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RESEARCH ARTICLE

Energetics explain predator occurrence and movement in pyrodiverse landscapes

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Abstract

Context Fire-adapted species have evolved to exploit resources in heterogenous landscapes that presumably maximize energy acquisition and minimize energetic expenditure. However, limited empirical work exists demonstrating the explicit energetic mechanisms that drive such adaptive responses to fire across diverse landscapes.

Objectives The California spotted owl (*Strix occidentalis occidentalis*) appears to benefit from landscape heterogeneity and preferentially uses smaller patches of severely burned forest, a behavior that has been hypothesized as adaptive. Here, we investigate empirical support for this hypothesis.

Methods We leveraged high-resolution GPS tracking and nest video monitoring to examine the hunting success, movement, and nest provisioning of 34 spotted owls in the Sierra Nevada and San Bernardino Mountains, California across burned and unburned landscapes.

Results Regardless of time since fire, individuals avoided foraging directly within moderately or severely burned patches. 1 to 2 years post-fire, individuals had more success capturing prey in unburned forest, and the energy individuals spent moving increased with the proportion of high-severity fire and decreased with the proportion unburned forest. Multiple years after a fire, individuals had more success capturing prey, spent less energy moving, and provisioned more energy to nests in landscapes with more low-severity fire.

Conclusions These results support the hypothesis that spotted owls are adapted to fire-prone landscapes and that disturbance events within this region's natural range of variation can ultimately promote hunting and provisioning. As fires deviate from regional norms across the globe, the negative impacts of fire may become more extreme and long-term benefits of fire may degrade for animals in fire-prone landscapes.

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Examining the mechanistic impacts of disturbance can allow us to better understand animal responses to rapidly changing landscapes.

Keywords Behavior · Fire · Movement · Predator · Pyrodiversity · Spotted owl

Introduction

Animals spend energy to obtain energy, and theory suggests that natural selection should favor behaviors that maximize energetic input for output (Pyke 1984). The balance between energetic acquisition and expenditure drives an individual's ability to survive and reproduce (Brown et al. 2004) and determines the extent of a species' range (Anderson and Jetz 2005). The structure and composition of landscapes can influence an individual's energetic expenditure by creating physical barriers, opening movement corridors, and altering the surface over which they move (Huey 1991; Dugger et al. 2014; Martin et al. 2020). Landscape heterogeneity can benefit mobile species through the juxtaposition of diverse habitat types suitable for different life history events, thus maximizing energetic acquisition for energetic expenditure (Dunning et al. 1992; Pope et al. 2000; Turner and Gardner 2015). For breeding individuals that must provision growing offspring, tradeoffs between the energetic costs of movement and access to food are particularly precarious (Zulla et al. 2023).

Landscape disturbances can shape tradeoffs between energetic expenditure associated with movement and resource acquisition. Disturbance processes like fire create and maintain heterogeneity in forest ecosystems (Turner et al. 1994), which can make energetic resources more accessible to animals (Nimmo et al. 2014). Pyrodiversity is a measure of habitat variation in a post-fire landscape (Jones and Tingley 2022). Greater heterogeneity in fire age, size, and severity can support greater biodiversity (Tingley et al. 2016) and the ecology of different species (Stillman et al. 2019; Kramer et al. 2021b). For example, some aerial insectivores and cavity nesting birds take advantage of burned patches and standing dead trees, which provide important movement corridors and nesting opportunities, but require standing green forest for foraging opportunities and juvenile survival (Kotliar et al. 2008; Latif et al. 2016; Stillman et al. 2023). In addition to supporting species' access to energetic resources, disturbance processes can impact the physical structure of the landscape over which animals move to acquire energetic resources. Fires can eliminate structural obstacles to movement and facilitate an individual's ability to detect and successfully obtain food, but changes to the availability of energetic resources are ephemeral and vary across species (Doherty et al. 2022). The benefits of fire to animals can also explicitly depend on time; as forests move from earlier to later seral stages after a fire, higher pyrodiversity begets avian species richness (Tingley et al. 2016). Thus, disturbance events like forest fires, especially after multiple years of post-fire vegetation regeneration, can create foraging habitat, make energetic resources more accessible, and minimize the energy an individual expends to obtain food.

Fires typical for a region's climate can create foraging opportunities and optimize movements for fire-adapted animals, which have evolved traits that facilitate their survival in burned landscapes (Jones et al. 2023). However, the widespread disruption of natural fire regimes—resulting from the prohibition of Indigenous land stewardship, suppression of natural fire disturbance, forest management over the past 150 years, and climate change (Westerling 2006, 2016; Taylor et al. 2016)—may threaten the ability of fire-adapted species to acquire sufficient energy to survive and reproduce (Jones et al. 2023). In drier climates, specifically in western North America, fires are creating larger and more severely burned areas where forests are converted to expansive early-seral environments, which regenerate more slowly than areas burned at lower severities (Westerling 2016; Hemes et al. 2023). These "megafires" create large areas of severely burned forest, spatially separate less severely burned patches, and reduce variation in forest structure (Steel et al. 2018). Thus, while fire-driven heterogeneity can maximize energetic acquisition for expenditure, homogenous high-severity fire may lead to unbalanced tradeoffs between foraging opportunities and expending energy to obtain those resources.

Predators often exhibit top-down control on the flow of energy through ecosystems, and understanding the impact disturbance events like fire have on higher trophic levels is vital to conserve biodiversity (Pace et al. 1999; Beschta and Ripple 2009). By driving the structure and composition of landscapes, fire presumably impacts how predators interact with their biological communities. However, there are no clear or general responses of predators to fire (Geary et al. 2020). Indeed, studies on the energetics of predators following fires are scarce (Doherty et al. 2022). One predator species that appears to respond to fire is the California spotted owl (*Strix occidentalis occidentalis;* hereafter "spotted owl"), an avian predator typically associated with closed-canopy forests and older, late-seral characteristics, especially for roosting and nesting (Gutiérrez et al. 1995). In the core part of their range, individuals forage in small, spatially complex patches of severely-burned forest where prey densities are presumed to be higher (Jones et al. 2020; Kramer et al. 2021b). However, when burned patches become more simplified and/or exceed a certain size (~10–100 ha), individuals begin to avoid forests burned at high-severity (Jones et al. 2020). Because this species evolved in fire-prone forests (Jones et al. 2023), this hierarchical response presumably reflects an adaptation to historical frequent-fire regimes typical for forests in their range, where pyrodiversity was high and high-severity patches rarely exceeded 100 ha in size (Safford and Stevens 2017). However, our current understanding of predator associations with burned landscapes is largely phenomenological. We have yet to identify a mechanistic explanation for spotted owls' responses to fire, as well as the responses for many other predators globally occurring in fire-prone landscapes (Geary et al. 2020).

