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Frequent burning and limited stand-replacing fire supports Mexican spotted owl pair occupancy

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Abstract

Changing fire regimes have the potential to threaten wildlife populations and communities. Understanding species' responses to novel fire regimes is critical to formulating effective management and conservation strategies in an era of rapid change. Here, we examined the empirical effects of recent and historical wildfire activity on Mexican spotted owl (*Strix occidentalis lucida*) populations in the southwestern United States. Using region-wide, standardized detection/non-detection data of Mexican spotted owl breeding pairs collected from 2015 to 2022, we found (*i*) higher rates of pair occupancy at sites that experienced more frequent fires in the three decades prior to the initiation of our study, and (*ii*) lower rates of local persistence at sites that experienced more extensive high-severity fire during the study. Historical fire regimes throughout much of our study area were characterized by high fire frequencies and limited high-severity components, indicating that Mexican spotted owls responded to wildfire in a manner consistent with their evolutionary environment. Management activities such as prescribed burning and mechanical thinning that aim to reduce stand-replacing fire risk and re-introduce the potential for frequent-fire regimes will likely benefit Mexican spotted owl conservation objectives, as well as promote more resilient forest landscapes.

Keywords Forest restoration, High-severity fire, Mixed-conifer, Occupancy, Old-forest, Restoration, Southwest, *Strix occidentalis lucida*, Wildfire

Resumen

Los cambios en los regímenes de fuego tienen el potencial de amenazar las comunidades y poblaciones de fauna silvestre. El entender la respuesta de las especies a los cambios en los nuevos regímenes de fuego, es crítico para poder formular estrategias de manejo y conservación efectivos en una era de rápidos cambios. Examinamos en este trabajo los efectos empíricos de la actividad de incendios históricos y recientes sobre poblaciones de búho moteado de México (Strix occidentalis lucida) en el sudoeste de los EEUU. Explorando un nivel regional amplio, datos estandarizados de detección/no detección de parejas de búho moteado de México coleccionadas desde 2015 a 2022, encontramos: (i) una mayor tasa de ocupación de parejas de búhos en sitios que experimentaron fuegos muy frecuentes en las tres décadas previas a la iniciación de nuestro estudio, y (ii) una menor tasa de persistencia en sitios que experimentaron severidades de fuego más extensas durante el período de estudio. Los regímenes de fuegos históricos, a través de la mayoría de nuestra área de estudio, se caracterizaron por fuegos de alta frecuencia y componentes de severidad

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limitados, lo que indica que el búho moteado de México responde al fuego de manera consistente con la evolución de su ambiente. Las actividades de manejo como las quemas prescriptas y el aclareo mecánico, que tienden a reducir el riesgo de los fuegos de reemplazo total de los rodales (stand-replacing fires) y reintroducen el potencial de regímenes de fuegos frecuentes, es probable que beneficien los objetivos de conservación del búho moteado de México, como así también promuevan paisajes forestales más resilientes.

Introduction

Fire regimes are changing globally (Bowman et al. 2020). Driven by land-use (e.g., land conversion, fire suppression) and climate change, many ecosystems are experiencing fire characteristics that fall outside of their historical range of variability (Seidl et al. 2016; Safford and Stevens 2017). For example, systems that historically experienced long-interval, high-intensity fire regimes are experiencing an "interval squeeze" (Turner et al. 2019; Le Breton et al. 2022), where shortened fire return intervals can lead to tree regeneration failure and subsequent ecosystem type conversion. Other ecosystems that historically experienced short-interval, low-intensity fires have experienced long periods of fire suppression, promoting uncharacteristically large and severe fires when they do occur because of an accumulation of fuels (Stevens et al. 2017; Steel et al. 2018). In these cases and in others, changing fire regimes are converting ecosystems from their natural state to novel conditions (Stevens-Rumann et al. 2018; Coop et al. 2020), with pervasive impacts to society via altered provisioning of ecosystem services.

Changing fire regimes are also having widespread effects on wildlife, with important conservation implications. Animals have accumulated adaptations that allow them to thrive in a fire environment consistent with their evolutionary past (Nimmo et al. 2021; Jones et al. 2023), yet it is estimated that changing fire regimes are a threat to >4400 species globally (Kelly et al. 2020). Uncharacteristic fires can produce mass animal mortality events (Tomas et al. 2021; Nimmo et al. 2022), but perhaps more often they will produce novel vegetation patterns to which animals may not be adapted (Stillman et al. 2021; Jones and Tingley 2022). To develop well-informed pre- and post-fire vegetation management plans, land managers and conservation workers must understand how species of concern respond to changing fire regimes. In some regions, such as the western United States, knowledge gaps about how certain species respond to wildfire have produced substantial barriers to implementing large-scale ecosystem restoration activities (Ganey et al. 2017; Peery et al. 2019; Stephens et al. 2020; North et al. 2021). Thus, understanding wildlife responses to changing fire regimes is a key component of ecosystem restoration.

