AVIAN CONSERVATION
& ECOLOGY

VOLUME 20, ISSUE 2, ARTICLE 13

Jones, H. H., B. D. Merriell, M. C. Swan, M. Johnson, and R. B. Siegel. 2025. Pinyon-juniper specialist birds are resilient to local-scale reduction of canopy cover and pinyon pines, but amount of understory shrub cover determines the composition of the insectivore guild. Avian Conservation and Ecology 20(2):13. https://doi.org/10.5751/ACE-02941-200213

Research Paper

Pinyon-juniper specialist birds are resilient to local-scale reduction of canopy cover and pinyon pines, but amount of understory shrub cover determines the composition of the insectivore guild

Harrison H. Jones[1], *Brandon D. Merriell*[2], *Megan C. Swan*[3], *Matthew Johnson*[3] *and Rodney B. Siegel*[1]
[1]The Institute for Bird Populations, [2]Trent University, [3]Southern Colorado Plateau Inventory & Monitoring Program

ABSTRACT. Drought-induced tree die-off and die-back in the southwestern United States is changing the structure and floristic composition of pinyon-juniper woodlands, a widespread middle-elevation community with high bird endemism. Amid increasing prevalence of high-severity wildfires in this habitat, managers have also turned to mechanical thinning to reduce fuel loads. Therefore, in this study, we asked how breeding-season bird densities are associated with microhabitat-scale structural features and floristic composition in pinyon-juniper woodlands, features likely to change with die-back and mechanical thinning. We fit Bayesian N-mixture models to eight years of monitoring data at three Colorado Plateau national parks and found supported responses to microhabitat variables across 18 of 25 species, though park-level effects were an order of magnitude larger than microhabitat effects. Pinyon-juniper specialists were resilient to loss of canopy cover at local scales, but generalist forest species showed supported associations with greater canopy cover. We found no threshold values of canopy cover, but nine species showed a supported negative effect of park on density at Bandelier National Monument after a large-scale (> 95%) pinyon pine die-off and associated reduction in canopy cover (< 15% remaining). Species also showed weak or no associations with pinyon-pine basal area, perhaps indicating a selection for both junipers and pinyons. Exceptions included positive associations of cavity-nesting birds with greater pinyon-pine basal area, and negative associations of species associated with canopy gaps. The extent of shrub foliage cover, which may increase in woodlands following thinning or die-off, shaped the composition of the insectivorous bird guild. Foliage-gleaning birds of both canopy and understory showed positive supported associations with increasing shrub cover, while aerial insectivore and bark forager densities were negatively affected. An ordination of species' responses to all covariates suggests the community segregated along a woodland successional gradient and was generally associated with a simplified vertical vegetation structure.

Les oiseaux spécialistes des forêts de pins pignons du Colorado et de genévriers s'adaptent bien à la réduction locale du couvert forestier et des pins pignons, mais la composition de la guilde d'insectivores dépend de la strate arbustive

RÉSUMÉ. La mortalité et le dépérissement des arbres induits par la sécheresse dans le sud-ouest des États-Unis sont en train de modifier la structure et la composition végétale des forêts de pins pignons du Colorado et de genévriers, une communauté très répandue à moyenne altitude qui présente un fort endémisme aviaire. Face à la hausse des incendies de forêt de grande ampleur dans cet habitat, les gestionnaires se sont également tournés vers l'éclaircissage systématique pour réduire la charge combustible. Dans la présente étude, nous avons donc cherché à déterminer dans quelle mesure la densité des oiseaux pendant la saison de nidification est associée aux caractéristiques structurelles à l'échelle du microhabitat et à la composition végétale des forêts de pins pignons et de genévriers, caractéristiques susceptibles de changer avec le dépérissement et l'éclaircissage. Nous avons appliqué des modèles bayésiens N-mixture à des données de suivi sur 8 ans dans trois parcs nationaux du plateau du Colorado et avons trouvé des associations aux variables du microhabitat pour 18 des 25 espèces, bien que les effets à l'échelle du parc aient été d'un ordre de grandeur supérieur aux effets à l'échelle du microhabitat. Les espèces spécialistes des forêts de pins pignons et de genévriers ont bien résisté à la perte de couvert forestier à l'échelle locale, mais les espèces forestières généralistes ont montré des associations avec un couvert forestier plus important. Nous n'avons pas trouvé de valeur seuil pour le couvert forestier, mais avons constaté un effet négatif du parc sur la densité pour 9 espèces au Bandelier National Monument, après un dépérissement à grande échelle (> 95 %) des pins pignons et une réduction concomitante du couvert forestier (< 15 % restant). Nous avons également constaté que les espèces ont été faiblement ou aucunement associées avec la surface terrière des pins pignons, ce qui pourrait indiquer que les espèces sélectionnent à la fois les genévriers et les pins pignons. Parmi les exceptions, nous avons observé des associations positives entre les oiseaux nichant dans des cavités et une plus grande surface terrière de pins pignons, ainsi que des associations négatives entre les espèces associées aux trouées dans la canopée. L'étendue du couvert arbustif, qui peut augmenter dans les forêts à la suite d'un éclaircissage ou d'un dépérissement, a influé sur la composition de la guilde des oiseaux insectivores. Les oiseaux glaneurs de feuillage, tant dans la canopée que dans la sous-strate, ont eu des associations positives avec l'augmentation du couvert arbustif, tandis que les densités d'insectivores aériens et d'espèces corticoles ont été négativement touchées. Une ordination des réactions des espèces à toutes les covariables indique que la communauté s'est séparée selon un gradient de succession des forêts et était généralement associée à une structure végétale verticale simplifiée.

Key Words: *Bayesian hierarchical models; breeding-season bird density; Colorado Plateau; foliage height diversity; pinyon pine die-off; canopy height*

Corresponding author: Harrison H Jones, hjones@birdpop.org

INTRODUCTION

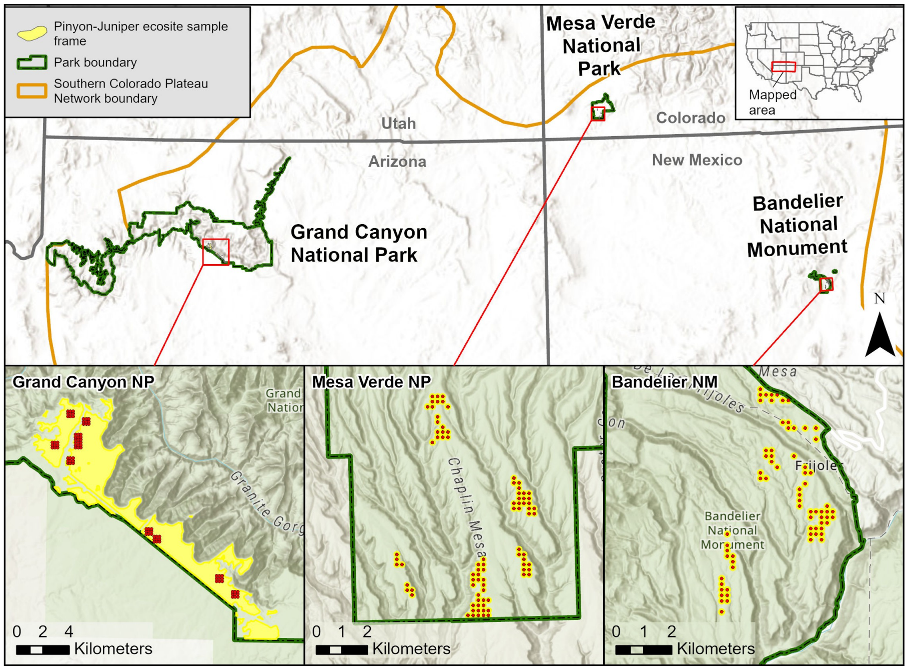
Populations of nearly half of all bird species are thought to be declining globally (Lees et al. 2022), with 57% of species in North America showing declining trends since 1970 (Rosenberg et al. 2019). Climate change likely plays a major role in these declines (Jenouvrier 2013, Bateman et al. 2020) through both direct demographic effects and indirect effects of climate on local habitat (e.g., Roberts et al. 2019, Cadieux et al. 2020, Ceresa et al. 2021). Birds are especially sensitive to these indirect climate effects on microhabitat, defined here as habitat features at or below the scale of the breeding territory (i.e., second- and third-order habitat selection *sensu* Johnson 1980), because their microhabitat associations are tied to both local floristic composition (Lee and Rotenberry 2005, Adams and Matthews 2019) as well as vegetation structural features (MacArthur and MacArthur 1961, Culbert et al. 2013). Microhabitat can play an important role in explaining avian breeding occupancy (Hack et al. 2023) and reproductive success (Shew et al. 2019, Kuile et al. 2023), perhaps because finer-scale habitat features are more closely linked to food resource availability and nesting locations. Long-term changes to climate are leading to latitudinal and elevational shifts in plant communities (Boisvert-Marsh and de Blois 2021), however, as well as the creation of no-analog plant communities (Urban et al. 2012). In the western United States, extreme drought and wildfire events have also led to high tree mortality, especially of drought-sensitive species (Allen et al. 2010, Fettig et al. 2013, Clark et al. 2016), which, in turn, alters habitat structure. Predicting how bird species will respond to climate change therefore requires understanding their associations with these changing aspects of habitat. However, bird-microhabitat associations also tend to differ, often substantially, among geographic regions within a species' range (Whittingham et al. 2007, Crosby et al. 2019, Zillig et al. 2023, Van Lanen et al. 2024), and predictive models of local habitat associations used for management decisions are more accurate when incorporating regional, rather than global, associations (Doherty et al. 2016, Crosby et al. 2019, Elliott et al. 2023, Schofield et al. 2023).

Climate-change effects are particularly pronounced in the Southwestern United States, which is currently in the grip of a 20-year megadrought (Overpeck and Udall 2020, Williams et al. 2022), leading to outsized negative effects on forest ecosystems (Buotte et al. 2019). One widespread Southwestern plant community of great ecological and cultural importance is pinyon-juniper woodlands, a mid-elevation, dwarf woodland dominated by pinyon pine (*Pinus edulis* or *monophyla*) and juniper (*Juniperus* spp.; Romme et al. 2009, Muldavin and Triepke 2020). These woodlands are home to many habitat-specialist birds (Paulin et al. 1999), which track their occurrence on the landscape (Van Lanen et al. 2023), yet climate-change mediated drought is profoundly altering the distribution, floristic composition, and structure of their habitat. Changing precipitation patterns and disturbance regimes have led to both upslope and downslope shifts in woodland distribution (Weisberg et al. 2007, Garbarino et al. 2020), part of a larger process of both contraction and infilling of open woodlands to dense stands (Amme et al. 2020, Filippelli et al. 2020) depending on climate and soil properties. These changes produce both higher and lower tree densities in existing woodlands as well as shifts in plant communities at the upper and lower ecotones. On a more immediate time scale, extreme drought events and associated outbreaks of bark beetles (Gaylord et al. 2013) have led to large-scale die-off and die-back (i.e., loss of foliage) of pinyon pines (Breshears et al. 2005, Hicke and Zeppel 2013, Meddens et al. 2015) and resulted in juniper-dominated woodlands (Mueller et al. 2005). In particular, *P. edulis* is projected to decline across its range with increasing regional drought (Shriver et al. 2022, Noel et al. 2025). These die-off events also lead to structural changes by reducing canopy cover (Clifford et al. 2011; Flake and Weisberg 2019), which in turn increases understory cover and changes understory plant composition (Flake and Weisberg 2021). Such changes are particularly concerning because many pinyon-juniper bird species are associated with specific structural elements such as canopy height and cover (Sedgwick 1987, Pavlacky and Anderson 2004) or tied to the presence of pinyon pines (Pavlacky and Anderson 2001, Fair et al. 2018) during the breeding season.

In addition to drought, management interventions are also changing habitat features of pinyon-juniper woodlands. With the increased prevalence and size of high-severity fires (Singleton et al. 2019), and infilling of woodlands due to historical fire suppression (Filippelli et al. 2020), managers have increasingly turned to mechanical thinning of pinyon-juniper to reduce both density-dependent drought mortality of trees (e.g., Greenwood and Weisberg 2008) and fuel loads (Huffman et al. 2009, Redmond et al. 2014a). Despite the widespread use of this management technique to increase pinyon-juniper fire resiliency, particularly near human infrastructure, questions remain regarding its effects on ecosystem dynamics and habitat-specialist wildlife (Hartsell et al. 2020, Redmond et al. 2023). In addition to reducing the density of pinyon and juniper, mechanical thinning appears to increase understory vegetation density over long time periods (Ernst-Brock et al. 2019, Almalki et al. 2023). While a recent review found that overall effects of pinyon-juniper thinning on wildlife were generally non-significant (Bombaci and Pejchar 2016), a growing body of evidence suggests thinning reduces the occupancy of pinyon-juniper specialist birds (Crow and van Riper 2010, Bombaci et al. 2017, Magee et al. 2019). For example, the Pinyon Jay (*Gymnorhinus cyanocephalus*), a habitat-specialist corvid that is a seed-dispersal mutualist of the pinyon pine, was found to avoid nesting in thinned pinyon-juniper stands (Johnson et al. 2018), and Gray Vireo (*Vireo vicinior*), another pinyon-juniper specialist, prefers to nest in areas with greater foliage density (Harris et al. 2020). Despite these apparent negative effects of thinning, the specific mechanisms that reduce habitat suitability (the ability for a habitat to support viable populations over ecological timescales; Kellner et al. 1992) for pinyon-juniper birds in thinned stands remain unknown and require an understanding of how specific floristic composition and physiognomy changes associated with thinning are impacting birds.

In this study, we used point-count surveys of breeding-bird communities, paired with local measures of floristic composition and vegetation structure, to model habitat relationships in three national parks on the southern Colorado Plateau. We examined these relationships across an eleven-year period (2008-2018) in three parks encompassing a gradient of structural complexity and floristic composition, including a large area of one park that was mechanically thinned. Our objectives were to: (1) quantitatively describe key floristic and structural variables explaining

Fig. 1. Location of point-count stations in three Southern Colorado Plateau Network parks and monuments. Count stations were placed in persistent pinyon-juniper woodland and placed as either a regular grid (Mesa Verde NP and Bandelier NM) or as 3 × 3 grid of count stations centered on a randomly placed GRTS point (Grand Canyon NP) within the ecosite sampling frame (yellow shading).



microhabitat associations for pinyon-juniper bird species on the Colorado Plateau, and (2) use these relationships to understand prospective species responses to drought-related tree die-off and mechanical thinning. As in other habitat studies, we predicted that the most important floristic and structural drivers of breeding-season density would vary greatly among species based on their particular foraging and nesting ecologies.

METHODS

Study sites and sampling design

Bird and habitat data were collected at national parks and monuments in the Southern Colorado Plateau Inventory & Monitoring Network (SCPN), located near the Four Corners region of the Southwestern USA (Fig. 1). These data were collected as part of the network's long-term vital signs bird monitoring program (Holmes et al. 2015) in three parks located in New Mexico, Arizona, and Colorado, respectively: Bandelier National Monument (Bandelier), Grand Canyon National Park (Grand Canyon), and Mesa Verde National Park (Mesa Verde). Bird and habitat variables were sampled in concurrent years, with sample visits to each park occurring every three years, starting in 2008 and running through 2018. Survey data at Bandelier were only collected once, however. The initial survey year varied by park, with habitat data initially gathered in 2008 at Bandelier, in 2009 at Mesa Verde, and in 2011 at Grand Canyon. The number of survey years was therefore variable across parks (N = 1 at Bandelier, 4 at Mesa Verde, 3 at Grand Canyon), and no survey data was collected at any park in 2010, 2013, and 2016. Monitoring efforts were limited to specific plant communities for each park; while a range of plant communities were monitored across the network, we only included pinyon-juniper monitoring points in our analysis. A spatial sampling frame for each plant community was originally created by overlaying National Park Service vegetation and soil classification maps to identify areas of overlap between the focal plant community and soil layers associated with that community (DeCoster et al. 2012, Appendix A). The sampling frame was further reduced by removing areas near roads, human structures, and archaeological sites; areas with a slope of > 30%; and areas more than 2 hours' travel time from crew campsites. Field crews visited all survey points prior to establishment to ground truth habitat assignations. A more complete description of the sampling frame delimitation is provided in Holmes et al. (2015, Appendix A).

The sample replicate for the analysis consisted of individual point-count survey locations, though the spatial sampling regime varied by park. In parks with smaller sampling frames (Bandelier, Mesa Verde), survey points were placed as a regular 200 m grid across the focal habitat (Fig. 1). At Grand Canyon, the large sampling frame precluded this approach, and the sampling scheme consisted of regular clusters of survey points (Fig. 1) placed throughout the sampling frame using the GRTS algorithm (Stevens and Olsen 2004). Clusters comprised 3 × 3 blocks of point-count stations 200 m apart. To account for spatial autocorrelation of survey data in the model, we grouped spatially aggregated survey points at Bandelier and Mesa Verde into clusters. All of the pinyon-juniper study sites were located within natural landscapes and consisted of relatively homogenous persistent woodlands (*sensu* Romme et al. 2009), defined as having moderate to relatively dense canopy cover and a variable but often sparse understory of shrubs, subshrubs, and forbs. The Mesa Verde sites were old-growth woodlands dominated by Utah juniper (*J. osteosperma*) and two-needle pinyon pine (*P. edulis*) with an understory of *Purshia tridentata*, *Artemisia tridentata*, *Cercocarpus montanus*, and *Amelanchier utahensis*. The Grand Canyon sites, located on the South Rim near Pasture Wash, were also dominated by *P. edulis* and *J. osteosperma*, but with a higher basal area of pinyon pine. The understory consisted of *Purshia stansburiana* and *A. tridentata*.

The sites at Bandelier are part of the Pajarito Plateau and represent the most disturbed woodlands. A mass die-off of pinyon pines occurred on the plateau in 2002-2003, resulting in a near total loss (> 95%) of pinyon pines. In addition, Bandelier mechanically thinned ~2,000 ha of the remaining woodlands starting in the spring of 2007 and running through 2010 to prevent soil erosion near archaeological sites. These areas were treated by cutting all live trees < 15 cm in diameter at the root crown, then lopping and scattering the cut vegetation in bare areas. This treatment was designed to mimic the mortality associated with historical surface fires at the site. Of the point-count stations in the monument, 33 (47%) were sampled after the thinning treatment (i.e., sites thinned in 2007 or 2008), 11 were sampled prior to thinning, and 26 stations were never thinned (Appendix 1: Fig. S1). Survey sites at Bandelier therefore represent both thinned and un-thinned sites which experienced pinyon pine die-off. The point-counts and associated vegetation surveys at Bandelier occurred in late May and mid-June 2008, after that year's thinning treatments took place. After treatments, the canopy cover was 10-20%, and the vegetation consisted of *J. monosperma* and very minimal *P. edulis* with a diverse understory of *Quercus undulata*, *Cercocarpus montanus*, and other shrubs and forbs.

Point-count surveys

Breeding-season densities of pinyon-juniper bird species were sampled using eight-minute, unlimited-radius point counts, following the methods described in Holmes et al. (2015, Standard Operating Procedure #4). During survey years, each point-count station was surveyed at least twice; the surveys at Bandelier in 2008 used three replicates, though we only included the first two surveys in analyses. The first surveys took place throughout May and the second surveys took place throughout June, depending on the park and year. In all cases, subsequent visits were separated by three or more weeks. Point-count surveys were conducted by a single trained observer, who identified all individuals seen or heard to species where possible. We subsequently updated the bird taxonomy to match the current American Ornithological Society checklist (Chesser et al. 2024). Surveys took place between a half hour before and four hours after local sunrise. Surveyors recorded the minute of first detection (1-8) and the estimated horizontal distance (in m) between the bird and the observer for each individual or flock detected. Before each survey, observers recorded the date, start time, and environmental factors likely to impact the detectability of birds. These included the estimated wind speed (0-6 on the Beaufort scale), background noise (not counting birdsong, 0-3 scale), and cloud cover (recorded to the nearest 10%). Prior to analysis, we removed any detections recorded as 'flyovers' (individuals flying over the point and not interacting with the local habitat). We also excluded aerially foraging species that are not strongly associated with the habitat variables that we measured: Violet-green Swallow (*Tachycineta thalassina*) and White-throated Swift (*Aeronautes saxatalis*).

Local habitat covariates

We modeled the effects of ten habitat covariates (Table 1), describing both floristic composition and vegetation structure, on breeding-season bird densities. We selected habitat variables that we predicted would change with tree die-off and thinning, and therefore could help explain mechanisms driving changes to breeding-season densities. Species associated with greater sapling density, greater canopy and subcanopy foliar cover, greater canopy height, and higher pinyon pine basal area should be most at risk to future tree die-off and thinning in the region, while species associated with higher juniper basal area, greater shrub foliar cover and height, and greater snag basal area may benefit from future disturbance (refer to Table 1 for a full list of predicted responses to thinning and vegetation die-off). Habitat variables were collected once per survey year at each point-count station following the methods described in Holmes et al. (2015, Standard Operating Procedure #5). Some covariates were collected using a plotless sampling technique directly from the count station, while others were collected in four circular subplots of two different radii (11.3 and 5 m, respectively). The sampling methods used were consistent across sites and years, and for any given habitat measure only a single method was used. The first subplot was centered on the count station, while the center points of the other three were located 30 m from the count station at 0°, 120°, and 240° bearings. Therefore, all habitat measurements represent the local area within ~40 m of the count station and are relatively independent across count stations, which were separated by 200 m. Measures of pinyon pine and snag basal area were collected directly from the count station using an angle gauge as part of a variable area plot technique. In both cases, the observer spun around the count station center point and counted as 'hits' all visible pinyon pines or snags larger than the 10 basal area factor aperture on the angle gauge. The basal area was averaged across subplots to give a mean value for each count station.

Six covariates were collected at the 11.3-m-radius subplot level: foliage height diversity, canopy height class, subcanopy foliar cover class, shrub height class, shrub foliar cover class, and dominant shrub species. Foliage height diversity, a measure of the vertical complexity of foliage strata, was derived from presence-absence data of five vegetation strata: emergent trees, canopy, subcanopy, shrub layer, and dwarf shrub layer (shrubs < 0.5 m tall at maturity; Appendix 1: Fig. S2). In the field, the subcanopy was defined as a distinct stratum of trees (not shrubs) below the canopy stratum, while emergent trees were those with a crown higher than the contiguous canopy. For each subplot, each vegetation stratum was determined to be present or absent. We then determined the proportion of subplots at which each stratum was present and calculated the Shannon's diversity index (*H'*) of these proportions. Higher diversity values are the result of greater proportions of more strata, and therefore represent a more complex vertical vegetation structure. To determine shrub and canopy layer height, observers calculated the average height of the stratum across the subplot using a clinometer and used this value to assign a height class to the subplot. Height classes

Table 1. Local habitat covariates fit to a model of breeding-season bird density. Predicted changes to each habitat element with extreme drought and mechanical thinning are listed.

Variable name	Habitat element measured	Definition	Predicted changes with drought and thinning
Canopy closure (%)	Vegetation structure	Percentage canopy closure calculated using a convex spherical densitometer	Tree die-off and die-back after drought will result in reduced canopy closure. Thinning removes trees, resulting in reduced canopy cover.
Sapling density (stems ha^{-1})	Vegetation structure	Density of 2.5-10 cm DBH saplings, measured in 5-m-radius subplots	Thinning and drought reduce the number of nurse plants for saplings and provide harsher microclimatic conditions for sapling establishment.
Canopy height class	Vegetation structure	Canopy height class (0.5,1,2,5,10,20) averaged across four subplots	Loss of older, taller trees and die-back of canopy foliage during drought should lower canopy height.
Subcanopy foliar cover class	Vegetation structure	Braun-Blanquet subcanopy foliar cover class averaged across four subplots	Subcanopy foliar cover will decrease due to die-off and die-back of trees during drought.
Shrub height class	Vegetation structure	Shrub height class (0.5,1,2,5,10,20) averaged across four subplots	A drought- or thinning-associated reduction in canopy cover should result in increased shrub height
Shrub foliar cover class	Vegetation structure	Braun-Blanquet shrub foliar cover class averaged across four subplots	Canopy die-back and a thinned canopy should provide more light for shrubs, increasing foliar cover.
Foliage height diversity (*H′*)	Vegetation structure	Shannon's diversity index calculated on the proportion of presence of five vegetation strata across four subplots	Foliage height diversity may increase following drought or thinning if understory strata increase in foliar cover.
Snag basal area (m^2 ha^{-1})	Vegetation structure	Basal area of snags (all species) calculated using an angle gauge with 10 basal area factor	Snag basal area will increase following tree die-off. Thinning may remove snags depending on methods used.
Pinyon pine basal area (m^2 ha^{-1})	Floristic composition	Basal area of *P. edulis*, calculated using an angle gauge with 10 basal area factor	Pinyon pines are more drought sensitive than junipers, resulting in greater proportional losses during drought.
Dominant shrub species	Floristic composition	Modal dominant shrub species listed across four subplots	Understory species turnover may drive a shift to less drought-sensitive shrub species.

consisted of 0.5, 1, 2, 5, 10, and 20, with each value representing the maximum height of that class in meters. For the subcanopy and shrub layers, the percentage foliar cover over each subplot was estimated using the Braun-Blanquet scale (1-7 values; Wikum and Shanholtzer 1978). In each case, we averaged the four subplot height and foliar cover class values to obtain a measurement for each count station. Lastly, observers listed the top three shrub species in each subplot in order of dominance (no shrubs were listed when no shrubs were present). We selected the modal most dominant shrub species for each count station (i.e., across the four subplots) in each year surveyed as a measure of understory plant composition.

Two additional covariates were collected within 5-m-radius subplots at each count station: percentage canopy closure and sapling density. Canopy closure was calculated in each cardinal direction from the center point of each subplot using a convex spherical densiometer; we averaged the canopy closure values from each cardinal direction at each subplot to calculate a measure for the count station as a whole. The total number of saplings with a DBH of 2.5 to < 10 cm were tallied for each subplot, and we calculated the stem density of saplings at each count station by dividing the total number of saplings counted by the total area surveyed.

Modeling habitat associations

We adapted a single-species Bayesian hierarchical mixture model developed by Amundson et al. (2014) to estimate bird density in each of the 3 parks using data from the first two surveys conducted at each count station in each survey year. Our model makes use of several sub-models including an *N*-mixture model of abundance (Royle, 2004) and models of detectability based on time removal (availability) and distance sampling (perceptibility; Farnsworth et al. 2002). This approach allows for the simultaneous estimation of availability (p_a; probability an individual was available for detection by signaling its presence), perceptibility (p_d; probability an available individual was perceived by an observer), and true abundance during survey k (N_k). We modeled N_k as a Poisson random variable with mean l_k (k in 1, ..., K surveys, where $K = \sum$ surveys/station/year) which was related to the survey-specific count (y_k) as

$$y_k \sim \text{Binomial}(n_k, p_{d[k]}) \qquad (1)$$

$$n_k \sim \text{Binomial}(N_k, p_{a[k]}) \qquad (2)$$

where n_k denotes the number of individuals available for detection.

We modeled survey-specific heterogeneity in p_a and p_d as detailed in Amundson et al. (2014). Briefly, the model assumes that individuals were available with probability a during each minute of an eight-minute survey period. As a result, the availability during interval j of survey k is given by $\pi_{jk} = a_k(1 - a_k)^{j-1}$. The corresponding conditional probability is given by

$$\pi_{jk}^{c} = \pi_{jk} / p_{a[k]} \qquad (3)$$

where $p_{a[k]} = \sum_j \pi_{jk}$ represents the probability an individual is available during at least one interval during survey k. Following Jones et al. (2024), we modeled availability as logit(1-a_k) = b_0 + $b_1$minute of day$_k$ + $b_2$ordinal date$_k$ + $b_3$ordinal date^2_k + $b_4$cloud cover$_k$. This model included fixed effects of minute of day, ordinal date (both linear and quadratic terms), and cloud cover (less than or greater than 50%). We modeled perceptibility using observed horizontal detection distances and considering the probability that an individual was detected in distance bin $b = 1, ..., B$ of survey k as $p_{d[k]} = \Sigma_b\ \pi_{d[bk]}$, with corresponding conditional probability

$$\pi^{c}_{d[bk]} = \pi_{d[bk]}/\Sigma_b \pi_{d[bk]} \tag{4}$$

We modeled detection distances using a half-normal distribution,

$$\pi_{d[bk]} = \exp(-r_b^2/2\sigma_k^2)(2r_b\delta_b/r_{max}^2) \tag{5}$$

where r_b is the midpoint distance of bin b, δ_b is the width of bin b, σ_k shapes the decline in detection probability with distance, and r_{max} is the species-specific maximum detection distance. We omitted either 5% or 10% of the farthest observations of each species to avoid fitting sparse data from the tail of the distribution of detection distances and to ensure that the detection interval and detection-distance bin were statistically independent. Where necessary, we truncated further distant detections until detection interval and detection-distance bin were statistically independent. We tested for independence using analysis of variance, making use of a conservative alpha value (0.10) where possible, or the standard alpha value (0.05) when necessary to avoid excessive truncation. Following Jones et al. (2024), heterogeneity in perceptibility was modeled as $\log(\sigma_k) = \log(\sigma_0) + b_1\text{noise}_k + b_{2k[\text{surveyor}]}$, which included a fixed effect of environmental noise during the survey and a random effect of surveyor.

