RESEARCH ARTICLE

Thinning alters avian occupancy in piñon–juniper woodlands

Patrick A. Magee,[1]*,[ORCID] Jonathan D. Coop,[2] and Jacob S. Ivan[3]

[1] Department of Natural and Environmental Sciences, Western Colorado University, Gunnison, Colorado, USA
[2] Center for Environment and Sustainability, Western Colorado University, Gunnison, Colorado, USA
[3] Colorado Parks and Wildlife, Fort Collins, Colorado, USA
* Corresponding author: pmagee@western.edu

ABSTRACT
Natural resource managers are increasingly applying tree reduction treatments to piñon–juniper woodlands to meet a range of ecological, social, and economic goals. However, treatment effects on woodland-obligate bird species are not well understood. We measured multiscale avian occupancy on 29 paired (control/treatment) sites in piñon–juniper woodlands in central Colorado, USA. We conducted point counts at 232 stations, 3 times each season in 2014 and 2015. We used hierarchical multiscale modeling to obtain unbiased estimates of landscape and local occupancy (i.e. probability of use) in treated and untreated sites for 31 species. Treatments reduced the occupancy of conifer obligates, including Mountain Chickadee (*Poecile gambeli*), Clark's Nutcracker (*Nucifraga columbiana*), and White-breasted Nuthatch (*Sitta carolinensis*), and increased occupancy of Lark Sparrow (*Chondestes grammacus*) and Mountain Bluebird (*Sialia currucoides*). Occupancy of Virginia's Warbler (*Oreothlypis virginiae*) and Gray Flycatcher (*Empidonax wrightii*), two piñon–juniper specialists, decreased at the landscape scale in treated sites, and Pinyon Jay (*Gymnorhinus cyanocephalus*) occupancy decreased at the local scale. Tree reduction treatments in piñon–juniper woodlands have the potential to reduce habitat quality for a suite of bird species of conservation concern. We suggest that treatments designed to retain higher tree density and basal area will benefit conifer-obligate and piñon–juniper specialist bird species.

Keywords: avian occupancy, mastication, piñon–juniper, pinyon pine, treatments, woodland birds

El raleo altera la ocupación de aves en bosques de piñón y enebro

RESUMEN
Los gestores de los recursos naturales aplican cada vez con mayor frecuencia tratamientos de raleo de árboles a los bosques de piñón y enebro para alcanzar una serie de objetivos ecológicos, sociales y económicos. Sin embargo, no se comprenden claramente los efectos de los tratamientos para las especies de aves que habitan de forma obligada en los bosques. Medimos la ocupación de las aves a múltiples escalas en 29 sitios pareados (control/tratamiento) en bosques de piñón y enebro en el centro de Colorado, EEUU. Realizamos conteos en puntos en 232 lugares, tres veces en cada estación en 2014 y 2015. Usamos modelos jerárquicos a escalas múltiples para obtener estimaciones no sesgadas de ocupación (i.e. probabilidad de uso) a escala de paisaje y local en sitios tratados y no tratados para 31 especies. Los tratamientos redujeron la ocupación de las especies que habitan en forma obligada los bosques de coníferas, incluyendo a *Poecile gambeli*, *Nucifraga columbiana* y *Sitta carolinensis*; y aumentaron la ocupación de *Chondestes grammacus* y *Sialia currucoides*. La ocupación de *Oreothlypis virginiae* y *Empidonax wrightii*, dos especialistas de los bosques de piñón y enebro, disminuyó a la escala de paisaje en los sitios tratados, y la ocupación de *Gymnorhinus cyanocephalus* disminuyó a escala local. Tres tratamientos de raleo de los bosques de piñón y enebro tienen el potencial de reducir la calidad de hábitat para un grupo de especies de aves de interés para la conservación. Sugerimos que los tratamientos diseñados para retener mayor diversidad de árboles y área basal beneficiarán a las especies de aves que habitan de forma obligada los bosques de coníferas y a las especialistas de piñón y enebro.

Palabras clave: aves de bosque, masticación, ocupación de aves, pino piñonero, piñón–enebro, tratamientos

INTRODUCTION

Piñon–juniper woodlands represent a diverse and ecologically important suite of North American forests, but one in which land managers may face particularly complex trade-offs and uncertainties (Romme et al. 2009). These woodlands are the third-largest vegetation type in the U.S.

(West 1984, Laylock 1999), encompassing 40 million ha of western North America (Tausch and Hood 2007, Romme et al. 2009). The piñon–juniper vegetation type varies considerably in taxonomic composition (comprised of multiple species of *Juniperus* and *Pinus* subsection *Cembroides*), structure, and disturbance regimes (Jacobs 2008, Romme et al. 2009). Piñon–juniper woodlands have experienced

large-scale regional expansions throughout much of the 20th century (Miller and Tausch 2001, Romme et al. 2009), but also abundant human efforts to reduce their extent. Drivers of expansion may include reduced herbaceous fuels and altered fire regimes associated with livestock grazing (Blackburn and Tueller 1970, Miller and Rose 1999, Miller and Tausch 2001, Tausch and Hood 2007), favorable recent climate variation (Blackburn and Tueller 1970, Miller and Rose 1999, Tausch and Hood 2007), woodland expansion and in-filling associated with recovery from older disturbance (Ko et al. 2011), and elevated atmospheric carbon dioxide (Soulé et al. 2004). Because these woodlands lacked commercial timber value (Johnson 1962), beginning in the 1940s, managers conducted large-scale deforestation primarily to provide forage for livestock (Box et al. 1966, Gottfried and Severson 1994). Piñon–juniper removal over large areas (e.g., chaining, cabling, bulldozing, burning, and use of chemical treatments) persisted until the 1970s when emerging concerns over multi-use management led to the implementation of smaller-scale treatments using different techniques (Aro 1971, Gottfried and Severson 1994).

Recently, tree removal in piñon–juniper woodlands has regained momentum and is increasingly applied in many western states to meet a variety of habitat management and fire mitigation objectives. To benefit at-risk sagebrush-obligate wildlife (Baruch-Mordo et al. 2013, Nelson and McAvoy 2013), managers frequently employ mastication, in which piñon and juniper trees are shredded and ground into mulch using heavy machinery (Miller et al. 2008, Frey et al. 2013; Knick et al. 2013, 2014). In the Great Basin, many projects employ hand-cutting with the intention of removing most trees (except old-growth juniper) while maintaining sagebrush cover (Holmes et al. 2017). Since the onset of the Sage Grouse Initiative (www.sagegrouseinitiative.com) in 2010, western juniper removal has increased by 1400% (Holmes et al. 2017). Managers have also thinned or eliminated large areas of piñon–juniper in recent years for fire hazard reduction as well as a variety of other wildlife habitat objectives (Brockway et al. 2002, Schwilk et al. 2009).

Tree removal treatments in piñon–juniper woodlands may have unintended impacts on a wide range of woodland-dependent biota, especially obligate birds already in decline. The piñon–juniper forest type provides nesting habitat for more breeding bird species than any other terrestrial ecosystem in the western U.S. (Balda and Masters 1980), including several at-risk woodland specialists experiencing long-term population declines (Sauer et al. 2017a, 2017b). Piñon–juniper bird communities differ substantially from those of other ecosystems and contribute significantly to landscape-scale avian biodiversity (Paulin et al. 1999, Francis et al. 2011). Among the obligate or near-obligate piñon–juniper birds, the Pinyon Jay (*Gymnorhinus cyanocephalus*) has declined 3.6% annually

in western forests since 1966 (Sauer et al. 2017a, 2017b). The Black-throated Gray Warbler (*Setophaga nigrescens*; −1.3%) and Virginia's Warbler (*Oreothlypis virginiae*; −1.4%) have also declined over the last 50 yr (Sauer et al. 2017a, 2017b). Piñon–juniper specialists are listed as species of high conservation concern by Partners in Flight (Colorado Partners in Flight 2000, Gillihan 2006), the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2008), and the Intermountain West Joint Venture (Intermountain West Joint Venture 2013).

