THESIS

POST-FIRE VEGETATION AND BIRD HABITAT USE IN PIÑON-JUNIPER WOODLANDS

Submitted by

Jamie Woolet

Department of Forest and Rangeland Stewardship

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2022

Master's Committee:

Advisor: Camille Stevens-Rumann

Jonathan Coop
Liba Pejchar

ABSTRACT

POST-FIRE VEGETATION AND BIRD HABITAT USE IN PIÑON-JUNIPER WOODLANDS

Global climate change has caused fire activity and behavior to shift from historical norms due to hotter and drier conditions. Although the ecological effects of changing fire regimes have been explored in many systems, the resilience of some forest types, such as piñon-juniper, are often overlooked. Piñon-juniper is a dominant forest type in the western US and provides breeding habitat for many obligate or semi-obligate bird species. Similarly, this system is supported by a critical mutualism, where the regeneration and infilling of these trees is reliant on several bird species that disperse piñon pine and juniper seeds. This study aimed to assess woodland resilience by evaluating post-fire forest structure and the associated avian communities one-year and 20+ years post-fire. More specifically, seedling regeneration and the habitat use of piñon-juniper obligate bird species, semi-obligates, piñon seed dispersers, and juniper seed dispersers were compared across burned, refugia, and unburned patches. Replicate patches of each habitat type were selected within three fire locations, and 3-4 bird point count stations and 1 forest inventory plot were established in each patch. No tree regeneration was observed 1-year post-fire, and after 25 years, there were few juniper seedlings and no piñon seedlings observed in burned plots. Seedling regeneration and forest structure in refugia and unburned plots were not different, regardless of fire age. Results from occupancy models indicated that Woodhouse's Scrub-jay, a piñon seed disperser, used all habitats equally. American Robin had the highest habitat use in the recent burned patches. Obligate and semi-obligate bird species

had differing responses to habitat types, with the habitat use of Ash-throated Flycatcher and Spotted Towhee not differing across habitat types, Virginia's Warbler having the highest habitat use in old burn and refugia patches, the Gray Vireo, Black-throated Gray Warbler, and Gray Flycatcher having highest habitat use in unburned, refugia, and recent burn patches, and the Blue-grey Gnatcatcher having the highest habitat use in the old burn. While there is a need for longer term studies, our work highlights that even 25 years post-fire, little tree recovery is observed and the associated bird species continue to differ, emphasizing the potential transition or long recovery time in these sensitive areas.

ACKNOWLEDGEMENTS

First, I would like to thank my advisor, Camille Stevens-Rumann, for taking me on as a student, allowing me freedom to create and pursue this project, for providing endless support, guidance, and laughter over the past two years, and for agreeing to continue to advise me for a PhD program.

I would also like to thank my committee members, Liba Pejchar and Jonathan Coop, for introducing me to this magical forest type, helping me design this study, and for always providing great feedback when I have questions.

This project could not have been done without the hard work and positive energy by my field crew, Maria Vicini and Gabriela Szyniec. You two are wonderful souls and made the 2021 field season unforgettable.

Thank you to the BLM Grand Junction Field Office for being an excellent point of contact for road conditions, permits, and location-specific advice.

Many thanks to the Joint Fire Science Program for assistance in funding this work, and to Gloria Edwards for providing a brilliant letter of support and a way to disseminate this research.

A big Thank You to Kate Wilkins and Larissa Bailey for pointing me towards resources to learn how to analyze my birds and for their advice and suggestions on occupancy modeling.

Lots of love and appreciation go to my husband, Joshua Wise, for his endless support and his listening ear. Thank you for always letting me talk-out ideas, for making me coffee when I need a boost, and reminding me to take a break and go for a walk or a run when I need a break.

Lastly, I would like to thank Thea Whitman for supporting me and offering amazing advice when I decided to go to graduate school, for reviewing my application materials, and for allowing me to still be a part of lab activities halfway across the US.

TABLE OF CONTENTS

ABSTRACT.....ii
ACKNOWLEDGEMENTS.....iv
Chapter 1 – POST-FIRE VEGETATION AND BIRD HABITAT USE IN PIÑON-JUNIPER WOODLANDS .1
Introduction 1
Methods..... 6
Study Area..... 6
Site Selection..... 7
Field Methods 8
Data Analysis.....9
Results..... 12
Vegetation Structure..... 12
Seedling Regeneration 13
Effects of Vegetation Characteristics on Seedling Regeneration 13
Bird Habitat Use 14
Discussion..... 15
Seedling Regeneration and Vegetation Characteristics 15
Bird Habitat Use 18
Management Implications 22
Limitations and Future Research 23
Conclusions 24
Figures and Tables 26
REFERENCES..... 36
APPENDIX.....46

CHAPTER 1

Introduction

Wildfire is an important disturbance globally, driving feedbacks that shape vegetation patterns and animal communities, influence biogeochemical processes, and control climate (Bowman et al. 2009, McLaughlin et al. 2020). Global climate change has caused fire activity and behavior to change from historical regimes due to hotter and drier conditions (Higuera and Abatzoglou 2020). In many ecosystems, such as in the western United States, fires are occurring more frequently, fire seasons are lengthening, and fires are burning more severely (Singleton et al. 2019, Westerling 2016, Higuera and Abatzoglou 2020). Recent research has made marked advances in beginning to outline the implications of fire regime change in various ecosystems, especially in terms of the resilience – the ability for an ecosystem to return to similar pre-disturbance conditions following a disturbance event – of these systems (e.g. Gill et al. 2017, Stevens-Rumann et al. 2018, Whitman et al. 2019, Chapman et al. 2020). Resilient communities often rely on intact ecological memory, such as seedbanks or nearby seed sources, and resilience can be degraded by novel disturbance regimes and changing climate that the ecosystems are not adapted to (Johnstone et al. 2016, Coop et al. 2020).

While much recent work has focused on the effects of changing climate and fire regimes on ponderosa pine and dry mixed conifer forests in the western US (e.g. Korb et al. 2019, Halofsky et al. 2020, Chapman et al. 2020), the resilience of other forest types to fire regime change, such as piñon-juniper (PJ), are frequently overlooked in the literature, even though they cover over 40 million ha across Colorado, New Mexico, Arizona, Utah, and Nevada

(Romme et al. 2009). Within this system, over- and understory vegetation structure vary, driven by spatial differences in climate, soil type, topography, elevation, and disturbance regimes (Romme et al. 2009). PJ woodlands, as opposed to PJ savannas or PJ shrublands, are categorized as areas where environmental conditions favor the growth of piñon and juniper with non-continuous understory growth (Romme et al. 2009). These woodlands provide critical habitat and food resources for several avian (Balda and Masters 1980, Gillihan 2006) and mammalian species (Gillihan 2006), and support habitat for several endemic or endangered plant species (Goodrich et al. 1999). Specifically, PJ woodlands exhibit a unique mutualism with the birds that live in this habitat. There are over 70 species of birds that use this habitat for breeding, 18 of which are obligate or semi-obligate species (Balda and Masters 1980), and these woodlands regenerate with the support from seed-dispersing birds (Chambers et al. 1999).

Fire in PJ woodlands generally occurs in the form of lightening ignitions that dissipate quickly due to rocks, bare ground, and separated surface fuel structure, usually resulting in a single torching event (Romme et al. 2003, Rocca et al. 2014). In these woodlands, large stand-replacing events are infrequent, however when they do occur, they are often associated with dry canopy fuels and driven by strong winds move the fire from tree crown to tree crown (Floyd et al. 2000, Romme et al. 2003). Since the 1980's, the total area burned has increased, individual fire sizes have gotten larger, and fire rotations -the time it takes in years for a particular area to burn - has decreased in PJ landscapes (Board et al. 2018). These changes are attributed to climate warming (Westerling et al. 2006, Keane et al. 2008) and changes to the vegetation structure, including a greater presence of highly flammable invasive grasses and more dead and dry canopy fuels due to drought, insects, and disease (Keane et al. 2008, Rocca et al. 2014).

Increases in fire size and shorter fire rotations may result in major shifts in PJ woodlands, because piñon pine and juniper do not have structural adaptions to fire – the needles and bark are highly flammable and cambium protection and insulation are not prevalent – thus even low-intensity fires commonly lead to tree death (Anderson 2002, Baker and Shinneman 2004). It can take up to several centuries for woodlands to fully recover after fire, with piñon pine and juniper recruitment often not observed for more than 30 years (Koniak 1985, Huffman et al. 2012, Bristow et al. 2014, Floyd et al. 2021). Fire may expedite the spread of flammable invasive vegetation, like cheatgrass, by creating patches of bare ground that are easy for them to establish (Urza et al. 2017, Floyd et al. 2021). This can create a feedback loop of frequent fires (Rocca et al. 2014) that may lead to subsequent reduced capacity for seedling regeneration due to the death of seed sources, undermining resilience in these systems.

Wildfire can impact bird species occupancy over short and long time scales, especially when the wildfire results in enduring cover type conversions with altered habitat structure and resource availability (Pons and Wendenburg 2005, Abella and Fornwalt 2015, Coop et al. 2020). The short-term impacts to bird communities is a function of the duration and severity of the fire, temporal scale, or life-history traits of the birds in question (Finch et al. 1997). The specific effects of fire on woodland bird communities are not well studied and create uncertainty regarding the duration of impact it may have on obligate and semi-obligate species, another consideration for woodland resilience. It has long been recognized that the breeding bird density in PJ is correlated with the density of piñon pine, total tree density, and piñon foliage volume (Masters 1979). Current research conducted in woodlands still supports this, as observed following thinning treatments, where there was a reduction in piñon-juniper obligate species (Magee et al. 2019, Crow and van Riper III 2010) and reduction in overall bird density in treated areas (Gallo and Pejchar 2017). Likewise, drought induced piñon mortality also caused a decrease in avian abundance and richness, with greater declines observed in areas that were subsequently thinned following tree mortality (Fair et al. 2018). While these studies can show potential responses bird communities may have when piñon and juniper are reduced in a system, they may not be an adequate analog for avian responses to fire (Gallo et al. 2017). Furthermore, fire often burns heterogeneously, creating a mosaic of burned areas intermixed with unburned or low severity burned islands within the fire perimeter, otherwise termed "refugia" (Meddens et al. 2018). These areas often serve as refuge for fire-sensitive and forest-dependent wildlife (Robinson et al. 2014, Steenvoorden et al. 2019), such as PJ obligate species that were displaced from the burned patches, although these relationships are not well understood.

Regeneration in burned PJ woodlands relies on several bird species that disperse piñon pine and juniper seeds. Piñon pine produces a cone crop every 5-7 years, from which the seeds are the most viable within the first year (Chambers et al. 1999). Piñon seed dispersers, such as Clark's Nutcracker (*Nucifraga columbiana*) and Pinyon Jay (*Gymnorhinus cyanocephalus*), collect these large and exposed seeds and move them up to 7 - 22 km away from the source tree, with a caching rate of around 120 – 330 seed per day (Persendorfer et al. 2016). Juniper, conversely, annually produces long-lived seeds that are available for dispersal on the tree itself as well as the ground underneath the canopy (Chambers et al. 1999). Juniper “berries” are eaten by frugivorous birds and intact seeds are defecated away from the parent tree (Salomonson 1978). Some research suggests that after consumption by birds, the fruitless cone is later picked up by rodents and buried elsewhere where it can germinate (Johnson 1962, Longland and Dimitri 2016). Understanding the habitat use of these birds in burned PJ woodlands and neighboring unburned areas, including refugia, can help to identify potential for natural regeneration of these woodlands, especially with larger fires occurring more often.

Findings from other disturbance events, like drought-induced mortality, show that successful regeneration of new piñon and juniper are largely dependent on two factors: seed availability and soil water moisture (Floyd et al. 2015, Redmond et al. 2015, Redmond et al. 2018). While seed sources for piñon and juniper following wildfire are limited to unburned edges, soil water moisture can be made available to seedlings via nurse objects, such as other live trees, logs, rocks, and shrubs, which create microhabitats with less solar exposure (Chambers et al. 1999 and sources therein). Other ground cover, such as perennial grasses, however, can reduce piñon regeneration and survival (Redmond et al. 2015, Redmond et al. 2018).

Given changing fire regimes and post-fire climate in PJ woodlands, it is important to understand how this landscape and associated obligate wildlife may respond to severe fire. Where fire results in tree mortality, resilience may be maintained by 1) the presence of seed-dispersing birds that move live seeds from neighboring unburned areas into the burned patches, and 2) the vegetation establishing in the developing woodland, by providing microclimates via nurse objects and overstory structure. The goal of this study aims to bridge current knowledge gaps on post-fire recovery of PJ woodlands by characterizing both post-fire forest structure and associated avian communities following a “recent fire” (one-year post-fire) and two “old fires” (20+ years post-fire), by comparing tree seedling regeneration and habitat use by piñon-juniper obligates and semi-obligates and avian seed dispersers across burned forest, unburned stands, and refugia. This research will address the following questions:

1) How does piñon and juniper seedling regeneration differ in burned, unburned, and refugia and how is this impacted by fire age and forest structure? 2) What is the habitat use of PJ obligates, PJ semi-obligates, piñon seed dispersers, and juniper seed dispersers in burned, unburned, and refugia? 3) Does the occupancy of seed dispersing birds effect seedling regeneration in burned areas?

