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A bird's eye view of ecosystem conversion: Examining the resilience of piñon-juniper woodlands and their avian communities in the face of fire regime change

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ABSTRACT

Climate change and land-use legacies have caused a shift in wildfires and post-fire growing conditions. These changes have strong potential to diminish the resilience of many ecosystems, with cascading effects and feedbacks across taxa. Piñon-juniper (PJ) woodlands are a diverse and widespread forest type in the western US and are home to many obligate and semi-obligate bird species. As such, this system is ideal for understanding wildfire resilience, or lack thereof, in terms of both vegetation and wildlife associations. This study evaluated post-fire vegetation structure and associated avian communities following three wildfires; one that burned one year prior to sampling (recent fire), and two that burned approximately 25 years previously (old fires). Vegetation characteristics and the habitat use of PJ-associated bird species were compared across severely burned patches, unburned refugia, and unburned sites outside of the burn perimeter. We expected wildfire to alter vegetation and bird usage for the first few years post-fire, which we observed in our recent burns. However, even 25-years post-fire, little recovery to PJ woodland had occurred and the associated bird communities had not returned, compared to unburned areas. No piñon regeneration was observed in any burned areas and no juniper regeneration in the recent fire. Piñon seedling densities in unburned sites and refugia averaged 80 ha^{-1} and 151 ha^{-1}, respectively, while juniper seedling densities were 220 ha^{-1} in both habitat types. Habitat use for thirteen PJ-associated species were modeled, three of which (Woodhouse's Scrub Jay, Ash-throated Flycatcher, and Virginia's Warbler) used all habitats. Four species (American Robin, Gray Vireo, Black-throated Gray Warbler, and Gray Flycatcher) were essentially absent from the old burn habitat, reflecting species-specific need for mature piñon or juniper trees and/or greater canopy cover. Conversely, birds that were present in the old burn habitat (including Virginia's Warbler, Blue-gray Gnatcatcher, Woodhouse's Scrub-jay, Ash-throated Flycatcher, and Spotted Towhee) are typically associated with habitat edges, high shrub cover, or cavity nests. Altered vegetation structure and bird habitat use in burned areas 25 years post-fire are evidence for enduring conversion to non-forest vegetation types. However, unburned refugia embedded in burned areas maintain forest attributes and support obligate bird communities, supporting ecological function and biological diversity.

1. Introduction

Wildfire is an important disturbance globally, shaping vegetation patterns and animal communities, influencing biogeochemical processes, and producing important climate feedbacks (Gavin et al., 2007, McLauchlan et al., 2020, Belcher et al. 2021). In many ecosystems, such as in the western United States, the past several decades have been marked by more frequent fires, lengthened fire seasons, and increased high-severity fire (Westerling 2016, Singleton et al. 2019, Higuera and Abatzoglou 2020). Recent research has advanced our understanding of the implications of fire regime change for components of ecosystem resilience (e.g. Gill et al. 2017, Stevens-Rumann et al. 2018, Whitman et al. 2019, Chapman et al. 2020). Resilience can be degraded by novel fire regimes, like uncharacteristic high-severity fire or shortened fire-

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free intervals, and warmer and drier climatic conditions post-fire that the ecosystems are not adapted to (Coop et al. 2020, Falk et al. 2022). Conversely, resilience can be maintained by intact reproductive material, such as seedbanks or nearby seed sources (e.g. proximity and density of fire refugia (Coop et al. 2019)), and environmental conditions that support seedling establishment and growth (e.g. microsite availability or understory vegetation (Falk et al. 2022)). However, while resilience is often studied through the lens of vegetation, it can also be assessed via other taxa that rely on the ecosystem for habitat, food, or nesting resources. Obligate bird species, for example, can serve as important indicators of whether or not a system is recovering towards prior conditions (Burger 2006).

Recent work in the western US has focused on the effects of changing climate and fire regimes on ponderosa pine and dry mixed-conifer forests (e.g. Korb et al. 2019, Halofsky et al. 2020, Chapman et al. 2020). However, within many other vegetation types, such as piñon-juniper (PJ) woodlands, resilience, or lack thereof, to changing fire regimes is relatively poorly described. In contrast to our understanding of the critical role of frequent surface fire in maintaining ecosystem function in ponderosa pine forests, the ecological role of fire in PJ is less understood. In this system, ignitions occur often, generally via lightning strikes that result in a single torching event under typical conditions, from which the ignition dissipates quickly due to rocks, bare ground, and discontinuous surface fuels (Romme et al. 2003, Rocca et al. 2014). Larger fires can occur; however, these events are infrequent and are associated with dry canopy fuels, and strong winds that promote spread fire from tree crown to tree crown (Floyd et al. 2000, Romme et al. 2003). Specifically, fire rotations – the time it takes in years for a particular area to burn – are generally between 400 and 1,428 years depending on the specific geographical region (e.g. Floyd et al. 2004, Floyd et al. 2017, Kennard and Moore 2013). Warmer and dryer conditions, increased presence of highly flammable invasive grasses, and more dead and dry canopy fuels from drought, insects, and disease (Keane et al. 2008, Rocca et al. 2014), have caused large fire events to occur more frequently compared to historical norms. Since the 1980′s, the number and size of fires have increased, and fire rotations have decreased in PJ landscapes (Board et al. 2018).

These altered fire regimes have implications for wildlife communities, as it can require up to several centuries for woodlands to fully recover, with piñon pine and juniper recruitment often not observed for several decades (Koniak 1985, Bristow et al. 2014, Floyd et al. 2021). Changing climate conditions, such as increased severity and frequency of drought, which the southwest has been experiencing the past several decades (Williams et al. 2022), have the potential to expand this recovery time by decreasing cone production (Redmond et al. 2012) and creating conditions that are too warm or too dry for juvenile establishment (Petrie et al. 2017, Kemp et al. 2019). This slow recovery may have minimal impacts on plant and animal communities under normal fire regimes and climate conditions, where only small areas are affected by high severity fire, but may be of much greater conservation concern when large landscapes are impacted.

Building on this, wildfire can affect bird species occupancy long-term 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, in general, 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). PJ woodlands provide critical habitat for over 70 species of birds, 18 of which are obligate or semi-obligate species (Balda and Masters 1980), which use this ecosystem as breeding habitat in the spring, and foraging habitat in the fall and winter seasons. The effects of fire on PJ woodland bird communities, specifically, are not well studied and substantial uncertainty exists regarding the duration of impacts to obligate and semi-obligate species, especially given the long recovery of this system. It has long been recognized that the breeding bird abundance in PJ is correlated with the density of piñon pine, total tree density, and piñon foliage volume (Masters 1979), all of which are removed from a system when a high severity fire occurs. Current research conducted in the context of changing disturbance regimes and PJ management interventions still supports this, as observed in studies where piñon-juniper obligate species declined as did overall bird density following thinning treatments (Crow and Van Riper 2010, Gallo and Pejchar 2017, Magee et al., 2019). Likewise, drought-induced piñon mortality caused a decrease in avian abundance and richness, with greater declines observed in areas that were thinned following tree mortality (Fair et al. 2018). While these studies show potential responses bird communities have when piñon and juniper are reduced in a system, either through thinning or mortality events, they may not serve as analogs for avian responses to fire, since fire can reset the successional trajectory of the entire plant community (Gallo and Pejchar 2017).