We modeled mean population size as $\log(l_k) = b_{0k[\text{cluster[station]}]} + b_{1k[\text{year}]} + b_{2k[\text{dominant shrub}]} + b_3\text{canopy closure}_k + b_4\text{sapling density}_k + b_5\text{snag basal area}_k + b_6\text{Pinyon pine basal area}_k + b_7\text{canopy height class}_k + b_8\text{subcanopy foliar cover}_k + b_9\text{shrub height class}_k + b_{10}\text{shrub foliar cover}_k + b_{11}\text{foliage height diversity}_k$. This model includes a random intercept term for station nested within cluster to account for spatial autocorrelation, as well as random intercept terms for the year and the dominant shrub species for each survey, and fixed slope effects for the other survey-specific habitat covariates (listed above). We chose to model the effects of both habitat structural features and plant species composition on abundance because birds are known to preferentially forage in specific plant species within a given stratum (e.g., Wood et al. 2012) and we were therefore interested in determining the relative importance of pinyon pine versus juniper in the canopy stratum and of specific shrub species in lower strata in shaping local abundance. We modeled the effect of the dominant shrub as a random effect due to the large number of taxa (19) and the fact we were already fitting a large number of fixed habitat effects in the abundance sub-model. While there are no tests of overfitting that have been developed for Bayesian hierarchical models, following the rough guideline of $N/k \geq 10$ (662 replicate surveys for each species / 9 fixed effects), our models are not overfit. We did not include park-specific effects within our model because only one park was surveyed per year, and Bandelier was only surveyed once (in 2008), and as a result the year effect for 2008 and the park effect for Bandelier would be confounded. Given this study design, the survey year captures information about both the year of the survey, as well as the park which was surveyed. Therefore, we report approximate 'park effects' which were calculated by stacking the posterior distributions of the random year effects for the years a given park was surveyed (Bandelier: 2008 only; Grand Canyon: 2011, 2014, and 2017; Mesa Verde: 2009, 2012, 2015, and 2018).

For each park, we reported the mean breeding-season density (birds ha^{-1}) across the sampled area while accounting for the species-specific sampled area (determined by the species-specific r_{max}) as

$$\text{mean}(\text{N}_{k[\text{park}]})/[\pi r_{max}^2/10{,}000] \tag{6}$$

We also calculated an overall density across parks as a weighted average of the proportion of the total sampling area of inference that occurred within each park (219.63 ha in Bandelier, 2138.68 ha in Grand Canyon, and 459.48 ha in Mesa Verde). Notably, individuals with home ranges that partially overlap the survey area violate the closure assumption of N-mixture models; therefore, our estimates of N_k, as well as our estimates of park-specific and overall density, should be interpreted as the number of individuals using the sampling area as opposed to the number permanently present therein (Latif et al. 2016).

Parameter estimation

We fit models in JAGS version 4.3.0 (Plummer 2003) using the 'jagsUI' package (Kellner 2024) in R version 4.3.3 (R Core Team 2024). We standardized all continuous covariates prior to analyses, and we only included complete cases in the analysis. Kendall's rank correlation was less than 0.5 for all included covariates. The variance inflation factor for all fixed covariates was < 3 (mean = 1.48, range = 1.06-2.12), suggesting a lack of multicollinearity in the data. We modeled the priors for fixed effects using a normal distribution with mean of 0 and precision of 0.01. The prior for the random station within cluster intercept was a normal distribution with a mean given by each station's cluster effect and precision t_{station}, with the prior for the cluster effects being normally distributed with a mean of 0 and precision t_{cluster}. Similarly, we assumed the random effects for year and dominant shrub species were normally distributed with a mean of 0 and precision t_{year} and t_{shrub}, respectively. We used a gamma distribution with both a shape and rate of 0.1 for the precision (t) of all random effects. We ran three chains for 110,000 iterations each, with a burn-in of 50,000 iterations. We thinned each chain by 30, yielding a joint posterior distribution of 6,000 samples. We assessed convergence of the chains via inspection of the MCMC summaries and the Gelman-Rubin statistic (R-hat; Gelman and Rubin 1992); chains were considered converged when R-hat < 1.2 (Kéry and Schaub 2012). Goodness-of-fit for the availability and perceptibility sub-models was assessed using posterior predictive checks in the form of Bayesian P-values derived from the posterior distributions, as suggested by MacKenzie et al. (2017) and as implemented in Jones et al. (2024). P-values near 0.5 indicate an adequate fit and $P < 0.2$ or $P > 0.8$ indicating an inadequate fit. We report the 90% Bayesian credible interval (BCI) for each parameter, which is thought to be more stable than the 95% credible interval (Kruschke 2015). We considered a relationship between a covariate and the relevant sub-model supported if the 90% BCI for its coefficient did not include zero. To obtain effect sizes for covariates across the full community, we stacked the joint posterior distributions of each parameter estimate for all species and derived the mean and 90% BCI.

Table 2. Pinyon-juniper bird species included in the study and associated functional traits. Species are listed in alphabetical order by four-letter Alpha Code. Bird taxonomy follows the 2024 American Ornithological Society checklist (Chesser et al. 2024). Categorical data on diet guild, foraging behavior and substrate, nest type, and height bands used within pinyon-juniper woodland were extracted from the Birds of the World database.

Alpha code	Common name	Latin name	Diet	Foraging behavior	Foraging substrate	Nest type	Height band(s)
ATFL	Ash-throated Flycatcher	*Myiarchus cinerascens*	Insectivore	Sally	Foliage, ground	Cavity	Midstory, understory
BCHU	Black-chinned Hummingbird	*Archilochus alexandri*	Nectarivore	Sally, glean	Generalist	Cup	Generalist
BEWR	Bewick's Wren	*Thryomanes bewickii*	Insectivore	Glean, probe	Foliage, branch	Cavity	Understory
BGGN	Blue-gray Gnatcatcher	*Polioptila caerulea*	Insectivore	Glean, flush-pursue	Foliage	Cup	Canopy, midstory
BHCO	Brown-headed Cowbird	*Molothrus ater*	Omnivore	Glean	Ground	Nest parasite	Ground
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	Omnivore	Glean	Foliage	Cup	Canopy, understory
BTHU	Broad-tailed Hummingbird	*Selasphorus platycercus*	Nectarivore	Sally, glean	Foliage, air	Cup	Understory
BTYW	Black-throated Gray Warbler	*Setophaga nigrescens*	Insectivore	Glean	Foliage	Cup	Canopy, midstory
BUSH	Bushtit	*Psaltriparus minimus*	Insectivore	Glean	Foliage	Pendent	Midstory, understory
CHSP	Chipping Sparrow	*Spizella passerina*	Omnivore	Glean	Ground, foliage	Cup	Understory, ground
CORA	Common Raven	*Corvus corax*	Omnivore	Glean	Ground	Platform	Ground
DUFL	Dusky Flycatcher	*Empidonax oberholseri*	Insectivore	Sally	Air	Cup	Midstory, understory
GRFL	Gray Flycatcher	*Empidonax wrightii*	Insectivore	Sally	Air, ground, foliage	Cup	Understory, ground
GRVI	Gray Vireo	*Vireo vicinior*	Insectivore	Glean	Foliage, branch	Cup	Understory, ground
HAWO	Hairy Woodpecker	*Dryobates villosus*	Insectivore	Peck	Trunk	Cavity	Midstory
JUTI	Juniper Titmouse	*Baeolophus ridgwayi*	Omnivore	Glean	Foliage, branch	Cavity	Canopy, midstory
MOCH	Mountain Chickadee	*Poecile gambeli*	Omnivore	Glean	Foliage, branch	Cavity	Canopy, understory
MODO	Mourning Dove	*Zenaida macroura*	Granivore	Glean	Ground	Platform	Ground
PIJA	Pinyon Jay	*Gymnorhinus cyanocephalus*	Omnivore	Glean, probe	Ground, foliage	Cup	Canopy, ground
PLVI	Plumbeous Vireo	*Vireo plumbeus*	Insectivore	Glean	Foliage, branch	Cup	Canopy, understory
SPTO	Spotted Towhee	*Pipilo maculatus*	Omnivore	Glean	Ground	Cup	Understory, ground
WBNU	White-breasted Nuthatch	*Sitta carolinensis*	Omnivore	Glean	Trunk, branch	Cavity	Canopy, midstory
WEBL	Western Bluebird	*Sialia mexicana*	Omnivore	Sally-pounce	Ground, foliage	Cavity	Canopy, ground
WETA	Western Tanager	*Piranga ludoviciana*	Insectivore	Glean, sally	Air, foliage	Cup	Canopy, midstory
WOSJ	Woodhouse's Scrub-Jay	*Aphelocoma woodhouseii*	Omnivore	Glean	Foliage, ground	Cup	Understory, ground

To visualize patterns of species responses across covariates, we ran a principal components analysis (PCA) on the mean effect sizes of each species to the nine fixed habitat covariates. We excluded three outlier species (Black-chinned Hummingbird [*Archilochus alexandri*], Brown-headed Cowbird [*Molothrus ater*], and Dusky Flycatcher [*Empidonax oberholseri*]) from the PCA to avoid biasing the ordination.

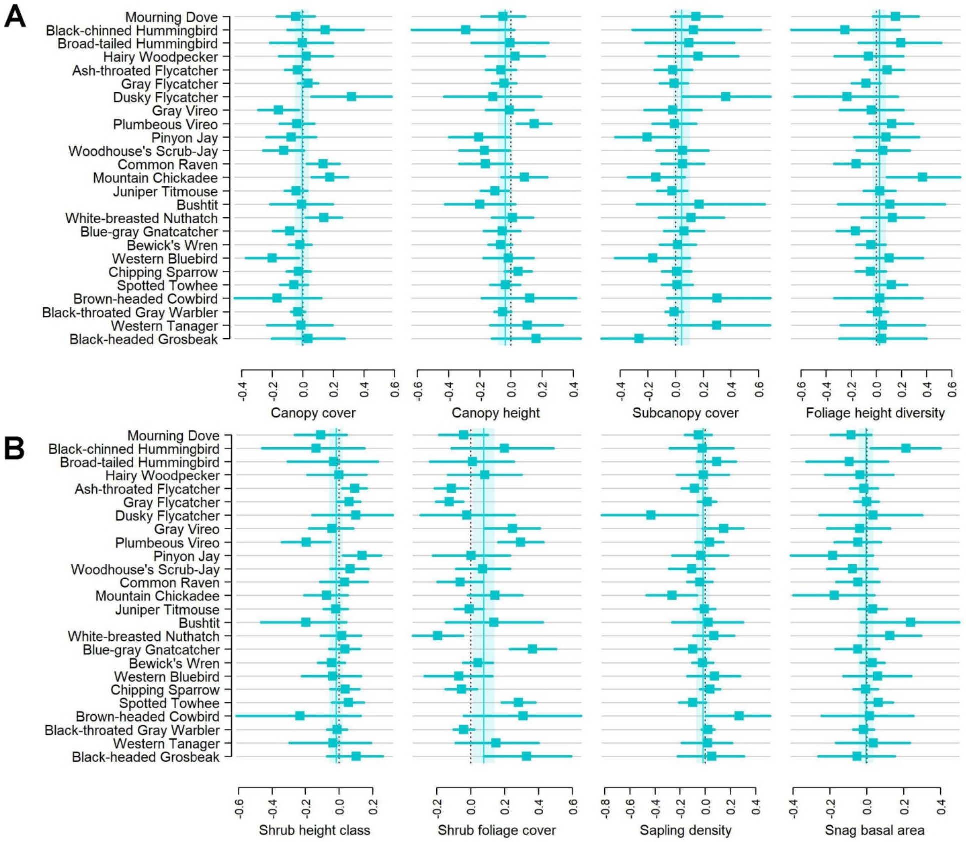
RESULTS

Point-count surveys and associated habitat data were collected in eight of the 11 years of the 2008-2018 timeseries, during which time 16 observers conducted 1,324 point-count surveys (after removing incomplete cases of habitat data) at 246 unique count stations (*N* of count stations = 70 at Bandelier, 90 at Grand Canyon, and 86 at Mesa Verde). Overall, both vegetation structure and plant species composition varied considerably across the three parks (described in the Supplemental Materials). Bird surveys resulted in 14,126 unique detections, of which 14,025 could be identified to species. Surveyors identified 93 species across all surveys (Appendix 1: Table S1); of these we modeled habitat relationships for 31 species with sufficient sample size of detections, and models converged for 25 species (Table 2). R-hat values were ≈ 1 for the parameters of interest for all modeled species, though some random effects of site showed R-hat values between 1.1 and 1.2. We fit the same model for all species modeled. Distance sampling model parameterizations for each species are reported in Appendix 1: Table S2; overall, we truncated 11.60 ± 6.55% of detections (mean ± SD), though the maximum detection distance (mean ± SD = 107.36 ± 64.40 m; range = 25-300 m) and effective area surveyed (mean ± SD = 4.87 ± 6.66 ha; range = 0.20-28.30 ha) varied significantly across species (Appendix 1: Table S2). The modeled estimates of availability were generally high (0.59 ± 0.27; mean ± SD of mean values of p_a; Appendix 1: Table S3, Fig. S3), though estimated average perceptibility was much lower (0.40 ± 0.14; mean ± SD of median values of p_d). We found a high goodness-of-fit for both detectability sub-models, as measured by Bayesian P-values (Appendix 1: Table S3, Fig. S3). We found supported responses for each of the five fixed covariates fit on the p_a and p_d sub-models, though the number of species with supported responses varied considerably across covariates (Appendix 1: Table S4, Fig. S4).

Breeding-season density across parks

We found an average overall breeding-season density of ~1 bird ha^{-1} (1.07 ± 1.60; mean ± SD of mean values), though density varied considerably among species, and, for some species, among parks (Appendix 1: Table S5, Fig. S5). The species with the highest mean densities across parks were Black-chinned Hummingbird (7.75 birds ha^{-1}), Black-throated Gray Warbler (*Setophaga nigrescens*; 3.28 birds ha^{-1}), Bushtit (*Psaltriparus minimus*; 2.14 birds ha^{-1}), Juniper Titmouse (*Baeolophus ridgwayi*; 1.90 birds ha^{-1}), and Gray Flycatcher (*Empidonax wrightii*; 1.89 birds ha^{-1}). We found large effect sizes, and numerous supported responses, of park effects on breeding-season density (Appendix 1: Table S6, Fig. S6); we estimated park effects by stacking the posterior distributions of all year effects for years in which a park was surveyed (only one park was surveyed per year). Notably, we found a relatively large negative effect size of Bandelier on density (-0.75 [-4.24, 1.01]; mean and 90% BCI of the stacked joint posterior distributions across species), with nine supported

Fig. 2. Log-scale beta effect sizes of microhabitat vegetation structure on the breeding-season densities of 25 Southwestern bird species in persistent pinyon-juniper woodlands. Bird species are listed in taxonomic order following the American Ornithological Society's 2024 checklist. Mean effect sizes and 90% Bayesian credible intervals are plotted for each covariate, while vertical lines and shaded area represent the mean and standard error of the effect size across species. Variables related to (A) canopy structure are plotted on the top row and (B) understory structure are plotted on the bottom row.

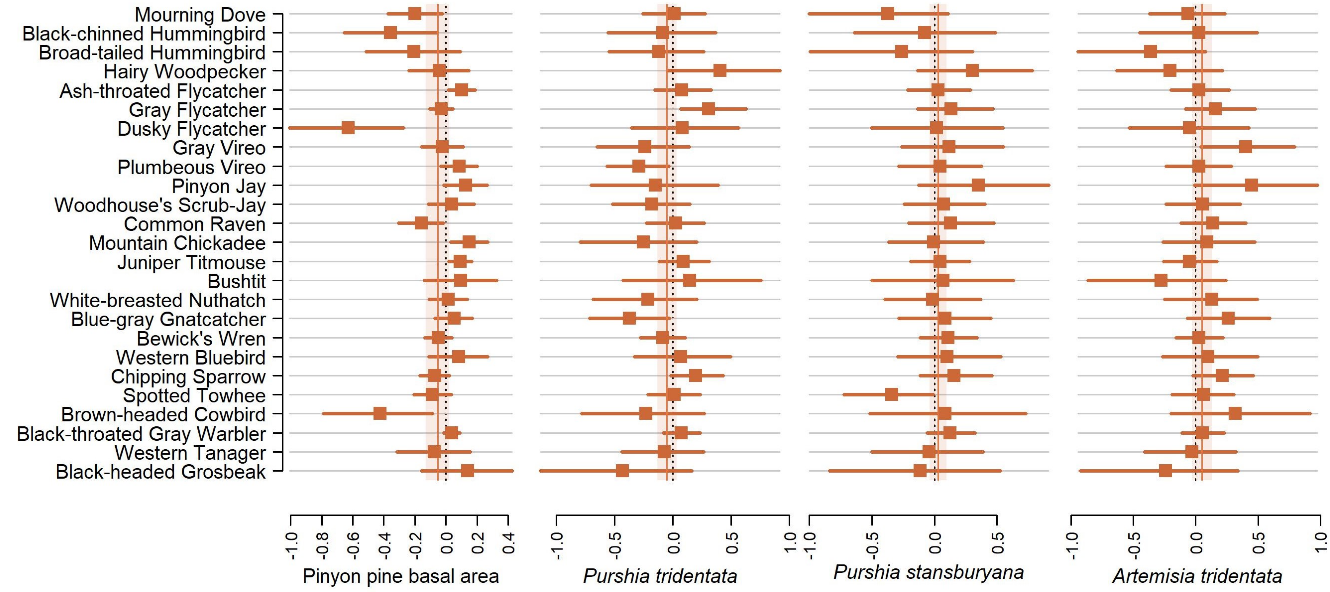


negative effects (4 supported positive effects). Six of the modeled species were either not detected (Mountain Chickadee [*Poecile gambeli*] and Gray Vireo) or detected in very low numbers (< 15 detections; Plumbeous Vireo [*Vireo plumbeus*], Pinyon Jay, Bushtit, and White-breasted Nuthatch [*Sitta carolinensis*]) at Bandelier. The park effect for Grand Canyon was also negative (-0.22 [-2.40, 1.62] mean and 90% BCI of the stacked joint posterior distributions across species), though there were fewer supported effects on density (5 supported negative effects, 3 supported positive effects). The Mesa Verde park effect had the smallest average effect size (-0.13 [-2.27, 1.52] mean and 90% BCI of the stacked joint posterior distributions across species), though species-level effect sizes were still generally large (3 negative supported effects, 4 supported positive effects).

Effects of floristic composition and vegetation structure on breeding-season density

Overall, we found supported responses to all ten microhabitat variables, and 18 of 25 species (72%) showed a supported effect of at least one of these covariates, though effect sizes on density were generally small. The effects of vegetation structure on density were generally better supported than those of floristic composition (Fig. 2, Fig. 3, Tables S7 and S8), though community mean effect sizes were near zero in most cases. In spite of the thinning and large-scale pinyon-pine die-off at Bandelier, we found few supported effects of canopy cover (-0.005 [-0.23, 0.26], mean and 90% BCI effect size of the stacked joint posterior distributions across species; 4 positive, 2 negative supported effects) and canopy height (1 positive, 3 negative supported effects) on breeding-season densities, though there was a trend of higher densities with decreasing canopy height (-0.04 [-0.31, 0.22]; mean and 90% BCI effect size across species). Instead, we found that a lower foliage stratum more strongly predicted density. Increasing foliage cover in the shrub layer (0.08 [-0.20, 0.41]; mean and 90% BCI effect size across species; 5 positive, 3 negative supported effects), but not the subcanopy (0.04 [-0.29, 0.44]; mean and 90% BCI effect size across species; 1 positive, 0 negative supported effects), was positively associated with breeding-season densities of some species, though community responses were variable (Fig. 2). While foliage cover in species-specific strata had supported effects on densities, the overall number of strata with foliage present (foliage height diversity) did not strongly influence densities for most species (0.02 [-0.31, 0.37]; mean and 90% BCI effect size across species; 1 positive, 1 negative supported effects).

Fig. 3. Log-scale beta effect sizes of microhabitat-level floristic composition on the breeding-season densities of 25 Southwestern bird species in persistent pinyon-juniper woodlands. Bird species are listed in taxonomic order following the American Ornithological Society's 2024 checklist. Mean effect sizes and 90% Bayesian credible intervals of the joint posterior distribution are plotted for each covariate, while the vertical lines and shaded area represent the mean and standard error of the mean effect sizes across species. The effect of pinyon pine basal area was fit as a fixed effect, while the effect of the dominant shrub species (estimated in the field by surveyors) was fit as a random effect on density. Effect of dominance of each of the three most abundant shrub species across parks is plotted.



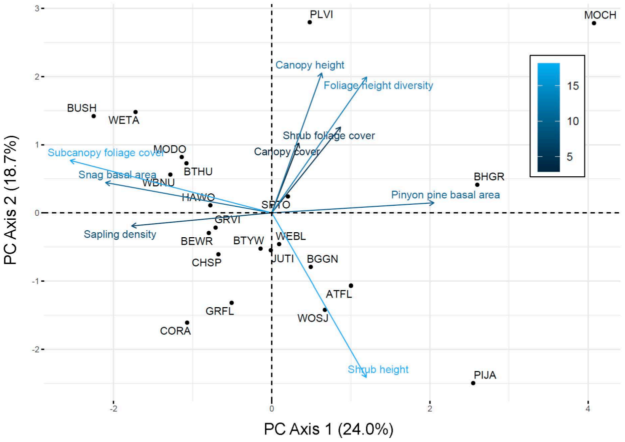
Other structural variables also had little effect on density, including shrub height (-0.02 [-0.28, 0.18]; mean and 90% BCI effect size across species; 2 positive, 1 negative supported effects), snag basal area (-0.003 [-0.23, 0.25]; mean and 90% BCI effect size across species; 1 positive, 0 negative supported effects), and sapling density (-0.02 [-0.30, 0.24]; mean and 90% BCI across species; 1 positive, 2 negative supported effects). Overall, species responses to structural variables were linear and generally small (Appendix 1: Fig. S8, Fig. S9), with the exception of non-linear positive responses to increasing shrub foliage cover (Appendix 1: Fig. S10).

We also found supported effects of floristic composition on breeding-season densities at the microhabitat scale (Fig 3 and Appendix 1: Fig. S6, Table S8). There was a small but negative overall effect of two-needle pinyon pine (*P. edulis*) basal area on bird densities (-0.05 [-0.52, 0.21]; mean and 90% BCI effect size across species) and many supported effects among individual species (5 negative, 3 positive supported effects). However, we found only 7 supported effects (4 negative, 3 positive) of dominant shrub species on breeding-season densities. Species responses were generally idiosyncratic, though there was a weak community trend of lower densities where antelope bitterbrush (*P. tridentata*) dominated (-0.05 [-0.58, 0.43]; mean and 90% BCI effect size across species) and higher densities where big sagebrush (*A. tridentata*) dominated (0.05 [-0.45, 0.53]; mean and 90% BCI effect size across species). Average effect sizes across species were near zero for most shrub species, however (Fig. 3, Appendix 1: Fig. S7). Blue-gray Gnatcatcher (*Polioptila caerulea*) responded most strongly to shrub composition, showing a supported negative effect of antelope bitterbrush (-0.37 [-0.71, -0.03]) and positive supported and near-supported effects of Utah serviceberry (*Amelanchier utahensis*; 0.74 [0.19, 1.31]) and alderleaf mountain mahogany (*C. montanus*; 0.36 [-0.04, 0.78]), respectively. Because other shrub species had low sample sizes of points at which they were classified as dominant (Appendix 1: Table S9), we do not report their effect sizes on bird density.

Patterns of species responses across habitat variables

Based on an examination of a scree plot and the axis Eigenvalues, we retained and plotted the first two PCA axes, representing 42.8% of the variance (Fig. 4). While this represents a smaller percentage of the total variance, the PCA did not include the year effects, which had much larger effect sizes on abundance. The first axis had an Eigenvalue of 2.16 and explained 24.0% of the variance (Appendix 1: Table S10). The species responses to pinyon pine basal area (0.43), foliage height diversity (0.25), snag basal area (-0.44), subcanopy foliage cover (-0.54), and sapling density (-0.37) loaded heavily on this axis (Appendix 1: Table S11), which we interpret as a measure of species' associations with early-successional or die-off associated woodlands characterized by high snag densities and many young conifers (negative values) or late-successional pinyon-pine-dominated (positive values) woodlands. The second axis had an Eigenvalue of 1.69 and

Fig. 4. PCA bi-plot of breeding-season density responses to microhabitat variables across a Southwestern persistent pinyon-juniper woodland community. The mean effect size of each covariate on each species was ordinated to visualize responses to groups of variables; we excluded Black-chinned Hummingbird (*Archilochus alexandri*), Brown-headed Cowbird (*Molothrus ater*), and Dusky Flycatcher (*Empidonax oberholseri*) from the ordination because these species had large outlier values. Length and direction of each arrow represents the size and magnitude of the loading of each variable on each axis, while arrows are color coded by their average contribution to the first two PC axes. Species codes follow the four-letter codes described in Appendix 1: Table S1; species scores are provided in Appendix 1: Table S10. Species scores indicate that the community is segregated by woodland successional stage (first axis), and that half of the species are associated with a reduced vertical vegetation complexity (second axis).



explained 18.7% of the variance, with high positive loadings of responses to canopy height (0.49), foliage height diversity (0.48), and shrub foliage cover (0.30) and high negative loadings of response to shrub height (-0.58). We, therefore, interpreted this axis as a measure of association with greater vertical foliage structure (positive values), typically characterized by greater presence of foliage strata in the shrub layer, midstory, and canopy. Overall, species scores were concentrated in the lower left quadrant (Appendix 1: Table S12; Fig. 4).

DISCUSSION

We found numerous supported responses to microhabitat variables across 18 of 25 species, though park-level effects were an order of magnitude larger than microhabitat effects. Our results suggest that pinyon-juniper specialist birds are relatively resilient to loss of canopy cover at local scales, with only generalist species of forests and woodlands showing a supported association with greater canopy cover (Fig. 2a). There were no clear threshold values in canopy cover affecting breeding densities (Appendix 1: Fig. S8), though nine species, including many insectivorous foliage gleaners, showed a supported negative effect of Bandelier on density after a large-scale pinyon pine die-off (and associated reduction in canopy cover; Appendix 1: Fig. S6), suggesting potential landscape-level canopy cover effects not captured in our models. Species also showed limited associations, positive or negative, with pinyon-pine basal area (Fig. 3), perhaps indicating a selection for both tree species. Exceptions to this trend included positive associations with greater pinyon pine basal area of cavity-nesting birds (3 species), and negative associations of species associated with canopy gaps (5 species). Our results suggest that the extent of shrub foliage cover in the woodland understory is a major factor in shaping the functional composition of the insectivorous bird guild in pinyon-juniper woodlands. Foliage gleaning bird species (5 species), of both canopy and understory, showed positive supported associations with shrub foliage cover, while aerial insectivores (2 species) and bark foragers (1 species) were negatively associated with this structural feature (Fig. 2b). An ordination of species' responses to all microhabitat features (Fig. 4) suggests that the community segregated along a woodland successional gradient, and generally preferred a simplified vertical vegetation structure.

Resilience of PJ-specialist birds to canopy cover loss, but potential landscape effects

We found few supported effects of canopy cover or height on density across the range of variables included in the study (~10-40% canopy cover), and estimated species densities showed gradual and largely linear changes across the gradient of canopy cover (Appendix 1: Fig. S9a, Fig. S10). When evaluating habitat associations over larger intervals of canopy cover (i.e., from mature woodland to treeless shrubland), other studies have found most pinyon-juniper bird species prefer more wooded conditions (Sedgwick 1987, Pavlacky and Anderson 2004, Knick et al. 2017). However, our results agree with Magee et al. (2019) in that most of the pinyon-juniper community was relatively resilient to moderate, local reductions in canopy cover. This may be due to the large variability inherent in pinyon-juniper woodlands, which encompass everything from open shrub-dominated savanna to closed-canopy woodlands (Romme et al. 2009, Muldavin and Triepke 2020). The persistent woodlands sampled in this study likely represent the more mesic, closed-canopy end of this gradient, and, therefore, lower canopy cover in this environment is likely well within the natural range of variation for the habitat. More open canopy structures may also have existed prior to European settlement (Landis and Bailey 2005), and open canopies may harbor a greater diversity of canopy arthropods (Müller et al. 2014). Unlike pinyon-juniper specialist species, we found supported effects of canopy cover on the densities of five generalist species of conifer forest and woodlands. Magee et al. (2019) also found that generalist forest species, including Mountain Chickadee and White-breasted Nuthatch, showed reduced occupancy in thinned pinyon-juniper landscapes, suggesting a sensitivity to reduced canopy cover. This relationship is unusual, because habitat-specialist birds are typically more sensitive to disturbance than generalists (e.g., Devictor et al. 2008), and may reflect adaptations by pinyon-juniper specialists to exploit the variable nature of their habitat.

Extreme thinning (removal of > 90% of tree cover), however, has resulted in local extirpations or reduced densities of many pinyon-juniper bird species (Crow and van Riper 2010, Bombaci et al. 2017, Johnson et al. 2018), and suggests that a minimum threshold of canopy cover may be necessary for maintaining pinyon-juniper woodland species. Although we found no evidence for such a minimum canopy cover threshold, local-scale habitat associations may also not be good predictors of landscape-level occupancy (Farrell et al. 2019), and negative effects of canopy cover loss on pinyon-juniper birds appear to be more pronounced at the landscape level (Magee et al. 2019). We found nine supported negative effects of Bandelier on breeding-season densities, including pinyon-juniper specialists, where a landscape-scale die-off resulted in > 95% loss of pinyon pines five years prior to sampling. While it is impossible to definitively conclude that the die-off, and resulting loss of canopy cover, was responsible for local declines and extirpations, this interpretation is supported by a concurrent long-term study on the adjacent Los Alamos National Laboratory property that found similar declines and extirpations during this time period (Fair et al. 2018). The pinyon pine die-off event and thinning are partially confounded at the Bandelier study sites, but Fair et al. (2018) found that declines occurred in both thinned and un-thinned stands following the die-off, with abundance and richness declining faster at the thinned sites. Therefore, the landscape-level loss of canopy cover may be important in driving declines in addition to any effects of the loss of pinyon pines *per se*. However, breeding bird density was significantly correlated with pinyon pine density in at least one study (Masters 1979).

