Research Article

Woodland Reduction and Long-Term Change in Breeding Bird Communities

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ABSTRACT Forested ecosystems in the western United States have been the focus of tree reduction efforts for decades, with the intent of improving forage for livestock and wildlife. Yet, the long-term consequences of tree removal for biodiversity are virtually unknown. We conducted bird and vegetation surveys in northwestern Colorado where trees were mechanically removed over 40 years ago. We evaluated differences in avian species richness and community composition, and used a Bayesian hierarchical approach to determine if tree removal had long-term effects on bird density. We found that tree reduction initiates a long-term change from dense pinyon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands to sagebrush scrub, fundamentally altering bird community composition. Disturbed sites were used by fewer species and largely dominated by shrubland-obligate birds. Further, bird densities were markedly different between historically disturbed sites and reference sites. Densities of many species were correlated with specific vegetative characteristics (e.g., mean tree diameter) that could be factored into management decisions to better sustain diverse natural communities. © 2016 The Wildlife Society.

KEY WORDS avian community, habitat, land conversion, pinyon-juniper, rank abundance distributions, richness, tree removal.

Deliberate and large-scale tree removal to increase forage for livestock or hunted wildlife species has been common and widespread for centuries (Aro 1971, Lewis et al. 1982, Yahner 1984, Fuschs et al. 2015). These practices are global in scale but particularly prevalent in the western United States where forested lands are converted to shrub or grasslands to increase forage quantity and quality (Aro 1971, Terrel and Spillett 1975, Evans 1988, Miller and Wigand 1994). Trees are removed using prescribed fire or mechanical techniques (Aro 1971, Miller and Wigand 1994, Redmond et al. 2013). Historically, chaining was the most widely used method to mechanically remove forest cover (Aro 1971). Chaining has been successful at reducing tree cover, killing a majority of older, larger trees in a stand, and increasing herbaceous forage for livestock and wildlife (Aro 1971).

Recent speculation about decreasing habitat for birds and mammals that depend on open habitats (e.g., greater sage-grouse [*Centrocercus urophasianus*], Schroeder and Baydack 2001, Knick and Connelly 2011; mule deer [*Odocoileus hemionus*], Bergman et al. 2015), and increased concerns about wildfire has renewed tree reduction efforts. In some cases, chaining is still employed (Redmond et al. 2013), whereas elsewhere it has been replaced with other mechanical tree removal methods (e.g., hydro ax) that have similar objectives and outcomes (Wästerlund and Hassan 1995).

During the last half-century, pinyon (*Pinus edulis*)—juniper (*Juniperus osteosperma*) ecosystems have been a major focus of forest conservation and tree reduction because of their large spatial extent, the ecosystem services they provide, and their natural or human-induced encroachment on shrubland and grassland ecosystems (Miller and Wigand 1994, Tausch and Tueller 1977, Redmond et al. 2013). Both pinyon and juniper trees have been expanding into grasslands and shrublands since the mid 1800s (Romme et al. 2009). The mechanisms for pinyon–juniper expansion are not well known but may include recovery from past natural disturbances, range expansion since the Holocene epoch, livestock grazing, fire suppression, and the effects of climatic variability and rising atmospheric carbon dioxide (Miller and Wigand 1994, Romme et al. 2009). Because pinyon–juniper expansion into grasslands and shrublands reduces forage for livestock and hunted species and decreases the amount of habitat for shrubland species of concern (e.g., greater sage-grouse and Brewer's sparrow [*Spizella breweri*]), tree reduction and thinning at the margins and interior of pinyon–juniper stands is an important component of current land management activities. Although removing tree cover has been a common land management practice for decades,

and is predicted to increase in frequency and intensity (Redmond et al. 2013), the long-term effects of tree removal on bird communities are virtually unknown.

Because all or most trees are removed during chaining, pinyon–juniper woodlands are replaced with open grasslands and shrublands (Tausch and Tueller 1977). Removing the majority of forest cover is likely to have an impact on the habitat use of forest-dwelling birds that respond to changes in vegetation structure and density (MacArthur and MacArthur 1961). In slow recovering systems, such as pinyon–juniper ecosystems (Schott and Pieper 1987), these changes in vegetation structure may have a lasting effect on bird community composition and habitat use. Inference about changes in species composition following habitat disturbance are typically drawn from surveys conducted shortly after initial disturbance (e.g., 1–3 yr; Debinski and Holt 2000), which may not predict long-term effects on community dynamics (Stouffer et al. 2011). The few studies on the short-term effects of pinyon–juniper removal on animal communities (Baker and Frischknecht 1973, O'Meara et al. 1981, Sedgwick and Ryder 1986) reported that pinyon–juniper removal has negative consequences on forest-obligate species (Bombaci and Pejchar 2016). Because long-term effects on species, particularly those that are rare and long-lived, can go unseen in short-term studies (Laurance et al. 2002, 2011), these studies provide the unique opportunity to revisit historically chained areas and compare short- and long-term changes to natural communities.

