

ARTICLE

Forest owl community response following the removal of an intraguild invader

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Abstract

Invasive predators can reshape native predator assemblages, triggering cascading changes in broader wildlife communities. In western North America, the barred owl (*Strix varia*) is an invasive apex predator with well-documented negative impacts on congeneric northern spotted owls (*Strix occidentalis caurina*), but impacts on other native forest owls are poorly understood. We coupled a large-scale removal experiment with a passive acoustic monitoring network to quantify species-specific and community-level responses of a five-species assemblage of native forest owls to the lethal removal of invasive barred owls. Our results supported predictions of intraguild predation theory, where smaller bodied, nocturnal species most susceptible to predation and resource competition from larger barred owls benefitted from removal, whereas a diurnally active owl species and a larger bodied species showed little to no response. We conclude that focused management actions limiting the occurrence of barred owls can provide spatial refugia for spotted owls and other sympatric native owl species, thereby promoting forest biodiversity.

KEYWORDS

barred owl, bioacoustics, intraguild predation, invasive species, multispecies occupancy, removal experiment, spotted owl, Strigidae

INTRODUCTION

High densities of invasive predators can rapidly alter the structure of native wildlife communities and trigger irretrievable loss of biodiversity. Consequently, the lethal removal of invasive predators has become a key strategy in combating global biodiversity loss (Doherty & Ritchie, 2017; Glen & Hoshino, 2020; Park, 2004). While the number and size of invasive predator control programs increase, studies of the benefits to wildlife communities after invasive animal removal remain limited (Kurle et al., 2021, but also see Jones et al., 2016). Rapid changes in the abundance of invasive, top predators can suppress populations of smaller

native predators (mesopredators), resulting in cascading changes to predation pressure on prey populations and ecosystem processes (Crooks & Soulé, 1999; Ritchie & Johnson, 2009). Outcomes of interactions between native and invasive predators may vary with resource availability, habitat complexity, or the underlying dynamics of localized predator–prey relationships. In this respect, biodiversity conservation through removal of invasive predators requires a community-level view to fully understand benefits, or unforeseen consequences, of removing invasives (Ritchie & Johnson, 2009; Ruscoe et al., 2011).

In western North America, the barred owl (*Strix varia*) is an invasive predatory bird with well-documented

negative competitive impacts to the federally threatened and closely related northern spotted owl (*Strix occidentalis caurina*; Long & Wolfe, 2019). The northern spotted owl, an obligate of old conifer forests, was listed in 1990 as a federally threatened subspecies because of population declines driven by the loss of old-forest habitats. Despite nearly 40 years of old-forest habitat protection on federally managed lands, populations of spotted owls have declined at an accelerating rate—largely due to the impacts of interspecific competition with rapidly expanding populations of barred owls (Dugger et al., 2016; Franklin et al., 2021). As the threat of barred owls mounted, large-scale removal experiments were implemented to determine if lethal control of barred owls could provide a viable management tool to benefit spotted owls (Diller et al., 2016; Wiens et al., 2021). Those experiments demonstrated that removal of barred owls stabilized populations of spotted owls in treated areas, whereas populations in control areas without removal continued to decline sharply. Experimental results have since been used to develop a management strategy for barred owls that includes lethal control measures across vast landscapes to offset the extinction risk of spotted owls (USFWS, 2024).

Beyond impacts to spotted owls, the rapid rise and establishment of a highly adaptable apex predator like the barred owl may trigger a series of broader, cascading ecological consequences (Holm et al., 2016). Such impacts may be prevalent within native guilds of sympatric forest owls (Barry et al., 2025), especially in areas where barred owls have become superabundant (Holm et al., 2016; Rugg et al., 2023). Small-bodied owl species are likely to be especially vulnerable to invading barred owls because of increasing levels of intraguild predation—the most extreme form of interference competition (Polis et al., 1989; Polis & Holt, 1992; Sergio & Hiraldo, 2008). Indeed, dietary studies of barred owls in western forests show this species commonly preys upon native, small-bodied owls including northern saw-whet owls (*Aegolius acadicus*), northern pygmy owls (*Glaucidium gnoma*), and western screech owls (*Megascops kennicottii*; Baumbusch, 2023; Hamer et al., 2001; Kryshak et al., 2022; Wiens et al., 2014). Where barred owls are well established, they have displaced western screech owls from preferred mature forests (Rugg et al., 2023), leading to declines in occurrence (Acker, 2012).

A superabundance of barred owls may also have consequences for larger bodied predators like the great horned owl (*Bubo virginianus*), a widespread and common intraguild predator of barred owls (Laidig & Dobkin, 1995), spotted owls (Wiens et al., 2014), and smaller owl species (Elliott, 2006; Hayward & Garton, 1988; Marti & Kochert, 1996). Changes in the distribution of great horned owls with increasing populations of barred owls have the

potential to indirectly affect a broad suite of smaller species whose choice of habitat is mediated by risk of predation from great horned owls (Grossman et al., 2008; Rohner & Krebs, 1996). Increases in abundance of barred owls in older forests may further increase predation pressure on sympatric forest owls by displacing them into more open habitats favored by great horned owls and other larger predators (e.g., red-tailed hawks *Buteo jamaicensis*; Wiens et al., 2014). A clear understanding of the possible benefits, or unintended consequences, of invader removal to the native forest owl community can inform management strategies for barred owls and associated forest wildlife.

