Ornithological Applications, 2026, 128, 1–14
https://doi.org/10.1093/ornithapp/duag008
Advance access publication 24 January 2026
Research Article

Ornithological Applications

Passive acoustic monitoring captures large-scale *Dryocopus pileatus* (Pileated Woodpecker) occupancy patterns in the Pacific Northwest, USA

Zachary J. Ruff[1,2,*], Damon B. Lesmeister[1,2], Julianna M. A. Jenkins[2], and Natalie M. Rugg[1,2]

[1]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA
[2]USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA

*Corresponding author: ruffz@oregonstate.edu

ABSTRACT

Dryocopus pileatus (Pileated Woodpecker) landscape use is widespread in the Pacific Northwest, especially in forested locations with structurally complex canopies, but declines at higher latitudes, higher elevations, and in areas of greater topographic complexity. High-use sites featured high conifer canopy cover and high *Abies grandis* (grand fir) basal area. These findings emerged from our analyses of ~1.7 million hours of acoustic recordings collected from 3,948 sites distributed across 10 million hectares of forest lands in the Pacific Northwest, USA. Data were processed using a deep learning model to detect species-specific vocalizations. Landscape use rates were high overall, with detections at 83% of surveyed locations. Detection probability decreased significantly over the field season and was negatively influenced by environmental noise and precipitation, emphasizing the need to account for these factors when interpreting acoustic monitoring data. The deep learning model detected *D. pileatus* vocalizations with high precision (>97% true positives among apparent detections). We corrected encounter histories based on precision, thereby improving the accuracy and reliability of ecological inferences. Passive acoustic monitoring, combined with machine learning and remotely sensed landscape variables, effectively uncovered nuanced patterns of occupancy and landscape use by *D. pileatus* at broad spatial scales. By elucidating patterns of landscape use, occupancy, and detectability, our results can help to guide conservation efforts and future research on this species. Given the role that *D. pileatus* plays as an ecosystem engineer, its distribution and habitat associations bear strongly on forest ecosystem management and biodiversity conservation in the context of changing forest conditions. This broad-scale assessment highlights the ecological importance of *D. pileatus* in shaping forest communities, influencing habitat availability for cavity-dependent species, and maintaining biodiversity across forested landscapes.

Keywords: bioacoustics, deep learning, ecosystem engineer, forest biodiversity, multi-state occupancy, occupancy modeling

How to Cite

Ruff, Z. J., D. B. Lesmeister, J. M. A. Jenkins, and N. M. Rugg (2026). Passive acoustic monitoring captures large-scale *Dryocopus pileatus* (Pileated Woodpecker) occupancy patterns in the Pacific Northwest, USA. Ornithological Applications 128:duag008.

LAY SUMMARY

- *Dryocopus pileatus* (Pileated Woodpecker) is a large woodpecker found in forests across North America. *Dryocopus pileatus* is an important ecosystem engineer—it excavates large tree cavities for nesting, roosting, and feeding, and these cavities are reused by other cavity-dependent species.
- We used an AI model to detect *D. pileatus* vocalizations in a collection of 1.7 million hours of audio recordings collected at nearly 4,000 field sites in the Pacific Northwest, USA in 2023.
- We used statistical models to identify landscape features that predicted *D. pileatus* landscape use (low intensity of vocal activity) and occupancy (high intensity of vocal activity).
- *Dryocopus pileatus* landscape use was higher in southern regions, at lower elevations, at sites with multi-layered tree canopies, and at sites with less variable terrain. Occupancy was more likely at sites with higher canopy cover of conifers, especially *Abies grandis* (grand fir).

Le suivi acoustique passif permet de saisir les schémas d'occupation à grande échelle de Dryocopus pileatus sur la côte nord-ouest du Pacifique, aux États-Unis

RÉSUMÉ

L'utilisation du paysage par *Dryocopus pileatus* est très répandue sur la côte nord-ouest du Pacifique, particulièrement dans les zones forestières où la canopée est structurellement complexe, mais elle diminue aux latitudes plus élevées, à des altitudes plus élevées et dans les zones de plus grande complexité topographique. Les sites les plus utilisés se caractérisaient par une couverture forestière dense en conifères et une grande

Submission Date: June 23, 2025; **Accepted:** November 7, 2025
Published by Oxford University Press for the American Ornithological Society 2026.

surface terrière en *Abies grandis*. Ces conclusions sont issues de nos analyses de ~1,7 million d'heures d'enregistrements acoustiques recueillis sur 3 948 sites répartis sur 10 millions d'hectares de forêts de la côte nord-ouest du Pacifique, aux États-Unis. Les données ont été traitées à l'aide d'un modèle d'apprentissage profond afin de détecter les vocalisations spécifiques à chaque espèce. Les taux d'utilisation du paysage étaient généralement élevés, avec des détections dans 83% des sites suivis. La probabilité de détection a significativement diminué au cours de la saison de terrain et elle était négativement influencée par le bruit environnemental et les précipitations, soulignant la nécessité de tenir compte de ces facteurs lors de l'interprétation de données de suivi acoustique. Le modèle d'apprentissage profond a détecté les vocalisations de *D. pileatus* avec une grande précision (> 97% de vrais positifs parmi les détections apparentes). Nous avons corrigé les historiques de rencontres en fonction de la précision, améliorant ainsi l'exactitude et la fiabilité des inférences écologiques. Le suivi acoustique passif, combiné à l'apprentissage profond et à des variables du paysage télédétectées, a permis de mettre en évidence de manière efficace les schémas d'occupation et d'utilisation du paysage par *D. pileatus* à grande échelle spatiale. En élucidant les schémas d'utilisation du paysage, d'occupation et de détectabilité, nos résultats peuvent contribuer à guider les efforts de conservation et les recherches futures sur cette espèce. Compte tenu du rôle que *D. pileatus* joue en tant qu'ingénieur de l'écosystème, sa répartition et ses associations d'habitats ont une forte incidence sur la gestion des écosystèmes forestiers et la conservation de la biodiversité dans le contexte de conditions forestières changeantes. Cette évaluation à grande échelle souligne l'importance écologique de *D. pileatus* dans la formation des communautés forestières, l'influence sur la disponibilité d'habitat pour les espèces cavicoles secondaires et le maintien de la biodiversité dans les paysages forestiers.

Mots-clés: bioacoustique, apprentissage profond, ingénieur de l'écosystème, biodiversité forestière, occupation multi-états, modélisation de l'occupation

INTRODUCTION

Forest-adapted ecosystem engineers play a major role in shaping forest structure and function, influencing biodiversity, nutrient cycling, and habitat complexity. Particularly important are those species whose activities significantly modify the physical environment, thereby creating niches and resources essential for many other organisms (Albertson et al. 2024, Sanders and Frago 2024). Woodpeckers are notable ecosystem engineers due to their cavity-excavating behaviors, which have far-reaching ecological effects within forested landscapes (van der Hoek et al. 2020). *Dryocopus pileatus* (Pileated Woodpecker), one of the largest extant woodpeckers, is a keystone species with a wide distribution in forested ecosystems across North America, playing a critical role in shaping habitat complexity and biodiversity (Aubry and Raley 2002b, Bull and Jackson 2020). By excavating large cavities in trees and snags for nesting and roosting, *D. pileatus* creates habitat resources that are subsequently used by a diverse community of cavity-dependent species, including owls, ducks, songbirds, and mammals (Bonar 2000, Aubry and Raley 2002b).

Consequently, understanding patterns of *D. pileatus* landscape use is valuable for broader ecosystem management and conservation planning. *Dryocopus pileatus* is generally associated with mature and old-growth forests and typically selects for mature forests with large-diameter trees for nesting and roosting, although it also uses younger forests, especially for foraging (Mellen et al. 1992). Loud and conspicuous vocalizations and drumming behavior, detectable over substantial distances (Bull et al. 1990), make *D. pileatus* highly detectable and well suited for passive acoustic monitoring (PAM). Recent advances in PAM now enable ecologists to gather extensive, objective, and long-term data on species presence, distribution, and behavior, and to complete habitat association analyses across large spatial extents (Sugai et al. 2019, Tosa et al. 2021).

Monitoring of the federally threatened *Strix occidentalis caurina* (Northern Spotted Owl) is mandated under the Northwest Forest Plan (NWFP; Lint et al. 1999), and in recent years, the monitoring approach has shifted from acoustic playback surveys and capture–mark–recapture demographic methods towards PAM in a stratified random sampling design (Lesmeister and Jenkins 2022). The region monitored under the NWFP represents a significant portion of the range of *D. pileatus* in Washington, Oregon, and California, USA; as such, the extensive PAM datasets generated by this program present an unprecedented opportunity to evaluate landscape use patterns of *D. pileatus* at large ecological scales in the Pacific Northwest.

Historically, *D. pileatus* was considered a management indicator species by national forests covered by the NWFP, making its ecology particularly relevant to regional management decisions (Aubry and Raley 2002a). The capacity of PAM to simultaneously monitor multiple species and generate permanent audio records provides valuable opportunities to understand broader community ecology and inform future ecological assessments (Tosa et al. 2021). Moreover, previous research has indicated home range sizes of *D. pileatus* in *Pseudotsuga menziesii* (douglas-fir) forests in western Oregon to be ~400–550 ha (Mannan 1984, Mellen et al. 1992), aligning closely with the 500-ha size of hexagons used in the NWFP PAM survey design. Although previous work has investigated habitat selection by *D. pileatus* based on remotely sensed landscape features at moderate scales (Hu and Tong 2022, Zeller 2024), to our knowledge, no previous attempt has been made to characterize *D. pileatus* landscape use on a scale comparable to the NWFP PAM program.

We analyzed *D. pileatus* detections from the large-scale NWFP PAM project using multi-state occupancy models. Our primary objectives were to characterize landscape use and occupancy patterns of *D. pileatus* within the NWFP monitoring area using detections from acoustic data. The relative persistence of vocal activity within a sampling period can be used as an indicator of territoriality as opposed to occasional or incidental site use (Reid et al. 2021). Hence, in this study, we use "landscape use" (or simply "use") to describe a state of infrequent or sporadic *D. pileatus* vocal activity and "occupancy" to describe a state of persistent vocal activity at a site, and we applied these definitions when constructing our encounter histories (MacKenzie et al. 2018). Additionally, we quantified factors influencing the detection probability of *D. pileatus*, including seasonal patterns of territorial vocal activity and environmental conditions which could affect sound attenuation. We anticipated that detection probability would be positively associated with recording effort, negatively associated with ambient noise levels, precipitation, and high temperatures, and would exhibit seasonal decline over the course of the monitoring season due to a reduction in territorial behaviors following nesting. We hypothesized that rates of *D. pileatus* landscape use and occupancy would vary geographically, with a positive association with mature and old-growth forest characteristics, including taller and larger-diameter trees, structurally complex canopies,

and higher prevalence of snags and coarse woody debris. We also predicted that occupancy would correlate with the prevalence of tree species previously documented as preferred or avoided nesting and roosting substrates for *D. pileatus*.

