Forest Ecology and Management 619 (2026) 124084

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

A keystone species underscores the importance of old trees and deadwood in green Sierra lodgepole pine forests of the Oregon Cascades

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ARTICLE INFO

Keywords:
Black-backed Woodpecker
Habitat Selection
Lodgepole Pine
Forest Management

ABSTRACT

Forest management can shape species' habitat quality, quantity, and configuration, thereby influencing biodiversity conservation efforts. The Black-backed Woodpecker (*Picoides arcticus*) is a keystone species typically associated with conifer forests recently burned at high severity. However, burned forests can become unsuitable for breeding 5–10 years post-fire, and this species also nests in unburned ("green") lodgepole pine (*Pinus contorta* var. *murrayana*) forests in the western portion of its range. Recently, woodpecker vital rates were found to be similar between burned and green forest, raising questions about how management of green forests may be undertaken to support this species. To address this issue, we used a combination of empirical and geospatial data to conduct a multi-level landscape-scale assessment of breeding habitat and nest tree selection in green forest. Our empirical model found Black-backed Woodpeckers were more likely to select lodgepole pine nest sites with greater snag density (≥191 snags/ha), more open forest conditions (live tree basal area 5 – 20 m^2/ha), and moderate cover (≥16.5%) of logs 10 – 30 cm in diameter. Our geospatial model predicted lodgepole pine forests to be more suitable for nesting if they were at least 160 years old (at the breeding home range scale; 324 ha), contained ca. 30 m^2/ha lodgepole pine basal area and ca. 20% canopy cover (both within a 0.8 ha scale). Black-backed Woodpeckers also preferred older nest trees that were 31.5 cm diameter at breast height. Despite lodgepole pine being widespread in the East-Cascades of Oregon, our model predicted that only a subset of lodgepole pine forest is suitable across the broader landscape. In an era of increasing megafires, green forests may provide temporally stable resources and thereby hold conservation value for cavity nesters.

1. Introduction

Habitat selection, defined as the disproportionate use of a resource relative to its availability (Block and Brennan, 1993), influences individual fitness and population persistence (Mayor et al., 2009, Tellería, 2016). Because organisms respond to environmental conditions at multiple scales, habitat selection occurs hierarchically, from the home range of individuals (level 2 selection) to the procurement of individual resources, such as a nest tree (level 4 selection; Johnson 1980b, McGarigal et al., 2016). Habitat loss has been shown to be a prominent driver in extirpation, extinction, and overall biodiversity loss (Fahrig, 1997, Betts et al., 2022). To conserve biodiversity, it is therefore critical to understand the habitat requirements and selection cues used by species of conservation concern, especially during key periods in their life cycle.

Within species, individuals can vary markedly in the types of resources they select across space and time (Orians and Wittenberger, 1991, Garshelis, 2000, Jones et al., 2019, Stillman et al., 2019b, Betts et al., 2020, Jones and Tingley, 2021). However, not all available habitats are of equal quality, and this can constrain those species that have a narrow habitat breadth and rely on one type of habitat for critical processes in the life cycle. More recently, some species once considered to be highly specialized have proven to be more varied in their use of habitat. For example, the California Spotted Owl (*Strix occidentalis occidentalis*) requires old growth forest characteristics for nesting and roosting but can preferentially forage in small patches recently disturbed by severe wildfire (Jones et al., 2020). Similarly, some woodpecker species that are often associated with disturbed forests, such as the

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https://doi.org/10.1016/j.foreco.2026.124084
Received 8 May 2026; Received in revised form 24 June 2026; Accepted 3 July 2026
Available online 10 July 2026

White-headed Woodpecker (*Picoides albolarvatus*) and Lewis's Woodpecker (*Melanerpes lewis*), use more intact forest structure than previously recognized (Hollenbeck et al., 2011, Kozma and Kroll, 2012, Blake et al., 2022). Viewing individual species—even those considered to be specialists—as having singular habitat requirements is a simplification and species may often be more flexible than they initially appear (Bolnick et al., 2002, Holtmann et al., 2017, Stillman et al., 2019b).

Within fire-adapted ecosystems, pyrodiversity can be defined as the spatial and temporal variations in fire characteristics, such as burn severity and time since fire, and it is thought that pyrodiversity begets biodiversity (see Jones and Tingley, 2021). However, mature and old forests are important components of pyrodiversity when embedded within fire-adapted landscapes, and these areas hold unique conservation benefits by acting as refugia via the retention of important structural elements after disturbance (Coop et al., 2019, Lesmeister et al., 2025). Within a pyrodiversity context, areas of old forest that have experienced greater time since stand-replacing fire provide distinctly different resources (e.g., regarding space, sunlight, dead wood, insect abundance) when compared to areas recently burned by moderate- to high-severity wildfire. In a departure from historic conditions, homogenous stand-replacing megafires are becoming increasingly prevalent (Abatzoglou and Williams, 2016, Abatzoglou et al., 2021) and even woodpeckers that readily use post-fire areas have been shown to avoid the interior core of high-severity burn areas (White et al., 2019). Population pulses of wood-boring insects (e.g., Buprestidae [jewel beetles], Cerambycidae [longhorn beetles], Siricidae [horntail wasps]) are thought to drive fluctuations in woodpecker populations, particularly in burned forests (Powell, 2000, Rota et al., 2015). However, these resources are ephemeral (Hutto, 2008) and post-fire forest management practices such as salvage logging can further reduce the availability of the nesting and foraging resource pulse that wildfire creates (Saab et al., 2007, Hanson and North, 2008). In pyrodiverse landscapes, unburned (hereafter "green") forests can provide refugia and more temporally stable resources than the ephemeral resource pulses created by recent wildfire (Tremblay et al., 2015a). This raises important landscape scale conservation implications for green forest within pyrodiverse forest systems—both for intact forest and burned forest associated species alike.

In forested systems, managing the habitat requirements for the entire suite of species in an ecosystem is infeasible; therefore, identifying keystone species and conserving their habitat can provide a more practical approach to maintaining broader elements of biodiversity (Mills et al., 1993, Hossack et al., 2015, Ollerton, 2017, McMillan et al., 2019). In green conifer forests, particularly those managed for timber, natural cavities are rare (Kroll et al., 2012, Bunnell, 2013). Woodpeckers are keystone species that, through their life history, create key habitat components for secondary cavity-nesting species (Martin and Eadie, 1999, Virkkala, 2006, Tremblay et al., 2020). Because of this relationship, woodpeckers are commonly used as indicators of biodiversity and structural targets in managed forests (Angelstam and Mikusinski, 1994, Martin et al., 2021, Menon and Shahabuddin, 2021). Without strong primary excavators (i.e., woodpeckers), the biodiversity of forest dwelling cavity nesting birds and mammals would likely decline (Bunnell, 2013, Drever et al., 2008, Drever and Martin, 2010). Presence of woodpeckers therefore provides cascading positive impacts on forest processes, for example, like seed dispersal and prey availability for predators (Raphael and White, 1984, Tarbill et al., 2015).

To understand the full breadth of a keystone species' habitat requirements, it is important to delineate and consider the drivers of each component and scale of habitat use (Krausman, 1999, Garshelis, 2000, Lindenmayer and Franklin, 2002, Lindenmayer et al., 2006). The Black-backed Woodpecker (*Picoides arcticus*) has been thought to be more specialized to recently burned forest than any other species (Hutto, 2008) and has therefore factored into the discussion of post-fire forest management (Hutto, 1995, 2008; Saab et al., 2007). Consistent with this view, green forest habitat was formerly considered to be a sink habitat for this species (Hutto, 1995). However, recent investigations show that this species can experience enhanced fitness when green forest is available to fledglings from burned forest nests (Stillman et al., 2021). Furthermore, this species has been found nesting successfully in green forest (Tremblay et al., 2009, 2015a,b) and has similar vital rates when nesting in green forest and adjacent forests that recently burned at high severity (Kerstens and Rivers, 2023). In the western portion of their range, nesting in green forest appears to be closely tied to Sierra lodgepole pine forests despite the availability of several other green forest types (Kerstens and Rivers, 2023; Kerstens et al., in review). Nevertheless, Black-backed Woodpecker habitat use in green forest remains understudied (Tremblay et al., 2009, 2015b) particularly in the western portion of its range (Fogg et al., 2014, Verschuyl et al., 2021, Kerstens and Rivers, 2023).