In contrast to the lack of effect of canopy cover, we found supported associations with lower canopy height for three pinyon-juniper specialist species: Juniper Titmouse, Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*), and Pinyon Jay. These species are thought to be year-round residents in pinyon-juniper woodlands, and their association with lower canopies may reflect a preference for drier microhabitats on south and east facing slopes. South-facing aspects in pinyon-juniper woodlands are known to have lower soil moisture and conifer cover (Westerband et al. 2015), lower primary productivity (Huang et al. 2012), and less conifer recruitment (Greenwood and Weisberg 2009), potentially leading to lower canopy heights and larger areas of bare ground. Lower canopy heights were also associated with less productive soil types in the Great Basin (Greenwood and Weisberg 2009). Woodlands with lower conifer cover have higher solar radiation and soil temperatures (Royer et al. 2012), likely reducing snow cover in winter and leading to warmer microclimates during the non-breeding season. Juniper Titmouse had a significantly higher occupancy on south-facing slopes in Wyoming (Pavlacky and Anderson 2001), and Pinyon Jay has been documented to use more open habitats during the non-breeding season (Johnson et al. 2016). In addition, all of these species likely engage in seed-caching behavior during the fall and winter months, with the two corvids in particular caching large numbers of pinyon pine seeds in bare ground (Vander Wall and Balda 1981, Marzluff and Balda 1992). Sites with low canopy cover may correspond with preferred caching and foraging locations, which tend to be south-facing, open microhabitats (Marzluff and Balda 1992, Boone et al. 2021, Sicich et al. 2025). A better understanding of how topography, particularly aspect and slope position, affect habitat suitability for pinyon-juniper specialist birds is needed.

Associations with pinyon pines are driven by nesting ecology and habitat preferences

At the microhabitat scale, pinyon-juniper bird species showed few associations with a specific floristic composition within persistent woodlands, with neither tree nor shrub species composition showing many supported effects on density. At the larger landscape scale, pinyon-juniper species are associated with pinyon pines and junipers over other conifer species (Zillig et al. 2023), and many obligate and semi-obligate species are not found in other habitat types throughout their western North American range (Paulin et al. 1999, Van Lanen et al. 2023). Within pinyon-juniper woodlands, however, both tree (typically two intermixed species) and shrub (dominated by one or two species; Appendix 1: Fig. S7) species richness at our sites was low, perhaps providing fewer opportunities for selection of individual plant species. While bird species are not strongly associated with pinyon pines over junipers at our relatively homogenous study sites, many pinyon-juniper birds showed a significant association with pinyon pine presence at a site in southwestern Wyoming where this tree is scarce (Pavlacky and Anderson 2001). Therefore, relative preferences for tree species may be tied to landscape-level tree distributions. Alternatively, species may be selecting for a balance of juniper and pinyon pine on the breeding territory. The vast majority of pinyon-juniper bird species studied in New Mexico preferentially nested in junipers relative to their abundance (Goguen et al. 2005, Francis et al. 2011). By contrast, studies of foraging substrates have found that many pinyon-juniper birds preferentially forage in pinyon pines (Laudenslayer and Balda 1976, Masters 1979). Keane and Morrison (1999) found, for example, that Black-throated Gray Warblers foraged more than twice as often in pinyon pines as in junipers, and that pinyon pines tended to contain higher arthropod abundances than junipers. Pinyon pines may also contain a greater foliage surface area (Laudenslayer and Balda 1976), and harbor a distinct arthropod community relative to junipers (Riskas 2021). Therefore, selecting for a mix of pinyon pine and juniper on the breeding territory may facilitate an optimization between nesting and foraging microhabitats.

The three species that showed supported responses to higher pinyon pine basal area were all cavity-nesting species: Mountain Chickadee, Juniper Titmouse, and Ash-throated Flycatcher (*Myiarchus cinerascens*; Table 2). Nest cavities may be a limiting resource on the breeding densities of these species, and Masters (1979) also found that pinyon pine densities explained the density of cavity-nesting species. Pinyon pines are more drought sensitive than junipers (Mueller et al. 2005) and are, therefore, more likely to be weakened by bark beetles or disease, facilitating cavity excavation. These bird species are secondary cavity nesters which frequently use woodpecker-excavated nest cavities (Youkey 1990), and the most common woodpecker species in this habitat (Hairy Woodpecker, *Dryobates villosus*) may preferentially nest in pinyon pines (Francis et al. 2011). Five species of woodland edge or treefall gaps also showed supported associations with lower pinyon pine basal area: Mourning Dove (*Zenaida macroura*), Black-chinned Hummingbird, Dusky Flycatcher, Common Raven (*Corvus corax*), and Brown-headed Cowbird. These species may select for canopy gaps that are often caused by local-scale pinyon-pine die-offs from fungal or beetle infestations (Floyd et al. 2003), and which, therefore, tend to have lower pinyon pine basal area. Alternatively, these species may prefer early-successional (e.g., stage I and stage II) woodlands, which tend to be juniper-dominated (Huffman et al. 2012, Miller et al. 2019).

Shrub foliage density shapes functional composition of the insectivore guild

We found numerous supported responses of insectivorous birds to the foliage cover of shrubs, with both positive and negative responses. Five species of foliage gleaning insectivores showed non-linear positive associations with greater shrub cover (Appendix 1: Fig. S8c, Fig. S10). Increasing shrub foliage cover from < 1% to 25-50% lead to estimated density increases of 205% for Blue-gray Gnatcatcher, 179% for Black-headed Grosbeak, 166% for Brown-headed Cowbird, 147% for Plumbeous Vireo, 136% for Spotted Towhee, and 114% for Gray Vireo, among others. While some birds prefer shrub-dominated shrubland-woodland ecotones in the Great Basin, the species that showed positive associations with shrubs at our sites are generally species that occur in woodland interior (Sedgwick 1987, Pavlacky and Anderson 2004). Blue-gray Gnatcatcher breeding densities are known to be positively associated with Rosaceae shrub density (Pavlacky and Anderson 2001) and Gray Vireo densities also increase with increasing shrub cover of big sagebrush (Schlossberg 2006). Both canopy and understory foliage gleaners (Table 2) were associated with greater understory shrub foliage, suggesting that species forage across a greater range of vertical foliage bands in this dwarf woodland. Understory shrub species are often the only deciduous vegetation in persistent pinyon-juniper woodlands, and arthropod community composition in this habitat is in part driven by plant primary productivity (Uhey et al. 2020). Keane and Morrison (1999) found that arthropod densities were significantly higher on understory bitterbrush and sagebrush than on canopy pinyon pines and junipers in May, and, therefore, shrubs may provide key foraging habitat for foliage gleaners during the peak of the breeding season.

By contrast, we found that two other foraging guilds, aerial and bark foragers, were negatively associated with increasing shrub cover, though these relationships were more gradual and linear (Appendix 1: Fig. S11). Both Gray Flycatcher and Ash-throated Flycatcher are aerially foraging species that prefer to capture insect prey at lower foraging heights, either on the ground or on low outer foliage of conifers (Schlossberg and Sterling 2020, Cardiff and Dittmann 2020). Therefore, extensive understory shrub foliage cover may reduce foraging microhabitat for these species. White-breasted Nuthatch is a bark-foraging specialist which prefers conifer trunks and large branches as foraging substrate (Grubb Jr. and Pravosudov 2020). Conifer biomass tends to be inversely correlated with shrub biomass in pinyon-juniper woodland (Roundy et al. 2014), so areas of high shrub foliage cover may contain less trunk foraging area. These responses suggest that small-scale tree die-off and moderate canopy thinning may change the composition of the insectivore guild by increasing understory shrub cover (Albert et al. 2004, Roundy et al. 2014, Ernst-Brock et al. 2019, Huffman et al. 2019). Such effects may be lagged by 10+ years (Huffman et al. 2019), with declines in shrub cover occurring in the first 2-3 years after thinning (Redmond et al. 2014b, Havrilla et al. 2017). Prescribed fire treatments in pinyon-juniper understories have also been shown to reduce shrub cover over long (10+ year) time periods (Roundy et al. 2014, Huffman et al. 2019). Additional assessments of a diversity of thinning treatments on wildlife habitat suitability are increasingly necessary at long timescales.

Community segregation by woodland successional stage and vegetation complexity

When we examined species responses to the microhabitat variables in aggregate, species showed segregation by woodland successional stage (PC axis 1, Fig. 4). Species segregated into those associated with early-successional (stage I and II) and die-off affected woodlands (negative values on PC 1) with a greater presence of snags, saplings, and young conifers and those associated with mature (stage III) woodlands with a higher canopy height, pinyon pine basal area, and foliage height diversity. These habitat features correlate with pinyon-juniper woodland maturity stages (Harper et al. 2003, Huffman et al. 2012, Miller et al. 2019), though tree die-off and die-back may act to reset the successional clock in mature woodlands (Clifford et al. 2011). Few studies have assessed bird community response to pinyon-juniper woodland succession, but our results mirror similar findings of changes to community composition along gradients of conifer cover (Sedgwick 1987, Rosenstock and Van Riper III 2001, Pavlacky and Anderson 2004, Knick et al. 2017). Of the pinyon-juniper bird community, roughly half of the species showed stronger associations with early-successional habitats, though these species were often also present in late-successional woodlands. Species also responded differentially to the vertical complexity of vegetation (PC axis 2), with higher densities associated with simplified vegetation structure for most species. Persistent pinyon-juniper woodlands have infrequent fire-related disturbance, with stand-replacing fires occurring at average fire return intervals of 300-400 years (Romme et al. 2009). Late-successional persistent woodlands also show decreasing understory vegetation components with increasing tree dominance (Roundy et al. 2014). Therefore, persistent pinyon-juniper woodlands tend toward even-aged stands where foliage is generally concentrated in one or two vertical strata (understory or canopy), and few species may have, therefore, evolved to exploit a more complex vertical vegetation structure. Finally, Pinyon Jay showed a unique response to microhabitat variables, with higher densities in late-successional woodlands with low vertical vegetation complexity. This response could be tied to the species' need for both closed-canopy woodlands for nesting and more open habitats for seed caching and arthropod foraging (Johnson and Sadoti 2023, Van Lanen et al. 2024, Sicich et al. 2025). Pinyon Jay may serve as a poor umbrella species for pinyon-juniper bird communities given its highly divergent local habitat associations.

Management implications

Our results suggest that most pinyon-juniper specialist birds are relatively resilient to tree mortality and thinning at the microhabitat (40-m-radius) scale, showing limited association with higher canopy cover or greater basal area of pinyon pine. Changes to density in response to canopy cover, both positive and negative, were gradual and linear, with no evidence of canopy cover thresholds (Figs. S9, S10). However, extreme (< 10% canopy cover remaining) removal of conifers has been shown to result in local declines and extirpations of pinyon-juniper specialist birds (Crow and van Riper 2010, Bombaci et al. 2017, Johnson et al. 2018). These negative effects could be due to a landscape loss of canopy cover, which may more adversely affect densities than local-scale losses (Magee et al. 2019). Evidence for positive effects of thinning on woodland health is sparse (Redmond et al. 2023), and negative effects of thinning and tree mortality may be amplified at landscape scales, so managers seeking to maximize habitat for birds should thin moderately and patchily where necessary (Darr et al. 2022), leaving a mosaic of dense and more open stands on the landscape. More landscape-level studies on the effects of thinning and conifer removal on bird communities are needed to inform pinyon-juniper management. Thinning and tree die-off may also affect bird communities through increases in understory shrub cover, which can shift the composition of the insectivore guild. Managers can increase shrub cover over long timescales through moderate thinning, which can dramatically increase the densities of some foliage gleaning insectivores, though shrub cover typically decreases in the 2-3 years after thinning. Persistent pinyon-juniper woodlands are not thought to be fire adapted (Romme et al. 2009), and prescribed fire treatments have led to the long-term (10+ year) loss of shrub cover, indicating that prescribed fire treatments may not be advisable if maintaining understory bird species is a management objective. Methods of thinning that leave understory shrubs in place are likely to increase bird densities immediately after treatment, but a better understanding of how treatment types affect understory plants is needed. Unlike pinyon-juniper specialists, many generalist birds of forest and woodland were more sensitive to local changes in canopy cover. Of these, Mountain Chickadee is most at risk to thinning and tree die-off, with higher densities associated with high canopy cover, greater pinyon pine density, and greater vertical vegetation structure. This species is, therefore, especially at risk to climate-change induced tree die-off and even moderate thinning, with local extirpations from pinyon-juniper woodlands likely following such events. Where Mountain Chickadee represents a species of conservation concern, managers may wish to conduct pre-treatment surveys for this species to identify the degree to which it is using areas that will be thinned.

Author Contributions:

Harrison Jones, Megan Swan, and Rodney Siegel helped conceive of the idea; Brandon Merriell and Harrison Jones developed the analytical methods and analyzed the data; and Matthew Johnson contributed substantial field data and funding. The first draft of the manuscript was written by Harrison Jones and all authors commented on drafts of the manuscript. All authors read and approved the final manuscript.

Acknowledgments:

The authors are indebted to the many field technicians that collected bird and habitat survey data for this project, as well as to Dr. Jennifer Holmes and Matthew Johnson for designing and managing the SCPN bird monitoring program. Kristin Straka provided maps of point count station locations and thinning locations at BAND. David Rakestraw provided clarification about how field habitat data were collected, while Kay Beeley provided additional details about the thinning treatment at BAND. Sarah Milligan and Paul Morey provided courtesy reviews that improved the manuscript.

Data Availability:

Code required to replicate the analyses in this paper are available in Appendix 1; data are archived on the National Park Service's Integrated Resource Management Applications website (https://doi.org/10.57830/2302328).

LITERATURE CITED

Adams, B. T., and S. N. Matthews. 2019. Diverse temperate forest bird assemblages demonstrate closer correspondence to plant species composition than vegetation structure. Ecography 42:1752-1764. https://doi.org/10.1111/ecog.04487

Albert, S., N. Luna, R. Jensen, and L. Livingston. 2004. Restoring biodiversity to piñon-juniper woodlands. Ecological Restoration 22:18-23. https://doi.org/10.3368/er.22.1.18

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259(4):660-684. https://doi.org/10.1016/j.foreco.2009.09.001

Almalki, Y. M., A. G. Fernald, C. G. Ochoa, A. F. Cibils, A. M. Faist, D. S. Cram, and R. L. Steiner. 2023. Understory vegetation response to thinning pinyon-juniper woodlands. Rangeland Ecology & Management 88:152-158. https://doi.org/10.1016/j.rama.2023.02.012

Amme, N., C. A. Pague, and M. D. Redmond. 2020. Change in pinon-juniper woodland cover since Euro-American settlement: expansion versus contraction associated with soil properties. Rangeland Ecology & Management 73(6):847-855. https://doi.org/10.1016/j.rama.2020.07.001

Amundson, C. L., J. A. Royle, and C. M. Handel. 2014. A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. Auk 131(4):476-494. https://doi.org/10.1642/AUK-14-11.1

Bateman, B. L., L. Taylor, C. Wilsey, J. Wu, G. S. LeBaron, and G. Langham. 2020. Risk to North American birds from climate change-related threats. Conservation Science and Practice 2(8): e243. https://doi.org/10.1111/csp2.243

Boisvert-Marsh, L., and S. de Blois. 2021. Unravelling potential northward migration pathways for tree species under climate change. Journal of Biogeography 48(5):1088-1100. https://doi.org/10.1111/jbi.14060

Bombaci, S., and L. Pejchar. 2016. Consequences of pinyon and juniper woodland reduction for wildlife in North America. Forest Ecology and Management 365:34-50. https://doi.org/10.1016/j.foreco.2016.01.018

Bombaci, S. P., T. Gallo, and L. Pejchar. 2017. Small-scale woodland reduction practices have neutral or negative short-term effects on birds and small mammals. Rangeland Ecology & Management 70(3):363-373. https://doi.org/10.1016/j.rama.2016.11.006

Boone, J. D., C. Witt, and E. M. Ammon. 2021. Behavior-specific occurrence patterns of Pinyon Jays (Gymnorhinus cyanocephalus) in three Great Basin study areas and significance for pinyon-juniper woodland management. PLoS ONE 16:e0237621. https://doi.org/10.1371/journal.pone.0237621

Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers, and C. W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences 102 (42):15144-15148. https://doi.org/10.1073/pnas.0505734102

Buotte, P. C., S. Levis, B. E. Law, T. W. Hudiburg, D. E. Rupp, and J. J. Kent., 2019. Near-future forest vulnerability to drought and fire varies across the western United States. Global Change Biology 25(1):290-303. https://doi.org/10.1111/gcb.14490

Cadieux, P., Y. Boulanger, D. Cyr, A. R. Taylor, D. T. Price, P. Sólymos, D. Stralberg, H. Y. H. Chen, A. Brecka, and J. A. Tremblay. 2020. Projected effects of climate change on boreal bird community accentuated by anthropogenic disturbances in western boreal forest, Canada. Diversity and Distributions 26:(6) 668-682. https://doi.org/10.1111/ddi.13057

Cardiff, S. W., and D. L. Dittmann. 2020. Ash-throated Flycatcher (Myiarchus cinerascens), version 1.0. In A. F. Poole, and F. B. Gill, editors. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.astfly.01

Ceresa, F., P. Kranebitter, J. S. Monrós, F. Rizzolli, and M. Brambilla. 2021. Disentangling direct and indirect effects of local temperature on abundance of mountain birds and implications for understanding global change impacts. Peer J 9:e12560. https://doi.org/10.7717/peerj.12560

Chesser, R. T., S. M. Billerman, K. J. Burns, C. Cicero, J. L. Dunn, B. E. Hernández-Baños, R. A. Jiménez, O. Johnson, A. W. Kratter, N. A. Mason, P. C. Rasmussen, and J. V. Remsen Jr. 2024. Sixty-fifth supplement to the American Ornithological Society's check-list of North American birds. Ornithology 141(3):1-20. https://doi.org/10.1093/ornithology/ukae019

Clark, J. S., L. Iverson, C. W. Woodall, C. D. Allen, D. M. Bell, D. C. Bragg, A. W. D'Amato, F. W. Davis, M. H. Hersh, I. Ibanez, S. T. Jackson, S. Matthews, N. Pederson, M. Peters, M. W. Schwartz, K. M. Waring, and N. E. Zimmermann. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22 (7):2329-2352. https://doi.org/10.1111/gcb.13160

Clifford, M. J., N. S. Cobb, and M. Buenemann. 2011. Long-term tree cover dynamics in a pinyon-juniper woodland: climate-change-type drought resets successional clock. Ecosystems 14:949-962. https://doi.org/10.1007/s10021-011-9458-2

Crosby, A. D., E. M. Bayne, S. G. Cumming, F. K. A. Schmiegelow, F. V. Dénes, and J. A. Tremblay. 2019. Differential habitat selection in boreal songbirds influences estimates of population size and distribution. Diversity and Distributions 25 (12):1941-1953. https://doi.org/10.1111/ddi.12991

Crow, C., and C. van Riper III. 2010. Avian community responses to mechanical thinning of a pinyon-juniper woodland: specialist sensitivity to tree reduction. Natural Areas Journal 30(2):191-201. https://doi.org/10.3375/043.030.0206

Culbert, P. D., V. C. Radeloff, C. H. Flather, J. M. Kellndorfer, C. D. Rittenhouse, and A. M. Pidgeon. 2013. The influence of vertical and horizontal habitat structure on nationwide patterns of avian biodiversity. Auk 130(4):656-665. https://doi.org/10.1525/auk.2013.13007

Darr, M., C. Beidleman, P. Cutler, M. Desmond, G. Garber, K. Granillo, L. Hay, J. Hayes, K. Johnson, M. Ramsey, C. Rustay, T. Supplee, and B. Thompson. 2022. Incorporating bird needs when thinning piñon-juniper woodlands. New Mexico Avian Conservation Partners, Albuquerque, New Mexico, USA.

DeCoster, J. K., C. L. Lauver, M. E. Miller, J. R. Norris, A. E. Snyder, M. C. Swan, L. P. Thomas, and D. L. Witwicki. 2012. Integrated upland monitoring protocol and standard operating procedures for the Southern Colorado Plateau Network. Fort Collins, CO; 2012. Report No.: NPS/SCPN/NRR-2012/577.

Devictor, V., R. Julliard, and F. Jiguet. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117(4):507-514. https://doi.org/10.1111/j.0030-1299.2008.16215.x

Doherty, K. E., J. S. Evans, P. S. Coates, L. M. Juliusson, and B. C. Fedy. 2016. Importance of regional variation in conservation planning: a rangewide example of the Greater Sage-Grouse. Ecosphere 7(10):e01462. https://doi.org/10.1002/ecs2.1462

Elliott, L. H., A. M. Bracey, G. J. Niemi, D. H. Johnson, T. M. Gehring, E. E. G. Giese, G. E. Fiorino, R. W. Howe, G. J. Lawrence, C. J. Norment, D. C. Tozer, and L. D. Igl. 2023. Application of habitat association models across regions: useful explanatory power retained in wetland bird case study. Ecosphere 14(5):e4499. https://doi.org/10.1002/ecs2.4499

Ernst-Brock, C., L. Turner, R. J. Tausch, and E. A. Leger. 2019. Long-term vegetation responses to pinyon-juniper woodland reduction treatments in Nevada, USA. Journal of Environmental Management 242:315-326. https://doi.org/10.1016/j.jenvman.2019.04.053

Fair, J. M., C. D. Hathcock, and A. W. Bartlow. 2018. Avian communities are decreasing with piñon pine mortality in the southwest. Biological Conservation 226:186-195. https://doi.org/10.1016/j.biocon.2018.06.035

Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating detection probabilities from point-count surveys. Auk 119 (2):414-425. https://doi.org/10.1093/auk/119.2.414

Farrell, C. E., L. Fahrig, G. Mitchell, and S. Wilson. 2019. Local habitat association does not inform landscape management of threatened birds. Landscape Ecology 34:1313-1327. https://doi.org/10.1007/s10980-019-00843-6

Fettig, C. J., M. L. Reid, B. J. Bentz, S. Sevanto, D. L. Spittlehouse, and T. L. Wang. 2013. Changing climates, changing forests: a western North American perspective. Journal of Forestry 111 (3):214-228. https://doi.org/10.5849/jof.12-085

Filippelli, S. K., M. J. Falkowski, A. T. Hudak, P. A. Fekety, J. C. Vogeler, A. H. Khalyani, B. M. Rau, and E. K. Strand. 2020. Monitoring pinyon-juniper cover and aboveground biomass across the Great Basin. Environmental Research Letters 15(2). https://doi.org/10.1088/1748-9326/ab6785

Flake, S. W., and P. J. Weisberg. 2019. Fine-scale stand structure mediates drought-induced tree mortality in pinyon-juniper woodlands. Ecological Applications 29(2):e01831. https://doi.org/10.1002/eap.1831

Flake, S. W., and P. J. Weisberg. 2021. Drought alters the understory of pinyon-juniper woodlands indirectly through tree dieback. Rangeland Ecology & Management 76:118-128. https://doi.org/10.1016/j.rama.2021.02.007

Floyd, M. L., M. Colyer, D. D. Hanna, and W. H. Romme. 2003. Gnarly old trees: canopy characteristics of old-growth piñon-juniper woodlands. In Floyd, M. L., editor. Ancient Piñon-Juniper Woodlands. University Press of Colorado, Boulder, Colorado, USA.

Francis, C. D., C. P. Ortega, and J. Hansen. 2011. Importance of juniper to birds nesting in piñon-juniper woodlands in northwest New Mexico. Journal of Wildlife Management 75(7):1574-1580. https://doi.org/10.1002/jwmg.200

Garbarino, M., F. Malandra, T. Dilts, S. Flake, L. Montalto, S. Spinsante, and P. J. Weisberg. 2020. Upper and lower treeline biogeographic patterns in semi-arid pinyon-juniper woodlands. Journal of Biogeography 47(12):2634-2644. https://doi.org/10.1111/jbi.13952

Gaylord, M. L., T. E. Kolb, W. T. Pockman, J. A. Plaut, E. A. Yepez, A. K. Macalady, R. E. Pangle, and N. G. McDowell. 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. New Phytologist 198(2):567-578. https://doi.org/10.1111/nph.12174

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7 (4):457-472. https://doi.org/10.1214/ss/1177011136

Goguen, C. B., D. R. Curson, and N. E. Matthews. 2005. Breeding ecology of the Gray Flycatcher in pinyon-juniper woodlands in New Mexico. Western Birds 36:286-295.

Greenwood, D. L., and P. J. Weisberg. 2008. Density-dependent tree mortality in pinyon-juniper woodlands. Forest Ecology and Management 255(7):2129-2137. https://doi.org/10.1016/j.foreco.2007.12.048

Greenwood, D. L., and P. J. Weisberg. 2009. GIS-based modeling of pinyon-juniper woodland structure in the Great Basin. Forest Science 55(1):1-12. https://doi.org/10.1093/forestscience/55.1.1

Grubb Jr., T. C., and V. V. Pravosudov. 2020. White-breasted Nuthatch (Sitta carolinensis), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.whbnut.01

Hack, B., C. A. Cansler, M. Z. Peery, and C. M. Wood. 2023. Fine-scale forest structure, not management regime, drives occupancy of a declining songbird, the Olive-sided Flycatcher, in the core of its range. Ornithological Applications 126(2):duad000. https://doi.org/10.1093/ornithapp/duad065

Harris, J. P., L. M. Smith, and S. T. McMurry. 2020. A multiscale analysis of Gray Vireo (Vireo vicinior) nest-site selection in central New Mexico. Avian Conservation and Ecology 15(1):12. https://doi.org/10.5751/ACE-01540-150112

Harper, K. T., S. C. Sanderson, and E. D. McArthur. 2003. Pinyon-juniper woodlands in Zion National Park, Utah. Western North American Naturalist 63:189-202.

Hartsell, J. A., S. M. Copeland, S. M. Munson, B. J. Butterfield, and J. B. Bradford. 2020. Gaps and hotspots in the state of knowledge of pinyon-juniper communities. Forest Ecology and Management 455. https://doi.org/10.1016/j.foreco.2019.117628

Havrilla, C. A., A. M. Faist, and N. N. Barger. 2017. Understory plant community responses to fuel-reduction treatments and seeding in an upland piñon-juniper woodland. Rangeland Ecology & Management 70(5):609-620. https://doi.org/10.1016/j.rama.2017.04.002

Hicke, J. A., and M. J. B. Zeppel. 2013. Climate-driven tree mortality: insights from the piñon pine die-off in the United States. New Phytologist 200(2):301-303. https://doi.org/10.1111/nph.12464

Holmes, J. A., M. J. Johnson, C. L. Lauver, J. R. Norris, A. E. C. Snyder, and L. P. Thomas. 2015. Habitat-based bird community monitoring protocol for the Southern Colorado PlateauNetwork. Fort Collins, CO; 2015. Report No.: NPS/SCPN/NRR—2015/1041.

Huang, C., G. P. Asner, and N. N. Barger. 2012. Modeling regional variation in net primary production of pinyon-juniper ecosystems. Ecological Modelling 227:82-92. https://doi.org/10.1016/j.ecolmodel.2011.12.016

Huffman, D. W., P. Z. Fulé, J. E. Crouse, and K. M. Pearson. 2009. A comparison of fire hazard mitigation alternatives in pinyon-juniper woodlands of Arizona. Forest Ecology and Management 257(2):628-635. https://doi.org/10.1016/j.foreco.2008.09.041

Huffman, D. W., J. E. Crouse, W. W. Chancellor, and P. Z. Fulé. 2012. Influence of time since fire on pinyon-juniper woodland structure. Forest Ecology and Management 274:29-37. https://doi.org/10.1016/j.foreco.2012.02.014

Huffman, D. W., M. T. Stoddard, J. D. Springer, J. E. Crouse, A. J. S. Meador, and S. Nepal. 2019. Stand dynamics of pinyon-juniper woodlands after hazardous fuels reduction treatments in Arizona. Rangeland Ecology & Management 72(5):757-767. https://doi.org/10.1016/j.rama.2019.05.005

Jenouvrier, S. 2013. Impacts of climate change on avian populations. Global Change Biology 19(7):2036-2057. https://doi.org/10.1111/gcb.12195

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61 (1):65-71. https://doi.org/10.2307/1937156

Johnson, K., T. B. Neville, J. W. Smith, and M. W. Horner. 2016. Home range- and colony-scale habitat models for Pinyon Jays in piñon-juniper woodlands of New Mexico, USA. Avian Conservation and Ecology 11(2):6. https://doi.org/10.5751/ACE-00890-110206

Johnson, K., N. Petersen, J. Smith, and G. Sadoti. 2018. Pinon-juniper fuels reduction treatment impacts pinyon jay nesting habitat. Global Ecology and Conservation 16:e00487. https://doi.org/10.1016/j.gecco.2018.e00487

Johnson, K., and G. Sadoti. 2023. A review of Pinyon Jay (Gymnorhinus cyanocephalus) habitat ecology. Wilson Journal of Ornithology 135(2):232-247. https://doi.org/10.1676/22-00103

Jones, H. H., C. Ray, M. Johnson, and R. Siegel. 2024. Breeding birds of high-elevation mixed-conifer forests have declined in national parks of the southwestern U.S. while lower-elevation species have increased, with responses to drought varying by habitat. Ornithological Applications 126(2):duae007. https://doi.org/10.1093/ornithapp/duae007

Keane, J. J., and L. L. Morrison. 1999. Temporal variation in resource use by Black-throated Gray Warblers. Condor 101 (1):67-75. https://doi.org/10.2307/1370447

Kellner, C. J., J. D. Brawn, and J. R. Karr. 1992. What is habitat suitability and how should it be measured? In D. R. McCullough, and R. H. Barrett, editors. Wildlife 2001: populations. Springer, Dordrecht, Netherlands. https://doi.org/10.1007/978-94-011-2868-1_36

Kellner, K., and M. Meredith. 2024. Package 'jagsUI': a wrapper around 'rjags' to streamline 'JAGS' analyses. Version 1.6.2.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, San Diego, California, USA.

