Received: 29 April 2024 | Revised: 21 August 2024 | Accepted: 17 September 2024

DOI: 10.1002/eap.3080

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Frequent, heterogenous fire supports a forest owl assemblage

Kate McGinn[1,2] | **Benjamin Zuckerberg**[1] | **Gavin M. Jones**[2,3] | **Connor M. Wood**[4] | **Stefan Kahl**[4,5] | **Kevin G. Kelly**[1] | **Sheila A. Whitmore**[1] | **H. Anu Kramer**[1] | **Josh M. Barry**[1] | **Elizabeth Ng**[1] | **M. Zachariah Peery**[1]

[1]Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, USA

[2]USDA Forest Service, Rocky Mountain Research Station, Albuquerque, New Mexico, USA

[3]Biology Department, University of New Mexico, Albuquerque, New Mexico, USA

[4]K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA

[5]Chemnitz University of Technology, Chemnitz, Germany

Correspondence
Kate McGinn
Email: mcginn4@wisc.edu

Funding information
National Fish and Wildlife Foundation; USDA Forest Service; USFS Pacific Southwest Research Station; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: DGE-1747503; Wisconsin Agricultural Experiment Station

Handling Editor: Sarah P. Saunders

Abstract

Fire shapes biodiversity in many forested ecosystems, but historical management practices and anthropogenic climate change have led to larger, more severe fires that threaten many animal species where such disturbances do not occur naturally. As predators, owls can play important ecological roles in biological communities, but how changing fire regimes affect individual species and species assemblages is largely unknown. Here, we examined the impact of fire severity, history, and configuration over the past 35 years on an assemblage of six forest owl species in the Sierra Nevada, California, using ecosystem-scale passive acoustic monitoring. While the negative impacts of fire on this assemblage appeared to be ephemeral (1–4 years in duration), spotted owls avoided sites burned at high-severity for up to two decades after a fire. Low- to moderate-severity fire benefited small cavity-nesting species and great horned owls. Most forest owl species in this study appeared adapted to fire within the region's natural range of variation, characterized by higher proportions of low- to moderate-severity fire and relatively less high-severity fire. While some species in this assemblage may be more resilient to severe wildfire than others, novel "megafires" that are larger, more frequent, and contiguously severe may limit the distribution of this assemblage by reducing the prevalence of low- to moderate-severity fire and eliminating habitat for a closed-canopy species for multiple decades. Management strategies that restore historical low- to moderate-severity fire with small patches of high-severity fire and promote a mosaic of forest conditions will likely facilitate the conservation of this assemblage of forest predators.

KEYWORDS
bioacoustics, disturbance, megafire, occupancy, owls, passive acoustic monitoring, wildfire

INTRODUCTION

Disturbance can increase biodiversity by supporting species with varying sensitivities to dynamic ecological processes (Connell, 1978). Fire is a driving agent of disturbance in many forest ecosystems (Bond & Keeley, 2005; Seavy et al., 2012; White et al., 2016), and the characteristics of a fire regime—severity, return interval, configuration, size, and seasonality—are driven by a region's elevation, latitude, and climate (Archibald et al., 2013; McLauchlan et al., 2020; Veblen et al., 2000). These features influence the suitability of burned habitat for both fire-associated and fire-avoidant species, and species often exhibit adaptations to iterative features of fire disturbance (Blakey et al., 2021; Fontaine et al., 2009; White et al., 2016). For example, species adapted to shorter interval, lower severity fire regimes, like those that occur in seasonally dry forests, often rely on different aspects of a dynamic mosaic of fire severity and successional stages (Jones & Tingley, 2022; Tingley et al., 2016). Animals that occur in fire-prone landscapes have varied relationships with burned forest depending on their natural histories, and species diversity is often high where fire promotes heterogeneity in forest age and structure (Ponisio et al., 2016; Taillie et al., 2018; Tingley et al., 2016).

While natural fire regimes can support biodiversity, novel fire dynamics potentially pose a substantial threat to some animals and biological communities even in forests adapted to frequent fires (Levine et al., 2022; Taylor et al., 2016; Westerling et al., 2011; Wood & Jones, 2019). In western North America, fire suppression has led to longer return intervals, broad homogenization of forests (Lydersen & Collins, 2018), and a reduction in biodiversity (Steel et al., 2019). Climate change, the suppression of natural forest fires, and the loss of indigenous fire management have broadly created more homogenous forest landscapes and contributed to large, stand-replacing, high-severity fires (Skinner & Chang, 1996). These large-scale, high-severity "megafires" can limit forest regeneration, threaten species that tend to avoid fire-disturbed landscapes, and reduce and sometimes reverse the value of fire disturbance for fire-associated species (Steel et al., 2022). While species show varied responses to fire, novel disturbance events often fail to yield forest heterogeneity typical of historical fires, eliminating habitat for forest specialists and potentially inducing novel interspecific dynamics in ecosystems (Delheimer et al., 2019; Jones et al., 2021; Steel et al., 2022).

Predators often exhibit top-down effects on biological communities, and the impacts of environmental change on higher trophic levels can cascade to entire ecosystems (Estes et al., 2011; Pace et al., 1999). Fire can mediate interactions between higher trophic levels and other species and shape communities through predator interactions with both competitors and prey (Geary et al., 2020). For example, *Canis dingo*, a predatory species adapted to hunting in open habitat, benefit from recently burned vegetation and, in turn, appear to suppress invasive foxes (Geary et al., 2018). However, as disturbance regimes change, the way fire influences predator interactions may shift as well. Globally, owls occupy apex positions in their respective food chains, but how changes in natural disturbance processes impact this guild of nocturnal predators is largely unknown (Wood, Gutiérrez, et al., 2019). The Sierra Nevada in California hosts a diverse and speciose assemblage of forest owls (Gutiérrez et al., 2007), but we know very little of how owl species associate with disturbed habitat in this region given their cryptic nature (Wood, Gutiérrez, et al., 2019). In this region, the historical percentage of areas burned at high severity was 5%–20%, with patches of high-severity fire ranging between 10 and 100 ha (Safford & Stevens, 2017). Over the past few decades, the proportion of high-severity fire has increased (Steel et al., 2018). An ecosystem-scale passive acoustic monitoring program that spans across the Sierra Nevada (Kelly et al., 2023) offers an opportunity to study interspecific variation in habitat associations following wildfires that vary in their resemblance to historical disturbance patterns in an understudied guild of avian predators.

Here, we conducted ecosystem-scale passive acoustic surveys across the Sierra Nevada bioregion to test the hypothesis that site occupancy for six forest owl species is related to the severity, spatial configuration, and temporal history of past fire disturbance. We first examined the effect of elevation, latitude, and the proportion of closed-canopy forest to account for broad spatial variation in site occupancy and examined species' associations with canopy characteristics. We predicted that all species would be less likely to occupy forests burned at higher severity the previous year due to a loss of live overstory, which is important for all species to varying degrees (Bennett & Bloom, 2005; Davis & Weir, 2010; Giese, 1999; Groce & Morrison, 2010; Gutiérrez et al., 2017; Linkhart et al., 1998). We further predicted that species that nest and roost in closed-canopy forest would be less likely to occupy forest burned at higher severity for extended periods of time due to the loss of overstory. We predicted that cavity-nesting species would be more likely to occupy habitat burned at low- to moderate-severity 2–10 years postfire due to increased nesting opportunities (Gehlbach & Stoleson, 2010; Reynolds & Linkhart, 1987), and species that forage in open forest would be more likely to occupy sites burned at higher severity after at least 5–10 years of shrub and hardwood regeneration, due to potential foraging opportunities (Johnson, 1992).

Finally, we predicted that patchier high-severity fire would immediately benefit all species by creating edges between older and younger forest (Jones et al., 2020). Understanding the impacts of past fire disturbance on the distribution of this predator assemblage is important to identify management strategies to conserve predator biodiversity in this and other regions as fire regimes continue to change and produce larger, more contiguously severe disturbance events.

METHODS

Study system

The species that comprise the owl assemblage in the Sierra Nevada co-occur at landscape scales but occupy distinct ecological niches (Wood, Gutiérrez, et al., 2019). While all forest owl species rely on trees for nesting, great horned (GHOW; *Bubo virginianus*) and western screech (WESO; *Megascops kennicottii*) owls occupy a wide variety of habitats and often forage where canopies are relatively open (Davis & Weir, 2010; Johnson, 1992). Flammulated owls (FLOW; *Psiloscops flammeolus*) breed in mid-successional mixed conifer forests often dominated by yellow pine and Douglas fir (Linkhart et al., 1998). California spotted owls (SPOW; *Strix occidentalis occidentalis*) rely on closed-canopy forest for roosting and nesting, while benefiting from forest heterogeneity—specifically edges between younger and more mature forest—for access to prey (Zulla et al., 2022). Northern pygmy (NOPO; *Glaucidium gnoma*) and northern saw-whet (NSWO; *Aegolius acadicus*) owls are more general in their habitat associations but often nest in mature forests (Groce & Morrison, 2010; Hayward & Garton, 1988; Hinam & St Clair, 2008). Finally, western screech, flammulated, northern pygmy, and northern saw-whet owls are secondary cavity nesters, nesting in cavities excavated by other species (Bull et al., 1997; Scott et al., 1977) that are more prevalent following fires (Tarbill et al., 2015) but are also present in unburned forest.

Acoustic monitoring in the Sierra Nevada

We conducted ecosystem-scale passive acoustic monitoring (PAM) surveys in 1648 sites across the Sierra Nevada in 2021. Our surveys spanned the western slope of the Sierra Nevada, including coverage in all seven national forests, three of the four national parks, and some private land (Kelly et al., 2023). We divided this area into 6236 4-km^2 hexagonal grid cells, which are comparable in size to SPOW and GHOW territories in this region (Bennett & Bloom, 2005; Kelly et al., 2023) and likely encompass smaller owl territories (Peery, 2000), to obtain a total sampling area of 24,494 km^2. In 2021, we surveyed 845 nonadjacent grid cells to reduce the possibility of double-counting potential SPOW and GHOW territories (Wood, Popescu, et al., 2019). Cells were excluded if they intersected highways, were over 50% water, or lacked road/trail access.

We deployed one to three, but generally two, autonomous recording units (ARUs; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in each surveyed grid cell. When possible, no ARUs in this project were closer than 500 m to one another and ARUs were placed at least 250 m from the edges of cells. ARUs had a single omnidirectional microphone with −25 dB sensitivity, 62 signal-to-noise ratio, and recorded 20:00–08:00 PDT at a sample range of 32 kHz, 16-bit resolution, and gain of +33 dB. We began deployments in early May, and surveys lasted through mid-July. Most locations were surveyed for approximately five weeks continuously.

