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ARTICLE

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Distinct bird assemblages emerge after fire versus forest harvest but converge with early seral forest development

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Abstract

Anthropogenic changes to disturbance regimes, including intensified forest management, have been hypothesized to drive population declines in early seral forest birds. Species adapted to early seral conditions can benefit from timber harvest, but intensively managed stands often lack key habitat features that exist after natural disturbances. To evaluate how early seral bird communities differ between areas regenerating from natural (i.e., wildfire) and anthropogenic (i.e., timber harvest) disturbance, we sampled stands across a chronosequence of 2–20 years post-disturbance in southwest Oregon, USA, in sites regenerating after wildfire, clearcut harvest with intensive management, or post-fire salvage logging. We found that fire-origin stands supported 8.8 more species (90% CI: 4.1, 14.1; 54% more) than clearcut stands immediately following disturbance (2–5 years), including a greater number of cavity-nesting species. These differences diminished somewhat with stand age, but fire-origin stands still supported 4.9 more foliage-gleaning species (90% CI: 3.2, 6.5; 102% more) 6–9 years after disturbance. Differences in species richness and composition between disturbance types attenuated as stands approached canopy closure (16–20 years), suggesting that intensive management may emulate natural stand-replacing disturbance for birds that occupy developmentally advanced early seral forests. Salvage-logged stands exhibited few differences from unlogged fire-origin stands, although they supported 1.8 fewer (90% CI: 0.0, 3.4) cavity-nesting species 6–9 years after fire. Overall, distinct bird communities in recently burned forests suggest that these areas may be especially valuable for promoting biodiversity. Guilds more strongly associated with

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recently burned forests than harvested stands tended to be associated with biological legacies, including deciduous shrub cover, large residual trees, and snags. Therefore, emulating post-fire structural legacies and early seral vegetation in managed forests should enhance their value for birds, including species experiencing long-term declines.

KEYWORDS
avian point counts, bird community composition, clearcut, early successional forest, intensive forest management, Klamath Mountains, occupancy modeling, Oregon, post-fire salvage logging, species richness, wildfire

INTRODUCTION

Understanding how species respond to forest management and disturbance regimes is critical for conservation in an era of rapid biodiversity loss (Millar & Stephenson, 2015; Rosenberg et al., 2019). Natural disturbance regimes filter species over time (Balmford, 1996) such that many taxa in temperate forest ecosystems are adapted to early seral conditions that follow stand-replacing disturbance (Kwit et al., 2014; Swanson et al., 2014). Where natural disturbance regimes have been modified—especially via fire suppression and forest management—the amount of contemporary early seral conditions may be below historical ranges of variability (Donato et al., 2020; Lorimer & White, 2003). Population declines in birds associated with early seral forests have been documented in several forest regions of North America (Betts et al., 2010; King & Schlossberg, 2014), and many of these declines are thought to be caused by habitat loss (Betts et al., 2022; Phalan et al., 2019). Therefore, it has become a priority to understand how natural and anthropogenic stand-replacing disturbances differ in the habitat they provide for early seral species.

Even-aged management has been suggested as a means for supporting biodiversity associated with early seral forests (DeGraaf & Yamasaki, 2003; Demarais et al., 2017; Yamaura et al., 2012). However, early seral stands originating from timber harvest often diverge from naturally disturbed stands in their structural complexity and vegetation characteristics, with potential implications for biodiversity (Swanson et al., 2011). Evaluating the conservation implications of forest management for early seral-associated species requires quantifying and comparing species assemblages to those that occur after natural disturbance, such as wildfire (Attiwill, 1994; North & Keeton, 2008). Although the degree to which forest harvest emulates wildfire has been studied for birds in boreal regions (Bognounou et al., 2021; Zimmerling et al., 2017), similar studies are needed in temperate forests to inform conservation planning and management practices.

In the Pacific Northwest, fire has been a key ecological process over long time scales (Baig & Gavin, 2023; Boyd, 2021; Walsh et al., 2010) and forest lands managed for diverse objectives provide an opportunity to compare early seral forests initiated by different disturbances within a temperate forest landscape. On large private forests, management practices typically include shortened rotations (35–50 years) using clearcut harvest, single-species conifer plantings of selected stock, and herbicides to control competing vegetation (Demarais et al., 2017; Talbert & Marshall, 2005). Intensive management practices that accelerate crop tree growth following harvest are increasingly common worldwide (FAO, 2022). Federal forests in the Pacific Northwest are managed for multiple uses and rarely undergo clearcut harvest or herbicide application (Kroll, Johnston, et al., 2020). However, salvage logging after natural disturbance often occurs to mitigate economic losses (Beschta et al., 2004; Lindenmayer et al., 2008), and is common after fire in both private and federal forests. For example, salvage logging accounted for 14% of the harvest area from 2013 to 2023 on lands managed by the USDI Bureau of Land Management in Oregon (BLM, 2024). Although intensive management approaches may benefit biodiversity conservation by reducing harvest pressure elsewhere on the forest land base (Pirard et al., 2016), whether early seral conditions in intensively managed forests support biodiversity at levels commensurate with forests that experience natural disturbance remains unclear.

Under natural conditions, early seral stands in the Pacific Northwest can be characterized by abundant broadleaf vegetation, even in conifer-dominated forests (Halpern, 1989; Stokely et al., 2018). In intensively managed forests, post-harvest herbicide application suppresses broadleaf vegetation (Wagner et al., 2004), which reduces the abundance of foliage-gleaning and shrub-nesting birds (Betts et al., 2013). Broadleaf vegetation may be disproportionately important in providing foraging and nesting opportunities for these guilds in early seral forests (Campbell & Donato, 2014; Ellis et al. 2012; Hagar et al., 2007). Alternatively, total vegetation cover may be more important than vegetation type (Jones et al., 2012), though broadleaf vegetation accounts for most of the variability in total vegetation among young managed stands. Moreover, conifer and broadleaf cover may provide similar foraging opportunities where sclerophyllous broadleaf species dominate early seral forests (Campbell & Donato, 2014).

Intensive forest management and salvage logging limit structural legacies, such as standing dead trees (snags) and live trees (Linden & Roloff, 2013), which characterize early seral stands after wildfire (Reilly et al., 2021). Snags in recently burned stands provide nesting and foraging resources for many avian taxa, including keystone species such as woodpeckers (Hutto & Gallo, 2006; Schulte & Niemi, 1998). Live trees contribute structural complexity and distinct habitat elements to post-fire stands (Dunn & Bailey, 2016; Franklin et al., 2000).

To understand how early seral bird communities vary in response to natural versus anthropogenic disturbances, we studied breeding bird assemblages following stand-replacing wildfire (fire-origin stands), clearcutting with intensive forest management (clearcut stands), and post-fire salvage logging in southwest Oregon, USA. We asked: (1) How do stand-scale responses of breeding bird assemblages vary among disturbance types? (2) Does variation between fire-origin and clearcut stands change with time since disturbance? and (3) Do structural legacies and vegetation characteristics explain variability in bird community response among disturbance types and stand ages? To do this, we evaluated variation in diversity (species richness and gamma diversity) and composition (species dissimilarity and guild-level species richness) across disturbance types and time since disturbance, and in relation to key stand characteristics. We hypothesized that fire-origin stands would support greater bird species richness than clearcut stands due to greater availability of snags, overall vegetation cover, and broadleaf vegetation cover. We also predicted that differences in bird communities would diminish with time since disturbance because of vegetation recovery (Kroll, Springford, et al., 2020) and the effects of snag attrition and decay (Dunn & Bailey, 2015; Ritchie et al., 2013) on snag-dependent bird species (Boulanger & Sirois, 2007; Hutto & Patterson, 2016; Saab et al., 2007).

