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RESEARCH ARTICLE

Bird associations with floristics and physiognomy differ across five biogeographic subregions of the Great Basin, USA

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ABSTRACT

The majority of management plans for birds on public lands across the western United States do not recognize the geographic variation in a given species' habitat. We examined associations of plant species and functional groups with occupancy of 19 bird species across 5 biogeographic subregions of the Great Basin (central, western, Sierra Nevada, northern, and eastern), USA. We hypothesized that occupancy was associated with floristics (individual plant species) within subregions, and with physiognomy (characterized by functional groups) across the Great Basin. We used two methods to evaluate bird-vegetation associations within and across subregions. First, we examined which covariates of floristics and physiognomy were significantly associated with occupancy in each subregion. Second, for each bird species, we compared covariate estimates between each of the 10 pairs of subregions. We classified the effects of covariates on occupancy in 2 subregions as significantly different if <5% of their posterior distributions overlapped. The plant species and functional groups that were associated significantly with occupancy varied considerably among subregions. Twenty-four percent of bird-plant associations that were significant at the Great Basin level were not significant in any subregion. Associations between occupancy and floristics differed the most between the Sierra Nevada and central or western subregions, and the least between the eastern and western subregions. Associations between occupancy and physiognomy differed the most between the Sierra Nevada and western and central subregions, and the least between the northern and western subregions. These differences and similarities may reflect variations in climate or bird communities or differences in sampling effort. In addition, the number and strength of associations between occupancy and floristic or physiognomic covariates varied substantially among bird species and subregions. We recommend that the management of birds across the Great Basin or other large ecoregions evaluate and account for geographic variation in environmental attributes associated with occupancy, and not assume bird-plant relations are consistent across the Great Basin.

Keywords: avian, floristics, Great Basin, management, occupancy, physiognomy, vegetation

LAY SUMMARY

- The majority of management plans for birds on extensive public lands across the western United States do not recognize geographic variation in a given species' habitat. Local identities of plant species (floristics) and vegetation structure (physiognomy) can affect availability of nesting sites, food, shelter, and protection from predators.
- We examined associations of floristics and physiognomy with occupancy of 19 species of birds across 5 biologically distinct subregions of the Great Basin (central, western, Sierra Nevada, northern, and eastern), USA. We hypothesized that associations between birds and floristics varied among subregions, whereas associations between birds and physiognomy were consistent.
- Associations between bird occupancy and floristics and physiognomy were inconsistent across the Great Basin. Associations in the Sierra Nevada subregion were the most distinct.
- A single, regional management approach may not be effective for some Great Basin bird species. We recommend that management plans for birds evaluate local associations with vegetation, and not assume bird-plant relations are consistent across the Great Basin.

Las asociaciones de aves con la florística y la fisonomía difieren en cinco subregiones biogeográficas de la Gran Cuenca, EEUU

RESUMEN

La mayoría de los planes de manejo de aves en tierras públicas a lo largo del oeste de Estados Unidos no reconocen la variación geográfica en el hábitat de una especie determinada. Examinamos asociaciones de especies de plantas y

grupos funcionales con la ocupación de 19 especies de aves en cinco subregiones biogeográficas de la Gran Cuenca (central, oeste, Sierra Nevada, norte y este), EEUU. Hipotetizamos que la ocupación estaba asociada con la florística (especies de plantas individuales) dentro de las subregiones y con la fisonomía (caracterizada por grupos funcionales) en toda la Gran Cuenca. Usamos dos métodos para evaluar las asociaciones de aves y vegetación dentro y entre subregiones. Primero, examinamos qué covariables florísticas y fisonomías estaban significativamente asociadas con la ocupación en cada subregión. Segundo, para cada especie de ave, comparamos estimaciones de covariables entre cada uno de los 10 pares de subregiones. Clasificamos los efectos de las covariables sobre la ocupación en dos subregiones como significativamente diferentes si <5% de sus distribuciones posteriores se superponen. Las especies de plantas y los grupos funcionales que se asociaron significativamente con la ocupación variaron considerablemente entre las subregiones. El 24% de las asociaciones de aves y plantas que fueron significativas a nivel de la Gran Cuenca no lo fueron en ninguna subregión. Las asociaciones entre ocupación y florística difirieron más entre Sierra Nevada y las subregiones central u oeste, y menos entre las subregiones este y oeste. Las asociaciones entre ocupación y fisonomía difirieron más entre Sierra Nevada y las subregiones oeste y central, y menos entre las subregiones norte y oeste. Estas diferencias y similitudes pueden reflejar variaciones en el clima o en las comunidades de aves, o diferencias en el esfuerzo de muestreo. Además, el número y la fuerza de las asociaciones entre la ocupación y las covariables florísticas o fisionómicas variaron sustancialmente entre las especies de aves y las subregiones. Recomendamos que el manejo de las aves en la Gran Cuenca u otras grandes ecorregiones evalúe y tome en cuenta la variación geográfica en los atributos ambientales asociados con la ocupación, y no asuma que las relaciones entre aves y plantas son consistentes en toda la Gran Cuenca.

Palabras clave: aviar, fisonomía, florística, Gran Cuenca, manejo, ocupación, vegetación

INTRODUCTION

Identification of species-specific habitat attributes can increase the success of ecological restoration and conservation efforts and may improve the accuracy of predictions of future species distributions in the face of climate and land-use change. Globally, avian distributions are affected by numerous factors including climate, physiological tolerances, intrinsic limits to population growth, and resource availability (Root 1988, Gill 2007, Rowhani et al. 2008, Jimenez-Valverde et al. 2011). At the local level, the species richness, abundance, and distribution of birds correspond in large part to the characteristics of vegetation. Vegetation composition (hereafter floristics) and structure (hereafter physiognomy) affect availability of nesting strata, food, and shelter; protection from predators; and cues about environmental conditions consistent with successful reproduction (James 1971, Cody 1981, Cubley et al. 2020).

Understanding associations between bird distributions and vegetation features has long been a goal in ornithology, with much research focusing on the relative effects of floristics and physiognomy (MacArthur and MacArthur 1961, Robinson and Holmes 1984, Mac Nally 1990). Early work found that because floristics and physiognomy are correlated, predictions of avian diversity that were based on both floristic and physiognomic diversity were no more accurate than those based on physiognomic diversity alone (MacArthur and MacArthur 1961). Subsequent research suggested that in grasslands and shrubsteppe, associations between bird distributions and vegetation varied among spatial extents: relations with floristics were stronger at small extents, and those with physiognomy were stronger at large extents (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Knopf et al. 1990). Across the central Great Basin, floristics was more strongly associated with the species composition of birds than was vegetation physiognomy or primary productivity (Fleishman and Mac Nally 2006), and in the Mojave Desert, species composition of birds was more closely related to floristics than to physiognomy (Fleishman et al. 2003). There is no consensus on the relative effects of floristics and physiognomy on avian diversity and distributions, or the spatial scale at which different vegetation attributes are most meaningful (Fisher and Davis 2010). However, bird-vegetation associations necessarily shift as floristics shift across large geographic areas. Relations of floristics or physiognomy with the distributions of single species may be more consistent than those with community metrics such as diversity.