Forest owl detections

To identify forest owl vocalizations, we used the BirdNET algorithm, a deep convolutional neural network designed to identify 984 North American and European bird species by sound (Kahl et al., 2021). We developed a customized version of BirdNET (Kahl et al., 2021) that was overfit to the vocalizations of species of interest in this region, including the six forest owls in this study. BirdNET outputs a unitless numeric prediction score, ranging from 0 to 1, for each species in every 3-s interval of audio data. This prediction score indicates confidence in the identification, with larger numbers indicating greater confidence.

Acoustic validation

For all species except SPOW, we designed species-specific probability-based thresholds in the prediction score to minimize false positives in our acoustic identifications. For each species, we manipulated thresholds for both the minimum BirdNET prediction score for an observation, as well as the minimum number of observations within an hour, such that an hour-long sample was marked as a true positive only if the number of BirdNET observations above a selected prediction score was above a selected number of calls per hour. For each of these species, we manually validated a random subset of at least 200 h-long acoustic data files that each contained at least one

BirdNET identification with a prediction score of at least 0.1. For each hour-long sample, we used RavenPro 2.0 (Cornell Lab or Ornithology, Ithaca, NY) to manually scan potential observations to either (1) confirm the presence of at least one true call or (2) identify false positives where no true calls were present. In each hour-long sample, we counted the number of BirdNET identifications over a series of prediction score thresholds (0.1, 0.2, …, 0.9, 0.91, …, 0.99). We then estimated the probability of a random hour of acoustic data representing a false positive as a function of the number of BirdNET observations over each prediction score. We fit logistic regressions in which the true-positive/false-positive status of an hour-long acoustic data file was the binary response and the number of BirdNET observations above a prediction threshold was the predictor (lme4; Bates et al., 2015). We did this for multiple prediction score thresholds for each species. We extrapolated false-positive rates to a seven-day sampling period using the following equation: $1-(1-\mathrm{FP})^n$, where FP is the false-positive rate per hour and n is the number of hours within the sampling period in which ARUs were recording (84 h total).

For FLOW and GHOW, we identified a call rate and score threshold at which the false-positive rate for the secondary sampling period was about 0.01 (Appendix S1: Figure S1). We used these thresholds to filter detections used in encounter histories. Maximizing precision for three species (NSWO, WESO, NOPO) with BirdNET thresholds produced recall too low to be usable for occupancy models, so we employed an alternative strategy for these species. First, we used a more liberal call rate and prediction score threshold that resulted in higher false-positive rates (Appendix S1: Figure S1). We manually validated all remaining BirdNET observations for these species, which were then included in encounter histories. All SPOW vocalizations above a threshold of 0.989 were validated separately from the other forest owl species as part of a separate, species-specific monitoring program (Kelly et al., 2023) and were included in a final encounter history for the species.

To account for imperfect detection, we divided the continuous sampling in 2021 into two 4-week-long secondary sampling periods starting on Julian day 130 and ending on 193. Each week of acoustic sampling was separated by one day. Specifically, the first week of sampling occurred on Julian days 130–136, the second week of sampling occurred on Julian days 138–144, and so on. We determined the presence of either a manually validated or threshold-validated detection in each secondary sampling period. If an ARU was not recording at any point during a particular secondary sampling period, we would consider that period null. For all smaller forest owls (FLOW, WESO, NSWO, NOPO), we evaluated detections at the scale of single ARUs. We made this decision because these species have smaller home ranges, and their calls are quieter and propagate over shorter distances than the larger species. For the larger species (GHOW and SPOW), we created encounter histories at the scale of sampling hexagons because these species have larger home ranges and there is a greater chance that multiple ARUs in a sampling hexagons are recording calls from the same individual (Reid et al., 2022).

Predictor variables

To account for the effects of spatial environmental variation on the probability of site occupancy for these six owl species, we calculated elevation and latitude at each ARU location. We averaged values between ARUs in the same sampling cell for covariates to be used in occupancy models for the two larger species (GHOW and SPOW). To account for the effects of spatial characteristics on the probability of detecting each species, which have vocalizations with different acoustic characteristics and likely different propagation across the landscape, we measured terrain ruggedness and the proportion of closed-canopy forest within the 250-m buffers and the hexagonal sampling cells. This buffer size was selected for the smaller species given the relative size of their territories (Davis & Weir, 2010; Giese & Forsman, 2003; Hinam & St Clair, 2008; Linkhart et al., 1998). We calculated terrain ruggedness as the SD of elevation in a sample buffer/cell (Duchac et al., 2021), and canopy cover was calculated as the proportion of a buffer/cell with canopy cover greater than 70% (Jones et al., 2016; Tempel et al., 2014). Canopy cover was downloaded from the California Forest Observatory Database (CFO; Salo Sciences, 2020). These are fine-scale estimates (10 m) created by imputing airborne lidar estimates of forest structure across the landscape using deep learning models that recognize forest structure patterns in satellite imagery.

We quantified fire variables at two severity classes: low- to moderate-severity fire (0%–75% overstory mortality) and high-severity fire (>75% overstory mortality). Generally, we considered fires with more low- to moderate-severity fire and smaller areas of high-severity fire to be within this region's natural range of variation and fires with larger proportions of severe fire to be more characteristic of "megafires" (Safford & Stevens, 2017; Steel et al., 2018). To estimate fire severity, we obtained fire data from the Monitoring Trend in Burn Severity (MTBS; https://www.mtbs.gov/) for fires larger than 400 ha. We binned fire data, stacking data by most recent disturbance, into five consecutive temporal groups that increased in duration: one year following a fire disturbance, 2–4 years, 5–10 years, 11–21 years, and 21–35 years. These categories have been shown to differentially influence animal responses to fire disturbance (Donato et al., 2016; Fontaine & Kennedy, 2012; González et al., 2022; McIver et al., 2008; Nappi & Drapeau, 2009).

Using the "landscapemetrics" package (version 1.5.6; Hesselbarth et al., 2019) in R version 4.2.1 (R Core Team), we calculated the proportion and patch density (number of patches/area) of both fire severity classes for each temporal group. Specifically, we calculated the proportion of low- to moderate-severity and high-severity burned area in 250-m buffers for small species and in hexagonal sampling cells for the two larger species. We used patch density to quantify the patch characteristics for each fire class within each 250-m buffer or 400-ha cell because it was less correlated with composition (proportion of each severity class) than other patch metrics. A lower value for patch density indicates a more contiguous landscape and a higher value indicates a patchier fire footprint.

Fire history analysis

To examine the effects of the severity, patchiness, and temporal history of fire on the occupancy of forest owls across the Sierra Nevada, we fit single-species, single-season occupancy models (MacKenzie et al., 2003), which enabled us to estimate the occupancy of a species of interest from our imperfect acoustic detection process. These models require repeated surveys at fixed locations, in this case ARUs, and allow spatial predictors to describe patterns in occupancy and detectability. All covariates used in the analyses were standardized.

We modeled the probability of detecting each species as univariate functions of terrain ruggedness, a continuous covariate related to the secondary sampling period, and the consecutive number of hours ARUs recorded throughout the summer. These variables have previously been shown to affect the detection probability of vocalizing owl species (Duchac et al., 2021). We ranked all univariate models using Akaike information criterion (AIC) and considered competitive models as those within 2 ΔAIC units of the top ranked model. We then added variables in order of rank until the resulting models were no longer within 2 AIC units of the top model. When a parameter was added to a top ranked model but did not provide a reduction of more than 2 AIC units, we considered the parameter to be uninformative (Arnold, 2010). We carried forward the top detection models that did not contain uninformative parameters.

The best detection models informed the next stage in which we modeled the probability of site occupancy. We fit three parallel sets of models in which we considered: (1) preliminary covariates to account for broad spatial variation in site occupancy; (2) the proportion of burned forest in sites to examine fire severity; and (3) the patch density of burned forest to examine the patchiness of burns at both severity classes. For the preliminary analysis, we examined the probability of site occupancy as univariate functions of elevation, latitude, and the proportion of a site with canopy cover over 70%. For proportion, we examined the probability of site occupancy as univariate functions of the proportion of a site burned at both severity classes for all time steps. For patch density, we examined the probability of site occupancy as univariate functions of patch density of both severity classes for all time steps. As above, we ranked univariate models and added variables in order of rank until resulting models were no longer within 2 AIC units of the top model. We did not run global models within each of the three subgroups because several covariates were correlated with one another.

We combined the top preliminary, proportion, and patch density models within 2 AIC units of the top model on their respective groups that did not contain uninformative parameters. In this final stage, we ran a global model and removed covariates until the top performing model did not contain uninformative parameters (as defined by Morin et al., 2020). In all stages of analyses, we did not include covariates that were highly collinear in the same model (Pearson correlation coefficient, $|r| > 0.7$; Dormann et al., 2013). We standardized all covariates and ran all models in the package "unmarked" (version 1.2.5; Kellner et al., 2023) in R version 4.2.1 (R Core Team). We assessed the model fit of the best-supported, species-specific occupancy models using the goodness-of-fit test (Pearson's χ^2 test) implemented with the mb.gof.test function in the package "AICcmodavg" (Mazerolle, 2023) and bootstrapped 1000 times to obtain a p value (MacKenzie & Bailey, 2004). We considered models to appropriately fit the data if p values were greater than 0.05 (MacKenzie & Bailey, 2004). Finally, if multiple models were competitive in the final model set, we averaged model outputs using the package "AICcmodavg."

RESULTS

Acoustic survey efforts

We screened 555,718 h (the equivalent of 63.4 years) of usable acoustic data from early May to late July 2021 using BirdNET. We obtained usable acoustic data from surveys across 1648 sites for smaller owls and 845 hexagonal sampling cells for the two larger species across sampled locations in the Sierra Nevada. We obtained a variable number of hours and sites with detections that met our species-specific thresholds designed to eliminate the potential for false-positive detections (Appendix S1: Figure S1). All six species were detected across the region (Figure 1).

