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Fuels management mitigates megafires to the benefit of old forest species

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ABSTRACT

Climate change and fire exclusion have changed disturbance regimes in forest ecosystems globally. In many seasonally dry forests, fuels management can mitigate severe wildfire behavior and create more resilient forests. Yet concern that fuels management might simplify forests and adversely impact biodiversity, particularly older forest associated species, has constrained the pace and scale of fuels management efforts. The California spotted owl (*Strix occidentalis occidentalis*), emblematic of this conundrum, will likely face local and widespread extirpation if wildfires continue to increase in size and severity. Here, we leveraged bioregional passive acoustic monitoring and a novel disturbance dataset in the Sierra Nevada, California to examine 1) the impact of disturbance legacies and fuels management on wildfire severity, 2) the effect of fuels management and wildfire severity on spotted owl occupancy across the bioregion, and 3) the net effects of fuels management on spotted owl occupancy via their direct (i.e., by altering habitat) and indirect effects (i.e., by changing fire behavior and mitigating severe fire effects). We found that the net effects of fuels management on spotted owl occupancy depended on their intensity. High-intensity fuels management (≥35 % reduction in canopy cover) resulted in net increases in spotted owl occupancy when implemented across 1–25 % of a landscape. Low-intensity management (<35 % reduction in canopy cover) resulted in net increases to spotted owl occupancy when implemented across up to 100 % of a landscape. Combining low levels of high-intensity fuels management and high levels of low-intensity fuels management in occupied owl sites—in addition to conserving existing nesting and roosting habitat—may effectively modify fire behavior and directly create habitat structures that benefit spotted owls. Our work suggests that restoring resilient forests through fuels management and conserving a vulnerable forest specialist can be viewed as complementary objectives.

1. Introduction

Disturbances can generate mosaics of characteristic patches of different ecological successional stages and, ultimately, support biodiversity (Bond and Keeley, 2005, Kelly et al., 2020). Many animal species that occur in frequently disturbed landscapes have evolved traits that allow them to survive disturbances as well as capitalize on resource pulses following natural disturbance events (Nimmo et al., 2019, Jones et al., 2023). For example, Verreaux's sifakas (*Propithecus verreauxi*) consume water-rich fruit and flowers during severe droughts, allowing them to cope with water scarcity through increased fat storage, metabolic water production, and water conservation. Black-backed woodpeckers *(Picoides arcticus)* preferentially excavate nests in standing dead trees (Seavy et al., 2012) and forage for woodboring beetle larvae near dead and dying trees (Powell, 2000). However, many fire-prone forest ecosystems across the globe are threatened by rapidly changing disturbance regimes (Senande-Rivera et al., 2022). Because of the suppression of Indigenous management (Taylor et al., 2016), many decades of fire

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exclusion (Collins et al., 2011), selective removal of large fire-resilient trees (Collins et al., 2015), fuels accumulation and compositional shifts in vegetation (Kreider et al., 2024), and increasingly warm temperatures with more variable precipitation (Abatzoglou and Williams, 2016), many forest ecosystems are now experiencing extreme drought and wildfire behavior (e.g., larger and more severe) that deviates substantially from historical ranges of variation (Stephens et al., 2018, Senande-Rivera et al., 2022, Parks et al., 2023). Animals, even those with physiological or behavioral adaptations to persist in disturbed landscapes, face extirpation as changing fire patterns rapidly alter the landscapes on which they occur (Kelly et al., 2020).

Seasonally dry forests in western North America, where mixed-severity fires historically burned every 5–20 years (Hessburg et al., 2005, Hagmann et al., 2021), have recently experienced massive drought-related tree mortality (Stephens et al., 2018) and larger, more frequent high-severity fires due to a combination of fire suppression and climate change (Hagmann et al., 2021). Wildfires are expected to continue to increase in size and severity across portions of the western US (Westerling, 2016), with important effects to wildlife. In California, for example, 100 vertebrate species experienced fire across at least 10 % of their geographic range during the 2020 and 2021 fires seasons alone (Ayars et al., 2023). In response to rapidly changing disturbance characteristics and potential threats to biodiversity and human communities (Kolden, 2020), modifying fire behavior through fuels management and redistribution has become a central management focus across the western United States. Land managers can proactively reduce fuel loads by implementing prescribed burns, mechanically thinning forests, or managing unplanned ignitions in a way that promotes forest resiliency (Agee and Skinner, 2005). Forest restoration and fuels management, including prescribed burns and fuels reduction, can reduce the spread, intensity, and severity of fires when they occur (Ager et al., 2007, Davis et al., 2024). For example, burn severity in the Rim Fire that occurred in the Sierra Nevada in 2013 was lower in previously treated areas or areas that experienced prior low-moderate severity burns (Lydersen et al., 2017). Similar results have been reported in association with the 2006 Boulder Complex Fire, the 2007 Antelope Complex Fire, the 2013 American Fire and the 2019 Walker Fire (Tubbesing et al., 2019, Low et al., 2023). By creating heterogenous structural conditions and disrupting fuel continuity, fuels management can increase the likelihood that subsequent fires will burn at lower intensities and promote forest resilience to future disturbances (Stephens et al., 2020).

The pace and extent of fuels management implementation is limited by several factors, including financial, operational, and legal constraints, as well as uncertainty about the direct impacts of fuels management strategies on wildlife habitat (North et al., 2015). There is some evidence for both positive and negative impacts of fuels management on different wildlife. For example, fuels management can create horizontal structural heterogeneity that benefits multiple species with unique life histories. In the eastern Cascades in Washington, multiple avian species of various nesting guilds responded positively to thinning followed by prescribed burning (Gaines et al., 2010). Pacific fishers (*Pekania pennanti*) can tolerate fuels management if adequate cover and large woody structures are retained (Smith et al., 2025). On the other hand, fuels management can directly decrease habitat quality for some animals. Management activities that remove trees can reduce habitat quality for arboreal northern flying squirrels (*Glaucomys sabrinus*) by hindering their movement in canopies and reducing food availability (Lehmkuhl et al., 2006). Mechanical thinning has been shown to negatively impact Pacific martens (*Martes caurina*), which rely on dense understories, by simplifying forest structure, creating barriers to movement, and reducing habitat connectivity (Moriarty et al., 2016). Fuels management alters the habitat of wildlife that depend on large, old trees, high canopy cover, and complex vertical structure (Tempel et al., 2014). Thus, promoting resilient forests while also conserving vulnerable mature forest species presents potential challenges.

While fuels management may negatively impact the habitat of some animals, especially those that rely on late-seral forest characteristics, the negative short-term consequences of fuels management may be outweighed by longer-term benefits of reducing the threat of severe-fire induced habitat loss. The spotted owl (*Strix occidentalis*), which uses mature forest structures for nesting, roosting, and often foraging (Jones et al., 2018, Zulla et al., 2022, McGinn et al., 2023a) has been the center of controversy regarding forest management and timber harvesting in fire-prone western regions for nearly five decades (Forsman, 1976, Verner et al., 1992, Gutiérrez et al., 1998, Franklin et al., 2021). In the Sierra Nevada, the California spotted owl (*S. o. occidentalis*) faces potential local and widespread extinction if fires continue to occur at their current frequency, size, and severity (Jones et al., 2016a, 2021, McGinn et al., 2025). At the same time, there is lingering uncertainty about the impact of fuels management on this closed-canopy associated species. While some work suggests that fuels management can directly promote foraging habitat for California spotted owls (Wright et al., 2023), other evidence suggests they limit nesting/roosting habitat in the absence of wildfire (Tempel et al., 2015, Hanson, 2021). A simulated study on the bioregional-effects of fuels management on future high-severity fire found that fuels management may ultimately increase spotted owl occupancy across the Sierra Nevada (Jones et al., 2022), but fuels management data in the study were hypothetical. Another study found that sites with higher proportions of more intense fuels management were less likely to be occupied by spotted owls, but the negative effects of fuels management were weaker than the negative effects of high-severity fire (Ng et al. in review). While Ng and colleagues used empirical fuels management data, they did not examine the impact of fuels management on fire and, therefore, did not examine the relative direct and indirect effects of fuels management of spotted owls. To date, we lack a comprehensive empirical study that examines the tradeoff between fuels management and conserving spotted owl habitat at a bioregional scale.