The Great Basin encompasses more than 425,000 km^2 of internal drainage across California, Nevada, Utah, Idaho, and Oregon, USA. The Great Basin is characterized by arid, expansive sagebrush shrubsteppe ecosystems and over 300 mountain ranges with diverse ecological communities. More than 70% of the Great Basin is public land, and conservation priorities for wild animals are determined on a state-by-state basis and described in state wildlife action plans and conservation plans (Wildlife Action Plan Team 2012; California Department of Fish and Wildlife 2015; Utah Wildlife Action Plan Joint Team 2015; Oregon Department of Fish and Wildlife 2016; Idaho Department of Fish and Game 2017). Goals for birds, and passerines in particular, are similar among the five state Wildlife Action Plans, and largely focus on the protection of sagebrush-dominated ecosystems and restoration of riparian areas. The majority of plans emphasize management actions over extensive areas of the Great Basin, such as reduction of cheatgrass (*Bromus tectorum*), a highly flammable, nonnative invasive grass that is increasingly common across elevations

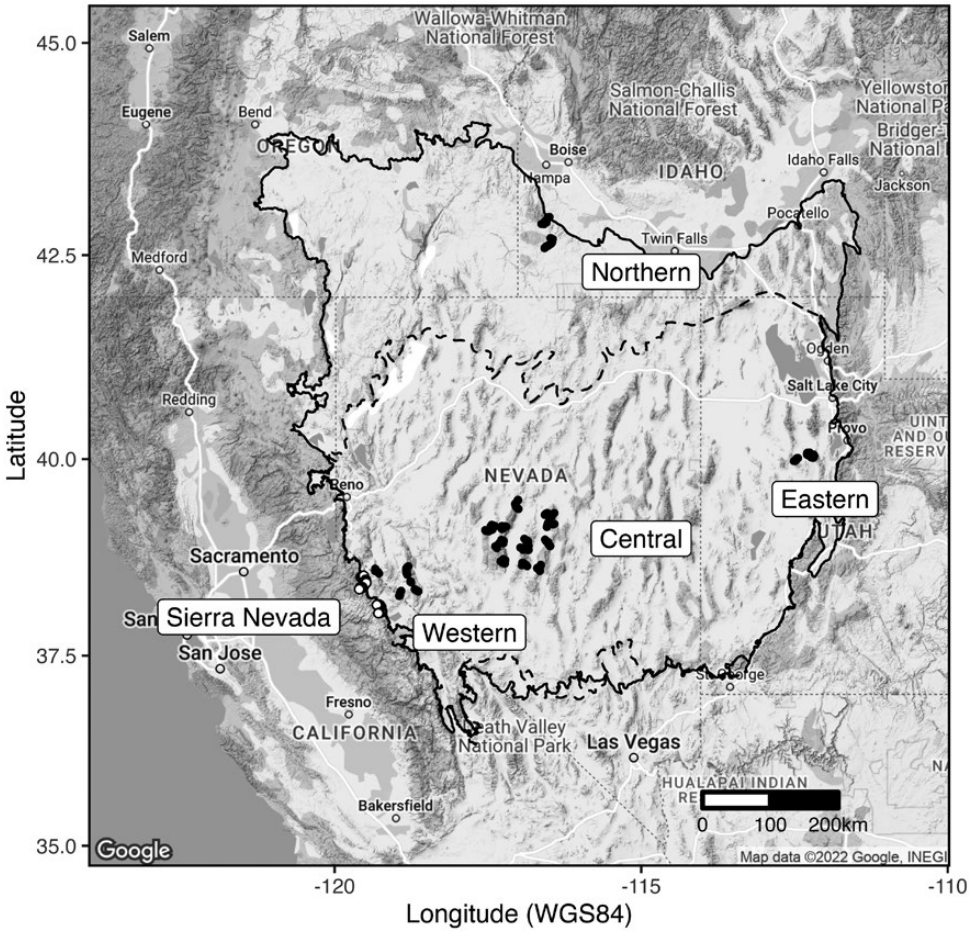

FIGURE 1. Great Basin and locations of survey points in each subregion. Points in the Sierra Nevada subregion are designated by white dots to better differentiate them from points in the western subregion. Dotted outline indicates The Nature Conservancy's delineation of the Great Basin. Solid black outline indicates the U.S. Environmental Protection Agency's Level III Ecoregion delineation of the Great Basin (Central Basin and Range and Northern Basin and Range).

and vegetation types (Williamson et al. 2020, Smith et al. 2022); restoration of sagebrush (*Artemisia* spp.); and increasing the sustainability of livestock grazing in valleys and riparian-upland watersheds (Pellant et al. 2004, Davies et al. 2011, Batchelor et al. 2015).

Management plans often assume that bird-environment relations that were characterized in one area of the Great Basin are representative of those relations across the entire ecoregion (e.g., Sage Grouse Initiative, https://www.sagegrouseinitiative.com/). However, differences in climate, hydrology, vegetation composition, geology, and insect and other animal communities across the Great Basin are well established (e.g., Brown 1978, Harper et al. 1978, Austin and Murphy 1987, Grayson 1993, Riddle et al. 2014). For example, more precipitation falls in the northern Great Basin than in the central or southern Great Basin, and from 1951 through 2013, maximum precipitation increased significantly in the eastern and northern Great Basin, but not in the western or southern Great Basin (Xue et al. 2017). A review of 170 published studies on Great Basin vegetation found that 95.1% of experiments identified significant spatial variation in phenotypic traits (Baughman et al. 2019). It is in part these differences that have led researchers to divide the Great Basin into subregions on the basis of geology, ecological and evolutionary processes, and species composition of plants, vertebrates, or invertebrates (Behle 1963, Holmgren 1972, Johnson 1978, Austin and Murphy 1987). Therefore, it is reasonable to assume that the habitat of species that occur throughout the Great Basin varies among subregions.

We investigated whether associations between bird occupancy and floristics or physiognomy differed among 5 biogeographic subregions of the Great Basin (Figure 1). Our data were collected over elevational gradients in montane canyons, which span vegetation types such as sagebrush shrubsteppe, pinyon-juniper woodlands, riparian zones, aspen groves, and, in some areas, closed-canopy conifer forests. We created plant functional

TABLE 1. Years and number of locations at which we conducted 100-m fixed radius point counts of birds in five subregions of the Great Basin. Sampling occurred from late May through early July of each year. All data are archived (Fleishman 2019a, b, c, d).