We used barred owl removal experiments replicated in three different study areas to test ecological predictions concerning the impacts of barred owls on local communities of forest owls and to identify possible species-specific benefits, or secondary consequences, of removal. We used a multispecies passive acoustic monitoring network (Lesmeister et al., 2022) in each study area to quantify the effects of removal experiments on the regional occurrence of five native forest owl species, including four smaller bodied owl species (northern spotted owl, northern saw-whet owls, northern pygmy owls, western screech owls) and one larger bodied species (great horned owl). All species share a limited supply of forest resources with non-native barred owls, but each species occupies a distinct niche in Pacific Northwest forests based on habitat and food habits, as well as diel patterns (Appendix S1: Table S1). We used passive acoustic monitoring coupled with a trained convolutional neural network (PNW-Cnet; Ruff et al., 2023) to detect species-specific vocalizations and estimate site use in paired treatment (barred owls removed) and control (no removal) landscapes. We implemented passive acoustic monitoring after a 4- to 5-year removal period across study areas, when the occurrence of territorial pairs of barred owls had been substantially reduced in treated landscapes (Wiens et al., 2020).

We hypothesized that the removal of barred owls would result in differential responses within the native assemblage of forest owls. Specifically, we predicted that landscape use by spotted owls would be greater in areas with removal relative to similar areas without removal due to competitive release from sympatric barred owls (Wiens et al., 2021). We also predicted that landscape use by small-bodied owl species most susceptible to intraguild predation from barred owls (saw-whet owls, screech owls, pygmy owls) would be greater in areas with barred owl removal. For the largest member of the forest owl guild (great horned owl), we hypothesized that barred owl removal could have a positive effect because of reduced competition for shared prey (Cromrich et al., 2002) or a negative effect because of reduced

opportunities to prey upon smaller barred owls and their young (Bosakowski et al., 1989).

METHODS

Study areas and barred owl removal experiment

We conducted passive acoustic monitoring on three experimental study areas with long-term demographic monitoring of spotted owls and barred owl removal: Cle Elum (CLE), Washington, and the Coast Range (COA) and Klamath (KLA) in western Oregon (Table 1, Figure 1). All study areas were part of the northern spotted owl effectiveness monitoring program for the Northwest Forest Plan (Dugger et al., 2016; Franklin et al., 2021) and part of a range-wide passive acoustic monitoring network (Lesmeister & Jenkins, 2022). Study areas varied in climate, vegetation composition, and topography (Wiens et al., 2021). Forests in the Oregon study areas were primarily dominated by Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*) forests interspersed with hardwood riparian areas, whereas drier forests of Cle Elum included more ponderosa pine (*Pinus ponderosa*). For the barred owl removal experiment, each study area was divided into two or more similar treatment (barred owls removed) and control (barred owls not removed) areas with respect to forest conditions and numbers of territories historically occupied by spotted owls (Wiens et al., 2021). Owl

species that may occur in our study areas but were not included in our analysis included flammulated owl (*Psiloscops flammeolus*), long-eared owl (*Asio otus*), and great gray owl (*Strix nebulosa*). These species were omitted from our analysis because they were not consistently detected in all study areas (Lesmeister et al., 2022) and tended to be more strongly associated with open, non-forested habitats relative to the owl species we did include.

We located and lethally removed barred owls throughout treatment landscapes using standardized protocols and a 12-gauge shotgun (Diller et al., 2014; Wiens et al., 2020). We removed barred owls across a 4- (KLA) or 5-year (CLE, COA) removal period (2015–2020; Table 1). We conducted regular follow-up visits to detect and remove recolonizing barred owls as needed throughout the year. The per visit detection rate of barred owls was high (0.66–0.74; Wiens et al., 2020), so we were confident that newly colonizing barred owls were quickly detected and removed over repeated visits. We removed a total of 2633 individual barred owls from treatment areas prior to passive acoustic monitoring in 2020, 467 of which were removed from 5-km² sample units with passive acoustic monitoring (Table 1; Appendix S1: Figure S1).

Passive acoustic monitoring and data processing

We collected acoustic data from 577 survey stations located in treatment ($n = 292$) and control ($n = 285$)

TABLE 1 Passive acoustic monitoring effort for six forest owl species in three study areas with (treatment) and without (control) barred owl removal in Washington and Oregon, USA, 2020.

Study area	Area (km ²)	Hexagons sampled (5-km ² each)	Acoustic survey stations	Barred owls removed ^a
Cle Elum (CLE)				
Control	670	14	50	
Treatment	604	28	114	574 (145)
Coast Range (COA)				
Control	1015	34	135	
Treatment	582	15	60	1280 (210)
Klamath (KLA)				
Control	698	25	100	
Treatment	783	30	118	779 (112)
All study areas				
Control	2383	73	285	
Treatment	1969	73	292	2633 (467)

^aTotal number of barred owls removed from treatment landscapes prior to passive acoustic monitoring in 2020, with numbers removed from 5-km² hexagons sampled with passive acoustic monitoring shown in parentheses. The removal period was Oct 2015–Aug 2020 in the CLE and COA study areas, and Oct 2016–Aug 2020 in KLA.