In the southwestern United States, historically frequent-fire forests are now experiencing uncharacteristically severe fires (Singleton et al. 2019), sometimes resulting in forest regeneration failure (Rodman et al. 2020). An iconic inhabitant of these at-risk forests is the Mexican spotted owl (*Strix occidentalis lucida*; Fig. 1), which tends to be associated with areas of higher canopy cover and larger, older trees (Ganey et al. 2016; Witt et al. 2022). The Mexican spotted owl is also a centerpiece of forest management policy and politics in the American Southwest. In 1993, the Mexican spotted owl was listed as threatened under the US Endangered Species Act (USFWS 1993); in the decades since, all forests in the

Fig. 1 An adult Mexican spotted owl (*Strix occidentalis lucida*) on the Lincoln National Forest in southern New Mexico, USA. Photo credit: USDA Forest Service

Southwestern Region of the USDA Forest Service have integrated Mexican spotted owl conservation into their forest and project planning, and numerous high-profile lawsuits have sought to protect the owl from real or perceived infringements on its habitat. For example, in 2019, a lawsuit relating to Mexican spotted owl habitat conservation resulted in an injunction on timber management actions on five national forests in New Mexico and one national forest in Arizona for 1 year (WildEarth Guardians v. USFWS et al. 2019).

As the pattern, frequency, and intensity of fires change within southwestern forests, concern over Mexican spotted owl habitat conservation will continue to grow because of the potential loss of nesting and roosting habitat (Jones et al. 2016). Yet to date, little published literature exists on Mexican spotted owl demographic responses to larger, more severe fires. Early studies suggested that Mexican spotted owl occupancy, survival, and reproduction may not be negatively affected by low-intensity fires (Bond et al. 2002; Jenness et al. 2004). However, recent studies have predicted Mexican spotted owl habitat loss resulting from larger, more severe fires (Wan et al. 2020; Jones et al. 2022b). Despite these advances, robust empirical studies are still lacking. Such information is critical to informing forest management and conservation actions that both safeguard owl habitat and promote resilient forests.

Here, we used detection/non-detection data collected from 2015 to 2022 across 200 sampling units in Arizona and New Mexico to develop a multi-season occupancy model (Royle and Kéry 2007). We used this model to examine the potential effects of wildfire on Mexican spotted owl pair occupancy, persistence, and colonization rates, while accounting for imperfect detectability. We focused our analysis on Mexican spotted owl pairs because pair occupancy represents the parameter of interest reflecting demographic drivers (i.e., potential reproductive behavior), and the inclusion of non-territorial floaters or wide-ranging individuals can bias site occupancy analyses (Berigan et al. 2018). Based on previous research on the California subspecies of spotted owl (*S. o. occidentalis*) (Jones et al. 2020, 2021; Kramer et al. 2021), we hypothesized that Mexican spotted owls occurring in forested habitat are adapted to a landscape that developed under a fire regime characterized by lower-severity, frequent fire. As such, we developed a set of predictions that, if supported by data, would provide evidence in support of our hypothesis. First, we predicted Mexican spotted owls would have higher pair occupancy rates in areas that experienced more frequent fires and less high-severity fire. Second, we predicted that Mexican spotted owl pairs would be less likely to colonize or persist in areas that experienced more extensive severe fire within these sites. Our study provides the first robust empirical estimates of the effect of wildfire on Mexican spotted owl pair occupancy at broad spatial and temporal scales and how these owls respond dynamically to changing fire landscapes.

Methods

Study area

Our study was conducted on National Forest System lands in Arizona and New Mexico that comprise the Southwestern Region of the USDA Forest Service (Fig. 2). The region experiences a wide variety of climate conditions, but is characterized by mild winters and hot, dry summers punctuated by heavy precipitation during the North American Monsoon (June through September). Forested habitat for Mexican spotted owls in the study area consists of pine-oak complexes at lower elevations and mixed-conifer forest at higher elevations. Pine-oak complexes are dominated by ponderosa pine (*Pinus ponderosa*), with a component of Gambel oak (*Quercus gambelii*). White fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*) limber pine (*Pinus flexilis*), and blue spruce (*Picea pungens*) comprise mixed conifer forest. Natural fire regimes in this region within these forest types range from understory to mixed-severity fires with relatively short return intervals (0 to 34 years; Brown and Smith 2000) and a limited stand-replacing component.

In some areas within our study region, Mexican spotted owls also inhabit rocky canyonlands characterized by steep canyon walls with large vertical cliffs containing caves, ledges, and other microsites that facilitate nesting and roosting activities (USFWS 2012). The majority of sites surveyed in this study (~97% or greater) occurred in forested as opposed to canyonland habitat; most canyonland habitat occurs on non-USFS managed lands. The majority of known Mexican spotted owl habitat occurs on lands under US federal jurisdiction (USFWS 2012).

Sampling design and data collection

The sampling design for this study is described in detail in Blakesley (2015), and we summarize it here. A sampling frame was developed containing vegetation cover and geophysical features considered to be potentially suitable for Mexican spotted owl nesting and roosting behaviors. Following guidance from the 2012 Mexican spotted owl Recovery Plan, a 1-km^2 grid (US National Grid System) was overlaid on the sampling frame to define potential sampling units, and grid cells containing < 50% National Forest System lands were eliminated. Potential sampling units were further eliminated if they did not match features of Mexican spotted owl habitat derived from a geophysical habitat model (Johnson 2003) and potential vegetation type (Wahlberg et al. 2014).