We addressed remaining uncertainty regarding this tradeoff by leveraging a bioregional passive acoustic monitoring program (Wood et al., 2019, Kelly et al., 2023) and a novel disturbance dataset spanning the Sierra Nevada (Kramer et al. in review). Our objective was to understand how fuels management directly and indirectly influenced spotted owl occupancy via its effects on modifying fire behavior as well as owl habitat. We accomplished this by developing a coupled Bayesian fire-owl modeling system. First, we modeled the effects of fuels management and disturbance legacies on fire behavior in the boundaries of the Caldor and Dixie fires: two large and severe fires that burned in 2021. Second, we modeled the direct effects of fuels management and disturbance legacies on spotted owl occupancy. Finally, we combined outputs from the first two stages to estimate the indirect effects of fuels management on spotted owl occupancy via its effects on fire behavior. In doing so, we sought to answer our central question: Are the net effects of fuels management on spotted owls positive or negative? As forests in western North America face an increasingly warmer climate and larger, uncharacteristically severe wildfires, it is important to understand the direct and indirect impacts of fuels management on at-risk wildlife to effectively balance potential tradeoffs and achieve co-benefits for conserving biodiversity and promoting resilient forests.

2. Methods

2.1. Study area

Our study areas included forestlands in the Sierra Nevada and Southern Cascade ecoregions and ranged from 226 to 3985 m in elevation. For the first objective of our study, we established a fire-only study area and examined fire characteristics within the boundaries of the Caldor and Dixie megafires, which occurred in 2021 and likely reflect the trajectory of future fire (Westerling, 2016). For the second and third objectives of our study, we established an acoustic study area and conducted passive acoustic monitoring surveys across 3,254,810 ha of foothill and montane forests in eastern California, USA from May to August 2022 (Fig. 1).

Most of our study area was comprised of forests managed by the USDA Forest Service (USFS). Some sampling areas within the boundaries of the Caldor and Dixie Fires overlapped forest managed by the National Park Service and privately owned land.

2.2. Passive acoustic monitoring

We divided our Sierra Nevada study area into 8087 400-ha hexagonal cells (Fig. 1), the approximate size of a spotted owl territory (Tempel et al., 2014). We selected non-contiguous cells for passive acoustic surveys if they did not intersect highways, were less than 50 % perennial water, and were within a walkable distance from a road over traversable topography. Cells with particularly steep topography and some wilderness areas were excluded, but these accounted for less than 5 % of possible survey cells (Kelly et al., 2023). We did not survey adjacent cells to reduce the possibility of the same individual owls being detected in multiple adjacent sampling cells (Wood et al., 2019).

Within each surveyed cell, we typically deployed two (range: 1–4) autonomous recording units, or ARUs (SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA). To maximize detection, ARUs were deployed at mid-slope and ridgetop locations with good sound propagation, in locations where roads and streams were absent (for reducing ambient noise), and secured to small-diameter trees at the height of 1.5–2 m above the ground. Individual ARUs were deployed (where possible) at least 500 m apart and at least 250 m from cell borders. If cells overlapped with a known spotted owl protected activity center (PAC; 121 ha of high-quality spotted owl habitat around historical spotted nest and roost sites), then we attempted to place at least one ARU inside the border of the PAC. Otherwise, deployments were conducted without prior knowledge of spotted owl occupancy.

ARUs were equipped with one omni-directional microphone with −25 dB sensitivity. We programmed them to record from 18:00–09:00 Pacific Daylight Time at a sample rate of 32 Hz, 16-bit resolution, and + 33 dB gain. We collected data over a ~5-week period per ARU deployment, which began in early April at the earliest and ended in early August at the latest.

2.3. Spotted owl detections

We exclusively examined acoustic data from 20:00–06:00, which constituted a "survey night" when spotted owls most often vocalize (Reid et al., 2022). We identified spotted owl vocalizations in the acoustic dataset using BirdNET, a deep neural network that automates call classification for > 6000 species (Kahl et al., 2021, Wood and Kahl, 2024). Our customized version of BirdNET was specifically tailored to classify different spotted owl vocalizations: the four-note, contact, crow bark, monkey hoot, and juvenile begging calls. The neural network analyzed acoustic data in 3-second segments and generated a confidence score ranging from 0 to 1 for each type of call in a segment. Confidence scores represent unitless expressions of the algorithm's predictive accuracy for a given classification (Kahl et al., 2021, Wood and Kahl, 2024).

We followed methods outlined in Kelly et al. (2023) to establish a threshold for confidence scores of 0.989 for all call types, which determined which of the algorithm's predictions would receive manual validation. The process is known to miss individual calls that fall below the confidence threshold, but cumulative seasonal spotted owl detection probabilities (i.e., once manually confirmed owl identifications are used as inputs for occupancy models) are close to one over the entire sampling period (Kelly et al., 2023). Thus, the effect of correct predictions excluded by our high threshold is negligible with regard to the inferences drawn from our modeling process. All potential spotted owl detections were manually validated using Raven Pro, a sound analysis

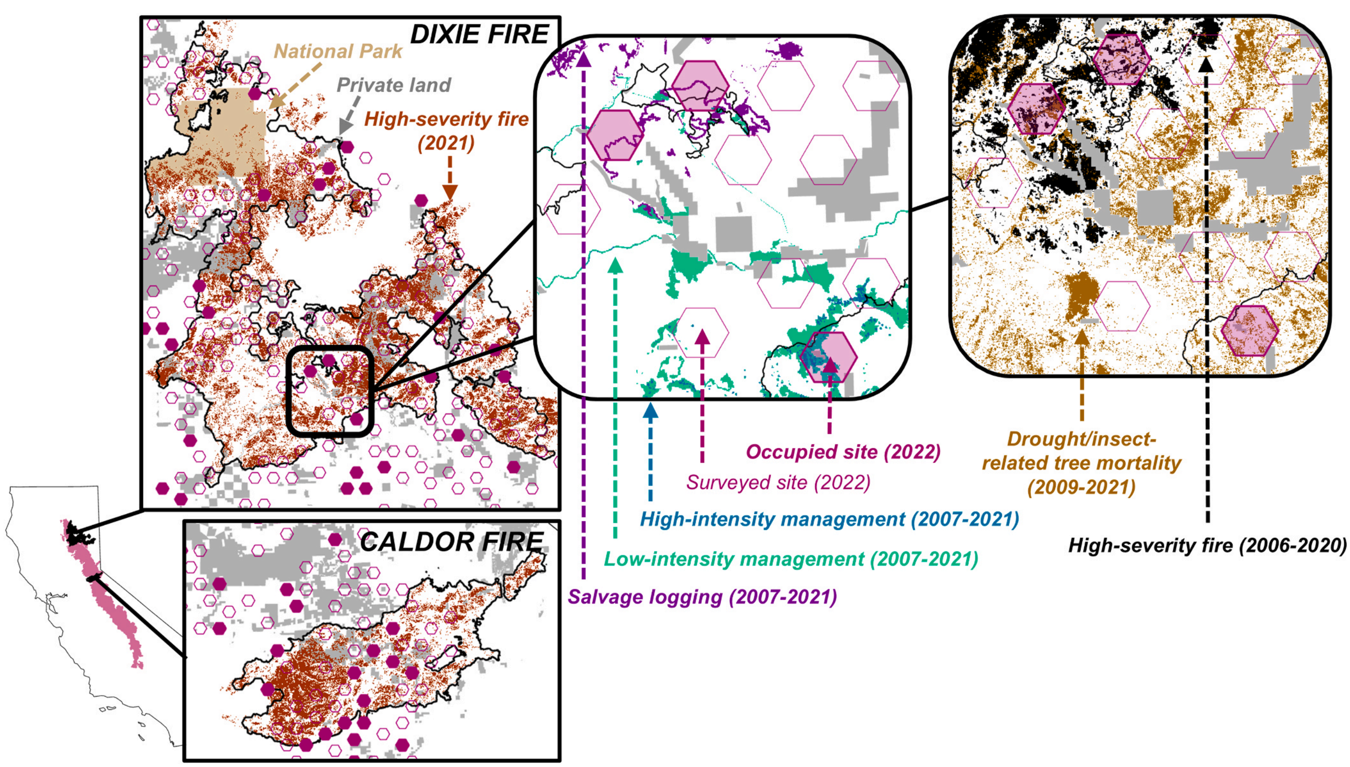

Fig. 1. Disturbance variables included in models. We estimated the proportion of disturbances within 452 ha circular landscapes (1200 m buffers) randomly placed within the boundaries of the Dixie and Caldor fires and within hexagonal survey cells (shown here) that we passively monitored using autonomous recording units. Shaded pink hexes are those occupied by spotted owls and unshaded pink hexes are those surveyed with no spotted owl detections. Note that disturbance data were obtained across different time periods for the first and second objectives of the study.

software (K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA). Manual validation is necessary to obtain accurate presence data and eliminate false-positive errors because even moderate indices of false-positives can severely bias occupancy and covariate estimates (McClintock et al., 2010, Berigan et al., 2019).