Here, we integrated high-resolution GPS tracking and nest video monitoring to examine the foraging behavior of a top predator, the spotted owl, following forest fires that largely resembled disturbance events typical for the region. We hypothesized that pyrodiversity (i.e., a mixture of post-fire characteristics) promotes energetic provisioning to nests, while larger areas of high-severity fire with decreased pyrodiversity hinder resource acquisition and increase the energetic cost of movement (Fig. 1). First, we predicted that spotted owls would preferentially capture prey in areas with higher fine-scale pyrodiversity, and that, in turn, higher pyrodiversity at a landscape-scale would result in higher energetic provisioning. Second, we predicted that spotted owls would be less likely to capture prey within areas of severely burned forest and would incur greater energetic movement costs within landscapes with greater proportions of high-severity fire. In addition to these core predictions, we also explored potential relationships between energetics/habitat selection and other post-fire burn characteristics that could explain additional variation, including low- moderate-severity fire. Finally, we predicted that the effects of fire would be stronger when disturbance was more recent. As natural disturbance regimes change, understanding how predators expend and obtain energy in burned landscapes is increasingly important.

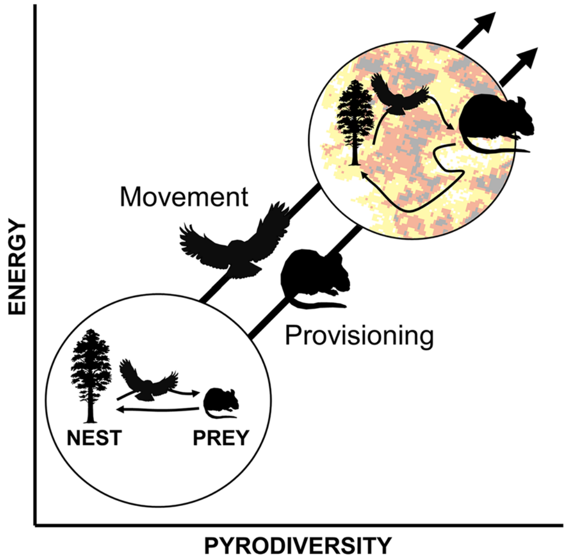

Fig. 1 Predicted relationship between pyrodiversity and energy. We expected that the energetic cost of movement, driven by distance traveled by owls, and energetic provisioning, driven by biomass of prey delivered to nests, would both increase with pyrodiversity at local and landscape scales

Materials and methods

Captures, tagging, and camera monitoring

Between 2019 and 2022, we tagged 34 breeding male spotted owls across the Sierra Nevada and in the San Bernardino Mountains in southern California (Fig. 2). Fourteen individuals had 95% kernel home ranges, described below, that partially burned less than a decade prior to sampling; we considered these sites to be in our "burned" sampling group. We considered sites to be "unburned" ($n=20$) if they had not experienced fire in the past decade prior to sampling. We focused on this time period to target recent fires specifically

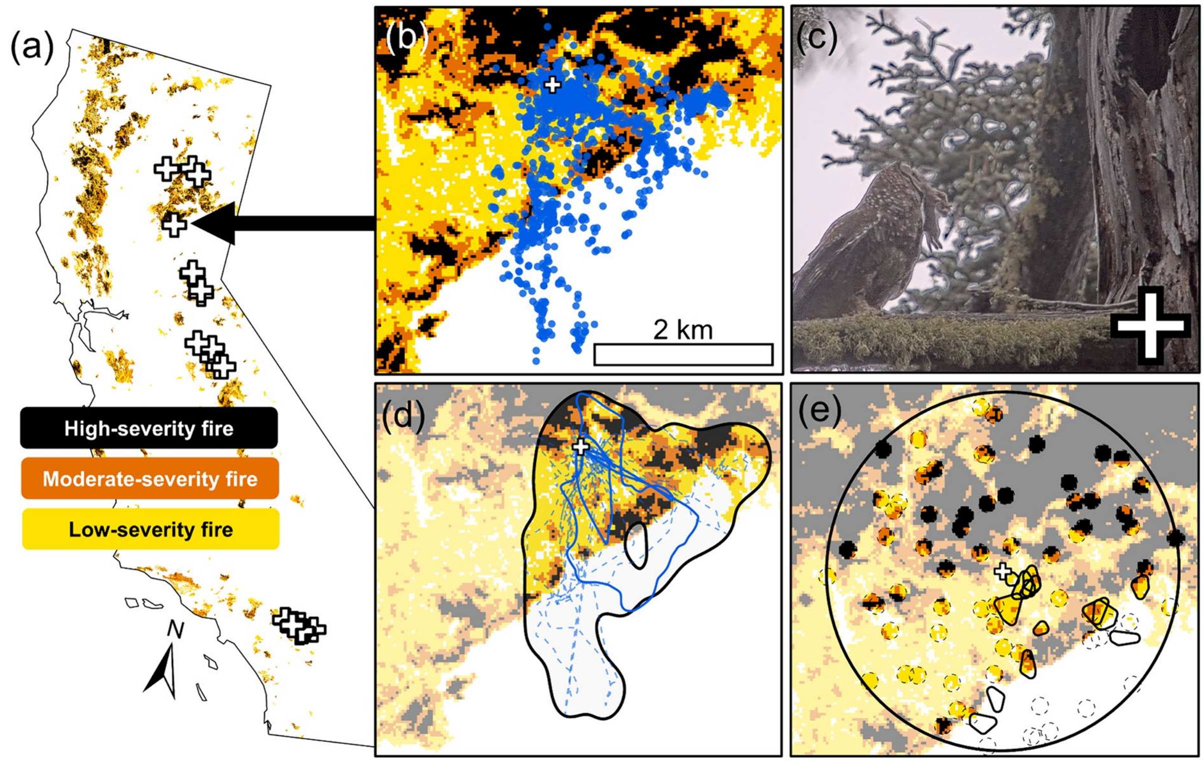

Fig. 2 Study area and GPS tagging. We tagged (**a**) 34 individual spotted owls across their range in the Sierra Nevada and in southern California, and 14 had home ranges that overlapped fires that occurred 1–10 years prior to sampling. **b** GPS tags attached to an individual spotted owl recorded fine-scale locations at night (black). **c** Cameras pointed at nests (white plus) recorded prey deliveries to nests. **d** We estimated 95% KDE (solid black line) and movement paths (blue lines). A single night's movement path is represented by a solid blue line. **e** Movement paths and camera footage were reviewed simultaneously to estimate capture polygons (black outlines) and available polygons (grey dashed outlines)

and control for temporal variation in post-fire forest regeneration (Tangney et al. 2022). All individuals tagged in 2021 were in southern California, and 2021 was the only year individuals were tagged in this region.