Understanding drivers of habitat use in green forest is relevant more broadly because it helps clarify the role of green forests in conserving cavity dependent species in fire-adapted forest landscapes, especially because forest structure may take more than a century to regenerate following stand-replacing disturbances, such as wildfire (Franklin et al., 2002). Coupled with recent findings about Black-backed Woodpecker habitat use and vital rates (White et al., 2019, Stillman et al., 2021, Kerstens and Rivers, 2023), this suggests that increasing prevalence of high severity megafires may actually be detrimental to this species considered to be a post-fire specialist. Thus, understanding the Black-backed Woodpecker's use of other forest types is important to ensure conservation strategies do not rely on the erroneous assumption that larger, more severe fires benefit this species in the long term.

Although Black-backed Woodpecker habitat requirements in recently burned forests are well documented (Powell, 2000, Hutto, 2008, Saab et al., 2009, Stillman et al., 2019a, Tremblay et al., 2020), comparatively little is known about their nesting habitat selection in green forests despite these areas occupying a much larger proportion of the western landscape (Fogg et al., 2014, Tremblay et al., 2015a, OFRI, 2021). In this study, our objective was to identify the landscape- and local-scale characteristics associated with Black-backed Woodpecker habitat selection when nesting in green conifer forests by evaluating selection at both the home range (level 2) and nest tree (level 4) scale. We leveraged geospatial forest structural data and empirical field-based measurements to assess habitat selection across multiple scales and predict suitable green forest breeding habitat for a fire-associated keystone species throughout the East Cascades Ecoregion of Oregon, USA. Previous work in green forests of the Black-backed Woodpecker's western range has demonstrated nesting is strongly associated with mature lodgepole pine stands containing snags, logs, and old live trees (Fogg et al., 2014; Kerstens and Rivers, 2023; Kerstens et al., in review).

Because Black-backed Woodpeckers are closely tied to the availability of dead wood (see Tremblay et al., 2020) and disproportionately use lodgepole pine stands for nesting in green forests, we first tested the hypothesis that available lodgepole pine stands contained greater deadwood abundance than other available green conifer forests. We also hypothesized that Black-backed Woodpeckers would preferentially select mature and older forest conditions that have had time to develop large potential nest trees with heartwood decay and accumulate dead wood for foraging (Tremblay et al., 2009; Kerstens et al., in review). Therefore, we predicted positive associations with large live trees, dead wood, and older stand ages. By identifying the structural characteristics and landscape conditions associated with Black-backed Woodpecker nesting habitat selection, our study provides the first multi-scale assessment of green forest habitat use in the western portion of the species' range and informs forest management in fire-prone landscapes.

2. Methods

2.1. Study area

We examined how the Black-backed Woodpecker selects nesting

habitat in the unburned landscape during the 2018, 2019, and 2021 breeding seasons (May-August) across ~165,000-ha in south-central Oregon (Fig. 1). This region included the xeric conifer-dominated Pumice Plateau and associated ecoregions (i.e., Pumice Plateau Basins, and High Southern Cascades Montane Forest; collectively "Pumice Plateau" hereafter) and ranged from 1280 to 1950 m above sea level (m. a.s.l.). Unburned conifer forests in our study area consisted of either a lodgepole pine (*Pinus contorta* var. *murrayana*) or ponderosa pine (*Pinus ponderosa*) dominated overstory; co-dominant mixed pine, which could also include western white pine (*Pinus monticola*) and sugar pine (*Pinus lambertiana*); and mixed conifer, which could include true firs (*Abies spp.*), Douglas-fir (*Pseudotsuga menziesii*) Engelmann spruce (*Picea engelmannii)* and/or mountain hemlock (*Tsuga mertensiana*). These forest types and their distributions are largely topographically and edaphically defined by the volcanic activity related to the Mazama and Newberry eruptions (Gara et al., 1985, Geist and Cochran, 1991, U.S. Environmental Protection Agency, 2016). Breeding season temperatures ranged from −6°C – 34°C (mean ca. 11°C). Precipitation over the same period ranged from 30 mm – 224 mm (SNOTEL weather station, Sun Pass, Oregon, 1646 m.a.s.l.). Prior to the 20th century, this landscape experienced frequent, widespread and low–mixed severity fires every 7–25 years (Merschel et al., 2018, Hagmann et al., 2019).

2.2. Nest searching

We searched for active Black-backed Woodpecker nests during the breeding seasons across the green forest types of the study area using both passive search measures and active playbacks. In 2018, nest searching was primarily focused around randomly located woodpecker point count transects spread across the landscape from a prior study in our system (Verschuyl et al., 2021). After the 2018 field season, it became clear that nest searching for Black-backed Woodpecker nests was most productive in lodgepole pine forest, thus in 2019 we prioritized searching in these areas. In 2021, to broaden our assessment back to the landscape, we resumed searching in random locations that represented all the major coniferous forest types of the system as well as in locations previously deemed productive for Black-backed Woodpeckers. Although we nest searched in all four representative coniferous forest