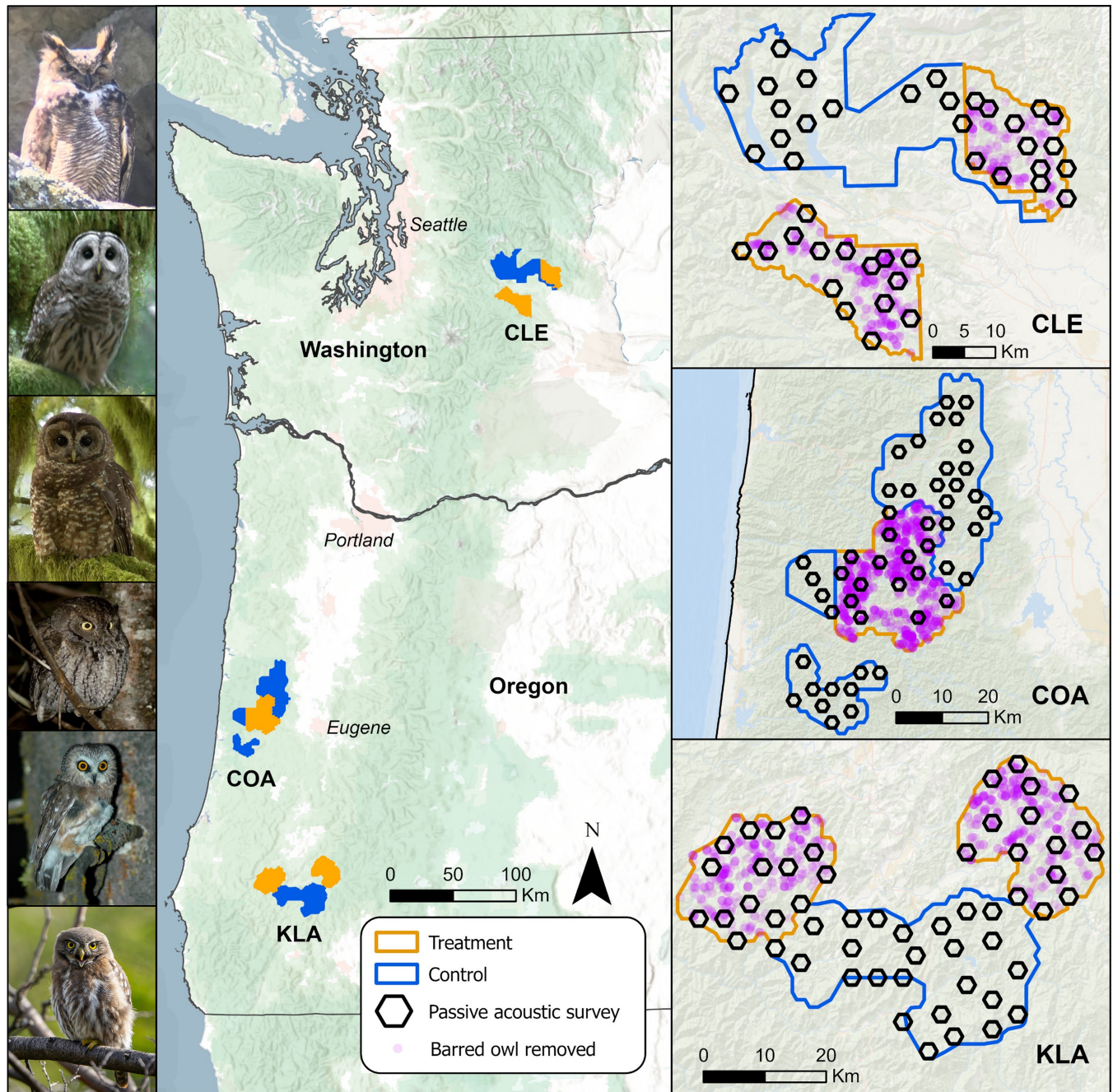


FIGURE 1 Distribution of passive acoustic surveys of six forest owl species relative to barred owl removal locations in three paired treatment (barred owls removed) and control (no removal) experimental study areas in Cle Elum, Washington (CLE), the Oregon Coast Range (COA), and Klamath, Oregon (KLA), USA. A total of 2633 barred owls were removed from treatment areas during 4 (KLA) to 5 (CLE, COA) years of removal effort prior to passive acoustic surveys in 2020. Owl species (shown in descending order of body size) included great horned owl, barred owl, northern spotted owl, western screech owl, northern saw-whet owl, and northern pygmy owl. Photo of northern pygmy owl by Ignacio Rafael Bas Molinari on Unsplash; all other photographs by Patrick Kolar, used with permission.

landscapes (Table 1). Three to four survey stations were placed within 5-km² hexagons ($n = 146$) that were randomly selected from a uniform sampling grid of hexagons to cover approximately 20% of federally managed lands in each study area (Lesmeister et al., 2021). Survey stations were spaced ≥ 500 m apart and located at least 50 m

from roads, trails, and streams. At each survey station, we attached an autonomous recording unit (ARU; Song Meter SM4, Wildlife Acoustics; Maynard, MA) to a tree (10–20 cm diameter) approximately 2-m aboveground (Lesmeister et al., 2021). We deployed ARUs for 6 weeks during March to mid-September 2020 (i.e., the end of the

4- to 5-year removal period) and programmed ARUs to record continuously during crepuscular periods (1 h before to 3 h after sunset, and 2 h before to 2 h after sunrise) and 10 min on the hour throughout the rest of the day and night using a sample rate of 32 kHz, sample range of 16 kHz, and gain of +16 dB. Mean elevation at ARU locations was 390 m in COA, 681 m in KLA, and 1206 m in CLE.

