

THESIS

THE IMPACT OF WILDFIRE ON AVIAN COMMUNITIES: EXPLORING HABITAT ASSOCIATIONS TWO  
DECADES AFTER FIRE

Submitted by

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## ABSTRACT

### THE IMPACT OF WILDFIRE ON AVIAN COMMUNITIES: EXPLORING HABITAT ASSOCIATIONS TWO DECADES AFTER FIRE

Large high-severity wildfires have been affecting ponderosa pine dominated systems for decades, yet minimal long-term research has been conducted to address how avian species are responding to vegetation recovery and wildfire-driven conversion multiple decades after wildfire in ponderosa pine ecosystems of the southwestern United States. Understanding how community dynamics differ between low- and high-severity portions of burned footprints, and how vegetation structure relates to species presence is crucial for species conservation efforts, especially as wildfires in the western U.S. continue to have larger proportions of high-severity fire compared to historical fires. To address this in the Southwest, our study sought to quantify vegetation recovery, avian community dynamics across low- and high-severity sites, and quantify species-specific relationships with current vegetation structure in two post-fire footprints two decades after fire. This study focused on the Ponil Complex Fire in northern New Mexico and the Hayman Fire in southern Colorado, both of which burned in 2002. We found continued divergence between vegetation recovery at low- and high-severity sites, though this divergence was more pronounced at the Hayman Fire. We found also significant dissimilarities in avian community composition between low- and high-severity sites, and significantly lower species richness at high-severity sites across both wildfires. Forest-associated bird species

presence was associated with more canopy cover and lower severity. Alternatively, lower canopy cover and higher severity were associated with the presence of a variety of grassland-, shrubland-, and desert-associated species. Our findings point to the importance of preserving pyrodiversity on the landscape to maximize suitable habitat for the greatest number of species, especially as it pertains to preserving adequate proportions of low-severity patches for forest-associated species who require intact canopy cover. However, large high-severity patches as the dominant component of the landscape will not support the most diverse array of bird communities 20+ years post fire.

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## CHAPTER 1 – The impact of wildfire on avian communities: exploring habitat associations two decades after fire

### 1.1 Introduction

Fires are an essential disturbance for a variety of terrestrial ecosystems across the globe (McLauchlan et al., 2020; Chia et al., 2015). Among the many influences wildfire exerts on ecosystem processes, wildfire shapes landscape heterogeneity through its influence on vegetation structure immediately after and in the decades following wildfire events (Bassett et al., 2017; Chia et al., 2015; Lyon, 2000; McLauchlan et al., 2020). This resulting landscape heterogeneity across burned areas leads to 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). High-severity patches in close proximity to low- and moderate-severity patches create distinct edge habitats for birds with different habitat requirements, and for species to fulfill the full extent of their foraging and nesting needs across both unburnt and burnt patches on a landscape (Fontaine and Kennedy, 2012; Stillman et al., 2019). Fire directly affects habitat importance for birds by altering the number of surviving mature trees, canopy cover, availability of snags, coarse woody debris, and understory vegetation structure. These factors influence prey abundance, nesting availability, and other factors that contribute to bird survival and reproductive success (George and Zack, 2008; Van Lear and Harlow, 2002). For example, the early seral-environment resulting from high-severity fire serves as a unique habitat type for bird species who require burned patches at different life stages and can lead to an increase in transitory habitat features such as woody debris, snags, and dense shrub cover, along with a short-term increase in prey (Hutto and Patterson, 2016; Smucker et al., 2005).

The influence of fire on wildlife habitat is particularly relevant in ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States, where wildfire is the principal disturbance, and spatial and temporal heterogeneity of wildfire is characteristic of the ecosystem's fire regime (Kaufmann et al., 2006; McKinney, 2019; Odion et al., 2014). Historically, ponderosa pine forests across the Southwest exhibited either a mixed-severity fire regime or primarily low-severity fire regime, depending on the geographical location within the Southwest. Ponderosa pine forests in Colorado, USA, historically exhibited a mixed-severity fire regime, whereas fires in these systems in New Mexico and Arizona historically had a more frequent, low-severity fire regime (Haffey et al., 2018). More specifically, the mixed-severity regime of Colorado ponderosa pine forests were comprised of frequent, low-severity fires (with mean fire interval (MFI) of 30 years or less) at lower elevations, and smaller, more variable, moderate- and high-severity fires occurring less frequently and further upslope (Kaufmann et al., 2005; McKinney, 2019; Woolman et al., 2022). In New Mexico and Arizona, frequent, low-severity fires historically occurred with some areas of high-severity fire patches in mixed-conifer forest and in areas with heavy fuel accumulations (Fulé et al., 1997; Swetnam and Baisan, 1996). Overall, forests consisted of mixed-age ponderosa pines (Savage and Mast, 2005), with a diverse range of spatial configurations, tree sizes, and varied tree clustering (Brown et al., 2015). This mosaic of patches provided a variety of potential habitat types within a relatively small geographical area (Singleton et al., 2021), and suited a wide variety of avian species adapted to the fire legacy (e.g., Kotliar et al., 2002; Kotliar et al., 2007; Fontaine and Kennedy, 2012; Latif et al., 2016; Vierling and Lentile, 2008).

However, since the later half of the 20th century, the fire regime of these ponderosa pine ecosystems has begun shifting toward larger and higher-severity fires due to a variety of compounding causes (Abatzoglou and Williams, 2016; Cassell et al., 2019; Mueller et al., 2020; Savage et al., 2013; Singleton et al., 2019). Euro-American settlement and the subsequent logging practices and livestock grazing of the late 1800s and early 1900s contributed to dense regeneration of ponderosa pine seedlings and saplings (Baker et al., 2007; Fitzgerald, 2005). At the same time, fire suppression became a main priority of the U.S. Forest Service, when it was established in the early 1900s. In turn, many previously open stands of ponderosa pine forests with only a few large, mature trees transformed into unnaturally dense, even-aged young ponderosa pine stands that contained more fine fuels than their historical counterparts (Baker et al., 2007; Fitzgerald, 2005). These densely-packed forests increased fuels and contributed to larger and higher-severity fires across the Southwest (Covington and Moore, 1994), with minimal research on how these larger, higher-severity fires influence avian community dynamics and species presence in the decades after wildfire in these areas.

Shifting fire regimes, due to land management over the last century, paired with climate change, present potential long-term ramifications for the resilience of ponderosa pine ecosystems and the long-term habitat availability for avian species who depend on forested ecosystems. After wildfire, successful seedling regeneration is critical for ecosystem recovery and resilience. Yet across the US Intermountain west, regeneration success has decreased in the 21st century, with the most dramatic shift in communities occurring in the southwestern US (Davis et al., 2023). As a result of regeneration failure, estimates have found that up to 16% of all ponderosa pine forests across the US intermountain West are at risk of wildfire-driven

conversion under certain climate warming scenarios (Davis et al., 2020; Woolman et al., 2022) which is defined as enduring and substantial change to the landscape, such as a change in the dominant species or vegetation type (Coop et al., 2020). The combination of wildfire-driven conversion and climate change potentially affect suitable avian habitat on multiple scales. At a large-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, which can lead to niche contraction (Hoecker and Turner, 2022). Species who occupy areas vulnerable to increased wildfire activity and vegetation-type conversion are likely most at-risk of more immediate niche contraction (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).

On a smaller scale, an increase in the area burned by high-severity fire also alters patch configuration and habitat structure across a burned landscape. Pyrodiversity, which is the variability of fire severity across a burn footprint, has been hypothesized to increase avian community diversity (Tingley et al. 2016). Yet as fire regimes shift, previously heterogeneous burned footprints with high pyrodiversity and a mix of smaller low-, moderate-, and high-severity patches will become more homogeneous in nature, leading to a larger proportion of high-severity patches outside a range of natural variability (Singleton et al., 2021), influencing how bird species utilize burn footprints after fire (Steel et al., 2021) and reducing overall pyrodiversity. These uncharacteristically large high-severity patches may undermine the benefits that high-severity fire has historically created for certain ponderosa-pine associated avian species, when high-severity patches were 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 burned and unburned habitat in the vicinity (i.e., these species would select burned habitat for potential snag abundance but select unburned habitat for live foraging opportunities (Latif et al., 2016)). Even burn specialists have been shown to utilize unburned habitat for foraging as juveniles, increasing their burned habitat usage as they mature (Stillman et al., 2019). Researchers who studied this topic in conifer forests of the Sierra Nevada and Southern Cascades found that overall bird community richness decreased as distance to patch edge increased (Steel et al., 2021). Results from Steel et al. (2021) pointed to patch interiors with fewer overall species, in addition to a shift in bird communities from forest-associated to non-forest associated species.

Despite the growing potential for forest-conversion in the Southwest after high-severity wildfire, few datasets exist on how forest and vegetation recovery impacts avian communities and their habitat associations multiple decades after wildfire in southwestern ponderosa pine ecosystems — especially in instances where the landscape does not follow historical recovery trajectories. Research on bird responses to wildfire prior to the early 2000s mostly treated wildfire as a homogenous disturbance, with little regard to fire severity (Hutto and Patterson, 2016). It was not until a study by Smucker et al. (2005) which incorporated severity metrics into the analysis that avian responses across studies became more aligned (Smucker et al., 2005; Hutto and Patterson, 2016). Many southwestern-focused publications that included fire severity metrics in analyses have mostly focused on time periods less than 20 years after fire.

As a result, research in these southwestern ponderosa pine ecosystems which addresses the link between long-term vegetation recovery and avian habitat associations is needed to better understand how vegetation structure is associated with species' presence and community patterns in the decades after wildfire. Understanding avian habitat associations are imperative to understand how avian communities are responding to vegetation succession in the long-term in these ecosystems, and whether these results indicate continued disparity between low- and high-severity burn patches. As "megafires" continue to occur (Stillman et al., 2019), potentially undermining expected recovery pathways and leading to novel habitat characteristics, understanding larger community dynamics are critical. This is especially relevant in southwestern ponderosa pine ecosystems because they are increasingly at risk of wildfire-driven forest conversion as a result of climate change and an increasing proportion of high-severity wildfire (Coop, 2023).

Here we examined two wildfires that burned in 2002. These fires were the Hayman Fire in southern Colorado and the Ponil Complex Fire in northern New Mexico. These fires provided a unique opportunity to study long post-fire periods that, though both burned in an extreme fire year for the Southwest, these wildfires had different patch configurations and proportion of high-severity patches (Hayes and Robeson 2011; Fornwalt et al., 2016; Coop et al., 2019). Specifically, we addressed three major objectives: 1) Determine how avian species richness differs across low- and high-severity sites two decades after fire, 2) Examine how avian community composition and vegetation structures differ across low- and high-severity sites two decades after fire, and 3) Quantify associations between frequently observed bird species and

vegetation structures two decades after fire, to understand habitat-bird associations in the post-fire landscape.

