

**THE DIVERSITY AND DISTRIBUTION OF AVIAN COMMUNITIES IN RELATION
TO THE SHRUBS *EPHEDRA CALIFORNICA* AND *LARREA TRIDENTATA* IN THE
CENTRAL CALIFORNIA DESERT**

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Abstract

Interactions between key landscape features in desert ecosystems can influence avian community assembly. Bird species may use resources provided by shrubs, including as thermal refuges and as a food source.

Citizen science data, such as eBird, is broadly accessible and has been underutilized in the study of fine-scale avian populations and distributions. eBird data offers opportunities for examining avian diversity and abundance across ecological gradients.

Using citizen science data, I tested the hypothesis that shrub density and aridity predict the abundance and diversity of bird communities throughout the Central California desert. Shrub density and aridity were important predictors of avian diversity and abundance, but this effect was not constant across species. eBird data offers promise for testing predictions at fine spatial scales, but limitations in the quality and availability of data across locations must be taken into consideration.

Keywords: plant-animal interactions, foundation species, desert, arid, density, landscape ecology, birds, citizen science, shrubs, conservation

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Table of Contents

Abstract	ii
Acknowledgments.....	iii
Table of Contents	iv
List of Tables	v
List of Figures	vi
Introduction.....	1
Research Objectives.....	14
Methods	18
Study sites.....	18
eBird data.....	21
Aridity indices.....	22
Sampling effort and bias.....	23
Bird species diversity.....	23
Statistical analyses.....	24
Results	28
Evaluation of eBird data by site.....	28
Effects of aridity and shrub density on avian abundance and diversity	36
Discussion	51
Implications.....	56
References	57

List of Tables

Table 1: Aridity index values and climate classification. Drylands are defined by the United Nations Environment Program as tropical and temperate areas with an aridity index of less than 0.65 (UNEP 1992).....	27
Table 2: List of bird species that were one of the top two most abundant species at each site across all checklists during summer or winter. See Fig. 6 for abundance values. Species selected for testing predictions are in bold; these were abundant and present in the greatest number of sites.....	34
Table 3: The relationship between proportion of species and shrub density, aridity, and the interaction of shrub density and aridity.	42
Table 4: The relationship between the mean Shannon index and shrub density, aridity, season, and the interaction of shrub density and aridity.....	43
Table 5: The relationship between <i>Zonotrichia leucophrys</i> abundance and shrub density, aridity, season, and the interaction of shrub density and aridity.....	44
Table 6: The relationship between <i>Passer domesticus</i> abundance and shrub density, aridity, and the interaction of shrub density and aridity.....	45
Table 7: The relationship between <i>Agelaius tricolor</i> abundance and shrub density, aridity, and the interaction of shrub density and aridity. Season was not found to be a significant predictor of relative abundance. $R^2 = 0.1975196$	46

List of Figures

Figure 1: The predicted associations between avian communities and shrubs by local aridity...	16
Figure 2: Map of study sites in the Central California desert. Sites indicated by blue circles were retained and sampled, while those indicated with red circles were excluded from the dataset.....	26
Figure 3: The cumulative number of checklists and species, by site and by season.	30
Figure 4: The mean proportion of species observed per log minute by site, season, and year....	31
Figure 5: The mean relative number of birds observed per site by season, with mean rate of birds used as a proxy for relative bird abundance.....	32
Figure 6: The cumulative abundance of the top two bird species per site per season, across all checklists per site.....	33
Figure 7: The mean Shannon Diversity Index values per site.....	35
Figure 8: Aridity index and the mean rate of bird observations, per species and by season. Species used for testing predictions are <i>Zonotrichia leucophrys</i> , <i>Passer domesticus</i> , and <i>Agelaius tricolor</i>	40
Figure 9: Shrub density and the mean rate of bird observations, per species and by season. Species used for testing predictions are <i>Zonotrichia leucophrys</i> , <i>Passer domesticus</i> , and <i>Agelaius tricolor</i>	41
Figure 10: Shrub density and the proportion of species observed. Shrub density values are specific to each site.....	47
Figure 11: Aridity and the proportion of species observed, by season and across sites.....	48
Figure 12: Aridity indices and mean Shannon diversity indices, across sites.....	49
Figure 13: Shrub density and mean Shannon diversity indices, across sites.....	50