We investigated whether tree removal to increase forage for livestock and enhance habitat for mule deer has altered bird communities in woodlands chained over 40 years ago, relative to reference woodlands that have not been subject to large-scale human or natural disturbances. Our research objectives were to evaluate differences in species richness and community composition between historically chained sites and reference sites, compare bird densities between historically chained sites and reference sites, and identify the vegetation characteristics associated with differences in bird densities. We predicted that >4 decades after initial disturbance, species richness and community composition would be similar in historically chained and reference sites (Wiens and Rotenberry 1981, Hobson and Schieck 1999). We further hypothesized that densities of individual species would differ between chained sites and reference sites, and that the influence of habitat characteristics would vary in their magnitude and direction depending on species' life-history strategies (i.e., foraging and nesting guilds, habitat preference).

STUDY AREA

This study was conducted in a pinyon–juniper ecosystem in the Piceance Basin, Northwest Colorado, USA on public land managed by the Bureau of Land Management. The Piceance Basin is a semiarid region characterized by warm, dry summers and cold winters with 30-year mean annual precipitation of 33 cm (Lendrum et al. 2013, Colorado 2016, Stephens et al. 2016). Our study area was bounded by

United States Highway 40 to the north, Colorado State Highway 139 to the west, the Roan Plateau to the south, and Colorado State Highway 13 to the east. Dominant land use activities in the area included oil and natural gas extraction and domestic livestock grazing (Northrup et al. 2015). Our study area ranged in elevation from approximately 1,500 m to 2,400 m. The topography consists of high plateaus and deeply incised valleys. Temperatures ranged from a 2-year mean of −18°C in January to 30°C in July (Colorado 2016). Woodlands were dominated by 2 tree species, pinyon pine and Utah juniper (Sedgwick 1987). In lower elevations, Utah juniper dominated the overstory, and the understory consisted of antelope bitterbrush (*Purshia tridentata*) and mountain mahogany (*Cercocarpus montanus*; Sedgwick 1987). At higher elevations pinyon pine dominated the overstory, and most of the low elevation grasses and forbs were present in greater proportions, along with arrowleaf balsamroot (*Balsamorhiza sagittata*) and lupine (*Lupinus* spp.). Typical high elevation shrubs included big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), antelope bitterbrush, mountain mahogany, common chokecherry (*Prunus virginiana*), and Saskatoon serviceberry (*Amelanchier alnifolia*; O'Meara et al. 1981, Sedgwick 1987). In addition to a diverse bird community (Sedgwick 1987), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), golden-mantled ground squirrels (*Callospermophilus lateralis*), chipmunks (*Tamias* spp.), and mountain cottontails (*Sylvilagus nuttallii*) were common mammal species (Gallo et al. 2016).

METHODS

Field Methods

We established sampling sites in historically chained pinyon–juniper woodlands (chained sites) and sampling sites in woodlands that were never mechanically disturbed (reference sites; Table A1, available online in Supporting Information). We identified areas that had been chained in the 1950s through the 1970s using local knowledge from land managers and aerial imagery. We then visited each location to verify that the site had not been disturbed since initial chaining by prescribed fire, wildfire, or mechanical tree removal. We confirmed that these areas had not been significantly disturbed since the initial chaining by observing the presence of many large, decaying, fallen trees and the absence of charred debris indicating fire. We considered disturbance from oil and natural gas extraction and domestic livestock grazing to be constant across our study area. We identified 9 historically chained areas embedded in a matrix of pinyon–juniper woodlands ranging in size from 3 to 1,243 ha. Using a geographic information system (GIS), we established 25 sampling sites throughout these chained areas. We placed a sampling site within each chained area by picking a random but accessible location in the approximate center of each area. We then placed additional sampling sites in each cardinal direction, such that the sites were ≥250 m

apart (i.e., the max. distance that most species can be detected; Ralph et al. 1995). Because of the irregular shape of some chained areas, some sites were located near undisturbed forest (∼35 m). However, we counted only birds detected within the chained area. Because we began selecting sites in the smallest chained areas first, our design allowed for 1 site in each of the smallest areas and up to 6 sampling sites in the largest areas.

Reference sampling sites ($n = 50$) had been previously established across the study area for an ongoing wildlife-monitoring program (Gallo et al. 2016). All reference sites were randomly placed on the landscape using GIS and were buffered from all forms of known anthropogenic disturbance (e.g., historically chained areas, energy well pads, roads) by ≥250 m. We ground-truthed each reference site to verify that it was within pinyon–juniper woodlands. To ensure a similar sampling effort between treatments and eliminate the possibility of differences in species and individual accumulation from uneven sampling (Magurran 2004), we used stratified random sampling to select 25 reference sites from this larger set of reference sites using GIS. Because 5 of the 9 chained areas were clustered together on the landscape, we stratified reference sites such that we randomly selected 13 sites from the vicinity of the cluster of chained areas, and 12 from the overall study area that encompassed the more geographically dispersed chained areas. We spaced reference sites so that the nearest reference site to the geographically dispersed chained sites was 3.6 km, and the nearest reference site to the cluster of chained sites was 1.23 km.