METHODS

Study Area

We conducted our study on federally managed forest lands within the NWFP area, which includes ~10 million ha of forested lands across western Washington, western Oregon, and northwest California States (Figure 1).

Due to its extensive size, our study area exhibited diverse terrain, climatic conditions, and forest types. Field sites ranged in elevation from 24 m above sea level (m.a.s.l.) in low-lying coastal areas to 2,350 m.a.s.l. in high elevation sites in the Cascade Mountains. Forest composition varied from coniferous forests dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla* (western hemlock), *Pinus monticola* (western white pine), *Pinus ponderosa* (ponderosa pine), and *Abies grandis* (grand fir) in northern regions, to mixed evergreen conifer-hardwood forests in southern areas (Reilly et al. 2018). Climate varied significantly, with northwest Washington receiving annual rainfall exceeding 4,600 mm, while sites in southwest Oregon, northern California, and the east side of the Cascades experienced warmer, drier conditions and received most precipitation as winter snowfall (Reilly et al. 2018). The NWFP encompasses 12 physiographic provinces representing broad differences in topography, climate, and vegetation (Thomas et al. 1993). We sampled 10 of these provinces, excluding the Washington Western Lowlands and Oregon Willamette Valley provinces (Figure 1).

Acoustic Data Collection

We selected study sites from a grid of 500-ha (5-km^2) hexagons covering the NWFP monitoring area (Lesmeister et al. 2021). Eligible hexagons had ≥25% federal management and ≥50% forest-capable land, meaning land capable of maintaining vegetative cover with the potential to develop into mature and old-growth forest, based on soil type, plant associations, and elevation (Davis et al. 2011). We used stratified random sampling, selecting 20% of eligible hexagons within several historical *S. o. caurina* demographic study areas and 2% outside these areas, resulting in 1,008 hexagons (total area = 5,040 km^2) sampled in 2023 (Figure 1; Lesmeister et al. 2021, Lesmeister and Jenkins 2022).

Within each hexagon, we deployed four autonomous recording units (ARUs; Wildlife Acoustics Song Meter SM4 or Song Meter Mini), spaced ≥500 m apart, ≥200 m from hexagon edges, and ≥50 m from roads, trails, and streams (Figure 1). We deployed ARUs on small trees (diameter at breast height <20 cm) positioned on mid to upper slopes. ARUs recorded daily in two 4-hr blocks around sunrise and sunset, plus the first 10 min of every hour outside of these blocks, totaling ~10.7 hr per day. ARU stations within each hexagon were deployed concurrently for approximately eight weeks between March and September 2023.

We calculated naïve landscape use as the proportion of ARU stations within each physiographic province with at least one detection. We report the mean number of detections per ARU station within each province; the mean call density, calculated as the number of detections divided by the total number of recording hours within each province; and the mean latency, defined as the mean time in days from the start of recording to the first detection at each station for stations with at least one detection.

Acoustic Data Processing

We trained a deep learning model (PNW-Cnet v5) to automate detections of 135 target classes, facilitating rapid processing of audio recordings, following the methods described by Ruff et al. (2023). We generated spectrogram images for non-overlapping 12-s segments of the audio data covering frequencies of 0–4,000 Hz and used PNW-Cnet v5 to generate class scores in the range [0,1] for each segment (Ruff et al. 2023). We analyzed detections of the PNW-Cnet v5 target class representing *D. pileatus* territorial vocalizations, specifically the rapid "cackle" and the slower "wuk" series call (Tremain et al. 2008), treating segments with scores ≥0.95 for this class as detections. We did not analyze drumming detections.

Deep learning models often generate false positives; therefore, estimating model precision (the proportion of apparent detections that are true positives) provides a robust method to account for these errors (Rainio et al. 2024). By multiplying the naïve apparent detection count by the precision rate, we obtained a precision-adjusted detection count. We evaluated PNW-Cnet v5 precision on the *D. pileatus* class by manually reviewing 3,500 randomly selected apparent detections (score ≥0.95) using spectrogram visualization (Kaleidoscope, Wildlife Acoustics, Inc.). We labeled detections based on which *D. pileatus* vocalizations, if any, were audible in the clip or visible in the spectrogram. We report the total number of calls and use the proportion of segments containing actual *D. pileatus* calls to estimate precision. We estimated classification precision to be >0.973, so multiplied apparent detections by 0.973 to obtain the precision-adjusted detection count.

Occupancy Analysis

We used a single-season multi-state occupancy framework (Mackenzie et al. 2018), defining the survey unit as an ARU station and the survey occasion as a week of recording by one ARU. Our ARUs likely detected *D. pileatus* vocalizations within several hundred meters—smaller than reported home range sizes in the Pacific Northwest. Thus, we assumed that ARU stations sampled a cell of potential habitat, centered on each ARU, which likely did not encompass an entire territory (Steenweg et al. 2018). Encounter histories had 3 states: no detections (State 0), detections on one, two or three days during the week (State 1), and detections on four or more days (State 2). State 2 indicated persistent vocal activity and therefore higher concentration of use, which can be an indicator of habitat quality (Tomasevic and Marzluff 2018). We truncated encounter histories at six weeks to reduce missing data due to ARU battery limitations. We omitted encounter histories from stations for which we did not have complete covariate information, leaving 3,948 ARU stations included in the analysis. To minimize the possibility of including false positives in the analysis, we manually reviewed all detections from stations that had ≤10 apparent detections in the first six weeks of recording and removed false positive detections from these stations before creating the encounter histories.

We constructed models using the conditional binomial parameterization (Nichols et al. 2007), estimating probability

of use (ψ), conditional probability of occupancy given use (*R*), detection probabilities for States 1 ($p^{[1]}$) and 2 ($p^{[2]}$), and probability of correctly classifying State 2 sites as such (δ; hereafter "classification"—note that this parameter is estimated at the level of the 1-week survey occasion and is distinct from precision, described above, which is calculated at the level of 12-s audio segments). Our analysis quantified relationships between these parameters and remotely sensed habitat features. We fit multi-state occupancy models using the *RPresence* package (MacKenzie and Hines 2024) in R 4.4.1 (R Core Team 2024).

The time-varying (i.e., survey) covariates that we considered for detection and classification probabilities (*p* and δ, respectively) included: total weekly recording effort (EFFORT; hr); mean ambient noise level (NOISE) measured in decibels below full scale (dBFS); mean, mean maximum, and maximum daily temperature during each survey week (TEMP_MN, TEMP_MNMAX, and TEMP_MAX; in °C), and mean and total daily precipitation during each survey week (PRECIP_MEAN, PRECIP_TOT; in mm). We measured noise levels within a 1/3-octave frequency band centered at 1,000 Hz using the sound pressure level (SPL) analysis tool in Kaleidoscope Pro (Wildlife Acoustics, Inc.) and averaged these values by week. We aggregated weather data at 4-km resolution from PRISM data (PRISM Climate Group 2024). We also considered several site-level covariates related to geography and terrain to account for possible differences in detection probability due to sound attenuation (Table 1). We tested for seasonal trends using ordinal date (DATE). We standardized all survey-level covariates prior to analysis.

We grouped site-level covariates by geography/climate, terrain, forest structure, and forest composition (Table 1). We aggregated multi-scale covariates derived from landscape raster data (LEMMA Group 2023) in 180-m and 360-m buffers around survey stations to characterize local conditions given the unknown location and distance of detected vocalizations. We included covariates for basal areas of tree species previously linked to *D. pileatus* nesting or roosting: *Abies amabilis* (pacific silver fir), *Abies grandis*, *Acer macrophyllum* (bigleaf maple), *Alnus ruber* (red alder), *Pinus ponderosa*, *Pseudotsuga menziesii*, *Thuja plicata* (western redcedar), and *Tsuga heterophylla* (Aubry and Raley 2002a, Hartwig et al. 2004, Tomasevic and Marzluff 2020). We standardized all continuous site-level covariates prior to analysis. We included physiographic

TABLE 1. Site-level covariates used to construct sub-models for probability of *D. pileatus* landscape use (ψ), probability of occupancy given use (*R*), and detection (*p*).

Covariate	Description	Group	Parameters
CHILI	Continuous heat insolation load index (Theobald et al. 2015)	Geography and Climate	ψ, *R*
CLIMWD	Climatic water deficit index	Geography and Climate	ψ, *R*
FR	Coverage of topoclimatic fire refugia (%; Krawchuk et al. 2023)	Geography and Climate	ψ, *R*
LATITUDE	Latitude (degrees)	Geography and Climate	ψ, *R*, *p*
LONGITUDE	Longitude (degrees)	Geography and Climate	ψ, *R*, *p*
PROV	Physiographic province (categorical)	Geography and Climate	ψ, *R*, *p*
DSTREAM	Distance to stream or surface water (m)	Terrain	ψ, *R*
ELEV_MN	Mean elevation (m)	Terrain	ψ, *R*, *p*
ELEV_SD	Standard deviation of elevation (m)	Terrain	ψ, *R*, *p*
MTPI	Multiscale topographic position index (Theobald et al. 2015)	Terrain	ψ, *R*
TOPO_DIV	Topographic diversity (Theobald et al. 2015)	Terrain	ψ, *R*
AGE_DOM	Mean age of dominant trees (y)	Forest Structure	ψ, *R*
CC_CON	Canopy cover of conifers (%)	Forest Structure	ψ, *R*
CC_HDW	Canopy cover of hardwoods (%)	Forest Structure	ψ, *R*
CC_LAYERS	Number of tree canopy layers	Forest Structure	ψ, *R*
DBH_CON	Mean conifer DBH, basal area-weighted (cm)	Forest Structure	ψ, *R*
DDI_MN	Diameter diversity index	Forest Structure	ψ, *R*
DOWN_COV	Areal coverage of down trees with diameter ≥25 cm (%)	Forest Structure	ψ, *R*
DOWN_MASS	Biomass of down trees with diameter ≥25 cm (kg ha^{-1})	Forest Structure	ψ, *R*
DOWN_VOL	Volume of down trees with diameter ≥25 cm (m^3 ha^{-1})	Forest Structure	ψ, *R*
OGSI_MN	Mean OGSI	Forest Structure	ψ, *R*
SNAG_MASS	Biomass of snags with DBH ≥25 cm (kg ha^{-1})	Forest Structure	ψ, *R*
SNAG_TPH	Density of snags with DBH ≥25 cm (stems ha^{-1})	Forest Structure	ψ, *R*
SNAG_VOL	Volume of snags with DBH ≥25 cm (m^3 ha^{-1})	Forest Structure	ψ, *R*
STAND_HGT	Stand height (m)	Forest Structure	ψ, *R*
TPH_50	Density of trees with DBH ≥50 cm (stems ha^{-1})	Forest Structure	ψ, *R*
TPH_75	Density of trees with DBH ≥75 cm (stems ha^{-1})	Forest Structure	ψ, *R*
BA_ABAM	Basal area of *Abies amabilis* (pacific silver fir; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_ABGRC	Basal area of *Abies grandis/concolor* (grand fir/white fir; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_ACMA	Basal area of *Acer macrophyllum* (bigleaf maple; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_ALRU	Basal area of *Alnus ruber* (red alder; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_PIPO	Basal area of *Pinus ponderosa* (ponderosa pine; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_PSME	Basal area of *Pseudotsuga menziesii* (douglas-fir; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_THPL	Basal area of *Thuja plicata* (western redcedar; m^2 ha^{-1})	Forest Composition	ψ, *R*
BA_TSHE	Basal area of *Tsuga heterophylla* (western hemlock; m^2 ha^{-1})	Forest Composition	ψ, *R*