Introduction

Deserts and Drylands

Drylands are broadly classified as ecosystems with low water availability (Safriel et al. 2005). Water availability can be broadly determined by an ecosystem's ratio of mean annual precipitation to mean annual potential evaporation and transpiration (evapotranspiration); this ratio is known as the aridity index (UNEP 1992). A lower aridity index indicates a more water-limited ecosystem; drylands have an aridity index below 0.65 (Middleton and Thomas 1997). As such, most dryland ecosystems have a potential mean annual evaporative demand at least 1.5 times greater than mean annual precipitation (Safriel et al. 2005, Hoover et al. 2020). This results in a very dry climate, with little water stored in the air or soil (UNEP 1992).

More than two billion people live in or rely on dryland ecosystems for resource production (Safriel et al. 2005, EMG 2011). Drylands cover approximately 41% of the Earth's surface (Safriel et al. 2005), and this number is estimated to be increasing (Huang et al. 2016). Drylands can provide ecological value in many ways. They are primarily used for livestock grazing (Asner et al. 2004); however, depending on water availability, drylands are also used for agriculture (Cherlet et al. 2018, Stavi et al. 2022). Dryland agriculture is responsible for 60% of the world's food production (UNESCO 2009). Because of their many and varied uses, drylands have a large economic footprint.

Drylands are useful for carbon sequestration. Vegetation present in drylands can store carbon in biomass both above and below ground (Hanan et al. 2021). The surface layer of soil is also able to store carbon (Plaza et al. 2018). Current estimates suggest that drylands are responsible for the containment of approximately 30% of the world's carbon (Hanan et al. 2021). Carbon sequestration is important because it helps to reduce the greenhouse effect. Gases that

would otherwise be present in the Earth's atmosphere and help to trap the sun's heat, thus resulting in atmospheric warming, are instead stored in biomass and in soil (Lal 1999). This helps to reduce the magnitude of global warming due to less heat being trapped in the Earth's atmosphere (IPCC 2022).

Carbon sequestration also helps to maintain soil integrity (Hussain et al. 2021). Water increases soil mineralization, which in turn results in less carbon being stored in the soil (Moyano et al. 2012). Wet soil is therefore more likely to lose accumulated carbon than dry soil. As a result, carbon remains in dryland soil for a longer period than in other, more temperate environments (Laban et al. 2018, Gifford et al. 1992).

Dryland ecosystems encompass a range of ecosystems. These include grasslands, savannas, shrublands, woodlands, and both cold and hot deserts (FAO 2011). The common factor across dryland ecosystems is that total evaporation is greater than total precipitation, which results in very low water availability in these ecosystems (UNEP 1992). Because these ecosystems lack water, plant cover and growth are low and soil quality is poor (Naorem et al. 2022); this has led to the incorrect notion that drylands lack ecological importance (White and Nackoney 2003).

One way in which drylands are ecologically valuable is their relatively high number of endemic and endangered species (Safriel et al. 2005). Many dryland species are highly adapted to survive in the more stressful climates found in drylands (IUCN 2017). As a result, drylands contain species that occupy highly specific niches. However, many of these endemic species are also vulnerable to habitat loss. Endemic species can quickly become endangered if conservation efforts are not undertaken to protect their habitats and populations (IPCC 2022). These endemic and endangered species can include flora such as trees, grasses, shrubs and cacti, and fauna such

as birds, reptiles, and mammals (Safriel et al. 2005). Examples of species that are endemic to drylands and denoted as threatened or endangered include the Kern mallow, the Bakersfield cactus, and the San Joaquin kit fox (Germano et al. 2011). These species all have highly specific habitat requirements; the Kern mallow, for example, grows only in California, often at the base of a few local shrub species, and usually in locations with less than 25% shrub cover (Williams et al. 1997). While the presence of so many endemic species makes drylands ecologically valuable, it also increases the need to protect dryland habitats.