Subregion	Years sampled	Number of canyons sampled	Number of points sampled	Elevational range of points (m)
Central	2001–2015, 2017–2020	25	303	1900–3220
Western	2012–2020	10	134	1660–2950
Sierra Nevada	2012–2020	10	134	1790–3190
Northern	2017–2018	5	92	1180–1880
Eastern	2017–2018	6	96	1650–2400

groups to approximate vegetation structure (i.e., physiognomy). Functional groups are sets of species with similar traits that relate to their ecological roles, and that respond to multiple environmental factors in similar ways (Lavorel et al. 1997, Diaz and Cabido 2009). Although functional groups are subjective, we considered vegetation traits that may be meaningful to birds (Lavorel et al. 1997), especially physical structure and association with riparian areas. These groups were analogous to physiognomic groups used in previous Great Basin bird research (Rotenberry and Wiens 1980, Fleishman et al. 2003, Fleishman and Mac Nally 2006). Understanding whether relations between birds and vegetation differ across geographic gradients could indicate how birds respond to environmental differences, including those caused by management actions. We hypothesized that occupancy of a given bird species was associated with different plant species among subregions, but with a given functional group of plants across the Great Basin.

METHODS

Study System

Our work spanned 5 subregions of the hydrographic Great Basin, which we reference as central, western, Sierra Nevada, northern, and eastern (Figure 1). Our delineations, which primarily are based on vegetation, are generally consistent with ecoregions as defined by The Nature Conservancy (The Nature Conservancy of Nevada 2001) and the U.S. Environmental Protection Agency's Level IV Ecoregions (Bryce et al. 2003). Dominant plant species in the Sierra Nevada subregion, which has expansive, closed-canopy, subalpine conifer forests, include lodgepole pine (*Pinus contorta*), Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), and red fir (*A. magnifica*). Conifers in the western and central subregions largely are dominated by juniper (*Juniperus osteosperma*) and single-leaf pinyon (*P. monophylla*). The northern subregion includes ponderosa pine (*P. ponderosa*) woodlands but few pinyon woodlands, whereas the eastern subregion includes plant species that are common in the Rocky Mountains but not much further west in the Great Basin, such as Douglas-fir (*Pseudotsuga menziesii*) (Grayson 1993).

Field Data

We sampled birds with 100-m fixed-radius point counts from late May through early July, which encompasses the breeding season of most birds in the Great Basin and ends before a high proportion of juveniles have fledged and before most movement to molting or wintering grounds. Across the 5 subregions, our survey points spanned elevations from 1,100 to 3,200 m (Table 1). In the central subregion, we sampled birds from 2001 to 2020, except for 2016 and 2017, at a total of 303 points in 25 canyons (Fleishman 2019b). In the western and Sierra Nevada subregions, we sampled birds from 2012 to 2020 at a total of 134 points in 10 canyons (Fleishman 2019a). In the northern and eastern subregions, we sampled birds from 2017 to 2018 at a total of 92 points in 5 canyons and 96 points in 6 canyons, respectively (Fleishman 2019c, d). Each canyon had an average of 12 survey points, and the centers of almost all points were at least 350 m apart.

We visited each point 3 times during each breeding season, with about 10–14 days between visits, and recorded all birds detected by sight or sound that perched or fed within the point for 8 min. In almost all cases, sampling was restricted to the first four hours after sunrise. A total of 52 observers conducted point counts across all subregions and years, with an average of 4 observers per year. We excluded fledglings and juveniles from analyses.

To characterize floristics and physiognomy, we measured 4 radial 50-m lines, one in each of the cardinal directions, from the center of each point. At 5-m intervals along each line (41 per point), we recorded the size of the closest tree within 1 m (height and either diameter at breast height or basal diameter, depending on plant morphology), canopy cover, and presence of dominant plant species that intersected the line (~25 taxa; most grasses and forbs were not differentiated). We estimated canopy cover with a concave spherical densiometer, which samples ~120 m^2 per measurement (Cook et al. 1995). These data were collected in 2013 in the central subregion, in 2016 and 2017 in the Sierra Nevada and western subregions, and in 2017 and 2018 in the northern and eastern subregions (Fleishman 2019e, f, g, h). Our annual observations, and those of experienced colleagues, suggested that point-level composition and abundances

TABLE 2. Functional groups of plants as defined in our analyses.

Species included	Functional group
Sagebrush (*Artemisia tridentata, A. arbuscula*), rabbitbrush (*Ericameria* spp., *Chrysothamnus* spp.), saltbush (*Atriplex* spp.), horsebrush (*Tetradymia* spp.), hopsage (*Grayia spinosa*), bitterbrush (*Purshia tridentata*)	Low shrub
Pinyon (*Pinus monophylla*), juniper (*Juniperus* spp., primarily *J. osteosperma*)	Arid conifer
Aspen (*Populus tremuloides*), alder (*Alnus* spp.), water birch (*Betula occidentalis*), cottonwood (*Populus angustifolia*, *P. fremontii*)	Riparian tree
Chokecherry (*Prunus virginiana*), bitter cherry (*P. emarginata*), Woods' rose (*Rosa woodsii*), willow (*Salix* spp.)	Riparian shrub
Limber pine (*Pinus flexilis*), Jeffrey pine (*P. jeffreyi*), lodgepole pine (*P. contorta*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), white fir (*A. concolor*)	Montane conifer

of trees and shrubs were relatively stable over the period of this study.

Floristics and Physiognomy

We examined associations between bird occupancy and the abundance of 13 plant species that occurred in our survey locations in at least 3 of the 5 subregions and are among the dominant taxa where they occur: sagebrush (*Artemisia tridentata, A. arbuscula*), Woods' rose (*Rosa woodsii*), bitterbrush (*Purshia tridentata*), desert peach (*Prunus andersonii*), rabbitbrush (*Ericameria* spp., *Chrysothamnus* spp.), aspen (*Populus tremuloides*), cottonwood (*P. angustifolia, P. fremontii*), pinyon, juniper (*Juniperus* spp.), mountain mahogany (*Cercocarpus ledifolius*), willow (*Salix* spp.), limber pine (*Pinus flexilis*), and fir (*Abies magnifica, A. concolor*). The extensive distributions and dominance of these species allowed for comparison of associations with bird species among subregions. We also included each of these species within a functional group (Table 2).

We defined 5 functional groups of plants (Table 2) on the basis of our 30 years of field experience and discussions with other experts on the ecology of the Great Basin. For example, we included sagebrush, rabbitbrush, saltbush (*Atriplex* spp.), horsebrush (*Tetradymia* spp.), hopsage (*Grayia spinosa*), and bitterbrush in the low shrub functional group. We hypothesized that birds view these shrub species as functionally equivalent given that they are relatively short, grow in dry microclimates, and may provide breeding habitats for birds that build their nests in shrubs. These functional groups are analogous to physiognomic groups used in previous research on Great Basin birds (Rotenberry and Wiens 1980, Fleishman and MacNally 2006).

Every functional group except montane conifers, which was not present in the northern subregion, was present in all subregions, but the species composition of the functional group often differed among subregions. For example, in the central subregion, the riparian tree functional group included aspen, cottonwood, water birch (*Betula occidentalis*), and dogwood (*Cornus sericea*); whereas in the western subregion, the same functional group included aspen, cottonwood, dogwood, and alder (*Alnus* spp.).

