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Invasive barred owls select old-forest structure: Functional habitat loss for spotted owls and a threat to old-forest fauna

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ABSTRACT

Invasive predators are leading drivers of native species decline, and their impact is heaviest where they concentrate in the habitats native species most depend on. The barred owl (*Strix varia*) is a generalist predator invading old forests across western North America. Using GPS telemetry of 56 barred owls across the range of the northern spotted owl (*Strix occidentalis caurina*) in northwestern California, we found consistent selection for an old-forest axis integrating high canopy cover, tall stands, large trees, diverse tree sizes, and old age. Because these attributes define old forest, selection concentrated owls in stands sustaining a distinctive old-forest fauna, and disproportionately in habitat of the spotted owl, an umbrella species for this forest, peaking in its highest-quality nesting and roosting forest. Each owl also appropriated a large area, roughly 28 times the home range recorded in its native range, magnifying the invasion's per-individual footprint. Because habitat is defined by the conditions permitting occupancy, pervasive barred owl presence converts structurally intact forest into functional non-habitat for the spotted owl, a biotic habitat loss invisible to structure-based monitoring, while concentrating novel predation on naive old-forest prey. Because the forest persists, removing barred owls can restore this habitat: we estimate each territorial pair removed frees several square kilometers, though gains require sustained control and are not spatially additive. More broadly, where an invader co-opts the structure defining a specialist's habitat, protecting that structure is necessary but not sufficient: the specialist becomes conservation-reliant, dependent on managing the invader itself.

1. Introduction

Habitat loss and biological invasions rank among the foremost drivers of the ongoing global biodiversity crisis, and although the two are often studied in isolation, they increasingly act in concert. Habitat degradation and fragmentation not only erode the native systems on which specialists depend, but also render those systems more susceptible to colonization and dominance by widespread generalist invaders, so that the two pressures compound rather than simply add (Didham et al., 2007). Invasions are, moreover, a growing driver in their own right as alien species now rank among the leading causes of documented extinctions, and their toll continues to mount with expanding global trade and connectivity (Bellard et al., 2016; Pyšek et al., 2020; Simberloff et al., 2013). Understanding how invaders reshape native communities—and where their impacts fall most heavily—is now a central concern of biological conservation.

The most damaging invaders are frequently competitively dominant generalists that exploit native species lacking a shared evolutionary history with them. Because native prey and competitors are often naive to such novel enemies, invasive predators and competitors can depress or displace them far more severely than ecologically similar native counterparts (Salo et al., 2007; Sih et al., 2010). Invasive predators alone

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are implicated in the majority of recent vertebrate extinctions (Doherty et al., 2016), and competitively superior invaders can replace ecologically similar natives across entire regions, as the introduced eastern gray squirrel (*Sciurus carolinensis*) has done to the native red squirrel (*Sciurus vulgaris*) across much of Britain and Italy (Gurnell et al., 2004). Critically, such impacts are rarely uniform in space—they intensify where an invader concentrates its activity in the very habitats that native species most depend on, aligning competitive and predatory pressure with the areas of greatest conservation value. Anticipating these impacts therefore hinges on knowing where an invader settles on the landscape and how much habitat each individual effectively appropriates.

The relative importance of these drivers varies among biomes (Leclerc et al., 2018; Sala et al., 2000), but their combined pressure is particularly acute in the world's remaining old-growth and late-successional forests, which sustain a disproportionate share of forest biodiversity yet continue to decline worldwide (Lindenmayer et al., 2012; Watson et al., 2018). In temperate western North America, late-successional and old-growth forests have been disproportionately reduced by decades of industrial timber harvest, yet the remnants of these forests support exceptional biological diversity (DellaSala et al., 1999; Spies et al., 2018). Structurally, late-seral forests are characterized by high canopy closure, tall dominant trees, large-diameter stems, diverse diameter distributions, and complex vertical layering (Franklin et al., 2002; Spies et al., 2018). These attributes sustain a distinctive community of associated fauna—including the northern spotted owl (*Strix occidentalis caurina*), long designated as an umbrella species for old-growth forest conservation (Thomas et al., 1990), marbled murrelets (*Brachyramphus marmoratus*), fishers (*Pekania pennanti*), Humboldt martens (*Martes caurina humboldtensis*), flying squirrels (*Glaucomys* spp.), tree voles (*Arborimus* spp.), diverse amphibian assemblages, and rich arthropod communities (Carey, 1995; Carey and Johnson, 1995; Holm et al., 2016; Lattin, 1993; Lesmeister et al., 2018; Thomas et al., 1990). Federal conservation policy in western United States, principally the Northwest Forest Plan (NWFP), was designed to protect remaining late-seral forest, largely through the lens of spotted owl habitat, making the fate of these forests inseparable from the species they support (Davis et al., 2022a; Franklin et al., 2021).

The barred owl (*Strix varia*) is native to eastern North America but has expanded its range westward throughout western North America over the past century, and now represents a novel biotic threat to old-forest ecosystems across the region (Franklin et al., 2021; Holm et al., 2016; Long and Wolfe, 2019; Wiens et al., 2014). Range-wide passive acoustic monitoring for northern spotted owl shows that barred owls now occupy more than 90% of forest in Washington and Oregon, with lower but increasing occupancy (63%) in California (Jenkins et al., 2025). Barred owls are large-bodied, generalist predators with a remarkably broad diet (Hamer et al., 2001; Kryshak et al., 2022; Wiens et al., 2014). DNA metabarcoding of barred owl digestive tracts identified 78 prey types spanning mammals, amphibians, birds, reptiles, fish, and invertebrates (Kryshak et al., 2022). Mammals composed the majority of vertebrate prey by dietary weight, but amphibians were detected in nearly a third of individuals and reptiles in roughly a fifth—prey groups largely absent from spotted owl diets (Kryshak et al., 2022). This dietary breadth, combined with population densities that can exceed those of the congeneric spotted owls they displace, has raised concern about novel trophic cascades affecting old-forest prey communities, native competitors, and ecosystem processes (Holm et al., 2016). Critically, if barred owls preferentially select the structural attributes of late-seral forest, their competitive and predatory pressure would be spatially concentrated in the areas most important for old-forest-dependent fauna.

The northern spotted owl decline is the best-documented manifestation of barred owl effects on old-forest fauna, driven by extensive niche overlap and competitive dominance. The interaction exemplifies the competitive exclusion principle, which holds that species cannot permanently coexist when a competitively superior species exploits similar limiting resources (Gause, 1935; Lotka, 1932; MacArthur and Levins, 1967; Volterra, 1926). Barred owls are larger, more aggressive, have higher fecundity and survival, broader habitat use, and a more generalized diet than spotted owls, and maintain smaller, more closely spaced home ranges that support higher local densities (Long and Wolfe, 2019). These traits position barred owls as the superior competitor wherever the two species co-occur, and indeed, spotted owl occupancy, survival, and reproduction are consistently depressed in areas of barred owl invasion (Franklin et al., 2021; Wiens et al., 2021). Landscape-scale removal experiments have shown that reducing barred owl densities triggers competitive release, stabilizing or reversing spotted owl population declines (Diller et al., 2016; Hobart et al., 2025; Wiens et al., 2021), and the United States' federal Barred Owl Management Strategy now identifies targeted lethal removal as the cornerstone of spotted owl recovery (USFWS, 2024). Yet this evidence documents the demographic outcome of competition, not its spatial basis. What remains less well understood is whether barred owls actually converge on the same structural attributes of late-seral forest that spotted owls—and the wider old-forest community—depend on, the shared dependence through which competitive exclusion would be realized in space.

Radio-telemetry studies conducted over the past two decades in the invaded range have consistently identified an association between barred owls and older, structurally complex forest, although the specific attributes documented vary among study areas and methods. Across studies, barred owls selected high canopy closure and large-crowned trees (Singleton et al., 2010), old conifer forest (Hamer et al., 2007; Wiens et al., 2014), tall stands (Jenkins et al., 2019), and high mean diameter and basal area of large trees (Irwin et al., 2017), while avoiding clearcuts, young plantations, and non-forest cover types (Irwin et al., 2017; Wiens et al., 2014). Both barred owls and spotted owls used old conifer forest at rates far exceeding landscape availability, but barred owls exhibited seasonal shifts in midstory density preference and selected lower topographic positions and gentler slopes (Jenkins et al., 2019; Singleton et al., 2010). Home range size decreased with increasing proportion of old forest (Hamer et al., 2007; Wiens et al., 2014). At the landscape scale, range-wide passive acoustic monitoring has shown that barred owl occupancy is positively associated with mature forest characteristics, including old-growth structure index and conifer canopy cover (Jenkins et al., 2025).

Collectively, these findings indicate that barred owls in the invaded range prefer forest with attributes characteristic of late-seral conditions, yet no prior method has resolved individual space use with enough fidelity to identify which structural features each owl selects. Early radio-telemetry studies relied on manual triangulation with limited temporal resolution and spatial coverage, precluding fine-scale inference about individual space use. Acoustic monitoring captures landscape-level associations but cannot resolve individual-level resource selection or quantify the area each owl commandeers. Animal-borne GPS tags now provide continuous, minimally biased sampling of individual space use (McKinnon and Love, 2018; Watson et al., 2023), and, as part of a broader transformation in animal tracking (Kays et al., 2015; Nathan et al., 2022), can reveal which structural features an invader selects (Alston et al., 2023; Noonan et al., 2019). Estimating individual home range size is essential for quantifying the spatial extent of each owl's competitive and predatory influence—the area within which it depletes shared resources and preys upon old-forest fauna. This per-individual sphere of influence, in turn, enables estimation of old-forests functionally recovered when barred owls are removed, linking habitat selection directly to management outcomes. To our knowledge, ours is the first study to use GPS telemetry to quantify barred owl resource selection within the invaded range. Earlier work there resolved individual space use with radio-telemetry (Singleton et al., 2010; Wiens et al., 2014) and landscape-scale distribution with acoustic detection (Jenkins et al., 2025); GPS tags have been deployed on barred owls in the region once before, but to estimate home-range size in support of an acoustic-monitoring design rather than to model selection (Watson et al., 2023).

GPS tracking of the species has otherwise focused on its native range (Clément et al., 2021; Jirinec et al., 2024).

We focus on third-order selection—the use of resources within an established home range (Johnson, 1980)—because this is the scale at which barred owl impact is exerted: an individual depletes prey and displaces competitors within the forest it actually occupies and hunts. The landscape-scale decline is a manifestation of these individual actions summed across owls, which makes within-home-range use the mechanistic scale underlying the broader pattern. GPS locations resolve this use at the individual level, tying each owl's selection directly to where it presses on old-forest fauna. Where owls place those home ranges within the landscape—second-order selection (Johnson, 1980)—is a complementary question we do not address here; range-wide acoustic surveys provide coarse-scale information on barred owl occupancy at that extent (Jenkins et al., 2025). We first estimated individual home range size, defining the spatial extent of each owl's competitive and predatory influence. We then hypothesized that barred owls select structural attributes of mature, closed-canopy forest—attributes central to the habitat requirements of spotted owls and other old-forest-dependent species—and that this selection generates substantial spatial overlap with old-forest. We tested three predictions in turn. First, we predicted that barred owls would select an integrated gradient of late-seral forest structure. Second, we predicted that this selection would translate into disproportionate use of mapped spotted owl habitat, intensifying with habitat quality. Third, we predicted that individual home ranges would encompass substantial proportions of high-quality spotted owl habitat, consistent with extensive competitive overlap. Beyond testing these predictions, we translated the observed overlap into estimates of spotted owl habitat functionally recovered through barred owl removals.

2. Material and methods

2.1. Study area

We tracked and removed barred owls in northwestern California (Fig. 1), within a study region that encompassed lands administered by federal and state agencies, tribal governments, and private entities. The area spans two major ecoregions: the Klamath Mountains and the Coast Range (Omernik and Griffith, 2014). Topography is complex, ranging from broad riparian corridors to steep river canyons, rugged ridgelines, and elevations ranging from sea level along the coast to over 2000 m in the interior mountains.