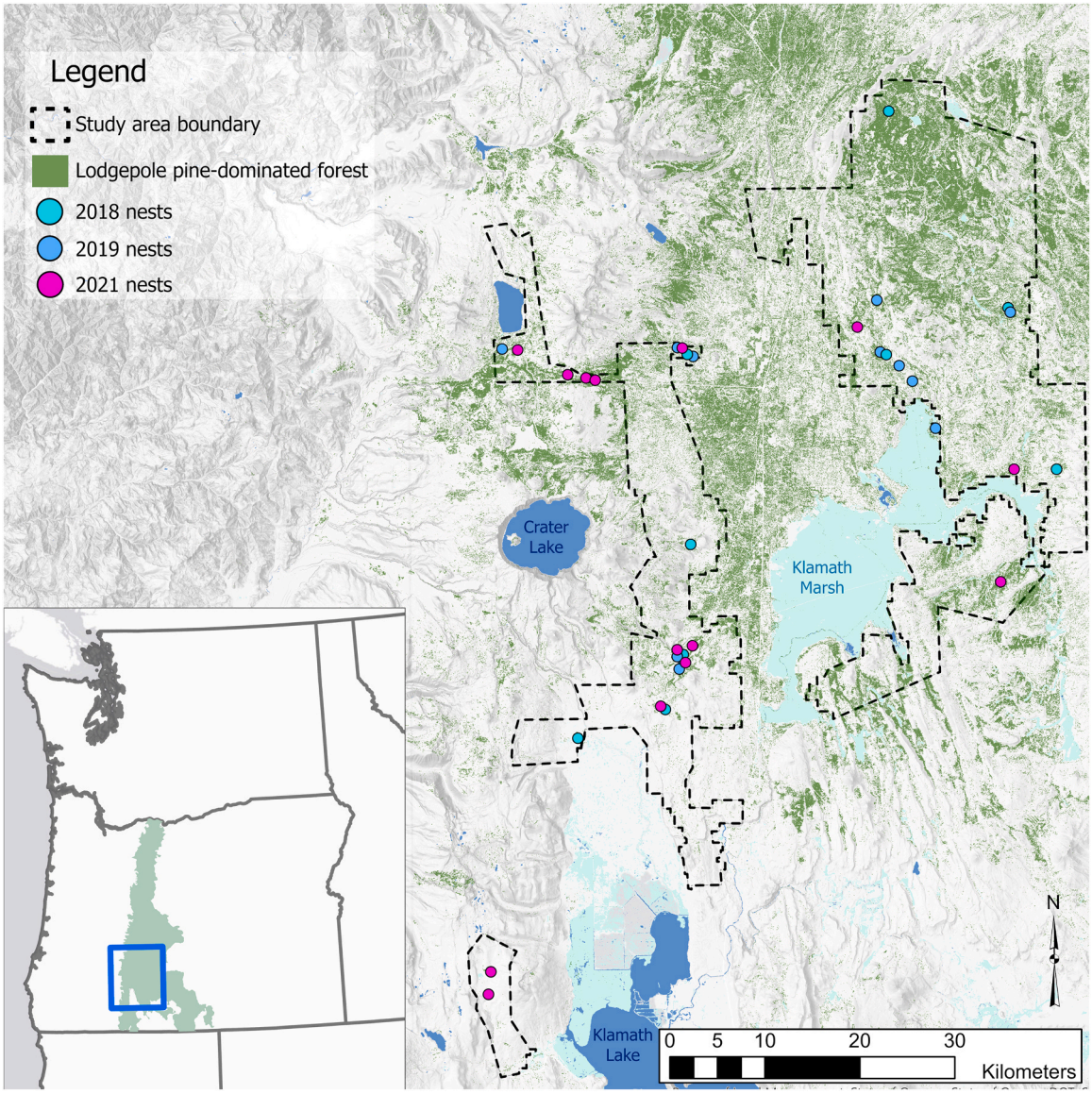

Fig. 1. Study area and Black-backed Woodpecker nest locations in south-central Oregon. Green areas represent lodgepole pine-dominated forest derived from GNN forest-type classifications; small lodgepole inclusions may not be visible at the scale of the figure. The inset map shows the location of the study area (blue box) within the East Cascades Ecoregion of Oregon.

types, we inadvertently spent more time searching in lodgepole pine forest since we often found Black-backed Woodpeckers exhibiting evidence of breeding (e.g., frequent drumming, snarl calls, evidence of a male and female within the same territory, and/or nestling begging calls) in these areas and spent time attempting to follow them to a nest. In contrast, while searching in the other forest types we typically did not find Black-backed Woodpeckers—and in the handful of occasions where we did, they were lone individuals not exhibiting territoriality or signs of breeding—and we therefore moved more quickly through these areas. In our experience, breeding Black-backed Woodpeckers are highly territorial and responsive to playbacks, and we often detected individuals quickly in lodgepole pine forests; therefore, simply spending more time searching in the other forest types was unlikely to yield additional nests in those areas. Indeed, we faced a tradeoff between reducing bias and maximizing our sample size across a large spatial extent; however, our field observations suggest that unequal search effort is unlikely to explain our observed patterns of nesting habitat use.

2.3. Empirical characterization of habitat at woodpecker nests and available locations

Because our objective was to identify habitat characteristics associated with nesting in green forests, all empirical habitat measurements were restricted to nests and available locations occurring within the green forest landscape. We measured nest site characteristics around active Black-backed Woodpecker nest sites in green forest. At each green forest nest site ($n = 35$), we measured forest structural metrics within a 0.03 ha plot (i.e., having a 10 m radius) centered on the nest tree. This included snag density, percent ground cover of logs $\geq$ 10 cm diameter (binned by 10 cm – 29 cm, 30 cm – 60 cm, and $\geq$60 cm), live tree basal area, and forest type. We recorded the tree species and measured characteristics of the nest tree, which included diameter at breast height (hereafter, "DBH"), and height. To characterize available habitat, we repeated the plot measurements as described above at randomly selected available sites ($n = 196$) across the unburned landscape of the study area in 2021. All randomly selected empirical ground-based vegetation plots were centered on potentially available nest trees, i.e., being at least 15 cm DBH and at least 1.5 m high (Forristal, 2009, Seavy et al., 2012, Verschuyl et al., 2021).

2.4. Extracting geospatially derived covariates at nests and available locations

In addition to using empirical ground-collected data to quantify Black-backed Woodpecker nest tree and nest site selection across the landscape, we used the 2017 geospatial Gradient Nearest Neighbor (GNN; Ohmann and Gregory, 2002) dataset provided by the Landscape Ecology Mapping, Modeling, and Analysis group (LEMMA Landscape Ecology Mapping Modeling and Analysis, 2021) to predict breeding home range selection. The GNN dataset contains geospatial forest attribute covariates (derived from US Forest Service Forest Inventory and Analysis surveys and 30 m Landsat imagery) for the entire study area and greater Pumice Plateau ecoregion. Open-source GNN raster layers (Table 1) were downloaded to match forest attributes that likely have ecological significance to nesting Black-backed Woodpeckers. These were clipped to the study area and resampled to reduce classification and spatial misalignment errors (Lillesand et al., 2015) using the moving window analysis in ArcGIS Pro at three ecologically relevant spatial scales. The spatial scales used in the breeding home range selection analysis were rounded to the nearest multiple of 30 m to align with the original GNN data resolution. This resulted in sampling at the finest effective grain supported by the smoothed GNN data (i.e., 90 m^2; hereafter, 0.8 ha) at the scale of the breeding home range (144 ha; Goggans et al., 1989; Tremblay et al., 2009) and at the scale of the landscape immediately surrounding the breeding home range (324 ha; Goggans et al., 1989; Tremblay et al., 2009). Since there was no data available on Black-backed Woodpecker pair breeding home range size estimates in green forest of our study system, we relied on the assumption that breeding pair home ranges in green forest in the eastern portion of their range (Tremblay et al., 2009), and home ranges of individuals during the breeding season in green forest near our study site (Goggans et al., 1989) could be used as a proxy in our study area. We find no reason for this to bias the results; while following individual breeders during nest searching, Black-backed Woodpeckers occupied similar sized home ranges to those elsewhere in their range (authors, personal observation). Our geospatial assessment included additional nest locations ($n = 5$) from the study conducted by Verschuyl et al. (2021) in our study area during 2015 for a combined sample size of $n = 40$.

Table 1
Imputed GNN variables used for modeling (LEMMA 2021).

Model Scale	Variable	Description
Level 2	AGE_DOM	Basal area weighted stand age based on dominant and codominant trees
	CANCOV	Canopy cover of live trees
	PICO_BA	Lodgepole pine basal area
Level 4	AGE_DOM	Basal area weighted stand age based on dominant and codominant trees
	MNDBHBA_con	Basal-area weighted mean diameter of live conifers
	STNDHGT	Stand height, computed as mean of heights of all dominant and codominant trees
	FORTYPBA	Forest type, which describes dominant tree species based on basal area

2.5. Dead wood across available forest types

All analyses were conducted in R version 4.1.2 (2021) using *tidyverse* (Wickham et al., 2019) and ArcGIS Pro 3.3 (2023). Before assessing which habitat features Black-backed Woodpeckers selected on the landscape, we wanted to assess how critical habitat components for woodpeckers—namely dead wood in the form of snags and logs—varied between the different forest types of the unburned landscape. As prior research in our system found Black-backed Woodpeckers mostly nesting in lodgepole pine, but occasionally in ponderosa pine (Kerstens et al., in review), we were most interested in comparing these two forest types. To gain a more holistic assessment of the landscape we also included mixed pine and mixed conifer—the other two dominant forest types—in this analysis. We therefore used empirically collected vegetation data around the ground-based available sites across the landscape to perform an ANOVA and test for differences in snag density and ground cover attributed to downed logs ($\geq$10 cm diameter) between lodgepole pine ($n = 80$), ponderosa pine ($n = 41$), mixed pine ($n = 43$), and mixed conifer ($n = 32$) stands.

2.6. Empirical breeding home range selection

To assess breeding pair home range selection in green forest, we employed a use versus availability framework (Johnson 1980a) and compared used nest sites against the available sites on the landscape. Using the empirically derived data, we fit a habitat selection function (HSF) using logistic regression within a binomial generalized linear modelling framework with a logit link (Table S1). Available sites were coded as 0 and used sites were coded as 1. The empirical breeding home range selection model included nest site characteristics as predictor variables. Predictor variables were selected a priori based on previous studies on Black-backed Woodpecker nesting ecology and our ecological hypotheses and specifically included snag density, live tree basal area, percent ground cover attributed to downed logs (10–30 cm diameter), and whether a stand was dominated by lodgepole pine. We only used the smaller log size category since logs in lodgepole pine forest rarely reach larger sizes (authors, personal observation). We calculated the relative

contribution of each parameter to the empirical model's predicted probability of nest site selection and used bootstrapping with 1000 replicates to calculate 95% confidence intervals around these estimates (Tremblay et al., 2015b) using the *boot* package (Canty and Ripley, 2025). To facilitate this comparison among predictor variables, we fit a standardized version of the empirical breeding home range selection model in which continuous predictors were z-standardized (mean = 0, SD = 1). We used the original un-standardized version of the model for ecological interpretation.

