**Foundation plants enhance avian community diversity: examining resource provision and habita heterogeneity.**

Malory Owen[[1]](#footnote-1), Christopher J. Lortie1, and Nargol Ghazian1\*

1Department of Biological Science, York University, 4700 Keele St, Toronto, ON M3J 1P3, Canada

\*Corresponding Author: Department of Biological Science, York University, 4700 Keele St, Toronto, ON, M3J 1P3, Canada. Email: [nargolg1@my.yorku.ca](mailto:nargolg1@my.yorku.ca)

# Abstract

Habitat heterogeneity is often a critical determinant of animal community composition and structure in some systems. Plants can increase habitat heterogeneity and resources for animal communities through provision of habitat, structure, and resources. However, interactions with plants can be species and life-stage specific. Here, we tested the hypothesis that foundation plant species, specifically cacti and shrubs, facilitate avian communities by providing structural complexity relative to open microsites. We used line transects to record habitat associations of birds at a protected site in the Mojave Desert, CA, USA. We found that the bird biodiversity and behaviour were not equally represented across all microhabitats or seasons. Diversity and evenness of the bird communities and territorial behaviors were significantly greater at shrubs microhabitats in spring. However, in the summer the diversity of birds was greater at cacti than in the open. Hence, seasonal timing is also an important component of the facilitative functions provided by foundation plants for bird communities in deserts. This study suggests that non-trophic interactions with plants in addition to direct resource provision are also important ecological mechanisms for maintaining local bird diversity in deserts.

**Keywords:** Arid, bird, cacti, community, desert, diversity, facilitation, foundation species, habitat heterogeneity, microhabitat, mutualism, positive interactions, shrubs.

# Introduction

Positive interactions are amongst some of the most important forms of ecological interactions across communities. Interactions such as 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 of associated species (Bertness and Callaway 1994; Bruno et al. 2003). 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). 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 are relatively limited when compared with plant-plant studies with most studies examining hypotheses that supported the function of shrubs as seed traps for beneficiary animals (Lortie et al. 2016). In the more specific example of bird-plant interactions, plants aid birds in foraging and defining their territory (Wiens 1973; Craig 1990; Devereux et al. 2000; Longland and Price 1991). All of these trophic and non-trophic interactions are ecologically relevant for desert bird species; however, the relative frequency of these interactions within a given system or for a specific community is not well documented.

In many ecosystems, including deserts, plants are foundation species. Foundation species are often benefactors that facilitate other species within an ecosystem using some or all of the mechanisms previously described including habitat provision, complexity, shelter, and direct resource provision (Angelini et al. 2011; Almeida and Mikich 2018). 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 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 variations are stressful for many species in the ecosystem (Siegal et al. 2013). 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. The species specificity of positive interactions is also an important ecological issue (Callaway 1998; Villarreal-Barajas and Martorell 2009) because we need to know whether the benefits are generic and thus more easily restored and managed or specific to certain foundation species.

Birds are able to be used 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). Birds also typically respond to the environmental changes with seasonal shifts - at times by migrating (Salewski and Bruderer 2007). Secondly, the timing of life cycles 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), and specifically, floral and fruiting timing of plants (Schwartz 2003; Beatley 1974; Jordan and Nobel 1982; Nobel and Hartsock 1981) is necessary for the success of birds during migration breeding seasons (Sillett and Holmes 2002; Runge and Tulloch 2017; Fahse et al. 1998). Thus examining the avian community provides a means to decouple pathways of animal-plan positive interactions and provides insight into temporal and seasonal variations that can influence these dynamics.

Climate change can introduce many novel drivers of change in natural systems and exacerbate existing challenges to local biota. 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). Furthermore, if positive effects are specific to certain functions provided by species or even their unique architecture, then their loss can ultimately translate to the loss of the associated taxa. 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). Additionally, the effects of extreme heat and drought on the avian community in the United States is not well understood (Albright et al. 2010). Many of these threatened interactions are species-specific and thus cannot be restored after their disappearance (Valiente-Banuet et al. 2015), and our study hence provides a framework for determining benchmarks for bird-plant interactions in desert ecosystems.

In this study, two common desert foundation plant species and the resident avian community were examined to explore the relative importance, specificity, and sensitivity of avian associations by behaviour with these dominant plants. We 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. We 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 are 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.

# Materials & 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 (Supplemental material A, Fig. 1). 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. Rainfall varies significantly throughout the year with a mean annual precipitation ranging from 34 to 310 mm per year (Urban et al. 2009). Typically, there is limited to no precipitation in the summer months. The July maximum and minimum temperatures are 33 C and 20 C respectively. 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”; 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 our 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, all three foundation species were fruitings.

## **Experimental Design**

A total of 27 surveys from 5/1/2019 to 5/10/2019 for spring observations and 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 7-10 am or 5-8 pm, 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. Most non-shrub or non-cactus spaces constituted a relatively open microhabitat, this included some vegetative areas. However, none of these open gaps had the level of heterogeneity that shrubs or cacti provide to their open surroundings. We recorded behaviour using an a priori design ethogram to classify observations (Supplemental material C Table 8). Microhabitat, geographic coordinates, and the time of the sighting/hearing were also recorded. We only included visual observations of birds in microhabitat and behavioural analyses as birds that were heard but not seen could not be documented at any microhabitat, and birds may have been exhibiting behaviors that should be prioritized over singing or calling as defined by the ethogram; though, these behaviors could not be observed. Flyovers (defined as birds flying roughly 25 feet above the highest vegetation at the site that did not land within sight) were not included as observations

## **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. We 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 are defined in this study as the number of individuals represented in each species, trophic guild, or migratory class. Species richness 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 that accounts for rare species, more so than Simpson’s Diversity which more heavily incorporates species evenness. We then compared contrasted terms using estimated marginal means with the *emmeans* function (Lenth and Herve 2019) in R Version 4.0.2 (R Development Core Team 2020). We repeated these analyses excluding the Black-throated Sparrow, which made up ~36% of observations to ensure that this abundant species was not unduly influencing detected outcomes. We also used a Non-metric Multidimensional Scaling analysis followed by a PERMANOVA (Legendre and Legendre 1998) to explore the influence of season on community composition and associations.

