Forest Ecology and Management 596 (2025) 123058

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Bird communities follow alternate recovery trajectories two decades after wildfire☆

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ARTICLE INFO

Keywords:
Fire
Habitat
Birds
Southwest
Ponderosa Pine

ABSTRACT

Wildfires are altering forested landscapes across western North America. These wildfires are increasingly burning with high severity across large areas and driving the conversion of forest to non-forest. Understanding how long-term vegetation structure differs between low- and high-severity portions of burned landscapes, and how fire severity and post-fire vegetation structure relate to avian species and communities, is crucial for avian conservation efforts. We quantified vegetation structure and avian species composition in low- and high-severity portions of two wildfires — the 2002 Ponil Complex Fire in northern New Mexico and the 2002 Hayman Fire in southern Colorado — two decades after burning. We found long-term divergence in vegetation structure attributes, such as live overstory basal area, overstory canopy cover and 1000-hour fuel loads, between low- and high-severity sites, particularly at the Hayman Fire. We also found dissimilarities in avian species composition between low- and high-severity sites, and higher species richness associated with low-severity sites, higher live overstory basal area, and shorter distances to refugia, indicating that avian species are following alternate recovery trajectories at low- versus high-severity sites. Forest-associated bird species tended to occur at sites with greater overstory canopy cover and low fire severity. Meanwhile, grassland-, shrubland-, and desert-associated bird species were most commonly found in areas with lower overstory canopy cover and high fire severity. Our findings point to the importance of pyrodiversity on the landscape for providing suitable habitat for the greatest number of species, as well as the importance of low-severity patches for supporting forest-associated species that require intact overstory canopy cover. Large high-severity patches as the dominant component of the landscape will likely not support the most diverse or characteristic array of bird species 20 + years post fire.

1. Introduction

Wildfires are an essential disturbance for terrestrial ecosystems across the globe (Chia et al., 2015; McLauchlan et al., 2020) and can shape avian habitat and avian species and communities through their influence on vegetation structure (Bassett et al., 2017; Chia et al., 2015; McLauchlan et al., 2020; Smucker et al., 2005). Landscapes that burned with a range of severities — including high-severity patches where all trees are killed as well as refugia patches with varying degrees of tree survivorship — commonly contain a variety of distinct habitat types for various avian species with different life requisites (Barton et al., 2014; Bassett et al., 2017; Roberts et al., 2020). Fire directly impacts various vegetation characteristics that creates landscape heterogeneity and in turn influences avian habitat suitability for different species, including the abundance of overstory canopy cover, snags, coarse woody debris, and the abundance and composition of understory vegetation (Rainsford et al., 2021). These factors influence prey abundance, nesting availability, thermal refugia, and other factors that contribute to bird survival and reproductive success (George and Zack, 2008; Van Lear and Harlow, 2002). A mix of burn severities within close proximity to each other, such as high-severity patches near refugia, may also enable species that require a wide variety of habitat conditions to meet their foraging and nesting needs (Fontaine and Kennedy, 2012; Puig-Gironès et al., 2023; Stillman et al., 2019).

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https://doi.org/10.1016/j.foreco.2025.123058
Received 17 March 2025; Received in revised form 30 July 2025; Accepted 31 July 2025
Available online 18 August 2025

The influence of wildfire on avian habitat, species, and communities is particularly relevant in ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States, where spatial and temporal heterogeneity of wildfire effects are characteristic of the ecosystem's relatively frequent low- to mixed-severity historical fire regime (Kaufmann et al., 2006; McKinney, 2019; Odion et al., 2014). This historical fire regime created and maintained relatively open ponderosa pine stands with a diverse range of tree sizes, ages, and spatial configurations (Battaglia et al., 2018; Brown et al., 2015; Rodman et al., 2017). It is also thought to have created and maintained a variety of habitat types that suited a multitude of avian species adapted to the fire legacy (Fontaine and Kennedy, 2012; Kotliar et al., 2007; Kotliar et al., 2002; Latif et al., 2016; Vierling and Lentile, 2008). However, aggressive logging and livestock grazing during the Euro-American settlement period of the late 1800s and early 1900s, and fire exclusion since the settlement period, have made forests denser and more homogeneous (Fitzgerald, 2005; Fulé et al., 2021; Hood et al., 2021). As a result, forests now commonly burn in an uncharacteristic manner, with high-severity effects across large, contiguous areas (Abatzoglou, Williams, 2016; Cassell et al., 2019; Mueller et al., 2020; Savage et al., 2013; Singleton et al., 2019). Anthropogenic climate change is further exacerbating the susceptibility of stands to uncharacteristically severe wildfire (Rocca et al., 2014).

Avian responses to vegetation structures after wildfire can serve as a useful indicator of ecosystem resilience (Woolet et al., 2023). In particular, the increasing prevalence of high-severity fire in ponderosa pine forests is altering the spatial and temporal patterns of avian habitat heterogeneity, with unknown long-term consequences for avian species and communities. Across the US West, post-fire regeneration success has decreased in the 21st century, with particularly dramatic declines in severely burned forests of the southwestern US (Davis et al., 2023). As a result of reduced regeneration, severely burned ponderosa pine forests are at increased risk of wildfire-driven conversion (Davis et al., 2020; Woolman et al., 2022). The combination of wildfire-driven forest conversion and continued climate change could affect suitable avian habitat and the resilience of avian communities at both broad geographical scales and at the landscape scale. Burned areas which experience conversion, paired with the growing impact of climate change, can lead to a geographical mismatch in suitable vegetation structures and climate conditions for forest-associated wildlife (Hoecker and Turner, 2022). Species that occupy areas vulnerable to increased wildfire activity and vegetation-type conversion are likely at the highest risk for this loss of suitable habitat (Hoecker and Turner, 2022). This risk is heightened for habitat specialists who cannot quickly adapt to immediate or pervasive habitat loss (O'Neil et al., 2020).

As fire regimes shift, previously heterogenous burned footprints with a mix of smaller unburned, low-, moderate-, and high-severity patches are becoming more homogeneous in nature, with a larger proportion of high-severity patches outside the range of natural variability (Singleton et al., 2021). Uncharacteristically large high-severity patches may undermine the benefits that high-severity fire historically created for certain ponderosa pine associated avian species, when smaller high-severity patches had edges close enough to remnant habitat patches that birds could utilize a variety of habitat types on the landscape. This is especially relevant for bird species that historically experienced mixed benefits from wildfire and have been documented to use contrasting patch types for different behaviors (Latif et al., 2016). For example, birds that nest in pre-existing cavities but forage in live canopy may need both high-severity and low-severity or unburned habitat in the vicinity (Latif et al., 2016). Even high-severity specialists have been shown to utilize refugia patches for foraging as juveniles, increasing their use of severely burned patches as they mature (Stillman et al., 2019). Assessing whether homogeneity within burn footprints reduced potential ecological benefits of high-severity fire for avian species in the study area was a key component of our study.

Despite the growing amount and extent of high-severity wildfire in southwestern ponderosa pine forests, few studies have examined how fire severity and proximity to refugia affect long-term post-fire avian habitat, species, and communities. Here we collected vegetation structure and avian species composition data in two 2002 southwestern wildfires to address this knowledge gap. Our work has three specific objectives: 1) Examine how vegetation structures differ across low- and high-severity site types two decades after fire; 2) Determine how vegetation structures, site distance to refugia, and site type (low- versus high-severity) influence avian species richness and avian species composition; and 3) Quantify associations between frequently observed bird species and vegetation structures to understand habitat-bird associations in the post-fire landscape. We expected that vegetation structures and avian species composition would be fundamentally different between low- and high-severity sites two decades following wildfire, with low-severity sites containing more live overstory trees and less woody fuels than their high-severity counterparts. We further expected that shrub cover and snag basal area would be greater at high-severity sites, with more conifer regeneration at low-severity sites. Finally, we expected species richness to decrease as distance to refugia increased.