METHODS

Study area

We conducted this study in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) forest types in the Klamath Mountains of southwest Oregon, USA (Figure 1). Douglas-fir-dominated forest types are widespread in the region and occur across a relatively broad range of site conditions (Agee, 1993; Skinner et al., 2006). Climatic conditions in this area include warm, dry summers and cool, wet winters, with a mean annual temperature of 11.4°C and a mean annual precipitation of 1550 mm in Douglas-fir-dominated forest types (for 1991–2020; PRISM Climate Group 2022, accessed 1/26/2023). High-severity fire is part of the historical mixed-severity fire regime in Douglas-fir-dominated forests of the region (Agee, 1993; Reilly et al., 2021), yet has increased in recent decades due to fire suppression and climate warming (Taylor et al., 2021). Stands are often quickly colonized by shrubs and broadleaf trees after stand-replacing disturbance, and conifer establishment can be protracted following severe fire (Shatford et al., 2007; Tepley et al., 2017).

In our study region, land ownership patterns are dominated by private lands managed by large companies and public lands managed by federal agencies (USDA Forest Service and USDI Bureau of Land Management). Companies managing forests for wood production often use intensive management techniques, including herbicide applications applied during site preparation and after planting seedlings to mitigate non-crop tree competition (Kroll, Johnston, et al., 2020). In contrast, public forest lands have multiple goals and are typically managed less intensively. Some public lands are salvage logged and replanted following fire, whereas others are planted or receive no post-fire management. When competing vegetation is controlled on federal lands, it typically involves mulch mats around planted seedlings or mechanical treatments (e.g., brushing; Lopez Ortiz et al., 2019).

Study design

We stratified sampling locations across three disturbance types and three stand age classes across the early seral period, using a chronosequence design. Disturbance types included stand-replacing high-severity fire (fire-origin stands), post-fire salvage logging (salvage-logged stands), and clearcut harvest with intensive forest management (clearcut stands). Stand age classes included: 2–5 years (young), 6–9 years (intermediate), and 16–20 years (advanced). For overlapping disturbances (i.e., fire followed by salvage logging), we based stand age on the timing of the initial disturbance event. We were constrained to sampling salvage-logged stands in the intermediate age class because of unexpected fire activity and management during site selection in 2018. Therefore, our final study design included seven distinct combinations of disturbance type and stand age: fire-origin and clearcut stands of young,

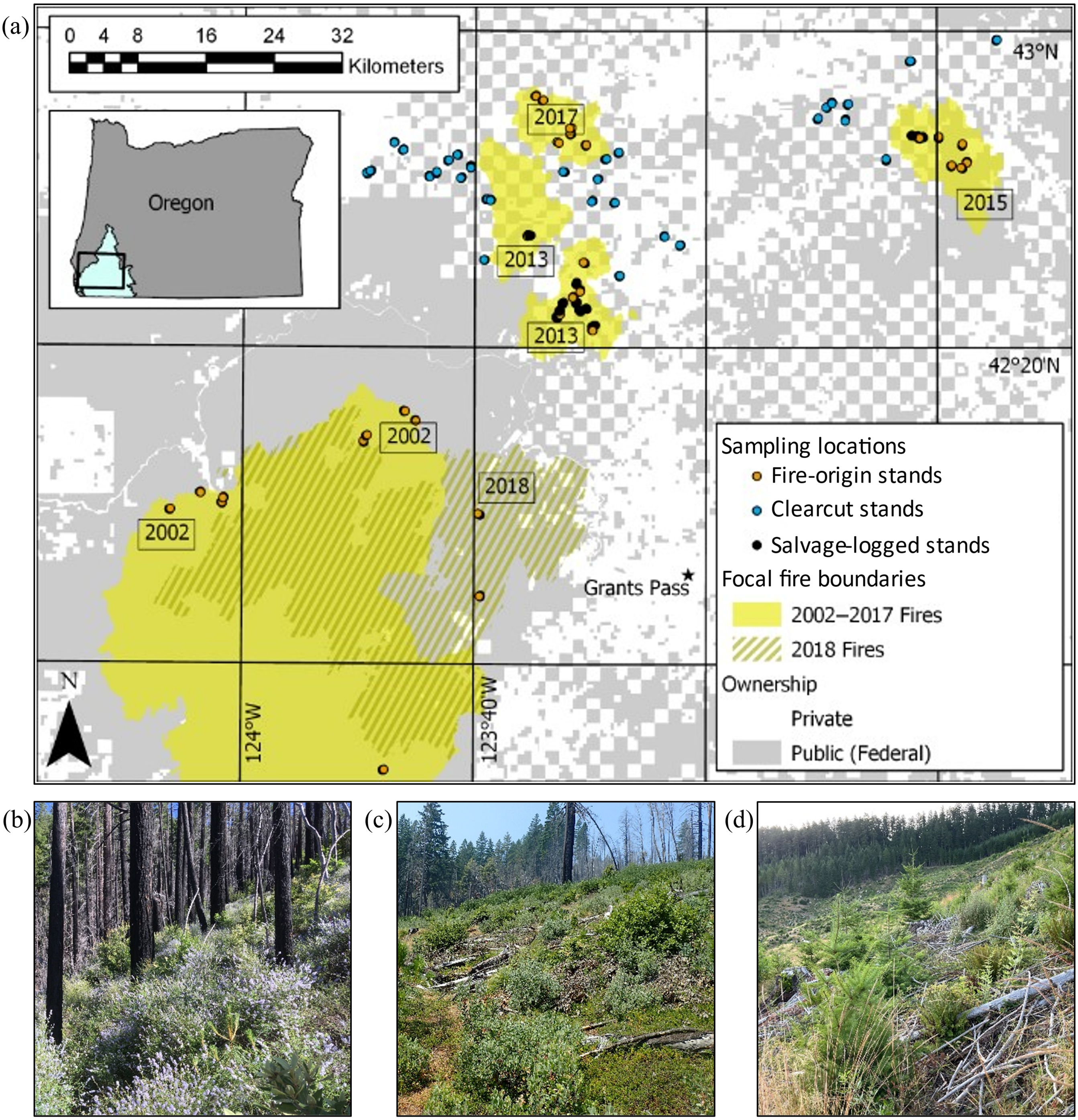

FIGURE 1 Map of study area and sampling locations (a) reproduced from Frank et al. (2025) under a Creative Commons license https://creativecommons.org/licenses/by-nc-nd/4.0/, and example photos of each disturbance type, including (b) fire-origin stand (stand age: 8 years), (c) post-fire salvage-logged stand (stand age: 8 years), and (d) clearcut stand with intensive forest management (stand age: 7 years). Photographs in panels (b–d) were taken by Graham S. Frank.

intermediate, and advanced age, and salvage-logged stands of intermediate age.

We used federal and private harvest records with fire severity maps and remotely sensed potential vegetation-type data to identify locations that met our experimental design criteria. We constrained sampling to Douglas-fir or Douglas-fir/tanoak (*Notholithocarpus densiflorus*) vegetation types (Henderson, unpublished report) and excluded stands that had experienced known disturbances within 45 years prior to fire or harvest. Fire-origin stands were those on federal lands that had burned at high severity (>75% basal area mortality) based on an RdNBR of 649 (Relativized difference in the Normalized Burn Ratio; Reilly et al., 2017).

These criteria led us to select stands that had burned in 2002 (Biscuit Fire), 2013 (Douglas Complex), 2015 (Stouts Creek Fire), 2017 (Horse Prairie Fire), and 2018 (Taylor Creek Fire). Some young and intermediate fire-origin stands were planted, but seedlings had little effect on vegetation structure due to suppressed growth and high mortality (GSF, personal observation). Salvage-logged stands met all criteria of fire-origin stands but also experienced clearcut harvest after fire. Salvage-logged stands were planted but not treated with herbicides, the typical practice on federal lands in our study area. Clearcut stands were those regenerating after clearcut timber harvests conducted on unburned, privately managed forestlands. Candidate stands had to be >4 ha and accessible by gravel logging roads (<30-min hike) to facilitate repeated sampling.

From the pool of potential locations, we selected 69 stands to match distributions of elevation and topographic heat load (heat load index, McCune & Keon, 2002) among the disturbance-age class categories ($n = 9$–11 per category; Table 1). Within each stand, we placed three avian point count stations that were ≥100 m apart from one another and ≥50 m from an identifiable stand boundary (i.e., harvest edge, road, or lower-severity burn). Nearly all plots (97%) were within 150 m of the next closest plot in a stand, though the irregular shape of some stands prevented us from implementing this as a strict criterion for plot placement. We prioritized sampling intensity (i.e., multiple point count stations within a stand) to improve avian detection probabilities while limiting travel time in this large, complex landscape.