Knick, S. T., S. E. Hanser, J. B. Grace, J. P. Hollenbeck, and M. Leu. 2017. Response of bird community structure to habitat management in piñon-juniper woodland-sagebrush ecotones. Forest Ecology and Management 400:256-268. https://doi.org/10.1016/j.foreco.2017.06.017

Kruschke, J. K. 2015. Doing Bayesian analysis: a tutorial with R, JAGS, and STAN. Second edition. Academic Press, London, UK. https://doi.org/10.1016/B978-0-12-405888-0.00008-8

Kuile, A. M.-T., K. Ogle, C. Cavanaugh, J. Dudley, A. Markus, V. Saab, M. Wright, and J. Sanderlin. 2023. Forest management, forest vegetation, and climate influence nesting ecology of a focal bird species in the western USA. Forest Ecology and Management 549:121443. https://doi.org/10.1016/j.foreco.2023.121443

Landis, A. G., and J. D. Bailey. 2005. Reconstruction of age structure and spatial arrangement of pinon-juniper woodlands and savannas of Anderson Mesa, northern Arizona. Forest Ecology and Management 204(2-3):221-236. https://doi.org/10.1016/j.foreco.2004.09.006

Latif, Q. S., M. M. Ellis, and C. L. Amundson. 2016. A broader definition of occupancy: Comment on Hayes and Monfils. Journal of Wildlife Management 80(2):192-194. https://doi.org/10.1002/jwmg.1022

Laudenslayer, W. F., and R. P. Balda. 1976. Breeding bird use of a pinyon-juniper ponderosa pine ecotone. Auk 93:571-586.

Lee, P. Y., and J. T. Rotenberry. 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. Journal of Biogeography 32(7):1139-1150. https://doi.org/10.1111/j.1365-2699.2005.01254.x

Lees, A. C., L. Haskell, T. Allinson, S. B. Bezeng, I. J. Burfield, L. M. Renjifo, K. V. Rosenberg, A. Viswanathan, and S. H. M. Butchart. 2022. State of the world's birds. Annual Review of Environment and Resources 47:231-60. https://doi.org/10.1146/annurev-environ-112420-014642

MacArthur, R. D., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42(3):594.598. https://doi.org/10.2307/1932254

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2017. Occupancy estimation and modelling, inferring patterns and dynamics of species occurrence. Academic Press, London, UK. https://doi.org/10.1016/B978-0-12-407197-1.00019-3

Magee, P. A., J. D. Coop, and J. S. Ivan. 2019. Thinning alters avian occupancy in pinon-juniper woodlands. Ornithological Applications 121(1):duy008. https://doi.org/10.1093/condor/duy008

Marzluff, J. M., and R. P. Balda. 1992. The Pinyon Jay: behavioral ecology of a colonial and cooperative corvid. T & AD Poyser Ltd., Calton, UK.

Masters, N. L. 1979. Breeding birds of pinyon-juniper woodland in north central Arizona. Northern Arizona University, Flagstaff, Arizona, USA.

Meddens, A. J. H., Hicke, J. A., Macalady, A. K., Buotte, P. C., Cowles, T. R., and C. D. Allen. 2015. Patterns and causes of observed pinon pine mortality in the southwestern United States. New Phytologist 206(1):91-97. https://doi.org/10.1111/nph.13193

Miller, R. F., J. C. Chambers, L. Evers, J. Williams, K. A. Snyder, B. A. Roundy, and F. B. Pierson. 2019. The ecology, history, ecohydrology, and management of pinyon and juniper woodlands in the Great Basin and Northern Colorado Plateau of the western United States. Gen. Tech. Rep. RMRS-GTR-403. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO. https://doi.org/10.2737/RMRS-GTR-403

Mueller, R. C., C. M. Scudder, M. E. Porter, R. T. Trotter, C. A. Gehring, and T. G. Whitham. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. Journal of Ecology 93(6):1085-1093. https://doi.org/10.1111/j.1365-2745.2005.01042.x

Muldavin, E., and F. J. Triepke. 2020. North American pinyon-juniper woodlands: ecological composition, dynamics, and future trends. Pages 516-531 in M. I. Goldstein, D. A. Dellasala, editors. Encyclopedia of the world's biomes. Science Direct, Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.12113-X

Müller, J., S. Bae, J. Röder, A. Chao, and R. K. Didham. 2014. Airborne LiDAR reveals context dependence in the effects of canopy architecture on arthropod diversity. Forest Ecology and Management 312:129-137. https://doi.org/10.1016/j.foreco.2013.10.014

Noel, A., D. R. Schlaepfer, B. J. Butterfield, M. C. Swan, J. Norris, K. Hartwig, M. C. Duniway, and J. B. Bradford. 2025. Most pinyon-juniper woodland species distributions are projected to shrink rather than shift under climate change. Rangeland Ecology & Management 98:454-466. https://doi.org/10.1016/j.rama.2024.09.002

Overpeck, J. T., and B. Udall. 2020. Climate change and the aridification of North America. Proceedings of the National Academy of Sciences 117(22):11856-11858. https://doi.org/10.1073/pnas.2006323117

Paulin, K. M., J. J. Cook, and S. R. Dewey. Pinyon-juniper woodlands as sources of avian diversity. Ecology and management of pinyon-juniper communities within the Interior West. 1999. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Provo, Utah, USA.

Pavlacky, D. C., and S. H. Anderson. 2001. Habitat preferences of pinyon-juniper specialists near the limit of their geographic range. Condor 103(2):322-331. https://doi.org/10.1093/condor/103.2.322

Pavlacky, D. C., and S. H. Anderson. 2004. Comparative habitat use in a juniper woodland bird community. Western North American Naturalist 64:376-384.

Plummer, M. 2003. JAGS: a program for analysis of bayesian graphical models using gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003):1-10.

R Core Team. 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://doi.org/10.32614/R.manuals

Redmond, M. D., E. S. Golden, N. S. Cobb, and N. N. Barger. 2014a. Vegetation management across Colorado Plateau BLM lands: 1950-2003. Rangeland Ecology & Management 67 (6):636-640. https://doi.org/10.2111/REM-D-13-00171.1

Redmond, M. D., T. J. Zelikova, and N. N. Barger. 2014b. Limits to understory plant restoration following fuel-reduction treatments in a piñon-juniper woodland. Environmental Management 54:1139-1152. https://doi.org/10.1007/s00267-014-0338-3

Redmond, M. D., A. K. Urza, and P. J. Weisberg. 2023. Managing for ecological resilience of pinyon-juniper ecosystems during an era of woodland contraction. Ecosphere 14(5):e4505. https://doi.org/10.1002/ecs2.4505

Riskas, H. L. 2021. Climate effects on canopy arthropod communities of pinyon pine and juniper trees. Northern Arizona University, Flagstaff, Arizona, USA.

Roberts, L. J., R. Burnett, J. Tietz, and S. Veloz. 2019. Recent drought and tree mortality effects on the avian community in southern Sierra Nevada: a glimpse of the future? Ecological Applications 29(2):e01848. https://doi.org/10.1002/eap.1848

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366(6461):120-124. https://doi.org/10.1126/science.aaw1313

Rosenstock, S. S., and C. Van Riper III. 2001. Breeding bird responses to juniper woodland expansion. Journal of Rangeland Management 54(3):226-232. https://doi.org/10.2307/4003238

Romme, W. H., C. D. Allen, J. D. Balley, W. L. Baker, B. T. Bestelmeyer, P. M. Brown, K. S. Eisenhart, M. L. Floyd, D. W. Huffman, B. F. Jacobs, R. F. Miller, E. H. Muldavin, T. W. Swetnam, R. J. Tausch, and P. J. Weisberg. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the western United States. Rangeland Ecology & Management 62(3):203-222. https://doi.org/10.2111/08-188R1.1

Roundy, B. A., R. F. Miller, R. J. Tausch, K. Young, A. Hulet, B. Rau, B. Jessop, J. C. Chambers, and D. Eggett. 2014. Understory cover responses to piñon-juniper treatments across tree dominance gradients in the Great Basin. Rangeland Ecology & Management 67(5):482-494. https://doi.org/10.2111/REM-D-13-00018.1

Royer, P. D., D. D. Breshears, C. B. Zou, J. C. Villegas, N. S. Cobb, and S. A. Kurc. 2012. Density-dependent ecohydrological effects of piñon-juniper woody canopy cover on soil microclimate and potential soil evaporation. Rangeland Ecology and Management 65(1):11-20. https://doi.org/10.2111/REM-D-11-00007.1

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60(1):108-115. https://doi.org/10.1111/j.0006-341X.2004.00142.x

Schofield, L. N., R. B. Siegel, and H. L. Loffland. 2023. Modeling climate-driven range shifts in populations of two bird species limited by habitat independent of climate. Ecosphere 14(2):e4408. https://doi.org/10.1002/ecs2.4408

Schlossberg, S. 2006. Abundance and habitat preferences of Gray Vireos (Vireo vicinior) on the Colorado Plateau. Auk 123 (1):33-44. https://doi.org/10.1093/auk/123.1.33

Schlossberg, S., and J. C. Sterling. 2020. Gray Flycatcher (Empidonax wrightii), version 1.0. Pages in A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.gryfly.01

Sedgwick, J. A. 1987. Avian habitat relationships in pinyon-juniper woodland. Wilson Bulletin 99:413-431.

Shew, J. J., C. K. Nielsen, and D. W. Sparling. 2019. Finer-scale habitat predicts nest survival in grassland birds more than management and landscape: a multi-scale perspective. Journal of Applied Ecology 56(4):929-945. https://doi.org/10.1111/1365-2664.13317

Shriver, R. K., C. B. Yackulic, D. M. Bell, and J. B. Bradford. 2022. Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions. Global Ecology and Biogeography 31(11):2259-2269. https://doi.org/10.1111/geb.13582

Sicich, B., A. C. Young, C. S. Bundy, F. Abadi, and M. J. Desmond. 2025. Open spaces and arthropod abundance are important foraging habitat components for Gymnorhinus cyanocephalus (Pinyon Jay) in south-central New Mexico. Ornithological Applications 127:duaf000. https://doi.org/10.1093/ornithapp/duaf046

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

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262-278. https://doi.org/10.1198/016214504000000250

Uhey, D. A., H. L. Riskas, A. D. Smith, and R. W. Hofstetter. 2020. Ground-dwelling arthropods of pinyon-juniper woodlands: arthropod community patterns are driven by climate and overall plant productivity, not host tree species. PLoS ONE 15. https://doi.org/10.1371/journal.pone.0238219

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B-Biological Sciences 279(1735):2072-2080. https://doi.org/10.1098/rspb.2011.2367

Vander Wall, S. B., and R. P. Balda. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift für Tierpsychologie 56(3):217-242. https://doi.org/10.1111/j.1439-0310.1981.tb01298.x

Van Lanen, N. J., A. P. Monroe, and C. L. Aldridge. 2023. Living on the edge: Predicting songbird response to management and environmental changes across an ecotone. Ecology and Evolution 13(11):e10648. https://doi.org/10.1002/ece3.10648

Van Lanen, N. J., A. P. Monroe, and C. L. Aldridge. 2024. Despite regional variation, Gymnorhinus cyanocephalus (Pinyon Jay) densities generally increase with local pinyon-juniper cover and heterogeneous ground cover. Ornithological Applications 126(4): duae036. https://doi.org/10.1093/ornithapp/duae036

Weisberg, P. J., E. Lingua, and R. B. Pillai. 2007. Spatial patterns of pinyon-juniper woodland expansion in central Nevada. Rangeland Ecology & Management 60(2):115-124. https://doi.org/10.2111/05-224R2.1

Westerband, A., M. Dovčiak, G. La Quay-Velázquez, and J. S. Medeiros. 2015. Aspect reduces soil moisture and tree cover, but not nitrogen mineralization or grass cover, in semiarid pinyon-juniper woodlands of the southwestern United States. The Southwestern Naturalist 60:21-29. https://doi.org/10.1894/FMO-18.1

Whittingham, M. J., J. R. Krebs, R. D. Swetnam, J. A. Vickery, J. D. Wilson, and R. P. Freckleton. 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecology Letters 10(1):25-35. https://doi.org/10.1111/j.1461-0248.2006.00992.x

Wikum, D. A., and G. F. Shanholtzer. 1978. Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. Environmental Management 2:323-329. https://doi.org/10.1007/BF01866672

Williams, A. P., B. I. Cook, and J. E. Smerdon. 2022. Rapid intensification of the emerging southwestern North American megadrought in 2020-2021. Nature Climate Change 12:232-234. https://doi.org/10.1038/s41558-022-01290-z

Wood, E. M., A. M. Pidgeon, F. Liu, and D. J. Mladenoff. 2012. Birds see the trees inside the forest: The potential impacts of changes in forest composition on songbirds during spring migration. Forest Ecology and Management 280:176-186. https://doi.org/10.1016/j.foreco.2012.05.041

Youkey, D. E. 1990. Bird and Rodent Nesting in Excavated Cavities in Pinon-juniper Woodland, Southeastern Colorado. Oregon State University, Corvallis, OR, USA.

Zillig, M. W., F. A. Fogarty, and E. Fleishman. 2023. Bird associations with floristics and physiognomy differ across five biogeographic subregions of the Great Basin, USA. Ornithological Applications 125. https://doi.org/10.1093/ornithapp/duac040

Editor-in-Chief: Jennifer L. Lavers
Subject Editor: Steven L. Van Wilgenburg

Appendix 1

RESULTS

Differences in vegetation structure and floristics

Sites at MEVE tended to have high canopy closure (30-40%) and height (10-15 m), high subcanopy foliar cover, high sapling densities, and high snag basal area (3-5 m^2/ha). The shrub foliar cover was high, but shrub height was generally low. By contrast, the survey points at GRCA had intermediate shrub cover and shrub height. Overall, canopy height (5-10 m) and closure (20-40%) at this park showed intermediate values, snag basal area was low (1-3 m^2/ha), and subcanopy and shrub foliar cover showed middling values. The sites at GRCA showed a higher average pinyon pine basal area than at MEVE (4-7 m^2/ha versus 3-5 m^2/ha at MEVE). Sites at BAND were most divergent in terms of vegetation structure. On average, these survey points showed a low canopy closure (10-20%) and height (5 m), non-existent sub-canopy foliar cover, high snag basal area (3-6 m^2/ha), and high shrub height (2 m).

Estimates of species detectability and model goodness-of-fit

The modelled estimates of availability were generally high (0.59 ± 0.27; mean ± SD of mean values of p_a; Table S3, Figure S2), with the exceptions being species that do not sing frequently or show nomadic behavior (hummingbirds, Hairy Woodpecker, corvids, Western Bluebird, etc.). By contrast, the estimated average perceptibility was much lower (0.40 ± 0.14; mean ± SD of median values of p_d). We found a high goodness-of-fit for both detectability sub-models, as measured by Bayesian P-values. For p_a, 23 species (92%) had a P-value between 0.4 and 0.6, and all species had a P-value between 0.2 and 0.8, while for the p_d sub-model 21 species (84%) had a Bayesian P-value between 0.4 and 0.6, and all species also had a P-value between 0.2 and 0.8 (Table S3, Figure S2). We found supported responses for each of the five fixed covariates fit on the p_a and p_d sub-models, though the number of species with supported responses varied considerably across covariates (Table S4, Figure S3). The effects of the linear term of ordinal date on availability were variable across species (0.07 [-0.48, 0.84], mean and 90% BCI of stacked joint posterior distribution across species; 6 supported positive effects, 4 supported negative effects), though the quadratic term showed a generally positive effect (0.13 [-0.63, 1.32], mean and 90% BCI; 9 supported positive effects, 7 supported negative effects). We also found a generally positive effect of minute of day on availability (0.15 [-0.25, 0.62], mean and 90% BCI; 11 supported positive effects, 1 supported negative effect). By contrast, both cloud cover (0.004 [-0.42, 0.42], mean and 90% BCI; 3 supported positive effects, 4 supported negative effects) and environmental noise (0.006 [-0.11, 0.18], mean and 90% BCI; 2 supported negative responses) showed few supported effects on detectability.

FIGURES

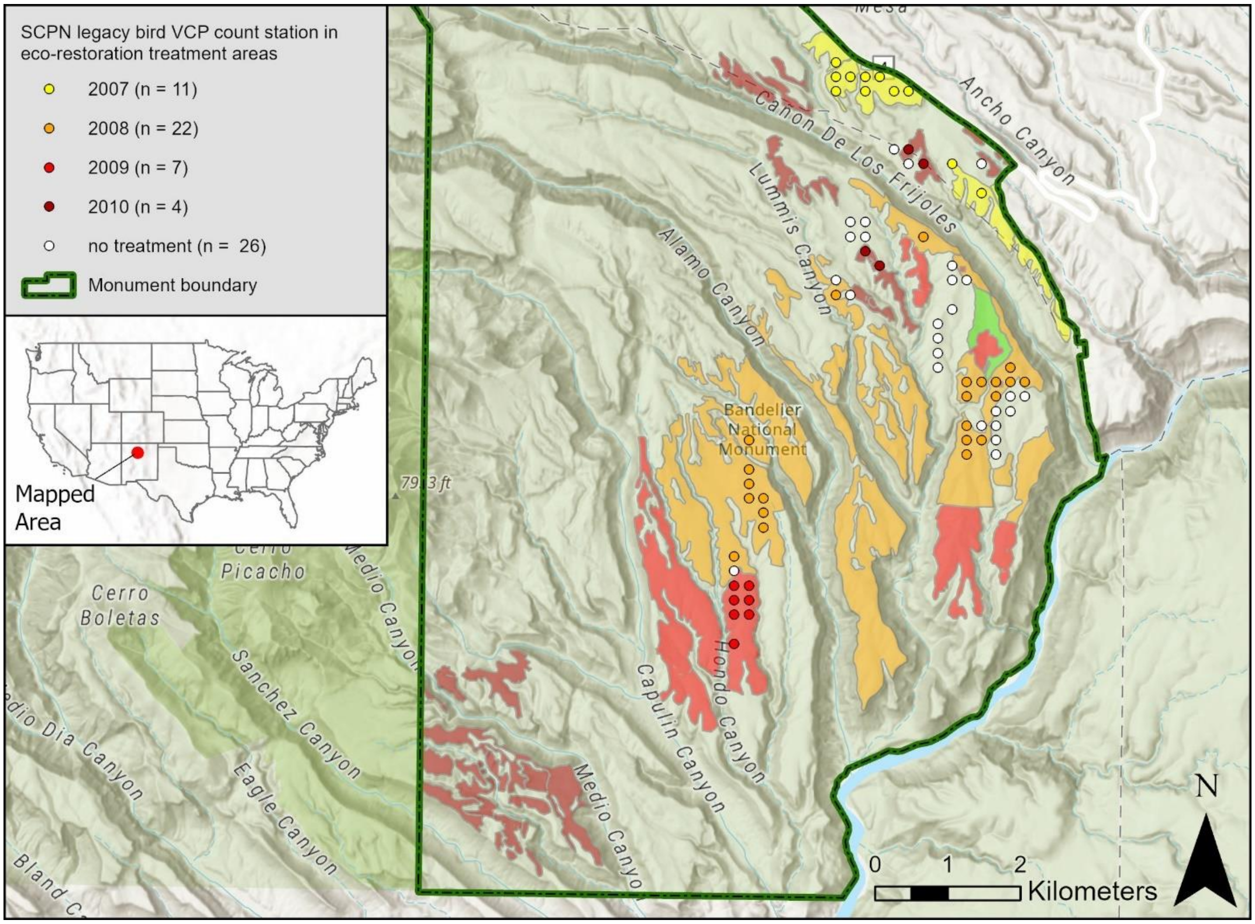


Figure S1. Location of point count stations in Bandelier National Monument in relation to mechanically thinned pinyon-juniper woodlands. Points represent count stations, established as a 250-m regular grid in pinyon-juniper woodland habitat. Points are color coded by the year in which the site was thinned, with white points indicating non-thinned count stations. Thinning consisted of mechanically cutting all live trees < 15 cm in diameter at the root crown, then lopping and scattering the cut vegetation in bare areas. Bird surveys were conducted in late May of 2008, after the thinning that year took place.

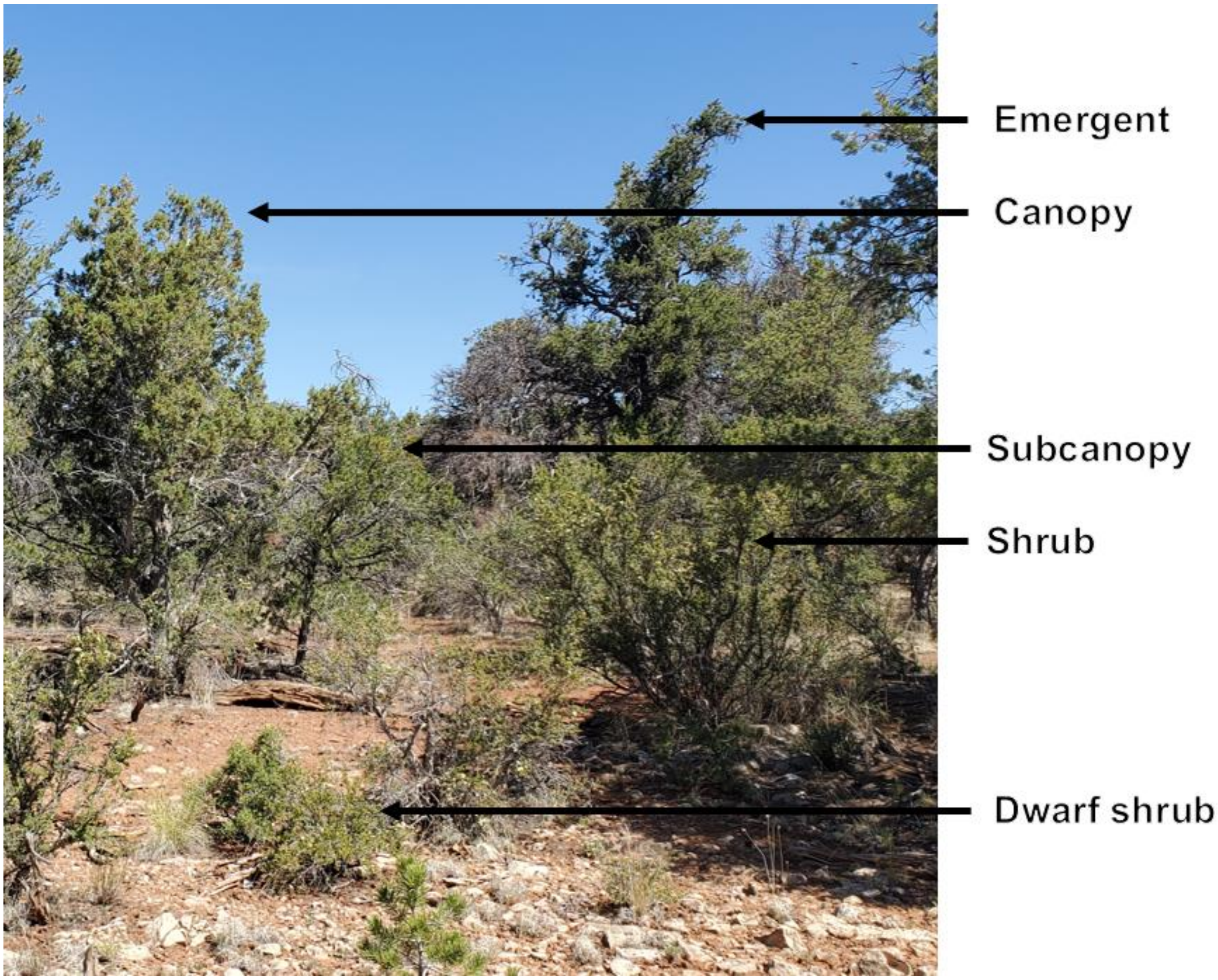


Figure S2. Vertical foliage strata used to calculate the foliage height diversity measure. The photo represents persistent pinyon-juniper woodland habitat at Grand Canyon National Park, with each foliage stratum denoted by an arrow. Emergent trees were those with a crown higher than the contiguous canopy, while the subcanopy was defined as a distinct stratum of young trees (not shrubs) below the canopy. Dwarf shrubs were defined as those below 0.5 m tall at maturity.

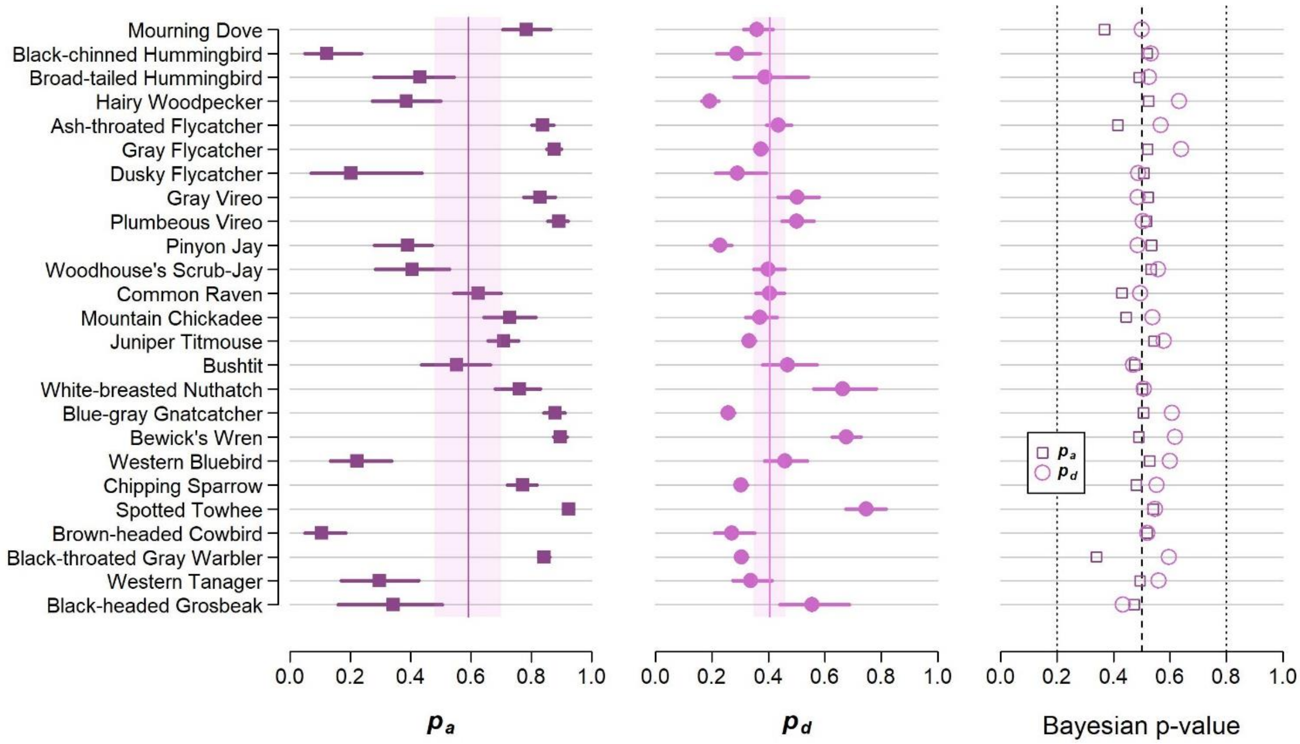


Figure S3. Species-specific estimates of probability of availability (p_a) and detectability (p_d) during point count surveys. Species are listed in taxonomic order, following the American Ornithological Society's 2024 taxonomy. Mean values and the 90% BCI are plotted, with vertical lines and shaded areas indicating the mean and standard error of the mean effect sizes across all species. Also plotted are posterior Bayesian P-values, a measure of sub-model goodness-of-fit for p_a and p_d.