2. Materials and methods

2.1. Study areas

We conducted our study across two wildfires in the southwestern US (Fig. 1). In the summer of 2002, lightning ignited the Ponil Complex Fire near Cimarron, New Mexico. This fire ultimately burned 36,051 ha, with 51 % of the area burning at moderate- to high-severity (Coop et al., 2019). The Ponil Complex Fire burned through a mix of primarily ponderosa pine forest, grassland, and shrubland, along with some mixed-conifer forest (ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*)) and pinyon-juniper woodland (two-needle pinyon (*Pinus edulis*), alligator juniper (*Juniperus deppeana*), and Rocky Mountain juniper (*Juniperus scopulorum*)) (Hayes and Robeson, 2011; Hayes and Robeson, 2009). The Hayman Fire burned in the summer of 2002, west of Colorado Springs, Colorado. In total, the fire burned 55,893 ha (Graham, 2003), with 65 % of the landscape experiencing moderate- to high-severity fire (Coop et al., 2019). The fire primarily burned through ponderosa pine and ponderosa pine - Douglas-fir dominated forests, as well as scattered aspen (*Populus tremuloides*) stands (Graham, 2003).

The historical fire regimes varied slightly between the two study areas. In the Ponil Complex Fire area in northern New Mexico, historical regimes primarily consisted of frequent, low-severity fires (Moore et al., 1999; Hayes and Robeson, 2011; Parks et al., 2018), though areas of mixed-conifer forest in the burn footprint may have historically burned with a higher proportion of moderate- and high-severity fire. Meanwhile, the Hayman Fire area experienced a fire regime dominated by less frequent mixed-severity fires consisting of low-, moderate-, and sometimes high-severity effects (Kaufmann et al., 2006; McKinney, 2019; Woolman et al., 2022).

The climate at both study areas is continental. Both study areas experience a summer monsoonal rain pattern. For the Ponil Complex Fire, the annual temperature between 1990 and 2020 averaged 9 °C, with an average minimum temperature of 0.3 °C and an average maximum temperature of 17.7 °C. Precipitation from 1990 to 2020 averaged 424 mm annually (PRISM, 2024). For the Hayman Fire, the average annual temperature between 1990 and 2020 averaged 6.2 °C, with an average minimum temperature of −1.6 °C and an average maximum temperature of 14.1 °C. Precipitation from 1990 to 2020 averaged 510 mm annually (PRISM, 2024). Elevations at Ponil Complex Fire sites ranged from 1836 m to 2490 m while elevations at Hayman Fire sites ranged from 2145 m to 2609 m.

2.2. Site selection

Prior to establishing sites at both fires, we determined fire severity

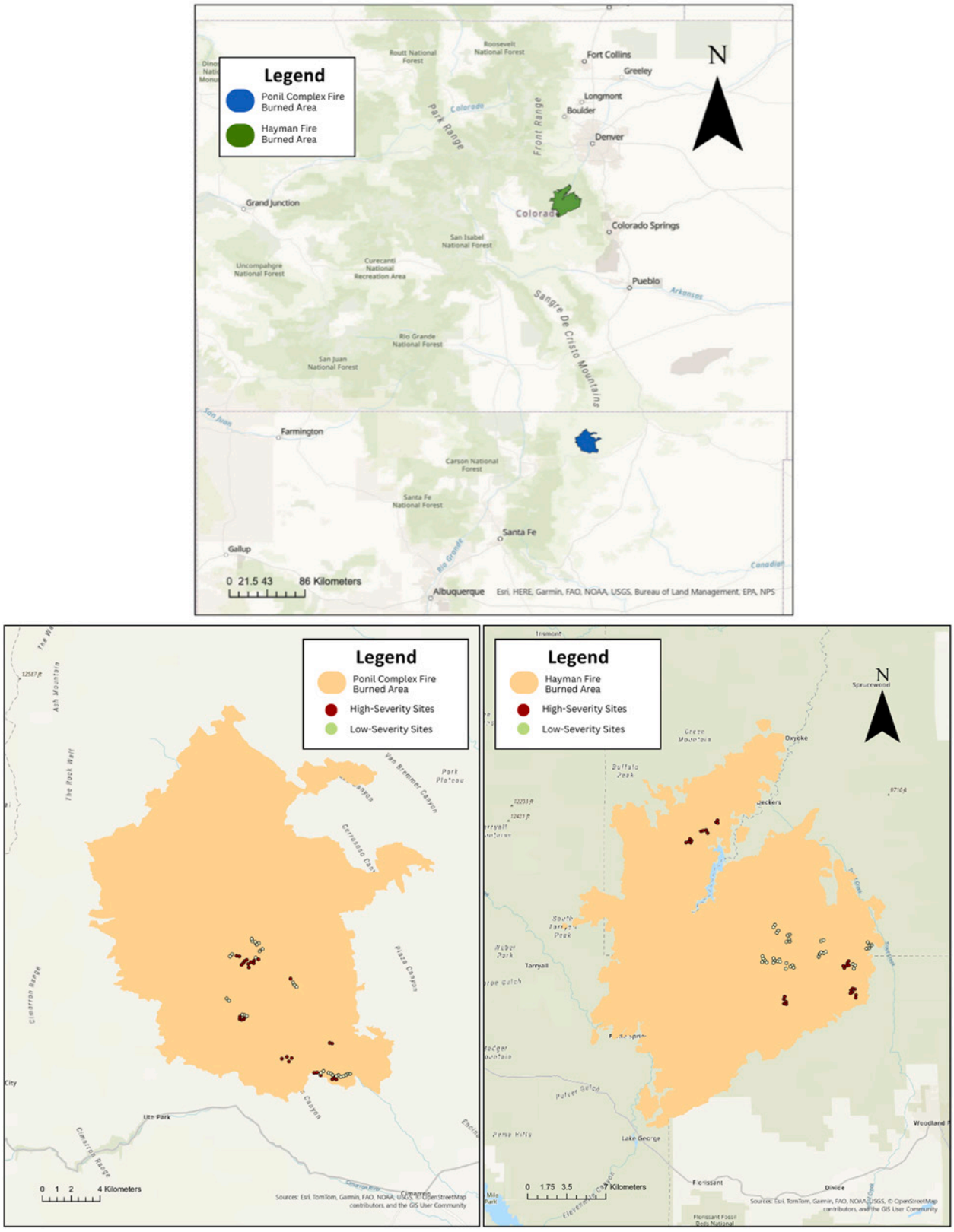

Fig. 1. Maps of the study areas with burned areas and low- and high-severity sites labeled.

via Monitoring Trends in Burn Severity fire data (Eidenshink et al., 2007). We reclassified the area within the burn perimeter as either low- or high-severity in ArcGIS Pro (Esri, 2024). We grouped unburned, low- and moderate-severity classifications together due to the possibility of surviving trees. We then used the resulting fire severity maps in the field to identify potential areas for site establishment in each fire severity type per fire. We randomly established sites at these potential areas if they were at least 50 m from the nearest public road, were in a ponderosa pine, ponderosa pine - Douglas-fir, or mixed-conifer forest pre-fire, were not planted post-fire, and had some evidence of having burned. Sites

were at least 150 m from another site to maintain no overlap between point counts at a 75 m radius. Two pairs of sites at the Ponil Complex Fire were several meters less than 150 m apart, likely due to GPS positioning error in the field. We ultimately established 130 sites in total (Fig. 1). Of these, 60 (30 high-severity and 30 low-severity) were in the Ponil Complex Fire within the Philmont Scout Ranch, and 70 (30 high-severity and 40 low-severity) were in the Hayman Fire footprint within the Pike-San Isabel National Forest. High-severity sites at both fires did not contain any surviving overstory trees, while low-severity sites had at least some overstory tree survival (Fig. 2).

2.3. Bird surveys

We measured bird species presence at the 130 sites between May and June of 2022 (Hayman Fire sites) and May and June of 2023 (Ponil Complex Fire sites) to align with the breeding bird season (Ralph et al., 1993). Prior to the 2022 and 2023 field seasons, we thoroughly trained technicians on species identification common to the study areas. We used previous local studies, field guides, and other relevant publications of birds to generate lists of species potentially occurring in the study sites (e.g., Bennetts et al., 1996; Finch et al., 1997; Morris et al., 1977). The aim of these lists was to reduce observer bias during point counts (Ralph et al., 1995). We further calibrated species identifications while establishing sites.