Data collection

Point counts

We collected data on bird species occurrence on stands using point counts (Ralph et al., 1995) conducted between May 16 and June 20 in one of 3 years: 2019, 2021, or 2022. Our point counts documented all birds detected within a 50 m radius during a 10-min period and were conducted by experienced technicians following 2 weeks of training in local species identification and distance estimation. Field crews conducted point counts at all three stations on each stand on three different occasions across the season to allow for separating detection processes from occupancy. When sampling, we randomized the first visit date to a stand within the first 3 weeks of the season and conducted the second visit 2 days later to facilitate sampling for a related study. We then randomized the date of the third visit within the fourth week of the season. We randomized observers across visits and the order of point count

TABLE 1 Mean (±SD) values for biophysical characteristics of early seral forest types stratified by disturbance and stand age, including explanatory variables included in occupancy models.

	Fire			Clearcut			Salvage
Variable	**2–5 years**	**6–9 years**	**16–20 years**	**2–5 years**	**6–9 years**	**16–20 years**	**6–9 years**
n	10	10	9	10	10	9	11
Stand age (years)	3.2 ± 1.2	7.4 ± 1.2	18.9 ± 1.2	3.7 ± 0.9	7.3 ± 1.3	18.2 ± 1.3	7.5 ± 1.1
Elevation (m)	656 ± 172	680 ± 137	807 ± 442	710 ± 410	689 ± 121	637 ± 121	767 ± 177
Heat load index	0.75 ± 0.17	0.69 ± 0.20	0.74 ± 0.15	0.77 ± 0.17	0.72 ± 0.15	0.75 ± 0.12	0.66 ± 0.17
Woody vegetation cover (%)	48 ± 31	108 ± 48	137 ± 67	16 ± 19	31 ± 20	119 ± 15	80 ± 30
Conifer	1 ± 3	4 ± 4	23 ± 17	1 ± 2	15 ± 12	79 ± 26	5 ± 6
Broadleaf	46 ± 31	104 ± 45	114 ± 59	14 ± 19	16 ± 10	40 ± 28	75 ± 31
Broadleaf tree	17 ± 17	30 ± 20	61 ± 40	7 ± 13	1 ± 2	15 ± 24	28 ± 26
Evergreen shrub	8 ± 7	31 ± 35	43 ± 24	4 ± 7	10 ± 10	15 ± 10	27 ± 27
Deciduous shrub	21 ± 27	43 ± 39	11 ± 18	3 ± 4	5 ± 5	9 ± 11	20 ± 21
Snag basal area (m^2 ha^{-1})	55.0 ± 7.0	48.3 ± 14.0	22.4 ± 18.2	0.7 ± 1.1	1.2 ± 1.3	1.7 ± 2.0	6.0 ± 4.4
Live tree basal area (m^2 ha^{-1})	1.7 ± 3.0	1.9 ± 3.2	3.8 ± 2.7	0.0 ± 0.0	0.0 ± 0.0	10.9 ± 3.7	0.4 ± 0.7
10–50 cm diameter	0.2 ± 0.7	0.2 ± 0.5	1.5 ± 1.6	0.0 ± 0.0	0.0 ± 0.0	10.3 ± 3.7	0.0 ± 0.0
>50 cm diameter	1.5 ± 2.6	1.8 ± 3.2	2.3 ± 2.1	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 1.0	0.4 ± 0.7

Note: Vegetation cover values were summed across four vertical strata and multiple species and may total >100. Variable names in bold were included as explanatory variables in the ecological process component of the explanatory model, and those in italics were included in the detection process components of both models. Heat load index ranges 0–1, with higher values representing greater topographic heat loads.

stations within the stand for each visit. Point counts started at sunrise and usually concluded by 10:00, with 2.2% of visits (14 of 630) conducted slightly later due to logistical challenges. Crews did not conduct point counts during high winds or heavy precipitation, and they excluded flyover individuals.

We classified each bird species observed during point counts according to the nest site and foraging substrates as described by the Cornell Lab of Ornithology (Appendix S1). We focused our analysis on four foraging guilds and four nesting guilds that corresponded to most species in our dataset. Four species with unclassified foraging substrates accounted for 6% of detections, and four other species with unclassified nesting locations accounted for <1% of detections.

Forest structure and vegetation

We measured structural and compositional elements that we expected to be important in explaining differences in occupancy. We used 25-m radius circular plots centered on point count stations to measure the dbh of each stem >50 cm in diameter to characterize large legacy elements. If there were fewer than three snags or live trees of this size in the plot, we expanded up to 50 m to measure these elements. We measured smaller stems 10–50 cm in diameter in four 100 m^2 subplots surrounding each point count station. To maximize coverage, we located subplots centered 18 m from a point count station at 0°, 120°, and 240°, with a fourth centered 9 m away at 60°, 180°, or 300°. For analyses, we summarized snag and legacy tree data into stand-level estimates of basal area (in square meters per hectare).

We characterized vegetation at each point count station by estimating foliage cover for each woody plant species within the subplots used to measure smaller snag and tree stems. To reduce variability among observers, crews estimated cover in discrete classes (Peet et al., 1998): <0.1%, 0.1%–1%, 1%–2%, 2%–5%, 5%–10%, 10%–25%, 25%–50%, 50%–75%, 75%–95%, and >95%. We accounted for the vertical structure of vegetation by separating cover estimates into four separate vertical strata: below 0.5 m, 0.5–2 m, 2–5 m, and >5 m. For each subplot, we converted ordinal cover estimates into percent cover by taking the midpoint of each cover class and summed estimates from all four vertical strata; thus, cover values could exceed 100%. We averaged cover estimates across subplots to generate a single stand-level estimate and summed these by plant growth form for analysis; these included coniferous trees (needle-leaf gymnosperms), broadleaf trees (angiosperms capable of attaining midstory or overstory positions; evergreen and deciduous combined), and evergreen and deciduous shrubs (other woody broadleaf angiosperms).

Statistical analysis

Modeling

We fit multispecies hierarchical occupancy models within a Bayesian framework to evaluate bird community- and guild-level associations with the seven disturbance-age categories and their vegetation characteristics while accounting for imperfect detection (Dorazio & Royle, 2005; Zipkin et al., 2010). We analyzed occupancy at the stand scale and collapsed point count data across stations on each stand to estimate detection for each species on each visit. Our models included all species detected at least twice (Appendix S1). We assumed that each detection represents species presence (occupancy), but that a non-detection could be the result of either a presence or an absence.

We developed two models, each with component submodels for detection and occupancy probabilities. The first model compared disturbance types and stand age classes (hereafter, the comparative model). The second model examined associations between species occupancy and stand characteristics (hereafter, the explanatory model), which we chose a priori to evaluate predictions about key characteristics of early seral bird habitat. The two models were identical in their structure and covariates for detectability but differed in the covariates used to model occupancy probability.

For the comparative model, we estimated logit occupancy probability at the stand level as a function of disturbance type, stand age class, disturbance type × stand age class interaction, and elevation. We chose to model stand age as a categorical variable due to the gap in ages between the intermediate and advanced age classes. For the explanatory model, we modeled logit occupancy probability as a function of the following stand characteristics: cover of conifers, broadleaf trees, deciduous shrubs, and evergreen shrubs; snag basal area; large live tree (>50 cm dbh) basal area; and elevation. We did not distinguish between deciduous and evergreen broadleaf trees because deciduous tree species were rarely encountered in field plots. We standardized all stand characteristics prior to model fitting and calculated means and SDs within each disturbance-age category (Table 1). Within each of these models, we allowed each species-specific slope parameter to vary as a function of foraging and nesting guild identity (Brown et al., 2014; Soto-Shoender et al., 2020).