Just as PJ woodlands are important for bird communities, PJ woodlands also rely on seed-dispersing birds to aid in post-fire recovery. Piñon produce a cone crop every 5–7 years, with seeds that are only viable for one year (Chambers et al. 1999). To establish in burned patches, seeds must be dispersed by piñon seed dispersers, such as Clark's Nutcracker (*Nucifraga columbiana*) and Pinyon Jay (*Gymnorhinus cyanocephalus*), which collect these large and exposed seeds and move them up to 7–22 km away from the source tree (Pesendorfer et al., 2016). Juniper produce long-lived seeds annually (Chambers et al. 1999) which provide food for frugivorous birds that defecate intact seeds away from the parent tree (Salomonson 1978). Because different bird species differentially use post-fire habitats and disperse seeds over varying distances, the mosaic of burn patterns within a wildfire footprint may impact habitat use and alter dispersal patterns, specifically with the formation of fire refugia.

Fire refugia are defined as unburned or low severity burned islands within the fire perimeter (Meddens et al. 2018). These areas can support resilience by serving as seed-sources within a burned patch, as well 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. Bird use of refugia can be constrained by the quality and size of refugia patch, as well as the potential for the bird to exploit resources in the nearby burned area (Berry et al. 2015). While these relationships are not well understood, refugia, especially larger (~5 ha and greater) patches, may also support PJ seed dispersers by providing intact habitat and access to seeds within the fire perimeter. Understanding the habitat use of PJ associated birds in burned PJ woodlands and neighboring unburned areas, including refugia, can help identify potential for natural regeneration of these woodlands (through support for seed dispersing birds) as well as the ecological impacts fire has on the bird communities in this system.

Given the potential widespread and enduring consequences of changing fire regimes, especially in dry western forests, it is important to understand how PJ woodlands and associated wildlife are responding to severe fires over short- and long-term time scales. This study investigates a "recent fire" (one-year post-fire) and two "old fires" (25- and 27- years post-fire) to examine and compare the immediate and long-term effect of fire on vegetation and bird communities. Specifically, this study explores 1) patterns and predictors of piñon pine and juniper seedling regeneration in burned, unburned, and refugia sites, 2) bird habitat use by PJ obligates, PJ semi-obligates, piñon seed dispersers, and juniper seed dispersers across burn mosaics, and 3) associations between the habitat use of seed dispersing birds in burned patches and tree seedling regeneration.

2. Methods

2.1. Study area

The study area was located in Garfield and Mesa Counties in western Colorado (U.S.) on Bureau of Land Management (BLM) land managed by the Grand Junction Field Office. Annual average precipitation is 41 cm at the nearest Western Regional Climate Center station, with most rainfall occurring in August through October (1947–2016; (Western Regional Climate Center, 2022); wrcc.dri.edu). Annual average temperature is 8.5 °C with an average maximum of 17 °C and average low of −0.39 °C (1991– 2020; https://www.ncei.noaa.gov/access/us-climate-normals, accessed 14 September 2021 (NOAA National Centers for Environmental Information, 2021)). The soils across sites consist of Calciborolls, Torriorthents, and Haploborolls (Web Soil Survey (Soil Survey Staff, 2021), 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 Mormon tea (*Ephedra nevadensis*), big sagebrush (*Artemisia tridentata*), mountain mahogany (*Cercocarpus montanus*), and perennial bunchgrasses (*Poaceae* spp.*)*.

Site Selection

Three wildfires in western Colorado were selected as study locations (Fig. 1). Details about the selected fires are located in Table 1. The BC and HT fires are categorized as "old" fires, and PG fire is the "recent" fire. These fires were selected as they have geographical, vegetative, and climatic similarities, and therefore are suitable for investigating long- and short-term effects of fire. Additional wildfires within PJ woodlands in this region were unavailable due to limited access given the high proportion of private ownership of rangelands and limited topographical accessibility from fires occurring on mesa tops. We also considered drought-induced tree mortality in site selection, as severe drought drove widespread tree death in many PJ woodlands in the early 2000 s (Breshears et al. 2005). To avoid studying compound disturbances, the fires selected for this study occurred in areas with minimal drought and insect induced mortality (USDA Forest Service, Pinyon-Juniper Woodland Mortality in Southwestern US 2000–2007, databasin.org (USDA Forest Service and FHTET, 2000–2007)), which were field-verified by visual observations in neighboring unburned stands to ensure they did not contain abundant dead piñon pine.

Table 1
Properties of the three Colorado fires selected for study. Note: the area of refugia and area of burned woodland do not add up to the size of the fire. This is due to the resolution of raster data (30 × 30 m) used for quantifying these values, thus losing a small amount of data.

Fire Name	Ignition Date	Size	Area of Refugia (ha)	Area of Burned Woodland (ha)
Buninger Canyon (BC)	June 26, 1994	748	394	380
Hatchet (HT)	July 23, 1996	2,301	669	1673
Pine Gulch (PG)	July 31, 2020	56,254	19,123	37,121

Within each fire, patches were characterized into the following habitat classes: burned, refugia, or unburned. Burned habitat are patches within the fire perimeter that had evidence of fire and, since piñon pine and juniper are highly flammable, resulted in nearly 100% tree mortality; refugia habitat were defined as patches within the fire perimeter that burned less-severely or did not burn at all, and thus supported intact live tree canopy. Refugia and burned patches 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 [https://www.mtbs.gov]). Continuous patches >5 ha were classified based on burn severity classes. This patch size was selected because, 1) it allowed for the placement of 3–4 bird observation point count stations 160+ m apart and at least 50-m from an edge, and 2) we aimed to define a patch size that would be most ecologically

