Thesis Citations

Malory Owen

6/21/2020

Introduction Background Habitat use, broadly defined, is the way an animal interacts with its surroundings, be they biotic or abiotic. The dimensions of habitat use that we study may take several forms; Macrohabitat use generally describes large-scale interactions with variety in participants, while microhabitat use refers to a homogenous scale of environment (Price 1978; Jorgensen 2004). Despite the “macro” and “micro” prefixes, these definitions are largely based on variability of a habitat-in-question, thus the reality of a macro/microhabitat is highly dependent on the ecosystem at large. For highly mobile individuals (such as birds), an individual’s surrounding microhabitat can rapidly shift as the individual transverses space. Microhabitat use relies on reactions based on a variety of environmental inputs. The plant taxonomic heterogeneity of a habitat provides resource partitioning (Schoener 1974), so access to food, water, shelter, etc. will be differentiated between space. Optimal foraging theory is based on this idea, to some extent, in that different microhabitats provide different resources (Pyke 1984). However, predator avoidance is another strong contributor to habitat selection based on the actor’s morphology, species, lifestage, life history, etc. (Longland and Price 1991).  
Desert habitats are generally stressful. Numerous factors including ultraviolet radiation, heat, water scarcity, wind, and other abiotic and biotic ecological factors contribute to this harshness relevant to plants and to animals (Maestre, Valladares, and Reynolds 2005; Bonanomi, Incerti, and Mazzoleni 2011). Positive interactions between plants and animals are thus relatively common in high-stress systems (Lortie and Callaway 2006). Facilitation is broadly defined as the association of a benefactor plant species with protegee plants or animals by increasing germination, growth, and recruitment of protegee species (Franco and Nobel 1989). In arid ecosystems, facilitation by foundation species can provide resources like water, shade, and pollinators (Flores-Torres and Galindo-Escamilla 2017; Miranda-Jácome, Montaña, and Fornoni 2013; Mitchell et al. 2009), or protection from trauma by herbivory, trampling, freezing temperatures, predation, and wind (Gómez-Aparicio et al. 2008; Parker 1989; Tewksbury and Lloyd 2001; Nobel 1980). Benefactor species which facilitate many interspecifics in an ecosystem are known as foundational species (Angelini et al. 2011; Almeida and Mikich 2018) and tend to dominate an ecosystem. Shrub species have been documented as the most common foundational species globally, though trees and cacti are two other common vegetative benefactors (Filazzola and Lortie 2014). These large, sturdy plants are largely responsible for habitat infrastructure of wildlife throughout an ecosystem (Callaway 1997; Gelmi-Candusso, Heymann, and Heer 2017). While most studies have focused on plant-plant facilitation (Callaway 2007), there is also evidence for the importance of plant-animal interactions in stressful environments (Lortie, Filazzola, and Sotomayor 2016; Bertness et al. 1999; Arsenault and Owen-Smith 2002). However, a more comprehensive understanding of what resources or services animals contribute to the interaction may illuminate pathways of habitat creation that, so far, is less understood. Most studies examining habitat use focus on single populations of interactors and one category of influence (i.e., a single resource or a single predator). However, these influences are difficult to untangle because they exist at a multitude of scales and are rarely independent themselves (Webb et al. 2010; Buler, Moore, and Woltmann 2007). Studies also tend to examine these relationships as a unidirectional flow rather than as a network of interactions that change depending on each party and other abiotic/biotic factors Moore and Aborn (2000)]. This work is critical; however, holistic studies that examine interactions at the community level paint more complete tableaus of critical interactions for ecosystem functioning. This concert of interacting species is, however, dependent on temporal and geographic limitations. Phenology in desert ecosystems can vary widely due to the extreme plasticity of temperature and precipitation (Henen et al. 1998) including cacti & shrubs (Schwartz 2003; Beatley 1974; Jordan and Nobel 1982; Nobel and Hartsock 1981) and bird migration and breeding seasons [Sillett and Holmes (2002); Runge and Tulloch (2017); Fahse, Dean, and Wissel (1998)). This suggests that for animals that rely on or associate with cacti for resources, timing is critical (Buler, Moore, and Woltmann 2007). Phenological mismatch has been studied in deserts (Kellermann and van Ripper III 2015) and is important to explore interactions through time and space at different reproductive stages of the foundation plant species or pollinating/seed dispersing birds in a system, as these limitations determine the capability of plant/bird reproduction to occur, and therefore, habitat creation. However, we must first determine the potentiality for these interactions to even occur before we can determine the implications of phenological mismatches. Phenology, however, does not solely determine the plant reproductive output and, consequently, resource value to interacting animals (like birds). Each plant species has different floral and fruiting output with varying numbers of reproductive structures that interacting animals may benefit from. This variety is linked to plant coevolution with interacting pollinators and seed dispersers (Jordano 1987). Even so, these reproductive output features are strongly influenced by other morphological characteristics of a plant due to a finite amount of nutrients, resources, and energy, thereby requiring tradeoffs between reproductive structures and non-reproductive structures (Bazzaz and Grace 1997). This allocation of resources in a plant determines factors such as plant size, chemical defenses, and reproductive output (Obeso 2004) often in an inverse relationship (Hasegawa and Takeda 2001). Two of these factors, physical size and reproductive output, influence plant-animal interactions that then influence a plant’s reproductive success and an animal’s resource availability. Physical size as a combination of plant height and canopy width is directly linked with pollination frequency for the plant individual itself as taller, larger plants stand out against their shorter neighbors, thereby attracting flying pollinators such as birds and insects (Wolf and Hainsworth 1991; Mitchell 1994). However, number of inflorescences also positively influences a plant’s number of pollination visitations (to diminishing returns), as showy floral displays similarly attract flying pollinators (Ohashi and Yahara 2001). These two features of a plant will then influence the relationship between pollinators and plants.  
However, the allocational tradeoffs between physical size and reproductive output, being two structural depositions of plant resources, are thus at odds as the plant’s morphological makeup. Despite the strong implications for agriculture and conservation fields of biology, these tradeoffs are not well documented. As a precursor to the primary portion of this study, we conducted a systematic review to examine the extent to which allocational tradeoffs between plant physical and reproductive structures were measured. In this study, we examined the hypothesis that there are associations between birds and foundation plant species such as shrubs and cacti which change with shifting phenology. In reference to “associations” we include presence/absence data as well as behavioral data. By including both metrics, we hope to more accurately reflect these interactions; associations alter functionality based on the birds’ behaviors. Our research question is: How do desert bird communities and associations with foundation plant microhabitats change between migratory/flowering seasons (hereafter referred to as spring) and breeding/fruiting seasons (hereafter referred to as summer)? We predict that 1) abundance and diversity of birds is greater near foundation plant species, 2) observed microhabitats will be defined by the birds’ functional and taxonomic diversity, and 3) seasonality changes the associations between foundation plants and the bird community.