The climate is Mediterranean, characterized by wet winters and hot, dry summers, with a strong gradient from the maritime, high-precipitation coast to increasingly continental and seasonally dry conditions inland. This environmental heterogeneity supports exceptional biological diversity, and the Klamath-Siskiyou region has been ranked among the most globally significant temperate forests (DellaSala et al., 1999; Whittaker, 1960). Dominant vegetation types across the study area include coast redwood (*Sequoia sempervirens*) forests, mixed-conifer stands of douglas-fir (*Pseudotsuga menziesii*), tanoak (*Notholithocarpus densiflorus*), pacific madrone (*Arbutus menziesii*), pines (*Pinus* spp.), and incense cedar (*Calocedrus decurrens*), as well as oak (*Quercus* spp.) woodlands, montane lakes, and meadows.

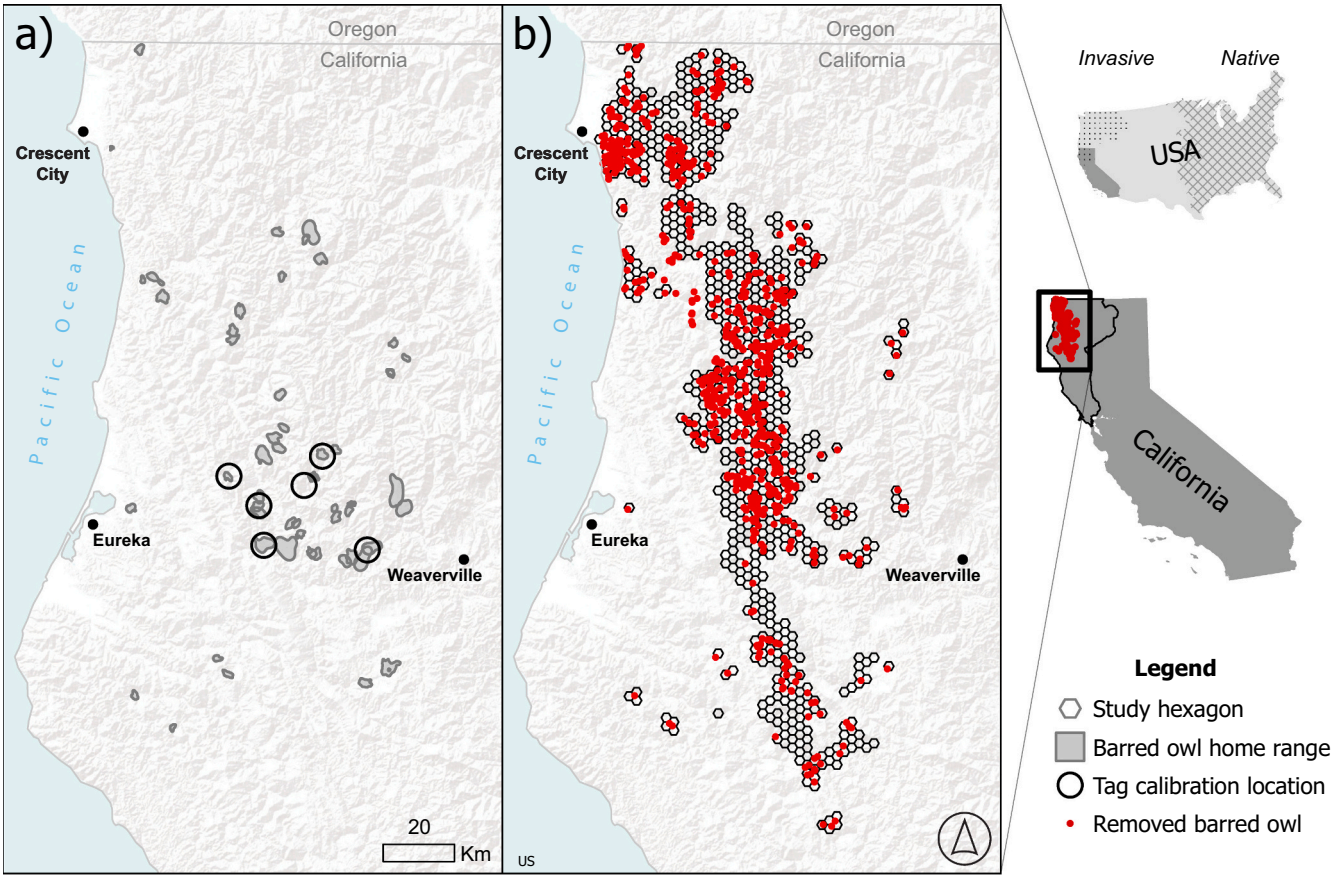

Fig. 1. (a) Home ranges (95% AKDE) for GPS-tagged barred owls (gray polygons, $n = 56$), and stationary GPS calibration tags (open circles, $n = 6$). (b) Survey grid of 5-km^2 hexagons (gray), and barred owl removals (red points). The inset shows the study area within the range of the northern spotted owl in California (black outline) and the western United States. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Field methods

Over a three-year period (14 August 2023 to 29 August 2025), an area of 4070 km^2 was surveyed for barred owl presence by trained personnel in tandem with an ongoing barred owl removal effort conducted across the study area (Fig. 1; Hobart et al., 2025). Live-capture for owl telemetry and removal were conducted as coordinated but operationally separate efforts across the study area. Field crews visited 5-km^2 survey hexagons at night and broadcast conspecific vocalizations to attract owls. These survey and humane-removal techniques followed established barred owl management methods (Diller et al., 2014; USFWS, 2024). The capture crew opportunistically attempted to live-capture owls for tagging across the study area, whereas removal crews independently surveyed and removed owls in areas not occupied by active telemetry subjects.

Live-captured owls were fitted with GPS tags following Jirinec et al. (2024). Conspecific vocalizations were broadcast to lure territorial individuals into mist nets (12 × 2.6 m; 127-mm mesh, 4 pockets) beginning after local sunset. Two nets were stacked and hoisted up to 10 m high using a Triple High Mist Net Pole System (Bat Conservation and Management, Carlisle, Pennsylvania, USA), depending on vegetation structure and bird behavior. Several individuals were also captured using snare poles. Following capture, owls were hooded to reduce stress, banded with a numerical lock-on band, and measured (wing cord, tail length, mass). A blood sample (≤1 mL) was collected via the brachial vein with a sterile 25-gauge needle for health assessment unrelated to this study. Sex was determined from vocalization characteristics and morphometrics (e.g., size, presence of brood patch) and confirmed during gross necropsy. Age of owls (both removals and live-captures) was assessed from feather characteristics and molt limits (Pyle et al., 1997, 2022; Weidensaul et al., 2011), and individuals were assigned into four age classes: juveniles (FCJ), subadults in their first molt cycle (FCF), subadults in at least their second molt cycle (M-SCB), and adults in at least their third molt cycle (M-TCB).

We preferentially deployed tags on individuals past their first molt cycle (M-SCB or older; >1 year), which were more likely to hold established territories and remain range-resident within the study area. One exception was a female (ID-55) tagged as FCF, who molted into SCB shortly thereafter while still tagged and collecting data. Apart from three pairs, only one individual per pair was tagged. Owls were equipped with a tag (~20 g; PinPoint VHF-450, Lotek Wireless, Newmarket, Ontario, Canada) ventrally reinforced with a 0.2 mm titanium plate (~0.7 g) to reduce risk of tag damage during lethal removal of the individual. Tags were attached with a backpack-style harness made from braided elastic (Bierregaard, 2014; Clément et al., 2021) and programmed to record one GPS fix every 4 h for 61 days, beginning at 00:00 GMT on the second night following capture (~24 h post-capture). Observers remotely downloaded location data from tags approximately every two weeks and any additional data were retrieved from recovered after removal. This schedule allowed for a maximum of 366 locations per bird, although actual samples were typically lower due to failed fixes, earlier battery depletion, or premature tag removal by the bird. Once an owl was tagged, the capture crew informed removal crews and provided updated locations as needed so that active telemetry subjects and the areas they occupied were avoided during ongoing removal operations. After the conclusion of the sampling schedule (typically after 61 days, though often removal occurred later), study individuals were humanely removed using approved methods by trained and permitted personnel using the same established removal protocols cited above.

Calibration tags were deployed within the study area to quantify GPS error for animal-borne locations (Fig. 1). Because GPS signal quality can be reduced by vegetation and topography (Jiang et al., 2008; Recio et al., 2011), we placed six stationary tags for a mean of 17.5 days (range: 9–28) across a gradient of conditions, from valley bottoms to ridge tops. Tags were affixed to trees at ~2 m above ground and positioned away from trunks, except for one tag placed inside a tree cavity to represent signal conditions induced by cavity-nesting owls.

2.3. Habitat data

2.3.1. Forest structure and topographic variables

To evaluate barred owl selection of individual forest structural attributes, we obtained nine continuous vegetation variables from gradient nearest neighbor (GNN) imputation maps (version GNN.2023.1, 2021 imagery year) produced by the Landscape Ecology, Modeling, Mapping, and Analysis group (Bell et al., 2023; LEMMA, 2023; Ohmann and Gregory, 2002). GNN integrates field plot data from the Forest Inventory and Analysis program with Landsat satellite imagery and mapped environmental data to produce forest structure and composition layers at 30-m resolution (Bell et al., 2023). As the sole non-structural, topographic predictor, we used a 30-m-resolution topographic wetness index (TWI) derived from a digital elevation model using triangular multiple flow direction (Hoylman, 2021). All ten predictors are described in Table 1.

The first six GNN variables—canopy cover, diameter diversity, stand height, large conifer density, mean tree diameter, and dominant stand age—represent core structural attributes of forest maturity (Franklin et al., 2002; Spies et al., 2018). The old-growth structure index (OGSI) integrates density of large live trees, diameter diversity, large dead tree (snag) density, and percent cover of dead wood into a composite index of late-successional and old-growth forest conditions (Davis et al., 2015, 2022a). Snag and down wood biomass capture the dead-wood component of old-growth structure independently of the composite index. TWI was the sole non-structural predictor: barred owls have been associated with riparian areas and moist lowland forest in parts of their invaded range (Hamer et al., 2007; Jenkins et al., 2019; McGee et al., 2024; Wiens et al., 2014), giving it the clearest prior support of any non-structural feature for selection by this species, and, being largely independent of the forest-structure gradient (Fig. S2), offering a reference against which the specificity of selection for late-seral structure can be judged.

Because GNN rasters were based on 2021 imagery and our telemetry data extended through 2025, we updated the structural layers to account for high-severity wildfire that occurred after the imagery date. We obtained burn severity maps for 2022–2024 from the Monitoring Trends in Burn Severity program (MTBS; www.mtbs.gov) and reclassified pixels burned at the highest severity class to zero for all nine GNN variables, reflecting the loss of forest structure in those areas. Non-forest pixels in the GNN rasters (coded as −1) were converted to zero prior to analysis. All ten predictors were then standardized (mean-centered and divided by one standard deviation) across the study area extent to enable comparison of selection coefficients on a common scale.

2.3.2. Spotted owl habitat layers

We used two spotted-owl-specific datasets in our selection analyses (Table 1). First, we used a landcover model of forest structure and composition used by northern spotted owls for nesting and roosting (hereafter “NR” forest; Davis et al., 2016, 2022b). The structural elements underlying this model included density of live large conifers, conifer canopy cover, mean conifer diameter, diameter diversity, and stand height. Species compositional elements included percentage of total stand basal area comprised of (and grouped by) pine, oak, subalpine, evergreen hardwoods, and redwoods. The NR forest layer classified forest into four categories: (1) unsuitable, (2) marginal, (3) suitable, and (4) highly suitable, representing increasing quality of forest structure and composition for spotted owl nesting and roosting, and thus habitat components important for spotted owl persistence. Secondly, we used a binary habitat/non-habitat layer (hereafter “NSO habitat” layer) modeled from environmental predictors related to the amount and spatial pattern of NR forests at multiple spatial scales, topography, and climate. Both models were trained and tested on 2809 northern spotted owl nest and pair day-roost locations collected circa 1993 (Davis et al.,

Table 1
Predictors used in resource selection function (RSF) analyses of barred owl habitat selection in northwestern California. Forest structure variables were obtained from gradient nearest neighbor (GNN) imputation maps (Bell et al., 2023; LEMMA, 2023). The a priori predicted direction of barred owl selection is shown for each predictor.