Methods

Study Area

The study area was located in Garfield and Mesa Counties in western Colorado on Bureau of Land Management (BLM) land managed by the Grand Junction Field Office. The climate of this region is semi-desert, with cool and dry winters, and hot and dry summers. Annual average precipitation is 41.78 cm at nearest Western Regional Climate Center station, with most rainfall occurring in August through October (1947-2016; WRCC; wrcc.dri.edu). Annual average temperature is 8.5°C with an average maximum of 17.44°C and average low of -0.39°C (1991– 2020; NOAA; www.ncei.noaa.gov/access/us-climate-normals, accessed 14 September 2021). The soils across sites consist of Calciborolls, Torriorthents, and Haploborolls (Web Soil Survey, downloaded 19 August 2021), on top of Cretaceous or Tertiary rocks (Alstatt 2003). The overstory tree vegetation is characterized by two-needle piñon (*Pinus edulis*) and

Utah juniper (*Juniperus osteosperma*), with understory vegetation dominated by Morman tea (*Ephedra nevadensis*), big sagebrush (*Artemisia tridentata*), mountain mahogany (*Cercocarpus montanus*), and perennial bunchgrasses (*Poaceae spp.)*.

Site Selection

Three wildfires were selected to study. The Buninger Canyon Fire (BC) burned 748 ha in 1994, the Hatchet Fire (HT) burned 2,301 ha in 1996, and the Pine Gulch Fire (PG) burned 56,254 ha in 2020 (Figure 1). The BC and HT fires are categorized as “old” fires, and PG fire is the “recent” fire. Within each fire, patches were characterized into the following habitat classes: burned, refugia, or unburned. Burned habitat are patches within the fire perimeter that burned severely and resulted in nearly 100% tree mortality; refugia habitat are patches within the fire perimeter that burned less-severely or did not burn at all. Boundaries for refugia and burned habitat classes were initially determined in ArcGIS Pro (version 2.7.0, ESRI, 2020) by using dNBR fire severity imagery from Monitoring Trends in Burn Severity (Eidenshink et al. 2007 [www.mtbs.gov]) and classifying patches that were greater than 5 ha based on burn severity. Burned patches were identified by medium and high severity burns, and refugia patches were identified by unburned or low severity burns. Habitat characterization was later verified in the field and were delineated by amount of observable tree mortality; burned patches had nearly 100% fire-caused mortality (as indicated by down or standing trees with visible charring; Figure 1.a and 1.b), whereas refugia had little to no tree mortality (Figure 1.c). Unburned patches were located near but outside the fire perimeter (Figure 1.d).

Point count stations were established in patches where 3-4 points could be placed at least 160 m apart and about 50 m away from a road or patch edge. In each patch, a vegetation plot was established either in the center of the patch's point count stations or offset from one of the point count stations, when patch shape did not lend itself to centering the forest plot (Figure 2). In total, there were 32 forest plots (6 old burn, 5 old refugia, 6 recent burn, 6 recent refugia, and 9 unburned), and 126 point count stations (24 old burn, 20 old refugia, 24 recent burn, 22 recent refugia, and 36 unburned), which were visited 3 times (n = 378).

Field Methods

To quantify avian communities, we performed point counts following McLaren et al. (2019). Briefly, 6-minute point counts were performed at each location from late April – early June. Birds were surveyed from dawn – 1030 hr. Date, time, cloud cover, wind, precipitation, and observer were recorded at the beginning of each count. All birds seen and heard were recorded, and their detection distances from the observer were logged. Birds that were flew over the patch without stopping were recorded but excluded from analysis. Similarly, unidentified birds were recorded, but excluded from analysis. Point counts were not conducted under heavy precipitation or at windspeeds that caused small trees to sway. Each point count location was visited three times during the season and at least one week apart. Observers were trained and tested at identification of birds by sight and aurally prior to survey period and were trained in-field before observing alone. The observer and time visited to point count was alternated for each point visit to mitigate observer and temporal bias.

To assess vegetation composition and structure, we established one 0.05-ha circular plot in each patch to obtain representative forest structure and patch characteristics. Two 25 x 25-m belt transects were established, intersecting at the 12.5-m mark, and directed in the four cardinal directions. Slope, aspect, and elevation were measured at plot center. Canopy cover was assessed by point intercept method along the four transects at 1 m intervals for a total of 50 observations. Species, diameter at root crown (DRC) (Vankat 2017), and mortality class (no mortality, partial mortality (50% or greater tree death), all mortality) of all standing live and dead trees in the plot were recorded. DRC was converted to diameter breast height (DBH) to calculate basal area (BA) using methods described by Chojnacky and Rogers (1999), DBH $= \sum_{i=1}^{n} d_i^2$, where *n* is the number of stems at DRC with diameter 2.5 cm or larger and d_i is the diameter of all stems at DRC that are 2.5 cm or larger. Distance to the nearest ten live seed sources for piñon pine and juniper, up to 200 m away, were recorded from plot center. Understory cover by functional group (grass, forb, shrub (including Gambel oak (*Quercus gambelii*)), and tree) and substrate type (litter, rock, and soil) were measured along the four transects using the pin-drop method at 0.5 m intervals for a total of 98 observations at each plot. All piñon seedlings, juniper seedlings, and Gambel oak resprouts were counted and the size class determined (0-10 cm, 10-30 cm, 30-60 cm, 60-137 cm) within the full 0.05 ha plot. Whether the piñon or juniper seedling was nursed or in the interspace was also noted. Nursed seedlings were growing in the shade of a rock or log, underneath a shrub, or under the canopy of a tree; seedlings in the interspace had little to no direct shading from another object or plant.

Data Analysis

All data analysis was performed in R Studio (version 2021.09.2) using R version 4.1.2 (R Core Team, 2021). R packages *dplyr* (Wickham et al. 2021) and *ggplot2* (Wickham 2016) were used for data manipulation and visualization.

Analysis of Variance (ANOVA) and Tukey Honest Significant Difference (HSD) tests were used to compare differences between the means for overstory structure (live tree BA per ha, percent canopy cover, total live trees per ha), substrate cover (percent bare ground and percent litter), and understory cover (percent forb, percent grass, percent shrub) across habitat groups(old burn, recent burn, old refugia, recent refugia, and unburned) using R packages *emmeans* (Lenth 2021) and *multcompView* (Graves et al. 2019).

Kruskal-Wallis tests were used to test whether seedling recruitment (total conifer seedlings, piñon seedlings, juniper seedlings, and Gambel oak) was different in old refugia, recent refugia, unburned habitat groups. Because only one burned plot had conifer seedlings present, burned habitat was only included in the Gambel oak category. This test was used because although there was no evidence for unequal variances (Levene Test, $p > 0.33$ for each seeding category), the seedling counts were not normally distributed for the total conifer seedlings and juniper seedlings categories (Shapiro-Wilks test, $p < 0.01$ for total conifer seedlings and juniper seedling categories).

To test for effects of forest structure variables on seedling regeneration (all conifer seedlings, piñon seedlings, and juniper seedlings) in unburn and refugia, R package *MASS* (Venables and Ripley 2002) was used to run Generalized Linear Models (GLM) using negative binomial regression. Negative binomial regression was chosen for the model because Poisson regression showed evidence of overdispersion. Pearson's correlation was used to verify that variables in the model were not correlated. All uncorrelated forest characteristic variables were put in a global model and different model combinations were tested to create a best-fitted model based on lowest AIC values.

Raw bird detections were filtered to exclude flyover observations, birds that were detected over 100 m away, and birds that were not identified. Old and recent refugia and old and recent unburned habitat groups were consolidated into two groups – refugia and unburned, due to similar forest characteristics across the habitat ages and the assumption that these habitats would have similar avian responses regardless of fire age. Single-season occupancy analysis (MacKenzie et al. 2017) was conducted to determine the occupancy of select species using the R package *unmarked* (Fiske and Chandler 2011). Because we cannot be absolutely certain that we meet the assumptions for determining species occupancy (MacKenzie et al. 2017), we instead use the term "habitat use". Four guilds were investigated: PJ obligates, PJ semi-obligates, piñon seed dispersers, and juniper seed dispersers. Guild designations are based on reports by Balda and Masters (1980), Paulin et al. (1999), and breeding ranges outlined by Cornell Ornithology Lab (allaboutbirds.org). Species included in PJ obligate and semi-obligate guilds are based on species' breeding habitats in the western US (e.g while the Blue-gray Gnatcatcher is observed throughout the continental US, the western populations generally breed in PJ or oak forests (Root 1967)).

Within each of these guilds, representative species that had adequate detection data were selected for analysis and each species was evaluated separately. Detection model covariates - observer, cloud, and wind (each categorical) – were individually tested in detection-only models to determine the variables that affect detection probability (p) compared to a null model, using R package *AICmodavg* (Mazerolle 2020). Occupancy-only model covariates were determined by testing a null occupancy hypothesis (habitat use is not different across habitat types) against several alternative hypothesis models formulated on the potential biological responses birds may have to habitat types: Hypothesis 1) Habitat use is different in each habitat type [OldBurn ≠ RecentBurn ≠ Refugia ≠ Unburned]; Hypothesis 2) Habitat use in burned habitat is different from habitat that did not burn [(OldBurn + RecentBurn) ≠ (Refugia + Unburned)]; and Hypothesis 3) Habitat use is different across fire ages [OldBurn ≠ RecentBurn ≠ (Refugia + Unburned)]. The best-fitting occupancy-only model was determined based on lowest AICc. Covariates from the detection-only model and the occupancy-only model were combined to create a full model to estimate ψ and p. Top models were assessed for over-dispersion using the MacKenzie-Bailey Goodness-of-fit test.

Results

Vegetation Structure

ANOVA tests between habitat groups (old burn, recent burn, old refugia, recent refugia, and unburned) indicated evidence for differences in live tree BA ha^{-1} ($p = 0.001$, f-value = 7.00), percent canopy cover of live and dead standing trees ($p = 0.01$, f-value = 4.11), number of live trees ha^{-1} ($p = 0.001$, $f = 6.94$), percent litter cover ($p < 0.001$, f-value = 9.45), percent of exposed bare ground ($p < 0.001$, f-value = 9.48), percent shrub cover ($p = 0.005$, f-value = 4.69), and percent grass cover ($p < 0.001$, f-value = 13.03). Percent forb cover was not different between habitat groups ($p = 0.104$, f-value = 2.137). Live tree BA per ha highest in recent refugia, old refugia, and unburned. Percent canopy cover of live and standing dead trees was highest in old refugia and lowest in old burn. Number of live trees per ha was highest in old refugia, recent refugia, and unburned, with no live trees recorded in either burned groups. The recent burn had the lowest percent of litter cover and the highest percentage of exposed bare ground the remaining habitats did not having meaningful differences in these categories.

Percent shrub cover was lowest in the recent burn and was highest in the old burn and recent refugia. Lastly, percent grass cover was highest in the old burn with no meaningful differences between remaining habitat groups. (Table 1, Table S2, Table S3).

Seedling Regeneration

Three juniper seedlings were counted at one old burned site, with no other conifer seedling recorded at other burned locations. Densities of Gambel oak resprouts in burned areas was 4,623 ha^{-1} (0 - 12,480 ha^{-1}) in the recent burn and 590 ha^{-1} (0 - 3,380 ha^{-1}) in the old burn (Figure 3, Table S1). In the unburned areas, the average conifer seedling density was 300 ha^{-1} (60 - 860 ha^{-1}) the average piñon seedling density was 80 ha^{-1} (0 - 460 ha^{-1}), the average juniper seedling density was 220 ha^{-1} (20 - 860 ha^{-1}), and the average Gambel oak density was 182 ha^{-1} (0 - 560 ha^{-1}). In refugia, the average total conifer seedling density was 371 ha^{-1} (20 - 1,020 ha^{-1}), the average piñon seedling density was 151 ha^{-1} (0 - 480 ha^{-1}), the average juniper seedling density was 220 ha^{-1} (20 - 540 ha^{-1}), and the average Gambel oak density was 1,196 ha^{-1} (0 - 5,080 ha^{-1})(Figure 3, Table S1). Across all sites, 73% of piñon seedlings and 50% of juniper seedlings were found under a nurse object. There was no effect of habitat type on total conifer seedling ($p = 0.807$), piñon seedling ($p = 0.274$), juniper seedling ($p = 0.782$), or Gambel oak resprout densities ($p = 0.159$).

Effects of Vegetation Characteristics on Seedling Regeneration

GLM models used to determine the effect forest characteristics have on number of seedlings are presented in Table 2. Number of live trees in the plot and the elevation at plot center had significant positive relationship on total number of seedlings and number of piñon seedlings. Number of live juniper trees in the plot had a significant positive relationship on juniper seedling counts. Percent shrub cover and live tree BA had significant negative relationship on the total number of seedlings. Percent shrub cover and BA of live juniper trees had a significant negative relationship on number of juniper seedlings (Table 3).

Bird Habitat Use

After excluding flyovers and birds detected over 100 m away, 58 unique bird species and 2,852 individual birds were detected. Full list of species and number of detections are presented in Table S4. Within the guilds of interest, the birds with adequate detections for occupancy analysis included: Woodhouse's Scrub-jay (*Aphelocoma woodhouseii*), American Robin (*Turdus migratorius*), Virginia's Warbler (*Oreothlypis virginiae*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Gray Vireo (*Vireo vicinior*), Spotted Towhee (*Pipilo maculatus*), Black-throated Gray Warbler (*Dendroica nigrescens*), Blue-gray Gnatcatcher (*Polioptila caerulea*), and Gray Flycatcher (*Empidonax wrightii*) (Table 5).

