et al. 2013)), the Canadian Centre for Climate Modeling and Analysis (CanESM2, see refs.

(Arora and Boer 2010, Christian et al. 2010)). These climate models represent a subset of models selected by California's Fourth Climate Change Assessment (CCCA4) (http://www.climateassessment.ca.gov/). A set of filters were applied by CCCA4 at global, regional, and California scales to obtain models that realistically represent variability for California in selected hydrologic variables and the climatological drivers of that variability. RCP 8.5 describes a world where emissions rise rapidly in coming decades. Climate scenarios were downscaled to a 1/16 degree lat/lon grid using the Localized Constructed Analogs (LOCA) statistical downscaling methodology (Pierce et al. 2014).

Fine scale (FS) model. We used historical fire severity data for the Sierra Nevada with vegetation and topography to develop a static presence/absence model of high severity fire at 30-m scale. We then used this model to create a set of 30-m probability surfaces of high severity fire for a range of fire size classes for the Sierra Nevada bioregion. Previous work found that topography was the most important predictor of high severity fire occurrence when sampling individual 30-m pixels (Dillon et al. 2011). We developed a suite of topographic variables from a 30-m digital elevation model (DEM). We transformed aspect to calculate the heat load index (HLI) and topographic radiation aspect index (TRASP) using the Geomorphometry and Gradient Metric toolbox in ArcGIS (Evans et al. 2014). We created topographic position indices (Jenness 2013) in four and six classes with 1-km and 2-km radii. We also created layers of elevation and percent slope. We used three hierarchical levels of vegetation information taken from the Landfire v.1.4.0 existing vegetation type (EVT) layer: EVT, existing vegetation type physiognomy (EVT_PHYS; e.g., conifer, hardwood, grassland), and plant functional type (PFT). PFT is the coarsest classification and results in 97 EVTs in the Sierra Nevada aggregated to six PFT's: forest, grass, shrub, riparian, exotic, and non-vegetated.

For all fires >400-ha, we calculated the distribution of fires where the total fire size was greater than or equal to 85% of the average vegetated area of the LS grid cells (1/16th degree) to align with prior Sierra Nevada modeling efforts (Westerling 2018). This produced a minimum fire size of 3290-ha. We ordered the fires that intersected the Sierra Nevada bioregion by total area burned. Applying the minimum fire size limit left 264 fires that we separated into seven fire size bins. With the exception of the largest bin, each bin includes fires that span the length of the fire severity record, 1984-2015. The largest fires have occurred since 2002, resulting in the largest bin including only the most recent fires. We chose 2-3 fires from each size class to build the downscaling model (Table S4). While we attempted to be as objective as possible in selecting fires for model development, a degree of subjectivity was necessary to achieve full spatial and temporal coverage of the study area. All fires selected for model development occurred after 2000 (the Landsat acquisition year for the imagery used in the Landfire existing vegetation and FRCC layers), and where possible, each bin contained fires that were distributed North-South. We selected twenty fires to train and test our downscaling model, choosing fires that produced the fullest coverage of year, ignition month, total fire area and fraction of BA90 (Table S4).

We used a presence/absence approach to model presence of high severity fire pixels in each fire. Individual fire pixels were classified as 0 (absent) or 1 (present), where 1 represented pixels that burned at BA90. The set of fires selected for training the downscaling model resulted in 556,444 pixels with nearly equal representation of presence and absence (47.8% of these had a value of 1, 52.2% had a value of 0). Having true absence values, especially when equivalent in number to presence ensures that accuracy assessments are unbiased and more robust. We used all training pixels to sample the independent variables and used the rfUtilities package in R (Murphy et al. 2010, Evans and Murphy 2018) to select the best model using a classification and regression tree approach, Random Forest (Breiman 2001). We evaluated model accuracy using Cohen’s Kappa and the area under the Receiver Operating Curve (AUC) using the rfUtilities package in program R (Evans and Murphy 2018). The best fit model included existing vegetation type (EVT), heat load index (HLI), elevation, percent slope, total fire size (ha), and six class topographic position index (Cohen’s Kappa = 0.8175, AUC = 0.9085, percent correctly classified = 90.88%) (Figure S16). We used the best model to create a set of probability surfaces corresponding to seven fire size class bins; each 30-m pixel was assigned a probability of burning at BA90 for fires in each bin. The remaining classification variables did not vary temporally so the same set of probability surfaces were used for all management and climate change scenarios.

The logit and generalized Pareto distribution models (LS), driven by GCM and fuel treatment scenarios, produce annual distributions of fire size and severity at 1/16th degree (LS). Each fire occurrence was assigned to the appropriate fire size bin and allocated to the 30-m landscape (FS) with a Monte Carlo simulation drawing from the probability surface for the corresponding fire size bin. Starting with a randomly assigned ignition point within the LS modeling pixel, FS pixels were allocated as BA90 (true/false) in an iterative fashion based on the probability surface until the predicted fire size was reached. This process was repeated 100 times for each unique treatment/climate combination. Tests of the simulation approach revealed that simulated BA90 probabilities very closely approximate empirical BA90 patterns from real fires (Fig. S17). To ensure that a pixel was not assigned to more than one fire in a given year or assigned a repeat fire in too short an interval, each pixel was deactivated for 9 years before it could be burned again. There is limited information on the actual time interval between high severity fires in the Sierra, but research suggests previous fire occurrence limited high severity fire for 9 years (Collins et al. 2009). After each fire was allocated to the landscape, the number of BA90 pixels intersecting owl territories was estimated for each year and passed to the spatial occupancy model.

We note that while the simulated probability of BA90 closely approximated the observed BA90 pattern (Fig. S17), there was a tendency within individual simulations for the simulated BA90 patches to have a more evenly sprinkled “salt shaker” type distribution, whereas the observed pattern would be expected to be more clumped. That is, spatial autocorrelation was relatively weak at fine spatial scales. We expect that the effects of that lack of clumping would average out over the 100 simulations of the FS model that were delivered to the spotted owl spatial occupancy model, but ultimately may have resulted in more conservative (less negatively impactful) severe fire effects to owls than would be expected (Jones et al. 2016a). Nevertheless, future revisions to the spatial allocation algorithm could include a spatial autocorrelation parameter that enforces clumping patterns that even more closely approximate real observed BA90 patches.

Population model

Spatial occupancy model for spotted owls. We completed repeat within-season detection/non-detection surveys in *n*=275 spotted owl sites on four demographic study areas between 1993-2011 (Tempel et al. 2016, Jones et al. 2018). On all study areas, Sierran mixed-conifer montane forest was the dominant vegetation type, elevations ranged from 300-3050 m, and climate was Mediterranean (Tempel et al. 2016). We used vocal lures during surveys to detect owls. A survey in which no owls were detected needed a total duration of ≥30-min to be included as an absence record. We excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique color leg-bands as part of a concomitant mark-recapture study) that occurred outside of a delineated territory boundary using a Geographic Information System (GIS) to eliminate potential spurious positive detections of transient owls not occupying the nominal sites. Extensive details about each study area and additional survey details have been published (Tempel et al. 2016).

We modeled site occupancy dynamics using a Bayesian multi-season spatial occupancy model (Chandler et al. 2015). The spatial dependence in the model's structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites that represented nearly all suitable habitat in the Sierra Nevada. The process model defines dynamics in the binary occupancy state of spotted owls across $i = 1, 2, \ldots, R = 1800$ sites and years $k = 1, 2, \ldots, K = 53$ as

$$z_{ik} \sim \begin{cases} Bernoulli(\psi_i), & if\ k = 1 \\ Bernoulli\big(\gamma_{i,k-1}(1 - z_{i,k-1}) + (1 - \varepsilon_i(1 - \gamma_{i,k-1}))z_{i,k-1}\big), & if\ k > 1 \end{cases}$$

where $z_{i,k} = 1$ denotes that site i is occupied in year k and $z_{i,k} = 0$ denotes that site i is not occupied in year k. In the initial year of the model, $z_{i,k}$ depends only upon the initial occupancy, ψ_i. In subsequent years $z_{i,k>1}$ is dependent upon the previous occupancy state of site i and its neighbors n_{ih}: it is sampled from the function $h(\gamma_{i,k-1}, \varepsilon_{i,k-1}, z_{i,k-1})$ where $\varepsilon_{i,k-1}$ and $\gamma_{i,k-1}$ respectively describe probabilities for extinction (transitioning from occupied to unoccupied) and colonization (transitioning from unoccupied to occupied). Covariates were selected *a priori* based on published information regarding spotted owl habitat-occupancy associations (Jones et al. 2018). Extinction probability ($\varepsilon_{i,k-1}$) was modeled as

$$\begin{aligned} logit(\varepsilon_i) = {} & \beta_0 + \beta_1 central_i + \beta_2 south_i + \beta_3 lgTree.hiCanopy_i + \beta_4 lgTree.medCanopy_i \\ & + \beta_5(lgTree.hiCanopy_i \times central_i) + \beta_6(lgTree.hiCanopy_i \times south_i) \\ & + \beta_7(lgTree.medCanopy_i \times central_i) + \beta_8(lgTree.medCanopy_i \times south_i) \end{aligned}$$

where $\beta_{0\text{-}2}$ were intercepts that varied by latitudinal bioregion (*north* was the reference category); $\beta_{3\text{-}4}$ were forest structural variables representing the proportion of each owl site containing the spatial intersection ($\cap$) of large trees (quadratic mean stand diameter ≥61 cm) and high canopy closure (≥70% canopy cover), and large trees and medium canopy closure (40-70% canopy cover), respectively (Jones et al. 2018); and $\beta_{5\text{-}8}$ were interactions that allowed the slopes of $\beta_{3\text{-}4}$ to vary across bioregions.

Defining colonization $\gamma_{i,k-1}$ began by defining the probability that site *i* was colonized by an individual from site *h* in year *k* as

$$\rho_{ik,h} = \rho_0 \exp\left(-\frac{d_{i,h}^2}{2\sigma^2}\right) z_{i,k-1} n_{ih}$$

where ρ_0 was the baseline colonization probability for coincident sites, $d_{i,h}$ was the Euclidean pairwise distance between sites, σ was the scale parameter determining the decay rate in colonization probability from ρ_0 as a function of distance, n_{ih} was an $i \times h$ neighborhood matrix that limited colonizing sites to those occurring within the approximate 95th percentile of breeding dispersal distances for spotted owls (25-km, ref. (Blakesley et al. 2006)). We used the neighborhood matrix to limit the number of potential colonizing sites, which helped facilitate model fitting; we note that truncating the dispersal distance is not likely to bias results (Zhao et al. 2017). This parameterization enforced the condition that site *i* could not be colonized by site *h* if $z_{h,k-1}$=0 (i.e., an unoccupied site does not contribute potential colonizers). The probability of a colonization event was thus

$$\gamma_{ik} = 1 - \{\prod_{h=1}^{M} 1 - \rho_{ik,h}\}$$

where *M* was the total number of sites in *i*'s neighborhood. Like ref. (Chandler et al. 2015) we also allowed for a pseudo-rescue effect (Brown and Kodric-Brown 1977) in which extinctions were less likely to be observed at highly connected sites than at isolated sites, because the former sites have a greater chance of being colonized immediately after extinction. The pseudo-rescue effect was modeled as

$$\phi_{i,k-1} = 1 - \varepsilon_i(1 - \gamma_{ik})$$

indicating that the probability that an occupied site remains occupied ($\phi_{i,k-1}$) was one minus the probability that it went extinct and was not recolonized.

The observation model was

$$y_{ik} = Bernoulli(z_{ik} * p_i)$$

$$logit(p_i) = \alpha_0 + \alpha_1 lgTree.hiCanopy_i + \alpha_2 lgTree.medCanopy_i$$

where p_{ijk} was the probability of detecting an individual when it was present, α_0 was the intercept, α_1 and α_2 were the regression coefficients for detection, and covariates were the same as those used to model the extinction process above. We included the same covariates when modeling detection as we did modeling extinction to account for potential detection biases associated with habitat covariates.

We chose flat prior distributions for all model parameters: *Uniform*(−40, 40) for all α and β coefficients because habitat-related covariate values were proportions ranging from 0 to 1; *Uniform*(0, 1) for ψ_1 and ρ_0; and *Uniform*(0, 40) for σ. After an adaptation phase of length 5000, we sampled posterior distributions using three Markov chains each of length 15,000. Markov-Chain Monte Carlo simulation was conducted using JAGS (Plummer 2003) in program R (v

3.3.2) using the package jagsUI (v 1.4.4) (Kellner 2016). Convergence was assessed using the Gelman-Rubin diagnostic ($\hat{R}$), where we considered values <1.1 to indicate convergence. We also assessed trace plots to ensure chains were not still moving toward the stationary distribution.

Development of the patch network. We developed a network of (*n* = 1844) California spotted owl sites spanning the Sierra Nevada, which acted as patches in the metapopulation model (Fig. S14). The metapopulation network began with *n* = 1422 known spotted owl protected activity centers (PACs) delineated by the USDA Forest Service (USFS) during 1993-2011. PACs represent approximately 121-ha of the highest quality surrounding the known location of every territorial owl, or pair of owls, that have been detected at any time on USFS land in the Sierra Nevada. Other ownerships, such as national parks or private lands, do not have PACs but still contain areas that are used by spotted owls throughout the Sierra Nevada. With additional known owl territories from non-USFS ownerships, we identified a total of (*n* = 1494) previously delineated PACs and territories in the Sierra Nevada (Fig. S14).

The spatial area that spotted owls actively defend is commonly referred to as the "territory", which is larger in size than the 121-ha PAC (254-639 ha) and increases with latitude (Tempel et al. 2016). For the sake of clarity we hereafter refer to all areas that were (*a*) originally delineated as PACs, (*b*) identified as owl territories but had no associated PAC, or (*c*) randomly generated *potential* spotted owl PACs/territories (see below) as "owl sites" or "patches" interchangeably. However, and as is described in more detail below, we collected site-specific covariate information at the scale of the owl *territory* to be used in our spatial occupancy model in part because habitat and disturbance covariates of interest in the present study have been strongly linked to owl occupancy dynamics at the territory scale (Jones et al. 2016a, 2018).

Therefore, the spatial extent of an "owl site" or "patch" is here best interpreted to be equivalent to an owl territory.

Some gaps were present within the known patch network, but it was unclear whether these gaps were ecologically meaningful or a sampling artifact because owl sites were identified incidentally, not systematically. We used a Sierra Nevada-wide spotted owl habitat suitability index (HSI; JJ Keane *unpublished data*) to identify areas most likely to contribute to the owl population where no patches were currently known to exist. To fill gaps in the patch network, we generated n = 350 of points at random locations across the Sierra Nevada, but constrained their locations to occur (1) at least the mean nearest neighbor distance from existing owl site centers in the network ($\bar{x}_{NND}$ = 2423.6 m) and (2) in areas with HSI values above the 50th percentile (i.e., of putative higher quality). These points represented site centers, so we buffered the new points to match region-specific territory sizes for covariate estimation. The generation of n = 350 new territories yielded territory densities that approximately matched densities from regions with known territory locations (Fig. S14).

Influence of treatments on owls. The current scientific literature lacks strong empirical evidence regarding temporal treatment effects on spotted owls. The detection of such effects might be obscured by the owl's long lifespan and high site fidelity; that is, spotted owls may continue to occupy territories long after they become sub-optimal (Jones et al. 2018). On the other hand, a number of empirical studies suggest spotted owl territories that contain greater amounts of large trees and/or high canopy cover tend to have higher occupancy, higher survival, and higher reproduction than territories that contain less of this forest type (Blakesley et al. 2005, Tempel et al. 2014a, 2016, Jones et al. 2016b, Gutiérrez et al. 2017). One approach for modeling potential treatment effects on spotted owls, therefore, involves a space-for-time substitution, positing that future processes can be predicted from existing spatial patterns (Pickett 1989). Using this approach we might reasonably assume, for example, that because owl territories with higher canopy cover have lower extinction rates, then extinction rates would be expected to increase if canopy cover is reduced as part of a treatment (Tempel et al. 2015a). Thus, in the present study, we approximated the effect of treatment on owls based on empirical relationships between forest characteristics and spotted owl occupancy rates (see below for additional details).

