Variety is the spice of desert bird life: foundation plant species provide habitat heterogeneity for bird communities in the Mojave Desert.

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Abstract

Plants provide habitat and resources to the desert animal community. However, these interactions are species specific and can depend on season. I tested the hypothesis that birds use different foundation species in deserts as microhabitat, and birds shift associations by flowering and fruiting life-stages. I used line transects to record habitat associations of birds at a protected site in the Mojave Desert. I found that the bird biodiversity and behaviour were not equally represented across all microhabitats or season. Diversity of birds and territorial behaviors were significantly greater at shrubs microhabitats in spring. Shrubs likely primarily provided structural heterogeneity for the avian community to use as perches, nests, and other non-trophic services because foraging and consumption were observed less often. Bird biodiversity was greater at cacti than at open summer microhabitats, which supported the least bird biodiversity. Non-trophic interactions with plants are important for maintaining local bird diversity in deserts.

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Table of Contents

List of Tables

List of Figures

Introduction

Background

In ecology, a microhabitat refers to a relatively fine-scale spatial area of a physical environment. However, size is not the only criterion that defines a microhabitat as size is often relative and subjective. A more appropriate definition takes the internal homogeneity of a microhabitat internal homogeneity relative to adjacent areas into account. In this study, I define a microhabitat by the way that microhabitat influences the conditional experience of an individual within the area in question; if the conditional experience of a visiting individual (e.g. a bird) differs from the average, typical conditions experienced by the rest of the population of the visiting individual, then the bounds of the first individual is a microhabitat (Denney et al. 2020). Simply put, a microhabitat is different relative to adjacent microhabitats in regard to certain characteristics, which are defined by the observer (Price 1978; Jorgensen 2004; Sandel 2015). It is the culmination of multiple, differing microhabitats together in a landscape that creates habitat heterogeneity (Maseko et al. 2019). For highly mobile species such as birds, proximity of an individual to different microhabitats can rapidly shift as the individual transverses a habitat. Heterogeneity has been documented as a key component of ecosystem functionality because this heterogeneity can provide resource partitioning among potential competitors (Fuhlendorf et al. 2017; Cockburn and Lidicker 1983). In this study, the microhabitats created by large plants in desert ecosystems were examined to explore their capacity to support diverse avian communities.

Plant-animal interactions are often positive. Positive interactions or facilitation at the landscape level can influence ecosystem infrastructure (Stachowicz 2001). Facilitation is defined as any positive interaction wherein a benefactor species increases the fitness or survival for associated species (Bertness and Callaway 1994; Bruno et al. 2003; Franco and Nobel 1989). Facilitative interactions can be commensalistic or mutualistic. The latter is a type of positive interaction where both interacting parties benefit (Bronstein 2009). However, competitive interactions often happen concurrently alongside facilitation (i.e. competition for pollinators between benefactors and beneficiaries) (Braun 2018). There are many mechanisms for facilitation between interacting taxa (Landero and Valiente-Banuet 2010), and several categories are common across plant-animal interactions with plants often providing food resources such as nectar, fruit, and seeds (Narango et al. 2017; Feinsinger 1987; Saracco et al. 2004; Guo et al. 1995). Benefactor plants can also indirectly facilitate carnivores or insectivores by attracting their prey items (Ruttan et al. 2016). Non-trophic interactions between plants and animals is the most well-documented type of facilitation, with most studies examining hypotheses that supported the function of shrubs as shelters or seed traps for beneficiary animals (Lortie et al. 2016). Benefactor plants can provide prey animals structural cover from their predators (Fischer 1980). Plants are also often nesting sites for small mammals and birds (Owen et al. 2019; Burnside et al. 2020). In the more specific example of a bird-plant interaction, birds can associate with a plant to use as a perching site that aids the bird in foraging and defining its territory (Wiens 1973; Craig 1990; Devereux et al. 2000; Longland and Price 1991). All of these trophic and non-trophic interactions can be relevant for desert birds; however, the relative frequency of these interactions is not well documented.

Different taxa or functional groups within a community can provide support to other species throughout an ecosystem particularly in more stressful environments (Zhang and Tielbörger 2020). Foundation species can be benefactors that facilitate other species within an ecosystem using some or all of the mechanism previously described (Kane et al. 2011; Angelini et al. 2011; Almeida and Mikich 2018). Foundation species are represented at many different levels in food webs and can be found in most ecosystems (Borst et al. 2018; Jones et al. 1994). The uniting characteristic among all foundation species is their strong influence on community composition (Dayton 1972). In many ecosystems, including deserts, plants are foundation species. The traits of a foundation plant species (such as growth pattern, life histories, and origins of neighbors and targets) can influence the mechanism of the interaction (He et al. 2013). Traits can also shift the net outcome of interactions from facilitative to competitive (Callaway and Walker 1997). Shrubs and cacti have been documented as common foundation species globally (Filazzola and Lortie 2014). These large, sturdy plants are often responsible for habitat infrastructure of wildlife throughout an ecosystem (Callaway 1997; Gelmi-Candusso et al. 2017). In relatively high-stress environments like deserts, events like mega-droughts and other inter-annual variation is stressful for many species in the ecosystem (Siegal et al. 2013). These foundation plant species are able to recover after stressful periods and provide some stability during and after harsh events, though their dieback after severe droughts does negatively impact facilitation (McAuliffe and Hamerlynck 2010). This physical stability helps maintain the presence of many other species in a habitat (Lortie et al. 2018). While most studies have focused on plant-plant facilitation (Callaway 2007), positive plant-animal interactions are also frequent in deserts (Lortie et al. 2016; Bertness et al. 1999; Arsenault and Owen-Smith 2002). A more comprehensive understanding of the types of associations between foundation plant species and animals will enable better predictions of how biodiversity will respond to a changing climate and to the relatively extreme existing variation in desert climates seasonally.

This study focuses on bird-plant interactions in a desert ecosystem. Desert plants benefit birds in many ways, but birds can also benefit foundation plant species. Pollination and seed dispersal are critical reproductive services that support sexual reproduction of plants, thereby maintaining genetic variation in shrub and cactus communities (Gorostiague and Ortega-Baes 2017; Godínez-Alvarez et al. 2002; Ebert 2006). Birds can function as indicator species for ecosystem health because they are easily tracked and respond to large- and small-scale changes in the environment (Carignan and Villard 2002). These responses include shifts in occurrence (Villard et al. 1995), abundance (Mazerolle and Villard 1999), and reproductive success (Villard et al. 1993) during ecological changes. Birds also typically respond to the environmental changes with seasonal shifts sometimes by migrating (Salewski and Bruderer 2007). Phenology in desert ecosystems can vary widely due to the extreme variation in temperature and precipitation inherent in these climates (Henen et al. 1998). For animals that rely on or associate with plants for resources (nectar, fruit, seeds, etc.), timing is critical (Buler et al. 2007). For example, floral and fruiting timing of plants (Schwartz 2003; Beatley 1974; Jordan and Nobel 1982; Nobel and Hartsock 1981) is critical for the success of birds during migration breeding seasons (Sillett and Holmes 2002; Runge and Tulloch 2017; Fahse et al. 1998). Therefore, it is important to explore bird-plant interactions at different plant reproductive stages.

