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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).

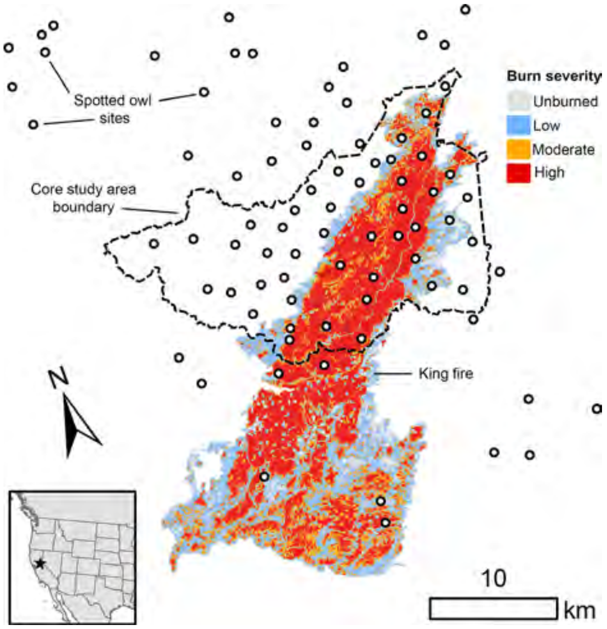

Figure 1 Study area map showing the distribution of spotted owl sites in relation to the 2014 King Fire. The Before–After Control-Impact natural experiment was made possible because a portion of sites was unburned (those outside the King Fire) while other sites experienced a gradient of burn severity. 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) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

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).

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

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.

unmarked owls (Franklin et al., 1996). Recent work has 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:

$$\text{logit}(p_{i,t}) = a_0 + a_1 repro_{i,t} + a_t$$

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:

$$\text{logit}(\psi_{i,1}) = b_0 + b_1 kf_i$$

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

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

and

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

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

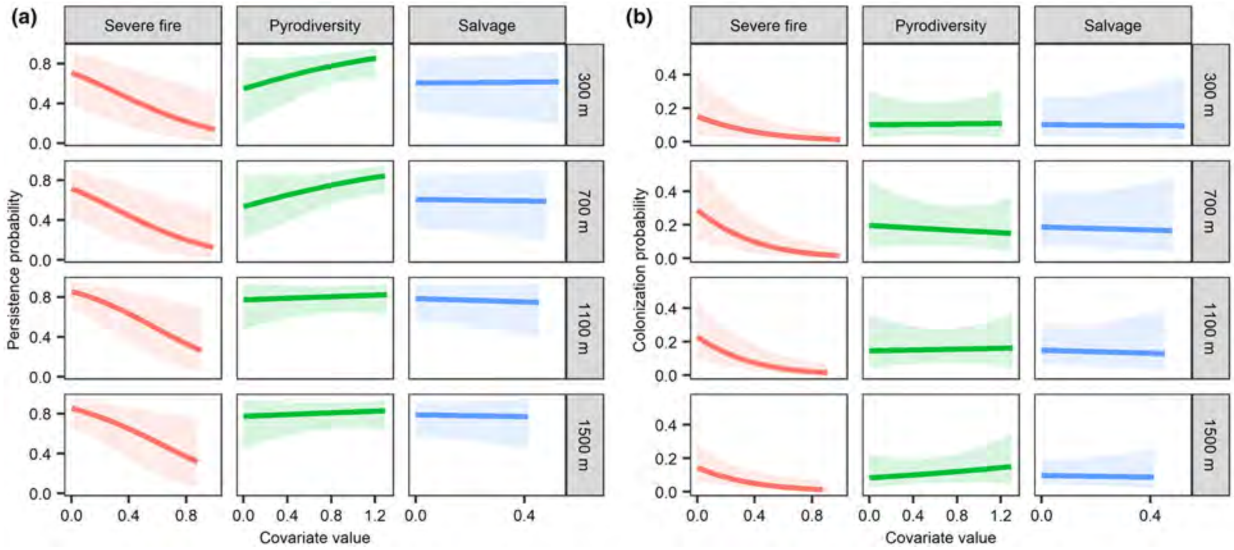

Figure 2 Predicted relationships between covariates (severe fire, pyrodiversity and salvage logging) and dynamic occupancy rates (persistence in panel a; colonization in panel b) across the four scales of analysis (nest area, 300 m; PAC, 700 m; territory, 1100 m and home range, 1500m). The thick colored 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 [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

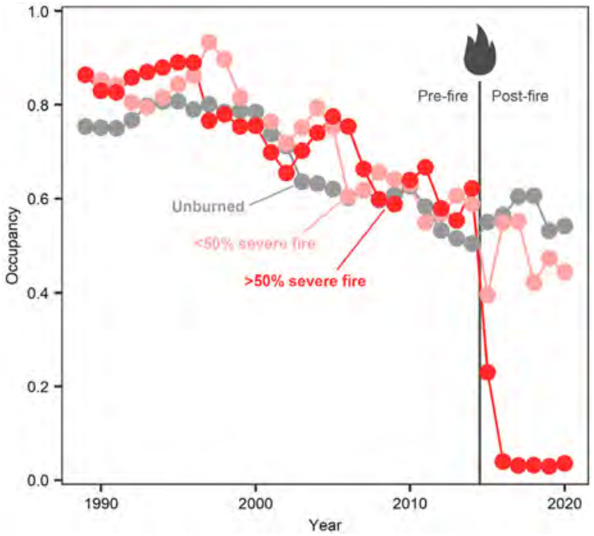

Figure 3 Derived annual occupancy from 1989 to 2020 for spotted owl sites grouped by the percentage of the home-range (1500 m) that experienced severe fire (unburned, <50% severe, >50% severe). The grey vertical line on the x-axis between years 2014 and 2015 indicates the timing of the 2014 King Fire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