Detection probabilities

For all results, we consider β estimates with 85% confidence that do not overlap zero to be significant (Sutherland et al., 2023). The probability of detecting GHOW increased with the average number of recording hours between ARUs in each cell and average ruggedness in cells (Table 1; Appendix S1: Table S2). The probability of detecting western screech owls WESO increased with terrain ruggedness and increased with time across the primary sampling period (Table 1; Appendix S1: Table S2). The probability of detecting FLOW and NOPO decreased with time across the primary sampling period (Table 1; Appendix S1: Table S2). The probability of detecting SPOW increased with the average number of recording hours between ARUs in each cell (Table 1; Appendix S1: Table S2). Top models for NSWO indicated a lack of fit.

General habitat associations

The occurrence of each of these six species of owl varied across the Sierra Nevada based on several general spatial characteristics (Figure 2). GHOW were less likely to occupy sites with a higher proportion of closed-canopy forest and were more likely to be at lower elevations and lower latitudes (Table 1, Figure 2). WESO were also less likely to occupy sites at lower elevations and latitudes (Table 1, Figure 2). FLOW were more likely to occupy sites at higher latitudes, while SPOW were more likely to occur at lower latitudes (Table 1, Figure 2). SPOW, NSWO, and NOPO were more likely to occur where there was a higher proportion of closed-canopy forest. Finally, NOPO were less likely to occur at higher elevations (Table 1, Figure 2).

Effect of fire on occupancy

The top occupancy models for each species indicated that associations with fire severity, history, and composition varied among species (Table 1). At some point postfire, occupancy was lower for five of six species in severely burned forests. Three of the six species in this study—SPOW, FLOW, and NOPO—showed negative associations with higher proportions of high-severity fire that burned one year prior (Figure 3). The odds (Jones & Peery, 2019) of FLOW occupying a site decreased by 9.4%, with every 1-ha increase in high-severity fire that burned 1-year prior, and the odds of NOPO occupying a site decreased by 14.3% (Table 1, Figure 3). Negative responses to severe fire persisted across time only for SPOW. Specifically, the odds of SPOW occupying a cell decreased by 11.2% for every 10-ha increase in high-severity fire that burned 1 year prior, decreased by 4.3% for every 10-ha increase in high-severity fire that burned 5–10 years prior, and decreased by 7.0% for every 10 ha increasing in high-severity fire that burned 11–20 years prior (Table 1, Figure 3). The odds of GHOW occupying a cell decreased by 27.8% for every 10-ha increase in high-severity fire that burned 2–4 years prior (Table 1, Figure 3).

Responses to low- to moderate-severity fire varied across species. The odds of WESO occupying a site increased by 11.1% for every 1-ha increase in low- to moderate-severity fire that burned 2–4 years prior while the odds of FLOW occupying a site increased by 7.4% with every 1-ha increase in low- to moderate-severity fire that burned 5–10 years prior (Table 1, Figure 3). The odds of GHOW occupying a cell increased by 6.2% for every 10-ha increase in low- to moderate-severity fire that burned 21–35 years prior, while the odds decreased by 12.8% with every 1-ha increase for FLOW (Table 1, Figure 3).

Higher density of burned patches generally yielded lower probabilities of occupancy for several forest owls (Figure 3). One year after a fire, WESO and SPOW were less likely to occupy sites with a higher patch density of low- to moderate-severity fire (Table 1, Figure 3). While most species' responses to the patch density of fire were largely neutral, GHOW showed a positive association with patchier high-severity fire that burned 21–35 years prior to sampling (Table 1, Figure 3).

DISCUSSION

The alteration to historical fire regimes leaves the fate of many species in disturbance-adapted ecosystems uncertain. This is the first study to examine the effect of fire on a predator guild across a bioregion, with a focus on understudied forest owls likely to have important top-down effects on multiple animal communities (Wood, Gutiérrez, et al., 2019). Our results suggest that these species have distinct associations with burned forests and that the status of this assemblage depends on a combination of fire severity, patchiness, and temporal history. While site occupancy in burned forests varied among

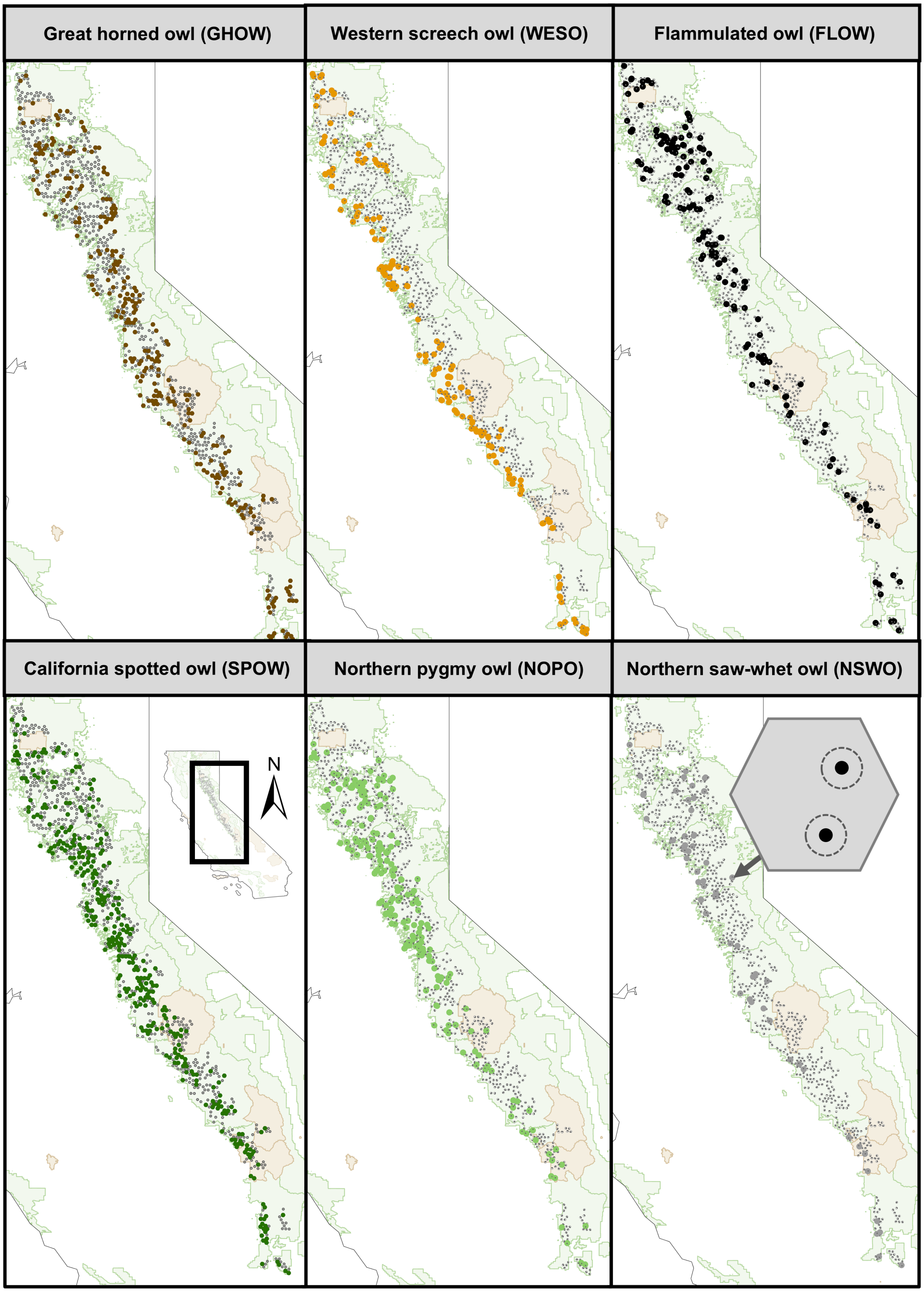

FIGURE 1 Sierra Nevada study area and forest owl detections. Colors correspond to validated occurrences of great horned owls, western screech owls, flammulated owls, spotted owls, northern pygmy owls, and northern saw-whet owls. The regional study area was divided into noncontiguous hexagonal sampling grids across seven national forests (green) and three national parks (brown). In 845 noncontiguous sampling hexagonal cells, we deployed one to three passive autonomous recording units (ARUs). We conducted analyses at the scale of the hexagonal sampling cells for the larger species and at the scale of 250-m buffers around ARUs for the smaller species. Note that spotted owl detections were all manually vetted, while the other five species were obtained using prediction score and call rate thresholds. The distributions of those five species are likely underestimated as a consequence of eliminating false positives.

TABLE 1 Top combined models for all species.

Species	Model structure	*p* value	Effect	Estimate	SE
GHOW	$p_{\text{hours+rugged}}, \psi_{\text{latitude+CC+elevation+LM21–35+H2–4}}$	0.07	Hours	0.33	0.15
			Rugged	0.09	0.11
			Latitude	−0.24	0.11
			Elevation	−0.31	0.13
			CC	−0.73	0.14
			LM21–35	0.23	0.12
			H2–4	−0.29	0.15
	$p_{\text{hours+rugged}}, \psi_{\text{latitude+CC+elevation+H21–35\_pd+H2–4}}$	0.07	Hours	−0.32	0.16
			Rugged	0.10	0.11
			Latitude	−0.23	0.10
			Elevation	−0.31	0.12
			CC	−0.73	0.14
			H21–35_pd	0.20	0.13
			H2–4	−0.28	0.15
WESO	$p_{\text{time+rugged}}, \psi_{\text{latitude+elev+LM2–4+LM1\_pd}}$	0.38	Rugged	−1.38	0.12
			Time	4.76	1.75
			Elevation	−1.35	0.12
			Latitude	−0.55	0.11
			LM2–4	0.21	0.08
			LM1_pd	−0.54	0.20
FLOW	$p_{\text{time}}, \psi_{\text{latitude+LM5–10+LM21–35+H1}}$	0.65	Time	−7.39	1.90
			Latitude	0.28	0.01
			LM5–10	0.27	0.08
			LM21–30	−0.33	0.16
			H1	−0.25	0.15
NOPO	$p_{\text{time}}, \psi_{\text{CC+elevation+H1}}$	0.79	Time	−7.63	1.54
			Elevation	−0.66	0.15
			CC	0.56	0.15
			H1	−0.39	0.13
NSWO	$p_{\text{time}}, \psi_{\text{CC+H5–10\_pd+H1}}$	0.05	Time	−8.16	2.78
			CC	1.01	0.47
			H5–10_pd	−0.60	0.48
			H1	−4.10	5.73
	$p_{\text{time}}, \psi_{\text{CC+LM5–10+H1}}$	0.05	Time	−8.20	2.79
			CC	1.00	0.43
			LM5–10	−0.33	0.28
			H1	−3.99	5.62
SPOW	$p_{\text{hours}}, \psi_{\text{CC+latitude+H1+H5–10+H11–20}}$	0.42	Hours	0.31	0.11
			CC	1.08	0.21
			Latitude	−0.49	0.10
			H_1	−0.63	0.14
			H_5–10	−0.18	0.09
			H_11–20	−0.18	0.10

TABLE 1 (Continued)

Species	Model structure	*p* value	Effect	Estimate	SE
	p_{hours}, $\psi_{\text{CC+latitude+LM20\_pd+H5–10+H11–20}}$	0.44	Hours	0.31	0.11
			CC	0.95	0.16
			Latitude	−0.49	0.10
			LM_1_pd	−0.67	0.15
			H_5–10	−0.19	0.09
			H_11–20	−0.18	0.10

Note: We report model structure, *p* values (which indicate suitable goodness-of-fit when over 0.05), and covariate estimates and SEs. We report multiple models for a species if multiple models are competitive. Fire covariates are labeled with the severity (LM = low to moderate, H = high), followed by the time bin (ex. H2–4 is high-severity fire that burned 2–4 years prior) and whether the variable described patch density (_pd).
Abbreviations: FLOW, flammulated owls; GHOW, great horned owls; NOPO, northern pygmy owls; NSWO, northern saw-whet owls; SPOW, spotted owls; WESO, western screech owls.

