Landsc Ecol (2025) 40:165
https://doi.org/10.1007/s10980-025-02171-4

REVIEW ARTICLE

Characterizing climate- and fire-driven habitat vulnerability for an old-forest species

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Received: 25 November 2024 / Accepted: 4 July 2025

Abstract
Context Changes in climate and associated disturbance regimes are altering patterns of biodiversity by shifting macroenvironmental conditions and modifying the structure and composition of critical habitat. These threats require understanding the climate vulnerability of species habitat to inform conservation planning.
Objectives We developed a framework to address this need for the Mexican spotted owl (*Strix occidentalis lucida*), a species whose range is experiencing widespread climate-driven increases in wildfire and drought that can have adverse impacts upon large, old trees, a vital habitat element for owl nesting and roosting.
Methods We leveraged broad-scale data describing owl habitat quality, predicted fire severity, and tree recruitment probability to quantify the vulnerability of this species' habitat in the southwestern United States.
Results Owl habitat quality was positively associated with predicted fire severity and negatively associated with tree recruitment potential, indicating that portions of the Mexican spotted owl's existing range may be vulnerable to forest recruitment failure and, under extreme weather, high-severity wildfire. Despite these patterns, we also identified large patches of high-quality habitat that have the potential to resist high-severity fire and foster tree recruitment, which are likely to sustain current forest communities, and owl nesting and roosting habitat in the near-term.
Conclusions In identifying the relative vulnerability of habitat across a broad spatial extent, our framework provides a valuable tool for the conservation of this and other old-forest-obligate species, and habitat specialists in general. More broadly, the framework we have developed may help prioritize limited conservation resources to effectively promote biodiversity in an increasingly dynamic world.

Keywords Habitat vulnerability · Fire refugia · Climate change · Fire-driven transformation · Rare ecological features · Mature and old-growth forest

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02171-4.

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Published online: 04 August 2025

Introduction

Climate change is driving species range shifts globally (Chen et al. 2011; Freeman et al. 2018b; McCain et al. 2021). Warming temperatures and shifting precipitation patterns are a primary factor governing geographic shifts in suitable environmental niche space (Freeman et al. 2018a; McCain and Colwell 2011). However, variation in individual species responses to climate change has led to the reshuffling of animal community composition (Princé and Zuckerberg 2015) and other idiosyncratic patterns that cannot simply be predicted by climate niche tracking alone (Fordham et al. 2012; HilleRisLambers et al. 2013; Tingley et al. 2012). Habitat specialization is one important factor that may mediate species ability to track shifts in suitable climate space (Bosco et al. 2022; Platts et al. 2019). When suitable climate space shifts, but important vegetation conditions do not, the vulnerability of habitat specialists to climate-driven local extirpation may increase (Fourcade et al. 2021; Le Feuvre et al. 2021). At the same time, habitat specialists may occupy climate change refugia, where local topographic conditions and habitat buffer a species against the larger-scale changes in climate conditions (Keppel et al. 2012). Thus, climate change responses by habitat specialists may be complex and difficult to predict.

As the climate warms, disturbance regimes—i.e., the typical size, frequency, severity, and spatial patterns of disturbance in a given area—are also shifting (Turner and Seidl 2023), having important effects on species habitat that could otherwise act as hold-outs or climate change refugia (Hannah et al. 2014; Keppel et al. 2012; Morelli et al. 2020). In forest ecosystems, fire and drought are both natural disturbance processes that produce spatio-temporal variation in vegetation patterns and thus species habitat (Jones and Tingley 2022; Turner 2010). But climate- and land-use-change are giving rise to increases in both fire size and the area burned at high severity, altering forest structure and landscape pattern (Collins et al. 2021; Parks and Abatzoglou 2020; Stephens et al. 2022). For habitat specialists, disturbance-driven losses of unique or rare forest conditions upon which they specialize may pose a greater threat than warming temperature itself (Hoecker and Turner 2022), with significant consequences for the availability and functionality of potential climate change refugia and the distribution of suitable habitat.

Ecologically rare features face heightened vulnerability to climate- and disturbance-driven losses (Foden et al. 2013, 2019). Large, old trees are some of the rarest features in ecosystems across the globe (Kane et al. 2023; Lindenmayer et al. 2012; Lutz et al. 2018), providing critical habitat for numerous wildlife species (Jones et al. 2018; Mazurek and Zielinski 2004). For example, greater gliders (*Petauroides volans*) in Australia are limited by the abundance of old, cavity-bearing trees (Smith et al. 2007), and the lack of old-growth forest in China constrains wild populations of giant pandas (*Ailuropoda melanoleuca*; Zhang et al. 2011). While many large, old trees have survived fire for centuries or millennia, novel fire regimes and environmental conditions can overwhelm their ability to persist (e.g., McClure et al. 2024) and provide habitat for the wildlife species that depend on them. For example, uncharacteristic fire regimes, combined with logging, led to a recent apparent collapse in Mountain Ash ecosystems in Australia, with concomitant declines in tree cavity-dependent wildlife (Lindenmayer and Sato 2018).

Given potentially heightened threats to rare and important habitat features, like large, old trees, quantifying the risks presented by changes in climate and disturbance regimes is necessary to understand the consequences for the species that rely upon them. Here, we implement a framework for identifying vulnerable habitat in an environment experiencing rapid changes to both climate and disturbance regimes: the southwestern United States. In this region, the Mexican spotted owl (*Strix occidentalis lucida*) is a federally threatened species that nests in large, old trees in the forested portion of its range (Seamans and Gutiérrez 1995). In other portions of its range, Mexican spotted owl will nest and roost in rocky canyons, cliffs, and caves (Ganey and Balda 1989); we focus here on the forested portion of the owl's range. The size and spatial arrangement of these old-forested habitats is critical for owls: nesting and roosting locations most commonly occur in locations with contiguous, high-quality habitat (i.e., a "core area") of at least 40 ha, which are identified and designated for additional protections as a part of this species' recovery plan (Bowden et al. 2015; U.S. Fish and Wildlife Service 2012; Jones unpublished data). The availability of these nesting and roosting habitats is thought to be the key limiting feature of the environment for owls, although this species uses a broader set of environmental conditions for other activities (such as foraging) and outside of the breeding season (Ganey et al. 2017). Forests throughout the American Southwest, including these old-forest, nesting and roosting habitats, are experiencing rapid shifts in fire regimes (Singleton et al. 2019) and forest recovery following severe fire is becoming less likely (Davis et al. 2023). Yet we lack a broader understanding of the vulnerability of existing Mexican spotted owl forest habitat to wildfire. We combined geospatial datasets describing forest resilience to climate and fire with a habitat suitability model for Mexican spotted owl to characterize the distribution, abundance, and spatial patterns of potentially vulnerable nesting and roosting habitat. We sought to answer the following three questions:

(1) What are the relationships between Mexican spotted owl habitat quality and indicators of high-severity wildfire and post-fire tree recruitment?
(2) Where do areas of low vulnerability to fire align with high-quality Mexican spotted owl habitat?
(3) Are potential refugia of a sufficient size (≥ 40 ha, the nest core area) to support nesting and roosting habitat for Mexican spotted owl mating pairs assuming widespread fire occurrence?