2.7. Geospatial breeding home range selection

For our geospatial assessment, we conducted a beta stabilization analysis using the raster for two of the covariates (i.e., lodgepole pine basal area and stand age) to determine the appropriate ratio of used versus available points (Fieberg et al., 2021). This stabilization occurred at a ratio of 40:16,000 used versus available points (Figure S1). After generating 16,000 available points in the study area, we extracted the covariate values at each used and available point for our HSF modeling analysis.

Although we initially wanted to use the same variables in both our empirical and geospatial HSF models, the dead wood measures in the GNN data were highly inaccurate for our area. This provided an impetus to test a separate binomial GLM that leveraged multi-scale landscape-level data that we were unable to empirically measure across the large spatial extent of interest. Thus, we excluded dead wood from our geospatial analysis and instead used metrics that can easily be integrated into management via retention standards and harvest schedules. The geospatial model therefore included lodgepole pine basal area, stand age, and percent canopy cover, again comparing used sites to available sites. We ran three versions of this geospatial model, with the data resampled at each of the three spatial scales of interest (i.e., 0.8 ha, 144 ha, and 324 ha). We used likelihood ratio tests (change in deviance) to evaluate the contribution of each covariate across these spatial scales to determine the most informative spatial scale for each covariate. Using the most informative respective scale for each of the three covariates, we built a full geospatial model to predict breeding home range selection. We performed leave one out cross validation (LOOCV) to test predictive fit for both the empirical and geospatial breeding home range selection models.

Finally, we created a predictive map of priority green forest Black-backed Woodpecker breeding habitat using the habitat selection function (Northrup et al., 2022) results from the full geospatial model (Table S1). The model was built using 2017 GNN data to best represent the spread of years during which the nests in this analysis were active. However, to allow the predictions to be as relevant as possible, we predicted back out to the landscape using the 2021 GNN data, which represented the most current available data (at the time of our analysis). Data for model training was collected from within the Pumice Plateau, Pumice Plateau Basins and High Southern Cascades Montane Forest level IV ecoregions (U.S. Environmental Protection Agency, 2016). We extended our predictions to include the Grand Fir Mixed Forest, Oak/-Conifer Foothills, Ponderosa Pine/Bitterbrush Woodland, Fremont Pine/Fir Forest, Southern Cascades Slope, Cascade Crest Montane Forest, and Cascade Subalpine/Alpine level IV ecoregions to provide a preliminary characterization of green forest nesting habitat in less studied portions of the Black-backed Woodpeckers western range. In summary, the combined landscape of our predictive model space spans the length of the Oregon Cascades along its crest and east-slope forests. We acknowledge that the strength of inference to the regions outside the Pumice Plateau and surrounding area is likely weaker. However, due to the limited study of Black-backed Woodpecker green forest breeding habitat in the western portion of their range, we felt that it would be fruitful to predict across this broader landscape. Recognizing that habitat suitability and use are not synonymous, and to minimize the risk of overlooking suitable green forest Black-backed Woodpecker breeding habitat, we used the upper 69% confidence interval from the combined geospatial model for the predictive mapping. This provides a buffer to better reflect potential habitat availability, since the raw model outputs predict relative probability of use. The 69% upper limit was determined by calculating Youden's J statistic to optimize the tradeoff between specificity and sensitivity in our habitat suitability predictions.

2.8. Nest tree selection

To broaden a prior assessment of empirically measured nest-tree selection (Kerstens et al., in review) to a larger spatial extent, we compared characteristics of used nest trees to geospatially derived dominant overstory characteristics at the 16,000 available points across the landscape. Using the same HSF framework as our prior models, we fit a binomial GLM with a logit link comparing used and available trees. Because GNN geospatial data was limited to a 30 m grain, we characterized available nest-tree characteristics using the pixel-level overstory attributes. GNN data represent the dominant forest structure in each pixel rather than measuring individual stems (Ohmann and Gregory, 2002); therefore, we treated pixel values as proxies for the characteristics of trees available for nesting at a given location. This approach assumes that the dominant overstory conditions at the 30 m scale were broadly representative of the structural attributes of trees within those pixels (Ohmann and Gregory, 2002) that could be available to nesting woodpeckers (Hollenbeck et al., 2011). Although nest-tree selection occurs at a finer spatial grain, stem-level data were not available across the extent of our study area. Further, our objective in this analysis was to assess stand-level structural characteristics of potential trees across the landscape rather than capture idiosyncratic attributes of individual trees. Imputed overstory variables for this analysis included tree age, height, DBH (modeled as linear and quadratic terms), and dominant tree species. The latter was defined as the tree species contributing the greatest basal area per pixel. Tree age for used nests was also estimated using imputed GNN data. Given the strong preference for lodgepole pine, we then subset the data for this analysis to only include lodgepole pine nest trees and available trees when modeling nest tree characteristics. Because we were also interested in assessing the optimal nest tree DBH these woodpeckers select, we used the delta method to find the derivative of the quadratic term for DBH with the *msm* package (Jackson, 2011).

2.9. Model interpretation and diagnostics

Since the goal of our analysis was to test relationships between Black-backed Woodpecker habitat selection and green forest metrics, we focused on estimating effect sizes and confidence intervals of specific a priori models rather than performing model selection. Because we fit models within a use versus availability framework, we interpreted coefficients as measures of habitat selection. We exponentiated coefficients to derive relative selection strength (hereafter, "RSS"; analogous to odds ratios from logistic regression), which represents the multiplicative change in relative probability of use associated with a one-unit increase in each covariate. Model predictions are calculated using an inverse logit transformation and represent the relative probability of use (given specified habitat values) rather than the absolute probability of occurrence (Fieberg et al., 2021, Northrup et al., 2022). Fixed effects included the corresponding habitat characteristics at each level (for used and available locations), and none of our models included random effects.

The mean-variance relationship was assessed for all models to assess the model fit. In instances where the dispersion parameter was greater than 1, we used a quasibinomial GLM. For all models in our analysis, we assessed model fit by examining the randomized quantile residuals using the *DHARMa* package (Hartig, 2022) to confirm that they were distributed between 0 and 1. All used nests and available points (i.e., the replicates) were independent of one another, and we tested for collinearity of the fixed effects. We checked the QQ residuals plot and the tests

for homogeneity and uniformity of variance to detect significant deviations and ensure model assumptions for each of our analyses were met.

3. Results

3.1. Dead wood across available forest types

In available sites across the green forest landscape, empirically measured dead wood in the form of snag density (ANOVA: $F_{3,192} = 2.77$, $p = 0.043$) and downed log cover (ANOVA: $F_{3,192} = 3.15$, $p = 0.026$) varied among forest types. Dead wood abundance was generally more abundant and similar across the mixed conifer, mixed pine, and lodgepole pine forest types relative to ponderosa pine forest (Fig. 2). In lodgepole pine forest, mean snag density was 37.4 snags per hectare (95% quantiles: 0, 256) while mean log cover ≥ 10 cm diameter was 14.3% (95% quantiles: 0%, 40.6%). In ponderosa pine sites, mean snag density was 5.4 snags per hectare (95% quantiles: 0, 31.8) and mean log cover ≥ 10 cm diameter was 8.1% (95% quantiles: 0%, 35.0%). Percent log cover was 1.8 times higher in lodgepole pine sites (6.2% greater; 95% CI 2.0%, 10.4%) compared to ponderosa pine sites (Tukey HSD $p = 0.014$). Small-diameter logs (10–30 cm) comprised the majority of total log cover across forest types, and particularly within lodgepole pine stands. Average snag density was 7 × greater in lodgepole pine relative to ponderosa pine forest (32 more snags per ha; 95% CI 14.1, 49.8; Tukey HSD $p = 0.053$). We did not detect measurable differences in dead wood abundance between mixed conifer or mixed pine forests relative to ponderosa pine forests (Fig. 2).