Individual survey characteristics and the biophysical environment influence detection probability. As noted above, we randomized observers and day of year during surveys to reduce variation in species detectability among disturbance types and age classes. Therefore, we modeled detection probability as a function of snag basal area and woody vegetation cover, which we expected to vary substantially across disturbance types and age classes and influence detection probabilities. We modeled species-specific slope parameters for detection covariates and intercepts for each sub-model as random effects drawn from community-level distributions (Zipkin et al., 2010). This community-level component of the multispecies model can increase the precision of species-specific parameters by sharing information across species, with estimates for rarely detected species shrinking toward the mean of the common distribution (Gelman & Hill, 2007).

We fit each model with JAGS in the R statistical software (version 4.2.3; R Core Team, 2023) using the R2jags package (Su & Yajima, 2021). For each model, we ran three chains of 40,000 iterations each, with 30,000 discarded as a burn-in period and a thin rate of 30, resulting in posterior distributions of 999 draws. We visually examined posterior draws and calculated potential scale reduction factors (R-hat) to evaluate convergence of parameter estimates for each parameter (Gelman & Rubin, 1992); R-hat values <1.05 and visual examination indicated convergence for all parameter estimates. We evaluated model fit using posterior predictive checks, which showed indications of good model fit. We calculated residuals for the occupancy component of each model following Wright et al. (2019) and used a Mantel test to evaluate whether differences in occupancy residuals were correlated with spatial distance between stands. Mantel tests showed no evidence of spatial autocorrelation in occupancy residuals for the comparative model ($r = -0.12$, $p = 0.94$) or the explanatory model ($r = -0.07$, $p = 0.81$). Additional model fitting details are in Appendix S2.

Comparisons of community metrics

To compare community- and guild-level diversity and composition, we calculated species richness, gamma diversity, and community dissimilarity for each posterior draw of parameters from the comparative model; this resulted in posterior distributions for each metric that incorporated uncertainty from the detection process. For inference, we calculated the medians and 90% Bayesian credible intervals for these distributions and for their comparisons between disturbance-age categories, as they are more computationally stable than 95% intervals and facilitate comparisons against zero. We provide complete descriptions of each community metric in Appendix S3.

We calculated species richness as the sum of expected occupancy probabilities for all species separately, as well as for each guild. We calculated gamma diversity (Whittaker, 1960) as the number of species occurring across stands within a disturbance-age category or across age classes within a disturbance type (Tingley et al., 2016). We compared overall species composition and foliage-gleaning species composition among disturbance-age categories using the Raup–Crick dissimilarity index (Raup & Crick, 1979; Vellend et al., 2007). Raup–Crick dissimilarity evaluates differences in species composition independent of differences in species richness (Chase et al., 2011). We calculated the mean Raup–Crick dissimilarity for each pairwise comparison with at least one fire-origin disturbance-age category and inferred differences in community composition by comparing the posterior distributions of between-category and within-category Raup–Crick dissimilarities. To supplement community- and guild-level metrics, we report species-specific occupancy responses in Appendix S4, including an indicator species analysis (De Cáceres et al., 2010; De Cáceres & Legendre, 2009; Dufrêne & Legendre, 1997; Urban et al., 2012).

Average predictive comparisons for environmental covariates

To evaluate the strength of associations between environmental covariates and species occupancy, species richness, and guild-level richness, we used average predictive comparisons (APCs; Gelman & Pardoe, 2007; Jones et al., 2012). We calculated comparisons for a fixed, interpretable difference in each occupancy covariate from the explanatory model while averaging over the distributions of other occupancy covariates. This approach is preferable to holding other variables at fixed values when a single value is not representative of the sample (e.g., for bimodal or highly variable distributions; Gelman & Pardoe, 2007). We evaluated APCs for differences of 10 percentage points for vegetation variables, 10 $\text{m}^2\ \text{ha}^{-1}$ snag basal area, 1 $\text{m}^2\ \text{ha}^{-1}$ large residual tree basal area, and 100 m elevation.

RESULTS

We conducted 621 point counts that yielded 2949 observations of 70 bird species (Appendix S1). This resulted in 1445 stand-level detections, and we estimated occupancy for 62 species that we detected more than once. Most species belonged to the foliage-gleaning and ground-foraging guilds, with 20 species (50.2% of detections) and 21 species (29.5% of detections), respectively. The five most frequently detected species were, in descending order, the Spotted Towhee (6.9%; a ground forager; scientific names in Appendix S1), Black-headed Grosbeak (5.7%), Lazuli

Bunting (5.6%), House Wren (5.5%), and Nashville Warbler (5.5%; all foliage gleaners). Detections were more evenly distributed among nesting guilds (Appendix S1: Table S2). Mean detection probabilities ranged among species from 0.08 to 0.73 for the comparative model (median = 0.27) and 0.07–0.73 for the explanatory model (median = 0.23), and detection probabilities varied with snag basal area and woody vegetation cover (Appendix S4: Figure S6).

Species richness

Fire-origin stands supported greater total bird species richness than clearcut stands in the years immediately following disturbance, but these differences lessened with stand age (Figure 2a). Young fire-origin stands (2–5 years) were the most species-rich category in our study, supporting an estimated 8.8 more species (90% CI: 4.1, 14.1; 54%) than similar age clearcut stands. At intermediate ages (6–9 years), the contrast in species richness between fire-origin and clearcut stands weakened, with an estimated 5.2 more species (90% CI: 0.9, 9.2; 29%) in fire-origin stands. We did not find strong evidence for differences in species richness in intermediate salvage-logged stands when compared to fire-origin stands, with an estimated difference of only 1.5 fewer species (90% CI: −2.3, 5.1). Advanced clearcut stands (16–20 years) supported an estimated 8.6 more species (90% CI: 4.5, 12.8; 51%) than young clearcut stands, resulting in similar species richness estimates between clearcut and fire-origin stands in the advanced age class (2.7 more species in clearcut stands, 90% CI: −1.5, 6.4; Figure 2).

Guild-level species richness

Young and intermediate clearcut stands supported lower species richness than fire-origin stands for several foraging and nesting guilds (Figure 2b,c). Compared to clearcut stands, fire-origin stands supported more foliage-gleaning

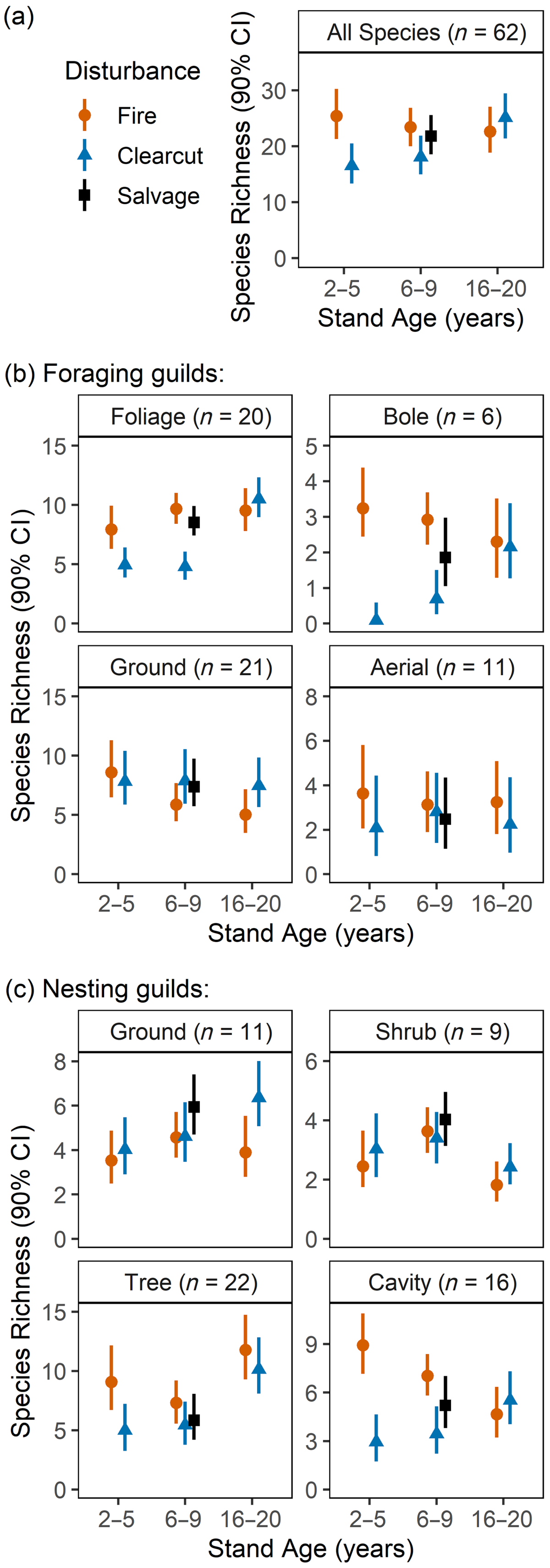

FIGURE 2 Stand-level species richness estimates for (a) all bird species, (b) specific foraging guilds, and (c) specific nesting guilds across disturbance-age categories of early seral forest in southwest Oregon. Estimates are expected values in a given disturbance-age category based on the sum of all species occupancy probabilities, after accounting for imperfect detection. Points and vertical lines represent the median and 90% Bayesian credible interval of the posterior distribution for this estimate. Note the different *y*-axis scales for each panel.