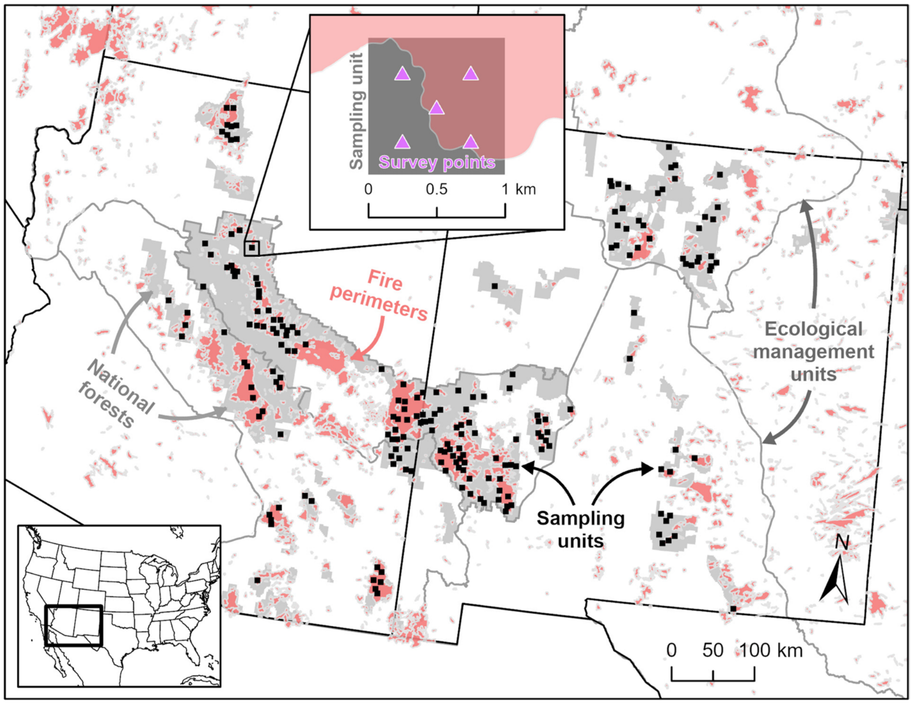

Fig. 2 Study area and sampling design. Black squares in the main map show the $n=200$ sampling units, and the inset map shows the five call points (purple triangles) nested within each sampling unit. Grey shading shows the boundaries of National Forest System in Arizona and New Mexico in which sampling units were placed. Grey border lines in the main map delineate the Ecological Management Units, among which sampling units were stratified. Red shading shows fires > 400 ha mapped by Monitoring Trends in Burn Severity (MTBS) program since 1984. Inset shows an example of a sampling unit that was affected by fire

Of the approximately 17,900 1-km^2 sampling units, a spatially-balanced random sample of 1000 was drawn. Sampling units were stratified across 5 Ecological Management Units, which are administrative boundaries governing recovery coordination for the species (Fig. 2). Then, based on estimated home range sizes of Mexican spotted owls (Peery et al. 1999; May and Gutiérrez 2002) sampling units falling within 5 km of each other were eliminated to reduce the likelihood of the closure assumption being violated (Rota et al. 2009), resulting in 465 sampling units. The 350 highest-ranked sampling units (in terms of potential Mexican spotted owl habitat quality) were surveyed during a pilot season (April–July 2014). Ultimately, because of logistical constraints, 200 of the 350 sampling units were selected and consistently surveyed from 2015 to 2022 as part of detection/non-detection surveys. Data collected during the pilot season were not included in the present analysis. Within each 1-km^2 sampling unit, five evenly-distributed survey points were placed; survey crews navigated to these locations to conduct callback surveys (Fig. 2).

Breeding season detection/non-detection surveys were conducted from April-August during the years 2015 through 2022. At each survey point, technicians used a FoxPro NX3 or NX4 digital game callers to broadcast pre-recorded Mexican spotted owl vocalizations in an attempt to elicit a territorial response (Forsman 1983). The pre-recorded audio files produced a mixture of male and female spotted owl vocalizations that played for 20 s, followed by 20 s of silence, for a 10-min period. After the 10-min broadcast cycle, technicians listened in silence for 5 min for responses from Mexican spotted owls. Owl detections were only considered valid if they occurred within the 1-km^2 sampling unit. If no owls were detected, technicians moved to a subsequent survey point, and surveys continued until a male-female pair of Mexican spotted owls were detected, or until all 5 points were surveyed. While attempts were made to visit all 5 survey points, sometimes points were not visited due to safety concerns, weather conditions (e.g., high winds), or other logistical issues. However, a minimum of 3 survey points were visited for a site to be considered fully "surveyed," unless a detection occurred sooner.