We collected bird observations via 8-minute point counts at all sites, with two separate point count visits total per site. Point counts began 20 min before sunrise and finished within 5 h after sunrise. Following the recommendation of other sources utilizing raw counts between sites, we established the *a priori* argument that p (detection probability) was equal in our low- and high-severity sites (Socolar et al., 2019). We are confident in this argument because we visited each site twice during the season to minimize detection probability differences between counts, which has been recommended as sufficient for improving model performance (Dettmers et al., 1999), determining bird presence vs absence, and calculating species richness (Siegel et al., 2001). When care is taken to ensure factors such as weather variables, observer differences, time of visit, and season of visit are similar across study sites, detection bias is likely to be minimal (MacKenzie et al., 2018). Thus, to further reduce detection bias, we did not conduct point counts in rain, snow, or wind speeds above 18 mph.

At the beginning of each point count, we noted the time, date, precipitation, wind speed, cloud cover, and observers. A primary observer conducted the point count at each site, with at least one additional crew member acting as secondary observer(s) at each site. Previous research has found that observer bias was the key source of detection bias between sites; therefore, our pooled method ensured we would not have this kind of variability between sites (Schmidt et al., 2023). During the count, we documented all bird species heard or seen within 200 m, estimating the distance to each bird (calibrated during pre-season training with a rangefinder). To eliminate any overlap between site observations and reduce detection bias, we eliminated bird species greater than 75 m from all statistical analyses, similar to methods from Vogeler et al., (2013). If we heard an unknown bird sound, we made an audio recording and identified the species later. We also documented the method of bird detection, including if a visual ID was made and the sex determined.

2.4. Vegetation structure measurements

At all 130 sites, we collected vegetation structure measurements within a circular 0.04 ha area (11.3 m radius) surrounding the site center. As with the bird surveys, measurements were conducted between

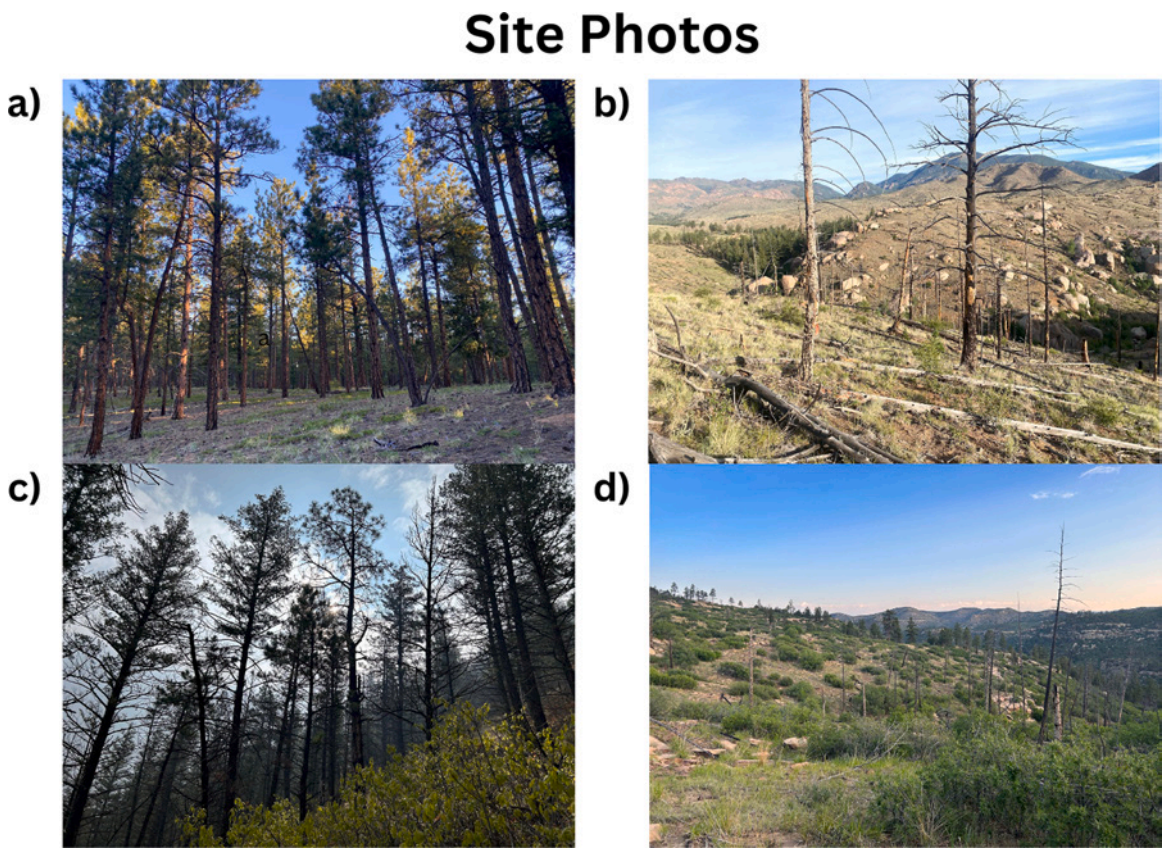

Fig. 2. Low- and high-severity sites across each fire. Photos in the top row are low-severity (a) and high-severity (b) sites at the Hayman Fire. Photos in the bottom row are low-severity (c) and high-severity (d) sites at the Ponil Complex Fire. Photos highlight the intact canopy cover across low-severity sites at both fires, and the more extensive tall shrub cover at all sites in the Ponil Complex Fire compared to the Hayman Fire.

May and June of 2022 (Hayman Fire sites) and May and June of 2023 (Ponil Complex Fire sites). From the site center, we extended four transects in the cardinal directions. Along each transect, we counted 1-hour (< 0.6 cm diameter), 10-hour (0.6–2.5 cm), and 100-hour (2.5–7.6 cm) woody fuels, and converted counts to loads using modified Brown (1974) methods. We counted 1-hour fuels on a 6 m transect, and 10-hour and 100-hour fuels along the entire 11.3 m transect. We also recorded the percent cover of understory plant functional groups (shrub, forb, graminoid, and tree) and substrates (rock, bare ground, litter, woody fuels, and moss) along each transect using the point-intercept method. We measured tall shrubs $\geq$ 0.61 m tall along each transect using modified Canfield (1941) protocols, where the recorder measured the length of space each shrub crossed on the transect. Gaps of greater than 0.30 m were considered a separate tall shrub. We used the average height of the entire tall shrub or continuous shrub patch to determine the average height. To characterize the overstory, we collected information including percent canopy cover via a densitometer every 1 m along each transect, and diameter at breast height (DBH) for all overstory trees and saplings across the entire site. We quantified 1000-hour (>7.6 cm diameter) woody fuel loads within a 6.0 m radius subplot at the plot center. For each log in this subplot, we measured its diameter at each end, its length, and whether it was sound or rotten. We counted all conifer tree seedlings by species across the site and estimated their ages using whorl counts. We also recorded aspect, slope, and site coordinates at the center of the site.

2.5. Statistical analyses

Statistical analyses were performed in R (version 2022.02.0 "Prairie Trillium") at an $\alpha = 0.05$ level. To compare vegetation structures between low- and high-severity sites at each fire (Objective one), we first assessed correlation between variables via Spearman Correlation Coefficients, excluding highly correlated variables in the subsequent analyses. We then performed Kruskal Wallis tests to examine differences in the remaining variables (overstory canopy cover, live overstory basal area, snag basal area, percent bare ground and rock cover, percent shrub cover, percent graminoid cover, and 1000-hour fuel loads) across low- and high- severity sites at each fire. We then performed post-hoc Dunn tests when significance was found. We also conducted a Fisher's Exact test on conifer tree seedling presence across low- and high-severity sites at each fire.

To address the relationship between avian species richness, vegetation structures, distance to refugia, and fire severity type (Objective two), we classified sites post-hoc in two ways. First, we used a spatial layer from Walker et al. (2019) to generate a continuous distance to refugia variable for sites across both fires. Given the potential ecological benefits of refugia for a variety of bird species, we incorporated this distance to refugia metric into analyses to assess the influence of proximity to live overstory cover within the burn footprints. We identified refugia as live tree patches at least 0.4 ha in area. We then classified sites into low- and high-severity interior and edge groups for the Ponil Complex Fire. We classified low-severity sites as "low-severity interior" if they were further than 100 m from a non-refugia patch at least 0.4 ha in area using the same spatial layer from Walker et al. (2019). Similarly, we classified high-severity sites as "high-severity interior" if they were further than 100 m from a refugia patch at least 0.4 ha in area. We attempted the same categorization for the Hayman Fire. However, despite extensive sampling across the burned area, our sample sizes for high-severity edge (n = 4) and low-severity interior (n = 5) sites were too small for robust categorical analysis. Thus, we retained our original low- and high-severity groups for the Hayman Fire.