species in the young age class (90% CI: 1.0, 5.1 more species) and this difference was even more pronounced in the intermediate age class (90% CI: 3.2, 6.5 more species). Species richness of cavity-nesting birds was also 3× higher in young fire-origin stands than in young clearcut stands (90% CI: 3.8, 8.1 more species; Figure 2c). Other guilds with markedly higher species richness in young fire-origin stands compared to young clearcut stands included bole-foraging species (90% CI: 2.3, 4.3 more species) and tree-nesting species (90% CI: 1.2, 7.3 more species).

When comparing fire-origin and salvage-logged stands in the intermediate age class, differences in guild-level species richness were smaller than those between fire-origin and clearcut stands (Figure 2b,c). Nonetheless, salvage-logged stands supported fewer cavity-nesting species (90% CI: 0.0, 3.4 fewer) and bole-foraging species (90% CI: −0.1, 2.1 fewer) than fire-origin stands. Foliage-gleaning species richness was not definitively lower in salvage-logged stands than in unlogged fire-origin stands (90% CI: −0.5, 2.7 fewer species), nor was tree-nesting species richness (90% CI: −0.8, 3.5 fewer species). Salvage-logged stands supported more ground-nesting species (1.4, 90% CI: 0.1, 2.8) and possibly more ground-foraging species (1.5, 90% CI: −0.3, 3.7) than unlogged fire-origin stands.

Changes through time in guild-level richness differed between clearcut and fire-origin stands, resulting in these metrics converging in the advanced age class (Figure 2). Advanced clearcut stands supported comparable species richness to fire-origin stands for each guild that characterized earlier differences between the two disturbance types, including foliage-gleaners (90% CI: −1.0, 2.9 more species), tree-nesters (90% CI: −4.3, 1.0 more species), cavity-nesters (90% CI: −1.0, 2.7 more species), and bole-foragers (90% CI: −1.4, 1.2 more species). In the advanced age class, the only guilds for which we found evidence of differences in species richness between disturbance types were ground-foraging and ground-nesting guilds (Figure 2b,c), with clearcut stands supporting greater species richness of both guilds than fire-origin stands (90% CI: 0.6, 4.5 more ground-foraging species; 90% CI: 1.0, 4.0 more ground-nesting species). We found no evidence that aerial insectivore or shrub-nesting species richness varied among disturbance types within the advanced age class or any other age classes (Figure 2).

Comparisons of early seral forest characteristics

The structure and composition of stands varied considerably across the chronosequence in our sample (Table 1). Woody vegetation cover developed more rapidly in fire-origin than in clearcut stands, with fire-origin stands having >3× as much cover in the intermediate age class ($\bar{x}$ = 108, SD = 48 vs. $\bar{x}$ = 31, SD = 20). Stands in the advanced age class had high total cover overall, but composition depended on disturbance type: Advanced clearcut stands were dominated by conifer cover ($\bar{x}$ = 67%, SD = 21% of total woody vegetation cover), whereas advanced fire-origin stands had abundant broadleaf vegetation cover, especially broadleaf trees ($\bar{x}$ = 46%, SD = 19% of total) and evergreen shrubs ($\bar{x}$ = 32%, SD = 16% of total). Snag basal area was high in fire-origin stands ($\bar{x}$ = 42, SD = 19 $\text{m}^2\,\text{ha}^{-1}$), though to a lesser degree in advanced fire-origin stands ($\bar{x}$ = 22, SD = 18 $\text{m}^2\,\text{ha}^{-1}$), yet was nearly absent from clearcut stands ($\bar{x}$ = 0.6, SD = 1.1 $\text{m}^2\,\text{ha}^{-1}$). Most salvage-logged stands contained some residual snag basal area ($\bar{x}$ = 5.1, SD = 3.8 $\text{m}^2\,\text{ha}^{-1}$), but snag basal area was the primary characteristic distinguishing salvage-logged stands from fire-origin stands of the same age class. Salvage-logged and fire-origin stands had relatively similar vegetation in the intermediate age class, though salvage-logged stands had slightly lower shrub cover (salvage: $\bar{x}$ = 47, SD = 30; fire: $\bar{x}$ = 74, SD = 37).

Species richness relationships with stand characteristics

Regenerating vegetation

Species richness responses were associated with regenerating vegetation, but these relationships depended on plant growth form (Figure 3a). Total species richness was more positively associated with conifer cover than broadleaf tree cover, with estimates from APCs corresponding to approximately nine more species (90% CI: 3.5, 14.7) across a 100 percentage-point increase in conifer cover compared to five fewer species (90% CI: −0.8, 9.8) for the same change in broadleaf tree cover, which was primarily comprised of sclerophyllous evergreen species.

Species richness relationships with regenerating vegetation varied among foraging and nesting guilds (Figure 3b). Foliage-gleaning species richness was positively associated with both conifer and deciduous shrub cover, resembling patterns in overall species richness, and had no clear relationship with evergreen shrubs or broadleaf trees (Figure 3b). We found clearer negative relationships with broadleaf cover for shrub-nesting species richness (APC for 10% change = −0.34, 90% CI: −0.47, −0.21) and ground-foraging species richness (APC = −0.58, 90% CI: −0.86, −0.32). Shrub- and tree-nesting guilds were the only groups to show distinct responses to deciduous shrub versus coniferous tree cover. Shrub-nesting species were positively associated with shrub cover, especially deciduous shrubs (APC = 0.33, 90% CI:

