Forest Ecology and Management 609 (2026) 123660

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Changes to vegetation structure and tree species composition drive bird species turnover following disturbance in southwestern United States mixed-conifer forest

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ARTICLE INFO

Keywords:
Indicator species
Bandelier National Monument
Grand Canyon National Park
Basal area
Shrub foliage cover
Snag

ABSTRACT

Mixed-conifer forests in the southwestern United States are vulnerable to climate-change-mediated disturbance, and provide habitat for many regionally declining birds. Drought stress and increased prevalence of high-severity wildfire can reshape the canopy structure, age distribution, and tree species composition of mixed-conifer forests, though there is little understanding of how these habitat features correlate with avian abundances. We fit Bayesian N-mixture models to eight years of monitoring data from Bandelier and Grand Canyon National Parks, including sites at Bandelier which experienced high-severity wildfire. We related breeding-season densities of 34 mixed-conifer forest bird species to 12 microhabitat variables to identify microhabitat associations. We also examined changes to bird and tree community composition over time. Tree and bird community composition significantly shifted following the high-severity wildfire, but smaller shifts also occurred after prescribed fire at Grand Canyon. There were no community-wide microhabitat associations with breeding-season density. Instead, declining canopy cover, subcanopy foliage cover, and foliage height diversity as well as increasing sapling density (perhaps a proxy for loss of mature trees) all affected distinct subsets of disturbance-sensitive birds. However, 62% of species were resilient to changes in canopy cover. Associations with tree species composition were also important, with declining local tree richness and subalpine tree (subalpine fir, quaking aspen, spruces) basal area, as well as increasing ponderosa pine dominance, each negatively associated with a subset of bird species. One third of the community responded negatively to increasing live tree basal area, however, suggesting the potential importance of disturbance in shaping breeding-season densities.

1. Introduction

The effects of climate change on natural systems have become increasingly pronounced in recent years (Ripple et al., 2023), with important effects on the health and resilience of global forests (Allen et al., 2010; Forzieri et al., 2022; Hartmann et al., 2022). Conifer forests of the western United States are among the most globally vulnerable to climate change effects (Wang et al., 2019), with montane conifer forests in Arizona and New Mexico predicted to be especially at risk (Loehman et al., 2018; Thorne et al., 2018; Williams et al., 2010). In the southwestern United States and northwestern Mexico, mixed-conifer forest typically occurs at elevations above 2400 m and consists of a variable assemblage of pines (*Pinus*), spruces (*Picea*), firs (*Abies*), Douglas fir (*Pseudotsuga menziesii*), and deciduous aspen (*Populus tremuloides*) stands depending on elevation and microclimate. These forests are particularly vulnerable because the Southwest region has been undergoing a megadrought since 2000 (Cayan et al., 2010; Overpeck and Udall, 2020; Williams et al., 2022), a climate pattern that is likely caused by, and will continue as a result of, a warming climate (Todd et al., 2025). Climate effects are exacerbated in geographically isolated sky island mountain ranges of the Southwest, where trees may be especially vulnerable due to small population sizes and reduced genetic variability (Love et al., 2023). Mixed-conifer forest trees are also often growing near the southern limit of their range in the Southwest, where physiological stresses from climate are more pronounced (Anderegg and HilleRisLambers, 2016; Ayres et al., 2024; Camarero et al., 2021). Taken together, these factors suggest a potential for rapid, climate-induced disturbances to reshape the structure and composition of southwestern

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https://doi.org/10.1016/j.foreco.2026.123660
Received 17 December 2025; Received in revised form 25 February 2026; Accepted 26 February 2026

forests.

Drought may be the most widespread of these climate change disturbances, and it can lead to changes in the structure, composition, and age distribution of trees (Clark et al., 2016). Severe drought, often paired with high temperatures and bark beetle outbreaks, is elevating mortality rates of trees in mixed-conifer forests (Allen et al., 2015; Ganey and Vojta, 2011; Park Williams et al., 2013; van Mantgem et al., 2009). This has led to instances of sudden mass mortality (Hartmann et al., 2022) and long-term population declines for many western United States tree species (Stanke et al., 2021), which changes forest structure by reducing mature tree density and canopy cover. Drought mortality also disproportionately affects Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) over more xeric-adapted species such as ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*; Mathys et al., 2017; Oswald et al., 2016; Stanke et al., 2021). This uneven mortality leads to shifts in tree species composition towards more xeric-adapted tree species and a homogenization of forest composition (Batllori et al., 2020; Loehman et al., 2018; Rodman et al., 2022; Seidl and Turner, 2022). Finally, drought shifts the age distribution of trees in mixed-conifer forests. Drought not only more frequently kills older, large-diameter trees (Bennett et al., 2015; Ganey and Vojta, 2011; Stanke et al., 2021), but also creates conditions in which sapling trees cannot establish (Crockett and Hurteau, 2024; Davis et al., 2019; Ganey and Vojta, 2011), leading to a lack of young trees in the understory and potential regeneration failure.

In addition to drought, the severity and extent of wildfires in southwestern montane mixed-conifer forests has greatly increased in recent years (Cunningham et al., 2024; Singleton et al., 2019), likely due to the hotter, drier climate (Harvey, 2016; Mueller et al., 2020). While fire is a natural disturbance in Southwestern mixed-conifer forest (Bock and Block, 2005), historic fire suppression starting in the nineteenth century has led to increased densities of many non-fire-adapted conifer species such as white and Douglas fir (Fulé et al., 2004; Strahan et al., 2016; Jaquette et al., 2021), which, when combined with hot, dry conditions, is yielding more frequent, higher-severity fires (Wasserman and Mueller, 2023). Because changing climatic and structural conditions in post-fire landscapes often prevent the re-establishment of conifers (Harvey et al., 2016; Rodman et al., 2020; Stevens-Rumann et al., 2018; Stevens-Rumann and Morgan, 2019), wildfire can lead to conversion to non-forested ecosystems (Coop et al., 2020; Guiterman et al., 2022), quaking aspen forest (Andrus et al., 2021), or oak shrublands (Guiterman et al., 2018). Therefore, post-fire mixed-conifer landscapes may be dominated by shrubby or deciduous vegetation and lacking in young conifers, while canopy cover may be permanently reduced or absent. Even when mature conifers remain in the post-fire landscape, high-severity wildfire disproportionately kills subalpine tree species, leading to a more homogenous and xeric-adapted species composition after fire (Cassell et al., 2019; Travis Belote et al., 2015). Delayed mortality after wildfire (Busby et al., 2024) may also continue to reduce tree density, leading to more open, park-like stands. Therefore, both tree die-off and wildfire can profoundly reshape the structure, species composition, and age distribution of mixed-conifer forests in the Southwest.

These structural and compositional changes may carry important consequences for wildlife that inhabit Southwestern mixed-conifer forests. Over fifty species of breeding birds, for example, inhabit this ecosystem in Arizona and New Mexico (Jones et al., 2024), many of which are confined to mixed-conifer forest in the region. Western forest birds are a strongly declining group in the United States (-29.5% population trend since 1970; Rosenberg et al., 2019), and mixed-conifer bird species in particular have shown declines in California's Sierra Nevada (Furnas, 2020; Roberts et al., 2019), and on the Colorado Plateau (Jones et al., 2024). While many mixed-conifer bird species are widespread, they are undergoing local population declines in the Southwest and are priority species for regional conservation: 26 mixed-conifer forest species are listed as Species of Greatest Conservation Need by the state of Arizona (Arizona Game and Fish Department, 2022), and 21 are listed in New Mexico (New Mexico Department of Game and Fish, 2025). Data from eBird indicate that mixed-conifer specialists as diverse as Dusky Grouse (*Dendragapus obscurus*; −37.2%), Williamson's Sapsucker (*Sphyrapicus thyroideus*; −33.5%), Ruby-crowned Kinglet (*Corthylio calendula*; −21.1%), Brown Creeper (*Certhia americana*; −33.5%), Pine Siskin (*Spinus pinus*; −20.6%), and Dark-eyed Junco (*Junco hyemalis*; −25.7%) have all undergone large-scale breeding-season declines in Arizona from 2012 to 2022 (Fink et al., 2025). While the drivers underpinning bird population declines are many and varied (Lees et al., 2022), forest habitat degradation through indirect effects of climate change may be an important mechanism in the Southwest mixed-conifer forest. Forest birds are known to select for specific structural features (Culbert et al., 2013; Sweeney et al., 2025; Vogeler et al., 2014) and plant species compositions (Adams and Matthews, 2019; Holmes and Robinson, 1981; Zillig et al., 2023) on their breeding territories, yet these habitat features can shift dramatically following disturbance stemming from drought and wildfire.

While the effects of wildfire and die-offs on montane conifer forests are well documented, it is less clear how these changes affect habitat suitability for birds. Many mixed-conifer forest birds preferentially forage in particular tree species (Airola and Barrett, 1985; Franzreb, 1978) and some prefer aspen-dominated forest over conifers (or vice versa; Swift et al., 2017). Similarly, a subset of bird species in mixed-conifer forest prefers late-successional seral stages (Sallabanks et al., 2006), taller canopy heights (Franzreb, 1983), and greater canopy cover (White et al., 2013a, 2013b). Specific functional groups, such as bark foragers, foliage gleaners, and aerial foragers, may also benefit from greater canopy cover (White et al., 2013b). Species and functional groups associated with closed-canopy, late-successional forests and subalpine tree species should be negatively impacted by tree die-off. However, many mixed-conifer birds in the Sierra Nevada are relatively insensitive to canopy cover effects, at least above a minimum threshold (Verner and Larson, 1989; White et al., 2013a), and a majority of species may show higher densities in more open canopy structures (Beedy, 1981), including those produced by mechanical thinning (Kalies et al., 2010; Latif et al., 2022; Siegel and DeSante, 2003; White et al., 2013b). Responses to wildfire are expected to be similarly heterogenous, with a small subset of species, such as the American Three-toed Woodpecker (*Picoides dorsalis*), being dependent upon high-severity wildfire and another subset showing preferences for unburned forest (Bock and Block, 2005; Hutto et al., 2020; Kotliar et al., 2002). These diverging preferences lead to species turnover along the fire severity gradient (Scott and Korb, 2024), though a plurality of species is often more abundant in medium- and high-severity burn patches in the Sierra Nevada (Ray et al., 2025; Roberts et al., 2021; Taillie et al., 2018), suggesting a general preference for disturbance. Species responses to fire are complex, however, and depend on specific combinations of time since fire and fire severity (Hutto and Patterson, 2016; Taillie et al., 2018), as well as heterogeneity in fire severity (pyrodiversity; Tingley et al., 2016). Specific structural and floristic features of the post-fire landscape, such as the density of snags and shrubs, are often tied to species presence (White et al., 2016).