Next, we constructed Poisson regression models in R, setting the total species richness at each site as the response variable. For each model, we tested for overdispersion and multicollinearity, and selected the top model based on the lowest AIC value. We selected three top models per fire to address each component of our objectives: one model assessing only vegetation structure variables, one model assessing the combination of vegetation structure variables and low- vs high-severity site type (including low-severity interior and edge, and high-severity interior and edge for the Ponil Complex Fire), and one model incorporating distance to refugia as a continuous variable. Vegetation structure variables tested included those collected in our vegetation structure measurements, including 1000-hour fuels, live overstory basal area, live overstory canopy cover, percent tall shrub cover, percent graminoid cover, percent bare ground/rock cover, and snag basal area.

To analyze avian species composition dynamics (Objective two), we created a dissimilarity matrix via Jaccard distance, which is used for binary classifications. We then conducted a non-metric multidimensional scaling analysis (NMDS) on the dissimilarity matrix using the Vegan package in R (Oksanen et al., 2022). For this analysis, we included all species observed within 75 m of a site across both fires (Table S1). NMDS results are assessed via a stress value, with the best results having a minimized stress value. Stress is minimized by selecting a higher number of dimensions (k) (Bakker, 2023). For both fires, we selected k = 3 dimensions. To assess species and vegetation structure variables significantly correlated with species composition, we then fit species and vegetation structure vectors onto results from NMDS using the envfit function in the Vegan package in R (Oksanen et al., 2022). The envfit function fits vectors of variables onto the ordination plot and assesses the significance of these fitted vectors using permutation. The resulting plot scales vectors such that stronger predictors have longer vectors. After testing vegetation structure variables for multi-collinearity, we included 1000-hour fuels, live overstory basal area, percent tall shrub cover, percent graminoid cover, percent bare ground/rock cover (for the Ponil Complex Fire only), and snag basal area as environmental variables. Following the fitting of these vegetation structure and species vectors, we conducted a permutational multivariate ANOVA (PERMANOVA) on the dissimilarity matrix using the ADONIS2 function in the Vegan package in R (Oksanen et al., 2022) to test for significant differences across sites based on site-severity type categories as the grouping factor. We also assessed percent tall shrub cover categories for the Ponil Complex Fire, which had adequate shrub cover for the analysis. We classified tall shrub cover categories into the following groups: Low cover consisted of sites with 0–20 % of the site having shrubs at least 0.61 m tall, moderate sites had between 20 % and 40 % cover, and high sites had above 40 % cover. We assessed the marginal effect of each term in the model. We then tested for homogeneity of dispersion via the betadisper function in the Vegan package, followed by a visual assessment of each NMDS ordination plot (Oksanen et al., 2022). To assess distance to refugia as predictor of avian species composition across sites, we also tested a univariate model on the dissimilarity matrix with distance to refugia set as a continuous explanatory variable, using the ADONIS2 function.

To quantify associations between frequently observed bird species and vegetation structures (Objective three), we conducted hypothesis testing across each fire for all species observed on at least 15 sites. We classified sites into a "present" and "non-present" group for each species following methods from Veech (2021). We assessed normality via Shapiro-Wilks testing in R. Due to non-normality, we selected Wilcoxon-Rank Sum Tests. We then conducted hypothesis tests on a variety of vegetation structure variables, depending on the associated habitat group for each species. For example, we conducted hypothesis tests for forest-associated species on canopy cover, snag basal area, and tall shrub cover across sites at each fire. Hypotheses varied based on habitat-associations for each species group.

3. Results

3.1. Vegetation structure across fire severities

Broadly, low- and high-severity sites had divergent vegetation structures twenty years post-fire (Table 1). At each fire, low-severity

Table 1
Mean vegetation characteristics at low- and high-severity sites across the Ponil Complex and Hayman Fires. Standard errors are in parentheses. Sites that do not share superscript letters are significantly different (based on Kruskal-Wallis and post-hoc Dunn tests with α =.05 significance level).

Fire	Site Type	% Canopy Cover	Live Basal Area (m^2 / ha)	Snag Basal Area (m^2/ ha)	% Tall Shrub (≥ 0.61 m)	% Bare Ground or Rock	% Graminoid	1000-Hour Fuels (mg/ ha)
Ponil Complex	High Severity	0.35 (0.29) [a]	0.00 (0.00) [a]	3.12 (0.54) [a]	22.12 % (2.82) [a]	37.20 (2.57) [a]	32.29 (2.85) [a]	12.82 (1.89)[a]
Ponil Complex	Low Severity	38.10 (2.36) [b]	19.89 (1.21) [b]	1.77 (0.43) [ab]	15.31 % (2.74) [ab]	10.38 (1.14) [b]	24.76 (2.37) [a]	2.64 (0.64) [b]
Hayman	High Severity	1.67 (0.69) [a]	0.13 (0.09) [a]	4.69 (0.72) [a]	2.70 % (0.55) [c]	47.28 (3.41) [a]	29.74 (2.27) [a]	20.32 (2.72) [a]
Hayman	Low Severity	39.03 (2.23) [b]	18.54 (0.96) [b]	1.56 (0.37) [b]	0.48 % (0.23) [d]	8.48 (1.60) [b]	16.36 (2.20) [b]	2.99 (0.60) [c]

sites had greater overstory canopy cover and live overstory basal area, and lower bare ground and rock cover and 1000-hour fuel loads. At the Hayman Fire, low-severity sites also had lower snag basal area, lower tall shrub cover, and lower graminoid cover than high-severity sites. Conifer seedling presence was also greater in low-severity sites than in high-severity sites at each fire (Table 2). At the Ponil Complex Fire, 86.7 % of low-severity sites had conifer regeneration, while only 56.7 % of high-severity sites had regeneration. Of these high-severity sites, 20.0 % only had two needle pinyon and/or juniper seedlings present, and 36.7 % exhibited the presence of ponderosa pine or Douglas-fir seedlings. At the Hayman Fire, 100.0 % of low-severity sites had conifer regeneration, compared to 43.0 % of high-severity sites.

3.2. Drivers of avian species richness and composition

Poisson regression models at both fires indicated the importance of distance to refugia and site type as predictors of species richness across fires. Results of these Poisson regression models and avian species richness findings for both the Ponil Complex Fire and Hayman Fire can be found in Table 3 (and Table S2 in the appendix). The top model for each fire when assessing site type as a categorical variable included both site type and percent graminoid cover as significant coefficients. Results of this model for the Ponil Complex Fire highlight that low-severity interior sites, low-severity edge sites, and sites with higher graminoid cover were associated with higher species richness. Similarly, low-severity sites and sites with higher graminoid cover were associated with higher species richness at the Hayman Fire. At the Ponil Complex Fire, the top performing model when assessing only vegetation structure variables indicated that greater live overstory basal area and lower percent bare ground and rock cover were associated with higher species richness. At the Hayman Fire, results of the same analysis indicated that higher live overstory basal area and higher graminoid cover were associated with higher species richness. Finally, the top model when including the distance to refugia metric included distance to refugia, live overstory basal area, and percent graminoid cover for the Ponil Complex Fire. As distance to refugia increased, species richness decreased, and as live overstory basal area and percent graminoid cover increased, species richness increased.

Table 2
Results of Fisher's Exact Test on the presence vs. absence of conifer seedling regeneration. PL represents low-severity sites at the Ponil Complex Fire. PH represents high-severity sites at the Ponil Complex Fire. HL represents low-severity sites at the Hayman Fire. HH represents high-severity sites at the Hayman Fire.