DBH = diameter at breast height; OGSI = old growth structure index.

province as a categorical covariate (excluding two unsampled provinces, Washington Western Lowlands and Oregon Willamette Valley), using the Oregon Klamath province as the reference level, against which the effects of other provinces were estimated on a relative basis.

We used a secondary candidate set model selection strategy (Morin et al. 2020), fitting sub-models separately for each model parameter—ψ (use), *R* (occupancy given use), *p* (detection), and δ (classification)—while using intercept-only sub-models for the non-focal parameters, then constructed a final candidate model set including all combinations of competitive sub-models (ΔAIC ≤10). We separately selected covariates and most supported covariate scales for each parameter using univariate sub-models ranked by Akaike's Information Criterion (AIC). Based on AIC support for the univariate sub-models, we grouped highly correlated covariates ($|r| \geq 0.60$) and used only the most supported covariate from each group in subsequent stages. Multivariate sub-models for probability of use (ψ) considered geography, climate, terrain, and forest structure, while those for probability of occupancy (*R*) additionally included forest composition. For detection and classification probabilities (*p*, δ), fewer covariates were initially considered, and after thinning highly correlated covariates as described above, all combinations of the remaining covariates were modeled.

We used the final, most-supported multi-state occupancy model to predict the probability of *D. pileatus* use and occupancy across all forested (≥50% forest capable) hexagons within the NWFP area. Values were estimated based on landscape variables measured at the center of each 5-km^2 hexagon to approximate conditions within the hexagon. In addition to ψ (use) and *R* (occupancy given use), we estimated the derived probabilities φ_0, φ_1, and φ_2, corresponding to the probabilities of each centroid being in State 0, State 1, or State 2, respectively. We calculated $\varphi_0 = 1 - \psi$, $\varphi_1 = \psi(1 - R)$, and the probability of occupancy = $\varphi_2 = \psi R$. We estimated standard errors for these derived estimates using the delta method (Powell 2007). We report the mean predicted probability of use and occupancy for each physiographic province.

RESULTS

We analyzed ~1.7 million hours of audio recorded at 3,948 ARU stations in 2023, divided into ~511 million 12-s audio segments for classification. Of these, 259,379 segments indicated *D. pileatus* vocalizations (PNW-Cnet v5 score ≥0.95), equivalent to 0.152 detections per recording hour, or one detection for every 6.6 hr of audio (Table 2). Naïve landscape use was high; 82.6% of ARU stations had at least one detection. The rate of occupancy was more variable, with 55.5% of all ARU stations being observed in State 2 during at least one survey week. The number of apparent detections per ARU station ranged from 0 to 1,525 (mean = 86.7, SE = 125.6). Naïve landscape use varied by physiographic province; average station-level use ranged from 53.3% to 100%, while the proportion of stations observed in State 2 ranged from 22.6% to 85.7%. Landscape use was generally lower in Washington than in Oregon or California, with the lowest rates of use and occupancy in the Washington West Cascades province (Table 2). Mean latency, the average time between the start of sampling and the first detection at a station, ranged from 3.5 days in the CA Coast Range province to 9.2 days in the WA West Cascades province, with an overall average of 5.7 days (Table 2).

We manually reviewed 3,500 randomly selected segments classified by PNW-Cnet v5 as *D. pileatus* detections (score ≥0.95) to estimate the precision of PNW-Cnet v5 on this class. Of these, 97.3% contained confirmed calls, while another 1.7% had attenuated signals representing possible or probable detections. Hence, a conservative estimate of classification precision when using a detection threshold of 0.95 is 0.973, although actual precision might be slightly higher. Of the clips with confirmed detections, 69.4% included "cackle" calls, 31.9% included "wuk" series calls, and 1.3% included both call types.

TABLE 2. Summary of recording effort and *D. pileatus* detections by physiographic province.

Province	Dets	Stations	Use Stns	State 2 Stns	Dets/ Stn (Mean)	Dets/ Stn (SE)	Dets/ hour (mean)	Dets/ hour (SE)	Latency (mean)	Latency (SE)
CA Cascades	3,336	72	60	38	46.33	63.81	0.10	0.14	7.49	9.42
CA Coast Range	8,411	42	42	36	200.26	242.11	0.45	0.55	3.45	5.28
CA Klamath	21,678	329	278	199	65.89	88.77	0.16	0.20	4.77	7.71
OR Coast Range	78,063	791	784	604	98.69	105.04	0.23	0.24	4.55	6.91
OR East Cascades	16,592	287	217	146	57.81	78.68	0.14	0.19	5.55	8.18
OR Klamath	41,909	346	339	281	121.12	122.21	0.28	0.28	4.12	7.04
OR West Cascades	55,507	844	739	506	65.77	83.70	0.15	0.19	4.39	7.03
WA East Cascades	10,683	413	271	115	25.87	53.03	0.06	0.12	8.73	10.26
WA Olympic	17,815	479	347	188	37.19	64.30	0.09	0.15	6.51	8.57
WA West Cascades	5,385	345	184	78	15.61	31.75	0.04	0.07	9.16	10.07
Overall	259,379	3,948	3,261	2,191	65.70	82.63	0.15	0.19	5.69	7.96

Detections ("Dets") are defined as 12-s audio segments that scored ≥0.95 for the PNW-Cnet v5 *D. pileatus* class. "Use" indicates recording stations with ≥1 detection. "State 2" indicates stations that were classified as occupied for the analysis, indicating there were detections on ≥4 days within one or more weeks during the first 6 weeks of sampling. Latency is the time in days from the start of recording to the first detection at each station for stations that had ≥1 detections. Summaries are based on the first 6 weeks of sampling at each station.

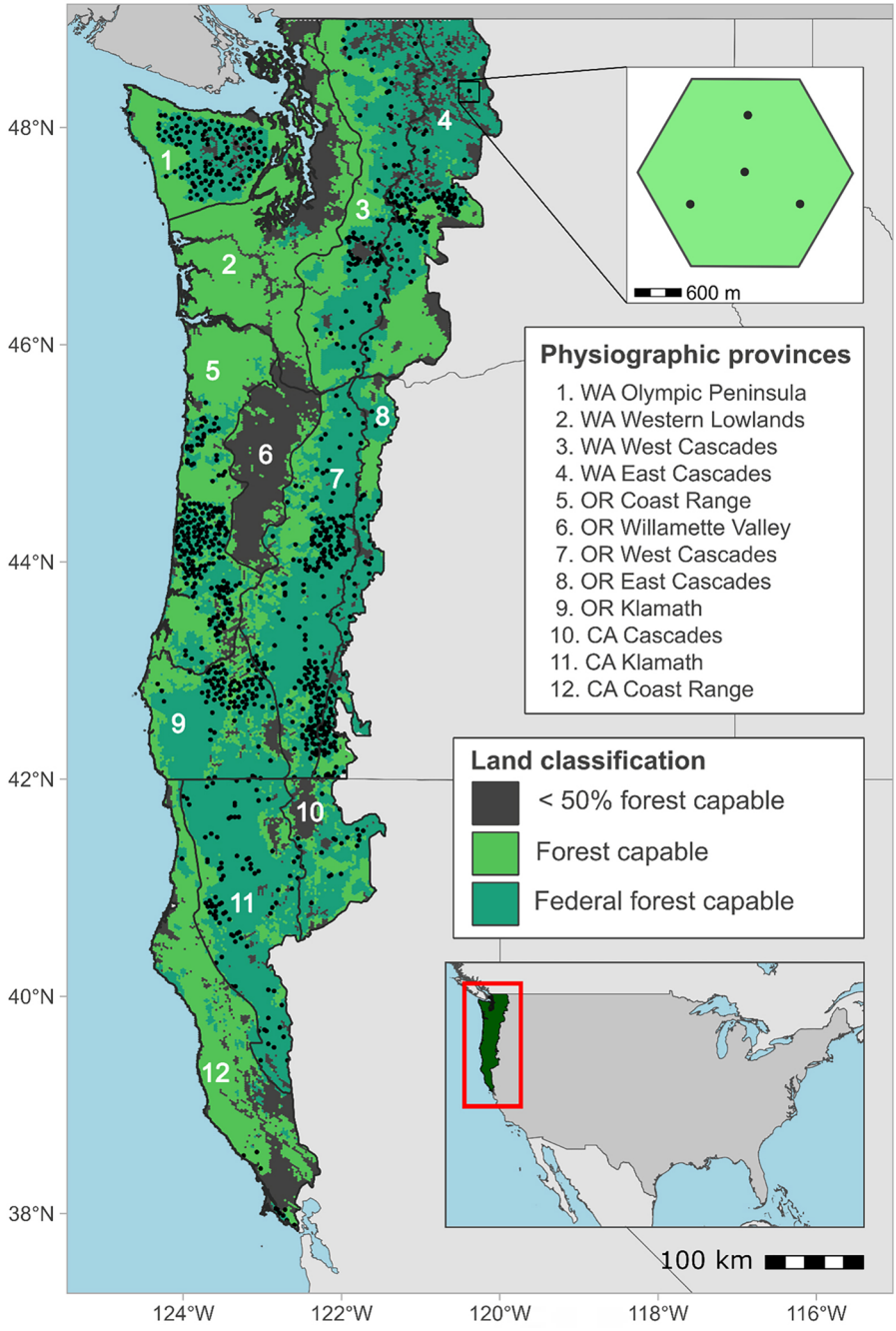

FIGURE 1. Area covered by the Northwest Forest Plan (NWFP) passive acoustic monitoring program and 2023 sampling locations. Sampling locations (black dots) were selected from a tessellation of 5-km² hexagons. Eligible hexagons were ≥25% federally managed and ≥50% "forest capable" (ie, capable of developing mature and old growth forest). We sampled 20% of eligible hexagons within several long-term *Strix occidentalis caurina* demographic study areas and 2% of eligible hexagons outside these areas ($n = 1{,}008$). (Upper inset) Typical deployment of 4 recording stations within a sampling hexagon. (Lower inset) NWFP monitoring area within the contiguous United States.