For bird species dependent on woodland canopy, tree removal treatments reduce habitat, with negative consequences for population persistence. In northwestern Colorado, after chaining treatments, abundance declined for 11 of 16 species studied, with greatest impacts on bark and foliage gleaners, as well as cavity nesters (O'Meara et al. 1981, Sedgwick and Ryder 1986). In the same area, woodland species such as the Black-throated Gray Warbler, Plumbeous Vireo (*Vireo plumbeus*), and Hermit Thrush (*Catharus guttatus*) declined in response to reduced canopy height and cover and lowered stand density (Sedgwick 1987). While forest bird species generally decline after thinning treatments (Bombaci and Pejchar 2016), edge and open habitat or shrubland species may increase, possibly balancing species richness across the landscape (Crow and van Riper 2010). A recent study showed positive responses by Brewer's Sparrow (*Spizella breweri*), Green-tailed Towhee (*Pipilo chlorurus*), and Vesper Sparrow (*Pooecetes gramineus*) to piñon–juniper removal by hand-thinning in sagebrush (Holmes et al. 2017).

We assessed the effects of piñon–juniper partial thinning on avian occupancy at both local and landscape scales. Partial thinning represents a slightly more nuanced tree reduction approach than clearcuts, but it is unclear whether this evolution in management manifests into positive consequences for birds. Due to the ecological breadth of the piñon–juniper bird community, we assessed avian responses to treatments in reference to 7 habitat associations: mature conifer obligates, open-conifer species, piñon–juniper specialists, piñon–juniper/shrubland species, forest-edge species, forest generalists, and generalists.

METHODS

Study Area

Study sites were located along the Arkansas River corridor between Salida and Cañon City, Colorado (Figure 1), and centered in Coaldale, Colorado (38.3465°N, 105.7648°W; WGS84 datum). Within this study area, the Bureau of Land Management (BLM) Royal Gorge Field Office (RGFO) completed ~10,000 ha of tree removal projects from 1998 to 2014 (M. Rustand personal communication). While the river corridor consists of a patchwork of public and private
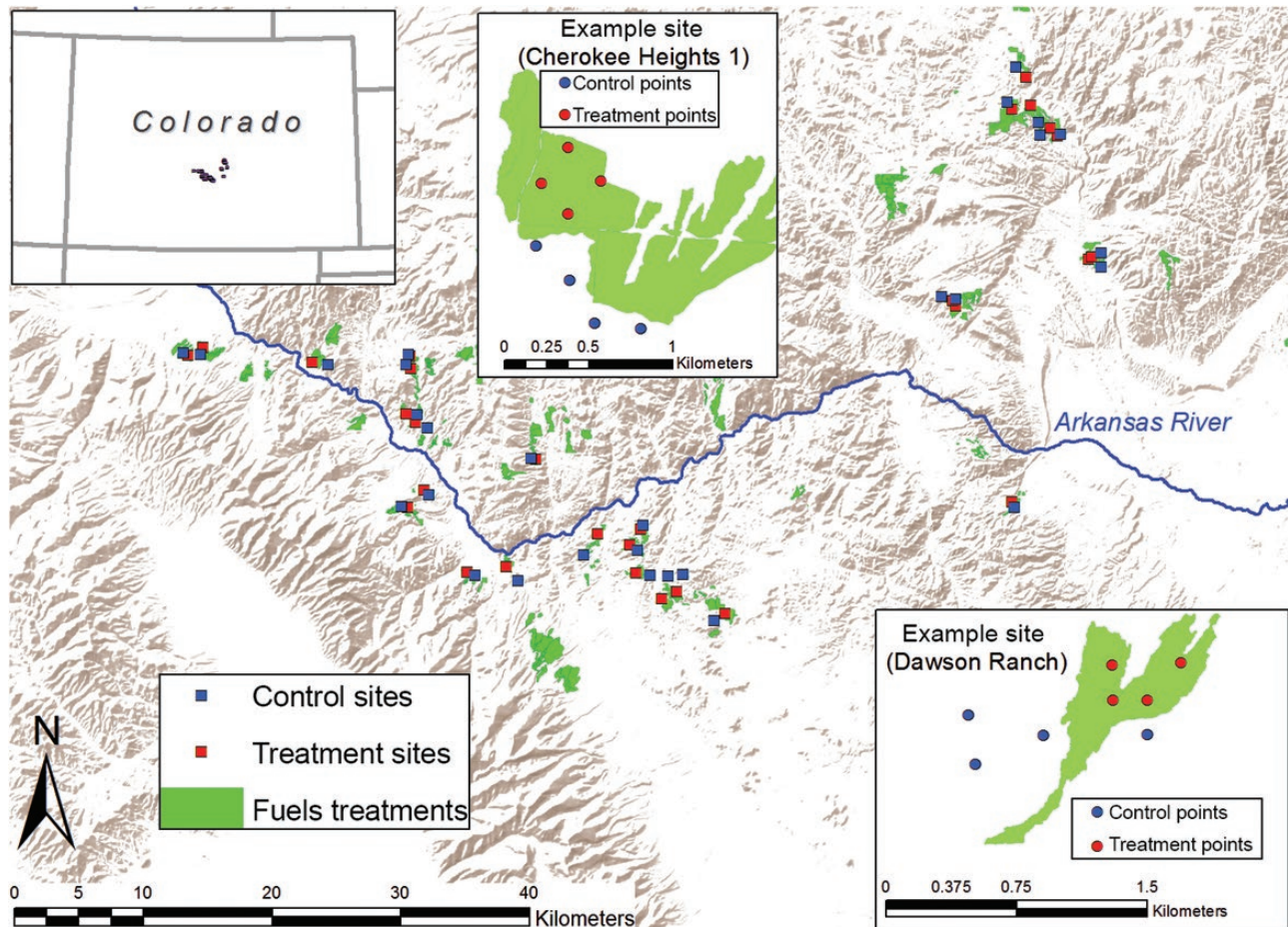
FIGURE 1. Sampling sites consisted of 29 mechanical thinning treatments and 29 paired controls in piñon–juniper woodlands in central Colorado.

lands, the BLM-RGFO manages much of the surrounding landscape for multiple uses including livestock grazing, recreation, and fuelwood gathering. Exurban development occurs near some study sites; others receive little human visitation.

The piñon–juniper landscape within the study area varies in topography, climate, and composition. The Arkansas River flows from west to east along a 545-m elevation gradient from Salida (2,160 m) to Cañon City (1,615 m.). Climate varies along this gradient with colder, drier conditions in Salida (mean annual temperature = 7.7°C, mean annual precipitation = 27.6 cm, 1897–2012) and warmer, wetter conditions toward Cañon City (mean annual temperature = 12.2°C, mean annual precipitation = 32.1 cm, 1931–2016; Colorado Climate Center; http://ccc.atmos.colostate.edu/cgi-bin/monthlydata.pl). Elevation of study plots ranged from 1,830 to 2,550 m. Below 2,500 m, piñon–juniper woodlands dominate the landscape; at higher elevations they generally intergrade with ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelii*). The climate gradient within our study area corresponds with a gradient in piñon–juniper woodland composition and structure, shifting from persistent woodland-type systems dominated by two-needle piñon (*Pinus edulis*) and intermixed with Rocky Mountain juniper (*Juniperus scopulorum*) at higher elevations in the cooler and drier western portions of the study area, toward more savanna-like stands dominated by oneseed juniper (*J. monosperma*) in the east.

Study Design and Data Collection

Natural resource managers designed and implemented piñon–juniper thinning treatments to mitigate fire risk and alter habitat prior to, and independent of, this post hoc investigation of treatment effects on bird communities. Our primary aim was to investigate general treatment effects, but we secondarily assessed 2 treatment types: mastication (n = 24) and hand-thinning (n = 5). Mastication, performed by a hydro-ax with a rotary motor or Fecon head, mulched trees. In hand-thinning, field crews used chainsaws and either lopped and scattered conifer trunks and branches over the treated area or piled branches to be burned in winter.

Managers nonrandomly implemented treatments broadly across an ecological range of sites throughout the study area (i.e. some at upper elevations intermixed with ponderosa pine, others within dense piñon–juniper stands, others adjacent to open meadows). Thinning treatments resulted in variable forest structures from evenly spaced residual trees on some sites to retention of tree clumps on other sites (Figure 2).