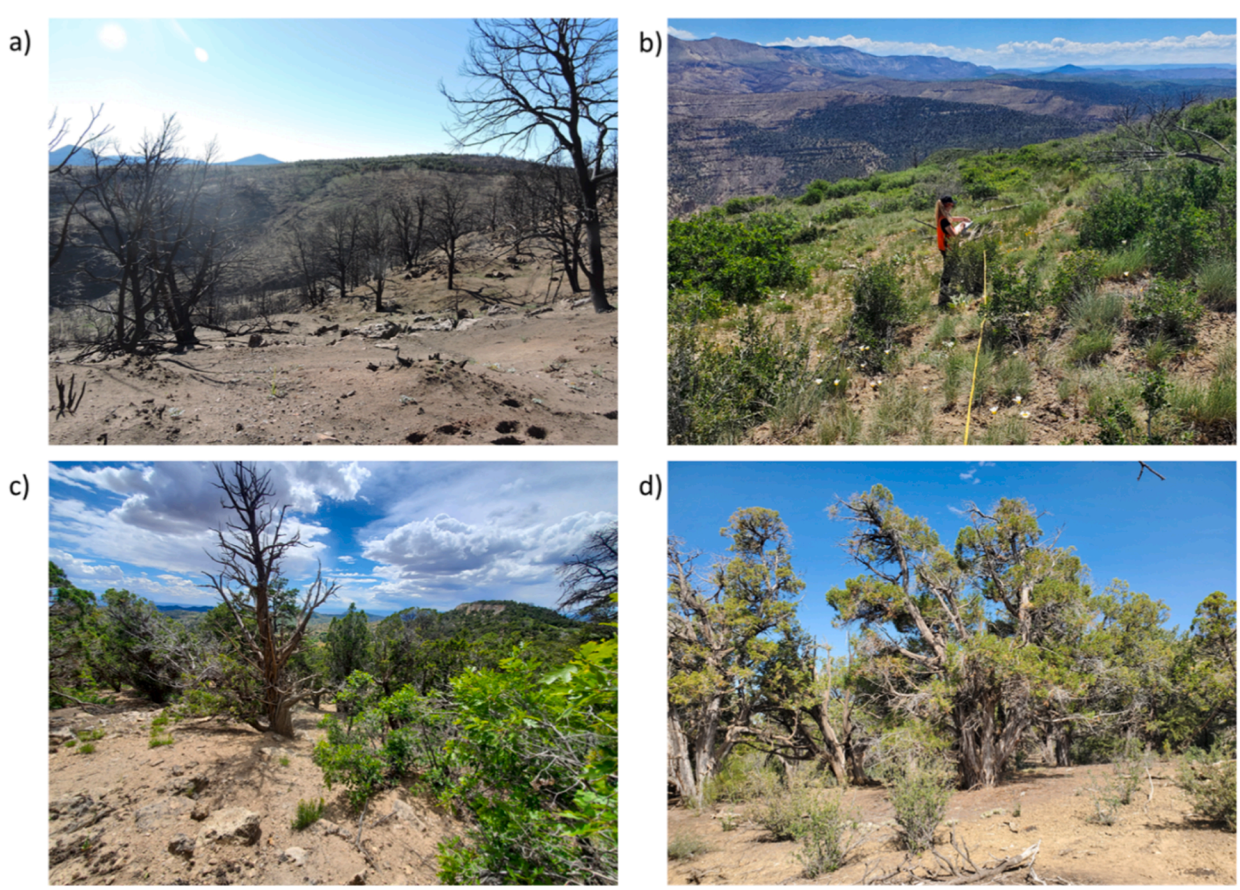

Fig. 1. Study area in piñon-juniper woodlands at various years post-fire a) recent burn; b) old burn c) refugia; d) unburned (Photo credit: Jamie Woolet).

significant and large enough to serve as habitat given the average home range size of many of our target bird species. Burned patches were identified by medium- and high-severity burns (dNBR classes 3–6), and refugia patches were identified by unburned or low severity burns (dNBR classes 1–2). Habitat characterization was later verified in the field and was confirmed by the amount of observable fire-caused tree mortality, as indicated by down or standing trees with visible charring. Burned patches, regardless of spatially-identified burn severity characterization, had nearly 100% fire-caused mortality (Fig. 1a and b), whereas refugia, regardless of spatially-identified burn severity characterization, had little to no fire-caused tree mortality (Fig. 1c). Unburned patches were located near but at least 100 m outside the fire perimeter (Fig. 1d).

Point count stations were established in patches where 3–4 points could be placed at least 160 m apart and at least 50 m away from a road or patch edge, to mitigate bird observation overlap and habitat-edge effects (Ralph et al. 1995). Site locations were selected via stratified random sampling, where, within continuous patches, 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 vegetation plot (Fig. 2). In total, there were 32 vegetation plots (6 old burn (3 HT, 3 BC), 5 old refugia (3 HT, 2 BC), 6 recent burn, 6 recent refugia, and 9 unburned (3 HT, 3 BC, 3 PG)), and 126 point count stations (24 old burn (12 HT, 12 BC), 20 old refugia (12 HT, 8 BC), 24 recent burn, 22 recent refugia, and 36 unburned (12 HT, 12 BC, 12 PG)), each of which were visited 3 times (N = 378). Plots within the recent burn (PG) are limited to the western portion of the fire perimeter due to forest cover type (transitioning to *Pinus ponderosa*-mixed conifer at higher elevation), accessibility (roads), and proximity to the older fires, allowing for better comparison of fire structure across sites. Additionally, the recent burn was 10 times larger than each of the old burns allowing for more sites to be supported with less concern for pseudo-replication.

2.2. Field methods

To assess vegetation composition and structure, in April – June 2021, we established one 0.05-ha circular plot in each patch to obtain representative vegetation structure and patch characteristics. Slope, aspect, and elevation were measured at plot center. Aspect in degrees was converted to folded aspect to approximate heat load using the following equation by McCune and Keon (2002): Folded Aspect = $|180 - |\text{Aspect} - 225||$, where southwest slopes have higher folded aspect values and are associated with higher heat load, as opposed to northeast slopes with lower folded aspect values and lower heat load (McCune and Keon 2002). Species, diameter at root crown (DRC) (Vankat 2017), and