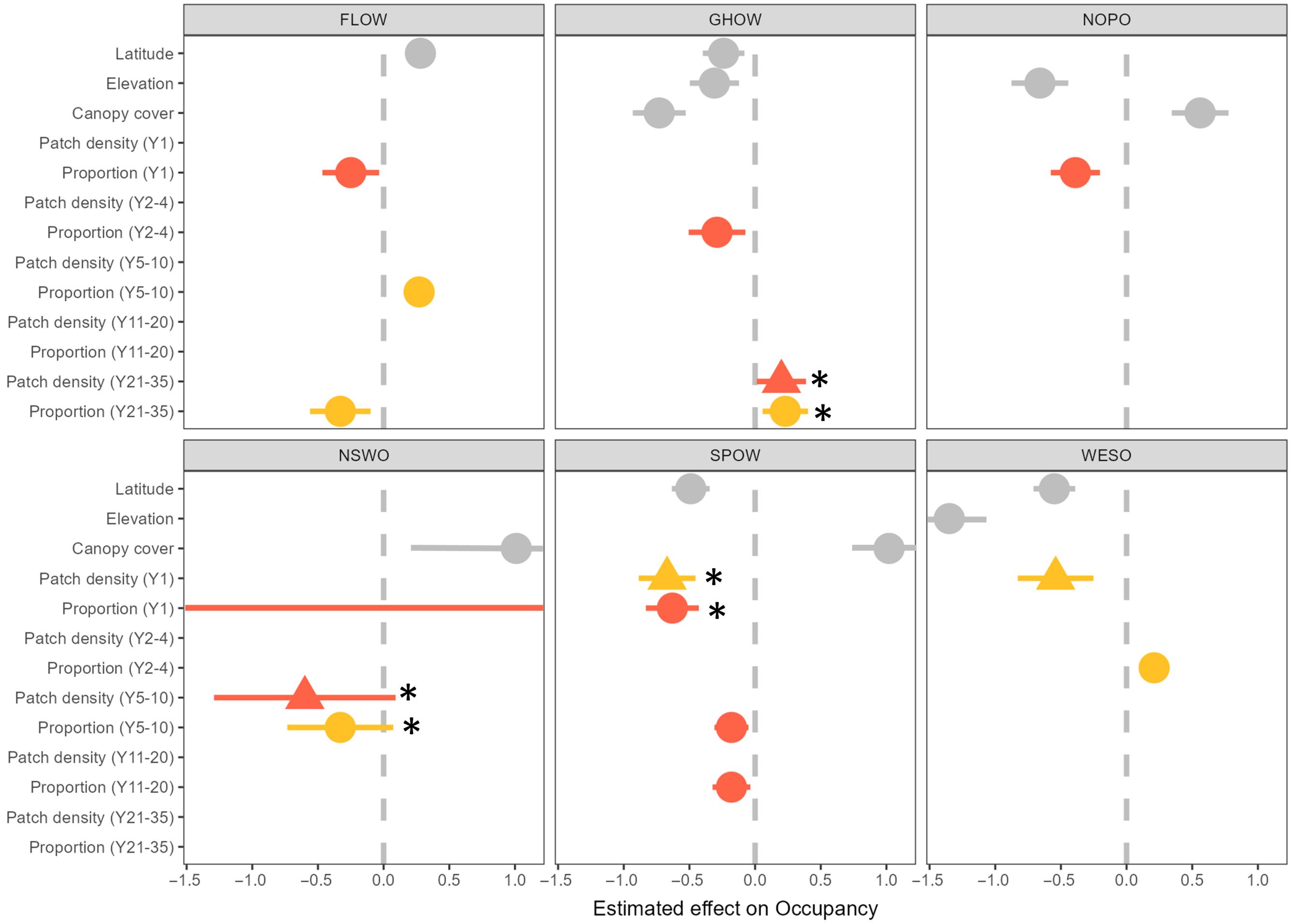

FIGURE 2 Covariate effect sizes from top ranked occupancy models for flammulated owls (FLOW), great horned owls (GHOW), northern pygmy owls (NOPO), northern saw-whet owls (NSWO), spotted owls (SPOW), and western screech owls (WESO). Gray indicates covariates that describe broad spatial associations, red indicates a fire covariate describing high-severity fire, and orange indicates a fire covariate describing low to moderate severity. Triangles indicate configuration covariates, and the square indicates an interaction between a composition and configuration covariate. Error bars show 85% CIs. The top model describing northern saw-whet owl occupancy contained estimated effect sizes with large values and CIs that overlapped zero, indicated by the horizontal error bars in the northern saw-whet panel. Parameter effects with asterisk indicate those that were unique to the first and second best models.

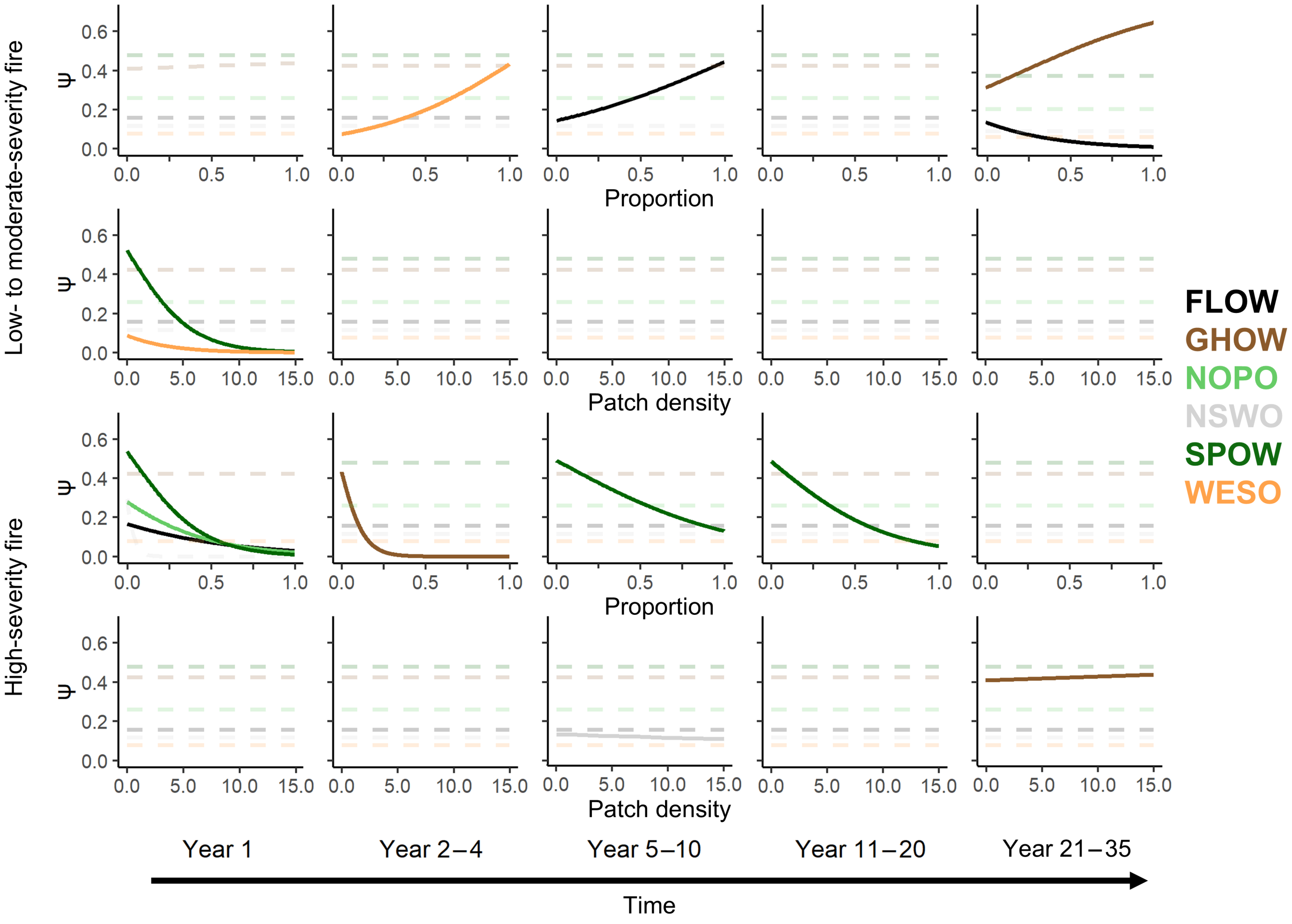

FIGURE 3 Predicted relationships between the proportion and patch density of low- to moderate-severity fire and high-severity fire and the probability of site occupancy (ψ) for six forest owl species. Solid lines indicate a predicted relationship between either patch density or proportion of both severity classes at each times step, and are shown only for covariates that comprise top models for each species. Dashed lines indicate species-specific estimates of mean occupancy. FLOW, flammulated owls; GHOW, great horned owls; NOPO, northern pygmy owls; NSWO, northern saw-whet owls; SPOW, spotted owls; WESO, western screech owls.

species, recent fires appeared to have a stronger influence on owl occupancy than older fires. Recent low- to moderate-severity fire promoted occupancy for two out of the four cavity-nesting species, and the negative impacts of high-severity fire appeared to be largely ephemeral for the assemblage of species. Thus, historically frequent and heterogenous fire likely supported this diverse assemblage of avian predators. SPOW—which are closely associated with closed-canopy forests—were largely absent from sites that experienced more high-severity fire within the past two decades. While higher proportions of severe fire—characteristic of novel "megafires"—may limit the distribution of multiple species immediately after a disturbance, we found direct evidence for prolonged negative consequences of severe fire only for SPOW. While other forest owl species may be more resilient to the potential long-term impacts of severe fire, disturbance events with increasingly higher proportions of stand-replacing fire may limit the habitat created by low- to moderate-severity fire.