3.2. Empirical breeding home range selection (Level 2)

We report parameter estimates for all habitat selection models in Table 2. Our empirical model for breeding home range selection was driven most strongly by whether a site was in lodgepole pine forest (relative contribution 69.8%; 95% bootstrapped CI: 48.3%, 96.0%), followed by similar contributions from snag density (11.1%; 95% bootstrapped CI: 0.9%, 30.8%) and live tree basal area (11.6%; 95% bootstrapped CI: 0.9%, 26.1% [Fig. 3]). Log cover accounted for 7.5% of the model contribution (95% bootstrapped CI: 0.3%, 21.2%). The empirical model predicted that Black-backed Woodpeckers were 17.1 × more likely to select nest sites dominated by lodgepole pine overstory relative to other green forest type (95% CI: 3.9, 76.1). Further, we detected a modest positive relationship for Black-backed Woodpeckers selecting sites with greater snag density, with the RSS increasing by 6.4% for every additional 10 snags per hectare (95% CI: 1.0%, 12.0%). For every 10 m^2 / ha decrease in live tree basal area, the RSS increased by 44.3% (95% CI: 2.9%, 102.4%), with a minimum observed live tree basal area of 4.6 m^2 / ha. Percent cover of logs 10–30 cm diameter had an imprecise positive relationship, and each 10% increase in log cover increased the RSS by 35.0% (95% CI: −11.8%, 106.8%). Our empirical model predicted that Black-backed Woodpeckers reached a 50% relative probability of selecting a site for breeding when snag density was least 174 snags (≥10 cm diameter) per ha, live trees basal area was most 20 m^2 per ha of (i.e., the observed mean at used sites), ground cover of logs 10–30 cm diameter was at least 16.5% (i.e., the observed mean at used sites), and the stand was dominated by lodgepole pine (Fig. 4). However, when accounting for model uncertainty, the lower 95% confidence interval for snag density indicated that at least 757 snags per ha (or 24 snags per 10 m radius of the nest tree) would be required to reach a 50% predicted relative probability of use. Cross validation yielded a mean accuracy of the model correctly predicting a nest at 35.6% (see Supplemental Figure 2).

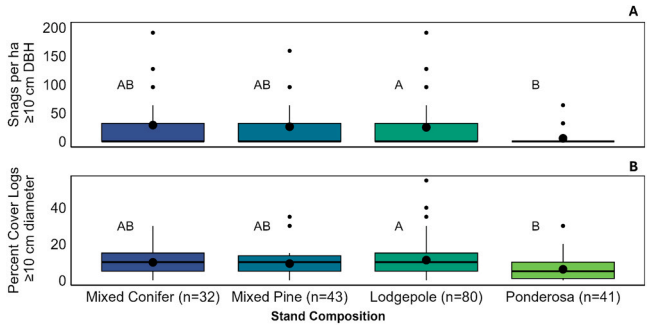

Fig. 2. Dead wood abundance in the form of snags (a) and logs (b) was lower at available sites in ponderosa pine forest relative to available sites in lodgepole pine forest. Letters above each box denote ANOVA results, using a $p \leq 0.05$ statistical threshold for differences between groups.

Table 2
Parameter estimates for Black-backed Woodpecker habitat selection models.

Model	Variable	Estimate	SE	Statistic	*p*-value
Empirical	Intercept	−3.670	0.864	−4.25	< 0.001
Breeding Home Range (Level 2)	Snag density (SPH)	0.0062	0.0027	2.32	0.020
	Small log cover (%)	0.0300	0.0217	1.38	0.167
	Live tree basal area (m^2/ha)	−0.0367	0.0173	−2.12	0.034
	Lodgepole pine (PICO)	2.841	0.761	3.73	< 0.001
Geospatial	Intercept	−7.876	1.198	−6.57	< 0.001
Breeding Home Range (Level 2)	Lodgepole pine basal area (0.8 ha)	0.1023	0.0275	3.72	< 0.001
	Stand age (324 ha)	0.0347	0.0115	3.01	0.003
	Canopy cover (0.8 ha)	−0.0545	0.0181	−3.02	0.003
Geospatial	Intercept	−12.658	1.572	−8.05	< 0.001
Nest Tree Selection (Level 4)	Tree age	0.0231	0.0098	2.36	0.018
	Tree height	0.3601	0.0628	5.73	< 0.001
	DBH (centered)	0.0196	0.0489	0.40	0.689
	DBH^2 (centered)	−0.0093	0.0048	−1.95	0.052

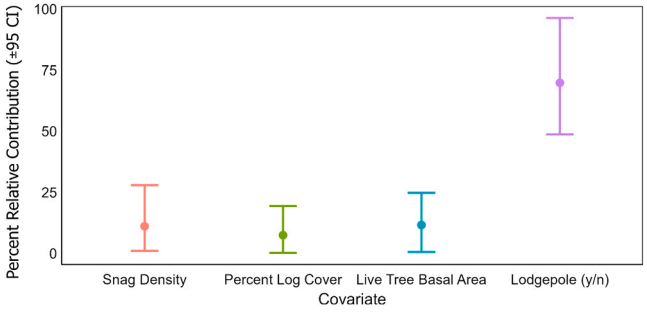

Fig. 3. Whether or not a stand was compromised of lodgepole pine had the strongest influence on whether Black-backed Woodpeckers selected a green forest site for nesting as measured by the empirical model. The other model parameters (i.e., snag density, percent log cover, and live tree basal area) had similar contributions to the influence of selection. Results show the relative contribution of each parameter to the model's predictions ± 95% bootstrapped confidence intervals.

3.3. Geospatial breeding home range selection (Level 2)

We found support from the geospatial breeding home range selection model that mean stand age had the most influential effect on breeding home range selection at the largest spatial scale (i.e., 324 ha), while lodgepole pine basal area and canopy cover were most influential at the finest scale (i.e., 0.8 ha; Fig. 5). The likelihood ratio tests showed the

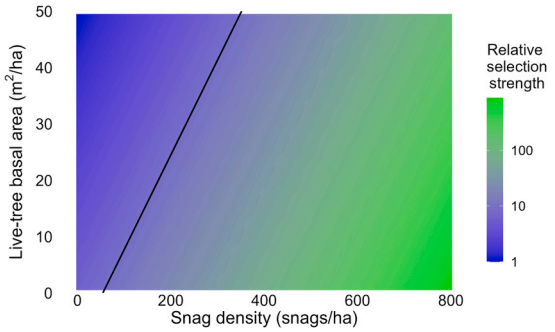

Fig. 4. Within green lodgepole pine dominated forest, the level 2 empirical breeding habitat selection model predicted relative selection strength of Black-backed Woodpecker nest sites increased with snag density and lower live tree basal area; the minimum live tree basal area observed at nest sites was 4.6 m^2/ha. Log cover was held at the observed mean (16.5%). The black line represents the threshold where the model predicts a 50% relative probability of use. Color scale is log_{10} transformed.

greatest reductions in deviance at these respective spatial scales. Our model showed Black-backed Woodpecker habitat selection was positively tied with older stands at the 324-ha scale that had greater lodgepole pine basal area at the 0.8 ha scale. RSS increased 2.94 × for every additional 10 m^2 / ha of lodgepole pine basal area at the 90 m scale (95% CI 1.71, 5.07), and 1.56 × greater for each 10-year increase in stand age at the 324 ha scale (95% CI: 1.2, 2.04). We found that Black-backed Woodpeckers select sites with decreasing canopy cover at the 0.8 ha scale (Fig. 5). The RSS increased 1.60 × for every 10% decrease in canopy cover (95% CI: 1.12, 2.29), with a minimum observed canopy cover value of 22.6%.