We surveyed birds by conducting 5-minute point counts at each of the 25 chained sites and 25 reference sites (Dunn et al. 2006). Three to 5 trained observers surveyed each site 4 times per year between April–June for 2 years (2013–2014). We conducted surveys at each site approximate 2 weeks apart, and rotated observers among sites and surveys. We detected birds visually or aurally and recorded their distances from the point count station using Nikon Prostaff range-finders (Nikon, Tokyo, Japan). We did not include raptors and birds flying over sites in subsequent analyses. We recorded aerial insectivorous birds (e.g., violet-green swallow [*Tachycineta thalassina*]) only if they perched within sites. All surveys started approximately 30 minutes after sunrise and, on average, ended by 1100. We rotated starting times among locations and surveys. We did not conduct surveys in fog, rain, or high winds (i.e., >3 on Beaufort scale). Bird survey procedures were approved by the Colorado State University Institutional Animal Care and Use Committee (Protocol #12-3277A).

To assess the relationship between bird densities and habitat characteristics, we measured a variety of vegetation parameters. In 2013, we sampled vegetation in 10×10-m plots, offset from each point count station by approximately 5 m in a random direction, to determine plant composition and cover (McElhinny et al. 2005). We defined trees (live and dead) as individuals with a height >1 m (Romme et al. 2009). We recorded species, tree height, crown area, trunk diameter at breast height (DBH), and condition (i.e., live,

dead, large-snag broken above 1 m, small-snag broken below 1 m, log, cut stump) for each tree in the 10×10-m plot following the methods used in Huffman et al. (2012). We measured diameter of trees that were <1.5 m in height at mid-trunk height. We calculated percent forest cover by dividing total crown area by plot size (100 m^2). We calculated an index of forest stand age, modified by McElhinny et al. (2005), by dividing the total DBH of all trees within the plot by the plot size (DBH/100 m^2). In 2013 and 2014, we classified all vegetation into 6 height classes (0–0.5 m, 0.6–1 m, 1.1–2 m, 2.1–5 m, 5.1–10 m, and >10 m), and measured percent cover of each height class, shrub and grass species richness, and percent cover using a 25-m line intercept beginning at each point count station and heading in a random compass direction (Canfield 1941). We tested for differences between years for each vegetation variable using analysis of variance (ANOVA) in R (R version 3.2.3, www.r-project.org, accessed Mar 2016), and did not find significant differences. Therefore, we averaged the 2 years of vegetation data for each variable at each site and incorporated these values into the analyses described below. We tested for differences between vegetation variables in chained and reference sites using a non-parametric Mann–Whitney U test in R.

Statistical Analyses

Density.—We used hierarchical open population binomial mixture models (Kéry and Royle 2010, Kéry and Schaub 2012) to quantify the effect of historical chaining on the abundance of each bird species (Model 1, code available online in Supporting Information) and the effect of vegetation parameters on bird densities (Model 2, code available online in Supporting Information). Binomial mixture models estimate abundance using repeated count data while taking into account imperfect detection (Kéry and Schaub 2012). Thus, they contain more information than estimating an occurrence or non-occurrence response, similar to the widely used occupancy modeling framework (MacKenzie et al. 2006, Kéry and Schaub 2012). We truncated bird detections at a 100-m radius from the point count station, making all surveyed areas 3.1 ha. Therefore, we infer our results as bird density (individuals/ha).

To quantify the long-term effect of tree removal on species density, we let y_{ijk} be the number of individuals counted at site i, during survey j, in year k (2013 and 2014). Assuming the population was closed over the course of each year, the observed counts arise as a binomial random variable,

$$y_{ijk} \sim \text{binomial}\left(N_{ik}, p_{ijk}\right),$$

where N_{ik} is the number of individuals available to be counted in year k at site i, and p_{ijk} is the survey-specific detection probability. We then modeled our latent variable N_{ik} as a Poisson random variable,

$$N_{ik} \sim \text{Poisson}\left(\lambda_{ik}\right),$$

where λ_{ik} is the expected abundance at site i for year k. To quantify the influence of historical chaining on the

Table 1. Hypothesized direction of effect (+ or −) for each vegetation parameter's influence on bird density in the Piceance Basin, Colorado, USA, 2013–2014. Shrub, tree, grass, and ground refer to proportion of shrub, tree, grass, and bare ground cover, respectively. Shrub richness refers to shrub-species richness, DBH refers to the mean tree diameter/100 m², and snag refers to the number of standing dead trees within a sampling plot. Log refers to the number of downed trees within a sampling plot. Parameters that were not included in the species-specific models are indicated by a 0.

Species	Covariates							
	Shrub	**Tree**	**Grass**	**Shrub richness**	**DBH**	**Ground**	**Snag**	**Log**
Mourning dove	+	−	+	+	0	0	0	0
Plumbeous vireo	−	+	0	0	+	−	0	0
Violet-green swallow	−	+	0	0	+	0	+	0
Juniper titmouse	−	+	0	0	+	0	+	0
Mountain chickadee	−	+	0	0	+	0	+	0
White-breasted nuthatch	−	+	0	0	+	0	0	+
Rock wren	+	−	+	0	0	+	0	0
Mountain bluebird	−	+	0	0	+	0	+	0
Green-tailed towhee	+	−	+	+	0	0	0	0
Spotted towhee	+	+	−	0	0	−	0	0
Vesper sparrow	+	−	+	0	0	+	0	0
Chipping sparrow	+	+	−	+	0	0	0	0
Brewer's sparrow	+	−	+	+	0	0	0	0
Dark-eyed junco	+	+	+	0	0	+	0	0
Cassin's finch (*Haemorhous cassinii*)	−	+	0	0	+	+	0	0