Methods Study Site The research was done at the Sweeney Granite Mountains Desert Research Center (34°48′20″N 115°39′50″W) in the Mojave Desert. The 3,600 hectares elevation ranges from 1,128 to 2,071 m and is not accessible to visitors and thus any disturbance. Rainfall varies significantly throughout the year with a mean annual precipitation ranging from 34 t 310 mm per year (Urban, Reynolds, and Fulton 2009), and no typically no precipitation in the summer months. The long-term July daily average minimum and maximum is 1°C and 40°C respectively ((1937-2007 records; Western Regional Climate Center, Reno, Nevada 2008). 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 156 birds, 42 mammals, 35 reptiles, 2 amphibians, and 504 species of vascular plants documented at the reserve [Gurin, La Doux, and Coe (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. *Larrea tridentata*, or Creosote Bush, is a large, long-lived deciduous shrub that is well documented as a benefactor species for plants and animals. *Yucca schideigera*, or Mojave Yucca, is a flowering plant native to the region with several specialist and generalist relationships with fauna of the region. While there are many other plant species found in the study site, these three are the most abundant of plant species and accounted for most interactions documented in this study.  
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 currently over 159 bird species on the Sweeney Granite Mountains Desert Research Center (Gurin, La Doux, and Coe 2012), and a complete list of all known avian species to the field site is available via the site’s website. 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, Tilghman, and Anderson 1985) was seen or heard at every sampling replication. Experimental Design We used a 500-meter line transect over two-hour period block to sample the bird community. Transects were deployed between 7-10am or 5-8pm depending on daily temperatures, which were associated with peak bird activity. Two individual line transects were used and spaced 80 meters apart. The starting coordinates for transect 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/juvenile hummingbirds were identified only to family due to the visual similarity between species. In each instance, microhabitat was also recorded as list the categories here.. However, we only included visual observations of birds in microhabitat and behavioral analyses. Flyovers (defined as birds flying roughly 25 feet above the highest vegetation at site that did not land within sight) were not included as an observation. In addition to species, we also recorded behavior as designated by an ethogram (Appendix C), 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). We also took photographs of birds using a Nikon D5300 camera equipped with a Sigma 150-600mm lens which served as identification aids and behavioral/microhabitat records (Supplemental Material A). Statistical Analyses Behavior and microhabitat functioned as dependent variables for each observation of a bird. Behavioral observations were then categorized into broader behaviors (active movement, cleaning, feeding, inactive, and territorial/mating). Microhabitat level observations were distilled into two levels (vegetative or non-vegetative) and three levels (cactus, shrub, or other). Trophic guild and migratory class were the metrics we used to define functional diversity. We categorized all observed species into trophic guilds using “Foraging Guilds of North America” (De Graaf, Tilghman, and Anderson 1985) and into migratory classes using Common Birds of the Sweeney Granite Mountains Desert Research Center (Gurin, La Doux, and Coe 2012). Taxonomic diversity was recorded to species level and thus represented in the statistical analyses. Using each line transect walk survey as a level of replication, we calculated species abundance (A), richness (S), turnover (T), and evenness (J) using the R Vegan Package (Oksanen et al. 2019). Additionally, we calculated Simpson’s Diversity Index (D) and Shannon’s Diversity Index (H) to encourage transparency on the influence of evenness or richness respectively (Morris et al. 2014). Using these different metrics for community structure, we used linear regression models to determine differences in community structure in spring and summer, excluding species richness (for which we used a general linear model due to a non-normal, Poisson distribution) (Mayorga, Bichier, and Philpott 2020). To assess the species variance impact on community structure, we conducted a principal components analysis of both spring and summer. We then composed two distance-based Moran’s eigenvector maps for each season as a visualization for the variance by species. To test our main hypothesis examining associations between birds and foundation plant microhabitats, we conducted general loglinear models (Donald et al. 2001). When considering species as the diversity index, the first model examined species count data present at each microhabitat, the second examined species richness at each microhabitat, and the third examined the behavior counts at each microhabitat. We also conducted two additional GLMs to assess the birds’ functional diversity metrics as indicators for mesohabitat use; functional diversity was first modelled first with trophic guilds and then with migratory classes (Table \*\*\* with models written out). However, it should be noted that to prevent overdispersion of our trophic guild model, we could not include trophic guild as a term in our model, though the counts of each trophic guild were still grouped by trophic guild. Microhabitats were simplified into one of three categories: open, cactus, or shrub, as these microhabitats provide different amenities to birds and vice versa. In these models, we included each survey as well as the mean average air temperature at the start of each survey session recorded by the research center’s weather station, as air temperature plays a role in animal behavior in desert ecosystems (Appendix A) (Ivey et al. 2020). Additionally, we conducted a general linear model contrasting seasons, microhabitats, and behaviors of only the most commonly spotted species, the Black-throated Sparrow, to assess if this dominant bird species replicates the findings of our community-wide statistics. All figures were plotted using the ggplot2 R package (Wickham 2016). All analyses were performed in R version 3.5.1 (Oksanen et al. 2019), and all R Markdown code can be found on GitHub at <https://github.com/maloryowen/Desert-Bird-Habitat-Use>. Photo documentation of birds can be found at <https://www.flickr.com/photos/189022785N06/albums/72157714811897947>.