The geospatial nest site model predicted that when lodgepole pine basal area at the 0.8 ha scale and stand age at the 324-ha scale were both at their observed maximum observed value (27.7 m^2 / ha and 158.4 years, respectively), and canopy cover at the 0.8 ha scale was at the minimum, the model predicted a high relative probability of use (0.316; 80% CI: 0.114, 0.623). LOOCV yielded a mean accuracy of correctly predicting a nest at 0.007. Using the model predictions from the upper 69% confidence interval, our geospatial nest site model for the Oregon Cascades region predicted that suitable Black-backed Woodpecker nesting habitat in green forest—that has not undergone major disturbance (e.g., wildfire or beetle kill)—was largely restricted to older lodgepole pine dominated forests within the Pumice Plateau Ecoregion and surrounding areas (Fig. 6).

3.4. Nest tree selection (Level 4)

The geospatial nest tree model predicted that used nest trees were estimated to be 109 years old on average (95% quantiles: 78, 165) and ranged from an estimated 69–201 years. The univariate geospatial nest-species model indicated that RSS for lodgepole pine nest trees was 24.4 × greater relative other available conifer species in green forests of the Pumice Plateau (95% CI: 7.4, 150.8), indicating strong positive selection for lodgepole pine nest trees. Although lodgepole pine was the most abundant available species we measured at empirical plots across the landscape, Black-backed Woodpeckers selected these sites at disproportionally greater abundance than ponderosa pine, which was the second most abundant available species present (Fig. 7).

For the multivariate geospatial nest tree model (restricted to lodgepole pine) the dispersion parameter exceeded 1, thus we fit a quasibinomial model. The resulting nest tree model estimated that the optimal nest tree DBH in lodgepole pine was 31.5 cm (95% CI: 26.7 cm, 36.3 cm; Fig. 8). Holding DBH at the estimated optimum and nest tree height at the mean, RSS increased strongly with tree age from 0.021 at 69 years (minimum) to 0.445 at 201 years (maximum), yielding a 21-fold increase across the observed range of used nest trees ages. In addition, for every 10-year increase in tree age, RSS increased by 26.0% (95% CI: 2.8%, 51.7%).

4. Discussion

4.1. Resource availability and use between green forest types

Black-backed Woodpeckers in our study area selected breeding habitat in mature and old lodgepole pine (var. *Murrayana*) forests containing abundant levels of deadwood, both as snags and logs. In fire-adapted landscapes, green lodgepole pine forests may contain greater abundances of important resources for breeding Black-backed Woodpeckers than other green forest types. For example, we found deadwood abundance to be greater in lodgepole pine relative to ponderosa pine stands, the other dominant conifer species present in our system. We did not find a measurable difference between deadwood abundance in lodgepole pine compared to mixed conifer or mixed pine stands, despite the lack of Black-backed Woodpecker nesting in mixed conifer and

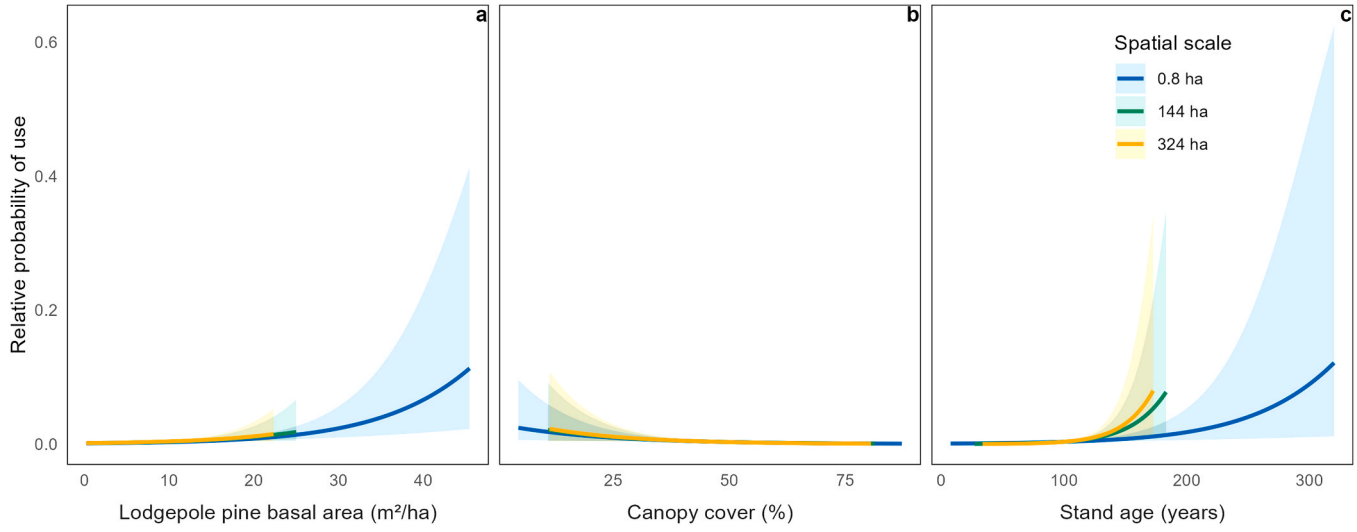

Fig. 5. Increasing lodgepole pine basal area (a) and decreasing canopy cover (b) were the best predictors of potential habitat suitability at the 0.8 ha scale (the smallest spatial scale we tested). Increasing stand age (c) was the best predictor of potential Black-backed Woodpecker green forest nest site suitability at the 324-ha scale (the largest spatial scale we tested). Results show relative probability of use from the level 2 geospatial breeding habitat selection model at each spatial scale.