Model Selection

The most supported sub-model for detection probability (p) included observed state (higher intercept for State 2), latitude (–), mean elevation (–; 360-m buffer), date (–), recording effort (+), and background noise (–; Table 3 and Figure 2), and had 100% of AIC weight. The most supported sub-model for classification accuracy (δ) included background noise (–), mean precipitation (–), and recording effort (+), also having 100% of AIC weight (Table 3 and Figure 2).

For use (ψ), one competitive sub-model emerged, which included effects of latitude (–), mean elevation (–; 360-m buffer), topographic diversity (–), and canopy layers (+; 180-m buffer; AIC weight 100%; Table 3 and Figure 2). For probability of occupancy given use (R), one competitive sub-model emerged, which included effects of latitude (–), mean elevation (–; 360-m buffer), conifer canopy cover (+; 360-m buffer), topographic diversity (–), and *Abies grandis* basal area (+; 360-m buffer; Table 3 and Figure 2). Four other sub-models for R appeared

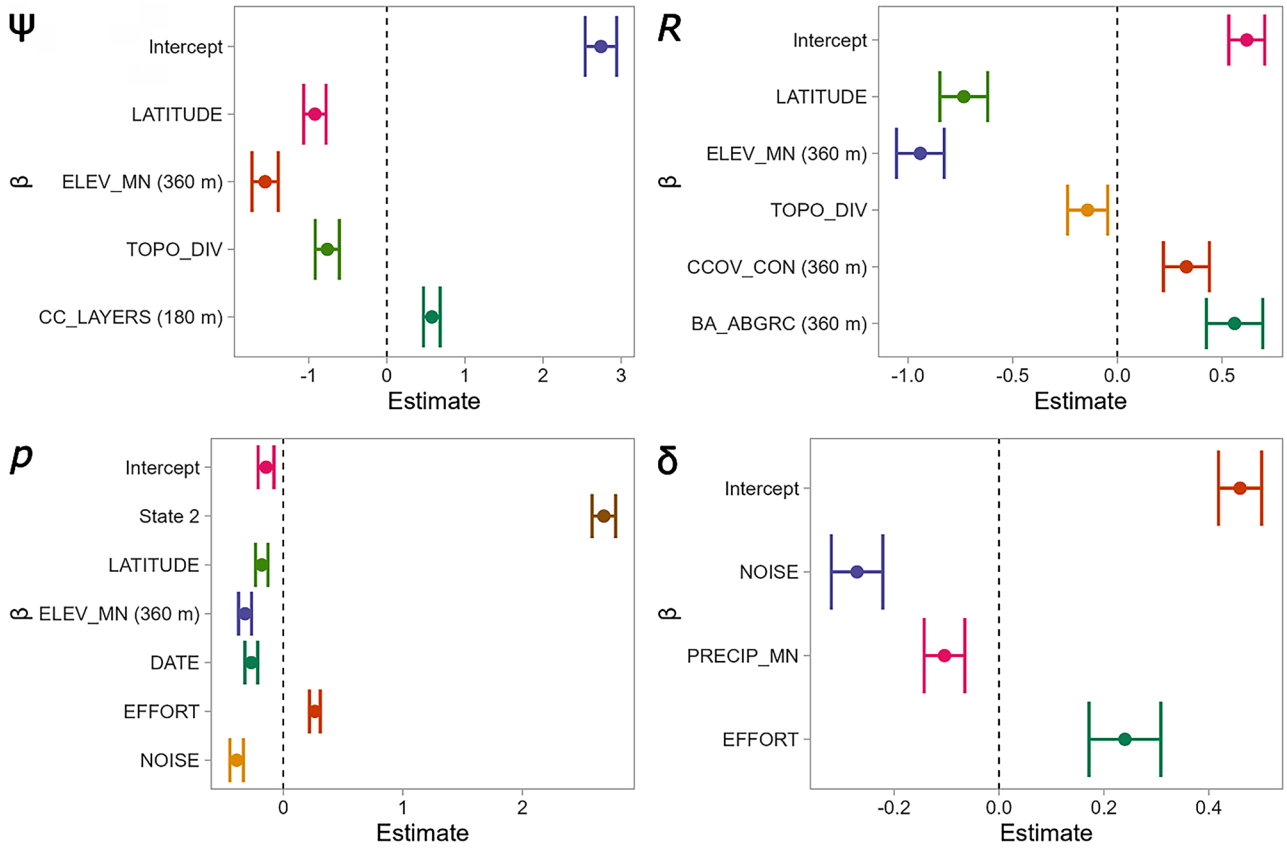

FIGURE 2. Point estimates and 95% confidence intervals for covariate beta coefficients from the full multi-state occupancy model on probability of *D. pileatus* use (ψ), occupancy given use (*R*), detection (*p*), and classification of the occupied state (δ). All covariates were Z-transformed prior to model fitting; hence, each point estimate represents the predicted multiplicative effect of increasing each covariate by 1 standard deviation on the odds of the parameter in question. Beta estimates for which the 95% confidence interval does not include 0 (dashed line) are considered statistically significant. Table 1 includes site-level covariate descriptions.

highly competitive (ΔAIC ≤ 2) but each of these simply added an extra covariate to the sub-model described above and did not significantly improve AIC (Supplementary Material Table 1); we considered these extra covariates uninformative and did not consider these sub-models in the final model selection.

As there was only one competitive sub-model for each of the model parameters ψ (use), *R* (occupancy), *p* (detection), and δ (classification), we simply combined these sub-models to obtain the full multi-state occupancy model and fitted it to the data to estimate covariate effect sizes. The full model had an AIC score of 36,078.1.

Covariate Effects

Geography and elevation were strong predictors of ψ (use) and *R* (occupancy given use), with negative relationships indicating lower use and occupancy in more northern and higher-elevation sites (Table 4 and Figures 2 and 3). Based on covariate estimates from the most-supported model, an increase of 2.5 degrees of latitude decreased the odds of use by 62.6% (95% CI: 56.4–67.9%) and decreased the odds of occupancy by 54.3% (CI: 48.4–59.5%). An increase of 200 m in elevation decreased the odds of use by 47.4% (CI: 43.6–50.9%) and decreased the odds of occupancy by 32.1% (CI: 28.8–35.2%). Topographic diversity negatively influenced both ψ and *R*, indicating greater probability of use and occupancy in flatter areas; an increase of 0.21 in topographic diversity (equal to the standard error for this covariate) decreased the odds of use by 53.4% (CI: 45.6–60.1%) and decreased the odds of occupancy by 13.2% (CI: 4.5–21.2%). Use was strongly positively influenced by the mean number of canopy layers within a 180-m buffer; increasing the mean canopy layers by 1 increased the odds of use by a factor of 3.1 (CI: 2.5–3.8).

R (occupancy given use) was positively influenced by both *Abies grandis* basal area and conifer canopy cover (Table 4 and Figures 2 and 4). Increasing *Abies grandis* basal area by 2.5 m^2 ha^{-1} increased the odds of occupancy by 31.3% (CI: 22.9–40.2%). Increasing conifer canopy cover by 10 percentage points increased the odds of occupancy by 19.7% (CI: 12.7–27.0%).

Of the eight tree species considered for potential effects on occupancy (*R*), *Alnus ruber* and *Pinus ponderosa* were unsupported in univariate models. *Tsuga heterophylla* was excluded due to correlation with latitude, while *Abies amabilis*, *Acer macrophyllum*, *Pseudotsuga menziesii*, and *Thuja plicata* were included in multivariate sub-models for *R* but we found to be uninformative when added to models that already included latitude, elevation, conifer canopy cover, and *Abies grandis* basal area. Hence, only *Abies grandis* (+) was included in the final model.

Weekly detection probability (*P*) was positively related to recording effort and negatively related to latitude, mean elevation, Julian date (indicating seasonal decline), and background noise. Sites that were observed in State 2 had substantially higher detection probability than those that were not; the odds of weekly detection were 14.6 times higher for State 2 sites