Predictor	Abbreviation	Units	Resolution	Type	Prediction	Description
Forest structure						
Canopy cover	CANCOV	%	30 m	Continuous	+	Canopy cover of all live trees
Diameter diversity index	DDI	index	30 m	Continuous	+	Structural diversity based on live tree densities across diameter classes; higher values indicate multistoried stands
Stand height	STNDHGT	m	30 m	Continuous	+	Mean height of dominant and codominant trees
Large conifer density	TPHC_GE_50	trees ha^{-1}	30 m	Continuous	+	Density of live conifers ≥50 cm DBH
Mean tree diameter	MNDBHBA	cm	30 m	Continuous	+	Basal-area-weighted mean diameter of all live trees
Dominant stand age	AGE_DOM	years	30 m	Continuous	+	Basal-area-weighted mean age of dominant and codominant trees
Old-growth structure index	OGSI	index	30 m	Continuous	+	Composite index integrating large live tree density, tree size diversity, large snag density, and down wood cover (Davis et al., 2022a)
Snag biomass	SBPH_GE_25	kg ha^{-1}	30 m	Continuous	+	Biomass of snags ≥25 cm DBH and ≥2 m tall
Down wood biomass	DBPH_GE_25	kg ha^{-1}	30 m	Continuous	+	Biomass of down wood ≥25 cm diameter at large end and ≥3 m long
Topography						
Topographic wetness index	TWI	index	30 m	Continuous	+	Tendency of a site to accumulate water based on upslope contributing area and local slope (Hoylman, 2021)
NSO habitat layers						
NSO habitat	–	binary	100 m	Categorical	+	Landscape-scale habitat suitability modeled from environmental predictors (Glenn et al., 2017; 2024 version)
NR forest suitability	–	4 classes	30 m	Categorical	+	Nesting and roosting forest classified as unsuitable, marginal, suitable, or highly suitable (Davis et al., 2016, 2022b; 2024 version)

2016; Glenn et al., 2017). The year 1993 was chosen because barred owls were still relatively uncommon, minimizing potential bias from interspecific competition in habitat selection (Dugger et al., 2016). Models were generated separately within physiographic modeling regions across the northern spotted owl range (Davis et al., 2016), so the layers applied to our study area were parametrized with local data. These models are projected to more recent environmental conditions and annually updated; we used the 2024 versions to align with the bulk of our telemetry data (Table S1). Across the northern spotted owl range, these layers best represent the suite of resources and conditions that support spotted owl occupancy (Hall et al., 1997; Krausman and Morrison, 2016; Lesmeister et al., 2018).

The NSO habitat layer is built at 100-m resolution, representing broader landscape-scale potential for occupancy, whereas the NR forest layer operates at 30-m resolution, capturing finer-scale variation in forest structure quality for nesting and roosting. The two layers together provide complementary perspectives on the degree to which barred owl space use overlaps with conditions important for spotted owls.

2.4. Analytical approach

We processed and analyzed barred owl telemetry data in R package *ctmm* v1.3.0 (Calabrese et al., 2016), a continuous-time movement-modeling framework that represents GPS location error and temporal autocorrelation explicitly. Calibration data from stationary tags (Section 2.2) indicated that topography substantially influenced GPS accuracy and occasionally produced outliers of up to several kilometers. Because unmodeled location error can bias inference if not properly addressed (Fleming et al., 2021), we implemented standardized filtering criteria based on spatial displacement, estimated speeds, and dilution of precision (DOP) values for each individual. Specifically, we removed GPS fixes that met any of the following thresholds: a) DOP > 20, b) distance from the geometric median of all locations for that individual > 5 standard deviations above the mean, c) distance from the geometric median > 99th percentile, or d) minimum speed required to explain successive locations > 10 standard deviations above the mean. Although heuristic, these criteria yielded a deliberately conservative estimate of barred owl space use and thus overlap with spotted owl habitat. The curated location dataset was used for both home range and habitat selection analyses.

2.4.1. Home range estimation

Home range areas were based on autocorrelated kernel density estimates (AKDE; Fleming and Calabrese, 2017, Noonan et al., 2019) implemented via the workflow described by Calabrese et al. (2016). First, to account for location error, we calibrated the curated dataset with information from all six stationary loggers following the framework of Fleming et al. (2021). Calibration data were first filtered using the same criteria applied to bird-borne data for consistency. Second, for each individual owl we used the *ctmm* select() function to compare a candidate set of movement models (Calabrese et al., 2016). The candidate set included isotropic and anisotropic Ornstein-Uhlenbeck (OU) models (Dunn and Gipson, 1977; Uhlenbeck and Ornstein, 1930), Ornstein-Uhlenbeck foraging (OUF) models and a constrained OUF variant with identical position and velocity autocorrelation timescales (Fleming et al., 2014), a central-place foraging model (Fleming et al., 2015), and an independently and identically distributed (IID) model representing no autocorrelation. We selected the best-supported movement model for each individual (Burnham and Anderson, 2004). Third, we estimated home ranges with AKDE using the selected movement model and enabled *ctmm*'s optimal temporal weighting, which adjusts for irregular sampling intervals among fixes (Fleming and Calabrese, 2017; Noonan et al., 2019). Home ranges were based on the 95% AKDE contour and group-level home range size estimates (all individuals, sex) were obtained using a hierarchical meta-analytic framework that propagates uncertainty, implemented with the mean() function in *ctmm* (Fleming et al., 2022). AKDE requires range-resident movement (Calabrese et al., 2016). One owl (ID-55) undertook a brief foray (~15 km from its normal area for 4 days) before returning. We censored this 4-day bout prior to model fitting to satisfy the range-residency assumption.

For comparability with earlier barred owl telemetry studies that reported minimum convex polygon (MCP) and fixed-kernel density estimates (KDE; using reference bandwidth), we also estimated 100% MCP, 95% fixed-kernel density (KDE, reference bandwidth), and 95% adaptive local convex hull (LoCoH; Getz et al., 2007) home ranges from the same filtered locations in R package *adehabitatHR* v0.4.22, selecting per individual the smallest adaptive parameter that yielded a hole-free 95% isopleth. These conventional IID estimators were used only for comparison and were not used for inference.

2.4.2. Habitat selection

We examined third-order selection (Johnson, 1980) using resource selection functions (RSFs) following the autocorrelation-informed workflow of Alston et al. (2023). RSFs contrasted used (observed) locations against availability defined by each individual's 95% AKDE utilization distribution. This approach accounts for temporal autocorrelation while minimizing pseudoreplication and bias in selection inference. Individual RSFs were fit with small-sample bias correction, then combined into population-level coefficients as described below.

To evaluate barred owl selection of forest structure, we first screened the ten standardized predictors (Table 1) for collinearity. On a uniform 100-m lattice within each barred owl's 95% AKDE home range, we computed a Spearman correlation matrix (Fig. S2) and variance inflation factors (VIF). The nine forest-structure attributes were strongly intercorrelated (many $|\rho| > 0.5$; VIF up to 18.6), whereas topographic wetness was effectively independent ($|\rho| < 0.07$). Because fitting the correlated attributes together produced unstable, mutually suppressed coefficients (Fig. S4), we did not interpret multivariate structural models and instead summarized structural selection with a single composite axis (below).

To build that axis, we reduced the nine attributes to their first principal component—an old-forest axis—with the prcomp() function in base R on centered and scaled predictors, oriented so that higher values denote more mature forest (Fig. 3). This axis was near-identical whether derived within home ranges or across the study region (Tucker's congruence coefficient ~ 1; Fig. S3), indicating it reflects the forest rather than where owls settled. We used the axis as our primary structural predictor and retained topographic wetness as an independent control; because the structural attributes are collinear (Fig. S2), the per-attribute univariate RSFs decompose this axis rather than provide independent effects.

Population-level coefficients were obtained with the same hierarchical meta-analytic estimator used for home ranges, implemented with the mean() function in ctmm (Fleming et al., 2022). This estimator propagates each owl's uncertainty and among-individual variation rather than naively averaging point estimates. As an independent check using a modeling framework that accounts for individual variation differently, we also fit the RSFs as weighted logistic mixed models with per-owl random intercepts and slopes (Muff et al., 2020).

To examine whether barred owl selection of forest structure translates into disproportionate use of mapped spotted owl habitat, we fit RSFs using the NSO habitat and NR forest layers described in Section 2.3.2 (Table 1). For the NSO habitat layer, we collapsed its unsuitable and non-forest classes into a single non-habitat category to allow a binary habitat/non-habitat contrast. For the NR forest layer, we recoded the four suitability classes into separate binary indicator rasters and fit them jointly, so each class coefficient reflects selection for that class relative to all other cover on the landscape, including non-forest.

To scale habitat release estimates, we multiplied the telemetry-derived mean area of NSO habitat and NR forest contained within a barred owl home range by the number of removals most likely to represent established, range-resident birds. Because removal tallies also include females and younger birds—some of which may be non-resident dispersers and floaters—we restricted scaling to removed males ≥ M-SCB (i.e., beyond the first molt cycle). This choice is conservative because it credits habitat release only to this subset, despite additional removals of females and younger birds that may also reduce competitive pressure within the same areas.

In addition to the additive scaling estimate, we quantified the unique spatial footprint of removals over the study interval. For removed males ≥ M-SCB, we created equal-area circular buffers centered on each removal location with area set to the mean home range size, dissolved overlapping buffers, and calculated the union area. This metric provides a conservative index of the non-additive area potentially affected by removals given clustered effort and repeated removals in the same locations over multiple years.

3. Results

We GPS-tagged 58 barred owls during a focal removal effort within a region where several partners have carried out barred owl removals for spotted owl conservation (Hobart et al., 2025). Of these tagged individuals, one owl was never detected again after capture and release. We adopted a minimum threshold of 10 tracking days for inclusion in analyses; one individual did not meet this criterion because its tag failed before 10 days, leaving 56 owls (~5% of all owls removed during the study interval) for analysis (Table S1). Tags were programmed for 61-day deployments, but some yielded shorter intervals because of earlier battery depletion, premature detachment by birds, or tags remaining on unrecovered birds at the time of analysis. Owls meeting the ≥10-day threshold were monitored for a mean of 56.0 days (range: 12–61) and provided a mean of 294.7 locations (range: 48–356) after outlier filtering. Calibration data from stationary tags indicated a mean horizontal location error of 47.2 m (95% CI = 45.0–49.4 m), well above the few-meter error often assumed for GPS telemetry and large enough to bias space-use estimates if not explicitly modeled (Fleming et al., 2021).

Barred owl home range size varied by individual but not by sex (Fig. 2). Mean home range area was 6.7 km^2 (95% CI = 5.1–8.9 km^2) overall, 7.2 km^2 (5.4–9.3 km^2) for males, and 6.2 km^2 (3.8–9.7 km^2) for females. The smallest home range estimate was 0.2 km^2 and the largest 29.1 km^2. For comparability with earlier studies, mean 95% KDE, 100% MCP, and 95% LoCoH home range areas were 7.9, 9.9, and 3.7 km^2, respectively (Table S2).