## **1.2 Methods**

### *1.2.1 Study Area*

This data was collected across two wildfires in the southwestern United States, with fires located in southern Colorado and northern New Mexico (Figure 1). In the summer of 2002, lightning caused the Ponil Complex Fire to ignite near Cimarron, New Mexico. Several days after burning as three separate fires, the fires merged into one fire (Hayes and Robeson, 2011). In its entirety, the fire burned across over 36,051 ha, and comprised a mix of primarily ponderosa pine forest, grasslands, and shrublands, along with mixed-conifer forest on some north-facing slopes, and pinyon-juniper woodlands (*Pinus edulis*, *Juniperus deppeana*, and *Juniperus scopulorum*) (Hayes and Robeson, 2009; Hayes and Robeson, 2011). The historical fire regime of this area consisted of frequent, low-severity fires (Moore et al., 1999; Hayes and Robeson, 2011; Parks et al., 2018), though areas of mixed-conifer in the burn footprint may have historically burned with a higher proportion of moderate- and high-severity fire. In total, 51% of the Ponil Complex Fire burned at moderate- to high-severity fire, out of a total of 36,051 ha (Coop et al., 2019). The burned area encompassed a range of private and public lands in northern New Mexico, including the Carson National Forest, Philmont Scout Ranch, and other private properties.

The Hayman Fire began burning in the summer of 2002 near Tappan Mountain, west of Colorado Springs and southwest of Denver, Colorado. In total, the fire burned 55,893 ha (Graham, 2003; Lewis et al., 2006). The Hayman Fire was the biggest wildfire in state history at the time and remains the fourth largest in the state at the time of publication (*Historical*

*Wildfire Information | Fire Prevention and Control*, n.d.). The fire primarily burned through forests consisting of ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) forests, and aspen (*Populus tremuloides*) stands (Graham, 2003). Historical fire regimes in the area reflected the mixed-severity fire regime of Colorado ponderosa pine forests, comprised of frequent, low-severity fires (MFI of 30 years or less) at lower elevations, and smaller, more variable, moderate- and high-severity fires occurring less often and further upslope (Kaufmann et al., 2005; McKinney, 2019; Woolman et al., 2022). The Hayman Fire burned with mixed-severity across its burn footprint. 65% of the Hayman Fire burned at moderate-to to high-severity, out of a total of 52,353 ha (Coop et al., 2019). Up to 70% of the post-fire landscape experienced total tree mortality which was unprecedented in its severity (Fornwalt et al., 2016).

To determine 30-year normals for the time period between 1991 and 2020 at each study location, we utilized the PRISM database (PRISM 2023). Research for the Ponil Complex Fire was conducted at the Philmont Scout Ranch, where temperatures peaked each August with a precipitation of 81.1 mm. Mean temps in the coldest month, January, averaged -0.6°C, and 19.9°C in the hottest month, July, throughout this time period. Research for the Hayman Fire was conducted near and within the Manitou Experimental Forest. 30-year normals indicated the highest precipitation in the month of August, peaking at 87.3 mm. August is also the hottest month on average, with a mean of 16.3°C, and coldest in January, with a mean of -4.1°C.

### *1.2.2 Site Selection*

In 2022, we established 70 sites within the Hayman Fire burn footprint, consisting of 30 high-severity and 40 low- to moderate-severity sites (Figure 1). Figure 2 provides an example picture for the site conditions at low- and high-severity sites for each fire. All sites were

established within the Pike-San Isabel National Forest. In 2023, we established 60 sites within the Ponil Complex Fire, consisting of 30 high-severity and 30 low- to moderate-severity sites. Elevations at Hayman Fire sites ranged from 2145 m to 2609 m. Elevations at Ponil Complex Fire sites ranged from 1836 m to 2490 m. All sites were established within the Philmont Scout Ranch. We measured bird presence between May and June of 2022 and 2023 to align with the breeding bird season (Ralph et al., 1993).

Prior to scouting both fires, we determined fire severity via the Monitoring Trends in Burn Severity (MTBS.gov last accessed on October 8, 2023) program data and reclassified the burn perimeter as either low- or high-severity in ArcGIS Pro (2021), with unburned, low- and moderate-severity grouped 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. Due to the high-severity nature of much of the Hayman Fire, in the field, we classified high-severity as 100% tree mortality for both fires. We classified low-severity and moderate-severity as any stand with evidence of trees that survived post-fire. A portion of the burned area in the Hayman Fire includes a 2700 ha high-severity patch ten times larger in size than any historical fire from the same area (Fornwalt et al., 2016; Graham, 2003). On account of the similar lack of overstory and wide extent for this large patch, we limited moderate- and high-severity site establishment to no more than 15 sites in that area. We established the remaining 15 sites in other moderate- or high-severity patches. Within both burn footprints, we established sites at least 50 m from the nearest public road, however, we did not avoid proximity to several private, emergency-only roads and hiking trails, because vehicle traffic was infrequent. We established sites at least 200 m from each other based on bird census recommendations from

Hutto et al., 1986. We avoided locations where post-fire management efforts were evident, including planting restoration efforts and salvage logging. We established sites only in areas with clear evidence of ponderosa pine or mixed-conifer forest to maintain consistency across both wildfires and their overlapping forest types.

### 1.2.3 Bird Surveys

Prior to the 2022 and 2023 field season, we thoroughly trained technicians on species identification for species common to the Hayman and Ponil Complex Fires. We used research studies from the area, local eBird data, field guides, and other relevant publications of birds associated with southwestern ponderosa pine, Douglas-fir, and aspen forests, as well as grassland- and shrubland associated species, to generate lists of species potentially occurring in the study sites (e.g., Bennetts et al., 1996; Morris et al., 1977; eBird, 2023; Finch, 1997). The aim of these lists were to serve as a reference guide for observers, based on recommendations from Ralph et al. (1995) to reduce observer bias toward certain species during point counts. During initial field days, we practiced species identification while establishing sites.

Once the sampling period began, we collected bird observation data each morning beginning 20 minutes before sunrise and finishing within 5 hours after sunrise via 8-minute point counts at each site. 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 extra care in study design was taken to minimize detection probability differences between counts. For example, each site was visited twice during the season (Ralph et al., 1995), which has been recommended as sufficient for improving model performance (Dettmers,

1999), determining bird presence vs absence, and calculating species richness (Siegel et al., 2001). At the beginning of each point count, we collected the following data points: start time, end time, date, precipitation, wind speed, cloud cover, and observers. To further reduce detection bias, we did not conduct point counts in heavy rain (anything above a light drizzle), snow, or wind speeds above 18 mph. During the count, we recorded all birds heard or seen within 200 m, by estimating the distance to each bird (after pre-season training with a rangefinder). We selected this distance to ensure accuracy across points and maintain independence across points. To combat any overlap between species and again reduce detection probability bias, we eliminated birds greater than 75 m from all statistical analyses, similar to methods from Vogeler et al., 2013.

We also recorded the method of bird detection, including if a visual ID was made and the sex was determined. The same experienced observer visited every point count across both seasons, with at least one additional crew member acting as an additional observer at each site. Following each count, observers thoroughly reviewed observations together to ensure no birds were double-counted or overlooked. 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). When applicable, we recorded unknown sounds and later identified them.

#### *1.2.4 Field Measurements*

We collected forestry measurements at all 130 sites where bird counts were conducted to capture immediate vegetation structure characteristics at each point count. The size of each site was 0.04 ha. From the site center, we extended four transects out to 12 m the cardinal

directions. Data collected at the site-level included aspect, slope, and site coordinates, which were recorded at the center of the site. Along each transect, we recorded 1-hour, 10-hour, and 100-hour fuels using modified Brown (1974) methods. We recorded 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 understory functional groups (shrub, forb, graminoid, and tree) and substrate (rock, bare ground, litter, woody debris, and moss) along each transect using the point-intercept sampling method and recording only the first vegetation “hit” going downwards. We quantified coarse woody debris via a subplot up to 6m on the transect. For each log in this subplot, we measured the diameter at each end of the log, the length of the log, and whether it was sound or rotten. We measured shrubs  $\geq 0.61$  m 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 shrub. We used the average height of the entire shrub or continuous shrub patch to determine the average height. We collected overstory information across the entire site, including percent canopy cover via a densitometer and diameter at breast height for all trees and saplings. We also counted and aged all seedlings. We aged ponderosa pine and Douglas-fir seedlings via the whorl-count method. We grouped aspen, pinyon pine, and juniper seedlings into four size classes based on height. Distance to the nearest five seed sources were calculated up to 200 m from site center for both ponderosa pine and Douglas-fir trees, along with juniper and pinyon pine when present.

#### *1.2.5 Statistical analysis*

Statistical analysis was performed in R (version 2022.02.0 “Prairie Trillium”). All analysis was performed at an  $\alpha = .05$  significance cutoff. To address Objective #1, we first classified sites

into high- and low-severity interior and edge groups for the Ponil Complex Fire. We created these classifications based on a spatial refugia layer from Walker et al. (2019). 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 via measurement in ArcGIS Pro. 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 classification for the Hayman Fire. However, despite extensive sampling across the burned area, our sample size for high-severity edge and low-severity interior sites were too small for analysis. Thus, we analyzed sites across simply low- vs high-severity sites. To categorize shrub cover groups across the fires, we split sites into low, moderate, and high shrub cover groupings. Low cover consisted of sites with 0-20% of the site having shrubs at least 0.61 m tall, moderate sites had between 20-40% cover, and high sites above 40% cover. Following this categorization, we assessed species richness across site types for normality via Shapiro-Wilks test in R using the *psynTur* package (Andrews, 2022), along with a visual assessment of Q-Q plots. Then, we ran a Two-Sample t-Test and One-Way Analysis of Variance (ANOVA) on these site-type categories to test for differences in species richness based on severity and shrub cover. We examined differences among groups using a Tukey's HSD test when ANOVA results were significant.

To assess vegetation and avian community dissimilarity across sites (Objective #2), we first created a summary table of vegetation structure variables. We assessed correlation between these variables via Spearman Correlation Coefficients and did not include highly correlated variables in the analysis. Due to non-normality, we performed Kruskal Wallis tests on canopy cover, live basal area, snag basal area, percent bare ground/rock, percent shrub,

percent graminoid, and 1000-hour fuels 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 seedling presence vs absence between low- and high-severity sites at each fire, including ponderosa pine, Douglas-fir, pinyon pine, and juniper seedlings (Table 3).

To analyze avian community dynamics at low- and high-severity sites, 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, 2022). 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). However, there is a tradeoff between complexity of interpretation and smaller stress values. For both fires, we selected K = 5 dimensions to get stress as close as possible to an acceptable value of 0.1, based on recommendations from Buttigieg and Ramette (2014). We then fit environmental and species vectors onto results from NMDS, to assess vegetation structure variables and species significantly correlated with the site distributions. We fit these vectors onto the NMDS using the *envfit* function in the *Vegan* package in R (Oksanen, 2022). The *envfit* function fits vectors of variables onto the ordination plot and assesses the significance of these fitted vectors using permutation of the selected variables (*Envfit Function - RDocumentation*, n.d.). The resulting plot scales vectors based on their correlation, so that stronger predictors have longer arrows pointed in the direction of the relationship in the resulting ordination plot.