Results Throughout the entirety of the study, we visually observed 755 birds and heard 467 birds. However, because only birds that were seen could be classified by behavior and microhabitat, those 467 heard-only birds were not included in the data analysis, though the complete visual and auditory dataset can be found at <https://github.com/maloryowen/Desert-Bird-Habitat-Use>. During the spring, 539 birds were seen while only 216 birds were seen in summer. Overall community structure between seasons Using Shapiro Normality Tests, we found that all metrics for community structure were normally distributed except species richness. All measures of avian community structure, except species turnover, were significantly greater in during the spring census (Linear Model/General Linear Model, Table ***; Fig. 1). Spring and summer mean ± standard error was 20.40 ± 1.78 & 10.15 ± 1.28 for species abundance, 1.86 ± 0.07 & 0.73 ± 0.12 for Shannon-Weaver Index, 8.56 ± 0.54 & 3.20 ± 0.41 for species richness, 0.80 ±0.02 & 0.38 ± 0.06 for Simpson’s Diversity Index, 0.88 ± 0.02 & 0.57 ± 0.07 for species evenness, and 0.67 ± 0.03 & 0.66 ± 0.05 for species turnover. Our Principle Components Analysis allows us to determine which species in each season vary together, thereby showing how variable the community species were in each season. For both seasons, we decided that the important principle components would be comprised of those at which 80% of variance was explained by the addition of a principle component. During the spring, this was delineated by the first six principle components, whereas in summer, the first two principle components reached 80% explanation of variance (Appendix E***  use barplots of relative eignevalues). To determine which species in a principle component were varying together, we chose the eigenvalue of 0.50 as a cut-off point for inclusion, as this value presented itself as a natural break in the principle component dataset. For spring species (Figure \*\*\* A), the first principle component (which accounted for 46% of variance) was composed of 3 species which varied together: the Black-tailed Gnatcatcher, the Black-throated Sparrow, and the Blue-gray Gnatcatcher. The second principle component accounted for 58% of variance and only the Blue-gray Gnatcatcher and White-throated Swift varied together. The third principle component consisted of 67% of the variance and only the White-throated Swift accounted for the variance; this is similar to the fourth principle component which accounted for 75% of the variance and represented only the Verdin as a variance. And finally, the sixth principle component for spring accounted for 81% of the variance of the dataset, with the White-throated Swift and Black-tailed Gnatcatcher varying together. For the summer species (Figure \*\*\* B use the eigenvalue map), the first principle component accounted for 66% of the community’s variance, with Gambel’s Quail supporting most of this variance alone. The second principle component, however, accounted for 89% of the community’s variance with Gambel’s Quail and the Black-throated Sparrow importantly varying together. Microhabitat & Behavior in Seasons Our model to compare species abundances between seasonal microhabitats only, we found that the only significant differences between seasonal microhabitats were found between open habitats in the spring and open habitats in the summer, with open summer microhabitats displaying higher species counts (Appendix E; General Linear Model, p-value = 0.0327). However, our model to compare species richness between seasonal microhabitats showed more complex results. Spring cactus microhabitats were less species rich than spring open and spring microhabitats (General Linear Model, p-value = 0.0233; p-value = 0.0144). However, open spring habitats were more species rich than summer cacti, summer open, & summer shrub habitats (General Linear Model, p-value = 0.0001, p-value < 0.0001, p-value = 0.0009). Lastly, spring shrub microhabitats were richer than summer cacti, summer open, and summer shrub microhabitats (General Linear Model, p-value < 0.0001, p-value < 0.0001, p-value = 0.0005). How, though, were bird behaviors represented at each seasonal microhabitat? We found that of all combinations of only microhabitats and behaviors, territorial/mating behaviors at shrub microhabitats were more common than inactivity or feeding behaviors at cacti (General Linear Model, p-value = 0.0026, p-value = 0.0231). However, including season as a term in our model revealed more information. A total of eleven combinations of behaviors at seasonal microhabitats were significantly different (Table \*\*\* ; Figure ***). These models used taxonomic diversity (as delineated by species), however, bird functional diversity also provided insight to the interactions between these foundation plant microhabitats and birds. Bird trophic guild abundance was significantly greater at spring shrubs than at spring cacti or spring open microhabitats (Appendix E; General Linear Model, p-value = 0.0318, p=value = 0.0384). However, when considering migratory class abundance, there were no significant differences between seasonal microhabitats (Appendix E). Black-throated Sparrows were visually observed 129 times throughout both seasons. When removing community diversity in the model by removing species as a grouping factor and comparing habitat use in only Black-throated Sparrows, we did not find any statistical difference among abundances of any behaviors in either season and microhabitats (General Linear Model, Appendix E, Table*** ). Discussion Positive interactions are responsible for habitat infrastructure across ecosystems where cohabitation can be beneficial for all parties involved (Cardinale, Palmer, and Collins 2002). This is particularly pressing in ecosystems where abiotic and biotic stressors are abundant, such as degraded arid systems and high-elevation alpine systems (Graff and Aguiar 2011; Choler, Michalet, and Callaway 2001). In this study, tested the hypothesis that there are associations between birds and foundation plant species such as shrubs and cacti which change with shifting phenology. Our results do indeed support our hypothesis to some degree, though the interaction links are complex. The presented evidence suggests that mutualistic interactions with foundation plants is ecologically important in this system, with bird habitat use (as presented by presence and behavior at microhabitats) being influenced by foundation plants. Our first prediction that “bird community structures in this desert system differ between spring and summer” was supported by our results. We were able to see that values for diversity metrics were higher in spring, a time of migration for birds and floral production in foundation plants (Rathcke and Lacey 1985). Additionally, our PCA revealed that species abundance was more variable during spring suggesting that the community composition is more diverse during this time. Typical changes in biodiversity due to the arrival and departure of migratory species have been shown to influence resident species’ success in reproduction and resource acquisition, though evidence is conflicting and anthropogenic changes may impact this (Cox 1968; Greenberg et al. 1993; Ramírez-Cruz et al. 2020). When considering plants in seasonal areas (where migration is most likely to occur) (Salewski and Bruderer 2007), spring is a period in which floral offerings to migratory birds benefit both species, with pollination being an act of mutualism (Linhart and Feinsinger 1980). This increased diversity during a migration season was expected, as summer conditions in deserts often result in lower frequencies of vertebrate activity due to intense conditions (Tonkin et al. 2017; Boyles et al. 2017; Geiser and Ruf 1995). This provided for a clear path forward to analyze how habitat