Drylands are vulnerable to both land use change and climate change (IPCC 2022). Traditionally, many drylands have been used by nomadic and travelling populations (Safriel et al. 2005). The mobility of these populations can act as an adaptation to changes in rainfall (Tugjamba et al. 2023). In dry seasons, these populations can move from locations where precipitation is highly seasonal to areas where precipitation is less seasonally dependent. Ecosystems are better able to recover from grazing pressures when precipitation is more constant across seasons (Ganguli and O'Rourke 2022). As land use changes have occurred and populations have become more static, these ecosystems are unable to recover in times of low rainfall; this results in dryland degradation and a loss of vegetation cover (Middleton and Thomas 1997).

A changing climate may increase the frequency and intensity of extreme weather events, which includes both droughts and floods (Seneviratne et al. 2021). Drylands are also expanding globally as greenhouse gas emissions increase, which in turn further fuels climate change (Feng et al. 2022). Ecosystems that are accustomed to consistently low water availability may be unable to adapt quickly enough to these climactic extremes. Organisms that inhabit extreme locations have adapted to survive in these conditions; however, adaptations may not occur

rapidly enough relative to the rate of change in both temperature and water supply (Vale and Brito 2015). As such, understanding both how organisms have adapted in the past to shifting environmental conditions and how some of these climactic shifts may be mitigated is a necessary step to help maintain and preserve dryland ecosystems.

Deserts are a subcategory of drylands (Mirzabaev et al. 2022). Specifically, deserts generally receive less than 10 inches of precipitation per year (Marshak 2009). Deserts can be classified as either arid or hyper-arid, depending on their aridity index (Mirzabaev et al. 2022). Deserts can be either hot or cold; both have low mean annual precipitation and are differentiated by either high or low mean annual temperature (Peel et al. 2007).

Deserts are a rich source of ecological biodiversity. Though deserts do not have high absolute biodiversity when compared to biodiversity hotspots such as tropical forests, desert biodiversity is relatively high (Safriel et al. 2005). Because of the harsh surrounding environment, desert organisms have adapted to survive in stressful conditions (Cloudsley-Thompson 1993). This results in highly specialized species that are uncommon or unique to one or few desert locations, or only present in specific niches (Safriel et al. 2005). Deserts also contain highly productive patches that increase localized biodiversity (Ward 2009) and can attract migratory species for use as either wintering grounds or as stopovers during migration (Lavee and Safriel 1974).

Desert ecosystems are constantly adapting to environmental variability, including fluctuating temperatures and intermittent precipitation (Maliva and Missimer 2012). Most of the annual precipitation deserts receive is in seasonal resource pulses, usually in summer and winter (Schwinning and Sala 2004). Due to the lack of water availability, many annual plants undergo very short lifecycles before spending the following seasonal period as seeds (Polis 2016). While

perennial plant abundances are more stable over time, significant changes to environmental conditions such as sustained drought will affect these populations as well (Munson et al. 2016). Animals are reliant on plant populations for a variety of purposes, including as food sources and for shelter. Any disruption at the bottom of the food chain, therefore, will influence the entire ecosystem (Scherber et al. 2010).

Furthermore, nighttime and daytime temperatures in deserts can vary widely (Sellers and Hill 1974). Many desert animals have developed behavioural adaptations, such as hunting or foraging at night. This helps to reduce their exposure to high daytime temperatures (Louw and Seely 1982, Walsberg 2000). In plants, many have adapted to minimize water loss, either through decreased surface area or through variations in photosynthesis (Mulroy and Rundel 1977). However, because these organisms have developed specific adaptations, any unexpected shift in temperature may affect the effectiveness of these mechanisms.

This thesis focusses on biotic interactions in Californian deserts. There are multiple deserts located in California (Germano et al. 2011, Hilberg et al. 2016, Randall et al. 2010). The San Joaquin Desert is in the Central Valley of California (Germano et al. 2011), while the Mojave Desert is located in the Mojave Basin (Berry et al. 2006). These deserts are of interest because they have undergone extreme severe and prolonged droughts beginning in the year 2000 (Williams et al. 2022).