We developed these questions without a priori expectations about what the relationships between owl nesting and roosting habitat and indicators of its vulnerability might be, or how these associations would be realized in space. We aimed to explore these questions to provide valuable information to guide managers in allocating limited resources for Mexican spotted owl conservation in the southwestern US, and, more broadly, demonstrate a framework for evaluating habitat vulnerability of imperiled species dependent on rare habitat elements in fire-prone regions.

Methods

Study area

Our study area included upland conifer forests of Arizona and New Mexico, USA (Online Resource Fig. S1). Typical tree species in this region include ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). The relative dominance of these species covaries with gradients of elevation, temperature, and precipitation. Ponderosa pine forests or pine-oak woodlands dominate warm, dry sites (typical of lower-elevation locations within upland forests). Douglas-fir and white fir become more common as conditions become cooler and more mesic at middle elevations, while subalpine fir and Engelmann spruce become prevalent at the highest elevations. Although many other tree species are present across the region, e.g., mesquite (*Prosopis spp.*), aspen (*Populus tremuloides*), locust (*Robinia* spp.), or oak (*Quercus spp.*), we focus on forests that contain at least one of these dominant coniferous tree species, since they make up a large proportion of total tree biomass in this region (Wilson et al. 2013) and have widely available post-fire recruitment data, which help to assess vulnerability to forest transformation (Davis et al. 2023). Furthermore, these forests represent a central portion of the Mexican spotted owl's range and host a significant percentage (likely > 80%) of its population within the US (Online Resource Fig. S1).

Mexican spotted owl data and models

To describe habitat quality for Mexican spotted owl throughout the study area, we relied on an existing field-survey database (Jones et al. 2023) and an associated species distribution model (Shirk et al. 2023). Briefly, the database incorporates information from 2,913 field-inventoried locations of Mexican spotted owl nest/roost sites from 1989 to 2020. These locations were compared to pseudo-absence points distributed across all forested habitat using a Random Forest classifier (Breiman 2001) to estimate the relative probability of Mexican spotted owl nest/roost site occurrence based upon topographic, climatic, and remotely sensed reflectance covariates (Shirk et al. 2023). Topographic values were fixed at static values for the entire study period, while climatic and reflectance covariates varied across years. The modeled relationships were then used to develop predictive maps across the Southwest in the form of annual raster layers (one raster for each year during the period from 1986 to 2020) at a ca. 30-m spatial resolution, representing the mean relative probability of Mexican spotted owl nest/roost occurrence. Although not explicitly included in the model, we expected that the relative probability of nest/roost occurrence should closely match the prevalence of mature, old growth trees in the region because Mexican spotted owls are dependent on this habitat type for nesting and roosting in forested environments (Seamans and Gutiérrez 1995), and such features might be identified through predictors such as spectral reflectance. A parallel study, conducted in concert with Shirk et al. (2023) and Jones et al. (2023), demonstrated that forest areas predicted as highly suitable Mexican spotted owl nest/roost habitat indeed contained higher densities of large trees (Witt et al. 2022). We focused specifically on habitat quality in 2020, as it was the latest year available in this dataset and aligned with the timing of the fire severity predictions (see *Forest Resistance and Recruitment*).

To aid visualization and analysis of nesting and roosting habitat vulnerability in 2020, we created a binary variable of owl habitat quality that defined areas as "high-" or "low-quality" in that year. To construct this variable, we extracted the predicted value of relative probability of nest/roost site occurrence from the species distribution model at both true nest/roost locations and pseudo-absence points. We performed this extraction in a time-dependent fashion, such that presence and pseudo-absence points received the probability value from the year of data collection (or generation in the case of pseudo-absence points). We used these predicted relative probability values to calculate the true skill statistic (Allouche et al. 2006), which maximizes the sum of sensitivity (true positive rate) and specificity (true negative rate). We treated the value of the statistic as the threshold between "high-" and "low-quality" owl nesting and roosting habitat and discretized the 2020 output of the species distribution model to facilitate interpretation of our results.

Forest resistance and recruitment

To assess the vulnerability of Mexican spotted owl nesting and roosting habitat to wildfire and tree regeneration failure, key drivers of forest transformation, we used recently developed maps predicting fire severity and post-fire tree recruitment potential throughout the study area. Rodman et al. (2023) developed predictive maps of fire severity using relationships between remotely sensed estimates of the composite burn index (CBI; Parks et al. 2019) and factors that are likely to influence fire behavior (i.e., weather, topography, fuels, past fire occurrence) across 1180 individual fire events. These empirical relationships were used to develop two predictive maps of fire severity in 2021 under moderate (75th percentile) and extreme (99th percentile) fire weather scenarios based on existing topography and fuels conditions. Davis et al. (2023) created species-specific maps of post-fire tree recruitment (i.e., the probability of at least 100 trees ha^{-1} of a given species establishing within 10 years of a theoretical fire event given the availability of seed) from hierarchical regression models developed with biophysical covariates and a database of over 10,000 field plots throughout the western US. These maps of tree recruitment highlight areas where recent (2001–2020) climatic and topographic conditions are most limiting to tree recruitment in the US Southwest (Rodman et al. 2023). Because thresholds of likely presence/absence of tree recruitment differed by tree species (Davis et al. 2023), we centered values around the probability value that maximized the true skill statistic (Allouche et al. 2006) and stretched them to the range of [0,1], placing all species-specific maps on a comparable scale. We then calculated community-weighted recruitment probability as the weighted average of individual tree species probabilities, with weights based on relative abundance in each 30-m pixel (Wilson et al. 2013). Taken together, our two maps of predicted fire severity and single map of tree recruitment probability characterize the capacity of Mexican spotted owl forest habitat to resist severe fire and maintain resilience at the end of 2020, heading into 2021.