Climate change can introduce many novel drivers of change in natural systems and exacerbate existing challenges to local biota. Specifically, climate change can generate phenological mismatches in desert bird and plant communities by shifting the timing of flowering and fruiting that animals fail to equally react to the changing climate (Kellermann and van Ripper III 2015). The changes in these desert systems will further intensify the frequency, strength, and duration of severe weather events such as droughts (Ye and Grimm 2013), mega-droughts (i.e. long-term sustained inter-annual drought events) (Williams et al. 2020), and significantly warming annual temperatures (Kunkel et al. 2013). If foundation species are extirpated or become functionally extinct locally, other species can also disappear (Berger et al. 2008; Säterberg et al. 2013). Desert bird communities have already severely declined primarily due to desert climate change (Iknayan and Beissinger 2018) because increased temperatures in already hot ecosystems are linked with decreases in the frequency of trophic interactions (Plessis et al. 2012). Many of these threatened interactions are species-specific and thus cannot be restored after their disappearance (Valiente-Banuet et al. 2015).

Research Objectives

In this study, two common desert foundation plant species and the resident avian community were examined to explore the relative importance and sensitivity to change of the avian association patterns. I tested the hypothesis that birds associate with different foundation species in deserts as microhabitats and temporal shifts in plant flowering and fruiting changes the frequency and nature of these associations. I used association patterns through time and at fine spatial scales to test the following predictions. (1) The abundance, richness, and diversity of a desert avian community is greater near foundation plants relative to open-gap microhabitats without a foundation plant. (2) The bird-plant associations estimated by observed bird behaviours will vary across microhabitats (cactus, shrub, or open) and by season (spring versus summer) because of changes in plant and bird reproductive timing.

Methods

Study Site

The field work was conducted at the Sweeney Granite Mountains Desert Research Center (34°48′20″N 115°39′50″W) in the Mojave Desert (Appendix A Fig. 4). The elevation of the 3600 hectares of land ranges from 1128 to 2071 m and is not accessible to the public and is thus safe from visitor disturbance (“Reserve Facts,” n.d.). Rainfall varies significantly throughout the year with a mean annual precipitation ranging from 34 to 310 mm per year (Urban et al. 2009), and typically no precipitation in the summer months. The July maximum and minimum temperatures are 33 C and 20 C, respectively, and the December maximum and minimum temperatures are 8 C and -1 C, respectively (“Reserve Facts,” n.d.). The site is dominated by perennial woody and succulent shrubs such as *Cylindropuntia acanthocarpa, Yucca mohavensis, Larrea tridentata, Ambrosia salsola, Pinus monophylla*, and numerous other shrub species (André 2006). There have been 159 birds, 42 mammals, 35 reptiles, 2 amphibians, and 504 species of vascular plants documented at the reserve (Gurin et al. 2012; “Mammals of the Granite Mountains,” n.d.; Stewart and Lappin 2008; André 2006).

Study species

While the Mojave boasts an array of diverse plants, a handful of foundational plant species dominate the landscape. *Cylindropuntia acanthocarpa*, or Buckhorn Cholla, is a shrub-like cactus with an irregular branching pattern (Pinkava 1999). *Larrea tridentata*, or Creosote Bush, is a large, long-lived deciduous shrub that is a highly reliable floral producer due to its low rainfall threshold (Bowers and Dimmitt, 1994). *Yucca schideigera*, or Mojave Yucca, is a flowering plant native to the region with several specialist and generalist relationships to fauna of the region. While there are many other plant species found in the study site, these three are the most abundant plant species and accounted for the greatest number of interactions documented in this study. Mojave Yucca, however, was included as a cactus in my study due to its succulent leaves ending in sharp points which make it functionally similar to other cacti in the region. All three of these species have been documented as foundation species in the region (Smith 1995; Schafer et al. 2012). During the spring surveys, these three species were flowering; in summer, however, all three had fleshy fruits available.

The avian community of the Mojave Desert includes typical species of the American Southwest but is also home to desert obligate species which rely on plant species only found in wild desert areas (e.g. the Cactus Wren, *Campylorhynchus brunneicapillus*). There are over 159 bird species documented frequenting the Sweeney Granite Mountains Desert Research Center protected area (Gurin et al. 2012). The most common bird documented over both seasons was *Amphispiza bilineata*, or the Black-throated Sparrow. An insectivore, herbivore, and granivore, this year long resident of southwestern deserts (De Graaf et al. 1985) was seen or heard at every sampling replication in 2019 during this experiment.

Experimental Design

We conducted observations during 27 surveys from 5/1/2019 to 5/10/2019 for spring observations and repeated 20 surveys recording the observations for summer from 8/14/2019 to 8/24/2019. A 500-meter line transect was used over two-hour period blocks to sample the bird community from 7-10am or 5-8pm, depending on daily temperatures. Two individual line transects were used and spaced 80 meters apart. The starting coordinates for transects 1 and 2 were (34.78299, -115.662) and (34.78303, -115.663), respectively. A single observer familiar with the local bird species recorded all visual or auditory bird cues and identified each observation to species. Some female or juvenile hummingbirds were identified only to family due to the visual similarity between species. In each instance, microhabitat was also recorded as specifically as possible. After recording, each microhabitat was binned into one of three categories: cactus, shrub, or open. As most non-shrub or non-cactus spaces constituted a relatively open microhabitat, this included some vegetative areas, but none with the level of heterogeneity that shrubs or cacti provide to their open surroundings. In addition to species, I also recorded behaviour as designated by an ethogram (Appendix C: Table 8), microhabitat, geographic coordinates, the time of the sighting/hearing, and an estimate of the distance from the transect (<25 meters, 25-50 meters, or >50 meters). I only included visual observations of birds in microhabitat and behavioural analyses for two reasons: 1) Birds that were heard but not seen could not be documented at any microhabitat, and 2) birds may have been exhibiting behaviors which should be prioritized over singing or calling as defined by the ethogram, but these behaviors could not be observed. Flyovers (defined as birds flying roughly 25 feet above the highest vegetation at site that did not land within sight) were not included as observations. I also took photographs of birds using a Nikon D5300 camera equipped with a Sigma 150-600mm lens which served as identification aids and behavioural/microhabitat records (Owen 2020).