Lasting negative impacts of high-severity fire for spotted owls

SPOW avoided burned forests for up to two decades following high-severity fire, whereas previous, shorter term studies have only shown that historical territories remain unoccupied for up to six years following disturbances that produced large areas of severely burned forest (Jones et al., 2022). Our study shows that the negative impacts of high-severity fire may persist longer than previously documented for this species. SPOW rely on older, closed-canopy forests for nesting and roosting, and such habitat also supports stable microclimates when conditions exceed physiological thresholds (Jones et al., 2016; McGinn et al., 2023). High-severity fire, especially when homogenous, leads to the loss of suitable nesting and roosting habitat that is unlikely to regenerate for many decades (Jones et al., 2022). While SPOW appeared to be largely absent from forests burned at high severity 1 year prior and 5–20 years prior (Figure 4), they had neither a negative nor positive relationship with forest burned at high severity 2–4 years prior. Hexagonal sampling cells that overlapped burns from 2017 to 2019 had a maximum proportion of high-severity fire of 0.27, while cells that overlapped fires from 2020 had a maximum proportion of 0.96. Therefore, there either (1) was not enough variation in the dataset to determine the relationship between high-severity fire from that timestep and SP occupancy or (2) SPOW in fire-adapted ecosystems are not particularly sensitive to high-severity fire if it burns less than a quarter of a site 2–4 years prior (see also Jones et al., 2016, 2021). Regardless, our results strongly suggest that SPOW face long-term loss of suitable habitat as fires become larger and more contiguously severe in the Sierra Nevada.

Lower severity fire is considered to be relatively benign, if not beneficial, for SPOW (Jones et al., 2018; Lee et al., 2012) potentially by promoting foraging habitat (Wilkinson et al., 2022; Zulla et al., 2022), and therefore, we expected that this species would be more likely to occur in areas burned at low to moderate severity. Contrary to our expectations, low- to moderate-severity patchiness appeared to reduce the suitability of sites immediately following a disturbance. We believe this was because the proportion of high-severity fire and patchiness of low- to moderate-severity fire were correlated such that the loss of habitat to contiguous high-severity fire outweighed the potential benefits of heterogeneity created by patchy low- to moderate-severity fire.

Varying effect of high-severity fire on occupancy

GHOW are widely distributed across North America and occur within a broad range of habitat types (Bennett & Bloom, 2005). Consistent with previous work, we found this species was less likely to occupy sites with more closed-canopy forests. Further, GHOW in the Sierra Nevada were less likely to associate with high-severity fire 2–4 years following a disturbance but more likely to associate with patchy high-severity fire 11–20 years following a disturbance. These findings corroborate

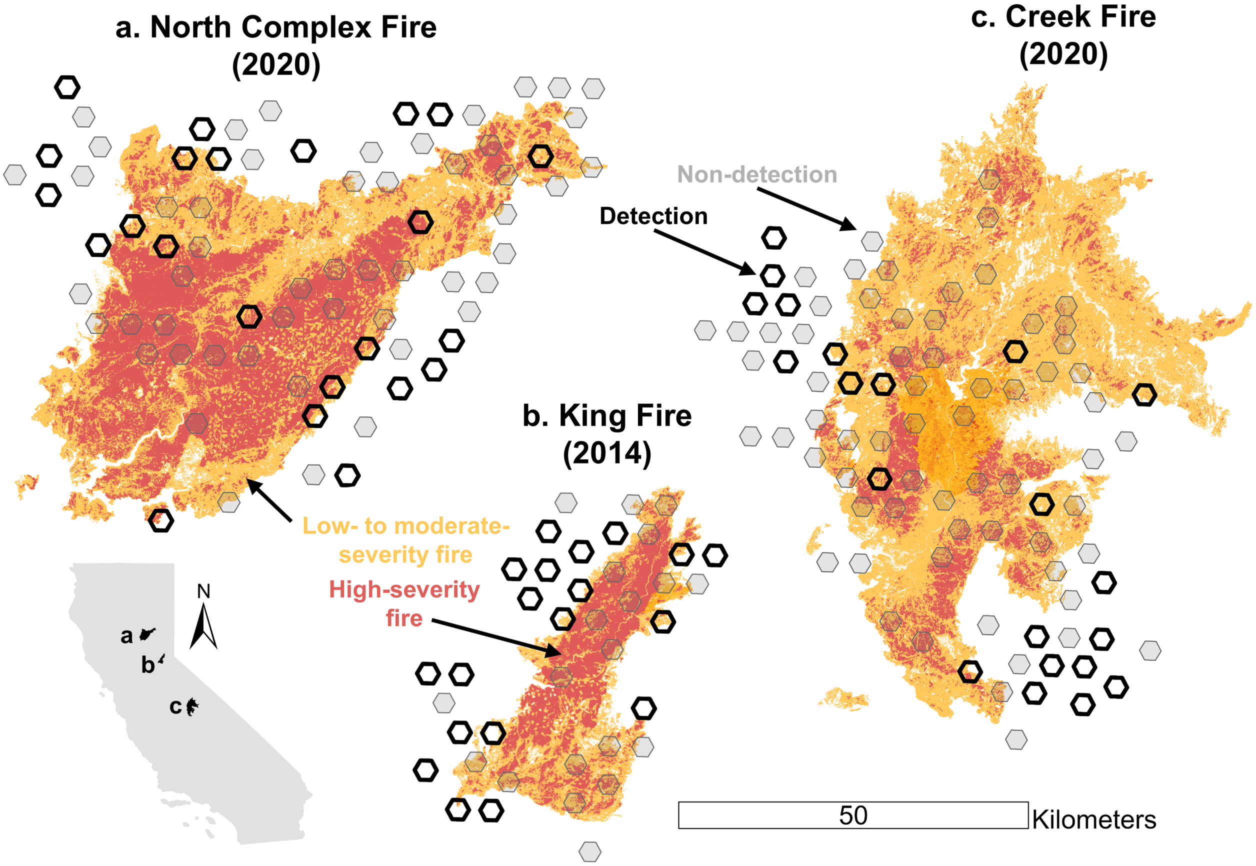

FIGURE 4 Validated SPOW detections included in the spotted owl occupancy models within and near the boundaries of the King, Creek, and North Complex Fires. Orange indicates low- to moderate-severity fire and red indicates high-severity fire. Bold hexes indicate sampling cells that contained at least one detection during the 2021 sampling period. Only a few spotted owls were detected within the boundaries of these fires, and none were detected within areas of contiguous high-severity fire.

previous studies in which GHOW tended to avoid forests burned at high severity a few years prior but benefited from heterogeneity in habitat types (Duchac et al., 2021; Grossman et al., 2008). Severe fire leads to a loss of standing overstory, followed by regrowth of early succession wildflowers and forbs in the few years following a disturbance. While this ephemeral vegetation provides potential food resources for other birds like mountain quail (Brunk et al., 2023), the mammalian prey that GHOW often hunt may not recolonize severely burned sites until shrubs regenerate (Culhane et al., 2022). A decade of regeneration in high-severity burns allows sufficient time for shrubs and small trees to grow, which small mammals use for foraging and cover (Torre & Díaz, 2004). A patchy configuration of such burns may afford GHOW enough access to edge habitat to take advantage of this prey resource.

WESO have previously been described as rare in the central Sierra Nevada (Groce, 2008), although our work demonstrates that they are currently distributed throughout the region (Figure 1). Previous research on forest owl occupancy in the Pacific Northwest showed that WESO were more likely to occupy sites burned at high severity two years prior (Duchac et al., 2021). However, we found that this species neither avoided nor preferred sites burned at high severity at any successional stage, but they were less likely to occupy sites with patchy low- to moderate-severity burns from fire the year prior. In this timestep, low- to moderate-severity patchiness was highly and positively correlated ($r = 0.75$) with the proportion of sites burned at high severity. In the Sierra Nevada, especially at mid-elevations, high-severity fire facilitates shrub regeneration but often hinders tree regrowth while low- to moderate-severity fire promotes regrowth (Collins & Roller, 2013; Crotteau et al., 2013). For WESO in this region, patchy low- to moderate-severity fire interspersed with more high-severity fire may limit any potential benefits of either resulting vegetation structure.

Low- to moderate-severity fire benefits small forest owls

The smaller forest owls in this study, specifically WESO, FLOW, NOPO, and NSWO, are secondary cavity nesters, which may explain the occupancy patterns we observed in relation to fire history. FLOW and WESO were more likely to occupy sites burned at low to moderate severity 2–10 years following a disturbance. Low- to moderate-severity fire reduces understory but leaves snags interspersed with surviving trees (Crotteau et al., 2013). Northern flickers (*Colaptes auratus*), pileated woodpeckers (*Dryocopus pileatus*), sapsuckers (*Sphyrapicus*), and hairy woodpeckers (*Dryocopus villosus*) create cavities in these standing dead trees that are suitable in size for the secondary cavity nesters in this study (Bull & Holthausen, 1993; Raphael & White, 1984). Standing dead trees following fires are a source of nesting habitat for some woodpecker species, but older burned areas can lose their value for individuals over time (Nappi & Drapeau, 2009; Tingley et al., 2018). Secondary cavity nesters may take advantage of potential nesting habitat created—and subsequently abandoned—by woodpeckers following a fire disturbance (Duchac et al., 2021). Our results suggest that smaller owl species may use nesting habitat created after low- to moderate-severity burns, indicating successional recolonization of different species following disturbance events like fire.