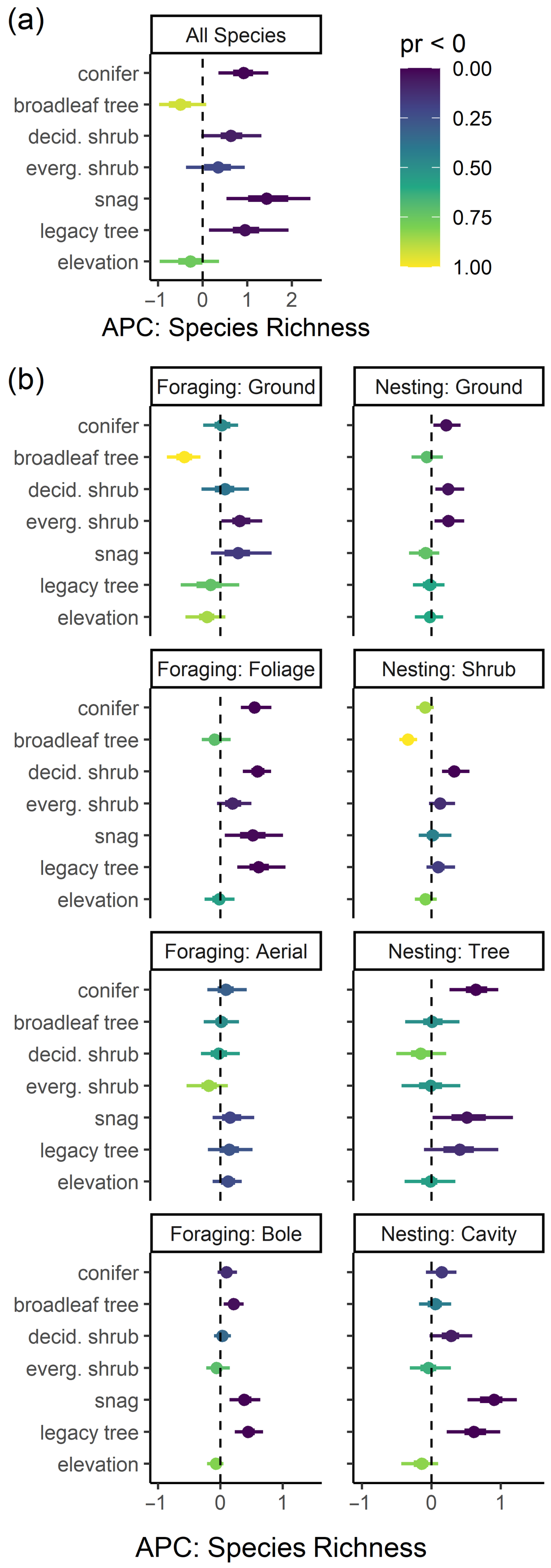

FIGURE 3 Average predictive comparisons (APCs) for (a) total or (b) guild-specific species richness across early seral structural and vegetation characteristics. Comparisons correspond to 10 percentage-point increases in conifer, broadleaf tree, deciduous shrub, or evergreen shrub cover, a 10 m^2 ha^{-1} increase in snag basal area, a 1 m^2 ha^{-1} increase in legacy tree (>50 cm diameter) basal area, or a 100-m increase in elevation. Points represent posterior medians, thick lines are 50% credible intervals, and thin lines are 90% credible intervals. Colors correspond to the proportion of posterior draws with estimates <0 (i.e., Bayesian *p*-values).

0.15, 0.55), but not conifer cover (APC = −0.09, 90% CI: −0.22, 0.03). Conversely, tree-nesting species responded positively to conifer cover (APC = 0.64, 90% CI: 0.26, 0.97) but not shrub cover (evergreen 90% CI: −0.43, 0.42; deciduous 90% CI: −0.51, 0.21). Notably, despite a foliage-gleaning species richness relationships to conifer cover and deciduous shrub cover being similar, species-specific responses to these two components of the vegetation were negatively correlated within the foliage-gleaning guild (*r* = −0.38, 90% CI: −0.65, −0.08; Appendix S4: Figures S2 and S3).

Structural legacies

Bird species richness was positively associated with structural legacies (Figure 3). The APC estimates for snags and large live trees (>50 cm dbh) corresponded to seven more species (90% CI: 2.7, 12.1) with a 50 m^2 ha^{-1} increase in snag basal area and five more species (90% CI: 0.7, 9.6) with a 5 m^2 ha^{-1} increase in large tree basal area. For the same change in snag basal area, guild-specific APC estimates corresponded to increases of nine cavity-nesting species (90% CI: 5.2, 12.3), four bole-foraging species (90% CI: 1.5, 6.4), five foliage-gleaning species (90% CI: 0.7, 10.0), and five tree-nesting species (90% CI: 0.2, 11.8). Guild-specific responses to large live trees were similar to those for snags. For a 5 m^2 ha^{-1} increase in large tree basal area, APC analysis estimated increases of two bole-foraging species (90% CI: 1.2, 3.4), three cavity-nesting species (90% CI: 1.1, 4.9), three foliage-gleaning species (90% CI: 1.3, 5.2), and weaker evidence for an increase of four tree-nesting species (90% CI: −1.1, 9.6).

Gamma diversity

Gamma diversity comparisons among disturbance-age categories resembled stand-scale richness patterns

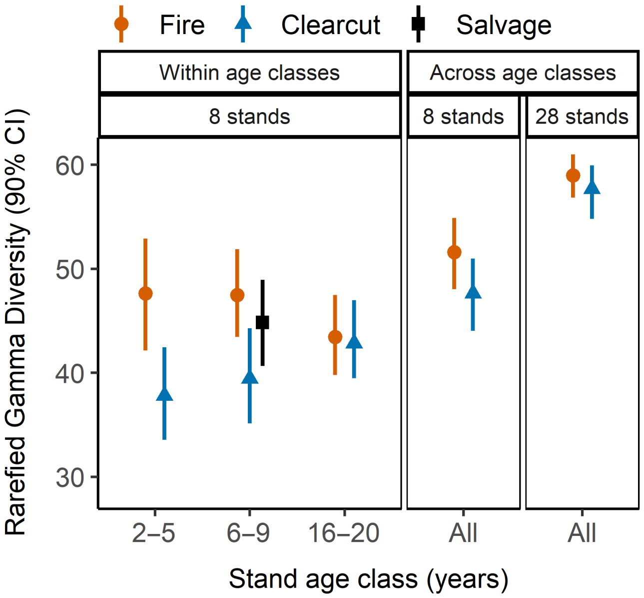

FIGURE 4 Comparisons of multi-stand richness (gamma diversity), rarefied to equal numbers of stands among groups. Gamma diversity represents the total number of species present across a collection of stands belonging to the same group and was calculated for categories of early seral conditions defined by stand age and disturbance type, and across all stand ages for a given disturbance type. Secondary panel headers indicate the number of stands used in rarefaction. Points and error bars represent posterior medians and 90% Bayesian credible intervals.

(Figure 4). However, when comparing gamma diversity calculated across all age classes for each disturbance type, there was only weak evidence for differences between fire-origin and clearcut stands (90% CI: −1.9, 5.2 more species across fire-origin stands).

Species composition

Raup–Crick dissimilarity analysis showed that young and intermediate fire-origin early seral forests supported distinct bird assemblages from clearcut stands, but that differences between disturbance types were reduced as stands aged (Figure 5). Within the young and intermediate age classes, pairs of clearcut and fire-origin stands were more dissimilar in composition than pairs of fire-origin stands alone (young: 0.26 greater, 90% CI: 0.14, 0.38; intermediate: 0.25 greater, 90% CI: 0.15, 0.38). Salvage-logged stands were more similar in composition to intermediate fire-origin stands, but still distinct (Figure 5). For the advanced age class, we found no evidence for differences in species composition between fire-origin and clearcut stands, relative to dissimilarity among advanced fire-origin stands (90% CI for contrast: −0.05, 0.14).

Raup–Crick dissimilarity analysis also revealed a strong gradient in bird species composition with stand age (Figure 5). For example, species composition in young fire-origin stands was more similar to young clearcut stands than to advanced fire-origin stands by 0.30 (90% CI: 0.12, 0.50). Species composition was more similar between fire-origin and clearcut stands in the advanced age class than between intermediate and advanced fire-origin stands (difference: 0.20, 90% CI: 0.05, 0.34) or advanced and young fire-origin stands (difference: 0.46, 90% CI: 0.28, 0.63).

Comparisons of dissimilarity in foliage-gleaning species composition generally resembled patterns for the entire community, but contrasts between disturbances were slightly weaker. The contrast in foliage-gleaning species composition between clearcut and fire-origin stands was strongest in the young age class, with average dissimilarity among pairs of young clearcut and fire-origin stands 0.18 higher (90% CI: 0.11, 0.26) than that among young fire-origin stands. Importantly, we did not find evidence for differences in foliage-gleaning species composition between advanced fire-origin and clearcut stands (90% CI for contrast: −0.02, 0.18). Similarly, differences in the composition of foliage-gleaning species between intermediate fire-origin and clearcut stands were weak (90% CI for contrast: 0.00, 0.13), especially considering the pronounced contrast in foliage-gleaning species richness between these categories.

DISCUSSION

Our study revealed that species composition in clearcut stands was distinct relative to fire-origin stands for at least the first 9 years after disturbance, including fewer species from nesting and foraging guilds associated with snags, large legacy trees, and deciduous shrubs. The differences in avian communities between post-fire and salvage-logged stands were similar but of lower magnitude than differences between post-fire and clearcut stands. Bird assemblages varied across both post-fire and post-harvest stand ages, highlighting the dynamic and ephemeral nature of early seral conditions (Harris & Betts, 2021; Kroll, Springford, et al., 2020; Raphael et al., 1987). Bird communities converged between disturbance types as stands aged, apparently driven by conifer regeneration in clearcut stands and snag loss in fire-origin stands. Our findings suggest that intensively managed forests emulate natural disturbance for birds that occupy developmentally advanced early seral forests, but that younger, recently burned forests are distinct for avian biodiversity relative to stands regenerating after clearcut harvests.