We monitored 29 treatment and 29 paired control sites from mid-May to early July 2014 and 2015. Treatment sites were defined as areas where managers removed piñon–juniper vegetation; these sites varied in shape, age (2003 to 2014), and size (18–77 ha). Control sites consisted of the immediate landscape surrounding treatments that was not masticated or hand-thinned. Control sites also varied in shape and size (20–117 ha), depending on topography and surrounding vegetation communities that often created natural boundaries for the controls (Figure 2). The close proximity of treatment and control sites reduced variation imposed by site factors. Steep terrain limits mastication machinery (slope constrained hand-thinned sites to a lesser degree), thus some of our controls occurred on steeper sites adjacent to flatter mastication treatments. However, slope did not strongly influence vegetation structure or composition independent of treatment effects within the study area (Coop et al. 2017). Other topographic variables did not differ between treatment and control sites (Coop et al. 2017). Control sites occupied an area large enough to contain 4 randomly selected, independent sampling stations. Neighboring vegetation communities bounded control sites, largely driven by topography, elevation, and soils. At 23 of the 29 control sites, sampling points were clustered in an adjacent area separate from the treatments. However, to ensure control samples represented the correct habitat type, at 6 sites control points were located in untreated habitat on more than one side of treatment units (e.g., Figure 1, Dawson Ranch). Some evidence of logged stumps and fire scars suggested that control sites

may have been disturbed historically, but probably not since the middle of the previous century.

We used a hierarchical multi-scale method for sampling and estimating avian occupancy (Nichols et al. 2008). Of all the fuels treatments completed and mapped by BLM (Figure 1), we selected 29 treatments of sufficient size to sample. In GIS, each of the 29 treatment monitoring sites was paired with a control, over which we placed a fishnet of 4-ha squares (to define 200 m × 200 m sampling spaces). We then randomly selected 4 of these within which we located a point count station. All point count stations were separated by a minimum of 250 m, and most had wider separation, especially between controls and treatments. We ground-truthed each site to insure the habitat was appropriate (treated piñon–juniper in treatments and untreated piñon–juniper in controls) and that point count stations were >100 m from the edge of the treatment or control. Thus, we were able to evaluate variation in occupancy among sites (landscape scale) as well as among points (point count stations) within sites (local scale; Nichols et al. 2008).

Avian sampling. We conducted 10-min point counts at each of the 232 point count stations during each of 3 sessions (May 15–31, June 1–15, and June 16 to July 2) in 2014 and 2015. With few exceptions, we surveyed birds within a 5-hr window (0500–1000 hr) each morning. During sampling, we identified and recorded every bird that was seen or heard. We recorded wind speed, sky conditions, and air temperature at the beginning of each point count from the point count station. Sampling was conducted under standardized weather protocols (Martin et al. 1997) restricted to precipitation-free mornings (2% of points in fog or light drizzle) on relatively calm days (wind speed <13 km hr^{-1} for 99% of samples, <8 km hr^{-1} for 92% of points). A total of 6 field personnel, 4 individuals each year (2 of these conducted surveys during both years), conducted point counts. We trained and tested field technicians in bird identification by sight and sound using a variety of methods. Observers rotated among sites

FIGURE 2. Examples of mastication, hand-thinned, and control sites.

between sampling sessions, and they all surveyed during the same time frame daily.

Occupancy analysis. We discarded bird detections >100 m from the sampling point. Of the total bird detections (n = 11,798), 8.9% were discarded; 41% of these were from surveys in the controls and 59% from treatment surveys. We estimated multi-scale occupancy (MacKenzie et al. 2006) using a modified hierarchical approach (Nichols et al. 2008) to examine variation in avian use of piñon–juniper sites as a function of tree thinning treatments (Hagen et al. 2016). The analysis includes estimation of 3 parameters: (1) Ψ, the probability that a species occurs within a site ("landscape occupancy"); (2) θ, the probability that a species occurs at a point (point count station), given that the site is occupied ("local occupancy"); and (3) p, the probability that a species is detected during a sampling occasion given that it occurs at the point and the site (MacKenzie et al. 2006). We assumed that (1) there was no un-modeled heterogeneity in detection and occupancy, (2) each point count station was closed to changes in occupancy over the survey season (e.g., May–June; note that we expected and modeled potential changes in detection over this same period), (3) detections of a species at each point count station were independent, and (4) the target species were never falsely detected (Nichols et al. 2008, Pavlacky et al. 2012). We acknowledge that for some species, the closure assumption may have been violated as the study period extended over 1.5 months, therefore what we estimated was the probability of use at a given site over the course of the sampling season, rather than strictly occupancy (Steenweg et al. 2018). We grouped the 31 bird species into 7 habitat associations: (1) mature conifer obligates, (2) open-conifer species, (3) piñon–juniper specialists, (4) piñon–juniper woodland/shrubland species, (5) forest generalists, (6) forest-edge species, and (7) generalists. We categorized birds into habitat groupings based on Birds of North America species accounts (https://birdsna.org/Species-Account/bna/home) and the Colorado Breeding Bird Atlas (Wickersham 2016).

We modeled avian occupancy using program Mark 8.0 (White and Burnham 1999). We only analyzed encounter histories for bird species with >100 total observations to allow for robust statistical analyses (i.e. higher likelihood of obtaining meaningful parameter estimates with tight confidence intervals). We arrived at this number via attempting to fit models to all species and realizing that 100 observations was the approximate cut point at which we began to note problems with model-fitting and parameter estimation (Welsh et al. 2013).

We treated year (2014 or 2015) as a group effect so that we could evaluate whether occupancy varied significantly between the 2 sampling seasons. This structure also allowed us to collapse all data (i.e. ignore the year effect) when it was unimportant, which was the case for all species

analyzed here, thus giving us more power to detect differences in treatment effects.

To efficiently assess avian response to treatments, we constructed models for each of the 31 species independently in 2-step fashion (Pavlacky and Sparks 2016). First, for each species we identified a best-fitting structure for modeling detection by considering several alternatives while holding other model parameters in their most general form. Second, we fixed the best-fitting structure for detection, then considered alternative structures for other model parameters to assess evidence for a general treatment effect on landscape scale (Ψ) or local scale (θ) occupancy, or both.

Detection probability. Following the approaches of Pavlacky et al. (2012), we binned observations for each of the 3 visits to a site into five 2-min intervals, which gave us flexibility in modeling detection as a function of visits only, minute interval only, combinations of both, and combinations in conjunction with visit- or interval-specific covariates. We chose to consider 8 possible structures for detection: a null model and all combinations of (1) the effects of observer (we grouped the 6 observers into 3 groups of 2 based on their experience level), (2) survey period (late May, early June, late June), and (3) treatment (control vs. treatment). Exploratory analyses with weather variables indicated that they did not significantly affect detection probability, so we did not consider these in further model development. We identified the best fitting structure based on the sample size-corrected Akaike Information Criterion (AIC$_c$; Burnham and Anderson 2002). For each species, we model-averaged detection probabilities to obtain baseline real estimates during visit one to represent the intercept for the species' top model. Beta estimates and 95% confidence intervals for the relevant covariates in the top model indicated how those covariates altered detection from the baseline (intercept).

Effect of treatment on landscape and local occupancy. In the second step, we developed 7 models for each species to evaluate potential impacts of treatments on landscape (Ψ) and local scale (θ) occupancy (Table 1). Psi or θ or both were specified to allow for a generic treatment effect (i.e. hand-thinning and mastication treatments were collapsed to a single 'treatment'), an effect where hand-thinning was allowed to be different from mastication, and a null structure in which there was no difference between control and treatment sites (Table 1). In all cases, probability of detection (p) was fixed to the best fitting structure for each species. We judged relative fit of models using AIC$_c$ as before and computed model-averaged values for Ψ and θ by treatment based on the entire model set. We assessed generic treatment effects for each species (26 of 31 for Ψ and 23 of 31 for θ) by noting the magnitude and direction of coefficients for treatment, whether or not 95% CIs for these overlapped zero, and by considering ΔAIC$_c$

TABLE 1. Treatment effects models developed for multi-scale occupancy estimation of 31 bird species in piñon–juniper woodlands in central Colorado.

Model	Model structure
1: Null	Ψ (.) θ (.) p (top model)
2: Ψ treatment	Ψ (treatment) θ (.) p (top model)
3: θ treatment	Ψ (.) θ (treatment) p (top model)
4: Ψ and θ treatment	Ψ (treatment) θ (treatment) p (top model)
5: Ψ mastication vs. hand-thin	Ψ (mast + hand) θ (.) p (top model)
6: θ mastication vs. hand-thin	Ψ (.) θ (mast + hand) p (top model)
7: Ψ and θ mastication vs. hand-thin	Ψ (mast + hand) θ (mast + hand) p (top model)

of models that included treatment effects (Burnham and Anderson 2002).