A primary proximate goal of treatments is to reduce the continuity of available fuels on the landscape. Treatments can act to reduce fuel continuity in at least two ways: decrease vertical continuity by removing ladder fuels that connect the understory to the canopy (increased vertical canopy separation), and decrease horizontal continuity by reducing overstory canopy cover (increased horizontal canopy separation) (Hessburg and Agee 2003, Agee and Skinner 2005). Changes in vertical continuity are more difficult to quantify than changes in horizontal continuity, and thus most approaches for measuring canopy cover estimate horizontal overstory closure. Therefore, although treatments that affect vertical continuity may alter important understory forest structures preferred by spotted owls, we focus hereafter on potential treatment effects to horizontal continuity and total canopy cover. In the Sierra Nevada, treatments often reduce total canopy cover in stands from greater than 70% to between 40% and 70% (North et al. 2007, Stephens et al. 2009).

The amount of forest in an owl territory characterized by both high total canopy cover (>70% overstory closure) and larger trees (>61 cm dbh) is the best predictor of spotted owl occupancy dynamics across the Sierra Nevada bioregion (Jones et al. 2018). Thus, one empirically-based approach to linking the potential effects of treatments to owl dynamics could involve re-allocating large tree/high canopy cover forest to large tree/medium canopy forest in proportion to the extent of treatment that is applied (Marc Meyer, *personal communication*). Preliminary analyses suggested local extinction probabilities were less positively (or sometimes negatively) associated with large tree/medium canopy cover forest compared to large tree/high canopy cover forest. Therefore, using this approach to approximate treatments would be expected to incur a mean negative effect on owl dynamics in the absence of any potential benefits related to the reduction of severe fire activity.

Treatment scenarios were applied to the entire Sierra Nevada using an algorithm that reduced FRCC classes 2 and 3 (i.e., forests outside of HRV) to FRCC class 1 (i.e., representative of HRV). When FRCC changed from class 2 or 3 to class 1 within portions of an owl site, we approximated potential effects to owls by re-allocating large tree/high canopy cover forest to large tree/medium canopy cover forest in proportion to the area treated. For example, if an owl site contained 100 ha of large tree/high canopy cover and 100 ha of large tree/medium canopy cover forest prior to treatment, and 25 ha of the owl site changed from FRCC 2 or 3 to FRCC 1, then following treatment the owl site would contain 75 ha of large tree/high canopy cover forest and 125 ha of large tree/medium canopy cover forest. Thus, we assumed that treatment would preferentially target large tree/high canopy cover forest. However, in practice, treatment likely targets a suite of forest types (not just large trees/high canopy cover), with particular focus on medium and small tree dominated types, so we also created scenarios that were more conservative where treatment effects were proportionally smaller (e.g., only 25% of treatments occurred in large tree/high canopy cover forest). We refer to the first and second scenarios as having “strong habitat effects” and “weak habitat effects”, respectively.

Forward projections of the population model. All posterior distributions achieved convergence ($\hat{R} < 1.1$) (Table S2). For each forward projection, we originally planned to combine each iteration of the FS fire model output (*n* = 100) with each posterior parameter draw (*n* = 45,000) to ensure projections covered the full range of variation from the two data sources. However, this resulted in a computationally intractable number of simulations for each treatment/climate scenario (100 fire runs × 45,000 posterior draws = 4,500,000 simulations per scenario). Thus, to make forward projections computationally tractable, we sampled from a thinned posterior distribution ($n_{sampled}$ = 500; n_{full} = 45,000). We used each posterior draw ($n_{sampled}$ = 500) and FS fire ouput (*n* = 100) to project the spotted owl population forward 500 × 100 = 50,000 times over the period 2012-2064 for each treatment/climate scenario. Treatment effects within individual owl territories were modeled by modifying forest-structure covariate values in a manner consistent with expected changes in horizontal canopy structure due to fuel treatments (i.e., reducing fuel continuity by reducing canopy cover). Thus, when fuel treatments occurred within an owls site (FRCC values within a pixel changed from FRCC 2 or 3 to FRCC 1), we approximated potential effects to owls by re-allocating large tree/high canopy cover forest to large tree/medium canopy cover forest in proportion to the area treated (see above). Severe fire effects were modeled by the addition of a parameter within the extinction function that represented an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a natural before-after control-impact experiment (Jones et al. 2016a) (Fig. S1):

$$\begin{aligned} logit(\varepsilon_{ik}) = \; & \beta_0 + \beta_1 central_i + \beta_2 south_i + \beta_3 lgTree.hiCanopy_i + \beta_4 lgTree.medCanopy_i \\ & + \beta_5(lgTree.hiCanopy_i \times central_i) + \beta_6(lgTree.hiCanopy_i \times south_i) \\ & + \beta_7(lgTree.medCanopy_i \times central_i) + \beta_8(lgTree.medCanopy_i \times south_i) \\ & + \boldsymbol{\beta_9 propSevere_{ik}} \end{aligned}$$

where β_9 was defined by a mean value of 8.23 (SD = 3.73) (Jones et al. 2016a), and *propSevere* was the proportion of an owl territory that experienced BA90 in a given year as determined by the FS fire model. Note that β_9 from ref. (Jones et al. 2016a) was generated using a broader definition of severe fire (75% mortality) than we use in this paper (90% mortality). We expect this means our simulations will yield severe fire effects on owls that are slightly more conservative (smaller in magnitude) than would be expected in reality. We generated a normal distribution of length n=45,000 for β_9 to match the length of posterior distributions for the other parameters used in the forward projection. To model potential semi-permanent vacancy of sites that experienced large amounts of severe fire (Jones et al. 2016a), we included a threshold effect (*q*) in the colonization function:

$$\gamma_{ik} = \begin{cases} 1 - \{\prod_{h=1}^{M} 1 - \rho_{ik,h}\} & if\ s_{i,1:k-1} < q \\ 0 & if\ s_{i,1:k-1} \geq q \end{cases}$$

where *s* was the proportion of the spotted owl site that experienced severe fire in year *k* of the forward simulation (via the fire model), and *q* was a threshold value (0.4, 0.5, or 0.6) that forced all future colonization probabilities to zero when exceeded. This parameterization allowed for (1) delayed extinction following high-severity fire because of the high site fidelity in spotted owls, which was observed following the 2013 Rim Fire (JJ Keane, *unpublished data*), and (2) severely-burned sites experiencing catastrophic habitat loss to be removed from the site network over the modeling period. For all inferences made in the paper, we used *q* = 0.5. However, we show the sensitivity of owl model results to varying the value of *q* to 0.4 or 0.6 in under the CNRM-CM5 GCM scenario in Figs. S18-S20.

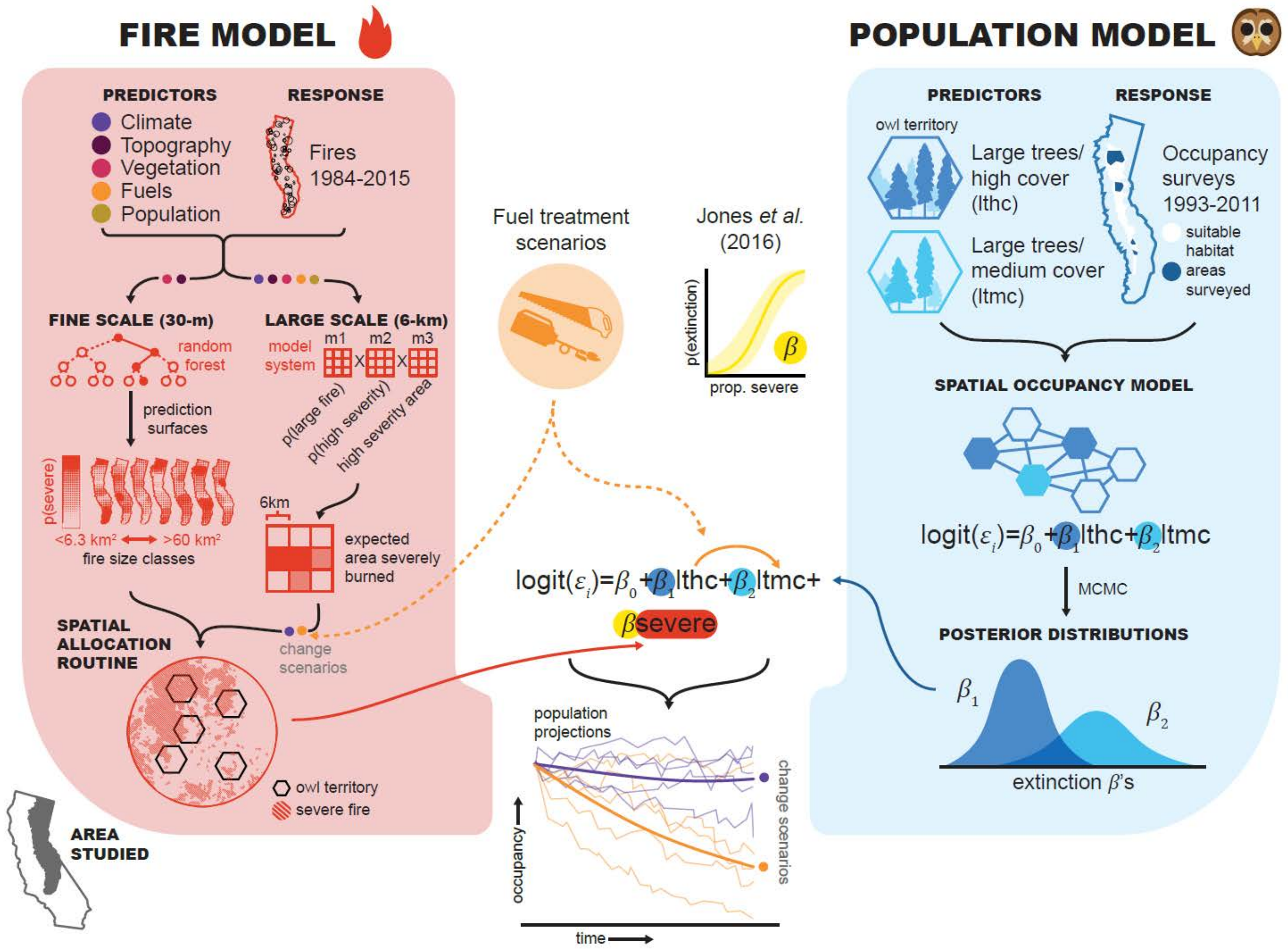

Fig. S1. Conceptual diagram showing the flow of information through the fire and population models and how they were linked during forward simulations.

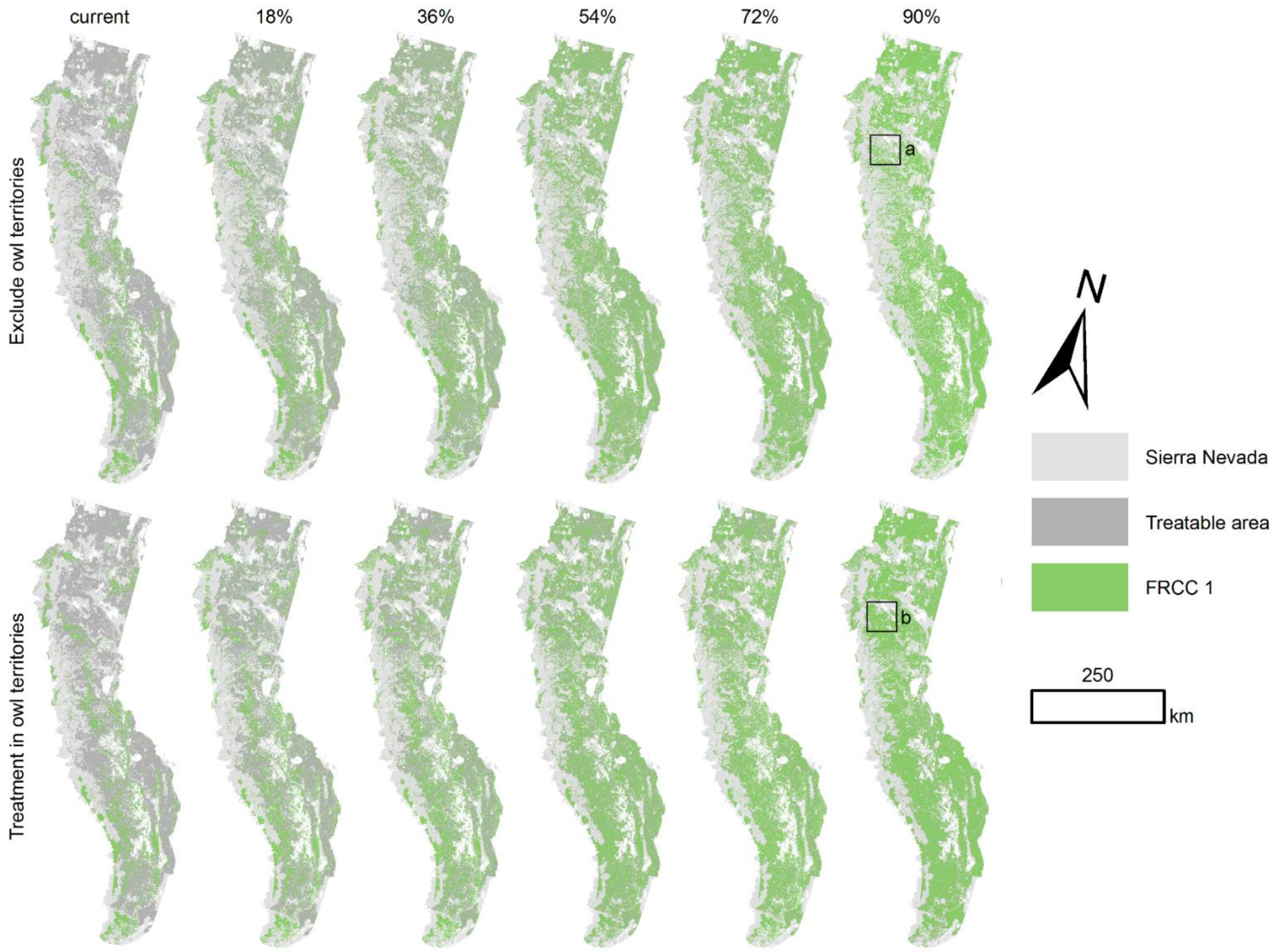

Fig. S2. Fuel treatment data that served as input data to the fire and population models.

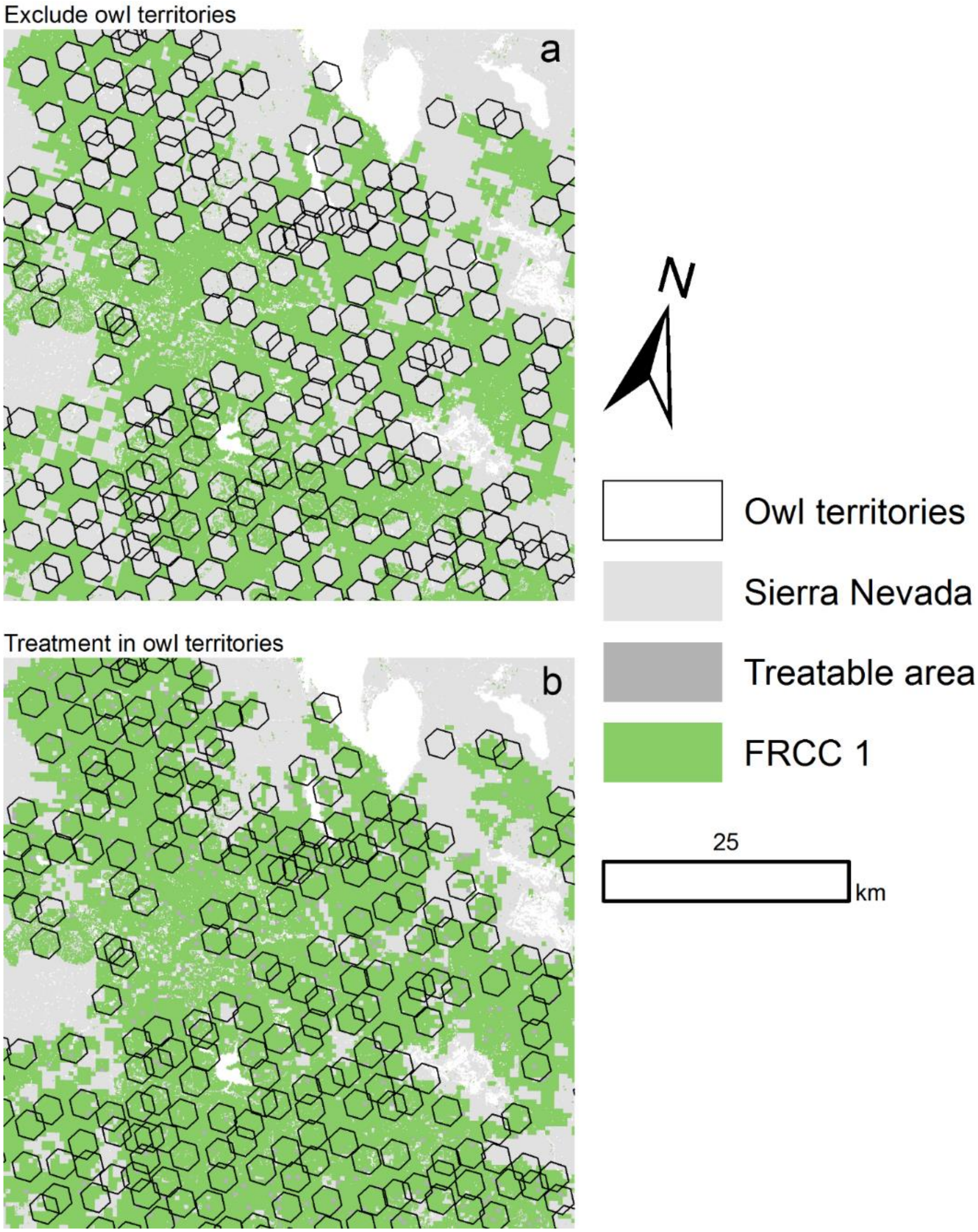

Fig. S3. Zoomed in figure showing fine scale effects of fuel treatment exclusion (corresponding with insets a and b from Figure S2).