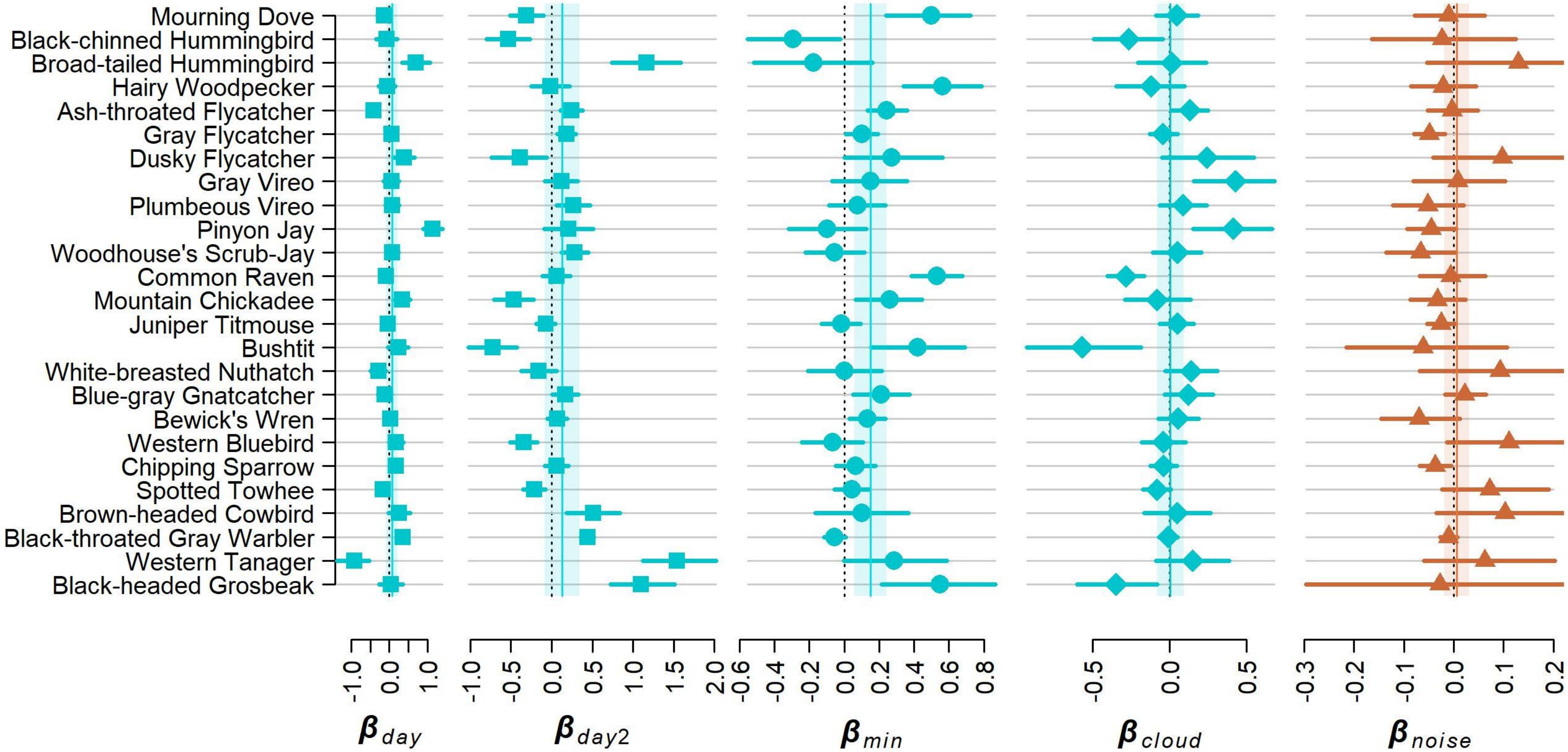


Figure S4. Plotted estimates of effect sizes of covariates on detectability sub-models. Covariates plotted in turquoise were fit on the availability (p_a) sub-model, while the covariate plotted in brown was fit on the perceptibility sub-model (p_d). Mean values and the 90% BCI are plotted, with vertical lines and shaded areas indicating the mean and standard error of the mean effect sizes across all species. Species are listed in taxonomic order, following the American Ornithological Society's 2024 taxonomy.

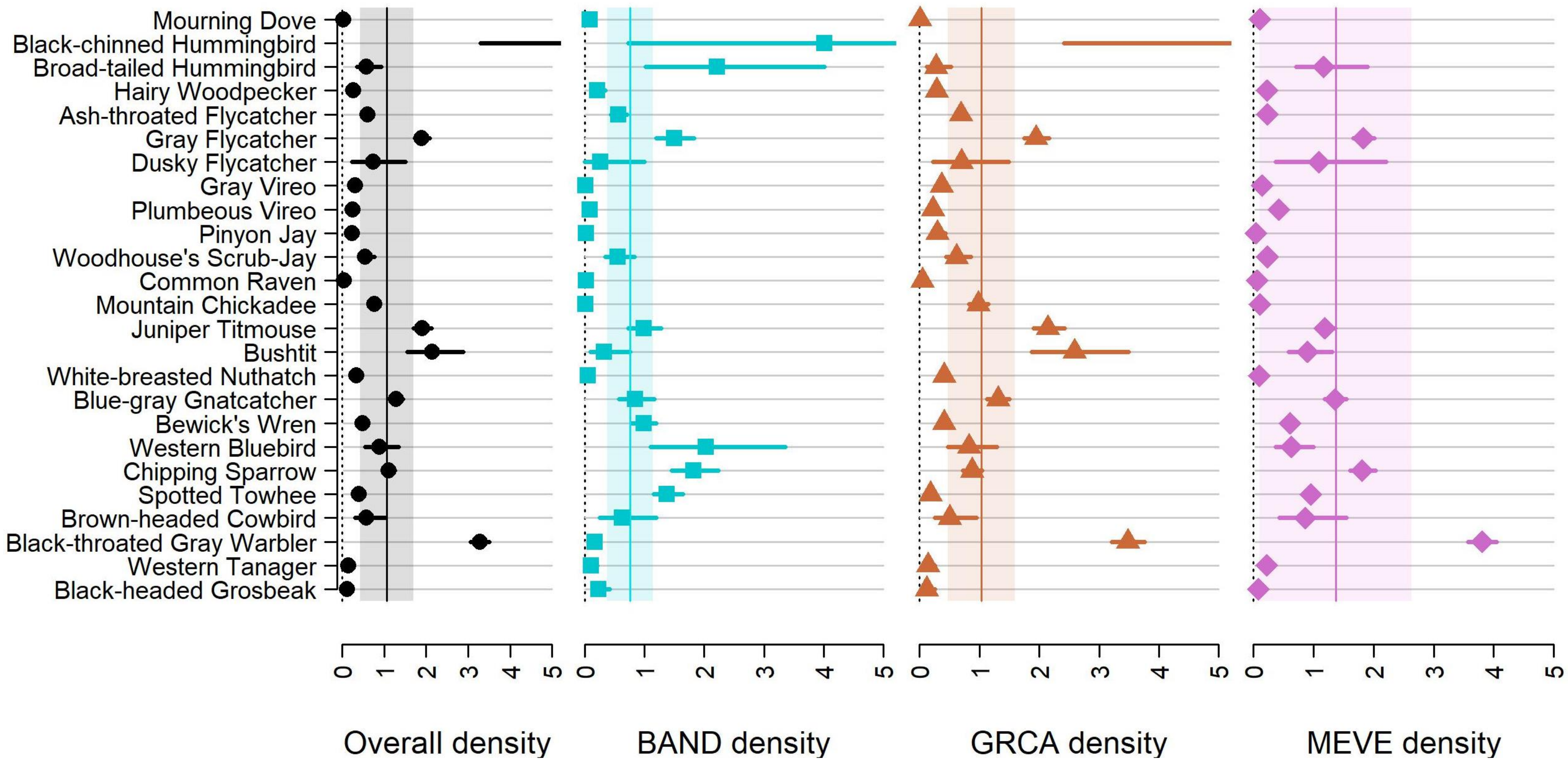


Figure S5. Park-specific densities in pinyon-juniper woodland habitat of 25 Southwestern bird species. Values represent the mean and 90% BCI of the estimated station-specific densities in birds ha^{-1} at each park, as well as across parks. Vertical lines and shaded areas represent the mean and standard error of the mean densities across species. Species are listed in taxonomic order following the American Ornithological Society's 2024 checklist. Densities of Black-chinned Hummingbird are not shown due to high estimated values.

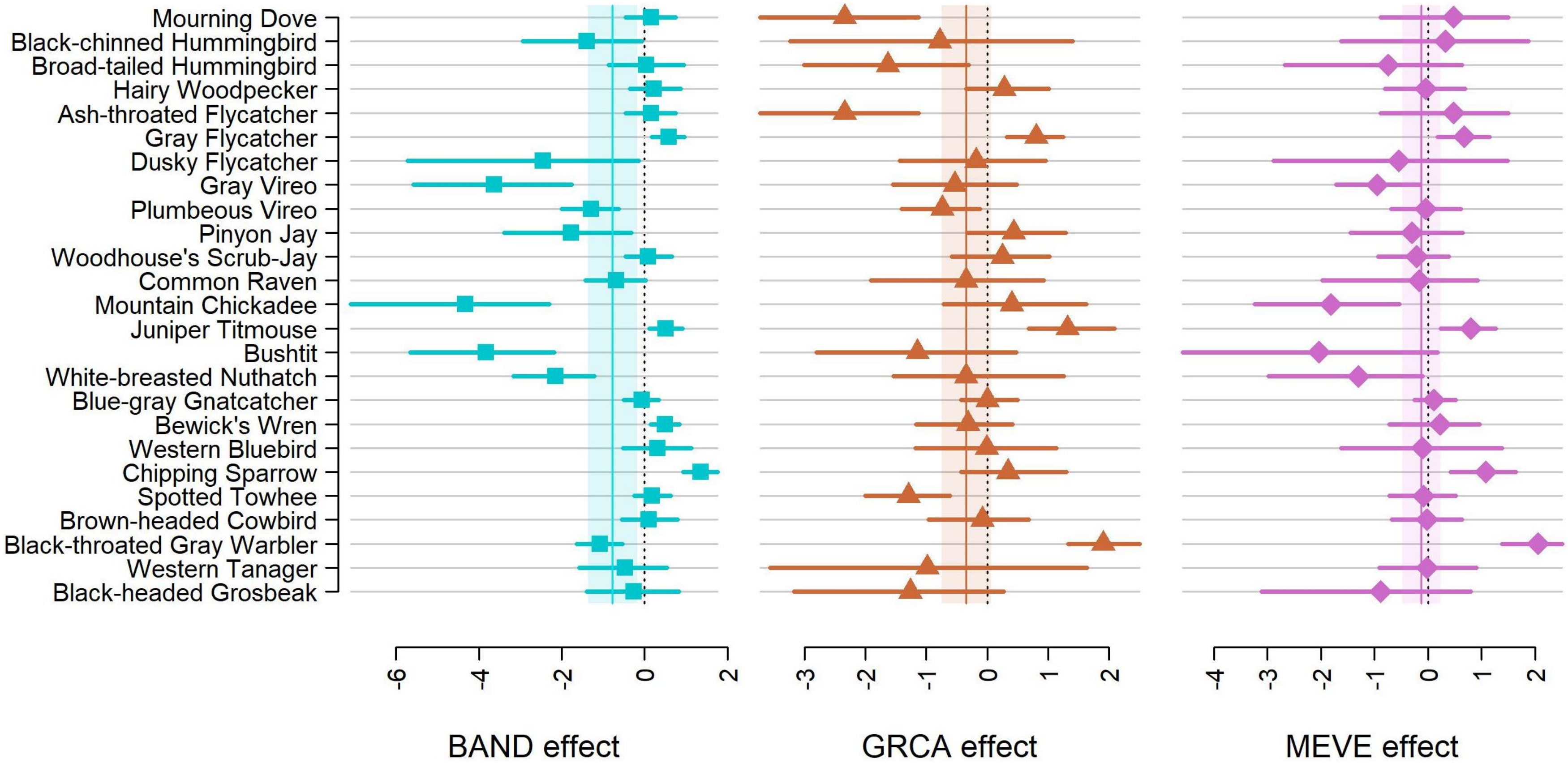


Figure S6. Park-specific year effects on densities in pinyon-juniper woodland habitat of 25 Southwestern bird species. Because only one park was surveyed per year, year effects averaged across all years in which a park was surveyed represent a general effect of each park on density. The mean value and 90% Bayesian credible interval are reported for each parameter, with vertical lines and shaded areas indicating the mean and standard error of the mean effect sizes across all species. Species are listed in taxonomic order following the American Ornithological Society’s 2024 checklist.

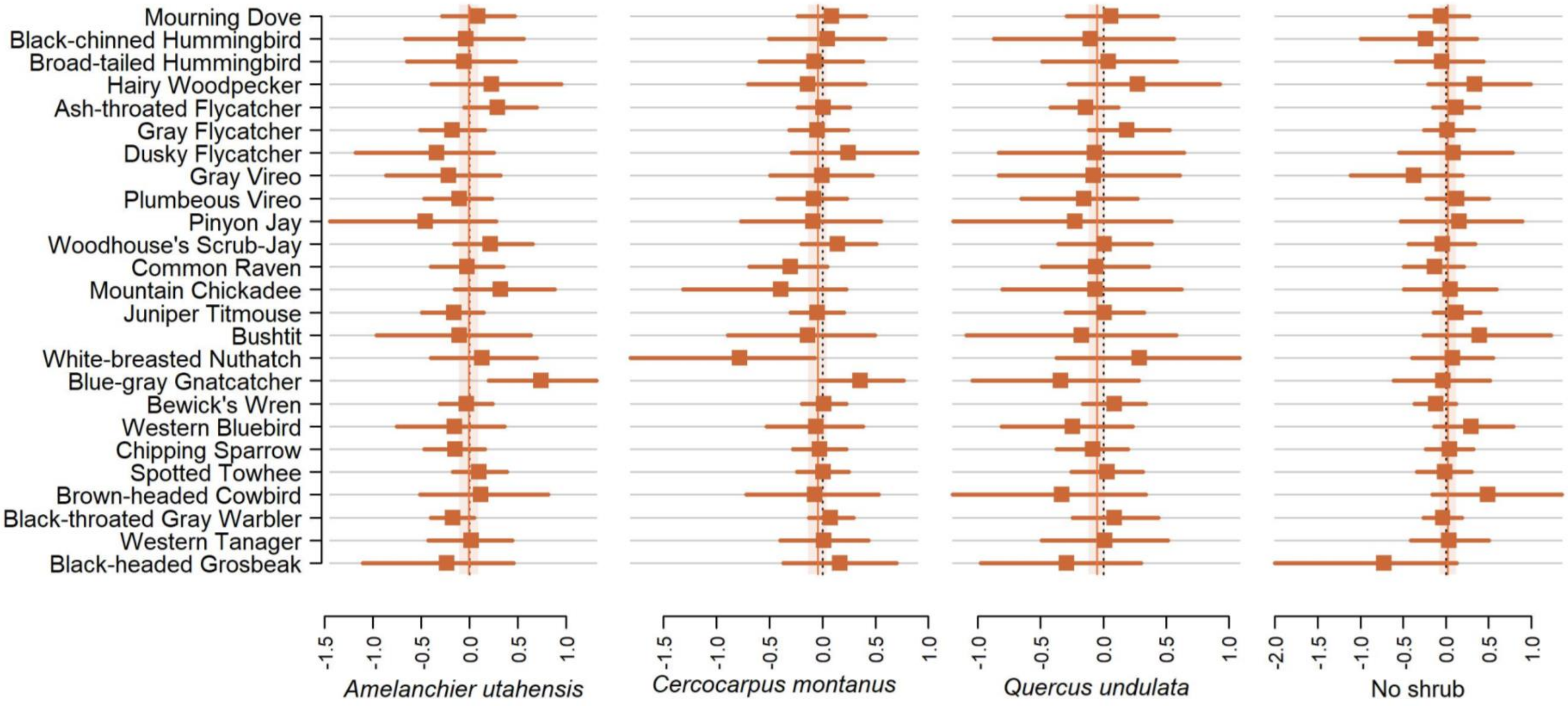


Figure S7. Additional effects of microhabitat-scale shrub-layer floristic composition on breeding-season densities of 25 Southwestern bird species in pinyon-juniper woodland. The mean and 90% Bayesian credible interval are plotted horizontally for each species, while the vertical line and shaded area represent the mean and standard error of the mean species level effect sizes. Bird species are listed in taxonomic order following the American Ornithological Society's 2024 checklist (Chesser et al. 2024).

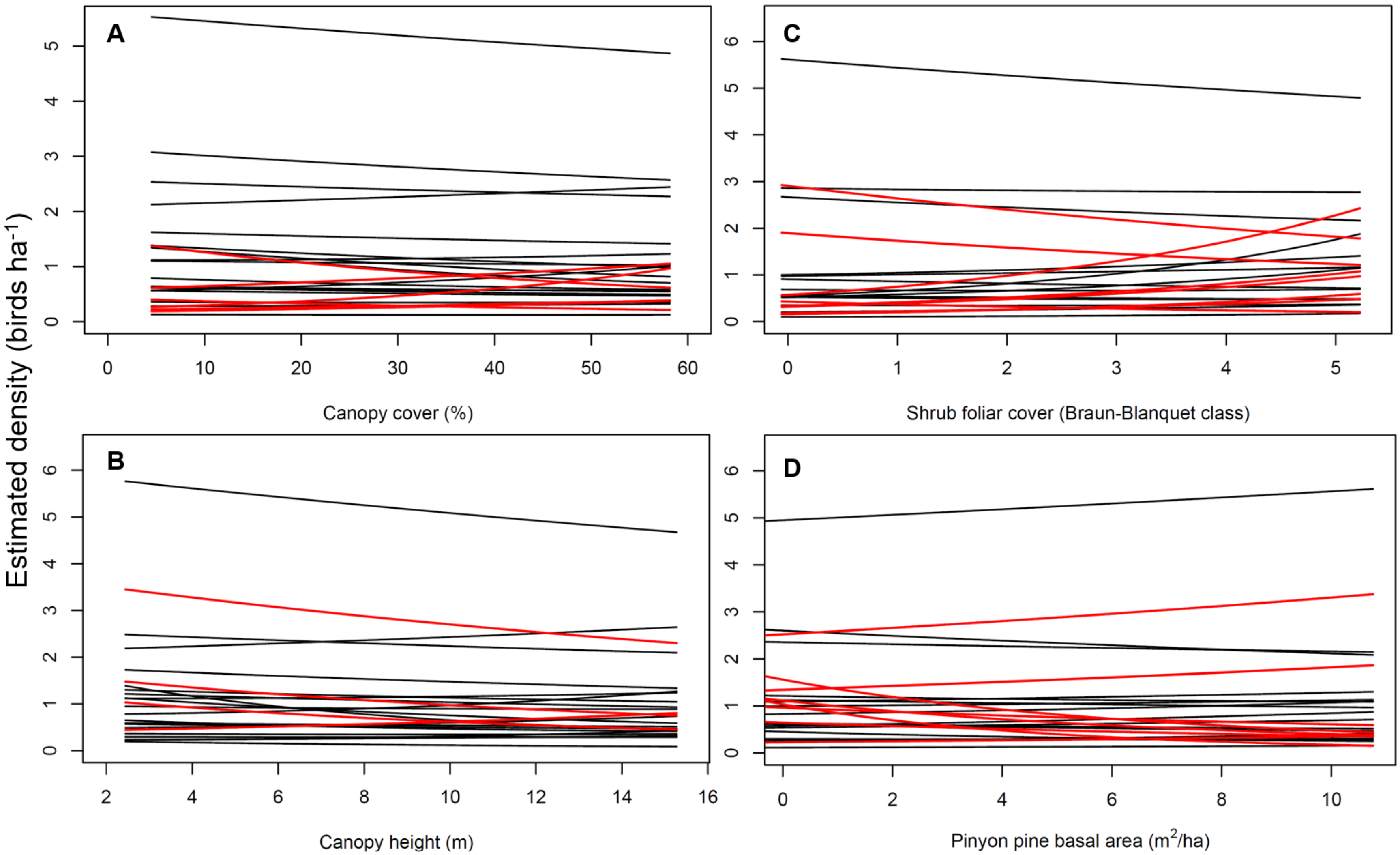
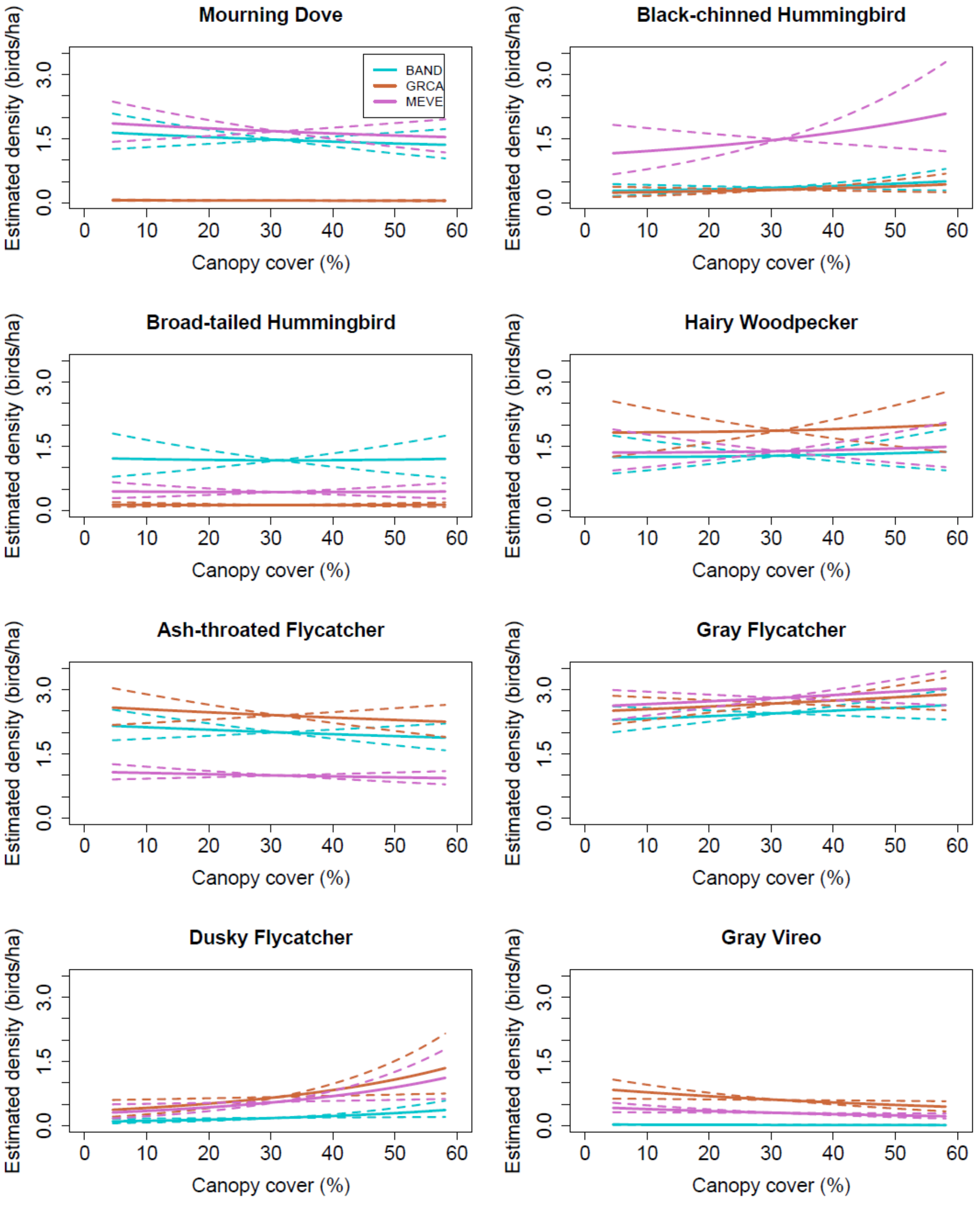


Figure S8. Estimated density of 25 bird species in persistent pinyon-juniper woodlands across gradients of canopy cover, canopy height, shrub foliage cover, and pinyon pine basal area. Estimated densities assume that all other covariates on density are held to their mean values. Species with supported effects of the covariate on density are plotted in red.


Mourning Dove

Black-chinned Hummingbird

Broad-tailed Hummingbird

Hairy Woodpecker

Ash-throated Flycatcher

Gray Flycatcher

Dusky Flycatcher

Gray Vireo

Figure S9. Estimated park-specific breeding-season densities of 25 bird species in persistent pinyon-juniper woodlands across a range of canopy cover. Park-specific density estimates are estimated from model output by assuming that fixed effects are held to park-specific mean values, while the shrub effect represents the most common dominant shrub in each park. We included the mean year effect of the years that each park was surveyed. Lines represent the mean and 90% BCI of the estimated density. Species are listed in taxonomic order following the American Ornithological Society's 2024 checklist.

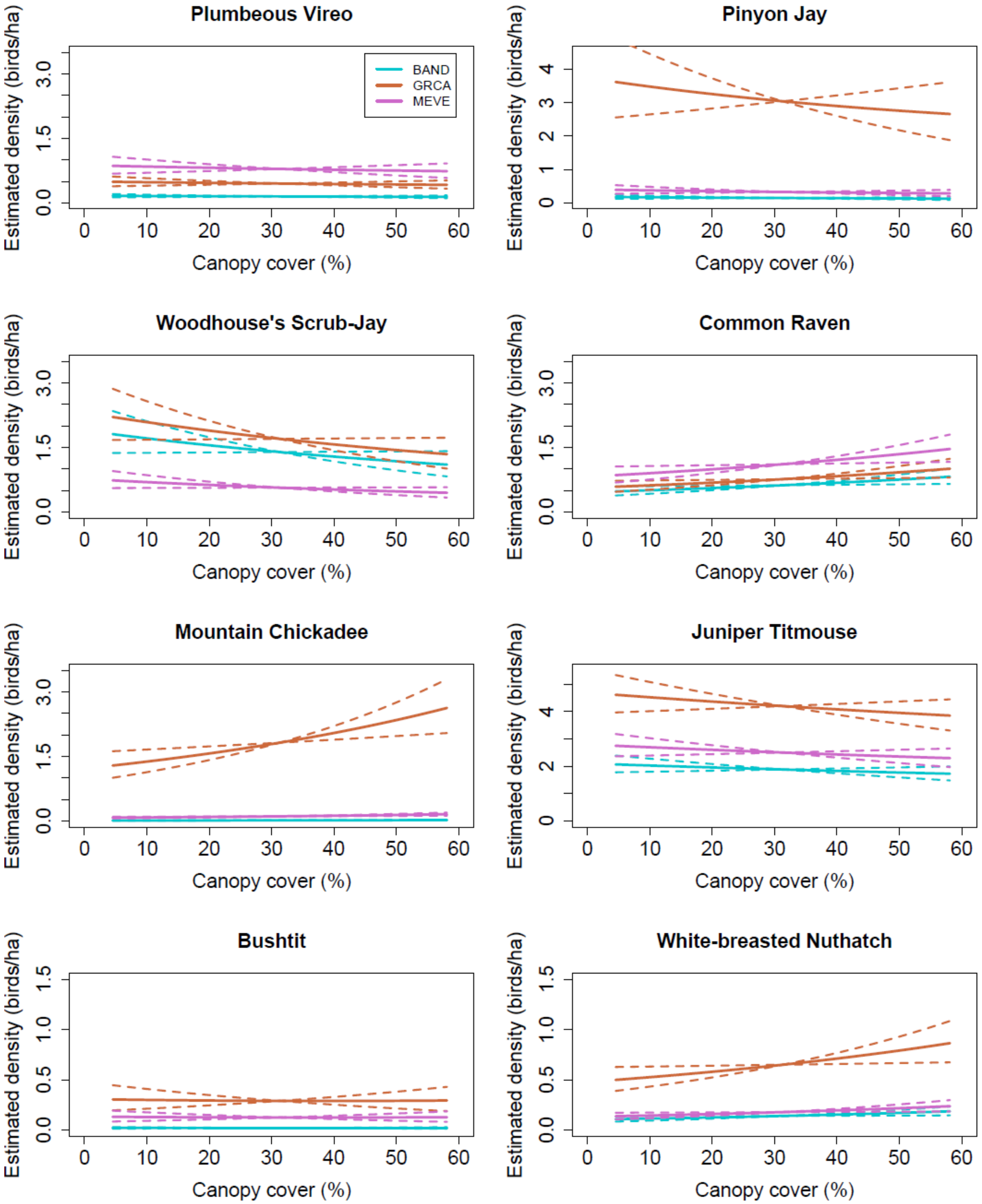


Figure S9 (continued).