RESULTS

Bird Community
We observed 77 bird species across all sites and seasons (Appendix Table 5) representing 9 avian orders with 78% of the bird assemblage from Passeriformes (60 species). We observed Spotted Towhee (*Pipilo maculatus*) more than any other species (n = 2,595), followed by Black-throated Gray Warbler (n = 1,022), Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*; n = 834), Chipping Sparrow (*Spizella passerina*; n = 806), Broad-tailed Hummingbird (*Selasphorus platycerus*; n = 731), Black-headed Grosbeak (*Pheucticus melanocephalus*; n = 703), Plumbeous Vireo (n = 682), Gray Flycatcher (*Empidonax wrightii*; n = 646), and Blue-gray Gnatcatcher (*Polioptila caerulea*; n = 545; Appendix Table 5). Habitat groupings included 2 mature conifer species, 6 open conifer species, 5 piñon–juniper specialists, 7 piñon–juniper/shrubland inhabitants, 5 forest generalist species, 3 forest-edge species, and 3 generalists (Table 2). Of the 77 species encountered, 46 were observed <100 times and several flyover species were not included in more detailed occupancy analyses (Appendix Table 5).

Detection Probability
The best-fitting structure for 20 of the 31 species included an observer effect (for 8 of these species, it was the only effect). For 18 of these 20 species, more experienced observers had higher detection probabilities than less experienced observers, with the exception of Gray Flycatcher and Bushtit (*Psaltriparus minimus*; Table 3). More experienced observers detected 14 of the 20 species at higher rates than intermediate-level observers. In addition to Gray Flycatcher and Bushtit, intermediate-level observers detected Common Raven (*Corvus corax*), Black-headed Grosbeak, Ash-throated Flycatcher (*Myiarchus cinerascens*), and Western Tanager (*Piranga ludociviana*) at higher rates than the most experienced observers.

Survey period appeared in 18 of the 31 species' top detection models. For 9 of these 18 species, detection was lower during mid-June compared to late May and for 13 species detection was lower in late June compared to late May. For 5 species, detection probability was higher after the first round of surveys in May including the highest detectability in early June for Virginia's Warbler and Western Bluebird (*Sialia mexicana*) and highest detection in late June for Common Nighthawk (*Chordeiles minor*), Western Wood-Pewee (*Contopus sordidulus*), and Ash-throated Flycatcher. Treatment appeared in 15 of the top detection models; 7 species (all conifer obligates plus Woodhouse's Scrub-Jay) had greater detection probabilities in controls and 7 species (all aligned more with open habitats) had greater detection probabilities in treatments. Baseline detection probabilities ranged from 0.02 for Common Nighthawk to 0.75 for Spotted Towhee.

Occupancy
Treatment effects. Three conifer-dependent species including Mountain Chickadee (mature conifer), Clark's Nutcracker (*Nucifraga columbiana*; open conifer woodlands), and White-breasted Nuthatch (*Sitta carolinensis*; forest generalist) showed negative treatment effects at the landscape scale (Tables 2 and 4, Figure 3). Virginia's Warbler and Gray Flycatcher (piñon–juniper specialists) likely had lower landscape-scale occupancy on treated sites (although for these species 95% CIs overlapped 0 slightly). In contrast, only 1 species, Mountain Bluebird (*Sialia currucoides*; edge species), responded positively to treatments at the landscape scale. Lark Sparrow (*Chondestes grammacus*; edge species) also had a strong positive generic treatment effect at the landscape scale, but the model had a ΔAIC_c > 7 and therefore was not reliable.

At the local scale, only one species had treatment effect confidence intervals that did not overlap 0 (Tables 2 and 4, Figure 4). Lark Sparrow occupied 2% of control sites at the local scale compared to 11% of hand-thinned and 62% of mastication sites, and therefore responded positively to treatments. Black-headed Grosbeak (generalist), Broad-tailed Hummingbird (forest generalist), Ash-throated Flycatcher (piñon–juniper shrublands), and Pinyon Jay (piñon–juniper specialist) tended to have lower local-scale occupancy in the treatments compared to control sites. American Robin (*Turdus migratorius*; forest generalist), Western Bluebird (open conifer woodlands), and Blue-gray Gnatcatcher (piñon–juniper shrublands) tended to show elevated local occupancy in treatments.

DISCUSSION

Treatment Effects on Avian Occupancy
Our results demonstrate that tree thinning treatments alter the occupancy of numerous bird species, and reduce the

TABLE 2. Model averaged landscape (Ψ) and local (θ) occupancy estimates for piñon–juniper birds in central Colorado during 2014–2015. Species are ordered by taxonomy within habitat grouping.

Species	Ψ			Θ		
	Control	Mastication	Hand-thin	Control	Mastication	Hand-thin
Piñon–juniper specialists						
Gray Flycatcher	0.96	0.89	0.89	0.90	0.87	0.86
Pinyon Jay	0.58	0.67	0.70	0.84	0.53	0.42
Juniper Titmouse	0.81	0.80	0.79	0.92	0.91	0.89
Virginia's Warbler	0.86	0.76	0.79	0.86	0.83	0.84
Black-throated Gray Warbler	0.99	0.89	0.95	0.93	0.93	0.93
Mature conifer						
Mountain Chickadee	0.90	0.74	0.82	0.87	0.89	0.89
Yellow-rumped Warbler	0.53	0.49	0.50	0.82	0.81	0.85
Open conifer						
Steller's Jay	0.53	0.40	0.89	0.97	0.83	0.97
Clark's Nutcracker	0.84	0.59	0.58	0.92	0.94	0.93
Western Bluebird	0.43	0.43	0.48	0.59	0.67	0.69
Townsend's Solitaire	0.61	0.56	0.59	0.97	0.92	0.91
Chipping Sparrow	0.99	0.99	0.99	0.87	0.88	0.87
Western Tanager	0.95	0.89	0.88	1.0	0.98	0.99
Piñon–juniper shrubland						
Common Nighthawk	0.47	0.99	0.97	0.40	0.42	0.42
Ash-throated Flycatcher	0.75	0.76	0.76	0.92	0.92	0.79
Plumbeous Vireo	0.94	0.96	0.96	0.95	0.95	0.95
Woodhouse's Scrub-Jay	0.96	0.98	0.96	0.99	0.99	0.69
Bushtit	0.89	0.87	0.87	0.75	0.64	0.62
Blue-gray Gnatcatcher	0.88	0.87	0.87	0.80	0.85	0.84
Spotted Towhee	0.99	0.97	0.98	0.97	0.98	0.98
Forest generalists						
Broad-tailed Hummingbird	0.96	0.95	0.94	0.89	0.85	0.84
Northern Flicker	0.61	0.48	0.94	0.96	0.95	0.97
Western Wood-Pewee	0.67	0.64	0.66	0.67	0.61	0.89
White-breasted Nuthatch	0.92	0.70	0.72	0.87	0.84	0.84
American Robin	0.72	0.74	0.86	0.66	0.83	0.85
Edge						
Mountain Bluebird	0.65	0.91	0.54	0.77	0.77	0.79
Lark Sparrow	0.84	0.82	0.84	0.02	0.62	0.11
Brown-headed Cowbird	0.65	0.64	0.65	0.88	0.95	0.95
Generalist						
Mourning Dove	0.92	0.90	0.90	1.0	1.0	1.0
Common Raven	0.70	0.71	0.69	0.95	0.97	0.98
Black-headed Grosbeak	0.93	0.93	0.94	0.88	0.81	0.75

occupancy of woodland specialists, in piñon–juniper habitats within our study area. Nineteen species had negative coefficients associated with landscape- and/or local-scale occupancy. These findings align with previous studies that document effects of piñon–juniper removal on bird communities both in the short and long term (O'Meara et al. 1981, Sedgwick and Ryder 1986, Crow and van Riper 2010, Bombaci et al. 2017, Gallo and Pejchar 2017). In an experimental study using 28 small treatment patches (1 ha) in the Piceance Basin of northwestern Colorado, woodland or open woodland bird habitat use declined in the first 2 yr following all treatment types (hydro-ax, roller chopping, and chaining) compared to control plots (Bombaci et al. 2017). In our study, 3 conifer obligates (Mountain Chickadee, White-breasted Nuthatch, and Clark's Nutcracker) exhibited strong negative effects of thinning and 5 other species exhibited lower

occupancy on treated sites at the landscape scale. Reduced occupancy by these species was linked to substantial reduction in canopy cover and tree density across our study sites (Coop et al. 2017). These findings (Figure 3) suggest that woodland reduction treatments have the potential to affect regional distributions and populations of forest birds (Pavlacky et al. 2012). For the 4 species that showed local-scale declines (Figure 4), thinning treatments may reduce the number of suitable territories in highly managed areas.