Statistical Analyses

We built models of the occupancy of 19 bird species for which we detected at least 40 individuals per subregion per year. For each species, all subregions were included in a single occupancy model, which allowed direct comparison of vegetation associations among subregions, and comparison to associations across the Great Basin when subregional data were pooled. We acknowledge that our sampling across the Great Basin was patchy, but for simplicity, refer to the latter associations as Great Basin level. Occupancy estimates the probability that a species is present while accounting for imperfect detection (MacKenzie et al. 2002, Royle and Nichols 2003).

We modeled detection probability for each species as

$$C_{ijk} \sim \text{Binominal}\ (p_{ijk}, Z_{ik})$$

$$\text{logit}\ (p_{ijk}) = \alpha 0 + \alpha 1 * \text{observer}_{ikj}$$

$$\alpha 1 \sim \text{Normal}\ (0,\ tau)$$

$$tau \sim \text{Uniform}\ (0, 5)$$

where C_{ijk} is the observed presence or absence of the species at point i during visit j in year k, and p is the probability of detecting the species given its presence. We used a logit link function to model the random effects of observer on detection probability. $\alpha 0$ is the mean point-level detection probability for the species, and $\alpha 1$ is a random effect of observer identity on detection, with a mean of 0 and a precision of tau.

We linked the detection process to the occupancy process through Z_{ik}, which we treated as a Bernoulli random

variable defined by the probability that point i is occupied in year k (ψ):

$$Z_{ik} \sim \text{Bernoulli}\ (\psi_{ik})$$

$$\text{logit}\ (\psi_{ik}) = \beta 0_S + \beta 1 * year_{ik} + \beta 2 * point_{ik} + \beta 3_S * X_{ik},$$

$$\beta 0_S \sim \text{Normal}\ (mu,\ tau0)$$

$$mu \sim \text{logit}(mu0)$$

$$mu0 \sim \text{Uniform}(0, 1)$$

$$tau0 \sim sd0^2$$

$$sd0 \sim \text{Uniform}\ (0, 10)$$

$$\beta 2 \sim \text{Normal}\ (0,\ tau1)$$

$$tau1 \sim \text{Uniform}\ (0, 1)\ ,$$

where Z_{ik} is the occupancy state (0 = absent, 1 = present) at point i in year k. We applied a logit link function to ψ to model occupancy covariates. $B0_S$ is an intercept that varies among subregions S and is defined by a normal distribution with a mean of mu and precision of tau0. $\beta 1$ is the fixed effect of year, and $\beta 2$ is a point-level random effect with a mean of 0 and precision of tau1. $B3_S$ is a vector of covariate values indexed by subregion S for every variable in **X** at each point i. **X** is a matrix of point-level covariate estimates for each subregion. The variables in **X** were percent cover of the 5 plant functional groups (Table 2) and the prevalence of the 13 plant species listed above. We classified a covariate's association with occupancy as significant if >95% of its posterior distribution was above or below zero.

We implemented models with Bayesian methods in JAGS (Plummer 2003) with the *jagsUI* package (Kellner 2019) in R (R Core Team 2020). Code for the final model is available at https://github.com/MarthaZillig/vegetation_associations_code. We based posteriors on 3 chains of 50,000 iterations after a 10,000 sample for both the burn-in and adaptive phase. We classified convergence as Rhat <1.10 (Gelman and Hill 2007), and visually examined traceplots of the Markov chains to further assess convergence. We calculated collinearity of all pairs of candidate covariates (those included in **X**). A priori, we determined that if pairs of variables had a correlation coefficient of >0.8, we would exclude the variables of the pair that we deemed less ecologically relevant on the basis of our experience and the variables' information content. In two subregions, the collinearity between one plant species and one functional group was 100% because the functional group only contained that plant species (central subregion: limber pine and nonarid conifer functional group; northern subregion: cottonwood and riparian tree functional group). In these instances, we removed the functional group from the analysis because it provided less information than the plant species. All collinearity matrices are included in Supplementary Material Table S1.

We examined model fit on the basis of separate Bayesian *P*-values for the detection and occupancy processes, and classified the fit of the model as good if both Bayesian *P*-values were 0.05–0.95. Additionally, we examined estimated detection probability and classified the fit of the model as good if mean detection probability was >15%. Models of 13 of the 19 species passed all goodness of fit tests (Bayesian *p*-values and detection threshold); we only report the results of those models (Figure 2). The 13 species represent multiple ecological guilds (Gonzalez-Salazar et al. 2014) and land-cover associations. Models of Western Wood-Pewee (*Contopus sordidulus*), Vesper Sparrow (*Pooecetes gramineus*), Song Sparrow (*Melospiza melodia*), Orange-crowned Warbler (*Leiothlypis celata*), Yellow Warbler (*Setophaga petechia*), and Lazuli Bunting (*Passerina amoena*) did not pass goodness of fit tests.

We used 2 methods to evaluate whether estimated associations between the occupancy of a given species of bird and a particular covariate were significantly different between two subregions. First, we examined which covariates were significantly associated with occupancy (>95% of the posterior distribution above or below zero) in each subregion. Second, we compared covariate estimates of vegetation associations between each of the 10 pairs of subregions. If the posterior densities in the two subregions overlapped by <5%, we classified the covariate's effect on bird occupancy in the 2 subregions as significantly different. The association of a given covariate with occupancy could differ significantly between subregions regardless of whether the association was significant in both subregions. For example, say 97% of the posterior distribution of a covariate in one subregion was above zero (significant, positive association with occupancy), whereas 93% of the posterior distribution of the covariate in another subregion was above zero (nonsignificant association with occupancy). Although we would consider the former association significant and the latter non-significant, the overlap between the two posterior distributions was >5%. Therefore, we would not consider the covariate's association with occupancy in the two subregions to be significantly different. This method allowed us to evaluate subregional differences in bird-vegetation associations that might not be apparent solely on the basis of significant associations with occupancy.

RESULTS

Mean Great Basin-level occupancy of the 13 species was 0.34, and mean occupancy within each subregion was