Captures, GPS tagging, and camera installations followed methods described in detail previously (Wood et al. 2021; Wilkinson et al. 2022; Zulla et al. 2023). Briefly, we used call-based surveys to locate breeding spotted owls (Franklin et al. 1996), which we tagged and monitored between early May and late June in all sampling years. At each site, we captured males using noose poles and hand capture techniques, attaching GPS tags via tail mounts (Kramer et al. 2021a; Wood et al. 2021). GPS tags (Alle-300, Ecotone, Poland, 10 g) were programmed to record locations every two minutes between 2000 – 0600 PDT over the battery life of the tags (range: 3–12 days). Median positional error of tags was 45 m (15–74 m S.A. Whitmore and H.A. Kramer, unpublished data). One male was tagged with an acoustic Vesper tag (Reid et al. 2022). We attempted to recapture owls and remove tags at the end of the breeding season, with the remainder of tags expected to be dropped via molting of tail feathers in ≤ 1 year.

Using methods described in previous studies (Wilkinson et al. 2022; Zulla et al. 2022, 2023), we installed infrared cameras (AXIS Q1786 – LE, 4 megapixel) in trees near nest trees to observe nests during the same 10 hr period that GPS tags were collecting locations, plus an additional 30 min each morning (10.5 h total). Cameras were installed in trees 10–50 m from nest sites (to minimize disturbance to nesting activities) using single rope technique to avoid climbing spurs, reduce subsequent damage to trees, and increase safety for climbers

(Anderson et al. 2015). Cameras were powered by deep cycle lithium batteries and programmed using AXIS Companion (Canon Inc, Lund, Sweden) to specify image quality and recording period, and videos were saved to an SD card, downloaded, and reviewed to detect and identify prey delivered to nests.

To identify successful capture locations, we reviewed all video data and noted the time of all prey deliveries and species delivered when possible. We then reviewed GPS data to identify clusters of locations just before a relatively straight movement path back to nests (Marsh et al. 2014; Wood et al. 2021). Clusters were defined as containing up to 10 GPS locations prior to an individual's return to the nest, such that all cluster points were required to occur over 20 min or less with fewer than 250 m between points (Wilkinson et al. 2022; Zulla et al. 2022, 2023). Prey deliveries observed in video recordings were linked to GPS point clusters, and minimum convex polygons (hereafter "capture polygons") were calculated around points in clusters. Available polygons were established by first creating a 2018 m buffer around nest locations, which corresponds to the average home range size of California spotted owls (1279 ha; Roberts 2017). Thirteen nests in this study were located within 2 km of burned forest. For each capture polygon, we randomly established five circles within the 2018 m buffer equal in size to the average prey capture polygon (0.679 ha). We buffered all capture and available polygons with 50 m buffers to account for potential GPS positional error (Zulla et al. 2022, 2023).

Characterizing burned landscapes

We obtained all covariates describing the most recent decade of fire prior to sampling (2011–2021) on the landscape from the Monitoring Trend in Burn Severity dataset (MTBS; https://www.mtbs.gov/). We established four classes of fire severity depending on the proportional loss of live overstory in any 30 m pixel: unburned (0% overstory mortality within the boundaries of a fire), low-severity fire (0–25% overstory mortality), moderate-severity fire (25–75% overstory mortality), and high-severity fire (> 75% overstory mortality).

In each capture polygon and available polygon, we used the package landscapemetrics (V 1.5.6; Hesselbarth 2023) to calculate the proportion of used and available areas burned at low-, moderate, and high-severity. In used and available polygons, we also calculated pyrodiversity as the Shannon diversity index of all fire severity classes and unburned space within the fire boundaries (Jones and Tingley 2022). To calculate these fire characteristics at a landscape scale, we first defined approximate home ranges using 95% kernel density estimates (KDEs) of each tagged owl, estimated using fixed kernel width using the abehabitatHR package (0.4.21; Calenge 2024) in R (V 4.2.2). In each KDE that overlapped fire which occurred within the last decade ($n = 14$), we calculated the proportion of each burn severity class and pyrodiversity as above. Finally, in both capture polygons and home ranges, we calculated the proportion of unburned or unchanged forest by subtracting the total proportion of all severity classes from 1.

Resource selection

We examined the relationship between fire and the probability of an area facilitating successful prey capture for all individuals in home ranges that overlapped an area burned at most one decade prior to sampling ($n = 14$). For all analyses, we fit generalized linear mixed-effects models in the program R (V 4.4.0) with package glmmTMB (V 1.1.9; Mollie et al. 2017) to test the prediction that spotted owls select for pyrodiversity and against high-severity fire for capturing prey. Specifically, we fit two sets of generalized mixed-effects models in which the binary response was the use of a capture polygon, and the fixed effects were pyrodiversity, the proportion of each burn severity class, and the proportion of unburned/unchanged forest within a capture polygon. In the first set of analyses, we fit models that allowed for individual random intercepts to allow for background variation in the abundance of different habitat types experienced by different individuals in each territory (Duchesne et al. 2010). In the second set of analyses, we fit separate models for each territory ($n = 14$) independently to examine territory-specific differences in foraging behavior. We attempted to fit a single mixed model with individual territory as a random slope, but that model did not converge. In both sets of analyses, we examined each fire characteristic in univariate models, and in the first set of analyses, we examined interactions between each fire characteristic and a site-level variable describing time-since-fire (either 1–2 years or 5–10 years). We chose these two temporal categories for time-since-fire because other studies have examined the impact of fire on spotted owl using similar time-frames (Lee and Bond 2015; Jones et al. 2016, 2021), and these categories have been shown to influence animal responses to fire (Fontaine and Kennedy 2012; González et al. 2022). In all models, we weighted available polygons ($W = 1000$) to enable convergence to the inhomogeneous Poisson process (Muff et al. 2020). We did not include distance to nest as a covariate in our design (Benhamou and Courbin 2023). We evaluated the goodness-of-fit of home-range scale models by calculating Count Pseudo-R^2—the number of correctly predicted outcomes divided by the total count—which is useful for evaluating models with binary responses.