All code is published on Zenodo (Owen and Lortie 2020a). Photo documentation of birds is published at Figshare (Owen 2020), and a complete dataset of bird observation is published in the Knowledge Network for Biocomplexity Data Repository (Owen and Lortie 2020b).

# Results

A total of 755 birds were observed and an additional 467 bird calls were recorded during both seasons for a cumulative number of 1222 bird records over a an entire duration of 94 hours. Birds that were not seen were excluded because these instances could not be classified by microhabitat or behaviour. During the spring, 539 individual birds were visually observed, and 216 birds were visually observed in summer. Thus, there were significantly more individual birds observed in spring than in summer (Fig. 1; Table 1; post-hoc contrast at p = 0.0327).

Avian communities associated with shrubs in spring were the most species-rich and diverse (Fig. 1; Table 1; GLM richness; p = 0.024; post-hoc contrast at p = 0.0144; GLM Shannon index; p = 0.0001; post-hoc contrast at p = 0.0038). Open microhabitats in summer had the lowest bird species richness and biodiversity across all census periods (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 lowest at open microhabitats in spring (Fig. 1; Table 1; GLM; p = 0.0254; post-hoc contrast at p = 0.0327). All iterative analyses findings were robust that excluded the Black-throated Sparrow (Supplemental material 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 (Supplemental Material E Table 10 and Figure 4; PERMANOVA; F2 = 1.523; R2 = 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 we 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); thus, there was no termporal effect for these factors.

# Discussion

Plant-animal interactions in deserts provides a key means to better understand community assembly patterns in many ecosystems such as deserts. The hypothesis that foundation plant species provide non-trophic, i.e. not resource-driven, benefits to the resident bird communities was supported in the Mojave Desert. The two ecological contexts that we predicted to influence positive outcomes for birds including species and seasonal specificity were also supported suggesting that these dynamics are consistent but warrant deeper examination. Avian species richness, diversity, 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 foundation plant species effects are species-specific at a given site within a region, or that different species of birds use these habitats differently, and uniquely influence community composition (Ellison 2019). Foundation plants change community structure by modifying community assembly and generally support a higher α-diversity and a larger species pool relative to the open-gap (Kikvidze et al. 2015). Both mechanisms were likely relevant drivers of the observed bird-plant association patterns in this system. Additionally, the mean frequencies of behaviours varied both by season and by microhabitat. Benefits estimated through observed behaviors were primarily non-trophic such as using plants for structural purposes as we observed increased territorial displays at shrubs in the spring. Thus, foundation species are structural agents of facilitation that aid in increasing the diversity of the local avian community but interactions with these microhabitats differ seasonally.

Habitat heterogeneity, being fine-scale differences of habitats between microsites, revise was observed as important for bird community composition. Open and cacti microhabitats supported some birds though to a much lesser extent than shrubs in both spring and summer. 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 reason for desert birds to be in open sites. While cacti can provide services like cover from predator and nesting sites to many species (Kozma and Mathews 1997), the family Cactaceae is morphologically diverse (Boke 1980) and unique cactus species thus provide functionally different opportunities for animals. The importance of cacti for birds in regions with other dominant cactus species has been well-documented (Drezner 2014). Furthermore, the use of vegetation where the structure is conducive to cooler temperatures is an important driver of habitat selection by birds, particularly during the warmest of days (Kline et al. 2019). Our findings suggest that it is hence not one or the other (shrub or cacti) that enhances community assembly, but in fact, it is the existence of both species in the area, as well as the open-gap, even in times of trophic resource abundance such as spring that contributes to heterogeneity and heterogeneity itself is crucial for the maintenance of biodiversity in arid ecosystems. Good but could use one more edit for simplicity and direct writing if you have the mojo still Nargol :)

Resource availability through summer fruits 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 such as for perching sites as territorial displays. Territorial displays allow birds to express honest signals to potential mates (Searcy et al. 2006) and provide population key information to conservationists such as reproductive status and population viability? (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). Birds likely associate more with foundation plants as they possibly provide structural resources through architecture, shade, branching, height, spatial continuity, or even the presence of some animals near them and not other species. Future work could 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 stress in desert ecosystems is likely to increase in future. Temporal environmental fluctuations influence bird diversity from spring to summer in deserts (Tonkin et al. 2017), and thus the decrease in bird individuals in summer was expected. 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). This study supports other published work that has clearly documented avoidance by vertebrates of open gaps in desert summer landscapes. This suggests that birds likely used foundation species structure as perches and shade to avoid experiencing the peak of environmental stressors, including temperature and solar radiation. Shelter by foundation plant species is thus a critical form of habitat for avian communities in these ecosystems and is species specific.