Statistical Analyses

Behaviour and microhabitat were treated as dependent variables for each independent bird observation documented. Behavioural observations were then categorized into broader behaviours (active movement, cleaning, feeding, inactive, and territorial/mating). Microhabitats were classified as cactus, shrub, or open gap. Trophic guild and migratory class abundances, defined as the number of individuals within a trophic guild or migratory class at a seasonal microhabitat during a particular survey, were used to define functional diversity in further detailed analyses. I categorized all observed species into trophic guilds using "Foraging Guilds of North America" (De Graaf et al.1985) and into migratory classes using *Common Birds of the Sweeney Granite Mountains Desert Research Center* (Gurin et al. 2012). Taxonomic diversity was recorded to species level and is thus represented in the primary statistical analyses.

Generalized linear models (GLM) were used to compare bird abundance, richness, diversity, trophic guild abundance, migratory class, or behaviour with microhabitat type and season while including average maximum air temperature for the hour and survey replication as random factors (Donald et al. 2001; Morris et al. 2014). Species, trophic guild, or migratory class abundance (A) are defined in this study as the number of individuals represented in each species, trophic guild, or migratory class. Species richness (R) is the number of species in a community (i.e. a seasonal microhabitat during one survey). Diversity is represented as the Shannon Index, a biodiversity measure which accounts for rare species, more so than Simpson's Diversity which more heavily incorporates species evenness. I then compared contrasted terms using estimated marginal means (using the emmeans function in R). I repeated these analyses excluding the Black-throated Sparrow, which made up ~36% of observations, to account for the skew this abundant species may have imposed on the data. All models were tested for overdispersion using the dispersion.test function in R and fit to either a quasi-poisson or gaussian distribution as appropriate. Additionally, to explore how species composition changed between seasonal microhabitat communities, I conducted a Non-metric Multidimensional Scaling analysis followed by a PERMANOVA (Legendre and Legendre 1998). I set the reduced dimensions to 2 for the NMDS and used the Bray-Curtis method of distance calculation for the PERMANOVA.

All analyses were performed in R version 4.0.2 (R Dev team 2020), and all R Markdown code is published on Zenodo (Owen and Lortie 2020a). Photo documentation of birds are published at Figshare (Owen 2020), and a complete dataset of bird observation are published in the Knowledge Network for Biocomplexity Data Repository (Owen and Lortie 2020b).

Results

I visually observed 755 birds and heard 467 birds during both seasons for a total of 1222 bird records over a total of 94 hours, though our spring observations had six additional surveys. However, because birds that were not seen could not be classified by microhabitat or behaviour at the same level of fineness as visually observed species, those 467 heard-only birds were not included in the subsequent data analysis. During the spring, 539 individual birds were visually observed, and 216 birds were visually observed in summer.

There were more individual birds observed in spring than in summer (Fig. 1; Table 1; post-hoc contrast at $p = 0.0327$). The highest species richness of birds detected within the community were associated with shrubs in the spring (Fig. 1; Table 1; GLM; $p = 0.024$; post-hoc contrast at $p = 0.0144$). Similarly, bird diversity was also greatest at shrubs in spring (Shannon index, Fig. 1; Table 1; GLM; $p = 0.0001$; post-hoc contrast at $p = 0.0038$). Open microhabitats in summer had the lowest bird species richness and biodiversity (Fig. 1; Table 1; Richness: GLM; $p = 0.024$; post-hoc contrast at $p < 0.0001$; Shannon index: GLM; $p = 0.0001$; post-hoc contrast at $p = 0.0216$). The total abundances of birds were, however, greatest at open microhabitats in summer and smallest at open microhabitats in spring (Fig. 1; Table 1; GLM; $p = 0.0254$; post-hoc contrast at $p = 0.0327$). To explore sensitivity to dominant species and to highlight abundant species, I conducted a second set of GLMs that reanalyzed the datasets excluding the most common species (the Black-throated Sparrow). All findings were robust and consistent with my previous findings that had included the Black-throated Sparrow (Appendix D). Bird trophic guild abundances were highest at shrubs in spring (Fig. 1; Table 2; GLM; $p = 0.0233$; post-hoc contrasts at $p = 0.0384$, respectively). However, there was no difference in the abundance of birds by migratory class between microhabitats or by season (Fig. 1; Table 1; $p = 0.318$). There was no significant difference between the composition of the avian communities by season or by microhabitats (Appendix E Table 10 and Figure 4; PERMANOVA; $F_2 = 1.523$; $R^2 = 0.0081$; $p = 0.178$).

The most frequent activity observed was territorial behaviours in the spring at shrubs (Fig. 2; Table 3; GLM; p-value < 0.0001; post-hoc contrast at $p = 0.0291$). Cleaning behaviours were the least common, and I observed cleaning at shrubs four times in spring and once in the summer (Fig. 2; Table 3; GLM; p-value < 0.0001; post-hoc contrast at $p = 0.0291$). Feeding, active, and cleaning behaviors at all communities were equally frequent (Fig. 2; Table 3; GLM; p-value < 0.0001).

Discussion

The relative importance of two foundation plant species for the avian community was examined through associational pattern analyses by season. The hypothesis that birds use different foundation species in deserts as microhabitats and plant flowering and fruiting shifts these interactions was supported. The prediction that birds will associate with foundation plants was supported because bird species richness, biodiversity, and trophic guild abundances were higher at foundation plants. Diverse bird communities were most likely to be associated with foundation shrubs rather than at open or cacti microhabitats. This suggests that while all foundation plant species do not benefit all species equally at a given site within a region, they are still important for community composition (Ellison 2019). Foundation plants can provide food resources to small animals (Thompson et al. 1991) in addition to shelter from harsh abiotic conditions and from predators (Westphal et al. 2018). Both mechanisms were likely relevant drivers of the observed bird-plant association patterns in this system. The second prediction that foundation plants support certain behaviors was also supported because bird behaviour varied by season and microhabitat. Birds used foundation plant species for structural purposes as I observed increased territorial displays at shrubs in the spring. Nectarivores (like hummingbirds), frugivores (like orioles), and omnivores (like sparrows) engaged in trophic interactions at foundation plants; however, trophic behaviours were much less common compared to territorial behaviours, though feeding behaviours were still more common at foundation plants than in open microhabitats. Facilitation theory for plant-animal interactions was supported for bird communities. While non-trophic benefits were particularly important for birds, the value of trophic interactions was still evident.