Treatments reduced habitat suitability for several forest-obligate species and, simultaneously, enhanced habitat for some generalists and non-forest species. The strongest positive responses to treatments came from Mountain Bluebird at the landscape scale and the Lark Sparrow at the local scale. Both species strongly associate with ecotones (Power and Lombardo 1996, Martin and Parrish 2000) and

TABLE 3. Top detection (p) structures associated with occupancy modeling for 31 bird species in treated and untreated piñon–juniper woodland landscapes in central Colorado during 2014–2015. Real estimates and betas of model parameters are given along with the 95% confidence interval. p = detection probability.* obs = observer (3 groups of 2 based on experience; KE included the least experienced observer, PJ included observers with intermediate experience, the intercept included the 2 most experienced bird counters), visit = survey period (the intercept = May 15–31, V2 = June 1–15, V3 = June 16 to July 2), trtm = treatment (the intercept represented control sites). The intercept is presented on the real scale to facilitate comparison between species and with work from previous studies. Covariate coefficients are presented on the logit scale to facilitate assessment of the direction and magnitude of their effect relative to the intercept.

Habitat	Species	Top detection model	p Real estimate	B KE	B PJ	B V2	B V3	B Tmt
Piñon–juniper specialists	Gray Flycatcher	p(visit + obs)	0.44 (0.41, 0.50)	0.4 (0.1, 0.6)	0.5 (0.3, 0.7)	-0.2 (-0.4, 0.0)	-0.3 (-0.5, -0.1)	NA
	Pinyon Jay	p(obs)	0.18 (0.14, 0.23)	-0.8 (-1.4, -0.2)	-0.2 (-0.6, 0.2)	NA	NA	NA
	Juniper Titmouse	p(obs + trtm)	0.38 (0.34, 0.41)	-0.0 (-0.3, 0.3)	-0.2 (-0.4, 0.0)	NA	NA	-0.4 (-0.6, -0.2)
	Virginia's Warbler	p(visit + obs + trtm)	0.23 (0.18, 0.27)	-0.8 (-1.2, -0.5)	-0.8 (-1.0, -0.5)	0.9 (0.6, 1.1)	0.5 (0.2, 0.8)	-0.6 (-0.8, -0.3)
	Black-throated Gray Warbler	p(visit + trtm)	0.61 (0.58, 0.67)	NA	NA	0.1 (-0.1, 0.3)	-0.2 (-0.3, 0.0)	-0.6 (-0.8, -0.5)
Mature conifer	Mountain Chickadee	p(visit + trtm)	0.41 (0.34, 0.47)	NA	NA	-0.3 (-0.5, -0.0)	-0.4 (-0.6, -0.1)	-0.3 (-0.5, -0.1)
	Yellow-rumped Warbler	p(visit)	0.38 (0.30, 0.44)	NA	NA	-1.1 (-1.6, -0.7)	-1.9 (-2.4, -1.3)	NA
Open conifer	Steller's Jay	p(obs)	0.14 (0.10, 0.18)	-0.2 (-0.8, 0.3)	-0.7 (-1.2, -0.1)	-0.9 (-1.2, -0.6)	-0.8 (-1.1, -0.5)	-0.5 (-0.9, -0.2)
	Clark's Nutcracker	p(visit + trtm)	0.41 (0.30, 0.50)	NA	NA	0.6	0.1	NA
	Western Bluebird	p(visit + obs)	0.14 (0.05, 0.23)	-0.2 (-0.7, 0.3)	-0.9 (-1.4, -0.3)	0.1 (0.1, 1.1)	-0.4 (-0.4, 0.6)	NA
	Townsend's Solitaire	p(visit)	0.30 (0.27, 0.38)	NA	NA	-0.9 (-1.3, -0.4)	-1.0 (-1.4, -0.6)	NA
	Chipping Sparrow	p(obs + trtm)	0.27 (0.23, 0.30)	-0.5 (-0.7, -0.2)	-0.7 (-0.9, -0.5)	NA	NA	1.1 (0.9, 1.3)
	Western Tanager	p(visit + obs + trtm)	0.30 (0.23, 0.34)	-0.1 (-0.4, 0.2)	0.5 (0.3, 0.7)	0.1 (-0.1, 0.3)	-0.4 (-0.6, -0.1)	0.1 (-0.1, 0.3)
Piñon–juniper shrubland	Common Nighthawk	p(visit)	0.02 (-0.00, 0.04)	NA	NA	2.8 (1.6, 3.9)	3.2 (2.1, 4.4)	NA
	Ash-throated Flycatcher	p(visit + obs + trtm)	0.27 (0.23, 0.38)	-0.1 (-0.4, 0.2)	0.4 (0.2, 0.6)	0.3 (0.0, 0.5)	0.4 (0.1, 0.6)	0.3 (0.1, 0.5)
	Plumbeous Vireo	p(visit + trtm)	0.44 (0.41, 0.50)	NA	NA	-0.1 (-0.3, 0.1)	-0.1 (-0.3, 0.1)	-0.2
	Woodhouse's Scrub-Jay	p(visit + obs + trtm)	0.47 (0.44, 0.50)	-0.3 (-0.5, -0.1)	-0.2 (-0.4, -0.0)	0.1 (-0.3, 0.1)	-0.1 (-0.3, 0.1)	-0.3 (-0.3, 0.0)
	Bushtit	p(obs)	0.10 (0.05, 0.10)	0.3 (-0.4, 1.0)	0.8 (0.3, 1.4)	-0.1 (-0.1, 0.3)	-0.3 (-0.3, 0.0)	-0.1
	Blue-gray Gnatcatcher	p(trtm)	0.34 (0.30, 0.38)	NA	NA	NA	NA	0.2 (-0.0, 0.4)
	Spotted Towhee	p(obs)	0.75 (0.73, 0.76)	-0.3 (-0.5, -0.2)	-0.2 (-0.4, -0.1)	NA	NA	NA

TABLE 3. Continued

Habitat	Species	Top detection model	P Real estimate	B KE	B PJ	B V2	B V3	B Tmt
Forest generalists	Broad-tailed Hummingbird	p(visit + obs + trtm)	0.53	−0.3	−0.3	−0.1	−0.5	0.2
			0.47, 0.58	−0.5, −0.0	−0.5, −0.1	−0.3, 0.1	−0.7, −0.3	0.0, 0.3
	Northern Flicker	p(obs)	0.14	−0.6	−0.1	NA	NA	NA
			0.10, 0.23	−1.2, 0.0	−0.5, 0.3			
	Western Wood-Pewee	p(visit + obs + trtm)	0.10	−0.8	−0.2	0.9	1.1	0.6
			0.05, 0.18	−1.4, −0.3	−0.6, 0.1	0.4, 1.3	0.7, 1.6	0.1, 1.1
	White-breasted Nuthatch	p(obs)	0.23	−0.9	−0.5	NA	NA	NA
			0.18, 0.27	−1.3, −0.5	−0.7, −0.2			
	American Robin	p(visit + obs)	0.18	−0.6	−2.0	−0.3	−0.5	NA
			0.14, 0.27	−1.0, −0.2	−2.6, −1.5	−0.7, −0.0	−0.9, −0.2	
Edge	Mountain Bluebird	p(trtm)	0.23	NA	NA	NA	NA	0.7
			0.18, 0.27					0.4, 1.0
	Lark Sparrow	p(trtm)	0.10	NA	NA	NA	NA	4.7
			0.0, 0.99					3.3, 6.2
	Brown-headed Cowbird	p(visit)	0.18	NA	NA	−0.8	−0.7	NA
			0.14, 0.27			−0.5, 0.3	−1.2, −0.3	
Generalists	Mourning Dove	p(obs)	0.27	−0.9	−0.8	NA	NA	NA
			0.27, 0.30	−1.2, −0.6	−1.0, −0.5			
	Common Raven	p(visit + obs)	0.23	−0.3	0.2	0.0	−0.6	NA
			0.18, 0.27	−0.6, 0.2	−0.1, 0.6	−0.3, 0.4	−1.0, −0.2	
	Black-headed Grosbeak	p(obs)	0.47	−0.2	0.1	NA	NA	NA
			0.41, 0.50	−0.4, 0.1	−0.0, 0.3			

*Real estimates of p were originally derived from Mark by model averaging the detection probability on visit one in the first 2-min bin. We converted these to represent the overall detection probability on visit one using the following equation: $p_{new} = 1-(1-p)^{\wedge}5$.