Movement cost

To estimate movement cost, we first measured the average distance each individual traveled each night they were tagged. GPS locations were initially filtered out by battery life (> 3.7 V) because tags with low battery power were more likely to yield imprecise locations (Zulla et al. 2022). To establish smoothed movement paths traveled by each bird per night, we removed any location that was farther from both the previous and subsequent locations than the distance between the previous and subsequent points (McGinn et al. 2023b). This approach eliminated 21% of GPS locations. We additionally removed clusters of locations that were more than 3 km away from nest locations, which correspond to locations that did not accurately represent the true location of an individual or outlier locations that indicate prospecting, roosting, or another behavior distinct from foraging behaviors. We smoothed each movement path using polynomial approximation with an exponential kernel algorithm to estimate the distance each bird flew per night.

We estimated the energetic cost of distance traveled each day using the following conversion: movement cost $= 15.8 + 0.00628d \;/\; M^{0.71}$ (McGinn et al. 2023; Fig. SI 1), in which d is the distance individuals moved each day (m), and M is an individual's mass, which we recorded during the initial capture and used to scale estimates of the energetic cost of movement (Hudson et al. 2013). If mass was not recorded for an individual, we supplemented that value with the mean of all males in that region. Finally, we averaged movement cost across the period individuals were tagged (kJ d^{-1}). We did not include any partial days of GPS tracking in analyses examining the impact of fire characteristics on movement cost.

To examine the impact of fire characteristics on average movement cost, we fit four models specifying a Gamma distribution with a log link, in which the fixed effects were a binary variable denoting burn status of 95% KDEs ("unburned" vs. "burned"), a continuous fire variable (pyrodiversity or the proportion of each burn severity class in 95% KDEs), a binary time-since-fire variable differentiating sites that burned 1–2 years prior to sampling and sites that burned 5–10 years prior to sampling, and an interaction between fire and time-since-fire. Daily movement cost was the response variable. We treated "Year" as a random effect to account for variation between years and regions. Note that all individuals tagged in 2021 were in southern California, and all individuals tagged in 2019, 2020, and 2022 were in the Sierra Nevada. We examined each fire characteristic in separate models because these variables were functionally dependent on one another.

Provisioning

To estimate energetic provisioning, we first calculated prey delivery rates and the biomass delivered to nests each day cameras recorded video. We counted the number of deliveries captured on video, as described above, per night. We only considered deliveries in which we were confident that the transfer of prey from adult to young was successful. Prey were identified to the most specific taxonomic group possible. We additionally estimated biomass using values from previous research and the literature, which are available in the supplementary material (Table SI 1); mass estimates for prey species in the Sierra Nevada were obtained from (Zulla et al. 2022), whereas estimates for species in southern California were obtained from Wilkinson et al. (2022). For all unidentifiable prey deliveries (18.5%) where relative size could be observed, we averaged the masses of possible prey from the literature (Zulla et al. 2022; Wilkinson et al. 2022). For all prey deliveries where we could not identify either taxonomic group or size class (5.5%), we considered mass to be an average of all other prey delivered to nests in the region. We removed one individual from analysis because the nest camera only captured one night of prey deliveries. We did not include potential prey deliveries when it was uncertain whether prey was delivered to the nest.

We calculated energetic provisioning for each day cameras recorded prey deliveries, using gross energy (kJ g^{-1}) of prey based on wet mass reported in the literature (Weathers et al. 2001). For species that did not have estimates of gross energy, we assigned a value based on estimates for species of similar masses (Weathers et al. 2001). For prey not identified to species, we considered gross energy conversion to be an average across all prey types. The average biomass delivered to nests each day and average energetic provisioning were highly correlated with one another ($r=0.999$), indicating these choices did not have a major impact in our analyses. We estimated energetic provisioning as 77% of gross energy delivered to nests, which—assuming nestlings ate all food delivered to nests and assimilated energy as efficiently as adult spotted owls—corresponds to the biologically available energy consumed by nestlings (Weathers et al. 2001). Finally, we averaged provisioning across the amount of time cameras recorded video (kJ d^{-1}). We examined the impact of fire characteristics on energetic provisioning to nests by running four models, specifying a Gamma distribution with a log link, and maintaining model structure as above, in which the average daily provisioning was the response. We evaluated the goodness-of-fit of home-range scale models by calculating Conditional R^2_{GLMM} (Nakagawa and Schielzeth 2013) using the package MuMIn (V 1.47.5; Barton 2024).

Extrapolation analysis

In a post-hoc analysis described in the supplementary material, we extrapolated our predictions of provisioning and movement cost to estimate the number of flying squirrels that would be needed to compensate for the energetic requirements of individuals based on fire characteristics in historical spotted owl territories.

Results

Resource selection

For pairs with nests within 2 km of burned areas ($n=14$), we identified 177 prey capture locations, as well as the prey species captured in those locations. Of these prey captures, 62% were located within the perimeter of fires that occurred 1–10 years prior to sampling, 58% overlapped low-severity fire, 23% overlapped with moderate-severity fire, and 16% overlapped with high-severity fire. More detailed descriptions of prey are in the supplemental materials (Fig. SI 2). Individuals were less likely to successfully capture and deliver prey in polygons with a higher proportion of high-severity fire or moderate-severity fire (Fig. 3; $\beta_H=-3.39$, 95% CI = [− 5.08, −1.69]; $\beta_M=-2.36$, [−3.48, −1.24]). Spotted owls captured prey in low-severity burned areas in proportion to its availability 1–2 years post-fire but were more likely to successfully capture prey in areas with more low-severity fire 5–10 years post-disturbance (Fig. 3; $\beta_{L*Y}=0.96$, [0.01, 2.00]). Finally, spotted owls were more likely to capture prey in polygons with more unburned forest 1–2 years prior (Fig. 4; $\beta_U=1.11$, [0.68, 1.54]) but captured prey in unburned areas in proportion to its availability 5–10 years post-fire (Fig. 4; β_{U*Y} = -0.99, [-1.74, -0.25]).

Our second set of resource selection analyses examined each territory individually and revealed differences in the driving components of site selection for foraging. For several sites analyzed individually, models did not converge due to a low proportion of capture polygons in burned areas (Table SI 5). The proportion of high severity fire in capture polygons negatively impacted the probability of their use in all sites. The proportion of moderate severity fire also negatively impacted the probability of successful prey capture, while low-severity fire had variable effects on the probability of successful prey capture (Fig. 3). The effect of pyrodiversity on the probability of use varied between territories, such that spotted owls selected for pyrodiversity in some sites and against it in others (Fig. 3). Finally, the proportion of unburned forest positively impacted the probability of successful prey capture in sites that burned 1–2 years prior (Fig. 4).