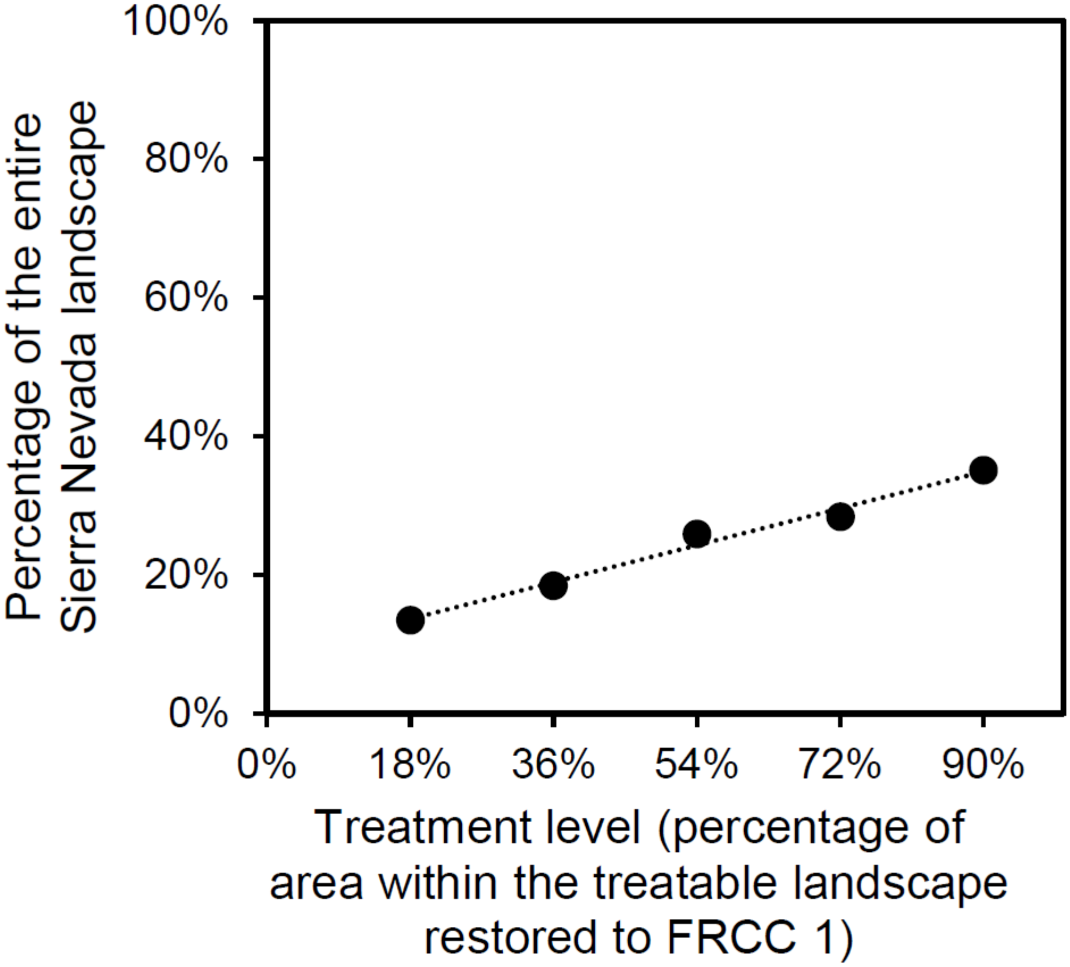

Fig. S4. Relationship between treatment levels (18%, 36%, 54%, 72%, 90%) and the percent area of the total Sierra Nevada landscape that each level comprises.

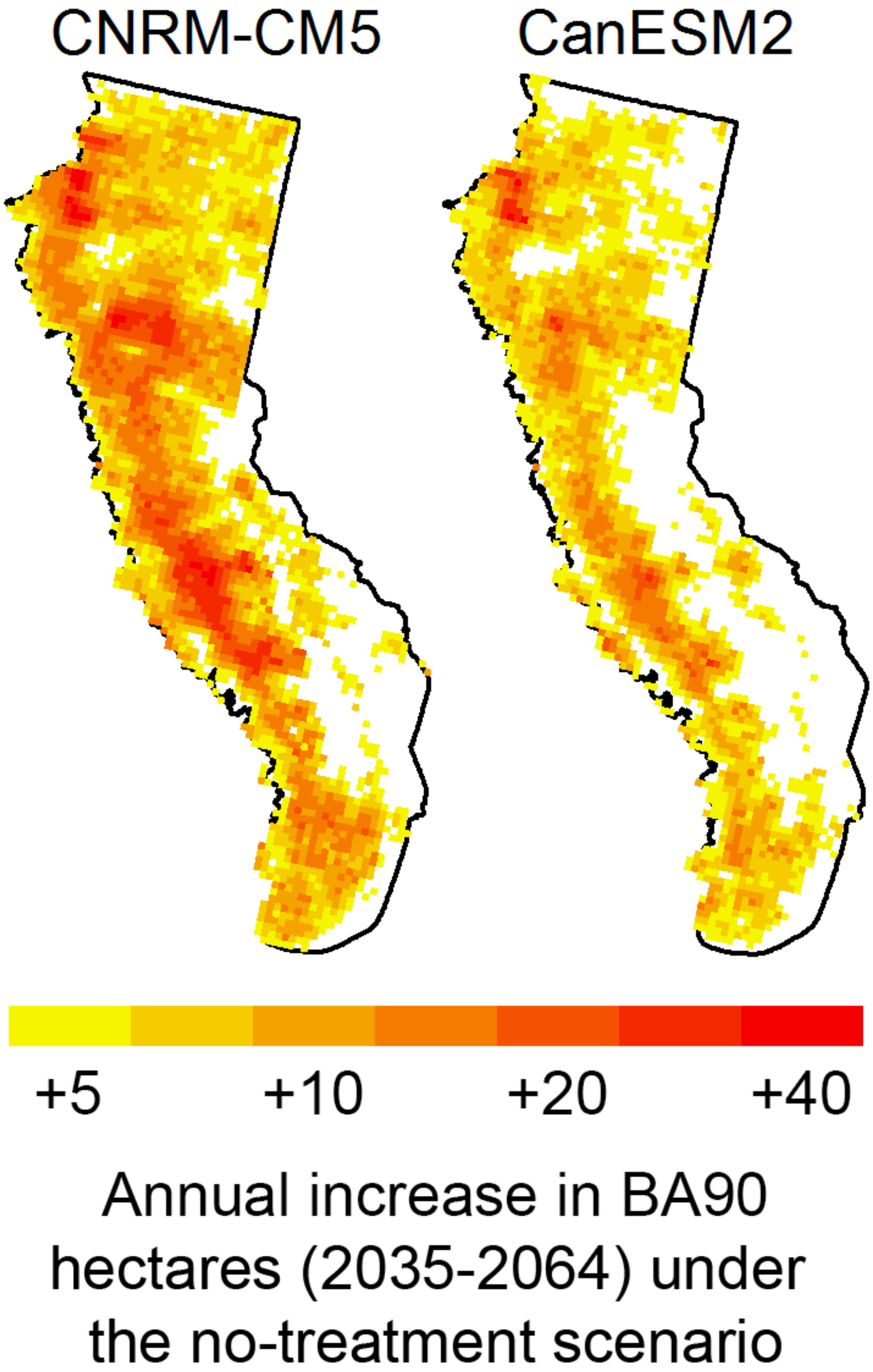

Fig. S5. Annual rate of change in BA90 area (hectares) from 2035-2064 under the no-treatment scenario for each GCM (CNRM-CM5 and CanESM2).

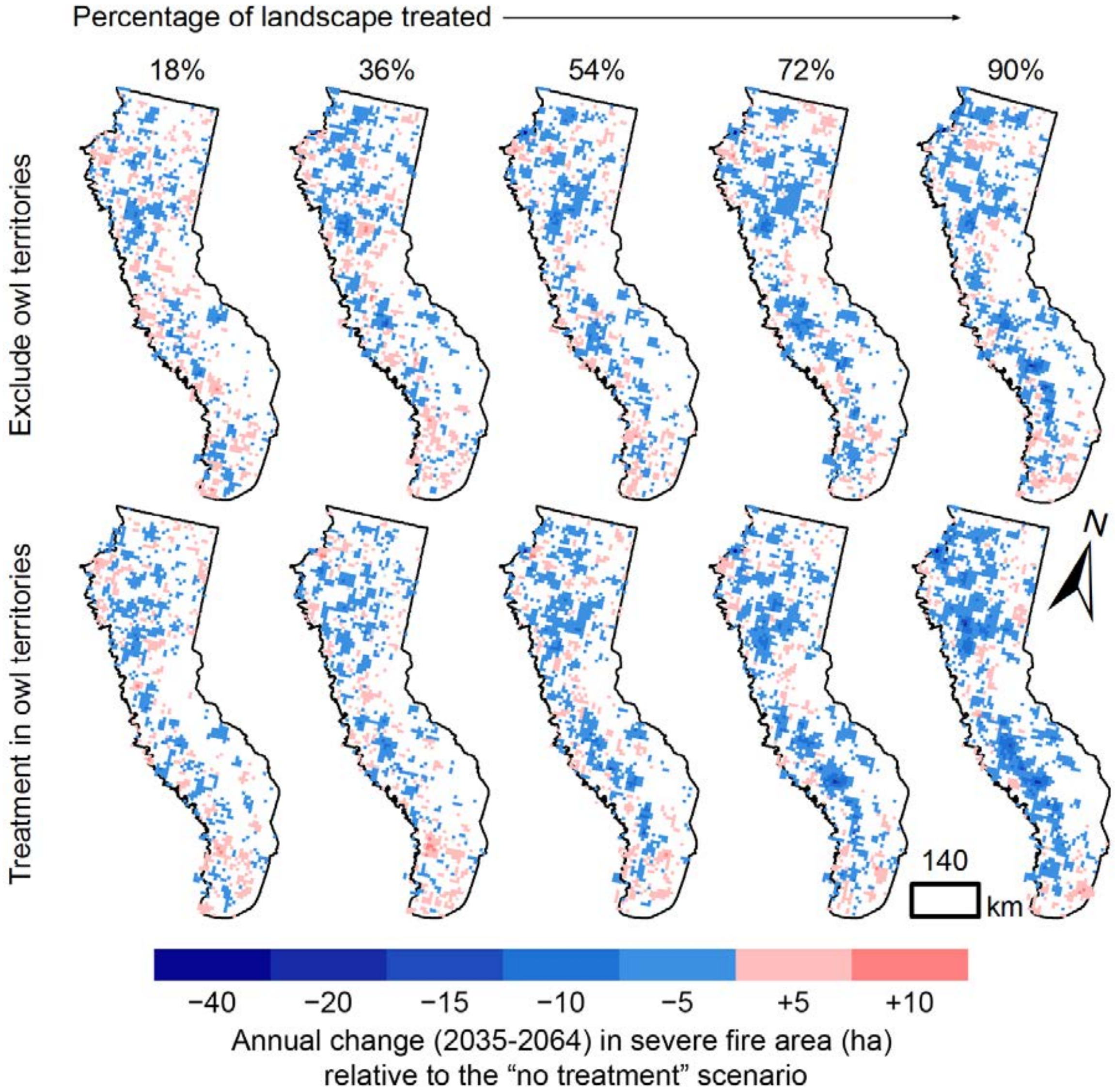

Fig. S6. Changes in severe fire (BA90) extent by mid-century (2035-2064) compared to the baseline no-treatment (0%) scenario. This figure is a repeat of Fig. 1 from the main text but for the CanESM2 GCM.

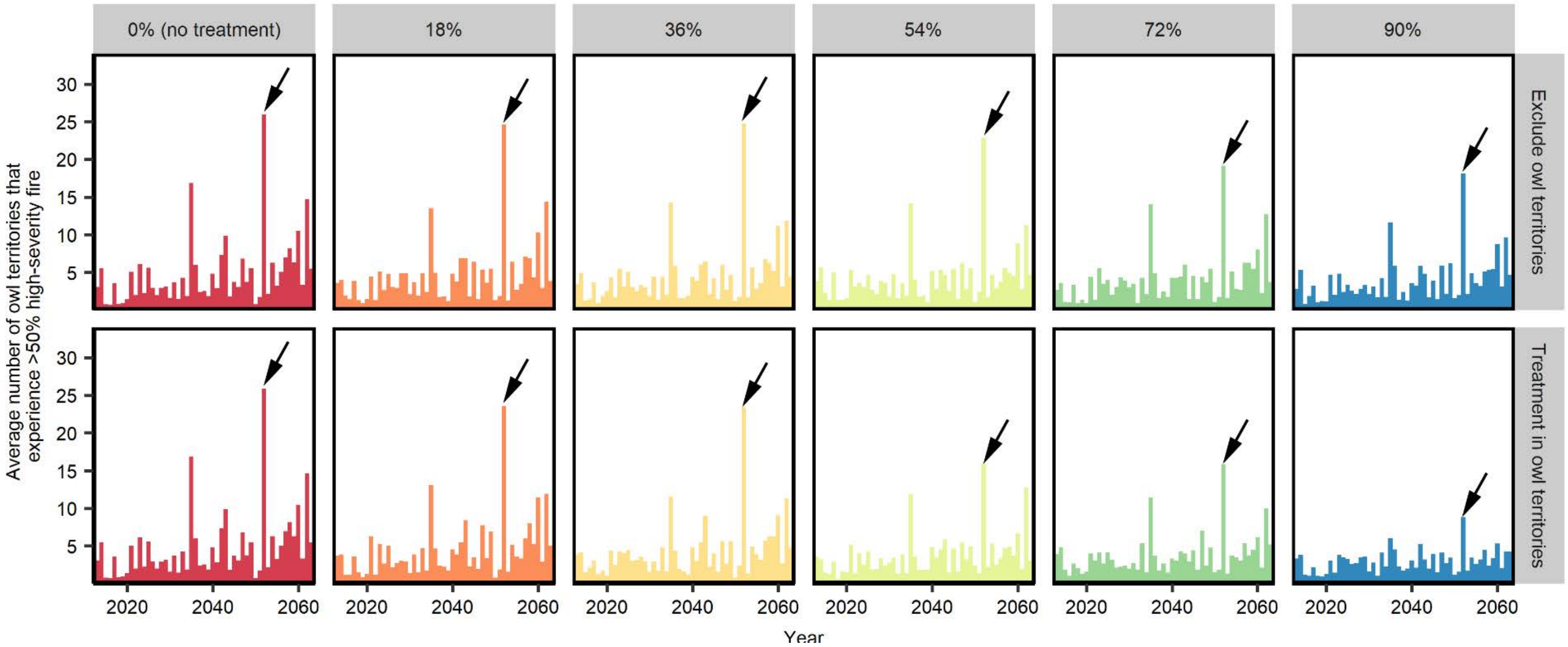

Fig. S7. Predicted changes in spotted owl territory exposure to extinction-inducing severe fire (>50% territory area burned at BA90) in the Sierra Nevada from 2012-2064. Each bar represents the number of owl territories per year affected by >50% severe fire averaged across 100 simulations of the fire model. The CRNM-CM5 global circulation model was used. Arrows point to an extreme fire year (2052).