In the present analysis, we only considered detections of a male-female pair to constitute a "detection" (i.e., a "1" in the detection history). Detections of single males or females were treated as "non-detections" (i.e., a "0" in the detection history) because the inclusion of non-territorial floaters or wide-ranging individuals can bias site occupancy analyses (Berigan et al. 2018). We also limited the analysis to pairs because diurnal visits to check reproductive status were not conducted, an approach that facilitates a multi-state occupancy analysis using reproductive states (Rockweit et al. 2023). In the absence of reproductive status, the presence of a pair of owls at least tells us that the conditions at the site may be of sufficient quality to support a breeding pair, which is more biologically meaningful than the presence of a potentially transient individual. In each year, sampling units were surveyed two times, which formed the secondary sampling periods in our occupancy model (see below). In 2021 and 2022, for logistical reasons, sites were not visited a second time if a detection occurred on the first visit; we account for this potential source of variation in detectability using "year" as a random effect in our detection model. During each survey, technicians recorded wind speed on the Beaufort scale and ambient noise levels on an index ranging from 0 (no noise) to 4 (very loud). In 2020, no surveys were conducted because of the COVID-19 pandemic. Thus, we analyzed data collected from 2015 to 2022, excluding 2020.

Statistical analysis

We used a multi-season occupancy model in a Bayesian formulation (Royle and Kéry 2007) to evaluate correlates of site occupancy. We formulated the model to contain parameters for initial occupancy ($\psi_{i,1}$), colonization ($\gamma_{i,\ t}$), persistence ($\phi_{i,\ t}$, the complement of extinction, $\varepsilon_{i,\ t}$), and detection probability ($p_{i,\ j,t}$). Sampling locations (i) referred to the 1-km^2 sampling grid, primary sampling periods (t) were breeding seasons (April–August in this dataset), and the secondary sampling periods (j) were repeated surveys that occurred twice each year (see above).

We computed covariates from remotely sensed spatial datasets within circular buffered areas centered on sampling locations to evaluate the potential effects of fire on initial occupancy, persistence, and colonization rates of Mexican spotted owls. To account for potential scale-dependence of effects (Jackson and Fahrig 2015), we constructed occupancy models that varied the scale at which covariates were summarized to approximate administrative or biological scales of interest: the scale of the sampling unit that was actually surveyed (100-ha), the protected activity center (PAC) scale (250-ha) (US Fish and Wildlife Service 2012), and the home range scale (400-ha) (estimated to range from 346 to 452 ha; Peery et al. 1999; May and Gutiérrez 2002). At each scale, we computed (i) the number of times the area burned during the pre-study period (1984–2014; complete fire records begin in 1984), (ii) the cumulative proportion of the area that burned severely (> 75% canopy mortality; RdNBR > 572, Miller et al. 2009) during the pre-study period (1984–2014; complete fire records began in 1984), and (iii) the annual proportion of the area that burned severely during the study period (2015–2022). Fire data were obtained from the Monitoring Trends in Burn Severity project (http://mtbs.gov/), which maps fires over 400-ha in size (thus, smaller fires are excluded). We originally calculated a metric of within-site pyrodiversity (Jones and Tingley 2022) as a model covariate, but this variable was highly correlated with the proportion of each site that burned severely, so we excluded it from further consideration. Previous analyses of fire effects on California spotted owls have evaluated the potential confounding effects of post-fire salvage logging (Jones et al. 2016, 2021); however, the spatial extent of salvage logging is extremely limited in Arizona and New Mexico forests, so we did not include it as a potential explanatory covariate.

We developed an a priori model that described site occupancy dynamics as a function of fire-related covariates using a before-after control-impact formulation (Popescu et al. 2012). We modeled detection probability as a logit-linear function of survey covariates:

$$logit\left(p_{i,j,t}\right) = a_0 + a_1 julian.date_{i,j,t} + a_2 wind_{i,j,t} + a_3 noise_{i,j,t} + a.year_t$$

where a_0 was the intercept, a_1 was the fixed effect of Julian date (day of year) of the survey, a_2 was the fixed effect of wind (measured on the Beaufort scale) during the survey, a_3 was the fixed effect of the noise index during the survey, and $a.year_t$ was a random year effect to account for unmodeled temporal heterogeneity in p.

We modeled initial occupancy in the first year of our study (2015) as a logit-linear function of several fire-related variables:

$$logit\left(\psi_{i,1}\right) = b_0 + b_1 fire_i + b_2 n.burn_i + b_3 high.severity_i$$

where b_0 was the intercept, $fire_i$ was an indicator variable for areas within a fire perimeter during the study period (2015–2022), to account for potential background differences in occupancy rates of these groups; $n.burn_i$ was a continuous variable ranging from 0 to 3 describing the number of times a sampling unit experienced fire during the pre-study period (1984–2014); and $high.severity_i$ was a variable describing the cumulative proportion of each site that experienced high-severity fire (> 75% canopy mortality) in the pre-study period (1984–2014).