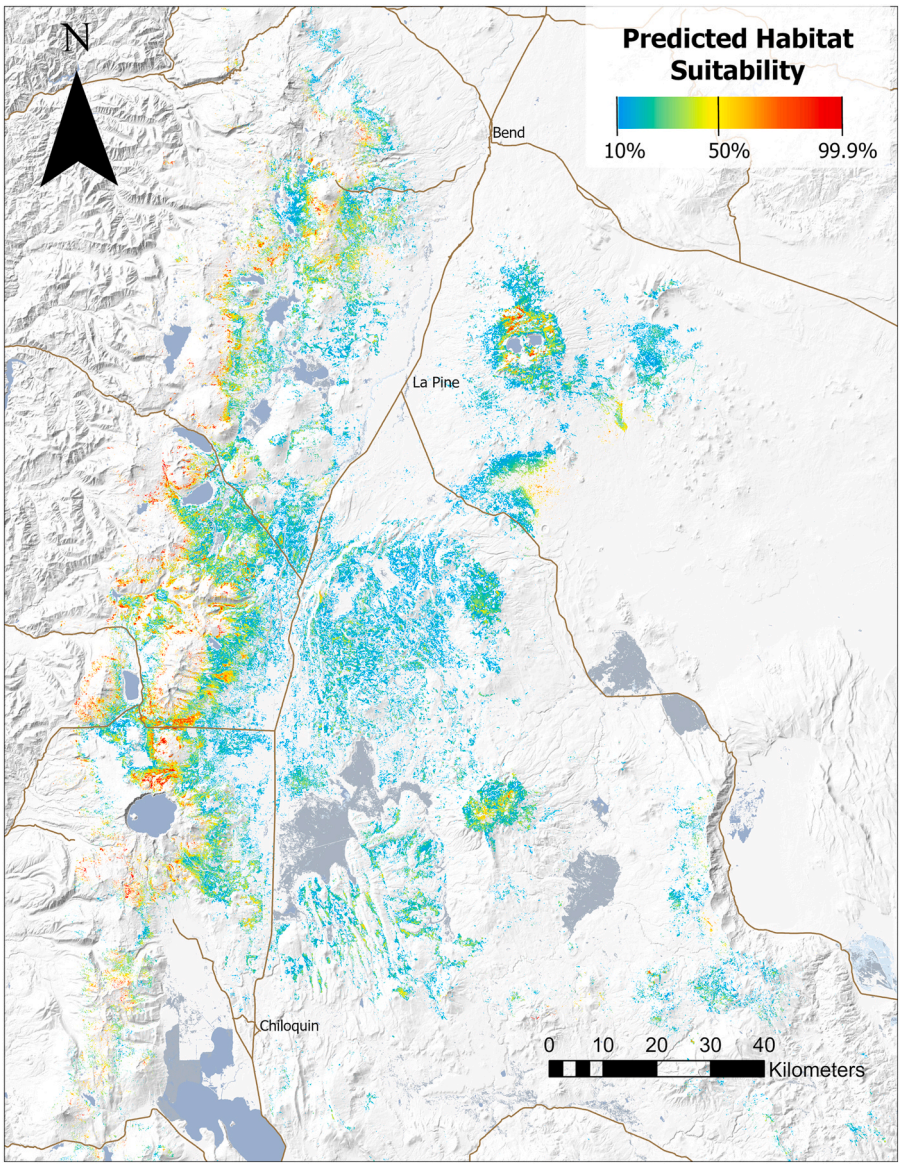

Fig. 6. Predicted suitability of potential habitat for green forest Black-backed Woodpecker breeding sites in the Oregon Cascades Ecoregion as of 2021. Colored regions predict potential habitat suitability > 10%. Areas of the Oregon Cascades not shown in the map had limited predicted suitable habitat.

mixed pine stands. Because mixed conifer and mixed pine forests are occupied by a greater diversity of woodpeckers, we hypothesize that Black-backed Woodpeckers may face greater competition in those forest types, and their use of lodgepole pine may allow for landscape-scale niche partitioning and reduced intraguild competition (Bull et al., 1986). Notably, used nest sites in mature and old forest averaged 3 × as many snags relative to the available lodgepole pine sites (Kerstens et al., in review) that included a range of age classes. Although lodgepole pine forest is widespread in our system, the geospatial model predicted that sites with > 50% suitability were limited and our results suggest not all green lodgepole pine forests are suitable for nesting.

Black-backed Woodpecker fledglings originating from burned natal sites have been found to have improved juvenile survival in green mixed conifer forests (Stillman et al., 2019b). However, we did not observe nesting in green mixed conifer forests. Mixed conifer forests may provide adequate foraging substrates for adult and fledgling Black-backed Woodpeckers but may lack the necessary nesting substrates required for breeding.

We propose that patches of older forests containing overstory legacy trees that have survived wildfire for a century or more play an equally important role relative to recently burned ephemeral resource pulses when considering the landscape level pyrodiversity-biodiversity hypothesis (e.g., by providing temporally stable breeding habitat for cavity nesting species; Tremblay et al., 2015a). Indeed, we have observed territories repeatedly occupied in successive years (authors, personal observation). On the Pumice Plateau and surrounding areas, the historical frequent mixed severity fire regime combined with chronic underlying bark beetle presence likely maintained a pyrodiverse and heterogenous mosaic of conditions (Franklin and Dyrness, 1973, Agee, 1981, Gara et al., 1985, Hagmann et al., 2019, Shaw et al., 2022). These frequent, lower-severity disturbances likely created a diverse array of habitat patches that supported the coexistence of eleven woodpecker species.

4.2. Nest site selection

Our empirical model of nest-site selection suggested that lodgepole pine dominance was the most important predictor of nest-site selection. Dead wood quantity and live tree basal area had comparable influence but less than lodgepole pine dominance. Despite our sample size, cross-

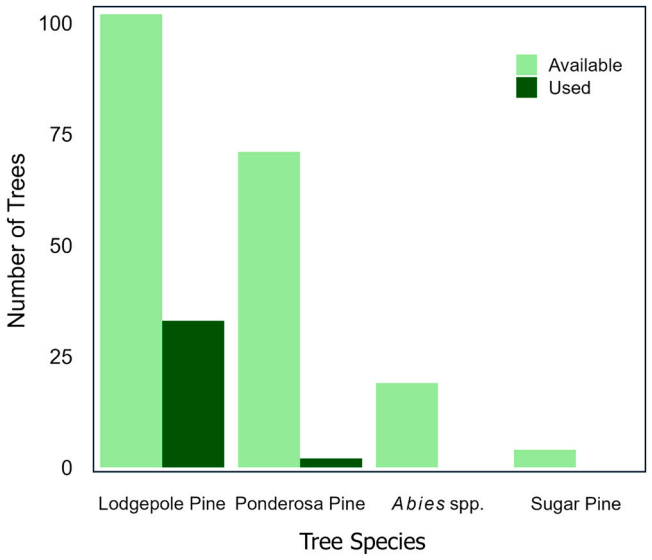

Fig. 7. Tree species of used nest trees in green forest relative to empirically measured available trees on the landscape.

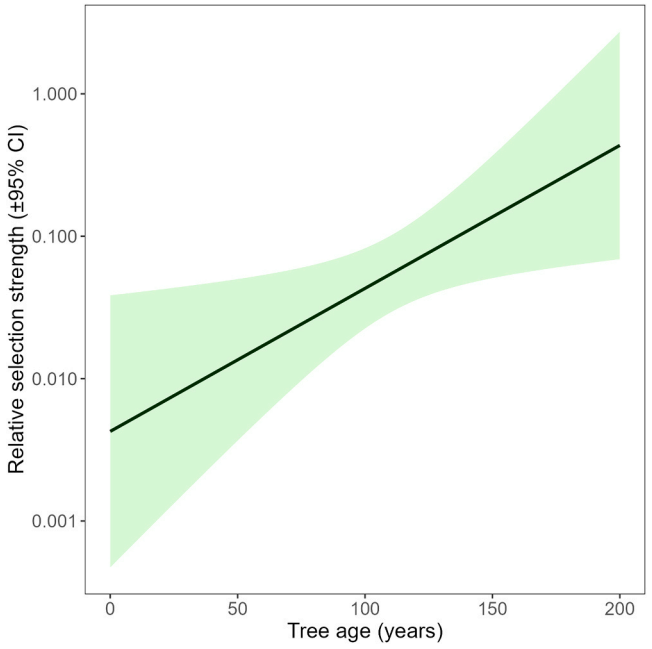

Fig. 8. Relative selection strength of a tree being selected for nesting in green forest increases with tree age, as predicted by the level 4 geospatial nest tree model when DBH was held at 31.5 cm (i.e., the predicted "optimal" size) and height was set to the mean (20 m). The y-axis is displayed on a $\log_{10}$ scale.

validation of our empirical model yielded modest accuracy in predictive performance. In the eastern portion of their range, Black-backed Woodpeckers preferentially nest in jack pine (*Pinus banksiana*; Tremblay et al., 2015b)—a close relative of lodgepole pine (Critchfield, 1985). Similar green forest structural retention requirements across these systems suggest that mature lodgepole/jack pine provide important green forest breeding habitat throughout much of the Black-backed Woodpecker's range (Tremblay et al., 2015b). Although the uneven-aged lodgepole-dominated forests in our study area exhibited legacies of biological disturbance agents, such as periodic bark beetle outbreaks, stem breakage associated with butt rot or western gall rust (*Endocronartium harknessii*), and/or tree wounding from animals (Shaw et al., 2022), they lacked clear evidence of major recent disturbance. In the western portion of their range, we speculate that Black-backed Woodpeckers may be adapted to nest in these lodgepole pine forests that have not experienced recent stand-replacing disturbance, in contrast to other forest types where disturbances of greater severity are needed to provide an adequate dead wood supply for nesting.

Our geospatial model predicted that Black-backed Woodpeckers were more likely to select breeding home ranges in stands that were older at the 324 ha scale (i.e., the largest spatial scale we examined). Conversely, lodgepole pine basal area and canopy cover were predicted to be most important at the 0.8 ha scale (i.e., the smallest scale). Although, the geospatial model also predicted a negative relationship with canopy cover around nest sites, nests did not occur in areas below 22.6% canopy cover. This suggests Black-backed Woodpeckers select relatively open stands while still requiring a minimum level of live overstory structure, indicating a potential nonlinear response that we were unable to evaluate given our nest sample size.