Group 1	Group 2	N	Adjusted p
HH	HL	70	< 0.0001
HH	PH	60	0.44
HH	PL	60	0.002
HL	PH	70	0.0009
HL	PL	70	0.03
PH	PL	60	0.02

For the Hayman Fire, the top model included only distance to refugia and also revealed an inverse relationship with species richness. AIC was lower for all Ponil Complex Fire models compared to Hayman Fire models. The top model for the Ponil Complex Fire across all model types indicated a combination of percent graminoid cover and site type was the best predictor of species richness, based on an assessment of AIC and residual deviance values. Alternatively, the model with only distance to refugia included was the best predictor of species richness across the Hayman Fire regression models.

Species composition differed significantly by fire severity within each fire footprint, as revealed by NMDS and PERMANOVA analyses (Fig. 3 and Fig. 4). For the Ponil Complex Fire, the stress value was 0.147, indicating an acceptable fit for the NMDS. Overall, 26 species were significantly correlated with the site distribution patterns. Environmental variables that were significantly correlated with avian site composition across the ordination plot included live overstory basal area, percent overstory canopy cover and percent bare ground and rock cover (Table 4). For the Hayman Fire NMDS, the stress value was 0.155, again indicating an acceptable fit. Overall, 22 species drove site distribution patterns, similar to the Ponil Complex fire with the addition of tall shrub cover, percent grass cover and 1000-hour fuels. Results of PERMANOVA on the dissimilarity matrix for the Ponil Complex Fire indicated a significant difference between site types (Table 5). It also indicated a non-significant difference between shrub cover categories. Results of PERMANOVA on the dissimilarity matrix for the Hayman Fire indicated a significant difference between low- and high-severity site types (Table 5). However, results for the Hayman Fire indicated heterogeneity of variance between low- vs. high-severity site types. The subsequent visual assessment of low- vs high-severity sites in the NMDS ordination plot showed non-overlapping ellipses for low- vs high-severity site type. This visual assessment of our NMDS ordination plot highlights the distinction in low- vs high-severity site composition, indicating that the significant PERMNOVA result is likely a result of significant differences in group means, rather than an erroneous result of heterogeneity of variance. Still, PERMANOVA results for the Hayman Fire should be interpreted with some caution. Results from our univariate model testing of distance to refugia as a continuous explanatory variable revealed similar findings for both the Ponil Complex Fire and Hayman Fire (Table 6). Distance to refugia was a significant predictor variable in both models, explaining 13.1 % of variation in avian species composition across sites at the Ponil Complex Fire, and 13.8 % of variation in avian species composition across Hayman Fire sites.

3.3. Habitat associations of frequently observed species

There were 37 species observed at least 15 times at either fire for which we analyzed species-habitat associations and associated hypotheses (Table 7 and Table S3). At the Ponil Complex Fire, nine species from tree nesting or cavity nesting guilds were associated with higher overstory canopy cover, while only one species, the Dusky Flycatcher

Table 3
Results of Poisson regression models assessing the relative influence of vegetation structure, proximity to refugia, and low- vs high-severity site classification on species richness across both fires. Site Type for the Ponil Complex Fire included high-severity interior sites, high-severity edge sites, low-severity interior sites, and low-severity edge sites. Site Type for the Hayman Fire included high-severity sites, and low-severity sites.

FIRE	Model	AIC	Null Deviance	Residual Deviance	Key Predictors
Ponil Complex Fire	Vegetation Structure Only	313.84	91.09	60.37	Live Overstory Basal Area, Percent Bare Ground/Rock Cover
Ponil Complex Fire	Vegetation Structure + Distance to Refugia	307.78	91.09	52.31	Live Overstory Basal Area, Percent Graminoid Cover, Distance to Refugia
Ponil Complex Fire	Vegetation Structure + Site Type	302	91.09	44.53	Percent Graminoid Cover, Site Type
Hayman Fire	Vegetation Structure Only	374.14	102.79	77.25	Live Overstory Basal Area, Percent Graminoid Cover
Hayman Fire	Vegetation Structure + Distance to Refugia	363.89	102.79	69.01	Distance to Refugia
Hayman Fire	Vegetation Structure + Site Type	366.75	102.79	69.87	Percent Graminoid Cover, Site Type

(*Empidonax oberholseri*), a flycatching shrub nester, was associated with lower overstory canopy cover. Foraging guilds varied more for species associated with higher canopy cover, comprising a mix of flycatcher, foliage gleaner, and ground forager guilds. Tall shrub cover at the Ponil Complex Fire was negatively associated with two species, a tree nester and foliage gleaner, the Western Tanager (*Piranga ludoviciana*), and a tree nester and flycatcher, the Western Wood-Pewee (*Contopus sordidulus*). Finally, the Black-headed Grosbeak (*Pheucticus melanocephalus*), a tree nester and foliage gleaner, was associated with significantly lower snag basal area.

At the Hayman Fire, 11 species were associated with higher canopy cover, but guild associations varied, encompassing a wide range of nesting and foraging guilds. These included shrub, tree, and ground nesters, and ground forager, flycatcher, foliage gleaner, and bark forager foraging guilds. Four species were associated with lower overstory canopy cover. These species were Dusky Flycatcher, Mountain Bluebird (*Sialia currucoides*), Green-tailed Towhee (*Pipilo chlorurus*), and Rock Wren (*Salpinctes obsoletus*), comprising a mix of shrub nester, ground nester, and cavity nester guilds, and the flycatcher and ground forager guilds. The three species associated with higher tall shrub cover, Dusky Flycatcher, Rock Wren, and Green-tailed Towhee, belonged to the shrub nester or ground nester guilds, and the ground forager or flycatching guilds. Two of these species, the Green-tailed Towhee and Rock Wren, were also associated with higher graminoid cover. Four species were associated with lower snag basal area (Pygmy Nuthatch (*Sitta pygmaea*), Steller's Jay (*Cyanocitta stelleri*), Western Tanager, and Western Wood-Pewee).

4. Discussion

4.1. Overview

Vegetation and avian species composition at low- and high-severity burned sites were divergent 20 years following the Ponil Complex and Hayman Fires. Low-severity sites, greater live overstory basal area, greater graminoid cover, and smaller distances to refugia were associated with higher species richness at both fires. Higher percent overstory canopy cover was consistently a driving factor for occurrence across a variety of individual species. In addition, the distinct differences in vegetation structure and conifer regeneration between severities at both fires highlight the enduring impact of high-severity wildfire on vegetation-type conversion, supporting prior research which has shown southwestern ponderosa pine ecosystems are increasingly at risk of wildfire-driven conversion (Coop et al., 2020; Guiterman et al., 2022). Lack of live seed sources within the interior of high-severity patches and potentially unfavorable climatic conditions for regeneration may act as barriers to forest regeneration at high-severity sites (Chambers et al., 2016; Stevens-Rumann et al., 2017; Davis et al., 2023). These differences in vegetation structure and the associated species composition, paired with signs of fine-scale conversion, indicate that bird composition is likely to remain significantly divergent at sites of different severity in the coming decades. This also points to reduced potential suitable habitat for forest-associated species that require mature canopy cover from ponderosa pine or mixed-conifer stands and other features associated with low-severity sites. As fire regimes shift across the Southwest, fires with a greater proportion of large, high-severity patches may follow similar recovery patterns (Coop et al., 2020).

4.2. Vegetation structure, avian species composition, and distance to refugia

Post-fire vegetation structures shape avian species composition (Barton et al., 2014), and there is a relationship between species richness and foliage height diversity, as well as mean canopy height (Culbert et al., 2013). High-severity patches in both study fires lacked vertical structure diversity, which limited avian species richness compared to low-severity patches with more structural complexity. Especially large, high severity patches act as ecological filters, excluding forest-obligate species due to the lack of canopy cover and favoring generalists or shrubland/grassland species through the presence of non-forest vegetation structures such as shrubs and downed woody debris. Low-severity sites and greater live overstory basal area were correlated with higher species richness as well as a greater number of species in NMDS ordination plots. This follows relationships observed within previous studies, and reflects research in southwestern ponderosa pine forests that found the highest breeding bird abundance and richness in forest stands with mature ponderosa pine trees (Culbert et al., 2013; MacArthur and MacArthur, 1961; Rosenstock, 1996; Wood et al., 2013).