For subsequent years (2015–2022), we modeled site occupancy as a process dependent on the true occupancy state ($z_{i,\,t}$), the probability that an unoccupied site would be colonized ($\gamma_{i,\,t}$), and the probability that an occupied site would remain occupied ($\phi_{i,\,t}$):

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

where rates of colonization and persistence were influenced by site and time-varying covariates related to fire effects in a before-after control-impact formulation:

$$\begin{aligned} logit\left(\gamma_{i,t-1}\right) = & c_0 + c_1 fire_i + c_2 after_{i,t} + c_3 fire_i after_{i,t} \\ & + c_4 fire_i after_{i,t} high.severity_{i,t} + c.year_t \end{aligned}$$

and

$$\begin{aligned} logit\left(\phi_{i,t-1}\right) = & d_0 + d_1 fire_i + d_2 after_{i,t} + d_3 fire_i after_{i,t} \\ & + d_4 fire_i after_{i,t} high.severity_{i,t} + d.year_t \end{aligned}$$

where $fire_i$ was an indicator variable for areas that were within a fire perimeter during the study period (2015–2022) as described above for the initial occupancy sub-model; $after_{i,t}$ was an indicator variable for post-fire years, where at each site "0" would represent pre-fire years and "1" would indicate post-fire years; $high.severity_{i,t}$ was a continuous time-varying covariate representing the proportion of each sampling unit that experienced stand-replacing fire in years when $after_{i,t} = 1$; and $c.year_t$ and $d.year_t$ were annual random effects that accounted for unmodeled temporal heterogeneity in both sub-models.

We fit our a priori model at each of the three spatial scales of interest (100 ha, 250 ha, and 400 ha) using JAGS (Plummer 2003) in the R statistical programming environment (version 4.3.2). All coefficients were given normally distributed priors with $\mu = 0$ and $\sigma = 1.4$, which are uninformative priors in occupancy models (Northrup and Gerber 2018). We ran three chains of 5000 iterations, an adaptation phase of 1500 and a thin rate of 10, yielding 1500 posterior samples for each parameter across all chains. We evaluated convergence using the Gelman-Rubin statistic (all values < 1.1). We made inferences about model parameters by examining the direction and magnitude of mean effects, the extent to which posterior distributions overlapped zero, and by examining the proportion of the posterior distribution that was positive or negative. We square-root transformed the variable representing the proportion of a sampling unit that experienced severe fire to account for anticipated non-linear or threshold-type effects. We used the square-root instead of the natural logarithm transformation because the range of values in the predictor variable included zero. We z-standardized all continuous covariates to facilitate model fitting and coefficient interpretation (Schielzeth 2010).

Results

The direction and magnitude of fire effects did not change considerably across spatial scales examined, but we found the strongest biological effect sizes at the 400-ha scale. Thus, we report posterior means and Bayesian credible intervals on the logit scale from the 400-ha scale in the main text (Table 1); full results from all spatial scales can be found in the Supporting Information (Table S1).

Table 1 Summary of posterior distributions from the multi-season occupancy model (400-ha scale). Results are organized by sub-model component (detection, initial occupancy, colonization, and persistence). *SD* standard deviation, *LCL* lower 95% Bayesian credible limit, *UCL* upper 95% Bayesian credible limit, *f* proportion of posterior distribution with the same sign as the mean (i.e., probability of effect being in the direction of the mean). All coefficient values are on the logit scale

	Mean	SD	LCL	UCL	*f*
Detection (p)					
Intercept	− 0.862	0.394	− 1.613	− 0.081	0.983
Wind	− 0.166	0.089	− 0.341	0.002	0.972
Julian date	0.013	0.002	0.008	0.018	1.000
Noise	− 0.404	0.126	− 0.659	− 0.173	0.999
Year (random effect)[a]	6.615	4.837	1.185	19.031	1.000
Initial occupancy (ψ1)					
Intercept	− 0.172	0.229	− 0.613	0.278	0.787
Fire (grouping variable)	0.236	0.330	− 0.381	0.907	0.761
Number of burns (1984–2014)	0.345	0.319	− 0.248	0.974	0.857
High-severity (1984–2014)	− 0.013	0.206	− 0.433	0.389	0.521
Colonization (γ)					
Intercept	− 2.619	0.448	− 3.376	− 1.723	0.998
Fire (grouping variable)	− 0.573	0.717	− 2.103	0.681	0.781
After	0.397	1.084	−1.671	2.470	0.644
Fire × after	0.374	1.083	− 1.713	2.532	0.637
Fire × after × high-severity	0.057	0.274	− 0.494	0.481	0.653
Year (random effect)[a]	5.892	6.179	0.216	22.25	1.000
Persistence (φ)					
Intercept	2.560	0.352	1.908	3.268	1.000
Fire (grouping variable)	0.498	0.601	− 0.632	1.746	0.799
After	− 0.255	1.120	− 2.421	1.959	0.590
Fire × after	−0.242	1.082	− 2.346	1.885	0.603
Fire × after × high-severity	− 0.484	0.193	− 0.889	− 0.120	0.992
Year (random effect)[a]	6.991	6.993	0.539	24.879	1.000

[a] The random effect for year is represented as precision, or 1 divided by the variance

Areas were more likely to be occupied by Mexican spotted owl pairs if they experienced more frequent fire in the three decades (1984–2014) prior to the initiation of the study (posterior mean $b_2 = 0.345$, 95% Bayesian credible interval $[-0.248, 0.974]$) (Fig. 3A; Table 1). Although the 95% Bayesian credible interval for this effect overlapped zero, 86% of the posterior distribution was positive, indicating evidence of a positive effect of fire frequency on initial occupancy. The amount of severe fire experienced by sampling units in the three decades prior to the study period had no discernable effect on Mexican spotted owl initial pair occupancy ($b_3 = -0.013$ $[-0.433, 0.389]$).