Species habitat use in burned, unburned, and refugia was different across and within guild categories (Table 6, Figure 4). Habitat use for Woodhouse's Scrub-jay (piñon seed disperser and obligate species), Ash-throated Flycatcher (obligate), and Spotted Towhee (semi-obligate) was not affected by habitat type. The American Robin (juniper seed disperser) and the Gray Flycatcher (semi-obligate) had the highest habitat use in the recent burned habitats. The Virginia's Warbler (obligate) and the Blue-gray Gnatcatcher (semi-obligate) had the highest habitat use in the old burn patches (although both species also had high habitat use in refugia and unburned habitats). The Gray Vireo (obligate) and Black-throated Gray Warbler (semi-obligate) had the highest habitat use in refugia and unburned habitats.

Model detection covariates varied among bird species. The observer affected the detection probabilities of six of the nine species modeled, wind speed effected the detection of one species, and cloud cover effected the detection for three species (Table S5).

Discussion

Our two mechanisms that suggest how woodland resilience may be maintained wildfire were: 1) seed-dispersing birds using these habitats for scatter-hoarding seeds and 2) the vegetation structure in developing woodlands facilitating seedling germination and survival. While we found little conifer regeneration in the burned areas, regeneration in refugia and unburned habitat types was positively associated with number of live tree and elevation, and negatively associated with percent shrub cover and live tree basal area. Bird guilds and individual species varied in their response to each habitat type, but generally, PJ obligate and semi-obligate occupancy was either higher in unburned and refugia habitats or remained unchanged across habitat types, piñon seed disperser occupancy did not differ between habitats, and juniper seed dispersers had the highest occupancy in recent burn.

Seedling Regeneration and Vegetation Characteristics

In the old burn, we expected that seedling regeneration would increase with higher shrub cover and decrease with more grass cover. Only one plot had any regeneration present, so it is difficult to assign forest characteristics that may support seedling growth, especially as these burned areas have a different structure than areas that did not burn. While findings from other PJ regeneration studies in different regions are variable, current climatic stress may be driving this observed lack of regeneration. In Mesa Verde National Park, Floyd et al. (2021) observed no recovery in PJ woodlands 30 years following wildfires, whereas in Arizona, Huffman et al. (2012)

observed recovery starting at six years post-fire and increasing with time since last fire. However, research suggests that piñon and juniper recovery rates after fire are reduced by drought (Hartsell et al. 2020, Vanderhoof et al. 2020). The southwestern US, including the current study region, has been experiencing a megadrought that has not been seen in ~2,000 years, including the driest conditions in within the past 22-years (Williams et al. 2022), so this lack of regeneration in the old burn can in part be attributed to current climatic conditions. Proximity to seed source is a known factor to contribute to revegetation in most forest types (Chambers et al. 2016, Coop et al. 2019). With seeds that are bird-dispersed, it is possible that this proximity-constraint could be lessened, especially for piñon, as birds disperse seeds several kilometers away from its source (Chambers et al. 1999, Persendorfer et al. 2016). While this has been observed in other forested systems (Coop and Schoettle 2009), this is still yet to be seen in these burned patches. However, proximity to seed source may be more crucial for juniper regeneration, as dispersal generally occurs at shorter distances (Salomonson 1978, Chambers et al. 1999). Of note, the one old burn plot that had juniper regeneration was distinct from the other burned plots – it was the only old burned plot that had live seed sources within 50 m (Table S3).

Unsurprisingly, we did not observe piñon or juniper seedling regeneration in the recent burn. We did, however observe and count resprouting Gambel oak, which had quickly grown in the newly burned sites (average 4,623 stems/ha across recent burned plots, Table S1). Some past research suggest that Gambel oak stands are key for PJ woodland establishment by providing microclimates that protect recently-germinated seedlings (Floyd 1982), and recent work has built on this, showing a higher survival rate for piñon seedlings that were planted under Gambel oak (Crocket and Hurteau 2022). Further monitoring these sites in the upcoming decades will be critical to understand how the abundance of Gambel oak contributes to piñon and juniper regrowth in burned areas.

We expected refugia and unburned areas would have similar regeneration patterns, regardless of fire age, and that sites with higher live tree basal area would have more seedlings, as this metric is often used as a surrogate for seed availability in post-drought recovery studies (Redmond et al. 2015). While refugia and unburned plots had comparable regeneration and vegetation characteristics, seedling regeneration decreased with increasing BA and increased with number of live trees. For context, the number of live trees was correlated with canopy cover, so as live tree density increased, canopy cover increased. This suggests a more-interconnected canopy with greater amounts of forest-floor shading when tree density is higher. This shading may provide more suitable microclimates (Meagher 1943), free from the intense solar radiation of western Colorado, compared to areas that have larger but fewer trees.

Further, regeneration decreased with increasing shrub cover for total seedlings and juniper seedlings, with a larger negative effect on juniper seedlings in unburned and refugia plots. Regeneration studies in drought-affected PJ woodlands showed that shrubs had a facilitating effect on regeneration, especially for piñon (Redmond et al. 2012). However, our study did not show a linear relationship, rather as shrub cover increased, number of seedlings increased, until around 11-14% shrub cover, after which seedlings dramatically decreased as shrub cover increased (Table S1 and Table S2). Redmond et al. (2012) measured shrub cover up to ~14%, while we measured shrub cover up to 40%. This indicates there may be a threshold for shrub cover in facilitating conifer regeneration, where at higher cover this relationship is competitive and prohibits seedling growth.

Bird Habitat Use

Piñon-juniper woodlands are important for avian biodiversity, with over 70 bird species known to use this habitat and 18 of these species requiring this habitat to breed in the Western US (Balda and Masters 1980). In this study, we observed 13 obligate or semi-obligate species. The dynamics of guilds and individual species are important to identify species that may be of concern in a future with more fire and classify the potential for future seed dispersal into burned areas.

We expected that PJ obligates and semi-obligates would have a higher occupancy in unburned and refugia habitat compared to burned sites; while this was true for several species, there were also several exceptions. The Gray Vireo, Black-throated Gray Warbler, and Gray Flycatcher all had the lowest habitat use in the old burn and highest habitat use in refugia or unburned sites. Interestingly, these three birds also had high habitat use in the recent burn patches. Since the recent fire occurred after the breeding season the previous year, it is possible that these migratory birds returned to their former nesting sites (Schlossberg 2009), and were observed before moving on to more suitable habitats. These birds are also insectivorous, it is possible that these birds were exploiting insects that are of higher abundances 1-year post-fire (Swengel 2001). Regardless, other post-fire avian studies suggest that it can take several years to observe meaningful responses to fire (Smucker et al. 2005), so verifying whether these birds truly occupy recently burned habitat may require additional years of study. Somewhat opposite of these species is the Blue-gray Gnatcatcher, which had a high habitat use in the old burn, as well as refugia and unburned. These species often nest in shrubby areas near intact woodlands (Root 1967), so the current stage of vegetation growth in the old burn may provide suitable habitat for this species.

Contrary to our hypothesis, several species were not strongly affected by habitat type, with similar occupancy in each habitat, including the Ash-throated Flycatcher, Woodhouse's Scrub-jay, Spotted Towhee, and Virginia's Warbler. Resource use in each habitat was not quantified (nesting, foraging, etc.), but varying habitat structure may provide access to key resources for certain species. For example, the open-ness of the burned habitats might provide abundance of preferred insects, such as moths and wasps (Hansen 1986), for the Ash-throated Flycatcher. Similarly, the greater amount of shrub cover in the old burn sites may provide an abundance of nesting areas for Virginia's Warbler in lieu of trees (Saab et al. 2005).

A PJ obligate of concern is the Gray Vireo. Currently, this species has a stable population across its range (Breeding Bird Survey 2019), however, it is projected to have future declines in parts of its range due to its requirement for mature juniper woodlands and its sensitivity to unsuitable habitat and forest structure (Harris et al. 2021). This species was not observed in the old burn, likely due to the absence of juniper trees, and this can be expected to persist for at least several more decades until more prolific regeneration and maturation occurs. Further, thinning treatments within PJ woodlands have been reported to also eliminate Gray Vireo from occupying treated sites (Crow and Van Riper 2010). With fire in PJ woodlands burning larger areas, more Gray Vireo habitat will be effected by fire than it has in the past, with multi-decade lasting effects.

Woodhouse's Scrub-jay was present and active in all habitat types and was also one of the most frequently observed birds in this study. While this species is less-dependent on piñon and has a lower caching capabilities compared to other piñon dispersers (Vander Wall and Balda 1981), it still has an important role in seed dispersal. Woodhouse's Scrub-jay often stays within its home area for foraging, caching seeds within established stands and into nearby openings, rarely dispersing seeds further than 500 m away (Vander Wall and Balda 1981). This implies that seeds sourced from refugia are likely to be moved into nearby burned patches. Woodhouse's Scrub-jay also has a less effective spatial memory than other piñon seed dispersing birds (Bedkenoff et al. 1997), so seeds cached by this species may have a higher likelihood of germinating the next year instead of being consumed. Furthermore, this species is known to consume other food, such as oak acorns or insects (Vander Wall and Balda 1981), thus it may be less likely to leave a disturbed area in search of cone-producing piñon stands.

Clark's Nutcracker and Pinyon Jay are most known for their piñon seed caching abilities, however, few were observed (Table S4). The relative absence of these birds could be driven by several factors, such as regional drought, range-wide population declines, and seasonal habitat use (Vander Wall and Balda 1981, Christensen et al. 1991, Boone et al. 2019). Persistent drought and regional warming, which the western US has been experiencing since the early 2000s (Williams et al. 2022), is known to cause piñon cone production to decrease (Redmond et al. 2012). While less cone production is known to reduce foraging behavior of seed dispersing birds (Christensen et al. 1991), we did not collect data on this, thus we cannot confirm that as a factor driving the lack of observations. The Pinyon Jay is one of the quickest-declining land birds in the southwest US, having lost about 85% of its population over the past 50 years (Boone et al. 2019), so the lack of observations may be due to the range-wide population decline. The Clark's Nutcracker tends to breed at high-elevation coniferous forests, not appearing in PJ woodlands until seeds begin to ripen in August (Vander Wall and Balda 1981), so not observing this bird in the spring is also not surprising. However, the lack of these keystone species and absence of post-fire piñon regeneration in our study sites may be linked, and if so, an indicator of diminishing woodland resilience to high-severity fire.

We expected juniper dispersers to have a higher probability of occupying burned areas, as several of these species have been documented to increase in abundance post-fire (e.g. Kotliar et al. 2007). Consistent with our hypothesis, the American Robin had a higher habitat use in the recent burn compared to other habitats. American Robins are often observed more in burned areas compared to unburned areas, although not always (Smucker et al. 2005). Similar to the obligate and semi-obligate species, the American Robin's prevalence in the recently burned habitat may be due to returning to past breeding sites, however, unlike the other species analyzed in this study, the American Robin had a much lower habitat use in the refugia and unburned habitats, possibly indicating preference for the recent burned areas over intact woodlands.

We were unable to fully assess our last question regarding how the presence of seed dispersing birds influenced seedling regeneration in burned areas due to little regeneration in burned plots. The presence of the American Robin in the recent burn and the Woodhouse's Scrub-jay in all habitats may offer potential modes of seed dispersal in these woodlands for future regeneration. However, under a changing climate, these seedlings must establish under more extreme climate than the parent trees had several centuries ago (Stevens-Rumann et al.

2018). In unburned and refugia, elevation was a significant driver for seedling regeneration, so at higher elevations, regeneration was more successful. It is possible that burned areas may reflect this as well, with less regeneration success in burned areas at lower elevations. Others have observed this “trailing edge” of forest and woodlands, where new tree conifer establishment is limited at lower elevation/latitudes within a species range (Kemp et al. 2019, Parks et al. 2019).

Management Implications

Results from this study present several relevant findings for management, specifically showing how refugia contribute to the maintenance of both key vegetation attributes (piñon pine and juniper trees and seedlings) and attendant biota (PJ-associated birds). As fire effects a higher proportion of the landscape, refugia are key for retaining live seed sources nearer to the burned patches and providing patches of intact habitat for associated birds. Managers can provide protection of refugia that is created during a wildfire and promote refugia before a fire starts. To promote refugia, managers can create gaps in the canopy and understory to minimize fire spread in woodlands that are at risk for a large fire (Coop et al. 2019, Stevens et al. 2021), such as woodlands with denser canopy, higher prevalence of tree mortality, and more continuous understory. Promoting refugia will also limit the continuity of large burned patches, which will help to maintain avian diversity in these forests (Steel et al. 2022).

For restoration activities, managers can select priority areas by investigating the presence of piñon and juniper dispersing birds in fire-effected areas. Avian surveys should be multi-year, multi-season, and include mast years and non-mast years to ensure that all seed dispersing behaviors are captured. If seed dispersers are absent from the landscape, these areas should take precedent for planting actions. While research on optimal site conditions in burned areas is necessary, land managers can promote seeding germination and success by ensuring adequate nurse objects (Chambers et al. 1999). While important overstory characteristics are lacking in burned areas, other factors, such as shrub cover and grass cover can be monitored and controlled. Lastly, it is important to recognize that current climate conditions may not support the return of these woodlands in burned areas; in this case, managers can support trailing edge forests and monitor seedling establishment occurring at higher elevations, as these regions may be important for the persistence of this important woodland habitat.

Limitations and Future Research

While this study advanced knowledge on tree regeneration and bird responses to fire, these are several limitations. First, limited sample size may be a constraint for lack of regeneration observations in the old burn plots, with there being only six old burned plots that were surveyed. However, anecdotally, while performing point counts and hiking extensively in these burned regions, little tree regeneration was observed, with scattered juniper and few, if any, piñon observed intermittently, so these findings are not necessarily confounded. Second, we collected data during late spring/early summer, before piñon seeds are ripe and after caches have been utilized, so unfortunately, the behaviors that would display bird interactions with piñon seeds were likely missed. Third, studies are often not in agreement regarding bird responses to recent fire in different landscapes, and in many cases, there is a delayed response to fire. This indicates that observing a certain species in the recently burned habitat does not necessarily mean that they prefer this kind of environment.