We processed a total of 247,474 h of audio data from 577 survey stations (Appendix S1: Table S2), averaging 428.9 h per station. The resulting audio data were converted to spectrogram images and processed using a multistep workflow that integrated a trained convolutional neural network model (PNW-Cnet) for automated species identification (Lesmeister & Jenkins, 2022; Ruff et al., 2023). PNW-Cnet had high performance in detecting all six of the focal owl species (Ruff et al., 2021), and we reviewed resulting detections manually to confirm species detections within each week of sampling at survey stations (Lesmeister et al., 2022). Call-playback surveys of spotted owls, barred owls, and pygmy owls occasionally overlapped sample sites with acoustic monitoring, so we removed acoustic surveys occurring in the same night as call-playback surveys. We assumed that station-level surveys were independent because the recording radius around individual ARUs was less than the ≥ 500 -m spacing among stations. We summarized daily recordings and species-specific vocal detections/non-detections from each survey station into six weekly survey occasions for data analysis. We calculated naïve occupancy as the proportion of survey stations where each species was detected at least once.

Community occurrence model

We developed a Bayesian hierarchical community occurrence model (Dorazio & Royle, 2005; Zipkin et al., 2010) to estimate species-specific and community-level occurrence of six forest owl species in landscapes with and without barred owl removal (Appendix S1: Section S1). The model estimated the probability that a survey station was used during the sampling season by ≥ 1 vocalizing owl, while accounting for imperfect detection. The model provided a powerful framework to estimate differential responses of multiple forest owl species (including barred owls) to removal while accounting for underlying variations among species' detection rates and occurrence among study areas. The hierarchical approach also increased the precision of inferences for rare species (e.g., spotted owls) by treating species-specific model coefficients as random effects drawn from common community-level distributions (Zipkin et al., 2010).

The goal of our analysis was to test our predictions concerning differential effects of barred owl removal on species-specific and community-level occurrence (i.e., probability of use at a given survey station; ψ_{ij}). The barred owl removal experiment treated each study area as a unit of spatial replication, so we combined detection/non-detection data from all study areas and included "area" effects on ψ_{ij} in our model. We tested for additive effects of study area and treatment level on occurrence parameters via the logit-link function: $\text{logit}(\psi_{ij}) = \beta_{0i} + \beta_{1-2i}(\text{area})_j + \beta_{3i}(\text{TRT})_j$, where ψ_{ij} is the probability that species i used the 250–500-m recording radius around survey station j , β_{0i} is the intercept for species i , β_{1-2i} are the species-specific coefficients for each study area, and $\beta_{3i}(\text{TRT})_j$ is the species-specific coefficient for treatment level at survey station j (i.e., 1 if a hexagon received barred owl removal, 0 otherwise). To estimate the mean response of the five native owl species to barred owl removal, we excluded detection/non-detection data on barred owls and refitted the model to obtain community-level estimates of ψ_{ij} in areas with and without barred owl removal. In early iterations of the model, we explored using forest covariates (mean percent forest canopy cover, proportion of area with large conifer trees) to account for possible spatial heterogeneity in forest conditions among survey stations. Models including forest covariates had little support from the data, and forest cover conditions were approximately similar between paired treatment and control areas (Appendix S1: Section S1, Figure S2), so we omitted these uninformative covariates from the final model. We also tested a model that included a random effect at the grid-cell level (i.e., hexagon) to examine consequences of possible nonindependence among survey sites on inferences regarding treatment effects. This model exhibited poor convergence for some model parameters (i.e., Effective Sample Sizes < 400), but inferences were generally similar between models with and without the random effect term (Appendix S1: Section S1, Table S2). Consequently, we relied upon the model without the random effect term for primary inferences but provided details on possible consequences of nonindependence on parameter estimates in Appendix S1.

Our detection submodel was specified as $\text{logit}(p_{ij,k}) = \alpha_{0i} + \alpha_{1i}(\text{hours})_j + \alpha_{2i}(\text{noise})_j + \alpha_{3i}(\text{date})_j + \alpha_{4i}(\text{date}^2)_j + \alpha_{5i}(\text{TRT})_j$, where $p_{ij,k}$ was the probability of detecting species i at survey station j for replicate survey k , α_{0i} was the intercept for species i , and α_{1-5i} were the species-specific regression coefficients representing the station level, log-linear effects of the number of hours of recording time (in hours), background noise level (noise), the nonlinear effect of ordinal date (day 1 = Jan 1) of the first day of each weekly survey occasion (date , date^2), and barred owl

treatment level (TRT). Recording time, noise level, and survey date have been shown to consistently affect the detectability of forest owls during passive acoustic monitoring (Duchac et al., 2020, 2021; Rugg et al., 2023; Weldy et al., 2023). We defined hours of recording time as the total hours recorded per week at each monitoring station. We used Kaleidoscope Pro Sound Pressure Level Analysis between 250 and 1000 Hz to generate estimates of background noise levels (Wildlife Acoustics, 2021). We averaged background noise level at each station daily, then averaged within survey occasions. We included an effect of barred owl removal on detection because the presence of barred owls may suppress vocal activity (and thus detectability) of sympatric owl species (Crozier et al., 2006; Duchac et al., 2020; Rugg et al., 2023).