2.4. Disturbance data

To assess disturbance and management processes affecting forest structure, we used methods outlined in Kramer et al. (in review) to categorize drivers of canopy cover change across USFS-owned portions of the study area (Fig. 1). We calculated fire severity at a 30-meter resolution following Cova et al. (2023) and within fire perimeters from the California Department of Forestry and Fire Protection Fire and Resource Assessment Program (CAL FIRE FRAP), which included wildfire greater than 4 ha from both accidental human ignitions and natural ignitions. Prescribed fire was included in the forest management dataset (see below). We classified a given pixel as having experienced high severity fire effects when the composite burn index (CBI) was ≥ 2.25, which is consistent with typical severity classification strategies (Miller and Thode, 2007, Miller et al., 2009, Cova et al., 2023).

To characterize patterns in severe drought- and insect-related tree mortality, we used the Ecosystem Disturbance and Recovery Tracker (eDaRT) Mortality Magnitude Index (MMI; (Koltunov et al., 2020, Slaton et al., 2025). The eDaRT algorithm used Landsat imagery to estimate the probability that canopy cover changed at 8- or 16-day intervals at a 30 m resolution. The MMI product used eDaRT to estimate the magnitude of these disturbances on an annual time scale. Each pixel value ranged from 0 to 100, representing an estimated 0–100 % loss of canopy cover. We used MMI data to identify areas of severe drought-related tree mortality when a pixel was not within a fire perimeter or a fuels management area, as well as to characterize the intensity of fuels management (described below). Importantly, while the majority of these cases represented drought- or insect-related tree mortality, we could not rule out less common causes or mortality (such as windfall), which were included in this disturbance class. We used an MMI threshold of 12 because it visually matched a known gradient in drought mortality (Fettig et al., 2019) and provided a large enough sample size of cells with non-zero values.

We mapped fuels management activities using a modified version of the USFS Forest Activity Tracking System (FACTS), which contains spatial records of all USFS activities (USDA Forest Service 2020). We filtered entries for those specifically associated with fuels management codes, accounted for activities lacking completion data, and applied temporal buffers that captured 91 % of landscape change associated with fuels management activities. We classified these fuels management pixels as salvage (when the FACTS activity code corresponded to 3132 - Recreation Removal of hazard trees and snags, 4231 - Salvage Cut, or 4232 - Sanitation Cut), maybe salvage (when they occurred within 3 years after fire) or non-salvage fuels management (when they were an activity type other than salvage and did not occur shortly after fire). We characterized fuels management pixels that we had high confidence did not reflect salvage logging as "low-intensity" if their pixel-scale eDaRT MMI value was less than 35 (corresponding to less than 35 % canopy loss) and "high-intensity" if their MMI value was greater than or equal to 35 (corresponding to less than 35 % canopy loss). Assuming no canopy impact, prescribed fire would be represented as "low-intensity" management.

We compiled and combined annual rasters of 1) low- and high-intensity fuels management across two 15-year time frames (2006–2020 and 2007–2021), 2) high-severity fire across a 15-year time frame (2006–2020) and for the year 2021, and 3) drought- or insect-related tree mortality across 13-year spans (2008–2020 and 2009–2021). The time periods ending in 2020 contributed to the "fire model" in which the response was the proportion of high-severity fire that occurred in 2021. The time periods ending in 2021 contributed to the "owl model" in which the response was spotted owl occupancy in 2022. Although a pixel could only be assigned a single disturbance type for any given year, pixels in the composite could have experienced multiple disturbances.

For the first objective of our study (the "fire model"), we established 1000 random locations within the boundaries of both the Caldor and Dixie fires, ensuring they were at least 1200 m from the fire perimeters. The 1200 m buffer size was selected because resulting landscapes were similar in size to spotted owl territories (Tempel et al., 2014). We created 1200 m buffers around each random location and calculated the proportional area affected by each disturbance type prior to 2021. For the second and third objectives (the "owl model" and tradeoff predictions), we estimated the proportional area affected by each disturbance type prior to 2022. For both sets of analyses, we calculated the proportion of private, National Park, and USFS land. Although the MMI data covered all land ownerships, we could not differentiate between drought-related tree mortality and forest management on non-USFS managed land (see below), so we were only able to estimate drought-related tree mortality and fuels management on USFS managed land. Low- and high-intensity fuels management did not appear to be implemented non-randomly across different slope angles, aspects, and positions at the scale of our analyses; we used Pearson correlations to assess the relationship between the proportion of low- and high-intensity management and the proportion of six different landscape management units and found only very weak (± 0.02 to ± 0.15) relationships. Additionally, we found no significant differences in the proportion of any of the landscape management units between either unmanaged and managed landscapes or occupied and unoccupied landscapes (Supplemental Figure 1).

2.5. Fire model

We fit a Bayesian formulation of a binomial model to examine the relationship between previous natural and anthropogenic disturbance and the proportion of landscapes (1200 m buffered areas) burned at high severity within the boundaries of the Caldor and Dixie megafires (Fig. 2). Pixels within 1200 m buffers that burned at high severity were "successes," and pixels that did not burn at high severity were "failures." The response variable was the proportion of pixels in a buffered area that were a success. The precision of the underlying latent variable (τ) was modeled as the exponential of a normally-distributed parameter (t_0):

$$\tau = \exp(t_0),\ t_0 \sim N(0,0.5)$$

The likelihood function described the probability of observing the data given the model parameters. For each observation i, the probability of success, μ_i, was modeled as the logistic function of a linear combination of predictors:

$$\mathrm{logit}(\mu_i) = \beta_0 + \beta_1 highIntensityTx_i + \beta_2 highIntensityTx_i highIntensityTxPr_i +$$

$$\beta_3 lowIntensityTx_i + \beta_4 lowIntensityTx_i\ lowIntensityTxPr_i +$$

$$\beta_5 highSeverityFire_i + \beta_6 highSeverityFire_i highSeverityFirePr_i +$$

$$\beta_7 droughtMortality_i + \beta_8 droughtMortality_i droughtMortalityPr_i +$$

$$\beta_9 private_i + \beta_{10} nationalPark_i$$

where β_0 was the intercept and β_{1-10} were the effects of binary and continuous disturbance variables. To account for the nested nature of the data—specifically the fact that only disturbed sites could experience a non-zero continuous proportion of a particular disturbance type—we included interaction terms between "dummy" indicator variables denoting whether a site was disturbed and explanatory variables describing the proportion of the disturbance. $highIntensityTx_i$ was a binary variable indicating whether a buffered area was managed at high-