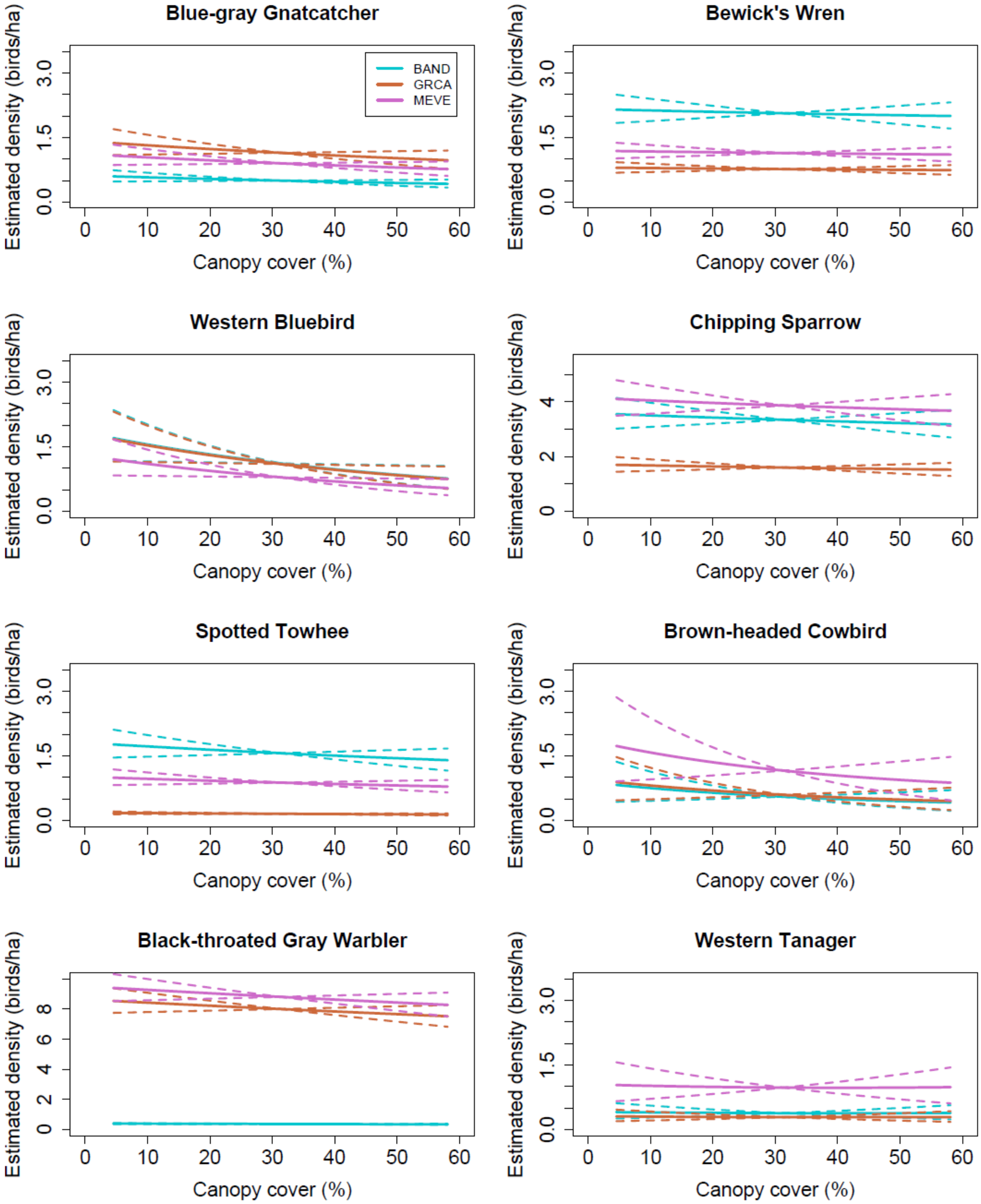


Figure S9 (continued).

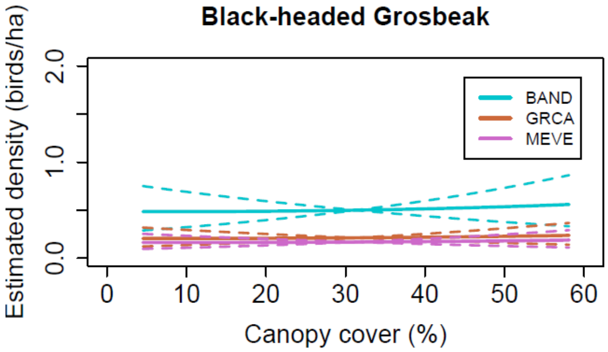


Figure S9 (continued).

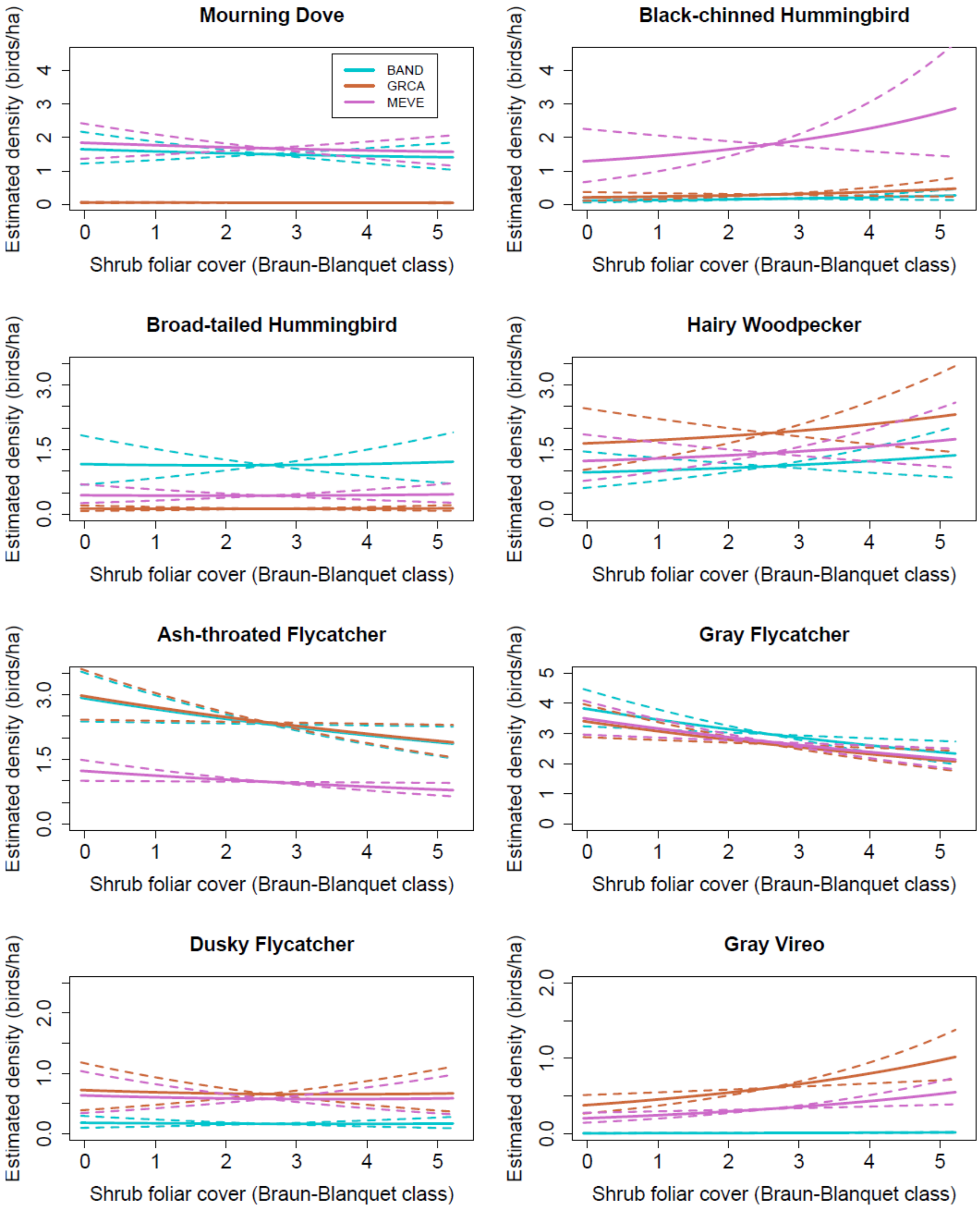


Figure S10. Estimated park-specific breeding-season densities of 25 bird species in persistent pinyon-juniper woodlands across a range of shrub foliage cover. A shrub cover score of 1 indicates < 1% foliage cover while a score of 5 indicates 25-50% foliage cover. Park-specific densities are estimated from model output where fixed effects are held to park-specific mean values and the shrub effect represents the most common dominant shrub in each park. We included the mean year effect of the years that each park was surveyed. Lines represent the mean and 90% BCI of the estimated density. Species are listed in taxonomic order following the American Ornithological Society's 2024 checklist.

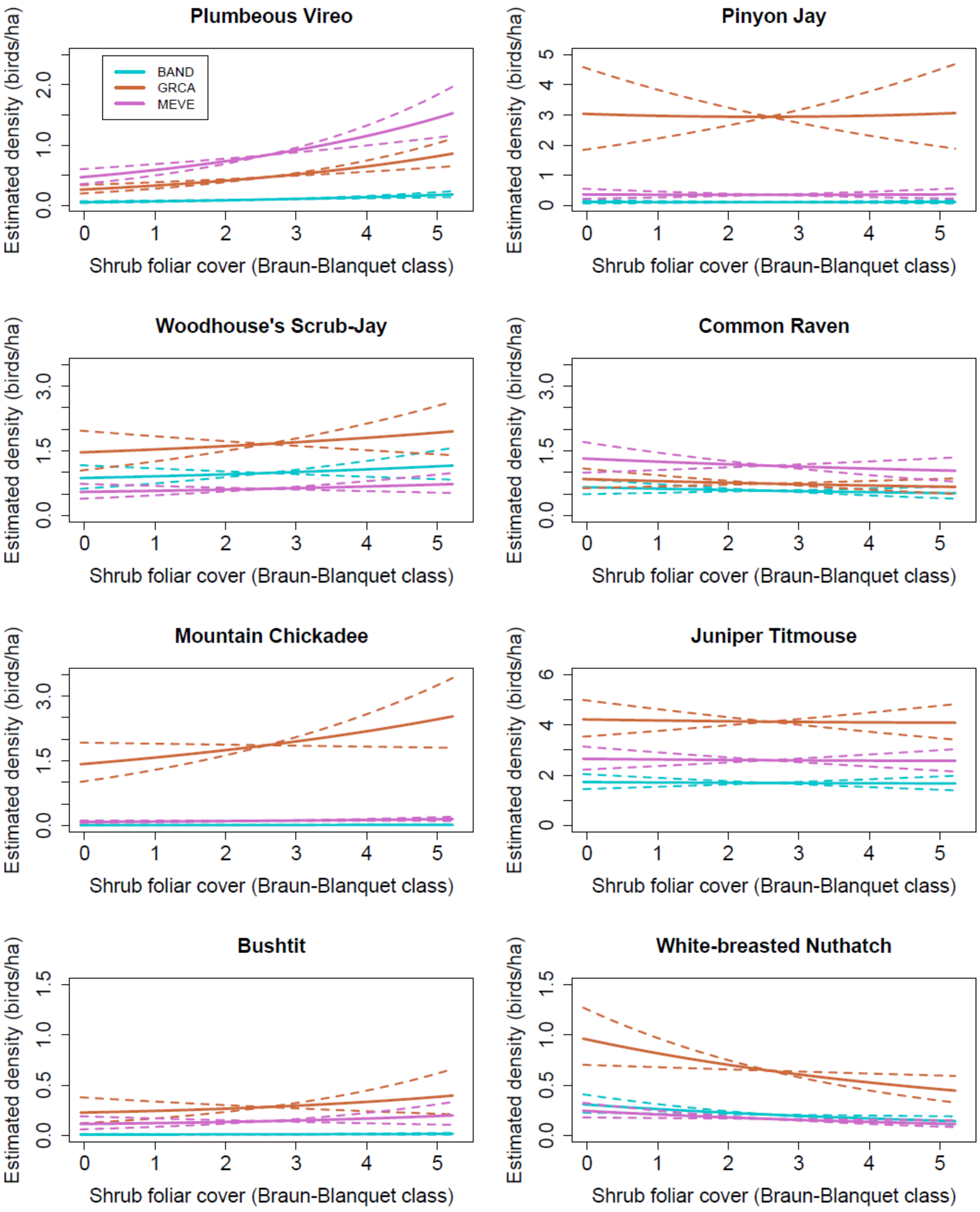


Figure S10 (continued).

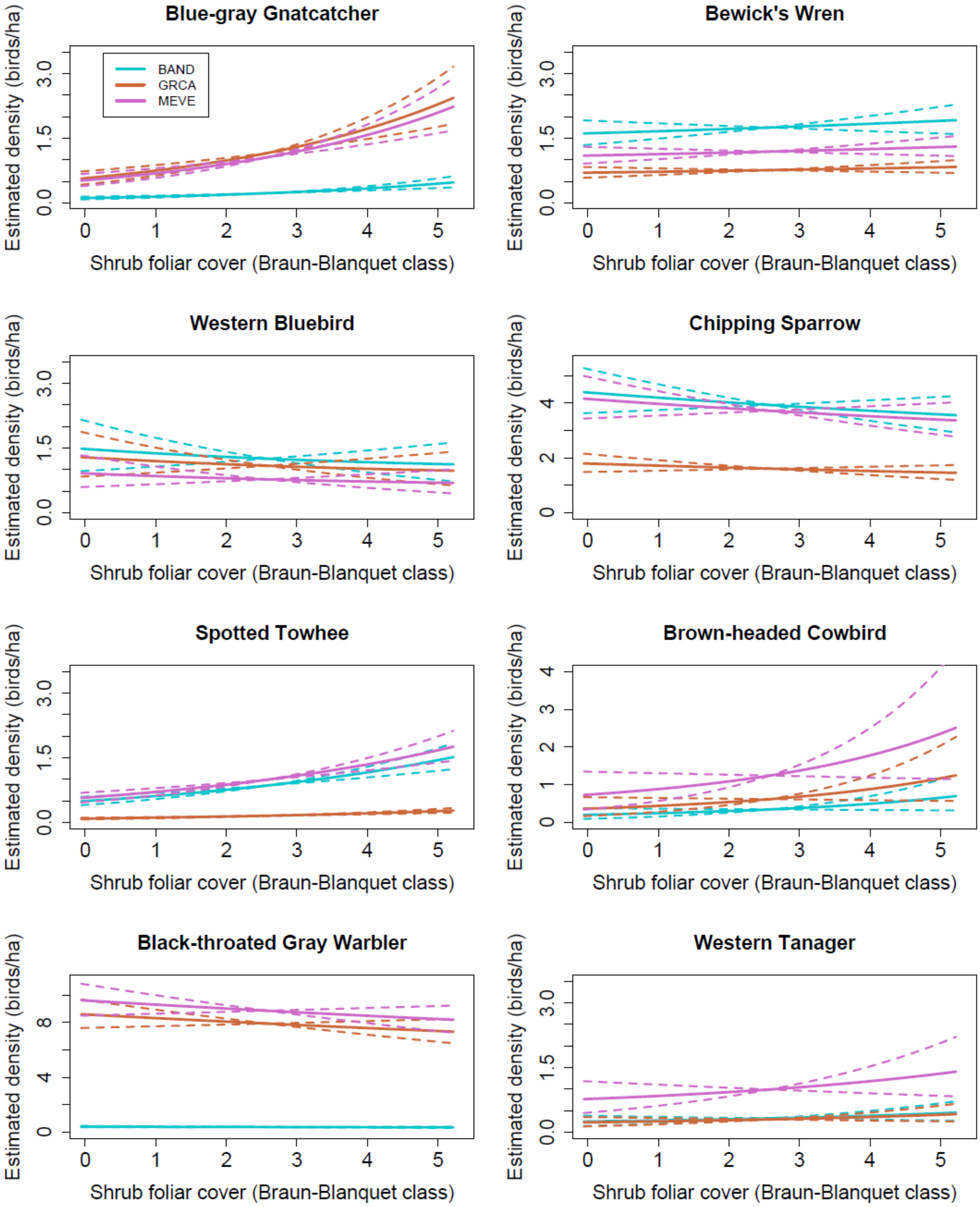


Figure S10 (continued).

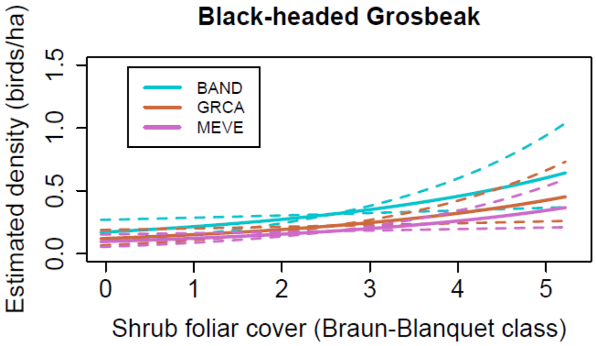


Figure S10 (continued).

TABLES

Table S1. Sample sizes of bird species detections in pinyon-juniper woodland across three parks on the southern Colorado Plateau. Detections represent the cumulative detections of each species across survey years with two replicate surveys conducted per year. Total number of survey years varied by park ($N = 1$ at Bandelier, 4 at Mesa Verde, 3 at Grand Canyon), and listed detections exclude surveys for which habitat data was not available. Species are listed in taxonomic order, and bird taxonomy follows the 2024 American Ornithological Society checklist. Bolded species were those modelled in the analysis.

Alpha Code	Common Name	Scientific Name	BAND	GRCA	MEVE	Total
SCQU	Scaled Quail	*Callipepla squamata*	0	0	4	**4**
WITU	Wild Turkey	*Meleagris gallopavo*	0	0	36	**36**
EUCD	Eurasian Collared-Dove	*Streptopelia decaocto*	0	0	1	**1**
WWDO	White-winged Dove	*Zenaida asiatica*	20	0	0	**20**
MODO	**Mourning Dove**	*Zenaida macroura*	65	9	324	**398**
GRRO	Greater Roadrunner	*Geococcyx californianus*	0	0	1	**1**
CONI	Common Nighthawk	*Chordeiles minor*	2	0	0	**2**
COPO	Common Poorwill	*Phalaenoptilus nuttallii*	0	0	1	**1**
WTSW	White-throated Swift	*Aeronautes saxatalis*	6	16	94	**116**
BCHU	**Black-chinned Hummingbird**	*Archilochus alexandri*	2	18	67	**87**
BTHU	**Broad-tailed Hummingbird**	*Selasphorus platycercus*	19	13	106	**138**
GBHE	Great Blue Heron	*Ardea herodias*	0	0	1	**1**
TUVU	Turkey Vulture	*Cathartes aura*	18	5	7	**30**
SSHA	Sharp-shinned Hawk	*Accipiter striatus*	0	1	0	**1**
COHA	Cooper's Hawk	*Accipiter cooperii*	1	1	9	**11**
AGOS	American Goshawk	*Accipiter atricapillus*	0	2	0	**2**
RTHA	Red-tailed Hawk	*Buteo jamaicensis*	1	1	0	**2**
WESO	Western Screech-Owl	*Megascops kennicottii*	0	0	1	**1**
GHOW	Great Horned Owl	*Bubo virginianus*	1	0	1	**2**
NOPO	Northern Pygmy-Owl	*Glaucidium gnoma*	0	0	2	**2**
NSWO	Northern Saw-whet Owl	*Aegolius acadicus*	0	0	2	**2**
HAWO	**Hairy Woodpecker**	*Dryobates villosus*	17	86	62	**165**
NOFL	Northern Flicker	*Colaptes auratus*	44	44	14	**102**
AMKE	American Kestrel	*Falco sparverius*	9	0	2	**11**
PEFA	Peregrine Falcon	*Falco peregrinus*	0	2	1	**3**
ATFL	**Ash-throated Flycatcher**	*Myiarchus cinerascens*	151	383	269	**803**
CAKI	Cassin's Kingbird	*Tyrannus vociferans*	30	0	10	**40**
WEWP	Western Wood-Pewee	*Contopus sordidulus*	10	5	21	**36**
HAFL	Hammond's Flycatcher	*Empidonax hammondii*	0	0	1	**1**
GRFL	**Gray Flycatcher**	*Empidonax wrightii*	125	433	610	**1168**
DUFL	**Dusky Flycatcher**	*Empidonax oberholseri*	0	31	56	**87**
SAPH	Say's Phoebe	*Sayornis saya*	10	0	2	**12**
GRVI	**Gray Vireo**	*Vireo vicinior*	0	190	110	**300**
PLVI	**Plumbeous Vireo**	*Vireo plumbeus*	12	106	300	**418**
WAVI	Warbling Vireo	*Vireo gilvus*	0	0	7	**7**
PIJA	**Pinyon Jay**	*Gymnorhinus cyanocephalus*	2	168	36	**206**
STJA	Steller's Jay	*Cyanocitta stelleri*	0	29	5	**34**
WOSJ	**Woodhouse's Scrub-Jay**	*Aphelocoma woodhouseii*	54	172	87	**313**

Alpha Code	Common Name	Scientific Name	BAND	GRCA	MEVE	Total
CLNU	Clark's Nutcracker	*Nucifraga columbiana*	0	0	9	**9**
CORA	**Common Raven**	*Corvus corax*	27	82	394	**503**
BCCH	Black-capped Chickadee	*Poecile atricapillus*	0	0	1	**1**
MOCH	**Mountain Chickadee**	*Poecile gambeli*	0	318	45	**363**
JUTI	**Juniper Titmouse**	*Baeolophus ridgwayi*	66	542	437	**1045**
TRES	Tree Swallow	*Tachycineta bicolor*	0	0	2	**2**
VGSW	Violet-green Swallow	*Tachycineta thalassina*	34	9	71	**114**
BARS	Barn Swallow	*Hirundo rustica*	0	1	8	**9**
CLSW	Cliff Swallow	*Petrochelidon pyrrhonota*	0	0	3	**3**
BUSH	**Bushtit**	*Psaltriparus minimus*	1	123	49	**173**
RCKI	Ruby-crowned Kinglet	*Corthylio calendula*	1	6	2	**9**
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	1	0	2	**3**
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	1	5	1	**7**
WBNU	**White-breasted Nuthatch**	*Sitta carolinensis*	6	279	84	**369**
PYNU	Pygmy Nuthatch	*Sitta pygmaea*	0	4	0	**4**
BGGN	**Blue-gray Gnatcatcher**	*Polioptila caerulea*	31	207	262	**500**
ROWR	Rock Wren	*Salpinctes obsoletus*	10	0	2	**12**
CANW	Canyon Wren	*Catherpes mexicanus*	3	0	3	**6**
BEWR	**Bewick's Wren**	*Thryomanes bewickii*	155	260	533	**948**
NHWR	Northern House Wren	*Troglodytes aedon*	0	0	4	**4**
NOMO	Northern Mockingbird	*Mimus polyglottos*	4	0	0	**4**
WEBL	**Western Bluebird**	*Sialia mexicana*	49	82	81	**212**
MOBL	Mountain Bluebird	*Sialia currucoides*	0	0	29	**29**
TOSO	Townsend's Solitaire	*Myadestes townsendi*	1	2	7	**10**
HETH	Hermit Thrush	*Catharus guttatus*	3	1	32	**36**
AMRO	American Robin	*Turdus migratorius*	13	0	32	**45**
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	7	0	7	**14**
HOFI	House Finch	*Haemorhous mexicanus*	84	2	54	**140**
CAFI	Cassin's Finch	*Haemorhous cassinii*	0	0	17	**17**
PISI	Pine Siskin	*Spinus pinus*	37	2	31	**70**
LEGO	Lesser Goldfinch	*Spinus psaltria*	4	7	94	**105**
AGOL	American Goldfinch	*Spinus tristis*	0	0	2	**2**
LASP	Lark Sparrow	*Chondestes grammacus*	0	0	1	**1**
CHSP	**Chipping Sparrow**	*Spizella passerina*	136	202	641	**979**
BRSP	Brewer's Sparrow	*Spizella breweri*	4	0	3	**7**
DEJU	Dark-eyed Junco	*Junco hyemalis*	7	0	2	**9**
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	0	0	2	**2**
CANT	Canyon Towhee	*Melozone fusca*	4	0	0	**4**
GTTO	Green-tailed Towhee	*Pipilo chlorurus*	1	0	5	**6**
SPTO	**Spotted Towhee**	*Pipilo maculatus*	172	98	558	**828**
YHBL	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	0	0	1	**1**
WEME	Western Meadowlark	*Sturnella neglecta*	0	0	31	**31**
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	0	0	1	**1**
BHCO	**Brown-headed Cowbird**	*Molothrus ater*	17	14	57	**88**
BRBL	Brewer's Blackbird	*Euphagus cyanocephalus*	0	0	2	**2**
OCWA	Orange-crowned Warbler	*Leiothlypis celata*	0	0	1	**1**
VIWA	Virginia's Warbler	*Leiothlypis virginiae*	13	0	45	**58**

Alpha Code	Common Name	Scientific Name	BAND	GRCA	MEVE	Total
MGWA	MacGillivray's Warbler	*Geothlypis tolmiei*	3	0	0	**3**
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	3	3	7	**13**
GRWA	Grace's Warbler	*Setophaga graciae*	5	0	0	**5**
BTYW	**Black-throated Gray Warbler**	*Setophaga nigrescens*	22	893	1488	**2403**
HETA	Hepatic Tanager	*Piranga flava*	1	0	0	**1**
WETA	**Western Tanager**	*Piranga ludoviciana*	7	18	93	**118**
BHGR	**Black-headed Grosbeak**	*Pheucticus melanocephalus*	33	35	54	**122**
LAZB	Lazuli Bunting	*Passerina amoena*	0	0	10	**10**

Table S2. Distance sampling sub-model parameterizations of breeding season densities of Southwestern birds. The bin type and number of bins indicate how distance values were collapsed into distance categories for the distance sampling analysis. The initial truncation percentage represents the percentage of the distance observations initially retained in the perceptibility sub-model, while the actual truncation percentage represents the total percentage truncated to ensure that detection interval and detection-distance bin were statistically independent. A conservative alpha value (0.10) was used to test for this statistical independence (by ANOVA) except when small sample size combined with a conservative alpha led to excessive truncation of the tail of the detection distance distribution. The maximum detection distance is the farthest detection distance after truncation of the observation distances. The effective survey area at each point count station was estimated as the area of the circle defined by the maximum detection distance and centered on the count station. Species are listed in alphabetical order by four-letter species code; full species names are given in Table S1.

Species Code	**Bin Type**	***N* Bins**	**Initial truncation percentage**	**Alpha value**	**Truncation percentage**	**Maximum detection distance (m)**	**Effective survey area (ha)**
ATFL	equalDensity	4	0.9	0.05	10.87	120	4.52
BCHU	equalArea	3	0.9	0.1	12.82	25	0.20
BEWR	equalArea	3	0.95	0.05	25.85	8	2.11
BGGN	equalDensity	4	0.95	0.05	4.87	66	1.37
BHCO	equalDensity	4	0.95	0.1	4.29	104	3.40
BHGR	equalArea	3	0.9	0.1	10.08	129	5.23
BTHU	equalWidth	3	0.9	0.1	8.00	46	0.67
BTYW	equalDensity	5	0.95	0.1	4.93	87	2.38
BUSH	equalArea	4	0.9	0.1	10.12	35	0.39
CHSP	equalDensity	5	0.9	0.05	9.85	86	2.32
CORA	equalWidth	5	0.9	0.1	10.44	300	28.30
DUFL	equalDensity	5	0.95	0.1	4.71	78	1.91
GRFL	equalDensity	4	0.9	0.05	14.50	69	1.50
GRVI	equalArea	5	0.9	0.1	12.59	92	2.66
HAWO	equalDensity	5	0.9	0.1	9.62	147	6.79
JUTI	equalDensity	4	0.95	0.05	6.87	84	2.22
MOCH	equalDensity	5	0.9	0.1	10.03	88	2.43
MODO	equalDensity	4	0.9	0.1	9.87	260	21.20
PIJA	equalDensity	3	0.95	0.1	4.21	210	13.90
PLVI	equalArea	4	0.9	0.1	16.95	87	2.38
SPTO	equalArea	3	0.9	0.1	32.28	66	1.37
WBNU	equalDensity	4	0.9	0.1	17.86	90	2.54
WEBL	equalDensity	4	0.9	0.05	15.61	85	2.27
WETA	equalDensity	5	0.9	0.1	9.73	138	5.98
WOSJ	equalDensity	5	0.9	0.1	12.96	110	3.80

Table S3. Mean estimates of availability and perceptibility for 19 Southwestern bird species during point-count surveys in pinyon-juniper woodland. The mean probability of availability for detection (p_a) and probability of perceptibility by the observer (p_d) are given along with the 90% BCI (5th and 95th centiles of the joint posterior distribution), the estimated sample size (ESS), and the R-hat value (a measure of model convergence) for each parameter. The Bayesian P-value (Bp), a measure of model goodness of fit, is also listed; Bayesian P-values between 0.4 and 0.6 are considered indicative a good model fit. Species are listed in alphabetical order by four-letter species code; full species names are given in Table S1.