We fitted our model using the *spOccupancy* package in R (Doser et al., 2022; R Core Team, 2022). We centered and standardized continuous covariates and specified uninformative priors (normal distribution, mean = 0, variance = 2.72) for model parameters (Broms et al., 2016; Doser et al., 2022). We ran three Markov chains for 200,000 iterations with a burn in of 100,000 and a thinning rate of 10, resulting in a posterior sample of 30,000. We calculated the mean, SD, and the 2.5th and 97.5th percentiles of posterior distributions (i.e., 95% Bayesian credible interval; BCI) of model coefficients. We evaluated strength of model coefficients by examining the direction and magnitude of mean effects, the extent to which the 95% BCI overlapped zero, and the proportion of the posterior distribution that was positive or negative (f , or the probability of an effect being in the same direction as the mean). We visually examined trace plots and used the Gelman-Rubin statistic ($\hat{R}$; Gelman & Rubin, 1992) to determine if chains showed adequate mixing; values of $\hat{R}$ in our final model were ≤ 1.1 , indicating good convergence. We evaluated model fit using a posterior predictive check with a Bayesian p -value, where values < 0.1 or > 0.9 indicated poor model fit (Hooten & Hobbs, 2015). Data and code used for our analysis are available at Wiens (2025).

RESULTS

Over 3041 weekly sampling occasions, we confirmed vocal detections of at least one of the six owl species at 551 (95%) of 577 survey stations and detected all six species in all study areas (Appendix S1: Table S3). The most frequently detected species across study areas and treatment levels was the northern pygmy owl (naïve occupancy = 0.76), followed by barred owl (0.68), northern saw-whet owl (0.60), great horned owl (0.54),

western screech owl (0.52), and northern spotted owl (0.18). We observed 0 and 1 weekly detections of spotted owls in the control areas of CLE and COA, respectively. The mean number of owl species detected per survey station was 1.17 (SD = 0.04, max = 4) in CLE, 2.13 (SD = 1.22, max = 5) in COA, and 2.78 (SD = 1.33, max = 6) in KLA (Appendix S1: Figure S3).

Estimates of species-specific probability of use varied considerably among owl species, study areas, and treatment levels (Figure 2). As expected, we found strong support for a negative effect of removal on landscape use by barred owls, with a probability of 1.0 that use was lower in treated areas relative to controls (Figure 3; Appendix S1: Table S5). Differences in probability of use by barred owls between control and treatment areas were greatest in CLE, but nominal in COA and KLA where vocal detections of barred owls were more ubiquitous. In agreement with our predictions, spotted owls and two of the three small owls (screech owls, saw-whet owls) showed a positive association with barred owl removal (Figures 2 and 3). We found no response to removal by the largest species (great horned owl). Contrary to predictions, we found a weak, negative effect of treatment area on the probability of use by pygmy owls (a mostly diurnal owl species).

The probability of detection during weekly survey occasions ranged from a low of 0.29 for spotted owls in control areas to a high of 0.62 for barred owls in control areas (Appendix S1: Figure S4). Detection rates were greater in treatment relative to control areas for spotted owls, saw-whet owls, screech owls, and great horned owls and reduced in treatment areas for barred owls and pygmy owls (Appendix S1: Table S6). Detection varied nonlinearly with survey date for all owl species and decreased with increasing levels of background noise for five of six species. The effect of survey effort (in hours of recording time) varied among species. The Bayesian p -value for the final six-species model was 0.62 (Appendix S1: Table S7), indicating adequate model fit.

The reduced five-species model (excluding barred owls) indicated a weak, positive effect of barred owl removal on the native forest owl community (Figure 3; Appendix S1: Table S8). Community-level probability of use ranged from a low of 0.469 in the CLE control area to a high of 0.846 in the KLA treatment area (Table 2). There was high variance in community-level hyperparameters, reflecting large differences in landscape use among species, study areas, and treatment levels (Appendix S1: Table S8). The mean community-level probability of detection during weekly surveys was 0.385 and 0.470 in control and treatment areas, respectively. The Bayesian p -value for the reduced five-species model (0.582) indicated good fit.