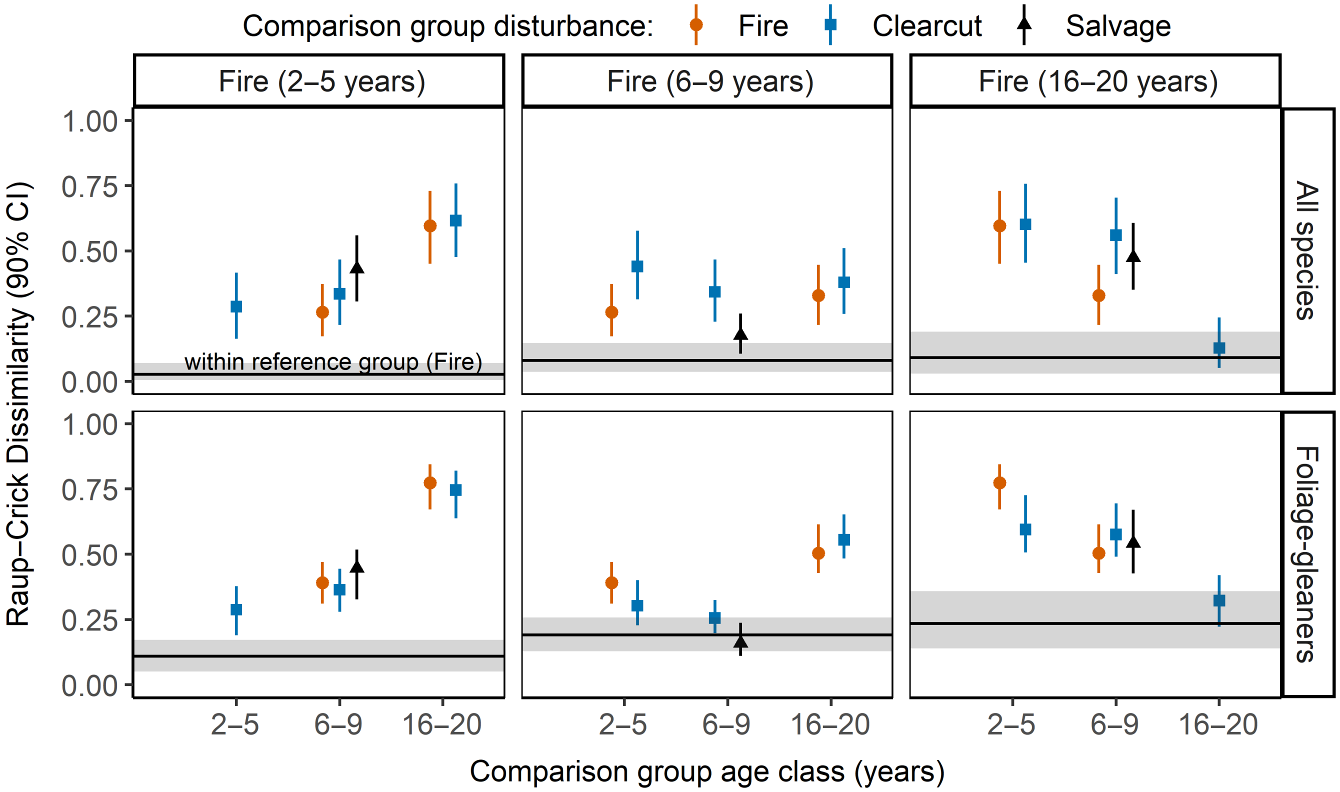

FIGURE 5 Comparisons of avian community composition among disturbance-age categories. Points and error bars are posterior medians and 90% credible intervals of the mean Raup–Crick dissimilarity among all pairs of stands in the "reference group" (indicated by panel header) and each other disturbance-age category ("comparison group"). Horizontal lines and shaded area indicate the posterior median and 90% credible interval of mean Raup–Crick dissimilarity among reference group stands.

Both cavity-nesting and bole-foraging species contributed to variation in composition between disturbance types and stand ages in stands experiencing fire, pointing to the importance of snags in our system. Our findings are consistent with studies from boreal mixedwood forests, where cavity-nesting species distinguished initial post-fire and post-harvest communities (Hobson & Schieck, 1999; Van Wilgenburg & Hobson, 2008). However, differences in cavity-nesting and bole-foraging species richness among disturbance types were smaller than might be expected from stand structure alone. This finding may reflect responses to snags that are non-linear or mediated by other factors. For example, cavity-nesting species often exhibit threshold responses to nest site availability (Berl et al., 2015) and snags in adjacent stands may complement low snag abundance within a stand (Dunning et al., 1992). Similarly, abundant snags surrounding fire-origin stands may reduce competition for these habitat elements, whereas scarce snags surrounding clearcut stands may increase demand (Kroll et al., 2012). The value of snags as nesting and foraging substrates also declines with decay over time (Barry et al., 2018; Boulanger & Sirois, 2007; Farris et al., 2002; Nappi et al., 2010), which supports our observation that bole-foraging species richness declined steadily with post-fire stand age. The bole-foraging guild was also associated with live legacy trees and regenerating tree cover, reflecting more generalist foraging preferences compared to post-fire snag specialists in some systems (Hutto, 1995). Indeed, the Hairy Woodpecker, the most common bole-foraging species detected in our study, frequently forages on small diameter Douglas-fir that dominated the vegetation in advanced clearcut stands (Ouellet, 1997).

In the stand-replacing disturbances we examined, large live trees contributed to elevated species richness in post-fire stands relative to harvested stands, even in small amounts. Large Douglas-fir—the dominant tree species of mature forests in our study area—is relatively fire resistant due to its thick bark (Dunn & Bailey, 2016); therefore, patches of stand-replacing fire commonly contain individual or groups of surviving trees (Franklin et al., 2002; fire refugia). In contrast, we observed few large legacy trees in the interior of clearcut stands, as tree retention requirements in clearcut forests in our area are typically met by leaving trees in riparian buffers or at stand edges (Linden & Roloff, 2013), which were not captured by our sampling design. Nonetheless, our results support findings from other studies that post-harvest bird species richness is positively related to the retention of live legacy trees (Hanle et al., 2020; Linden et al., 2012). Opportunities to retain large legacy trees may be limited by management history, especially in intensively managed landscapes. The value of large legacy trees for avian biodiversity we found is likely relevant to a range of forest management practices, and it underscores the importance of managing for forest resilience so that such legacies are maintained in the face of increasing fire extent and severity (Halofsky et al., 2020).

Reduced woody vegetation in young and intermediate clearcut stands compared to fire-origin stands corresponded to lower species richness for the foliage-gleaning guild and distinct community composition. These patterns support the prediction that intensive forest management delays the development of early seral habitats for foliage-gleaning birds. Differences in vegetation development between fire-origin and clearcut stands were likely caused by a combination of factors, including herbicide application as well as biological legacies and fire effects (Fites-Kaufman et al., 2006; Roberts, 2004). Our findings align with the results of a controlled experiment that studied a range of post-harvest herbicide application intensities in the Oregon Coast Range, which showed that foliage-gleaning species responded negatively to greater postharvest herbicide intensities initially (Betts et al., 2013), but that these differences attenuated by year 8 of stand growth (Kroll et al., 2017; Kroll, Springford, et al., 2020). Most foliage-gleaning species in our study peak in abundance as stands transition into closed-canopy forests (Harris & Betts, 2021), so a truncated period of occupancy due to delayed colonization may have population-level consequences for these species (Hayes et al., 2005). However, additional research is needed to connect stand-scale occupancy to landscape-scale populations. Evaluating whether the shorter duration of early seral bird habitat in clearcut stands is ameliorated by the high disturbance frequency of intensively managed landscapes will be particularly valuable.