Q1: What are the relationships between Mexican spotted owl habitat quality and indicators of high-severity wildfire and post-fire tree recruitment?

To answer Q1, we intersected maps of owl nesting and roosting habitat quality (in 2020), predicted fire severity (under moderate and extreme fire weather with 2021 fuel conditions), and community-weighted recruitment probability (based upon measurements from 2001 to 2020) across ~ 3.8 Mha in the US Southwest, a total of > 43 M 30-m pixels. To incorporate uncertainty in predictions of fire severity, we performed this overlay for the mean ± 1 standard error

(SE) of the prediction for both moderate and extreme fire weather conditions. Likewise, we incorporated prediction uncertainty in species-specific recruitment maps using the mean prediction ± 1 SE for each species. For all 30-m pixels within the study area, we visualized the relationships among models using non-linear regression (i.e., generalized additive models) to evaluate how predicted fire severity and community-weighted recruitment probability varied with owl habitat quality across a range of fire weather conditions. Specifically, we fit a series of univariate GAMs with cubic shrinkage splines and Gaussian error structure to model the mean, mean + 1 SE, and mean − 1 SE of predicted fire severity under moderate and extreme conditions, and community-weighted recruitment probability as a function of the continuous probability of Mexican spotted owl nesting/roosting habitat. To improve the computational tractability of these models, we used a random 10% sample of pixels (4.3 M pixels) to fit our GAMs. Comparisons across 10% samples revealed no qualitative differences in the overall shape of the predicted relationships between owl nesting and roosting habitat quality and predicted fire severity or tree recruitment probability.

Q2: Where do areas of low vulnerability to fire align with high-quality Mexican spotted owl habitat?

To answer Q2, we categorized levels of vulnerability within high-quality owl nesting and roosting habitat as follows: 'not resistant' areas with high predicted fire severity (composite burn index [CBI] ≥ 2.25); 'resistant − recruitment' areas with low predicted fire severity (CBI < 2.25) and a low community-weighted recruitment probability (< 0.5); resistant + recruitment areas with both a low predicted fire severity (CBI < 2.25) and high community-weighted recruitment probability (≥ 0.5). To describe broader spatial patterns of vulnerability throughout the study area, we summarized and plotted the proportion of each vulnerability class within U.S. Geological Survey HUC12 watersheds (United States Geological Survey 2023). Within each watershed, we calculated the proportion of pixels assigned to each vulnerability category under moderate and extreme fire weather conditions. We then excluded all watersheds with < 1 ha of total area covered by our Mexican spotted owl nesting and roosting habitat maps and vulnerability layer. After investigating broad-scale patterns across the study area, we assessed fine-grained patterns of habitat vulnerability classes across several areas of interest, particularly those that showed strong differences between moderate and extreme fire weather conditions and within two large, landscape restoration projects managed by the USDA Forest Service (the Four Forests Restoration Initiative in northern Arizona and the South Sacramento Restoration Project in southern New Mexico). These focal maps allowed us to view the spatial patterns of nesting and roosting habitat vulnerability at the native, 30-m resolution of the raster in key areas.

Q3: Are potential refugia of a sufficient size (≥ 40 ha, the nest core area) to support nesting and roosting habitat for Mexican spotted owl mating pairs assuming widespread fire?

To answer Q3, we assessed spatial patterns of each vulnerability class within potential high-quality owl nesting and roosting habitat assuming widespread fire. For these analyses, we restricted the maps of vulnerability (developed for each weather scenario) to areas with high-quality Mexican spotted owl nesting and roosting habitat in two ways: (1) using data-driven species distribution model and threshold value noted above; and (2) using Mexican spotted owl protected activity centers (PACs), which are USDA Forest Service administrative boundaries used to protect key habitat elements used by spotted owl pairs, including nest and roost trees. Our analysis of PACs was intended to help assess the vulnerability of current protected areas and identify potential mismatches with future habitat vulnerability, which could inform or prioritize future PAC delineation in new locations.

Under each fire weather scenario, we calculated landscape metrics using our vulnerability raster of not resistant, resistant − recruitment and resistant + recruitment classes, restricted to high-quality nesting and roosting habitat as defined above. Within high-quality nesting and roosting habitats, we identified individual patches of each vulnerability class by converting this raster to polygons using eight-neighbor pixel contiguity (i.e., Queen contiguity) (Bivand 2022; Turner et al. 2001). We removed any polygons with area ≤ 0.09 ha (i.e., isolated 30-m pixels). We used the area and perimeter of each polygon to calculate the shape index of all polygons as:

$$s = 0.25\frac{perimeter}{\sqrt{area}}$$

following Patton (1975).

We also used cumulative frequency distributions of patch size to describe the total area and number of patches in each vulnerability class that exceeded Mexican spotted owl nest core area size (40.47 ha). We then calculated the percentage of the total area and number of patches larger than the nest core area size within each vulnerability class and across the entire study extent. For this analysis of landscape patterns relative to the nest core area size, we constructed an additional vulnerability class, 'all resistant', which combined resistant − recruitment and resistant + recruitment patches, because these two classes would both resist high-severity fire and could theoretically provide high-quality nesting and roosting habitat for Mexican spotted owl in the immediate aftermath of a fire. For the study-extent composition of the all-resistant class, we summed the total area or number of all-resistant and not-resistant patches in the denominator. Finally, we examined the mean shape index as a function of patch size across the range of patch sizes observed and visualized them using generalized additive models for each set of weather conditions and vulnerability class.

Results

Q1: What is the relationship between Mexican spotted owl habitat quality and indicators of high-severity wildfire and post-fire tree recruitment?

We found that owl habitat quality for nesting and roosting was positively associated with fire severity under both moderate (Pearson's $r = 0.45$) and extreme weather conditions ($r = 0.40$), where predicted CBI increased up to a point (~ 0.6 probability of an owl nest/roost) and then plateaued (Fig. 1). This pattern held true regardless of weather conditions, although predicted high-severity fire (CBI ≥ 2.25) was rare under moderate conditions but frequently observed in extreme conditions (Fig. 1). Under moderate weather conditions, low-quality owl habitat had a median predicted CBI of 0.5 and high-quality owl habitat had a median predicted CBI of 1.1, with high-severity fire predicted across 9,875 ha (0.3% of the study extent), 2,530 ha (0.1%) of which would be high-quality owl habitat. In contrast, under extreme weather conditions, low-quality owl habitat had a median predicted CBI of 1.5 and high-quality owl habitat had a median predicted CBI of 2.1, with high-severity fire predicted across 567,981 ha (14.6% of the study extent), 115,516 ha (3.0%) of which would be high-quality owl habitat. We noted a high degree of uncertainty in our models of fire severity, although this uncertainty did not qualitatively impact the relationship between owl nesting and roosting habitat quality and fire severity—the high-quality owl habitat was consistently less resistant to high-severity fire after accounting for prediction uncertainty (Fig. 1).