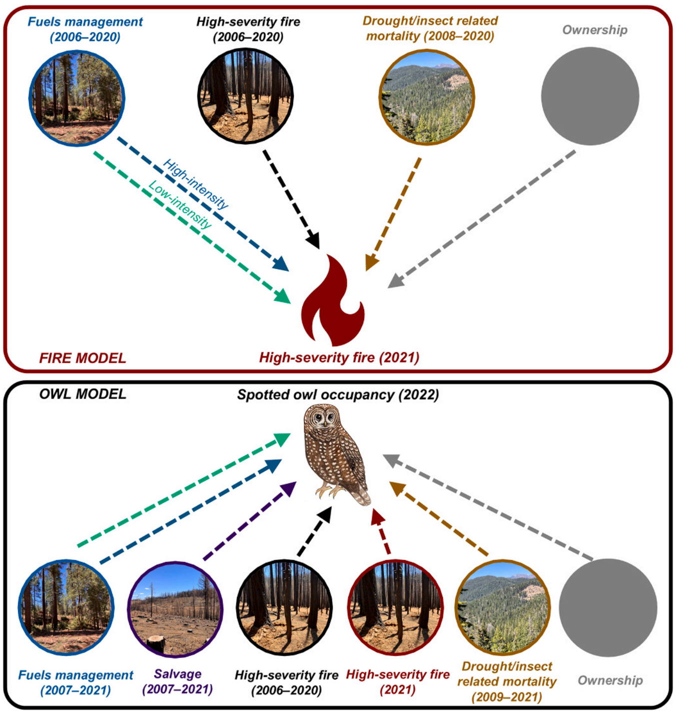

Fig. 2. Conceptual diagram of the fire and owl models. In the fire model, the response variable was the proportion of 1200 m buffers that burned at high-severity in 2021. In the owl model, the response variable was the probability of spotted owl occupancy in surveyed hexagonal cells in 2022.

intensity 2006–2020, $lowIntensityTx_i$ indicated whether a buffered area was managed at low-intensity between 2006 and 2020, $highSeverityFire_i$ indicated whether a buffered area burned at high-severity between 2006 and 2020, and $droughtMortality_i$ indicated whether a buffered area experienced drought- or insect-related tree mortality between 2008 and 2020. Variables denoted with "*Pr*" were the non-zero continuous proportions of buffered areas affected by the disturbance. $private_i$ was the proportion of privately owned land, $nationalPark_i$ was the proportion of land designated as a national park, and the proportion of USFS-managed land was the reference category. The probability μ_i was then used to define the Beta distribution parameters p_i and q_i, with:

$$p_i = \mu_i\tau$$

$$q_i = (1\text{-}\mu_i)\tau$$

The response variable y_i was assumed to follow a Beta distribution with parameters p_i and q_i, which are derived from a logistic transformation of the linear predictor, and y_i was modeled as:

$$y_i \sim \text{Beta}(p_i, q_i)$$

where y_i represents the observed outcome for the i^{th} observation, and p_i and q_i are the shape and rate parameters of the Beta distribution.

2.6. Owl model

We fit a Bayesian formulation of a single-season occupancy model to describe associations between disturbance variables and territory occupancy across the Sierra Nevada (Fig. 2). First, we modeled detection probability as a logit-linear function:

$$\text{logit}(p_i) = a_0 + \text{a}_1\text{Effort}_\text{i}$$

where a_0 was the intercept and a_1 was the effect of survey effort defined as the number of hours ARUs were recording during a secondary sampling period. We then modeled occupancy during 2022 at each territory ψ_i using the following logit-linear function:

$$\text{logit}(\psi_i) = b_0 + b_1 highIntensityTx_i + b_2 highIntensityTx_i highIntensityTxPr_{ii} +$$

$$b_3 lowIntensityTx_i + b_4 lowIntensityTx_i\ lowIntensityTxPr_i +$$

$$b_5 highSeverityFire15y_i + b_6 highSeverityFire15y_i highSeverityFire15yPr_i +$$

$$b_7 highSeverityFire1y + b_8 highSeverityFire15y_i highSeverityFire1yPr_i +$$

$$b_9 droughtMortality_i + b_{10} droughtMortality_i droughtMortalityPr_i +$$

$$b_{11} salvage_i + b_{12}\text{salvage}_\text{i} salvagePr_i +$$

$$b_{13} private_i$$

where b_0 was the intercept and $b_{1\text{–}13}$ were the effects of disturbance variables on occupancy. As above, we included interaction terms between "dummy" indicator variables denoting whether a site was disturbed and non-zero continuous variables describing the proportion of the site that experienced the disturbance. $HighIntensityTx_i$ was a binary variable indicating whether a surveyed hex was managed at high-intensity between 2007 and 2021, $lowIntensityTx_i$ indicated whether a hex was managed at low-intensity between 2007 and 2021, $highSeverityFire15y_i$ indicated whether a hex burned high-severity between 2006 and 2020, $highSeverityFire1y_i$ indicated whether a hex burned at high-severity in 2021, $droughtMortality_i$ indicated whether a hex experienced either drought- or insect-related tree mortality between 2009 and 2021, and $salvage_i$ indicated whether a hex was salvaged logged after a fire between 2007 and 2021. Variables denoted with "*Pr*" were the proportion of surveyed hexes affected by the disturbance, and $private_i$ was the proportion of privately owned land in hexes.

We fit Bayesian formulations of the "fire model" and "owl model" to the data using JAGS (Just Another Gibbs Sampler) and the package "rjags" (V4.15, Plummer, 2023) in the R statistical programming environment (V4.4.0, R Core Team, 2024). All coefficients in both models were assigned uninformative Gaussian priors with $\mu = 0$ and $\alpha = 0.5$ (Northrup and Gerber, 2018). We ran three chains of 10000 iterations, an adaptation phase of 1500, and a thin rate of 10 yielding 3000 posterior samples for each parameter across all chains. We assessed convergence using the Gelman-Rubin statistics (all values <1.1). We made inferences about parameters based on their direction, magnitude, and the degree to which the posterior distribution overlapped with zero.

2.7. Predicting fuels management tradeoff effects

The fire model and owl model in the previous sections (Fig. 2) examined the impacts of prior disturbances, including fuels management, on high-severity fire and spotted owl occupancy, respectively. We additionally sought to examine the direct and indirect impacts of high- and low- intensity fuels management on spotted owls by combining the predictions from the fire and owl models to examine tradeoff effects (Fig. 3). First, using the fitted fire model, we predicted management-dependent high-severity fire across the full range of observed values for high-intensity and low-intensity fuels management, while using full posterior distributions and mean covariate values for all other model terms. Second, we substituted the predicted management-dependent high-severity fire into the owl model as the high-severity fire (1-year prior to acoustic surveys) covariate value, predicting spotted owl occupancy across the full range of observed values for high-intensity and low-intensity fuels management. In this second step, we similarly used the mean covariate values for all other model terms, including high-severity fire 2–16 years prior to acoustic surveys. Finally, we predicted management-dependent high-severity fire and spotted owl occupancy across the full range of observed values for high-intensity and low-intensity fuels management. In this step, we used combinations of different covariate values for high-and low-intensity fuels management, adding up to no more than 1, and used the mean covariate values for no-