TABLE 4. Beta estimates and 95% CI for Ψ and θ from best-fit treatment effects models. N.E. = no estimate generated for occupancy parameter.

Species	Parameter	β	95% CI Lower	95% CI Upper
Piñon–juniper specialists				
Gray Flycatcher	Ψ Treatment	−1.65	−3.57	0.26
Pinyon Jay	Ψ Treatment	1.06	−0.68	2.80
	θ Treatment	−2.11	−4.47	0.25
Juniper Titmouse	Ψ Treatment	−0.23	−1.18	0.72
Virginia's Warbler	Ψ Treatment	−1.04	−2.16	0.07
Black-throated Gray Warbler	Ψ Treatment	N.E.	N.E.	N.E.
Mature conifer				
Mountain Chickadee	Ψ Treatment	−1.21	−2.36	−0.07
Yellow-rumped Warbler	Ψ Treatment	−0.39	−1.20	0.43
Open conifer				
Steller's Jay	Ψ Hand-thin	N.E.	N.E.	N.E.
	Ψ Mastication	−0.76	−1.72	0.20
Clark's Nutcracker	Ψ Treatment	−1.39	−2.37	−0.41
Western Bluebird	θ Treatment	0.87	−0.51	2.24
Townsend's Solitaire	Ψ Treatment	−0.48	−1.34	0.37
Chipping Sparrow	Ψ Treatment	N.E.	N.E.	N.E.
Western Tanager	Ψ Treatment	−1.55	−3.99	0.90
Piñon–juniper shrubland				
Common Nighthawk	Ψ Treatment	N.E.	N.E.	N.E.
Ash-throated Flycatcher	θ Hand-thin	−1.88	−4.59	0.83
	θ Mastication	0.21	−2.92	3.35
Plumbeous Vireo	Ψ Treatment	0.90	−1.12	2.93
Woodhouse's Scrub-Jay	θ Hand-thin	N.E.	N.E.	N.E.
	θ Mastication	N.E.	N.E.	N.E.
Bushtit	θ Treatment	−1.05	−3.70	1.60
Blue-gray Gnatcatcher	θ Treatment	0.65	−0.39	1.69
Spotted Towhee	Ψ Treatment	N.E.	N.E.	N.E.
Forest generalists				
Broad-tailed Hummingbird	θ Treatment	−0.76	−1.94	0.42
Northern Flicker	Ψ Hand-thin	N.E.	N.E.	N.E.
Western Wood-Pewee	θ Hand-thin	N.E.	N.E.	N.E.
	θ Mastication	−0.42	−2.00	1.16
White-breasted Nuthatch	Ψ Treatment	−1.76	−3.31	−0.21
American Robin	θ Treatment	1.36	−0.13	2.86
Edge				
Mountain Bluebird	Ψ Hand-thin	−0.57	−1.99	0.85
	Ψ Mastication	1.80	0.44	3.15
Lark Sparrow	θ Hand-thin	1.84	0.14	3.55
	θ Mastication	4.42	3.17	5.66
Brown-headed Cowbird	θ Treatment	N.E.	N.E.	N.E.
Generalists				
Mourning Dove	Ψ Treatment	−0.64	−2.15	0.85
Common Raven	θ Treatment	N.E.	N.E.	N.E.
Black-headed Grosbeak	θ Hand-thin	−1.41	−2.53	−0.30
	θ Mastication	−0.58	−1.51	0.35

their habitat structure was likely boosted by thinning treatments, especially where tree retention within the treatment area was prescribed.

Only one species, Pinyon Jay, showed inconsistent occupancy responses to treatments at the 2 different scales we modeled. At the local scale, occupancy was lower on treated sites (Figure 4), whereas at the landscape scale occupancy appeared to be higher in treatments (Figure 3). Pinyon Jays live in cohesive flocks and occupy large home ranges (Balda and Bateman 1971). They generally nest and roost in dense patches of piñon pine, but may forage for and cache pine seeds in relatively open forest stands that can be distant from the roost or nest (Johnson et al. 2011, K. Johnson personal communication). Thus, it may be that Pinyon Jays find treated landscapes suitable for occupancy as long as they contain sufficiently dense forest patches (that could accommodate nesting flocks numbering over 100 individuals). At finer scales of habitat use, Pinyon Jays may abandon treated forest patches that remove too much cover for nesting and roosting or severely reduce piñon pine seed availability.
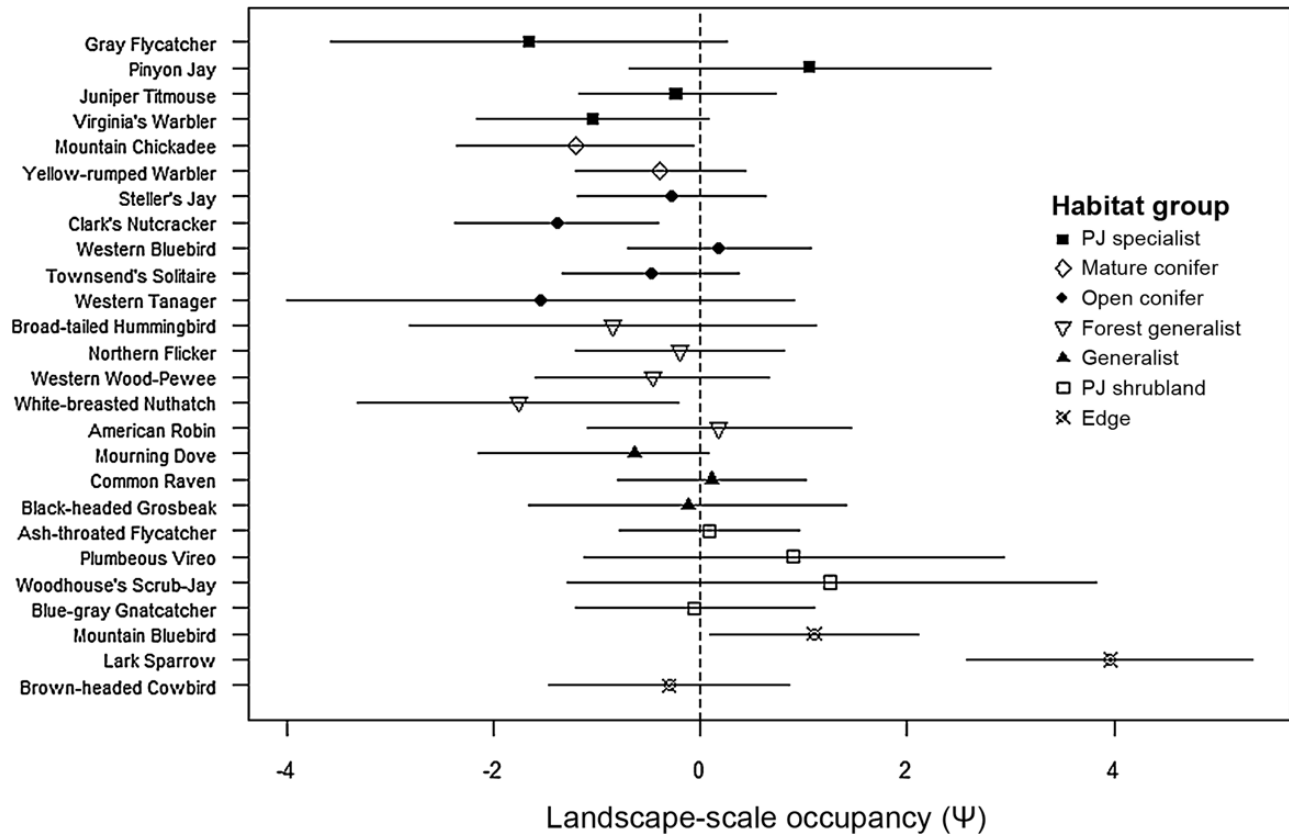
FIGURE 3. Modeled treatment effect of landscape-scale occupancy (Ψ) in masticated and hand-thinned piñon–juniper woodlands in central Colorado during 2014–2015. Horizontal axis is the modeled occupancy β value and 95% CI derived from the top generic treatment model for each species based on AIC_c. PJ refers to piñon–juniper.