Environmental managers and conservationists must make restoration decisions regarding planting, genetic provenance for restoration, and distribution of limited resources like seeds, seedlings, and fencing (amongst other things) to support plant growth (Aavik and Helm 2018). Developing spatial tools for seed-sourcing for keystone species is also a critical decision in drylands (Shryock, DeFalco, and Esque 2018). Commonly, managers establish 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 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 habitats, managers may better protect bird communities, which rely on habitat heterogeneity.

**Acknowledgments**

We gratefully thank the Sweeney Granite Mountains Desert Research Station team, Jim André, and Tasha La Doux for providing safe and accessible accommodations and field sites, as well as their input on conditions, timing, and experimental design. Thank you as well to Anza-Borrego Foundation for providing support through the Paul Jorgensen Bird Research Grant. CJL was supported by an NSERC and NG and MO were supported by FGS funding from York University. The authors declare no conflicts of interest.

**Author’s Contributions**

CJL and MO conceived the ideas and the experimental design; MO collected the data; MO analyzed the data with input from CJL; MO led the writing on the manuscript; NG and CJL thoroughly edited the manuscript and contributed critically to drafts for publication.

**Data Availability**

The dataset of bird observation is published in the Knowledge Network for Biocomplexity Data Repository: Owen, M., and C. Lortie. 2020c. Mojave Desert Bird Microhabitat and Behavioral Line Transect Observations. All other codes and data are publicly available on Zenodo and Figshare: Owen, M., and C. Lortie. 2020a. Mojave Desert Bird Survey Photos 2019; Owen, M., and C. Lortie. 2020b. Desert Bird Microhabitat Associations Analyses.

**Literature cited**

Aavik, T., and A. Helm. 2018. Restoration of plant species and genetic diversity depends on landscape-scale dispersal. Restoration Ecology 26:S92–S102.

Albright, Thomas P., Anna M. Pidgeon, Chadwick D. Rittenhouse, Murray K. Clayton, Brian D. Wardlow, Curtis H. Flather, Patrick D. Culbert, and Volker C. Radeloff. 2010. “Combined Effects of Heat Waves and Droughts on Avian Communities across the Conterminous United States.” *Ecosphere* 1 (5): art12. https://doi.org/10.1890/ES10-00057.1.

Almeida, A. de, and S. B. Mikich. 2018. Combining plant–frugivore networks for describing the structure of neotropical communities. Oikos 127:184–197.

André, J. M. 2006. Vascular flora of the Granite Mountains. Crossosoma 32:38–74.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation. BioScience 61:782–789.

Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313–318.

Barrientos, R., A. Barbosa, F. Valera, and E. Moreno. 2007. Temperature but not rainfall influences timing of breeding in a desert bird, the trumpeter finch (Bucanetes githagineus). Journal of Ornithology 148:411–416.

Barthélémy, D., and Y. Caraglio. 2007. Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Annals of Botany 99:375–407.

Beatley, J. C. 1974. Effects of Rainfall and Temperature on the Distribution and Behavior of Larrea Tridentata (Creosote-Bush) in the Mojave Desert of Nevada. Ecology 55:245–261.

Beck, M. J., and T. L. George. 2000. Song Post and Foraging Site Characteristics of Breeding Varied Thrushes in Northwestern California. The Condor 102:93–103.

Bergamo, P. J., N. Susin Streher, A. Traveset, M. Wolowski, and M. Sazima. 2020. Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. Ecology Letters 23:129–139.

Berger, K. M., E. M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. Ecology 89:818–828.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80:2711–2726.

Boke, N. H. 1980. Developmental Morphology and Anatomy in Cactaceae. BioScience 30:605–610.

Bowers, J. E., and M. A. Dimmitt. 1994. Flowering Phenology of Six Woody Plants in the Northern Sonoran Desert. Bulletin of the Torrey Botanical Club 121:215–229.

Braun, J. 2018. Pollinator-mediated interactions of foundation plants in the mojave desert. PhD thesis, York University.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802.

Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112:143–149.

Callaway, Ragan M. 1998. “Are Positive Interactions Species-Specific?” *Oikos* 82 (1): 202.

Callaway, R. M. 2007. Positive Interactions and Interdependence in Plant Communities. First. Springer, Dordrecht.

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Carignan, V., and M.-a. Villard. 2002. Selecting Indicator Species to Monitor Ecological Integrity: A Review. Environmental Monitoring and Assessment 78:45–61.

Collins, S. L. 1981. A comparison of nest-site and perch-site vegetation structure for seven species of warblers. Wilson Bull. 93:542–547.

Cooney, C. R., H. E. A. MacGregor, N. Seddon, and J. A. Tobias. 2018. Multi-modal signal evolution in birds: Re-examining a standard proxy for sexual selection. Proceedings of the Royal Society B: Biological Sciences 285.

Cox, G. W. 1968. The Role of Competition in the Evolution of Migration. Evolution 22:180–192.

Craig, R. 1990. Foraging Behavior and Microhabitat Use of Two Species of White-Eyes (Zosteropidae) on Saipan, Micronesia. The Auk 107:500–505.

De Graaf, R. M., N. G. Tilghman, and S. H. Anderson. 1985. Foraging Guilds of North American Birds. Environmental management 9:493–536.

Devereux, C. L., R. Slotow, and M. R. Perrin. 2000. Territoriality and habitat use of fiscal shrikes (Lanius collaris) in South Africa. The Ring 22:95–104.