Seasonality bring shifts in both abiotic and biotic factors relevant to ecological interactions between plants and animals. In this study, desert bird communities strongly associated with shrubs in spring but not summer. My findings support previous work detailing the importance of foundation shrub species on desert animal behaviours such as foraging, mating, and thermoregulation (Aukemab and Martínez Del Rio 2002; Bauwens et al. 1996; Westphal et al. 2018). In spring, many plants undergo a blooming period that provides direct facilitation to nectarivores (and pollination is provided to the plants by the pollinators) (Linhart and Feinsinger 1980). During this season, much of the bird community is undergoing migration, a particularly stressful period in bird life histories (Rathcke and Lacey 1985; Guglielmo et al.

2001; Rattenborg et al. 2004). Migration can lead to increased physical stress which requires stopovers at resting sites (Gutierrez et al. 2019). Spring shrubs also facilitate plant-animal-animal interactions by providing services to insects, which then are a resource for insectivores (Braun and Lortie 2019; Ruttan et al. 2016) such as birds. These results fall neatly within the well-documented idea that animals must behaviourally adapt to harsh environments and situations (Filazzola et al. 2017; Peinetti et al. 2011), with birds adapting to an intense desert climate by taking advantage of shrubs as physical structures in less stressful periods like spring

However, food availability was not the primary driver of bird community diversity at shrub microhabitats. Birds in this system were typically observed associating with shrub microhabitats for their structural benefits, i.e. perching sites for territorial displays. Territorial displays allow birds to express honest signals to potential mates (Searcy et al. 2006) and provide population information to conservationists (Lewis et al. 2020). These findings support previous research that shrubs are valuable to migrating birds in the spring when they are seeking new territories (Lima 2009) and that perching sites are used differently for foraging and territorial displays (Collins 1981; Beck and George 2000). The expression of these behaviors is necessary for birds to maintain social connections and territories, both of which are important for bird reproductive success (Wilkins et al. 2013; Cooney et al. 2018).

Habitat heterogeneity, being a distinction between microsites along a niche dimension, was observed as important for bird community composition. Open and cactus microhabitats supported some birds though to a much lesser extent than shrubs in both spring and summer and were functionally equivalent. Abiotic factors such as ultraviolet radiation, water scarcity, and heat are more intense in summer, which accounts for the lower diversity of many vertebrate species in open microhabitats in deserts (Koyama 2015). However, we observed some birds at cacti and open microhabitats, which can provide seeds and nest sites to birds (Simons and Martin 1990; Kelt et al. 2004). For example, when seeds and fruit begin to drop beneath the canopy of the mother plant, seed predators (i.e. granivorous birds) forage for these trophic resources (Racskó et al. 2007; Janzen 1970); but this is equally common in open areas (Milesi et al. 2019). However, summer foraging at open sites was not observed in this study, and thus is likely not a reasoning for desert birds to be in open sites. Additionally, ground nesting is obligatory for some desert bird species, and species can nest in the open and not under canopies in deserts (Kozma and Mathews 1997). Cacti provide cover from predators and unique nesting habitat to birds like the Cactus Wren and the Black-throated Sparrow, as well as many other vertebrates (Kozma and Mathews 1997). While cacti can provide these services to many species, the family Cactaceae is morphologically diverse (Boke 1980) and unique cactus species thus provide functionally different opportunities for animals. Because many positive interactions are species-specific (Filazzola et al. 2020; Callaway 1998; Bonanomi et al. 2011), my findings that cacti were not any more valuable to birds than open microhabitats may be different in other desert communities. For example, perch height differences are important determinants for bird perch use (Portugal et al. 2017; Polak 2014). The higher level of bird diversity at one particular microhabitat (i.e. shrubs) thus does not exclude the value other microhabitat types, but instead suggests that, even in times of trophic resource abundance such as spring, ecosystem heterogeneity is important for many species within a desert bird community. Indeed, the importance of cacti for birds in regions with other dominant cactus species has been well-documented (Drezner 2014). Bird species richness has recently been linked to habitat heterogeneity throughout many ecosystems (Farwell et al. 2020), though my study supports these findings at an even finer scale. Ultimately, diverse plant microhabitats across a landscape support diverse bird communities.

While spring shrubs offer stopover refuge for migrating birds and perches for territorial displays, summer also brings certain resources to bird communities. During summer, there is increased fruit production for frugivorous birds in many ecosystems (McGrath et al. 2009), and this is true at my study site as well. Despite these benefits of summer, the intense environmental conditions previously mentioned often result in a decrease in bird diversity from spring to summer in deserts (Tonkin et al. 2017; Boyles et al. 2017; Geiser and Ruf 1995), and thus a fewer number of bird individuals in summer was expected. Indeed, open microhabitats in summer became nearly vacant in regard to species richness and diversity. Increased seasonal temperatures in summer pressure birds to avoid hotter areas in the open, as has been documented among other vertebrates (Ivey et al. 2020). Open gaps between vegetation in deserts are particularly harsh for animals and plants due to increased seasonal temperatures (Ivey et al. 2020; Lortie et al. 2016; Smith et al. 2018), and this decrease in bird richness and diversity from spring to summer suggests that temperatures at fine scales can be an environmental limitation for bird communities (Barrientos et al. 2007). Changes in biodiversity due to the arrival and departure of migratory species (in addition to anthropogenic impacts) have been shown to influence resident species' success in reproduction and resource acquisition (Cox 1968; Greenberg et al. 1993; Ramírez-Cruz et al. 2020). My study supports previous work that has clearly documented avoidance by vertebrates of open gaps in desert summer landscapes.

Season and microhabitat influenced species richness and diversity, but bird abundance was not different by season and microhabitat. This may be due to the presence of several generalist species which dominate the desert bird community, the most common in this study being the Black-throated Sparrow. Because generalists may associate with multiple microhabitats more than specialists which obligately associates with different microhabitats across a heterogeneous landscape, this may inflate the number of individuals at a site only amenable to a generalist. Generalist birds have thrived as invasive, non-native species across the globe, with high counts of generalists found throughout many homogenous environments (Chace and Walsh 2006; Schneiberg et al. 2020; Vallejos et al. 2016). Trends among bird community composition in this heterogenous ecosystem did not shift when I excluded this common species. The preservation of the importance of shrubs in spring for the entire bird community after these exclusion analyses showed that foundation plant microhabitats are important to the bird community at large, not just for a common species.

Future Directions, Implications, and Conclusions

The reproductive output of plants can influence bird visitation. Different floral syndromes (such as flower number, scent, color, and height) determine pollinator visitation for animal-pollinated plants (Faegri and van der Pijl 1979), and fruit production is connected with endozoochoric seed dispersal (Gelmi-Candusso et al. 2017). However, these studies frequently focus solely on the reproductive success of plants and not the success of the nectarivore or frugivore. Birds are not only the beneficiaries in bird-plant interactions, but they can provide service to foundation plants by distributing seeds in areas surrounding their perch (Holl 1998). Understanding how birds provide reproductive services to foundation plants will further advance how habitat is maintained and created by plants. Thus, research that is able to both document association patterns and better estimate reciprocity will help conservationists make predictions about how certain restoration efforts will indirectly impact other taxa.