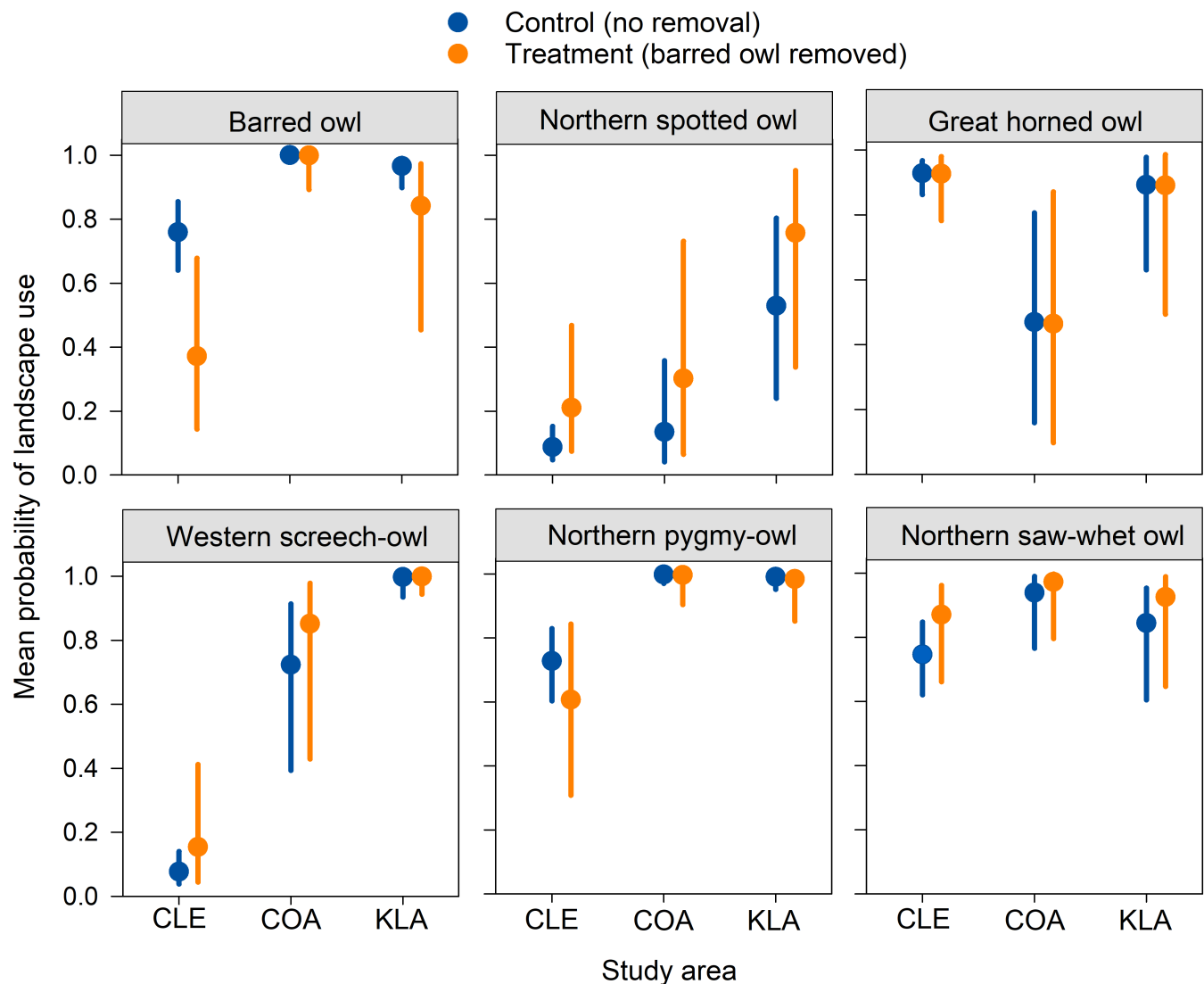


FIGURE 2 Mean probability of landscape use (with 95% credible intervals) by six forest owl species in areas with (treatment) and without (control) barred owl removal in Cle Elum, Washington (CLE), the Oregon Coast Range (COA), and Klamath, Oregon (KLA), USA. Estimates are from 2020, following four (KLA) to five (CLE, COA) years of continuous barred owl removal effort in treated areas.

DISCUSSION

We coupled barred owl removal experiments with passive acoustic monitoring to investigate responses of five native forest owl species to the removal of an invasive intraguild predator. The assemblage of forest owls varied in their responses to removals, but all species were affected, as shown by species-specific differences between areas with and without barred owl removal in probabilities of site use, detectability, or both. Three native owl species exhibited higher use in treatment areas relative to controls (with ≥ 0.82 probability), one (pygmy owl) exhibited lower use in treated areas (with 0.74 probability), and one (great horned owl) showed no detectable difference. Except for diurnally active pygmy owls, the

species-specific patterns we observed supported predictions of intraguild predation theory, with smaller bodied, nocturnal species (northern spotted owl, western screech owl, northern saw-whet owl) benefiting the most from removing larger barred owls. This finding further indicated a mesopredator release situation, where the suppression of a superabundant invasive predator had cascading, asymmetrical effects down the predator dominance hierarchy (Chakarov & Krüger, 2010; Mueller et al., 2016).

Passive acoustic monitoring was implemented across our experimental study areas at the end of the 4- to 5-year barred owl removal period. As a result, our study was limited to post-removal comparisons between paired treatment and control landscapes. Evidence of a