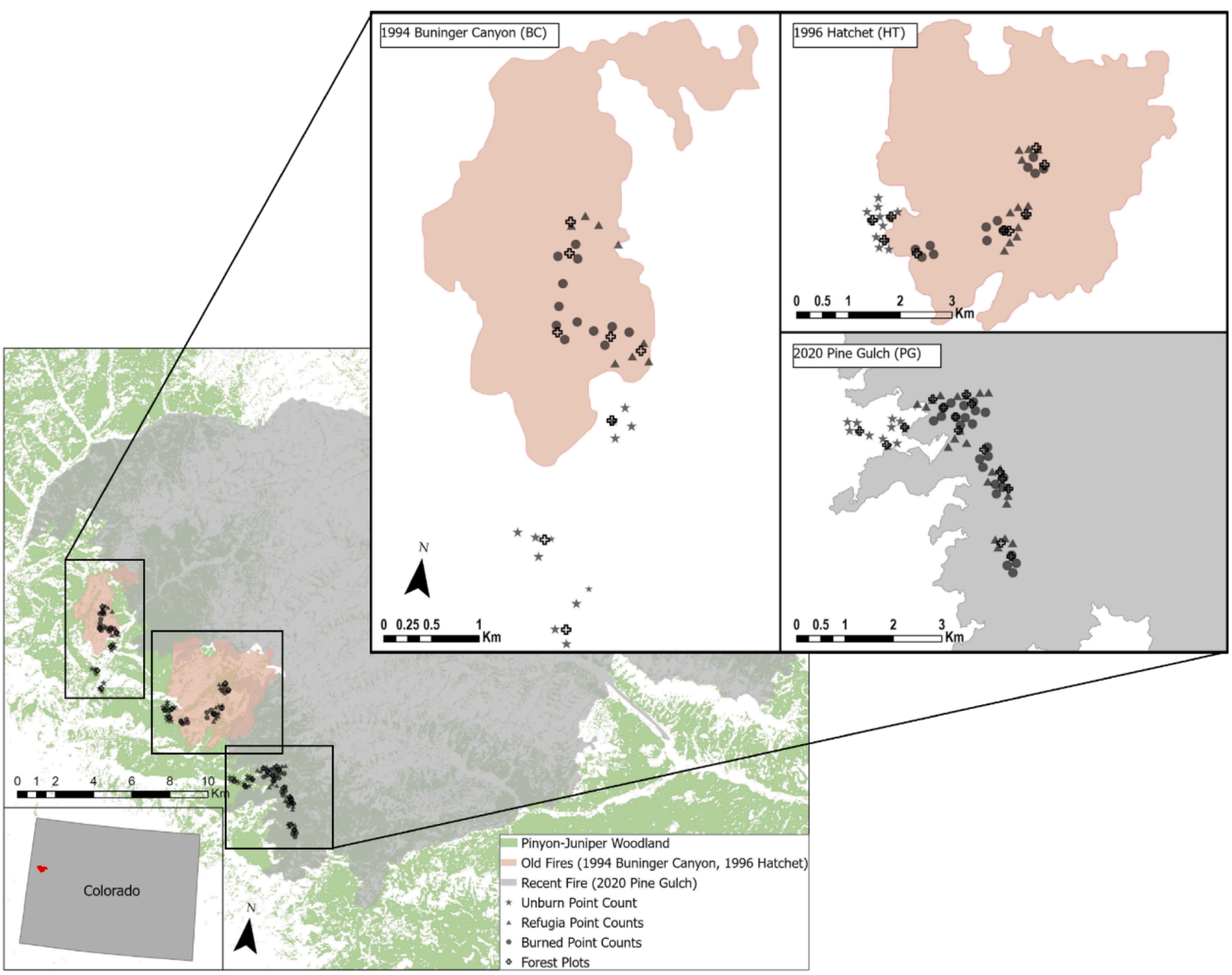

Fig. 2. Map of the three fires included in the study and distribution of study sites. The fires were located in western Colorado and burned in 1994, 1996, and 2020. The two older fires (1994 Buninger Canyon Fire (BC) and 1996 Hatchet Fire (HT)), are shown in light red and the recent fire (2020 Pine Gulch Fire (PG)) is shown 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 (Landfire, 2016) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 is a common method used in this ecosystem where trees have multiple stems or low branching. 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 (Chojnacky and Rogers 1999). Distance to the nearest ten live seed sources for piñon pine and juniper, up to 200 m away, were recorded from plot center. All piñon seedlings, juniper seedlings, and Gambel oak stems (a common early successional tree-shrub) 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.

Two, 25-m transects, within the same plots described above, were extended in the four cardinal directions. Canopy cover was assessed by point intercept method along the transects at 1-m intervals for a total of 50 observations using a GRS densiometer, live and dead material was considered "canopy". Understory cover by functional group (grass, forb, shrub (including Gambel oak (*Quercus gambelii*)), and tree) and substrate type (litter or bare ground (rock and soil) were measured along the transects every 0.5-m for a total of 98 observations at each plot.

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 2021, which corresponds with the period when birds are most readily detected (e.g, the breeding season). Birds were surveyed from approximately 0500hr – 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 flew over the patch without stopping were recorded but excluded from analysis. Similarly, birds we could not identify (<1% detections) were recorded but excluded from analysis. Point counts were not conducted under heavy precipitation or at windspeeds that caused small trees to sway (approximately ≥32 km/hr). 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 point count start-time were alternated for each point visit to mitigate observer and temporal bias.

2.3. 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 (piñon seedlings, juniper seedlings, and Gambel oak stems) were different in old burn, recent burn, old refugia, recent refugia, and unburned habitat groups. This test was used because although there was no evidence for unequal variances for the juniper and piñon seedling groups (Levene Test, $p = 0.14$, $p = 0.09$, $p < 0.001$ for juniper, piñon, and Gambel oak, respectively), the seedling densities were not normally distributed for any seedling group (Shapiro-Wilks test, $p < 0.001$). Because the burned habitat had zero to few piñon and juniper seedlings, regardless of fire age, additional tests were performed on the unburned and refugia habitat types to determine if regeneration was different across "intact" woodland groups.

To test for effects of vegetation structure variables on seedling regeneration at the plot scale (piñon seedlings, juniper seedlings, Gambel oak stems) in old burned, recent burned, old refugia, recent refugia, and unburned, 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 vegetation site variables in the model were not correlated; only variables that had a zero or were not significantly ($\alpha = 0.05$) positively or negatively correlated were used. Final variables (live tree BA, live juniper BA, live pinon BA, percent grass cover, percent shrub cover, total live tree, total live juniper trees, total live pinon trees, elevation, and folded aspect) were put in a global model and reverse stepwise variable selection was performed to drop variables from the model until a best-fitted model was created, based on the variable's contribution to AIC values. Because the burned habitat had no piñon and few juniper seedlings, additional GLMs that included only the unburned and refugia habitat types were investigated to look for seedling establishment trends in intact woodlands.

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 vegetation characteristics 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 habitat use of select species using the R package *unmarked* (Fiske and Chandler 2011). This modeling approach used Bayesian approaches to combine two probabilities – detection probability (p), which is the probability of detecting a species at the time of observation if it is present at the site (i.e. a lower p indicates the variable(s) that decrease the probability of detecting a bird when it is actually present), and occupancy probability (ψ), which is the probability that the species is present at the site (a lower ψ means the species is not likely the occupy the study site). Because we cannot be absolutely certain that we meet the assumptions for determining species occupancy (Hayes and Monfils 2015), we instead use the term "habitat use". Initially, four guilds were investigated: PJ obligates, PJ semi-obligates, piñon seed dispersers, and juniper seed dispersers (Supplementary data 1 TableS4). Guild designations are based on reports by Balda and Masters (1980), Paulin et al. (1999), and breeding ranges outlined by Cornell Ornithology Lab (Cornell Lab of Ornithology, 2019) (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)). *Post hoc*, we quantified the habitat use of other highly detected bird species to better understand bird habitat use in burned patches.

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). Next, occupancy-only model covariates to determine habitat use probability (ψ) 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 [old burn ≠ recent burn ≠ refugia ≠ unburned]; Hypothesis 2) Habitat use in burned habitat is different from habitat that did not burn [(old burn + recent burn) ≠ (refugia + unburned)]; and Hypothesis 3) Habitat use is different across vegetation ages [old burn ≠ recent burn ≠ (refugia + unburned)]. Covariates from the best-fitting occupancy-only model and best-fitting detection-only model were determined based on lowest AICc. Covariates that performed better than the null from the detection-only model and covariates that performed better than the null from the occupancy-only models, if any, were combined to create a full model to estimate ψ and *p*. Model combinations were compared to determine the best-fitting full model. The top model for each species was assessed for over-dispersion using the MacKenzie-Bailey Goodness-of-fit test.