Future work can also examine the importance of structural characteristics for bird communities. Benefactor rocks have been shown to facilitate plants and provide habitat for desert birds (Peters et al. 2008; Warning and Benedict 2015). Plant architecture, i.e. the nature and relative arrangement of a plant's parts (Barthélémy et al. 2007), has already been documented as important for bird communities, and should be examined in desert ecosystems more fully. Perch height is an important influencer of bird aggression, and thus plant and branch height should continue to be explored. Anthropogenic development of the American Southwest has provided an abundance of structures that may be beneficial to birds, such as fence posts and solar panels (Prather and Messmer 2010). However, these artificial structures may have negative implications such as the loss of seed dispersal over a landscape as birds over-use towers and poles. Careful attention should be paid to comparisons between these natural and non-natural or biotic and abiotic structures to see what native species are restored through these interactions and how they are mixed, locally.

Environmental managers and conservationists must make restoration decisions regarding planting, genetic management, and distribution of expensive resources like seeds, seedlings, and fencing (among other things) to support plant growth (Aavik and Helm 2018). Commonly, managers may resort to planting one easily accessible plant species that is functionally similar to a rarer plant to provide microhabitat at lower costs and effort (Holl and Howarth 2000). However, birds (and likely other vertebrate species) require a range of microhabitats in environments with varying degrees of stress and varying types of pressures so as to exclude competitors; for successful, community-wide restoration efforts, this shifting range of needs must be fully considered. By protecting current plant diversity and investing in a diverse set of plant microhabitats when restoring degraded habitat, managers may better protect bird communities which rely on habitat heterogeneity.

Figures & Tables

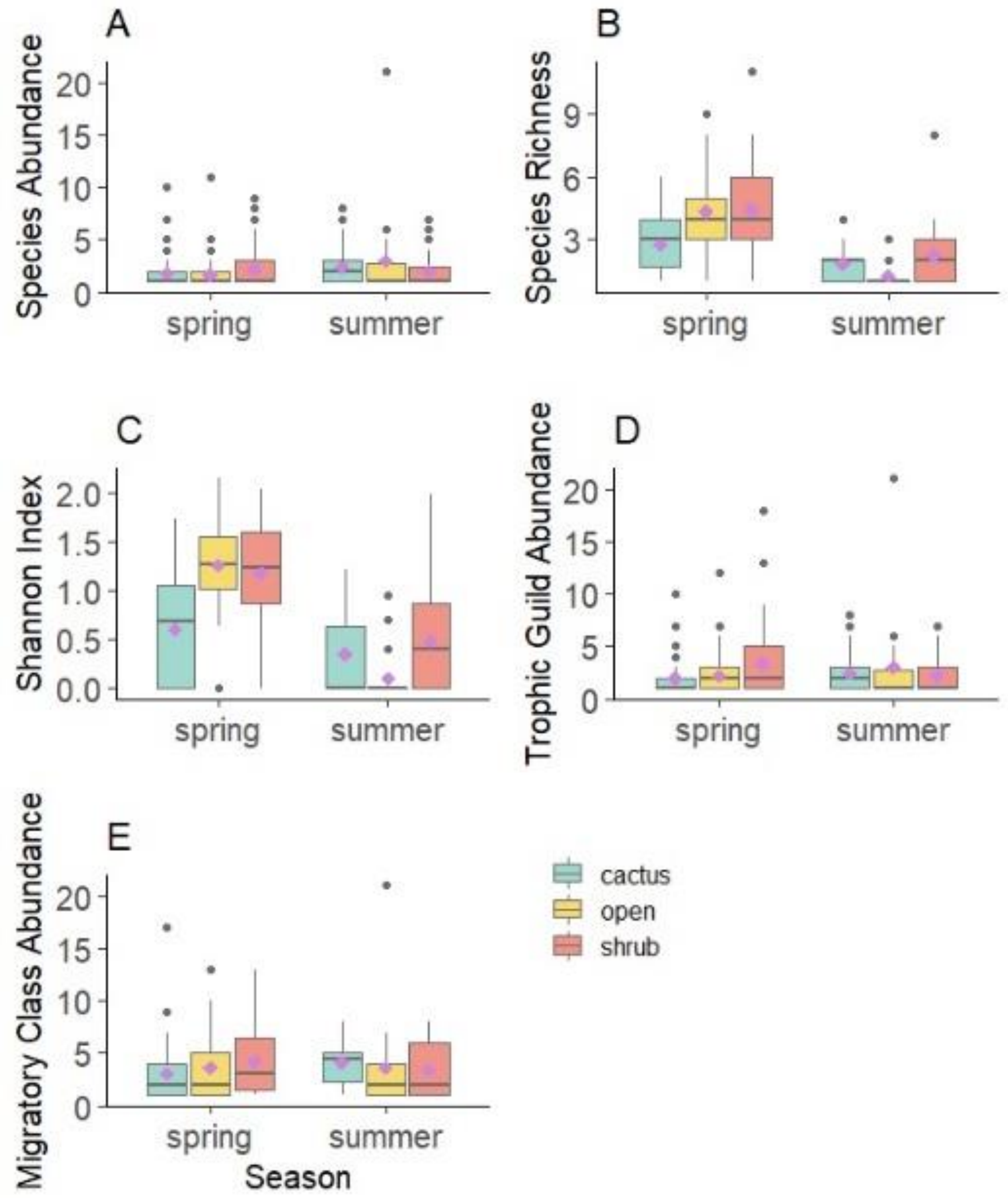

Figure 1: Comparative Boxplots of (A) species abundance, (B) species richness, (C) species diversity as the Shannon Index, (D) trophic guild abundance, and (E) migratory class abundance of all visually observed birds at either cacti, shrub, or open microhabitats in both spring (N=27)

and summer (N=20). Purple diamonds represent the means value among surveys of each bird community metric. Shrubs in spring had the highest species richness (p = 0.024) and species diversity (p < 0.0001) relative to all other seasonal microhabitats.