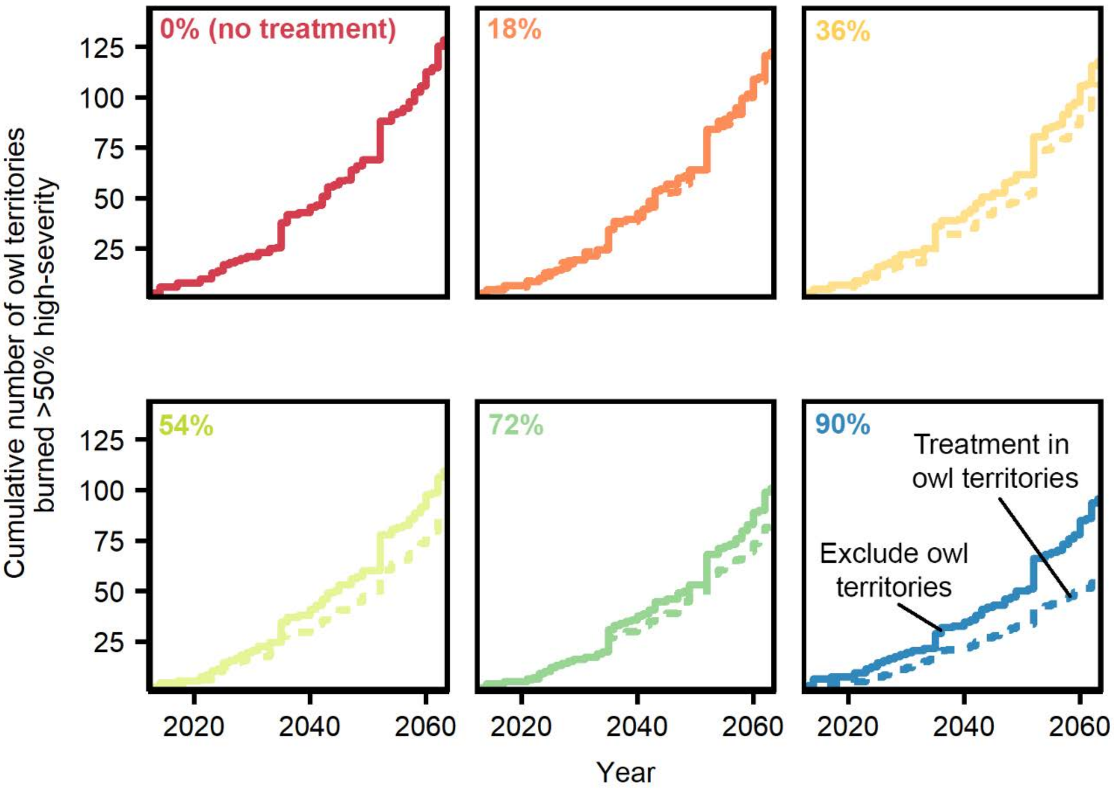

Fig. S8. Expected cumulative number of spotted owl territories exposed to extinction-inducing severe fire (>50% territory area burned severely) in the Sierra Nevada from 2012-2064 for each treatment level, averaged across 100 simulations of the fire model. Results produced using CNRM-CM5 GCM.

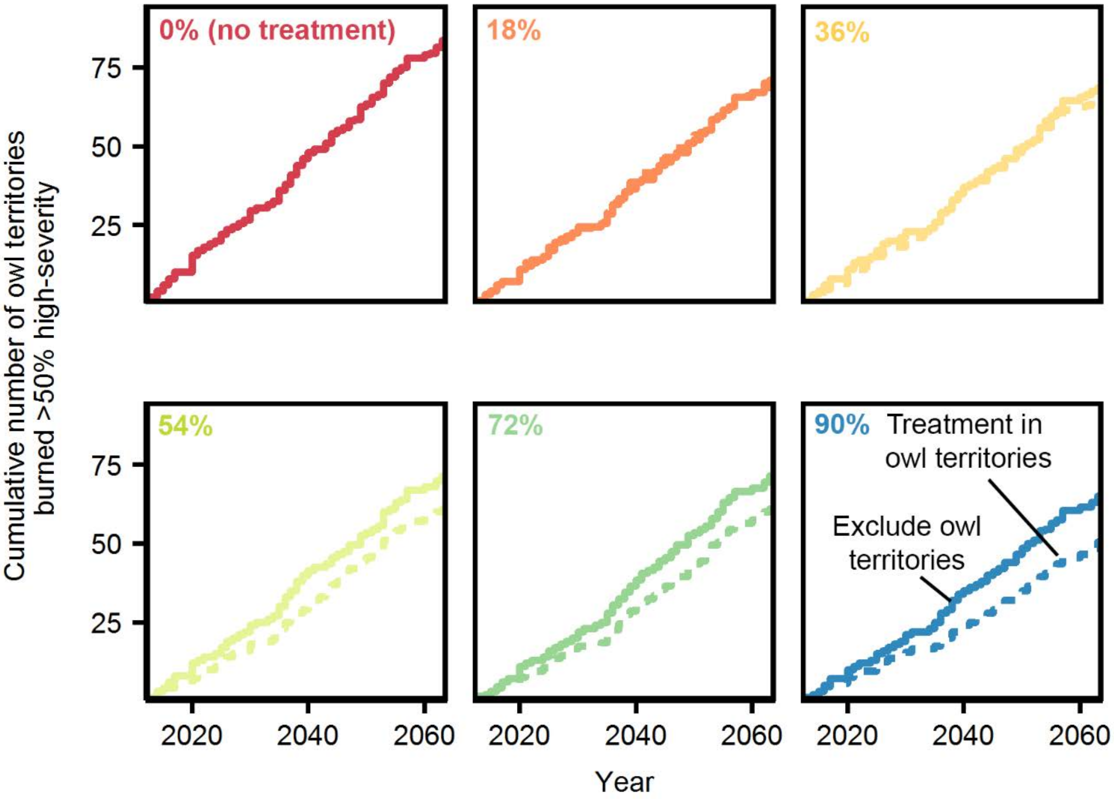

Fig. S9. Expected cumulative number of spotted owl territories exposed to extinction-inducing severe fire (>50% territory area burned severely) in the Sierra Nevada from 2012-2064 for each treatment level, averaged across 100 simulations of the fire model. This is a repeat of Figure S8 but for the CanESM2 GCM.

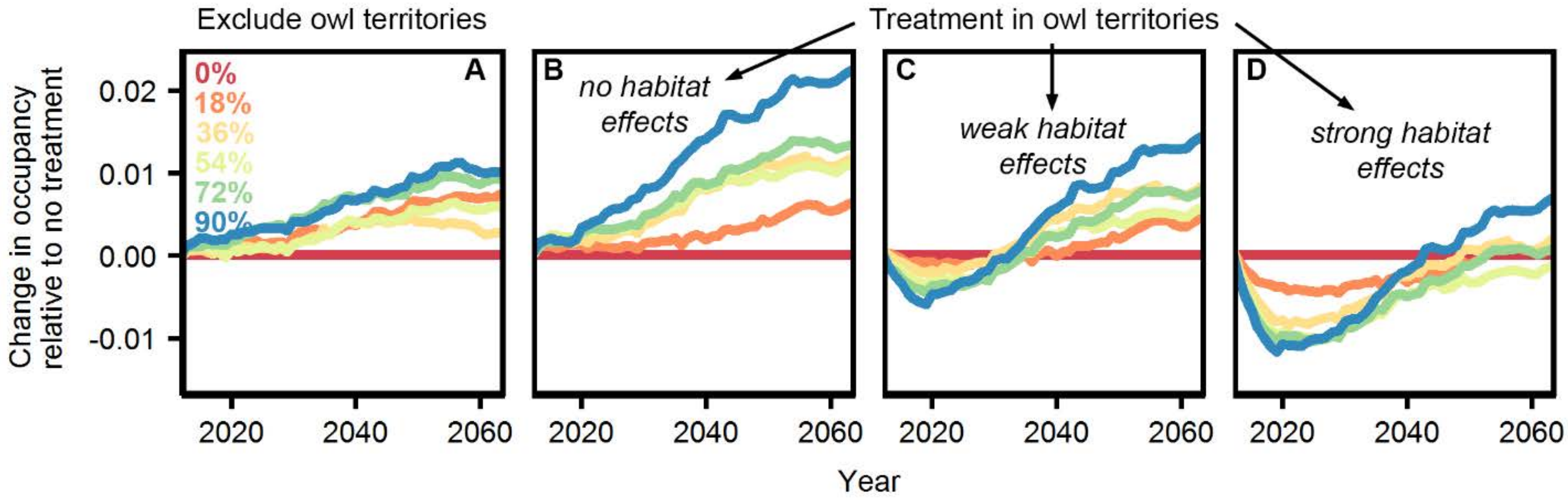

Fig. S10. Summary effects of treatment on spotted owls in the Sierra Nevada showing annual range-wide occupancy for each treatment scenario relative to the baseline no-treatment scenario (red line). This is a repeat of Figure 2 from the main text but for the CanESM2 GCM.

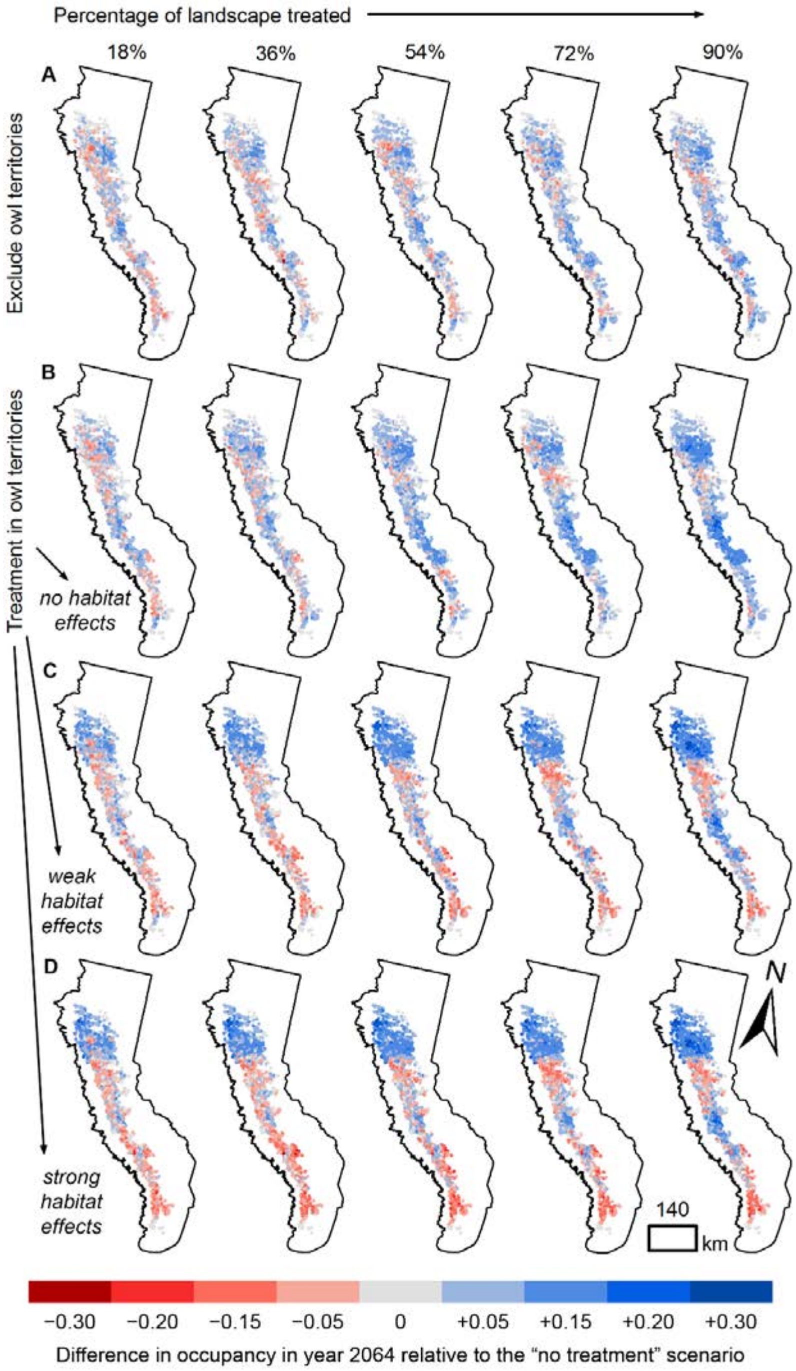

Fig. S11. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is an expanded version of Figure 3 from the main text, but also showing results from simulations that assumed "weak" habitat effects of fuel treatments (middle row). Figure 3 in the main text shows the top row (exclude treatment) and the bottom row ("strong" habitat effects).

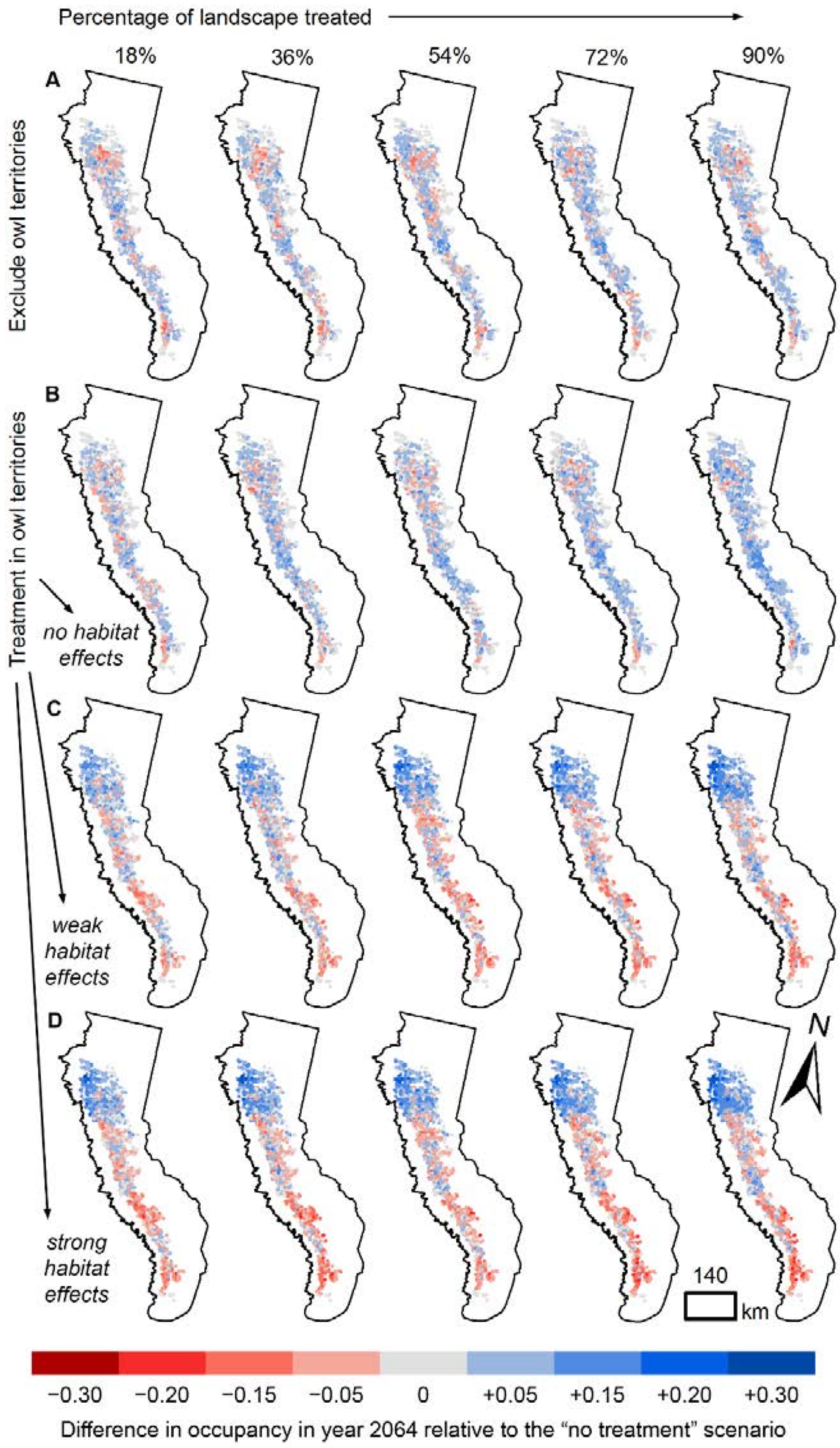

Fig. S12. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is a repeat of of Figure S11 text but for the CanESM2 GCM.