Following the fitting of these environmental 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, 2022), to test for significant differences across sites based on site-type and shrub-type categories as grouping factors. We assessed the marginal effect of each term in the model.

To address Objective #3, 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 habitat 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 shrub cover across sites at each fire. Hypotheses varied based on habitat-associations for each species group (Table 1).

To further explore Objective #3, we fit logistic regression models when possible for all species observed within 75 m of at least 15 sites at either fire, as well as for species with enough observations at both fires to fit a logistic regression model across both fires. To fit models, we used the *Caret* package in R (Kuhn, 2023). We split data for each species into training and testing sets. We selected models with Area under the Curve (AUC) values of at least .7 (Mandrekar, 2010), and with a combined Sensitivity and Specificity value minimum as close to 1.5 as possible (Power et al., 2012). For each model, we tested a range of habitat variable combinations based on predictions about the ecological importance of various vegetation structures for each species (e.g., we tested percent grass cover for grassland-associated species). Due to multicollinearity among many vegetation structure variables, we calculated a variance inflation factor (VIF) for each potential model, and only considered

models with VIF values of < 10 (James et al., 2013). Models also had to have residual deviance values lower than the null deviance to be selected. From this point, we selected final models based on those which had the best overall AUC value based on results of the testing set, followed by the highest Receiver Operating Characteristic curve (ROC) value when AUC values were equal.

## **1.3 Results**

### *1.3.1 Vegetation structure across fire severities:*

Broadly, sites of the same severity had similar vegetation structures across the two fires for almost all variables tested (Table 2). For both canopy cover and live basal area, we found significant differences between low- and high-severity sites irrespective of the fire, and low-severity sites had significantly higher live basal area and canopy cover than high-severity sites. There were no significant differences for either of these variables when comparing values between low-severity sites of the Hayman vs Ponil Complex Fire, and similarly, no significant differences when testing values between high-severity sites of the Hayman vs Ponil Complex Fire. There were significant shrub cover differences between the fires, and the Ponil Complex Fire had greater overall shrub cover. There was also a significant difference in shrub cover between low- and high-severity sites at the Hayman Fire, but not between low- and high-severity sites at the Ponil Complex Fire. Snag basal area was significantly different between low- and high-severity at the Hayman Fire, with higher snag area at high-severity sites. However, it was not significantly different across low-severity comparisons between the fires, high-severity comparisons between the fires, or between low- and high-severity sites at the Ponil Complex Fire. Similarly, percent grass cover was significantly different between low- and high-severity at

the Hayman Fire, but was not significantly different between low- and high-severity sites at the Ponil Complex Fire. Percent bare ground/rock and 1000-hour fuels were both significantly different between low- and high-severity at the Hayman Fire and at the Ponil Complex Fire, and were not significantly different between similar severities across the fires. Conifer seedling presence was not significantly different between sites of the same severity across fires, but was significantly different between low- and high-severity sites at each fire (Table 3).

### 1.3.2 Avian community patterns across fire severities

We observed 65 species in total within 75 m of a site across both fires (Table 5). NMDS results demonstrate broad species groupings by severity within each fire, as well as significant species drivers of dissimilarity across the sites (Figure 3). For the Ponil Complex Fire, the stress value was 0.09. 25 species were significantly correlated with the site distribution patterns on the ordination plot at a significance value of  $p \leq 0.01$ , based on permutation tests of their fitted vectors from the Vegan package (Oksanen, 2022) (Figure 3; *only the species with  $p \leq .001$  are plotted for ease of interpretation*). Of these 25 species, species associated with high-severity edge and high-severity interior sites included the Woodhouse's Scrub Jay (*Aphelocoma woodhouseii*) and Green-tailed Towhee (*Pipilo chlorurus*). Blue-gray Gnatcatchers (*Poliophtila caerulea*) and Rock Wrens (*Salpinctes obsoletus*) were also generally observed at similar, high-severity edge sites. Low-severity edge sites consisted of Warbling Vireo (*Vireo gilvus*) and Cordilleran Flycatcher (*Empidonax occidentalis*) at similar sites, along with Northern Flicker (*Colaptes auratus*), Hammond's Flycatcher (*Empidonax hammondii*), Hairy Woodpecker (*Leuconotopicus villosus*), Steller's Jay (*Cyanocitta stelleri*), Mountain Chickadee (*Poecile gambeli*), and Townsend's Solitaire (*Myadestes townsendi*) at similar low-severity edge sites.

Species associated with low-severity, but more closely with low-severity interior sites, included House Wren (*Troglodytes aedon*), Yellow-rumped Warbler (*Setophaga coronata*), Western Wood-Pewee (*Contopus sordidulus*), Plumbeous Vireo (*Vireo plumbeus*), and Western Tanager (*Piranga ludoviciana*). Species who generally occurred at similar sites, but who did not exhibit a clear distinction for being more associated with low- or high-severity sites included Mourning Dove (*Zenaida macroura*), Lesser Goldfinch (*Spinus psaltria*), Cassin's Kingbird (*Tyrannus vociferans*), Bullock's Oriole (*Icterus bullockii*), and American Robin (*Turdus migratorius*). Virginia's Warbler (*Vermivora virginiae*) and Black-headed Grosbeak (*Pheucticus melanocephalus*) were also grouped together, without clear affinity for high- or low-severity sites. Environmental vectors also highlighted which vegetation characteristics influenced the distribution of sites along the NMDS ordination (Figure 4). Significant environmental vectors for the Ponil Complex Fire included percent canopy cover, live basal area, and percent bare ground/rock at each site (Table 6). Percent graminoid cover was trending toward significant at  $p = 0.063$ . However, due to high correlation among all these variables, only live basal area was included in the final result ( $p = 0.001$ ,  $R^2 = 0.65$ ). Results of PERMANOVA on the dissimilarity matrix indicated a significant difference between site types (Table 7;  $p = 0.0001$ ,  $F = 5.4$ ,  $R^2 = 0.22$ ). It also indicated a non-significant difference between shrub cover categories (low, moderate, and high shrub cover sites).

For the Hayman Fire, the stress value was 0.10. 23 species significantly drove site distribution patterns at a significance value of  $p \leq 0.01$  (Figure 3; *only the species with  $p \leq .001$  are plotted*). Of these 23 species, some clear groupings emerged in the data. Species composition at high-severity sites generally included Green-tailed Towhee, Mountain Bluebird

(*Sialia currucoides*), Vesper Sparrow (*Pooecetes gramineus*), Rock Wren, Sage Thrasher (*Oreoscoptes montanus*), Canyon Wren (*Catherpes mexicanus*), and Brewer's Sparrow (*Spizella breweri*). There were many species generally driving the low-severity site distribution, which likely reflects the significantly higher species richness at low-severity sites. These species included Chipping Sparrow (*Spizella passerina*), Mountain Chickadee, Townsend's Solitaire, Hammond's Flycatcher, Yellow-rumped Warbler, Pygmy Nuthatch (*Sitta pygmaea*), and Western Tanager. Western Wood-Pewee, White-breasted Nuthatch (*Sitta carolinensis*), and Steller's Jay also were generally associated with low-severity sites, but in a separate clustering from the previously mentioned species. Hairy Woodpecker did not naturally tend to occur with any other species, landing between low- and high-severity sites on the NMDS ordination plot. Other species not generally associated with low- or high-severity sites, but generally clustering together, included Northern Flicker, American Robin, Black-headed Grosbeak, House Wren, and Olive-sided Flycatcher (*Contopus cooperi*). Significant environmental vectors shaping the distribution of sites for the Hayman Fire included 1000-hr fuels, percent canopy cover, tall shrub cover, percent bare ground/rock, live basal area, snag basal area, and percent graminoid. Similar to the Ponil Complex Fire, highly-correlated variables were eliminated, and only those explaining the highest proportion of variance were kept in the final analysis. These significant variables were 1000-hour fuels, tall shrub cover, live basal area, snag basal area, and percent graminoid cover (Table 6). Live basal area had the highest R<sup>2</sup>, at 0.64 (p = 0.001). Results of PERMANOVA on the dissimilarity matrix indicated a significant difference between low- and high-severity site types (Table 7; R<sup>2</sup> = 0.16, F stat = 12.9, p < 0.0001).

### 1.3.3 Species richness across low- and high- severity sites

For both the Ponil Complex and Hayman Fires, species richness was significantly higher at all low-severity sites compared to all high-severity sites (Figure 5). Post-hoc testing for significance between edge vs interior sites at the Ponil Complex Fire indicated only overall significance between low- and high-severity at large, but not between any groupings of edge or interior sites. However, the difference in species richness between high-severity edge and high-severity interior sites at the Ponil Complex Fire were trending toward significant ( $p = 0.07$ ). After testing for species richness differences between severities, we tested for differences between shrub cover categories as well. Species richness was not significantly higher between low, moderate, and high shrub cover sites at the Ponil Complex Fire, but was trending toward significance ( $p = 0.06$ ).

#### *1.3.4 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 (Table 4). Our hypotheses were sometimes but not always supported, depending on the species and vegetation structure metric being measured (Table 1). At the Ponil Complex Fire, forest-associated species who supported our hypothesis that sites where these species were present would exhibit significantly higher percent canopy cover than sites where these species were not observed, included the Cordilleran Flycatcher, Mountain Chickadee, Plumbeous Vireo, Western Tanager, and Yellow-rumped Warbler. Sites where the Black-headed Grosbeak was observed did not have a significant relationship with canopy cover. Woodland-associated species who reflected trends we would expect based on their nesting guilds included the Warbling Vireo (higher canopy cover), Western Wood-Pewee (higher canopy cover), and Dusky Flycatcher (*Empidonax oberholseri*) (lower canopy cover), American

Robin, and Northern Flicker. Virginia's Warbler did not exhibit a significant difference in canopy cover between sites, nor did the House Wren, the only frequent scrub-associated species. Regarding other vegetation structure metrics, there were less apparent trends for most species. Out of all species, only the Western Tanager and Western Wood-Pewee exhibited significant, negative relationships with tall shrub cover. Out of all species, only the Black-headed Grosbeak had a significant, negative relationship with snag basal area.