We also found that owl nesting and roosting habitat quality was negatively associated with community-weighted tree recruitment probability ($r = -0.21$; Fig. 2). Recruitment probability generally declined with increasing owl habitat quality, then plateaued between ~ 0.2–0.4 probability of an owl nest/roost, before declining further with increasing owl habitat quality (Fig. 2). This pattern produced a median recruitment probability of 0.38 in low-quality owl habitat and 0.31 in high-quality owl habitat. A substantial portion of our study area – 3.3 Mha (86% of the study extent)—was unlikely to experience post-fire recruitment of coniferous tree species (recruitment probability < 0.5), and 264,154 ha (6.8%) of this area occurred in high-quality owl habitat. In comparison, just 36,008 ha (0.9% of the study extent) of high-quality owl habitat had recruitment probability ≥ 0.5. We noted relatively less uncertainty (i.e., narrower prediction intervals) in our model of community-weighted recruitment probability as compared to the model of fire severity. In addition, uncertainty in our recruitment model did not impact the qualitative patterns between owl nesting and roosting habitat quality and recruitment probability—high-quality owl habitat was less likely to have successful tree recruitment after fire (Fig. 2).

Q2: Where do areas of low vulnerability to fire align with high-quality Mexican spotted owl habitat?

High-quality owl nesting/roosting habitat with the lowest vulnerability, resistant + recruitment class (CBI < 2.25, community-weighted recruitment probability ≥ 0.5), was most common in Arizona's Kaibab Plateau and Mogollon Rim. Still, some isolated

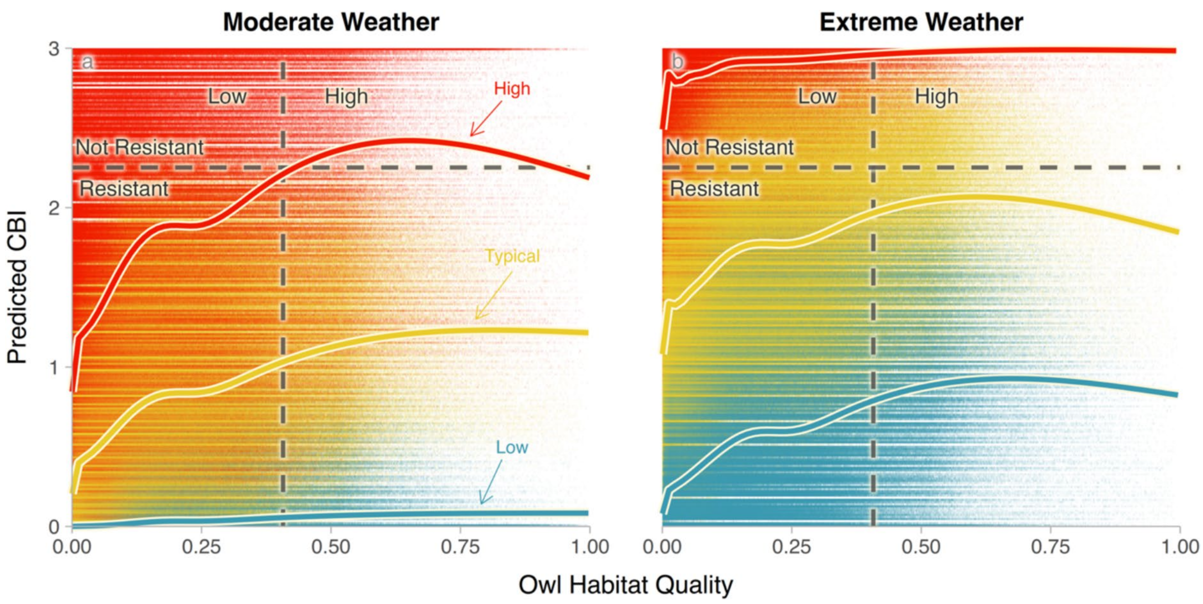

Fig. 1 Predicted fire severity (composite burn index; CBI) under two fire weather scenarios throughout Arizona and New Mexico forests as a function of Mexican spotted owl nesting and roosting habitat quality in 2020. Moderate fire weather (**a**) corresponds to 75th percentile daily fire weather and extreme fire weather (**b**) conditions corresponds to 99th percentile daily fire weather. The predicted risk of high-severity fire increased under extreme fire weather and, to a lesser extent, with increasing owl nesting and roosting habitat quality. Yellow points represent the typical (mean) fire severity outcome in individual pixels, while red and blue points represent the same in upper (mean + 1 standard error [SE]) and lower (mean − 1 SE) prediction intervals within each weather scenario, respectively. Points are a 10% subsample of the data (i.e., 4.3 M pixels). Colored lines are a non-linear regression (i.e., generalized additive model) for points of the same color to capture the overall trend in fire severity as a function of owl habitat quality. The horizontal, dark gray dashed line represents the boundary between fire-resistant and not fire-resistant pixels (CBI = 2.25). The vertical, dark gray dashed line represents the boundary between low- and high-quality owl nesting and roosting habitat (ca. 0.41)

reserves were present in New Mexico's mountains (Fig. 3). When compared to moderate conditions (Fig. 3a), extreme weather (Fig. 3b) reduced the prevalence of the resistant + recruitment class at the watershed scale, especially in the mountains of New Mexico. A more detailed look revealed that this pattern results from a contraction in the extent of this vulnerability class and not its local elimination (Fig. 3c, d, f, g). This resistant + recruitment class was present in 12.0% (35,882 ha) and 8.0% (25,198 ha) of all high-quality owl nesting and roosting habitat under moderate and extreme conditions, respectively (Fig. 3i, j), although the extent of this class varied some when accounting for the prediction uncertainty in our models of fire severity and recruitment probability (Online Resource Figs. S2, S3, S4).