use changed among these differing communities. Our second and third predictions, being “abundance and diversity of birds is greater near foundation plant species” and “seasonality changes the associations between foundation plants and the bird community”, while supported, require more nuanced interpretation to understand fully. Foundation species are not important factors for bird species counts, as only open sites experience any difference between seasons. In summer, we see increased fruit production for frugivorous birds in many ecosystems (McGrath, Van Riper, and Fontaine 2009) (anecdotally, we often saw orioles and other frugivores at the Mojave Yucca eating their ripe fruit), a benefit to birds and plants. We also see harsher ultraviolet radiation, water scarcity, and intense heat in desert summers. In regard to counts, we may not have observed more birds associating with foundation species in summer; but birds were not exposing themselves to open habitat as often in summer—where these conditions are harsher (Lortie, Filazzola, and Sotomayor 2016). It is interesting to consider that many birds may be reducing their habitat use of open spaces in summer but are not necessarily finding refuge in foundation plants. It should be noted that this study site is nestled within large granitic rock formations that support a slightly different plant community, but these locations were outside our sampling space. This is important as we know benefactor rocks, or nurse rocks, have been shown to be facilitators for plants and provide habitat for desert birds (Peters, Martorell, and Ezcurra 2008; Warning and Benedict 2015). However, these results suggesting that foundation plants are not important for birds during harsher seasons only applies to species abundances, not species richness. In fact, species richness may in fact be a better indicator of biodiversity, and therefore health, of an ecosystem (Tilman, Isbell, and Cowles 2014). In either season, shrubs are the most species rich microhabitat, though spring is richer than summer. Cacti support the least species richness compared to other microhabitats in any season, and do not differ within seasons. This was surprising, considering that we including Mojave Yucca as a cactus microhabitat, which produced large, fleshy, edible fruits in summer (though it is not actually a cactus, we argue that it is functionally similar in terms of fleshy perches and sharp points providing protection from larger predators, a major threat to bird nest survival) (Ricklefs 1969). Our previous results suggesting that open environments are less attractive to birds in summer held true, continuing to support the idea that open areas are less inhabited in desert summers, likely due to higher ultraviolet radiation, water scarcity, and heat. Our findings also support previous work detailing the importance of foundation shrub species for desert animals and their behaviors (Aukema and Martínez Del Rio 2002; Bauwens, Hertz, and Castilla 1996). However, the shrub-specific findings do illuminate caveats to a simple definition stress-gradient hypothesis as shrub species were richer during less stressful environmental season, though some studies have already discussed the importance of scale in regards to the stress-gradient hypothesis [Lortie and Callaway (2006); Maestre, Valladares, and Reynolds (2005)). Instead, we suggest that it is the stress the mobile species (in this study, birds) undergo which determines associations between interactors. It was, however, the use of these habitats, behaviorally, that provided significant, albeit complex, insight into these associations. As presented in Table \*\*\*, open microhabitats with feeding birds in summer expressed significantly higher avian species abundances than several other metrics, as did spring shrub territorial/mating behaviors (though the former still exceeded the latter). This aligns with our previous findings that spring shrubs are important for migrating birds, which are seeking new territories for rest and nests (Lima 2009). However, the importance of open summer microhabitats for feeding birds conflicts somewhat with our earlier conclusion that open microhabitats in summer are less occupied by birds. Here, we see that summer open microhabitat feeding behaviors dominate summer open inactivity and territorial/mating behaviors, summer cactus feeding behaviors, and spring shrub territorial/mating and cleaning behaviors. This is reality that foraging, specifically, is still necessary in open microsites, particularly as seeds and fruit begin to drop beneath the canopy of the mother plant, but are quickly foraged by seed predators (i.e. granivorous birds) (Racskó et al. 2007; Janzen 1970). This is to say that in terms of food acquisition, birds cannot operate as we would expect under the stress gradient hypothesis if it is true that food is not available as frequently with the foundation plants during this particularly harsh time. When considering, however, that migration is a highly intensive period for birds (Guglielmo, Piersma, and Williams 2001; Rattenborg et al. 2004) we can see that stress is still influencing the association with foundation plants. In fact, this concept falls neatly within the well-known idea that animals must behaviorally adapt to harsh environments (Filazzola et al. 2017). However, further investigations should more closely monitor the reproductive output of plants which do and do not secure bird visitations and behaviors at different seasons. When considering only one species, the Black-throated Sparrow, we did not see that variety was still important. But when we consider this species’ flexibility in niche, this is not surprising. As a generalist (Kozma and Mathews 1997), Black-throated Sparrows have an ability to function with multiple habitats (Kozma et al. 2017). To avoid increasing pressures on a particular microhabitat at a particular time of year in a particular behavioral fashion by a large population, like the Black-throated Sparrow, multiple microhabitats must be available. Without this, more specialist species which overlap in niche with the Black-throated Sparrow may be outcompeted to some degree (Julliard et al. 2006). It is thanks to this variety of microhabitats that generalists are indeed able to partition microhabitat use, as has been thoroughly documented in small mammals (Price 1978; Jorgensen 2004). We suggest that these findings are significantly helpful to environmental managers and conservationists who must make decisions about how restoration—which largely takes the form of plant choice, genetic management, and distribution (Aavik and Helm 2018)—should take place. Commonly, managers may resort to planting one, functionally-similar-to-a-rarer-plant plant species 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, and for successful, community-wide restoration efforts, this range of needs must be fully considered. Conclusion Considering both ends of plant-animal interactions forms a greater understanding of the needs of both interactors. Conservationists and ecologists should be sure include all pressures a target species must face. This study specifically addresses the need for comprehensive knowledge on 1) abiotic, ecosystem-wide forces like temperature & water, 2) situational, temporal pressures like migration & territory establishment, 3) species-specific functionalities like trophic guild, and 4) microhabitat provisions like cover, fruit, & floral resources; but many more pressures exist and should be investigated as unique, though interconnected influencers on associations. Our study focuses on desert microhabitats and birds as this ecosystem provides stark differences and consistently mapped pressures, but this heuristic can be applied to any ecosystem. With this knowledge, we can make more holistic management choices that preserve ecosystem functionality.