Site severity also significantly influenced avian species composition across sites. This was expected, given significant differences in vegetation structures between low- and high-severity sites. Previous literature has demonstrated species-specific habitat requirements as a strong driving factor in wildlife responses to fire (e.g., Van Lear and Harlow, 2002; Vierling and Lentile, 2008; Woolet et al., 2023). Features associated with high-severity sites, such as greater shrub cover, lower canopy cover, greater snag basal area, and downed woody debris were correlated with the presence of a variety of shrub-, woodland-, or desert-associated species, such as the Green-Tailed Towhee, Dusky Flycatcher, and Rock Wren. For example, adequate shrub cover is a nesting requirement for the Dusky Flycatcher, and greater snag basal area is considered favorable for Mountain Bluebird habitat (Liebezeit, George, 2002; Saab et al., 2009).

Low-severity sites across fires had greater mature canopy cover than high-severity sites, which provides improved foraging and protection from predators for wildlife (Barton et al., 2014). Thus, canopy cover had

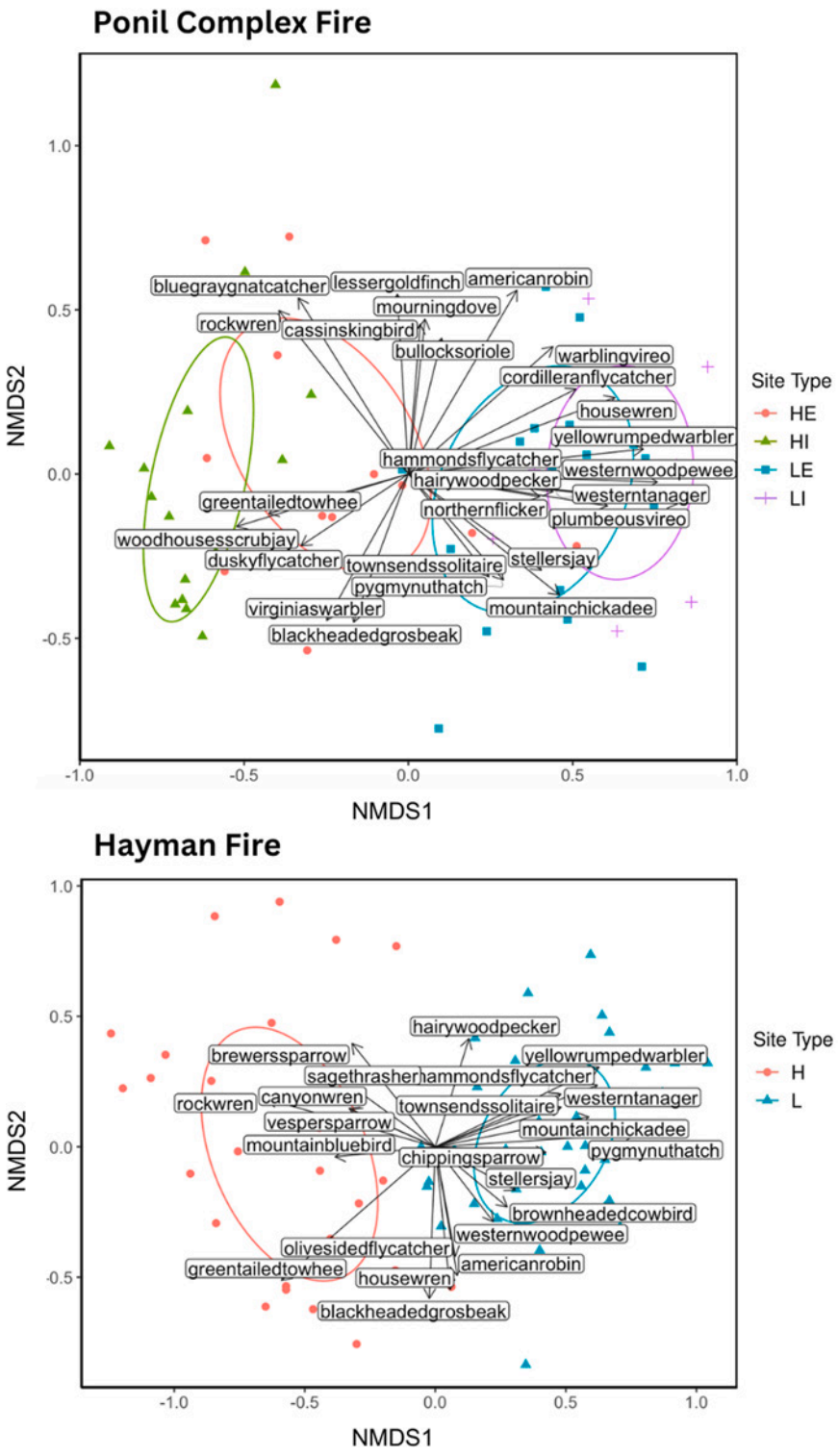

Fig. 3. NMDS ordination plots with species vectors for each fire. Significant species vectors are species that influenced the distribution of sites on the NMDS ordination plot. Species with a p-value $\leq .001$ are included. Site types at the Ponil Complex Fire indicate high-severity interior (HI), high-severity edge (HE), low-severity edge (LE), and low-severity interior (LI) sites. Site type at the Hayman Fire indicates high-severity (H) and low-severity (L) sites.

the strongest association with individual species presence and was correlated with species whose life history traits require greater forest cover. For example, the Pygmy Nuthatch, a secondary cavity nester which requires mature canopy for foraging, was highly associated with low- severity sites (Ghalambor and Dobbs, 2006). As a whole, almost all species associated with higher canopy cover at both fires were species that nest in tree foliage or are cavity nesters, with the exception of the Dark-eyed Junco (*Junco hyemalis*), Chipping Sparrow (*Spizella passerina*), and Townsend's Solitaire (*Myadestes townsendi*) on the Hayman Fire.

We found that distance to refugia played a significant role in predicting species richness and species composition across sites at both fires, with high-severity interiors acting as functional trait filters for forest-associated species. In both fires, as the distance to live tree cover