3. Results

3.1. Vegetation structure

Comparisons of stand characteristics among habitat groups (old burn, recent burn, old refugia, recent refugia, and unburned) indicated that live tree BA ha^{-1} was highest in recent refugia, old refugia, and unburned ($p = 0.001$, $F = 7.00$; Table 2 and Supplementary data 1 Table S2). We also found that percent canopy cover of live and standing dead trees was highest in old refugia and lowest in old burn ($p = 0.01$, $F = 4.11$), and that the number of live trees ha^{-1} was highest in old refugia, recent refugia, and unburned, with no live trees recorded in either burned groups ($p = 0.001$, $F = 6.94$). The percent litter cover was lowest in recent burn ($p < 0.001$, $F = 9.45$; Supplementary data 1 Table S3), and the percent of exposed bare ground was highest in recent burn ($p < 0.001$, $F = 9.48$). Percent shrub cover was lowest in the recent burn and was highest in the old burn and recent refugia ($p = 0.005$, $F = 4.69$), and percent grass cover was highest in the old burn ($p < 0.001$, $F = 13.03$). Percent forb cover was not different among habitat types ($p = 0.104$, $F = 2.137$).

3.2. Seedling regeneration and site drivers of regeneration

Densities of Gambel oak in burned areas were 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 (Fig. 3, Supplementary data 1 Table S1). The average Gambel oak density was 182 ha^{-1} (0–560 ha^{-1}) in unburned areas and 1,196 ha^{-1} (0–5,080 ha^{-1}) in refugia, and these densities were not statistically significant across all habitat types ($p = 0.159$). Three juniper seedlings were counted at one old burned site, with no other conifer seedling recorded at other burned locations. In the unburned areas, 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}), while in refugia, the average piñon seedling density was 151 ha^{-1} (0–480 ha^{-1}) and the average juniper seedling density was 220 ha^{-1} (20–540 ha^{-1}). Piñon and juniper seedling densities, being predominantly zero in burned areas, were different when comparing across all habitat types ($p = 0.001$ and $p = 0.0003$ for piñon and juniper seedlings, respectively). However, piñon and juniper seedling densities were not different between old refugia, recent refugia, and unburned ($p = 0.27$ and $p = 0.78$ for piñon and juniper seedling densities, respectively).

Across all habitat types, the total number of live trees in a plot had significant and positive associations with the number of piñon seedlings and the number of juniper seedlings (Table 3). Across all habitat types, folded aspect had a significant and positive association with the number of Gambel oak stems. For GLMs testing seedling establishment trends in intact woodlands (unburned and refugia only), total live juniper trees in a plot was positively associated with number of juniper seedlings, and percent shrub cover and live juniper BA was negatively associated with juniper seedlings. Total number of live trees in a plot and elevation were positively associated with number of piñon seedlings. In other words, across all habitat types, regeneration of both juniper and piñon in the plot was more likely when there was greater number of live trees, and the density of Gambel oak stems was dependent on the direction of the slope face. In intact woodlands, more juniper seedlings were observed in plots with greater number of juniper trees and lower percent shrub cover and lower live juniper basal area, and greater piñon seedlings were observed at higher elevation and plots with a greater number of live trees.

3.3. Bird habitat use

After excluding flyovers and birds detected >100 m away, 58 unique bird species and 2,852 individual birds were detected (Supplementary data 1 Table S4). Within PJ-associated guilds (obligate, semi-obligate, piñon seed dispersing, and juniper seed dispersing), the birds with adequate detections for occupancy analysis (>45 detections) 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 4). Additional species with enough detections for analysis were Black-headed Grosbeak (*Pheucticus melanocephalus*), Lazuli Bunting (*Passerina amoena*), Chipping Sparrow (*Spizella passerina*), Mourning Dove (*Zenaida macroura*), and Rock Wren (*Salpinctes obsoletus*).

Species that were not affected by habitat type were Woodhouse's Scrub-jay (piñon seed disperser and obligate species; ψ(all habitats) = 0.79), Ash-throated Flycatcher (obligate; ψ(all habitats) = 1.00), and Spotted Towhee (semi-obligate; ψ(all habitats) = 0.98) (Fig. 4, Supplementary data 1 Table S5). Species that used recent burned habitat more than the other habitat types were the American Robin (juniper seed disperser; ψ(old burn) = 0.19, ψ(recent burn) = 0.72, ψ(not burned) = 0.48) and the Gray Flycatcher (semi-obligate; ψ(old burn) = 0.49, ψ(recent burn) = 1.00, ψ(not burned) = 0.98). Species that used old burn habitat more than other habitat type were Virginia's Warbler (obligate; ψ(old burn) = 1.00, ψ(recent burn) = 0.77, ψ(refugia) = 1.00, ψ(unburned) = 0.83) and the Blue-gray Gnatcatcher (semi-obligate; ψ(old burn) = 1.00, ψ(recent burn) = 0.44, ψ(not burned) = 0.94), although both species also had high habitat use in refugia and unburned habitats. Species more likely to use refugia and unburned habitat were the Gray Vireo (obligate; ψ(old burn) = 0.00, ψ(recent burn) = 0.73, ψ(not burned) = 0.88) and Black-throated Gray Warbler (semi-obligate; ψ(old burn) = 0.43, ψ(recent burn) = 0.88, ψ(not burned) = 0.98).

For additional species modeled, the habitat use of Chipping Sparrow was not different across habitat types (ψ(all habitats) = 0.68). The species more likely to be observed in the burned patch compared to other habitat types was the Black-headed Grosbeak (ψ(old burn) = 1.00, ψ(recent burn) = 0.68, ψ(not burned) = 0.85). The species with higher habitat use in the recent burn were the Rock Wren (ψ(old burn) = 0.06, ψ(recent burn) = 0.56, ψ(refugia) = 0.53, ψ(unburned) = 0.25),

Table 2
Tukey HSD for differences in means of 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 habitats (α = 0.05). Full dataset can be found in Supplementary data 1 Table S2 and Table S3.

	BA		Percent Canopy Cover		Total Live Trees		Percent Shrub Cover		Percent Grass Cover	
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
Unburned	35.2	b	27.0	ab	341.0	b	10.3	ab	12.4	a

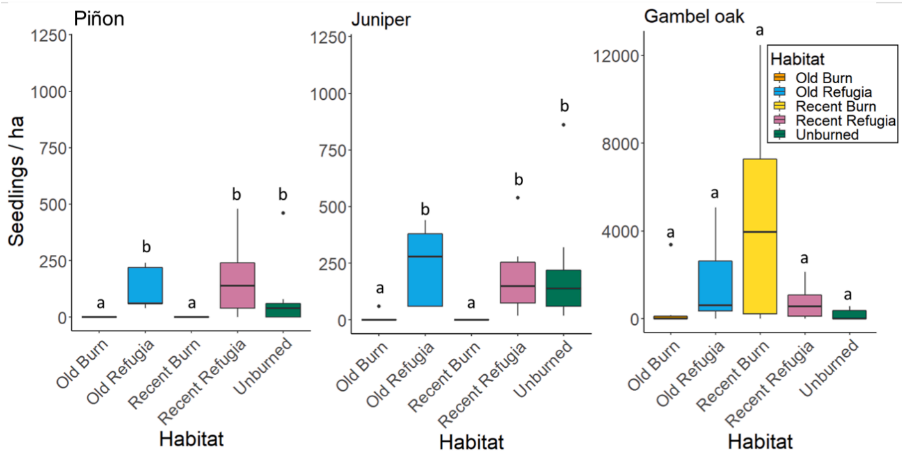

Fig. 3. Box plots displaying piñon seedlings per ha, juniper seedlings per ha, and Gambel oak stems per ha by habitat type (old burn, old refugia, recent burn, recent refugia, unburned). Boxes are colored by habitat type (orange = old burn, blue = old refugia, yellow = recent burn, pink = recent refugia, and green = unburned). Note the change in y-axis scale for Gambel oak stems. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Generalized linear model results for the top-performing model in each seedling category (piñon seedlings, juniper seedlings, Gambel oak stems) across all habitat types (old burn, recent burn, old refugia, recent refugia, and unburned) and across non-burned habitat types (old refugia, recent refugia, and unburned). These models were conducted at the plot scale to be consistent across all variables.