Donald, P. F., D. L. Buckingham, D. Moorcroft, L. B. Muirhead, A. D. Evans, and W. B. Kirby. 2001. Habitat use and diet of skylarks Alauda arvensis wintering on lowland farmland in southern Britain. Journal of Applied Ecology 38:536–547.

Drezner, T. D. 2014. The keystone saguaro (Carnegiea gigantea, Cactaceae): A review of its ecology, associations, reproduction, limits, and demographics. Plant Ecology 215:581–595.

Ellison, A. M. 2019. Foundation Species, Non-trophic Interactions, and the Value of Being Common. iScience 13:254–268.

Fahse, L., W. R. J. Dean, and C. Wissel. 1998. Modelling the size and distribution of protected areas for nomadic birds: Alaudidae in the Nama-Karoo, South Africa. Biological Conservation 85:105–112.

Filazzola, A., and C. J. Lortie. 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Global Ecology 23:1335–1345.

Gelmi-Candusso, T. A., E. W. Heymann, and K. Heer. 2017. Effects of zoochory on the spatial genetic structure of plant populations. Molecular Ecology 26:5896–5910.

Greenberg, R., D. K. Niven, S. Hopp, and C. Boone. 1993. Frugivory and Coexistence in a Resident and a Migratory Vireo on the Yucatan Peninsula. The Condor 95:990–999.

Gurin, C., T. La Doux, and S. Coe. 2012. Checklist for Birds of the Granite Mountains. Pages 79–84. First. Natural Reserve System University for California.

Harris, J. A. 1916. The Variable Desert. The Scientific Monthly 3:41–50.

He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters 16:695–706.

Henen, B. T., C. C. Peterson, I. R. Wallis, K. H. Berry, K. A. Nagy, K. H. Berry, and K. A. Nagy. 1998. Effects of Climatic Variation on Field Metabolism and Water Relations of Desert Tortoises. Oecologia 117:365–373.

Holl, K. D., and R. B. Howarth. 2000. Paying for restoration. Restoration Ecology 8:260–267.

Iknayan, K. J., and S. R. Beissinger. 2018. Collapse of a desert bird community over the past century driven by climate change. Proceedings of the National Academy of Sciences of the United States of America 115:8597–8602.

Ivey, K. N., M. Cornwall, H. Crowell, N. Ghazian, E. Nix, M. Owen, M. Zuliani, C. J. Lortie, M. Westphal, and E. Taylor. 2020. Thermal ecology of the federally endangered blunt-nosed leopard lizard (Gambelia sila). Conservation Physiology 8:1–11.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104:501–528.

Jordan, P. W., and P. S. Nobel. 1982. Height distribution of two species of cacti in relation to rainfall, seedling establishment, and growth. Botanical Gazette 143:511–517.

Kahle, D., and H. Wickham. 2013. ggmap: Spatial Visualizations with ggplot2. The R Journal 5:144–161.

Kelt, D. A., P. L. Meserve, M. L. Forister, L. K. Nabors, and J. R. Gutiérrez. 2004. Seed predation by birds and small mammals in semiarid Chile. Oikos 104:133–141.

Kline, Holley N., Timothy E. Fulbright, Eric D. Grahmann, Fidel Hernández, David B. Wester, Leonard A. Brennan, and Michael W. Hehman. 2019. “Temperature Influences Resource Use by Chestnut-Bellied Scaled Quail.” *Ecosphere* 10 (2): e02599. https://doi.org/10.1002/ecs2.2599.

Kozma, J. M., L. M. Burkett, A. J. Kroll, J. Thornton, and N. E. Mathews. 2017. Factors associated with nest survival of Black-throated Sparrows, desert-breeding nest-site generalists. Journal of Field Ornithology 88:274–287.

Kikvidze, Zaal, Robin W. Brooker, Bradley J. Butterfield, Ragan M. Callaway, Lohengrin A. Cavieres, Bradley J. Cook, Christopher J. Lortie, et al. 2015. “The Effects of Foundation Species on Community Assembly: A Global Study on Alpine Cushion Plant Communities.” *Ecology* 96 (8): 2064–69.

Kunkel, K. E., L. E. Stevens, S. E. Stevens, and L. Sun. 2013. Regional Climate Trends and Scenarios for the U.S. National Climate Assessment: Part 4. Climate of the U.S. Great Plains.

Landero, J. P. C., and A. Valiente-Banuet. 2010. Species-specificity of nurse plants for the establishment, survivorship, and growth of a columnar cactus. American Journal of Botany 97:1289–1295.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Second editions. Elsevier Science, Amsterdam, The Netherlands.

Lenth, R, and M Herve. 2019. *Emmeans, Estimated Marginal Means, Aka Least-Squared Means.*

(version 1.1.2).

Lewis, R. N., L. J. Williams, and R. T. Gilman. 2020. The uses and implications of avian vocalizations for conservation planning. Conservation Biology 00:1–14.

Longland, W. S., and M. V. Price. 1991. Direct Observations of Owls and Heteromyid Rodents: Can Predation Risk Explain Microhabitat Use? Ecology 72:2261–2273.

Lortie, C. J., A. Filazzola, and D. A. Sotomayor. 2016. Functional assessment of animal interactions with shrub-facilitation complexes: A formal synthesis and conceptual framework. Functional Ecology 30:41–51.

Lortie, C. J., E. Gruber, A. Filazzola, T. Noble, and M. Westphal. 2018. The Groot Effect: Plant facilitation and desert shrub regrowth following extensive damage. Ecology and Evolution 8:706–715.