Movement cost

We collected 51,787 locations from 34 owls, with an average of 1523 (SD = 804) locations for every individual over an average of 8.29 (SD = 3.37) nights. The average size of a home range estimated using 95% KDE for these individuals was 5.64 km^2 (SD = 3.84 km^2), and individuals traveled, on average, 8010 m day^{-1} (SD = 3890 m day^{-1}). We

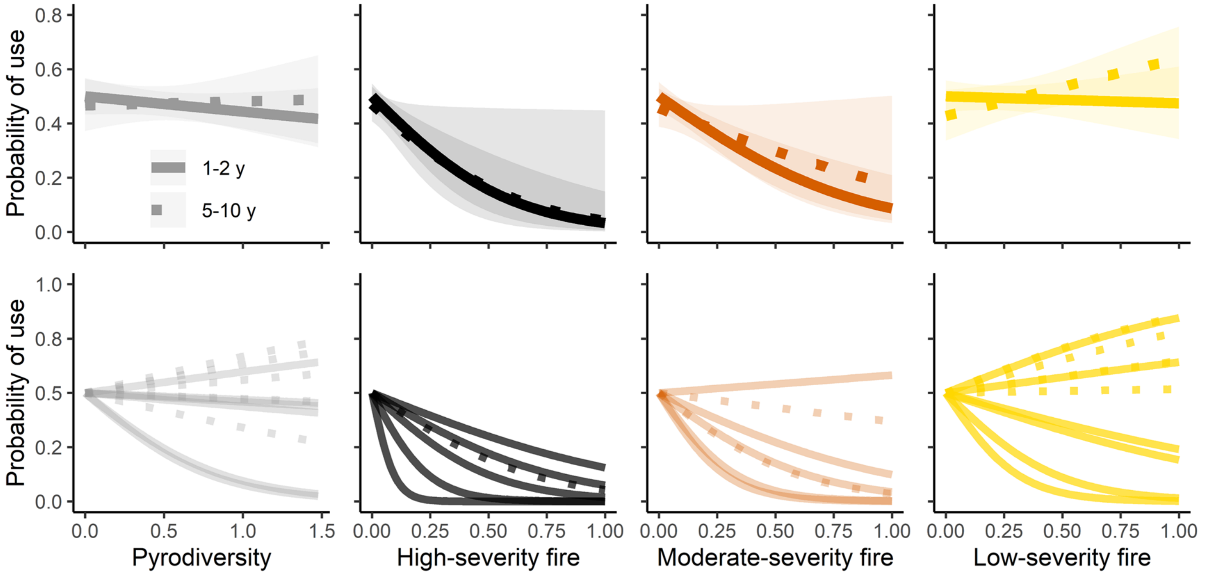

Fig. 3 Predicted effects of fire on resource selection. The top row shows the predicted effects of fire on the probability of successful prey capture, including 95% confidence intervals (shaded areas), from the first set of resource selection analyses in which all territories that bordered fires were pooled. Solid lines indicate predictions for coefficients in territories that burned 1–2 years prior to sampling and dotted lines indicate predictions for coefficients in territories that burned 5–10 years prior to sampling. The bottom row shows results from the second set of analyses in which territories were examined separately, and each line indicates the predicted effect of fire on the probability of successful prey capture for a separate territory

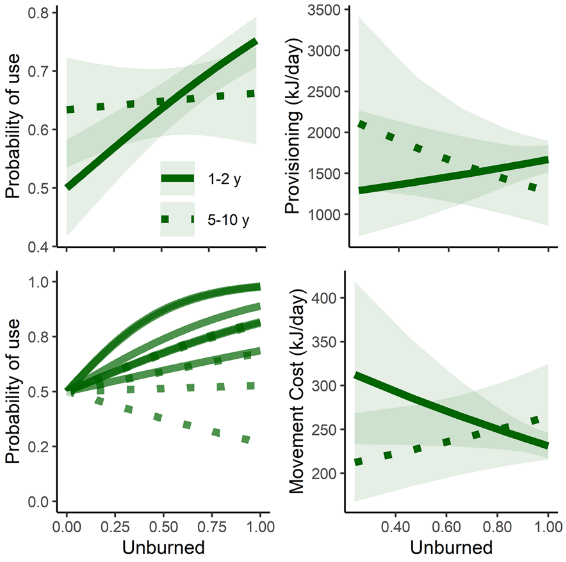

Fig. 4 Predicted effects of the proportion of unburned forest on resource selection, provisioning, and movement costs. Lines indicate predicted relationships between the proportion of unburned forest in capture polygons or home ranges and shaded areas indicate 95% confidence intervals. Solid lines show predicted relationships for sites burned 1–2 years prior and dotted lines show sites burned 5–10 years prior

estimated that individuals spent, on average, 236 kJ day^{-1} (SD = 38.6 kJ day^{-1}), which is comparable to previous estimates of daily energetic expenditure of 269 kJ day^{-1} (McGinn et al. 2023b) and 249 kJ day^{-1} (Weathers et al. 2001). In sites that burned 1–2 years prior, the energetic cost of movement increased with pyrodiversity and the proportion of high-severity fire (Fig. 5, $\beta_{Pyro}=0.34$, [0.07, 0.61]; $\beta_{H}=2.68$, [1.09, 4.27]) and tended to decrease with the proportion of unburned forest (Fig. 4, $\beta_{U} = -0.40$, [$-$0.80, 0.00]). However, the effects of fire characteristics (Fig. 5; $\beta_{Pyro*Y}=-0.43$, [-0.78, -0.11]; $\beta_{H*Y}=-3.69$, [-6.28, $-$ 1.10]; $\beta_{M*Y}=-1.80$, [-3.37, -0.23]; $\beta_{L*Y}=-1.04$, [-1.88, -0.19]) and unburned forest (Fig. 4, $\beta_{U*Y}=0.69$, [0.22, 0.47]) on movement cost depended on time. Specifically, 5–10 years post-fire, movement cost tended to decrease with the proportion of moderate-severity fire, decreased with the proportion of low-severity fire, and increased with the proportion of unburned forest (Figs. 4 and 5).