For the Hayman Fire, forest- and woodland-associated species that were present at sites with significantly higher percent canopy cover (as hypothesized) included the Dark-eyed Junco (*Junco hyemalis*), Hammond's Flycatcher, Mountain Chickadee, Pygmy Nuthatch, Steller's Jay, Western Tanager, Yellow-rumped Warbler, Chipping Sparrow, Townsend's Solitaire, and Western Wood-Pewee. Surprisingly, Brown-headed Cowbird (*Molothrus ater*), a grassland-associated species, was also associated with higher percent canopy cover at sites where it was observed. Dusky Flycatcher and Mountain Bluebird are the only two woodland-associated species who exhibited an association with lower percent canopy cover, along with the Green-tailed Towhee (scrub-associated) and Rock Wren (desert-associated). When analyzing canopy cover, other species' results were not significant. Similar to the Ponil Complex Fire, fewer species had significant relationships with tall shrub cover and dead basal area between present vs non-present sites, compared to canopy cover as a habitat metric. Forest- or woodland-associated species with a significant, negative relationship with tall shrub cover included the Pygmy Nuthatch, Steller's Jay, Western Tanager, Townsend's Solitaire, and Western Wood-Pewee. Species with a significant, positive relationship with tall shrub cover at present sites included the Dusky Flycatcher, Green-tailed Towhee, and Rock Wren. Finally, sites where the

Pygmy Nuthatch, Steller's Jay, Western Tanager, and Western Wood-Pewee were observed had lower dead basal area. The Dusky Flycatcher was associated with higher dead basal area. Finally, Green-tailed Towhee and Rock Wren were associated with higher percent grass cover, as expected.

### *1.3.5 Vegetation structures associated with individual species presence*

We tested logistic regression models for the same set of species observed at least 15 times at each fire (Table 8). For the Ponil Complex Fire, we successfully fit logistic regression models for three species. These species included two forest-associated species, the Western Tanager (AUC = 1.00) and Plumbeous Vireo (AUC = 0.83), and one open-woodland associated-species, the Western Wood-Pewee (AUC = 0.75). For all three of these species, univariate models performed best, with site type as the sole predictor. In all instances, these species were associated with low-severity sites. For the Plumbeous Vireo, a competing model with site type and canopy cover as predictor had a lower AUC (0.93), but higher ROC (0.88).

For the Hayman Fire, we successfully fit logistic regression models for Mountain Chickadee, Pygmy Nuthatch, Green-tailed Towhee, Rock Wren, and Yellow-rumped Warbler (Table 8). Of these, Mountain Chickadee, Pygmy Nuthatch, and Yellow-rumped Warbler are forest-associated species. Top models for these three forest-associated species' models included just percent canopy cover as a predictor (Pygmy Nuthatch, AUC = 1.00), percent canopy cover and dead basal area as predictor variables combined (Yellow-rumped Warbler; AUC = 0.90, VIF < 5), or with site type and dead basal area as predictors (Mountain Chickadee; AUC = 0.83, VIF < 10). Overall, species exhibited a positive relationship with low-severity sites and higher canopy cover, as one might expect for forest species. It is interesting to note that

the higher dead basal area was also an almost-significant predictor for the Mountain Chickadee ( $p = 0.06$ ), a secondary cavity nester. While higher dead basal area was not a significant predictor for the Yellow-rumped Warbler, including it in the final model slightly out-performed other model candidates that combined canopy cover and site type, canopy cover alone, or site type alone. The remaining two successful models were for a desert-associated species, Rock Wren, and a scrub-associated species, Green-tailed Towhee. For the Rock Wren model, simply including site type as a predictor fit a successful model (AUC = 0.88). For Green-tailed Towhee, a combination of site type and tall shrub cover as predictors created the best model (AUC = 0.79). Opposite to the forest-associated species, these species were associated with high-severity sites. In the case of Green-tailed Towhee, the model also indicated a positive relationship with greater tall shrub cover.

Finally, two species' models performed successfully across the two fires, the Yellow-rumped Warbler and Western Tanager. For the Yellow-rumped Warbler model, a combination of site type and percent canopy cover was best (AUC = 0.82, VIF <5). For the Western Tanager model, a combination of site type, fire type, and percent canopy cover performed best (AUC = 0.92, VIF < 10). As a whole, site type (i.e., severity) and percent canopy cover were frequently the most important predictors for models across species at either or both fires.

## **1.4 Discussion**

### *1.4.1 Overview*

We examined bird communities and their response to fire severity and vegetation structure two decades after wildfire in southwestern ponderosa pine forests. To accomplish this, we analyzed differences in composition and species richness across low- and high-severity

sites and investigated species-specific associations with severity and vegetation structure on the post-fire landscape. We found that severity had mixed effects on avian community dynamics at a fine habitat scale. Avian community composition at low- and high-severity sites continue to be divergent 20 years post-fire, and high-severity sites had significantly lower species richness compared to low-severity sites. Burn severity and canopy cover were consistently the most associated factors with species presence of individual bird species. To date, there is minimal research that addresses the long-term avian response to vegetation succession in ponderosa pine-dominated ecosystems of the southwestern United States at least 20 years post-fire. Our findings indicate the continual importance of pyrodiversity, or mixed-severity wildfire mosaics, for maximizing species richness in these frequent fire ecosystems (Bowman et al., 2016; Tingley et al., 2016). These findings also indicate that wildfires with a large proportion of high-severity patches do not facilitate bird species richness in the long-term compared to wildfires with greater heterogeneity. A mix of low-severity and high-severity patches prompted overall greater richness of bird species with different habitat requirements, and low-severity patches supported the most species 20 years after fire. Finally, the distinct differences in vegetation structure and conifer regeneration between low vs high-severity sites at both fires, paired with the significant differences in the associated bird communities, highlight the enduring influence of high-severity wildfire in these systems. Southwestern ponderosa pine ecosystems are increasingly at risk of wildfire-driven conversion (Coop et al., 2020; Guiterman et al., 2022), and our results indicate that conversion in high-severity patches at these fires has led to significantly different bird communities at least two decades after fire.

#### *1.4.2 Influence of severity on species richness*

Overall, the lower species richness at high-severity sites reflects what we expected based on the characteristics of the post-fire landscape for both fires. Research has shown that vegetation structure in burned areas shapes the effect of fire on bird community composition (Barton et al., 2014), and there is a relationship between species richness and foliage height diversity (Culbert et al. 2013; MacArthur and MacArthur, 1961; Wood et al., 2013), as well as mean canopy height (Culbert et al., 2013). At the Hayman Fire, our research supports these findings, because there continued to be minimal tree regeneration, low shrub cover, and minimal canopy cover across high-severity sites at the Hayman Fire. These high-severity patches in the Hayman post-fire landscape, with large swathes of non-forested area and minimal shrub cover, lacked the vegetation structure necessary to support a greater number of species compared to low-severity sites with extensive canopy cover. The Ponil Complex post-fire landscape had higher tall shrub cover at high-severity sites (an average of 22% cover compared to just 2% cover at Hayman Fire high-severity sites). However, similar to the Hayman Fire, high-severity sites lacked live canopy cover from mature trees. Our lower species richness findings at high-severity sites at the Ponil Complex Fire indicate that despite more tall shrub cover at high-severity sites, this mid-story cover still did not offset the overall impact of burn severity and enduring canopy cover loss at high-severity sites for species richness. This was further supported by our findings that species richness was not significantly different across different shrub cover categories. Our results echo findings that found lower species richness in high-severity patches across boreal and hemiboreal Northern American regions (Zlonis et al., 2019), and conifer forests of California (Tingley et al., 2016), but contradict those in the upper-mixed conifer zone of Oregon (Fontaine et al. 2009). Ultimately, our species richness findings at

these two wildfires highlight the enduring impact of high-severity fire in ponderosa-pine dominated ecosystems at least twenty years post-fire, and potentially further if similar vegetation structure persists in the coming decades as a result of wildfire-driven conversion.

Recent research into high-severity patch size has also found lower species richness at high-severity interiors than at high-severity edges, with high-severity interiors containing a subset of the species present at high-severity edge sites (Steel et al., 2021). Similarly, a study highlighting a woodpecker indicator species found higher species occupancy in areas with more varied severities, such as in high-severity patches in proximity to low-severity areas (Stillman et al., 2023). While our species richness results were non-significant between high-severity interior and high-severity edge sites at the Ponil Complex Fire, high-severity interior sites had the lowest species richness of any group and were trending toward significant ( $p = 0.07$ ), warranting further study into how increasingly large high-severity patches will influence bird communities in these systems differently than historically smaller high-severity patch sizes.

#### *1.4.3 Influence of severity on vegetation structure and avian community composition*

Literature regarding avian response to wildfire often uses time-since-fire as a proxy for vegetation recovery (e.g., Hutto and Patterson, 2016; Smucker et al. 2005; Taillie et al., 2018). Yet additional research into how vegetation recovery shapes avian responses further than 10 years post-fire is warranted (Franklin et al., 2022; Vierling & Lentile, 2008), with evidence that findings may not transfer across ecosystems (Rainsford et al., 2021). Therefore, we prefaced our analysis of community composition at low- vs high-severity sites with an analysis of vegetation recovery across the sites. Based on significant differences in percent canopy cover, live basal area, dead basal area, percent graminoid cover, 1000-hour fuels, percent shrub cover,

and conifer regeneration between low- and high-severity sites at both fires, we concluded there are still significantly different recovery patterns occurring at low- vs high-severity sites 20 years post-fire, similar to other findings (Fornwalt et al., 2018).

Likewise, avian community composition at low- and high-severity sites diverged considerably across both fires. Our multivariate analysis pointed to distinct avian communities across severities, with low-severity associated birds, high-severity associated birds, and species without a clear distinction for preference between the two (generalist species, edge specialists, etc.). This was expected, given that vegetation structure differed significantly between low- and high-severity sites and previous literature has highlighted species-specific habitat requirements as a strong driving factor in wildlife responses to fire (e.g., Vierling and Lentile, 2008, Van Lear and Harlow, 2002). Thus, severity continued to contribute to divergent bird communities at least 20 years after fire.

We also found that more overall species had a strong association with low-severity sites than high-severity sites at both fires. Low-severity sites typically included mature ponderosa pine trees and extensive canopy cover, which reflects other research in southwestern ponderosa pine forest that found the highest breeding bird abundance and richness in forest stands with mature ponderosa pine trees (Rosenstock, 1996). Fewer bird species were clearly associated with high-severity sites or their vegetation structure (e.g., lower canopy cover) and this was more pronounced at the Ponil Complex Fire than at the Hayman Fire. At the Ponil Complex Fire, features such as shrub cover, grass cover, and snag basal area, which benefit non-forest-associated species, were not significantly different between low- and high-severity sites. Thus, we hypothesize that shrub-associated species like Virginia's Warbler could meet their

habitat requirements at sites of any severity at the Ponil Complex Fire, rather than exclusively at high-severity sites. In addition, while high-severity fire creates many ephemeral habitat benefits for bird species immediately post-fire, including an increase in prey and suitable cavity nester habitat (White et al., 2015), these benefits would have dissipated 20 years post-fire.