Avian habitat associations are well documented for Sierra Nevada mixed-conifer forests, but generally lacking for similar habitat in the Southwest. In this study, we combined long-term monitoring point-count data from two southwestern protected areas on the Colorado Plateau with microhabitat-level field measurements of vegetation structure and floristic composition. We measured the response of breeding-season bird density to natural variation in habitat features expected to shift with tree die-offs and wildfire (Table 1), and took advantage of a natural experiment which occurred when the high-severity Las Conchas Fire burned through long-term monitoring sites in 2011, introducing additional microhabitat heterogeneity. We modelled avian breeding-season densities during two years of pre-fire

Table 1
Microhabitat covariates included in an N-mixture model of breeding-season mixed-conifer forest bird density. A short description of how each variable was measured or derived from measured values is provided, along with predictions about changes to these variables with high-severity wildfire and drought-induced tree die-off.

Variable Name	Habitat Feature Category	Definition	Predicted Changes with Wildfire and Die-off
Canopy closure (%)	Vegetation structure	Percentage canopy closure calculated using a convex spherical densitometer, averaged across four subplots	Wildfire and tree die-off should result in reduced canopy closure from dead trees and reduced tree growth
Sapling density (stems ha^{-1})	Vegetation structure	Density of 2.5–10 cm DBH saplings, measured in 5-m-radius subplots	Drought and post-wildfire conditions should result in reduced sapling recruitment
Standing snag basal area (m^2 ha^{-1})	Vegetation structure	Basal area of snags (all species) calculated using an angle gauge with 10 basal area factor	Snag basal area should increase following tree die-off and wildfire
Live tree basal area (m^2 ha^{-1})	Vegetation structure	Basal area of live trees (all species) calculated using an angle gauge with 10 basal area factor	Live tree basal area should decline after tree death due to loss of large-diameter trees, though remaining trees may grow larger after release from competition
Canopy height class	Vegetation structure	Canopy height class (0.5,1,2,5,10,20) averaged across four subplots	Canopy height will decrease following die-off and wildfire as large emergent trees die, though remaining post fire trees may grow taller over time
Subcanopy foliage cover class	Vegetation structure	Braun-Blanquet subcanopy foliar cover class averaged across four subplots	Subcanopy trees should be negatively impacted by wildfire, but may benefit from the die-off of mature canopy trees
Shrub foliar cover class	Vegetation structure	Braun-Blanquet shrub foliar cover class averaged across four subplots	Shrubs will be negatively impacted by wildfire, but may benefit from more open canopies after tree die-offs
Foliage height diversity (*H'*)	Vegetation structure	Shannon's diversity index calculated on the proportion of presence of five vegetation strata across four subplots	Foliage height diversity will decline as overall foliage declines after wildfire or die-offs
Tree richness	Floristic composition	Total tree species detected during plotless basal area sampling with 10 BAF angle gauge	Tree richness will decline after wildfire and drought-related die-off, as more susceptible subalpine tree species are lost
Proportion of deciduous tree basal area	Floristic composition	Proportion of total live tree basal area belonging to deciduous species (aspen and oak)	Aspen are generally more drought and fire sensitive, but can quickly resprout from the root stock to colonize burned areas
Mesic-xeric tree species composition	Floristic composition	PCA axis derived from an ordination of species-specific tree basal areas at each count station in each survey year. Negative values indicate more mesic, subalpine tree compositions	Tree species compositions should shift away from mesic-adapted subalpine tree species following wildfire and drought, and compositions should be more homogenized (closer to zero) following these disturbances
Ponderosa pine dominance	Floristic composition	PCA axis derived from an ordination of species-specific tree basal areas at each count station in each survey year. Negative values indicate a greater dominance of ponderosa pine	Ponderosa pine dominance should increase following both fire and drought because this is a fire-adapted and drought tolerant plant which is more likely to survive and recolonize following disturbance

and three years of post-fire data at Bandelier National Monument while comparing with three years of mixed-conifer data at Grand Canyon National Park that experienced a prescribed fire application. Our study objectives were to: (1) identify breeding-season habitat associations between mixed-conifer forest bird species and structural and floristic composition variables that are expected to change with drought-induced tree die-off and wildfire in the Southwest (for specific predictions, see Table 1), (2) examine whether bird and tree assemblages at both parks changed over the monitoring period, and (3) determine which bird species' densities showed increases and decreases at Bandelier after the high-severity Las Conchas Fire. We predicted that (1) bird species would respond to both structural and floristic elements of microhabitat, but that species responses would vary idiosyncratically based on unique aspects of their natural history. Second, we (2) predicted that bird and tree species composition would shift at both parks due to effects of the wildfire at Bandelier and both prescribed fire and potential tree die-offs effects at Grand Canyon. Finally, if bird communities respond similarly to those in the Sierra Nevada, we expected that (3) a majority of species would show resilience to declining canopy cover, and a preference for moderate disturbance, but that a subset of species would be tied to closed-canopy, old-growth forest.

2. Methods

2.1. Study sites and sampling design

Long-term bird and habitat monitoring data were collected at Bandelier National Monument (Bandelier) and Grand Canyon National Park (Grand Canyon), located on the Colorado Plateau near the Four Corners region of the Southwestern USA (Fig. 1). The data were collected as part of the Southern Colorado Plateau Inventory and Monitoring Network's (SCPN) long-term vital signs monitoring program (Holmes et al., 2015). Bird and habitat data were collected concurrently at each site, though the two parks were sampled in different years. The full dataset spans an eleven-year (2008–2018) time period, but the initial survey year varied by park, with monitoring starting in 2008 at Bandelier and in 2011 at Grand Canyon. The total number of survey years for each park was therefore variable, with five at Bandelier (2008, 2009, 2012, 2015, 2018) and three at Grand Canyon (2011, 2014, 2017). Neither park was surveyed in 2010, 2013, or 2016. Monitoring locations at both parks were habitat specific, selected to sample mixed-conifer forest at the time the sample design was created. The spatial sampling frame was

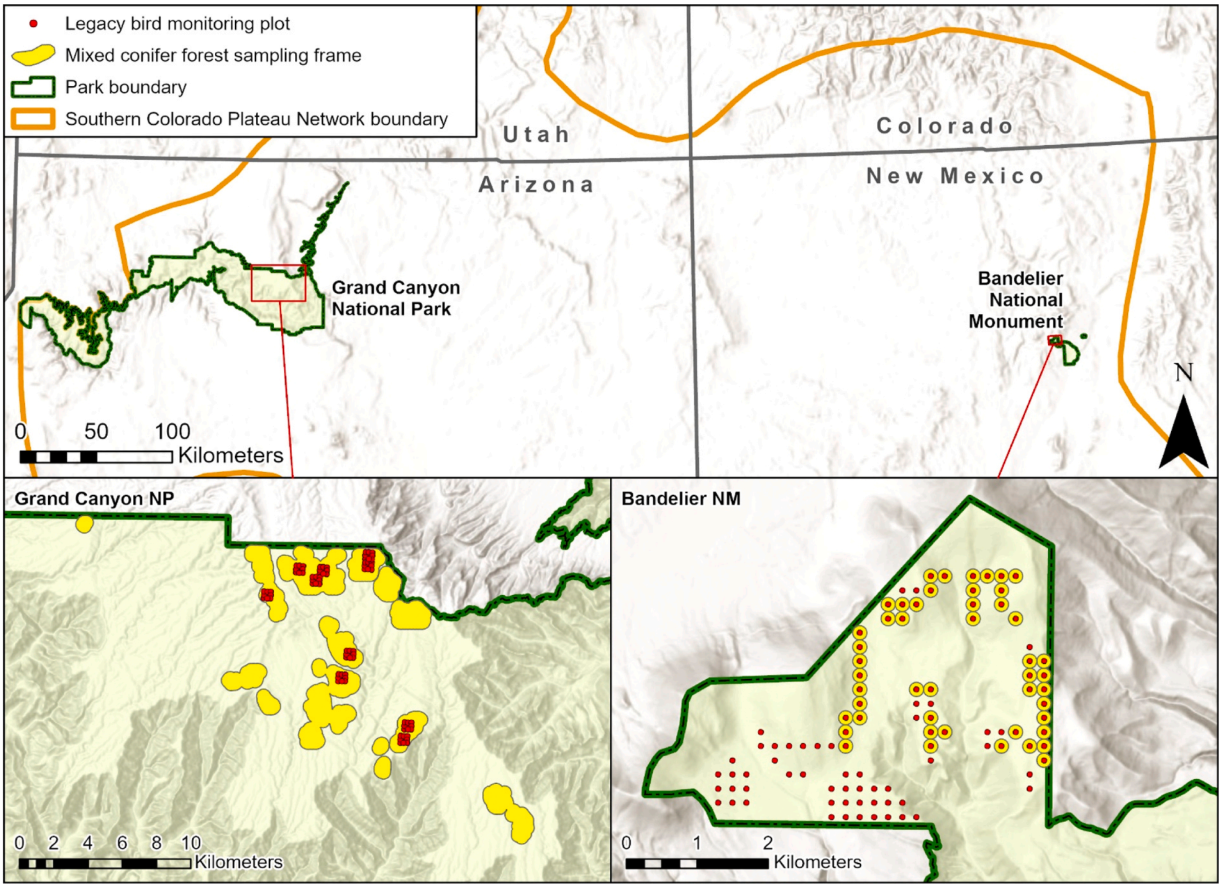

Fig. 1. Locations of point-count stations in two Colorado Plateau parks. Sampling locations at Grand Canyon were arrayed in 3 × 3 regular grids, while the sampling locations at Bandelier were arrayed in a regular grid across all areas of appropriate mixed-conifer habitat. Count stations highlighted in yellow represent the reduced sampling frame after the 2011 Las Conchas fire at Bandelier, and were the only survey locations sampled in 2012 and 2015.

developed for each park by intersecting areas with specific soil and plant community classifications and elevation values (see Holmes et al., 2015, Appendix A for more detail). Field validation was used to ensure that habitat categorizations were accurate.

The spatial sampling regime differed between the two parks. For Bandelier, a 200-m regular grid of point-count stations was overlaid on the sampling frame. At Grand Canyon, the sampling frame was much larger, and random center points of regular, 200-m 3 × 3 grids of count stations were placed within the sampling frame using the Generalized Random-Tessellation Stratified algorithm (GRTS; Stevens Jr. and Olsen, 2004). Sampling locations were further restricted to sites > 100 m away from non-focal habitats, roads, and other human infrastructure; those with < 30% slopes; those which had not recently experienced moderate or high-severity wildfires in 2008; and those which required less than two hours to access for field personnel. At Bandelier, the total number of point-count stations monitored varied from year to year. An initial 100 count stations were surveyed in 2008 and 2009, but following the Las Conchas Fire in 2011, 52 count stations with high or moderate vegetation burn severity were decommissioned and not surveyed in 2012 and 2015 (Figure A.1, Appendix A). However, all 100 original point-count stations were resurveyed in 2018, providing a direct comparison of bird densities and microhabitat conditions at Bandelier after the wildfire. All sites at Grand Canyon were surveyed in all years, though 23 point-count stations were treated with prescribed fire in 2012 (Thompson and Range fires, Figure A.2). In both parks we considered the sample replicate for both bird and microhabitat data to be the point-count station.