abundance of bird species, we modeled λ_{ik} as a function of disturbance or non-disturbance at site i using a log link,

$$\log(\lambda_{ik}) = \omega_{g[i]} + x_i\beta_1$$

In this equation, we set up our data vector (x_i) so that we gave reference sites a 0 and chained sites a 1. To account for potential site dependency within a disturbed patch, we used a multilevel model to include a random effect (ω) on geographical grouping ($g = 7$). We assigned each historically chained area its own group with the exception of the cluster of chained sites, which we placed together in a single group. We had 5 disturbance groups. We divided reference sites into 2 groups: the clustered reference sites and the geographically dispersed reference sites. We then modeled the group level parameters using a normal distribution and allowing each group to have a common mean (μ_{ω}) and standard deviation (σ_{ω}),

$$\omega_g \sim \text{normal}\left(\mu_{\omega}, \sigma_{\omega}^2\right).$$

This distribution has the effect of drawing the estimates of ω_g toward the mean level (μ_{ω}) but not entirely, thus creating a partial-pooling compromise among the estimates (Gelman and Hill 2007). Based on previous analyses (T. Gallo, Colorado State University, unpublished data) observers conducting point count surveys had the greatest influence on the detection probability for all species. Therefore, we modeled the detection probability as a function of the observer conducting the survey at site i, survey j, and year k on the logit scale:

$$\text{logit}\left(p_{ijk}\right) = \alpha_o + \alpha_1 observer_{ijk}$$

We used conventional vague priors for all parameters. Specifically, we assumed $\beta \sim \text{normal}(0,100)$, $\alpha \sim \text{normal}(0,100)$, $\mu \sim \text{normal}(0,100)$, and $\sigma \sim \text{uniform}(0,100)$.

For those species showing a positive or negative response to historically chained sites (i.e., 90% credible intervals not overlapping 0) we developed *a priori* hypotheses for which vegetation parameters may best explain variation in density based on foraging (DeGraaf et al. 1985) and nesting guilds (DeGraaf and Wentworth 1986) and habitat preference (Rodewald 2015; Table 1 and Table A2, available online in Supporting Inforfmation). To be cautious of over parameterizing our model, we chose only 4 vegetation covariates/species that we thought would have the greatest influence on density (Table 1). We then used the same hierarchical open population binomial mixture model (Kéry and Royle 2010, Kéry and Schaub 2012) described above to quantify the effect of habitat characteristics on species abundance. However, in this model X_i represents a matrix of continuous predictor variables scaled to have mean 0 and standard deviation 1 (Gelman et al. 2008):

$$log(\lambda_{ik}) = \omega_{g[i]} + X_i\beta$$

We tested for correlations among covariates that appeared in the same model to ensure that no covariates were highly correlated ($|r| > 0.7$).

We estimated posterior distributions of model coefficients using Markov chain Monte Carlo (MCMC) methods implemented in JAGS using the rjags package in R (Plummer et al. 2006). We ran models with 3 chains of 200,000 iterations each, a thinning rate of 1, and a burn-in rate of 50,000. We checked for model convergence by visually inspecting the trace plots of MCMC samples, and by checking that the Gelman-Rubin diagnostic statistic for each parameter was <1.1 (Gelman and Rubin 1992). Because of a small sample size and the desire to suggest reasonable management recommendations, we chose local-scale vegetation covariates that could be readily incorporated into land management practices. We also used relatively simple models to examine main effects alone, without considering additive effects or interactions. To assess the relative influence of disturbance and vegetation parameters on species density, we compared the posterior

distribution of model coefficients and examined overlap of their distributions with 0.

Species richness and community composition.—When calculating species richness and community composition, we again used bird detection data truncated at 100 m to ensure similar sampling effort and plot sizes among sites and to ensure independence from adjacent sites (Magurran 2004). To account for species-specific detection probabilities, we first calculated the mean number of detections for each species at each site by dividing the number of detections by the number of visits ($n = 8$; $\bar{d}_i = detections_i/8$). We then adjusted the count data for each species by dividing the mean number of detections at each site by the median posterior value of site- and survey-specific detection probabilities $\left(C_i = \bar{d}_i/p_i\right)$ estimated from the species-specific binomial mixture models described above $\left(p_i = median\left(p_{ijk}\right)\right)$. For species that were too rare to fit a binomial mixture model, we used a borrowing rule based on maximum detection distance before truncation and the vegetation strata in which the species most often sings or displays as suggested by Alldredge et al. (2007). We based behavior information on field observations and information obtained from Rodewald (2015). We first grouped all species into 4 general groups: maximum detection distance of ≤ 50 m, maximum detection distance of >50 m and ≤ 100 m, >100 m and ≤ 150 m, and >150 m. We then grouped them into 3 secondary groups: species that generally display near the ground, species that generally display in the mid-level vegetation strata, and species that generally display in the canopy (Table A3, available online in Supporting Information). We then borrowed detection information from within groups.