Species Code			p_a					p_d			**Bp p_a**	**Bp p_d**
	Mean	5%	95%	ESS	R-hat	Mean	5%	95%	ESS	R-hat		
ATFL	0.84	0.80	0.87	893	1.002	0.43	0.39	0.48	6000	1.000	0.42	0.57
BCHU	0.12	0.05	0.24	33	1.078	0.29	0.22	0.37	559	1.004	0.52	0.53
BEWR	0.90	0.87	0.92	6000	1.000	0.68	0.63	0.73	738	1.004	0.49	0.62
BGGN	0.88	0.84	0.91	1093	1.002	0.26	0.23	0.28	1076	1.002	0.51	0.61
BHCO	0.11	0.05	0.18	72	1.004	0.27	0.21	0.35	2631	1.000	0.52	0.52
BHGR	0.34	0.16	0.50	655	1.003	0.55	0.44	0.69	851	1.004	0.47	0.43
BTHU	0.43	0.28	0.54	718	1.006	0.39	0.28	0.54	101	1.022	0.49	0.52
BTYW	0.84	0.82	0.86	1255	1.001	0.31	0.29	0.33	6000	1.000	0.34	0.60
BUSH	0.55	0.44	0.66	501	1.006	0.47	0.38	0.57	524	1.004	0.47	0.47
CHSP	0.77	0.72	0.82	665	1.003	0.30	0.28	0.33	1488	1.001	0.48	0.55
CORA	0.62	0.54	0.70	198	1.011	0.40	0.36	0.46	198	1.011	0.43	0.49
DUFL	0.20	0.07	0.44	31	1.047	0.29	0.21	0.39	693	1.010	0.51	0.49
GRFL	0.88	0.85	0.90	1175	1.002	0.37	0.35	0.40	359	1.006	0.52	0.64
GRVI	0.83	0.77	0.88	2334	1.000	0.50	0.43	0.58	642	1.006	0.52	0.48
HAWO	0.39	0.27	0.50	513	1.008	0.19	0.16	0.23	2370	1.001	0.52	0.63
JUTI	0.71	0.66	0.76	536	1.004	0.33	0.31	0.35	579	1.003	0.54	0.58
MOCH	0.73	0.64	0.81	2168	1.001	0.37	0.32	0.43	1162	1.001	0.44	0.54
MODO	0.78	0.70	0.86	147	1.014	0.36	0.31	0.42	197	1.012	0.37	0.50
PIJA	0.39	0.28	0.47	318	1.010	0.23	0.19	0.27	296	1.007	0.54	0.49
PLVI	0.89	0.85	0.92	3936	1.000	0.50	0.45	0.56	1859	1.002	0.52	0.50
SPTO	0.92	0.90	0.94	4142	1.001	0.75	0.67	0.82	437	1.015	0.54	0.55
WBNU	0.76	0.68	0.83	1198	1.000	0.66	0.56	0.78	377	1.003	0.50	0.51
WEBL	0.22	0.13	0.34	59	1.040	0.46	0.39	0.54	5787	1.000	0.53	0.60
WETA	0.30	0.17	0.43	184	1.012	0.34	0.27	0.41	6000	1.000	0.49	0.56
WOSJ	0.40	0.28	0.53	273	1.009	0.40	0.35	0.46	1125	1.002	0.53	0.56

Table S4. Effects of covariates on detectability during point-count surveys of 25 bird species in pinyon-juniper woodlands. Species are listed in alphabetical order by four-letter Alpha Code; full species names are given in Table S1. The mean and 90% BCI are given for the joint posterior distribution for each covariate, along with the estimated sample size (a measure of autocorrelation in the MCMC chains) and R-hat value (a measure of model convergence). Species are listed in alphabetical order by four-letter species code; full species names are given in Table S1.

Species	Ordinal Date (baD)					Ordinal Date^2 (baD^2)					Minute of Day (baM)				
	Mean	5%	95%	ESS	R-hat	Mean	5%	95%	ESS	R-hat	Mean	5%	95%	ESS	R-hat
ATFL	-0.41	-0.55	-0.26	1164	1.002	0.24	0.11	0.38	1370	1.001	0.24	0.13	0.36	6000	1.000
BCHU	-0.07	-0.35	0.21	734	1.004	-0.53	-0.80	-0.27	1554	1.008	-0.29	-0.55	-0.02	1346	1.001
BEWR	0.03	-0.09	0.15	6000	1.000	0.07	-0.05	0.19	3640	1.001	0.13	0.03	0.24	3984	1.000
BGGN	-0.12	-0.30	0.05	6000	1.000	0.17	0.01	0.33	6000	1.000	0.21	0.05	0.37	1219	1.001
BHCO	0.26	-0.02	0.54	4846	1.001	0.51	0.19	0.84	3310	1.001	0.10	-0.17	0.37	1863	1.000
BHGR	0.04	-0.27	0.36	3700	1.001	1.10	0.72	1.51	1042	1.002	0.55	0.22	0.86	4603	1.001
BTHU	0.70	0.33	1.06	6000	1.000	1.17	0.74	1.59	2897	1.001	-0.18	-0.52	0.16	2963	1.001
BTYW	0.35	0.28	0.42	3983	1.000	0.44	0.36	0.52	2362	1.001	-0.05	-0.12	0.01	6000	1.000
BUSH	0.23	-0.03	0.50	2273	1.002	-0.73	-1.02	-0.43	1404	1.003	0.42	0.15	0.69	1898	1.002
CHSP	0.18	0.05	0.31	784	1.002	0.06	-0.09	0.21	1555	1.001	0.07	-0.05	0.18	6000	1.000
CORA	-0.09	-0.25	0.06	2799	1.001	0.06	-0.11	0.23	1174	1.001	0.53	0.39	0.68	6000	1.000
DUFL	0.38	0.12	0.65	1377	1.001	-0.39	-0.74	-0.06	1347	1.006	0.27	0.00	0.56	877	1.004
GRFL	0.07	-0.04	0.17	2381	1.001	0.18	0.07	0.30	6000	1.001	0.10	0.01	0.19	6000	1.000
GRVI	0.05	-0.15	0.26	3558	1.001	0.12	-0.08	0.32	2820	1.002	0.15	-0.07	0.36	4308	1.001
HAWO	-0.06	-0.28	0.16	6000	1.000	-0.01	-0.25	0.22	1717	1.001	0.57	0.34	0.79	4090	1.000
JUTI	-0.03	-0.14	0.08	3304	1.001	-0.07	-0.19	0.04	1274	1.001	-0.02	-0.13	0.09	6000	1.000
MOCH	0.34	0.13	0.54	5015	1.001	-0.47	-0.71	-0.22	2114	1.002	0.26	0.07	0.45	6000	1.000
MODO	-0.14	-0.31	0.03	1156	1.002	-0.31	-0.51	-0.10	400	1.005	0.50	0.24	0.72	258	1.008
PIJA	1.14	0.89	1.38	6000	1.000	0.20	-0.09	0.51	6000	1.000	-0.10	-0.32	0.12	6000	1.000
PLVI	0.08	-0.10	0.25	6000	1.000	0.27	0.06	0.47	6000	1.000	0.07	-0.09	0.24	6000	1.000
SPTO	-0.17	-0.28	-0.05	5901	1.000	-0.21	-0.35	-0.08	5314	1.000	0.04	-0.05	0.14	5901	1.000
WBNU	-0.29	-0.49	-0.09	3381	1.000	-0.16	-0.37	0.06	2753	1.001	0.00	-0.21	0.21	3498	1.000
WEBL	0.18	-0.01	0.36	6000	1.000	-0.34	-0.51	-0.17	6000	1.000	-0.07	-0.25	0.11	3194	1.001
WETA	-0.92	-1.37	-0.53	2081	1.001	1.54	1.12	2.02	2382	1.001	0.29	0.00	0.59	1577	1.001
WOSJ	0.07	-0.09	0.23	3088	1.001	0.28	0.12	0.45	3477	1.000	-0.05	-0.22	0.11	6000	1.001

Table S4 (continued).

Species	**Cloud Cover (baC)**					**Environmental Noise (bdN)**				
	Mean	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**
ATFL	0.13	0.02	0.25	6000	1.000	0.00	-0.05	0.05	1716	1.001
BCHU	-0.27	-0.49	-0.04	3551	1.001	-0.02	-0.16	0.12	1705	1.001
BEWR	0.05	-0.07	0.19	4413	1.000	-0.07	-0.15	0.01	3349	1.000
BGGN	0.12	-0.03	0.28	6000	1.000	0.02	-0.02	0.06	1169	1.001
BHCO	0.05	-0.17	0.27	1294	1.002	0.10	-0.03	0.28	1589	1.002
BHGR	-0.35	-0.60	-0.08	1192	1.003	-0.03	-0.30	0.32	470	1.020
BTHU	0.01	-0.21	0.24	6000	1.000	0.13	-0.05	0.35	1284	1.002
BTYW	-0.01	-0.07	0.05	5309	1.000	-0.01	-0.03	0.01	6000	1.000
BUSH	-0.57	-0.93	-0.19	2195	1.001	-0.06	-0.22	0.11	2475	1.023
CHSP	-0.04	-0.13	0.05	6000	1.000	-0.04	-0.07	-0.01	1166	1.002
CORA	-0.28	-0.40	-0.17	621	1.003	-0.01	-0.07	0.06	6000	1.000
DUFL	0.24	-0.05	0.55	1577	1.002	0.10	-0.04	0.27	1868	1.266
GRFL	-0.04	-0.13	0.05	3655	1.000	-0.05	-0.08	-0.02	3783	1.000
GRVI	0.43	0.16	0.68	3267	1.000	0.01	-0.08	0.10	3932	1.000
HAWO	-0.12	-0.35	0.10	6000	1.000	-0.02	-0.09	0.04	6000	1.000
JUTI	0.05	-0.06	0.16	946	1.002	-0.03	-0.05	0.00	6000	1.000
MOCH	-0.08	-0.29	0.14	6000	1.000	-0.03	-0.09	0.02	6000	1.000
MODO	0.05	-0.09	0.18	1303	1.001	-0.01	-0.08	0.06	3209	1.001
PIJA	0.41	0.15	0.67	3443	1.001	-0.05	-0.09	0.00	5348	1.001
PLVI	0.09	-0.06	0.24	4239	1.000	-0.05	-0.12	0.02	2577	1.001
SPTO	-0.08	-0.17	0.01	5901	1.001	0.07	-0.02	0.19	2813	1.231
WBNU	0.14	-0.03	0.31	3574	1.000	0.09	-0.07	0.33	268	1.006
WEBL	-0.04	-0.18	0.10	6000	1.000	0.11	-0.01	0.26	6000	1.001
WETA	0.15	-0.09	0.39	2222	1.001	0.06	-0.06	0.20	1552	1.001
WOSJ	0.05	-0.11	0.21	2141	1.001	-0.07	-0.14	0.00	6000	1.000

Table S5. Overall (across-park) and park-specific densities in persistent pinyon-juniper woodland for 25 Southwestern bird species. Overall densities, in birds ha^{-1}, represent weighted averages across all parks in which a species commonly occurred, with densities weighted by the total area of inference (i.e., area covered by the focal habitat) in each park. Park-specific densities are averages of all point-count stations in each park. Densities represent habitat-specific densities in mature pinyon-woodland rather than densities across all habitats in each park. Species are listed in alphabetical order by four-letter species code; full species names are listed in Table S1.

Species	Overall Density			BAND Density			GRCA Density			MEVE Density		
	Mean	5%	95%	Mean	5%	95%	Mean	5%	95%	Mean	5%	95%
ATFL	0.61	0.55	0.67	0.56	0.44	0.71	0.69	0.62	0.77	0.24	0.20	0.27
BCHU	7.75	3.29	14.68	4.01	0.73	10.26	6.37	2.41	13.17	15.97	6.65	29.69
BEWR	0.49	0.44	0.54	0.99	0.80	1.20	0.41	0.36	0.47	0.61	0.56	0.67
BGGN	1.28	1.13	1.45	0.84	0.58	1.17	1.31	1.13	1.51	1.36	1.19	1.55
BHCO	0.58	0.31	1.02	0.62	0.26	1.19	0.51	0.25	0.95	0.87	0.43	1.54
BHGR	0.12	0.06	0.25	0.23	0.12	0.42	0.12	0.05	0.25	0.09	0.05	0.16
BTHU	0.57	0.35	0.93	2.21	1.02	4.01	0.27	0.12	0.52	1.17	0.71	1.90
BTYW	3.28	3.06	3.51	0.17	0.11	0.26	3.49	3.21	3.77	3.81	3.58	4.04
BUSH	2.14	1.55	2.88	0.33	0.09	0.76	2.59	1.88	3.50	0.90	0.59	1.32
CHSP	1.10	0.97	1.25	1.82	1.46	2.23	0.88	0.72	1.04	1.81	1.61	2.03
CORA	0.05	0.04	0.06	0.02	0.01	0.04	0.05	0.03	0.06	0.07	0.05	0.08
DUFL	0.74	0.24	1.51	0.27	0.00	1.01	0.71	0.22	1.49	1.09	0.37	2.21
GRFL	1.89	1.72	2.08	1.50	1.20	1.83	1.95	1.75	2.17	1.83	1.66	2.02
GRVI	0.31	0.26	0.36	0.01	0.00	0.05	0.37	0.31	0.44	0.15	0.12	0.18
HAWO	0.27	0.20	0.36	0.21	0.11	0.35	0.28	0.20	0.39	0.23	0.15	0.34
JUTI	1.90	1.70	2.13	0.99	0.73	1.29	2.15	1.90	2.42	1.19	1.04	1.36
MOCH	0.77	0.64	0.90	0.01	0.00	0.04	0.98	0.83	1.15	0.11	0.08	0.15
MODO	0.03	0.02	0.04	0.09	0.06	0.12	0.00	0.00	0.01	0.11	0.09	0.14
PIJA	0.24	0.17	0.34	0.03	0.00	0.07	0.30	0.21	0.43	0.04	0.03	0.07
PLVI	0.25	0.21	0.28	0.08	0.05	0.13	0.22	0.18	0.27	0.43	0.37	0.49
SPTO	0.40	0.36	0.45	1.37	1.15	1.65	0.18	0.15	0.22	0.96	0.86	1.07
WBNU	0.33	0.27	0.39	0.05	0.03	0.10	0.41	0.33	0.49	0.10	0.08	0.13
WEBL	0.89	0.54	1.34	2.03	1.10	3.36	0.83	0.47	1.29	0.63	0.37	1.00
WETA	0.15	0.08	0.26	0.10	0.04	0.21	0.14	0.06	0.26	0.23	0.14	0.36
WOSJ	0.55	0.40	0.76	0.55	0.35	0.84	0.62	0.44	0.86	0.24	0.16	0.33

Table S6. Average effects of park on density of 25 Southwestern birds in persistent pinyon-juniper woodland. Park effects represent the average of the stacked posterior distributions of year effects during which a park was surveyed. The mean and 90% Bayesian credible interval are provided for each park effect. A park and year effect were not fit separately because BAND was only surveyed in one year, presenting identifiability problems. Because the park effects were estimated a posteriori, ESS and R-hat values are not provided. Species are listed in alphabetical order by four-letter species code; full species names are listed in Table S1.

Species	**BAND Effect**			**GRCA Effect**			**MEVE Effect**		
	Mean	**5%**	**95%**	**Mean**	**5%**	**95%**	**Mean**	**5%**	**95%**
ATFL	0.16	-0.46	0.75	-2.34	-3.73	-1.13	0.48	-0.89	1.49
BCHU	-1.40	-2.94	-0.06	-0.78	-3.23	1.39	0.33	-1.62	1.88
BEWR	0.49	0.14	0.85	-0.31	-1.17	0.41	0.23	-0.73	0.96
BGGN	-0.07	-0.50	0.34	0.01	-0.43	0.49	0.11	-0.26	0.52
BHCO	0.10	-0.54	0.80	-0.09	-0.96	0.68	-0.02	-0.68	0.63
BHGR	-0.27	-1.40	0.82	-1.26	-3.17	0.27	-0.88	-3.10	0.80
BTHU	0.04	-0.87	0.94	-1.63	-3.00	-0.31	-0.74	-2.67	0.64
BTYW	-1.08	-1.64	-0.53	1.91	1.33	2.50	2.05	1.38	2.51
BUSH	-3.83	-5.66	-2.18	-1.14	-2.80	0.47	-2.04	-4.58	0.17
CHSP	1.36	0.94	1.76	0.34	-0.42	1.30	1.08	0.43	1.63
CORA	-0.69	-1.43	0.02	-0.35	-1.90	0.93	-0.16	-1.97	0.93
DUFL	-2.45	-5.72	-0.14	-0.19	-1.44	0.96	-0.54	-2.89	1.49
GRFL	0.58	0.17	0.96	0.80	0.32	1.24	0.68	0.18	1.15
GRVI	-3.64	-5.59	-1.75	-0.53	-1.55	0.49	-0.95	-1.71	-0.16
HAWO	0.22	-0.36	0.87	0.28	-0.35	1.01	-0.04	-0.80	0.70
JUTI	0.51	0.11	0.92	1.32	0.68	2.08	0.80	0.24	1.27
MOCH	-4.33	-7.10	-2.30	0.40	-0.72	1.63	-1.81	-3.24	-0.53
MODO	0.16	-0.46	0.75	-2.34	-3.73	-1.13	0.48	-0.89	1.49
PIJA	-1.78	-3.39	-0.33	0.43	-0.33	1.28	-0.30	-1.45	0.65
PLVI	-1.29	-2.01	-0.62	-0.74	-1.40	-0.12	-0.04	-0.69	0.61
SPTO	0.18	-0.26	0.62	-1.30	-2.00	-0.62	-0.08	-0.73	0.51
WBNU	-2.15	-3.17	-1.22	-0.35	-1.54	1.25	-1.30	-2.98	-0.10
WEBL	0.31	-0.52	1.13	-0.01	-1.18	1.13	-0.10	-1.62	1.39
WETA	-0.48	-1.58	0.54	-0.98	-3.57	1.63	-0.02	-0.91	0.90
WOSJ	0.09	-0.46	0.66	0.25	-0.58	1.02	-0.21	-0.93	0.39

Table S7. Effects of vegetation structure on breeding-season densities of 25 Southwestern bird species in persistent pinyon-juniper woodland. The mean and 90% BCI are given for the joint posterior distribution for each covariate, along with the estimated sample size (a measure of autocorrelation in the MCMC chains) and R-hat value (a measure of model convergence). Species are listed in alphabetical order by four-letter species code; full species names are given in Table S1.

Species	**Canopy Cover (bnCanC)**					**Canopy Height (bnCanH)**					**Subcanopy Foliage Cover (bnScanfc)**				
	Mean	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**
ATFL	-0.03	-0.12	0.05	2758	1.001	-0.06	-0.16	0.03	356	1.006	-0.02	-0.15	0.12	4383	1.000
BCHU	0.15	-0.10	0.40	384	1.004	-0.29	-0.64	0.02	250	1.001	0.13	-0.31	0.62	351	1.011
BEWR	-0.02	-0.09	0.06	6000	1.000	-0.07	-0.14	0.01	6000	1.000	0.02	-0.11	0.15	3617	1.000
BGGN	-0.09	-0.20	0.02	664	1.003	-0.06	-0.17	0.06	1695	1.001	0.06	-0.08	0.21	2045	1.001
BHCO	-0.17	-0.45	0.12	346	1.004	0.12	-0.19	0.42	301	1.011	0.30	-0.06	0.69	290	1.007
BHGR	0.04	-0.20	0.27	811	1.003	0.16	-0.12	0.45	1121	1.003	-0.26	-0.54	0.02	356	1.006
BTHU	0.00	-0.21	0.20	1126	1.002	-0.01	-0.25	0.24	1153	1.002	0.10	-0.22	0.43	3021	1.001
BTYW	-0.03	-0.08	0.02	569	1.003	-0.05	-0.11	0.00	3604	1.001	-0.01	-0.07	0.05	1578	1.001
BUSH	-0.01	-0.22	0.20	1185	1.000	-0.20	-0.43	0.03	1131	1.003	0.17	-0.28	0.65	519	1.005
CHSP	-0.03	-0.11	0.05	6000	1.000	0.05	-0.04	0.14	937	1.002	0.01	-0.10	0.12	6000	1.000
CORA	0.13	0.02	0.24	1745	1.001	-0.16	-0.33	0.01	2737	1.001	0.05	-0.10	0.21	2044	1.001
DUFL	0.32	0.05	0.58	405	1.013	-0.12	-0.43	0.20	285	1.006	0.36	0.05	0.69	533	1.006
GRFL	0.03	-0.03	0.10	2066	1.001	-0.04	-0.12	0.04	2207	1.001	-0.01	-0.11	0.09	6000	1.000
GRVI	-0.16	-0.29	-0.03	1683	1.000	-0.01	-0.16	0.14	1595	1.000	-0.02	-0.23	0.19	1779	1.003
HAWO	0.02	-0.16	0.20	569	1.004	0.03	-0.17	0.22	6000	1.000	0.16	-0.12	0.45	1607	1.001
JUTI	-0.04	-0.12	0.03	6000	1.001	-0.10	-0.19	-0.01	6000	1.000	-0.02	-0.13	0.08	6000	1.000
MOCH	0.18	0.06	0.30	4536	1.000	0.09	-0.06	0.23	1065	1.002	-0.14	-0.34	0.07	6000	1.000
MODO	-0.05	-0.17	0.08	5117	1.001	-0.05	-0.19	0.09	4642	1.000	0.15	-0.03	0.34	2648	1.002
PIJA	-0.08	-0.24	0.09	6000	1.000	-0.21	-0.40	-0.01	2140	1.002	-0.21	-0.44	0.03	177	1.012
PLVI	-0.04	-0.15	0.07	653	1.003	0.15	0.03	0.26	1990	1.001	-0.01	-0.17	0.15	2466	1.001
SPTO	-0.06	-0.15	0.03	3351	1.000	-0.03	-0.13	0.06	2821	1.000	0.01	-0.10	0.12	4160	1.000
WBNU	0.14	0.02	0.26	2296	1.002	0.01	-0.12	0.14	2245	1.001	0.11	-0.12	0.35	1644	1.002
WEBL	-0.20	-0.37	-0.03	1077	1.002	-0.02	-0.18	0.15	6000	1.000	-0.17	-0.44	0.10	6000	1.000
WETA	-0.01	-0.24	0.20	834	1.002	0.10	-0.13	0.33	6000	1.003	0.30	-0.05	0.68	525	1.005
WOSJ	-0.12	-0.26	0.01	6000	1.000	-0.17	-0.33	-0.01	753	1.003	0.05	-0.14	0.24	6000	1.000

Table S7 (continued).

Species	Foliage Height Diversity (bnFHD)					Shrub Height (bnShrubH)					Shrub Foliage Cover (bnShrubfc)				
	Mean	5%	95%	ESS	R-hat	Mean	5%	95%	ESS	R-hat	Mean	5%	95%	ESS	R-hat
ATFL	0.09	-0.05	0.22	340	1.006	0.09	0.02	0.17	3191	1.000	-0.11	-0.21	-0.01	3553	1.001
BCHU	-0.25	-0.68	0.19	398	1.002	-0.14	-0.46	0.15	280	1.017	0.20	-0.11	0.49	365	1.001
BEWR	-0.04	-0.16	0.07	6000	1.000	-0.04	-0.13	0.03	3094	1.001	0.04	-0.05	0.13	1354	1.001
BGGN	-0.17	-0.32	-0.01	1640	1.001	0.04	-0.06	0.12	6000	1.000	0.37	0.23	0.50	884	1.003
BHCO	0.03	-0.34	0.37	355	1.003	-0.23	-0.61	0.13	242	1.002	0.31	-0.04	0.65	318	1.007
BHGR	0.04	-0.29	0.40	240	1.009	0.10	-0.07	0.26	3169	1.000	0.33	0.08	0.59	1209	1.002
BTHU	0.19	-0.14	0.52	1887	1.006	-0.03	-0.31	0.23	299	1.007	0.01	-0.24	0.26	622	1.003
BTYW	0.01	-0.07	0.09	6000	1.000	-0.01	-0.07	0.05	6000	1.000	-0.04	-0.10	0.02	2476	1.001
BUSH	0.11	-0.31	0.55	798	1.002	-0.20	-0.47	0.04	790	1.002	0.14	-0.15	0.42	885	1.001
CHSP	-0.04	-0.17	0.08	6000	1.000	0.04	-0.05	0.12	1748	1.001	-0.05	-0.15	0.04	6000	1.000
CORA	-0.16	-0.34	0.02	2211	1.001	0.03	-0.11	0.17	6000	1.001	-0.06	-0.19	0.08	1856	1.001
DUFL	-0.23	-0.65	0.17	336	1.014	0.10	-0.16	0.32	423	1.004	-0.02	-0.29	0.26	507	1.001
GRFL	-0.08	-0.20	0.03	6000	1.000	0.06	-0.01	0.13	1299	1.001	-0.12	-0.20	-0.04	2567	1.001
GRVI	-0.04	-0.29	0.22	1319	1.004	-0.04	-0.18	0.08	1652	1.002	0.25	0.08	0.41	1526	1.002
HAWO	-0.06	-0.33	0.22	1765	1.001	0.00	-0.19	0.16	528	1.005	0.09	-0.13	0.30	6000	1.000
JUTI	0.03	-0.10	0.15	1585	1.001	-0.02	-0.09	0.05	3346	1.000	-0.01	-0.10	0.08	5361	1.000
MOCH	0.37	0.08	0.67	3404	1.001	-0.07	-0.21	0.05	938	1.003	0.14	-0.02	0.30	6000	1.000
MODO	0.15	-0.03	0.34	3745	1.001	-0.11	-0.26	0.05	760	1.003	-0.04	-0.18	0.10	1752	1.001
PIJA	0.08	-0.18	0.34	358	1.006	0.14	0.02	0.25	1259	1.002	0.00	-0.22	0.23	361	1.005
PLVI	0.12	-0.05	0.29	6000	1.000	-0.20	-0.34	-0.05	6000	1.000	0.30	0.16	0.43	6000	1.000
SPTO	0.12	-0.01	0.25	3562	1.001	0.06	-0.04	0.15	2876	1.000	0.28	0.18	0.38	3355	1.000
WBNU	0.13	-0.12	0.38	1801	1.001	0.02	-0.11	0.13	2285	1.001	-0.19	-0.34	-0.04	2182	1.001
WEBL	0.10	-0.16	0.37	668	1.003	-0.04	-0.22	0.13	934	1.003	-0.07	-0.27	0.13	613	1.004
WETA	0.05	-0.29	0.39	664	1.003	-0.04	-0.30	0.19	1348	1.002	0.15	-0.09	0.40	6000	1.000
WOSJ	0.05	-0.16	0.27	2781	1.001	0.07	-0.05	0.17	824	1.002	0.07	-0.08	0.23	1259	1.001

Table S7 (continued).

Species	**Sapling Density (bnSap)**					**Snag Basal Area (bnSnag)**				
	Mean	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**
ATFL	-0.09	-0.19	0.01	606	1.003	-0.01	-0.09	0.06	1679	1.001
BCHU	-0.02	-0.28	0.22	484	1.005	0.21	0.02	0.40	539	1.001
BEWR	-0.02	-0.10	0.06	1272	1.001	0.03	-0.03	0.10	4764	1.000
BGGN	-0.10	-0.24	0.04	6000	1.001	-0.05	-0.17	0.07	2200	1.001
BHCO	0.27	0.01	0.52	391	1.005	0.02	-0.25	0.25	389	1.018
BHGR	0.05	-0.22	0.31	6000	1.001	-0.05	-0.26	0.15	6000	1.001
BTHU	0.09	-0.07	0.24	6000	1.000	-0.09	-0.33	0.12	1711	1.003
BTYW	0.02	-0.03	0.08	1324	1.001	-0.02	-0.07	0.04	1024	1.002
BUSH	0.02	-0.26	0.30	998	1.002	0.24	-0.03	0.50	859	1.001
CHSP	0.04	-0.04	0.12	1868	1.001	0.00	-0.07	0.06	6000	1.000
CORA	-0.04	-0.14	0.06	6000	1.000	-0.05	-0.17	0.07	6000	1.000
DUFL	-0.43	-0.82	-0.06	319	1.016	0.04	-0.26	0.30	368	1.010
GRFL	0.02	-0.06	0.09	6000	1.000	0.00	-0.07	0.07	6000	1.000
GRVI	0.15	-0.02	0.30	1810	1.001	-0.04	-0.22	0.13	1260	1.001
HAWO	-0.01	-0.22	0.19	2178	1.001	-0.04	-0.23	0.14	1157	1.002
JUTI	-0.01	-0.09	0.08	3646	1.000	0.03	-0.04	0.11	842	1.003
MOCH	-0.26	-0.47	-0.07	4210	1.000	-0.18	-0.40	0.04	843	1.002
MODO	-0.05	-0.16	0.05	2438	1.001	-0.08	-0.20	0.03	3764	1.000
PIJA	-0.03	-0.26	0.18	1093	1.002	-0.19	-0.41	0.03	295	1.008
PLVI	0.04	-0.08	0.15	5660	1.000	-0.05	-0.17	0.08	1111	1.002
SPTO	-0.10	-0.21	0.01	3758	1.000	0.06	-0.01	0.14	4241	1.000
WBNU	0.07	-0.10	0.23	1893	1.003	0.13	-0.04	0.29	1305	1.001
WEBL	0.07	-0.14	0.28	246	1.010	0.06	-0.13	0.24	2134	1.001
WETA	0.02	-0.19	0.22	5741	1.001	0.04	-0.17	0.23	4397	1.001
WOSJ	-0.11	-0.29	0.07	1702	1.002	-0.08	-0.22	0.06	6000	1.000

Table S8. Effects of floristic composition on breeding-season densities of 25 Southwestern bird species in persistent pinyon-juniper woodlands. The mean and 90% BCI are given for the joint posterior distribution for each covariate, along with the estimated sample size (a measure of autocorrelation in the MCMC chains) and R-hat value (a measure of model convergence). Species are listed in alphabetical order by four-letter species code; full species names are given in Table S1.