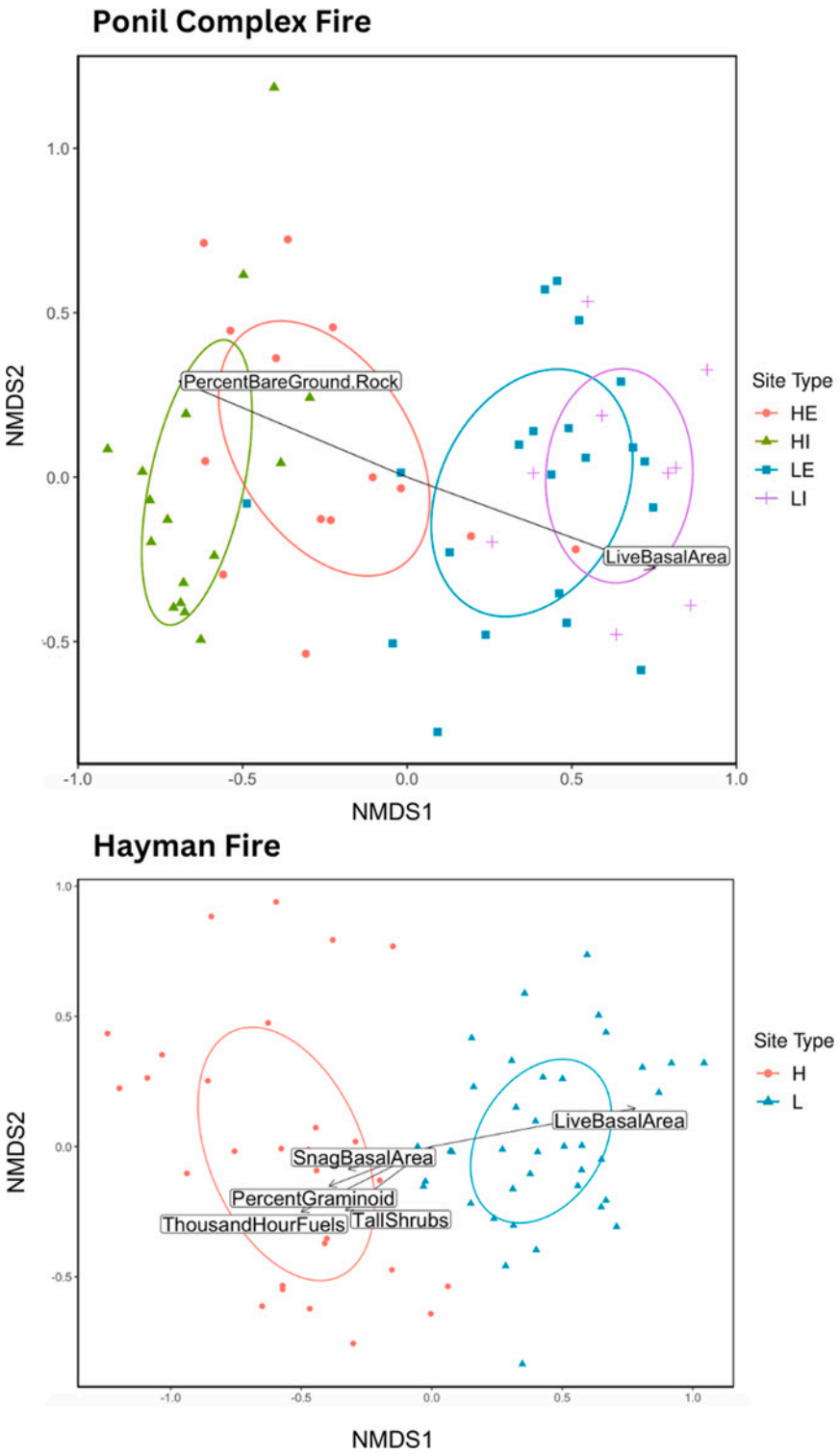

Fig. 4. NMDS ordination plots with significant vegetation structure vectors for each fire, excluding highly-correlated variables. Significant vectors are vegetation structure variables that influenced the distribution of sites on the NMDS ordination plot. Vegetation structure variables with a p-value $\leq .05$ are included. Site types at the Ponil Complex Fire indicate high-severity interior (HI), high-severity edge (HE), low-severity edge (LE), and low-severity interior (LI) sites. Site type at the Hayman Fire indicates high-severity (H) and low-severity (L) sites.

increased, species richness significantly decreased. This was especially relevant at the Hayman Fire, where the top regression model included only distance to refugia. High-severity patch proximity to unburned, low- or moderate-severity patches dictates whether bird species can utilize a variety of burn severities (termed habitat complementation) and is important for a variety of species (Stillman et al., 2023; Watson et al., 2012). Thus, these interior areas may have acted as an ecological filter for species who are generally associated with mature canopy cover, and reduced the ability for bird species to utilize a mix of burn severities in nearby proximity, limiting high-severity use at some interior sites to generalist species and/or birds with grassland- or desert habitat associations, such as the Western Meadowlark (*Sturnella neglecta*), Rock

Table 4
Results of fitting environmental vectors on the NMDS ordination plots. Significant vectors are in bold.

Ponil Complex Fire: Vegetation Structure Variable	NMDS1	NMDS2	r^2	(Pr (>r)
Thousand Hour Fuels	−0.97	−0.24	0.08	0.08
Tall Shrub Cover	−0.93	0.37	0.05	0.26
Live Basal Area	**0.94**	**−0.34**	**0.64**	**0.01**
Snag Basal Area	−0.43	0.90	0.05	0.22
Percent Bare Ground/Rock Cover	**−0.92**	**0.39**	**0.57**	**0.01**
Percent Graminoid	−0.65	−0.76	0.03	0.44
Hayman Fire: Vegetation Structure Variable	**NMDS1**	**NMDS2**	**r^2**	**(Pr (>r)**
Thousand Hour Fuels	**−0.89**	**0.45**	**0.31**	**0.01**
Tall Shrub Cover	**−0.80**	**0.60**	**0.17**	**0.04**
Live Basal Area	**0.98**	**0.19**	**0.63**	**0.01**
Snag Basal Area	**−0.97**	**0.36**	**0.11**	**0.03**
Percent Bare Ground/Rock Cover	**−1.00**	**0.09**	**0.68**	**0.01**
Percent Graminoid	**−0.93**	**−.036**	**0.18**	**0.03**

Table 5
PERMANOVA results quantifying the difference in avian community composition between Site Type and Shrub Cover groups. Site Type for the Ponil Complex Fire included high-severity interior sites, high-severity edge sites, low-severity interior sites, and low-severity edge sites. Site Type for the Hayman Fire included high-severity sites, and low-severity sites.

Ponil Complex Fire	df	Sum of squares	R^2	F	Pr(>F)
Site Type	**3**	**3.38**	**0.21**	**5.20**	**0.01**
Shrub Cover Group	2	0.42	0.03	0.96	0.49
Hayman Fire	**df**	**Sum of squares**	**R^2**	**F**	**Pr(>F)**
Site Type	**1**	**3.57**	**0.16**	**12.90**	**0.01**

Table 6
Univariate model results quantifying the difference in avian community composition across sites using distance to refugia as a continuous explanatory variable in the model.

Ponil Complex Fire	df	Sum of squares	R^2	F	Pr(>F)
Distance to Refugia	**1**	**2.08**	**0.13**	**8.73**	**0.01**
Hayman Fire	**df**	**Sum of squares**	**R^2**	**F**	**Pr(>F)**
Distance to Refugia	**1**	**3.09**	**0.14**	**10.87**	**0.01**

Wren, and Vesper Sparrow (*Pooecetes gramineus*). While distance to refugia was still a significant variable in the respective regression model at the Ponil Complex Fire, distance to refugia alone was not the best indicator of species richness for this fire. This may highlight the difference between large high-severity patches at the Hayman Fire and the relatively more heterogeneous landscape of the Ponil Complex Fire. These findings warrant the need for additional research addressing how increasingly large, high-severity fires may alter bird communities in southwestern ponderosa pine ecosystems, possibly in ways that mirror patterns observed in systems like the Sierra Nevada (Steel et al., 2021).

Overall, different species compositions existed at low- and high-severity sites, along with a variety of generalist and edge-associated species present at both fires. This supports the pyrodiversity-biodiversity hypothesis, which posits that heterogeneity in fire severity across the landscape is important for maximizing the number of species on the landscape (Tingley et al., 2016). This echoes foundational work such as the habitat-heterogeneity hypothesis, which proposes that an increase in heterogeneous habitat types maximizes species diversity (MacArthur and MacArthur, 1961). Both hypotheses have been exemplified in a variety of wildlife studies where an increase in the variety of vegetation structures, and therefore an increase in potential habitat niches, increases species richness and/or diversity (Böhning-Gaese, 1997; MacArthur and MacArthur, 1961; Verschuyl et al., 2008; Vogeler et al., 2014). However, our findings also showed significantly more species benefited from low-severity sites and their associated vegetation structures. It is critical to consider the proportion of high-severity and spatial heterogeneity patterns of different severities across the burn footprint. Our findings point to the potential reduced availability of suitable habitat for forest obligate species if future wildfire footprints of the Southwest burn with greater proportions of high-severity patches, as expected (Singleton et al., 2019). While our study incorporated only species richness counts into analyses due to study design limitations (i.e. lack of detection probability analysis and distance sampling methods), future studies should incorporate species abundance, along with rare species analyses for species with low detection probability, to assess whether similar patterns are observed, and to glean additional insights regarding associations with vegetation structures that were likely masked due to the overarching influence of canopy cover.

Post-fire vegetation structures and limited regeneration potential in high-severity patches suggest long-term divergence of avian communities across low- vs high-severity patches. Furthermore, conifer regeneration, or the lack thereof, point to signs of fine-scale wildfire-driven conversion at some high-severity sites. These findings support research which shows regeneration failure is increasing in prevalence in ponderosa pine ecosystems as fire regimes and climate conditions shift (Haffey et al., 2018; Petrie et al., 2023). Natural ponderosa pine regeneration is unlikely in areas greater than about 90–200 m from a surviving seed source, thus making tree regeneration in the interior of large high-severity patches less likely (Korb et al., 2019). Lack of seed availability, in combination with increasingly unfavorable climate conditions for regeneration is likely to continue this shift to non-ponderosa pine dominated systems in post-high severity landscapes with divergent avian communities (Kemp et al., 2019; Stevens-Rumann et al., 2022). These enduring ecosystem conversions may reduce overall suitable forest habitat for species in post-fire landscapes. The post-fire trajectories at our study sites likely reflect broader regional trends across the southwestern United States, where wildfires are increasingly burning with larger high-severity patches and at a greater frequency (Singleton et al., 2019).