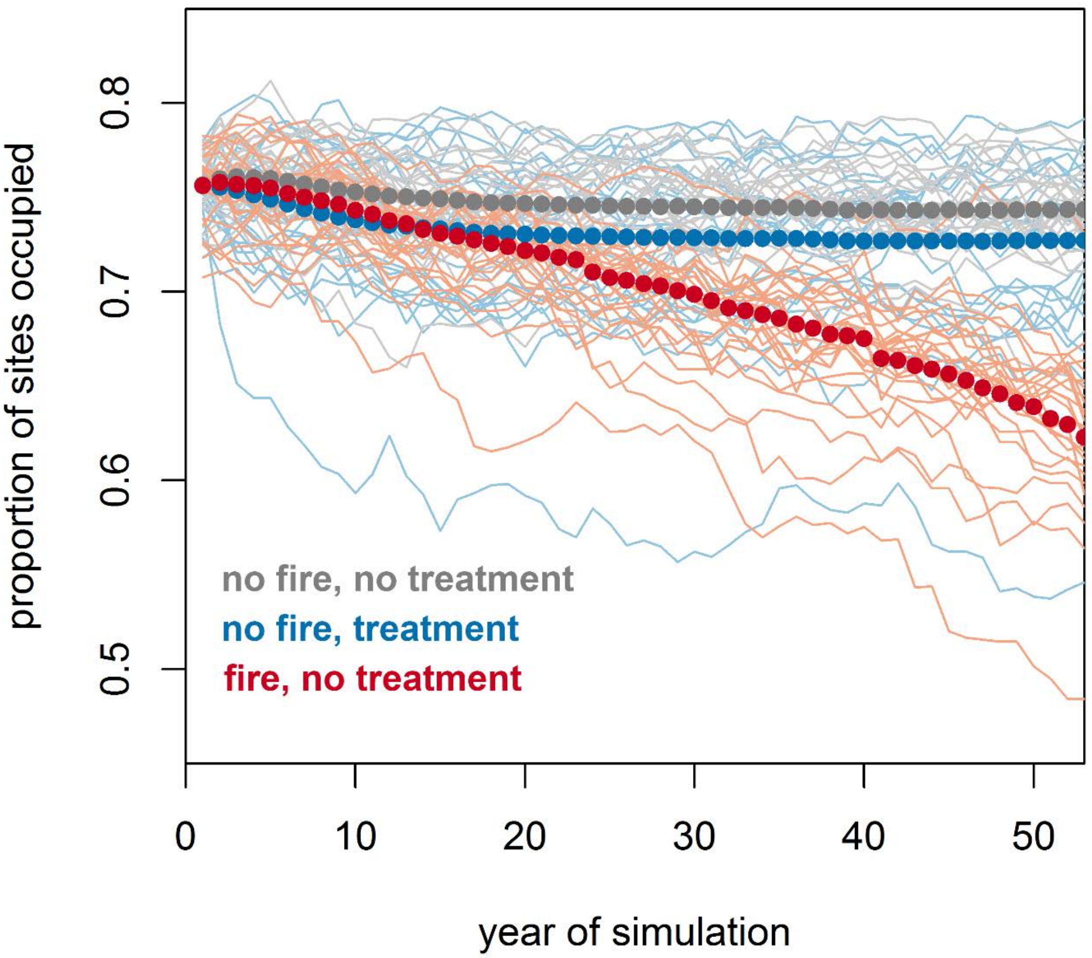

Fig. S13. Relative influence of fire and treatment on projected spotted owl occupancy compared to a baseline "no fire, no treatment" scenario. Projections were run using the CNRM-CM5 GCM.

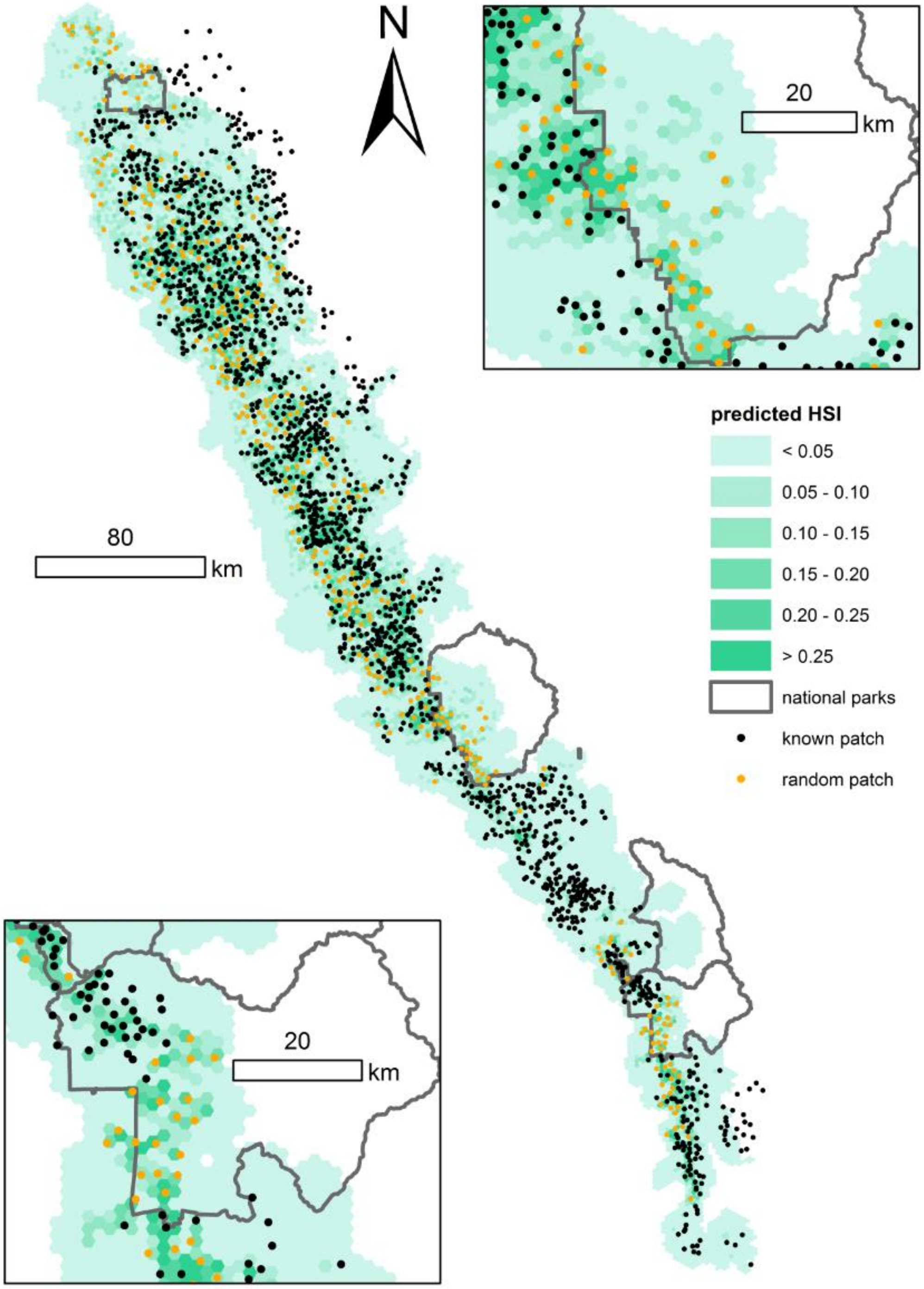

Fig. S14. Patch network used in the spatial occupancy model for spotted owls. Random patches (orange dots) were placed in areas with above-average habitat suitability and that were located at least the mean nearest neighbor distance from known patches. HSI = habitat suitability index (green shading) predicts the probability of spotted owl presence in each ~324-ha hexagonal grid cell across the Sierra Nevada bioregion (JJ Keane, unpublished data).

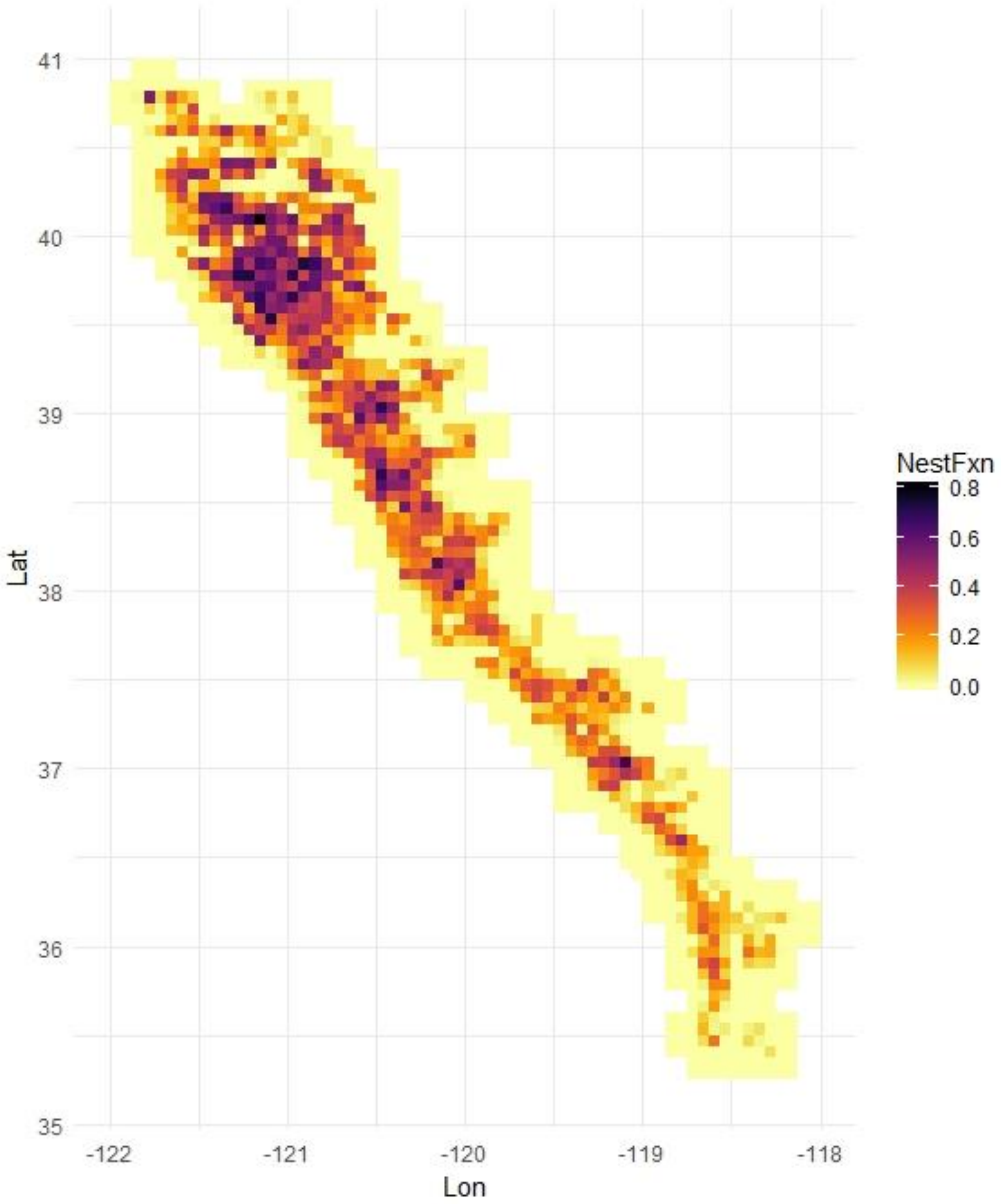

Fig. S15. Proportion of each 6-km grid cell filled by spotted owl territories.

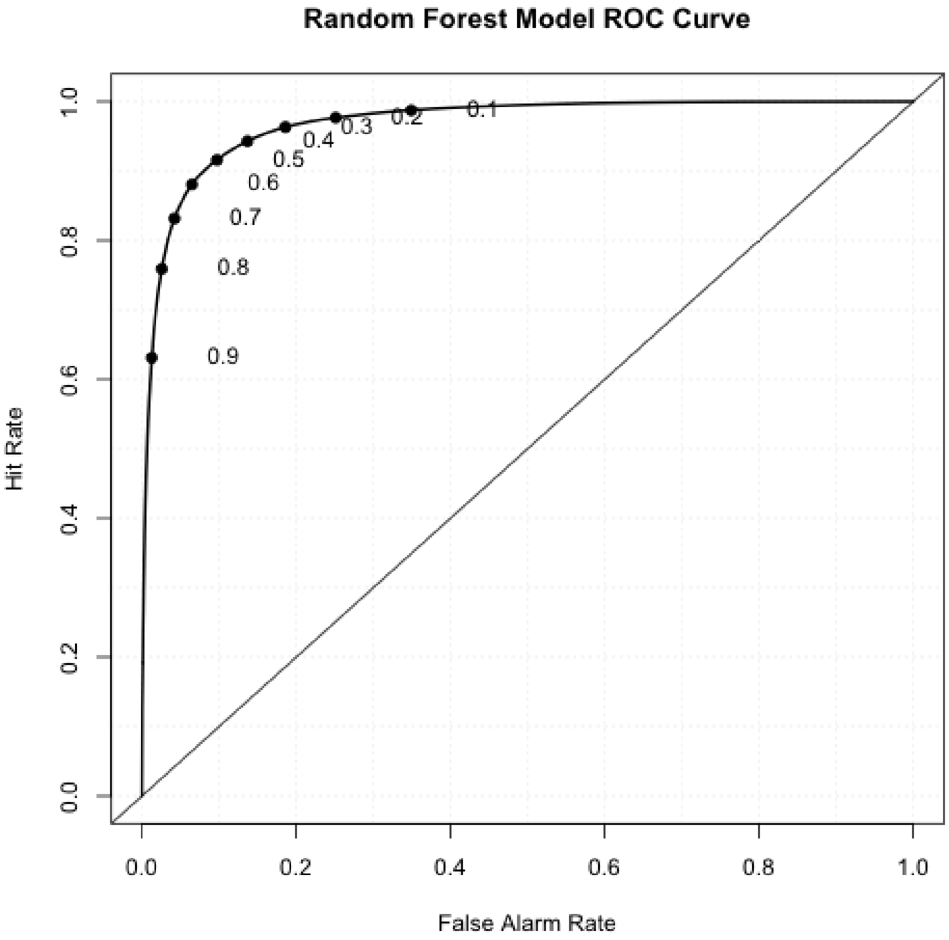

Fig. S16. Area under the receiver-operating curve (AUC) for the downscaling model. AUC = 0.9085. An area of 0.50, a curve corresponding to the 1:1 line, indicates a hypothetical model with skill equivalent to chance.