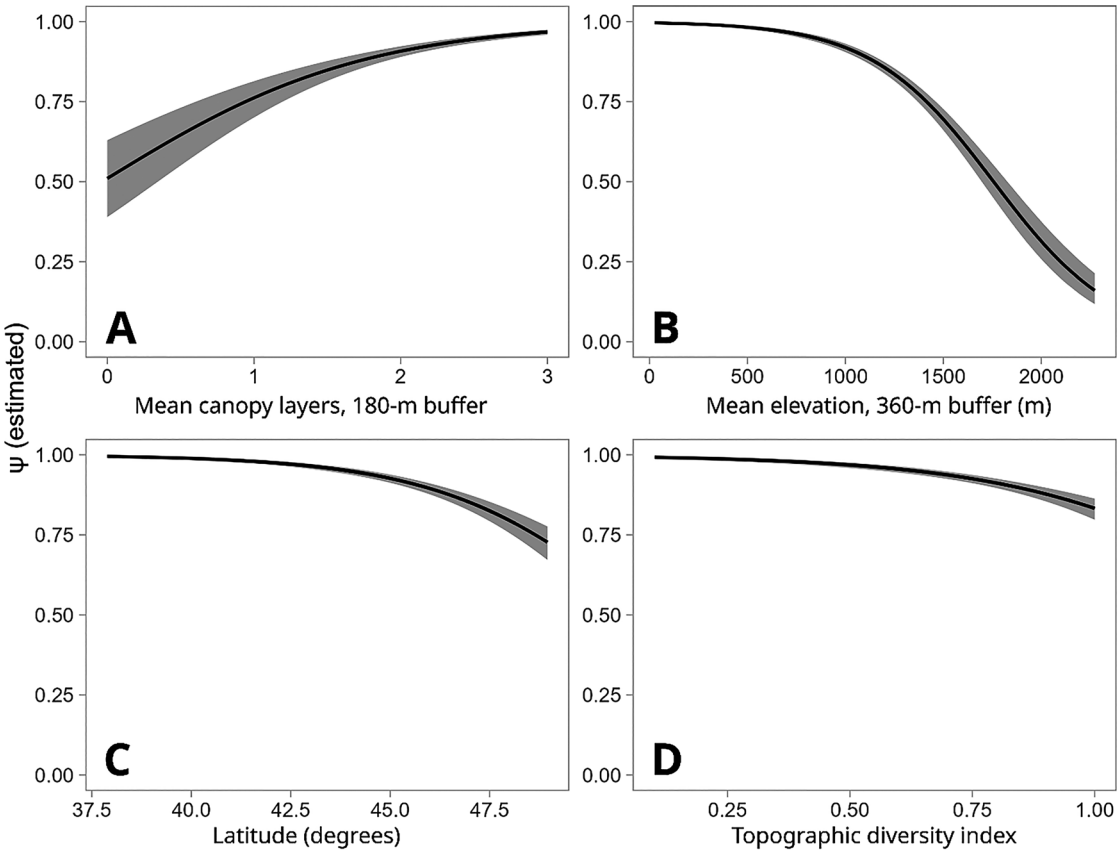

FIGURE 3. Effects of site-level covariates CC_LAYERS (**A**), ELEV_MN (**B**), LATITUDE (**C**), and TOPO_DIV (**D**) on predicted use (ψ) of *D. pileatus* based on beta estimates from the full multi-state occupancy model over the range of observed values for each covariate. Non-focal covariates for each subplot were held constant at their respective means. 95% confidence envelopes were calculated using the delta method. See Table 1 for covariate descriptions. ψ increases with the number of canopy layers and decreases with mean elevation, latitude, and topographic diversity.

than for non-State 2 sites (CI: 13.2–16.1 times higher). Increasing latitude by 2.5 degrees decreased the odds of weekly detection by 17.5% (CI: 12.8–22.0%). Increasing mean elevation by 200 m decreased the odds of weekly detection by 12.4% (CI: 10.4–14.3%). Shifting the survey date 2 weeks later in the season decreased the odds of detection by 8.4% (CI: 6.8–10.0%). Increasing recording effort by 5 hr increased the odds of detection by 26.2% (CI: 21.3–31.4%). Increasing mean background noise in the 1000 Hz band by 5 dB decreased the odds of detection by 23.5% (CI: 20.5–26.4%).

Classification accuracy (δ) decreased with higher background noise levels and higher mean precipitation but increased with higher recording effort. Increasing mean background noise in the 1000 Hz band by 5 dB decreased the odds of correct classification by 16.9% (CI: 14.0–19.7%). Increasing mean weekly precipitation by 5 mm decreased the odds of correct classification by 15.3% (CI: 9.9–20.5%). Increasing recording effort by 5 hr increased the odds of correct classification by 23.6% (CI: 16.4–31.4%).

Maps of predicted probability of *D. pileatus* landscape use (ψ) and occupancy (φ_2) across the NWFP area illustrate the influence of latitude and elevation, with predicted use close to 1 in low-lying areas throughout the study area but markedly lower and more variable in higher-elevation sites, particularly in Washington (Figure 5). Predicted occupancy was more variable overall but still significantly higher in coastal areas in the southern portion of the study area (Figure 5). The overall mean predicted use of 38,256 forested hexagon centroids across the NWFP area was 0.865 while the overall mean predicted probability of occupancy given use (R) was 0.634. The mean predicted probability that a hexagon centroid was in State 0, State 1, and State 2 was 0.135, 0.276, and 0.589, respectively. Physiographic provinces in Washington had the highest mean predicted probability of non-use φ_0: 0.457 in the WA East Cascades province, 0.267 in the WA West Cascades province, and 0.134 in the WA Olympic Peninsula province.

DISCUSSION

We detected widespread landscape use and occupancy by *D. pileatus* across forested landscapes of the Pacific Northwest, underscoring its continued presence and ecological influence across much of its range. These findings have strong conservation relevance, as they demonstrate that structurally complex, late-successional forests remain critical to sustaining *D. pileatus* populations and, by extension, the many cavity-dependent species that rely on them. The high rates of landscape use we observed in mature coniferous forests with multi-layered canopies highlight the importance of protecting and promoting forest structures that support this ecosystem engineer (Bull and Jackson 2020). Conservation strategies that maintain large-diameter trees, multi-layered canopies, and moderate levels of disturbance will likely provide the dual benefits of supporting *D. pileatus* and preserving the broader cavity-nesting community it facilitates. As forest ecosystems in the Pacific Northwest continue to experience accelerating changes from wildfire, logging, and other landscape-scale shifts in vegetation

TABLE 3. Results of sub-model selection for detection probability (*p*), classification accuracy (δ), use (ψ), and occupancy (*R*).

Parameter	Sub-model	AIC	*k*	ΔAIC	modlike	w_i
p	STATE + LATITUDE + ELEV_MN (360 m) + DATE + EFFORT + NOISE	37,864.3	10	0.0	1.000	1.000
δ	NOISE + PRECIP_MN + EFFORT	42,686.5	7	0.0	1.000	1.000
ψ	LATITUDE + ELEV_MN (360 m) + TOPO_DIV + CC_LAYERS (180 m)	41,805.8	8	0.0	1.000	0.998
R	LATITUDE + ELEV_MN (360 m) + TOPO_DIV + CCOV_CON (360 m) + BA_ABGRC (360 m)	42,627.4	9	0.2	0.918	0.286

We fit sub-models separately for each parameter while using intercept-only sub-models for non-focal parameters. The top *R* sub-model listed had the highest AIC support among *R* sub-models that did not include uninformative covariates. See Table 1 for site covariate descriptions. AIC = Akaike's Information Criterion; *k* = number of sub-model parameters; ΔAIC = difference in AIC from the most supported sub-model; w_i = AIC weight within each sub-model set. See Supplementary Material Table 1 for full sub-model selection results.

TABLE 4. Estimated covariate effects from the full multi-state occupancy model on probability of *D. pileatus* landscape use (ψ), probability of occupancy given use (*R*), detection (*p*), and classification of the high use state (δ).

Parameter	Beta	Estimate	Standard error	95% CI lower	95% CI upper
ψ	Intercept	2.741	0.101	2.539	2.943
	CC_LAYERS (180 m)	0.576	0.053	0.469	0.683
	ELEV_MN (360 m)	–1.560	0.084	–1.728	–1.392
	LATITUDE	–0.922	0.072	–1.066	–0.779
	TOPO_DIV	–0.763	0.077	–0.918	–0.608
R	Intercept	0.618	0.043	0.532	0.704
	BA_ABGRC (360 m)	0.560	0.067	0.425	0.695
	CCOV_CON (360 m)	0.330	0.055	0.220	0.439
	ELEV_MN (360 m)	–0.941	0.057	–1.055	–0.827
	LATITUDE	–0.734	0.057	–0.848	–0.620
	TOPO_DIV	–0.142	0.048	–0.238	–0.046
p	Intercept	–0.145	0.033	–0.211	–0.079
	State 2	2.681	0.049	2.583	2.780
	ELEV_MN (360 m)	–0.321	0.027	–0.375	–0.267
	EFFORT	0.263	0.023	0.218	0.309
	DATE	–0.269	0.027	–0.322	–0.215
	LATITUDE	–0.181	0.026	–0.233	–0.129
	NOISE	–0.391	0.028	–0.448	–0.335
δ	Intercept	0.460	0.021	0.418	0.501
	EFFORT	0.240	0.034	0.172	0.309
	PRECIP_MN	–0.104	0.019	–0.143	–0.065
	NOISE	–0.271	0.025	–0.320	–0.221

All covariates were Z-transformed prior to model fitting; hence, each estimate represents the predicted multiplicative effect of increasing each covariate by 1 standard deviation on the odds ratio of the parameter in question. Beta estimates for which the 95% confidence interval does not include 0 are considered statistically significant; this includes all covariates shown. See Table 1 for site-level covariate descriptions.

and disturbance dynamics, the persistence of *D. pileatus* can serve as a key indicator of forest integrity and habitat continuity. Integrating its habitat requirements into forest management planning therefore has broad implications for biodiversity conservation and the maintenance of ecological resilience.

The functional role of *D. pileatus* as an ecosystem engineer derives partly from its ability to excavate large nesting and roosting cavities, which directly supports a community of cavity-dependent taxa, including larger-bodied cavity-nesting birds such as owls and ducks (Bull et al. 1990, Martin et al. 2004). The limited availability of sufficiently large cavities in many forest ecosystems positions *D. pileatus* as a critical facilitator of biodiversity. Indeed, several studies have documented positive associations between *D. pileatus* and other cavity nesters, underscoring its potential as an indicator species for biodiversity, forest habitat quality, and availability of nesting resources (Bull et al. 1990, Bonar 2000, Scholer et al. 2018). Future research incorporating multi-species occupancy analyses could further elucidate the ecological interactions facilitated by *D. pileatus* activity, especially cavity excavation.

Our analysis focused exclusively on *D. pileatus* vocalizations due to the current limitations of our acoustic classification model, which prevented species-specific identification of woodpecker drumming. However, drumming represents a significant component of woodpecker communication, influencing territorial defense and mate attraction (Tremain et al. 2008, Bull and Jackson 2020). Recent studies, such as Zeller et al. (2024), highlight the value of analyzing drumming in addition to vocalizations to understand broader behavioral patterns. Future improvements to PNW-Cnet to distinguish woodpecker species based on drumming patterns would enable more comprehensive assessments of the acoustic ecology and behavioral responses to habitat variation of *D. pileatus* and other woodpeckers.

Based on these passive recordings, we were unable to estimate the number of different individuals detected by each ARU or the precise location of vocalizing individuals, which precluded us from estimating overall population size or local abundance. Additionally, because our results are based only on data from 2023, we could not estimate trends in use or occupancy.