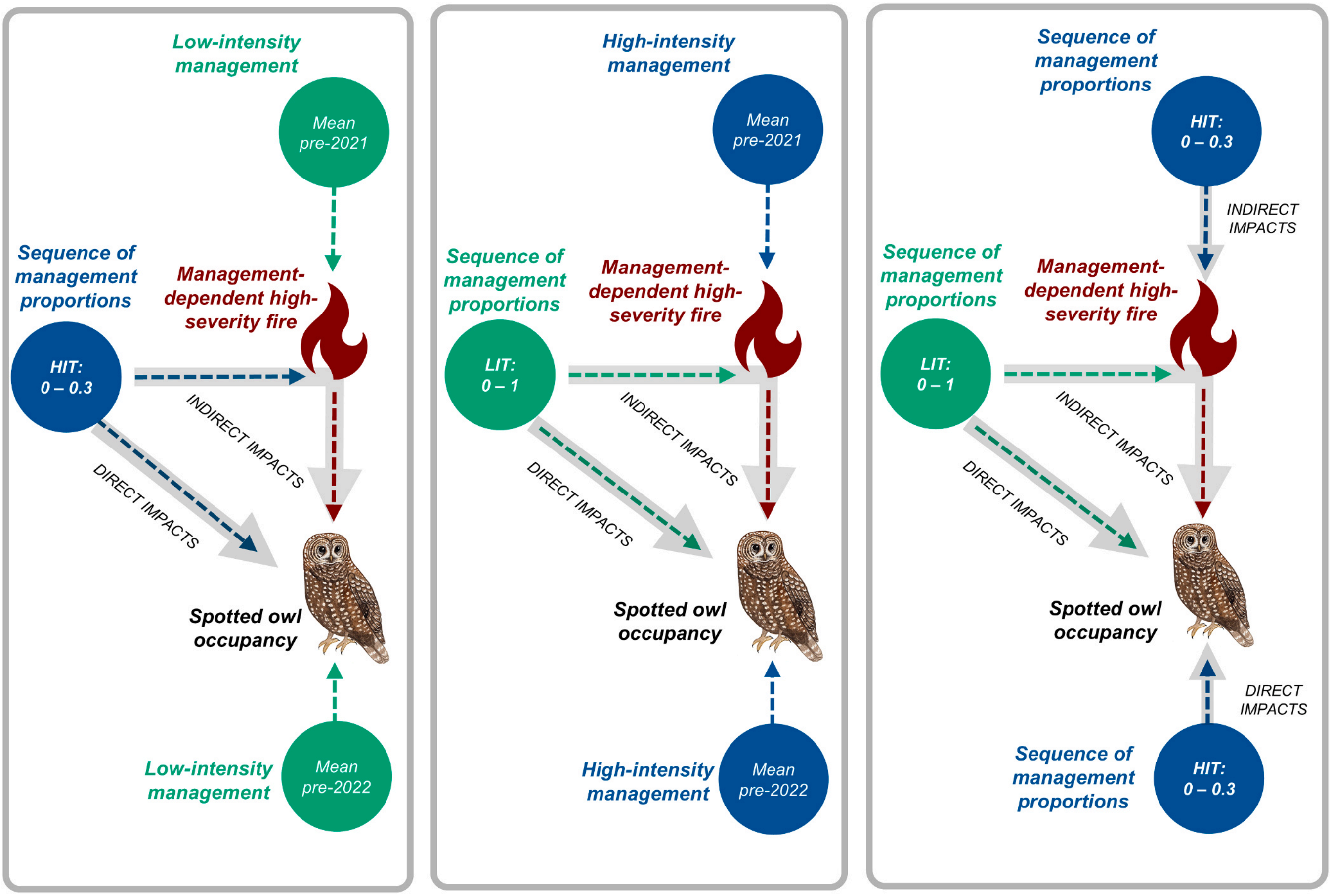

Fig. 3. Conceptual diagram of tradeoff effects. We predicted spotted owl occupancy based on a sequence of high- and low-intensity fuels management proportions. First, we predicted the proportion of high-severity fire in surveyed hexes using our fire model. All other variables in the model other than the target fuels management intensity were held constant. We then predicted spotted owl occupancy using our owl model based on the sequence of fuels management proportions and management-dependent high-severity fire. All covariates other than the target fuels management intensities and high-severity fire one year prior to surveys (management-dependent high-severity fire) were held constant.

management model terms. For all steps in this section, we predicted management-dependent high-severity fire and spotted owl occupancy using the full posterior distributions of all coefficients in the "fire model" and "owl model".

3. Results

3.1. Prior disturbance impacts on fire severity

Most (1661) of the 2000 buffered sites within the boundaries of the Caldor and Dixie Fires did not experience severe fire within the last 15 years, but the maximum proportion of a site burned at high severity was nearly 1.0. Contrastingly, 1905 of the 2000 sites experienced some drought- or insect-related tree mortality, though the maximum proportion of a site impacted by drought- or insect- related mortality was 0.50. Low-intensity fuels management was more prevalent (1442 sites, mean = 0.13) within the boundaries of the fires than high-intensity fuels management (1182 sites, mean = 0.02) and salvage logging (315, mean = 0.01). The maximum proportion of a site managed at low-intensity was 1.00, the maximum proportion managed at high-intensity was 0.25, and the maximum proportion of a site that was salvaged logged was 0.76.

Buffered sites within the boundaries of the Caldor and Dixie megafires with higher proportions of privately owned land experienced more high-severity fire than sites with more USFS managed land ($\beta_9 = 0.34$, 95 % Bayesian credible interval [0.15, 0.54]). Sites with higher proportions of land managed by the National Park Service experienced less high-severity fire in 2021 than sites with more privately owned land or sites with more land managed by the USFS ($\beta_{10} = -0.86$, [-1.43, -0.33]). Sites with higher proportions of high-intensity fuels management implemented 1–15 years prior to the 2021 fire season experienced less high severity fire in 2021 than sites with lower proportions of high-intensity fuels management (Fig. 4; $\beta_2 = -5.71$, [-7.02, -4.40]); posterior densities did not overlap zero, indicating there was nearly a 100 % chance that sites with more high-intensity fuels management experienced less high-severity fire. Sites with higher proportions of low-intensity fuels management implemented 1–15 years prior to the 2021 fire season experienced more high-severity fire in 2021 than sites with lower proportions of low-intensity fuels management (Fig. 4; $\beta_4 = 0.33$, [0.08, 0.58]). Additionally, sites with more drought- or insect-related tree mortality experienced more high-severity fire in 2021 than sites with less drought- or insect-related tree mortality ($\beta_8 = 4.13$, [3.66, 4.59]). The posterior densities indicated there was a 99 % chance that sites with more low-intensity fuels management experienced more high-severity fire and nearly a 100 % chance that sites with more drought- or insect-related tree mortality experienced more high-severity fire. Sites with higher proportions of forest burned at high-severity 1–15 years prior to the 2021 fire season tended to experience less high-severity fire in 2021 (Fig. 4; $\beta_6 = -0.16$, [-0.58, 0.28]. However, the 95 % Bayesian credible interval overlapped zero, and the posterior density indicated there was a 78 % chance that sites with higher proportions of previous high-severity fire experienced less high-severity fire in 2021.

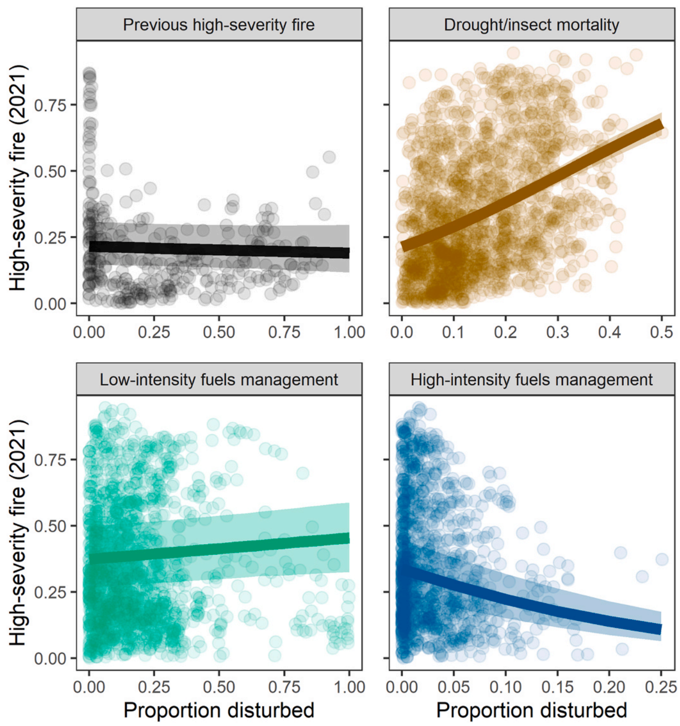

Fig. 4. Predicted proportion of high-severity fire in 1200 m buffers around random points within the boundaries of the Caldor and Dixie fires. Points indicate raw estimates of disturbance proportions within each buffered area, lines indicate the predicted relationship between prior disturbances and high-severity fire in 2021, and the transparent shading around lines indicate 95 % credible intervals. Fire and management disturbance variables were obtained from 2006 to 2020 and drought- or insect-related mortality was obtained from 2008 to 2020.