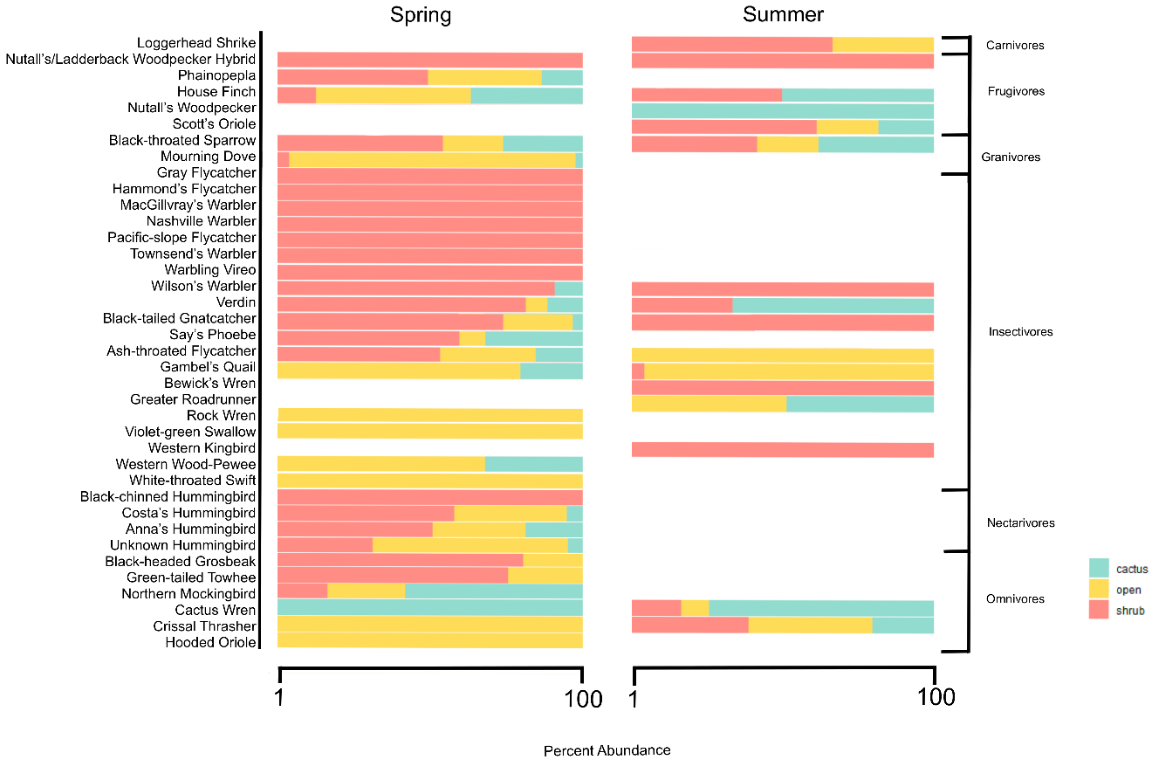

Figure 2: Species frequency as a percent of all observed avian species at cactus, shrub, and open microhabitats during spring and summer. More species and more individuals were present in

spring than in summer, with community variation being explained by a fewer number of species in summer than in spring.

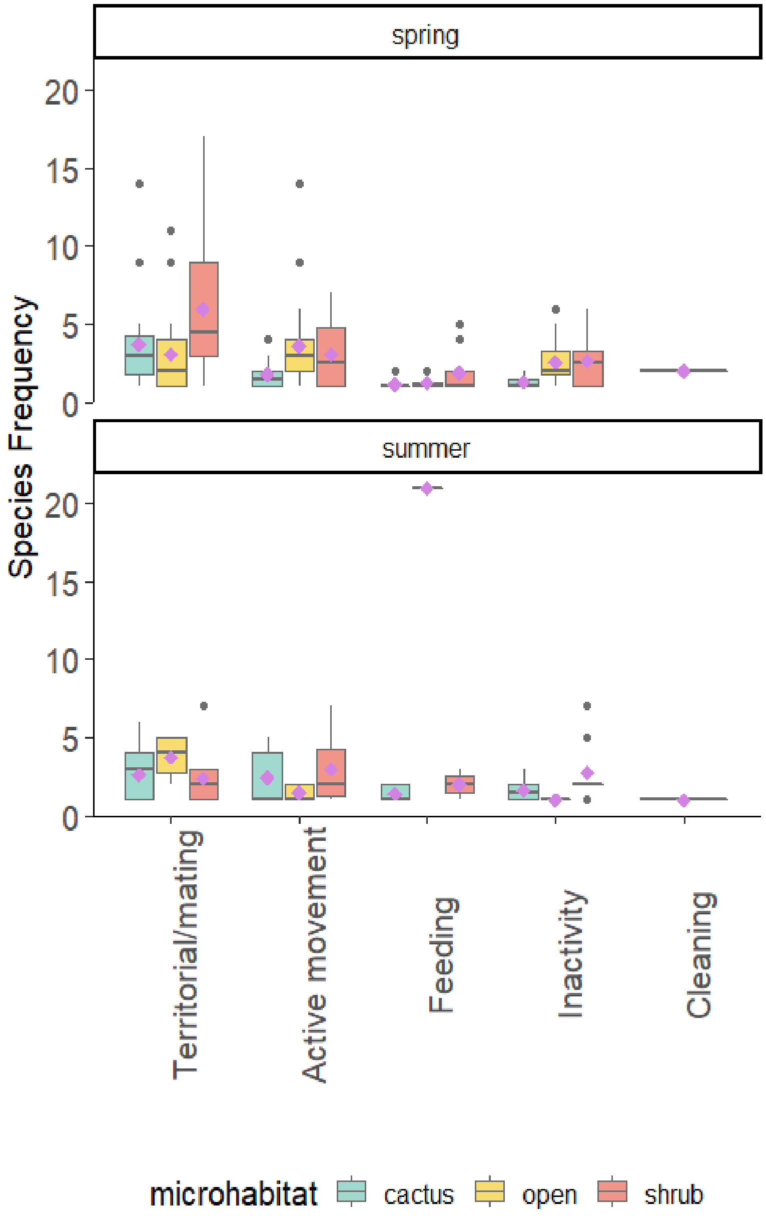

Figure 3: Comparative boxplots of the frequencies of behaviours exhibited by birds at cactus, shrub, and open microhabitats during spring and summer. The purple diamonds represent mean

frequencies of each behaviour with survey as the level of replication. The most common behaviour exhibited at a single seasonal microhabitat was territorial/mating behaviours at spring shrubs ($p < 0.0001$).

Table 1: General linear models testing the responses taxonomic abundance, richness, and Shannon Diversity index to three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer). Bold values show statistically significant models.