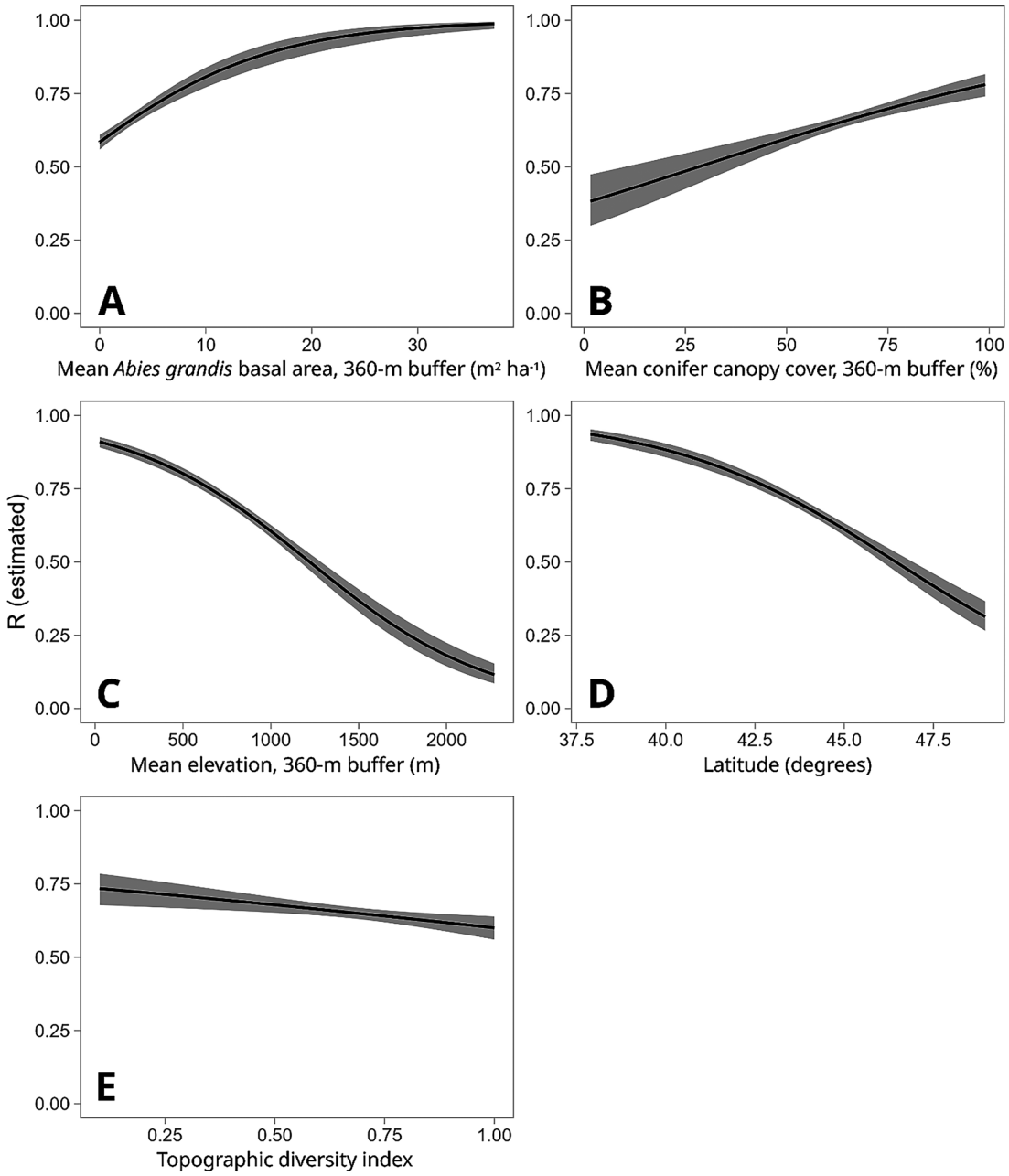

FIGURE 4. Effects of site-level covariates BA_ABGRC (**A**), CCOV_CON (**B**), ELEV_MN (**C**), LATITUDE (**D**), and TOPO_DIV (**E**) on predicted probability of occupancy given use (*R*) by *D. pileatus* based on beta estimates from the full multi-state occupancy model over the range of observed values for each covariate. Non-focal covariates for each subplot were held constant at their respective means. 95% confidence envelopes were calculated using the delta method. See Table 1 for covariate descriptions. *R* increases with *Abies grandis* basal area and conifer canopy cover and decreases with increasing mean elevation, latitude, and topographic diversity.

However, documenting landscape use by *D. pileatus* in the NWFP area as of 2023 establishes a baseline with which future occupancy estimates can be compared to detect evidence of expansion or decline. Future work may incorporate multiple years of data in a dynamic occupancy framework to estimate overall trends and rates of site turnover and to explore factors influencing site-level colonization and extinction of *D. pileatus*. Support for such analyses is a virtue of long-term monitoring programs generally, and the benefit is compounded in programs like the NWFP PAM program that encompass a variety of taxa (Lesmeister and Jenkins 2022).

Compared to previous *D. pileatus* studies relying on direct observation or radiotelemetry methods at smaller scales (e.g., Bull 1987, Aubry and Raley 2002a, Hartwig et al. 2004, Tomasevic and Marzluff 2020), our large-scale passive acoustic monitoring approach provided coarser location information over a much larger area. The difference in scale may explain some apparent discrepancies between our findings and those of earlier studies. For example, although previous studies have identified several species of tree as preferred nesting or roosting cover for *D. pileatus* (e.g., *Abies amabilis*, Aubry and Raley 2002a), in most cases we found no evidence that basal area of

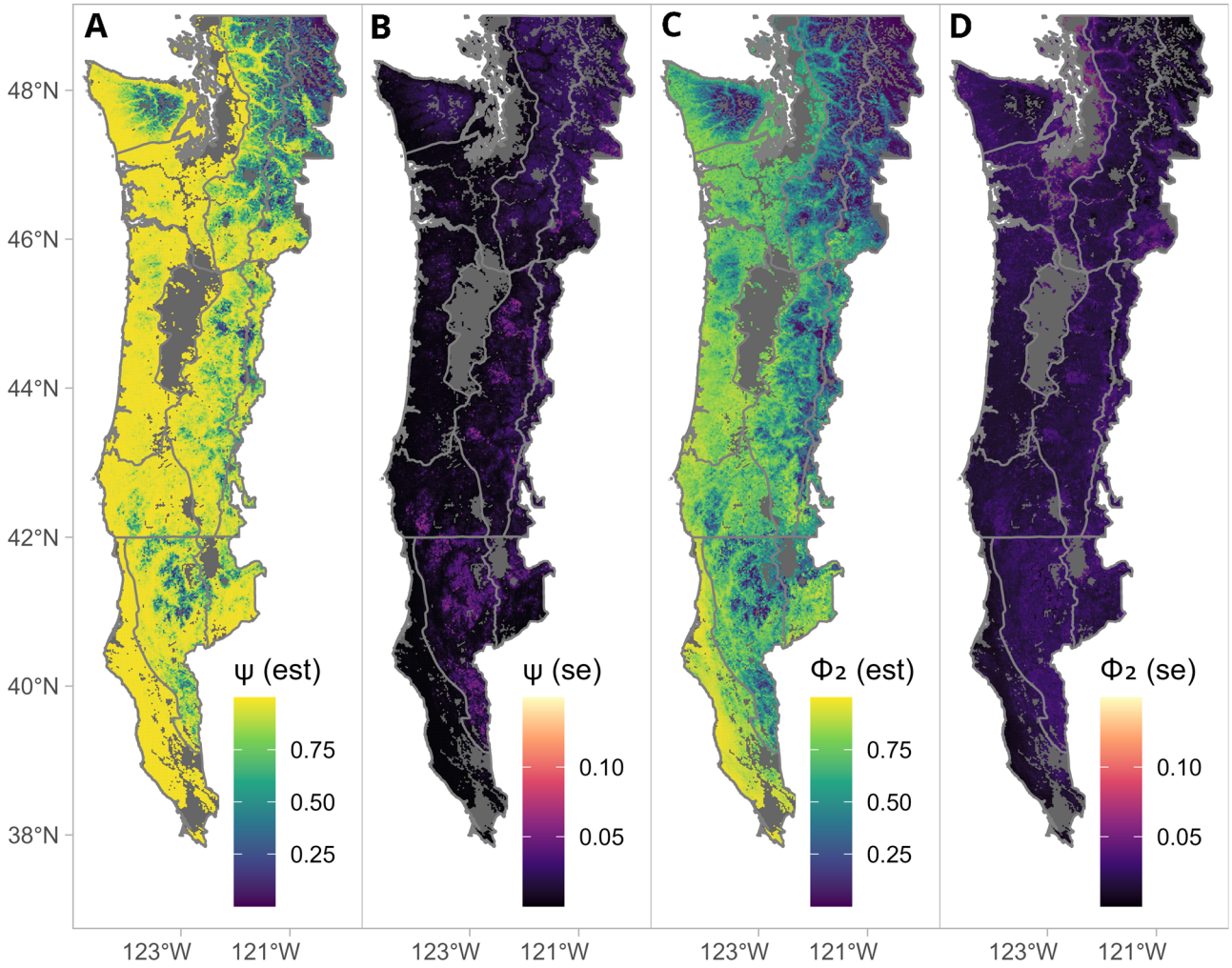

FIGURE 5. Predicted *D. pileatus* use (ψ; **A** = point estimates, **B** = standard errors) and occupancy (State 2; $\varphi_2 = \psi * R$, where R = probability of occupancy given use; **C** = point estimates, **D** = standard errors) for 38,256 forested 5-km² hexagons within the Northwest Forest Plan monitoring area based on a multi-state occupancy model. Estimates were based on covariate values at each hexagon's centroid. Non-forested hexagons are shaded gray. Supplementary Material Table 2 lists averages by physiographic province. Predicted use and occupancy are higher and more uniform in low-lying and coastal areas and more variable in mountainous areas.

these tree species influenced landscape use or occupancy by *D. pileatus* once other site variables were accounted for. This apparent discrepancy may reflect the broad spatial coverage of our study, which encompassed diverse forest compositions and ecological conditions across the Pacific Northwest. Tree species preference by *D. pileatus* varies regionally, influenced by local ecological contexts (Hartwig et al. 2004, Raley and Aubry 2006). Incorporating geographic interactions with habitat variables in future analyses could better capture these spatially nuanced relationships. However, we did find a positive effect of *Abies grandis* basal area on *D. pileatus* occupancy; this matches previous findings from multiple regions, including Vancouver Island and northeastern Oregon (Bull 1987, Hartwig et al. 2004), suggesting a selection of *A. grandis* stands in a range of ecological contexts.