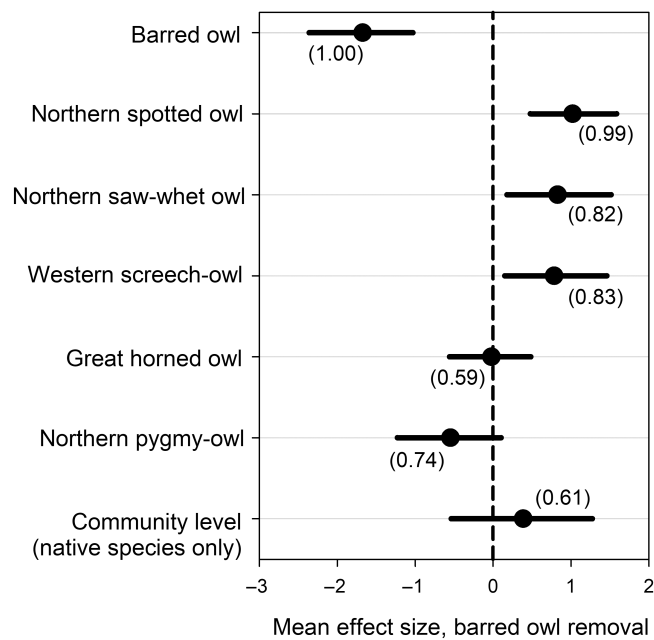


FIGURE 3 Mean effect size (logit scale with 95% credible intervals) of barred owl removal on species-specific and community-level probability of site use for six forest owl species in Cle Elum, Washington (CLE), the Oregon Coast Range (COA), and Klamath, Oregon (KLA), USA. We show the proportion of the posterior distribution with the same sign as the mean in parentheses (i.e., probability of an effect being in the direction of the mean). The community-level estimate is from the reduced, five-species model without barred owls included.

treatment effect on the two focal management species (spotted owls and barred owls) based on passive acoustic monitoring data was corroborated by long-term, before–after control-impact results demonstrating experimental reductions in barred owls with concurrent increases in territory occupancy, survival, and annual rate of population change of northern spotted owls (Wiens et al., 2020, 2021). There was unlikely to be any systematic bias affecting our results because of the duration and intensity of the barred owl removal effort prior to passive acoustic monitoring, the extent of spatial replication across different study areas and forest types, and the similarities in forest conditions between paired treatment and control sites. We concluded that the invasion, population expansion, and subsequent lethal removal of barred owls led to shifts in vocal behaviors and patterns of landscape use by the native forest owl community.

Removal effectiveness

Removals limited the use of treatment areas by vocalizing barred owls relative to control areas, but the effectiveness

TABLE 2 Mean expected probability of community-level site use ($\hat{\psi}$), with SD and lower (LCI) and upper (UCI) 95% credible intervals, for five native forest owl species in three study areas with (treatment) and without (control) barred owl removal in Washington (CLE) and Oregon (COA, KLA), USA.

Study area	$\hat{\psi}$	SD	LCI	UCI
CLE				
Control	0.46	0.71	0.12	0.84
Treatment	0.53	0.79	0.07	0.94
COA				
Control	0.67	0.88	0.04	0.99
Treatment	0.74	0.92	0.02	0.99
KLA				
Control	0.78	0.90	0.03	0.98
Treatment	0.83	0.94	0.01	1.00

Note: Estimates are from the five-species model without barred owls included.

of removals in limiting barred owls was highly variable among study areas. The impact of removal on barred owls was most pronounced in CLE, where the use of treatment areas was 39% lower relative to controls after removing 574 barred owls. In COA and KLA, however, barred owls used approximately 100% of the control areas, and we observed only minor reductions in the use of treatment landscapes after removing 2059 barred owls. Post-removal use of treatment areas by barred owls remained high in western Oregon because of an elevated rate of recolonization from surrounding landscapes with a remarkably high density of reproductive pairs (Wiens et al., 2014, 2020). These findings exemplify the challenges associated with reducing the use of landscapes by invasive barred owls where they are superabundant. In comparison, removal studies conducted near the presumed invasion front of barred owls in California reported widespread declines in barred owl occupancy from 0.19 to 0.03 after removing fewer than 70 individuals (Hofstadter et al., 2022).

Our estimates of landscape use by barred owls did not account for likely differences in movements and vocalization behaviors of well-established territorial pairs occupying control areas versus those of non-territorial, younger owls prospecting for territories and mates across vacated territories in treatment areas. Prior to passive acoustic monitoring in our study areas, there was a steep decline in the numbers of territorial pairs of adult (owls ≥ 3 -years old) barred owls collected from treatment areas, with subsequent recolonization by mostly subadults (owls 1–2-years old; Wiens et al., 2020). We suggest that increased space use and vocalization frequency by

predominantly younger non-territorial barred owls prospecting for mates in post-removal landscapes devoid of established territorial pairs can overestimate site use, as determined by passive acoustic monitoring. Approaches to estimate abundance (e.g., Kelly et al., 2023) or pair status of barred owls from passive acoustic data may provide better insight into the effectiveness of lethal removal in limiting invasive populations of barred owls.

Species-specific responses

As in previous studies (Diller et al., 2016; Hofstadter et al., 2022; Weldy et al., 2023; Wiens et al., 2021), spotted owls showed a positive response to barred owl removal across different study areas. Spotted owls were also the rarest owl species, and by 2020, this species was largely absent from control landscapes in two of three study areas. This finding mirrored results from concurrent mark-recapture studies of spotted owls in our study areas (Franklin et al., 2021; Wiens et al., 2021), highlighting the pending extirpation of this critically threatened species in regions where barred owls are most abundant and have been established the longest. Like spotted owls, western screech owls and northern saw-whet owls also showed a positive response to barred owl removal, presumably due to experimental reductions in direct predation (Hausleitner et al., 2015) and habitat displacement (Rugg et al., 2023). In agreement with previous findings from our study areas (Rugg et al., 2023), screech owls were relatively uncommon in the dry, high-elevation forests of CLE (use <0.15) but ubiquitous (use ~1.0) in the more mesic, lower elevation forests of COA and KLA. Little is known about the population status of northern saw-whet owls in our study region, including the degree to which populations seasonally migrate (Rasmussen et al., 2020). Saw-whet owls were well distributed across all study areas (use >0.70), but use of landscapes was up to 12% greater in areas with barred owl removal. Our findings on small-bodied owls not only supported previously hypothesized negative effects of invasive barred owls on native avian mesopredators (Holm et al., 2016) but also provided novel insight into the status and distribution of small-bodied owls in the Pacific Northwest.