Black-backed Woodpeckers likely respond to habitat features at larger scales than our 0.03 ha empirical plots, especially for foraging. However, selection processes were consistent across our nested geospatial and empirical spatial scales, thus finer scale measures around nests may function both as descriptors of micro-scale habitat and as indicators of surrounding patch structure. The predicted positive relationship with lodgepole pine basal area contradicts the negative relationship with live tree basal area from our empirical model. Within this context, the positive relationship with lodgepole pine basal area likely reflects selection for nest sites dominated by this tree species rather than selection for dense live structure. Decreased canopy cover (geospatial model) and live-tree basal area (empirical model) are consistent with the historically open forest conditions that characterized the southern east-slope Cascade montane forests (Agee, 1981, Hagmann et al., 2019) and to which Black-backed Woodpeckers likely adapted to (Goggans et al., 1989, Tremblay et al., 2009). Cavity nesters have been found to select nest sites with reduced foliar cover (Belles-Isles and Picman, 1986, Li and Martin, 1991) as dense and continuous forest cover can provide protection for mammals (Cox et al., 2012) that depredate cavity nests (Christman and Dhondt, 1997, Purcell and Verner, 1999) and make it harder for parents to detect and defend against potential predators (Belles-Isles and Picman, 1986, Li and Martin, 1991). Thus, our observation of the Black-backed Woodpecker selecting sites in green forest with reduced tree densities and canopy cover may serve two functions: such conditions may simultaneously permit adequate nest defense while still leveraging the green forest's predation protection for vulnerable fledglings.

4.3. Nest tree selection

Our landscape-scale geospatial assessment of nest tree selection in green forest supported the empirical results from a companion study (Kerstens et al., in review) that Black-backed Woodpeckers selected lodgepole pine nest trees with increased diameter and age relative to availability. Woodpeckers likely require numerous potentially suitable trees to select a nest site, and only a subset of them may have sufficient decay for nest construction. As trees age, they have more opportunity to develop internal decay (see Hennon and Mulvey, 2014), and such decay is likely critical in reducing wood hardness and facilitating cavity excavation (Lorenz et al., 2015). These processes should therefore increase their suitability as potential nest trees.

4.4. Deadwood in lodgepole pine forests

The stand dynamics of lodgepole pine forests in our system may be more susceptible to chronic low-level patchy disturbance that creates a regular supply of dead wood without removing the legacy material compared to the other forest types in the region (Franklin and Dyrness, 1973, Geiszler et al., 1980, Hagmann et al., 2013). This dynamic applies throughout the successional trajectory of lodgepole pine, from

micro-scale "disturbances" following cohort establishment (i.e., individual tree die-off due to density dependent effects in regenerating thickets) to episodic and/or chronic low-level disturbances in mature stands from biotic and abiotic disturbance agents like bark beetles, porcupines, bears, fungi, fire, and/or drought (Shaw et al., 2022).

Although dead wood in the form of snags is more limited in green forest relative to the recently burned forests Black-backed Woodpeckers are typically associated with, green forest nest sites have higher abundances of deadwood in the form of downed logs (Kerstens et al., in review). Logs likely provide critical Black-backed Woodpecker foraging substrates in green forests (Nappi et al., 2015) when snags are less abundant. These substrates may provide supplemental foraging resources that facilitate certain green forests to be suitable nesting habitat for Black-backed Woodpeckers. Their relationship with dead wood has been well studied in recently disturbed forests (Murphy and Lehnhausen, 1998, Bonnot et al., 2009, Saab et al., 2009, Nappi et al., 2015), but only more recently examined in green forests (Tremblay et al., 2015b, Martin et al., 2021). We found that Black-backed Woodpeckers selected late-seral lodgepole pine stands with high quantities of dead wood relative to available sites. Deadwood is often limiting in managed forests (Thorn et al., 2020) despite providing many ecological benefits (Harmon et al., 2004). Based on our findings, deadwood in green forests may be crucial for providing habitat for keystone species like the Black-backed Woodpecker, so management that retains deadwood should both support biodiversity conservation efforts in addition to supporting other forest functional values.

4.5. Management considerations

Lodgepole pine forests are an extensive, unique and important ecological community (Franklin and Dyrness, 1973, Geiszler et al., 1980, Agee, 1981, Stuart et al., 1989, Hagmann et al., 2019). Yet, conservation and restoration in some fire-adapted forest systems are often focused on ponderosa pine and fir (*Abies*) (Charnley et al., 2017). In contrast, management for lodgepole pine includes clearcutting on 80-year rotations (Charnley et al., 2017) and does not appear to be considered an important forest type for biodiversity conservation planning. Woodpeckers are often used as management indicators due to their keystone processes (Bull et al., 1986, 1990, Wisdom et al., 2000, Gaines et al., 2007, Menon and Shahabuddin, 2021); however, the woodpecker species used as indicators in other forest types are not associated with lodgepole pine forests in fire-adapted landscapes (Bull and Jackson, 2020, Ferris et al., 2026). Currently, we are unaware of management indicators for lodgepole pine forests and argue that these forests should be managed for their biodiversity value, in addition to their value for timber.

Using a singular indicator species across expansive and variable landscapes is unlikely to be an effective approach. Rather, multiple complementary indicators are needed to promote biodiversity across the landscape. In this context, our research supports previous work by Goggans et al. (1989) that the Black-backed Woodpecker is well suited as an indicator species for mature and old lodgepole pine forests. Managing for Black-backed Woodpecker's habitat requirements in these systems—and understanding how forest management activities influence habitat use and fitness—should provide conservation opportunities for additional wildlife species residing in these forests (Martin and Eadie, 1999, Virkkala, 2006, Tremblay et al., 2020). More broadly, our findings suggest that conservation of fire-associated species may require maintaining unburned forest conditions that promote chronic recruitment of dead wood and old trees, not solely the protection of recently disturbed habitat. Our findings underscore the importance of place-based management that recognizes the ecological value of low-productivity, edaphically constrained lodgepole pine systems. Maintaining these compositionally simple yet structurally complex stands—characterized by multiple age classes and abundant dead wood—may be critical for conserving Black-backed Woodpecker habitat across this landscape.

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

During the preparation of this work the authors used ChatGPT to assist with coding in RStudio and for occasional suggestions to improve readability. After using this tool, the authors tested, reviewed and edited the code and content and take full responsibility for the published article.

Funding

Funding for this research was provided by the National Council for Air and Stream Improvement, the Fish and Wildlife Habitat in Managed Forests Research Program in the College of Forestry at Oregon State University, the Oregon Department of Forestry, the Animal Behavior Society, the Association of Field Ornithologists, and the Klamath Basin Audubon Society. The funders were not involved with study design, data collection and analysis, publication decisions, or preparation of the manuscript.

CRediT authorship contribution statement

Jonathan B. Dinkins: Writing – review & editing, Validation, Methodology. **Mark E. Kerstens:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **James W. Rivers:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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

Acknowledgements

We thank J. Verschuyl, A. Stillman, T. Lorenz, N. Palazzotto, D. Shaw, C. Schwarz, and A. Merschel for valuable discussion and feedback; D. Gannon for statistical consultation; M. Johnson, J. Welch, C. Weekly, J. Pellissier, M. Gostin, A. Markus, D. Antle, J. Easter, J. Swingle, D. Mainwaring, J. Dachenhaus, E. Woodis, A. Holland, B. Howland, C. Brock, M. Kuzel, V. Hawk, C. Ross, N. Quatier, L. Bee, J. Ford, and K. Nicolato for outstanding logistical support; and one anonymous reviewer for helpful comments on a previous version of the manuscript.

Author contributions

M.E.K. conceived the idea for the original research as an extension to an investigation developed by J.W.R. All authors contributed to designing the associated methods. M.E.K conducted the research, analyzed the data, and drafted the initial version of the manuscript. All authors contributed extensively to the review and editing of the final manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124084.

Data availability

Data will be made available on request.

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