	Seedling Category	Covariate	Estimate	SE	z-value	p-value	AIC
All Habitat Types	Juniper Seedlings	# Live Trees	0.084	0.012	7.11	< 0.001 *	163.79
	Piñon Seedlings	# Live Trees	0.074	0.015	4.94	< 0.001 *	130.01
		Elevation	0.003	0.002	1.59	0.113	
	Gambel oak Stems	% Shrub	−0.056	0.043	−1.31	0.190	260.06
		Folded aspect	0.031	0.009	3.57	< 0.001 *	
		% Grass	−0.018	0.031	−0.60	0.549	
Old Refugia, Recent Refugia, and Unburned Habitats	Juniper Seedlings	% Shrub	−0.045	0.021	−2.13	0.033 *	129.58
		# Live Juniper	0.046	0.010	4.43	< 0.001 *	
		Live Juniper BA	−0.345	0.125	−2.75	0.006 *	
		Elevation	0.002	0.001	1.83	0.067	
	Piñon Seedlings	# Live Trees	0.044	0.012	3.58	< 0.001 *	110.00
		% Shrub	−0.052	0.030	−1.72	0.086	
		Live Tree BA	−0.262	0.169	−1.55	0.121	
		Elevation	0.004	0.001	3.30	< 0.001 *	

although the habitat use for this species was similar in refugia. Lazuli Bunting (ψ(old burn) = 0.65, ψ(recent burn) = 0.36, ψ(refugia) = 0.34, ψ(unburned) = 0.82) and Mourning Dove (ψ(old burn) = 0.65, ψ(recent burn) = 0.83, ψ(refugia) = 0.59, ψ(unburned) = 0.99) had the highest habitat use probability in the unburned.

Model detection covariates varied among bird species. Observer was included in the model for six of the nine PJ-associated bird species modeled (Supplementary data 1 Table S5), wind speed was included in the model for one species, and cloud cover was included in the model for three species.

4. Discussion

4.1. Bird habitat use as a measure of ecological resilience to fire

PJ woodlands are a critical, yet often understudied, habitat in western North America. This ecosystem is facing rapid changes in disturbance regimes and climate, with consequences for plant and animal communities. We found essentially no recovery toward pre-fire tree composition of habitat structure between 1- and 25-years post-fire. This persistent vegetation shift is confirmed in the bird community structure, where we saw a lower probability of PJ-associated birds (American Robin, Gray Vireo, Black-throated Gray Warbler, and Gray Flycatcher) using the old burned habitat. As climate change causes larger and more frequent fires, our findings are particularly concerning for PJ-obligate and semi-obligate bird species, some of which also play critical roles in seed dispersal and forest regeneration.

Given previous research on PJ woodland recovery, we expected that 25 years post-fire was adequate for observing tree regeneration, even if in the form of very young seedlings (e.g. Koniak 1985, Huffman et al. 2012, Bristow et al. 2014). Yet, only one burned site had any seedling regeneration present, thus vegetation characteristics and avian communities that may support seedling growth in the post-fire landscape cannot be assigned with certainty in this study. However, in unburned and refugia, our models show that piñon regeneration is supported by greater density of live trees in an area and higher elevation, and juniper regeneration is supported by greater density of live juniper trees, lower shrub cover and lower live juniper basal area (perhaps indicating that a greater number of smaller mature trees provides more canopy shading than an area comprised of fewer larger trees) – all of which is opposite of what was observed in burned plots. This further reiterates the long-time scale of regeneration in PJ, and the potential usefulness of incorporating other measures of resilience, such as wildlife studies, to quantify early signs of resilience when tree regeneration is expected to lag so long after fire events. Further, while we did not observe piñon or juniper seedling regeneration in the recent burn, we did observe abundant Gambel oak, which had high densities across all burned plots, even one-year post-fire (average 4,623 stems/ha across recent burned sites, Supplementary data 1 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). Recent experimental work has also demonstrated a higher survival rate for piñon seedlings that

Table 4
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	Detection covariates (p)	Occupancy covariates (ψ)	AICc
Piñon Seed Dispersers	Woodhouse's Scrub-jay	Null	Null	431.42
Juniper Seed Dispersers	American Robin	Observer	Hyp 3 [old burn ≠ recent burn ≠ (refugia + unburned)]	265.14
PJ Obligates	Ash-throated Flycatcher	Observer	Null	518.57
	Gray Vireo	Cloud	Hyp 3 [old burn ≠ recent burn ≠ (refugia + unburned)]	262.03
	Virginia's Warbler	Observer	Hyp 1 [old burn ≠ recent burn ≠ refugia ≠ unburned]	507.55
PJ Semi-obligates	Black-throated Gray Warbler	Observer + wind	Hyp 3 [old burn ≠ recent burn ≠ (refugia + unburned)]	457.86
	Blue-gray Gnatcatcher	Cloud	Hyp 3 [old burn ≠ recent burn ≠ (refugia + unburned)]	488.27
	Gray Flycatcher	Observer	Hyp 3 [old burn ≠ recent burn ≠ (refugia + unburned)]	468.55
	Spotted Towhee	Observer + cloud	Null	341.89

were planted under Gambel oak (Crockett and Hurteau, 2022). Additionally, while only a single observation point, the site that had juniper regeneration in the old burn was also the only old burn plot that had a relatively high density of Gambel oak stems (Supplementary data 1 Table S1), and it was only 50 m from an unburned edge. Proximity to a seed source, which has shown to be important in other forest types (Chambers et al. 2016, Coop et al. 2019) and more important for juniper (Salomonson 1978, Chambers et al. 1999), in combination with Gambel oak cover, may be associated with this observed regeneration. Further monitoring of these sites in the upcoming decades will be critical to understand the relative influence of Gambel oak abundance as well as distance to piñon and juniper seed source on piñon and juniper regrowth in burned areas.