Findings from this study reveal several areas for future research. First, while proximity to live seed sources is a known controlling factor for regeneration (Chambers et al. 2016, Coop et al. 2019), and these trees require dispersal agents to move seed into burned patches to successfully revegetate (Chambers et al. 1999), future work can focus on building understanding on dispersal distance dynamics into burned patches. This will inform whether increasingly larger burned patches have the potential to regenerate naturally. Second, little is known about site-specific controlling factors for piñon and juniper establishment in burned areas, thus, future work can investigate smaller scale vegetation structure and environmental conditions that are most suitable for piñon and juniper establishment in the current climate, such as optimal shrub cover or nurse object preferences. Third, future avian-focused work can investigate long-term bird occupancy post-fire – i.e. across the landscape, what species most commonly occupy burned areas and how long does this persist? What species do not occupy burned areas and under what conditions will they return? Do more frequent fire have long lasting effects on piñon-juniper obligate and semi obligate species, creating conservation concerns? Is there a limit to the size of burned patch that will successfully be re-seeded by seed dispersing birds?

Conclusions

Much is left to be discovered regarding woodland resilience to changing fire regimes as well as changing climate. This study found that after 25 years, tree regeneration in burned PJ woodlands is minimal, likely driven by microsite conditions, seed availability, and seed dispersal since neighboring unburned and refugia have regeneration of conifers at various size classes. Similarly, while many representative species did not have different habitat use across habitat types, there were several PJ obligate and semi-obligate species that were either absent or had a low habitat use in the burned regions. These two findings either reinforces the idea of long-recovery time for these woodlands, or the potential transition to non-forest cover type. Further research is needed to better understand the biotic and abiotic factors that influence regeneration in this system after fire over longer periods of time, as well as the habitat characteristics that support key bird species.

Figures and Tables

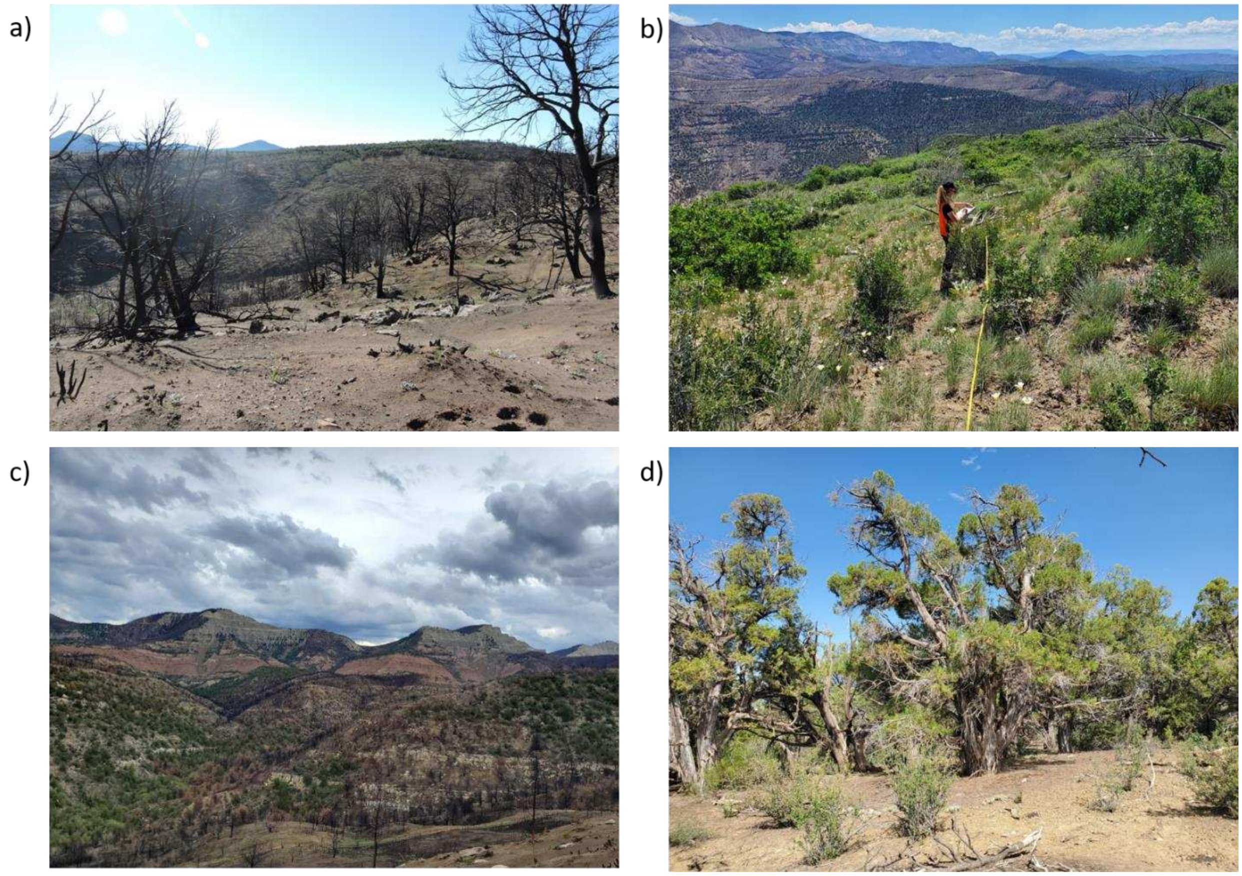

Figure 1. Study area in piñon-juniper woodlands at various years post-fire a) recent burn; b) old burn c) refugia, right and left side of photo; d) unburned/refugia (Photo credit: Jamie Woolet)

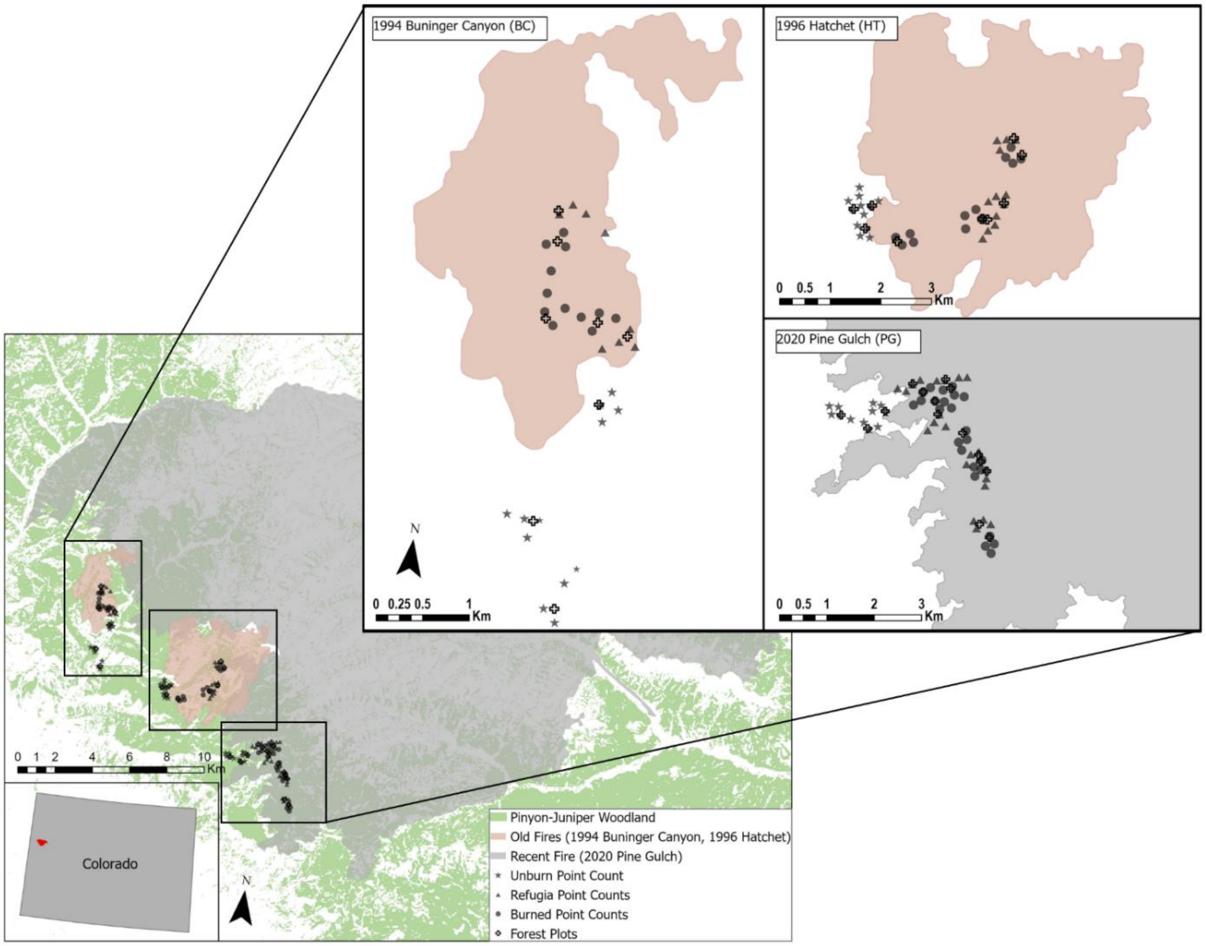

Figure 2. Map of the three fires included in the study and distribution of study sites. The fires were located in western Colorado and burned in 1994, 1996, and 2020. The two older fires (1994 Buninger Canyon Fire (BC) and 1996 Hatchet Fire (HT)), are colored in light red and the recent fire (2020 Pine Gulch Fire (PG)) is colored in grey. Study sites and habitat type are distinguished by symbols: stars = unburn, triangle = refugia, circle = burned. Forest plots are represented by empty cross symbol. Piñon-juniper Woodland vegetation layer is based on existing vegetation type data obtained from landfire.gov.

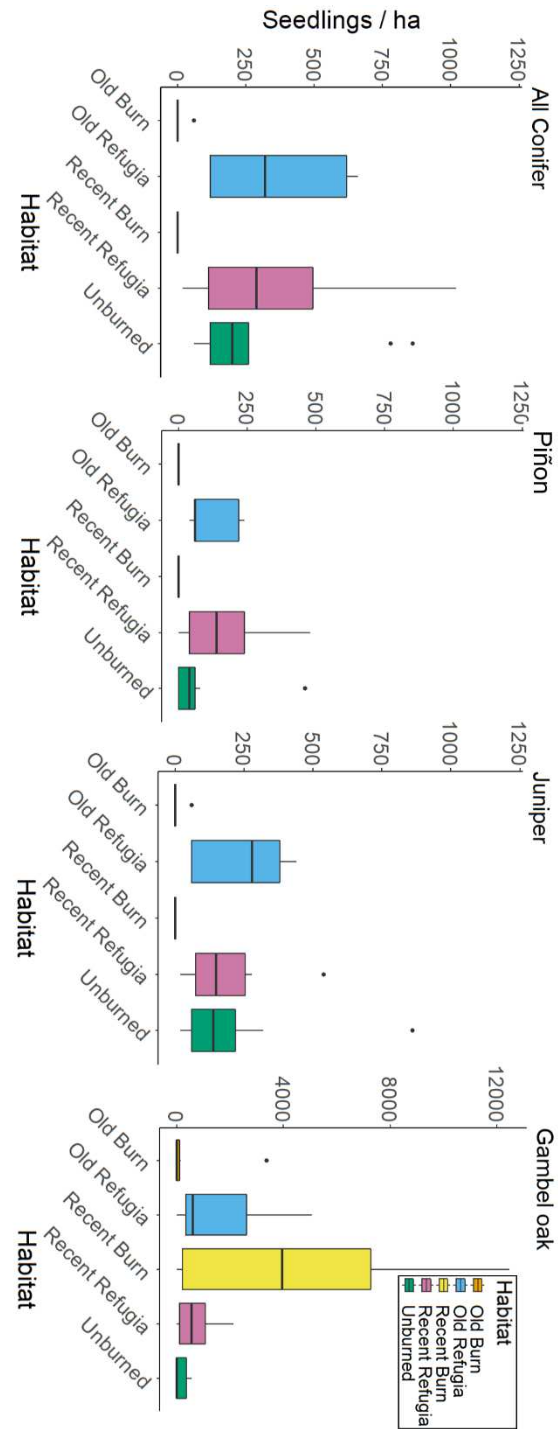

Figure 3. Box plots displaying total conifer seedlings per ha, piñon seedlings per ha, juniper seedlings per ha, and Gambel oak stems per haby habitat type (old burn, old refugia, recent burn, recent refugia, unburned). Boxes are colored by habitat type (orange = old burn, blue = old refugia, yellow = recent burn, pink = recent refugia, and green = unburned). Note the change in y-axis scale for Gambel oak resprouts.