After controlling for background differences in dynamic pair occupancy rates between burned vs. unburned sites and during the pre- and post-fire periods, we found no discernible effect of severe fire on post-fire pair colonization rates ($c_4 = 0.057$ $[-0.494, 0.481]$). In contrast, post-fire pair persistence declined as a function of severe fire exposure ($d_4 = -0.484$ $[-0.889, -0.120]$), with over 99% of the posterior distribution having negative values (Fig. 3B; Table 1).

All covariates examined in the pair detection sub-model were statistically meaningful and biologically sensible. Detectability decreased as a function of wind ($a_1 = -0.166$ $[-0.341, 0.002]$) and ambient noise ($a_3 = -0.404$ $[-0.659, -0.173]$) and increased as a function of Julian date ($a_2 = 0.013$ $[0.008, 0.018]$) (Table 1).

Discussion

In the southwestern US, a region experiencing rapid changes to fire regimes, Mexican spotted owls appear to be responding to fire in a manner somewhat consistent with their evolutionary history. The low- to mid-elevation pine-oak and mixed conifer forests inhabited by Mexican spotted owls had a historical fire regime characterized by low-severity, high-frequency fire. Some areas in the southwestern US, where land managers have promoted active fire management, are still experiencing predominately frequent and low-severity fire effects, including parts of the Gila National Forest (Holden et al. 2010; Hunter et al. 2011) and the Coronado National Forest (Villarreal et al. 2020). However, many contemporary fires have been characterized by large, high-severity patches that fall outside of the historical range of variation (Singleton et al. 2019). Our results suggest that these novel fire characteristics may be incompatible with conservation of Mexican spotted owls. As such, forest management that reduces the extent of severe fire and re-introduces frequent lower severity fire effects, while maintaining key habitat structures (e.g., large, old trees), will likely support Mexican spotted owl conservation objectives (e.g., Fig. 4).

Frequent, low-severity fire can be self-reinforcing (Holden et al. 2010), generating a heterogeneous environment while maintaining legacy structures such as large, old trees (Woolman et al. 2022). A landscape with spatial variation in cover type and forest age provides important foraging habitat for Mexican spotted owls, while large, old trees provide nesting and roosting habitat (Ganey and Balda 1994; Ganey et al. 1999). Thus, frequent, low-severity fire may promote landscape complementation (Dunning et al. 1992), which is the spatial juxtaposition of multiple resources required by animals to satisfy their

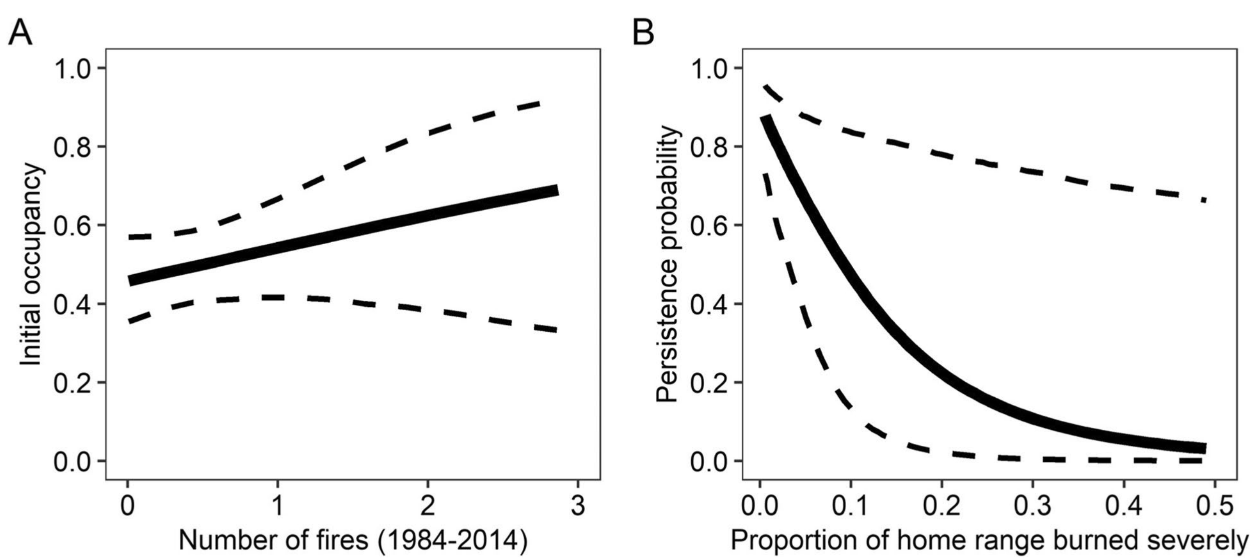

Fig. 3 Marginal plots showing continuous relationship between **A** number of fires that occurred prior to the initiation of the study and the initial site occupancy probability at the 400-ha scale and **B** the severe fire proportion and the probability of site persistence at the 400-ha scale. Black solid lines show the mean posterior prediction, and the black dashed lines show the upper and lower 95% Bayesian credible interval. The x-axis limits in each panel reflect the range of observed values from the study