3.1. Barred owl selection of forest structural attributes

Barred owls showed consistent positive selection for structural attributes associated with forest maturity (Fig. 3). Barred owls selected the old-forest axis (PC1)—a single maturity gradient summarizing the nine intercorrelated structural attributes—more than expected from availability ($\beta = 0.125$, 95% CI = 0.066–0.184). Projecting this relationship across the California portion of the spotted owl range illustrates where old-forest structure, and thus predicted barred owl use, is concentrated (Fig. 4). Because the structural predictors were strongly collinear (Section 2.4.2), this axis provides the clearest single-model summary of structural selection; decomposing it into univariate RSFs showed that selection was broad rather than driven by any single feature. Six of the nine structural variables had positive coefficients with 95% confidence intervals that excluded zero: canopy cover ($\beta = 0.147$, 95% CI = 0.071–0.223), diameter diversity index ($\beta = 0.123$, 95% CI = 0.063–0.182), stand height ($\beta = 0.122$, 95% CI = 0.059–0.185), large conifer density ($\beta = 0.115$, 95% CI = 0.053–0.177), mean tree diameter ($\beta = 0.090$, 95% CI = 0.034–0.146), and dominant stand age ($\beta = 0.075$, 95% CI = 0.026–0.125). Selection coefficients for the remaining three GNN variables—old-growth structure index ($\beta = 0.060$, 95% CI = −0.005–0.126), snag biomass ($\beta = 0.049$, 95% CI = −0.004–0.103), and down wood biomass ($\beta = 0.024$, 95% CI = −0.009–0.057)—were positive but had confidence intervals overlapping zero. The topographic wetness index, which loaded independently of the old-forest axis, showed no evidence of selection ($\beta = -0.008$, 95% CI = −0.088–0.072). A mixed-model robustness check with per-owl random intercepts and slopes (Muff et al., 2020) recovered the same direction and gradient of selection (Figs. S4–S6).

3.2. Barred owl selection of spotted owl habitat

Barred owls selected spotted owl habitat more than expected based on availability ($\beta = 0.266$, 95% CI = 0.064–0.469; Fig. 5), corresponding to an intensity ratio of 1.30 (95% CI = 1.07–1.60). Thus, barred owls used mapped spotted owl habitat about 30% more intensively than non-habitat across the landscape, consistent with disproportionate space use of spotted owl habitat.

Across the landscape, barred owls showed a consistent increase in

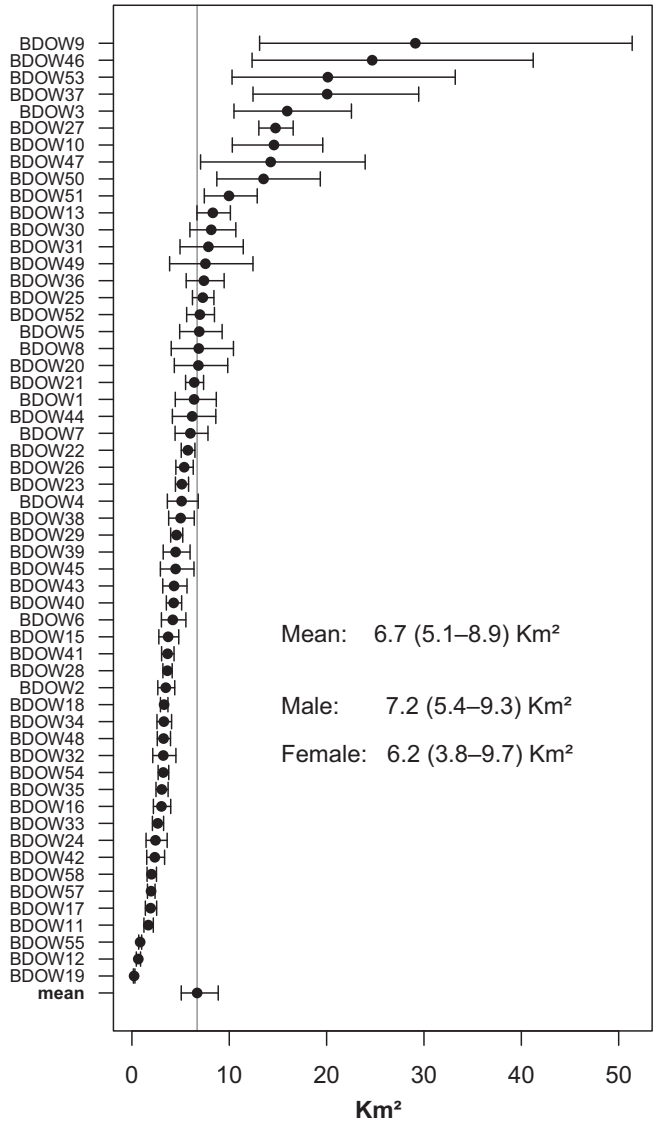

Fig. 2. Individual and population-level home range estimates of GPS-tagged barred owls in northwestern California, USA. Autocorrelated kernel density estimate (95% AKDE) home range areas (km^2) are shown for each tagged barred owl (black points ± 95% CI). The bottom row denotes the overall mean (±95% CI) across all individuals: 6.7 km^2 (5.1–8.9). Group-level means were 7.2 km^2 (5.4–9.3) for males and 6.2 km^2 (3.8–9.7) for females.

selection strength from unsuitable to highly suitable spotted owl NR forest classes. Estimated intensity ratios were 0.84 for unsuitable forest, 1.27 for marginal forest, 1.46 for suitable forest, and 1.52 for highly suitable forest, all relative to the mixed baseline that included non-forest (Fig. 5). The coefficient for highly suitable forest was strongly positive ($\beta = 0.421$, 95% CI = 0.139–0.703), corresponding to an intensity ratio of 1.52 (95% CI = 1.15–2.02), indicating roughly 50% greater use than the landscape baseline.

3.3. Spotted owl habitat within barred owl home ranges

Barred owl home ranges contained substantial amounts of northern spotted owl habitat and NR forest (Fig. 6). Specifically, the 56 barred owls with available home ranges contained collectively 214.4 km^2 of spotted owl habitat, and 98.3 km^2, 71.9 km^2, 71.1 km^2, 131.7 km^2 of unsuitable, marginal, suitable, and highly suitable NR forests, respectively. The average area of spotted owl habitat within barred owl home ranges was 3.83 km^2, and 1.28 km^2, 1.27 km^2, 2.35 km^2 of marginal, suitable, and highly suitable NR forests, respectively (Table S1). This translated into 64% of the average barred owl home range comprising spotted owl habitat, and 20%, 20%, and 38% for marginal, suitable, and highly suitable NR forests, respectively.

A total of 1171 barred owls were removed from the study area during the study interval. This included 619 males and 547 females; sex was unknown for 5 individuals. Age classes included 9 FCJ (juveniles), 190 FCF (subadults), 293 M-SCB (older subadults), and 676 M-TCB (adults); age was unknown for 3 individuals.

For habitat availability scaling, we focused on removed males ≥ M-SCB ($n = 489$) as the subset most likely to represent established, territorial birds. We multiplied this count by the mean area of spotted owl habitat contained within a barred owl home range (3.83 km^2; Table S1). This yields an estimated 1873 km^2 of spotted owl habitat made available for potential spotted owl recolonization. Applying the same approach to NR forest yielded 628 km^2 of marginal, 621 km^2 of suitable, and 1149 km^2 of highly suitable NR forest made available by removals.

Because removals were spatially clustered and occurred over multiple years, the habitat-release totals above are not strictly additive in space. The dissolved equal-area buffer footprint of removed males (≥M-SCB; see Methods) yielded a unique spatial extent of 1851 km^2—about 57% of the naive additive footprint (489 × 6.7 = 3276 km^2)—highlighting that many removals occurred in the same areas as barred owls recolonized.

4. Discussion

Invasive barred owls in northwestern California select the structural hallmarks of old forest strongly and consistently, and that single result carries a substantial consequence. Selection loaded on a single gradient of forest maturity—an old-forest axis—and intensified toward the highest-quality forest, concentrating each owl's pressure in the most structurally developed stands on the landscape. To quantify what that concentration means for the fauna these forests support, we used the northern spotted owl as a mapped lens: its habitat layers are built from the same structural gradients barred owls selected, and it has long served as an umbrella species for this forest type (Thomas et al., 1990). Seen through that lens, barred owls disproportionately used spotted owl habitat—most strongly its highest-quality class, which formed the single largest component of the average home range. By tracking individuals with GPS and modeling space use with explicit accounting for location error, we resolved the spatial mechanism behind the barred owl's competitive exclusion of spotted owls and translated it into a quantity managers can act on: the area of functional spotted owl habitat reclaimed when a resident barred owl pair is removed. And because the spotted owl is an umbrella for a wider old-forest community, the pressure a large-bodied generalist exerts in this forest plausibly extends beyond spotted owls to co-occurring old-forest species—through predation as much as competition—an implication our habitat-based results point to but do not directly measure.

4.1. Selection for old-forest structure

Barred owls selected the structural attributes of mature, closed-canopy forest, as we predicted. Selection loaded on a coherent old-forest axis, and decomposing that axis showed the response was broad rather than driven by any single feature, with nine of ten attributes positive and six of them individually significant (Fig. 3). Canopy cover, diameter diversity, stand height, large-conifer density, mean tree diameter, and stand age all excluded zero. This directionality corroborates and extends earlier radio-telemetry studies that linked barred owls to old conifer forest, large trees, and tall stands (Hamer et al., 2007; Irwin et al., 2017; Jenkins et al., 2019; Wiens et al., 2014), but resolves the response as selection for the living architecture of late-seral forest. The three attributes describing dead wood and decay were positive but non-significant. As sit-and-wait predators that hunt from elevated