Previous work on *D. pileatus* both within and outside the Pacific Northwest has consistently found positive association with large trees, snags, and logs, at both the patch and individual tree level (Conner et al. 1975, Bull 1987, Renken and Wiggers 1993, Shackelford and Conner 1997, McClelland and McClelland 1999). This appears to reflect a need for trees capable of supporting large cavities, commensurate with the relatively large body size of *D. pileatus*. However, in urban settings, *D. pileatus* are known to nest in significantly smaller trees than those used in nearby natural areas, with no apparent reduction in nest survival (Tomasevic and Marzluff 2020). In the Miami metropolitan area, *D. pileatus* nests extensively in palm snags and even utility poles, with mean diameter at breast height of only 36.8 cm (Diamond et al. 2020). In fact, *D. pileatus* uses a wide variety of tree species and size classes across its range, tending simply to select large trees relative to what is locally available (Hartwig et al. 2004). Our final model did not include effects of tree size, although the second-most supported sub-model for landscape use included a positive effect of mean conifer diameter (Supplementary Material Table 1).

Heartwood decay fungi, which soften wood and facilitate cavity excavation, are a major component of *D. pileatus* habitat in hardwood forests; this implies selection of older forests, which are characterized by larger and more decayed trees (Conner et al. 1975, McClelland and McClelland 1999). In coniferous forests *D. pileatus* is capable of excavating cavities in healthy trees, as conifers typically have softer wood (Bull

1987). However, some amount of decaying wood (in snags, logs or decadent live trees) is necessary to support populations of carpenter ants (*Camponotus* spp.), a major food resource for *D. pileatus* (McClelland and McClelland 1999, Raley and Aubry 2006). Despite this apparent dependence on decaying wood, we did not observe any effect of the density, areal coverage, volume, or biomass of snags or down wood on landscape use or occupancy. This may be because our dead wood covariates used a fairly modest size threshold (≥25 cm DBH or diameter at largest end) and thus included relatively small snags and logs, whereas previous work has shown that *D. pileatus* prefer larger, widely spaced snags rather than dense clusters of smaller snags, which are common in post-disturbance forests (Renken and Wiggers 1993, Bull et al. 2007). In Quebec, Savignac et al. (2000) found no effect of dead wood on *D. pileatus* habitat selection at the patch scale; they speculate that this may have been due to the abundance of dead wood exceeding the foraging requirements of this woodpecker. Our results do not rule out the possibility that dead wood influences patterns of *D. pileatus* landscape use or occupancy but may suggest that the absolute quantity of dead wood is less important than its size characteristics or spatial arrangement.

We omitted several site-level covariates from our multivariate models because they were highly correlated with covariates that had more support in univariate sub-models. A nuanced view of these omitted covariates may help to explain the landscape use and occupancy patterns we observed. For example, sites with more canopy layers also had higher conifer canopy cover, diameter diversity index, and stem density of medium-to-large trees (Supplementary Material Table 3). Hence, sites with high intensity of use by *D. pileatus* can be broadly described as having dense, multi-layered coniferous canopies, with high diversity of tree sizes and density of medium-to-large trees, which corroborates the common association of *D. pileatus* with mature and old-growth forest. Further, sites at higher latitude, which had lower rates of use and occupancy, had lower climatic water deficit and higher basal area of *Tsuga heterophylla* (Supplementary Material Table 3). Previous studies from the Pacific Northwest, USA found that *D. pileatus* select against *Tsuga heterophylla* for nesting and roosting (Aubry and Raley 2002a, Hartwig et al. 2004), so the negative effect of latitude could be attributable to greater prevalence of this avoided tree species. Hartwig et al. (2004) also found that patches containing nest and roost cavities had lower mean elevation than non-use patches.

Detection probability of *D. pileatus* was influenced by geographic, temporal, and environmental factors. Detection decreased at northern latitudes and higher elevations, suggesting lower densities or reduced vocal activity in these areas. We found that detection probability declined throughout the monitoring period, potentially reflecting reduced territorial vocal behaviors post-breeding (Tremain et al. 2008, Zeller et al. 2024). Detection probability and classification accuracy were negatively affected by ambient noise and precipitation, but increased with more survey effort. These results echo findings from previous studies of other species in this region (e.g., Duchac et al. 2020, Rugg et al. 2023, Jenkins et al. 2025) and emphasize the importance of optimizing recording conditions, particularly when modeling occupancy and habitat associations based on acoustic detections. For surveys and monitoring efforts specifically targeting *D. pileatus*, these relationships can inform study design to maximize detection probability and determine the level of survey effort required to achieve suitable detection power.

D. pileatus exhibits highly localized habitat selection that can vary widely in different parts of its range, and many authors caution against sweeping recommendations on best management practices to support the species (e.g., McClelland and McClelland 1999, Hartwig et al. 2004). The widespread distribution of *D. pileatus* that we observed suggests that the species is likely to persist in the Pacific Northwest, USA in the near term. Locally, however, populations may be limited by the availability of suitable habitat for nesting, roosting, or foraging. Our results suggest that management and conservation efforts to support *D. pileatus* are likely to be most successful at lower elevations and by expanding the distribution of structurally complex forests that have high conifer canopy cover, diversity of tree sizes, density of medium-to-large trees, and basal area of *Abies grandis*, while reducing basal area of *Tsuga heterophylla*. Because late-successional forests cannot be readily created, efforts to support *D. pileatus* may initially focus on preserving existing forest types with these characteristics. *D. pileatus* populations have been described to endure disturbance events resulting in moderate tree mortality if dead wood is not removed (Bull et al. 2007). However, *D. pileatus* is negatively impacted by high-intensity disturbance such as clearcut logging and stand replacement-level fires (Bull et al. 2007), which aligns with our finding that *D. pileatus* is more likely to use sites with more structurally heterogeneous forests. Hence, the increasing frequency of large-scale, high-intensity wildfire is likely to diminish the proportion of the landscape used by *D. pileatus*, in addition to its negative impacts on other old-forest species in the Pacific Northwest, USA (Lesmeister et al. 2018, Duchac et al. 2021).

Our results demonstrate the effectiveness of passive acoustic monitoring combined with machine learning and multi-state occupancy models for generating ecological insight at broad spatial scales. By elucidating patterns of landscape use, our results contribute to a deeper understanding of *D. pileatus* ecology within the broader framework of forest ecosystem engineers. Given their influential role in forest community dynamics and biodiversity, ongoing research incorporating multi-species analyses and improved acoustic classification methods promises valuable insights into ecological interactions and forest management practices that support biodiversity conservation.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

Acknowledgments

We are especially grateful to the many field and laboratory staff who deployed and retrieved ARUs and assisted with data processing and validation.

Funding statement

Funding and support for this study was provided by the interagency Northwest Forest Plan partnership between the US Bureau of Land Management, US National Park Service, US Forest Service Pacific Northwest Region, and US Forest Service Pacific Northwest Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official U.S. Government

determination or policy. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Government of any product or service.

Ethics statement

No live animals were involved in this work.

Conflict of interest statement

The authors declare that they have no conflicts of interest.

Author contributions

Zachary Ruff: Conceptualization, Methodology, Formal Analysis, Writing—Original Draft; Damon Lesmeister: Conceptualization, Resources, Supervision, Project administration, Funding acquisition, Writing—Review & Editing; Julianna Jenkins: Software, Writing—Review & Editing; Natalie Rugg: Data Curation, Writing—Review & Editing.

Data availability

Analyses reported in this article can be reproduced using data and code provided by Ruff et al. (2026).

LITERATURE CITED

Albertson, L. K., L. S. Sklar, B. B. Tumolo, W. F. Cross, S. F. Collins, and H. A. Woods (2024). The ghosts of ecosystem engineers: Legacy effects of biogenic modifications. *Functional Ecology* 38:52–72.

Aubry, K. B., and C. M. Raley (2002a). Selection of nest and roost trees by Pileated Woodpeckers in coastal forests of Washington. *The Journal of Wildlife Management* 66:392.

Aubry, K. B., and C. M. Raley (2002b). The Pileated Woodpecker as a keystone habitat modifier in the Pacific Northwest. In *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 1999 November 2–4 Reno NV* (Laudenslayer W. F., Shea P. J., Valentine B. E., Weatherspoon C. P., and Lisle T. E., Editors). USDA Forest Service General Technical Report PSW-GTR-181. pp. 257–274.

Bonar, R. L. (2000). Availability of Pileated Woodpecker cavities and use by other species. *The Journal of Wildlife Management* 64:52–59.

Bull, E. L. (1987). Ecology of the Pileated Woodpecker in Northeastern Oregon. *The Journal of Wildlife Management* 51:472–481.

Bull, E. L., R. S. Holthausen, and M. G. Henjum (1990). Techniques for monitoring Pileated woodpeckers. USDA Forest Service General Technical Report PNW-GTR-269.

Bull, E. L., and J. A. Jackson (2020). Pileated Woodpecker (*Dryocopus pileatus*), version 1.0. In *Birds of the World* (Billerman S. M., Keeney B. K., Rodewald P. G., and Schulenberg T. S., Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.pilwoo.01

Bull, E. L., N. Nielsen-Pincus, B. C. Wales, and J. L. Hayes (2007). The influence of disturbance events on Pileated Woodpeckers in Northeastern Oregon. *Forest Ecology and Management* 243:320–329.

Bull, E. L., A. L. Wright, and M. G. Henjum (1990). Nesting habitat of Flammulated Owls in Oregon. *Journal of Raptor Research* 24:52–55.

Conner, R. N., R. G. Hooper, H. S. Crawford, and H. S. Mosby (1975). Woodpecker nesting habitat in cut and uncut woodlands in Virginia. *The Journal of Wildlife Management* 39:144–150.

Davis, R. J., K. M. Dugger, S. Mohoric, L. Evers, and W. C. Aney (2011). Northwest Forest Plan—the First 15 Years (1994–2008): Status and Trends of Northern Spotted Owl Populations and Habitat. USDA Forest Service General Technical Report PNW-GTR-850. https://www.fs.usda.gov/pnw/pubs/pnw_gtr850.pdf

Diamond, J. M., M. S. Ross, H. Liu, and J. T. Heinen (2020). Palm snags are a critical nesting resource for woodpeckers in an urbanized tropical region. *Urban Ecosystems* 23:67–78.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, and R. J. Davis (2021). Differential landscape use by forest owls two years after a mixed-severity wildfire. *Ecosphere* 12: e03770.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, Z. J. Ruff, and R. J. Davis (2020). Passive acoustic monitoring effectively detects Northern Spotted Owls and Barred Owls over a range of forest conditions. *The Condor: Ornithological Applications* 122: duaa017.