Although tree regeneration was not observed, the presence of the Woodhouse's Scrub-jay across all habitats may offer potential modes of piñon seed dispersal into these burned landscapes for future regeneration. These birds often stay within their home area for foraging, caching seeds within established stands and into nearby openings, but rarely dispersing seeds >500 m from seed sources (Vander Wall and Balda, 1981). In spite of this, regeneration was still non-existent <500 m from seed sources. Clark's Nutcracker and Pinyon Jay are most known for their piñon seed caching abilities, however, few were observed (Supplementary data 1 Table S4). The relative absence of these birds could be driven by several factors, such as regional drought (Christensen et al. 1991), range-wide population declines (Boone et al. 2018), and seasonal habitat use (Vander Wall and Balda, 1981). However, the lack of these keystone species and absence of post-fire piñon regeneration in our study sites may be linked, and if so, indicate a diminishing woodland resilience to high-severity fire.

Ecological resilience is necessarily inclusive of a broad range of post-disturbance biotic elements and ecological processes, and we posit that bird habitat use is a particularly strong metric of resilience, as it demonstrates the extent to which birds recognize the post-fire vegetation state as similar to, or different from, the prior ecological state. The old burned, recent burned, and intact (unburned and refugia) habitats had distinct vegetation structure, in the form of differences in shrub, grass, and tree cover, which reflect differences in the bird community structure observed in these habitats. Thirteen obligate or semi-obligate bird species were observed in this study, three of which (Woodhouse's Scrub Jay, Ash-throated Flycatcher, and Virginia's Warbler) used all habitats nearly indiscriminately. Four bird species (American Robin, Gray Vireo, Black-throated Gray Warbler, and Gray Flycatcher) were least likely to use the old burn habitat, reflecting differences in habitat needs from birds that did continue to use the old burn habitat (including Virginia's Warbler, Blue-gray Gnatcatcher, Woodhouse's Scrub-jay, Ash-throated Flycatcher, and Spotted Towhee). Birds that were relatively absent from the old burn (excluding American Robin) are typically more reliant on mature piñon or juniper trees and/or greater canopy cover (e.g.Pavlacky and Anderson 2001, Sedgwick 1987, Harris et al. 2020), while the birds that did use the old burn are often associated with habitat edges, high shrub cover, or cavity nests (i.e. snags) (Root 1967, Pavlacky and Anderson 2001, Sedgwick 1987, Saab et al. 2005).

Of the species absent from the old burn habitats, the Gray Vireo is a PJ obligate of particular concern. Currently, this species has a stable population across its range (Pardieck et al. 2018); however, it is projected to experience future declines 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 pattern is likely to persist for at least several more decades until more prolific regeneration and maturation occurs, if at all. With fire in PJ woodlands burning larger areas, more Gray Vireo habitat will be affected by fire than it has in the past, with multi-decade effects, as observed in this study. The Gray Vireo, however, was observed in refugia and used this habitat no differently than unburned woodland, showing evidence that refugia of at least 5 ha can be important for maintaining Gray Vireo populations while woodlands are recovering after wildfire.

All PJ-associated species of interest, besides the Blue-gray Gnatcatcher, were observed using the recently burned habitats. 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, perhaps, before moving on to more suitable habitats. It is possible that the recent burned patches act as an ecological trap, where a sudden change (e.g. a recent fire) causes the birds to choose a less-suitable habitat which may reduce the species' fitness (Schlaepfer et al. 2002). Thus, while bird species may be present and using these recently burned patches, fitness may be diminished for these birds due to less optimal habitat characteristics (O'Neil et al. 2020). Conversely, all of these birds are known to consume insects for either all or a portion of their diets, so it is also possible that these birds were exploiting insects that are of higher abundances one-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, or were present briefly and moved on, will require additional years of study.

We find it important to note, here, that interpretation of habitat use probability, especially when the estimate of ψ is equal to 1, should be done with caution when the detection probability (p) is <0.15 (MacKenzie et al. 2002). Model results where p < 0.15 were few

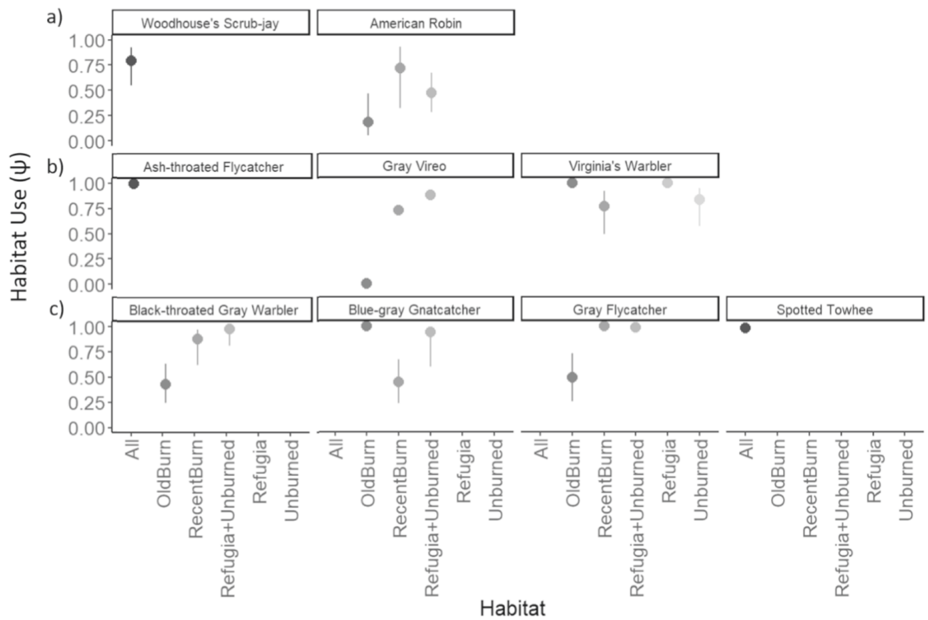

Fig. 4. Occupancy results for species of interest based on the species top occupancy model. Note that for species with occupancy estimates near 1 or 0, confidence intervals are excluded, as the Maximum Likelihood Estimates used to create these estimates often fail to produce reliable confidence intervals 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.

(Supplementary data 1 Table S5), but occurred with American Robin (Observer 2) and Gray Vireo (Cloud cover 0 and Cloud cover 1). This means that Observer 2 was less likely to detect American Robin when actually present, and Gray Vireo was less likely to be detected when actually present when there was less cloud cover. However, since point count observer was alternated for each visit and neither of these species had $\psi = 1$ for any habitat type, observer bias should not be an issue for these species.

4.2. Management implications

Past research has suggested that contemporary fuel conditions in PJ woodlands (including presence of invasive grasses, dry canopy fuels, and tree mortality – although not necessarily increased tree densities), more extreme weather events, and a warming and drying climate, are driving shortened fire rotations and increasing the annual area burned (Linn et al., 2013, Floyd et al. 2021, Board et al. 2018). Management actions that attempt to restore historical fire regimes may not be consistently achievable. These changing fire regimes, combined with post-fire environmental conditions that are frequently warmer and drier, suggest that managers may need to explore alternate and feasible strategies and interventions to promote woodland persistence. Our findings demonstrate that refugia contribute to the maintenance of both key vegetation attributes (piñon pine and juniper trees and seedlings) and attendant biota (PJ-associated birds), supported by birds utilizing the refugia similar to the unburned reference areas. As fire impacts 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.