Low- to moderate-severity fire may also create foraging habitat by opening the understory for these small predators to access prey. Both WESO and FLOW prey upon insects and other arthropods, which can recover quickly following fires (Choi, 2018). These two species often forage by either catching insects in the air or gleaning insects from the needles of large conifer trees, and a more open understory following a disturbance may facilitate these behaviors (Hayward & Garton, 1988; Reynolds & Linkhart, 1987). FLOW did not have any association with closed-canopy forest, which corroborates prior research on the species in other mid-elevation, dry forest ecosystems where they preferred large trees with more open understories (Linkhart et al., 1998; Yanco & Linkhart, 2018). WESO often hunt small mammals, which can increase in abundance after fires (Culhane et al., 2022). Forest regeneration 2–4 years following low- to moderate-severity fire may create forest structures where there is simultaneously enough understory regeneration for prey species to benefit from protection and food resources and enough standing overstory for WESO to access their prey from trees (Reid et al., 2006).

Lessons learned in acoustic surveys

Our acoustic survey program deploying 1648 ARUs across 25,800 km^2 is one of the largest acoustic monitoring programs in North America and the first to quantify the distribution of most of these species across an entire bioregion. We were successfully able to obtain enough detections for five of six forest owl species to examine the effects of fire on site occupancy for a cryptic guild of predators using a combined effort of manual validation and automated, machine learning-based detections. However, we obtained fewer detections for NSWO than all other species. Based on our field observations, NSWO appeared to cease territory vocalizations earlier than the other small forest owl species. Our acoustic surveys may have only overlapped the tail end of their vocalization behaviors. Additionally, while occupancy estimates for SPOW were derived from comprehensive and manually validated encounter histories—and likely reflect a reasonable estimate for the true proportion of sites in the Sierra Nevada occupied by SPOW (Kelly et al., 2023)—the five other species' occupancy estimates may be underestimated given our strategy to minimize false positives at the expense of potential true positives. Future research may consider lowering the initial prediction score thresholds and performing a comprehensive manual validation of all potential detections for species of interest.

Importance of fire heterogeneity for diverse assemblage

Here, we found that while there is an immediate negative impact of fire—potentially due to a loss of critical habitat—for four of the six species in this assemblage 1–4 years after fire, high-severity fire has apparent long-lasting impacts on the distribution of only one species. In fact, low- to moderate-severity fire increased occupancy for half of this assemblage at some point in time. While the loss of critical habitat may limit the distribution of some species, assemblages of similar species may broadly be more resilient to disturbance events. In a community of bats in the Sierra Nevada, most species were more likely to occur where severity or pyrodiversity was higher, likely due to increased heterogeneity and access to foraging opportunities (Steel et al., 2019). Potential trade-offs between heterogeneity and habitat loss occur across taxa, and while heterogeneity in burned forests can benefit some species, there is no unequivocal evidence that variation in postfire landscape characteristics, or pyrodiversity, inherently increases biodiversity (Jones & Tingley, 2022; Turner et al., 2013). Often, the potential benefits of heterogeneity following fire disturbance depend on broader ecological contexts. For example, at a finer scale, SPOW prefer pyrodiverse areas where the surrounding landscape is homogenous but avoid pyrodiverse areas where the surrounding landscape has more heterogeneity in forest structure (Jones et al., 2020; Kramer et al., 2021). Thus, there appears to be some critical threshold for heterogeneity that can be either facilitated by patchy fire or hindered where fire contributes to the loss of critical habitat. Such trade-offs are likely dictated by scale.

We examined only the proportion and patchiness of two burn classes, and while patchier landscapes can often be considered as more pyrodiverse (Lawes et al., 2015; McGranahan et al., 2018; Menges & Quintana-Ascencio, 2004), our study was not adequately comprehensive to directly examine pyrodiversity per se. Future work that seeks to quantify the effect of pyrodiversity on this assemblage of predators could consider trade-offs between heterogeneity and habitat loss, which are likely influenced by species-specific ecologies, the scale at which animals move across the landscape, the temporal dynamics of forest regeneration, and interspecific variation in recolonization following forest fires.

The breakdown of historical fire regimes

The forest owls in the Sierra Nevada have unique associations with burned habitat, and spatiotemporal diversity in fire severity across the landscape likely benefits this assemblage of avian predators. Other species in this region also show variable associations with burned habitat, and understanding interspecific variation in response to fire is necessary to conserve biodiversity in a rapidly changing environmental context (Brunk et al., 2023; Jones & Tingley, 2022; Taillie et al., 2018). Management following Euro-American colonization led to a buildup of fuels in western dry forest ecosystems, which can negatively impact other bird species that rely on pulse disturbance processes. A combination of rising temperatures, more variable precipitation events, and fire suppression has created a perfect storm for massive fires that burn the majority of live overstory (Steel et al., 2023; Westerling, 2016). This assemblage may be threatened by disrupted fire regimes on multiple fronts. (1) Fire suppression limits the distribution of this assemblage on the landscape; (2) novel megafires reduce the proportion of low- to moderate-severity fire that benefits some species; and (3) increasingly large and severe fires threaten the persistence of SPOW.

We did not examine the effect of postfire management on the occupancy of forest owl species because management data across this bioregion were not yet available. However, postfire management like salvage logging potentially exacerbates and prolongs the negative impacts of fire on predators by disrupting forest regeneration (Jones et al., 2022; Lee et al., 2013). Most species in this assemblage nest in dead trees, and salvage logging may introduce persistent negative impacts of fire for species that are otherwise resilient to high-severity fire. Future work will examine the impact of pre- and postfire management on this assemblage of forest owls across the Sierra Nevada, as well as the impacts of management on the severity and configuration of wildfire. When fire mitigation practices reduce habitat suitability for some species, more nuanced and spatially explicit approaches to forest restoration may be necessary to preserve biodiversity (Jones et al., 2022). Management that seeks to conserve biodiversity in the context of degrading disturbance processes should consider interspecific variation in associations with burned habitat and variable temporal scales over which fire impacts habitat suitability for wildlife.

AUTHOR CONTRIBUTIONS

Kate McGinn conceived the ideas for this manuscript under the mentorship of Benjamin Zuckerberg and M. Zachariah Peery. Kate McGinn processed data, ran analyses, created figures, and developed the manuscript. Gavin M. Jones assisted in analyzing data and conceptualizing figures. Connor M. Wood and M. Zachariah Peery developed the passive acoustic monitoring program and assisted in conceptualizing data processing strategies. Stefan Kahl developed the machine learning algorithm BirdNET. Kevin G. Kelly, Sheila A. Whitmore, and H. Anu Kramer organized data collection. Kate McGinn, Josh M. Barry, and Elizabeth Ng processed and validated acoustic data. All authors edited this manuscript.

ACKNOWLEDGMENTS

Many technicians made this research possible. Max Ciaglo provided comments on the initial drafts of this manuscript. Jake Holshuh supported the development of BirdNET. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program (DGE-1747503). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. This work was also supported by the Wisconsin Agricultural Experiment Station, the National Fish and Wildlife Foundation, the USDA Forest Service Region 5, and the USDA Forest Service Pacific Southwest Research Station.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Geographic locations of autonomous recording units from which detections were obtained are sensitive; these data are owned by the Department of Forest and Wildlife Ecology at the University of Wisconsin-Madison and are available to qualified researchers by contacting the principal investigator of the Sierra Nevada Acoustic Monitoring Program (M. Zachariah Peery; Email: mpeery@wisc.edu) and requesting access to the 2021 field season metadata. Anonymized encounter histories used in occupancy analyses (McGinn et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.w6m905qzc.

ORCID

Kate McGinn https://orcid.org/0000-0003-4647-1847
Gavin M. Jones https://orcid.org/0000-0002-5102-1229
Connor M. Wood https://orcid.org/0000-0002-0235-5214
H. Anu Kramer https://orcid.org/0000-0003-2014-0070

REFERENCES

Archibald, S., C. E. R. Lehmann, J. L. Gómez-Dans, and R. A. Bradstock. 2013. "Defining Pyromes and Global Syndromes of Fire Regimes." *Proceedings of the National Academy of Sciences of the United States of America* 110: 6442–47.

Arnold, T. W. 2010. "Uninformative Parameters and Model Selection Using Akaike's Information Criterion." *The Journal of Wildlife Management* 74: 1175–78.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Bennett, J. R., and P. H. Bloom. 2005. "Home Range and Habitat Use by Great Horned Owls (*Bubo virginianus*) in Southern California." *Journal of Raptor Research* 39: 119–126.

Blakey, R. V., E. B. Webb, D. C. Kesler, R. B. Siegel, D. Corcoran, J. S. Cole, and M. Johnson. 2021. "Extent, Configuration and Diversity of Burned and Forested Areas Predict Bat Richness in a Fire-Maintained Forest." *Landscape Ecology* 36: 1101–15.

Bond, W. J., and J. E. Keeley. 2005. "Fire as a Global 'Herbivore': The Ecology and Evolution of Flammable Ecosystems." *Trends in Ecology & Evolution* 20: 387–394.

Brunk, K. M., R. J. Gutiérrez, M. Z. Peery, C. A. Cansler, S. Kahl, and C. M. Wood. 2023. "Quail on Fire: Changing Fire Regimes May Benefit Mountain Quail in Fire-Adapted Forests." *Fire Ecology* 19: 19.

Bull, E. L., and R. S. Holthausen. 1993. "Habitat Use and Management of Pileated Woodpeckers in Northeastern Oregon." *The Journal of Wildlife Management* 57: 335–345.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. *Trees and Logs Important to Wildlife in the Interior Columbia River Basin*. Gen. Tech. Rep. PNW-GTR-391. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station 55. 391 pp.

Choi, S.-W. 2018. "A High Mountain Moth Assemblage Quickly Recovers after Fire." *Annals of the Entomological Society of America* 111: 304–311.

Collins, B. M., and G. B. Roller. 2013. "Early Forest Dynamics in Stand-Replacing Fire Patches in the Northern Sierra Nevada, California, USA." *Landscape Ecology* 28: 1801–13.

Connell, J. H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs." *Science* 199: 1302–10.

Crotteau, J. S., J. Morgan Varner, and M. W. Ritchie. 2013. "Post-Fire Regeneration across a Fire Severity Gradient in the Southern Cascades." *Forest Ecology and Management* 287: 103–112.

Culhane, K., R. Sollmann, A. M. White, G. L. Tarbill, S. D. Cooper, and H. S. Young. 2022. "Small Mammal Responses to Fire Severity Mediated by Vegetation Characteristics and Species Traits." *Ecology and Evolution* 12: e8918.

Davis, H., and R. D. Weir. 2010. "Home Ranges and Spatial Organization of Western Screech-Owls in Southern British Columbia." *Northwestern Naturalist* 91: 157–164.