References:

Aavik, Tsipe, and Aveliina Helm. 2018. “Restoration of plant species and genetic diversity depends on landscape-scale dispersal.” *Restoration Ecology* 26 (June): S92–S102. <https://doi.org/10.1111/rec.12634>.

Almeida, Adriana de, and Sandra Bos Mikich. 2018. “Combining plant–frugivore networks for describing the structure of neotropical communities.” *Oikos* 127 (2): 184–97. <https://doi.org/10.1111/oik.04774>.

André, J. M. 2006. “Vascular flora of the Granite Mountains.” *Crossosoma* 32 (2): 38–74.

Angelini, Christine, Andrew H. Altieri, Brian R. Silliman, and Mark D. Bertness. 2011. “Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation.” *BioScience* 61 (10): 782–89. <https://doi.org/10.1525/bio.2011.61.10.8>.

Arsenault, Randal, and Norman Owen-Smith. 2002. “Facilitation versus competition in grazing herbivore assemblages.” *Oikos* 97 (3): 313–18. <https://doi.org/10.1034/j.1600-0706.2002.970301.x>.

Aukema, Juliann E., and Carlos Martínez Del Rio. 2002. “Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment.” *Ecology* 83 (12): 3489–96. [https://doi.org/10.1890/0012-9658(2002)083[3489:WDAFEB]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083%5B3489:WDAFEB%5D2.0.CO;2).

Bauwens, Dirk, Paul E. Hertz, and Aurora M. Castilla. 1996. “Thermoregulation in a lacertid lizard: The relative contributions of distinct behavioral mechanisms.” *Ecology* 77 (6): 1818–30. <https://doi.org/10.2307/2265786>.

Bazzaz, Fakhri A., and John Grace. 1997. *Plant Resource Allocation*. 9th ed. San Diego: Academic Press.

Beatley, Janice 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 (2): 245–61. <https://doi.org/10.2307/1935214>.

Bertness, Mark D., George H. Leonard, Jonathan M. Levine, Paul R. Schmidt, and Aubrey O. Ingraham. 1999. “Testing the relative contribution of positive and negative interactions in rocky intertidal communities.” *Ecology* 80 (8): 2711–26. [https://doi.org/10.1890/0012-9658(1999)080[2711:TTRCOP]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080%5B2711:TTRCOP%5D2.0.CO;2).

Bonanomi, Giuliano, Guido Incerti, and Stefano Mazzoleni. 2011. “Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems.” *Plant Ecology* 212 (11): 1777–90. <https://doi.org/10.1007/s11258-011-9948-5>.

Boyles, Justin G., Nigel C. Bennett, Osama B. Mohammed, and Abdulaziz N. Alagaili. 2017. “Torpor patterns in desert hedgehogs (Paraechinus aethiopicus) represent another new point along a thermoregulatory continuum.” *Physiological and Biochemical Zoology* 90 (4): 445–52. <https://doi.org/10.1086/691542>.

Buler, Jeffrey J., Frank R. Moore, and Stefan Woltmann. 2007. “A multi-scale examination of stopover habitat use by birds.” *Ecology* 88 (7): 1789–1802. <https://doi.org/10.1890/06-1871.1>.

Callaway, Ragan M. 1997. “Positive interactions in plant communities and the individualistic-continuum concept.” *Oecologia* 112: 143–49.

———. 2007. *Positive Interactions and Interdependence in Plant Communities*. First. Dordrecht: Springer.