Two actions managers can perform are 1) provide protection of refugia that were created during a wildfire and 2) promote refugia before a fire starts. To protect refugia that were formed during a wildfire, managers can "edge harden" previously burned areas by reducing fuel loading underneath and next to live tree patches to reduce the risk of future fire spreading into these landscape features (Stevens et al. 2021), especially by preventing and reducing the establishment of cheatgrass and other invasive grasses that increase understory connectivity. While we did not distinguish between native and non-native grass cover, the prevalence of non-native grass may exacerbate an increase in fire activity (Bradley et al. 2018) and promote conversion (Floyd et al. 2021). To promote refugia before a fire occurs, managers may be able to create fuel breaks via gaps in the canopy and understory, especially efforts to minimize abundance of non-native grasses, 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 more dead trees and more continuous understory. We do not advocate for extensive and uniform canopy, as this would be against the historic variability of woodland structure, and not likely to reduce wildfire risk (Shinneman and Baker 2009; Rocca et al. 2014) and treatments themselves can disturb both vegetation and bird communities (Magee et al. 2019; Gallo and Pejchar 2017). However, the promotion and protection of refugia will help limit the continuity of large burned patches, and help maintain avian diversity across a heterogeneous landscape (Steel et al. 2022).

Though pre- and post-fire management activities can help support refugia, it is important to recognize that changing climate conditions and shortened fire rotations may reduce the role these sites can play in promoting forest recovery, where increasingly hot and dry conditions prevent tree seedling regeneration. Additional actions in burned areas should be considered, especially to mitigate the colonization of non-native vegetation (e.g. cheatgrass) which can influence fire activity and negatively impact native revegetation. Actions, such as increasing native perennial cover via seeding and planting, and pausing or limiting grazing to allow native vegetation to recover (Redmond et al. 2023) would be beneficial in these areas. In some settings, such as burned areas at higher elevation, post-fire conditions may allow for the return of these woodlands; in these cases, managers can monitor and support seedling establishment through planting actions following recommendations in North et al (2019), such as targeting regions further within a burned interior and sites that are more conducive for conifer survival and resilience. Planting action is crucial, especially as seed dispersers may be absent from or less active in these disturbed areas. New tree conifer establishment may be limited at lower elevation/latitudes within a species range (Kemp et al. 2019, Parks et al. 2019), thus at these lower elevations, planting may not be suitable for future conditions, and conversion to non-forested ecosystem may be expected. Especially with low densities of piñon caching birds, active management, where climate is suitable, may be necessary to reestablish PJ woodlands post-fire.

4.3. Limitations and future research

While this study advances our knowledge on PJ woodland regeneration, bird responses to fire, and the link between post-fire vegetation recovery and bird habitat use, we acknowledge several limitations. First, while sample size was robust regarding repeated measures of bird counts, the corresponding vegetation plots were limited in sample size, which may limit the observed regeneration in the old burn sites. However, anecdotally, scattered juniper seedlings, and few, if any, piñon seedlings were observed by field crews while conducting point counts and hiking extensively through these burned regions across three visits (J. Woolet, personal observation). Second, we collected data during late spring/early summer, before piñon seeds are ripe and after caches have likely been revisited by birds (Vander Wall and Balda, 1981), so bird interactions with piñon seeds were likely not observed. Bird counts were conducted during the spring as this is the height of the bird breeding season and the time when most birds are actively singing and can thus be observed (Gallo and Pejchar 2017), but we acknowledge the seasonality of usage and presence that may have been missed with this timing. Third, studies are often not in agreement regarding bird responses to recent fire in different landscapes, and in many cases, there is an immediate delay in the response to fire. This indicates that observing a certain species in the recently burned habitat (as we did in this study) does not necessarily mean that they prefer or thrive in this kind of environment (as we also observed, with the absence of some of these species in the older burned habitats). Studies that move beyond estimating occupancy to also measure survival, reproductive success, and movement across these areas are necessary to demonstrate whether burned areas are serving as an ecological traps (Schlaepfer et al. 2002; O'Neil et al. 2020) for some bird species.

Findings from this study reveal several areas for future research. First, proximity to live seed sources is a known controlling factor for tree regeneration by many species (Chambers et al. 2016, Coop et al. 2019), and dispersal agents may be essential to move seeds into large burned patches to successfully recover (Chambers et al. 1999). Future work focusing on dispersal distance dynamics into burned PJ woodlands is necessary, especially given that avian dispersal is critical for improving conservation strategies for bird-dispersed tree species (e.g. Coop and Schoettle 2009, Cavallero et al. 2013). This can inform whether increasingly larger burned patches have the potential to regenerate naturally (Gill et al. 2022), especially as the loss of key seed dispersers due to climate change are thought to hinder these processes (Fricke et al. 2022). Further, although assessing rodent-mediated dispersal or seed predation was beyond the scope of this study, it is known to have an important role in juniper regeneration, as juniper may be facilitated by diplochory, where a cone that was consumed and defecated by a bird is picked up by rodents and buried elsewhere (Longland and Dimitri 2016). These non-avian forms of seed dispersal and predation are important to understand more thoroughly.

Little is known about site-specific controlling factors for piñon and juniper establishment in burned areas, thus, future work should investigate the fine-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. Our model indicated that in unburned and refugia, piñon regeneration increased as elevation increased (Table 3); further research specifically investigating elevation trends and its potential for buffering climate-induced challenges for piñon regeneration is needed.

4.4. Conclusions

This study found that 25–27 years post-fire, tree regeneration in burned PJ woodlands is essentially non-existent, likely driven by lack of nearby seed sources, limited seed dispersal, and harsher environmental conditions (all of which are compounded by declining seed production and more intense droughts), since neighboring unburned and refugia have regeneration of conifers at various size classes. Similarly, several PJ obligate and semi-obligate species were either absent or had a low habitat use in the burned regions. These findings, both from the perspective of vegetation and bird communities, indicate these woodlands have a long recovery time, or that these woodlands are potentially transitioning to non-forest cover types. In addition, we demonstrate that large refugia patches (>5 ha) are critical for preserving plant and animal diversity within the interior of wildfires, as they shared similar characteristics to the unburned reference sites. These unburned islands may support resilience via the persistence of woodland structure and associated biota on the landscape, even though recovery processes in burned patches may be delayed or lost due to high-severity fire and an increasingly harsh and novel climate. Of the more abundant PJ-associated bird species, all species, except for the American Robin, had a high probability (>79%) of using refugia or unburned habitats, with five of these birds treating refugia and unburned habitats similarly, showing evidence for the importance of refugia for maintaining PJ-associated bird populations within fire perimeters. Often, we assess recovery post-fire through metrics of plant reestablishment, however this study indicates that considering how multiple taxa respond may provide a more complete picture of ecosystem recovery or lack thereof, even 25+ years post-fire.

CRediT authorship contribution statement

Jamie Woolet: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Supervision, Project administration, Funding acquisition. **Camille S. Stevens-Rumann:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition. **Jonathan D. Coop:** Conceptualization, Methodology, Writing – review & editing. **Liba Pejchar:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121368.

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