3.2. Disturbance impacts on spotted owl occupancy

Spotted owls were less likely to occupy cells that experienced more high-severity fire the year prior and 2–16 years prior to passive acoustic surveys than cells with more unburned or less severely burned forest (Fig. 5; $b_8 = -1.62$, [-2.86, -0.46]; $b_6 = -2.54$, [-3.62, -1.51]). Spotted owls were more likely to occupy cells that experienced more drought- or insect-related tree mortality (Fig. 5; $b_{10} = 3.21$, [2.12, 4.25]). Posterior densities indicated there was a near 100 % chance that spotted owl occupancy decreased with the proportion of high-severity fire and increased with the proportion of drought- or insect- related tree mortality. Spotted owls tended to be more likely to occupy cells with more low-intensity fuels management (Fig. 5; $b_4 = 0.18$, [-0.95, 1.76]) but less likely to occupy cells with more high-intensity fuels management (Fig. 5; $b_2 = -1.29$, [-3.87, 1.19]). Posterior densities indicated there was a 84 % chance that spotted owls were less likely to occupy cells with more high-intensity fuels management and a 64 % chance they were more likely to occupy cells with more low-intensity fuels management. There was no detectable relationship between spotted owl occupancy and the proportion of sites that were salvage logged (Fig. 5; $b_{12} = -0.05$, [-2.41, 2.18]).

3.3. Direct and indirect impacts of fuels management on spotted owl occupancy

Predicted spotted owl occupancy increased with the proportion of high-intensity fuels management until about 17 % of a cell was “fuels managed” at high-intensity. As the percentage of high-intensity fuels management continued to increase to 25 % (the maximum percentage of a landscape fuels managed within the boundaries of the Caldor and Dixie fires), predicted spotted owl occupancy began decreasing from its peak but remained higher than expected if no management occurred (Fig. 6). On the other hand, spotted owl occupancy increased continuously with the proportion of low-intensity fuels management in a cell (Fig. 6). Predicted spotted owl occupancy was highest (0.31) when 83 % of a cell was managed at low-intensity and 17 % of a territory was managed at high-intensity. Predicted occupancy was lowest when 0 % of the cell was

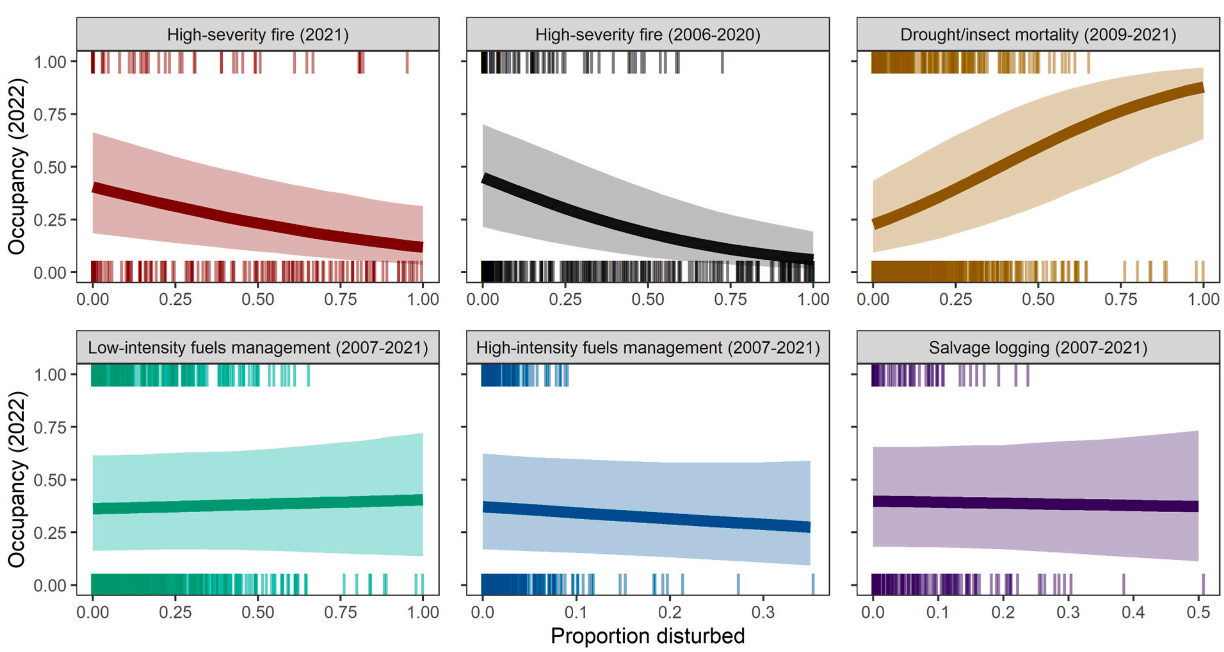

Fig. 5. Predicted spotted owl occupancy across disturbed landscapes. Small vertical tick marks indicate naive occupancy in passively monitored sites across the Sierra Nevada, where the marks at the top indicate sites where there was at least one detection, and marks at the bottom indicate sites where there were no detections. Lines indicate the predicted relationship between disturbance variables and spotted owl occupancy in 2022, and shading indicates 95 % credible intervals. We predicted spotted owl occupancy across the range of disturbance proportions represented in our dataset.

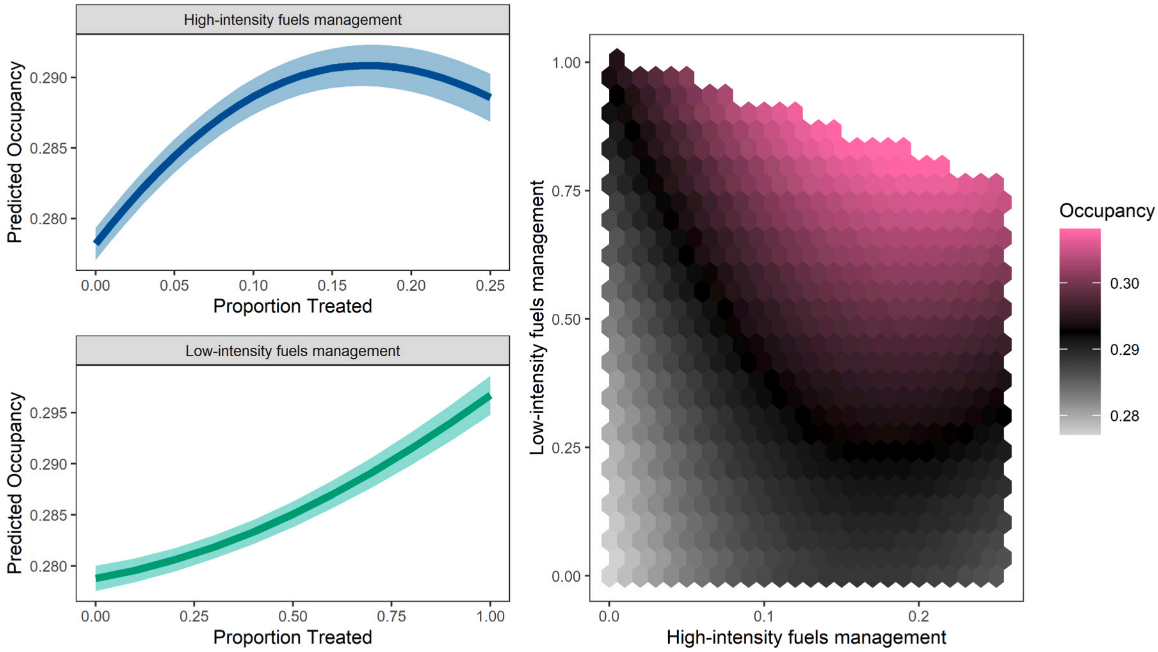

Fig. 6. Predicted occupancy under variable fuels management scenarios. In the left panels, we predicted occupancy across a range of fuels management scenarios while holding the "non-target" fuels management intensity and other disturbance variables constant at their mean values. Lines indicate the mean predicted spotted owl occupancy, and shading indicates one standard error around the mean. In the right panel, we predicted occupancy across a range of fuels management scenarios while holding "unmanaged" disturbance variables constant at their mean values.

managed at either intensity.