At both parks, monitoring locations were located within intact natural landscapes with little pre-fire disturbance. The study sites at Bandelier were located in the Jemez Mountains, at elevations of ~2700–3000 m.a.s.l. Pre-fire forests were characterized by high densities of a xeric-adapted assemblage of white fir (*A. concolor*), Douglas fir (*P. menziesii*), ponderosa pine (*P. ponderosa*), limber pine (*P. flexilis*), and quaking aspen (*P. tremuloides*), with the sparse understory shrub component consisting of common juniper (*Juniperus communis*) and Woods' rose (*Rosa woodsii*) and a strong understory herbaceous layer. The study sites at Grand Canyon were located on the Kaibab Plateau at elevations from 2550 to 2750 m.a.s.l. The plant community composition at this park was more variable, with cold-wet tree assemblages in mesic microhabitats, particularly steep drainages, dominated by Engelmann's (*P. engelmannii*) and blue (*P. pungens*) spruce, corkbark subalpine fir (*A. lasiocarpa* var. *arizonica*), and quaking aspen alongside more xeric microhabitats with warm-dry mixed-conifer trees including white fir, Douglas fir, and ponderosa pine. These varying compositions align closely with the described warm-dry to cold-wet continuum of mixed-conifer forest composition in the Southwest (Romme et al., 2009, Table V-1). The understory primarily consisted of common juniper and bare ground, with occasional Fendler's ceanothus (*Ceanothus fendleri*).

2.2. Point count surveys

Breeding-season densities of the mixed-conifer forest bird community were sampled using eight-minute, unlimited-radius point counts incorporating distance and time removal sampling, as outlined in Holmes et al. (2015); Standard Operating Procedure #4). Each count station was surveyed two or three times in each survey year, though we only retained the first two surveys for analyses. The first round of surveys occurred in late May to early June, while the second round of surveys occurred in mid-to-late June; subsequent surveys were separated by three or more weeks. Surveys were conducted by single, trained observers, and took place from a half hour before to four hours after local sunrise. All individual birds or flocks seen or heard were identified to species where possible, and we later updated the taxonomy to follow the 2025 American Ornithological Society checklist (Chesser et al., 2025). For each detection, surveyors recorded the minute of first detection (1−8), and estimated the horizontal distance to the nearest meter to the detected individual with the help of a laser rangefinder. Individuals which were flying over the canopy and judged in the field to not be behaving in a way that would suggest a link to the habitat below were recorded as 'flyover' detections; we removed all flyover detections from the dataset prior to analysis. Surveyors also collected environmental data likely to influence bird detectability during the count: wind speed (Beaufort scale), cloud cover (recorded to the nearest 10%), and background noise level (excluding noise related to bird vocalizations, 0–3 scale).

2.3. Microhabitat variables

We selected twelve local habitat covariates, representing both floristic composition and structural features of mixed-conifer forest habitat, for inclusion in models of bird habitat associations (Table 1). These habitat features were characteristics that we predicted would change with wildfire and drought-related tree die-off, and which should be related to breeding-season habitat suitability for birds (see Table 1 for predicted changes to these habitat features). Habitat variables were collected once per survey year at each point-count station, and sampling methods were consistent across years and parks (Holmes et al., 2015; Standard Operating Procedure #5). Habitat covariates were collected at three different scales: angle count sampling of tree basal area from each count station, and within circular subplots with radius 11.3 and 5 m. Each count station contained four subplots, sampled at two scales (see above), with one centered on the count station itself and three other subplots located 30 m from this point at 0°, 120°, and 240° bearings. The measurements from these four subplots therefore capture an area within ∼40 m of each count station; because count stations were separated by 200 m, we consider these values to be relatively independent from each other. Two habitat variables were collected at the smallest, 5-m-subplot scale: canopy closure and sapling density. Canopy closure was measured using a convex spherical densiometer (Lemmon, 1956) at elbow level. Readings were taken in each of the cardinal directions from the center point of each of the four subplots. We averaged these values to calculate a canopy closure value for each count station. Sapling density was measured as the total number of trees with a diameter at breast height (DBH) of 2.5 to < 10 cm within each subplot. We summed sapling abundances across subplots and divided by the total area (in ha) to obtain a sapling density.

Four habitat variables were measured at the intermediate 11.3-m-radius subplot scale: foliage height diversity, canopy height class, subcanopy foliage cover, and shrub foliage cover. Foliage height diversity is a measure of the vertical complexity of foliage strata, and was derived from presence-absence data of five foliage layers collected at each of the four subplots: dwarf shrubs, shrubs, subcanopy, canopy, and canopy emergent. A foliage stratum was considered present in a subplot if it occurred within the 11.3-m-radius cylinder centered on the subplot. Dwarf shrubs were defined as shrubs less than 0.5 m tall when mature, while the subcanopy was defined as a stratum of trees below the canopy stratum. For each station-year combination, we determined the proportion of subplots at which each foliage layer was present, and then calculated the Shannon's diversity index (H') of these proportions. Increasing values of this variable indicate forest structures with foliage present in more strata at more subplots. Canopy height was estimated in the field (in m) for each subplot using a clinometer and then binned into height class categories defined by the maximum value of canopy height: 5, 10, 20, 30, and 40. We averaged the height class categories of each of the four subplots to obtain a measure of canopy height for each count station. The total percentage of foliar cover for the subcanopy and shrub strata were estimated for each subplot using a modified Braun-Blanquet scale (1–7 values; Wikum and Shanholtzer, 1978). Cover categories correspond to < 1, 1–5, 5–10, 10–25, 25–50, 50–75, and 75–100 % of the area within each subplot. We averaged the values across the four subplots to obtain an average for each count station.

The approximate basal areas of both living and standing dead trees were calculated from the center point of each of the four subplots at each count station. Surveyors tallied all trees larger than the aperture of a 10 basal area factor (BAF) angle gauge held at 63.5 cm from the eye in a 360° arc. These measurements of basal area were collected for all standing dead trees (snags), regardless of species, and for each individual species of living tree. Tree counts were converted to basal area in m^2 ha^{-1}, and we then summed the tree and snag basal areas for each subplot to obtain a total live tree and snag basal area for each count station. We derived the proportion of live tree basal area from deciduous species by dividing the basal area of the three deciduous species, Rocky Mountain maple (*Acer glabrum*), Gambel's oak (*Quercus gambelii*), and quaking aspen, by the total tree basal area for each count station. To characterize the tree species composition at each count station, we also calculated species-specific basal areas for each count station and ordinated these species-by-site basal areas using Principal Components Analysis (PCA; Jolliffe and Cadima, 2016) to reduce the dimensionality of these data. Finally, we summed the number of unique tree species detected at each subplot during basal area sampling as a measure of the species richness of mature trees for each point-count station.

2.4. Measuring changes to bird and tree community composition

To examine changes to bird and tree communities over the monitoring period, we visualized community composition using Non-metric Multidimensional Scaling (NMDS; Kruskal, 1964) with Bray-Curtis dissimilarities. Analyses were conducted in R version 4.3.3 (R Core Team, 2025) using the *metaMDS* function of the *vegan* package (Oksanen et al., 2025). We ordinated both bird and tree communities at Bandelier and Grand Canyon separately; at Bandelier we only ordinated community data from the three years in which the whole sampling frame was surveyed (2008, 2009, 2018). To avoid circularity in analyses, and to include species that we could not model in the *N*-mixture model framework (see below), we used raw bird abundance values from field surveys. To partially account for imperfect detectability, we selected the higher abundance value of the two survey replicates for each bird species at each site in each survey year. The sample replicate for all compositional analyses was therefore the site-year combination. Prior to analysis, we excluded vagrant and passage migrant species, unidentified individuals, and species groupings poorly sampled by point-count surveys (nocturnal species, raptors). For trees, we used the site-by-year basal area of each detected tree species for the ordination. We selected the optimal dimensionality (k) for the ordination based on examination of scree and Shepard plots, and evaluated model fit using the stress statistic. In cases where $k > 2$, we only plotted the scores for the first two axes for ease of interpretation. We plotted 95% ellipses for each survey year in each park to show changes in species composition. We also tested for overall and pairwise differences in composition across years at each park using an ANOSIM statistical test (Clarke, 1993) implemented with the *anosim* function in the *vegan* package; bird abundance data were Hellinger transformed prior to each test, and communities with no species (only present in the tree dataset) were removed prior to analysis. Finally, we tested for species representative of each survey year using indicator species analysis (Dufrêne and Legendre, 1997) using the *multipatt* function in the *indicspecies* package (Cáceres et al., 2025). We did not include tests of indicators for multi-year groupings, and did not test for indicator species when there was no significant difference in community composition with year.

2.5. Modelling breeding-season microhabitat associations

We used single-species models to estimate breeding-season avian densities at each count station in each survey year. We adapted a hierarchical *N*-mixture model developed by Amundson et al. (2014) which was implemented in a Bayesian framework. This model includes two detectability sub-models using both time removal data (availability component of detectability) and distance sampling (perceptibility; Farnsworth et al., 2002) in addition to the N-mixture process sub-model of abundance (Royle, 2004). In this approach, estimation of detectability is split into the availability (p_a) component, or probability that an individual was present and available for detection by vocalizing or otherwise signaling its presence, and perceptibility (p_d) component, the probability that an available individual was perceived by the observer, thereby allowing for estimation of true abundance of individuals during each survey k (N_k). We estimated true abundance N_k as a Poisson random variable with mean λ_k (k in 1, …, K surveys, where K $= \sum$ surveys/station/year) which was related to the survey-specific count (y_k) as

$$y_k \sim \text{Binomial}(n_k, p_{d[k]})$$

$$n_k \sim \text{Binomial}(N_k, p_{a[k]})$$

where n_k denotes the number of individuals available for detection.

We modelled survey-specific differences in the p_a and p_d subcomponents of detectability following Amundson et al. (2014). Briefly, the model assumes that individuals were available with probability a during each minute of an eight-minute survey period. Therefore, the probability that an individual is first available during interval j of survey k is given by $\pi_{jk} = a_k(1 - a_k)^{j-1}$. The corresponding conditional probability is given by $\pi^c_{jk} = \pi_{jk}/p_{a[k]}$, where $p_{a[k]} = \sum_j \pi_{jk}$ represents the probability an individual is available during at least one interval during survey k. We modelled species' availability as logit(1-a_k) $=$ b$_0$ $+$ b$_1$minute of day$_k$ $+$ b$_2$ordinal date$_k$ $+$ b$_3$ordinal date^2_k $+$ b$_4$cloud cover$_k$. This sub-model included fixed effects of minute of day, ordinal date (linear and quadratic terms), and cloud cover (binned into categories of $<$ or $\geq$ 50%), covariates predicted to influence avian singing rates. Perceptibility was modelled using horizontal detection distance estimates binned into three, four, or five distance categories (whichever best approximated a half-normal distribution), and we considered the probability that an individual was detected in distance bin $b = 1, \ldots, B$ of survey k as $p_{d[k]} = \sum b \quad \pi d[bk]$, with corresponding conditional probability $\pi^c_{d[bk]} = \pi d[bk]/\sum b\pi d[bk]$. We modelled detection distances using a half-normal distribution, $\pi_{d[bk]} = \exp(-r_b^2/2\sigma_k^2)(2r_b\delta_b/r_{\max}^2)$, where r_b is the midpoint distance of bin b, δ_b is the width of bin b, σ_k shapes the decline in detection probability with distance, and r_{max} is the species-specific maximum detection distance after truncation. We omitted either 5% or 10% of the most distant observations for each species to exclude sparse data from the tail of the distribution of detection distances and to make sure that detection interval and detection-distance bin were not significantly correlated. Where necessary, we truncated further distant detections until detection interval and detection-distance bin were statistically independent. We tested for independence of these variables using analysis of variance (ANOVA), using a conservative alpha value (0.10) where possible, or a more standard alpha value (0.05) when necessary to avoid excessive data loss. We modelled heterogeneity in perceptibility as $\log(\sigma_k) = \log(\sigma_0)$ $+$ b$_1$noise$_k$ $+$ b$_{2k[\text{surveyor}]}$; this formulation includes a fixed effect of environmental noise during the survey and a random effect of surveyor.