Measure	Effect	d.f.	Deviance Residuals	P-value
Species Abundance (A)	Microhabitat	2	3.3587	0.3618
	Season	1	4.9182	0.0845
	Microhabitat x Season	**2**	**12.1427**	**0.0254**
	Survey	0	0	-
	Temperature	0	0	-
Species Richness (S)	**Microhabitat**	**2**	**23.528**	**0.0071**
	Season	**1**	**121.103**	**<0.0001**
	Microhabitat x Season	**2**	**22.262**	**0.024**
	Survey	0	0	-
	Temperature	0	0	-
Shannon Index (H)	**Microhabitat**	**2**	**5.0558**	**0.0036**

Season	**1**	**26.459**	**<0.0001**
Microhabitat x Season	**2**	**8.0337**	**0.0001**
Survey	0	0	-
Temperature	0	0	-

Table 2: General linear models testing function diversity metrics for bird communities, as defined by bird trophic guild and migratory class between three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer). Bold values show statistically significant models.

Measure	Effect	d.f.	Deviance Residuals	P-value
Trophic Guild				
Abundance	**Microhabitat**	**2**	**14.6185**	**0.0363**
	Season	1	0.1855	0.7718
	Microhabitat x Season	**2**	**16.5826**	**0.0233**
	Survey	0	0	-
	Temperature	0	0	-

Migratory Class Abundance	Microhabitat	2	2.7772	0.6178
	Season	1	0.032	0.916
	Microhabitat x Season	2	6.6078	0.318
	Survey	0	0	-
	Temperature	0	0	-

Table 3. General linear model testing for differences in behaviour frequency at three different microhabitats (shrub, cactus, and open sites) between two different seasons (spring and summer). Bold values show statistically significant models.

Measure	Effect	d.f.	Deviance Residual	P-value
Behaviour Abundance	**Microhabitat**	**2**	**20.282**	**0.0012**
	Season	1	5.133	0.0642
	Behaviour	**4**	**44.712**	**<0.0001**
	Microhabitat x Season	2	4.011	0.2624
	Microhabitat x Behaviour	**6**	**25.668**	**0.0088**

Season x Behaviour	**4**	**33.332**	**0.0002**
Microhabitat x Season x Behaviour	**6**	**45.038**	**<0.0001**
Survey	0	0	-
Temperature	0	0	-

Table 4: The main hypothesis was tested using general linear models that include all species observed during line transect surveys. Species abundance, richness, or diversity were used metrics for taxonomic community structure dependent variables while trophic guild and migratory class abundance represented functional diversity metrics for community structure dependent variables.

Model	R Code
Species abundance at different seasonal microhabitats	glm(counts~microhabitat*season + (1 |survey) + (1|temp), family = quasipoisson, data = data_species)
Species richness at different seasonal microhabitats	glm(richness~microhabitat*season + (1 |survey) + (1|temp), family = gaussian, data = data_richness)

Shannon Index at different seasonal microhabitats	glm(shannon~microhabitat*season + (1 |survey) + (1|temp), family = quasipoisson, data = data_diversity
Species abundance of different behaviours at different seasonal microhabitats	glm(totals~microhabitat*season*behaviour_simple + (1|survey) + (1|temp), family = quasipoisson, data = data_behaviour)
Trophic guild abundance at different seasonal microhabitats	glm(counts~microhabitat*season + (1 |survey) + (1|temp), family = quasipoisson, data = data_trophic)
Migratory class abundance at different seasonal microhabitats	glm(counts~microhabitat*season + (1 |survey) + (1|temp), family = quasipoisson, data = data_migratory)
Black-throated Sparrow abundance at different seasonal microhabitats	glm(counts~microhabitat*season*behaviour_simple + (1|survey) + (1|temp), family = quasipoisson, data = data_sparrow)

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Appendices

Appendix A: Site Map

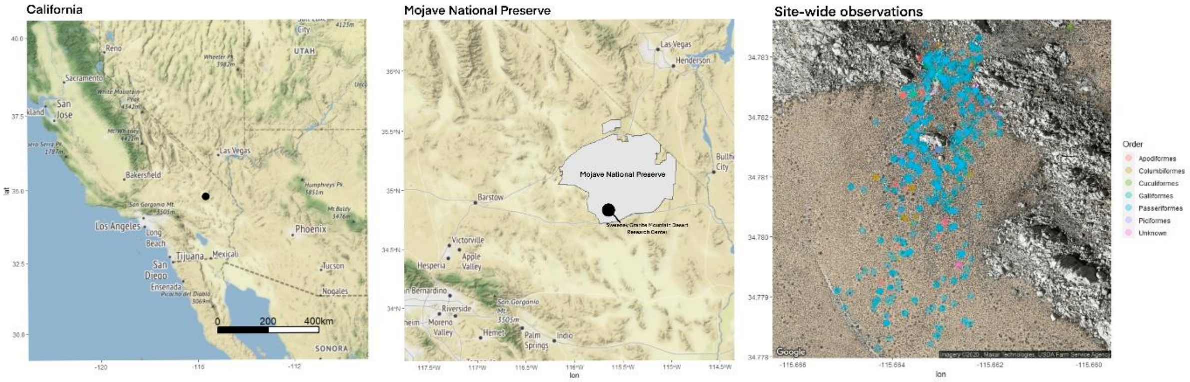

Figure 4: Maps of American southwestern region, Mojave National Preserve, and study sit4e with all observations group by taxonomic order. Passiformes dominated this study (Kahle and Wickham 2013; Mojave National Preserve Tract and Boundary Data 2019).

Appendix B: Species, trophic guild, and migratory class lists of all observation bird species and their frequencies throughout both seasons.

Table 5: Excluding unidentifiable birds, 39 distinct species were observed in spring and summer 2019 at the Granite Mountains site. In total, 755 individual birds were visually observed, 539 in spring and 216 in summer.

Bird Species	Spring Abundance	Summer Abundance
Anna's Hummingbird	10	0
Ash-throated Flycatcher	23	1

Bewick’s Wren	0	3
Black-chinned Hummingbird	1	0
Black-headed Grosbeak	5	0
Black-tailed Gnatcatcher	18	2
Black-throated Sparrow	144	131
Blue-gray Gnatcatcher	65	6
Cactus Wren	1	11
Costa’s Hummingbird	14	0
Crissal Thrasher	1	5
Gambel’s Quail	9	22
Gray Flycatcher	3	0
Greater Roadrunner	0	2
Green-tailed Towhee	4	0
Hammond’s Flycatcher	1	0
Hooded Oriole	1	0
House finch	9	0
Loggerhead Shrike	0	3

MacGillivray’s Warbler	2	0
Mourning Dove	25	0
Nashville Warbler	1	0
Northern Mockingbird	36	0
Nuttall’s Woodpecker	0	1
Nuttall’s/Ladderback Woodpecker Hybrid	1	1
Pacific-slope Flycatcher	2	0
Phainopepla	33	0
Rock Wren	36	0
Say’s Phoebe	12	0
Scott’s Oriole	0	5
Townsend’s Warbler	3	0
Verdin	18	9
Violet-green Swallow	9	0
Warbling Vireo	1	0
Western Kingbird	0	1
Western Wood-pewee	3	0

White-throated Swift	18	0
Wilson’s Warbler	9	1
Unknown Hummingbird	16	0
Unknown Passerine	1	1
Unknown	7	0

Table 6: Migratory classes of all visually observed birds were mostly residents in both seasons..