Macías-Duarte, A., A. O. Panjabi, E. H. Strasser, G. J. Levandoski, I. Ruvalcaba-Ortega, P. F. Doherty, and C. I. Ortega-Rosas. 2017. Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert. Journal of Field Ornithology 88:374–386.

Mammals of the Granite Mountains. (n.d.)..

Milesi, F. A., J. Lopez De Casenave, and V. R. Cueto. 2019. Are all patches worth exploring? Foraging desert birds do not rely on environmental indicators of seed abundance at small scales. BMC Ecology 19:1–17.

Mojave National Preserve Tract and Boundary Data. 2019.. NPS - Land Resources Division.

Morris, E. K., T. Caruso, F. Buscot, M. Fischer, C. Hancock, T. S. Maier, T. Meiners, C. Müller, E. Obermaier, D. Prati, S. A. Socher, I. Sonnemann, N. Wäschke, T. Wubet, S. Wurst, and M. C. Rillig. 2014. Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. Ecology and Evolution 4:3514–3524.

Narango, D. L., D. W. Tallamy, and P. P. Marra. 2017. Native plants improve breeding and foraging habitat for an insectivorous bird. Biological Conservation 213:42–50.

Nobel, P. S., and T. L. Hartsock. 1981. Shifts in the optimal temperature for nocturnal CO2 uptake caused by changes in growth temperature for cacti and agaves. Physiologia Plantarum 53:523–527.

Owen, M., and C. Lortie. 2020a. Mojave Desert Bird Survey Photos 2019.

Owen, M., and C. Lortie. 2020b. Desert Bird Microhabitat Associations Analyses.

Owen, M., and C. Lortie. 2020c. Mojave Desert Bird Microhabitat and Behavioral Line Transect Observations.

Peters, E. M., C. Martorell, and E. Ezcurra. 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (Mammillaria) in the Tehuacán Valley, Mexico. Journal of Arid Environments 72:593–601.

Pinkava, D. J. 1999. Cactaceae Cactus Family: Part Three: Cylindropuntia (Engelm.) Knuth Chollas. Journal of the Arizone-Nevada Academy of Science 32:32–47.

Plessis, K. L. du, R. O. Martin, P. A. R. Hockey, S. J. Cunningham, and A. R. Ridley. 2012. The costs of keeping cool in a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. Global Change Biology 18:3063–3070.

Prather, P. R., and T. A. Messmer. 2010. Raptor and Corvid Response to Power Distribution Line Perch Deterrents in Utah. Journal of Wildlife Management 74:796–800.

R Development Core Team. 2020. *R* (version 4.0.2).

Racskó, J., G. B. Leite, J. L. Petri, S. Zhongfu, Y. Wang, Z. Szabó, M. Soltész, and J. Nyéki. 2007. Fruit drop: The role of inner agents and environmental factors in the drop of flowers and fruits. International Journal of Horticultural Science 13.

Ramírez-Cruz, G. A., I. Solano-Zavaleta, M. Méndez-Janovitz, and J. J. Zúñiga-Vega. 2020. Demographic and spatial responses of resident bird populations to the arrival of migratory birds within an urban environment. Population Ecology 62:105–118.

Runge, C., and A. I. T. Tulloch. 2017. Solving problems of conservation inadequacy for nomadic birds. Australian Zoologist 39:280–295.

Ruttan, A., A. Filazzola, and C. J. Lortie. 2016. Shrub-annual facilitation complexes mediate insect community structure in arid environments. Journal of Arid Environments 134:1–9.

Salewski, V., and B. Bruderer. 2007. The evolution of bird migration–A synthesis. Naturwissenschaften 94:268–279.

Saracco, J. F., J. A. Collazo, and M. J. Groom. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. Oecologia 139:235–245.

Säterberg, T., S. Sellman, and B. Ebenman. 2013. High frequency of functional extinctions in ecological networks. Nature 499:468–470.

Schafer, J. L., E. L. Mudrak, C. E. Haines, H. A. Parag, K. A. Moloney, and C. Holzapfel. 2012. The association of native and non-native annual plants with Larrea tridentata (creosote bush) in the Mojave and Sonoran Deserts. Journal of Arid Environments 87:129–135.

Schwartz, M. D. 2003. Phenology: An integrative environmental science. Pages 1–610. Second. Springer Science+Business Media, New York.

Searcy, W. A., R. C. Anderson, and S. Nowicki. 2006. Bird song as a signal of aggressive intent. Behavioral Ecology and Sociobiology 60:234–241.

Shryock, Daniel F., Lesley A. DeFalco, and Todd C. Esque. 2018. “Spatial Decision-Support Tools to Guide Restoration and Seed-Sourcing in the Desert Southwest.” *Ecosphere* 9 (10): e02453. https://doi.org/10.1002/ecs2.2453.

Siegal, Z., H. Tsoar, and A. Karnieli. 2013. Effects of prolonged drought on the vegetation cover of sand dunes in the nw negev desert: Field survey, remote sensing and conceptual modeling. Aeolian Research 9:161–173.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Simons, L. S., and T. E. Martin. 1990. Food Limitation of Avian Reproduction: An Experiment with the Cactus Wren. Ecology 71:869–876.

Smith, C. J., R. J. Kramer, G. Myhre, P. M. Forster, B. J. Soden, T. Andrews, O. Boucher, G. Faluvegi, D. Fläschner, Hodnebrog, M. Kasoar, V. Kharin, A. Kirkevåg, J. F. Lamarque, J. Mülmenstädt, D. Olivié, T. Richardson, B. H. Samset, D. Shindell, P. Stier, T. Takemura, A.