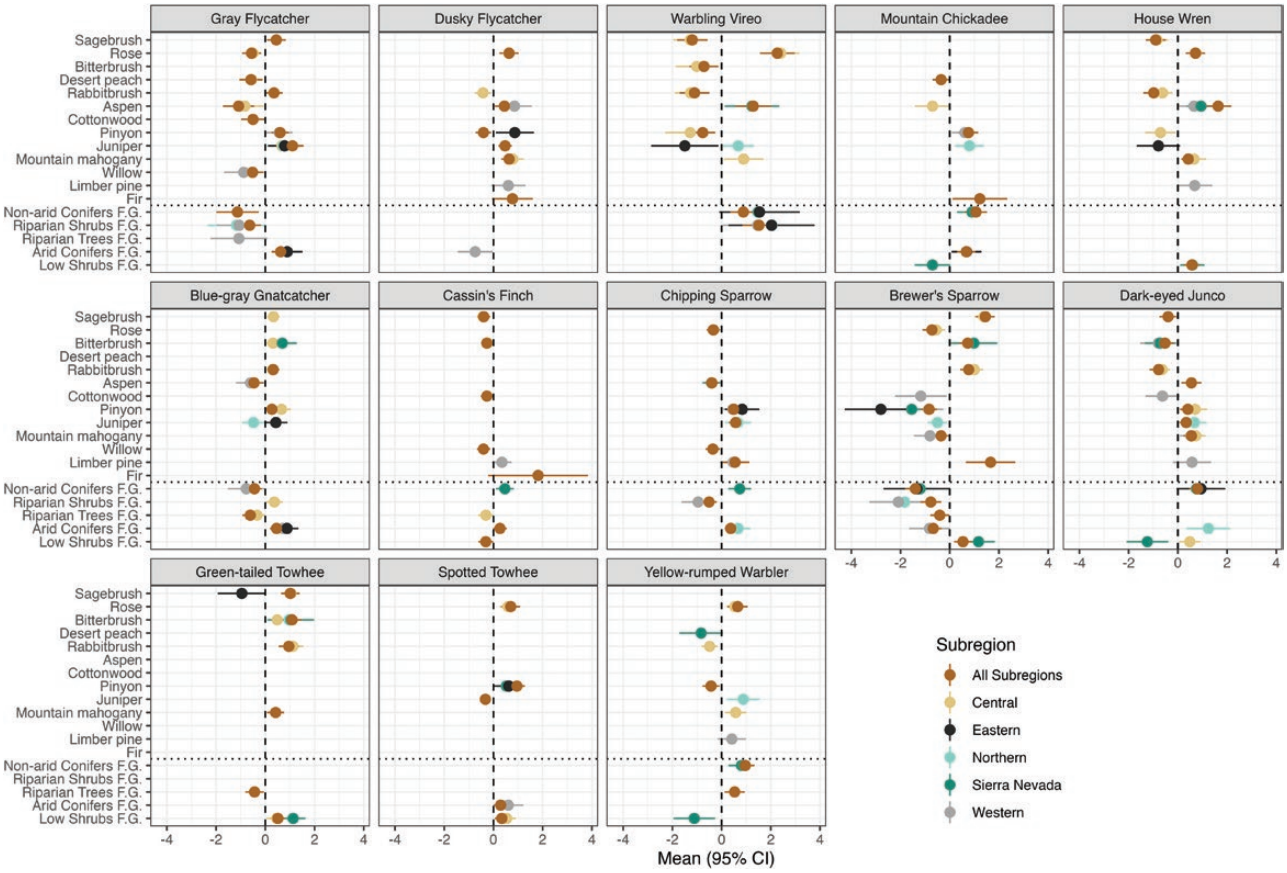

FIGURE 2. Model estimates of the effects of plant species and plant functional groups on bird occupancy at the Great Basin level (all subregions) and in each subregion. Values are means and 95% confidence intervals (CIs) of associations for which >95% of the posterior density was above or below zero. F.G., functional group. Horizontal dotted line separates plant species and functional groups. Overlapping points were moved slightly for readability.

0.30–0.38 (Supplementary Material Table S2). Mean occupancy at the subregion level varied among species, from a low of 0.11 for House Wren (*Troglodytes aedon*) to a high of 0.82 for Green-tailed Towhee (*Pipilo chlorurus*). Occupancy of some species was relatively consistent among subregions (e.g., Green-tailed Towhee), whereas occupancy of others was more variable. For example, mean occupancy of Mountain Chickadee (*Poecile gambeli*) was 0.02 in the northern subregion and 0.82 in the Sierra Nevada subregion. Full model outputs and covariate estimates for the 13 bird species are included in Supplementary Material Table S3.

No bird species' occupancy was associated significantly with the same plant species or functional group in more than 3 subregions (Figure 2). Three species were associated with the same plant species in three subregions, and the signs of the associations were the same: Gray Flycatcher (*Empidonax wrightii*; positive association with juniper), Brewer's Sparrow (*Spizella breweri*; negative association with pinyon), and Green-tailed Towhee (positive association with bitterbrush). The number of significant associations between occupancy of a given bird species and vegetation was greater at the Great Basin level than in any subregion. In 22 of 93 instances (24%), an association at the Great Basin level was not apparent in any subregion. For example, Cassin's Finch (*Haemorhous cassinii*) was negatively associated with cottonwood and willow and positively associated with fir at the Great Basin level, but was not associated with those plant species in any subregion (Figure 2). In general, associations that were consistent between a subregion and the Great Basin had the same sign. However, in 2 instances, the signs differed. The association between Dusky Flycatcher and pinyon was positive in the eastern subregion but negative at the Great Basin level, and the association between Green-tailed Towhee and sagebrush was negative in the eastern subregion but positive at the Great Basin level (Figure 2).

Of the 234 possible associations between a bird species and a plant species or functional group, 102 (44%) were significant in at least 1 subregion. Of those 102 associations, 18 (18%) were significant in >1 subregion, and the sign of 4 of the 18 associations differed between subregions. For

example, the association between occupancy of Dark-eyed Junco (*Junco hyemalis*) and the low shrub functional group was positive in the central subregion but negative in the Sierra Nevada subregion (Figure 2). Across all bird species and biogeographic subregions, 10% of possible associations between occupancy and floristics, and 13% of possible associations between occupancy and physiognomy, were significant.

With the exception of fir, which was not associated significantly with occupancy of any bird species at the subregion level, associations of all species of plants and functional groups with occupancy varied significantly between at least 2 subregions (Tables 3, 4; Supplementary Material Table S4). The associations of bird occupancy with juniper and pinyon, and with all functional groups except riparian shrubs, were especially variable (Supplementary Material Table S4). Particular pairs of subregions dominated these differences. Associations between occupancy and floristics differed the most between the Sierra Nevada and central subregions and between the western and central subregions (16% of realized differences), and differed the least between the eastern and western subregions (4%) (Supplementary Material Table S5). Associations between occupancy and physiognomy differed the most between the Sierra Nevada and western (18%) and central (17%) subregions, and differed the least between the northern and western subregions (3%). For example, associations of low shrubs with occupancy of 6 bird species significantly differed between the Sierra Nevada and central subregions. Associations of montane conifers with occupancy of 10 bird species differed between the Sierra Nevada and western subregions (6 species) and Sierra Nevada and central subregions (5 species) (Table 4).

DISCUSSION

Contrary to assumptions in state or regional wildlife action plans and conservation plans, our work did not yield evidence that associations between occupancy of birds and either floristics or physiognomy consistently were transferable among subregions of the Great Basin. Furthermore, significant differences in associations between occupancy of a given species and a given covariate among subregions would not have been apparent from analysis of significant occupancy associations alone. For example, the positive association between occupancy of Green-tailed Towhee and rabbitbrush was only significant in the central subregion and at the Great Basin level (Figure 2). Moreover, the association with rabbitbrush was significantly stronger in the central subregion than in any other (Figure 3B), suggesting that Green-tailed Towhee's use of rabbitbrush in the central subregion may be distinct.