The composition of regenerating vegetation helped explain some variability in bird communities. However, we found no evidence that the broadleaved vegetation characteristic of fire-origin stands corresponded to persistent differences in bird communities compared to clearcut stands. Fire-origin stands of advanced age were dominated primarily by broadleaf trees (e.g., tanoak and canyon live oak [*Quercus chrysolepis*]) and contained little deciduous shrub cover relative to younger fire-origin stands. Foliage-gleaning species richness was more strongly associated with deciduous shrub cover than evergreen shrub or broadleaf tree cover, a pattern that may reflect greater arthropod biomass in deciduous foliage (Campbell & Donato, 2014; Hagar et al., 2007; Hammond & Miller, 1998). High forage availability can promote species richness by allowing for smaller breeding season territories (Marshall & Cooper, 2004). Our finding that conifer cover and deciduous shrub cover showed similar relationships to foliage-gleaning species richness is harder to reconcile with this forage availability–richness mechanism. However, prior research focused on managed early seral forests in the Oregon Coast Range also found foliage-gleaning richness responses to conifer cover that matched—or exceeded—responses to any other cover type (Jones et al., 2012). One explanation may be the high live foliage biomass of conifers relative to broadleaf species in the western United States (McGinnis et al., 2010), which may allow them to support similar arthropod densities per unit land area even if they support fewer arthropods per unit biomass. Importantly, clearcut stands in our study were dominated by Douglas-fir, a native tree species that may support more native biodiversity elements than stands of non-native tree species, which are common in other temperate regions globally (Peralta et al., 2018).

We designed our study to cover most of the temporal breadth of the early seral period in clearcut stands (Harris & Betts, 2021), but the early seral period often lasts longer in post-fire stands. Extended post-fire establishment of Douglas-fir stands is likely where conifer regeneration is limited by seed availability and competition (Tepley et al., 2014) and this condition may have been common historically (Freund et al., 2014). A longer early seral period in fire-origin stands could mean that the convergence we observed in bird species richness and composition between older fire-origin and clearcut early seral stands is only temporary (Zimmerling et al., 2017). Sites to evaluate extended durations of early seral forest are limited in the Pacific Northwest, however, due to legacies of fire suppression and the susceptibility of early seral stands to reburning (Reilly et al., 2022; Weber et al., 2022). Nevertheless, permanent plots replicated over biophysical gradients (e.g., Laughlin et al., 2023) will provide opportunities for evaluating temporal dynamics of early seral forests. Quantifying the biodiversity response to fire- and harvest-generated stands over longer developmental periods, especially where multiple disturbances converge (e.g., drought, insect outbreaks, wildfire), remains an important area for continued study.

Our conclusions are based on community metrics derived from occupancy probabilities, which require less data to estimate than abundance and allowed us to incorporate uncommon species in our analyses while still accounting for imperfect detection. Although occupancy probabilities do not necessarily reflect patterns in abundance, nor habitat quality (Van Horne, 1983), widely distributed species also tend to occur at higher local densities (Gaston et al., 2000; Ten Caten et al., 2022; Venier & Fahrig, 1998), and density is usually correlated with demographic parameters reflecting habitat quality (Bock & Jones, 2007; Johnson, 2007). In some cases, anthropogenic disturbance can create an ecological trap by decoupling habitat quality from the cues used by breeding birds during settlement (Robertson & Hutto, 2007; Titeux et al., 2020). However, herbicide treatments in clearcut stands did not affect the demographic responses of the White-crowned Sparrow or House Wren in the Oregon Coast Range (Rivers et al., 2019, 2020), suggesting that these early seral forests do not serve as an ecological trap for the species studied to date.

Comparisons of gamma diversity among disturbance-age categories resembled stand-level species richness comparisons, suggesting that among-stand variability (i.e., beta diversity) did not vary substantially among categories in our study. This may have to do with our decision to focus on patches of stand-replacing fire within the mixed-severity fire regime of the Klamath-Siskiyou region, a decision motivated by the distinctive value of early seral forest structure for biodiversity (Swanson et al., 2014) and the prevalence of intensively managed stands in the Pacific Northwest. At landscape scales, mixed-severity fire regimes create a mosaic that often supports more diverse bird assemblages than high-severity fire alone (Stephens et al., 2015; Tingley et al., 2016). Future research should examine the degree to which combinations of management intensities at broad landscape scales (e.g., the TRIAD approach; Seymour & Hunter, 1992) emulate the diversity of forest birds supported by mixed-severity fire regimes.

Management implications

Our study has implications for forest structure mapping, post-fire management, and silvicultural practices. Many Pacific Northwest landscapes are currently or were recently deficient in complex early seral forests (Donato et al., 2020; Phalan et al., 2019). Our findings indicate that these more complex forms of early seral forests provide habitat for distinct and more species-rich bird assemblages than young, intensively managed stands. Landscape assessments of early seral forest extent, which can inform priorities for coarse-scale conservation planning and ecosystem restoration (e.g., DeMeo et al., 2018), should therefore differentiate intensively managed stands from other early seral forest conditions, especially for the youngest stand ages.

For managing post-fire environments, salvage logging may have only modest effects on bird communities in the medium term during which we sampled, a finding consistent with studies of short-term salvage logging effects in the Pacific Northwest (Fontaine, 2007; Giovanini et al., 2013). Importantly, the salvage-logged stands studied here were not treated with herbicides and most contained small amounts of standing dead wood (Table 1); applying principles of retention harvesting to salvage harvests can improve their value for birds (Hutto & Gallo, 2006; Saab et al., 2007).

Our findings suggest that managers of forestlands with broad objectives can integrate wood production and conservation goals by retaining elements characteristic of fire-origin early seral forest (e.g., snags, deciduous shrubs, legacy trees; Arnett et al., 2010; Hanle et al., 2020; Linden et al., 2012; Owens et al., 2014; Kroll, Springford, et al., 2020), an approach that has been applied in some public and private forests across the Pacific Northwest (Franklin & Donato, 2020). In intensively managed forests, productivity and safety considerations may limit opportunities to modify early seral stand management practices (Kroll, Johnston, et al., 2020), though these forests can contribute to biodiversity conservation by alleviating extraction pressure from other parts of the forest land base (Harris & Betts, 2023; Pirard et al., 2016). Elsewhere, fine-scale vegetation management, such as limiting herbicides to spot treatments around individual seedlings (Harrington, 2006), may allow managers to incorporate vegetative complexity into early seral stands while also managing forest growth. The development of uncrewed aerial spraying systems (Richardson, 2024) may also reduce safety concerns associated with retaining snags and legacy trees during harvest. However, policies requiring rapid reforestation with conifers (ODF, 2023) may constrain post-harvest management options; thus, reconsidering policy to allow greater latitude for biodiversity objectives may help non-industrial landowners provide habitat for early seral bird species.

AUTHOR CONTRIBUTIONS

Graham S. Frank: Methodology; investigation; data curation; formal analysis; writing—original draft; visualization; project administration. **Matthew G. Betts:** Conceptualization; methodology; funding acquisition; formal analysis; writing—review and editing. **Andrew J. Kroll:** Conceptualization; methodology; funding acquisition; formal analysis; writing—review and editing. **Jake Verschuyl:** Conceptualization; methodology; funding acquisition; formal analysis; writing—review and editing. **James W. Rivers:** Conceptualization; methodology; funding acquisition; writing—review and editing. **Mark E. Swanson:** Conceptualization; methodology; funding acquisition; writing—review and editing. **Meg A. Krawchuk:** Conceptualization; methodology; funding acquisition; project administration; supervision; resources; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

Andrew J. Kroll was employed by Weyerhaeuser Company, one of the landowners in this study, at the time the research was conducted. Neither the landowners nor the companies that indirectly funded this work influenced the study design, data analysis, interpretation, or decision to publish.

DATA AVAILABILITY STATEMENT

Data and code (Frank et al., 2025) are available in the Open Science Framework (OSF) at https://doi.org/10.17605/OSF.IO/FM8UV.

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SUPPORTING INFORMATION

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

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