In high-quality owl nesting and roosting habitat, the intermediate vulnerability class, resistant − recruitment (CBI < 2.25, community-weighted recruitment probability < 0.5), occurred widely across the study area (Fig. 3). This class was the most common, occupying 87.2% (261,750 ha) and 53.1% (159,448 ha) of all high-quality owl habitat under moderate and extreme conditions, respectively (Fig. 3i, j) and its coverage varied relatively little when considering prediction uncertainty (Online Resource Figs. S2, S3, S4). The most vulnerable class, not resistant (CBI ≥ 2.25), tended to replace some areas of resistant − recruitment class under extreme conditions. The prevalence of the not resistant class increased from < 1% (2,530 ha) of all high-quality owl habitat under moderate weather to 38.5% (115,516 ha) under extreme weather (Fig. 3i, j). This turnover in vulnerability classes was most evident in New Mexico (Fig. 3a, b) and could be seen at finer spatial scales (Fig. 3e, h), despite uncertainty in the predictions of fire severity (Online Resource Fig. S2, S3, S4).

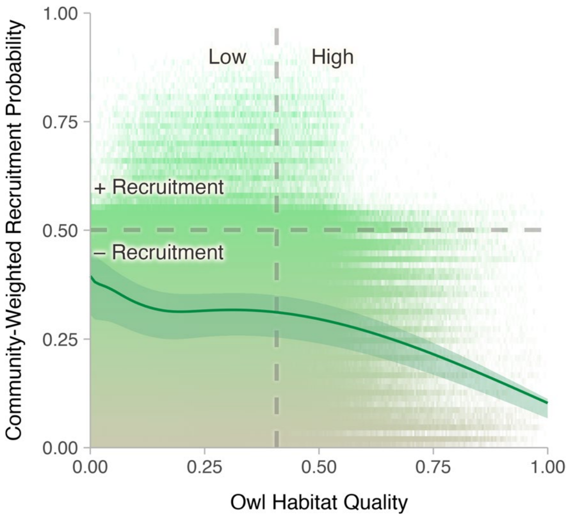

Fig. 2 Community-weighted recruitment probability for major coniferous tree species based on 2001–2020 environmental conditions across Arizona and New Mexico forests as a function of Mexican spotted owl nesting and roosting habitat quality in 2020. Higher values of recruitment probability (green points) indicate that sites remain highly suitable for regeneration of existing tree species, whereas lower values (brown points) indicate greater vulnerability to recruitment failure. Points are a 10% subsample of the data (i.e., 4.3 M pixels). The green line is a non-linear regression (i.e., generalized additive model) for the background points to capture the typical (mean) pattern of recruitment probability with variation in owl nesting and roosting habitat quality. The green shaded ribbon provides a prediction interval (i.e., mean ± 1 standard error of the prediction) from the model of community-weighted recruitment probability. The horizontal, dark gray dashed line represents the boundary (recruitment probability = 0.5) between pixels more likely to recruit coniferous tree species than not ("+ Recruitment") and pixels where the reverse is true ("– Recruitment"). The vertical, dark gray dashed line represents the boundary between low- and high-quality owl nesting and roosting habitat (ca. 0.41)

Q3: Are potential refugia of a sufficient size (≥ 40 ha, the nest core area) to support nesting and roosting habitat for Mexican spotted owl mating pairs assuming widespread fire?

Based on maps of high-quality nesting and roosting habitat derived from species distribution models and assuming all this habitat burned, most resistant + recruitment area (i.e., low-vulnerability habitat) was contained in small patches (i.e., < 10 ha, Fig. 4a, b). Still, if Mexican spotted owl forest habitat burned under moderate conditions, we predicted 2.2% of the study extent (74 patches; Online Resource Fig. S5a, b, Table S1) would be contained in low-vulnerability, resistant + recruitment areas larger than the Mexican spotted owl nest core area size. Similarly, if forest habitat burned under extreme conditions, we predicted that 1.1% of the landscape covered by our predictive maps of fire severity, tree recruitment probability and high-quality owl nesting and roosting habitat (36 patches; Online Resource Table S1) would be in low vulnerability patches larger than the nest core area size. While the patch distributions of resistant + recruitment habitat did not vary substantially with fire weather, the patch distribution of the more vulnerable habitat (i.e., not resistant and resistant – recruitment) strongly differed between moderate and extreme conditions. For example, if Mexican spotted owl forest habitat burned under moderate conditions, 39.2% of the study extent (0.5% of all patches) occurred in patches of the resistant – recruitment class that were larger than the nest core area size, as opposed to 13.8% of the study extent (0.1% of patches) if Mexican spotted owl habitat burned under extreme conditions (Online Resource Table S1). This decline in the resistant – recruitment class was mirrored by an increase in the not-resistant class. If forest habitat burned under moderate weather, < 0.1% of the study extent occurred in large not-resistant patches, whereas if Mexican spotted owl habitat burned under extreme conditions, 12.2% of study extent occurred in not-resistant patches larger than the Mexican spotted owl nest core area size (Online Resource Table S1).

If Mexican spotted owl PACs burned under moderate weather, 8.7% of the total extent of all PACs occurred in resistant + recruitment patches larger than the nest core area size, whereas if PACs burned under extreme conditions, 0% of the PAC extent occurred in resistant + recruitment patches larger than the nest core area size (Fig. 4c, d, Online Resource Table S1). Similarly, if PACs burned, 0.5% (moderate weather) and 0.0% (extreme weather) of individual patches occurred in the low-vulnerability class and were larger than the nest core area size (Online Resource Fig. S5c, d). Patch sizes of the resistant – recruitment class were meaningfully influenced by fire weather in PACs. If PACs burned under moderate weather, 75.5% of the PAC extent was in patch sizes of this class larger than the nest core area size, as opposed to just 0.2% if PACs burned under extreme weather (Fig. 4c, d; Online Resource Table S1). Similarly, 2.8% (moderate weather) and 0.1% (extreme weather) of individual