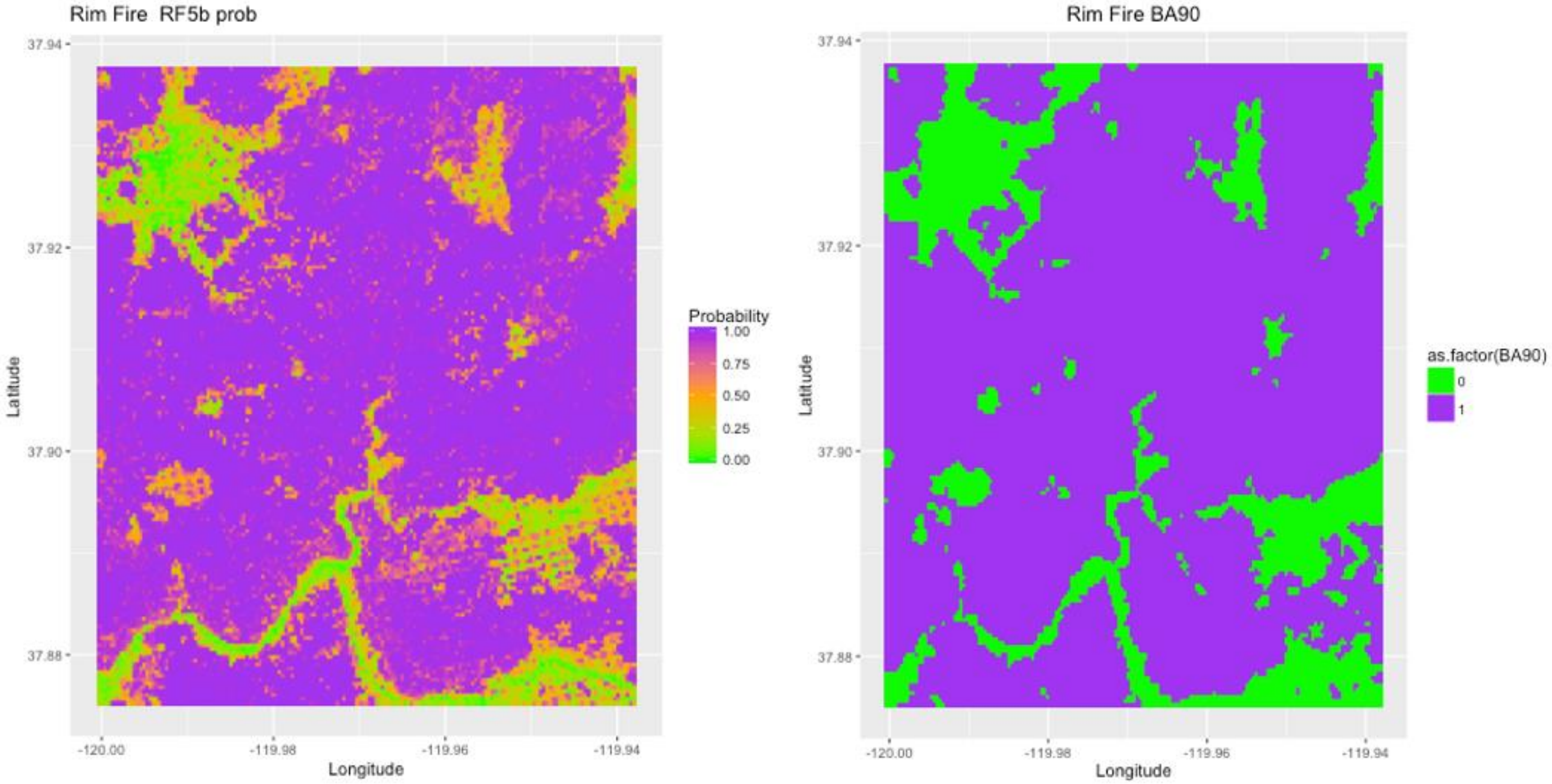

Fig. S17. The predicted probability of BA90 presence (left) produced with the Random Forest fine-scale fire model is paired with observed BA90 presence (right) for area containing the 2013 Rim Fire. These plots demonstrate the performance of the FS model relative to observations. This predicted probability uses the actual fire size; for our FS probability surfaces, we created seven surfaces similar to this for the entire Sierra Nevada bioregion, each with a different pattern of probability according to the fire size bin. These probabilities are drawn from to assign pixel values in the allocation algorithm.

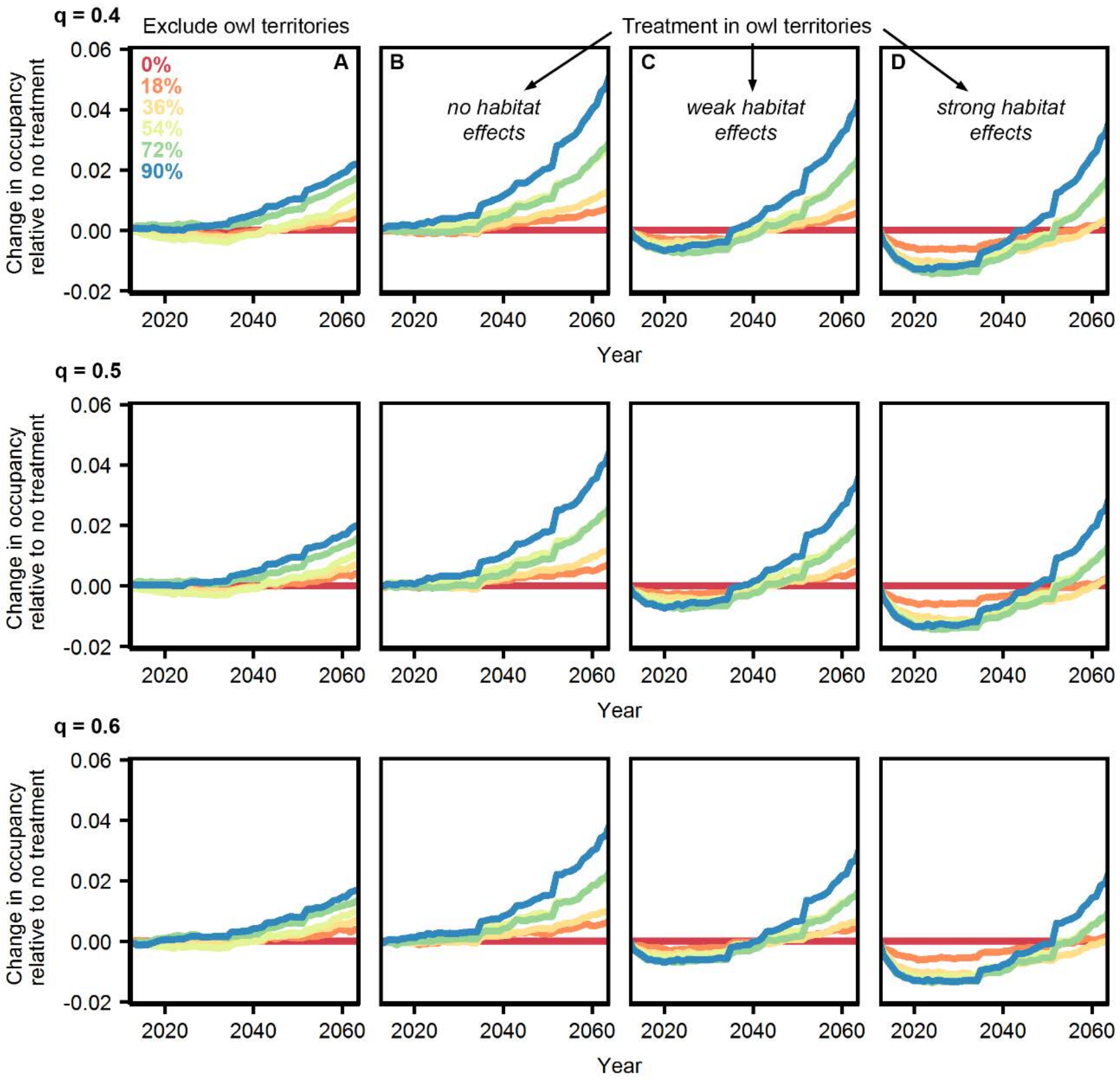

Fig. S18. Summary effects of treatment on spotted owls in the Sierra Nevada showing annual range-wide occupancy for each treatment scenario relative to the baseline no-treatment scenario (red line). This is a repeat of Figure 2 from main text, but showing the effects of different assumptions about the proportion of severe fire in an owl territory that will induce a semi-permanent extinction event (q=0.4, 0.5, 0.6). The middle row is equivalent to Figure 2 from the main text, included here for comparison. Results are shown from the CNRM-CM5 GCM only.

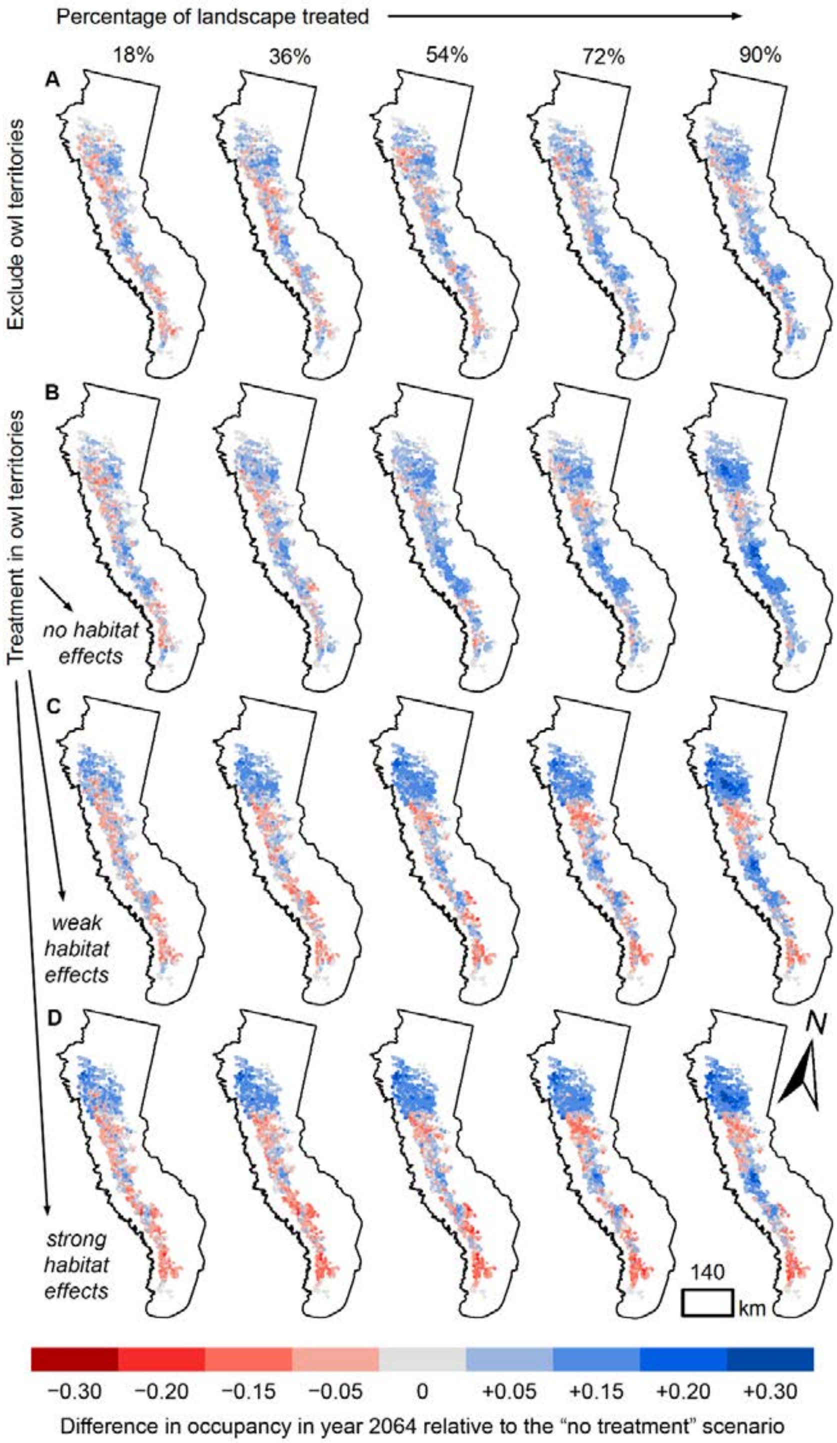

Fig. S19. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is a repeat of Figure 3 from main text showing q=0.4 (CNRM-CM5 only).

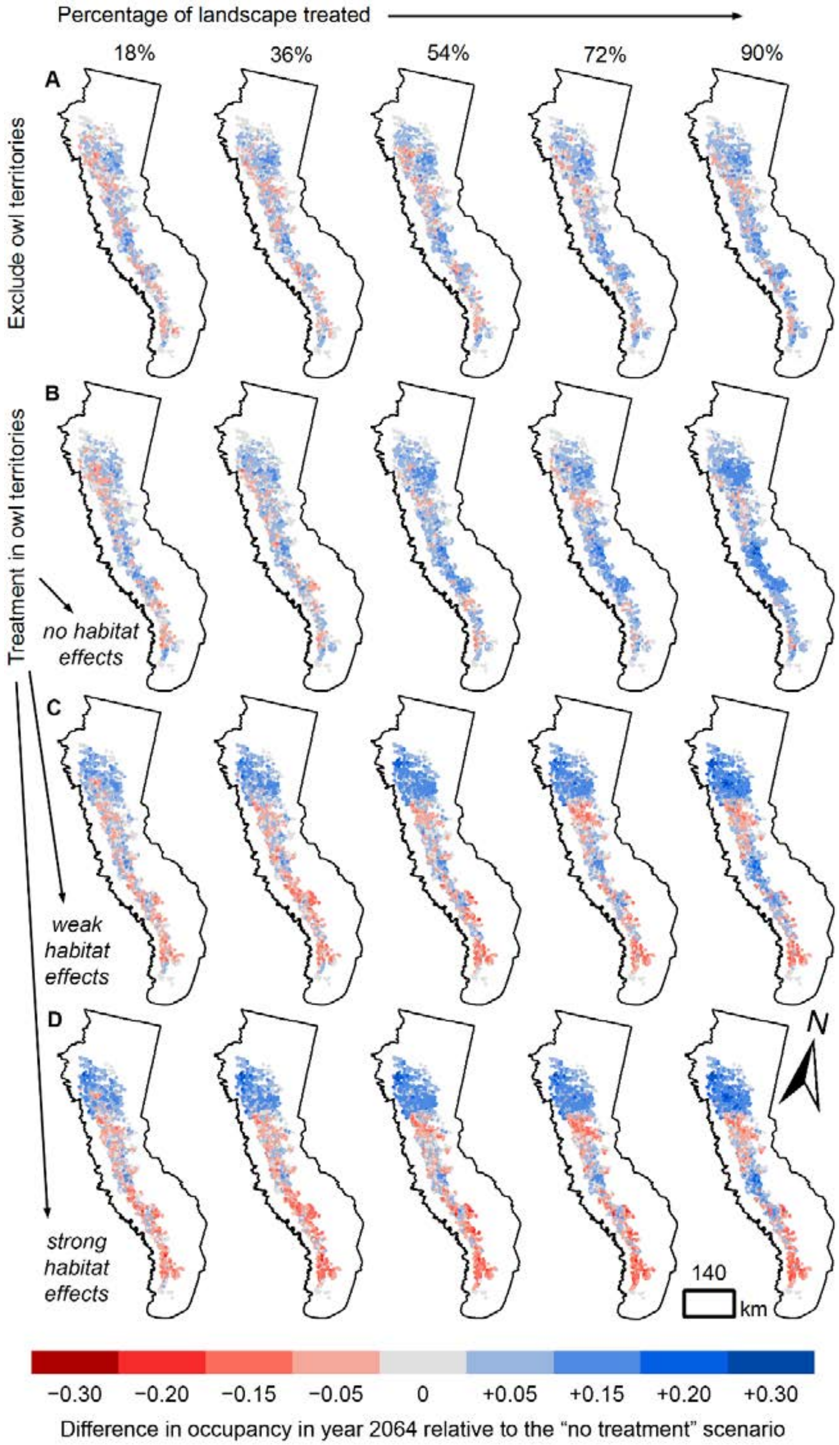

Fig. S20. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is a repeat of Figure 3 from main text showing q=0.6 (CNRM-CM5 only).

Table S1. Change in predicted BA90 area compared to the baseline (no treatment) scenario for the LS fire model.