Piñon–juniper woodland bird occupancy may remain highest in the absence of thinning, or if treatments are conducted, where tree canopy removal is minimized. Previous researchers found that woodland bird species responded negatively to treatments, especially entirely deforested patches (Bombaci and Pejchar 2016). To benefit woodland birds, researchers suggest avoiding clearcuts and, instead, retaining large pines and conifer patches (Gillihan 2006, Gaines et al. 2010). In piñon–juniper stands specifically, woodland birds have been shown to benefit both by preserving relatively high piñon density and also retaining abundant juniper (Balda and Masters 1980, Pavlacky and Anderson 2001, Francis et al. 2011, Gallo and Pejchar 2017). Higher piñon pine density correlates with presence of specialist woodland species that glean insects from bark and foliage or that use cavities as nest sites (Masters 1979; Pavlacky and Anderson 2001, 2004); juniper provides vital canopy nesting substrate for many species (Francis et al. 2011). The thinning levels in masticated units in our study reduced mean canopy cover from 36% in controls to 5% in treatments (Coop et al. 2017). Our results suggest that this level of tree canopy reduction may be below a required threshold for several piñon–juniper specialists and conifer obligates.

For example, Parrish et al. (2002) determined that the Black-throated Gray Warbler requires a minimum of 15% canopy cover for nesting habitat.

The duration of tree-removal treatment effects on piñon–juniper bird communities was beyond the scope of our research, but we anticipate they will be extended. Given sparse tree regeneration in treatments, reductions in piñon–juniper canopy cover, density, and basal area within our study area are expected to persist for many decades (Coop et al. 2017). Within 2 yr of treatments in northwestern Colorado, no birds responded positively to small clearcuts and woodland species rarely used treated sites (Bombaci et al. 2017). By contrast, our estimates of avian occupancy occurred over a 1–11 yr post-treatment timeframe. Four decades after chaining treatments, woodlands had lower bird species richness with shrubland species dominating, compared to reference sites where woodland species had higher richness and dominated in abundance (Gallo and Pejchar 2017).

Avian Community Composition and Diversity in Piñon–Juniper Woodlands

We observed 77 bird species during this study, confirming the reportedly high avian diversity of piñon–juniper woodlands
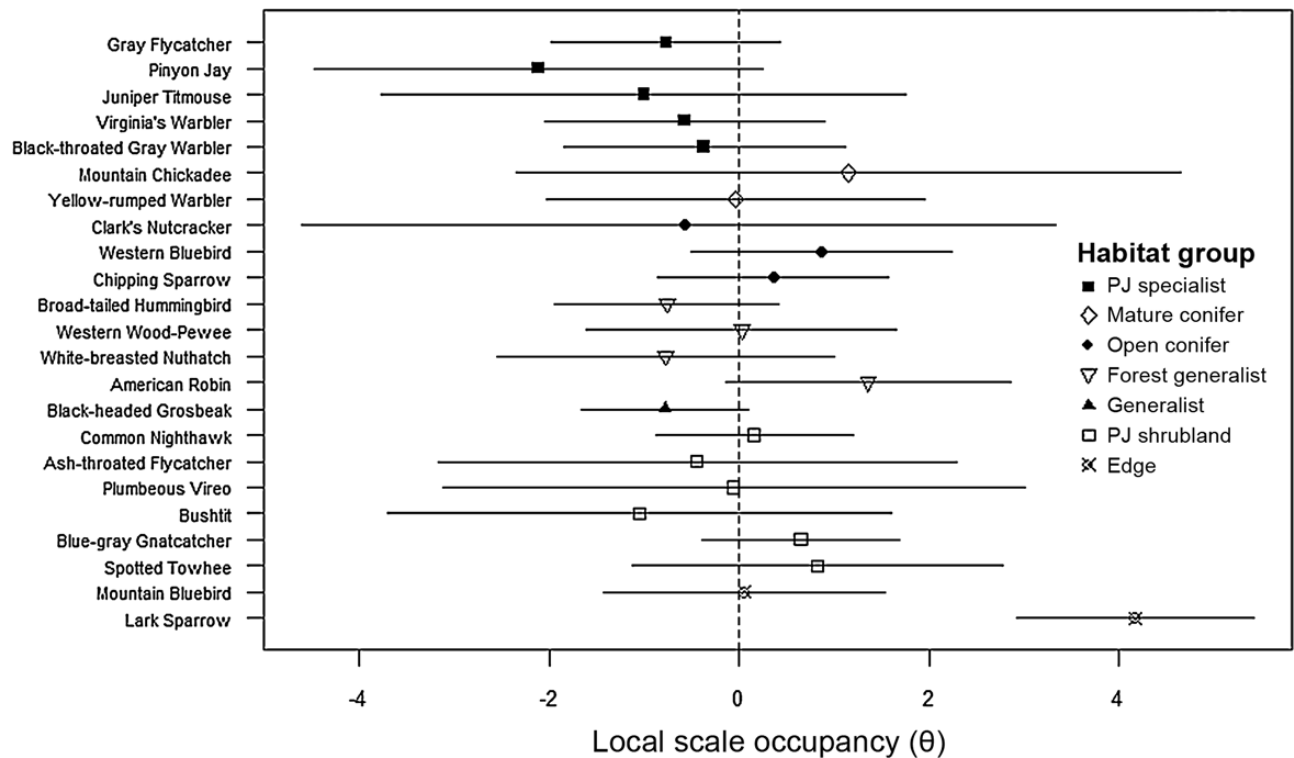
FIGURE 4. Modeled treatment effect of local scale occupancy (θ) in masticated and hand-thinned piñon–juniper woodlands in central Colorado during 2014–2015. Horizontal axis is the modeled occupancy β value and 95% CI derived from the top generic treatment model for each species based on AIC_c. PJ refers to piñon–juniper.

(Balda and Masters 1980, Paulin et al. 1999, Bombaci et al. 2017). The most abundant bird species detected matched those recorded in other studies; however, the species richness was higher than that documented in piñon–juniper systems elsewhere across the range of this ecosystem (Balda and Masters 1980, Bombaci et al. 2017, Gallo and Pejchar 2017). The Arkansas River corridor spans a relatively large and geographically complex region including piñon–juniper woodlands of diverse structural and taxonomic characteristics which may have accounted for the high number of species recorded in our study. Alternatively, the piñon–juniper bird community in our study area may reflect a regional hot spot of avian biodiversity.

Study Design and Appropriate Metrics
Resource managers require a clear understanding of how birds and other species respond to management interventions such as woodland tree removal (Kroll et al. 2014). Occupancy measures presence or absence and is relatively easy to quantify compared to abundance (distance sampling or mark/recapture) or avian productivity or performance metrics (nest success, survival). However, occupancy is a relatively coarse metric and can remain unchanged while substantial increases or decreases in abundance take place. Small or null changes in occupancy may mask relatively large and important changes in abundance, survival,

or nest success. Therefore, our analysis should be viewed as a conservative means of detecting bird responses, and as such, suggests that thinning treatments may have other impacts on the avian community beyond what we measured in this study. For ubiquitous species, limitations of relying on occupancy to assess treatment effects may be accentuated. For example, occupancy estimates of 4 of the most frequently encountered species in the study—Spotted Towhee (*n* = 2,595), Black-throated Gray Warbler (*n* = 1,022), Woodhouse's Scrub-Jay (*n* = 834), and Chipping Sparrow (*n* = 806)—were functionally 1.0, yet for Black-throated Gray Warbler and Chipping Sparrow, naive counts of the number of detections indicated that abundance may have been substantially different between treatments and controls, a result that was masked by the coarse nature of occupancy estimation.

Management Implications
Land managers are increasingly conducting tree removal projects in piñon–juniper woodlands to improve habitat for target wildlife species, reduce fire risk, and increase livestock forage production. However, these treatments may catalyze numerous unintended consequences for biodiversity (Holmes et al. 2017). Given that avian assemblages generally encompass a diverse suite of habitat preferences, diets and foraging adaptations, and life histories,

any specific management action would not be expected to produce uniform effects across all bird species within a community (Hurteau et al. 2008, Crow and van Riper 2010, Gaines et al. 2010). Our results and those of other studies (Bombaci and Pejchar 2016, Bombaci et al. 2017) demonstrate that conifer removal negatively impacts piñon–juniper specialists and other woodland birds that are vulnerable to habitat loss and fragmentation. Among the most vulnerable are 2 listed as Species of Greatest Conservation Need by Colorado Parks and Wildlife (2015): Virginia's Warbler and Pinyon Jay. Both of these species are experiencing survey-wide, long-term population declines (Sauer et al. 2017a, 2017b), and both responded negatively to piñon–juniper thinning in this study.