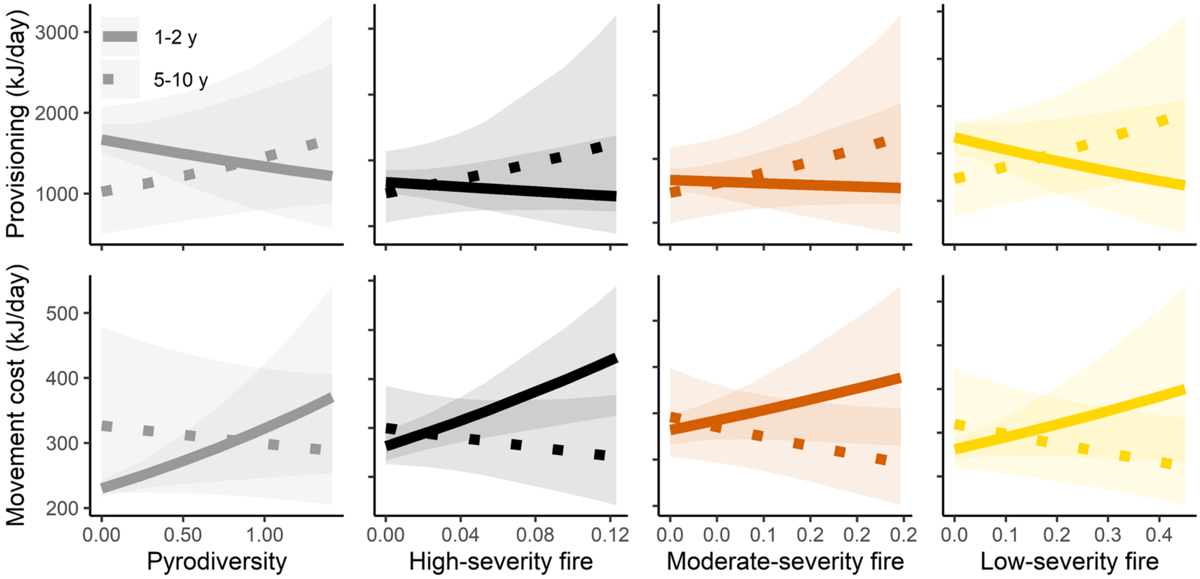

Fig. 5 Predicted effects of fire on provisioning and movement costs. Lines indicate predicted relationships between fire covariates and energetic metrics, and shaded areas indicate predicted 95% confidence intervals. Solid lines show predicted relationships for sites burned 1–2 years prior to sampling and dotted lines show predicted relationships for sites burned 5–10 years prior to sampling

Provisioning

In 95% KDEs, the proportion of high severity fire ranged from 0 to 0.12, the proportion of moderate severity fire ranged from 0 to 0.25, the proportion of low severity fire ranged from 0 to 0.45, and the proportion of unburned forest ranged from 0 to 1. We observed 975 prey deliveries by spotted owls at the 33 nests where we observed more than one night of prey deliveries, and of these, 671 were identified to taxonomic class, family, genus, or species. Woodrats were the most common prey item captured and provisioned to nests, accounting for 26% of all prey items in burned capture locations and 21% in unburned capture locations (Fig. SI 2). Only 10 capture locations experienced fire across 100% of their area. On average, 3.40 (SD = 1.90) prey deliveries were made per night. On average, breeding pairs delivered 387 g day^{-1} (SD = 236 g day^{-1}) of prey each night to nests. The average energetic provisioning to nests was 1670 kJ day^{-1} (SD = 1010 kJ day^{-1}). Average daily provisioning tended to decrease with low-severity fire that burned 1–2 years prior (Fig. 5; $\beta_L = -0.80$, [−2.05, 0.45]). However, 5–10 years post-fire, provisioning increased with the proportion of low-severity fire (Fig. 5; $\beta_{L*Y} = 1.80$, [0.21, 3.39]) and decreased with the proportion of unburned (Fig. 4; β_{U*Y} = − 1.00, [0.00, 2.00]). That is, in a site where 50% of an individual's territory burned at low severity 5–10 years prior, offspring benefited from an additional ~ 1.5 flying squirrels (considering the caloric value of an averaged sized flying squirrel and spotted owl assimilation efficiency) per day, compared to ~ 1.0 flying squirrels per day in an unburned site.

Extrapolation analysis

One to 2 years post-fire, we predicted that an individual in a territory with a mosaic of severity classes would deliver 1410 kJ to a nest and expend 440 kJ of energy each day and an individual in a territory with a higher amount of high-severity fire and relatively less low-severity fire would deliver 1780 kJ to a nest and expend 2370 kJ (Fig. 6). Five-ten years post-fire, we predicted that an individual in a territory with relatively more low-severity fire would deliver 1910 kJ to a nest and expend 190 kJ of energy each day and an individual in a severely burned territory would deliver 1430 kJ to a nest and expend 100 kJ (Fig. 6). Finally, we predicted that an individual in an unburned territory would deliver 1670 kJ to a nest and expend 230 kJ (Fig. 6c).

Discussion

Many animal species are adapted to take advantage of resources in post-fire environments, but as landscape-scale patterns of wildfire severity and configuration change rapidly, the mechanisms for species persistence in burned landscapes are not well understood. We have only a general understanding of spotted owl preferences for habitat in burned landscapes, and the species is ideal to examine these mechanisms because we do not yet understand why those preferences occur. As a fire-adapted species, spotted owls exhibit behaviors that appear to facilitate their persistence in fire-prone landscapes. In the core of their range, individuals hunt in small, spatially complex high-severity burned patches, but avoid foraging where fire burns large areas at high severity, suggesting an adaptation to historical fire regimes (Jones et al. 2020; Kramer et al. 2021b). Here, we offer the first mechanistic explanation for this phenomenon. While individuals avoided foraging in moderate- to high-severity burned patches, we found evidence that low-severity fire promoted individual energetics following multiple years of post-fire forest succession. Spotted owls appeared to exhibit resiliency to fire—and benefited from fire in the long run—where fire characteristics fell within the region's historical range of variability.