	Percentage of landscape treated				
CNRM-CM5	18%	36%	54%	72%	90%
Annual change in BA90 hectares (2035-2064)					
Treatment in owl territories	−1668.5	−2568.9	−4240.3	−4892.9	−7150.1
Exclude owl territories	−1551.6	−1927.9	−3099.2	−3845.2	−5021.4
Total change in BA90 hectares (2035-2064)					
Treatment in owl territories	−48386	−74498	−122970	−141895	−207353
Exclude owl territories	−44996	−55909	−89876	−111511	−145619
Percent reduction in BA90 (2035-2064) compared to no-treatment					
Treatment in owl territories	7.1%	11.0%	18.1%	20.9%	30.5%
Exclude owl territories	6.6%	8.2%	13.2%	16.4%	21.4%
CanESM2					
Annual change in BA90 hectares (2035-2064)					
Treatment in owl territories	−665.8	−871.8	−1334.3	−2049.6	−3048.4
Exclude owl territories	−386.2	−836.7	−1149.0	−1534.3	−1786.3
Total change in BA90 hectares (2035-2064)					
Treatment in owl territories	−19308	−25283	−38694	−59438	−88403
Exclude owl territories	−11200	−24264	−33320	−44495	−51803
Percent reduction in BA90 (2035-2064) compared to no-treatment					
Treatment in owl territories	2.8%	3.7%	5.7%	8.7%	13.0%
Exclude owl territories	1.6%	3.6%	4.9%	6.5%	7.6%

Table S2. Parameter estimates from the spatial occupancy model (point estimates and Bayesian credible intervals).

parameter	description	mean	SD	2.50%	97.50%	$\hat{R}$
extinction						
β_0	intercept for north (reference) bioregion	−1.537	0.177	−1.931	−1.223	1.013
β_1	difference in intercept from β_0 for central bioregion	0.427	0.303	−0.133	1.055	1.040
β_2	difference in intercept from β_0 for south bioregion	0.316	0.238	−0.142	0.814	1.008
β_3	slope of lgTree.hiCanopy for north (reference) bioregion	−3.577	2.236	−7.82	0.950	1.005
β_4	slope of lgTree.medCanopy for north (reference) bioregion	−11.18	2.899	−14.837	−4.005	1.017
β_5	difference in slope of lgTree.hiCanopy from β_3 for central bioregion	−2.737	3.371	−9.408	3.629	1.017
β_6	difference in slope of lgTree.hiCanopy from β_3 for south bioregion	−4.408	2.816	−9.995	1.116	1.006
β_7	difference in slope of lgTree.medCanopy from β_4 for central bioregion	6.231	5.063	−5.129	14.352	1.019
β_8	difference in slope of lgTree.medCanopy from β_4 for south bioregion	8.207	3.475	0.026	13.753	1.020
ρ_0	baseline colonization probability for coincident sites (d=0)	0.009	0.001	0.007	0.012	1.001
σ	scale parameter describing decay rate in colonization function	13.291	1.380	10.878	16.247	1.002
detection						
α_0	intercept	0.923	0.026	0.871	0.975	1.000
α_1	slope for detection effect of lgTree.hiCanopy	1.062	0.200	0.666	1.461	1.001
α_2	slope for detection effect of lgTree.medCanopy	−0.754	0.293	−1.325	−0.184	1.001
occupancy in 2011						
ψ_{2011}	proportion of sites occupied in 2011; input data for year 0 of projection	0.757	0.016	0.725	0.787	1.002
derived parameters						
β_{0+1}	intercept for central bioregion	−1.111	0.259	−1.596	−0.6	1.024
β_{0+2}	intercept for south bioregion	−1.222	0.165	−1.553	−0.904	1.001
β_{3+5}	slope of lgTree.hiCanopy for central bioregion	−6.315	2.648	−11.567	−1.109	1.011
β_{3+6}	slope of lgTree.hiCanopy for south bioregion	−7.985	1.829	−11.834	−4.656	1.006
β_{4+7}	slope of lgTree.medCanopy for central bioregion	−4.948	4.183	−13.702	2.110	1.012
β_{4+8}	slope of lgTree.medCanopy for south bioregion	−2.973	2.075	−7.397	0.747	1.005

Table S3. Logistic regression model specification for large fire presence (LS fire model).

for $q_m(X_{mij})$ terms:	**variable**	**description**
$q_m(X_{mij}) =$	$q(CWD_{ij})$	basis spline of cumulative monthly climate water deficit
	$q(T_{ij})$	basis spline of average temperature
	$q(VFR_{ij})$	basis spline of vegetation fraction
	$q(POP_{ij})$	basis spline of population
	$CWD0_{ij}$	cumulative water year climate water deficit
	$CWD1_{ij}$	lagged cumulative water year climate water deficit
	AET_{ij}	cumulative monthly actual evapotranspiration
	Emu_i	mean elevation
	$M_{78} * TRjja_{ij}$	Regional JJA temperature interacted with a factor for month = July or August
	M	factor for month of the year
for $\sum \boldsymbol{\beta}_m \times X_{mij}$ terms:	**variable**	**description**
$X_{mij} =$	$CWD_{ij} * AET_{ij}$	interaction between cumulative monthly climate water deficit and cumulative monthly actual evapotranspiration
	FSR_i	standardized fraction of grid cell in federal or state protection responsibility areas
	$Tmam_{ij}$	average March-April-May (MAM) temperature

Table S4. The distribution of fires within each fire size bin.

Fire size range (ha)	Total number of fires	Number after year 2000	Years spanned	Size midpoint (ha)
3291-6300	93	58	1985-2015	4500
6301-10,000	54	26	1987-2015	8000
10,001-15,000	34	28	1987-2015	12,500
15,001-20,000	21	11	1987-2014	17,500
20,001-30,000	21	11	1985-2015	25,000
30,001-60,000	30	11	1985-2015	45,000
60,001-199,555	11	11	2002-2013	60,000

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Forest restoration limits megafires and supports species conservation under climate change

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Climate change and fire suppression have altered disturbance regimes in forest ecosystems globally. In the seasonally dry forests of western North America, large-scale restoration may reduce severe fire and increase forest resilience but also eliminate existing habitat for sensitive wildlife species. We modeled bioregional-scale effects of forest restoration on future severe fire activity and occupancy dynamics of an old-forest species declining in abundance, the spotted owl (*Strix occidentalis*), in the Sierra Nevada mountains of California. Our findings suggest restoring historical forest structure may mitigate severe fire activity as the climate warms, particularly when restoration occurs in owl habitat. On average, benefits provided by restoration to owls (reduced severe fire) were found to exceed potential costs (direct habitat alteration) by mid-century. However, the magnitude and direction of restoration trade-offs varied spatially, which informs restoration planning. When large, old trees are maintained, forest restoration can provide co-benefits to old-forest species and forest ecosystem resilience under climate change.

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Climate change is profoundly altering forest distribution and disturbance regimes worldwide (Seidl *et al.* 2017). Humans also continue to shape forests globally. In the seasonally dry forests of western North America, a century of fire suppression and large-tree logging has transformed forest structure away from historical conditions (Collins *et al.* 2017). Forests that were historically open with low tree densities now have high densities of small- and medium-sized trees and a deficit of large trees (Safford and Stevens 2017). These altered forest structures combined with climate change have led to larger, more severe fires (Steel *et al.* 2015; Westerling 2016) and widespread drought-related tree mortality (Fettig *et al.* 2019), with substantial impacts to humans and forests. These increasingly common "mega-disturbance" events pose a major threat to forest persistence, and to forest species and ecosystem services (Stephens *et al.* 2018; Wood and Jones 2019).

Landscape-scale forest restoration may increase seasonally dry forest ecosystem resilience (Stephens *et al.* 2020). Thinning and prescribed/managed fire can reduce accumulation and increase heterogeneity of fuels (Knapp *et al.* 2017); promote development of large, fire-resistant trees (Agee and Skinner 2005); alter fire behavior and lower severe fire likelihood (Tubbesing *et al.* 2019); and reduce risk of drought-related tree mortality (Bradford and Bell 2016). However, restoration alters forests inhabited by wildlife that depend on large, old trees, high canopy cover, and complex vertical structure (Tempel *et al.* 2014). Concern over wildlife habitat has limited the pace and scale of forest restoration efforts (North *et al.* 2015a). Thus, restoring seasonally dry forest ecosystems while safeguarding vulnerable populations of old-forest species presents a conservation conundrum: how can restoration occur without jeopardizing species that use "departed" forest conditions (Peery *et al.* 2017)?

Solving this conundrum involves understanding whether or how the potential negative short-term impacts of restoration on old-forest species can be outweighed by reducing habitat loss to future severe wildfires. To address this question, we developed a novel bioregional-scale severe fire model (hereafter, "fire model") that generates robust, fine-grain (30-m) predictions of future severe fire activity linked to climate and vegetation (eg fuels) conditions. We coupled the severe fire model with a spatial occupancy model ("occupancy model") to evaluate relative and scale-dependent effects of restoration and severe fire on a focal old-forest species, the spotted owl (*Strix occidentalis*) (Figure 1), across the Sierra Nevada mountains of California (~120,000 km^2). In doing so, we assessed two central questions about bioregional-scale forest restoration. First, can restoration effectively reduce future severe fire activity in a changing climate? Second, can restoration provide co-benefits to old-forest species?

Methods

We fit the fire and occupancy empirical models independently over the period for which common historical data existed (1984–2015), then linked them together during forward simulations of restoration- and climate-induced changes in patterns of severe fire and owl occupancy dynamics (through 2064; WebFigure 1). Climate-change effects in the fire model

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Figure 1. An adult male spotted owl (*Strix occidentalis*) located in Sequoia and Kings Canyon National Parks in the southern Sierra Nevada, California.

were represented using the Representative Concentration Pathway 8.5 (RCP8.5) and the global circulation model (GCM) CNRM-CM5. We chose RCP8.5 because it reflected a "business-as-usual" emissions scenario; however, we considered only projections through mid-century, when the divergence between RCP8.5 and other more optimistic scenarios is modest compared to the final decades of the 21st century. The CNRM-CM5 model typically reflects moderate to warmer conditions than other commonly used GCMs and therefore represents a "higher end" warming scenario that produced greater future fire activity in our model. The fire model produced annual realizations of severe fire occurrence across the Sierra Nevada through mid-century (2064) that fed into the occupancy model. The behavior of both models was linked to a factorial design that varied the extent and location of restoration activities (changes to "fire regime condition class" [FRCC]; see WebPanel 1) across the landscape (Westerling 2018). By using changes in FRCC to reflect effects of restoration activities (eg fuels reduction), we assume that such activities, however implemented, can return forests to their historical range of variability.

Restoration (or "treatment") was simulated in areas without substantial mechanical operability constraints on non-subalpine federal lands (hereafter "treatable" lands; Collins *et al.* 2010; North *et al.* 2015a), with total treatment extent varying in equal intervals (20%, 30%, 40%, 50%, and 60% of the Sierra Nevada bioregion treated). Treatable lands (approximately 60,000 km^2) excluded wilderness areas, inaccessible areas, and other sensitive areas that cannot be treated under current regulatory frameworks. The highest treatment level (60%) represented ~90% of the total "treatable" area in the Sierra Nevada. A second set of treatment scenarios maintained the same total treatment extent but excluded treatment from spotted owl territories. Restoration treatments were introduced into the fire and owl occupancy models in year one of the forward projection and were implemented "instantaneously", meaning that treatment effects were immediate. Consequences of this simplifying assumption likely include an overestimation of the short-term effects of treatments (because they cannot be implemented across such large scales immediately) both in terms of their ability to reduce severe fire behavior and their effects on owl habitat. We evaluated the effect of our assumptions about how treatments would alter owl habitat by conducting a sensitivity analysis in which we varied the extent to which treatment modified habitat within the occupancy model ("no habitat alteration", "weak habitat alteration", "strong habitat alteration"; see WebPanel 1).

Fire model

We developed a novel multiscale fire model using remotely sensed burn severity data (WebFigure 1; WebPanel 1). We defined high severity as 90% basal area killed (hereafter "stand-replacing" or "severe" fire). The multiscale fire model consisted of large-scale (~6-km) and fine-scale (30-m) "submodels" that interacted to produce spatial realizations of severe fire. We developed the large-scale submodel by fitting a spatially explicit logistic regression model on a ~6-km grid to estimate the monthly probabilities of the occurrence of at least one fire >400 ha as a function of topography, human population, vegetation fraction, and climate (WebPanel 1; Westerling 2018). Then, for each fire >400 ha, the probability of a minimum threshold (>50 ha) burning in a stand-replacing fire was estimated by fitting a logistic regression with climate covariates. To estimate conditional extent of stand-replacing burned area, we fitted a generalized Pareto distribution with climate and FRCC covariates for each fire with >50 ha stand-replacing burned area (WebFigure 2). We used this model system to simulate large-scale stand-replacing burned area for each climate and treatment scenario (see WebPanel 1).

We developed the fine-scale submodel (a mapping algorithm) by selecting 20 fires for model training that yielded the most complete coverage of latitude, year, ignition month, fire size, and severity in the Sierra Nevada (WebTable 1). Random Forests, a machine-learning algorithm, was used to predict occurrence of stand-replacing fire pixels (30 m) on the landscape as a function of topography, vegetation type, and fire size, and a spatial allocation algorithm was developed to link the large- and fine-scale model to assign severely burned pixels to the 30-m landscape surface using a Monte Carlo simulation. Starting with a randomly assigned ignition point (using a uniform distribution) within the large-scale modeling pixel, the algorithm assigned 30-m pixels as stand-replacing fire (true/false) in an iterative fashion based on the modeled fine-scale probability surface until the predicted fire size from the large-scale model was reached. This procedure was repeated for the entire suite of models 100 times for each unique treatment scenario, and each individual simulation was delivered to the spatial occupancy model for spotted owls (see below). Full model description, evaluation, accuracy and error assessments, and allocation examples are provided in WebPanel 1.

Occupancy model

We modeled spotted owl territory (hereafter, "site") occupancy using a Bayesian spatial occupancy model (Chandler *et al*. 2015) with detection/non-detection data from $n = 275$ owl survey areas collected between 1993 and 2011 (WebFigure 1; Tempel *et al*. 2016). The spatial dependence in the model's structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites representing nearly all suitable habitat in the Sierra Nevada (see Jones 2019). Site extinction probability and detection probability were modeled as a function of forest structural variables representing the proportion of each owl site containing large trees (quadratic mean stand diameter ≥61 cm) and high canopy closure (≥70% canopy cover), and large trees and medium canopy closure (40–70% canopy cover), respectively (WebFigure 1; WebPanel 1; Jones *et al*. 2018).

We combined output from the multiscale fire model with 500 multivariate posterior draws of parameter distributions to project the spotted owl population forward over the period 2012–2064 while incorporating the full parameter uncertainty (WebFigure 1; WebPanel 1). Simulated treatment effects within individual owl territories were modeled by modifying forest structure covariate values (see above) in a manner consistent with expected changes in horizontal canopy structure due to treatments (ie reducing fuel continuity by reducing canopy cover). Severe fire effects were modeled using an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a before–after control–impact natural experiment (WebFigure 1; Jones *et al*. 2016). In forward projections of the model system, we focused on reporting expected (mean) outcomes to guide discussion of management implications, but we also acknowledge and discuss the role of prediction uncertainty in interpretation of results. For full model description and reporting, see WebPanel 1.

Results

In the absence of forest restoration treatments, severe fire was predicted to burn an average of ~24,000 ha/year (maximum annual prediction 235,000 ha) in the Sierra Nevada, or a total of ~720,000 ha (range 453,585–1,068,009 ha over 100 simulations) during the years 2035–2064 (Figure 2a; WebFigure 2). Restoration changed the expected severe fire area by a minimum of −6.8% (a reduction of 45,930 ha of severe fire) to −55.8% (a reduction of 257,880 ha of severe fire) over the period 2035–2064 depending on treatment extent and location (Figure 2, b and c). However, uncertainty in annual decreases of severe fire extent across the stochastic fire replicates resulting from treatment effects was large (orders of magnitude; WebFigure 2). More extensive treatments consistently reduced expected severe fire area across the landscape, and this effect was proportionally larger when treatments were included in owl territories (Figure 2c; WebFigure 2). For example, treating 60% of the landscape but restricting treatments to occur outside of owl territories reduced severe fire area by 29%, whereas allowing treatments to occur in owl territories reduced severe fire by nearly 56%. Moreover, higher levels of treatment (eg >40% of the Sierra Nevada) appeared to reduce expected severe fire activity even in years when climate models produced extreme fire conditions, most notably when treatments were included in owl territories (WebFigure 3).