Using our adjusted count data, we calculated total species richness (pooled) for chained and reference sites using the non-parametric Chao gamma diversity estimator and mean species richness per sampling site for chained and reference sites using the R packages vegan and BiodiversityR (Kindt and Coe 2005, Oksanen et al. 2015). To compare dominant bird species between chained and reference sites, we calculated rank abundance distributions and curves using BiodiversityR (Kindt and Coe 2005). Rank abundance distributions are commonly used to compare community composition between assemblages (Magurran 2004).

RESULTS

We fit our hierarchical open population binomial mixture model to 21 species (Table 2 and Table A4, available online in Supporting Information). Eleven species demonstrated a long-term negative relationship with chaining. In contrast, 5 species showed a long-term positive relationship with chaining and 5 showed little to no relationship to chaining (Table 2).

Most measured habitat characteristics differed between chained and reference sites (Table 3). Chained sites had a 45% higher mean percent cover of shrubs than reference sites and a 30% greater number of logs present (Table 3). Reference sites had a 90% higher percent cover of trees and a 100% greater overall number of snags (Table 3). However, proportion of bare ground and shrub species richness was similar across site types, and neither chained nor reference sites had trees >10 m tall (Table 3). We found that at least 1 measured habitat characteristics demonstrated a significant relationship with the density of each bird species. However, the effect size and direction of effects of habitat characteristics varied by bird species (Fig. 1). We were unable to fit our vegetation model to American robin (*Turdus migratorius*) because of lack of model convergence.

We observed 37 bird species in historically chained sites and 56 bird species in reference sites (Table A4). Chao gamma diversity estimates were 38.32 ± 4.62 (SE) and

Table 2. Median posterior distributions values and 90% credible intervals (CI) for the open population binomial mixture model used to assess the long-term effects of habitat disturbance on the density of bird species in the Piceance Basin, northwest Colorado, USA, 2013–2014. Species are organized by the direction that habitat disturbance affected density.

Direction of effect	Species	β	Lower CI	Upper CI
Negative	Vesper sparrow	−3.20	−6.37	−0.59
	Plumbeous vireo	−3.11	−4.26	−2.27
	Dark-eyed junco	−2.62	−5.53	−0.20
	Mourning dove	−1.66	−2.22	−1.16
	Cassin's finch	−1.55	−2.46	−0.82
	Violet-green swallow	−1.32	−2.24	−0.60
	Juniper titmouse	−1.28	−2.70	−0.17
	American robin	−1.16	−2.24	−0.10
	White-breasted nuthatch	−1.13	−1.64	−0.69
	Spotted towhee	−0.72	−1.27	−0.26
	Mountain chickadee	−0.69	−1.32	−0.10
Positive	Brewer's sparrow	2.50	2.07	2.94
	Mountain bluebird	1.55	1.17	1.91
	Rock wren	1.31	0.46	2.16
	Chipping sparrow	0.79	0.25	1.29
	Green-tailed towhee	0.64	0.28	0.98
No effect	Ash-throated flycatcher (*Myiarchus cinerascens*)	0.46	−0.23	1.12
	Empidonax flycatcher	0.39	−0.05	0.80
	Black-throated gray warbler	−0.43	−0.97	0.17
	Broad-tailed hummingbird (*Selasphorus platycercus*)	−0.47	−1.92	0.42
	Northern flicker (*Colaptes auratus*)	−0.76	−1.92	0.26

Table 3. Summary statistics of vegetative parameters ($\bar{x}$ and SE) in historically chained sites and reference sites in northwestern Colorado, USA, 2013–2014. Asterisks indicate significant differences.

Parameter	Chained ($\bar{x}$)	SE	Reference ($\bar{x}$)	SE
Shrub cover	0.27	0.03	0.15	0.03***
Grass cover	0.11	0.01	0.09	0.02
Proportion of bare ground	0.36	0.03	0.34	0.07
Forest cover	0.03	0.01	0.28	0.06***
Cover of height class 0–0.5 m	0.13	0.01	0.09	0.02
Cover of height class 0.6–1 m	0.10	0.01	0.03	0.01***
Cover of height class 1.1–2 m	0.10	0.01	0.05	0.01**
Cover of height class 2.1–5 m	0.04	0.01	0.18	0.04**
Cover of height class 5.1–10 m	0.00	0.00	0.10	0.02***
Cover of height class >10 m	0.00	0.00	0.00	0.00
Diameter at breast height (cm)	0.07	0.02	0.79	0.16***
Tree height (m)	1.02	0.24	3.12	0.62***
Snag height (m)	0.00	0.00	1.12	0.22**
No. logs	3.24	0.67	2.20	0.44
No. snags above 1.37 m	0.00	0.00	0.36	0.07
No. shrub species	2.80	0.28	2.28	0.46

**Significant at $P < 0.005$.
***Significant at $P < 0.001$.

71 ± 12.59 for chained and reference sites, respectively. Mean species richness/site differed significantly between chained (11 ± 3.61) and reference sites (15.48 ± 3.37; $F_{1, 48} = 20.61$, $P \leq 0.001$).