4. Discussion

4.1. Summary of results

Disturbance regimes are rapidly changing across the globe. In the seasonally dry forests of western North America, pyrodiverse fires historically burned with relatively high frequency (Hagmann et al., 2021). Following decades of fire exclusion and climate change, megafires now threaten the persistence of multiple wildlife species (Ayars et al., 2023), including the spotted owl (Jones et al., 2016a, 2021). Fuels management is the main adaptation strategy to modify fire behavior (Fulé et al. 2012, Hessburg et al., 2015). Fuels management that significantly alters canopy characteristics may have negative consequences for forest animals that rely on late-seral forest characteristics (Lehmkuhl et al., 2006, Moriarty et al., 2016). However, we found that fuels management can directly and indirectly increase California spotted owl occupancy in the Sierra Nevada. Landscapes with more high-intensity management which reduced canopy cover by at least 35 % experienced less high-severity fire in 2021, and thus high-intensity fuels management appeared to indirectly benefit spotted owls where up to 25 % of landscapes were managed. Landscapes with more low-intensity fuels management which reduced canopy cover by less than 35 % but which did not experience wildfire were more likely to be occupied by spotted owls, suggesting that low-intensity fuels management directly benefits spotted owls in the absence of fire. Therefore, if managers seek to conserve spotted owls in the Sierra Nevada, fuels management, including prescribed fire, constitutes an important component of any management strategy.

4.2. Forest management and disturbance legacies alter fire characteristics

We found that landscapes which experienced more drought- and insect-related tree mortality over the 13 years prior to the 2021 fire season experienced more high-severity fire within megafire footprints. Disturbances result in physical and biological legacies that influence the rate and trajectory of post-disturbance recovery and resilience to future disturbance (Pickett and White, 1985, Turner et al., 1993). For example, expansive tree mortality across the Sierra Nevada results from acute drought and fire exclusion, and the accumulation of dry, combustible woody fuel will likely contribute to uncharacteristically large, severe fires in the future (Stephens et al., 2018), where pre-fire drought increases post-fire tree mortality (Cansler et al., 2024). These predominantly severe wildfires can exaggerate the severity of subsequent disturbance events like bark beetle outbreaks, while mixed-severity fires can dampen and ultimately delay subsequent disturbance events (Seidl et al., 2016). As the climate continues to warm and precipitation events become more variable, individual disturbances—and interactions among disturbances—can combine to degrade ecosystem resilience (Johnstone et al., 2016). These feedback loops among disturbance legacies can have disproportionate effects on individuals, species, and communities, and contribute to ecological state shifts or novel ecosystems (Turner and Seidl, 2023).

While landscapes with more drought- and insect-related tree mortality experienced more high-severity fire, landscapes that burned at high-severity 1–15 years prior to the 2021 fire season tended to experience less high-severity fire in 2021. This result conflicts with previous work finding that forests that burn at high-severity in fuels limited systems are often more susceptible to burning at high intensity in the future (van Wagtendonk et al., 2012, Harris and Taylor, 2017, Povak et al., 2020). In the Sierra Nevada, moderate- to high-severity fires lead to an increase in standing snags and shrub vegetation, which interact with severe fire weather to increase the spread of higher-severity fires in subsequent burns (Coppoletta et al., 2016). Vegetation that persists after a high-severity fire, including species that are fire-adapted, can become more flammable after a severe fire. Prior work in the Sierra Nevada found that the length of time elapsed for fuels to accumulate contributes to the severity of subsequent fires; the dampening effects of previous fires on subsequent fire severity lasted up to 17 years (Collins et al., 2007). Our work supports this timeframe, though we did not explicitly test time-since-fire and instead binned fires that occurred 1–15 years prior, assuming a linear relationship across time to describe what is likely a non-linear process. In fuels-limited systems like the dry, mixed-conifer forests of the Sierra Nevada, fuels in the form of understory vegetation and felled snags may require more than 15 years to accumulate after a high-severity fire burns through fuel loads. After at least 15 years of fuels accumulation, sites previously burned at high-severity may be more likely to burn at high-severity once more.

Landscapes with more high-intensity fuels management experienced less high-severity fire. Fuels management that includes the full removal of surface and ladder fuels in dry mixed conifer forests can effectively reduce fire severity and canopy tree mortality by preventing crown fires (Safford et al., 2012). On the other hand, we found that landscapes with more low-intensity fuels management tended to experience more high-severity fire. This result contradicted our expectations, but several considerations may help explain it. First, USFS fuel management work tends to occur in a contiguous area of mixed management intensity; reductions in canopy cover vary across the managed area. Therefore, sites with a greater proportion of the area managed at low intensity would have lower amounts of high intensity fuels management. The observed relationship between low-intensity fuels management and high-severity fire could be more indicative of the importance of higher-intensity fuels management in moderating fire behavior. The effects of this tradeoff may be particularly acute in the high-risk areas where the USFS typically prioritizes fuels management work. Lighter treatments may not be sufficient to reduce severity in these sites, especially after a fire has reached some threshold of intensity. Second, forested areas that experience thinning without follow-up prescribed fire or biomass removal can be hazardous due to an increase in forest floor residues, which, when ignited by wildfire, result in high-severity burns (Weston et al., 2022). However, most of the landscapes in our study where low-intensity fuels management were implemented presumably had follow-up prescribed fire that removed residue. Untreated slash piles may increase subsequent fire severity, but in many cases slash is either piled or chipped and scattered. One major limitation in this study is that we lumped many different management scenarios under a single “low intensity” category. While we found a positive relationship between low intensity fuels management and high severity fire, the relationship was weak; any small increases to high-severity fire did not incur an ultimate cost to spotted owls. This suggests that the effect of low intensity fuels management we found on high-severity fire may be indicative of other dynamics and not be ecologically meaningful.

4.3. Effects of forest management and disturbance on spotted owl occupancy

Large high-severity burns have been shown to limit the distribution of spotted owls in California for multiple decades (Jones et al., 2016a, 2021, McGinn et al., 2025) by reducing the availability of nesting and roosting habitat (Stephens et al., 2016, Jones et al., 2021) and increasing energetic expenditure associated with foraging (McGinn et al., 2024). Our work provides further empirical evidence that uncharacteristically severe wildfires pose an existential threat to spotted owls in California. Megafires burn large areas at high-severity where fire-related tree mortality occurs in a simple, contiguous configuration. The subsequent loss of disturbance-driven spatial heterogeneity can lead to energetic consequences for spotted owls through both a loss of foraging opportunities and increased exposure to stressful ambient temperature (McGinn et al., 2023b, 2024) and ultimately limit the distribution of the species (McGinn et al., 2025).

The 2012–2016 California drought was potentially the most extreme in the last 1000 yr (Robeson, 2015, Fettig et al., 2019), and had major consequence for wildlife in the Sierra Nevada (Roberts et al., 2019). However, we found that spotted owls were more likely to occur in landscapes with a greater area of drought- or insect-related tree mortality. Other vulnerable forest species have also shown resilience to extreme drought. Fishers (*Pekania pennanti*) in the Sierra Nevada have exhibited high plasticity in their diet and shown resilience to rapid environmental change due to drought-related tree mortality by retaining atypical diet items like fungi (Smith et al., 2022). Beyond having a diet that buffers fitness costs of disturbance, spotted owls may directly benefit from drought- or insect- related tree mortality. Tree mortality can increase understory cover by creating openings in the canopy to allow more sunlight to reach the forest floor and increase the growth of shade-intolerant understory vegetation (Facciano et al., 2023). Dusky-footed woodrats (*Neotoma fuscipes*), which dominate spotted owl diets at lower elevations (Hobart et al., 2019), are more likely to occur in forests with higher understory cover and dead and down debris (Kuntze et al., 2025). Notably, at the scale of a spotted owl home range, drought- and insect- related tree mortality occurs in a complex configuration. If drought- or insect-related tree mortality indeed creates foraging opportunities for spotted owls, then the natural configuration of these disturbance processes may improve the juxtaposition of nesting/roosting habitat and foraging habitat for spotted owls (Jones et al., 2025b). Thus, tree mortality at a small scale may create forest heterogeneity that improves spotted owl foraging success (Zulla et al., 2022). Tree mortality at a large scale, however, may pose either a direct or indirect threat to spotted owls as temperatures continue to warm. Closed canopies shield individuals from stressful ambient temperatures, and a loss of such refugia may result in territory extinctions as temperatures continue to warm (McGinn et al., 2023b). Additionally, landscapes that experience drought- and insect-related tree mortality are more vulnerable to burning at high-severity and becoming unsuitable for spotted owls.