The degree to which owl territories were exposed to local extinction-inducing severe fire depended on the spatial extent of simulated restoration treatments and whether treatments were allowed within owl territories (WebFigure 3). Forest restoration has the potential to provide expected net benefits to spotted owls inhabiting the Sierra Nevada by the mid-21st century under all scenarios considered (Figure 3). When treatments were excluded from owl territories (Figure 3a), owl populations experienced expected net benefits that increased with more treatment, but the long-term benefits were lower compared to scenarios where owl territories received treatments (Figure 3, b–d). Owls were expected to benefit most when treatments occurred within territories and when treatments avoided modifying large tree/high canopy cover forest (Figure 3b). When treatments occurred inside territories and owl habitat was modified (Figure 3, c and d), a downward pressure was imposed on owl populations over initial years of the simulation but varied in degree depending on assumptions made about the extent to which treatment directly altered owl habitat. The expected net costs of treatment were offset by the cumulative benefits of reduced severe fire exposure by the 2040s and 2050s for all treatment scenarios (Figure 3, c and d). Importantly, the scenarios involving treatment in owl territories (and therefore simulated changes to forest structure in the owl model) introduced additional variability into the model system because of uncertainty associated with effects of habitat alteration, which resulted in wider prediction intervals (WebFigure 4).

When averaged across the entire Sierra Nevada, expected treatment effects on population occupancy were apparent but modest in magnitude (eg −0.01 to +0.04; Figure 3). However, larger expected effects that varied considerably in space were apparent at the territory scale (eg ±0.30; Figure 4; WebFigure 4). When treatments were excluded from owl territories, there were relatively uniform expected benefits to mid-century territory occupancy compared to a no-treatment scenario (eg –0.06 to +0.11; range of 99th percentile of values; Figure 4b). These benefits grew (eg –0.07 to +0.20) when treatments were simulated to occur within owl territories but were assumed to avoid modifying large tree/high canopy cover forest (Figure 4c). When simulated treatments were applied in owl territories and treatment was assumed to modify owl habitat, strong regional-scale patterns in trade-offs emerged (eg –0.11 to +0.22; Figure 4d). Broad-scale patterns in trade-offs were driven by regionally varying treatment effects to owl habitat estimated from occupancy data (WebTable 2) and spatial variation in future severe fire exposure (Figure 2).

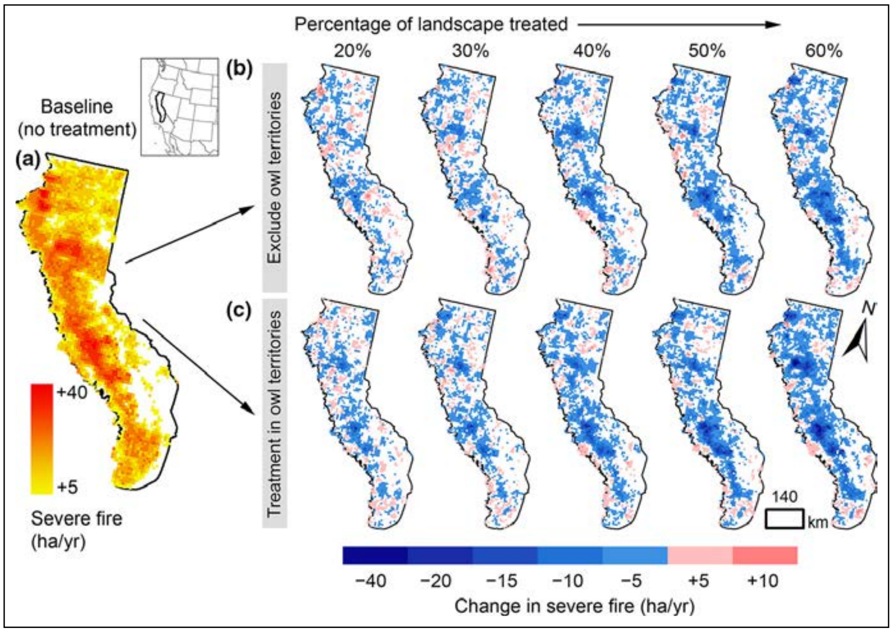

Figure 2. Severe fire activity in the Sierra Nevada is expected to increase by mid-century but was altered by treatment location and extent. (a) Mean annual increase in severe fire (90% basal area killed) over a mid-century climate period (2035–2064) under the baseline no-treatment (0%) scenario; (b) expected effects of treatment on severe fire activity when treatments excluded from spotted owl (*Strix occidentalis*) territories at varying levels of treatment extent (increasing from left to right); (c) expected effects of treatment on severe fire activity when treatments are included in owl territories. The polygon outlined in black depicts the boundary of the Sierra Nevada bioregion. The rectangle in the bottom right is the scale bar, where the horizontal length is equivalent to 140 km. Note that the color ramp intervals for change in severe fire are not all equal.

Discussion

Our analysis indicates that climate change will result in increased severe fire extent in the Sierra Nevada through mid-century, but that bioregional-scale restoration has the potential to offset this increase. Restoration also appears to support spotted owl conservation, suggesting co-benefits between forest resilience and old-forest species conservation objectives. Owls experienced relatively large expected benefits from treatment in areas where treatments considerably reduced future severe fire (Figures 2 and 4). Conversely, areas where owls experienced net negative treatment effects (eg southern Sierra Nevada) were characterized by lower future exposure to severe fire, more pronounced direct treatment impacts on predicted territory extinction rates, or both (Figures 2 and 4; WebTable 2). When treatments occurred in owl territories but were assumed not to alter key owl habitat, benefits were nearly universal and larger than other scenarios (Figures 3b and 4b) with less prediction uncertainty (WebFigure 4). Optimal management strategies might therefore entail a mixed approach where treatments are excluded from owl territories or designed to avoid high-quality owl habitat in certain regions where expected negative impacts of treatment are greatest, and included elsewhere where expected direct effects

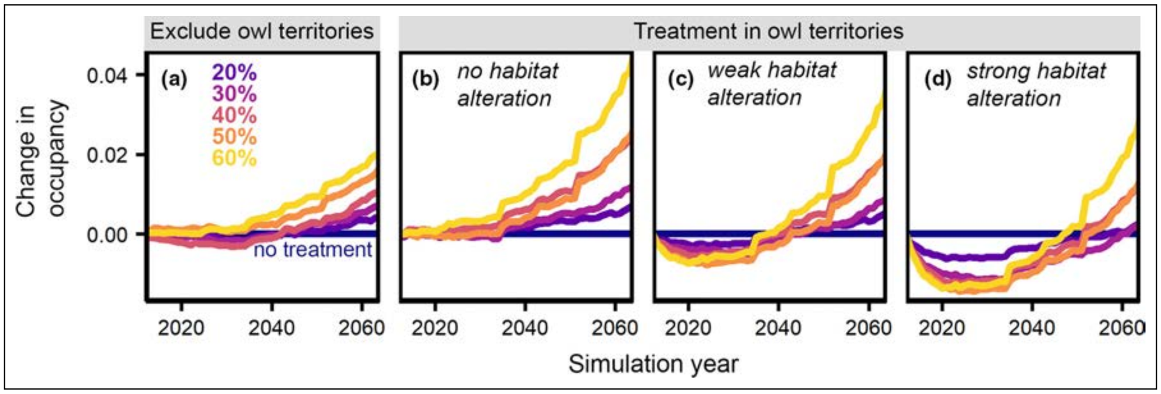

Figure 3. Sierra Nevada-wide site occupancy trajectories for each treatment scenario relative to the baseline no-treatment scenario (dark blue line). (a) Occupancy when treatments are excluded from owl territories; (b–d) occupancy when treatment occurs within owl territories but assumptions about the extent to which treatments alter owl habitat vary (no habitat alteration, weak habitat alteration, strong habitat alteration; see WebPanel 1). Trajectories represent means across 50,000 simulations. For full uncertainty across stochastic replicates, see WebFigure 4.

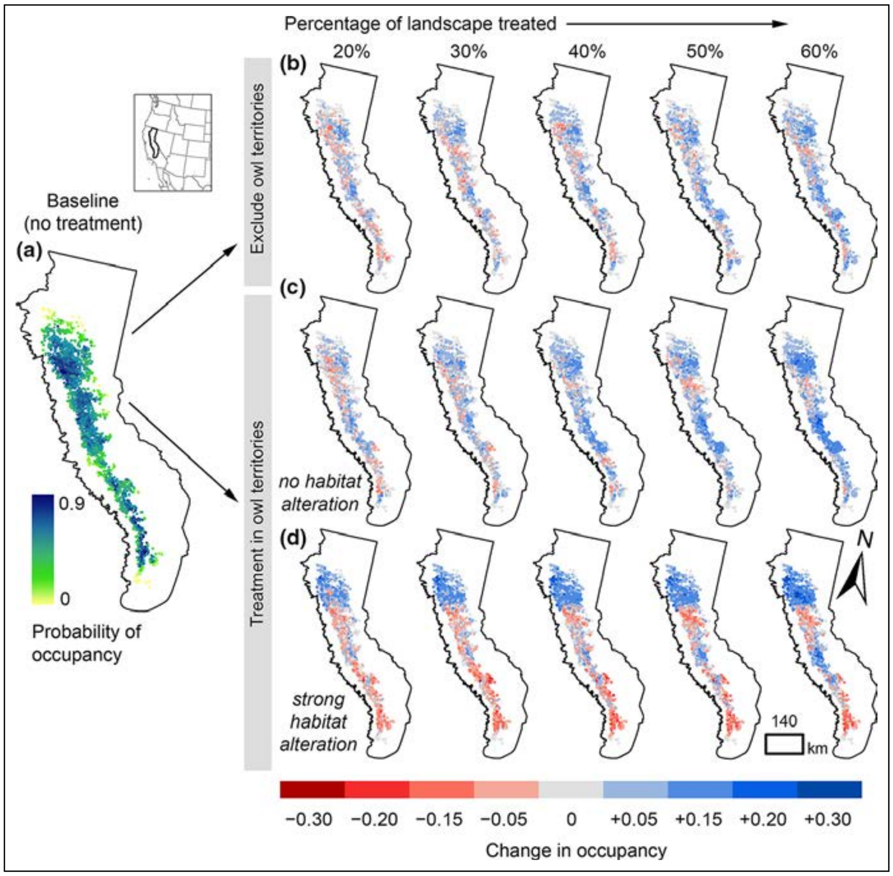

Figure 4. Spatial variation in effects of the location and extent of fuel treatments on spotted owl site occupancy by mid-century (2064). (a) Expected mid-century site occupancy under a no-treatment scenario; (b) difference in occupancy when treatments are implemented but are excluded from owl territories at varying levels of treatment extent (increasing from left to right); (c, d) difference in occupancy when treatment occurs within owl territories but assumptions about the extent to which treatments alter owl habitat vary (see WebFigure 4 for "weak habitat alteration"). Values represent the average across 50,000 simulations (WebPanel 1). The polygon outlined in black depicts the boundary of the Sierra Nevada bioregion. The rectangle in the bottom right is the scale bar, where the horizontal length is equivalent to 140 km. Note that the color ramp intervals for change in occupancy are not all equal.

of treatment are less negative or are positive (Figure 4).

Landscape fuel treatments will never stop a fire but they can change how fires burn, thereby mediating fire-related tree mortality and resulting effects to species and ecosystems. Both model simulations (eg Collins *et al.* 2011; Tempel *et al.* 2015) and empirical studies (eg Safford *et al.* 2012; Tubbesing *et al.* 2019) have suggested landscape fuel treatments are effective in altering fire behavior and can greatly reduce severe fire activity in seasonally dry forests. In accordance with these findings, our results suggest that returning forest conditions to within the historical range of variability reduces expected high-severity burned area at a bioregional scale (Figure 2; WebFigure 2). Although this was an expectation for fuel-limited seasonally dry forest ecosystems, concern exists that fuels management may be inadequate to modify severe wildfire in a changing climate when extreme fire conditions become more common on an annual basis (Schoennagel *et al.* 2017). Indeed, we observed some degree of increase in severe fire activity under all treatment scenarios with climate warming (eg WebFigure 3). However, as more of the landscape was treated, expected future severe fire extent was reduced (Figure 2) even in years with extreme fire weather, an effect that was particularly notable when larger proportions of landscapes were treated (eg >40%; WebFigure 3). At high levels of treatment extent, expected increases in severe fire activity were completely offset by expected reductions in severe fire due to treatment in some areas (Figures 2 and 4), although real changes could be much larger or smaller because of prediction uncertainty (WebFigure 2). These results suggested that large-scale forest restoration efforts have the potential to meaningfully alter severe fire activity and reduce fire-related risk to spotted owls in a changing climate.

Although our model offers a robust starting point for forecasting wildfire and population dynamics across this large bioregion, we made simplifying assumptions to make our model tractable. We assumed stationarity in fire–climate relationships over the forward simulation period, which may become less likely further into the future (Parks *et al.* 2016; Littell *et al.* 2018). Vegetation (ie fuels) within our models were static, and treatments were introduced once at the beginning of forward simulations and assumed to be maintained when in reality treatments would take decades to implement and maintenance would be variable. As such, effects of treatments to owls via direct habitat alteration only occurred once, whereas maintenance of treated areas could result in recurring effects. We also assumed that treatment applications varying in their direct effects to owl habitat (eg Figure 3, b–d) would all be equally effective at altering fire behavior, which is unlikely; in addition, we only considered how the expected changes in forest structure resulting from treatment interacted with our models, not potential effects of the treatment method itself (eg prescribed burning, hand-removal of small trees, thinning and/or logging of medium-sized trees). Finally, treatments were simulated randomly across the landscape because the fine-scale spatial patterning would not influence our statistical fire model, but strategic placement in areas with high baseline fire risk can make treatments more effective at lower treatment extents in the real world (McGarigal *et al.* 2018; Tubbesing *et al.* 2019).

Forest restoration currently occurs below desired levels because of legal, administrative, and financial constraints (Collins *et al.* 2010; North *et al.* 2015a). Increasing the pace and scale of restoration to levels that will alter fire activity at the bioregional scale (Figure 2) will require greater funding, more effective integration of silvicultural approaches with prescribed and managed fire to increase treatment extent at the landscape scale (North *et al.* 2012, 2021; York *et al.* 2021), and a recognition that while short-term costs may be high, they will be eclipsed by future costs under the status quo (North *et al.* 2015b). Over the past several decades, treatments have sometimes been implemented within portions of owl territories (~300–600 ha), but generally not within the "core" areas of the territory corresponding to management units called "protected activity centers" (PACs; ~121 ha). Our study treated the entire territory as the management unit (including the smaller PAC) and therefore we did not estimate potential effects of treatments at the PAC scale alone. Previous syntheses have recommended lower-intensity fuel treatments at the scale of the activity center (nest, roost) to reduce potential habitat-related negative effects to owls (Peery *et al.* 2017). Our results suggest that implementing treatments within owl territories could have an outsized effect on reducing future severe fire activity in the Sierra Nevada compared to treating the same area outside of owl territories (Figure 2).

Dry forest ecosystems, like those in the Sierra Nevada, face an increased probability of disturbance-initiated transition to non-forest landscapes without active management to restore ecologically appropriate forest conditions and reduce accumulated fuels (Stephens *et al.* 2020). Broadening forest restoration efforts in dry forests has the potential to enhance forest resilience and reduce risk of severe fire that negatively impacts forests, carbon storage, water supply, air quality, and local communities as the climate changes (Wood and Jones 2019; Stephens *et al.* 2020). As a complement to previous mechanistic work that examined forest restoration trade-offs at smaller spatial scales (Scheller *et al.* 2011; Tempel *et al.* 2015), our work suggests bioregional-scale forest restoration appears to be largely compatible with conservation of old-forest-dependent wildlife species.

Fire-suppressed forests that are well outside their historical range of variability are prone to severe fire and are also preferred by many forest-dependent wildlife species. Treatments within these forests are likely to reduce severe fire extent and therefore provide greater long-term benefits to species like the spotted owl. Treatments that increase landscape-scale heterogeneity are likely to provide shorter-term benefits as well by promoting habitat for key prey species (Hobart *et al.* 2019; Kramer *et al.* 2021). Additional targeted research that narrows uncertainties about the effects of different types of treatments (eg hand removal, pre-commercial thinning, prescribed fire) on species habitat will be needed to better inform planning. However, to minimize the effects of fuel reduction and forest restoration on spotted owls and other old-forest species, including the fisher (*Pekania pennanti*), northern goshawk (*Accipiter gentilis*), and American marten (*Martes americana*), it is essential that large, old trees and core nesting/roosting areas within territories be maintained (Jones *et al.* 2018). When large, old trees are maintained and recruited, fuel reduction and forest restoration in the Sierra Nevada can benefit both old-forest species, forest ecosystem resilience, and people in a changing climate.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2450/suppinfo