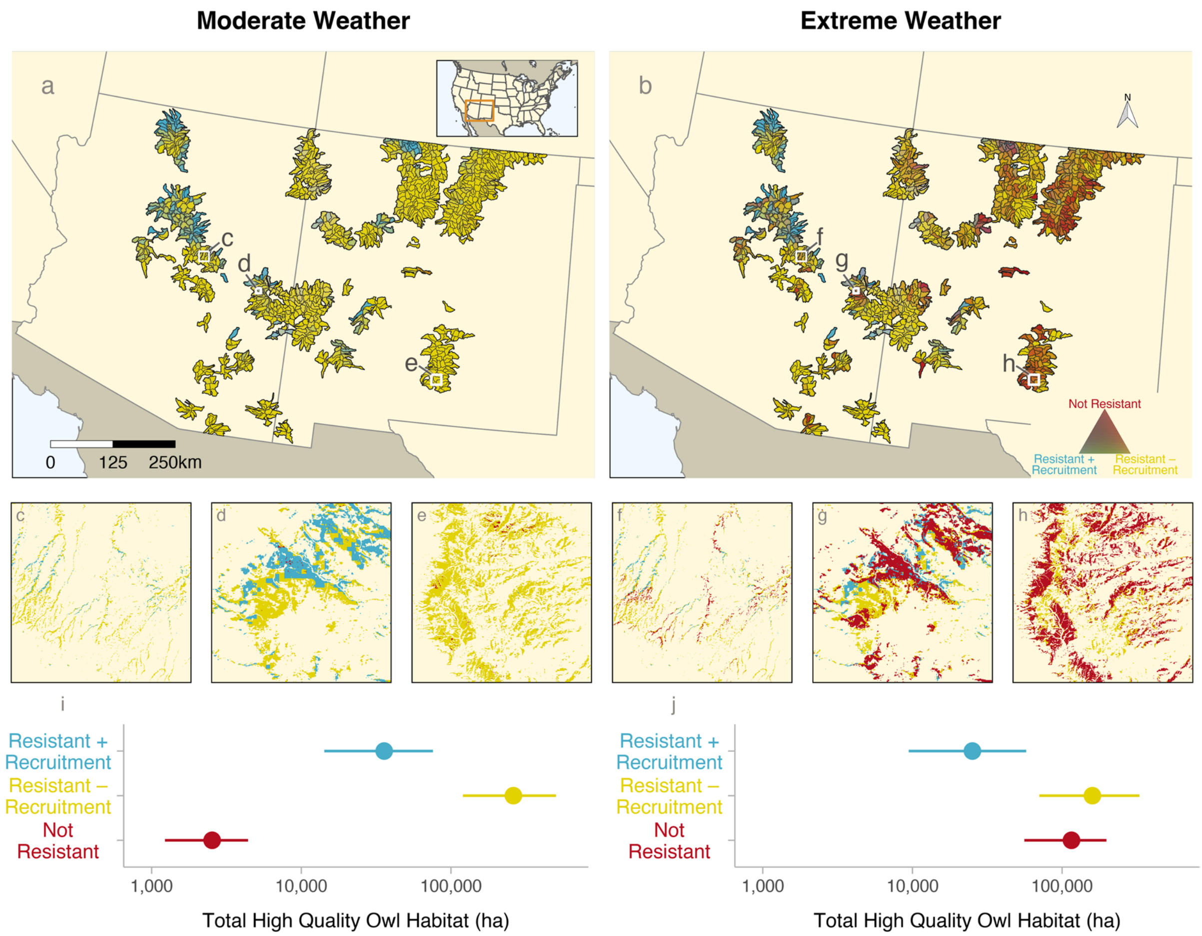

Fig. 3 Predicted fire refugia under moderate (**a**) and extreme (**b**) fire weather across high-quality Mexican spotted owl nesting and roosting habitat (in 2020) across Arizona and New Mexico forests. The color of each watershed represents its vulnerability class composition: from not resistant (red) to resistant – recruitment (yellow) to resistant + recruitment (blue). Intergraded colors represent the relative frequencies of these vulnerability classes in each watershed. The white boxes labeled with lower-case letters in panels (**a**, **b**) give the location of detailed areas, showing the full resolution, 30-m vulnerability raster for moderate (**c–e**) and extreme (**f–h**) weather. Panels (**i**, **j**) show the total area (ha) of high-quality owl nesting and roosting habitat in each vulnerability class for moderate (**i**) and extreme (**j**) weather. The point represents the habitat area assuming the estimated threshold between low- and high-quality nesting and roosting habitat (ca. 0.41) and the interval represents the habitat area with changes to this threshold (i.e., ± 0.1)

patches occurred in the resistant – recruitment class and were larger than the nest core area size if PACs burned (Online Resource Fig. S5c, d, Table S1). Large patches of the vulnerable, not-resistant class were uncommon within PACs under moderate fire weather (0% of the study extent) but were widespread under extreme fire weather (93.3% of the study extent; Online Resource Table S1). Finally, patch shapes did not depend strongly on the definition of high-quality Mexican spotted owl habitat used, weather conditions or vulnerability classes (Online Resource Fig. S6).

Discussion

Here, we developed a novel approach to quantify the habitat vulnerability of the Mexican spotted owl, an old-forest associated species threatened by rapid changes to climate and fire regimes, across a core part of its range in the southwestern US. Our analyses demonstrated that high-severity fire was common under extreme weather conditions, and predicted fire severity increased with habitat quality for owl nesting and roosting (Fig. 1). At the same time,