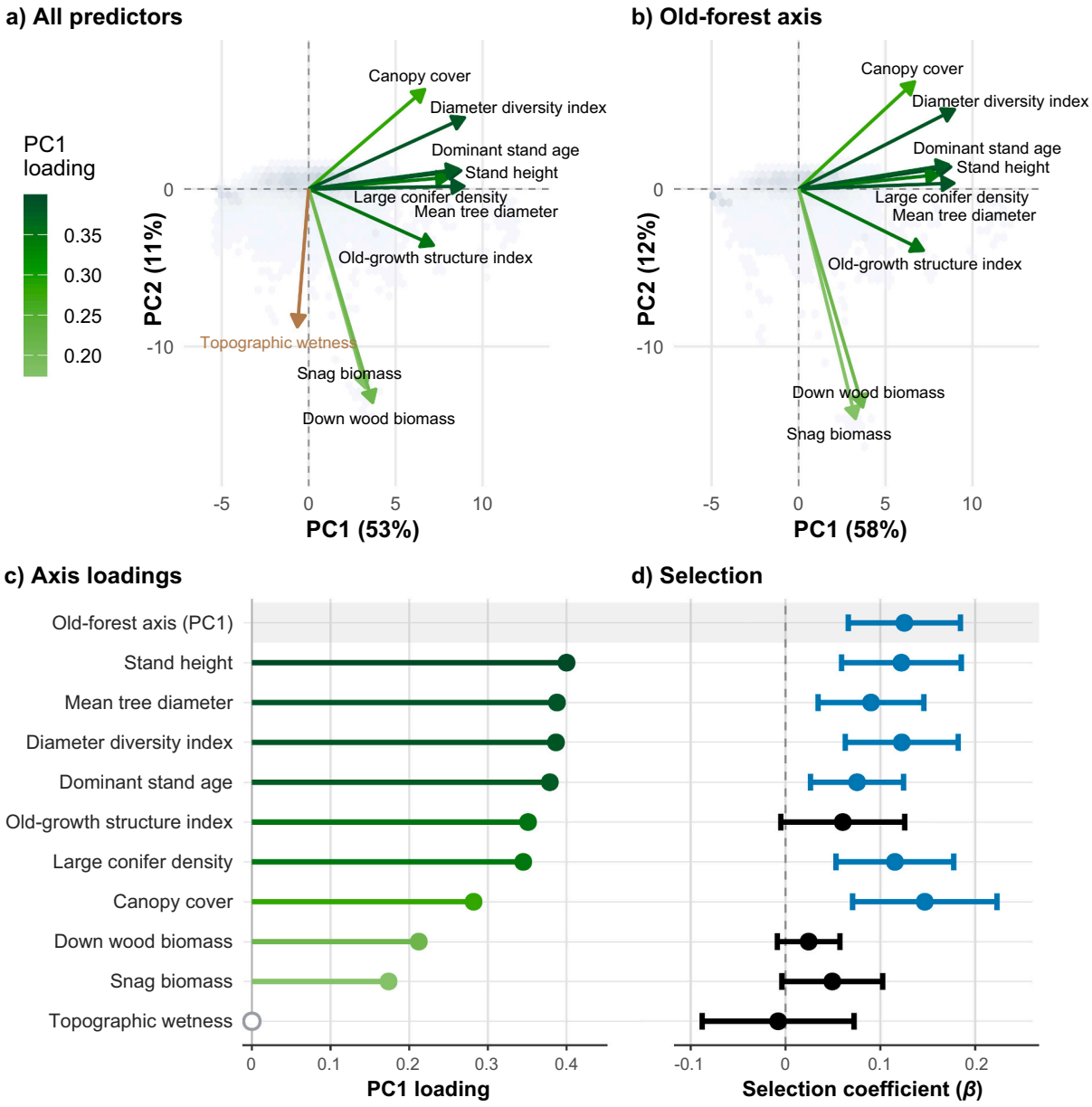

Fig. 3. Forest structure of the barred owl selection space, summarized by a single old-forest axis. (a) Principal component analysis (PCA) of all 10 forest-structure and topographic predictors and (b) of the 9 forest-structure predictors alone (topographic wetness index, TWI, excluded), each shown as a biplot of the first two components. Arrows are predictor loadings and shaded by their loading on the first component (PC1). PC1 is the "old-forest axis," on which positive values correspond to older, taller, more structurally complex forest; it explains 53% of the variance among all predictors and 58% among the structural predictors alone, and TWI loads roughly orthogonally to the old-forest cluster. (c) PC1 loadings for each predictor, ordered by loading. (d) Univariate selection coefficients (±95% CI) for each predictor, each from an independent single-predictor RSF fitted to a standardized predictor layer. Barred owls showed consistent positive selection for predictors associated with late-successional forest structure and for the old-forest axis.

perches, barred owls plausibly respond to the vertical space and prey base that tall, large-diameter, structurally diverse stands provide rather than to decay elements per se (Bierregaard et al., 2025; Wiens et al., 2014). Large-diameter trees supply the cavities they nest in, and high canopy closure with tall, multi-layered stands creates the sheltered, structurally complex setting that conceals a hunting owl and sustains its prey (Sillett and Van Pelt, 2007; Spickler et al., 2006). Dead wood also adds to that complexity and supports prey (Carey, 1995), so the weaker dead-wood signal more likely reflects owls tracking the living scaffold of the forest than indifference to decay. The old-growth structure index illustrates the point, as this composite of live- and dead-structure elements returned only an intermediate, non-significant coefficient, consistent with strong selection for its live-structure components offset by a weak dead-wood signal, though we cannot fully separate biology from the lower mapping accuracy of dead-wood layers (Bell et al., 2023).

4.2. *Overlap with spotted owl habitat and the old-forest community*

This structural selection scaled up, as predicted, to disproportionate use of mapped spotted owl habitat, with intensity rising across nesting and roosting suitability classes and peaking in the highest-quality forest (Fig. 5). Because those layers are built from the same structural gradients the old-forest axis captures (Davis et al., 2016; Lesmeister et al., 2018), the overlap is a predictable consequence of shared dependence on late-seral structure, and it matches range-wide occupancy patterns

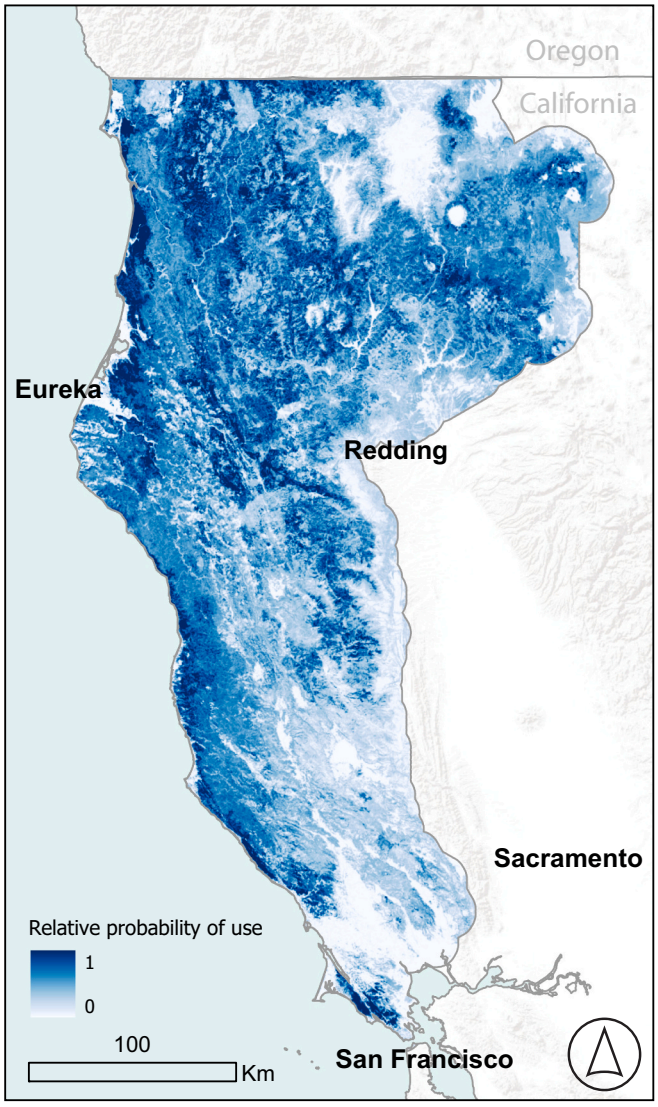

Fig. 4. Predicted relative probability of use by barred owls along the old-forest structural axis (PC1). The univariate selection relationship (Fig. 3d), fitted within the surveyed study area (Fig. 1), is projected here across the California portion of the northern spotted owl range. Barred owl use increased with old-forest structure—the tall, old, structurally complex forest that supports a suite of old-forest-associated species. The mapped surface is aggregated and Gaussian-smoothed for display; all analyses used the native 30-m resolution.

(Jenkins et al., 2025) and territory-scale evidence that barred owl presence raises spotted owl extinction risk (Yackulic et al., 2019). Our data give this competition a spatial signature, as barred owls have co-opted much of the forest most important for spotted owl persistence. Spotted owl survival, the dominant driver of population growth rate, is most tightly tied to nesting and roosting forest in the territory core, whereas reproduction depends more on landscape heterogeneity, with the highest-fitness territories interleaving older forest and roughly 40% other vegetation types (Dugger et al., 2005; Franklin et al., 2000; Olson et al., 2005). Because barred owls selected most strongly for exactly this high-quality nesting and roosting forest, their competitive displacement of spotted owls from it poses an acute demographic threat—one that helps explain why spotted owls keep declining even as structural nesting and roosting forest holds steady or increases on federal lands (Davis et al., 2022b; Franklin et al., 2021).

Individual home ranges bore this out. On average, 64% of a barred owl's home range was spotted owl habitat and 38% was the highest-quality nesting and roosting forest, about twice the share of lower-quality classes (Fig. 6). Each territorial owl therefore concentrates its competitive and predatory influence within the best remaining old forest, and the consequences reach beyond spotted owls. Because the attributes barred owls select also define habitat for the wider old-forest community (Carey, 1995; Franklin et al., 2002; Lesmeister et al., 2018; Thomas et al., 1990), and because barred owls are dietary generalists that take flying squirrels, tree voles, woodrats, salamanders, and small carnivores at densities several times those of the owls they displace (Kryshak et al., 2022; Wiens et al., 2014, 2021), their space use concentrates novel predation pressure where old-forest prey communities are richest, with the potential to propagate into trophic cascades and altered ecosystem processes (Holm et al., 2016). Many of these prey, including amphibians, reptiles, and small carnivores such as western spotted skunks (Tosa et al., 2022), are rare or absent in spotted owl diets and have no evolutionary experience of an avian predator hunting old forest at these densities (Kryshak et al., 2022; Sih et al., 2010), and small mammals such as flying squirrels and tree voles are themselves ecological linchpins that disperse mycorrhizal fungi and cycle nutrients essential to forest regeneration. Concentrated predation on such species is precisely the kind of top-down perturbation known to cascade through communities and ecosystem processes (Estes et al., 2011), so the stakes of this invasion extend well beyond a single competitor to the integrity of the old-forest community itself.

4.3. *Home-range size and the footprint of invasion*

A defining feature of these home ranges is their size in the invaded range. The mean of 6.7 km^2 is roughly 28 times the 0.24 km^2 we recorded for barred owls in their native range in Louisiana using the same continuous-time movement framework (Jirinec et al., 2024), a gap consistent with the general expansion of space requirements as resources thin toward higher latitudes. Because both estimates arise from the same analytical approach, the contrast is directly comparable, and its meaning is more than ecological. Each territorial owl in the invaded range concentrates its competitive and predatory influence over an area more than an order of magnitude larger than a conspecific holds at home, magnifying the per-individual footprint of the invasion across the old forest that spotted owls and other specialists depend on. Autocorrelated kernel density estimation propagated the calibrated location error—modeled for each fix from its GPS precision and averaging ~47 m—through each owl's fitted movement model, yet the resulting home ranges were smaller than the conventional, error-agnostic estimators most comparable to earlier barred owl studies (95% fixed-kernel KDE and 100% MCP; Table S2, Fig. S1). This confirms that accounting for error and autocorrelation did not inflate home-range size.

4.4. *Limitations*

Several limitations qualify these inferences. We relied on modeled spotted owl habitat layers and imputation-based structural maps, which simplify ecological complexity but remain the standard tools for spotted owl recovery planning, and selection was consistent across independently derived structural metrics (Bell et al., 2023). GPS error was substantial (~47 m; Table S3) and biased against detecting the very features the owls selected, because dense canopy and steep drainages both degrade GPS performance and characterize the forest these owls use, making our selection estimates conservative (Alston et al., 2023; Fleming et al., 2021). Because the structural predictors were too collinear to separate cleanly, our primary structural inference rests on the old-forest axis rather than on individual attributes, which should be read as a decomposition of a shared maturity gradient rather than as independent effects. Finally, the absence of topographic-wetness selection contrasts with northern study areas where barred owls favored lower elevations, gentler slopes, and stream margins (Hamer et al., 2007; Jenkins et al., 2019; McGee et al., 2026; Wiens et al., 2014), though it aligns with the lack of a stream effect reported elsewhere

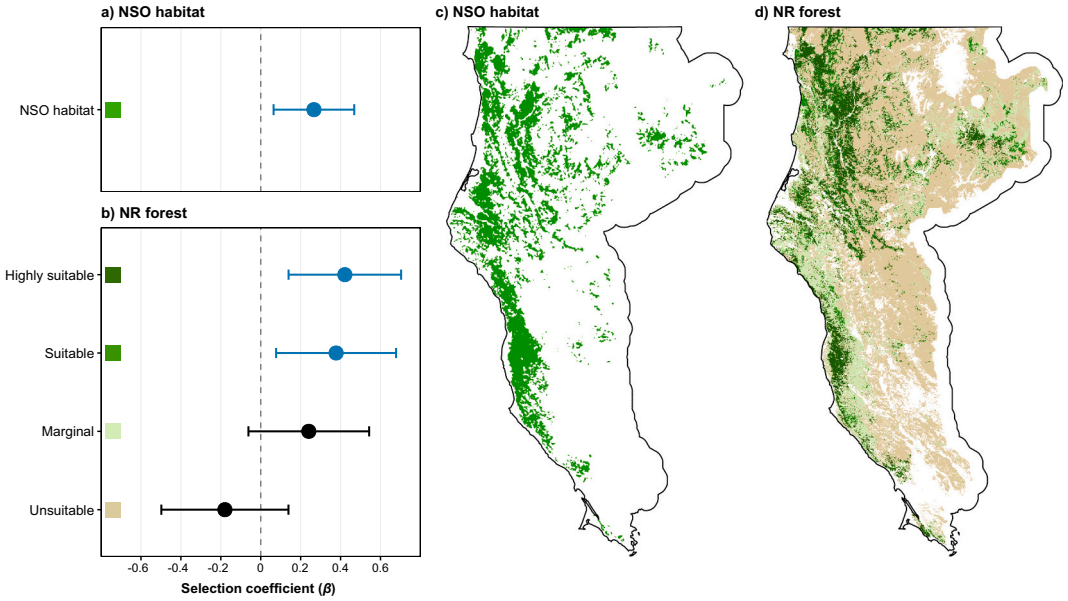

Fig. 5. Barred owl resource selection in relation to northern spotted owl (NSO) habitat—one old-forest-associated species for which suitable habitat is mapped across the region. Left, selection coefficients (±95% CI) for (a) the binary NSO "habitat" layer (Glenn et al., 2017, updated 2024) and (b) the four classes of the NSO nesting and roosting (NR) suitability layer (Davis et al., 2022b). Right, the corresponding layers mapped across the California portion of the NSO range: (c) NSO habitat and (d) NR forest. Barred owls selected NSO habitat overall, and selection increased across NR classes toward highly suitable forest. The maps in (c) and (d) are aggregated and smoothed for display at the grain of Fig. 4; coefficients were estimated from the native 30-m layers.