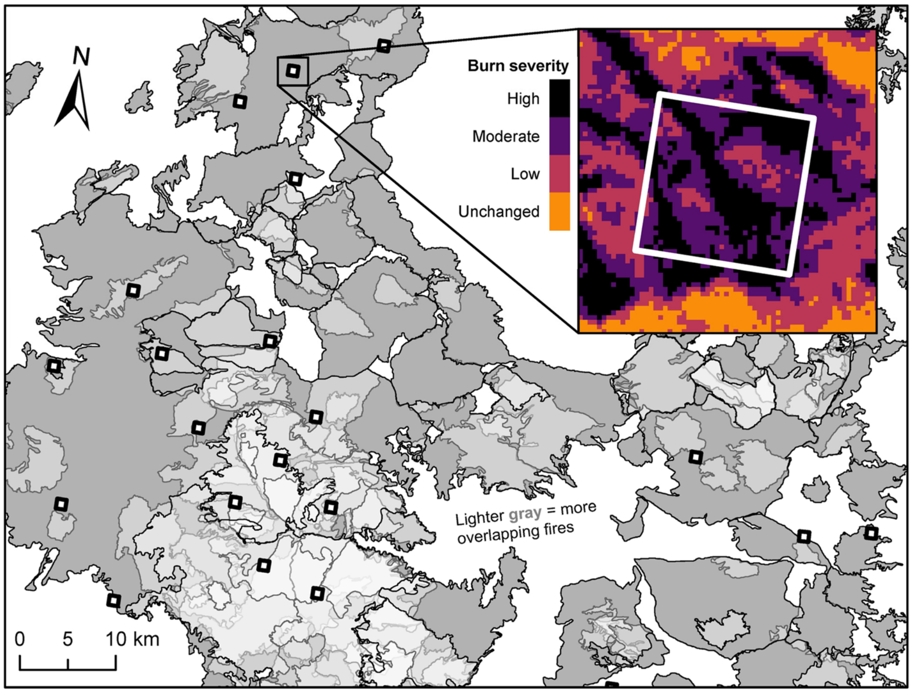

Fig. 4 Example of landscape features that influence Mexican spotted owl site occupancy on the Gila National Forest, New Mexico. The large map shows fire perimeters from 1984 to 2021 in gray shading with black outlines. In places where multiple fires overlap, the gray shading becomes lighter; sites that experience higher fire frequencies have higher predicted site occupancy. The inset map shows a sampling unit (white square) that experienced larger amounts of high-severity fire; sites with more high-severity fire experience lower rates of persistence

ecological needs. Our result showing that Mexican spotted owl pair occupancy is higher in areas with more frequent fire may be driven by this mechanism. Moreover, we found evidence suggesting a tendency for sites that never burned to have lower persistence than sites that burned (fire grouping variable, Table 1). Such an effect strengthens the argument that frequent, low-severity fire enhances complementation, leading to higher overall site persistence. Landscape complementation is one proposed mechanism underlying positive pyrodiversity-biodiversity relationships (Kelly et al. 2017; Jones and Tingley 2022). Therefore, theory would predict that frequent, low-intensity fire in these forests could generate higher local species richness (via high pyrodiversity), apparently benefiting both Mexican spotted owls as well as the broader biological community (Latif et al. 2016b; Barton and Poulos 2021; Saab et al. 2022).

While landscape complementation could explain Mexican spotted owl response to frequent, low-intensity fire, their response to high-intensity fire is more likely explained by local loss of important nest structures (Ganey et al. 2017). Recruitment of large, old trees that are sufficiently structurally complex and decadent to support nesting activities is sometimes a centuries-long process (Lindenmayer and Laurance 2017; Brown et al. 2019) that is made possible by low-intensity fires that facilitate adult tree survival. When fires burn at very high intensity, they can kill dominant overstory trees that act as Mexican spotted owl nesting habitat. This mechanism could explain why, in our study, pair persistence declined in areas that experienced more extensive severe fire effects. However, an alternative explanation is that more extensive patches of severe fire are less suitable for foraging owls, as has been shown in California spotted owls (Jones et al. 2020; Kramer et al. 2021). Large, homogenous patches of severely-burned forest represent poor habitat for the small mammal prey of spotted owl (Roberts et al. 2015; Culhane et al. 2022).

We predicted that severe fire would reduce local colonization rates, but we detected no such effects (Table 1). This lack of effect could be explained by at least two factors. First, there may have been little remaining variation in colonization rates that could be explained by the "fire × after × high-severity" covariate after other effects were accounted for; background colonization rates in the "burned" group were lower to begin with, and colonization rates appeared to increase, albeit marginally, at burned sites post-fire ("fire × after" covariate). Second, other factors besides patterns of burn severity may be more likely to cause spotted owls to colonize a given territory, including the presence of large, old trees that constitute ideal nesting structures. At the same time, the loss of such structures through high-severity fire may be very likely to lead to local extinction, and thus the observed relationship between extensive high-severity fire and lower persistence (Fig. 3B). Other factors, including imperfect knowledge of habitat quality and territoriality, could drive non-ideal territory colonization patterns.