Subregional differences in associations between floristics and occupancy of a given bird species likely have multiple mechanisms. For example, species richness, composition, and interspecific interactions of birds vary among subregions, which may reflect subregional differences in floristics (MacArthur 1962; Rice et al. 1983). Abundance of predators can influence selection of nest sites by females, and areas with low predator abundance may have characteristic but subregionally distinct vegetation (Lanyon 1981; LaManna et al. 2015) as a result of differences in climate, hydrology, and geology. For instance, Steller's Jay (*Cyanocitta stelleri*), a common nest predator in the western, Sierra Nevada, and eastern subregions, generally breeds in forest (Andrews and Righter 1992). Potential prey species in these subregions may nest in open, lower vegetation or in forest edges to avoid nest predation by Steller's Jays. Additionally, birds may be evaluating habitat quality on the basis of vegetation configuration, heterogeneity, or other elements at larger extents than is captured by our 50-m measurement radius.

There are at least 3 possible explanations for why associations between occupancy and physiognomy varied among subregions. First, our functional groups may not reflect plant traits or taxa that affect bird occupancy. We think this explanation is unlikely given that our functional groups included virtually all dominant species of shrubs and trees, and the plant species in each functional group had a similar structure and microclimate associations. Second, not all members of a given functional group occur or are equally abundant in all subregions. For example, water birch, a member of the riparian tree functional group, was abundant in the central subregion and absent from our survey locations in the other 4 subregions. As a result, associations between the riparian tree functional group and occupancy of any species that was attracted to or avoided water birch, and the direction of the associations, may have differed among subregions. Third, as our data suggest, bird species indeed may be associated with different functional groups in different parts of the Great Basin.

Our results suggested that relations between occupancy and physiognomy in the Sierra Nevada subregion may be distinct from those in the western or central subregions, despite the fact that no more than 30 km separated many of our points in the western and Sierra Nevada subregions. Those differences may reflect differences in subregional climate, geology, and vegetation. The east slope of the Sierra Nevada captures considerably more precipitation from Pacific cyclonic storms than mountain ranges immediately to the east (Grayson 1993). Additionally, soils in the Sierra Nevada have low pH and low concentrations of extractable phosphorus, which supports ponderosa pine and Jeffrey pine woodlands that are absent further east (DeLucia et al. 1988; Schlesinger et al. 1989).

TABLE 3. Associations between bird occupancy and floristics that were significantly different between subregions. Letters indicate the subregions: C = central; E = eastern; N = northern; S = Sierra Nevada; W = western.

Species	Plant species	Pairs of subregions in which the difference was significant
Gray Flycatcher	Bitterbrush	C-N, N-E, W-N
	Willow	C-W
Dusky Flycatcher	Rose	C-W
	Bitterbrush	C-S
	Rabbitbrush	C-S
	Aspen	C-W, S-W
	Pinyon	C-E, W-E, S-E
	Willow	S-E, W-N
Warbling Vireo	Rose	C-S, C-W, C-E
	Rabbitbrush	C-N
	Aspen	C-S
	Pinyon	C-E, C-W
	Juniper	N-E, C-N
Mountain Chickadee	Aspen	C-W, C-S, C-E
	Juniper	N-E
House Wren	Bitterbrush	C-N, C-S
	Pinyon	C-E, C-S
	Juniper	N-E, S-E
	Mountain mahogany	C-S, S-N
Blue-gray Gnatcatcher	Bitterbrush	C-W, W-E, S-W
	Aspen	S-W
	Willow	C-N, W-N
	Pinyon	C-E, C-W
	Juniper	C-N, N-E
Cassin's Finch	Aspen	S-E
Chipping Sparrow	Pinyon	S-E
	Juniper	N-E, S-N, W-N
Brewer's Sparrow	Sagebrush	C-N
	Bitterbrush	S-W
	Rabbitbrush	C-N, C-W
	Cottonwood	C-W
	Pinyon	C-E, C-S, N-E, W-E
	Mountain mahogany	W-N
Dark-eyed Junco	Rabbitbrush	C-S
	Aspen	C-W
	Cottonwood	C-W, S-W
	Pinyon	C-S
	Juniper	C-N, N-E, S-N, W-N
	Willow	C-W
Green-tailed Towhee	Sagebrush	C-E, N-E, W-E, S-E
	Rabbitbrush	C-N, C-E, C-W, C-S
	Cottonwood	C-W
	Willow	C-N
Spotted Towhee	Willow	C-N, S-N
Yellow-rumped Warbler	Bitterbrush	C-E, S-E
	Desert peach	C-S
	Rabbitbrush	C-S
	Juniper	C-N, N-E, W-N

Occupancy of some species, such as Cassin's Finch, Mountain Chickadee, and Spotted Towhee (*Pipilo maculatus*), was associated with relatively few covariates (Figure 2), and the directions of those associations differed little between subregions (Tables 3 and 4). These results suggest that the 3 species, none of which migrate far from the Great Basin, may have relatively similar and general vegetation associations across the ecoregion. Such generality is one way in which resident species may adapt to resource fluctuations across large areas (Martin and Fahrig 2018).

Occupancy of other species of birds was associated with different covariates in different subregions. Brewer's Sparrow is considered a sagebrush obligate in state wildlife action plans or conservation plans (e.g., Wildlife Action Plan Team 2012; Oregon Department of Fish and

TABLE 4. Associations between bird occupancy and physiognomy (functional groups) that were significantly different between subregions. Letters indicate the subregions: C = central; E = eastern; N = northern; S = Sierra Nevada; W = western.

Species	Functional groups	Pairs of subregions in which the difference was significant
Gray Flycatcher	Arid conifer	C-E, C-W, C-S
	Riparian tree	C-W
Dusky Flycatcher	Arid conifer	C-W, S-W
	Riparian tree	C-E, C-W, C-S
	Riparian shrub	S-E, S-W
	Montane conifer	W-E, S-W
Warbling Vireo	Riparian tree	C-W
	Montane conifer	C-E, C-S, W-E, S-W
Mountain Chickadee	Low shrub	C-S
	Riparian tree	C-S
	Montane conifer	C-S, S-W, W-E
House Wren	Arid conifer	W-E
Blue-gray Gnatcatcher	Low shrub	C-S
	Arid conifer	C-E, C-W, N-E, S-E, S-W, N-W
	Riparian shrub	C-W, S-W
	Montane conifer	S-E, S-W
Cassin's Finch	Riparian tree	C-E
	Montane conifer	S-W
Chipping Sparrow	Arid conifer	C-N
	Riparian shrub	C-W, S-W
	Montane conifer	S-W
Brewer's Sparrow	Low shrub	S-E, C-S, S-N
	Arid conifer	C-W
	Riparian shrub	C-N, C-W, W-E, S-W, S-N
	Riparian tree	C-S
	Montane conifer	C-S
Dark-eyed Junco	Low shrub	C-N, C-S, N-E, S-N, S-W
	Arid conifer	C-N, N-E, S-N, W-N
	Montane conifer	C-N, C-S
Green-tailed Towhee	Low shrub	C-N, C-S, S-N, S-W, S-E
	Riparian shrub	C-E, N-E, W-E
	Riparian tree	C-E, W-E, S-E
Spotted Towhee	Low shrub	C-N, C-E, S-N
	Arid conifer	N-E, S-W, W-N
	Montane conifer	S-E
Yellow-rumped Warbler	Low shrub	C-S, S-E, S-W, S-N
	Montane conifer	C-E, C-W, C-S