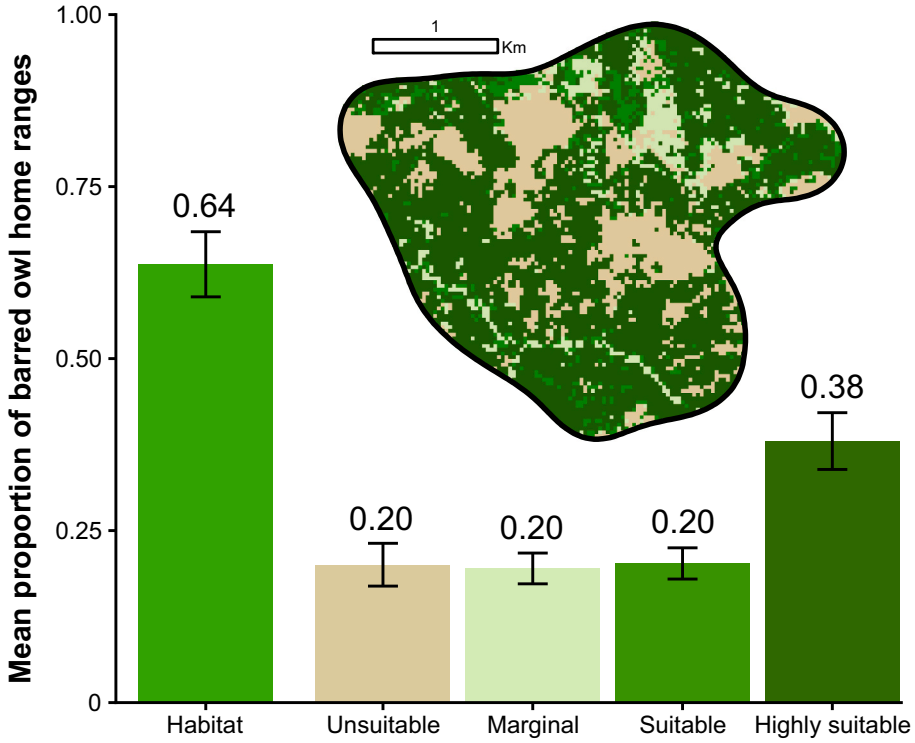

Fig. 6. Mean proportion of northern spotted owl habitat classes contained within barred owl home ranges (95% AKDE, $n = 56$). Bars show the mean proportion across individuals, with 95% confidence intervals. On average, 64% of a barred owl home range consisted of spotted owl habitat, and 38% of highly suitable nesting and roosting forest. The inset shows an example home range (BDOW13) overlaid on NR suitability (Davis et al., 2022b).

(Irwin et al., 2017; Singleton et al., 2010). In the steep, dissected Klamath terrain of our study area, riparian bottoms are narrow and spatially constrained, which may blunt how sharply topographic wetness differentiates barred owl space use rather than signaling indifference to moist sites.

4.5. Functional habitat loss and the case for sustained management

Our results reframe what habitat means for spotted owls. Under the ecological definition of habitat as the resources and conditions that produce occupancy (Hall et al., 1997; Krausman and Morrison, 2016),

much structurally suitable forest no longer functions as spotted owl habitat, because barred owls actively prevent occupancy, a biotic form of habitat loss that structure-based monitoring cannot see. This distinction carries practical weight, because under the U.S. Endangered Species Act the designation of habitat shapes where protections apply and how recovery is judged, so a widening gap between mapped structural habitat and forest that can actually support occupancy has direct management consequences. The situation also differs fundamentally from classically unoccupied habitat, where a species is simply too sparse to fill every suitable area (Hall et al., 1997), because here occupancy is actively suppressed by a competitor even where the forest remains intact, a reading anticipated by early recognition that monitoring maps depict potentially occupied habitat (Davis and Lint, 2005). Protecting forest structure, the central mechanism of the Northwest Forest Plan, is therefore necessary but not sufficient. Where barred owls are removed and structure persists, our results and previous evidence suggest this suppressed carrying capacity can rebound. With barred owls now occupying about 87% of forest-capable lands across the range (Jenkins et al., 2025), the area that can actually support spotted owls is far smaller than structural metrics imply. The corollary, however, is hopeful. Because the forest itself remains, removing barred owls should restore functional habitat. A spotted owl territory is not freed while either resident barred owl remains, so this recovery follows removal of the pair, which vacates on average an estimated 3.83 km^2 of spotted owl habitat (Table S1). Since we could not determine how many of the removed birds formed pairs, we scaled release conservatively by the number of removed territorial males (Section 3.3), yielding on the order of 1873 km^2 reclaimed in additive terms, in line with experiments where sustained removal stabilizes or reverses spotted owl declines and with the federal strategy that makes targeted removal the cornerstone of recovery (Diller et al., 2016; USFWS, 2024; Wiens et al., 2021).

These gains, however, are neither permanent nor spatially additive. Because barred owls recolonize quickly and removals cluster in the same places over time, the reclaimed area is not strictly additive, and an equal-area footprint of the removed territorial males spanned roughly 1850 km^2, about 57% of the 3276 km^2 expected had their home ranges not overlapped. Recovery will therefore hinge on sustained removal targeted where the highest-quality forest and the strongest barred owl selection coincide, which should maximize the habitat reclaimed per owl removed. Co-occurrence models built to guide barred owl management point the same way (Srivastava et al., 2026), and the practical case for sustained lethal control has been argued in detail (Dumbacher and Franklin, 2025). Because barred owls occupy the same old forest that supports the broader late-seral community, this management may also relieve predation and competitive pressure on other old-forest species, a co-benefit that remains to be tested directly.

4.6. *Conservation where habitat loss and invasion coincide*

More broadly, our findings speak to a challenge that recurs wherever habitat loss and biological invasion coincide, the two most pervasive drivers of the biodiversity crisis, and drivers that increasingly act in concert rather than in isolation (Didham et al., 2007; Pyšek et al., 2020). Invaders are damaging in part because they can outcompete or displace ecologically similar natives through competitive exclusion and niche displacement (Mooney and Cleland, 2001), and because native prey and competitors are often naive to enemies with which they share no evolutionary history (Salo et al., 2007; Sih et al., 2010). Alien species now figure in far more recent extinctions than native ones (Bellard et al., 2016; Blackburn et al., 2019), and their harm is greatest not when they merely occur within valuable native habitat but when they concentrate there, aligning competitive and predatory pressure with the areas of highest conservation value. The barred owl joins a broad set of such cases. The introduced eastern gray squirrel has replaced the native red squirrel across much of Britain and Italy (Gurnell et al., 2004), invasive Pacific lionfish have risen to nearly 40% of predator biomass on some Atlantic reefs, driving native prey-fish declines exceeding 60% and reducing native reef-fish recruitment by roughly 79% in controlled experiments (Albins and Hixon, 2008; Green et al., 2012), and introduced generalist predators have erased naive endemics across oceanic islands (Doherty et al., 2016). In each, a competitively superior generalist concentrates novel pressure on communities with little defense against it, a form of apex-level disruption increasingly recognized as a pervasive driver of ecological change (Estes et al., 2011).

The cautionary lesson from our system is that protecting habitat structure cannot, by itself, conserve species threatened by such invaders. Because barred owls select the very structure that defines spotted owl habitat, structurally intact forest can remain fully suitable on the map yet be biologically unavailable in practice, a form of functional habitat loss that vegetation-based monitoring does not capture. Where habitat degradation and a spreading competitor coincide, habitat set-asides risk becoming empty refuges, and the native specialist becomes a conservation-reliant species, dependent on continuing management of the biotic threat rather than on habitat protection alone (Scott et al., 2010). Conserving specialists under invasion therefore requires anticipating where an invader will concentrate its impact and sustaining management there, an effort that may prove as central to their persistence as protecting the habitat itself.

CRediT authorship contribution statement

Vitek Jirinec: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mourad W. Gabriel:** Writing – review & editing, Resources, Investigation, Conceptualization. **J. Mark Higley:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Raymond J. Davis:** Writing – review & editing, Methodology. **Jonathan E. Tenberge:** Writing – review & editing, Methodology, Investigation, Data curation. **Christina P. Varian:** Writing – review & editing, Investigation. **Daniel F. Hofstadter:** Writing – review & editing, Supervision, Investigation, Funding acquisition. **M. Zachariah Peery:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Julianna M.A. Jenkins:** Writing – review & editing, Formal analysis. **Alan B. Franklin:** Writing – review & editing. **Greta M. Wengert:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT and Claude in order to copyedit the manuscript and debug R code. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: J. Mark Higley reports a relationship with Hoopa Valley Tribe that includes: funding grants. M. Zachariah Peery reports a relationship with University of Wisconsin-Madison that includes: funding grants. If there are other authors, they 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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112035.

Data availability

LEMMA GNN layers and northern spotted owl habitat and nesting and roosting forest layers are publicly available and updated annually (available at the NWFP NSO mapping portal: https://r06-nwfp.projects.earthengine.app/view/nwfp-nso-cts-mspa-trend-view). Barred owl GPS telemetry locations (and derived home range polygons) are not publicly available because they contain sensitive spatial information and could enable inference about illicit trespass cannabis cultivation sites within the study area, posing risks to ongoing conservation and enforcement activities. Summary data supporting the analyses are provided in Supplemental materials. De-identified data may be shared with qualified researchers upon reasonable request to the corresponding author, subject to approval and a data-use agreement.

References

Albins, M.A., Hixon, M.A., 2008. Invasive Indo-Pacific lionfish Pterois volitans reduce recruitment of Atlantic coral-reef fishes. Mar. Ecol. Prog. Ser. 367, 233–238.

Alston, J.M., Fleming, C.H., Kays, R., Streicher, J.P., Downs, C.T., Ramesh, T., Reineking, B., Calabrese, J.M., 2023. Mitigating pseudoreplication and bias in resource selection functions with autocorrelation-informed weighting. Methods Ecol. Evol. 14, 643–654. https://doi.org/10.1111/2041-210X.14025.

Bell, D.M., Gregory, M.J., Palmer, M., Davis, R.J., 2023. Guidance for forest management and landscape ecology applications of recent gradient nearest neighbor imputation maps in California, Oregon, and Washington. In: Gen. Tech. Rep. PNW-GTR-1018. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR (41 pp. (Online only). 1018).

Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. Biol. Lett. 12, 20150623.

Bierregaard, R.O., 2014. A technique to facilitate the fitting of telemetry transmitter harnesses. J. Raptor Res. 48. https://doi.org/10.3356/JRR-13-00016.1.

Bierregaard, R.O., Livezey, K.B., Pyle, P., Mazur, K.M., James, P.C., 2025. Barred owl (Strix varia), version 2.1. In: Birds of the World. https://doi.org/10.2173/bow.brdowl.02.1.