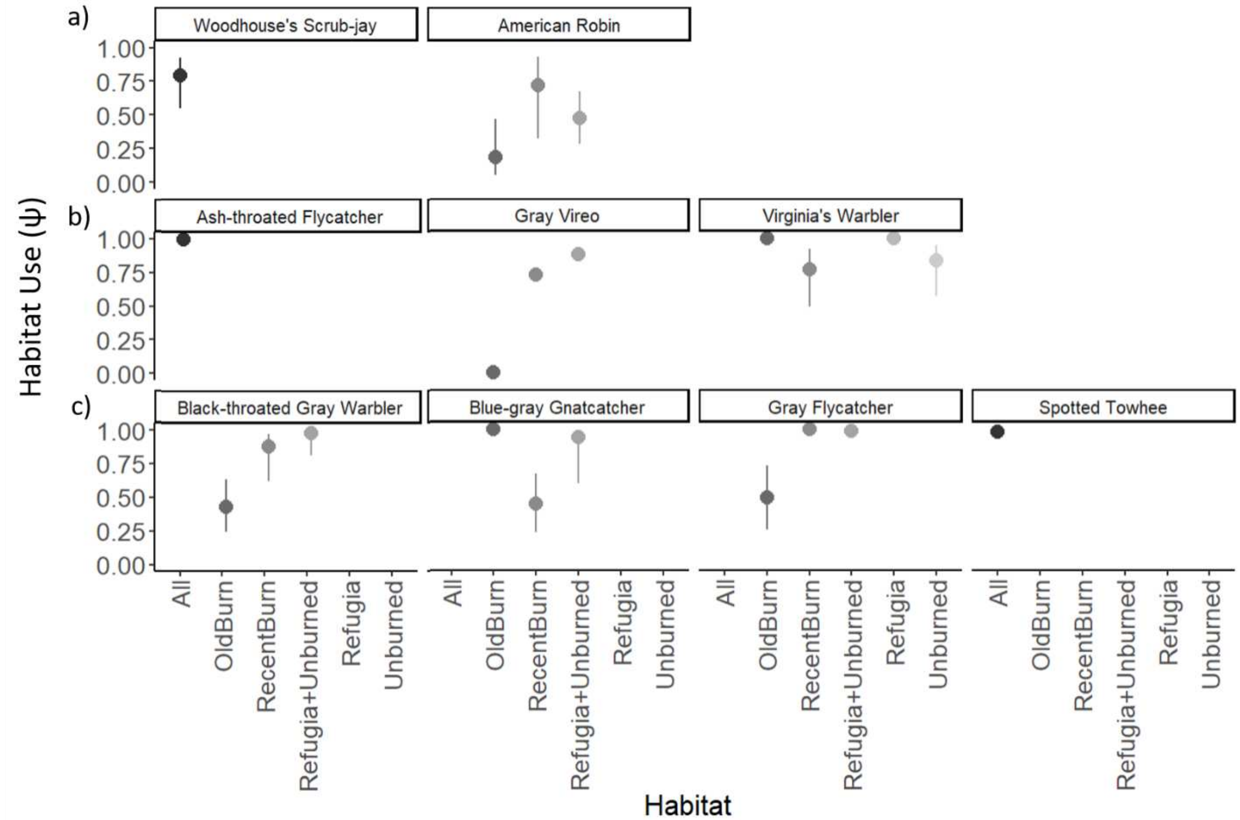

Figure 4. Occupancy results for species of interest based on the species top occupancy model. Note that for species with occupancy estimates near 1 or 0, confidence intervals are excluded, as the Maximum Likelihood Estimates used to create these estimates often fail to produce reliable confidence intervals when the estimate is near a boundary (Cooch and White 2018). Rows are organized by guild: a) piñon and juniper seed dispersers, b) piñon-juniper obligates, c) piñon-juniper semi-obligates.

Table 1. Tukey HSD for differences in live tree basal area per ha (BA), percent canopy cover, total live trees per ha, percent shrub cover, and percent grass cover across habitat types. Letters indicate significant differences from other habitat groups (α = 0.05).

	BA		Percent Canopy Cover		Total Live Trees		Percent Shrub		Percent Grass	
	Mean	TukeyHSD	Mean	TukeyHSD	Mean	TukeyHSD	Mean	TukeyHSD	Mean	TukeyHSD
Old Burn	0.0	a	6.1	a	0.0	a	19.5	b	35.2	b
Recent Burn	0.0	a	8.7	ab	0.0	a	0.8	a	1.3	a
Old Refugia	46.4	b	33.0	b	468.0	b	11.0	ab	7.8	a
Recent Refugia	48.7	b	26.5	ab	453.0	b	16.6	b	6.2	a
Unburn	35.2	b	27.0	ab	341.0	b	10.3	ab	12.4	a

Table 2. Generalized linear model equation used for each seedling class (total seedlings, juniper seedlings, piñon seedlings).

Top Model	**AIC**	**df**	**Null Deviance**	**Residual Deviance**
Total Seedlings ~ Elevation + Aspect + Live Tree BA + # Live Trees + % Shrub	137.47	13	70.33	21.04
Juniper Seedlings ~ Elevation + Aspect + Live Juniper BA + % Shrub + # Live Juniper	126.29	13	52.47	19.92
Piñon Seedlings ~ Elevation + Aspect + % Shrub + # Live Trees	107.87	14	45.19	23.48

Table 3 The effects of site characteristics on seedling regeneration using Generalized Linear Model with negative binomial regression

	Coefficient	Estimate	SE	z-value	p-value
All Conifer Seedlings	% Shrub Cover	-0.052	0.019	-2.735	0.006 *
	# Live Trees	0.040	0.010	3.928	< 0.001 *
	Live Tree BA	-0.337	0.112	-3.005	0.003 *
	Elevation	0.002	0.001	2.981	0.003 *
	Aspect	0.001	0.002	0.324	0.746
Juniper Seedlings	% Shrub	-0.049	0.022	-2.200	0.028 *
	# Live Juniper	0.046	0.014	3.215	0.001 *
	Live Juniper BA	-0.375	0.135	-2.773	0.006 *
	Aspect	0.000	0.002	-0.081	0.935
	Elevation	0.002	0.001	1.819	0.069
Piñon Seedlings	# Live Trees	0.044	0.018	2.399	0.016 *
	% Shrub	-0.027	0.027	-1.027	0.304
	Aspect	-0.001	0.003	-0.450	0.653
	Elevation	0.004	0.001	2.994	0.003 *

Table 4. Top occupancy models for determining detection probability and probability of occupancy for each species of interest. The model with the lowest AICc value was used to estimate occupancy. Hypotheses for occupancy covariates are based on potential biological responses a species may have to habitat types. Null Hypothesis: Habitat use is not different across habitat types, Hypothesis 1: Habitat use is different in each habitat type, Hypothesis 2: Habitat use in burned habitat is different from habitat that did not burn, Hypothesis 3: Habitat use is different across vegetation stages.

Guild	Species	Top Models	AICc	ΔAICc
Piñon seed dispersers	Woodhouse's Scrub-jay	p(null)psi(null)	431.42	0.00
		p(null)psi(Hypothesis3)	432.59	1.17
Juniper seed dispersers	American Robin	p(obs)psi(Hypothesis3)	265.14	0.00
		p(obs)psi(Hypothesis1)	266.29	1.15
PJ Obligates	Ash-throated Flycatcher	p(obs)psi(null)	518.57	0.00
	Gray Vireo	p(cloud)psi(Hypothesis3)	262.03	0.00
		p(cloud)psi(Hypothesis1)	262.04	0.01
	Virginia's Warbler	p(obs)psi(Hypothesis1)	507.55	0.00
		p(obs + cloud)psi(Hypothesis1)	507.56	0.01
PJ Semi-obligates	Black-throated Gray Warbler	p(obs+wind)psi(Hypothesis3)	457.86	0.00
		p(obs)psi(Hypothesis3)	459.84	1.98
	Blue-gray Gnatcatcher	p(cloud)psi(Hypothesis3)	488.27	0.00
		p(cloud +wind)psi(Hypothesis3)	489.44	1.17
	Gray Flycatcher	p(obs)psi(Hypothesis3)	468.55	0.00
	Spotted Towhee	p(obs + cloud)psi(null)	341.89	0.00
		p(obs + cloud)psi(Hypothesis3)	342.37	0.48
		p(obs + cloud)psi(Hypothesis2)	343.01	1.12

Table 5. Bird detections within 100 m for each habitat type. Guild designations are based on reports by Balda and Masters (1980), Paulin et al. (1999), and breeding ranges delineated by Cornell Ornithology Lab (allaboutbirds.org). Species that were used for occupancy models are indicated by [a]. Species that fall into a seed dispersing category but also an obligate or semi-obligate category are indicated by [b] or [c], respectively.

Guild	Species	Old Burn	Recent Burn	Refugia	Unburn	Total
Piñon seed dispersers	Woodhouse's Scrub Jay [a b]	43	16	38	28	125
	Pinyon Jay [c]	2	0	3	3	8
	Stellar's Jay	1	0	1	2	4
	Clark's Nutcracker	0	0	1	2	3
Juniper seed dispersers	American Robin [a]	3	18	14	18	53
	Mountain Bluebird	7	15	7	1	30
	Western Bluebird	0	2	4	1	7
	Townsend's Solitaire	0	0	1	2	3
PJ Obligates	Virginia's Warbler [a]	65	25	82	58	230
	Ash-throated Flycatcher [a]	29	26	75	84	214
	Gray Vireo [a]	0	9	17	26	52
	Juniper Titmouse	0	4	14	11	29
PJ Semi-obligates	Spotted Towhee [a]	157	98	195	153	603
	Black-throated Gray Warbler [a]	16	37	174	114	341
	Blue-gray Gnatcatcher [a]	45	15	56	64	180
	Gray Flycatcher [a]	11	35	50	56	152
	Bewick's Wren	6	3	16	14	39
	Lark Sparrow	7	4	4	5	20
	Bushtit	3	0	2	0	5

Table 6. Occupancy model results for each species of interest. Ψ is the probability of a species using a habitat type and *p* is the probability of the species being detected if present presented as a range.

Guild	Species	Habitat	ψ	CI	SE	*p*
Piñon seed dispersers	Woodhouse's Scrub-jay	All	0.79	0.55, 0.92	0.096	0.32
Juniper seed dispersers	American Robin	RecentBurn	0.72	0.32, 0.93	0.173	0.08 - 0.46
		Refugia + Unburn	0.48	0.29, 0.67	0.104	0.08 - 0.46
		OldBurn	0.19	0.06, 0.47	0.105	0.08 - 0.46
PJ Obligates	Ash-throated Flycatcher	All	1.00	0.00, 1.00	0.002	0.38 - 0.54
	Gray Vireo	Refugia + Unburn	0.88	0.10, 1.00	0.225	0.13 - 0.39
		RecentBurn	0.72	0.14, 0.98	0.282	0.13 - 0.39
		OldBurn	0.00	0.00, 1.00	0.002	0.13 - 0.39
	Virginia's Warbler	OldBurn	1.00	0.00, 1.00	0.001	0.29 - 0.57
		Refugia	1.00	0.00, 1.00	0.000	0.29 - 0.57
		Unburn	0.83	0.57, 0.95	0.094	0.29 - 0.57
		RecentBurn	0.77	0.49, 0.92	0.112	0.29 - 0.57
PJ Semi-obligates	Black-throated Gray Warbler	Refugia + Unburn	0.98	0.82, 1.00	0.026	0.22 - 0.82
		RecentBurn	0.88	0.62, 0.97	0.081	0.22 - 0.82
		OldBurn	0.43	0.25, 0.64	0.105	0.22 - 0.82
	Blue-gray Gnatcatcher	OldBurn	1.00	0.00, 1.00	0.006	0.25 - 0.49
		Refugia + Unburn	0.94	0.60, 0.99	0.066	0.25 - 0.49
		RecentBurn	0.44	0.24, 0.67	0.118	0.25 - 0.49
	Gray Flycatcher	RecentBurn	1.00	0.00, 1.00	0.020	0.22 - 0.44
		Refugia + Unburn	0.98	0.00, 1.00	0.090	0.22 - 0.44
		OldBurn	0.49	0.26, 0.73	0.132	0.22 - 0.44
	Spotted Towhee	All	0.98	0.93, 1.00	0.014	0.63 - 0.98

REFERENCES

Abella, Scott R. and Paula J. Fornwalt. 2015. "Ten Years of Vegetation Assembly after a North American Mega Fire." *Global Change Biology* 21(2): 789–802. https://doi.org/10.1111/gcb.12722.

Alstatt, David K. 2003. "Soil Survey of Douglas-Plateau Area, Colorado, Parts of Garfield and Mesa Counties." United States Department of Agriculture, Natural Resources Conservation Service.

Anderson, Michele. D. 2002. "Pinus edulis. In: Fire Effects Information System". U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available: https://www.fs.fed.us/database/feis/plants/tree/pinedu/all.html

Baker, William L. and Douglas J. Shinneman. 2004. "Fire and Restoration of Piñon-Juniper Woodlands in the Western United States: A Review." *Forest Ecology and Management* 189 (1–3): 1–21. https://doi.org/10.1016/j.foreco.2003.09.006.

Balda, Russel P. and Nancy Masters. 1980. "Avian communities in the pinyon–juniper woodland: a descriptive analysis." In: DeGraff, R.M., Tilghman, N.G. (Eds.), Proceedings: Management of Western Forests and Grasslands for Nongame Birds. *USDA Forest Service Gen. Tech. Rep. INT-86,* Ogden, Utah, pp. 146–169.

Bednekoff, Peter A., Russell P. Balda, Alan C. Kamil, Arla G. Hile. 1997. "Long-term spatial memory in four seed-caching corvid species." *Animal Behaviour* 53 (2): 335-341. https://doi.org/10.1006/anbe.1996.0395.

Board, David I., Jeanne C. Chambers, Richard F. Miller, and Peter J. Weisberg. 2018. "Fire patterns in piñon and juniper land cover types in the Semiarid Western United States from 1984 through 2013." *RMRS-GTR-372*. Fort Collins, CO: U.S Department of Agriculture, Forest Service, Rocky Mountain Research Station. 57 p.