More high-severity sites at the Ponil Complex Fire were considered edge sites located closer to a refugia patch than at the Hayman Fire, where all our sites were greater than 100 m from a refugia patch. High-severity patch proximity to unburnt 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). In addition, while the Hayman Fire burned with an unprecedented amount of high-severity (Fornwalt et al., 2016), researchers studying the Ponil Complex Fire found that there was not a large change in the patch structure across the landscape after the fire, meaning the fire mirrored historic burn severity patterns, with a mosaic of low-, moderate-, and high-severity patches (Hayes and Robeson, 2009). At the Ponil Complex Fire, this likely influenced the presence of edge-associated species who may not have displayed a clear affinity for high-severity sites in the results, but likely benefited from edge sites where they could take advantage of features across both low- and high-severity sites (Zlonis et al., 2019). For example, the Olive-Sided Flycatcher is an edge-associated species who may not have shown a clear affinity for high-severity sites, but may opt for edge sites, where they can benefit from vegetation features across both low- and high-severity (Zlonis et al., 2019). At the same time, large high-severity patch sizes with greater amounts of patch interior at the Hayman Fire likely reduced the ability for species to benefit fully from a variety of habitat types, limiting high-severity habitat use to mostly birds with clear

grassland- or desert-type habitat requirements (such as the Western Meadowlark, Rock Wren, and Vesper Sparrow).

Overall, the different avian communities at low- and high-severity sites, along with the variety of generalist and edge-associated species present at both fires (e.g., American Robin, Olive-sided Flycatcher, Black-headed Grosbeak, etc.), support the pyrodiversity-biodiversity hypothesis, which posits that heterogeneity across the landscape is important for maximizing the number of species on the landscape (Tingley et al., 2016). At the same time, however, our findings pointed toward the presence of more species that benefited from low-severity vegetation structures. Thus, while grassland-, desert- and shrubland-associated species utilized high-severity sites in our fires, we conclude that a large proportion of high-severity fire still reduces the overall species richness on the landscape 20 years after fire. This is especially relevant in instances of large high-severity patches with large interior space, where these interiors supported fewer species than edges in other ecosystems (Steel et al., 2021), though our sampling design did not properly capture this variability.

#### *1.4.4 Species-specific habitat associations*

Canopy cover and severity had the strongest associations with individual species presence. A combination of these variables predicted the detection of many common forest-associated species that had a positive association with higher canopy cover and a negative association with high-severity fire sites (including species such as Pygmy Nuthatch, Mountain Chickadee, Western Tanager, and Plumbeous Vireo). For some shrubland-, grassland-, and desert-associated species, the flipside also remained true, where lower canopy cover and high-severity fire were associated with Dusky Flycatcher presence at the Ponil Complex Fire, and

several species at the Hayman Fire, including the Rock Wren and Green-tailed Towhee. The major influence of fire severity and canopy cover in our study reflects other sources which hypothesize that greater overstory cover provides improved foraging and protection from predators for wildlife (Barton et al., 2014), as well as research that found fire severity drove variations in habitat structure across burned areas multiple decades after fire (Roberts et al., 2020). Additional post-fire literature has also highlighted the importance of canopy cover in moderating the effect of fire on bird species, and recommended utilizing canopy cover and structure when managing for canopy-associated species (Franklin et al., 2023).

At the Ponil Complex Fire in particular, canopy cover was almost the sole important metric for predicting species presence, compared to the relatively minimal correlations between species and shrub cover, grass cover, or snag area. Higher/lower snag and shrub cover were associated with only a few species, despite what we expected due to research that the presence of mature ponderosa pine, large snags, and gambel oak (*Quercus gambelii*) cover are all generally important predictors for southwestern bird communities (Rosenstock, 1996), and the fact that species such as the Pygmy Nuthatch, Mountain Chickadee and Western Wood-Pewee are cavity nesters who utilize snags. Due to the high correlation between live basal area and canopy cover at our sites, live basal area likely also exhibits this relationship with bird species across our sites. We also did not measure associations between species presence and 1000-hour fuels due to the high multicollinearity between this and other variables selected, though a study in Nebraska ponderosa pine forests found that coarse woody debris was an important factor for determining cavity nester distributions (Keele et al., 2019).

#### *1.4.5 Management implications*

As our findings and other research shows, management actions which aim to preserve both low- and high-severity patches and reduce the overall proportion of high-severity patches across the landscape 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). Furthermore, unburned and low-severity patches serve as an important source of habitat for forest-associated species in post-fire landscapes (Reynolds et al., 2022; Woolet et al., 2023). Managers should ideally identify desired forested habitats on the landscape before a fire occurs, to proactively incorporate preservation into fire planning, as suggested by Meddens et al. (2018). Managers can accomplish this by promoting forest resilience before a fire occurs, via actions such as pre-fire thinning and prescribed burning, to reduce fuel loads on the landscape (Parks et al., 2023) and maintain habitat heterogeneity across the landscape.

In instances where a fire has already occurred, managers should aim to allocate planting resources to the interiors of large high-severity patches, where natural regeneration is unlikely to occur (Chambers et al., 2016; Coop et al., 2020), and bird species richness will most likely be the lowest a couple decades after the fire (Steel et al., 2021). In addition, managers should aim to retain large diameter snags as habitat structures in post-fire landscapes, so that bird species can benefit from the ephemeral benefits of high-severity fire (Chambers and Mast, 2005).

#### *1.4.6 Study Limitations and additional research needs*

The overarching influence of canopy cover and lack of abundance data in our study likely masked fine-scale habitat associations for a variety of species at our study sites, such as the requirement of snag availability for cavity nesters (Ganey, 2016). Future studies that capture abundance metrics, or quantify behavioral differences such as nest selection, foraging

behavior, or reproductive success, could further quantify fine-scale habitat associations for bird species. Furthermore, we took many precautions to reduce detection probability bias by limiting observations to within 75 m, only conducting counts in good weather, and visiting sites twice during the season. 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). Therefore, we are confident in our modeled results for more commonly observed species. However, we did not examine habitat relationships for difficult to observe, rare, or more variable species due to detection probability differences. Capturing these habitat relationships in future studies would help to better understand the full range of bird community dynamics.

Further, we would improve our study by adding additional edge and patch metric data into analysis. More detailed data on patch configuration across the entire landscape could better model species responses and community richness patterns across a patch gradient. Similarly, remote sensing products could offer insight into more-detailed vertical vegetation structure differences between sites or provide more detailed insights into habitat and nesting selection for bird species (e.g., Vogeler et al., 2016). Future studies should aim to better quantify different layers of the canopy structure to capture additional vegetation metrics such as more detailed midstory information. While our study focused on fine-scale habitat selection based on site-specific measurements, future work should incorporate remote sensing products to capture a continuous gradient of vegetation structure across larger scales. This could help to compare these post-fire habitat associations at both small and large scales and determine which scale is most important for various bird species and their post-fire habitat selections.

Finally, because species-specific relationships may vary based on geographical locations, even within other frequent fire systems, managers and researchers alike need to be cautious when interpreting results across different ecosystems. Future research may aim to include a chronosequence across future decades, to understand whether our findings persist for more decades post-fire, especially under changing climate regimes.

#### *1.4.7 Conclusions*

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). Ultimately, whether successful regeneration occurs in future decades in these burned landscapes will have widespread implications for whether our findings 20 years post-fire persist into the coming decades. Our results provide a foundation for site conditions 20 years post-fire and warrant additional investigation into longer time scales in these ecosystems. Our findings highlight the importance of mixed-severity mosaics across post-fire landscapes by demonstrating that low- and high-severity fire patches support bird species and distinct bird communities with contrasting habitat needs two decades after fire. Our results also show that patches of low-severity fire had significantly higher species richness than high-severity patches at both fires. This is especially relevant as “megafires” increase the proportion of high-severity fire across the landscape, because these findings indicate high-severity patches support fewer overall species than low-severity patches. Managers must consider the extent to which high-severity patches dominate burned landscapes in future fires, and how to manage these landscapes for the biodiversity of these forests. The availability of a mosaic landscape with both high-severity patches paired with a suitable amount of low-severity habitat will become an increasingly

important consideration for avian species conservation in the western U.S. (Stillman et al., 2023; Tingley et al., 2016), given increases in high severity wildfires (Mueller et al., 2020; Parks and Abatzoglou, 2020).

## 1.5 Tables and Figures

### 1.5.1 Tables

**Table 1:** Habitat association hypotheses for the species and variables tested by Wilcoxon-Rank Sum Tests. In the Wilcoxon-Rank Sum results table, species are organized into the same habitat association categories provided by this table.

Habitat association	Canopy Cover Hypothesis	Shrub Cover Hypothesis	Dead Basal Area Hypothesis	Grass Cover Hypothesis
<b>Forest-Associated Species</b>	<i>Sites where this species was detected will have <b>higher % canopy cover</b> than sites where it was not detected.</i>	<i>Sites where this species was detected will have <b>lower % shrub cover</b> than sites where it was not detected.</i>	<i>Sites where cavity nester species within this group were detected will have <b>higher dead basal area</b> than sites where it was not detected. Other nesting guilds will not exhibit a preference.</i>	<i>Not tested</i>
<b>Open-Woodland Associated Species</b>	<i>Sites where tree or cavity nesters species within this group were detected will have <b>higher canopy cover</b>. Sites where scrub or ground nester species were detected will have <b>lower canopy cover</b>.</i>	<i>Sites where tree or cavity nesters species within this group were detected will have <b>lower shrub cover</b>. Sites where scrub or ground nester species were detected will have <b>higher shrub cover</b>.</i>	<i>Sites where cavity nesters or flycatcher species within this group were detected will have <b>higher dead basal area</b>. Species belonging to other foraging and/or nesting guilds will not exhibit a preference.</i>	<i>Not tested</i>
<b>Scrub-Associated, Desert-Associated Species, or Grassland-Associated Species</b>	<i>Sites where this species was detected will have <b>lower % canopy cover</b> than sites where it was not detected.</i>	<i>Sites where this species was detected will have <b>higher % shrub cover</b> than sites where it was not detected.</i>	<i>Not tested</i>	<i>Sites where this species was detected will have <b>higher % grass cover</b> than sites where it was not detected.</i>

**Table 2:** Mean vegetation characteristics at low- and high-severity sites across the Hayman and Ponil Complex 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  $\alpha = .05$  significance level).