Villarreal-Barajas, Tania, and Carlos Martorell. 2009. “Species-Specific Disturbance Tolerance, Competition and Positive Interactions along an Anthropogenic Disturbance Gradient.” *Journal of Vegetation Science* 20 (6): 1027–40.

Voulgarakis, and D. Watson-Parris. 2018. Understanding Rapid Adjustments to Diverse Forcing Agents. Geophysical Research Letters 45:12, 023–12, 031.

Smith, F. A. 1995. Den Characteristics and Survivorship of Woodrats (Neotoma lepida) in the Eastern Mojave Desert. The Southwestern Naturalist 40:366–372.

Stewart, G. R., and A. K. Lappin. 2008. Amphibians and reptiles of the Seychelles.

Team, R. C. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Thompson, D. B., J. H. Brown, and W. D. Spencer. 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology 72:852–863.

Tonkin, J. D., M. T. Bogan, N. Bonada, B. Rios-Touma, and D. A. Lytle. 2017. Seasonality and predictability shape temporal species diversity. Ecology 98:1201–1216.

Urban, F. E., R. L. Reynolds, and R. Fulton. 2009. The Dynamic Interaction of Climate, Vegetation, and Dust Emission, Mojave Desert, USA. Pages 1–62 *in* F.-B. A. and M. A. De La Rosa, editors. Arid environments and wind erosion. Nova Science Publishers, Inc.

Valiente-Banuet, A., M. A. Aizen, J. M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M. B. García, D. García, J. M. Gómez, P. Jordano, R. Medel, L. Navarro, J. R. Obeso, R. Oviedo, N. Ramírez, P. J. Rey, A. Traveset, M. Verdú, and R. Zamora. 2015. Beyond species loss: The extinction of ecological interactions in a changing world. Functional Ecology 29:299–307.

Warning, N., and L. Benedict. 2015. Overlapping home ranges and microhabitat partitioning among Canyon Wrens (Catherpes mexicanus ) and Rock Wrens (Salpinctes obsoletus ). The Wilson Journal of Ornithology 127:395–401.

Westphal, M. F., T. Noble, H. S. Butterfield, and C. J. Lortie. 2018. A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard. Ecology and Evolution 8:12153–12162.

Wiens, J. A. 1973. Interterritorial Habitat Variation in Grasshopper and Savannah Sparrows. Ecology 54:877–884.

Wilkins, M. R., N. Seddon, and R. J. Safran. 2013. Evolutionary divergence in acoustic signals: Causes and consequences. Trends in Ecology and Evolution 28:156–166.

Williams, A. P., E. R. Cook, J. E. Smerdon, B. I. Cook, J. T. Abatzoglou, K. Bolles, S. H. Baek, A. M. Badger, and B. Livneh. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. Science 368:314–318.

Ye, L., and N. B. Grimm. 2013. Modelling potential impacts of climate change on water and nitrate export from a mid-sized, semiarid watershed in the US Southwest. Climatic Change 120:419–431.

**Tables**

**Table 1.** General linear models testing taxonomic abundance, richness, and Shannon index at three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 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 | - |

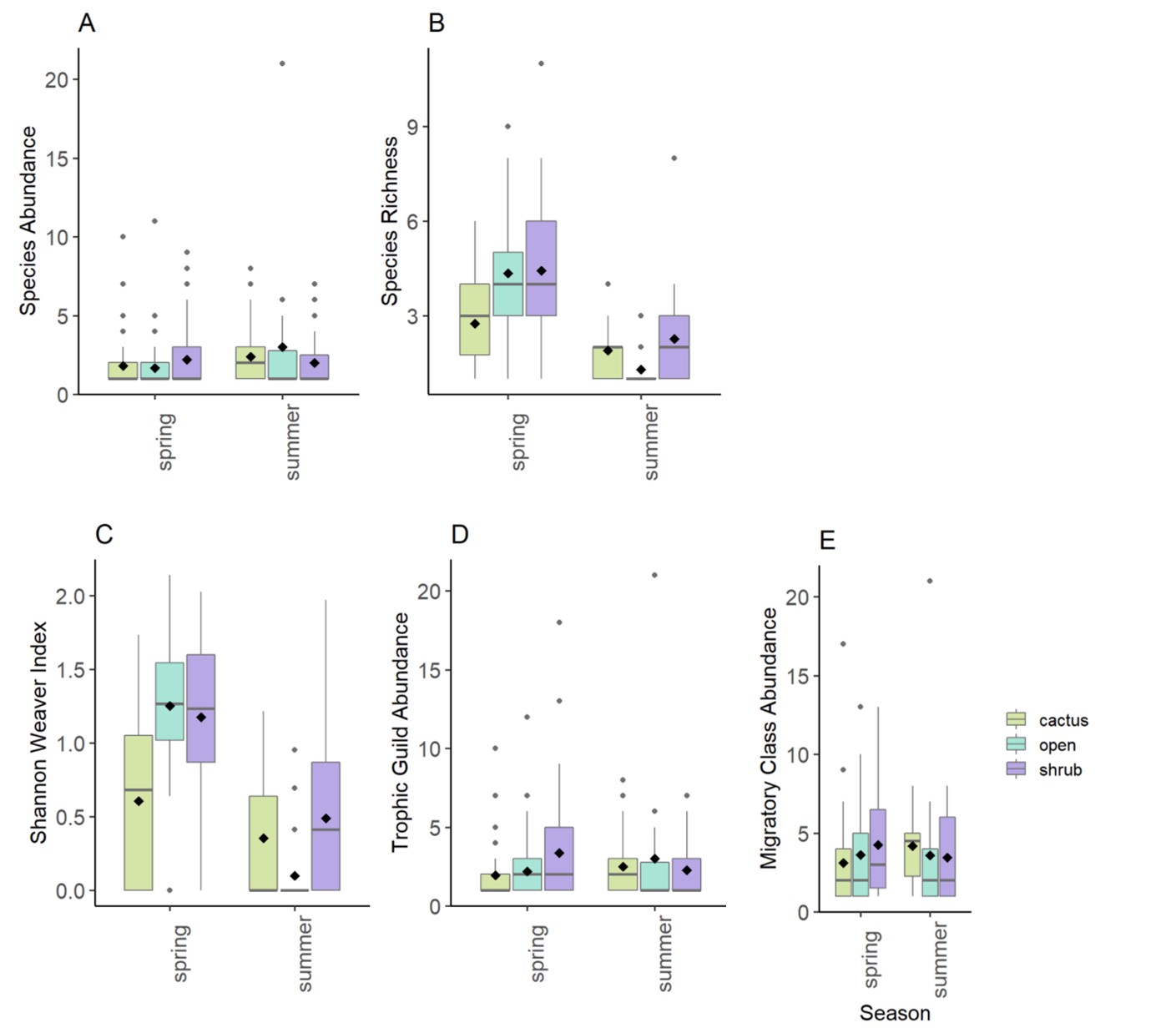
**Table 2.** General linear models testing functional diversity metrics for bird communities as defined by bird trophic guild and migratory class between three microhabitats (shrub, cactus, and open) during two different seasons (spring and summer).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 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 | - |