Boone, John D., Elisabeth Ammon, and Kristine Johnson. 2018. "Long-term declines in the Pinyon Jay and management implications for piñon-juniper woodlands." *Trends and traditions: avifaunal change in western North America. Studies of Western Birds* 3: 190-197. https://doi.org/10.21199/SWB3.10

Bowman, David M.J.S., Jennifer K. Balch, Paulo Artaxo, William J. Bond, Jean M. Carlson, Mark A. Cochrane, Carla M. D'Antonio, et al. 2009. "Fire in the Earth System." *Science* 324 (5926): 481–84. https://doi.org/10.1126/science.1163886.

Bristow, Nathan A., Peter J. Weisberg, and Robin J. Tausch. 2014. “A 40-Year Record of Tree Establishment Following Chaining and Prescribed Fire Treatments in Singleleaf Pinyon (Pinus Monophylla) and Utah Juniper (Juniperus Osteosperma) Woodlands.” *Rangeland Ecology and Management* 67 (4): 389–96. https://doi.org/10.2111/REM-D-13-00168.1.

Chambers, Jeanne C., Stephen B. Vander Wall, and Eugene W. Schupp. 1999. “Seed and Seedling Ecology of Pinyon and Juniper Species in the Pygmy Woodlands of Western North America.” *The Botanical Review* 65 (MARCH): 1–38.

Chambers, Marin E., Paula J. Fornwalt, Sparkle L. Malone, and Mike A. Battaglia. 2016. "Patterns of conifer regeneration following high severity wildfire in ponderosa pine–dominated forests of the Colorado Front Range." *Forest Ecology and Management* 378: 57-67. https://doi.org/10.1016/j.foreco.2016.07.001

Chapman, Teresa B., Tania Schoennagel, Thomas T. Veblen, and Kyle C. Rodman. 2020. “Still Standing: Recent Patterns of Post-Fire Conifer Refugia in Ponderosa Pine-Dominated Forests of the Colorado Front Range.” *PLoS ONE* 15 (1): e0226926. https://doi.org/10.1371/journal.pone.0226926.

Chojnacky, David C. and Paul Rogers. 1999. "Converting tree diameter measured at root collar to diameter at breast height." *Western Journal of Applied Forestry* 14 (1): 14-16. https://doi.org/10.1093/wjaf/14.1.14

Christensen, Kerry M., Thomas G. Whitham and Russel P. Balda. 1991. “Discrimination among pinyon pine trees by Clark's nutcrackers: effects of cone crop size and cone characters.” *Oecologia* 86 (3): 402–407. https://doi.org/10.1007/BF00317608.

Cooch, Evan G. and Gary C. White. 2018. “Program MARK: A Gentle Introduction.” http://www.phidot.org/software/mark/docs/book/

Coop, Jonathan D., and Anna W. Schoettle. 2009. “Regeneration of Rocky Mountain Bristlecone Pine (Pinus Aristata) and Limber Pine (Pinus Flexilis) Three Decades after Stand-Replacing Fires.” *Forest Ecology and Management* 257 (3): 893–903. https://doi.org/10.1016/j.foreco.2008.10.034.

Coop, Jonathan. D., Timothy J. DeLory, William M. Downing, Sandra L. Haire, Meg A. Krawchuk, Carol Miller, Marc-André Parisien, Ryan B. Walker. 2019. “Contributions of fire refugia to resilient ponderosa pine and dry mixed-conifer forest landscapes.” *Ecosphere* 10 (7): e02809. https://doi.org/10.1002/ecs2.2809

Coop, Jonathan D., Sean A. Parks, Camille S. Stevens-Rumann, Shelley D. Crausbay, Philip E. Higuera, Matthew D. Hurteau, Alan Tepley, et al. 2020. “Wildfire-Driven Forest Conversion in Western North American Landscapes.” *BioScience* 70 (8): 659–73. https://doi.org/10.1093/biosci/biaa061.

Cornell Lab of Ornithology. 2019. All About Birds. Cornell Lab of Ornithology, Ithaca, New York. https://www.allaboutbirds.org Accessed January 2022.

Crow, Claire, and Charles Van Riper III. 2010. “Avian Community Responses to Mechanical Thinning of a Pinyon-Juniper Woodland: Specialist Sensitivity to Tree Reduction.” *Natural Areas Journal* 30 (2): 191–201. https://doi.org/10.3375/043.030.0206.

Eidenshink, Jeff, Brian Schwind, Ken Brewer, Zhi-Liang Zhu, Brad Quayle, and Stephen Howard. 2007. "A project for monitoring trends in burn severity." *Fire Ecology* 3(1): 3-21.

ESRI 2020. ArcGIS Pro, version 2.7.0.

Fair, Jeanne M., Charles D. Hathcock, and Andrew W. Bartlow. 2018. “Avian Communities Are Decreasing with Piñon Pine Mortality in the Southwest.” *Biological Conservation* 226 (June): 186–95. https://doi.org/10.1016/j.biocon.2018.06.035.

Finch, Deborah M., Joseph L. Ganey, Wang Yong, Rebecca T. Kimball, Rex Sallabanks. 1997. “Effects and interactions of fire, logging, and grazing.” In: Block, William M.; Finch, Deborah M. (Tech. eds.). Songbird ecology in southwestern ponderosa pine forests: a literature review. *Gen. Tech. Rep. RM-292.* Fort Collins, CO: U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. p. 103-136.

Fiske, Ian and Richard Chandler. 2011. “unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance.” *Journal of Statistical Software* 43(10): 1–23. https://www.jstatsoft.org/v43/i10/

Floyd, Mary E. 1982. “The Interaction of Piñon Pine and Gambel Oak in Plant Succession near Dolores, Colorado.” *The Southwestern Naturalist* 27 (2): 143–47. https://doi.org/10.2307/3671138.

Floyd, M. Lisa, William H. Romme and David D. Hanna. 2000. “Fire History and Vegetation Pattern in Mesa Verde National Park, Colorado USA.” *Ecological Applications* 10 (6): 1666-1680. https://doi-org/10.1890/1051-0761

Floyd, M. Lisa, William H. Romme, Monique E. Rocca, Dustin P. Hanna, and David D. Hanna. 2015. “Structural and Regenerative Changes in Old-Growth Piñon-Juniper Woodlands Following Drought-Induced Mortality.” *Forest Ecology and Management* 341: 18–29. https://doi.org/10.1016/j.foreco.2014.12.033.

Floyd, M. Lisa, William H. Romme, and David D. Hanna. 2021. “Effects of Recent Wildfires in Piñon-Juniper Woodlands of Mesa Verde National Park, Colorado, USA.” *Natural Areas Journal* 41 (1): 28–38.

Gallo, Travis, and Liba Pejchar. 2017. "Woodland Reduction and Long-Term Change in Breeding Bird Communities." *Journal of Wildlife Management* 81 (2): 259–68. https://doi.org/10.1002/jwmg.21188.

Gill, Nathan S., Florencia Sangermano, Brian Buma, and Dominik Kulakowski. 2017. "Populus Tremuloides Seedling Establishment: An Underexplored Vector for Forest Type Conversion after Multiple Disturbances." *Forest Ecology and Management* 404 (May): 156–164. https://doi.org/10.1016/j.foreco.2017.08.008.

Gillihan, Scott W. 2006. "Sharing the land with pinyon-juniper birds." Salt Lake City, Utah, USA: Partners in Flight Western Working Group.

Goodrich, Sherel. 1999. "Multiple use management based on diversity of capabilities and values within pinyon-juniper woodlands." Pp. 164- 171 in S. B. Monsen and R. Stevens, compilers. Proceedings: ecology and management of pinyon-juniper communities within the Interior West. *USDA Forest Service RMRS-P-9.* Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 411 p.

Graves, Spencer, Hans-Peter Piepho, and Luciano Selzer with help from Sundar Dorai-Raj. 2019. "multcompView: Visualizations of Paired Comparisons." R package version 0.1-8. https://CRAN.R-project.org/package=multcompView

Halofsky, Jessica E., David L. Peterson, and Brian J. Harvey. 2020. "Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA." *Fire Ecology* 16 (1): 1-26.

Hansen, James D. 1986. "Comparison of insects from burned and unburned areas after a range fire." *The Great Basin Naturalist* 46 (4): 721–727. http://www.jstor.org/stable/41712293

Harris, Jonathan, Loren Smith, Scott McMurry. 2021. "Fine-scale plasticity in nest placement can compensate for poor quality junipers as nesting trees for gray vireos." *PeerJ* 9:e12477 https://doi.org/10.7717/peerj.12477

Higuera, Philip E. and John T. Abatzoglou. 2020. "Record-Setting Climate Enabled the Extraordinary 2020 Fire Season in the Western United States." *Global Change Biology* 27 (1): 1–2. https://doi.org/10.1111/gcb.15388.

Huffman, David W., Joseph E. Crouse, W. Walker Chancellor, and Peter Z. Fulé. 2012. "Influence of Time since Fire on Pinyon-Juniper Woodland Structure." *Forest Ecology and Management* 274: 29–37. https://doi.org/10.1016/j.foreco.2012.02.014.

Johnsen, Thomas N. 1962. "One-Seed Juniper Invasion of Northern Arizona Grasslands." *Ecological Monographs* 32 (3): 187–207. https://doi.org/10.2307/1942398.

Johnstone, Jill F., Craig D. Allen, Jerry F. Franklin, Lee E. Frelich, Brian J. Harvey, Philip E. Higuera, Michelle C. Mack, et al. 2016. “Changing Disturbance Regimes, Ecological Memory, and Forest Resilience.” *Frontiers in Ecology and the Environment* 14 (7): 369–78. https://doi.org/10.1002/fee.1311.

Keane, Robert E., James K. Agee, Peter Fulé, Jon E. Keeley, Carl Key, Stanley G. Kitchen, Richard Miller, and Lisa A. Schulte. 2008. “Ecological Effects of Large Fires on US Landscapes: Benefit or Catastrophe?” *International Journal of Wildland Fire* 17 (6): 696–712. https://doi.org/10.1071/WF07148.

Kemp, Kerry B., Philip E. Higuera, Penelope Morgan, and John T. Abatzoglou. 2019. “Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA.” *Ecosphere* 10 (1): e02568. https://doi.org/10.1002/ecs2.2568

Koniak, Susan. 1985. “Succession in Pinyon-Juniper Woodlands Following Wildfire in the Great Basin.” *Great Basin Naturalist* 45 (3): 556–66.

Korb, Julie E., Paula J. Fornwalt, and Camille S. Stevens-Rumann. 2019. "What drives ponderosa pine regeneration following wildfire in the western United States?" *Forest Ecology and Management* 454 (2019): 117663. https://doi.org/10.1016/j.foreco.2019.117663

Kotliar, Natasha B., Patricia L. Kennedy, and Kimberly Ferree. 2007. “Avifaunal Responses to Fire in Southwestern Montane Forests along a Burn Severity Gradient.” *Ecological Applications* 17 (2): 491–507. https://doi.org/10.1890/06-0253.

LANDFIRE. 2016. “Existing Vegetation Type Layer”, U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed 20 February 2020 at http://landfire.cr.usgs.gov/viewer/.

Lenth, Russel V. 2021. “emmeans: Estimated Marginal Means, aka Least-Squares Means.” R package version 1.7.0. https://CRAN.R-project.org/package=emmeans

Longland, William S. and Lindsay A. Dimitri. 2016. "Are Western Juniper Seeds Dispersed Through Diplochory?" *Northwest Science* 90 (2): 235-244.

MacKenzie, Darryl I., James D. Nichols, J. Andrew Royle, Kenneth H. Pollock, Larissa L. Bailey, and James E. Hines. 2017. “Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.” Elsevier.

Magee, Patrick A., Jonathan D. Coop, and Jacob S. Ivan. 2019. “Thinning Alters Avian Occupancy in Piñon-Juniper Woodlands.” *Condor* 121 (1): 1–17. https://doi.org/10.1093/condor/duy008.

Masters, Nancy Louise. 1979. Breeding birds of pinyon-juniper woodland in north central Arizona. *M.S. Thesis. Dept. of Sial. Sciences*, Northern Arizona University, Flagstaff, Ariz., 78 pp.

Mazerolle, Marc J. 2020. "AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)." R package version 2.3-1. https://cran.r-project.org/package=AICcmodavg.

McLaren, Matthew F., Chris M. White, Nicholas J. Van Lanen, Jeff J. Birek, Jenny M. Berven, and David J. Hanni. 2019. "Integrated Monitoring in Bird Conservation Regions (IMBCR): Field protocol for spatially-balanced sampling of land bird populations." Unpublished report. Bird Conservancy of the Rockies, Brighton, Colorado, USA.

McLauchlan, Kendra K., Philip E. Higuera, Jessica Miesel, Brendan M. Rogers, Jennifer Schweitzer, Jacquelyn K. Shuman, Alan J. Tepley, et al. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers." *Journal of Ecology* 2020;00: 1–23. https://doi.org/10.1111/1365-2745.13403.

Meagher, George S. 1943. "Reaction of pinyon and juniper seedlings to artificial shade and supplemental watering." *Journal of Forestry* 41 (7):480-482.

Meddens, Arjan J.H., Crystal A. Kolden, James A. Lutz, Alistair M.S. Smith, C. Alina Cansler, John T. Abatzoglou, Garrett W. Meigs, William M. Downing, and Meg A. Krawchuk. 2018. "Fire Refugia: What Are They, and Why Do They Matter for Global Change?" *BioScience* 68 (12): 944–54. https://doi.org/10.1093/biosci/biy103.

NOAA National Centers for Environmental Information. 2021. "U.S. Climate Normals 2020: U.S. Annual/Seasonal Climate Normals (1991-2020)", 14 September 2021, https://www.ncei.noaa.gov/access/search/data-search/normals-annualseasonal-1991-2020.