Migratory Class	Spring Abundance	Summer Abundance
Migrant	30	1
Resident	358	201
Summer resident	143	13
Unknown	8	1

Table 7: Trophic guilds of all visually observed birds were most commonly granivores and insectivores in spring and summer.

Trophic Guild	Spring Abundance	Summer Abundance
Carnivore	0	3

Frugivore	44	4
Granivore	169	131
Herbivore	9	22
Insectivore	221	34
Nectarivore	41	0
Omnivore	47	21
Unknown	8	1

Appendix C: Bird Ethogram

Table 8: Ethogram of bird behaviours observed during surveys.

Behaviour	Description
Eating Fruit	Eating part or whole of fruit from plant
Pollinating Flower	Body part (usually head or bill) sticks into flower and moves to a new flower on same or different plant
Building nest	Constructing nest at the location of nest site
Occupied nest	Sitting on nest
Carrying nest materials	Finding twigs, grass, hair, etc. and carrying in mouth to different location

Preening	Using bill to clean feathers
Singing	Individual vocalizing for that species song
Calling	Individual vocalizing, but is not the species song
Distraction Display	Individual attempting to lure predator (may be observer) away from nest, often feigning injury or aggressive behaviour
Copulation	Male mounts female, may be very quick
Foraging	Searching for food, eating in place where food is found.
Sparring	Displaying aggressive behaviour towards another bird
Fleeing	Moving away from predator (may be observer) in a sudden fashion (not casually moving)
Courtship Display	Male displaying for female in physical display (not just singing)
Feeding young	Feeding nestlings (usually regurgitation).
Carrying food	Taking food from one place to another, distance greater than 5 meters
Flying on plant	Flying to multiple branches on same plant
Flying between plants	Flying from one plant to another without landed on ground
Flying	Flying from one point to another

Standing on Plant	Standing without feet leaving same location, on top of a plant that supports weight of bird
Standing on Ground	Standing without feet leaving same location, on ground (ok if grass/small plants between bird and ground)

Appendix D: Black-throated Sparrow Exclusion Results

Table 9: Statistical output for general linear models testing taxonomic abundance, richness, and diversity at three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer) when Black-throated Sparrows, the most commonly observed bird species, was excluded. These results are consistent (though not identical) with analyses including Black-throated Sparrows.

Measure	Effect	d.f.	Deviance Residuals	P-value
Species Abundance (A)	Microhabitat	2	3.1512	0.2832
	Season	1	0.0029	0.9617
	Microhabitat x Season	**2**	**18.0492**	**0.0007**
	Survey	0	0	-
	Temperature	0	0	-

Species Richness (S)	**Microhabitat**	**2**	**10.2451**	**0.0027**
	Season	**1**	**28.2986**	**<0.0001**
	Microhabitat x Season	2	2.433	0.2446
	Survey	0	0	-
	Temperature	0	0	-
Shannon Index (H)	**Microhabitat**	**2**	**6.018**	**0.0039**
	Season	**1**	**37.884**	**<0.0001**
	Microhabitat x Season	**2**	**5.2**	**0.0083**
	Survey	0	0	-
	Temperature	0	0	-

Appendix E: Non-metric Multidimensional *Scaling and PERMANOVA Results*

Figure 5: Non-metric Multidimensional Scaling of bird communities at seasonal microhabitats. Seasonal microhabitat communities were not statistically distinct from any other seasonal microhabitat communities within the first dimension (x-axis) or second dimension (y-axis).

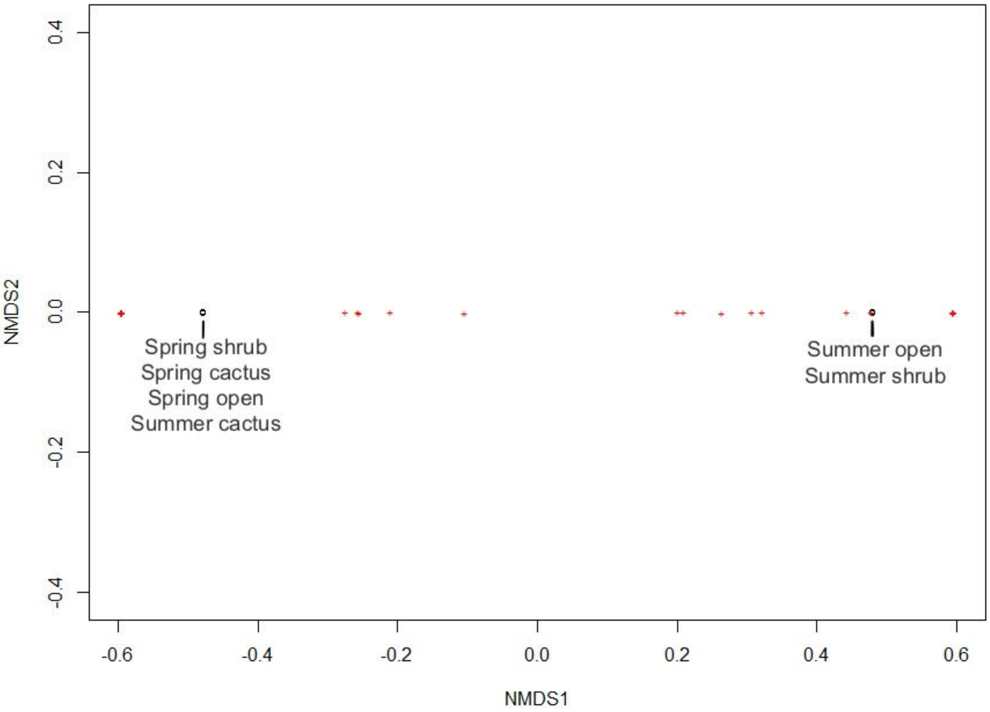

Table 10: A PERMANOVA of bird community NDMS scores by season and microhabitat.

Effect	DF	Sum of Squares	Mean Squares	F Value	R^2	p-value
Microhabitat	2	0.2078	0.1039	1.4983	0.00794	0.226
Season	1	0.0893	0.0892	1.2869	0.00342	0.239

Microhabitat x Season	2	0.2212	0.1056	1.5225	0.00807	0.178
Residuals	370	25.6625	0.0694	-	0.98058	