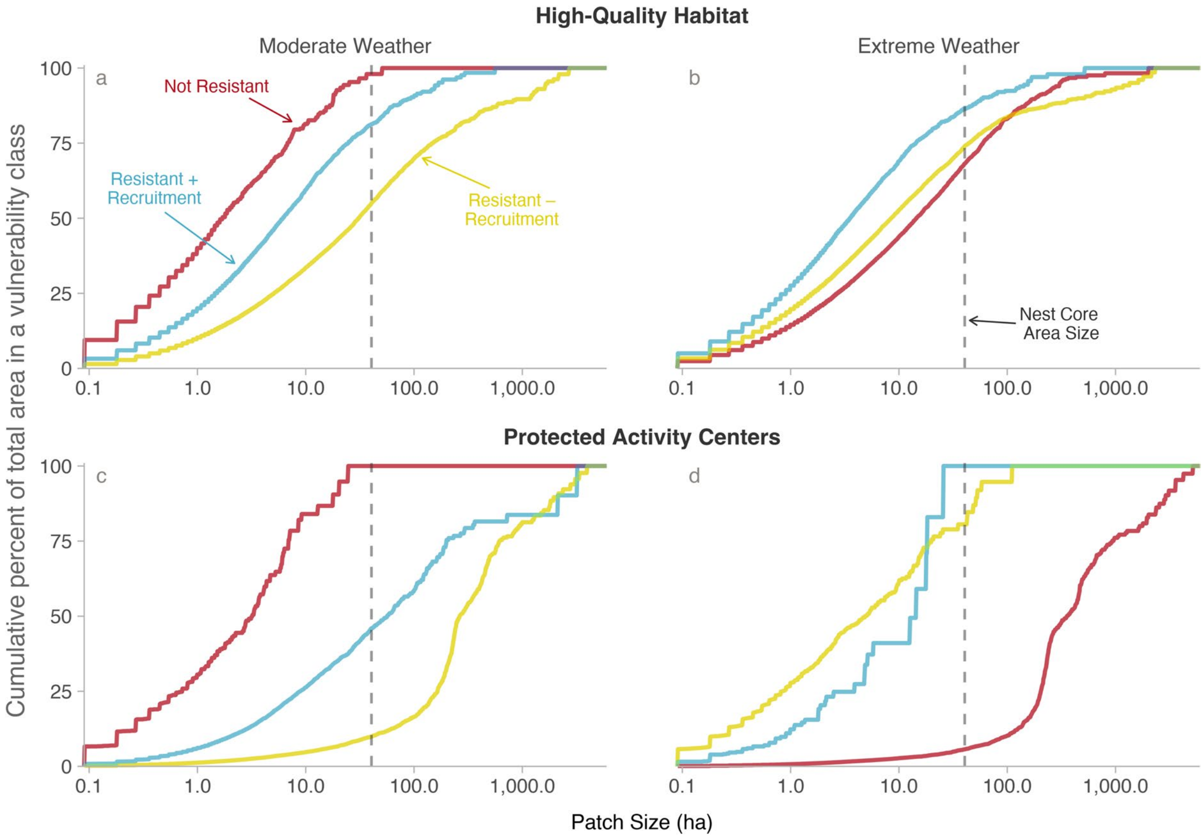

Fig. 4 Spatial patterns of Mexican spotted owl habitat vulnerability across Arizona and New Mexico forests. Lines show the cumulative frequency distribution of patch area within each vulnerability class (i.e., % of class in Online Resource Table S1) inside high-quality owl nesting and roosting habitat areas (in 2020) (**a**, **b**) and within existing protected activity centers (**c**, **d**). Panels (**a**, **c**) are based on moderate fire weather conditions, whereas panels (**b**, **d**) are based on extreme weather conditions. Under moderate conditions most area of not resistant habitat occurs in small patches, while resistant − recruitment and resistant + recruitment habitat occurs in large, contiguous patches. Under extreme conditions and especially within protected activity centers, much of the area of resistant − recruitment and resistant + recruitment habitat occurs in small patches, while relatively more area of not resistant habitat occurs in larger patches. The vertical, gray dashed line corresponds to a patch size of 40.47 ha, the nest core area size for Mexican spotted owls

the probability of tree regeneration following fire declined as owl nesting and roosting habitat quality increased (Fig. 2). Overall, these patterns indicate that low tree recruitment for existing species presented the most widespread challenge to the longer-term stability of Mexican spotted owl nesting and roosting habitat, but a lack of fire resistance may also pose a significant near-term challenge to high-quality nesting and roosting habitat under extreme fire weather (Fig. 3). Nevertheless, we also identified key areas that exhibited both resistance to fire and a high probability of tree recruitment that may serve as important refugia for Mexican spotted owl in the years ahead (Fig. 3). Moreover, these low-vulnerability areas include some patches that are large enough to be ecologically relevant for this species (Fig. 4).

Large, old trees—key features of Mexican spotted owl nesting and roosting habitat (Witt et al. 2022)—are just one example of ecologically rare features that are threatened by global change. In the face of increased warming and drought-like conditions, large trees face a disproportionate risk of drought-caused mortality (Bennett et al. 2015). The combined effects of drought and subsequent wildfire can lead to widespread forest loss (Cansler et al. 2024; Stephens et al. 2018), with mature forests being heavily impacted by such losses (Steel et al. 2023). Previous work has suggested that one of the most important factors explaining long-term

(1986–2020) declines in Mexican spotted owl nesting and roosting habitat in the southwestern US was region-wide drought-related tree mortality in the early 2000's (Jones et al. 2023). The present study extends these findings to demonstrate that Mexican spotted owl nesting and roosting habitat will be vulnerable to climate- and fire-driven forest loss in the coming decades. However, encouragingly, 8–12% of our study area appears that it may be resistant to these broader patterns of nesting and roosting habitat loss, particularly if weather conditions remain more moderate, and thus may act as climate change refugia (Keppel et al. 2012).

Will these resistant, but rare and potentially isolated, refugia provide value to Mexican spotted owl conservation? It depends. Refugia have the potential to act as holdouts and stepping-stones that can facilitate range shifts (Hannah et al. 2014) while increasing habitat connectivity, genetic diversity, and evolutionary potential (Morelli et al. 2017). Even small or isolated refugia can provide value. In recent years, conservation biologists have increasingly recognized the outsized role of 'small natural features', including large, old trees (Lindenmayer 2017), in the achievement of conservation objectives (Hunter et al. 2017). In fact, large, old trees are just one example of features that provide a disproportionate benefit to species and ecosystems and, as such, they have been called "keystone ecological structures" (Lindenmayer et al. 2014). Thus, their continued persistence in some areas will provide ecosystem benefits beyond providing habitat for Mexican spotted owls. Over time, increases in habitat fragmentation may lower population connectivity and reduce genetic diversity in Mexican spotted owls (Wan et al. 2018). Still, for Mexican spotted owls, the identification of these spatial refugia (Fig. 3) can act as cornerstones of climate change adaptation planning. More broadly, our framework offers a methodology to identify potential climate change refugia for other species and regions.

Once identified, how should these refugia be protected? Spotted owls exemplify a tension between current conservation policies and increasingly dynamic landscapes. The dominant conservation mechanism for spotted owls has been the delineation of PACs where territorial individuals are found (or were found in the recent past), which then tend to receive more limited forest management and treatment activities (e.g., prescribed fire and mechanical thinning). These "static" conservation strategies have yielded great success in maintaining species and biodiversity (Gray et al. 2016), largely by preventing the loss of habitat to extractive human land uses, e.g., timber harvest, mining, and land clearing for agriculture (Barber et al. 2014; Duncanson et al. 2023). However, the specter of climate change and altered disturbance regimes raise critical questions about the efficacy of this static strategy to conserve species or habitat refugia in a rapidly changing world. Steel et al. (2023) show that PACs for California spotted owls in the Sierra Nevada have experienced a greater decline in forest canopy cover relative to areas outside of PACs during 2011–2020, a decade of extreme drought and wildfire. Similarly, our analysis of vulnerability to wildfire inside of PACs showed a large reduction in the numbers (115 patches) and extent (17,675 ha) of low-vulnerability habitat inside of PACs under more extreme fire weather conditions. This dramatic increase in vulnerability within protected areas suggests that the status-quo reserve-based approach may not maintain sufficient habitat for species persistence in a future with more frequent and severe disturbances, occurring under historically extreme conditions. Landscapes, especially those subject to frequent disturbance regimes, vary over space and time (Shirk et al. 2023; Stoetzel et al. 2020) and resisting this fundamental property may prove counterproductive to achieving conservation and policy goals (Gaines et al. 2022; Hessburg et al. 2021; Rissman et al. 2018). Successful conservation in the face of rapid changes in climate and disturbance regime will require dynamic conservation tools.