We modelled mean breeding-season abundance for each species as $\log(\lambda_k)$ $=$ b$_{0k[\text{cluster[station]}]}$ $+$ b$_{1k[\text{year}]}$ $+$ b$_2$canopy closure$_k$ $+$ b$_3$sapling density$_k$ $+$ b$_4$snag basal area$_k$ $+$ b$_5$live tree basal area$_k$ $+$ b$_6$proportion of deciduous tree basal area$_k$ $+$ b$_7$tree species richness$_k$ $+$ b$_8$canopy height class class$_k$ $+$ b$_9$shrub foliar cover$_k$ $+$ b$_{10}$subcanopy foliar cover$_k$ $+$ b$_{11}$foliage height diversity$_k$ $+$ b$_{12}$mesic-xeric tree composition$_k$ $+$ b$_{13}$ponderosa pine dominance$_k$. This formulation includes a random intercept of point-count station nested within cluster to account for pseudoreplication from repeat surveys and spatial autocorrelation of clustered monitoring sites, as well as a random intercept of year. We did not include park effects in the model because only one park was surveyed in each year, and the random survey year effect therefore captures information about both year and park effects. We are able to report approximate park effects by stacking the posterior distributions of the random year effects for all survey years at each park. For eight species with low detections at Grand Canyon, we made two modifications to the model structure to facilitate model convergence; in all cases models for these species did not converge with the standard formulation. For five species which were absent or nearly absent ($\leq$ 6 detections) at Grand Canyon, we modelled N_k using a pseudo-zero-inflated-Poisson approach where

$$N_k \sim \text{Poisson}(\lambda_k \times \text{Park}_k)$$

and Park represents a survey-specific vector with values of zero for replicates at Grand Canyon and of one for replicates at Bandelier. This formulation therefore sets the estimated abundance for these species to zero for all surveys conducted at Grand Canyon. For another three species with small numbers of detections at Grand Canyon, we collapsed the three Grand Canyon levels of the random intercept of year (2011, 2014, and 2017) into a common Grand Canyon effect. These model formulations were identical to the original formulation in all other respects.

2.6. Parameter estimation

We fit our models in JAGS version 4.3.1 (Plummer, 2003) using the *jagsUI* package (Kellner and Meredith, 2024) in R version 4.3.3 (R Core Team, 2025). We column standardized (i.e., mean = 0, standard deviation = 1) all quantitative covariates prior to analysis and only included complete cases in the analysis. The Kendall's rank correlation was < 0.5 and the Pearson's correlation was ≤ 0.61 for all pairs of covariates; the variance inflation factor (VIF) for all covariates was < 2.5 (mean $= 1.79$, range $= 1.26$–2.30), indicating little multicollinearity in the dataset. The fixed effect covariates on all sub-models were modelled using 'uninformative' priors drawn from a normal distribution with a mean of 0 and precision of 0.01. The prior for the random count station within cluster intercept was also a normal distribution with a mean given by α_0, representing the baseline mean across all clusters, plus each station's cluster effect, and precision τ_{station}, with the prior for the cluster effects being normally distributed with a mean of 0 and precision τ_{cluster}. We also specified an 'uninformative' normal distribution with a mean of 0 and precision of 0.01 for a prior for α_0. Similarly, we assumed the random effects for year were normally distributed with a mean of 0 and precision τ_{year}. We modelled the precision (τ) of all random effects using a gamma distribution with a shape and rate of 0.1. We ran models with three chains of 110,000 iterations each and a burn-in of 50,000 iterations. The thin rate of each chain was 30, resulting in a joint posterior distribution of 6000 samples. We assessed convergence of the chains by visually inspecting the Markov chain Monte Carlo summaries and examining the Gelman-Rubin statistic (or R-hat value; Gelman and Rubin, 1992). We considered chains converged when R-hat < 1.2 (Kéry and Schaub, 2012). We measured goodness-of-fit of the availability and perceptibility sub-models using posterior predictive checks in the form of Bayesian P-values which were derived from the joint posterior distributions, a method suggested by MacKenzie et al. (2017) and implemented in Jones et al. (2024). Bayesian P-values between 0.6 and 0.4 indicate a good model fit.

We report the mean and 90% Bayesian credible interval (BCI) for parameters of interest; this uncertainty interval is thought to be more stable than the 95% credible interval (Kruschke, 2015). We considered a covariate relationship supported when the 90% BCI did not overlap zero. To calculate effect sizes for the full community, we stacked the joint posterior distributions across all species and calculated the mean and 90% BCI of this distribution. Because we measured habitat variables at the 40-m-radius scale, we consider covariate relationships to be representative of habitat associations within the breeding territory (second- or third-order selection; Johnson, 1980). We calculated the breeding-season density (birds ha^{-1}) for each species during each survey by dividing the estimated true abundance (N_k) by the species-specific

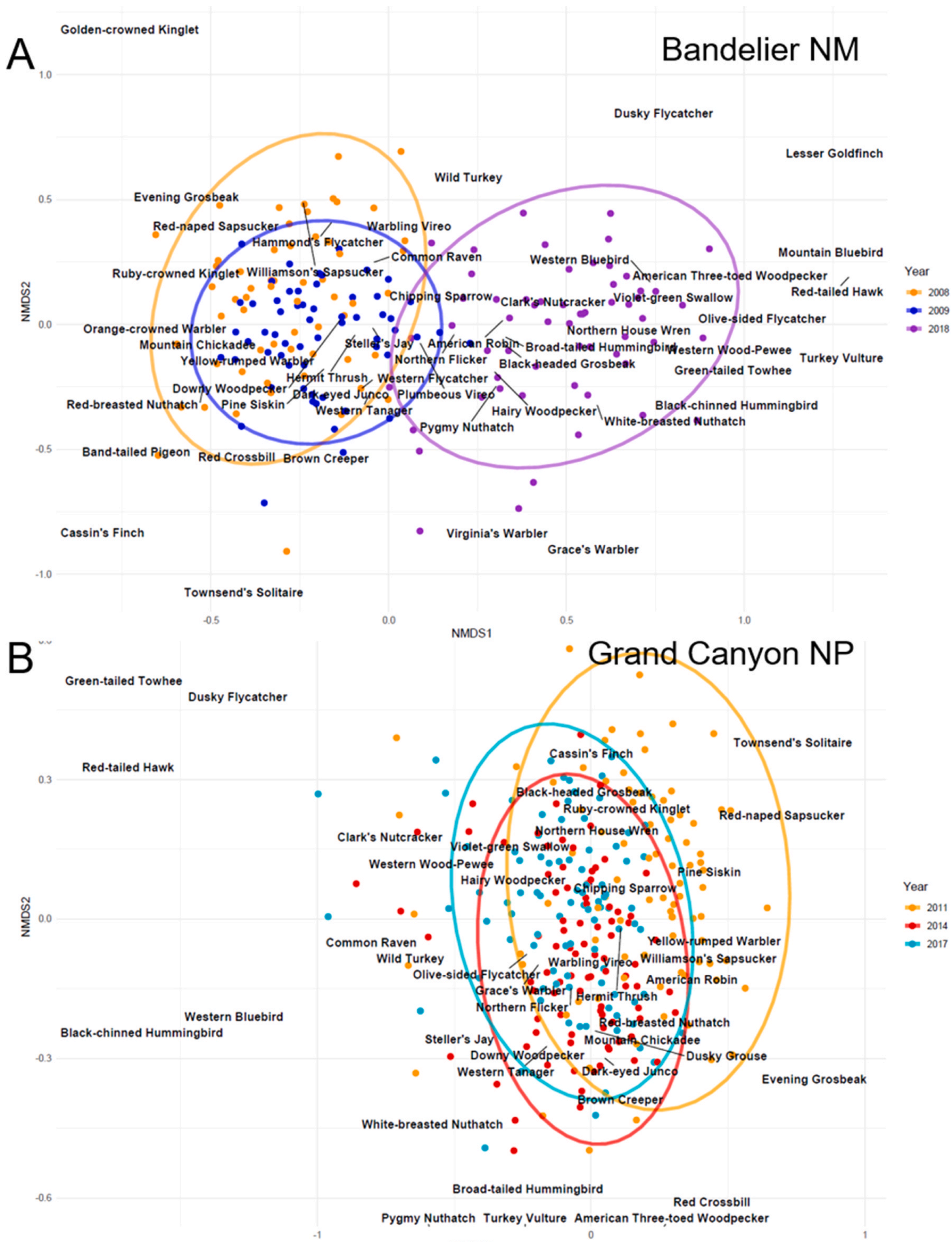

Fig. 2. NMDS ordinations of bird community composition at two parks on the Colorado Plateau. Figures show all complete survey years at Bandelier (A) and Grand Canyon (B). Ordinations use Hellinger-transformed raw abundance data with Bray-Curtis dissimilarities, and the higher of the two counts from replicate surveys selected for each species in each site-year. The 95% ellipses of community composition for each year are plotted to show differences in composition. Points represent site-year bird assemblages, while species scores are plotted in black. At Bandelier, data from 2008 and 2009 represent pre-fire assemblages, while the 2018 data represents seven-year post-fire assemblages.

sampled area (a circle with radius r_{max}, the maximum detection distance after data truncation). We calculated a mean breeding season density for each park and park-year combination as mean($N_{k[park]}$)/ [πr^2_{max}/10, 000]. We also calculated overall density across both parks as a weighted average of the proportion of the total sampling area of inference within each park (150.6 ha in Bandelier, 5363.0 ha in Grand Canyon). Changes to density at Bandelier pre- and post-fire were calculated by stacking the posterior distributions for parkwide density in 2008 and 2009 and comparing this pre-fire distribution to the 2018 density estimates. We did not include density estimates from 2012 or 2015 because surveys in these years included only a subset of the monitored sites. We considered changes to density supported when overlap between the pre- (i.e., 2008 and 2009) and post-fire (2018) distributions was < 10%. Because birds are a mobile taxon, and the home ranges of some individuals will only partially overlap the surveyed area at each site, our point count data violate the closure assumption of *N*-mixture models. We therefore consider our estimates of density to represent the number of individuals using each sampling area rather than the number permanently present at