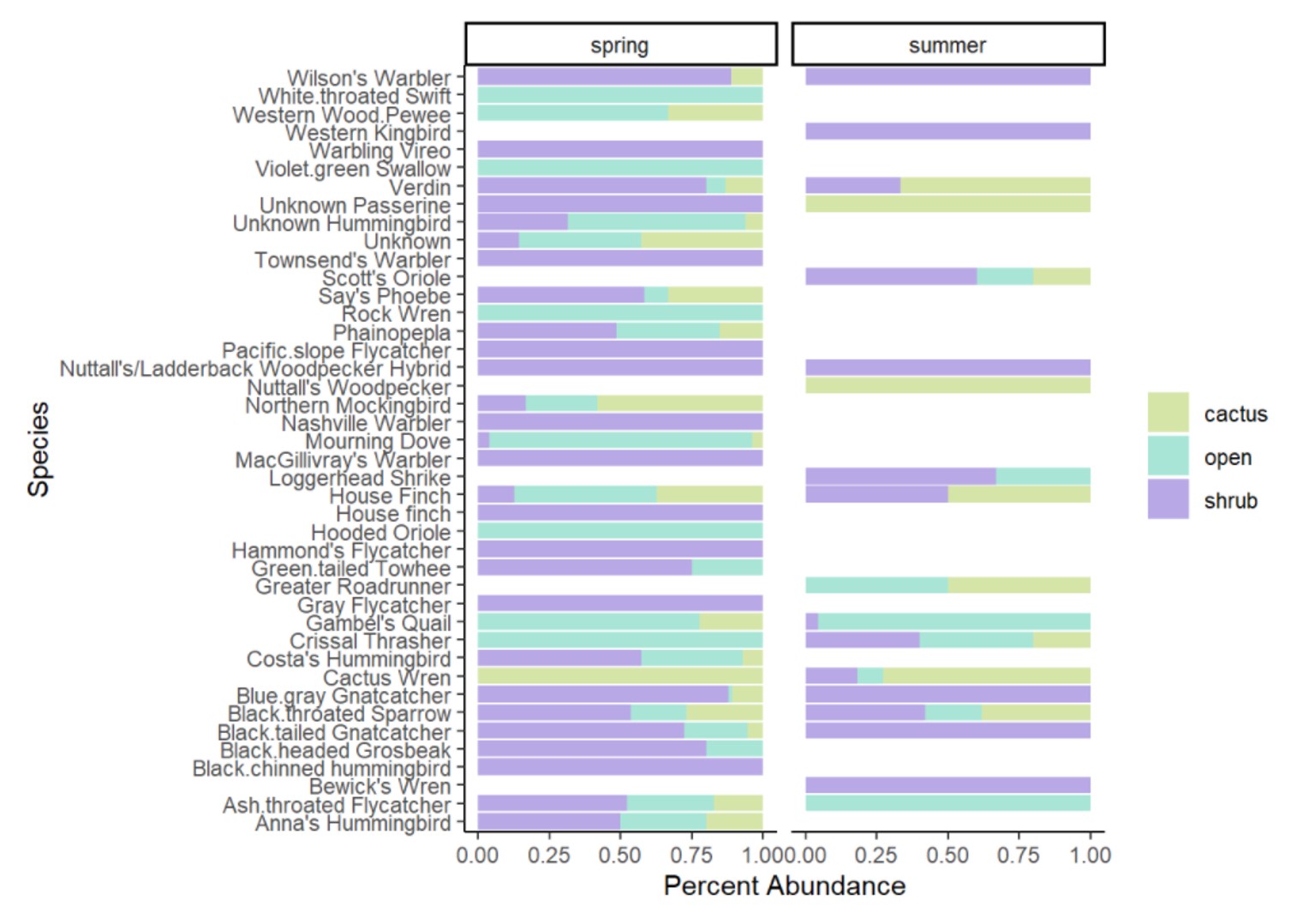
**Table 3.** Statistical output of the general linear model testing for differences in behavior frequency at three different microhabitats (shrub, cactus, and open sites) between two different seasons (spring and summer).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Measure | Effect | d.f. | Deviance Residual | P-value |
| Behavior Abundance | **Microhabitat** | **2** | **20.282** | **0.0012** |
|  | Season | 1 | 5.133 | 0.0642 |
|  | **Behavior** | **4** | **44.712** | **<0.0001** |
|  | Microhabitat x Season | 2 | 4.011 | 0.2624 |
|  | **Microhabitat x Behavior** | **6** | **25.668** | **0.0088** |
|  | **Season x Behavior** | **4** | **33.332** | **0.0002** |
|  | **Microhabitat x Season x Behavior** | **6** | **45.038** | **<0.0001** |
|  | Survey | 0 | 0 | - |
|  | Temperature | 0 | 0 | - |