Hartwig, C. L., D. S. Eastman, and A. S. Harestad (2004). Characteristics of Pileated Woodpecker (*Dryocopus pileatus*) cavity trees and their patches on southeastern Vancouver Island, British Columbia, Canada. *Forest Ecology and Management* 187:225–234.

Hu, R., and S. T. Y. Tong (2022). The use of remotely sensed data to model habitat selections of Pileated Woodpeckers (*Dryocopus pileatus*) in fragmented landscapes. *Forest Ecology and Management* 521:120433.

Jenkins, J. M. A., N. M. Rugg, R. J. Davis, S. A. Gremel, A. Henderson, E. Henson, M. Higley, H. D. Horan, C. McCafferty, T. Munger, D. Press, S. Reffler, Z. J. Ruff, J. K. Swingle, E. Tevini, A. D. Thomas, K. Wert, and D. B. Lesmeister (2025). Congener conflict: Invasive Barred Owl landscape use across the range of the Northern Spotted Owl. *Journal of Biogeography* 52: e70070.

Krawchuk, M. A., J. Hudec, and G. W. Meigs (2023). Manager's brief: Integrating fire refugia concepts and data into vegetation management decisions. A case study on the Gifford Pinchot National Forest, Little White Salmon Project Area, Washington. https://firerefugia.forestry.oregonstate.edu/export/krawchuk_fire_refugia_managers_brief_LWS_2023_final.pdf

Landscape Ecology Modeling, Mapping, & Analysis (LEMMA) Group. (2023). Gradient Nearest Neighbor (GNN) raster dataset (version 2023.1). Modeled forest vegetation data using direct gradient analysis and nearest neighbor imputation. https://lemma.forestry.oregonstate.edu/data. Accessed September 2024.

Lesmeister, D. B., C. L. Appel, R. J. Davis, C. B. Yackulic, and Z. J. Ruff (2021). Simulating the effort necessary to detect changes in Northern Spotted Owl (*Strix occidentalis caurina* populations using passive acoustic monitoring. USDA Forest Service Research Paper No. PNW-RP-618.

Lesmeister, D. B., R. J. Davis, P. H. Singleton, and J. D. Wiens (2018). Northern Spotted Owl habitat and populations: Status and threats. In *Synthesis of Science to Inform Land Management within the Northwest Forest Plan Area* (Spies T. A., Stine P. A., Gravenmier R., Long J. W., and Reilly M. J., Editors). USDA Forest Service General Technical Report PNW-GTR-966. pp. 245–298.

Lesmeister, D. B., and J. M. A. Jenkins (2022). Integrating new technologies to broaden the scope of Northern Spotted Owl monitoring and linkage with USDA forest inventory data. *Frontiers in Forests and Global Change* 5:966978.

Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey (1999). Northern Spotted Owl effectiveness monitoring plan for the Northwest Forest Plan. USDA Forest Service General Technical Report PNW-GTR-440. https://www.fs.usda.gov/pnw/pubs/pnw_gtr440.pdf

MacKenzie, D. I., and J. E. Hines (2024). RPresence: R Interface for Program PRESENCE. R package version 2.15.8. https://www.usgs.gov/software/presence

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines (2018). *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*, second edition. Academic Press, Cambridge, MA, USA.

Mannan, R. W. (1984). Summer area requirements of Pileated Woodpeckers in western Oregon. *Wildlife Society Bulletin* 12:265–268.

Martin, K., K. E. H. Aitken, and K. L. Wiebe (2004). Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *The Condor* 106:5–19.

McClelland, B. R., and P. T., McClelland (1999). Pileated woodpecker nest and roost trees in Montana: links with old-growth and forest "health." *Wildlife Society Bulletin* 27:846–857.

Mellen, T. K., E. C. Meslow, and R. W. Mannan (1992). Summertime home range and habitat use of Pileated Woodpeckers in western Oregon. *The Journal of Wildlife Management* 56:96–103.

Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, D. B. Lesmeister, C. K. Nielsen, J. Reid, and E. M. Schauber (2020). Is your ad hoc model selection strategy affecting your multimodel inference? *Ecosphere* 11: e02997.

Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutiérrez (2007). Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88:1395–1400.

Powell, L. A. (2007). Approximating variance of demographic parameters using the delta method: A reference for avian biologists. *The Condor* 109:949–954.

PRISM Climate Group. (2024). PRISM Gridded Climate Data, Oregon State University, https://prism.oregonstate.edu

R Core Team (2024). R: A language and environment for statistical computing (Version 4.4.1). R Foundation for Statistical Computing. https://R-project.org

Rainio, O., J. Teuho, and R. Klén (2024). Evaluation metrics and statistical tests for machine learning. *Scientific Reports* 14:6086.

Raley, C. M., and K. B. Aubry (2006). Foraging ecology of Pileated Woodpeckers in coastal forests of Washington. *The Journal of Wildlife Management* 70:1266–1275.

Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, J. J. Keane, S. C. Sawyer, P. A. Shaklee, H. A. Kramer, K. G. Kelly, A. Reiss, N. Kryshak, R. J. Gutiérrez, H. Klinck, and M. Z. Peery (2021). Noisy neighbors and reticent residents: Distinguishing resident from non-resident individuals to improve passive acoustic monitoring. *Global Ecology and Conservation* 28: e01710.

Reilly, M. J., T. A. Spies, J. Littell, R. Butz, and J. B. Kim (2018). Chapter 2: Climate, disturbance, and vulnerability to vegetation change in the Northwest Forest Plan area. In *Synthesis of Science to Inform Land Management Within the Northwest Forest Plan Area* (T. A. Spies, P. A. Stine, R. Gravenmier, J. W. Long, and M. J. Reilly, Technical Coordinators). USDA Forest Service General Technical Report PNW-GTR-966. pp. 29–92.

Renken, R. B., and E. P. Wiggers (1993). Habitat characteristics related to Pileated Woodpecker densities in Missouri. *The Wilson Bulletin* 105:77–83.

Ruff, Z. J., D. B. Lesmeister, J. M. A. Jenkins, and N. M. Rugg (2026). Data from: Passive acoustic monitoring captures large-scale *Dryocopus pileatus* (Pileated Woodpecker) occupancy patterns in the Pacific Northwest, USA. *Ornithological Applications* 128:duag008. 10.5281/zenodo.15706949 [Dataset].

Ruff, Z. J., D. B. Lesmeister, J. M. A. Jenkins, and C. M. Sullivan (2023). PNW-Cnet v4: Automated species identification for passive acoustic monitoring. *SoftwareX* 23:101473.

Rugg, N. M., J. M. A. Jenkins, and D. B. Lesmeister (2023). Western Screech-Owl occupancy in the face of an invasive predator. *Global Ecology and Conservation* 48: e02753.

Sanders, D., and E. Frago (2024). Ecosystem engineers shape ecological network structure and stability: A framework and literature review. *Functional Ecology* 38:1683–1696.

Savignac, C., A. Desrochers, and J. Huot (2000). Habitat use by Pileated Woodpeckers at two spatial scales in eastern Canada. *Canadian Journal of Zoology* 78:219–225.

Scholer, M. N., M. Leu, and J. R. Belthoff (2018). Patterns of co-occurrence in woodpeckers and nocturnal cavity-nesting owls within an Idaho forest. *Avian Conservation and Ecology* 13: art18.

Shackelford, C. E., and R. N. Conner (1997). Woodpecker abundance and habitat use in three forest types in eastern Texas. *The Wilson Bulletin* 109:614–629.

Steenweg, R., M. Hebblewhite, J. Whittington, P. Lukacs, and K. McKelvey (2018). Sampling scales define occupancy and underlying occupancy-abundance relationships in animals. *Ecology* 99:172–183. https://doi.org/10.1002/ecy.2054

Sugai, L. S. M., T. S. Silva, J. W. Ribeiro, and D. Llusia (2019). Terrestrial passive acoustic monitoring: Review and Perspectives. *BioScience* 69:15–25.

Theobald, D. M., D. Harrison-Atlas, W. B. Monahan, and C. M. Albano (2015). Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. *PLoS One* 10: e0143619.

Thomas, J. W., M. G. Raphael, R. G. Anthony, E. D. Forsman, A. G. Gunderson, R. S. Holthausen, B. D. Marcot, G. H. Reeves, J. R. Sedell, and D. M. Solis (1993). Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. USDA Forest Service. https://archive.org/details/CAT10656784

Tomasevic, J. A., and J. M. Marzluff (2018). Use of suburban landscapes by the Pileated Woodpecker (*Dryocopus pileatus*). *The Condor: Ornithological Applications* 120:727–738.

Tomasevic, J. A., and J. M. Marzluff (2020). Roosting, reproduction, and survivorship of Pileated Woodpeckers (*Dryocopus pileatus*) in a suburban setting. *Avian Conservation and Ecology* 15: art13.

Tosa, M. I., E. H. Dziedzic, C. L. Appel, J. Urbina, A. Massey, J. Ruprecht, C. E. Eriksson, J. E. Dolliver, D. B. Lesmeister, M. G. Betts, C. A. Peres, and T. Levi (2021). The rapid rise of next-generation natural history. *Frontiers in Ecology and Evolution* 9:698131.

Tremain, S. B., K. A. Swiston, and D. J. Mennill (2008). Seasonal variation in acoustic signals of Pileated Woodpeckers. *The Wilson Journal of Ornithology* 120:499–504.

van der Hoek, Y., G. V. Gaona, M. Ciach, and K. Martin (2020). Global relationships between tree-cavity excavators and forest bird richness. *Royal Society Open Science* 7:192177.

Zeller, A. C. (2024). Detection probability of the Pileated Woodpecker (*Dryocopus pileatus*): Implications for developing habitat use models. MSc Thesis, University of Alberta, Edmonton, Alberta, Canada. https://era.libr′ary.ualberta.ca/items/01d53164-99f7-49bd-b0fa-1e2d23b8b31c

Zeller, A., E. Bayne, and C. L. Mahon (2024). An ecological perspective on the temporal variation in Pileated Woodpecker (*Dryocopus pileatus*) drumming behavior in Alberta, Canada. *Avian Conservation and Ecology* 19: art11.

Published by Oxford University Press for the American Ornithological Society 2026.
This work is written by (a) US Government employee(s) and is in the public domain in the US. Ornithological Applications 2026 128(2) 1–14
https://doi.org/10.1093/ornithapp/duag008
Research Article