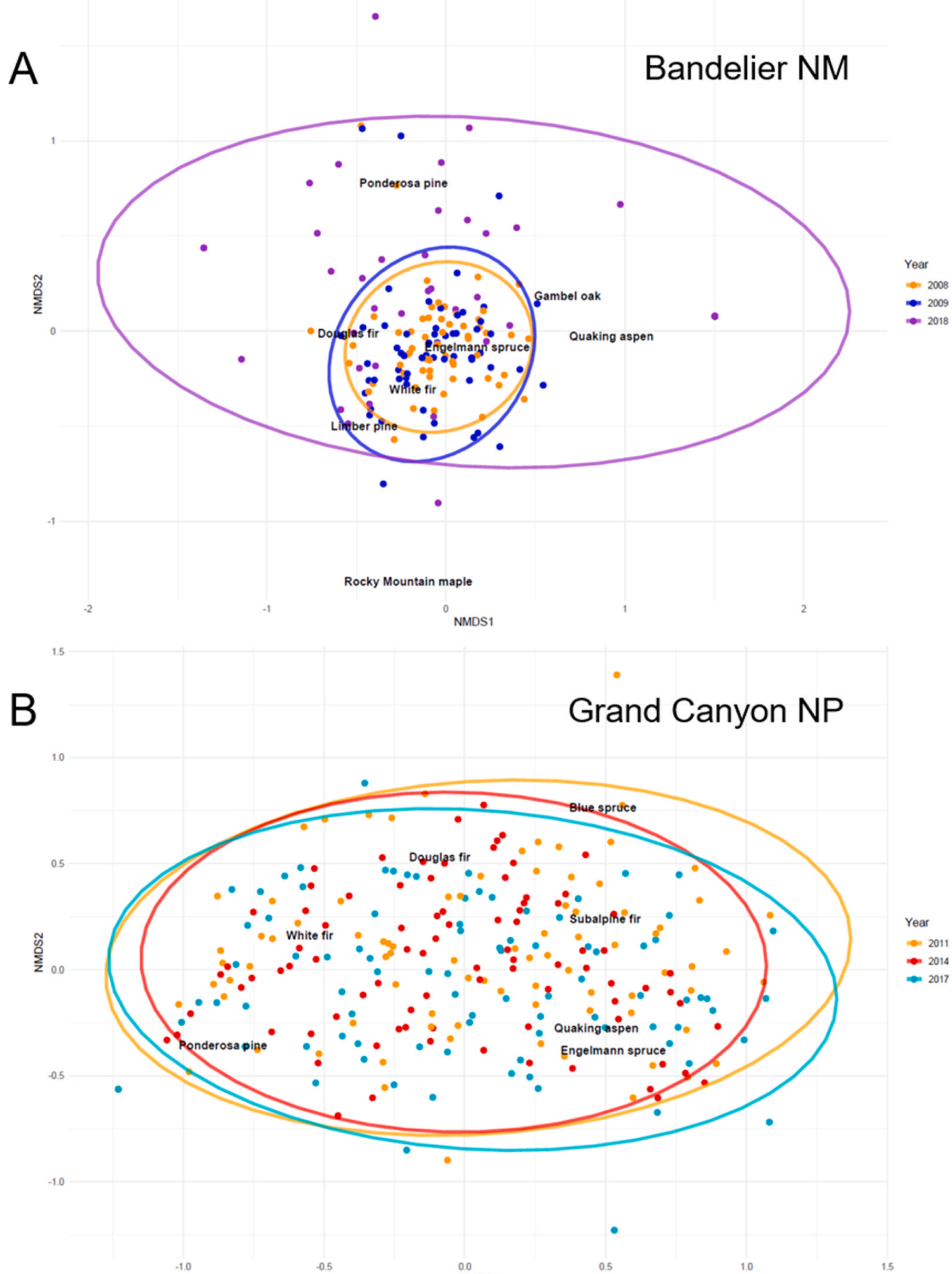

Fig. 3. NMDS ordination of tree species composition across survey years in two parks on the Colorado Plateau. Figures show all complete survey years at Bandelier (A) and Grand Canyon (B). Ordinations use raw biomass data (basal area of each species, in $m^2\ ha^{-1}$) with Bray-Curtis dissimilarities. The 95% ellipses of community composition for each year are plotted to show differences in composition. Points represent site-year compositions, while species scores are plotted in black. At Bandelier, data from 2008 and 2009 represent pre-fire assemblages, while the 2018 data represents seven-year post-fire assemblages.

the site (Latif et al., 2016). To visualize patterns of species responses to all covariates included in the abundance models, we ordinated the mean effect size of the twelve fixed covariates on abundance for each species using PCA.

3. Results

3.1. Survey data and changes to bird and tree community composition

Point-count and microhabitat data were collected during eight years of the 2008–2018 timeseries. After excluding third replicate surveys and cases of incomplete data, our dataset consisted of 1332 surveys conducted by 16 observers at 190 count stations (*N* of count stations = 100 at Bandelier, 90 at Grand Canyon) representing 666 unique site-year combinations. Surveys yielded 19,111 bird detections, of which 19,046 could be identified to species; 71 unique bird species were detected across all sites and years (Table A.1). During 2664 plotless tree surveys, surveyors counted 7216 individual live trees belonging to 10 species (Table A.2); no trees were counted using the angle gauge during 149 plotless surveys. We included 52 bird species (denoted with asterisks in Table A.1) and 10 tree species in the NMDS ordinations of community composition. Based on examination of scree plots, we selected 3 dimensions for NMDS ordinations of birds at both Bandelier (stress = 0.20, non-metric $R^2 = 0.96$, linear $R^2 = 0.76$) and Grand Canyon (stress = 0.22, non-metric $R^2 = 0.95$, linear $R^2 = 0.72$). There was incomplete overlap in the 95% ellipses of bird community composition across survey years at both parks (Fig. 2), though overlap was higher at Grand Canyon (Fig. 2b). We found significant changes to bird community composition over the timeseries using ANOSIM at both Bandelier (R = 0.48, $p < 0.001$) and Grand Canyon (R = 0.10, $p < 0.001$). All pairwise compositional differences were significant ($p < 0.001$ in all cases), but ANOSIM statistics were much higher for differences between pre- and post-fire years at Bandelier ($R \approx 0.65$) than before and after the prescribed fire at Grand Canyon ($R \leq 0.15$). We found statistically significant indicator species for all survey years at both parks, though there were larger numbers of indicator species at Bandelier (33 species, Table A.3) than at Grand Canyon (18 species, Table A.4).

We selected 2 dimensions for the NMDS ordination of the tree communities at both Bandelier (stress = 0.16, non-metric $R^2 = 0.97$, linear $R^2 = 0.92$) and Grand Canyon (stress = 0.19, non-metric $R^2 = 0.97$, linear $R^2 = 0.84$). Based on the 95% ellipses, the pre-fire tree composition at Bandelier represented a subset of the post-fire community in 2018 (Fig. 3a), while tree composition at Grand Canyon was essentially unchanged (Fig. 3b). We found a significant difference in tree composition across survey years at Bandelier (R = 0.20, $p < 0.001$), and pairwise differences were also significant, though the ANOSIM statistic was near-zero for the 2008–2009 comparison (R = 0.03, $p = 0.01$; 2008–2018, R = 0.32, $p < 0.001$; 2009–2018, R = 0.30, $p < 0.001$). We did not find a significant effect of survey year on tree community composition at Grand Canyon (R = 0.01, $p = 0.06$). We found four indicator tree species at Bandelier (Table A.5), all for the year 2008, with three having indicator statistics near 0.7.

3.2. Ordination of tree composition

After examining a scree plot and the axis Eigenvalues, we retained and plotted the first two PCA axes of tree species composition (Figure S3), representing 33.4% of the total variance (Table A.6). The first axis had an Eigenvalue of 2.00 and explained 20.03% of the variance. Basal area of the subalpine trees, Engelmann spruce (-0.75) and subalpine fir (-0.70), were strongly negatively loaded on this axis while the montane trees, Douglas fir (0.52) and white fir (0.46), were positively loaded (Table A.7). We interpreted this axis as a measure of mesic-adapted (subalpine) versus xeric-adapted (montane) tree composition. The second axis had an Eigenvalue of 1.34 and explained 13.4% of the total variance. This axis had a strong negative loading of ponderosa pine (-0.66) and positive loadings of white fir (0.61), quaking aspen (0.52), and Douglas fir (0.41). We interpreted this axis as a measure of ponderosa pine dominance, as the positively loaded tree species co-occur with ponderosa pine at more mesic sites, particularly ones that have been fire suppressed. Tree species contributions for each axis are provided in Table A.8.

3.3. Breeding-season bird density over time

We modeled breeding-season densities and habitat associations for 34 bird species for which models converged (bolded in Table A.1). R-hat values were ≈ 1 for all parameters of interest, though some random effects of site or transect had R-hat values between 1.1 and 1.2. We fit the standard model for 26 species (76%), the pseudo-ZIP formulation for 5 species, and the model version with a single ('year') effect for Grand Canyon for 3 species (Table A.9). We report distance sampling sub-model parameterizations in Table A.9. On average, we truncated 8.80 $\pm$ 6.10% (mean $\pm$ SD), and the maximum detection distance (mean $\pm$ SD = 99.00 $\pm$ 40.86 m; range = 41–250 m) and effective area surveyed (mean $\pm$ SD = 3.59 $\pm$ 3.49 ha; range = 0.53–19.60 ha) varied considerably across species. We found a high estimated availability on average (0.69 $\pm$ 0.18; mean $\pm$ SD of mean estimates of p_a; Table A.10, Figure A.4), but perceptibility was generally much lower (0.45 $\pm$ 0.13; mean $\pm$ SD of mean estimates of p_d). Goodness of fit, as measured by Bayesian P-values, was high for both sub-models (Table A.10, Figure A.4). All Bayesian P-values were between 0.2 and 0.8, and 30 of 34 P-values (88%) were between 0.4 and 0.6 for both p_a and p_d, indicating good model fit. We found supported responses to each of the five fixed-effect covariates fit on the detectability sub-models, though effect sizes and number of supported effects varied across covariates (Table A.11, Figure A.5).

The mean of species-specific breeding-season densities across parks and years was less than one bird per hectare (0.73 $\pm$ 1.35 birds ha^{-1}; mean $\pm$ SD of mean densities across both parks; Table A.12), though we found sometimes large differences in density across parks (Table A.12). The species with the highest densities across parks were Yellow-rumped Warbler (*Setophaga coronata*; 7.34 birds ha^{-1}), Violet-green Swallow (*Tachycineta thalassina*; 2.60 birds ha^{-1}), Northern House Wren (*Troglodytes aedon*; 2.32 birds ha^{-1}), and Western Warbling-Vireo (*Vireo swainsoni*; 1.68 birds ha^{-1}). We found numerous differences in parkwide breeding-season densities at Bandelier before (2008 and 2009) and after (2018) the 2011 Las Conchas fire (Table A.13, Figure A.6). Overall, we found that 17 species showed no supported change in density (i.e., overlap of the pre- and post-fire posterior distributions for mean density was > 10%), 11 species showed supported local population declines, and 6 species showed supported local population increases (Table A.13). The average pre- to post-fire difference in density across the community was -0.13 ± 1.03 birds ha^{-1} (mean $\pm$ SD), while the average difference for species with locally declining populations was -0.85 ± 0.84 birds ha^{-1} (mean $\pm$ SD; Table A.13). On average, these changes represented 74.20% $\pm$ 18.24% (mean $\pm$ SD) decreases for declining species. The species with the fastest declining breeding-season populations were Red-breasted Nuthatch (*Sitta canadensis*; −94.62%), Evening Grosbeak (*Coccothraustes vespertinus*; −94.41%), Red-naped Sapsucker (*Sphyrapicus nuchalis*; −92.51%), Ruby-crowned Kinglet (-81.79%), and Mountain Chickadee (*Poecile gambeli*; −79.28%). Conversely, the modelled species with the greatest population increases were Green-tailed Towhee (*Pipilo chlorurus*; 2069.03%), Western Bluebird (*Sialia mexicana*; 464.23%), Northern House Wren (319.23%), Western Wood-Pewee (*Contopus sordidulus*; 274.23%), and White-breasted Nuthatch (*Sitta carolinensis*; 241.22%).