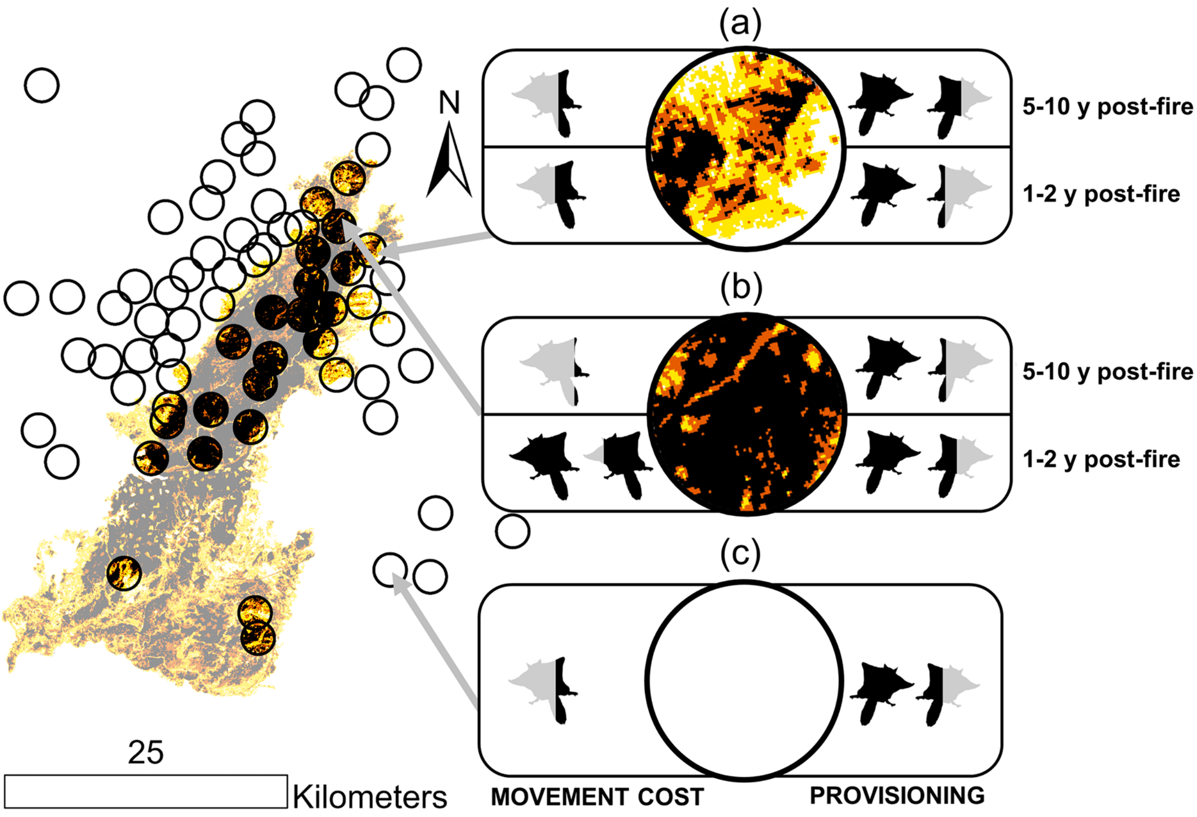

Fig. 6 Predicted movement costs and provisioning for historical spotted owl territories. We show predicted movement cost and energetic provisioning for three territories as the number of average sized flying squirrels (170 g) necessary per day which would satisfy those requirements. Solid black images represent 1 flying squirrel required per day, and partial images represent a proportion of a flying squirrel required per day. We show three hypothetical energetic requirements for three historical spotted owl territories with (**a**) a mosaic of severities including a moderate amount of low-severity fire (0.33) and high-severity fire (0.24), **b** a low amount of low-severity fire (0.07) and a high amount of high-severity fire (0.80) and **c** no fire

Fire incurs immediate energetic cost

Within burned territories with conditions similar to historical fire regimes (Williams et al. 2023), successful prey captures were less likely where there were greater amounts of high- and moderate-severity fire regardless of time-since-fire. Spotted owls generally consume small mammal species like woodrats (*Neotoma* spp.) and pocket gophers (*Thomomys* spp.), semi-arboreal and fossorial species, and flying squirrels (*Glaucomys oregonensis*), a smaller and less energetically efficient arboreal species (Hobart et al. 2021). While there is some evidence that semi-arboreal and fossorial species prefer recently burned habitat and younger forest (Borchert et al. 2014; Roberts et al. 2015), other evidence suggests that woodrats and flying squirrels are restricted to unburned areas after fire (Zwolak and Foresman 2007). Regardless of whether fire creates habitat for some small mammal species, prior work has shown that spotted owls consume more flying squirrels in landscapes that have experienced more extensive and frequent fire, presumably due to potential changes in flying squirrel abundance or availability (Hobart et al. 2021). Here, we demonstrate that in burned landscapes, spotted owls actively avoid foraging within moderately or severely burned patches, an avoidance observed in other forested species like northern goshawks (*Accipiter gentilis*) and American martens (*Martes americana atrata*) as well (Gosse et al. 2005; Blakey et al. 2020). Indeed, we found that 1–2 years post-fire, individuals had higher capture success in unburned forest. Even if fires create suitable habitat for woodrats and pocket gophers, spotted owls rely on standing trees for hunting, and even an intermediate reduction in live canopies that occurs in forests that burn at moderate-severity may limit the ability of spotted owls to access energetically efficient prey.

Home ranges in this study were burned no more than 15% at high-severity, indicating potential territory-level avoidance of areas with greater proportions of high-severity fire and supporting prior research showing spotted owls select for areas with smaller high-severity patches surrounded by ‘green’ forest (Jones et al. 2020; Kramer et al. 2021b). Avoidance, both immediate and time-lagged, of forest burned at high-severity is observed for other forest species as well, including other owls (Duchac et al. 2021), amphibians (Hossack et al. 2013), and mammals (Law et al. 2023). In landscapes with a relatively larger proportion of high-severity fire that burned 1–2 years prior to sampling, individuals in our study traveled further and spent more energy acquiring resources, corroborating the fine-scale avoidance of high-severity patches we observed in this study. In landscapes with more high-severity fire, suitable foraging habitat may be located further from nests or occur at lower densities, forcing individuals to travel further and spend more energy to acquire sufficient prey to sustain rapidly growing offspring. However, 5–10 years post-fire, the movement cost of high-severity fire was no longer apparent, indicating that spotted owls may be resilient to high-severity fire where it occurs across smaller extents.

Energetic benefits of fire

Individuals experienced higher capture success in sites with more low-severity fire and captured prey in unburned forest in proportion to its availability where sites burned 5–10 years prior (Figs. 3 and 4). Arboreal species like flying squirrels may persist in live canopies following low-severity fire, and fires that burn at lower severity may retain sufficient green forest to support spotted owl access to semi-arboreal and fossorial prey species like woodrats, pocket gophers, and mice if they do indeed avoid burned forests (Jones and Tingley 2022). Great horned owls (*Bubo virginianus*) benefit from edges between stands of different ages for access to small mammal species (Johnson 1992). The benefits of fire for hunting may require multiple years of regeneration to promote structures that facilitate spotted owl hunting behaviors. Potential prey habitat in the understory typically takes multiple years to regenerate after a fire (Zwolak and Foresman 2007), and edges between younger and older forest created by fire may take time to achieve the structure necessary to allow these perch-and-pounce predators access to prey. Additionally, this time-lag in selection for low-severity burns may reflect a post-disturbance learning curve, such that individuals may require time to identify foraging habitat in a changed landscape (Rahman and Candolin 2022).