Pardieck, Keith L., David J. Ziolkowski Jr., Michael Lutmerding, and Marie-Anne R. Hudson. "North American breeding bird survey dataset 1966–2017, version 2017.0." *US Geological Survey, Patuxent Wildlife Research Center* 10 (2018): F76972V8.

Parks, Sean. A., Solomon Z. Dobrowski., John D. Shaw, and Carol Miller. 2019. "Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non forest." *Ecosphere* 10 (3): e02351. https://doi.org/10.1002/ecs2.2568

Paulin, Kathleen M., Jeffery J. Cook, and Sarah R. Dewey. 1999. "Juniper woodlands as sources of avian diversity." In: Monsen, S.B., Stevens (Eds.), Proceedings: Ecology and Management of Pinyon–Juniper Communities within the Interior West. *USDA Forest Service Proceedings RMRS-P-9*, Ogden, UT, pp. 240–243.

Pesendorfer, Mario B., T. Scott Sillett, Walter D. Koenig, and Scott A. Morrison. 2016. "Scatter-Hoarding Corvids as Seed Dispersers for Oaks and Pines: A Review of a Widely

Distributed Mutualism and Its Utility to Habitat Restoration." *Condor* 118 (2): 215–37. https://doi.org/10.1650/CONDOR-15-125.1.

Pons, Pere and Clara Wendenburg. 2005. "The Impact of Fire and Forest Conversion into Savanna on the Bird Communities of West Madagascan Dry Forests." *Animal Conservation* 8 (2): 183–93. https://doi.org/10.1017/S1367943005001940.

R Core Team. 2021. "R: A language and environment for statistical computing." R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Redmond, Miranda. D., Frank Forcella, and Nichole N. Barger. 2012. "Declines in pinyon pine cone production associated with regional warming." *Ecosphere* 3 (12):1-14. http://dx.doi.org/10.1890/ES12-00306.1

Redmond, Miranda D. and Nichole N. Barger. 2013. "Tree Regeneration Following Drought- and Insect-Induced Mortality in Piñon-Juniper Woodlands." *New Phytologist* 200 (2): 402–12. https://doi.org/10.1111/nph.12366.

Redmond, Miranda D., Neil S. Cobb, Michael J. Clifford, and Nichole N. Barger. 2015. "Woodland Recovery Following Drought-Induced Tree Mortality across an Environmental Stress Gradient." *Global Change Biology* 21 (10): 3685–95. https://doi.org/10.1111/gcb.12976.

Redmond, Miranda D., Peter J. Weisberg, Neil S. Cobb, and Michael J. Clifford. 2017. "Woodland Resilience to Regional Drought: Dominant Controls on Tree Regeneration Following Overstorey Mortality." *Journal of Ecology* 106 (2): 625–39. https://doi.org/10.1111/1365-2745.12880.

Robinson, Natasha M., Steven W.J. Leonard, Andrew F. Bennett, and Michael F. Clarke. 2014. "Refuges for birds in fire-prone landscapes: the influence of fire severity and fire history on the distribution of forest birds." *Forest Ecology and Management* 318: 110-121.

Rocca, Monique E., Peter M. Brown, Lee H. MacDonald, and Christian M. Carrico. 2014. "Climate Change Impacts on Fire Regimes and Key Ecosystem Services in Rocky Mountain Forests." *Forest Ecology and Management* 327: 290–305. https://doi.org/10.1016/j.foreco.2014.04.005.

Romme, William H., Lisa Floyd-Hanna, David D. Hanna. 2003. "Ancient Piñon-Juniper Forests of Mesa Verde and the West: A Cautionary Note for Forest Restoration Programs." Pages 335-350. In: Omi, Philip N.; Joyce, Linda A. (technical editors). Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings: 16-18 April 2002: Fort Collins, Colorado. *Proceedings RMRS-P-29*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Romme, William H., Craig D. Allen, John D. Bailey, William L. Baker, Brandon T. Bestelmeyer, Peter M. Brown, Karen S. Eisenhart, et al. 2009. "Historical and Modern Disturbance Regimes, Stand Structures, and Landscape Dynamics in Piñon-Juniper Vegetation of the Western United States." *Rangeland Ecology and Management* 62 (3): 203–22. https://doi.org/10.2111/08-188R1.1.

Root, Richard B. 1967. "The niche exploitation pattern of the Blue-gray Gnatcatcher." *Ecological Monographs* 37 (4): 317- 350.

Saab, Victoria A., Hugh D.W. Powell, Natasha B. Kotliar, and Karen R. Newlon. 2005. "Variation in Fire Regimes of the Rocky Mountains: Implications for Avian Communities and Fire Management." *Studies in Avian Biology* 30: 76–96.

Salomonson, Michael G. 1978. "Adaptations for animal dispersal of one-seed juniper seeds." *Oecologia* 32:333-339.

Schlossberg, Scott. 2009. "Site fidelity of shrubland and forest birds." *The Condor* 111 (2):238-246.

Singleton, Megan P., Andrea E. Thode, Andrew J. Sánchez Meador, and Jose M. Iniguez. 2019. "Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015." *Forest Ecology and Management* 433 (2019): 709-719. https://doi.org/10.1016/j.foreco.2018.11.039

Smucker, Kristina M., Richard L. Hutto, and Brian M. Steele. 2005. "Changes in Bird Abundance After Wildfire: Importance of Fire Severity and Time Since Fire." *Ecological Applications* 15 (5): 1535-1549. https://doi.org/10.1890/04-1353

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey, 08 August 2021, http://websoilsurvey.sc.egov.usda.gov/.

Steel, Zachary L., Alissa M. Fogg, Ryan Burnett, L. Jay Roberts, Hugh D. Safford. 2022. "When bigger isn't better—Implications of large high-severity wildfire patches for avian diversity and community composition". *Diversity and Distributions* 28 (3): 439– 453. https://doi.org/10.1111/ddi.13281

Steenvoorden, Jasper, Arjan J.H. Meddens, Anthony J. Martinez, Lee J. Foster, and W. Daniel Kissling. 2019. "The Potential Importance of Unburned Islands as Refugia for the Persistence of Wildlife Species in Fire-Prone Ecosystems." *Ecology and Evolution* 9 (15): 8800–8812. https://doi.org/10.1002/ece3.5432.

Stevens, Jens T., Collin M. Haffey, Jonathan D. Coop, Paula J. Fornwalt, Larissa Yocom, Craig D. Allen, Anne Bradley et al. 2021. "Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States." *Forest Ecology and Management* 502: 119678. https://doi.org/10.1016/j.foreco.2021.119678

Stevens-Rumann, Camille S., Kerry B. Kemp, Philip E. Higuera, Brian J. Harvey, Monica T. Rother, Daniel C. Donato, Penelope Morgan, and Thomas T. Veblen. 2018. "Evidence for Declining Forest Resilience to Wildfires under Climate Change." *Ecology Letters* 21 (2): 243–52. https://doi.org/10.1111/ele.12889.

Swengel, Ann B. 2001. "A literature review of insect responses to fire, compared to other conservation managements of open habitat." *Biodiversity & Conservation* 10(7): 1141-1169.

Urza, Alexandra K., Peter J. Weisberg, Jeanne C. Chambers, Jessica M. Dhaemers, and David Board. 2017. "Post-Fire Vegetation Response at the Woodland–Shrubland Interface Is Mediated by the Pre-Fire Community." *Ecosphere* 8 (6). https://doi.org/10.1002/ecs2.1851.

Vander Wall, Steven B. and Russell P. Balda. 1981. "Ecology and Evolution of Food-storage Behavior in Conifer-seed-caching Corvids." *Zeitschrift für Tierpsychologie* 56: 217-242. https://doi.org/10.1111/j.1439-0310.1981.tb01298.x

Vankat, John L. 2017. "Methods for sampling density and basal area of multi-trunked trees: *Juniperus osteosperma* in pinyon-juniper vegetation," *Western North American Naturalist* 77(2): 195-203. https://doi.org/10.3398/064.077.0207

Venables, William N., Brian D. Ripley. 2002. *Modern Applied Statistics with S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0, https://www.stats.ox.ac.uk/pub/MASS4/.

Westerling, A. LeRoy, Hugo G. Hidalgo, Daniel R. Cayan, and Thomas W. Swetnam. 2006. "Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity." *Science* 313 (5789): 940–43. https://doi.org/10.1126/science.1128834.

Westerling, A. LeRoy. 2016. "Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring." *Philosophical Transactions of the Royal Society* 371: 20150178. http://dx.doi.org/10.1098/rstb.2015.0178

Western Regional Climate Center. "Altenbern, Colorado Period of Record Monthly Climate Summary: 1947-2016." WRCC, accessed 8 February 2022, https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?co0214

Whitman, Ellen, Marc André Parisien, Dan K. Thompson, and Mike D. Flannigan. 2019. "Short-Interval Wildfire and Drought Overwhelm Boreal Forest Resilience." *Scientific Reports* 9 (1): 1–12. https://doi.org/10.1038/s41598-019-55036-7.

Wickham, Hadley. 2016. "ggplot2: Elegant Graphics for Data Analysis." Springer-Verlag New York, 2016.

Wickham, Hadley, Romain François, Lionel Henry and Kirill Müller. 2021. "dplyr: A Grammar of Data Manipulation." R package version 1.0.7. https://CRAN.R-project.org/package=dplyr

Williams, A. Park, Benjamin I. Cook, and Jason E. Smerdon. 2022. "Rapid intensification of the emerging southwestern North American megadrought in 2020–2021." *Nature Climate Change* 12(3): 232-234.

APPENDIX

Table S1. Seedling counts per 0.05 ha plot and density per hectare. Total seedlings include combined numbers from juniper and piñon pine.

SiteID	Fire Age	Habitat	Total Seedlings	Total Seedlings/ha	Juniper Seedlings	Juniper Seedlings/ha	Piñon Seedlings	Piñon Seedlings/ha	Gambel Stems	Gambel Stems/ha
BCB1	old	burn	0	0	0	0	0	0	0	0
BCB2	old	burn	0	0	0	0	0	0	8	160
BCB3	old	burn	0	0	0	0	0	0	0	0
BCR2	old	refugia	31	620	19	380	12	240	31	620
BCR3	old	refugia	6	120	3	60	3	60	0	0
BCU1	old	unburn	6	120	6	120	0	0	0	0
BCU2	old	unburn	13	260	10	200	3	60	0	0
BCU3	old	unburn	12	240	11	220	1	20	0	0
HTB1	old	burn	0	0	0	0	0	0	0	0
HTB2	old	burn	0	0	0	0	0	0	0	0
HTB3	old	burn	3	60	3	60	0	0	169	3380
HTR1	old	refugia	6	120	3	60	3	60	131	2620
HTR2	old	refugia	16	320	14	280	2	40	18	360
HTR3	old	refugia	33	660	22	440	11	220	254	5080
HTU1	old	unburn	6	120	2	40	4	80	0	0
HTU2	old	unburn	10	200	7	140	3	60	19	380
HTU3	old	unburn	43	860	43	860	0	0	28	560
PGB1	recent	burn	0	0	0	0	0	0	624	12480
PGB2	recent	burn	0	0	0	0	0	0	353	7060
PGB3	recent	burn	0	0	0	0	0	0	0	0
PGB4	recent	burn	0	0	0	0	0	0	0	0
PGB5	recent	burn	0	0	0	0	0	0	43	860
PGB6	recent	burn	0	0	0	0	0	0	367	7340
PGR1	recent	refugia	11	220	6	120	5	100	33	660
PGR2	recent	refugia	4	80	3	60	1	20	0	0
PGR3	recent	refugia	51	1020	27	540	24	480	61	1220
PGR4	recent	refugia	1	20	1	20	0	0	23	460
PGR5	recent	refugia	27	540	14	280	13	260	0	0
PGR6	recent	refugia	18	360	9	180	9	180	107	2140
PGU1	recent	unburn	3	60	3	60	0	0	0	0
PGU2	recent	unburn	3	60	1	20	2	40	7	140
PGU3	recent	unburn	39	780	16	320	23	460	28	560

Table S2. Understory measurements for each plot. NR indicates a data point that was not recorded in the field.

SiteID	Habitat	Elevation	Slope	Aspect	% Bareground	% Litter	% Grass	% Shrub	% Forb
BCB1	OldBurned	2118	27	42	74	26	34	11	15
BCB2	OldBurned	2062	8	130	30	70	47	10	5
BCB3	OldBurned	2001	35	250	30	70	46	19	2
BCR2	OldRefugia	2126	34	80	70	30	23	10	10
BCR3	OldRefugia	1849	60	124	72	28	10	1	4
BCU1	OldUnburned	1832	45	70	67	33	20	9	0
BCU2	OldUnburned	1733	24	70	50	50	3	4	5
BCU3	OldUnburned	1675	12	338	58	42	2	0	0
HTB1	OldBurned	2063	65	320	22	78	26	21	24
HTB2	OldBurned	2042	63	52	28	72	31	28	10
HTB3	OldBurned	2014	32	274	21	79	27	28	14
HTR1	OldRefugia	2003	21	154	41	59	3	17	1
HTR2	OldRefugia	2065	34	172	38	62	0	19	10
HTR3	OldRefugia	2091	55	253	13	87	3	8	2
HTU1	OldUnburned	2029	44	33	47	53	36	19	14
HTU2	OldUnburned	1928	89	NR	64	36	18	9	5
HTU3	OldUnburned	1866	62	296	57	43	24	14	7
PGB1	RecentBurned	1925	45	308	82	18	0	2	0
PGB2	RecentBurned	1963	38	212	85	15	3	0	6
PGB3	RecentBurned	2065	35	358	84	16	0	2	7
PGB4	RecentBurned	2125	24	186	96	4	5	0	8
PGB5	RecentBurned	2184	35	300	95	5	0	0	1
PGB6	RecentBurned	2179	16	276	75	25	0	1	1
PGR1	RecentRefugia	1942	45	210	63	37	5	18	9
PGR2	RecentRefugia	1995	58	108	35	65	0	40	0
PGR3	RecentRefugia	2086	24	208	34	66	14	11	14
PGR4	RecentRefugia	2199	27	154	35	65	11	21	1
PGR5	RecentRefugia	2194	19	272	32	68	4	8	4
PGR6	RecentRefugia	2199	25	192	26	74	3	2	8
PGU1	RecentUnburned	1900	34	130	49	51	4	7	4
PGU2	RecentUnburned	1894	36	171	39	61	1	22	1
PGU3	RecentUnburned	1872	16	304	17	83	4	9	7

Table S3. Overstory measurements within each 0.05 ha plot. NR indicated a data point that was not recorded in the field. Nearest Juniper and Nearest Piñon are the nearest live juniper or piñon seed sources to plot center; a “-“ signifies that the nearest seed source was in the plot.