3.4. Effects of floristic composition and vegetation structure on breeding-season density

We found supported responses of breeding-season bird density to all twelve microhabitat covariates included in the abundance sub-model, and all modelled bird species showed supported responses to at least one covariate. Models supported associations between bird densities and both structural (Table A.14) and floristic composition (Table A.15) variables, though effect sizes were generally small (i.e., < 1 and > -1). Despite the high variability in canopy cover in the dataset, we found that a majority of bird species were resilient to changes in this variable (Table A.14, Fig. 4a). There were 7 positive and 6 negative supported responses to increasing canopy cover, though the mean effect size was near zero (-0.01 $\pm$ 0.31; mean $\pm$ SD of mean beta values across species). Non-linear effects were most pronounced at canopy cover values below 35% or above 80% for the species with supported negative and positive responses, respectively (Figures A.7a, A.8). There were fewer supported responses to canopy height (6 negative, 3 positive; -0.02 ± 0.17, mean $\pm$ SD of mean species responses) and sub-canopy foliage cover (3 positive, 3 negative; 0.004 ± 0.19, mean $\pm$ SD of mean species responses). We found a general trend of increasing densities with greater foliage height diversity, but only three supported positive species responses (2 near-supported positive responses, 0 supported negative responses; 0.05 ± 0.18, mean $\pm$ SD of mean species responses). We found more numerous supported responses to elements of lower vegetation strata and tree basal area (Table A.14, Fig. 4b). There was a community trend of lower densities at sites with greater sapling densities (10 negative, 1 positive responses; -0.12 ± 0.23, mean $\pm$ SD of mean species responses), though the effect of this variable on density was largely linear (Figure A.7d). Shrub foliage cover had little effect on densities (4 negative, 3 positive responses; -0.02 ± 0.15, mean $\pm$ SD of mean species responses). We also found community-wide trends of negative responses to increasing snag basal area (6 negative, 2 positive responses; -0.08 ± 0.18, mean $\pm$ SD of mean species responses) and increasing live tree basal area (12 negative, 0 positive responses; -0.12 ± 0.18, mean $\pm$ SD of mean species responses). A subset of these species

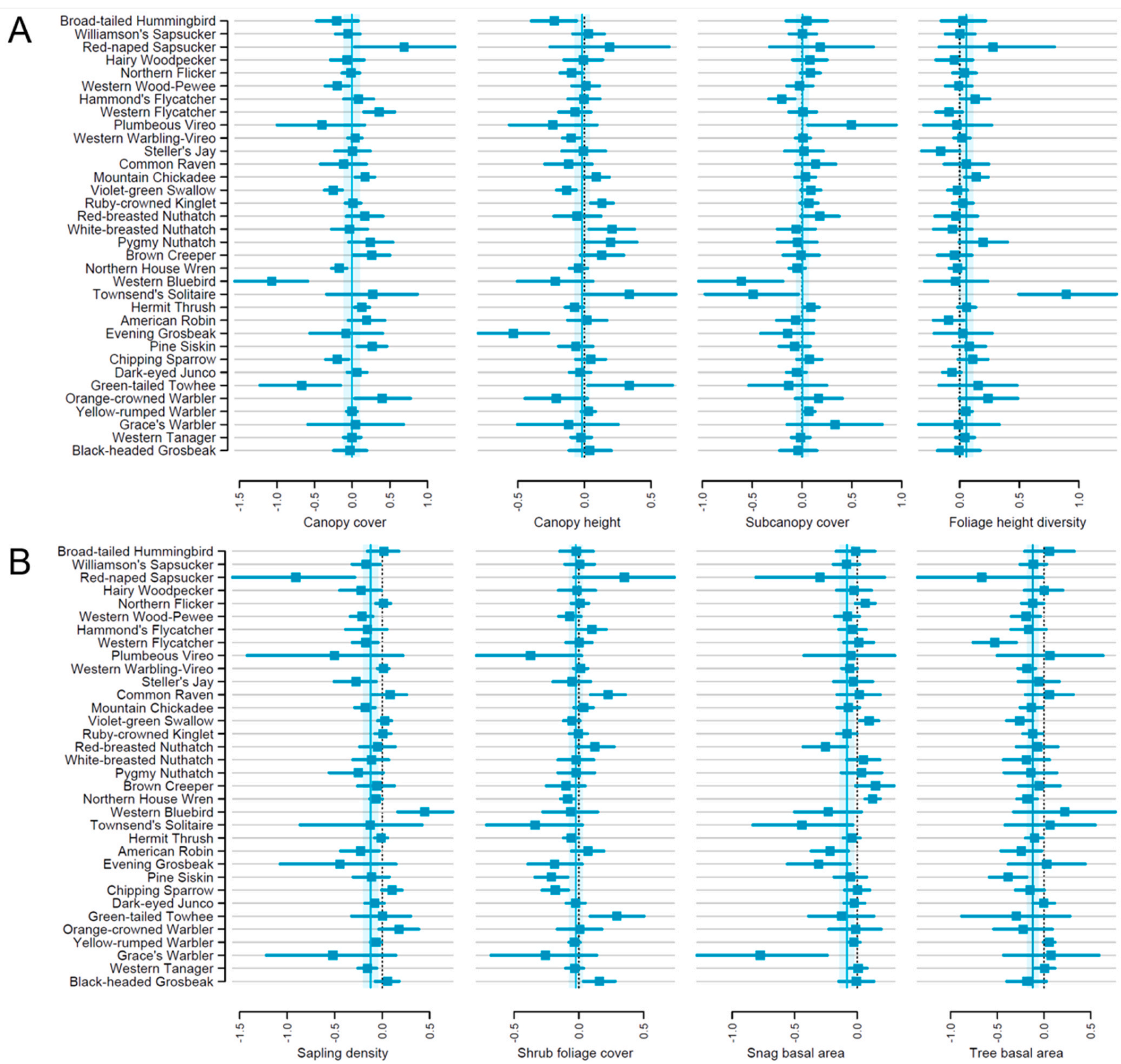

Fig. 4. Forest plot of mean effect sizes of eight structural microhabitat covariates on breeding-season abundance of 34 mixed-conifer forest birds. The mean and 90% Bayesian credible interval are plotted for each species, while vertical lines and shaded areas represent the mean and standard deviation of the mean effect sizes across the full community. Species are listed in taxonomic order following the American Ornithological Society's 2025 checklist.

responded non-linearly to live tree basal area values below 20 m^2/ha (Figure A.7c).

We also found supported responses to tree species composition (Table A.15, Fig. 5). A subset of species showed higher abundances associated with more mesic (6 species) or xeric (4 species) tree species compositions, though there was no community-wide pattern of association (-0.03 ± 0.30, mean ± SD of mean species responses; negative values indicate more mesic tree composition). Species responses were frequently non-linear at high values of both mesic and xeric tree assemblages (Figures A.9b, A.10). We similarly found associations with greater ponderosa pine dominance (3 supported responses) versus white fir and quaking aspen dominance (5 supported responses) in more xeric microhabitats, again without any community-wide trend (-0.03 ± 0.19, mean ± SD of mean species responses). Independent of tree species identity, we generally found higher bird densities at microsites with higher tree species richness (10 positive, 0 negative supported responses; 0.06 ± 0.21, mean ± SD of mean species responses). The subset of responsive species showed non-linearly increasing densities at ≥ 5 tree species at a site (Figure A.9a). Finally, there was a general trend of declining abundances with increasing deciduous biomass (-0.04 ± 0.11, mean ± SD of mean species responses), though there were few supported responses to this variable (4 positive, 3 negative).

3.5. Patterns of bird species responses across covariates

We retained and plotted the first two axes of ordinated bird responses to habitat variables (Fig. 6), representing 43.6% of the total variance (Table A.16). The first PC axis had an Eigenvalue of 2.92 and explained 24.3% of the total variance. This axis had high positive loadings for associations with canopy cover (0.60), tree richness (0.67), and subcanopy foliage cover (0.48), and high negative loadings for associations with xeric tree species composition (-0.77), proportion of deciduous basal area (-0.71), and sapling density (-0.68; Table A.17). We interpreted this axis as a measure of species association with disturbance, with more positive species scores indicating an association with old-growth, undisturbed mixed-conifer forest. The second PC axis had an Eigenvalue of 2.31 and explained 19.3% of the variance. This axis had high positive loadings for associations with canopy height (0.75), canopy cover (0.55), and foliage height diversity (0.51) and high negative loadings for associations with live tree basal area (-0.65) and sapling density (-0.43). We considered this axis a measure of a species' associations with foliage height diversity, with positive values indicating associations with more vertically complex vegetation strata. Variable contributions are provided in Table A.18.

4. Discussion

Our results suggest that forest habitat degradation through indirect effects of climate change (i.e., drought-related tree die-off, wildfire) is a plausible mechanism for declining populations of mixed-conifer forest birds in the Southwest. Vegetation structure, tree species composition, and bird community composition shifted over time following high-severity wildfire at Bandelier, but changes to microhabitat structure and bird community composition also occurred following prescribed fire at Grand Canyon. Bird species exhibited both local population increases and decreases during this time at both parks, suggesting that species turnover was driving changes to bird community composition. Moreover, local bird breeding-season densities showed supported associations with microhabitat variables predicted to shift with wildfire and drought-related die-off, including measures of both vegetation structure and floristic composition. There were no community-wide drivers of breeding-season density, with no more than a third of the community showing supported responses to any one covariate. Instead, a diversity of structural changes likely drove changes to local densities following disturbance: declining canopy cover, subcanopy foliage cover, and foliage height diversity as well as increasing sapling density and snag basal area. Just as important were changes to tree community composition, with the loss of local overall tree richness and subalpine tree species (subalpine fir, quaking aspen, spruces) basal area as well as increasing ponderosa pine dominance following wildfire each affecting a subset of bird species. However, 35% of the community showed negative responses to increasing live tree basal area, highlighting the importance of disturbance in shaping breeding-season densities of many species.