The impact of human-driven landcover changes on spotted owl occupancy depended on their timing and intensity. Spotted owl occupancy was insensitive to salvage logging. Prior research has found that post-fire salvage logging can locally reduce habitat quality and exacerbate the negative effects of high-severity fire for northern (*S. o. caurina*) and California spotted owls (Clark et al., 2013, Lee et al., 2013, Jones et al., 2020), and many other avian species respond negatively to salvage logging (Fogg et al., 2022). At a bioregional scale in the Sierra Nevada, however, the probability of spotted owls occurring in severely burned landscapes may be so low that post-fire salvage logging operations have no apparent significant effect. Alternatively, the full effects of salvage logging on spotted owls in the Sierra Nevada may take longer than 1–15 years to become apparent. While spotted owl territories remain unoccupied for multiple decades after a high-severity fire (McGinn et al., 2025, McGinn et al. in Review), they may eventually recolonize burned habitat. Salvage logging and subsequent replanting can damage seedlings or saplings, interfere with vegetation recovery, help invasive species establish, and lead to slower forest regeneration (Titus, 2009, Lindenmayer et al., 2012). While we found no evidence that salvage logging negatively impacted spotted owl occupancy within a 15-year period, salvage logging may prolong the negative consequences of high-severity fire and ultimately limit the distribution of spotted owls. Other evidence suggests that salvage logging does not have a ubiquitous detrimental effect on tree regeneration (Leverkus et al., 2020), and that salvage logging can reduce subsequent fire severity by removing heavy fuels or promote regrowth of some vegetation species (Royo et al., 2016). Future work should investigate the long-term impacts of salvage logging on forest regeneration and subsequent recolonization rates of spotted owls.

Low-intensity fuels management tended to directly benefit spotted owls, likely by creating foraging habitat. Small mammal biomass across landscapes can increase after fuels management treatments are implemented (Converse et al., 2006). In a simulated study conducted across the Sierra Nevada, accelerated forest management resulted in a higher abundance of woodrat habitat (Jones et al., 2025b). Typical woodrat habitat, comprised of “brushy” conditions (Kuntze et al., 2023), initially decrease following mechanical fuels management but increase and exceed original levels 8-years post-treatment (Vaillant et al., 2015). Sparsely treed forests and early-seral forests with smaller trees also comprise woodrat habitat (Kuntze et al., 2023), and these conditions may be created by clearing forest understories, piling wood, and creating small gaps in forest canopies that reset forest succession. On the other hand, spotted owls in our study tended to avoid landscapes that experienced more high-intensity management, which corroborates other studies that suggest there are some negative consequences of higher-intensity fuels management for the species (Ng et al. in review). The loss of high-quality nesting and roosting habitat may outweigh the benefits of structural heterogeneity introduced by fuels management if treatments are both intense and implemented across large areas (i.e. more than 100 ha). Alternatively, spotted owls may be more likely to occur in the same sites where managers implement low-intensity treatments. If that is the case, we found no evidence that low-intensity fuels management negatively impacts the occurrence of spotted owls

5. Management implications

While fuels management strategies could reduce the loss of forests and increase ecosystem resilience (North et al., 2021, Jones et al., 2022), there is considerable concern that fuels management activities could also reduce habitat for vulnerable species like the spotted owl (Jones et al., 2016b, Hanson, 2021, McGinn et al., 2023a). Landscapes with more high-intensity fuels management can be less suitable for spotted owls than untreated landscapes (Ng in Review), likely due to a loss of contiguous canopies that comprise high-quality nesting and roosting habitat (McGinn et al., 2023a). However, there is increasing evidence that fuels management may mutually create resilient forests and promote spotted owl conservation by preventing large, high-severity fires (Jones et al., 2022), creating foraging habitat (Wright et al., 2023), and improving the spatial juxtaposition of nesting/roosting and foraging habitat (Jones et al., 2025b). Our results provide strong empirical support for this hypothesis; when 0–25 % of a landscape was managed at high-intensity, the apparent negative effects of reducing canopy cover were outweighed by the benefits of reducing high-severity fire. We found that predicted occupancy was highest for sites where 17 % of the area was managed at high-intensity and the rest of the area was managed at low-intensity. A prerequisite for spotted owl occupancy is access to suitable nesting and roosting habitat (forests with closed canopies and tall, trees that support stable microclimates), especially as temperatures continue to rise (McGinn et al., 2023a, 2023b). Our results suggest that combining low levels of high-intensity fuels management and high levels of low-intensity fuels management—in addition to conserving existing nesting and roosting habitat—in occupied owl sites may effectively modify fire behavior and directly create habitat structures that benefit spotted owls. Management efforts are often under logistic constraints, in which case prioritizing strategic implementation of high-intensity fuels management in small patches (<100 ha) may be most cost effective. Other forest carnivores also appear to ultimately benefit from fuels management; a simulated study conducted in the Sierra Nevada found that the negative effects of fuels management on fisher population size were outweighed by the positive effects of reducing high-severity fire (Scheller et al., 2011, Jones et al., 2025a). Additional high-intensity fuels management outside of sites occupied by spotted owls and other forest specialists may further reduce the risk of high severity fire to the landscape as a whole.

6. Conclusions

Disturbance regimes in western North America are rapidly changing, and disturbance legacies on landscapes can exaggerate these changes. Future work should consider the indirect impacts other disturbance processes can have on wildlife, especially considering the influence disturbance legacies can have on one another. Our work demonstrates that anthropogenic disturbance through fuels management can directly and indirectly benefit spotted owls. Spotted owls serve as a surrogate species for at least 13 other avian species (Brunk et al., 2025); management aimed at conserving spotted owls will likely have implications for other wildlife. Many other forest species face the threat of increasingly large and severe wildfires. For example, fishers have experienced rapid declines in habitat across the southern Sierra Nevada following multiple large, predominately high-severity fires (Hart et al., 2025), and simulation work suggests that without management intervention, the species will be locally extirpated within 75 years (Jones et al., 2025a). Forest-dependent northern goshawks (*Accipiter gentilis*) also respond negatively to high-severity fire due to a loss of foraging and roosting habitat (Blakey et al., 2020). Like spotted owls in the Sierra Nevada, these forest specialists may directly benefit from horizontal forest heterogeneity created by fuels management and indirectly benefit from a reduction in the proportion of high-severity fire when wildfires do occur. Fuels management and the conservation of forest specialists are not necessarily at odds with one another. The climate is projected to continue to warm, and disturbance regimes are expected to increasingly deviate from historical patterns (Westerling, 2016). Land managers that seek to restore forest resilience through management interventions in vulnerable ecosystems can simultaneously conserve sensitive wildlife of concern by cautious implementing of targeted fuels management across relatively small proportions of landscapes.

CRediT authorship contribution statement

Gavin M. Jones: Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Kate McGinn:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sheila A. Whitmore:** Writing – review & editing, Resources, Project administration, Data curation. **H. Anu Kramer:** Writing – review & editing, Resources, Project administration, Methodology, Data curation. **Jason M. Winiarski:** Writing – review & editing, Resources, Project administration, Data curation. **Connor M. Wood:** Writing – review & editing, Software, Resources, Methodology, Funding acquisition, Data curation. **Elizabeth Ming-Yue Ng:** Writing – review & editing, Methodology, Data curation. **Craig Thompson:** Writing – review & editing, Resources, Funding acquisition. **Sarah C. Sawyer:** Writing – review & editing, Resources, Funding acquisition. **Peery M. Zachariah:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123316.

Data availability

Data will be made available on request.

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