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

**Table 3:** 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	LL	70	< 0.0001
HH	PH	60	0.44
HH	PL	60	0.002
LL	PH	70	0.0009
LL	PL	70	0.03
PH	PL	60	0.02

**Table 4:** 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. Frequently observed species are defined here as those that were observed as present on at least 15 sites. + \* denotes positive relationship, significance of  $p \leq .05$ ; + \*\* denotes positive relationship, significance of  $p \leq .001$ ; — \* denotes negative relationship, significance of  $p \leq .05$ ; — \*\* denotes negative relationship, significance of  $p \leq .001$

<b>Ponil Complex Fire: Forest-Associated Species</b>	<b>% Canopy Cover</b>	<b>% Tall Shrub Cover</b>	<b>Dead Basal Area (Snag Area)</b>
<b>Black-headed Grosbeak</b>			— *
<b>Cordilleran Flycatcher</b>	+ *		
<b>Mountain Chickadee</b>	+ **		
<b>Plumbeous Vireo</b>	+ **		
<b>Western Tanager</b>	+ **	— *	
<b>Yellow-rumped Warbler</b>	+ **		
<b>Ponil Complex Fire: Woodland-Associated Species</b>	<b>% Canopy Cover</b>	<b>% Tall Shrub Cover</b>	<b>Dead Basal Area (Snag Area)</b>
<b>American Robin</b>	+ *		
<b>Dusky Flycatcher</b>	— *		
<b>Northern Flicker</b>			
<b>Virginia's Warbler</b>			
<b>Warbling Vireo</b>	+ *		
<b>Western Wood-Pewee</b>	+ **	— *	
<b>Ponil Complex Fire: Scrub-Associated Species</b>	<b>% Canopy Cover</b>	<b>% Tall Shrub Cover</b>	<b>% Grass Cover</b>
<b>House Wren</b>	+ *		
<b>Hayman Fire:</b>	<b>% Canopy Cover</b>	<b>% Tall Shrub Cover</b>	<b>Dead Basal Area (Snag Area)</b>

<b>Forest-Associated Species</b>			
<b>Black-headed Grosbeak</b>			
Dark-eyed Junco	+	*	
<b>Hammond's Flycatcher</b>			
Mountain Chickadee	+	**	
<b>Pygmy Nuthatch</b>			
	+	**	—*
Steller's Jay	+	*	—**
<b>Western Tanager</b>			
	+	**	—*
<b>White-breasted Nuthatch</b>			
<b>Yellow-rumped Warbler</b>			
	+	**	
<b>Hayman Fire:</b>	<b>% Canopy Cover</b>	<b>% Tall Shrub Cover</b>	<b>Dead Basal Area (Snag Area)</b>
<b>Woodland-Associated Species</b>			
<b>American Robin</b>			
<b>Broad-tailed Hummingbird</b>			
Chipping Sparrow	+	**	
Dusky Flycatcher	—*	+	*
<b>Mountain Bluebird</b>			
	—	**	
<b>Northern Flicker</b>			
<b>Townsend's Solitaire</b>			
	+	*	—*
<b>Warbling Vireo</b>			
<b>Western Bluebird</b>			
<b>Western Wood-Pewee</b>			
	+	*	—*

Hayman Fire: Grassland- Associated Species	% Canopy Cover	% Tall Shrub Cover	% Grass Cover
Brown-headed Cowbird	+*		
Vesper Sparrow			
Hayman Fire: Scrub-Associated Species	% Canopy Cover	% Tall Shrub Cover	% Grass Cover
Green-tailed Towhee	—**	+**	+*
House Wren			
Hayman Fire: Desert-Associated Species	% Canopy Cover	% Tall Shrub Cover	% Grass Cover
Rock Wren	—**	+*	+*

**Table 5:** List of all species observed within 75 m of a site at either fire. Habitat associations categorized based on classifications from AllAboutBirds.org, a website from the Cornell Lab.

Species Name	Scientific Name	Fire	Foraging Behavior	Nesting Guild	Habitat Association
American Bushtit	<i>Psaltriparus minimus</i>	Ponil	Foliage Gleaner	Tree	Scrub
American Kestrel	<i>Falco sparverius</i>	Ponil	Aerial Diver	Cavity	Grasslands
American Robin	<i>Turdus migratorius</i>	Both	Ground Forager	Tree	Open Woodlands
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	Ponil	Flycatcher	Cavity	Open Woodlands
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	Both	Foliage Gleaner	Tree	Forests
Blue-Gray Gnatcatcher	<i>Polioptila caerulea</i>	Ponil	Foliage Gleaner	Tree	Forests
Brewer's Sparrow	<i>Spizella breweri</i>	Hayman	Foliage Gleaner	Shrub	Scrub
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	Both	Hovering	Tree	Open Woodlands
Brown-headed Cowbird	<i>Molothrus ater</i>	Both	Ground Forager	Tree	Grasslands
Bullock's Oriole	<i>Icterus bullockii</i>	Ponil	Foliage Gleaner	Tree	Open Woodlands

<b>Canyon Wren</b>	<i>Catherpes mexicanus</i>	Hayman	Ground Forager	Cliff	Deserts
<b>Cassin's Finch</b>	<i>Haemorhous cassinii</i>	Hayman	Ground Forager	Tree	Forests
<b>Cassin's Kingbird</b>	<i>Tyrannus vociferans</i>	Ponil	Flycatcher	Tree	Open Woodlands
<b>Chipping Sparrow</b>	<i>Spizella passerina</i>	Both	Ground Forager	Shrub	Open Woodlands
<b>Clark's Nutcracker</b>	<i>Nucifraga columbiana</i>	Both	Foliage Gleaner	Tree	Forests
<b>Cliff Swallow</b>	<i>Petrochelidon pyrrhonota</i>	Ponil	Aerial Forager	Cliff	Lakes and Ponds
<b>Common Raven</b>	<i>Corvus corax</i>	Both	Ground Forager	Cliff	Forests
<b>Cordilleran Flycatcher</b>	<i>Empidonax occidentalis</i>	Both	Flycatcher	Tree	Forests
<b>Dark-eyed Junco</b>	<i>Junco hyemalis</i>	Both	Ground Forager	Ground	Forests
<b>Dusky Flycatcher</b>	<i>Empidonax oberholseri</i>	Both	Flycatcher	Shrub	Open Woodlands
<b>Evening Grosbeak</b>	<i>Coccothraustes vespertinus</i>	Ponil	Ground Forager	Tree	Forests
<b>Grace's Warbler</b>	<i>Setophaga graciae</i>	Ponil	Foliage Gleaner	Tree	Forests
<b>Gray Flycatcher</b>	<i>Empidonax wrightii</i>	Ponil	Flycatcher	Shrub	Open Woodlands
<b>Green-tailed Towhee</b>	<i>Pipilo chlorurus</i>	Both	Ground Forager	Shrub	Scrub
<b>Hairy Woodpecker</b>	<i>Leuconotopicus villosus</i>	Both	Bark Forager	Cavity	Forests
<b>Hammond's Flycatcher</b>	<i>Empidonax hammondii</i>	Both	Flycatcher	Tree	Forests
<b>Hermit Thrush</b>	<i>Catharus guttatus</i>	Both	Ground Forager	Ground	Open Woodlands
<b>House Wren</b>	<i>Troglodytes aedon</i>	Both	Foliage Gleaner	Cavity	Scrub
<b>Lark Sparrow</b>	<i>Chondestes grammacus</i>	Hayman	Ground Forager	Ground	Grasslands
<b>Lesser Goldfinch</b>	<i>Spinus psaltria</i>	Both	Foliage Gleaner	Tree	Open Woodlands
<b>Lewis's Woodpecker</b>	<i>Melanerpes lewis</i>	Ponil	Aerial Forager	Cavity	Open Woodlands
<b>MacGillivray's Warbler</b>	<i>Geothlypis tolmiei</i>	Ponil	Foliage Gleaner	Shrub	Open Woodlands
<b>Mountain Bluebird</b>	<i>Sialia currucoides</i>	Both	Flycatcher	Cavity	Open Woodlands
<b>Mountain Chickadee</b>	<i>Poecile gambeli</i>	Both	Foliage Gleaner	Cavity	Forests

<b>Mourning Dove</b>	<i>Zenaida macroura</i>	Both	Ground Forager	Tree	Open Woodlands
<b>Northern Flicker</b>	<i>Colaptes auratus</i>	Both	Ground Forager	Cavity	Open Woodlands
<b>Olive-sided Flycatcher</b>	<i>Contopus cooperi</i>	Both	Flycatcher	Tree	Open Woodlands
<b>Pinyon Jay</b>	<i>Gymnorhinus cyanocephalus</i>	Ponil	Ground Forager	Tree	Open Woodlands
<b>Plumbeous Vireo</b>	<i>Vireo plumbeus</i>	Ponil	Foliage Gleaner	Tree	Forests
<b>Pygmy Nuthatch</b>	<i>Sitta pygmaea</i>	Both	Bark Forager	Cavity	Forests
<b>Red Crossbill</b>	<i>Loxia curvirostra</i>	Hayman	Foliage Gleaner	Tree	Forests
<b>Red-breasted Nuthatch</b>	<i>Sitta canadensis</i>	Hayman	Bark Forager	Cavity	Forests
<b>Red-headed Woodpecker</b>	<i>Melanerpes erythrocephalus</i>	Hayman	Flycatcher	Cavity	Open Woodlands
<b>Red-tailed Hawk</b>	<i>Buteo jamaicensis</i>	Both	Soaring	Tree	Forests
<b>Red-winged Blackbird</b>	<i>Agelaius phoeniceus</i>	Hayman	Ground Forager	Shrub	Marshes
<b>Rock Wren</b>	<i>Salpinctes obsoletus</i>	Both	Ground Forager	Ground	Deserts
<b>Sage Thrasher</b>	<i>Oreoscoptes montanus</i>	Hayman	Ground Forager	Shrub	Scrub
<b>Say's Phoebe</b>	<i>Sayornis saya</i>	Hayman	Flycatcher	Building	Grasslands
<b>Song Sparrow</b>	<i>Melospiza melodia</i>	Both	Ground Forager	Shrub	Open Woodlands
<b>Spotted Towhee</b>	<i>Pipilo maculatus</i>	Both	Ground Forager	Ground	Scrub
<b>Steller's Jay</b>	<i>Cyanocitta stelleri</i>	Both	Ground Forager	Tree	Forests
<b>Townsend's Solitaire</b>	<i>Myadestes townsendi</i>	Both	Flycatcher	Ground	Open Woodlands
<b>Vesper Sparrow</b>	<i>Poocetes gramineus</i>	Both	Ground Forager	Ground	Grasslands
<b>Violet-Green Swallow</b>	<i>Tachycineta thalassina</i>	Both	Aerial Forager	Cavity	Open Woodlands
<b>Virginia's Warbler</b>	<i>Vermivora virginiae</i>	Both	Foliage Gleaner	Ground	Open Woodlands
<b>Warbling Vireo</b>	<i>Vireo gilvus</i>	Both	Foliage Gleaner	Tree	Open Woodlands
<b>Western Bluebird</b>	<i>Sialia mexicana</i>	Both	Flycatcher	Cavity	Open Woodlands
<b>Western Meadowlark</b>	<i>Sturnella neglecta</i>	Hayman	Ground Forager	Ground	Grasslands
<b>Western Tanager</b>	<i>Piranga ludoviciana</i>	Both	Foliage Gleaner	Tree	Forests

<b>Western Wood-Pewee</b>	<i>Contopus sordidulus</i>	Both	Flycatcher	Tree	Open Woodlands
<b>White-Breasted Nuthatch</b>	<i>Sitta carolinensis</i>	Both	Bark Forager	Cavity	Forests
<b>Woodhouse's Scrub-Jay</b>	<i>Aphelocoma woodhouseii</i>	Ponil	Ground Forager	Tree	Scrub
<b>Yellow Warbler</b>	<i>Setophaga petechia</i>	Ponil	Foliage Gleaner	Shrub	Open Woodlands
<b>Yellow-breasted Chat</b>	<i>Icteria virens</i>	Ponil	Foliage Gleaner	Shrub	Scrub
<b>Yellow-rumped Warbler</b>	<i>Setophaga coronata</i>	Both	Foliage Gleaner	Tree	Forests

**Table 6:** Results of fitting environmental vectors on the NMDS ordination plots. Envfit results show the relative contribution of selected environmental variables to site distribution/separation. Highly correlated variables were eliminated from analysis (i.e., canopy cover, and percent bare ground/rock). Significant vectors are in bold.