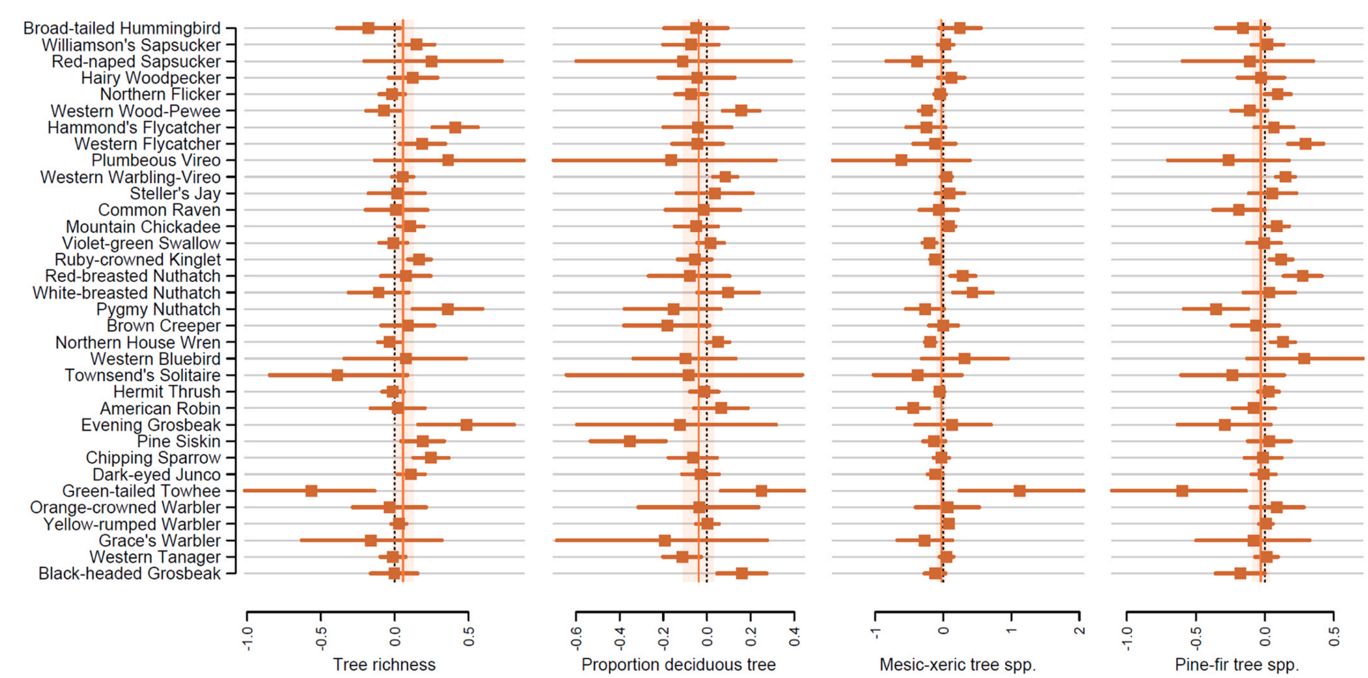

Fig. 5. Forest plot of mean effect sizes of four floristic-composition microhabitat covariates on breeding-season abundance of 34 mixed-conifer forest birds. The mean and 90% Bayesian credible interval are plotted for each species, while vertical lines and shaded areas represent the mean and standard deviation of the mean effect sizes across the full community. Species are listed in taxonomic order following the American Ornithological Society's 2025 checklist.

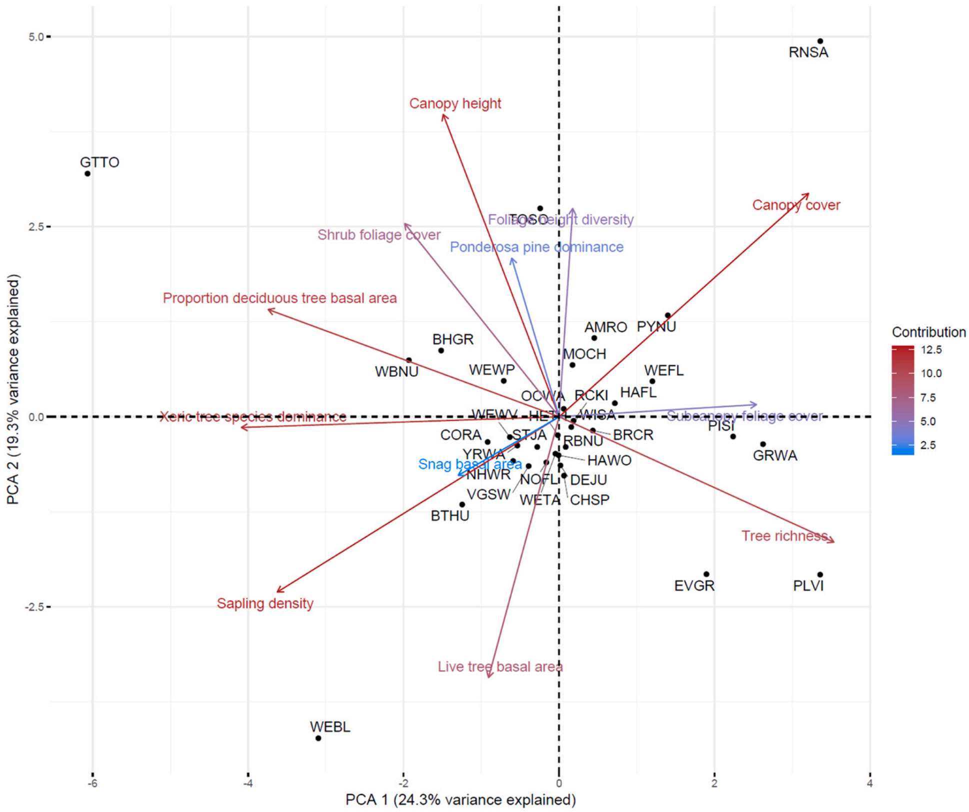

Fig. 6. PCA bi-plot of bird species associations with twelve microhabitat variables in southwestern US mixed-conifer forests. Arrows indicate the loadings on the first and second PC axes, while species responses are color coded by variable contribution. Points denote bird species, and are labeled with the four-letter codes provided in Table S1. The sign of the second PC axis (ponderosa pine dominance) was inverted so that positive values indicate higher ponderosa pine basal area in the local tree assemblage.

4.1. Shift in bird community composition following wildfire: species turnover

The bird community at Bandelier shifted over time, with important changes to species composition occurring after the 2011 Las Conchas fire. We observed statistically significant changes to community composition, and identified numerous indicator species for both the pre- and post-fire bird communities. Affected species exhibited both supported local population declines and increases over the monitoring period, suggesting that species turnover occurred. While we did not model burn effects directly, the large number of monitoring points within moderate or high severity burn areas at Bandelier (52%), and the fact that all but one of the monitored locations burned in 2011 (Figure A.1), indicate that wildfire effects likely played a large role in driving changes to the community. A subset of the 34 modelled species showed local population declines (32%) or increases (17%), while half of the species showed no supported change in local density. This response pattern mirrors reported responses of avian communities to wildfire in mixed-conifer forests across the western United States (Hutto et al., 2020; Kotliar et al., 2002; Taillie et al., 2018). Bird communities in nearby Southwestern mixed-conifer forests have also been shown to undergo community turnover following high-severity wildfire (Kotliar et al., 2007; Scott and Korb, 2024). However, we cannot preclude other factors such as increased forest fragmentation and edge effects (Hejl et al., 2002), reduced conifer masting in younger trees (Wion et al., 2023; Wright et al., 2021), direct demographic effects of drought on avian productivity (DeSante and Saracco, 2021; Saracco et al., 2018), and structural and floristic changes to remaining forest stands (see below) as additional drivers of change within the bird community over the timeseries.

We identified a suite of species which declined at Bandelier following the fire and which may be particularly reliant on unburned forests in the Southwest. These included Red-breasted Nuthatch, Mountain Chickadee, Ruby-crowned Kinglet, Hermit Thrush (*Catharus guttatus*), Western Flycatcher (*Empidonax difficilis*), Dark-eyed Junco, Brown Creeper, and many warblers (Yellow-rumped, Orange-crowned [*Leiothlypis celata*]), woodpeckers (Williamson's and Red-naped Sapsuckers, Downy Woodpecker [*Picoides pubescens*]), and finches (Evening Grosbeak, Pine Siskin, Red Crossbill [*Loxia curvirostra*]). Many of these species consistently show negative responses to wildfire in western mixed-conifer forests (Kalies et al., 2010; Kotliar et al., 2007; Roberts et al., 2021; Scott and Korb, 2024), though the junco and some warbler, sapsucker, and finch species show divergent, positive wildfire responses at more northerly latitudes (Kotliar et al., 2002). The subset of the community that increased over time and likely benefits from wildfire included both species that occur in unburned forest at lower densities (e.g., Northern House Wren, Western Wood-pewee, Violet-green Swallow) as well as specialist species of higher-severity fire (American Three-toed Woodpecker, Olive-sided Flycatcher [*Contopus cooperi*], Green-tailed Towhee). Our results therefore suggest that a subset of the Southwestern mixed-conifer forest bird community benefits from moderate to high-severity wildfire disturbance (Bock and Block, 2005; Hutto et al., 2020). We stress, however, that our 2018 results represent a single snapshot of the bird community seven years after the wildfire. Bird responses to fire are known to vary in relation to both fire severity and time since fire (Hutto and Patterson, 2016; Ray et al., 2025; Roberts et al., 2021; Taillie et al., 2018), which influence specific post-fire habitat attributes such as snag and shrub density that are associated with species' presence at a site (Raphael et al., 2018; White et al., 2016). Our data therefore likely do not capture the full spectrum of species responses to the post-fire landscape at Bandelier.

4.2. Structural microhabitat associations: diverse drivers across vertical strata

We found supported associations with all eight of the vegetation structure covariates at the microhabitat scale. Canopy cover was an important driver of breeding-season abundance, with 13 species (38%) showing supported responses to this variable. However, though the gradient of canopy cover included in the study was extensive (~5–95%), over 60% of species did not show supported responses to this variable. Those that did tended to show non-linear responses above 80% or below 35–40% canopy cover (Figure A.8). While these results mirror similar species responses from the Sierra Nevada (White et al., 2013a), in the Southern Rockies a majority of species showed positive responses to lower canopy cover, though the subset of species preferring closed canopy forest was nearly identical (Latif et al., 2022). Other studies have largely found that 35–40% canopy cover is an important threshold for species that prefer lower canopy cover (Sallabanks et al., 2006), or as a minimum threshold for the presence of some avian foraging guilds and species in mixed-conifer forest (Latif et al., 2022; White et al., 2013b). Therefore, while many Southwestern mixed-conifer birds appear to be resilient to loss of canopy cover, a subset of species are tied to closed canopies and are lost under more open canopy conditions, as is the case in the Sierra Nevada and Southern Rockies (Latif et al., 2022, 2020; Ray et al., 2025; White et al., 2013a, 2013b).