The rank abundance distributions (Fig. 2) indicated that historically chained sites were dominated by fewer species and most of those species were shrubland-obligate species. Sixty-five percent of the detections in chained sites were represented by 5 species: blue-gray gnatcatcher (*Polioptila caerulea*), mountain bluebird (*Sialia currucoides*), Brewer's sparrow, and chipping sparrow (*Spizella passerina*). In contrast, the relative proportion of bird species in reference sites was somewhat more even, and these sites were characterized by more woodland birds. The 5 most dominant species in reference sites were spotted towhee (*Pipilo maculatus*), black-throated gray warbler (*Setophaga nigrescens*), *Empidonax* flycatcher (*Empidonax* spp.), plumbeous vireo (*Vireo plumbeus*), and blue-gray gnatcatcher. These species combined represented 35% of the total detections in reference sites (Fig. 1).

DISCUSSION

Our findings demonstrate marked differences in bird community composition and species densities between historically chained sites and undisturbed woodlands. Contrary to our hypothesis, we found higher species richness and a more even community composition in undisturbed woodlands. These results are consistent with studies conducted in the first few years after tree removal at the same sites (O'Meara et al. 1981, Sedgwick and Ryder 1986). In the first 2 years following chaining, O'Meara et al. (1981) reported disturbed areas were dominated by shrubland-obligate species (e.g., Brewer's sparrows, green-tailed towhees [*Pipilo chlorurus*]), and woodland-obligate species (e.g., mountain chickadees [*Poecile gambeli*], white-breasted nuthatches [*Sitta carolinensis*], black-throated gray warblers) were most common in reference sites. Our rank-abundance

distributions demonstrate similar differences in community composition 40 years after disturbance. Specifically, historically chained sites were dominated by a smaller number of species and these dominant species were shrubland-obligate birds, whereas woodland-obligate birds dominated undisturbed woodlands.

Species habitat use was differentially affected by disturbance based on known habitat preferences. Similar to studies conducted shortly after chaining (O'Meara et al. 1981, Sedgwick and Ryder 1986), we found tree removal was negatively related to densities of white-breasted nuthatch, mountain chickadee, juniper titmouse (*Baeolophus ridgwayi*), and violet-green swallow. In 1976, after initial chaining and the 4 subsequent years following, mourning dove (*Zenaida macroura*), *Empidonax* flycatcher, mountain chickadee, plumbeous vireo, and black-throated gray warbler had higher densities in the undisturbed woodlands (Sedgwick and Ryder 1986), whereas, green-tailed towhee and Brewer's sparrow had higher densities in chained sites. We were unable to precisely relocate study sites or obtain original data from the O'Meara et al. (1981) and Sedgwick and Ryder (1986) studies. Therefore, we were unable to recreate or combine their data quantitatively. However, our analysis demonstrated similar results >40 years later, with the exception of *Empidonax* flycatcher and black-throated gray warbler. *Empidonax* flycatchers are air sallying birds and require plant structural diversity for pursuing insects from perches (Sabo and Holmes 1983). Although taller trees and snags were initially removed during tree removal activities, some structural diversity had recovered since the initial disturbance, possibly to a state of structural diversity beneficial for air sallying birds. Black-throated gray warblers are woodland-obligate birds and used nest sites within the canopy of trees (Guzy and Lowther 2012). However, in pinyon–juniper systems, black-throated gray warblers forage on big sagebrush up to 23% of the time (Guzy and Lowther 2012). Although
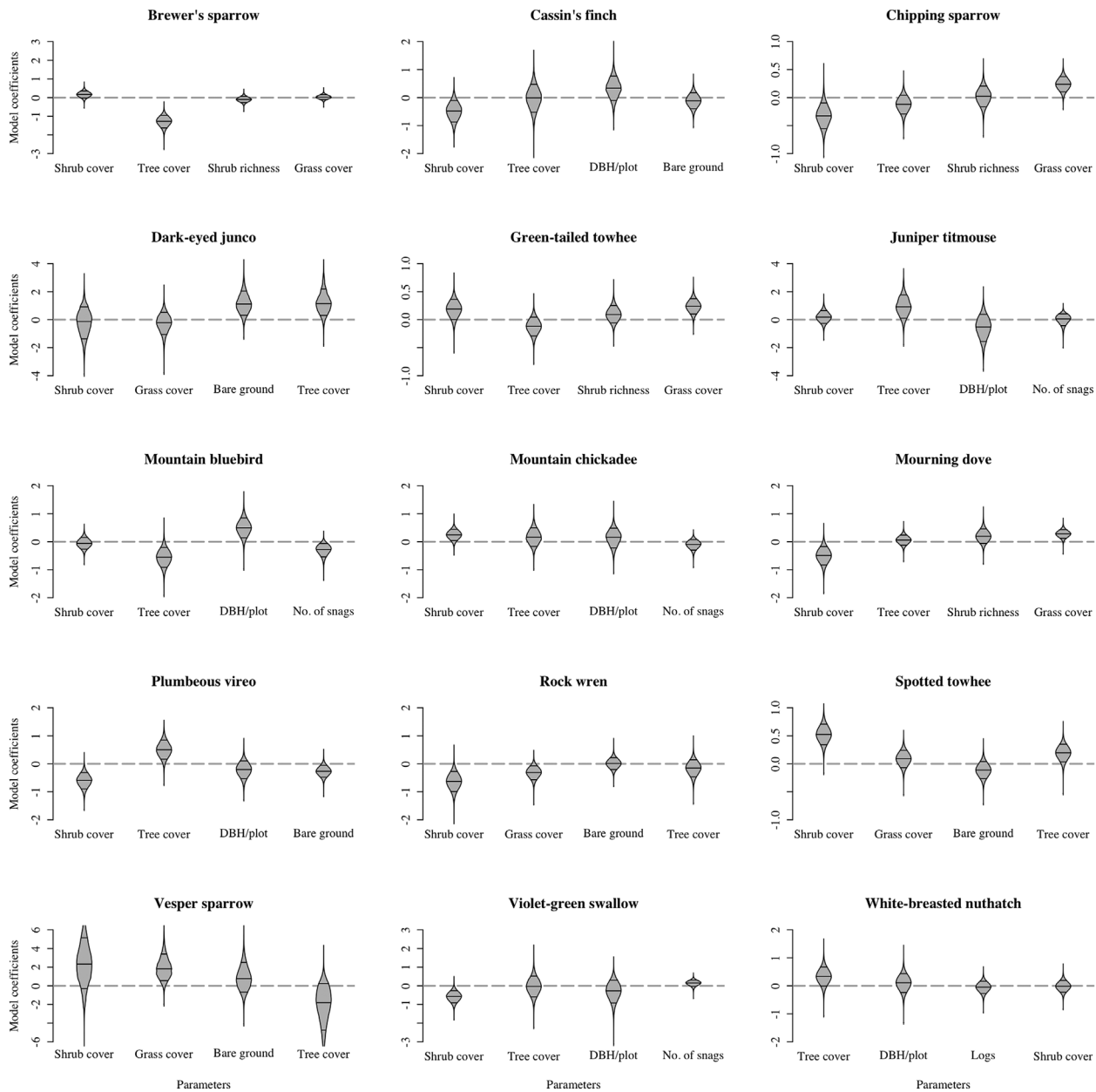
Figure 1. Posterior distributions of vegetation covariates for bird species that experienced a long-term response to tree removal in the Piceance Basin, Colorado, USA, 2013–2014. Dashed line indicates coefficient value of 0. Solid black lines within the posterior distributions indicate the median value and the 90% credible limits.