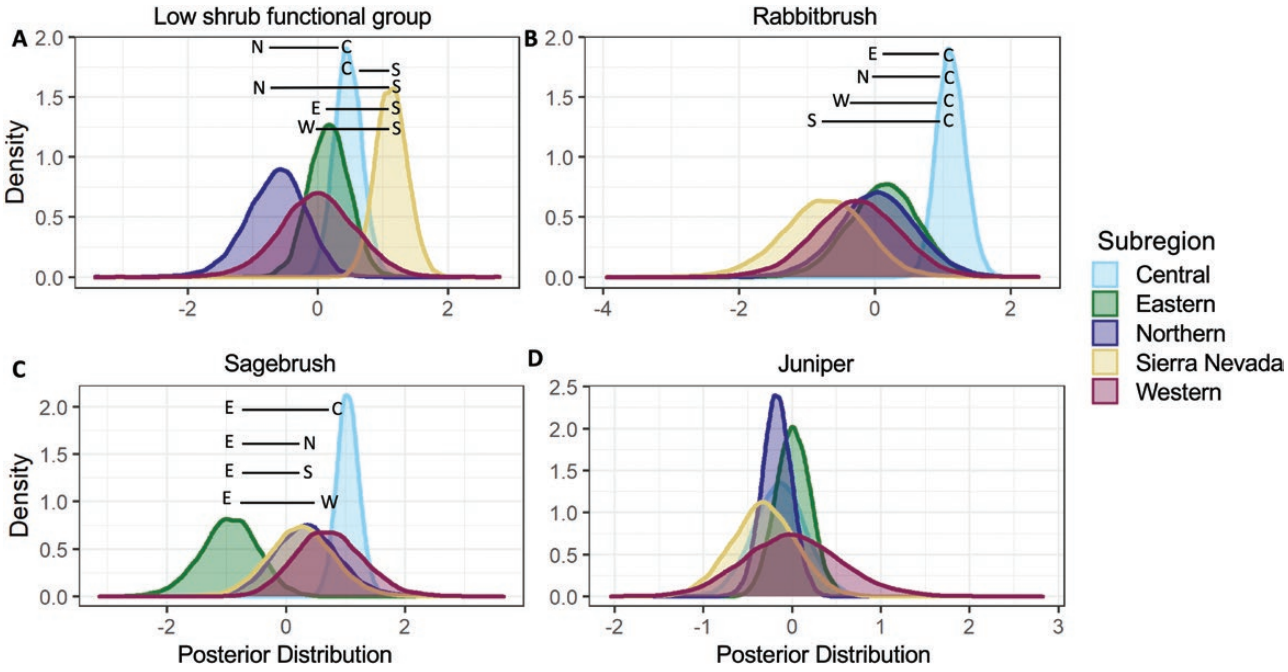

FIGURE 3. Associations between Green-tailed Towhee occupancy and floristics and physiognomy differed significantly among 5 subregions of the Great Basin. Posterior distributions of (**A**) low shrub functional group; (**B**) rabbitbrush; (**C**) sagebrush; and (**D**) juniper. A line between two peaks indicates >95% confidence that the posterior distributions of two subregional estimates are significantly different. Letters indicate subregions that significantly differed: C = central; E = eastern; N = northern; S = Sierra Nevada; W = western.

Wildlife 2016), albeit the ornithological literature tends to consider Brewer's Sparrow as a sagebrush associate rather than an obligate (Rotenberry et al. 2020). Its presence often is interpreted as an indication that sagebrush ecosystems are in good condition, particularly after a change in management (e.g., mechanical manipulation or changes in the intensity of livestock grazing) (McAdoo et al. 1989; Magee et al. 2011; Golding and Dreitz 2017). For example, on the basis of North American Breeding Bird Survey (BBS) data at 4 km^2 resolution and LANDFIRE data on vegetation type at 120 m^2 and 6.4 km^2 resolution, Donnelly et al. (2017) found strong associations between Brewer's Sparrow and sagebrush cover across the Great Basin. They concluded that protecting sagebrush that serves as habitat for Greater Sage-Grouse (Centrocercus urophasianus) would provide significant conservation benefits to Brewer's Sparrow and other sagebrush-obligate songbirds (Sage Grouse Initiative 2016; Donnelly et al. 2017). However, these inferences were based on data that are sparse throughout the Great Basin, particularly in Nevada (34 Breeding Bird Survey routes in Nevada, 97 in Utah, and 58 in Idaho; https://www.pwrc.usgs.gov/bbs/). Moreover, the vegetation data used by Donnelly et al. (2017) emphasized land-cover type rather than floristics or physiognomy. Sagebrush as classified by LANDFIRE may be similar to our low shrub functional group. LANDFIRE vegetation-type data are derived from multiple sources (e.g., Landsat imagery, decision tree models, field data) that rarely identify individual plants to species (https://www.landfire.gov/evt.php).

In contrast, our data suggested that associations between occupancy of Brewer's Sparrow and sagebrush or the low shrub functional group were inconsistent among subregions. The association between occupancy of Brewer's Sparrow and sagebrush was positive in the central subregion and at the Great Basin level, and the association between occupancy and the low shrub functional group was positive in the Sierra Nevada subregion and at the Great Basin level (Figures 2 and 4). However, Brewer's Sparrow occupancy was negatively associated with pinyon in the eastern, western, and Sierra Nevada subregions and at the Great Basin level. Our results suggest that Brewer's Sparrow may not be a sagebrush obligate, but instead is responding to the presence of any low shrubs and the absence of conifers. This inference is further supported by the fact that Brewer's Sparrows were not associated with sagebrush in the Sierra Nevada subregion, but were positively associated with bitterbrush, another low shrub (Figure 2).