In thinned piñon–juniper forests, woodland-obligate birds are most likely to decline, whereas species of open or edge habitats are likely to benefit. To reduce risk to priority conservation woodland birds and piñon–juniper specialists, canopy reduction should only occur when social and/or ecological benefits of treatment outweigh the loss of functional woodland habitat.

Piñon–juniper thinning prescriptions may vary by thinning method and extent of woodland canopy reduction. In our study, managers used 2 thinning treatments, mastication and hand-thinning. We did not detect differences in occupancy between methods. Similarly, other researchers have shown birds do not respond differentially to tree removal methods (rollerchop, mastication, chaining) in piñon–juniper woodlands (Bombaci et al. 2017) or ponderosa pine dry forests where thinning and burning were employed (Hurteau et al. 2008, Gaines et al. 2010). Regardless of the method, to sustain habitat use by forest-obligate birds, thinning should retain more trees. We also encourage managers to explore alternate means to achieve the goals in thinning prescriptions. For example, reductions of surface and ladder fuels may facilitate the retention of larger piñon pines and junipers, at higher densities and with greater canopy cover, that benefit forest-dependent species and still meet fire mitigation objectives.

A range of disturbances projected to increase under future climates (e.g., Williams et al. 2013), may also fully negate the need for thinning and tree removal in some settings. Strong evidence points to major piñon–juniper woodland losses in some areas, driven by climate-mediated drought, fire, and insect impacts (Breshears et al. 2005, Romme et al. 2009, Clifford et al. 2013, Meddens et al. 2015). Additional information is needed to effectively design and implement treatments in a balanced way to sustain avian biodiversity and achieve other objectives such as fuels mitigation. The social and ecological trade-offs of piñon–juniper management, and particularly application of thinning treatments, are complex. Decisions should consider the importance of retaining ecological integrity and conservation of habitat-obligate bird species.

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APPENDIX TABLE 5. Bird species composition and ranked abundance in piñon–juniper woodlands in central Colorado during 2014–2015. Ranked abundance based on number of observations (n = 15,541).

Rank	Species	Scientific name	Number of observations	Percent of observations
Top ten				
1	Spotted Towhee	*Pipilo maculatus*	2,595	16.7%
2	Black-throated Gray Warbler	*Setophaga nigrescens*	1,022	6.6%
3	Woodhouse's Scrub-Jay	*Aphelocoma woodhouseii*	834	5.4%
4	Chipping Sparrow	*Spizella passerina*	806	5.2%
5	Broad-tailed Hummingbird	*Selasphorus platycercus*	731	4.7%
6	Black-headed Grosbeak	*Pheucticus melanocephalus*	703	4.5%
7	Plumbeous Vireo	*Vireo plumbeus*	682	4.4%
8	Gray Flycatcher	*Empidonax wrightii*	646	4.1%
9	Blue-gray Gnatcatcher	*Polioptila caerulea*	545	3.5%
10	Ash-throated Flycatcher	*Myiarchus cinerascens*	491	3.2%
More than 100 observations per species				
11	Mountain Chickadee	*Poecile gambeli*	446	2.9%
12	Mourning Dove	*Zenaida macroura*	437	2.8%
13	Western Tanager	*Piranga ludoviciana*	435	2.8%
14	Virginia's Warbler	*Oreothlypis virginiae*	431	2.8%
15	Juniper Titmouse	*Baeolophus ridgwayi*	423	2.7%
16	Mountain Bluebird	*Sialia currucoides*	392	2.5%
17	Clark's Nutcracker	*Nucifraga columbiana*	322	2.1%
18	White-breasted Nuthatch	*Sitta carolinensis*	295	1.9%
19	Common Raven	*Corvus corax*	229	1.5%
20	Lark Sparrow	*Chondestes grammacus*	223	1.4%
21	American Robin	*Turdus migratorius*	220	1.4%
22	Western Wood-Pewee	*Contopus sordidulus*	206	1.3%
23	Pinyon Jay	*Gymnorhinus cyanocephalus*	171	1.1%
24	Yellow-rumped Warbler	*Setophaga coronata*	169	1.1%
25	Townsend's Solitaire	*Myadestes townsendi*	150	1.0%
26	Common Nighthawk	*Chordeiles minor*	149	1.0%
27	Brown-headed Cowbird	*Molothrus ater*	136	0.9%
28	Western Bluebird	*Sialia mexicana*	113	0.7%
29	Bushtit	*Psaltriparus minimus*	107	0.7%
30	Northern Flicker	*Colaptes auratus*	107	0.7%
31	Steller's Jay	*Cyanocitta stelleri*	104	0.7%
More than 50 observations per species				
32	Pine Siskin*	*Spinus pinus*	83	0.5%
33	Hermit Thrush	*Catharus guttatus*	82	0.5%
34	Lesser Goldfinch	*Spinus psaltria*	73	0.5%
35	Vesper Sparrow*	*Pooecetes gramineus*	73	0.5%
36	Rock Wren	*Salpinctes obsoletus*	70	0.5%
37	Bewick's Wren	*Thryomanes bewickii*	69	0.4%
38	Violet-green Swallow*	*Tachycineta thalassina*	66	0.4%
39	Dusky Flycatcher	*Empidonax oberholseri*	55	0.3%
40	Common Poorwill	*Phalaenoptilus nuttallii*	52	0.3%
41	Canyon Wren	*Catherpes mexicanus*	51	0.3%
More than 20 observations per species				
42	Hairy Woodpecker	*Dryobates villosus*	48	0.3%
43	Red-breasted Nuthatch	*Sitta canadensis*	47	0.3%
44	Wild Turkey	*Meleagris gallopavo*	46	0.3%
45	Black-chinned Hummingbird	*Archilochus alexandri*	27	0.2%
46	House Wren	*Troglodytes aedon*	27	0.2%
47	Evening Grosbeak	*Coccothraustes vespertinus*	27	0.2%
48	White-throated Swift*	*Aeronautes saxatalis*	26	0.2%
49	Dark-eyed Junco	*Junco hymenalis*	26	0.2%
50	Pygmy Nuthatch	*Sitta pygmaea*	24	0.2%
51	Hammond's Flycatcher	*Empidonax hammondii*	22	0.1%

APPENDIX TABLE 5. Continued

Rank	Species	Scientific name	Number of observations	Percent of observations
Less than 20 observations per species				
52	American Crow	*Corvus brachyrhynchos*	15	0.1%
53	Turkey Vulture	*Cathartes aura*	14	0.1%
54	Red Crossbill	*Loxia curvirostra*	13	0.1%
55	Green-tailed Towhee	*Pipilo chlorurus*	12	0.1%
56	Cassin's Finch	*Haemorphous cassinii*	11	0.1%
57	Ruby-crowned Kinglet	*Regulus calendula*	9	0.1%
58	Cooper's Hawk*	*Accipiter cooperi*	8	0.1%
59	Cordilleran Flycatcher	*Empidonax occidentalis*	8	0.1%
60	House Finch	*Haemorphous mexicanus*	8	0.1%
61	Cassin's Kingbird	*Tyrannus vociferans*	7	<0.1%
62	Warbling Vireo	*Vireo gilvus*	7	<0.1%
63	Red-tailed Hawk*	*Buteo jamaicensis*	6	<0.1%
64	Black-billed Magpie	*Pica hudsonia*	5	<0.1%
65	Great-horned Owl	*Bubo virginianus*	5	<0.1%
66	Golden Eagle*	*Aquila chrysaetos*	4	<0.1%
67	Olive-sided Flycatcher	*Contopus cooperi*	4	<0.1%
68	American Goldfinch	*Spinus tristis*	3	<0.1%
69	Say's Phoebe	*Sayornis saya*	3	<0.1%
70	American Kestrel	*Falco sparverius*	2	<0.1%
71	Western Kingbird	*Tyrannus verticalis*	2	<0.1%
72	Williamson's Sapsucker	*Sphyrapicus thyroideus*	2	<0.1%
73	Yellow Warbler	*Setophaga petechia*	2	<0.1%
74	Bullock's Oriole	*Icterus bullockii*	1	<0.1%
75	Eurasian Collared-Dove	*Streptopelia decaocto*	1	<0.1%
76	Eurasian Starling	*Sturnus vulgaris*	1	<0.1%
77	White-crowned Sparrow	*Zonotrichia leucophyrs*	1	<0.1%

*No analyses were run on these species because they we primarily detected using aerial habitat or grasslands adjacent to study plots.