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 6 years post-fire, which further indicated that severe fire was more likely of these two forces driving local extirpation and

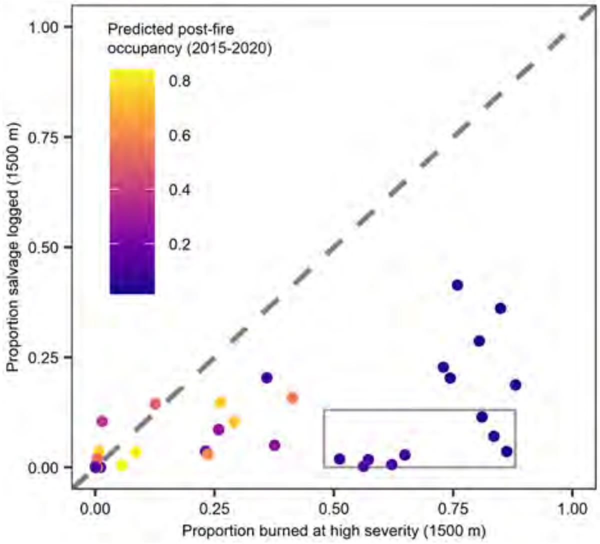

Figure 4 Comparison of the relative extent of salvage logging (y-axis) and severe fire (x-axis) at the home-range (1500 m) scale, where each point represents one spotted owl site. Points are colored by the predicted post-fire (2015–2020) occupancy at each spotted owl site. Points above the grey dashed 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 [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

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

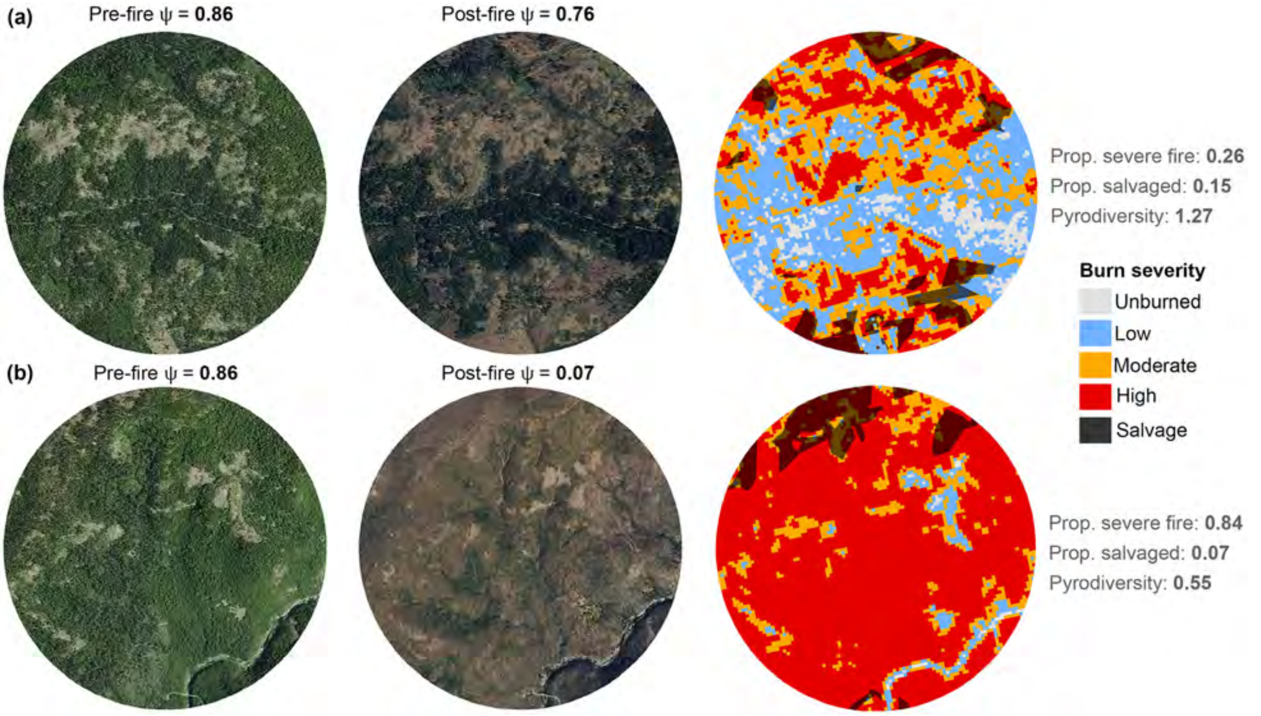

Figure 5 Two selected spotted owl sites (shown at the home-range scale, 1500 m) illustrating the effects of fire severity, pyrodiversity and salvage logging on site occupancy. The owl site in the top row (a; “site A”) and bottom row (b; “site B”) had the same predicted pre-fire occupancy probability ($\psi = 0.86$). 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 [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

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 recolonization 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