Species	**Pinyon Pine Basal Area (bnPied)**					***Purshia tridentata***					***Purshia stansburyana***				
	Mean	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**
ATFL	0.10	0.02	0.19	1499	1.001	0.03	-0.21	0.29	3646	1.000	0.08	-0.15	0.33	1559	1.001
BCHU	-0.36	-0.66	-0.06	312	1.004	-0.08	-0.64	0.49	824	1.007	-0.09	-0.55	0.37	598	1.008
BEWR	-0.05	-0.13	0.04	4902	1.000	0.11	-0.11	0.34	4171	1.000	-0.08	-0.28	0.11	6000	1.000
BGGN	0.05	-0.07	0.17	2289	1.001	0.08	-0.28	0.45	6000	1.000	-0.37	-0.71	-0.03	744	1.002
BHCO	-0.42	-0.79	-0.09	205	1.004	0.09	-0.51	0.73	402	1.006	-0.23	-0.78	0.27	377	1.007
BHGR	0.14	-0.16	0.42	1143	1.003	-0.11	-0.83	0.52	1891	1.001	-0.43	-1.14	0.16	3125	1.001
BTHU	-0.21	-0.51	0.09	3486	1.002	-0.26	-0.99	0.30	650	1.003	-0.12	-0.55	0.26	1404	1.001
BTYW	0.04	-0.01	0.09	1766	1.002	0.13	-0.06	0.32	4087	1.001	0.07	-0.08	0.23	620	1.003
BUSH	0.10	-0.14	0.33	1057	1.002	0.07	-0.50	0.63	3128	1.000	0.14	-0.43	0.76	1448	1.005
CHSP	-0.07	-0.17	0.02	1493	1.001	0.16	-0.11	0.46	1332	1.001	0.19	-0.02	0.43	5853	1.000
CORA	-0.16	-0.30	-0.02	6000	1.000	0.13	-0.20	0.48	6000	1.001	0.02	-0.23	0.27	2711	1.001
DUFL	-0.63	-1.01	-0.27	276	1.023	0.02	-0.50	0.54	1029	1.004	0.08	-0.35	0.56	967	1.013
GRFL	-0.03	-0.10	0.04	1375	1.001	0.13	-0.13	0.47	4862	1.000	0.31	0.07	0.62	1562	1.002
GRVI	-0.02	-0.16	0.11	1893	1.002	0.12	-0.26	0.55	2284	1.001	-0.24	-0.65	0.14	2385	1.002
HAWO	-0.04	-0.24	0.15	163	1.013	0.30	-0.13	0.78	550	1.003	0.40	-0.04	0.92	2644	1.002
JUTI	0.09	0.02	0.16	4789	1.001	0.04	-0.19	0.28	4940	1.000	0.09	-0.12	0.31	6000	1.000
MOCH	0.15	0.03	0.27	1758	1.001	-0.01	-0.36	0.39	2238	1.002	-0.25	-0.79	0.20	891	1.002
MODO	-0.20	-0.37	-0.02	6000	1.001	-0.37	-1.00	0.11	4594	1.001	0.01	-0.26	0.28	4188	1.000
PIJA	0.13	-0.01	0.26	2244	1.001	0.35	-0.13	0.91	188	1.011	-0.15	-0.70	0.39	3577	1.001
PLVI	0.09	-0.03	0.20	790	1.003	0.05	-0.29	0.38	1340	1.002	-0.29	-0.56	-0.03	614	1.003
SPTO	-0.09	-0.21	0.04	2754	1.000	-0.34	-0.72	-0.01	3013	1.001	0.01	-0.21	0.23	4579	1.001
WBNU	0.02	-0.11	0.14	2568	1.002	-0.01	-0.39	0.37	3816	1.003	-0.21	-0.68	0.20	2270	1.000
WEBL	0.08	-0.11	0.27	502	1.004	0.10	-0.29	0.53	6000	1.000	0.07	-0.33	0.50	488	1.005
WETA	-0.08	-0.31	0.16	1913	1.001	-0.04	-0.50	0.39	1367	1.002	-0.07	-0.43	0.26	6000	1.000
WOSJ	0.04	-0.11	0.18	421	1.005	0.07	-0.24	0.40	534	1.004	-0.18	-0.52	0.14	914	1.002

Table S8 (continued).

Species		***Artemisia tridentata***					***Amelanchier utahensis***					***Cercocarpus montanus***		
	Mean	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**
ATFL	0.03	-0.20	0.27	675	1.003	0.29	-0.05	0.69	4061	1.001	0.01	-0.23	0.26	6000	1.000
BCHU	0.03	-0.45	0.49	778	1.002	-0.04	-0.67	0.56	1232	1.001	0.05	-0.50	0.59	1163	1.010
BEWR	0.03	-0.16	0.22	3381	1.001	-0.03	-0.31	0.24	6000	1.000	0.01	-0.20	0.23	6000	1.000
BGGN	0.26	-0.07	0.59	1653	1.001	0.74	0.19	1.31	2302	1.001	0.36	-0.04	0.77	1319	1.003
BHCO	0.32	-0.20	0.92	317	1.006	0.12	-0.51	0.81	1050	1.006	-0.07	-0.72	0.53	992	1.004
BHGR	-0.24	-0.92	0.34	1260	1.002	-0.24	-1.10	0.45	1437	1.001	0.17	-0.37	0.70	2490	1.001
BTHU	-0.36	-0.95	0.08	303	1.008	-0.05	-0.65	0.48	1007	1.002	-0.08	-0.59	0.38	1976	1.001
BTYW	0.05	-0.11	0.23	3051	1.000	-0.18	-0.40	0.05	6000	1.000	0.08	-0.13	0.29	5124	1.000
BUSH	-0.28	-0.86	0.24	1752	1.001	-0.11	-0.96	0.63	2136	1.000	-0.14	-0.89	0.50	1567	1.002
CHSP	0.21	-0.02	0.46	5835	1.000	-0.15	-0.47	0.16	6000	1.000	-0.03	-0.28	0.23	6000	1.000
CORA	0.14	-0.12	0.40	1869	1.001	-0.02	-0.40	0.35	6000	1.001	-0.30	-0.69	0.05	1888	1.002
DUFL	-0.05	-0.53	0.42	917	1.002	-0.34	-1.18	0.25	1063	1.001	0.25	-0.29	0.90	1029	1.002
GRFL	0.16	-0.08	0.48	2839	1.001	-0.18	-0.51	0.16	2990	1.001	-0.05	-0.31	0.24	3832	1.000
GRVI	0.40	0.04	0.79	1628	1.001	-0.22	-0.86	0.32	2692	1.001	0.00	-0.49	0.47	2409	1.005
HAWO	-0.21	-0.63	0.21	359	1.006	0.23	-0.40	0.95	1449	1.002	-0.14	-0.70	0.41	1344	1.002
JUTI	-0.05	-0.26	0.17	4514	1.000	-0.16	-0.49	0.15	5614	1.000	-0.05	-0.30	0.21	5410	1.000
MOCH	0.09	-0.26	0.47	1064	1.004	0.32	-0.16	0.88	381	1.006	-0.39	-1.31	0.23	168	1.032
MODO	-0.06	-0.37	0.24	1826	1.001	0.08	-0.29	0.47	6000	1.000	0.09	-0.23	0.41	2230	1.001
PIJA	0.45	-0.01	0.98	166	1.012	-0.46	-1.44	0.28	1795	1.004	-0.09	-0.77	0.55	318	1.007
PLVI	0.03	-0.24	0.29	1252	1.001	-0.11	-0.47	0.23	6000	1.000	-0.08	-0.42	0.23	1004	1.002
SPTO	0.06	-0.19	0.30	4742	1.002	0.10	-0.18	0.39	5114	1.002	0.01	-0.24	0.25	4964	1.000
WBNU	0.13	-0.25	0.49	3545	1.002	0.13	-0.40	0.69	3546	1.000	-0.78	-1.81	-0.07	642	1.005
WEBL	0.10	-0.26	0.50	6000	1.000	-0.16	-0.76	0.36	6000	1.000	-0.06	-0.53	0.39	3820	1.001
WETA	-0.03	-0.41	0.32	4450	1.000	0.02	-0.43	0.44	1133	1.002	0.01	-0.40	0.43	1863	1.001
WOSJ	0.05	-0.24	0.36	620	1.003	0.21	-0.16	0.65	6000	1.001	0.14	-0.20	0.51	6000	1.000

Table S8 (continued).

Species	***Quercus undulata***					**No Shrub**				
	Mean	**5%**	**95%**	**ESS**	**R-hat**	**Mean**	**5%**	**95%**	**ESS**	**R-hat**
ATFL	-0.14	-0.42	0.12	2536	1.001	0.12	-0.15	0.39	6000	1.000
BCHU	-0.10	-0.87	0.56	1200	1.000	-0.24	-1.00	0.36	965	1.006
BEWR	0.09	-0.16	0.34	1528	1.001	-0.12	-0.37	0.12	2236	1.001
BGGN	-0.34	-1.04	0.28	4825	1.000	-0.04	-0.61	0.52	2867	1.001
BHCO	-0.33	-1.20	0.34	851	1.004	0.49	-0.16	1.36	543	1.006
BHGR	-0.29	-0.98	0.30	2831	1.000	-0.73	-2.01	0.13	906	1.005
BTHU	0.04	-0.49	0.59	2957	1.001	-0.04	-0.59	0.44	6000	1.000
BTYW	0.09	-0.25	0.44	6000	1.000	-0.04	-0.27	0.19	1298	1.001
BUSH	-0.18	-1.09	0.58	1530	1.007	0.39	-0.27	1.23	1303	1.004
CHSP	-0.08	-0.38	0.20	6000	1.000	0.04	-0.24	0.33	6000	1.000
CORA	-0.06	-0.49	0.36	6000	1.000	-0.13	-0.49	0.21	6000	1.000
DUFL	-0.07	-0.84	0.64	1359	1.005	0.08	-0.55	0.78	1104	1.001
GRFL	0.19	-0.12	0.53	4689	1.000	0.02	-0.26	0.33	936	1.002
GRVI	-0.08	-0.83	0.61	1855	1.001	-0.38	-1.12	0.19	1361	1.001
HAWO	0.27	-0.28	0.93	460	1.005	0.34	-0.21	1.00	1448	1.001
JUTI	0.01	-0.30	0.33	6000	1.000	0.12	-0.15	0.40	3002	1.001
MOCH	-0.06	-0.81	0.63	1852	1.005	0.05	-0.50	0.60	970	1.002
MODO	0.06	-0.29	0.43	3833	1.001	-0.06	-0.43	0.27	6000	1.000
PIJA	-0.23	-1.20	0.54	1422	1.001	0.16	-0.53	0.90	637	1.004
PLVI	-0.16	-0.65	0.27	1117	1.002	0.13	-0.23	0.51	2276	1.001
SPTO	0.03	-0.25	0.32	6083	1.000	-0.01	-0.34	0.30	4985	1.001
WBNU	0.29	-0.37	1.09	1477	1.001	0.08	-0.40	0.55	3401	1.001
WEBL	-0.24	-0.81	0.24	6000	1.000	0.29	-0.14	0.79	1352	1.001
WETA	0.01	-0.49	0.52	1729	1.001	0.04	-0.41	0.50	1699	1.001
WOSJ	0.01	-0.36	0.39	2822	1.001	-0.04	-0.44	0.34	6000	1.000

Table S9. Dominant shrub classifications across parks. Frequencies represent the sums of point-years in which each shrub species was classified in the field as the dominant species. Dominant species represent the modal shrub category across four subplots at and near the point-count station. The number of survey years varied by park (*N* = 1 at Bandelier, 4 at Mesa Verde, 3 at Grand Canyon), leading to uneven frequencies across parks.

Species	**Bandelier**	**Grand Canyon**	**Mesa Verde**
Amelanchier utahensis	0	1	18
Artemisia tridentata	0	115	46
Atriplex canescens	1	0	0
Cercocarpus montanus	14	0	24
Chrysothamnus nauseosus	2	0	0
Ephedra sp.	0	2	0
Ericameria nauseosa	0	1	0
Fallugia paradoxa	5	0	0
Fendleria rupicola	0	0	3
Gutierrezia sarothrae	5	0	0
No shrub	11	2	18
Opuntia sp.	4	0	2
Purshia stansburiana	0	147	0
Purshia tridentata	0	0	192
Quercus gambelii	1	0	10
Quercus undulata	20	0	0
Rhus aromatica	5	0	0
Ribes cereum	1	0	0
Yucca sp.	1	0	11

Table S10. Eigenvalues and percentage variance explained of a principal components analysis (PCA) of pinyon-juniper bird responses to habitat variables.

PC Axis	**Eigenvalue**	**Percentage variance explained**	**Cumulative Variance Explained**
Dim 1	2.16	24.04	24.04
Dim 2	1.69	18.77	42.81
Dim 3	1.48	16.44	59.25
Dim 4	1.11	12.31	71.56
Dim 5	0.96	10.70	82.25
Dim 6	0.79	8.83	91.08
Dim 7	0.37	4.09	95.17
Dim 8	0.26	2.85	98.02
Dim 9	0.18	1.98	100.00

Table S11. Variable loadings from a PCA of pinyon-juniper bird responses to vegetation structure and floristic composition. Each variable represents the mean effect size of the covariate on breeding density in permanent woodlands. The nine covariates included in the PCA were fixed effects fit on density. Loadings greater than 0.3 and less than -0.3 are thought to represent major contributions to each axis.

Variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
Canopy cover	0.07	0.24	0.59	0.08	0.28	0.53	0.33	0.29	0.17
Sapling density	-0.37	-0.05	-0.44	0.10	0.56	-0.17	0.21	0.24	0.45
Snag basal area	-0.44	0.11	-0.19	-0.46	0.11	0.45	-0.38	0.24	-0.35
Pinyon pine basal area	0.43	0.04	-0.31	-0.50	0.07	0.36	0.07	-0.41	0.40
Canopy height	0.13	0.49	-0.17	0.48	0.42	0.11	-0.29	-0.39	-0.24
Subcanopy foliage cover	-0.54	0.18	0.24	0.11	-0.32	0.08	-0.29	-0.36	0.53
Shrub height	0.25	-0.58	0.10	0.24	0.19	0.20	-0.61	0.18	0.23
Shrub foliage cover	0.18	0.30	-0.44	0.33	-0.51	0.26	-0.02	0.46	0.17
Foliage height diversity	0.25	0.48	0.20	-0.34	0.12	-0.48	-0.39	0.32	0.22

Table S12. Species scores from a PCA of pinyon-juniper bird breeding-season density responses to vegetation structure and floristic composition. Species are listed in alphabetical order by four-letter species code; full species names are provided in Table S1.

Species	**PC 1**	**PC 2**	**PC 3**	**PC 4**	**PC 5**	**PC 6**	**PC 7**	**PC 8**	**PC 9**
ATFL	1.00	-1.07	0.69	-0.97	0.31	0.12	-0.84	-0.64	0.05
BEWR	-0.80	-0.30	0.05	-0.06	-0.28	0.29	0.42	0.06	-0.63
BGGN	0.49	-0.79	-1.10	1.04	-2.13	1.26	0.03	-0.37	0.03
BHGR	2.60	0.41	-1.76	1.23	1.51	1.23	-0.13	0.75	0.07
BTHU	-1.08	0.73	0.85	1.12	0.66	-1.89	-0.05	0.82	0.51
BTYW	-0.14	-0.53	-0.13	-0.39	0.47	-0.10	0.36	-0.36	0.04
BUSH	-2.25	1.42	-0.65	-2.95	-1.06	0.92	0.45	0.65	0.31
CHSP	-0.68	-0.61	-0.01	0.87	1.00	0.01	-0.21	-0.36	-0.47
CORA	-1.07	-1.61	2.09	0.89	-0.20	0.88	1.23	0.54	-0.32
GRFL	-0.51	-1.32	0.68	0.25	1.00	0.58	0.25	-0.23	-0.29
GRVI	-0.71	-0.22	-2.43	0.89	-0.04	-0.77	0.49	0.28	0.30
HAWO	-0.78	0.11	0.44	1.12	-0.24	0.67	0.02	-0.61	0.29
JUTI	-0.01	-0.55	-0.34	-1.19	0.06	0.20	0.24	-0.20	-0.01
MOCH	4.08	2.78	2.29	-0.51	-0.34	0.05	0.30	-0.12	-0.20
MODO	-1.14	0.82	1.43	0.43	-0.79	-1.92	0.10	-0.14	-0.39
PIJA	2.55	-2.49	0.02	-0.64	-0.10	-0.96	0.37	0.32	0.80
PLVI	0.48	2.80	-1.64	0.37	-0.02	-0.27	0.88	-0.50	0.00
SPTO	0.20	0.24	-0.11	0.28	-1.19	0.24	-1.47	1.19	-0.66
WBNU	-1.28	0.56	1.34	-0.97	2.13	0.94	-0.54	0.11	0.47
WEBL	0.09	-0.46	-1.95	-1.46	1.06	-1.24	-0.31	-0.33	-0.81
WETA	-1.72	1.48	0.05	1.13	-0.25	0.37	-1.00	-0.58	0.55
WOSJ	0.67	-1.42	0.21	-0.48	-1.56	-0.60	-0.60	-0.28	0.36

MODEL CODE

JAGS model code to run single-species density models with distance sampling and time removal sub-models.

```
model {

  # PRIORS

  # model: augGaps.repAll.mindaycloudWindNoiseObsYxP

  ba0 ~ dnorm(0,0.01)     # availability intercept
  baD ~ dnorm(0,0.01)      # coefs of availability covars that affect
  baD2 ~ dnorm(0,0.01)     # Quadratic term of day of year
  baM ~ dnorm(0,0.01)      # the detection interval (like Day and Minute)
  baC ~ dnorm(0,0.01)      # coef for cloud cover during survey

  sigma0 ~ dunif(0,200)    # scale of detection fn, bounded for convergence
  # (0,200) or relaxed (0,500) for high-detection-prob situations (GCFL)
  bdN ~ dnorm(0,0.01)      # coefs of scale parameter covars like Noise,


  bnCanC ~ dnorm(0,0.01)
  bnSap ~ dnorm(0,0.01)
  bnSnag ~ dnorm(0,0.01)
  bnPied ~ dnorm(0,0.01)
  bnCanH ~ dnorm(0,0.01)
  bnScanfc ~ dnorm(0,0.01)
  bnShrubH ~ dnorm(0,0.01)
  bnShrubfc ~ dnorm(0,0.01)
  bnFHD ~ dnorm(0,0.01)

  #RANDOM STATION-WITHIN-CLUSTER EFFECT ON ABUNDANCE ONLY
  for (s in 1:nsta) {   # accounts for repeated measures...
   bn0cs[s] ~ dnorm(clusteff[unique_clust[s]],tau.sta)
  }
  for(t in 1:nclusts){
     clusteff[t] ~ dnorm(0, tau.clust) # ...and spatial autocorrelation
  }

##################################################################################

  #random year effect on abundance
  for (t in 1:nyears) {
   bnYear[t] ~ dnorm(0,tau.year)
  }
```

```
#random dominant shrub effect on abundance
for (d in 1:nshrub) {
  bnDshrub[d] ~ dnorm(0,tau.Dshrub)
}


# random observer effect on detection dist or interval
for (i in 1:nobservers) {
  obseff[i] ~ dnorm(0,tau.obs)
}

# overdispersion
#for (k in 1:nsurveys) {
#  od[m, k] ~ dnorm(0.0,tau.od[m])
#}
#tau.od[m] ~ dgamma(0.001,0.001)
#sd.od <- pow(tau.od,-0.5) # comment out unless tracking sd.od

# DETECTION PROBABILITY FUNCTIONS

for (k in 1:nsurveys) {

  # covariates of availability

  logit(q[k]) <- ba0 + baM*minute[k] + baD*day[k] + baD2*pow(day[k],2) + baC*cloud[k]

  # covariates of perceptibility/detection

  log(sigma[k]) <- log(sigma0) + bdN*noise[k] + obseff[observer[k]]  ###

  # distance-based estimation of detection probability

  for (b in 1:nbreaks) {

    log(g[b,k]) <- -mdpts[b]*mdpts[b]/(2*sigma[k]*sigma[k]) # half-norm density
    f[b,k] <- (2*mdpts[b]*delta[b])/(maxd*maxd) # delta[b] if bin widths vary
    #f[b,k] <- (2*mdpts[b]*delta)/(maxd*maxd)   # no [b] on delta: width static
    pi.d[b,k] <- g[b,k]*f[b,k]       # p(detection) per pt-bin
    pi.d.c[b,k] <- pi.d[b,k]/p.d[k]  # conditional form stdized by p(detected)

  } # b in 1:nbreaks

  p.d[k] <- sum(pi.d[,k]) # p.d is a sum over all dclass bins

  # removal-based estimation of availability given EQUAL detection intervals
```

```
  for (j in 1:J){
   ## next, p(available in a given interval and not before that)
   pi.a[j,k] <- (1-q[k])*pow(q[k],(j-1)) # Royle & Dorazio (2008) salamanders
   ## next, p(available in each interval j | available in at least one interval)
   pi.a.c[j,k]<- pi.a[j,k]/p.a[k] # conditional formulation
  }
  p.a[k] <- sum(pi.a[,k]) # p(available in at least one interval)


 } # k in 1:nsurveys

 # OBSERVATION-LEVEL MODEL

 for (i in 1:nobs) {

  # one binomial trial w/categorical distc linking dclass & tinterval to ptct
  dclass[i] ~ dcat(pi.d.c[,surveyid[i]])    # p(outcome=1 to nbreaks dclasses)
  tinterval[i] ~ dcat(pi.a.c[,surveyid[i]]) # p(outcome=1 to J intervals)

 } # i in 1:nobs

 # ABUNDANCE ESTIMATION

 for (k in 1:nsurveys) {

  # counts as a function of number available and detection probability

  y[k] ~ dbin(p.d[k],n.a[k])

  # number available for sampling as a function of abundance and p(available)

  n.a[k] ~ dbin(p.a[k],N[k])

  # abundance model

  N[k] ~ dpois(lambda[k]) # predicted abundance per survey (point-count)

  # covariates of abundance

  log(lambda[k]) <- bn0cs[sta[k]] + bnYear[Year[k]] + bnDshrub[Dshrub[k]] +
bnCanC*CanC[k] + bnSap*Sap[k] + bnSnag*Snag[k] + bnPied*Pied[k] + bnCanH*CanH[k] +
   bnScanfc*Scanfc[k] + bnShrubH*ShrubH[k] + bnShrubfc*Shrubfc[k] + bnFHD*FHD[k]

 } # k in 1:nsurveys
```

```
  # GOODNESS OF FIT STATS

  for (k in 1:nsurveys) {

    y.fit[k] ~ dbin(p.d[k],n.a[k]) # create new realization of model
    n.a.fit[k] ~ dbin(p.a[k],N[k])

    e.pa[k] <- p.a[k]*N[k]         # n.a value predicted by the model
    E.pa[k] <- n.a[k]-e.pa[k]      # components of the Bayesian P-value
    E.new.pa[k] <- n.a.fit[k]-e.pa[k]

    e.pd[k] <- p.d[k]*n.a[k]       # y value predicted by the model
    E.pd[k] <- y[k]-e.pd[k]        # components of the Bayesian P-value
    E.new.pd[k] <- y.fit[k]-e.pd[k]

  } # k in 1:nsurveys

  fit.pa <- sum(E.pa[])          # model deviation from observed data
  fit.new.pa <- sum(E.new.pa[])  # model deviation from predicted data
  bayesp.pa <- step(fit.pa-fit.new.pa[])

  fit.pd <- sum(E.pd[])
  fit.new.pd <- sum(E.new.pd[])
  bayesp.pd <- step(fit.pd-fit.new.pd[])

  # SUMMARY STATS AND DERIVED QUANTITIES

  mupavail <- mean(p.a[])
  mupdet <- mean(p.d[])      # mean probability of availability
  musigma <- mean(sigma[])      # mean scale parameter across stations

  ha <- maxd*maxd*3.14159/10000 # hectares surveyed at each sta for this sp
  #dens.ha <- mean(N[])/ha       # mean point-level density

  dens.band.ha <- mean(N[band_ind])/ha       # mean point-level density in band
  dens.grca.ha <- mean(N[grca_ind])/ha
  dens.meve.ha <- mean(N[meve_ind])/ha
  dens.ha <- dens.band.ha*0.078 + dens.grca.ha*0.759 + dens.meve.ha*0.163 #Weighted by
proportion of the area of inference in each park
  #Actual values are 219.6262 ha in BAND, 2138.676609 ha in GRCA, and 459.476255 ha in
MEVE

  N.2008 <- sum(N[ind_2008])
  N.2009 <- sum(N[ind_2009])
  N.2011 <- sum(N[ind_2011])
  N.2012 <- sum(N[ind_2012])
```

```
  N.2014 <- sum(N[ind_2014])
  N.2015 <- sum(N[ind_2015])
  N.2017 <- sum(N[ind_2017])
  N.2018 <- sum(N[ind_2018])

  #using length(ind_year) instead of nsta as below because not all stations were surveyed each year
  #not multiplying by 2 because indexing already accounts for both replicates at each station per year
  dens.2008 <- N.2008/(length(ind_2008)*ha)
  dens.2009 <- N.2009/(length(ind_2009)*ha)
  dens.2011 <- N.2011/(length(ind_2011)*ha)
  dens.2012 <- N.2012/(length(ind_2012)*ha)
  dens.2014 <- N.2014/(length(ind_2014)*ha)
  dens.2015 <- N.2015/(length(ind_2015)*ha)
  dens.2017 <- N.2017/(length(ind_2017)*ha)
  dens.2018 <- N.2018/(length(ind_2018)*ha)

  #none of the parks were surveyed in concurrent years
  #therefore, all surveys conducted within a given year represent surveys from unique parks
  #thus, below parameters are redundant to N.year[m] -- below naming just makes which park was surveyed in that year explicit
  N.2008.band <- N.2008
  N.2009.meve <- N.2009
  N.2011.grca <- N.2011
  N.2012.meve <- N.2012
  N.2014.grca <- N.2014
  N.2015.meve <- N.2015
  N.2017.grca <- N.2017
  N.2018.meve <- N.2018

  #redundant for same reason as above
  dens.2008.band <- dens.2008
  dens.2009.meve <- dens.2009
  dens.2011.grca <- dens.2011
  dens.2012.meve <- dens.2012
  dens.2014.grca <- dens.2014
  dens.2015.meve <- dens.2015
  dens.2017.grca <- dens.2017
  dens.2018.meve <- dens.2018

  logN.2008.band <- log(mean(N[ind_2008]))
  logN.2009.meve <- log(mean(N[ind_2009]))
  logN.2011.grca <- log(mean(N[ind_2011]))
  logN.2012.meve <- log(mean(N[ind_2012]))
  logN.2014.grca <- log(mean(N[ind_2014]))
```

```
logN.2015.meve <- log(mean(N[ind_2015]))
logN.2017.grca <- log(mean(N[ind_2017]))
logN.2018.meve <- log(mean(N[ind_2018]))

N.2008.rep1 <- sum(N[rep1_2008])
dens.2008.rep1 <- N.2008.rep1/(length(rep1_2008)*ha)
logN.2008.rep1 <- log(mean(N[rep1_2008]))
N.2008.rep2 <- sum(N[rep2_2008])
dens.2008.rep2 <- N.2008.rep2/(length(rep2_2008)*ha)
logN.2008.rep2 <- log(mean(N[rep2_2008]))

N.2009.rep1 <- sum(N[rep1_2009])
dens.2009.rep1 <- N.2009.rep1/(length(rep1_2009)*ha)
logN.2009.rep1 <- log(mean(N[rep1_2009]))
N.2009.rep2 <- sum(N[rep2_2009])
dens.2009.rep2 <- N.2009.rep2/(length(rep2_2009)*ha)
logN.2009.rep2 <- log(mean(N[rep2_2009]))

N.2011.rep1 <- sum(N[rep1_2011])
dens.2011.rep1 <- N.2011.rep1/(length(rep1_2011)*ha)
logN.2011.rep1 <- log(mean(N[rep1_2011]))
N.2011.rep2 <- sum(N[rep2_2011])
dens.2011.rep2 <- N.2011.rep2/(length(rep2_2011)*ha)
logN.2011.rep2 <- log(mean(N[rep2_2011]))

N.2012.rep1 <- sum(N[rep1_2012])
dens.2012.rep1 <- N.2012.rep1/(length(rep1_2012)*ha)
logN.2012.rep1 <- log(mean(N[rep1_2012]))
N.2012.rep2 <- sum(N[rep2_2012])
dens.2012.rep2 <- N.2012.rep2/(length(rep2_2012)*ha)
logN.2012.rep2 <- log(mean(N[rep2_2012]))

N.2014.rep1 <- sum(N[rep1_2014])
dens.2014.rep1 <- N.2014.rep1/(length(rep1_2014)*ha)
logN.2014.rep1 <- log(mean(N[rep1_2014]))
N.2014.rep2 <- sum(N[rep2_2014])
dens.2014.rep2 <- N.2014.rep2/(length(rep2_2014)*ha)
logN.2014.rep2 <- log(mean(N[rep2_2014]))

N.2015.rep1 <- sum(N[rep1_2015])
dens.2015.rep1 <- N.2015.rep1/(length(rep1_2015)*ha)
logN.2015.rep1 <- log(mean(N[rep1_2015]))
N.2015.rep2 <- sum(N[rep2_2015])
dens.2015.rep2 <- N.2015.rep2/(length(rep2_2015)*ha)
logN.2015.rep2 <- log(mean(N[rep2_2015]))
```

```
  N.2017.rep1 <- sum(N[rep1_2017])
  dens.2017.rep1 <- N.2017.rep1/(length(rep1_2017)*ha)
  logN.2017.rep1 <- log(mean(N[rep1_2017]))
  N.2017.rep2 <- sum(N[rep2_2017])
  dens.2017.rep2 <- N.2017.rep2/(length(rep2_2017)*ha)
  logN.2017.rep2 <- log(mean(N[rep2_2017]))

  N.2018.rep1 <- sum(N[rep1_2018])
  dens.2018.rep1 <- N.2018.rep1/(length(rep1_2018)*ha)
  logN.2018.rep1 <- log(mean(N[rep1_2018]))
  N.2018.rep2 <- sum(N[rep2_2018])
  dens.2018.rep2 <- N.2018.rep2/(length(rep2_2018)*ha)
  logN.2018.rep2 <- log(mean(N[rep2_2018]))

  #hyper-priors for random effects
  tau.sta ~ dgamma(0.1, 0.1)
  tau.clust ~ dgamma(0.1, 0.1)
  tau.year ~ dgamma(0.1, 0.1)
  tau.Dshrub ~ dgamma(0.1, 0.1)
  tau.obs ~ dgamma(0.1, 0.1)

}
```