Recent US national policy directives encourage land managers to reduce severe fire risk, increase forest resilience to fire, and restore frequent fires to southwestern US forests and across broader geographies (USDA 2022). Our results suggest that these objectives are consistent with the conservation of Mexican spotted owls in the southwestern US, as our model showed that higher fire frequency and reduced severe fire resulted in increased pair occupancy and persistence, respectively. These results are also consistent with recommendations in the Mexican spotted owl Recovery Plan (USFWS 2012) and with results from broader portions of the species range, especially in the range of the California spotted owl (Kramer et al. 2021). One important lingering uncertainty in the range of the Mexican spotted owl is how individuals and populations will respond to fuels reduction and forest restoration activities themselves, which often involves the removal of live trees (Ganey et al. 2017; Prichard et al. 2021); future research should address this uncertainty. However, in the Sierra Nevada, CA, recent research suggests both short- and longer-term benefits of fuels reduction to California spotted owls, from individual to population scales (Hobart et al. 2019; Jones et al. 2022a; Zulla et al. 2022; Wright et al. 2023). Evidence also supports the idea that broad-scale fuels reduction activities can benefit wildlife communities more broadly in the southwestern US (Hurteau et al. 2008; Latif et al. 2022). As the US Wildfire Crisis Strategy is implemented in the coming decade (USDA 2022), more research is needed to reduce uncertainties about how sensitive species and wildlife communities in general will respond.

While our research of fire responses by Mexican spotted owls provides some clarity about the potential benefits of restored frequent fire regimes, our study has limitations that must be acknowledged to appropriately interpret our inferences. First, detections of Mexican spotted owls primarily occurred at night, and previous work has demonstrated biases associated with relying on nocturnal detections of spotted owls for occupancy estimation because they may reflect wide-ranging, nonresident movements (Berigan et al. 2018). We attempted to limit this bias by only modeling pair detections, thus increasing the biological relevance of positive detection data (Yackulic et al. 2019). Nevertheless, our detections could reflect owls engaging in multiple types of non-territorial behaviors, including foraging and forays, and thus “occupancy” may be more safely interpreted as “use” (Latif et al. 2016a). Second, and on a related note, we generally think that Mexican spotted owl populations are limited by the availability of nesting rather than foraging habitat (Ganey et al. 2017). Because our detection data do not necessarily reflect occurrence at or near nesting habitat, or diurnal detections at roost sites, we are unable to make strong inferences about the potential effects of wildfire activity on potential nesting and roosting activity.

Third, our model did not include fire size, configuration, time-since-fire (Saab and Powell 2005), or interactions between fire and vegetation type because of sample size considerations, although these factors likely influenced Mexican spotted owl pair occupancy, colonization, and persistence rates. We conducted a post-hoc analysis that provided some evidence that effects of high-severity fire on Mexican spotted owl pair persistence might vary across vegetation types (Fig. S1), although these potential effects appear to vary only in degree rather than quality. Fourth, we found scale-invariant effects of fire on dynamic occupancy rates, but this scale-invariance could also be the result of poorly matched spatial data. Burn severity data obtained from MTBS does not map fires smaller than 400 ha, meaning that smaller, potentially important fires are not included in our modeling effort. The spatial extents over which we summarized data range from 100 to 400 ha. While we found marginally stronger effects at the 400-ha scale, this could simply reflect a better match with the scale of spatial data. It could also suggest that owls may respond dynamically to fire characteristics at broader spatial scales than were measured in our study (Jackson and Fahrig 2012). If true, effective fuels reduction and restoration treatments may require coordination across broader spatial scales than are captured by current administrative planning units (e.g., PACs). Given its high relevance to conservation planning and decision-making, future studies should consider better understanding the scale at which owls respond to fire characteristics across a range of landscape contexts.

Concluding remarks

The restoration of frequent-fire regimes in many southwestern US forests appears to be consistent with Mexican spotted owl conservation in the region given their response to recent fire activity. Some areas that have embraced prescribed fire and managed wildfire use, such as the Gila National Forest in western New Mexico and the Four Forests Restoration Initiative priority landscape (USDA 2022), are illustrative of the type of fire-mosaic landscape that could support both Mexican spotted owls and resilient forests (Fig. 4). Such “bright spots” can act as guideposts for restoration of fire regimes in the southwestern US. As the pace and scale of forest restoration accelerates (USDA 2022), maintaining the slow-to-recruit legacy features of large, old trees will be critical in promoting landscape complementation and overall compatibility between fuels reduction and Mexican spotted owl conservation.

Supplementary Information

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Supplementary Material 1.

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Authors' contributions

GMJ conceived of the idea, analyzed the data, visualized results, wrote the first draft, coordinated manuscript revisions, integrated reviewer feedback; MAC conceived of the idea, oversaw field data collection, performed data QA/QC, and contributed to manuscript revisions; CEL conceived of the idea, provided administrative support, and contributed to the manuscript revisions; MEW helped prepare spatial covariates for analysis and contributed to manuscript revisions; JSS contributed to manuscript revisions and analytical decisions; SJH helped develop the study design, provided logistical and administrative support, and contributed to manuscript revisions; BK helped secure funding to support field data collection, provided logistical and administrative support, and contributed to manuscript revisions.

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Declarations

Ethics approval and consent to participate

Mexican spotted owl surveys were performed under USFWS permit ESPER0036357.

Competing interests

None declared.

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