Biomass and corresponding energetic value of prey delivered to nests increased with the proportion of low-severity fire and decreased with the proportion of unburned forest in sites that burned 5–10 years prior. Spatial heterogeneity has long been thought to stabilize trophic interactions over time (Kareiva and Wennergren 1995; Ellner et al. 2001), specifically by promoting both hunting grounds and prey refugia (Kuntze et al. 2023; Quévreux et al. 2023). In Yellowstone National Park, a model system for predator-prey interactions, landscape-scale heterogeneity promotes refugia for prey species like elk (*Cervus elaphus*) and hunting habitat for wolves (*Canis Lupus*), allowing the coexistence of multiple trophic levels (Kauffman et al. 2007). Spotted owls often hunt for prey at the edges between younger and older forest, which constitutes an intersection between suitable prey habitat and typical predator habitat (Kuntze et al. 2023; Zulla et al. 2023). Heterogeneity has been shown to positively influence spotted owl prey deliveries, and fire—specifically that which leaves standing patches of green forest—may have been a historical driver for the heterogeneity in this region and in others (Kuntze et al. 2023). While we observed an immediate negative impact of fire on provisioning, low-severity fire appeared to benefit spotted owls by creating structural heterogeneity in the understory after multiple years of post-fire regeneration.

Temporal tradeoffs between movement and provisioning

Assuming fire composition and configuration do not impact the accessibility of prey species—though they likely do—we predicted in our post-hoc analysis that individuals in severely burned territories would need to spend more energy to provision less energy than individuals in unburned landscapes (Fig. 6). Spotted owls in sites burned by fires typical for this region—with a mosaic of severity types and small patches of high severity fire (Williams et al. 2023)—incurred some energetic cost immediately but benefited from higher energetic acquisition after multiple years of post-fire succession. From our extrapolation, the delayed energetic benefits of low-severity fire approached and exceeded the energetic benefits of unburned forest. Indeed, our results showed that individuals did not preferentially forage in unburned forests within fire perimeters that burned 5–10 years prior but had more success capturing prey within areas burned at low severity. However, many of the territories that burned predominately at high-severity in the 2014 King Fire (Fig. 6) have remained unoccupied for nearly a decade after the fire disturbance (Jones et al. 2021), indicating that a loss of nesting habitat in green, closed-canopy forest may preclude any delayed benefits of low-severity fire to foraging. Additionally, individuals that occur within severely burned landscapes—that are presumably still occupied despite a loss of nesting habitat—may incur more energetic cost immediately and lose access to energetic resources over time in the absence of low-severity fire.

Alternative mechanisms for variation in spotted owl foraging and energetics

We found evidence that variation in spotted owl hunting success and energetic tradeoffs may be explained by fire characteristics. While we controlled for unmodeled variation between home ranges in our study design, other mechanisms unexplored in this study may also drive spotted owl foraging behaviors and energetics in both burned and unburned forests. Pre-fire characteristics, specifically edges between differently aged forest stands and large trees, may impact the overall hunting success and energetic acquisition and expenditure of foraging spotted owls (Zulla et al. 2022, 2023). Energetics may also be influenced by warm daytime temperatures, which can be associated with shorter nocturnal movements, and the distribution of large trees with closed canopies, which support stable microclimate that can function as energetic “refugia” (McGinn et al. 2023b). However, sampling in this study occurred before temperatures approached or exceed physiological thresholds shown to impact movement or instigate the use of cool microclimates (McGinn et al. 2023a). Finally, foraging behaviors of animals can be influenced by the risk of predation (Haswell et al. 2020) or interspecific interactions with competitors (Austin et al. 2021). While barred owls, a primary competitor of spotted owls, have been effectively removed from the Sierra Nevada (Hofstadter et al. 2022) and do not occur in southern California, interactions with great horned owls or other raptor species may influence spotted owl foraging behaviors.

Conclusions

Predators show disparate responses to fire depending on their hunting strategies and associations with habitat cover, though the vast majority of studies that examine predator responses to fire focus on abundance, occurrence, or home-range level habitat selection and examine responses by comparing those metrics between burned and unburned areas (Geary et al. 2020). Here, we found that one of the drivers of such poignant variation in predator responses to fire may be the natural variation in fire regimes across the landscape. Spotted owls appear to benefit from landscape changes following fires that resemble those the species typically experienced in its evolutionary environment, but changes to such fire characteristics could incur increases in energetic expenditure or decreases in energetic acquisition. Future work may further examine the nuanced impacts of fire and interactions with other factors that influence spotted owl foraging. As the climate continues to warm and fires leave footprints that exceed historical thresholds of extent, severity and/or frequency (Moritz et al. 2012), some of the dynamic forces that drive natural heterogeneity may collapse. This is not an inconsequential problem: over 4400 species across many different taxa and regions face threats associated with disrupted fire regimes (Kelly et al. 2020).

One challenge for land managers in the context of rapidly changing disturbance regimes is balancing the resiliency of disturbance-prone landscapes and the conservation of sensitive species. In western North America, fire-suppression may negatively impact forest species on two fronts: (1) the loss of foraging opportunities in the absence of stabilizing, frequent-fire regimes that generate heterogeneity and (2) the loss of nesting/resting opportunities following atypically large and severe fires that exceed regional norms (Ayars et al. 2023). While fuels reduction treatments may incur some cost to habitat suitability for species that rely on closed-canopy forests (Jones et al. 2022), prescribed fire or mechanical restoration strategies like increasing canopy base height, reducing ladder fuels, and reducing canopy bulk density may ultimately promote forest resilience (Hagmann et al. 2021) and improve spotted owl foraging habitat (Wright et al. 2023). Fire regimes are projected to continue to change not just in western forests (Abatzoglou and Kolden 2011) but across forests globally (Joshi and Sukumar 2021), and it is increasingly important to identify restoration strategies that limit atypical disturbance events while promoting the structural heterogeneity necessary for animals, particularly predators, to obtain sufficient energetic resources required to survive and reproduce.

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Author contributions KM helped conceive the ideas, conducted analyses, led the writing of the manuscript, and designed the figures. CZ, ZW, BD, and KR developed field methods and collected data. MW helped conceive the ideas and plan analyses. JK acquired funding and helped acquire resources in the field. ZP and GJ conceived the ideas of the manuscript. All authors contributed to interpreting results, drafting/revising the article, and gave final approval for publication.

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Data availability Upon acceptance, data will be made available in a Dryad repository.

Declarations

Competing interests The authors declare no competing interests.

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