Delheimer, M. S., K. M. Moriarty, M. A. Linnell, and B. V. Woodruff. 2019. "If a Tree Falls in a Forest: Implications of Forest Structure Persistence for the Pacific Marten (*Martes caurina*)." *Ecosphere* 10: e02819.

Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. "Regeneration of Montane Forests 24 Years after the 1988 Yellowstone Fires: A Fire-Catalyzed Shift in Lower Treelines?" *Ecosphere* 7: e01410.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, and P. J. Leitão. 2013. "Collinearity: A Review of Methods to Deal with It and a Simulation Study Evaluating Their Performance." *Ecography* 36: 27–46.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, and R. J. Davis. 2021. "Differential Landscape Use by Forest Owls Two Years after a Mixed-Severity Wildfire." *Ecosphere* 12: e03770.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333: 301–6.

Fontaine, J. B., D. C. Donato, W. D. Robinson, B. E. Law, and J. B. Kauffman. 2009. "Bird Communities Following High-Severity Fire: Response to Single and Repeat Fires in a Mixed-Evergreen Forest, Oregon, USA." *Forest Ecology and Management* 257: 1496–1504.

Fontaine, J. B., and P. L. Kennedy. 2012. "Meta-Analysis of Avian and Small-Mammal Response to Fire Severity and Fire Surrogate Treatments in U.S. Fire-Prone Forests." *Ecological Applications* 22: 1547–61.

Geary, W. L., T. S. Doherty, D. G. Nimmo, A. I. T. Tulloch, and E. G. Ritchie. 2020. "Predator Responses to Fire: A Global Systematic Review and Meta-Analysis." *Journal of Animal Ecology* 89: 955–971.

Geary, W. L., E. G. Ritchie, J. A. Lawton, T. R. Healey, and D. G. Nimmo. 2018. "Incorporating Disturbance into Trophic Ecology: Fire History Shapes Mesopredator Suppression by an Apex Predator." *Journal of Applied Ecology* 55: 1594–1603.

Gehlbach, F. R., and S. H. Stoleson. 2010. *Western Screech-Owl (Megascops kennicottii)* 511–523. Raptors of New Mexico. Albuquerque, NM: University of New Mexico Press.

Giese, A. 1999. "Habitat Selection by Northern Pygmy-Owls on the Olympic Peninsula, WA." https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/2b88qh550

Giese, A., and E. Forsman. 2003. "Breeding Season Habitat Use and Ecology of Male Northern Pygmy-Owls." *Journal of Raptor Research* 37: 117–124.

González, T. M., J. D. González-Trujillo, A. Muñoz, and D. Armenteras. 2022. "Effects of Fire History on Animal Communities: A Systematic Review." *Ecological Processes* 11: 11.

Groce, J. E. 2008. "Habitat Associations of Cavity-Nesting Owls in the Sierra Nevada." Thesis, Texas A&M University.

Groce, J. E., and M. L. Morrison. 2010. "Habitat Use by Saw-Whet Owls in the Sierra Nevada." *The Journal of Wildlife Management* 74: 1523–32.

Grossman, S. R., S. J. Hannon, and A. Sánchez-Azofeifa. 2008. "Responses of Great Horned Owls (*Bubo virginianus*), Barred Owls (*Strix varia*), and Northern Saw-Whet Owls (*Aegolius acadicus*) to Forest Cover and Configuration in an Agricultural Landscape in Alberta, Canada." *Canadian Journal of Zoology* 86: 1165–72.

Gutiérrez, R. J., M. Cody, S. Courtney, and A. B. Franklin. 2007. "The Invasion of Barred Owls and Its Potential Effect on the Spotted Owl: A Conservation Conundrum." *Biological Invasions* 9: 181–196.

Gutiérrez, R. J., P. N. Manley, and P. A. Stine. 2017. *The California Spotted Owl: Current State of Knowledge*. Gen. Tech. Rep. PSW-GTR-254. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station 254.

Hayward, G., and E. Garton. 1988. "Resource Partitioning among Forest Owls in the River of No Return Wilderness, Idaho." *Oecologia* 75: 253–265.

Hesselbarth, M., M. Sciaini, K. With, K. Wiegand, and J. Nowosad. 2019. "Landscapemetrics: An Open-Source R Tool to Calculate Landscape Metrics." *Ecography* 42: 1648–57.

Hinam, H. L., and C. C. St Clair. 2008. "High Levels of Habitat Loss and Fragmentation Limit Reproductive Success by Reducing Home Range Size and Provisioning Rates of Northern Saw-Whet Owls." *Biological Conservation* 141: 524–535.

Johnson, D. H. 1992. "Spotted Owls, Great Horned Owls, and Forest Fragmentation in the Central Oregon Cascades." MS thesis, Oregon State University.

Jones, G. M., R. J. Gutiérrez, D. J. Tempel, B. Zuckerberg, and M. Z. Peery. 2016. "Using Dynamic Occupancy Models to Inform Climate Change Adaptation Strategies for California Spotted Owls." *Journal of Applied Ecology* 53: 895–905.

Jones, G. M., J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2018. "Declining Old-Forest Species as a Legacy of Large Trees Lost." *Diversity and Distributions* 24: 341–351.

Jones, G. M., H. A. Kramer, S. A. Whitmore, W. J. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, et al. 2020. "Habitat Selection by Spotted Owls after a Megafire Reflects Their Adaptation to Historical Frequent-Fire Regimes." *Landscape Ecology* 35: 1199–1213.

Jones, G. M., H. A. Kramer, W. J. Berigan, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2021. "Megafire Causes Persistent Loss of An Old-Forest Species." *Animal Conservation* 24: 925–936.

Jones, G. M., A. R. Keyser, A. L. Westerling, W. J. Baldwin, J. J. Keane, S. C. Sawyer, J. D. J. Clare, R. J. Gutierrez, and M. Z. Peery. 2022. "Forest Restoration Limits Megafires and Supports Species Conservation under Climate Change." *Frontiers in Ecology and the Environment* 20: 210–16.

Jones, G. M., and M. Z. Peery. 2019. "Phantom Interactions: Use Odds Ratios or Risk Misinterpreting Occupancy Models." *The Condor* 121: duy007.

Jones, G. M., and M. W. Tingley. 2022. "Pyrodiversity and Biodiversity: A History, Synthesis, and Outlook." *Diversity and Distributions* 28: 386–403.

Kahl, S., C. M. Wood, M. Eibl, and H. Klinck. 2021. "BirdNET: A Deep Learning Solution for Avian Diversity Monitoring." *Ecological Informatics* 61: 101236.

Kellner, K., A. Smith, J. Royle, M. Kery, J. Belant, and R. Chandler. 2023. "The Unmarked R Package: Twelve Years of Advances in Occurrence and Abundance Modelling in Ecology." *Methods in Ecology and Evolution* 14: 1408–15.

Kelly, K. G., C. M. Wood, K. McGinn, H. A. Kramer, S. C. Sawyer, S. Whitmore, D. Reid, et al. 2023. "Estimating Population Size for California Spotted Owls and Barred Owls across the Sierra Nevada Ecosystem with Bioacoustics." *Ecological Indicators* 154: 110851.

Kramer, H. A., G. M. Jones, S. A. Whitmore, J. J. Keane, F. A. Atuo, B. P. Dotters, S. C. Sawyer, S. L. Stock, R. J. Gutiérrez, and M. Z. Peery. 2021. "California Spotted Owl Habitat Selection in a Fire-Managed Landscape Suggests Conservation Benefit of Restoring Historical Fire Regimes." *Forest Ecology and Management* 479: 118576.

Lawes, M. J., B. P. Murphy, A. Fisher, J. C. Z. Woinarski, A. C. Edwards, J. Russell-Smith, M. J. Lawes, et al. 2015. "Small Mammals Decline with Increasing Fire Extent in Northern Australia: Evidence from Long-Term Monitoring in Kakadu National Park." *International Journal of Wildland Fire* 24: 712–722.

Lee, D. E., M. L. Bond, M. I. Borchert, and R. Tanner. 2013. "Influence of Fire and Salvage Logging on Site Occupancy of Spotted Owls in the San Bernardino and San Jacinto Mountains of Southern California." *The Journal of Wildlife Management* 77: 1327–41.

Lee, D. E., M. L. Bond, and R. B. Siegel. 2012. "Dynamics of Breeding-Season Site Occupancy of the California Spotted Owl in Burned Forests." *The Condor* 114: 792–802.

Levine, J. I., B. M. Collins, Z. L. Steel, P. de Valpine, and S. L. Stephens. 2022. "Higher Incidence of High-Severity Fire in and near Industrially Managed Forests." *Frontiers in Ecology and the Environment* 20: 397–404.

Linkhart, B. D., R. T. Reynolds, and R. A. Ryder. 1998. "Home Range and Habitat of Breeding Flammulated Owls in Colorado." *The Wilson Bulletin* 110: 342–351.

Lydersen, J. M., and B. M. Collins. 2018. "Change in Vegetation Patterns over a Large Forested Landscape Based on Historical and Contemporary Aerial Photography." *Ecosystems* 21: 1348–63.

MacKenzie, D. I., and L. L. Bailey. 2004. "Assessing the Fit of Site-Occupancy Models." *Journal of Agricultural, Biological, and Environmental Statistics* 9: 300–318.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. "Estimating Site Occupancy, Colonization, and Local Extinction When a Species Is Detected Imperfectly." *Ecology* 84: 2200–2207.

Mazerolle, M. 2023. "AICcmodavg: Model Selection and Multimodel Inference based on (Q)AIC(c)." R Package Version 2.3.3. https://cran.r-project.org/package=AICcmodavg.

McGinn, K., B. Zuckerberg, G. Jones, C. Wood, S. Kahl, K. Kelly, S. Whitmore, et al. 2024. "Frequent, Heterogenous Fire Supports a Forest Owl Assemblage [Dataset]." Dryad. https://doi.org/10.5061/dryad.w6m905qzc.

McGinn, K. A., M. Z. Peery, C. J. Zulla, W. J. Berigan, Z. A. Wilkinson, J. M. Barry, J. J. Keane, and B. Zuckerberg. 2023. "A Climate-Vulnerable Species Uses Cooler Forest Microclimates during Heat Waves." *Biological Conservation* 283: 110132.