Cardinale, Bradley J., Margaret A. Palmer, and Scott L. Collins. 2002. “Species diversity enhances ecosystem functioning through interspecific facilitation.” *Nature* 415 (6870): 426–29. <https://doi.org/10.1038/415426a>.

Choler, Philippe, Richard Michalet, and Ragan M. Callaway. 2001. “Facilitation and competition on gradients in alpine plant communities.” *Ecology* 82 (12): 3295–3308. [https://doi.org/10.1890/0012-9658(2001)082[3295:FACOGI]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082%5B3295:FACOGI%5D2.0.CO;2).

Cox, George W. 1968. “The Role of Competition in the Evolution of Migration.” *Evolution* 22 (1): 180–92.

De Graaf, Richard M, Nancy G. Tilghman, and Stanley H. Anderson. 1985. “Foraging Guilds of North American Birds.” *Environmental Management* 9 (6): 493–536.

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 (3): 536–47. <https://doi.org/10.1046/j.1365-2664.2001.00618.x>.

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 (1-2): 105–12. <https://doi.org/10.1016/S0006-3207(97)00137-7>.

Filazzola, Alessandro, and Christopher J Lortie. 2014. “A systematic review and conceptual framework for the mechanistic pathways of nurse plants.” *Global Ecology* 23: 1335–45. <https://doi.org/10.1111/geb.12202>.

Filazzola, Alessandro, Michael Westphal, Michael Powers, Amanda Rae Liczner, Deborah A. Smith Woollett, Brent Johnson, and Christopher J. Lortie. 2017. “Non-trophic interactions in deserts: Facilitation, interference, and an endangered lizard species.” *Basic and Applied Ecology* 20: 51–61. <https://doi.org/10.1016/j.baae.2017.01.002>.

Flores-Torres, Arnoldo, and Andrea Galindo-Escamilla. 2017. “Pollination biology of Agave horrida (Agavaceae) in the Chichinautzin mountain range, Central Mexico.” *Botanical Sciences* 95 (3): 423–31. <https://doi.org/10.17129/botsci.1022>.

Franco, A C, and P S Nobel. 1989. “Effect of Nurse Plants on the Microhabitat and Growth of Cacti.” *Journal of Ecology* 77 (3): 870–86.

Geiser, Fritz, and Thomas Ruf. 1995. “Hibernation versus Daily Torpor in Mammals and Birds: Physiological Variables and Classification of Torpor Patterns.” *Physiological Zoology* 68 (6): 935–66.

Gelmi-Candusso, Tiziana A., Eckhard W. Heymann, and Katrin Heer. 2017. “Effects of zoochory on the spatial genetic structure of plant populations.” *Molecular Ecology* 26 (21): 5896–5910. <https://doi.org/10.1111/mec.14351>.

Gómez-Aparicio, Lorena, Regino Zamora, Jorge Castro, and Jose A. Hódar. 2008. “Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores?” *Journal of Vegetation Science* 19 (2): 161–72. <https://doi.org/10.3170/2008-8-18347>.

Graff, Pamela, and Martín R. Aguiar. 2011. “Testing the role of biotic stress in the stress gradient hypothesis. Processes and patterns in arid rangelands.” *Oikos* 120 (7): 1023–30. <https://doi.org/10.1111/j.1600-0706.2010.19059.x>.

Greenberg, Russell, Daniel K. Niven, Steven Hopp, and Carol Boone. 1993. “Frugivory and Coexistence in a Resident and a Migratory Vireo on the Yucatan Peninsula.” *The Condor* 95 (4): 990–99. <https://doi.org/10.2307/1369434>.

Guglielmo, Christopher G., Theunis Piersma, and Tony D. Williams. 2001. “A sport-physiological perspective on bird migration: Evidence for flight-induced muscle damage.” *Journal of Experimental Biology* 204 (15): 2683–90.

Gurin, Catherine, Tasha La Doux, and Sharon Coe. 2012. *Checklist for Birds of the Granite Mountains*. First. Natural Reserve System University for California.

Hasegawa, S., and H. Takeda. 2001. “Functional specialization of current shoots as a reproductive strategy in Japanese alder (Alnus hirsuta var. sibirica).” *Canadian Journal of Botany* 79 (1): 38–48. <https://doi.org/10.1139/cjb-79-1-38>.

Henen, Brian T, Charles C Peterson, Ian R Wallis, Kristin H Berry, Kenneth A Nagy, Kristin H Berry, and Kenneth A Nagy. 1998. “Effects of Climatic Variation on Field Metabolism and Water Relations of Desert Tortoises.” *Oecologia* 117 (3): 365–73.

Holl, Karen D., and Richard B. Howarth. 2000. “Paying for restoration.” *Restoration Ecology* 8 (3): 260–67. <https://doi.org/10.1046/j.1526-100X.2000.80037.x>.

Ivey, Kathleen N., Margaret Cornwall, Hayley Crowell, Nargol Ghazian, Emmeleia Nix, Malory Owen, Mario Zuliani, Christopher J. Lortie, Michael Westphal, and Emily Taylor. 2020. “Thermal ecology of the federally endangered blunt-nosed leopard lizard (Gambelia sila).” *Conservation Physiology* 8 (1): 1–11. <https://doi.org/10.1093/conphys/coaa014>.

Janzen, D. H. 1970. “Herbivores and the number of tree species in tropical forests.” *The American Naturalist* 104 (940): 501–28.

Jordan, Peter W, and Park S Nobel. 1982. “Height distribution of two species of cacti in relation to rainfall, seedling establishment, and growth.” *Botanical Gazette* 143 (4): 511–17.

Jordano, Pedro. 1987. “Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution.” *The American Naturalist* 129 (5): 657–77.