Associations of bird occupancy with particular plant species and functional groups differed noticeably between the central subregion and other subregions. Also, Great Basin-level associations of multiple bird species, particularly Gray Flycatcher and Warbling Vireo, were similar to those in the central subregion (Figure 2). We have sampled birds in the central subregion for longer than in the other subregions, and the central subregion may have

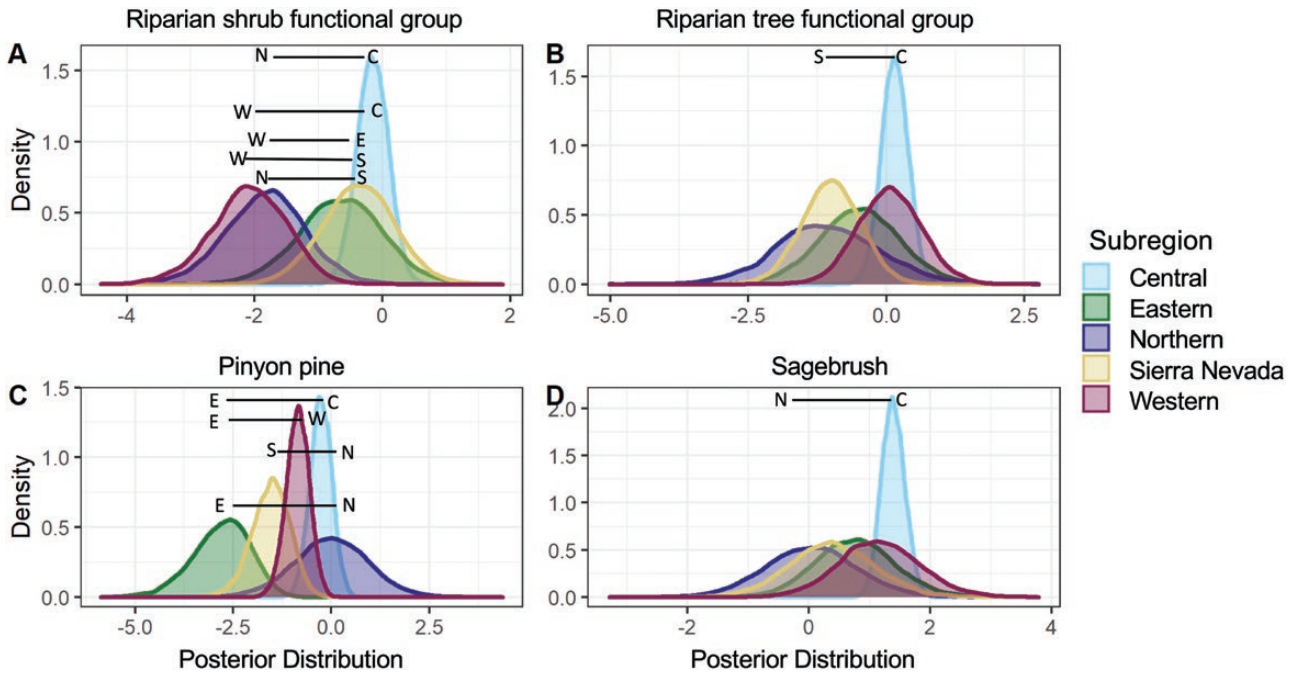

FIGURE 4. Associations between Brewer's Sparrow occupancy and floristics and physiognomy differed significantly among five subregions of the Great Basin. Posterior distributions of (A) riparian shrub functional group; (B) riparian tree functional group; (C) pinyon pine; and (D) sagebrush. A line between two peaks indicates >95% confidence that the posterior distributions of two subregional estimates are significantly different. Letters indicate subregions that significantly differed: C = central; E = eastern; N = northern; S = Sierra Nevada; W = western.

disproportionately contributed to the Great Basin-level estimates. We account for the difference in sampling effort in the subregional models, but could not account for the difference as effectively in the Great Basin-level models although the inclusion of a point-level random effect did account for some unmodeled variation between subregions.

Much of the interior Great Basin is similar to our sampling locations in the central subregion with respect to vegetation, geology, and climate, whereas our sampling locations in the other subregions (Figure 1) are more similar to adjacent ecoregions. For example, the northern subregion, which is adjacent to the Snake River Plain, is cooler and has greater water availability than the other subregions (Xue et al. 2017). Although species composition of birds and plants differs among subregions at the edges of the Great Basin, our results suggest that associations of occupancy with floristics and physiognomy may be more similar among edges than between edges and the interior of the ecoregion. Additionally, the number of years in which we conducted bird surveys in each subregion differed considerably (central, 18 years; western and Sierra Nevada, 8 years; northern and eastern, 2 years). It is possible that apparent vegetation associations in the northern and eastern subregions partially reflect stochasticity or avian population variability. Differences in sampling effort among subregions also may yield more or less overlap of posterior distributions and uncertainty around estimated means. Differences between subregions for which there was more uncertainty around the mean (e.g., eastern and northern) may be greater than those we estimated.

Floristics and physiognomy provide or are strongly correlated with resources necessary for successful bird reproduction. For example, floristics largely determines the types and abundances of food (e.g., fruits, seeds, insects) available to birds (Rotenberry 1985; Fleishman et al. 2003), whereas physiognomy affects predator avoidance and shelter from inclement weather. However, management that focuses exclusively on floristics or physiognomy would likely overlook fundamental aspects of bird habitat. To illustrate, both floristics and physiognomy were correlated with the diversity and abundance of migratory birds in riparian corridors that were dominated by tamarisk (*Tamarix ramosissima*), a non-native invasive species that is common throughout the southwestern United States (Walker 2008). Because tamarisk is structurally similar to some native riparian trees, its removal might be detrimental to migratory birds that use tamarisk at stopover sites (Fleishman et al. 2003; Walker 2008).

Management plans for wildlife in the Great Basin (e.g., Wildlife Action Plan Team 2012; Utah Wildlife Action Plan Joint Team 2015) tend to identify major vegetation types, associate individual bird species with those vegetation types, and then prioritize management actions for

each vegetation type. Such coarse-filter actions may indeed benefit many native birds, but they underestimate spatial variation in habitat that may be predictable. Similarly, a collaborative conservation strategy for birds in Nevada (Great Basin Bird Observatory 2010) emphasized that associations of a given species with vegetation composition and structure may be diverse, but did not reference potential subregional variation. For example, the strategy noted that Green-tailed Towhees were positively associated with dense shrubs, and suggested that conservation of areas with diverse, dense shrubs, along with conservation of montane shrublands, montane riparian, aspen, and pinyon and juniper, will benefit the species across the state. If subregional implementation of vegetation-focused conservation actions does not improve the status of a bird species, it may be assumed that the actions are flawed rather than that the actions did not target the species' subregional habitat.

Most previous efforts to characterize bird habitat in the Great Basin focused on sagebrush shrubsteppe and grasslands (Knopf et al. 1990, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981; but see Fleishman and Mac Nally 2006). Our work is among the first to address habitat for bird species in both upland and riparian communities in the montane Great Basin. Our research is consistent with evidence that attributes of bird habitat vary among resolutions and extents (Weins et al. 1987, Kristan 2006, Chave 2013), and does not support the theory that floristics and physiognomy are more closely related to bird occurrence at small and large spatial extents, respectively.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Data deposits: Bird and vegetation data included in our models are available at: https://www.fs.usda.gov/rds/archive/catalog/RDS-2011-0002-4, https://www.fs.usda.gov/rds/archive/catalog/RDS-2015-0031-2, https://www.fs.usda.gov/rds/archive/catalog/RDS-2019-0021, https://www.fs.usda.gov/rds/archive/catalog/RDS-2019-0017, https://www.fs.usda.gov/rds/archive/catalog/RDS-2019-0023, https://www.fs.usda.gov/rds/archive/catalog/RDS-2019-0019, https://www.fs.usda.gov/rds/archive/catalog/RDS-2015-0032-2, https://www.fs.usda.gov/rds/archive/catalog/RDS-2013-0007-2.

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