4.3. Management implications

Ponderosa pine ecosystems in the Southwest are particularly vulnerable to wildfire-driven conversion (Davis et al., 2020) and provide important habitat to a variety of bird species (Block and Finch, 1997). Our study builds upon these findings, demonstrating fine scale conversion to non-forested ecosystems at over half of Hayman Fire high-severity sites and to non-forested or pinyon-juniper woodlands at over 40 % of Ponil Complex Fire high-severity sites. Our findings also echo research from landscapes in numerous other fire-adapted ecosystems that serve as important overarching management conclusions, including the combined importance of both maintaining mixed-severity fire mosaics (Smucker et al., 2005), while recognizing the crucial need to maintain mature vegetation to preserve habitat for a variety of species (Puig-Gironès et al., 2023; Rainsford et al., 2021).

Overall, managers should consider the extent to which high-severity patches dominate burned landscapes in future fires. As our findings show, management actions which aim to preserve low- to moderate-severity fire, with small patches of high-severity fire, in ponderosa pine-dominated ecosystems will maximize species diversity by providing a range of distinct vegetation structures that suit species with different life history traits (Roberts et al., 2020; Stillman et al., 2023). This mixed mosaic of severity replicates the historically heterogeneous nature of these forests, supporting species diversity and functional resilience by creating distinct vegetation structure and habitats needed for different nesting and foraging guilds.

In particular, unburned and low-severity patches serve as an important source of habitat for forest-associated species in post-fire

Table 7
Results of Wilcoxon Rank-Sum tests on vegetation structure differences between sites where a species was detected vs. non-detected sites for each frequently observed species at each fire. The P-value for each test result and direction of the association is provided; the p-values were computed in R using approximations due to the presence of ties. + * denotes positive relationship, significance of p < =.05; + ** denotes positive relationship, significance of p < =.001; — * denotes negative relationship, significance of p < =.05; — ** denotes negative relationship, significance of p < =.001.

Ponil Complex Fire: Forest-Associated Species	**% canopy cover**	**% tall shrub cover**	**Dead Basal Area (snag area)**
Black-headed Grosbeak	0.88	0.40	**0.01** — *
Cordilleran Flycatcher	**0.002** + *	0.24	0.79
Mountain Chickadee	**< 0.0001** + **	0.15	0.12
Plumbeous Vireo	**< 0.0001** + **	0.09	0.18
Western Tanager	**< 0.0001** + **	0.03 — *	0.75
Yellow-rumped Warbler	**< 0.0001** + **	0.11	0.57
Ponil Complex Fire: Woodland-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**Dead Basal Area (Snag Area)**
American Robin	**0.01** + *	0.19	0.30
Dusky Flycatcher	**0.006** — *	0.62	0.13
Northern Flicker	0.03	0.17	0.14
Virginia's Warbler	0.06	0.09	0.75
Warbling Vireo	**0.01** + *	0.92	0.30
Western Wood-Pewee	**< 0.0001** + **	**0.04** — *	0.94
Ponil Complex Fire: Scrub-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**% Grass Cover**
House Wren	**0.002** + *	0.80	0.73
Hayman Fire: Forest-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**Dead Basal Area (Snag Area)**
Black-headed Grosbeak	0.64	0.93	1.0
Dark-eyed Junco	**0.03** + *	0.12	0.34
Hammond's Flycatcher	**0.002** + *	0.11	0.15
Mountain Chickadee	**< 0.0001** + **	0.11	0.15
Pygmy Nuthatch	**< 0.0001** + **	**0.0004** —**	**0.006** —*
Steller's Jay	**0.03** + *	**0.05** —*	**0.0003** —**
Western Tanager	**< 0.0001** + **	**0.009** —*	**0.002** —*
White-breasted Nuthatch	0.16	0.90	0.72
Yellow-rumped Warbler	**3.37e−07** + **	0.77	0.32
Hayman Fire: Woodland-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**Dead Basal Area (Snag Area)**
American Robin	0.80	0.66	0.10
Broad-tailed Hummingbird	0.80	0.81	0.24
Chipping Sparrow	**0.0007** + **	0.10	0.14
Dusky Flycatcher	**0.002** —*	**0.002** + *	**0.03** + *
Mountain Bluebird	**0.0003** —**	0.47	0.69
Northern Flicker	0.22	0.74	0.96

(*continued on next page*)

Table 7 (*continued*)

Hayman Fire: Woodland-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**Dead Basal Area (Snag Area)**
Townsend's Solitaire	**0.002** + *	**0.03** —*	0.30
Warbling Vireo	0.15	0.77	0.82
Western Bluebird	0.61	0.39	0.588
Western Wood-Pewee	**0.002** + *	**0.03** —*	**0.004** —*

Hayman Fire: Grassland-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**% Grass Cover**
Brown-headed Cowbird	**0.02** + *	0.24	0.88
Vesper Sparrow	0.26	0.87	0.26

Hayman Fire: Scrub-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**% Grass Cover**
Green-tailed Towhee	**< 0.0001** —**	**0.0001** + **	**0.002** + *
House Wren	0.39	0.60	0.51

Hayman Fire: Desert-Associated Species	**% Canopy Cover**	**% Tall Shrub Cover**	**% Grass Cover**
Rock Wren	**< 0.0001** —**	**0.02** + *	**0.004** + *

landscapes (Reynolds et al., 2022; Woolet et al., 2023). Managers can mitigate post-fire conversion and preserve patches of unburned and low-severity habitat by pre-emptively incorporating refugia protection into fire planning, as suggested by Meddens et al. (2018). This is often achieved through actions such as pre-fire thinning and prescribed burning, to reduce fuel loads on the landscape (Parks et al., 2023). Post-fire planting, particularly in the interior of high-severity patches, may help mitigate conversion (Stevens-Rumann and Morgan, 2019). If post-fire conversion has already occurred or is acceptable, working to minimize invasive species and promote productive non-forest ecosystems may be warranted.

4.4. Conclusions

Vegetation structure and avian species composition differed across low vs high severity patches 20 years post-fire, and we found evidence of fine scale vegetation-type conversion in some high-severity patches. This indicates the likely persistence of divergent avian species and forest recovery patterns into the coming decades and potential implications for reduced habitat availability for forest-associated bird communities in post-fire footprints with higher proportions of high-severity patches. Mixed-severity mosaics across post-fire landscapes support a diverse array of bird species and distinct bird communities within different severities based on vegetation structure two decades after fire. However, while some high-severity fire increases landscape scale diversity across a burn scar, patches of low-severity fire have higher species richness and are a critical component of this mosaic. Fire-driven homogenization toward large high-severity patches across the landscape limits forest bird community resilience post-disturbance. This finding is especially relevant as wildfire size and severity increase (Mueller et al., 2020; Parks and Abatzoglou, 2020). The availability of a mosaic landscape with both small high-severity patches paired with large proportions low-severity patches that mimics historical fire regimes of these landscapes will become increasingly important for avian species conservation in the western US (Stillman et al., 2023; Tingley et al., 2016).

CRediT authorship contribution statement

Maria R Vicini: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Camille S. Stevens-Rumann:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Jody C. Vogeler:** Writing – review & editing, Supervision, Conceptualization. **Paula J. Fornwalt:** Writing – review & editing, Supervision, Conceptualization.

Declaration of Competing Interest

Maria Vicini reports financial support was provided by Colorado State University. Maria Vicini reports a relationship with Intermountain West Transformation Network that includes: funding grants. 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

Thank you to Colorado State University and the Transformation Network (NSF Grant #2115169) for funding this research. Thank you as well to Sam Gunning, Ali Goodrich, Jamie Woolet, and Alex Smilor for your extensive help collecting field data. Thank you to Lee Hughes, the Philmont Scout Ranch, Steve Alton, and the Manitou Experimental Forest for your enthusiasm and willingness to facilitate field data collection. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official US government determination or policy.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123058.

Data availability

Data will be made available on request.

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