Jorgensen, Eric E. 2004. “Small Mammal Use of Microhabitat Reviewed.” *Journal of Mammalogy* 85 (3): 531–39. <https://doi.org/10.1644/ber-019>.

Julliard, Romain, Joanne Clavel, Vincent Devictor, Frédéric Jiguet, and Denis Couvet. 2006. “Spatial segregation of specialists and generalists in bird communities.” *Ecology Letters* 9 (11): 1237–44. <https://doi.org/10.1111/j.1461-0248.2006.00977.x>.

Kellermann, Jherime L, and Charles van Ripper III. 2015. “Phenological Synchrony of Bird Migration with Tree Flowering at Desert Riparian Stopover Sites.” In *Publication of an Organization Other Than the U.s. Geological Survey*, 133–44.

Kozma, Jeffrey M., Laura M. Burkett, Andrew J. Kroll, Jamie Thornton, and Nancy E. Mathews. 2017. “Factors associated with nest survival of Black-throated Sparrows, desert-breeding nest-site generalists.” *Journal of Field Ornithology* 88 (3): 274–87. <https://doi.org/10.1111/jofo.12209>.

Kozma, Jeffrey M., and Nancy E. Mathews. 1997. “Breeding bird communities and nest plant selection in Chihuahuan Desert habitats in South-Central New Mexico.” *Wilson Bulletin* 109 (3): 424–36.

Lima, Steven L. 2009. “Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation.” *Biological Reviews* 84 (3): 485–513. <https://doi.org/10.1111/j.1469-185X.2009.00085.x>.

Linhart, Yan B., and Peter Feinsinger. 1980. “Plant-Hummingbird Interactions: Effects of Island Size and Degree of Specialization on Pollination.” *Journal of Ecology1* 68 (3): 745–60.

Longland, William S., and Mary V. Price. 1991. “Direct Observations of Owls and Heteromyid Rodents: Can Predation Risk Explain Microhabitat Use?” *Ecology* 72 (6): 2261–73.

Lortie, Christopher J., and Ragan M. Callaway. 2006. “Re-analysis of meta-analysis: Support for the stress-gradient hypothesis.” *Journal of Ecology* 94 (1): 7–16. <https://doi.org/10.1111/j.1365-2745.2005.01066.x>.

Lortie, Christopher J., Alessandro Filazzola, and Diego A. Sotomayor. 2016. “Functional assessment of animal interactions with shrub-facilitation complexes: A formal synthesis and conceptual framework.” *Functional Ecology* 30 (1): 41–51. <https://doi.org/10.1111/1365-2435.12530>.

Maestre, Fernando T., Fernando Valladares, and James F. Reynolds. 2005. “Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments.” *Journal of Ecology* 93 (4): 748–57. <https://doi.org/10.1111/j.1365-2745.2005.01017.x>.

“Mammals of the Granite Mountains.” n.d. <https://doi.org/10.2307/3504060>.

Mayorga, Isabella, Peter Bichier, and Stacy M. Philpott. 2020. “Local and landscape drivers of bird abundance, species richness, and trait composition in urban agroecosystems.” *Urban Ecosystems* 23 (3): 495–505. <https://doi.org/10.1007/s11252-020-00934-2>.

McGrath, Laura J., Charles Van Riper, and Joseph J. Fontaine. 2009. “Flower power: Tree flowering phenology as a settlement cue for migrating birds.” *Journal of Animal Ecology* 78 (1): 22–30. <https://doi.org/10.1111/j.1365-2656.2008.01464.x>.

Miranda-Jácome, Antonio, Carlos Montaña, and Juan Fornoni. 2013. “Sun/shade conditions affect recruitment and local adaptation of a columnar cactus in dry forests.” *Annals of Botany* 111 (2): 293–303. <https://doi.org/10.1093/aob/mcs255>.

Mitchell, Randall J. 1994. “Effects of Floral Traits, Pollinator Visitation, and Plant Size on Ipomopsis aggregata Fruit Production.” *American Society of Naturalists* 143 (5): 870–89.

Mitchell, Randall J., Rebecca J. Flanagan, Beverly J. Brown, Nickolas M. Waser, and Jeffrey D. Karron. 2009. “New frontiers in competition for pollination.” *Annals of Botany* 103 (9): 1403–13. <https://doi.org/10.1093/aob/mcp062>.

Moore, Frank R., and David A. Aborn. 2000. “Mechanisms of en route habitat selection: how do migrants make habitat decisions during stopover?” *Studies in Avian Biology* 20 (1): 34–42.

Morris, E. Kathryn, Tancredi Caruso, François Buscot, Markus Fischer, Christine Hancock, Tanja S. Maier, Torsten Meiners, et al. 2014. “Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories.” *Ecology and Evolution* 4 (18): 3514–24. <https://doi.org/10.1002/ece3.1155>.

Nobel, Park S. 1980. “Morphology, Nurse Plants, and Minimum Apical Temperatures for Young Carnegiea gigantea.” *Botanical Gazette* 141 (2): 188–91.

Nobel, Park S., and Terry 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 (4): 523–27. <https://doi.org/10.1111/j.1399-3054.1981.tb02744.x>.

Obeso, José Ramón. 2004. “A hierarchical perspective in allocation to reproduction from whole plant to fruit and seed level.” *Perspectives in Plant Ecology, Evolution and Systematics* 6 (4): 217–25. <https://doi.org/10.1078/1433-8319-00080>.

Ohashi, Kazuharu, and Tetsukazu Yahara. 2001. “Behavioural responses of pollinators to variation in floral display size and their influences on the evolution of floral traits.” *Cognitive Ecology of Pollination*, 274–96. <https://doi.org/10.1017/cbo9780511542268.015>.