Conservation implications

Embracing the dynamic nature of landscapes will lead to more effective conservation strategies designed to resist, accept, or direct (sensu Aplet and Cole 2010) habitat changes for old-forest species. Many portions of the Mexican spotted owl's current range in the Southwest could be vulnerable to fire-driven transformation over upcoming decades. However, simulation studies indicate that forest restoration treatments, including management inside of PACs, can slow or reverse the contraction of spotted owl distributions relative to scenarios with more passive management approaches (Jones et al. 2022; Wood et al. 2018). Such treatments, when designed in ways that retain essential Mexican spotted owl nesting and roosting habitat elements such as large and mature trees, may help to resist near-term transformation and provide time for species adaptation, dispersal or migration to newly suitable areas. Indeed, while providing critical habitat for old-forest obligate species (Lindenmayer and Laurance 2017), larger trees are also the most fire-resistant individuals in many forests, including dry forests of the US Southwest (Cansler et al. 2020; Rodman et al. 2021). Thus, large-tree retention during mechanical treatments will help to maintain longer-term forest persistence in a future with increasing fire activity.

In addition to large-tree retention, other management practices that treat surface fuels may prove effective ways of maintaining old-forest habitats. In a recent meta-analysis, Davis et al. (2024) found that mechanical thinning with prescribed burns, mechanical thinning with pile burning, and prescribed burning alone led to net reductions in subsequent fire severity across a range of forest types and fire weather conditions, potentially limiting the extent of uncharacteristically severe wildfire. The efficacy of these treatments generally declined over time with most of the benefits diminishing within the first decade after treatment (Davis et al. 2024). In addition to these active management approaches, mounting evidence indicates that passive forest management (wildfires managed for resource benefits) can reduce the overall severity of subsequent wildfires in the ponderosa pine and interior mixed conifer forests of our study area (Davis et al. 2024; Parks et al. 2014; Rodman et al. 2023; Yocom et al. 2022), and ameliorating the impacts of drought (Willson and Hurteau 2025). Our results emphasize that using prescribed fires or allowing managed wildfires to burn under moderate weather conditions may be particularly effective ways of reaping these benefits without major, negative impacts to old-forest habitats. Over time, prescribed and managed wildfires may create a landscape mosaic that reduces the extent of uncharacteristically severe fire and increases the prevalence of fire refugia, even under extreme weather conditions (Downing et al. 2021; Krawchuk et al. 2020; Meddens et al. 2018). These habitat refugia can help resist broader scale ecosystem transformation and have important benefits for animal diversity (Senior et al. 2023).

Still, some portions of Mexican spotted owl nesting and roosting habitat in the Southwest are likely to lose forest cover or experience shifts in tree species composition over upcoming decades, regardless of management intervention (Flatley and Fulé 2016; Loehman et al. 2018). The data developed in the present study may help to prioritize treatments at broad spatial scales, in areas where they can be most useful (i.e., where Mexican spotted owl nesting and roosting habitat quality is high, and where mechanical treatments and/or fire could reduce vulnerability). Should large, severe fires drive transformations of existing Mexican spotted owl nesting and roosting habitat, areas with high community-weighted recruitment probabilities may be high-priority candidates for post-fire tree planting activities, which can help to accelerate forest recovery (Rodman et al. 2024; Sorenson et al. 2025). Alternatively, areas with low or moderate predicted fire severity could serve as anchor points for treatments that target surrounding areas, effectively expanding these fire-resistant zones. Maintaining Mexican spotted owl forest habitat across the region will also require new and creative solutions to management. As some vulnerable habitat patches are likely to be lost to fire, drought, and other factors over upcoming years, identifying newly suitable habitat patches, where the prevalence of old trees is increasing, or tree species compositions are shifting towards those preferred by Mexican spotted owl, will provide opportunities for accepting or directing forest transformation to maintain wildlife habitat and biodiversity.

Conclusions

Climate change and altered disturbance regimes are modifying the environmental features upon which plants and animals depend for their survival and/or reproduction. To persist, threatened species will depend upon reserves of suitable habitat that can resist change and/or foster resilience in the face of ecological transformation. Identifying such areas is an essential first step to conserving biodiversity. Once identified, appropriate management techniques may be able to strengthen, expand, and connect habitat refugia to enhance their benefits to sensitive species. The implementation of these stewardship activities should then be complemented by periodic reassessments of habitat vulnerability as climate, disturbance and ecological transformation unfold. This adaptive process provides the best path to conserving species and their habitat, as well as the ecosystem services rendered by these natural systems to humanity.

Acknowledgements We thank Joe Ganey for sharing some of the historical background of the Mexican Spotted Owl recovery plan and Dana Reid for providing data analysis to help contextualize Mexican spotted owl use of the nest core areas.

Author contributions All authors contributed to study conception and design. Data collection, preparation, and methodology performed by JFG and KCR. JFG conducted the analysis and created the visualizations. All authors contributed to the writing of the original draft and worked collaboratively towards the final draft. All authors read and approved the final draft.

Funding The authors declare that no funds, grants, or other support were received associated with conducting this research.

Data availability Spatial data related to predicted fire severity, tree recruitment probability and current (2020) owl habitat quality, and code used to process, analyze, and visualize data in this study are available through Zenodo via the following link:https://doi.org/10.5281/zenodo.15995952. Due to ethical concerns surrounding threatened and endangered species, the point locations of Mexican spotted owl nest and roost sites, and historical owl habitat quality (1986–2019) are excluded from the online repository, but are available upon reasonable request from the corresponding author.

Declarations

Conflict of interests The authors declare no competing interests.

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