**Ponil Complex Fire:**

Environmental Variable	NMDS1	NMDS2	r <sup>2</sup>	(Pr (>r))
<b>Thousand Hour Fuels</b>	-0.96	-0.27	0.09	0.06
Tall Shrub Cover	-0.97	0.24	0.05	0.24
<b>Live Basal Area</b>	<b>0.92</b>	<b>-0.40</b>	<b>0.65</b>	<b>0.001</b>
Snag Basal Area	-0.47	0.88	0.04	0.30
Percent Graminoid	-0.50	-0.86	0.03	0.37

**Hayman Fire:**

Environmental Variable	NMDS1	NMDS2	r <sup>2</sup>	(Pr (>r))
<b>Thousand Hour Fuels</b>	<b>-0.89</b>	<b>0.45</b>	<b>0.31</b>	<b>0.001</b>
<b>Tall Shrub Cover</b>	<b>-0.88</b>	<b>0.47</b>	<b>0.14</b>	<b>0.006</b>

Live Basal Area	1.00	-.10	0.64	0.001
Snag Basal Area	-0.93	0.36	0.11	0.03
Percent Graminoid	-0.98	0.19	0.18	0.003

**Table 7:** PERMANOVA results on dissimilarity matrix. PERMANOVA results quantify the difference in community composition between different groups (i.e., the difference between site types, between shrub cover groups). Df = degrees of freedom

**Ponil Complex Fire:**

	df	Sum of squares	R <sup>2</sup>	F	Pr(>F)
Site Type	3	3.48	0.22	5.40	0.0001
Shrub Cover Group	2	0.42	0.03	0.97	0.47

**Hayman Fire:**

	df	Sum of squares	R <sup>2</sup>	F	Pr(>F)
Site Type	1	3.57	0.16	12.90	0.0001

**Table 8:** Results of the top logistic regression models for species at each fire, and for species' models run for both fires combined. An AUC value of 0.50 indicates a test that performs no better than random; an AUC value 1.00 indicates a test with perfect accuracy. An ROC curve compares sensitivity and specificity values, to quantify test accuracy across a span of values.

Species	Fire	Predictors	AUC	ROC	Sens	Spec
Plumbeous Vireo	Ponil	Site Type	0.83	0.76	0.71	0.82
Western Tanager	Ponil	Site Type	1.00	0.85	0.83	0.87
Western Wood-Pewee	Ponil	Site Type	0.75	0.80	0.79	0.83
Mountain Chickadee	Hayman	Site Type, Dead Basal Area	0.83	0.85	0.60	0.89

<b>Pygmy Nuthatch</b>	Hayman	Canopy Cover	1.00	0.98	0.95	0.97
<b>Yellow-rumped Warbler</b>	Hayman	Site Type, Dead Basal Area	0.90	0.80	0.60	0.92
<b>Green-tailed Towhee</b>	Hayman	Site Type, Tall Shrub Cover	0.79	0.84	0.87	0.73
<b>Rock Wren</b>	Hayman	Site Type	0.88	0.79	0.76	0.82
<b>Western Tanager</b>	Both	Site Type, Fire Type, Canopy Cover	0.92	0.87	0.81	0.82
<b>Yellow-rumped Warbler</b>	Both	Site Type, Canopy Cover	0.82	0.82	0.81	0.68

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1.5.2 Figures

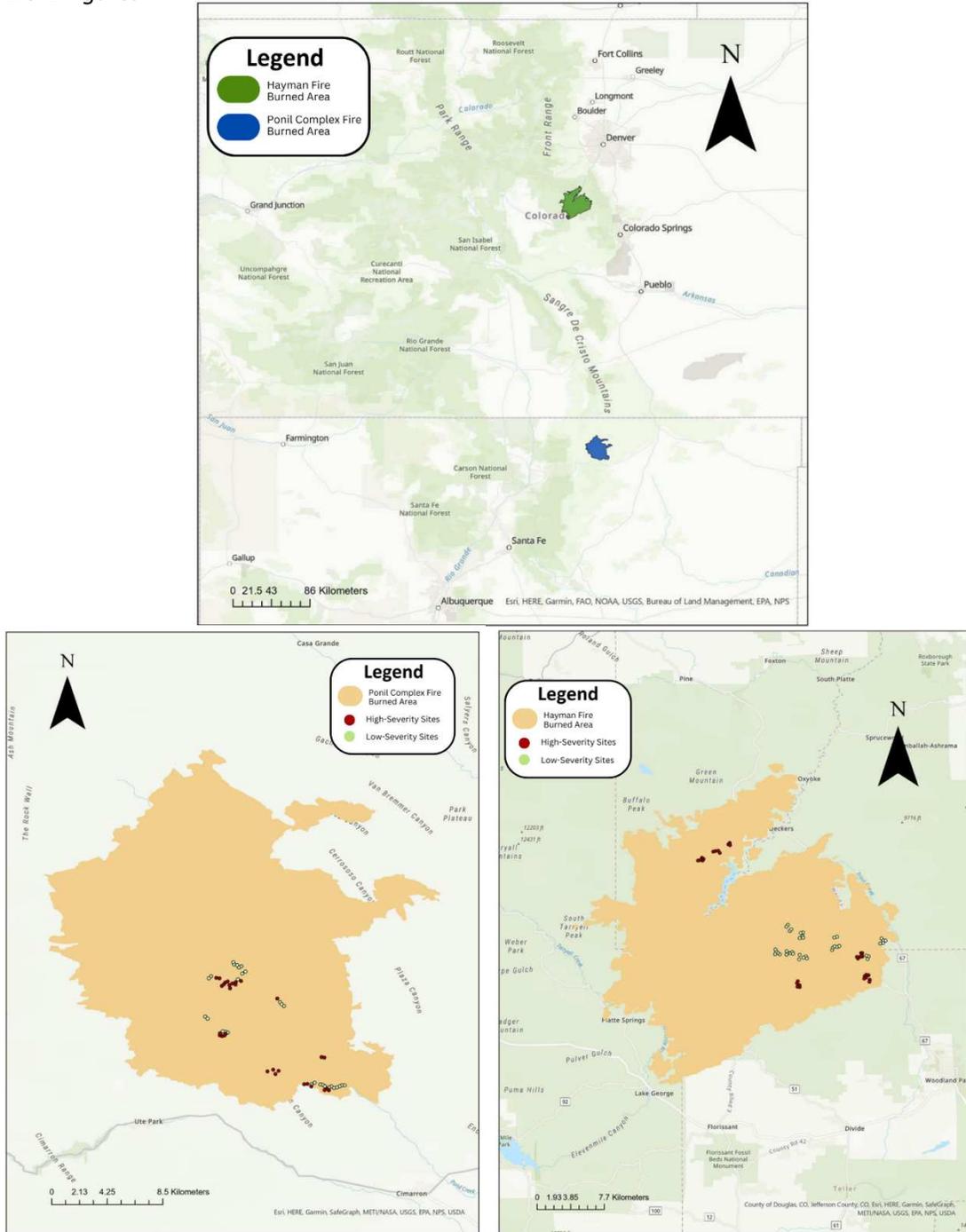
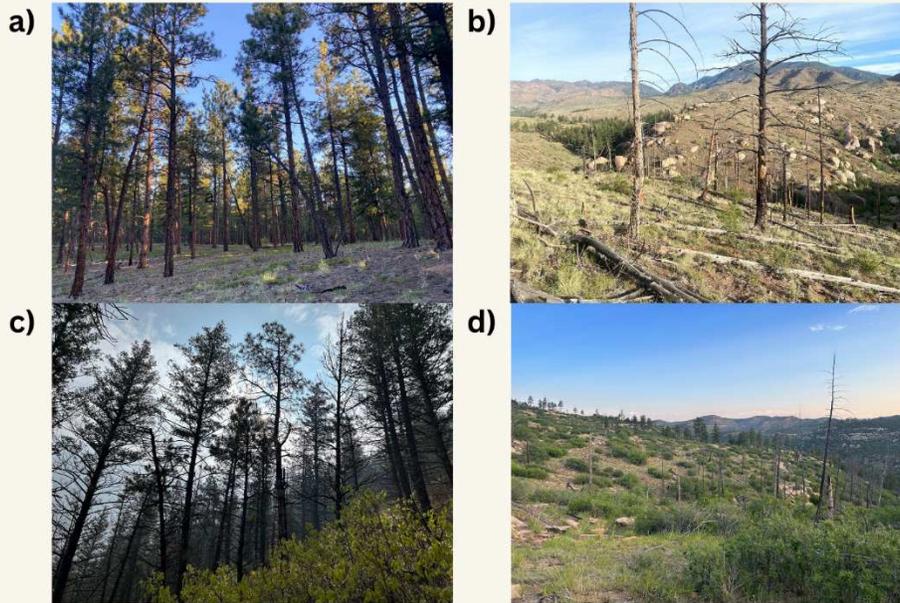
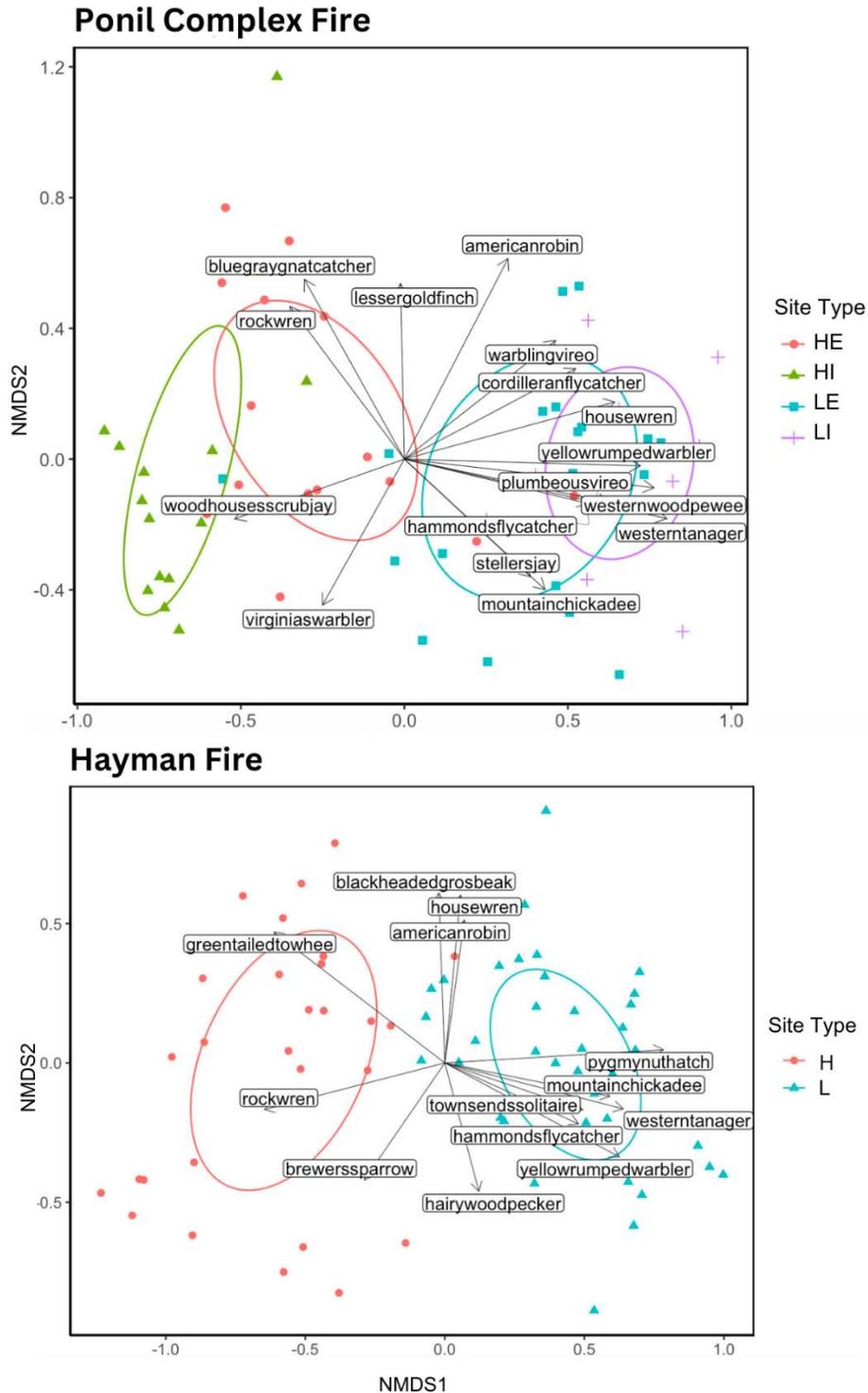