we did not measure foraging behavior, big sagebrush was the dominate shrub species in historically chained sites. This behavior may explain why black-throated gray warblers used chained sites.

Higher densities of some cavity nesters (e.g., juniper titmouse), tree nesters (e.g., plumbeous vireo), and bark gleaners (e.g., white-breasted nuthatch) were positively associated with tree cover and trees with larger DBH (Fig. 1). These results are consistent with previous studies demonstrating that tree cover and larger DBH trees are important habitat variables for these nesting and foraging guilds (Airola and Barrett 1985, Li and Martin 1991). Tree cover in disturbed sites was extremely low ($\bar{x}$ cover of vegetation 5.1–10 m and >10 m were both 0%, and $\bar{x}$ cover of vegetation

2.1–5 m was 4%; Table 3), and the trees that had regenerated since disturbance were relatively small compared to reference sites ($\bar{x}$ tree height = 1.02 m and $\bar{x}$ DBH/100 m^2 = 0.07 cm; Table 3). Because pinyon and juniper are slow-growing tree species (Tausch and Tueller 1977), it may take decades or even centuries for these trees to recover to a state preferred by cavity nesters, tree nesters, bark gleaners, and canopy gleaners.

Shrubland-obligate birds (e.g., green-tailed towhee, Brewer's sparrow) all had a positive relationship with chaining, but their association with individual vegetative characteristics differed. Higher densities of green-tailed towhee were associated with increased shrub and grass cover, which is unsurprising because green-tailed towhees
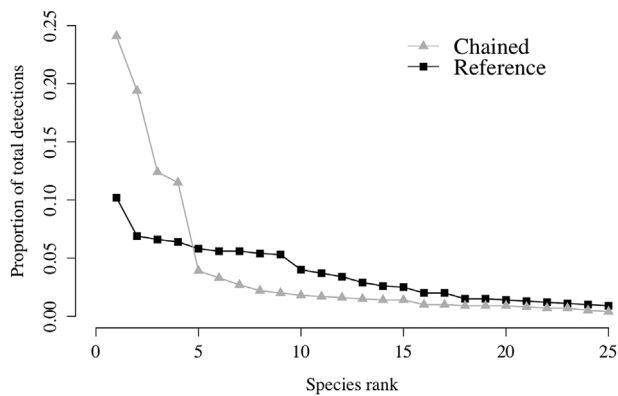
Figure 2. Rank abundance curves for bird species in historically chained sites and undisturbed reference sites in the Piceance Basin, Colorado, USA, 2013–2014.

tend to nest and forage amid dense shrubs and scattered grasses (Dobbs et al. 2012). Brewer's sparrow density had a positive relationship with increased shrub cover, but density declined with increased shrub species richness. Brewer's sparrows are closely associated with large open habitats dominated by big sagebrush (Wiens and Rotenberry 1981), and our results indicate that chaining had a stronger positive relationship with shrub cover than shrub species richness (Table 3). The spatial extent of big sagebrush in historically chained areas may have a stronger influence on Brewer's sparrow's habitat selection than local shrub species richness or composition (Petersen and Best 1987).