In addition to canopy cover, we found a small number of species associated with higher subcanopy foliar cover (Plumbeous Vireo [*Vireo plumbeus*], Hermit Thrush, Yellow-rumped Warbler) and foliage height diversity (Hammond's Flycatcher, Mountain Chickadee, Townsend's Solitaire [*Myadestes townsendi*], Orange-crowned and Yellow-rumped Warblers), structural features which decreased at Bandelier following the wildfire. These associations may represent preferences for foraging in the subcanopy stratum, or in multiple vertical strata (Airola and Barrett, 1985). In other cases, species may preferentially nest in or under understory or subcanopy vegetation with an overstory present. For instance, Orange-crowned Warbler prefers to nest under sub-canopy trees (Gilbert et al., 2020), while Hermit Thrush often places nests in young understory fir trees (Dellinger et al., 2020). Similarly, the richness of understory and ground nesting birds in mixed-conifer forest in the Northern Rockies was tied to the volume of both understory and canopy (> 2 m) foliage (Vogeler et al., 2014), though foliage height diversity is generally a poor metric of overall bird richness in western mixed-conifer forest (Verner and Larson, 1989; Vogeler et al., 2014). Foliage height diversity was also an important axis of bird-habitat associations for the full community (Fig. 6), and may therefore be an important factor for a subset of disturbance-averse mixed-conifer birds. More open forest canopies, and a lack of infilling, may help foster greater vertical vegetation complexity (Beedy, 1981).

About a third of the bird community showed supported negative associations with increasing sapling density, mirroring a similar avoidance of small (<15 cm DBH) trees by mixed-conifer birds in Idaho (Sallabanks et al., 2006). The responsive species included many woodpeckers (Williamson's and Red-naped Sapsuckers, Hairy Woodpecker [*Dryobates villosus*]), flycatchers (Western Flycatcher and Wood-Pewee), and other canopy-foraging insectivores (Mountain Chickadee, Western Tanager [*Piranga ludoviciana*], Yellow-rumped Warbler). These species are largely dependent upon mature trees for foraging and nesting. Saplings of light-tolerant conifers, such as ponderosa pine, are known to establish in more open microhabitats such as canopy gaps and burn patches where mature trees are lacking (Goodrich and Waring, 2017; Puhlick et al., 2012), and may represent the highest densities of saplings in post-fire landscapes (Zald et al., 2008). Mature trees provide a greater volume of foliage and trunk surface area for foraging, and represent preferred foraging microhabitat in relation to saplings, at least in some circumstances (Airola and Barrett, 1985; Franzreb, 1983). Therefore, the negative association with higher sapling densities may represent a positive association with mature tree density, an important determinant of species persistence in burned mixed-conifer landscapes (White et al., 2016).

4.3. Negative association with greater tree basal area: a preference for disturbance?

We found that 35% of the modelled bird community showed supported negative associations with increasing live tree basal area. Basal area is representative of both tree density and tree size class, and species may therefore be responding to either of these variables. However, basal area may emphasize large-diameter, old-growth trees when compared to other measures of mixed-conifer forest structure like canopy cover (Cade, 1997). While mixed-conifer bird species are often associated with either early or late successional stages (Sallabanks et al., 2006), both disturbance-adapted (Northern House Wren, Western Wood-Pewee, Chipping Sparrow) and purportedly disturbance-avoidant (Mountain Chickadee, Ruby-crowned Kinglet, Red-naped Sapsucker) species showed negative responses to basal area, suggesting that this result may not reflect preferences for young versus old forests. Instead, species may show negative associations with either heavily infilled forests after fire suppression or undisturbed climax communities. Infill of white and Douglas firs after fire suppression (e.g., Fulé et al., 2004; Jaquette et al., 2021) may increase tree basal area over baseline values. Notably, several studies have suggested that mixed-conifer forest birds prefer more open forest structures (Beedy, 1981), or show positive responses to treatments that thin out the canopy (Kalies et al., 2010; Kalies and Rosenstock, 2013; Siegel and DeSante, 2003; White et al., 2013a), possibly by creating more canopy gaps and fostering greater understory vegetation growth (Latif et al., 2020). Alternatively, or additionally, many species may breed at higher densities in areas experiencing mild or moderate wildfire disturbance versus unburned climax communities. Wildfire was a historical disturbance in mixed-conifer forest prior to fire suppression (Bock and Block, 2005; Romme et al., 2009), and many mixed-conifer forest birds show their highest abundances in moderately disturbed forests (Ray et al., 2025; Roberts et al., 2021; Taillie et al., 2018) or respond positively to increased structural heterogeneity (White et al., 2013b). For example, Mountain Chickadee showed higher breeding-season densities in low-severity burns than in unburned mixed-conifer forest, even though it responded negatively to high-severity burns (Ray et al., 2025). Therefore, disturbance is likely an important component of habitat suitability for many mixed-conifer forest birds in the Southwest, though it is unclear if the primary mechanism is thinning forest structure or creating patches of disturbed forest on the landscape. Ultimately, some species may require a mosaic of burn severities and disturbance levels to achieve their highest breeding-season densities (Tingley et al., 2016).

4.4. Positive responses to floristic composition: tree species matter too

A subset of mixed-conifer birds showed supported and often non-linear associations with tree species composition on both a mesic sub-alpine to xeric montane tree gradient and another gradient within xeric forests defined by pine versus fir dominance. While bird species show distinct associations with tree composition in other habitat types (Adams and Matthews, 2019; Lee and Rotenberry, 2005), and along mesic-xeric gradients in the boreal conifer forest (Kirk et al., 1996), this is, to our knowledge, the first documentation of this trend for conifer forests in the arid Southwest. Birds often favor specific tree species for foraging in mixed-conifer forest (Airola and Barrett, 1985; Franzreb, 1983), in part due to structural differences in the branching and foliage patterns of individual tree species. However, species may also be responding to other factors such as habitat-specific understory plant composition (Korb et al., 2007) or seed crops of favored tree species. Seven bird species also showed supported or near-supported negative relationships with increasing ponderosa pine dominance. These species may prefer the greater canopy cover and foliage available when white and Douglas fir are co-dominant (Gaines et al., 2007), as ponderosa-dominated forests generally have a more open structure (Covington and Moore, 1994). Species showed more supported associations with specific tree species combinations than with the more general coniferous-deciduous gradient that has been documented elsewhere (Clawges et al., 2008; Swift et al., 2017). This may be due in part to the fact that aspen stands, the primary deciduous tree at our study sites, support different bird species across the successional gradient (Hobson and Bayne, 2000; Schieck et al., 1995) and our measure of deciduous tree basal area may not be capturing aspen stand age. Overall, the loss of mesic subalpine tree species, and increasing dominance of ponderosa pine, in post-fire landscapes may decrease habitat suitability for a subset of the mixed-conifer community.

In addition to specific tree species compositions, ten bird species showed supported positive associations with increasing local tree species richness. Correlations between tree species richness and avian richness or abundance metrics are common in deciduous forests (Beason et al., 2023; James and Wamer, 1982; Poulsen, 2002), though these relationships have rarely been tested in single-species models. In other conifer-dominated systems, 'mixed-woods', in which no one tree species dominates stand composition, often show higher bird diversity (Hobson and Bayne, 2000; Lindbladh et al., 2022), though 'unmixed' aspen stands tend to show higher bird diversity (Hobson and Bayne, 2000; Hollenbeck and Ripple, 2007). This response might be due to differential use of different tree species, such as one species for foraging and another for nesting. For instance, Williamson's Sapsucker is thought to prefer aspens for nesting (Conway and Martin, 1993), but primarily forages in ponderosa pine and Douglas fir (Gyug et al., 2023). Therefore, the diversity of canopy microhabitats, with both open and closed vegetation and branching structures present, may be an important driver of breeding habitat suitability for some mixed-conifer species (Cavard et al., 2011). Alternatively, tree diversity may be higher in mesic microhabitats (Fernandes, 1992; Roach et al., 2021), such as snowmelt drainages, which are likely favored by some bird species. Specific functional groups were more likely to show a positive association with tree richness: ground-foraging sparrows (Chipping Sparrow, Dark-eyed Junco), aerial foragers (Hammond's and Western Flycatchers), and granivorous finches (Evening Grosbeak, Pine Siskin). Some resources may therefore be more limited by microhabitat diversity or microclimate than others. The potential for future climate and disturbance scenarios to result in homogenized tree compositions (e.g., Loehman et al., 2018) therefore represents a potential mechanism for reduction in habitat suitability for some mixed-conifer forest birds.

4.5. Management implications

During the breeding season, Southwestern mixed-conifer birds are both sensitive to and dependent on disturbance. A subset of species only appeared at the study sites following high-severity wildfire, while others were nearly extirpated by the same fire. Therefore, high-severity wildfire disturbance is likely to cause species turnover in Southwestern mixed-conifer bird communities. Tree die-off and prescribed fire are also likely to lead to structural changes and bird species turnover, though perhaps at different spatial and temporal scales. Species responded to divergent variables, with no more than a third of the modelled birds showing associations with any one covariate. Therefore, managing for any one variable is unlikely to affect the full bird community. Disturbance and vertical foliage complexity explained the largest amount of variation in breeding-season densities. A subset of species was sensitive to disturbance, and these species are largely identical to sensitive species in the Sierra Nevada and Southern Rockies. Both structural and floristic mechanisms explain the reduced densities of these species at the microhabitat scale following disturbance. On the structural side, the loss of canopy cover (particularly below a threshold value of 75%), subcanopy cover, mature trees, and foliage height diversity all decrease densities of different subsets of the bird community, which are likely to be negatively affected by thinning treatments and wildfire, and unable to persist in habitat which has undergone type conversion to non-forest. Maintaining forest mosaics with areas of higher canopy and subcanopy cover when thinning will allow more of these species to persist in treated landscapes. However, nearly two thirds (62%) of species were resilient to observed changes in canopy cover. With respect to tree species composition, subsets of bird species showed positive associations with subalpine spruce and fir trees and greater local tree species richness, and negative associations with greater ponderosa pine dominance. Fostering a higher diversity of trees, especially subalpine species, in disturbed landscapes will help maintain a higher diversity of bird species. A third of species, including disturbance adapted and disturbance avoidant birds, showed negative associations with higher live tree basal area. These species are likely dependent upon light-to-moderate wildfire disturbance to achieve their highest breeding-season densities, and may avoid fire-suppressed forests with high infill of Douglas and white fir. Maintaining a diversity of disturbed and undisturbed habitat on the landscape is therefore essential to create habitat for the full mixed-conifer bird community in the Southwest.

CRediT authorship contribution statement

Harrison Jones: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Brandon Merriell:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **Megan Swan:** Writing – review & editing, Conceptualization. **Matthew Johnson:** Writing – review & editing, Funding acquisition. **Rodney Siegel:** Writing – review & editing, Supervision, Project administration, 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

The authors are indebted to the many field technicians that collected bird and habitat survey data for this project, as well as to Dr. Jennifer Holmes and Matthew Johnson for designing and managing the SCPN bird monitoring program. Kristin Straka provided maps of point count station locations in relation to fire perimeters and wildfire severity at Bandelier and Grand Canyon. This work was supported by a grant from the National Park Service's Natural Resource Condition Assessment Program.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123660.

Data availability

Data required to replicate this analysis are published online at this address: https://catalog-beta.data.gov/dataset/scpn-habitat-based-bird-community-monitoring-data-2007–2018

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