Figure 1: Maps of the study areas with burned areas and low- and high-severity sites labeled.

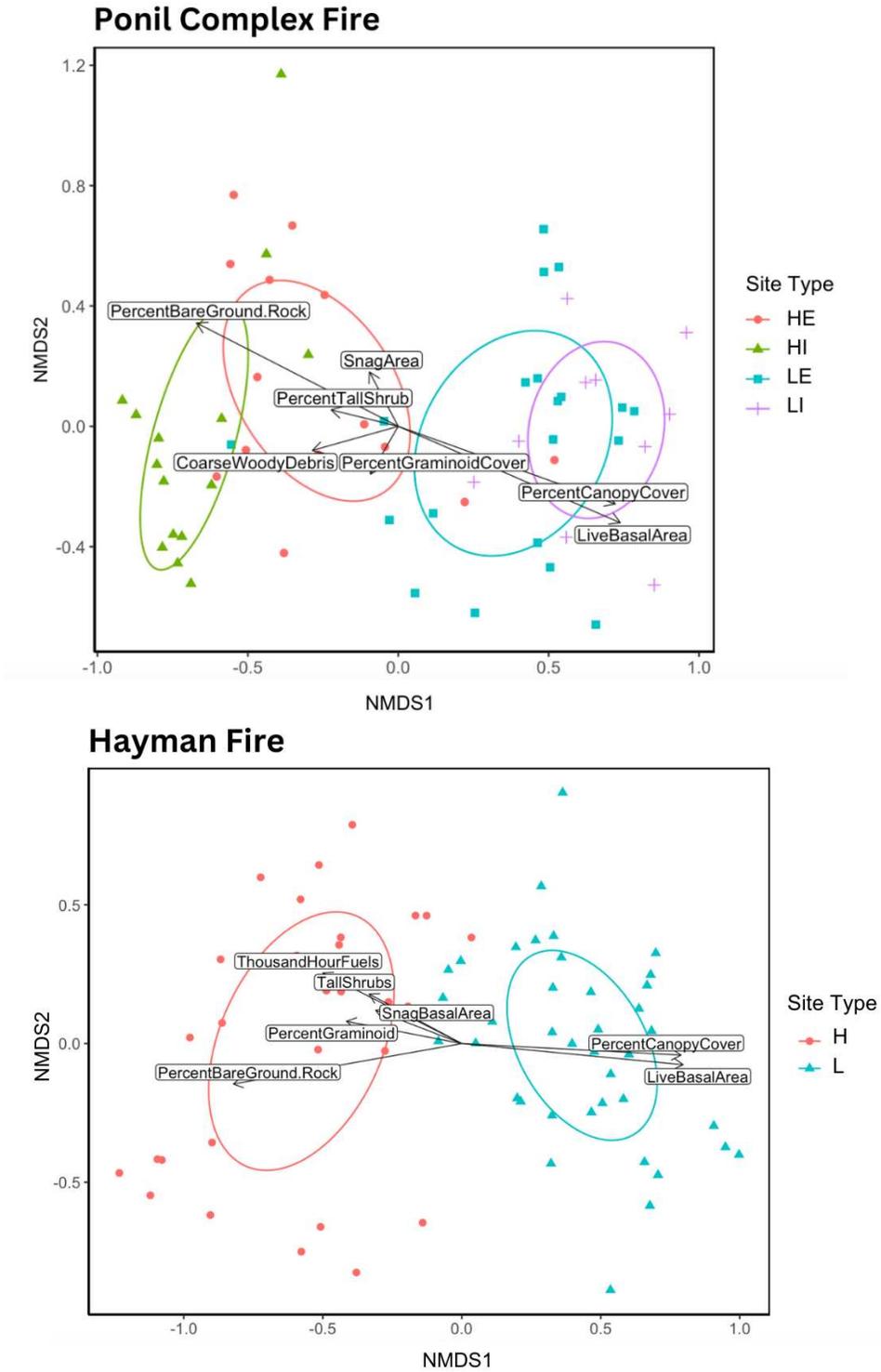
## Site Photos



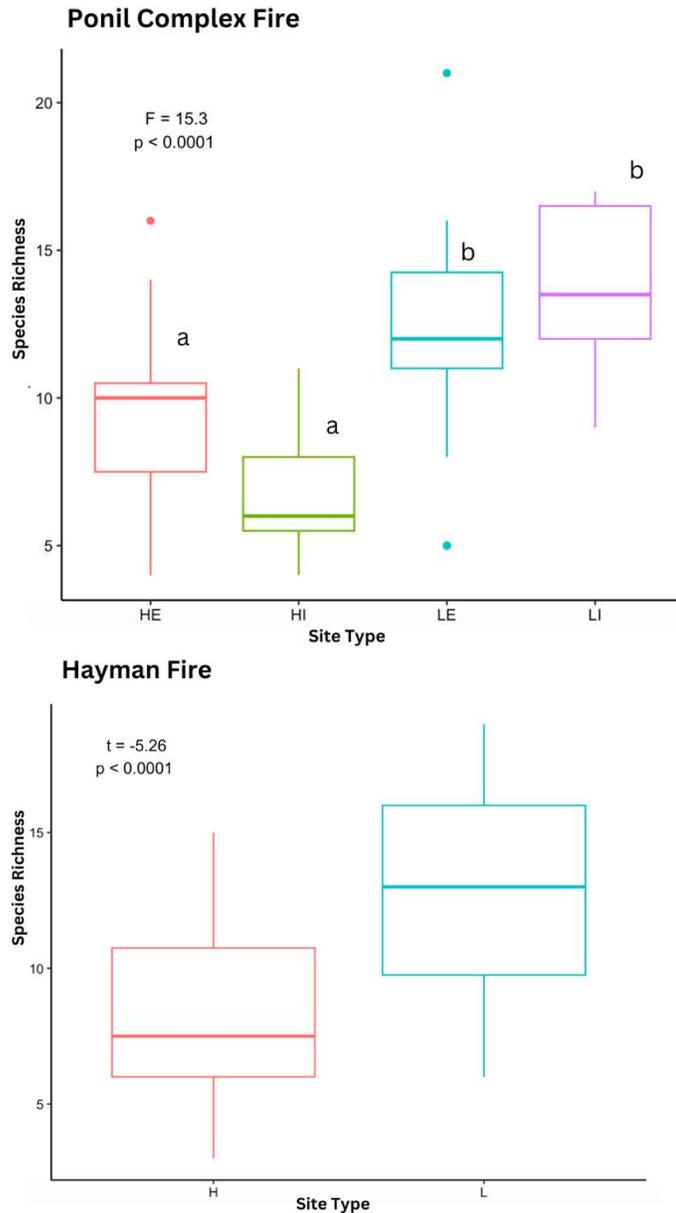
**Figure 2:** Low- and high-severity sites across each fire. Photos in the top row are low-severity (a) and high-severity (b) sites at the Hayman Fire. Photos in the bottom row are low-severity (c) and high-severity (d) sites at the Ponil Complex Fire. Photos highlight the intact canopy cover across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



**Figure 3:** NMDS ordination plot with species vectors for each fire. Species with a  $p$ -value  $\leq .001$  are included. Significant species vectors are species who significantly influenced the distribution of sites on the NMDS ordination plot. 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.



**Figure 4:** NMDS ordination plot for fires with all environmental vectors. 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.



**Figure 5:** Species Richness at both fires. Species Richness represents the count of individual species observed at each site. Site Type at the Hayman Fire indicates high-severity (H) and low-severity (L) sites. Site type at the Ponil Complex Fire indicate high-severity interior (HI), high-severity edge (HE), low-severity edge (LE), and low-severity interior (LI) sites. Sites in the Ponil Complex Fire Figure that do not share letters are significantly different (based on post-hoc Tukey tests with  $\alpha = .05$  significance level). For the Hayman Fire, results of the Two-Sample t-Test are included. Site types at the Hayman Fire indicate high-severity and low-severity.

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