The vegetation parameters that were associated with densities of ground-nesting birds were complex. Proportion of bare ground showed a positive relationship with dark-eyed junco (*Junco hyemalis*) densities yet had no effect on rock wren (*Salpinctes obsoletus*) or vesper sparrow (*Pooecetes gramineus*) densities. Further, dark-eyed junco and vesper sparrow showed a negative long-term relationship with tree removal, yet rock wren showed a positive long-term relationship with tree removal. In general, older pinyon–juniper woodlands have scarce understory vegetation (Tausch and Tueller 1977), which tends to increase the proportion of bare ground. In our study area, however, both references and chained sites had similar proportions of bare ground (Table 3). Areas where pinyon–juniper woodlands have been reduced or removed tend to have more perennial and annual grass and forb cover (Aro 1971), which could be used as cover from predation and nesting material for ground-nesting birds (Martin and Roper 1988). However, rock wren was negatively correlated, vesper sparrow positively correlated, and dark-eyed junco showed no correlation to increased grass cover. Measuring parameters at smaller, species-specific scales (e.g., nest site selection) could further explain patterns in ground-nesting bird densities.

Our results, combined with those of previous studies (O'Meara et al. 1981, Sedgwick and Ryder 1986) indicate a persistent state change in these human-disturbed landscapes from a woodland bird community to one dominated by a shrubland bird community without any evidence that the bird community is returning to its original condition 4 decades after disturbance. Consistent with our findings, long-term state changes in vegetative communities after pinyon–juniper removal have been observed in the Colorado Plateau (Redmond et al. 2013). However, succession in pinyon–juniper ecosystems after disturbance can sometimes take decades (Tausch and Tueller 1977, Schott and Pieper 1987). Although Tausch and Tueller (1977) and Schott and Pieper (1987) are careful to state that not all pinyon–juniper woodlands follow the same model of succession, they do emphasize that tree regrowth can take up to 50–60 years after mechanical disturbances. Thus, recovery from a mechanical disturbance in a slow recovering system may not be evident within 40–50 years. However, historically chained sites in our study area averaged only 4% cover of pinyon–juniper over 2 m tall, contained no trees over 5 m tall, and were dominated by shrub species, indicating that recovery to a woodland system even after 40 years may have only just begun, or alternatively, this community may continue to persist in an alternate shrub-dominated state. Our study reinforces the value of multi-decadal ecological monitoring (Lindenmayer and Likens 2009), and suggests careful consideration should be given to the long-term consequences of deliberate habitat disturbance for natural communities.

Our response metrics were limited to bird community composition, richness, and density. Future research should evaluate the long-term effects of disturbance on other demographic parameters of avian populations to more fully understand bird population dynamics in a slow recovering system. Birds may also be affected by mechanisms other than vegetation structure. Therefore, future research should evaluate whether tree removal causes long-term changes in other important ecological and environmental variables including predator–prey interactions and food composition (e.g., insect trophic structures). To our knowledge, there are no studies that have investigated the effect of deliberate and large-scale tree removal on bird communities in a chronological time series from initial disturbance decades ago until present day. Chaining as a means of tree reduction was used less frequently after the 1970s in pinyon–juniper ecosystems (Romme et al. 2009, 2013), making it difficult to test ecological theory (e.g., intermediate disturbance hypothesis) or measure changes in bird and plant communities using a space for time substitution for long-term data. The broad geographical distribution of pinyon–juniper woodlands supports a wide variety of vegetation types and bird communities (Balda and Masters 1980). These systems can also vary by soil type, precipitation, and elevation gradients, which could affect rates and patterns of regeneration after disturbance (Schott and Pieper 1987, Romme et al. 2009, Tausch et al. 2009). Therefore, we urge caution in generalizing our results to other woodland ecosystems, and encourage monitoring the effects of disturbance on diverse taxa wherever tree removal is employed as a form of habitat improvement or mitigation.

MANAGEMENT IMPLICATIONS

We suggest that future management actions that result in large-scale tree removal should explicitly measure intended and unintended long-term effects on birds and other taxonomic groups. The relationships we identified between bird densities and specific habitat characteristics could be factored into management and mitigation decisions to account for the long-term effects of tree removal on avian communities. For example, we found mean DBH/100 m^2 (i.e., a proxy for forest age) had the most significant positive correlation with habitat use of bark-gleaning birds. Therefore, leaving larger older trees within the treated areas would maintain habitat for bark-gleaning birds. Also, tree cover had a significant positive relationship with habitat use of upper canopy gleaners and tree nesters; therefore, selectively leaving patches of intact tree cover could mitigate the negative effects of tree removal on these groups. Our results can be used to adaptively guide management decisions, taking into account long-term costs and benefits to species of conservation value.

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