Blackburn, T.M., Bellard, C., Ricciardi, A., 2019. Alien versus native species as drivers of recent extinctions. Front. Ecol. Environ. 17, 203–207. https://doi.org/10.1002/fee.2020.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. https://doi.org/10.1177/0049124104268644.

Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol. Evol. 7, 1124–1132. https://doi.org/10.1111/2041-210X.12559.

Carey, A.B., 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Appl. 5, 648–661. https://doi.org/10.2307/1941974.

Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. Ecol. Appl. 5, 336–352. https://doi.org/10.2307/1942026.

Clément, M.A., Barrett, K., Baldwin, R.F., Bodinof Jachowski, C.M., Carter, A., Brinker, D., 2021. An unexpected backyard hunter: breeding Barred Owls exhibit plasticity in habitat selection along a development gradient. Urban Ecosyst. 24, 175–186. https://doi.org/10.1007/s11252-020-01031-0.

Davis, R.J., Lint, J., 2005. Chapter 3: Habitat status and trends. In: Lint, J. (Ed.), Northwest Forest Plan—The First 10 Years (1994–2003): Status and Trends of Northern Spotted Owl Populations and Habitat, PNWGTR. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, pp. 21–82.

Davis, R.J., Ohmann, J.L., Kennedy, R.E., Cohen, W.B., Gregory, M.J., Yang, Z., Roberts, H.M., Gray, A.N., Spies, T.A., 2015. Northwest Forest Plan–the first 20 years (1994-2013): status and trends of late-successional and old-growth forests. In: Gen. Tech. Rep. PNW-GTR-911. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR (112 p. 911).

Davis, R.J., Hollen, B., Hobson, J., Gower, J.E., Keenum, D., 2016. Northwest Forest Plan—the first 20 years (1994-2013): status and trends of northern spotted owl habitats. In: Gen. Tech. Rep. PNW-GTR-929. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. https://doi.org/10.2737/PNW-GTR-929 (54 p. 929).

Davis, R.J., Bell, D.M., Gregory, M.J., Yang, Z., Gray, A.N., Healey, S.P., Stratton, A.E., 2022a. Northwest Forest Plan—the first 25 years (1994–2018): status and trends of late-successional and old-growth forests. In: Gen. Tech. Rep. PNW-GTR-1004. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR (82 p. 1004).

Davis, R.J., Lesmeister, D.B., Yang, Z., Hollen, B., Tuerler, B., Hobson, J., Guetterman, J., Stratton, A., 2022b. Northwest Forest Plan—the first 25 years (1994–2018): status and trends of northern spotted owl habitats. In: Gen. Tech. Rep. PNW-GTR-1003. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. https://doi.org/10.2737/PNW-GTR-1003 (38 p. 1003).

DellaSala, D.A., Reid, S.B., Frest, T.J., Strittholt, J., Olson, D., 1999. A global perspective on the biodiversity of the Klamath-Siskiyou Ecoregion. Nat. Areas J. 19, 300–319.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol. Evol. 22, 489–496.

Diller, L.V., Dumbacher, J.P., Bosch, R.P., Bown, R.R., Gutiérrez, R.J., 2014. Removing barred owls from local areas: techniques and feasibility. Wildl. Soc. Bull. 38, 211–216. https://doi.org/10.1002/wsb.381.

Diller, L.V., Hamm, K.A., Early, D.A., Lamphear, D.W., Dugger, K.M., Yackulic, C.B., Schwarz, C.J., Carlson, P.C., McDonald, T.L., 2016. Demographic response of northern spotted owls to barred owl removal. J. Wildl. Manag. 80, 691–707. https://doi.org/10.1002/jwmg.1046.

Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R., 2016. Invasive predators and global biodiversity loss. Proc. Natl. Acad. Sci. USA 113, 11261–11265. https://doi.org/10.1073/pnas.1602480113.

Dugger, K.M., Wagner, F., Anthony, R.G., Olson, G.S., 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. Condor 107, 863–878.

Dugger, K.M., Forsman, E.D., Franklin, A.B., Davis, R.J., White, G.C., Schwarz, C.J., Burnham, K.P., Nichols, J.D., Hines, J.E., Yackulic, C.B., Doherty, P.F., Bailey, L., Clark, D.A., Ackers, S.H., Andrews, L.S., Augustine, B., Biswell, B.L., Blakesley, J., Carlson, P.C., Clement, M.J., Diller, L.V., Glenn, E.M., Green, A., Gremel, S.A., Herter, D.R., Higley, J.M., Hobson, J., Horn, R.B., Huyvaert, K.P., McCafferty, C., McDonald, T., McDonnell, K., Olson, G.S., Reid, J.A., Rockweit, J., Ruiz, V., Saenz, J., Sovern, S.G., 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. Condor 118, 57–116. https://doi.org/10.1650/CONDOR-15-24.1.

Dumbacher, J.P., Franklin, A.B., 2025. When avifauna collide: the case for lethal control of barred owls in western North America. Front. Ecol. Environ. 23, e2817. https://doi.org/10.1002/fee.2817.

Dunn, J.E., Gipson, P.S., 1977. Analysis of radio telemetry data in studies of home range. Biometrics 85–101.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science 333, 301–306. https://doi.org/10.1126/science.1205106.

Fleming, C.H., Calabrese, J.M., 2017. A new kernel density estimator for accurate home-range and species-range area estimation. Methods Ecol. Evol. 8, 571–579. https://doi.org/10.1111/2041-210X.12673.

Fleming, C.H., Calabrese, J.M., Mueller, T., Olson, K.A., Leimgruber, P., Fagan, W.F., 2014. From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. Am. Nat. 183, E154–E167. https://doi.org/10.1086/675504.

Fleming, C.H., Subaşı, Y., Calabrese, J.M., 2015. Maximum-entropy description of animal movement. Phys. Rev. E 91, 032107. https://doi.org/10.1103/PhysRevE.91.032107.

Fleming, C.H., Drescher-Lehman, J., Noonan, M.J., Akre, T.S.B., Brown, D.J., Cochrane, M.M., Dejid, N., DeNicola, V., DePerno, C.S., Dunlop, J.N., Gould, N.P., Harrison, A.-L., Hollins, J., Ishii, H., Kaneko, Y., Kays, R., Killen, S.S., Koeck, B., Lambertucci, S.A., LaPoint, S.D., Medici, E.P., Meyburg, B.-U., Miller, T.A., Moen, R. A., Mueller, T., Pfeiffer, T., Pike, K.N., Roulin, A., Safi, K., Séchaud, R., Scharf, A.K., Shephard, J.M., Stabach, J.A., Stein, K., Tonra, C.M., Yamazaki, K., Fagan, W.F., Calabrese, J.M., 2021. A comprehensive framework for handling location error in animal tracking data. https://doi.org/10.1101/2020.06.12.130195.

Fleming, C.H., Deznabi, I., Alavi, S., Crofoot, M.C., Hirsch, B.T., Medici, E.P., Noonan, M. J., Kays, R., Fagan, W.F., Sheldon, D., Calabrese, J.M., 2022. Population-level