SiteID	Habitat	% Canopy Cover	Total Live Trees	Live Juniper	Live Piñon	Live Tree BA	Live Juniper BA	Live Piñon BA	Nearest Juniper	Nearest Piñon
BCB1	OldBurned	4	0	0	0	0.00	0.00	0.00	195 m	> 200 m
BCB2	OldBurned	0	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
BCB3	OldBurned	4	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
BCR2	OldRefugia	16	12	8	4	1.20	1.13	0.07	-	-
BCR3	OldRefugia	18	17	16	1	3.32	3.32	0.00	-	-
BCU1	OldUnburned	21	24	0	24	1.62	1.62	0.00	NR	-
BCU2	OldUnburned	46	22	21	1	3.91	3.87	0.04	-	-
BCU3	OldUnburned	23	27	26	1	1.13	1.13	0.00	-	-
HTB1	OldBurned	0	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
HTB2	OldBurned	6	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
HTB3	OldBurned	23	0	0	0	0.00	0.00	0.00	14 m	28 m
HTR1	OldRefugia	33	26	17	9	2.47	2.18	0.29	-	-
HTR2	OldRefugia	33	19	13	6	1.92	1.75	0.17	-	-
HTR3	OldRefugia	65	43	24	19	2.68	2.02	0.65	-	-
HTU1	OldUnburned	0	6	4	2	0.07	0.06	0.01	-	-
HTU2	OldUnburned	12	13	12	1	0.86	0.82	0.05	-	-
HTU3	OldUnburned	27	37	37	0	0.81	0.81	0.00	-	13 m
PGB1	RecentBurned	17	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
PGB2	RecentBurned	10	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
PGB3	RecentBurned	8	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
PGB4	RecentBurned	0	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
PGB5	RecentBurned	13	0	0	0	0.00	0.00	0.00	> 200 m	> 200 m
PGB6	RecentBurned	4	0	0	0	0.00	0.00	0.00	67 m	82 m
PGR1	RecentRefugia	13	15	9	6	1.40	1.28	0.13	-	-
PGR2	RecentRefugia	2	11	8	3	0.75	0.73	0.01	-	-
PGR3	RecentRefugia	31	47	42	5	1.37	1.33	0.04	-	-
PGR4	RecentRefugia	23	11	9	2	2.82	2.76	0.06	-	-
PGR5	RecentRefugia	46	20	17	3	3.03	2.97	0.06	-	-
PGR6	RecentRefugia	44	32	28	4	5.23	4.90	0.33	-	-
PGU1	RecentUnburned	38	17	14	3	3.99	3.90	0.08	-	-
PGU2	RecentUnburned	26	5	2	3	0.44	0.37	0.07	-	-
PGU3	RecentUnburned	50	60	46	14	3.01	2.87	0.15	-	-

Table S4. Total detections of all observed birds in each habitat type within 100 m from observer after filtering out flyover species and unidentified birds.

Species	Species Name	Old Burn	Recent Burn	Refugia	Unburn	Total
SPTO	Spotted Towhee	157	98	195	153	603
BTYW	Black-throated Gray Warbler	16	37	174	114	341
VIWA	Virginia's Warbler	65	25	82	58	230
ATFL	Ash-throated Flycatcher	29	26	75	84	214
BGGN	Blue-gray Gnatcatcher	45	15	56	64	180
GRFL	Gray Flycatcher	11	35	50	56	152
BHGR	Black-headed Grosbeak	48	12	44	31	135
WOSJ	Woodhouse's Scrub-jay	43	16	38	28	125
CHSP	Chipping Sparrow	12	25	39	32	108
MODO	Mourning Dove	14	22	23	43	102
LAZB	Lazuli Bunting	17	6	8	29	60
AMRO	American Robin	3	18	14	18	53
GRVI	Gray Vireo	0	9	17	26	52
CORA	Common Raven	3	12	19	14	48
ROWR	Rock Wren	1	17	20	8	46
BEWR	Bewick's Wren	6	3	16	14	39
BRSP	Brewer's Sparrow	5	8	15	10	38
PLVI	Plumbeous Vireo	1	10	13	9	33
MOBL	Mountain Bluebird	7	15	7	1	30
JUTI	Juniper Titmouse	0	4	14	11	29
MOCH	Mountain Chickadee	1	3	12	11	27
YRWA	Yellow-rumped Warbler	4	2	7	9	22
LASP	Lark Sparrow	7	4	4	5	20
WEKI	Western Kingbird	9	3	3	2	17
WBNU	White-breasted Nuthatch	1	1	10	0	12
VESP	Vesper Sparrow	3	4	2	3	12
NOFL	Northern Flicker	2	2	6	2	12
CANW	Canyon Wren	1	0	8	3	12
GTTO	Green-tailed Towhee	1	5	1	3	10
WETA	Western Tanager	2	0	7	0	9
PIJA	Pinyon Jay	2	0	3	3	8
WEBL	Western Bluebird	0	2	4	1	7
BTSP	Black-throated Sparrow	5	2	0	0	7
MGWA	MacGillivray's Warbler	2	0	0	4	6
BUSH	Bushtit	3	0	2	0	5
WEWP	Western Wood Pewee	1	0	3	0	4
STJA	Steller's Jay	1	0	1	2	4
CAFI	Cassin's Finch	1	0	1	2	4
TOSO	Townsend's Solitaire	0	0	1	2	3
RCKI	Ruby-crowned Kinglet	2	0	1	0	3

HAWO	Hairy Woodpecker	1	2	0	0	3
DEJU	Dark-eyed Junco	0	0	3	0	3
CLNU	Clack's Nutcracker	0	0	1	2	3
WTSW	White-throated Swift	0	0	2	0	2
SAPH	Say's Phoebe	1	1	0	0	2
LOSH	Loggerhead Shrike	0	0	2	0	2
LBWO	Ladder-backed Woodpecker	0	0	2	0	2
HOWR	House Wren	0	0	2	0	2
CONI	Common Nighthawk	0	0	2	0	2
YEWA	Yellow Warbler	0	0	0	1	1
WIWA	Wilson's Warbler	0	0	1	0	1
WEME	Western Meadowlark	0	0	0	1	1
RTHA	Red-tailed Hawk	0	1	0	0	1
RBNU	Red-breasted Nuthatch	0	0	1	0	1
LEOW	Long-eared Owl	0	0	1	0	1
HOFI	House Finch	0	0	1	0	1
CAKI	Cassin's Kingbird	1	0	0	0	1
BTHU	Black-throated Hummingbird	0	0	0	1	1

Table S5. Species occupancy model results using the top model for each species. ψ indicates occupancy probability, p indicates detection probability for each covariate

Black-throated Gray Warbler: p(observer + wind)psi(Hypothesis3)

Habitat	ψ	lowerCI	upperCI	SE
OldBurn	0.4332	0.2489	0.6380	0.1047
RecentBurn	0.8783	0.6204	0.9696	0.0810
Refugia + Unburn	0.9761	0.8171	0.9973	0.0263

Observer	Wind	p	lowerCI	upperCI	SE
1	0	0.817477	0.720405	0.886172	0.042089
1	1	0.7531605	0.646517	0.835802	0.048544
1	2	0.6021289	0.41493	0.763562	0.092647
1	3	0.5839391	0.239643	0.862068	0.185145
1	4	0.6882322	0.098146	0.978156	0.329507
2	0	0.7405388	0.629209	0.827601	0.050972
2	1	0.6603747	0.529216	0.770818	0.062704
2	2	0.4909429	0.326588	0.657279	0.087655
2	3	0.4721262	0.169397	0.796844	0.187976
3	0	0.4789422	0.355737	0.604763	0.06489
3	1	0.385069	0.248538	0.54246	0.07712
3	2	0.2369844	0.12309	0.407313	0.073272
3	3	0.2236254	0.061255	0.559756	0.131529
3	4	0.3117909	0.021847	0.901863	0.32952

Woodhouse's Scrub-jay: p(null)psi(null)

ψ	lowerCI	upperCI	SE
0.7931047	0.549174	0.9234485	0.095978

p	lowerCI	upperCI	SE
0.3235552	0.241846	0.4176628	0.045238

Gray Flycatcher: p(observer)psi(Hypothesis3)

Habitat	ψ	lowerCI	upperCI	SE
OldBurn	0.492627	0.255846	0.732762	0.132394
RecentBurn	0.999080	0.000000	1.000000	0.020487
Refugia + Unburn	0.983902	0.000909	1.000000	0.089824

Observer	p	lowerCI	upperCI	SE
1	0.39015	0.301239	0.487014	0.047918
2	0.442598	0.340125	0.550203	0.054391
3	0.221068	0.1375489	0.335567	0.050636

Virginia's Warbler: p(observer)psi(Hypothesis1)				
Habitat	**ψ**	**lowerCI**	**upperCI**	**SE**
OldBurn	0.999983	0.000000	1.000000	0.001188
Refugia	1.000000	0.000000	1.000000	0.000214
Unburned	0.830991	0.570674	0.947883	0.093732
RecentBurn	0.770340	0.491226	0.920968	0.112410
Observer	**p**	**lowerCI**	**upperCI**	**SE**
1	0.506439	0.4197607	0.592732	0.044574
2	0.573332	0.4811871	0.660653	0.046273
3	0.291554	0.1974066	0.407789	0.054245

American Robin: p(observer)psi(Hypothesis3)				
Habitat	**ψ**	**lowerCI**	**upperCI**	**SE**
OldBurn	0.189111	0.057318	0.47216	0.10518
RecentBurn	0.718357	0.323054	0.931657	0.173018
Refugia + Unburn	0.475845	0.2861002	0.672829	0.104058
Observer	**p**	**lowerCI**	**upperCI**	**SE**
1	0.461556	0.2806248	0.653216	0.099827
2	0.084983	0.0364142	0.185841	0.035676
3	0.272467	0.1302489	0.483626	0.092706

Spotted Towhee: p(observer + cloud)psi(null)					
ψ	**lowerCI**	**upperCI**	**SE**		
0.9800077	0.92571	0.994841	0.013691		
Observer	**Cloud**	**p**	**lowerCI**	**upperCI**	**SE**
1	0	0.8826747	0.808593	0.930547	0.030493
1	1	0.9217427	0.818301	0.968558	0.035382
1	2	0.9841527	0.888872	0.99793	0.016309
1	3	0.9415691	0.843464	0.979671	0.03075
2	0	0.8079179	0.713549	0.876575	0.041478
2	1	0.868161	0.729711	0.941389	0.05207
2	2	0.9720044	0.818286	0.996278	0.028358
2	3	0.9000908	0.762775	0.961893	0.047271
3	0	0.6346894	0.512815	0.741448	0.059281
3	1	0.7311854	0.522205	0.87129	0.091436
3	2	0.9348176	0.652399	0.990957	0.063222
3	3	0.7881957	0.577019	0.910326	0.085478

Ash-throated Flycatcher: p(observer)psi(null)			
ψ	**lowerCI**	**upperCI**	**SE**
0.999943	0.000000	1.000000	0.001963

Observer	p	lowerCI	upperCI	SE
1	0.388556	0.315539	0.466943	0.038906
2	0.404434	0.325290	0.488882	0.042096
3	0.541199	0.434987	0.643796	0.054058

Gray Vireo: p(cloud)psi(Hypothesis3)

Habitat	ψ	lowerCI	upperCI	SE
OldBurn	0.000049	0.000000	1.000000	0.002067
RecentBurn	0.725452	0.140886	0.977052	0.282464
Refugia + Unburn	0.879468	0.101501	0.997883	0.225428

Cloud	p	lowerCI	upperCI	SE
0	0.135822	0.0701273	0.246729	0.043974
1	0.134962	0.0481184	0.325022	0.06713
2	0.385192	0.1686213	0.659327	0.136278
3	0.353672	0.1696242	0.594456	0.114921

Blue-gray Gnatcatcher: p(cloud)psi(Hypothesis3)

Habitat	ψ	lowerCI	upperCI	SE
OldBurn	0.999866	0.000000	1.000000	0.006187
RecentBurn	0.442705	0.237588	0.669420	0.117791
Refugia + Unburn	0.941958	0.600145	0.994334	0.066410

Cloud	p	lowerCI	upperCI	SE
0	0.488077	0.4056701	0.571136	0.042603
1	0.382966	0.2480085	0.538749	0.076231
2	0.437633	0.2726469	0.617674	0.091723
3	0.24751	0.1381533	0.402958	0.068303