The barred owl invasion of western forests may negatively affect a variety of native wildlife while also producing a few ecological “winners”—a scenario often observed in systems impacted by invasive predators (McKinney & Lockwood, 1999). We found that pygmy owls had a weak, negative response to removal, suggesting that the smallest and most common species of the forest owl assemblage may not be negatively

impacted by barred owls (also see Barry et al., 2025). All owl species in our study are primarily nocturnal except for pygmy owls, which are mostly diurnally active with a peak of activity near sunrise (Deshler, 2023). Barred owls are primarily nocturnal hunters but opportunistically take a wide range of diurnal prey (Hamer et al., 2001; Wiens et al., 2014), indicating that niche segregation between pygmy owls and barred owls may be large relative to other small owls. Great horned owls had reduced detection in our control areas but used landscapes with and without barred owl removal equally—a similar response of this species to barred owl removal in California (Barry et al., 2025). Together, these studies indicate that pygmy owls and great horned owls had little response to barred owl removal despite large underlying differences in density (and invasion stage) of barred owls. In eastern North America, barred owls exhibited spatial avoidance of great horned owls, likely due to interference competition or predation risk from the larger species (Laidig & Dobkin, 1995). Collectively, these findings illustrate the strong top-down roles of intraguild predation and body size in shaping community structure of forest owls (Marti et al., 1993; Gutiérrez et al., 2007).

Aside from pygmy owls, detection rates of native owls were consistently greater in areas with barred owl removal. Spotted owls and screech owls have been found to reduce their calling frequency (Crozier et al., 2006; Rugg et al., 2023) and avoid forests where barred owls are abundant, likely to mitigate competitive interactions or predation risk (Wiens et al., 2014). Such changes in vocalization behaviors and space use are expected to decrease detection probabilities in control areas, which were evident for four of five native owl species in our study. In contrast, pygmy owls may react to vocalizing barred owls by increasing the frequency of territorial calls, as has been suggested in flammulated owls (*Psilosops flammeolus*; Barry et al., 2025).

Community-level response

Our study provided compelling evidence that the barred owl invasion into western forests has the potential to lead to an overall less diverse community of forest owls. We observed high variance (uncertainty) in community-level estimates of use by the five-species assemblage of native forest owls, but community occurrence was consistently greater where barred owls were removed. Even in areas where vocalizing barred owls were ubiquitous, removals created spatial openings in their distribution that appeared to function as spatial refugia for spotted owls,

screech owls, and saw-whet owls, leading to a weak but positive effect on community-level use in treated landscapes. Similarly, in central Europe the diversity of a forest owl assemblage was largely determined by the distribution of a single large keystone predator, the eagle owl (*Bubo bubo*; Sergio & Hiraldo, 2008). Collectively, these studies and ours show how changes in the abundance of a dominant intraguild predator like the barred owl can cascade downward through effects on sympatric raptor and mammal meso-predators, potentially causing major alterations to food-web structures across a variety of forest conditions (Holm et al., 2016).

Prospects for biodiversity conservation

We provided a deeper understanding of species-specific and community-level responses of forest owls to the removal of invasive barred owls, thereby informing difficult decisions regarding the use of lethal control measures to promote threatened species recovery and biodiversity conservation. Barred owls were well distributed and common across a diversity of forest types in our study, resulting in little available forest habitat for spotted owls, screech owls, and saw-whet owls to avoid competitive interactions and predation risk from barred owls. Lethal control of barred owls is currently the only feasible, humane, and experimentally validated means of effectively reducing their impact on northern spotted owls and other species (Dumbacher & Franklin, 2025). Our results show that suppressing invasive populations of barred owls will increase the likelihood of co-occurrence with native forest owls, providing cascading benefits to a wide range of associated wildlife (Barry et al., 2025; Holm et al., 2016; Kryshak et al., 2022).

Pending decisions to implement broad-scale management of invasive barred owls to benefit threatened spotted owls have been controversial and will continue to be so given the history, scope, and complexity of this “wicked” conservation conundrum (Gutiérrez, 2020). Decades of unchecked population growth by barred owls in the Pacific Northwest have pressed forest managers into a realm of “forever management”, where dispersal by barred owls from unmanaged areas into managed landscapes inevitably necessitates removals in perpetuity, at least with current technology (Dumbacher & Franklin, 2025). Our study provided a compelling example of how community-level passive acoustic monitoring data can be coupled with multispecies occurrence models to evaluate the effects of forest management actions, including invasive species removal, on local communities of forest owls.

AUTHOR CONTRIBUTIONS

J. David Wiens and Katie M. Dugger directed barred owl removal experiments, Damon B. Lesmeister and Julianna M. A. Jenkins directed bioacoustics data curation and validation, and all authors contributed to conceptualization, methodology, and project funding. J. David Wiens performed data analyses and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Wiens, 2025) are available in the U.S. Geological Survey's ScienceBase repository at <https://doi.org/10.5066/P13TMSWW>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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