Oksanen, Jari F., Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, et al. 2019. “Vegan: Community Ecology Package.” <https://cran.r-project.org/package=vegan>.

Parker, Kathleen C. 1989. “Nurse plant retationships of columnar cacti in arizona.” *Physical Geography* 10 (4): 322–35. <https://doi.org/10.1080/02723646.1989.10642386>.

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 (5): 593–601. <https://doi.org/10.1016/j.jaridenv.2007.10.004>.

Price, Mary V. 1978. “The Role of Microhabitat in Structuring Desert Rodent Communities.” *Ecology* 59 (5): 910–21.

Pyke, Graham H. 1984. “Optimal Foraging Theory: A Critical Review.” *Annual Review of Ecology and Systematics* 15: 523–75. <https://doi.org/10.1146/annurev.ecolsys.15.1.523>.

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 (3). <https://doi.org/10.31421/ijhs/13/3/741>.

Ramírez-Cruz, Gonzalo A., Israel Solano-Zavaleta, Marcela Méndez-Janovitz, and J. Jaime Zúñiga-Vega. 2020. “Demographic and spatial responses of resident bird populations to the arrival of migratory birds within an urban environment.” *Population Ecology* 62 (1): 105–18. <https://doi.org/10.1002/1438-390X.12032>.

Rathcke, B., and E. P. Lacey. 1985. “Phenological patterns of terrestrial plants.” *Annual Review of Ecology and Systematics* 16: 179–214. <https://doi.org/10.1146/annurev.es.16.110185.001143>.

Rattenborg, Niels C., Bruce H. Mandt, William H. Obermeyer, Peter J. Winsauer, Reto Huber, Martin Wikelski, and Ruth M. Benca. 2004. “Migratory sleeplessness in the white-crowned sparrow (Zonotrichia leucophrys gambelii).” *PLoS Biology* 2 (7). <https://doi.org/10.1371/journal.pbio.0020212>.

Ricklefs, Robert E. 1969. “An analysis of nesting mortality in birds.” *Smithsonian Contributions to Zoology*, no. 9: 1–48. <https://doi.org/10.5479/si.00810282.9>.

Runge, Claire, and Ayesha I. T. Tulloch. 2017. “Solving problems of conservation inadequacy for nomadic birds.” *Australian Zoologist* 39 (2): 280–95. <https://doi.org/10.7882/AZ.2016.003>.

Salewski, Volker, and Bruno Bruderer. 2007. “The evolution of bird migration–A synthesis.” *Naturwissenschaften* 94 (4): 268–79. <https://doi.org/10.1007/s00114-006-0186-y>.

Schoener, Thomas W. 1974. “Resouce partitioning in ecological communities.” *Science* 185 (July): 27–39.

Schwartz, Mark D. 2003. *Phenology: An integrative environmental science*. Second. New York: Springer Science+Business Media. <https://doi.org/10.1007/978-94-007-6925-0>.

Sillett, T. Scott, and Richard T. Holmes. 2002. “Variation in survivorship of a migratory songbird throughout its annual cycle.” *Journal of Animal Ecology* 71 (2): 296–308. <https://doi.org/10.1046/j.1365-2656.2002.00599.x>.

Stewart, G. R., and A. K. Lappin. 2008. “Amphibians and Reptiles of the Granite Mountains.”

Tewksbury, Joshua J., and John D. Lloyd. 2001. “Positive interactions under nurse-plants: Spatial scale, stress gradients and benefactor size.” *Oecologia* 127 (3): 425–34. <https://doi.org/10.1007/s004420000614>.

Tilman, David, Forest Isbell, and Jane M. Cowles. 2014. “Biodiversity and Ecosystem Funcitoning.” *Annual Review of Ecology and Systematics*, 471–93. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.

Tonkin, Jonathan D., Michael T. Bogan, Núria Bonada, Blanca Rios-Touma, and David A. Lytle. 2017. “Seasonality and predictability shape temporal species diversity.” *Ecology* 98 (5): 1201–16. <https://doi.org/10.1002/ecy.1761>.

Urban, Frank E., Richard L. Reynolds, and Robert Fulton. 2009. “The Dynamic Interaction of Climate, Vegetation, and Dust Emission, Mojave Desert, USA.” In *Arid Environments and Wind Erosion*, edited by Fernandez-Bernal A. and M. A. De La Rosa, 1–62. Nova Science Publishers, Inc.

Warning, Nathanial, and Lauryn Benedict. 2015. “Overlapping home ranges and microhabitat partitioning among Canyon Wrens (Catherpes mexicanus ) and Rock Wrens (Salpinctes obsoletus ).” *The Wilson Journal of Ornithology* 127 (3): 395–401. <https://doi.org/10.1676/14-170.1>.

Webb, Elisabeth B., Loren M. Smith, Mark P. Vrtiska, and Theodore G. Lagrange. 2010. “Effects of Local and Landscape Variables on Wetland Bird Habitat Use During Migration Through the Rainwater Basin.” *Journal of Wildlife Management* 74 (1): 109–19. <https://doi.org/10.2193/2008-577>.

Western Regional Climate Center, Reno, Nevada, USA. 2008. “WRCC: Recent Climate in The West.” <https://wrcc.dri.edu/>.

Wickham, Hadley. 2016. “ggplot2: Elegant Graphics for Data Analysis.” New York: Springer-Verlag. <https://ggplot2.tidyverse.org>.

Wolf, Larry L., and F. Reed Hainsworth. 1991. “Hummingbird foraging patterns: visits to clumps of Ipomopsis aggregata inflorescences.” *Animal Behaviour* 41 (5): 803–12. <https://doi.org/10.1016/S0003-3472(05)80347-1>.