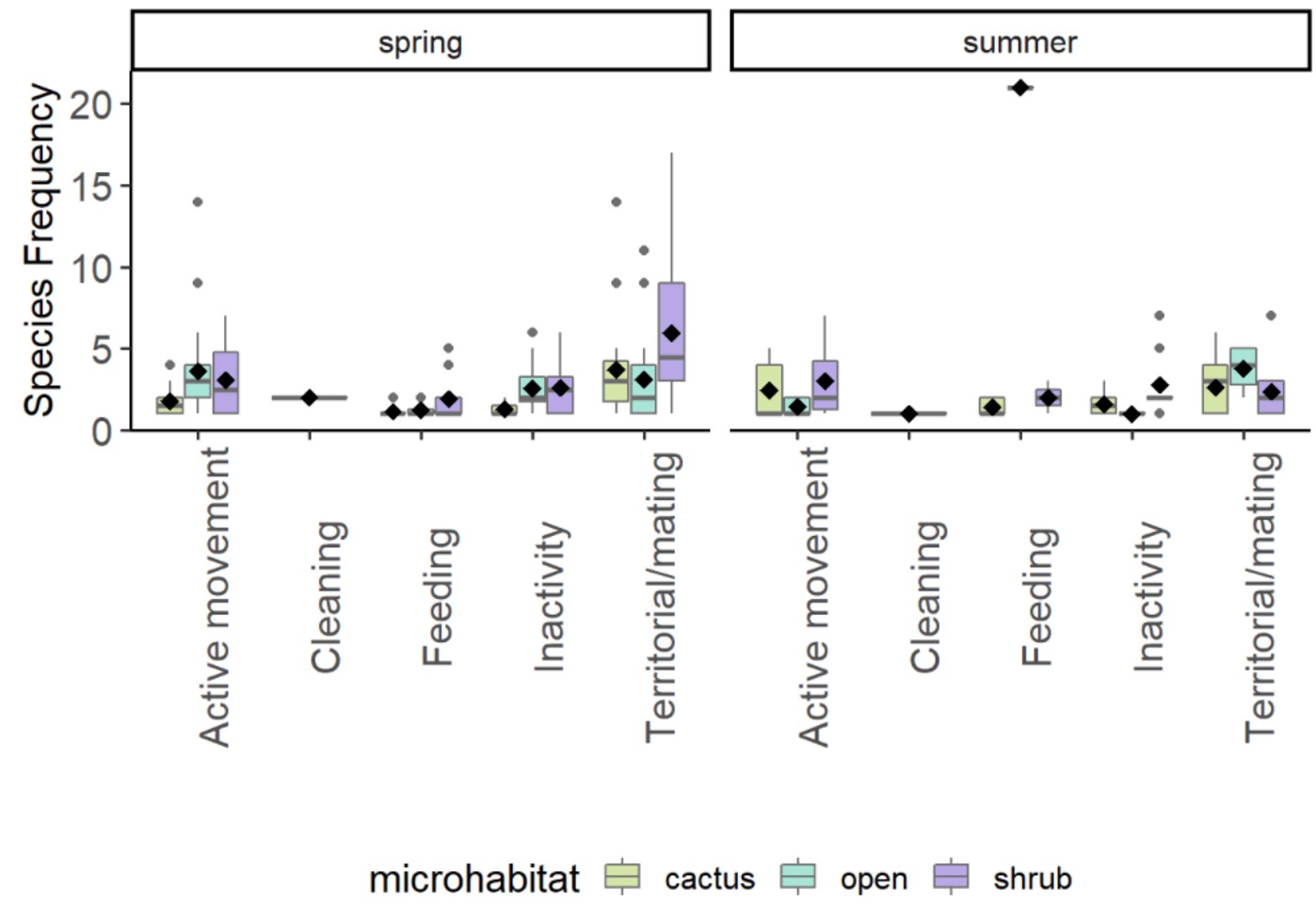
**Figures**

****

**Figure 1**. 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 and summer. Black diamonds represent the means value among surveys of each bird community metric. Shrubs in pring 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.



**Figure 3:** Boxplots of frequencies of behaviors exhibited by birds during surveys at cactus, shrub, and open microhabitats during spring and summer. Black diamonds represent the mean frequencies of each behavior with survey as the level of replication. The most common behavior exhibited at a single seasonal microhabitat was territorial/mating behaviors at spring shrubs (p < 0.0001).

1. [↑](#footnote-ref-1)