inference for home-range areas. Methods Ecol. Evol. 13, 1027–1041. https://doi.org/10.1111/2041-210X.13815.
Franklin, A.B., Anderson, D.R., Gutiérrez, R.J., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecol. Monogr. 70, 539–590. https://doi.org/10.1890/0012-9615(2000)070%5B0539:CHQAFI%5D2.0.CO;2.
Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manag. 155, 399–423. https://doi.org/10.1016/S0378-1127(01)00575-8.
Franklin, A.B., Dugger, K.M., Lesmeister, D.B., Davis, R.J., Wiens, J.D., White, G.C., Nichols, J.D., Hines, J.E., Yackulic, C.B., Schwarz, C.J., Ackers, S.H., Andrews, L.S., Bailey, L.L., Bown, R., Burgher, J., Burnham, K.P., Carlson, P.C., Chestnut, T., Conner, M.M., Dilione, K.E., Forsman, E.D., Glenn, E.M., Gremel, S.A., Hamm, K.A., Herter, D.R., Higley, J.M., Horn, R.B., Jenkins, J.M., Kendall, W.L., Lamphear, D.W., McCafferty, C., McDonald, T.L., Reid, J.A., Rockweit, J.T., Simon, D.C., Sovern, S.G., Swingle, J.K., Wise, H., 2021. Range-wide declines of northern spotted owl populations in the Pacific Northwest: a meta-analysis. Biol. Conserv. 259, 109168. https://doi.org/10.1016/j.biocon.2021.109168.
Gause, G.F., 1935. The Struggle for Existence. Williams and Wilkins Press, Baltimore, Maryland, USA.
Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., Wilmers, C.C., 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS One 2, e207.
Glenn, E.M., Lesmeister, D.B., Davis, R.J., Hollen, B., Poopatanapong, A., 2017. Estimating density of a territorial species in a dynamic landscape. Landsc. Ecol. 32, 563–579. https://doi.org/10.1007/s10980-016-0467-6.
Green, S.J., Akins, J.L., Maljković, A., Côté, I.M., 2012. Invasive lionfish drive Atlantic coral reef fish declines. PLoS One 7, e32596.
Gurnell, J., Wauters, L.A., Lurz, P.W.W., Tosi, G., 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. J. Anim. Ecol. 73, 26–35. https://doi.org/10.1111/j.1365-2656.2004.00791.x.
Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 25, 173–182.
Hamer, T.E., Hays, D.L., Senger, C.M., Forsman, E.D., 2001. Diets of Northern Barred Owls and Northern Spotted Owls in an area of sympatry. J. Raptor Res. 35, 221–227.
Hamer, T.E., Forsman, E.D., Glenn, E.M., 2007. Home range attributes and habitat selection of Barred Owls and Spotted Owls in an area of sympatry. Condor 109, 750–768. https://doi.org/10.1093/condor/109.4.750.
Hobart, B.K., Hofstadter, D.F., Higley, J.M., Hamm, K.A., Dotters, B.P., Roberts, K.N., Cormier, R.L., Franklin, A.B., Berigan, W.J., Keane, J.J., Merkle, W.W., Press, D.T., Peery, M.Z., 2025. Taking action to avoid extinction: successful regional-scale lethal control of barred owls supports a federal strategy to save spotted owls. Conserv. Lett. 18, e13121. https://doi.org/10.1111/conl.13121.
Holm, S.R., Noon, B.R., Wiens, J.D., Ripple, W.J., 2016. Potential trophic cascades triggered by the barred owl range expansion. Wildl. Soc. Bull. 40, 615–624. https://doi.org/10.1002/wsb.714.
Hoylman, Z.H., 2021. A 30m Topographic Wetness Index Dataset for the Continental United States. https://doi.org/10.5281/zenodo.4460354.
Irwin, L.L., Rock, D.F., Rock, S.C., 2017. Barred owl habitat selection in west coast forests. J. Wildl. Manag. 82, 202–216. https://doi.org/10.1002/jwmg.21339.
Jenkins, J.M.A., Lesmeister, D.B., Wiens, J.D., Kane, J.T., Kane, V.R., Verschuyl, J., 2019. Three-dimensional partitioning of resources by congeneric forest predators with recent sympatry. Sci. Rep. 9, 6036. https://doi.org/10.1038/s41598-019-42426-0.
Jenkins, J.M.A., Rugg, N.M., Davis, R.J., Gremel, S.A., Henderson, A., Henson, E., Higley, M., Horan, H.D., McCafferty, C., Munger, T., Press, D., Reffler, S., Ruff, Z.J., Swingle, J.K., Tevini, E., Thomas, A.D., Wert, K., Lesmeister, D.B., 2025. Congener conflict: invasive barred owl landscape use across the range of the northern spotted owl. J. Biogeogr., e70070 https://doi.org/10.1111/jbi.70070.
Jiang, Z., Sugita, M., Kitahara, M., Takatsuki, S., Goto, T., Yoshida, Y., 2008. Effects of habitat feature, antenna position, movement, and fix interval on GPS radio collar performance in Mount Fuji, central Japan. Ecol. Res. 23, 581–588. https://doi.org/10.1007/s11284-007-0412-x.
Jirinec, V., Bresnan, A.M., Clément, M.A., Colón, M.R., Long, A.M., Rhyne, G.S., Rodrigues, P.F., Stein, E.D., Pérez-Umphrey, A.A., Varian, C.P., Williams, S.T., Taylor, S.S., 2024. Home ranges, habitat selection, and energy expenditure of *Strix varia* (barred owls): understanding the full diel cycle matters for enhancing urban landscapes. Ornithol. Appl., duae038 https://doi.org/10.1093/ornithapp/duae038.
Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71. https://doi.org/10.2307/1937156.
Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. Science 348, aaa2478. https://doi.org/10.1126/science.aaa2478.
Krausman, P.R., Morrison, M.L., 2016. Another plea for standard terminology. J. Wildl. Manag. 80, 1143–1144. https://doi.org/10.1002/jwmg.21121.
Kryshak, N.F., Fountain, E.D., Hofstadter, D.F., Dotters, B.P., Roberts, K.N., Wood, C.M., Kelly, K.G., Schwarcz, I.F., Kulzer, P.J., Wray, A.K., Kramer, H.A., Dumbacher, J.P., Keane, J.J., Shaklee, P.A., Gutiérrez, R.J., Peery, M.Z., 2022. DNA metabarcoding reveals the threat of rapidly expanding barred owl populations to native wildlife in western North America. Biol. Conserv. 273, 109678. https://doi.org/10.1016/j.biocon.2022.109678.
Lattin, J.D., 1993. Arthropod diversity and conservation in old-growth northwest forests. Am. Zool. 33, 578–587.
Leclerc, C., Courchamp, F., Bellard, C., 2018. Insular threat associations within taxa worldwide. Sci. Rep. 8, 6393. https://doi.org/10.1038/s41598-018-24733-0.
LEMMA, 2023. Gradient Nearest Neighbor (GNN) raster dataset (version GNN.2023.1). Modeled forest vegetation data using direct gradient analysis and nearest neighbor imputation. https://lemma.forestry.oregonstate.edu/data (accessed 3.22.26).
Lesmeister, D.B., Davis, R.J., Singleton, P.H., Wiens, J.D., 2018. Northern spotted owl habitat and populations: status and threats. In: Spies, TA; Stine, PA; Gravenmier, R.; Long, JW; Reilly, MJ, tech. Coords. 2018. Synthesis of Science to Inform Land Management Within the Northwest Forest Plan Area. Gen. Tech. Rep. PNW-GTR-966. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 245–299 (966).
Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. Science 338, 1305–1306. https://doi.org/10.1126/science.1231070.
Long, L.L., Wolfe, J.D., 2019. Review of the effects of barred owls on spotted owls. J. Wildl. Manag. 83, 1281–1296. https://doi.org/10.1002/jwmg.21715.
Lotka, A.J., 1932. The growth of mixed populations: two species competing for a common food supply. J. Wash. Acad. Sci. 22, 461–469.
MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101, 377–385. https://doi.org/10.1086/282505.
McGee, K.R., Doherty, P.F., Franklin, A.B., Bailey, L., Hart, S., 2024. Occupancy Dynamics of Barred Owls on a Spotted Owl Landscape. Colorado State University, Fort Collins, Colorado.
McGee, K.R., Franklin, A.B., Carlson, P.C., Rex, A., Doherty, P.F., 2026. Interspecific interaction, habitat, or neighborhood occupancy? Long-term dataset reveals factors influencing the barred owl invasion through time. Biol. Conserv. 318, 111835. https://doi.org/10.1016/j.biocon.2026.111835.
McKinnon, E.A., Love, O.P., 2018. Ten years tracking the migrations of small landbirds: lessons learned in the golden age of bio-logging. Auk 135, 834–856. https://doi.org/10.1642/AUK-17-202.1.
Mooney, H.A., Cleland, E.E., 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. USA 98, 5446–5451. https://doi.org/10.1073/pnas.091093398.
Muff, S., Signer, J., Fieberg, J., 2020. Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. J. Anim. Ecol. 89, 80–92. https://doi.org/10.1111/1365-2656.13087.
Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.Ø., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J. R., Orchan, Y., Pauwels, I.S., Říha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilk, O., Westrelin, S., Whiteside, M.A., Jarić, I., 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. Science 375, eabg1780. https://doi.org/10.1126/science.abg1780.
Noonan, M.J., Tucker, M.A., Fleming, C.H., Akre, T.S., Alberts, S.C., Ali, A.H., Altmann, J., Antunes, P.C., Belant, J.L., Beyer, D., Blaum, N., Böhning-Gaese, K., Cullen, L., de Paula, R.C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., Ford, A.T., Goheen, J.R., Janssen, R., Jeltsch, F., Kauffman, M., Kappeler, P.M., Koch, F., LaPoint, S., Markham, A.C., Medici, E.P., Morato, R.G., Nathan, R., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., Paviolo, A., Ramalho, E.E., Rösner, S., Schabo, D.G., Selva, N., Sergiel, A., da Silva, M.X., Spiegel, O., Thompson, P., Ullmann, W., Zięba, F., Zwijacz-Kozica, T., Fagan, W.F., Mueller, T., Calabrese, J.M., 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. Ecol. Monogr. 89, e01344. https://doi.org/10.1002/ecm.1344.
Ohmann, J.L., Gregory, M.J., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest- neighbor imputation in coastal Oregon, U.S.A. Can. J. For. Res. 32, 725–741. https://doi.org/10.1139/x02-011.
Olson, G.S., Anthony, R.G., Forsman, E.D., Ackers, S.H., Loschl, P.J., Reid, J.A., Dugger, K.M., Glenn, E.M., Ripple, W.J., 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. J. Wildl. Manag. 69, 918–932. https://doi.org/10.2193/0022-541X(2005)069%5B0918:MOSODF%5D2.0.CO;2.
Omernik, J.M., Griffith, G.E., 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environ. Manag. 54, 1249–1266. https://doi.org/10.1007/s00267-014-0364-1.
Pyle, P., Howell, S.N.G., Ruck, S., 1997. Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing, and Sexing Waterbirds, Diurnal Raptors, and Gallinaceous Birds in the Hand. Anatidae to Alcidae. Slate Creek Press.
Pyle, P., Gahbauer, M., Johnson, E.I., Ryder, T.B., Wolfe, J.D., 2022. Application of a global age-coding system ("WRP"), based on molts and plumages, for use in demographic and other studies of birds. Ornithology 139, ukab063. https://doi.org/10.1093/ornithology/ukab063.
Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. Biol. Rev. 95, 1511–1534. https://doi.org/10.1111/brv.12627.
Recio, M.R., Mathieu, R., Denys, P., Sirguey, P., Seddon, P.J., 2011. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. PLoS One 6. https://doi.org/10.1371/journal.pone.0028225.
Sala, O.E., Stuart Chapin III, F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770.

Salo, P., Korpimäki, E., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more dangerous than native predators to prey populations. Proc. R. Soc. B Biol. Sci. 274, 1237–1243.

Scott, J.M., Goble, D.D., Haines, A.M., Wiens, J.A., Neel, M.C., 2010. Conservation-reliant species and the future of conservation. Conserv. Lett. 3, 91–97. https://doi.org/10.1111/j.1755-263X.2010.00096.x.

Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S., Vonesh, J.R., 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119, 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x.

Sillett, S.C., Van Pelt, R., 2007. Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy. Ecol. Monogr. 77, 335–359. https://doi.org/10.1890/06-0994.1.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: what's what and the way forward. Trends Ecol. Evol. 28, 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Singleton, P.H., Lehmkuhl, J.F., Gaines, W.L., Graham, S.A., 2010. Barred owl space use and habitat selection in the eastern Cascades, Washington. J. Wildl. Manag. 74, 285–294. https://doi.org/10.2193/2008-548.

Spickler, J.C., Sillett, S.C., Marks, S.B., Welsh, H.H., 2006. Evidence of a new niche for a North American salamander: *Aneides vagrans* residing in the canopy of old-growth redwood forest. Herpetol. Conserv. Biol. 1 (1), 16–27.

Spies, T.A., Hessburg, P.F., Skinner, C.N., Puettmann, K.J., Reilly, M.J., Davis, R.J., Kertis, J.A., Long, J.W., Shaw, D.C., 2018. Old growth, disturbance, forest succession, and management in the area of the Northwest Forest Plan. In: Spies, TA; Stine, PA; Gravenmier, R.; Long, JW; Reilly, MJ, tech. Coords. 2018. Synthesis of Science to Inform Land Management Within the Northwest Forest Plan Area. Gen. Tech. Rep. PNW-GTR-966. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 95–243 (966).

Srivastava, V., Van Lanen, N.J., Parshad, R.D., 2026. Modeling species co-occurrence effects to inform invasive barred owl management and recovery of the northern spotted owl. Ecol. Appl. 36, e70195. https://doi.org/10.1002/eap.70195.

Thomas, J.W., Forsman, E.D., Lint, J.B., Meslow, E.C., Noon, B.R., Verner, J., 1990. A Conservation Strategy for the Northern Spotted Owl. Portland, Oregon.

Tosa, M.I., Lesmeister, D.B., Levi, T., 2022. Barred owl predation of western spotted skunks. Northwest. Nat. 103, 250–256. https://doi.org/10.1898/1051-1733-103.3.250.

Uhlenbeck, G.E., Ornstein, L.S., 1930. On the theory of the Brownian motion. Phys. Rev. 36, 823–841. https://doi.org/10.1103/PhysRev.36.823.

USFWS, 2024. Final Barred Owl management strategy. https://www.fws.gov/media/final-barred-owl-management-strategy (accessed 10.7.25).

Volterra, V., 1926. Variations and fluctuations of the number of individuals in animal species living together. In: Chapman, R.N. (Ed.), Animal Ecology. McGraw-Hill, New York, New York, USA.

Watson, J.E., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., 2018. The exceptional value of intact forest ecosystems. Nat. Ecol. Evol. 2, 599–610.

Watson, W.A., Wood, C.M., Kelly, K.G., Hofstadter, D.F., Kryshak, N.F., Zulla, C.J., Whitmore, S.A., O'Rourke, V., Keane, J.J., Peery, M.Z., 2023. Passive acoustic monitoring indicates Barred Owls are established in northern coastal California and management intervention is warranted. Ornithol. Appl. 125, duad017. https://doi.org/10.1093/ornithapp/duad017.

Weidensaul, C.S., Colvin, B.A., Brinker, D.F., Huy, J.S., 2011. Use of ultraviolet light as an aid in age classification of owls. Wilson J. Ornithol. 123. https://doi.org/10.1676/09-125.1.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338. https://doi.org/10.2307/1943563.

Wiens, J.D., Anthony, R.G., Forsman, E.D., 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. Wildl. Monogr. 185, 1–50. https://doi.org/10.1002/wmon.1009.

Wiens, J.D., Dugger, K.M., Higley, J.M., Lesmeister, D.B., Franklin, A.B., Hamm, K.A., White, G.C., Dilione, K.E., Simon, D.C., Bown, R.R., Carlson, P.C., Yackulic, C.B., Nichols, J.D., Hines, J.E., Davis, R.J., Lamphear, D.W., McCafferty, C., McDonald, T. L., Sovern, S.G., 2021. Invader removal triggers competitive release in a threatened avian predator. Proc. Natl. Acad. Sci. USA 118, e2102859118. https://doi.org/10.1073/pnas.2102859118.

Yackulic, C.B., Bailey, L.L., Dugger, K.M., Davis, R.J., Franklin, A.B., Forsman, E.D., Ackers, S.H., Andrews, L.S., Diller, L.V., Gremel, S.A., Hamm, K.A., Herter, D.R., Higley, J.M., Horn, R.B., McCafferty, C., Reid, J.A., Rockweit, J.T., Sovern, S.G., 2019. The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls. Ecol. Appl. 29, e01861. https://doi.org/10.1002/eap.1861.