McGranahan, D. A., T. J. Hovick, R. D. Elmore, D. M. Engle, and S. D. Fuhlendorf. 2018. "Moderate Patchiness Optimizes Heterogeneity, Stability, and Beta Diversity in Mesic Grassland." *Ecology and Evolution* 8: 5008–15.

McIver, J. D., R. E. J. Boerner, and S. C. Hart. 2008. "The National Fire and Fire Surrogate Study: Ecological Consequences of Alternative Fuel Reduction Methods in Seasonally Dry Forests." *Forest Ecology and Management* 255: 3075–80.

McLauchlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, et al. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers." *Journal of Ecology* 108: 2047–69.

Menges, E. S., and P. F. Quintana-Ascencio. 2004. "Population Viability with Fire in *Eryngium cuneifolium*: Deciphering a Decade of Demographic Data." *Ecological Monographs* 74: 79–99.

Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, D. B. Lesmeister, C. K. Nielsen, J. Reid, and E. M. Schauber. 2020. "Is Your Ad Hoc Model Selection Strategy Affecting your Multimodel Inference?" *Ecosphere* 11: e02997.

Nappi, A., and P. Drapeau. 2009. "Reproductive Success of the Black-Backed Woodpecker (*Picoides arcticus*) in Burned Boreal Forests: Are Burns Source Habitats?" *Biological Conservation* 142: 1381–91.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. "Trophic Cascades Revealed in Diverse Ecosystems." *Trends in Ecology & Evolution* 14: 483–88.

Peery, M. Z. 2000. "Factors Affecting Interspecies Variation in Home-Range Size of Raptors." *The Auk* 117: 511–17.

Ponisio, L. C., K. Wilkin, L. K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, T. Griswold, and C. Kremen. 2016. "Pyrodiversity Begets Plant–Pollinator Community Diversity." *Global Change Biology* 22: 1794–1808.

Raphael, M. G., and M. White. 1984. "Use of Snags by Cavity-Nesting Birds in the Sierra Nevada." *Wildlife Monographs* 86: 3–66.

Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, H. A. Kramer, N. F. Kryshak, J. J. Keane, et al. 2022. "Breeding Status Shapes Territoriality and Vocalization Patterns in Spotted Owls." *Journal of Avian Biology* 2022: e02952.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCRACKEN, and P. Monaghan. 2006. "Spatial Variation in Demography and Population Growth Rate: The Importance of Natal Location." *Journal of Animal Ecology* 75: 1201–11.

Reynolds, R., and B. D. Linkhart. 1987. "The Nesting Biology of Flammulated Owls in Colorado." In *Biology Ad Conservation of Northern Forest Owls*. USDA Forest Service, 239–48. Gen. Tech. Rep. RM-142.

Salo Sciences. 2020. CFO Forest Strucuture. California Forest Observatory forest strucutre. https://forestobservatory.com/

Safford, H. D., and J. T. Stevens. 2017. *Natural Range of Variation for Yellow Pine and Mixed-Conifer Forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California, USA*. Gen. Tech. Rep. PSW-GTR-256. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station 229. 256 pp.

Scott, V. E., K. E. Evans, D. R. Patton, and C. P. Patton. 1977. *Cavity-Nesting Birds of North American Forests*. Agriculture Handbook. Washington, D.C: U.S. Forest Service, U.S. Government Printing Office.

Seavy, N. E., R. D. Burnett, and P. J. Taille. 2012. "Black-Backed Woodpecker Nest-Tree Preference in Burned Forests of the Sierra Nevada, California." *Wildlife Society Bulletin* 36: 722–28.

Skinner, C. N., and C. Chang. 1996. "Fire Regimes, Past and Present." In: *Sierra Nevada Ecosystem Project: Final Report to Congress*. Vol. II. Assessments and Scientific Basis for Management Options. Wildland Resources Center Report No. 37. Centers for Water and Wildland Resources, University of California, Davis, 1041–69.

Steel, Z. L., B. Campos, W. F. Frick, R. Burnett, and H. D. Safford. 2019. “The Effects of Wildfire Severity and Pyrodiversity on Bat Occupancy and Diversity in Fire-Suppressed Forests.” *Scientific Reports* 9: 16300.

Steel, Z. L., A. M. Fogg, R. Burnett, L. J. Roberts, and H. D. Safford. 2022. “When Bigger Isn’t Better—Implications of Large High-Severity Wildfire Patches for Avian Diversity and Community Composition.” *Diversity and Distributions* 28: 439–453.

Steel, Z. L., G. M. Jones, B. M. Collins, R. Green, A. Koltunov, K. L. Purcell, S. C. Sawyer, et al. 2023. “Mega-Disturbances Cause Rapid Decline of Mature Conifer Forest Habitat in California.” *Ecological Applications* 33: e2763.

Steel, Z. L., M. J. Koontz, and H. D. Safford. 2018. “The Changing Landscape of Wildfire: Burn Pattern Trends and Implications for California’s Yellow Pine and Mixed Conifer Forests.” *Landscape Ecology* 33: 1159–76.

Sutherland, C., D. Hare, P. J. Johnson, D. W. Linden, R. A. Montgomery, and E. Droge. 2023. “Practical Advice on Variable Selection and Reporting Using Akaike Information Criterion.” *Proceedings of the Royal Society B: Biological Sciences* 290: 20231261.

Taillie, P. J., R. D. Burnett, L. J. Roberts, B. R. Campos, M. N. Peterson, and C. E. Moorman. 2018. “Interacting and Non-Linear Avian Responses to Mixed-Severity Wildfire and Time since Fire.” *Ecosphere* 9: e02291.

Tarbill, G. L., P. N. Manley, and A. M. White. 2015. “Drill, Baby, Drill: The Influence of Woodpeckers on Post-Fire Vertebrate Communities through Cavity Excavation.” *Journal of Zoology* 296: 95–103.

Taylor, A. H., V. Trouet, C. N. Skinner, and S. Stephens. 2016. “Socioecological Transitions Trigger Fire Regime Shifts and Modulate Fire–Climate Interactions in the Sierra Nevada, USA, 1600–2015 CE.” *Proceedings of the National Academy of Sciences of the United States of America* 113: 13684–89.

Tempel, D. J., R. J. Gutiérrez, S. A. Whitmore, M. J. Reetz, R. E. Stoelting, W. J. Berigan, M. E. Seamans, and M. Z. Peery. 2014. “Effects of Forest Management on California Spotted Owls: Implications for Reducing Wildfire Risk in Fire-Prone Forests.” *Ecological Applications* 24: 2089–2106.

Tingley, M. W., V. Ruiz-Gutiérrez, R. L. Wilkerson, C. A. Howell, and R. B. Siegel. 2016. “Pyrodiversity Promotes Avian Diversity over the Decade Following Forest Fire.” *Proceedings of the Royal Society B: Biological Sciences* 283, no. 1840: 201617032.

Tingley, M. W., A. N. Stillman, R. L. Wilkerson, C. A. Howell, S. C. Sawyer, and R. B. Siegel. 2018. “Cross-Scale Occupancy Dynamics of a Postfire Specialist in Response to Variation across a Fire Regime.” *Journal of Animal Ecology* 87: 1484–96.

Torre, I., and M. Díaz. 2004. “Small Mammal Abundance in Mediterranean Post-Fire Habitats: A Role for Predators?” *Acta Oecologica* 25: 137–142.

Turner, M. G., D. C. Donato, and W. H. Romme. 2013. “Consequences of Spatial Heterogeneity for Ecosystem Services in Changing Forest Landscapes: Priorities for Future Research.” *Landscape Ecology* 28: 1081–97.

Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. “Climatic and Human Influences on Fire Regimes in Ponderosa Pine Forests in the Colorado Front Range.” *Ecological Applications* 10: 18.

Westerling, A. L. 2016. “Increasing Western US Forest Wildfire Activity: Sensitivity to Changes in the Timing of Spring.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150178.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. “Continued Warming Could Transform Greater Yellowstone Fire Regimes by Mid-21st Century.” *Proceedings of the National Academy of Sciences of the United States of America* 108: 13165–70.

White, A. M., P. N. Manley, G. L. Tarbill, T. W. Richardson, R. E. Russell, H. D. Safford, and S. Z. Dobrowski. 2016. “Avian Community Responses to Post-Fire Forest Structure: Implications for Fire Management in Mixed Conifer Forests.” *Animal Conservation* 19: 256–264.

Wilkinson, Z. A., H. A. Kramer, G. M. Jones, C. J. Zulla, K. McGinn, J. M. Barry, S. C. Sawyer, et al. 2022. “Tall, Heterogenous Forests Improve Prey Capture, Delivery to Nestlings, and Reproductive Success for Spotted Owls in Southern California.” *Ornithological Applications* 121: duac048.

Wood, C. M., R. J. Gutiérrez, and M. Z. Peery. 2019. “Acoustic Monitoring Reveals a Diverse Forest Owl Community, Illustrating Its Potential for Basic and Applied Ecology.” *Ecology* 100: e02764.

Wood, C. M., and G. M. Jones. 2019. “Framing Management of Social-Ecological Systems in Terms of the Cost of Failure: The Sierra Nevada, USA as a Case Study.” *Environmental Research Letters* 14: 105004.

Wood, C. M., V. D. Popescu, H. Klinck, J. J. Keane, R. J. Gutiérrez, S. C. Sawyer, and M. Z. Peery. 2019. “Detecting Small Changes in Populations at Landscape Scales: A Bioacoustic Site-Occupancy Framework.” *Ecological Indicators* 98: 492–507.

Yanco, S. W., and B. D. Linkhart. 2018. “Changing Fire Regimes and Faunal Responses: Habitat Use by Flammulated Owls after Fire in Colorado.” In *Trends and Traditions: Avifaunal Change in Western North America*, edited by W. D. Shuford, R. E. Gill, and C. M. Handel, 419–431. Camarillo, CA: Western Field Ornithologists.

Zulla, C. J., H. A. Kramer, G. M. Jones, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, et al. 2022. “Large Trees and Forest Heterogeneity Facilitate Prey Capture by California Spotted Owls.” *Ornithological Applications* 124: duac024.

SUPPORTING INFORMATION

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

How to cite this article: McGinn, Kate, Benjamin Zuckerberg, Gavin M. Jones, Connor M. Wood, Stefan Kahl, Kevin G. Kelly, Sheila A. Whitmore, et al. 2025. “Frequent, Heterogenous Fire Supports a Forest Owl Assemblage.” *Ecological Applications* 35(1): e3080. https://doi.org/10.1002/eap.3080