These long periods of intense drought are known as megadroughts and may have profound effects on the survival of desert organisms (Godfree et al. 2019, Kannenberg et al. 2021). These megadroughts, while infrequent, can result in losses of plant cover and potentially loss of biodiversity and resultant ecosystem collapse (Finger-Higgins et al. 2023).

Understanding how to mitigate the effects of these destructive climactic events is an important component of understanding how to maintain the health of desert ecosystems over time.

Drylands and deserts are both ecologically and economically valuable (Safriel et al. 2005). They are important sources of biodiversity, and they provide resources for much of the world's population. Focusing on understanding the mechanisms and interactions that help drive ecosystem and landscape stability will be useful in ensuring the continuing success and longevity of these dryland and desert ecosystems.

Foundation Species

Foundation species are abundant within their local ecosystems (Soulé et al. 2003). These species are responsible for structuring ecosystems; simply put, they control the biodiversity of associated species and help to regulate ecosystem processes (Ellison 2019). The interactions between foundation species and other organisms within the ecosystem are usually non-trophic (Borst et al. 2018); as such, the types of interactions that occur and involve foundation species can be positive, negative, or neutral (Stachowicz 2001). In contrast, trophic interactions are usually positive for one organism and negative for the other (Landi et al. 2018). Because foundation species are usually involved in non-trophic interactions, these interactions can be direct or indirect (Ellison 2019). Indirect species interactions are important for ecosystem stability and may have wide-ranging effects on other organisms within the ecosystem (Danet et al. 2020).

Foundation species can produce structural changes in an ecosystem (Ellison 2019). These changes can be due to additional biomass provided, the creation and maintenance of microclimates, protection against shoreline erosion, and nutrient recycling. Increased biomass can provide ground cover, which can be used as a habitat and a shelter for other species in the

ecosystem. Douglas fir trees, for example, provide habitats in both live trees and in fallen logs, and their foliage controls the microclimate and regulates the amount of light that reaches the forest floor from the forest canopy (Ellison et al. 2005). A key ecological theory is that the habitat provided by vegetation can enhance local biodiversity (Karr and Roth 1971). An important factor that distinguishes foundation species from others is their structural effects that are disproportionately greater than their abundance or the amount of biomass they provide would suggest. Notably, a reduction in the abundance of a foundation species, such as through forest logging, will have a disproportionately large effect and will lead to the decline of the local ecosystem (Ellison 2019).

In desert ecosystems, foundation species are usually shrubs (Lortie et al. 2018). Shrubs can survive in deserts due to lower water needs and have developed adaptations to manage the high rates of evapotranspiration present in these climates (Peguero-Pina et al. 2020). As foundation species, shrubs can create microclimates under their canopies (Lortie et al. 2022). This microclimate can facilitate the survival of organisms that live underneath or near the shrub canopy and indirectly benefits organisms that rely on shrub-dependent species (Jankju 2013). Biotic interactions between foundation species and other species in an ecosystem may help to buffer the ecosystem from the effects of climate change (Angelini et al. 2011).

In the San Joaquin Desert, a foundation species is the shrub *Ephedra californica* (Braun et al. 2021, Lortie et al. 2022), while in the Mojave Desert, two codominant foundation shrub species are *E. californica* and *Larrea tridentata* (Braun et al. 2021). *E. californica* is a dioecious shrub that is wind-pollinated. It does not flower every year, and only after a significant rainfall occurs (Meyer 2008). *L. tridentata* is a flowering shrub found in the southwestern United States (Betancourt et al. 1990, Braun and Lortie 2020). It has a low rainfall threshold, and so it flowers

more reliably relative to other desert plants (Barbour et al. 2007). These shrubs can provide both direct and indirect benefits to other organisms (Lortie et al. 2022, Braun and Lortie 2020, Newman et al. 2018). *E. californica* can act as a thermal refuge for species such as the blunt-nose leopard lizard (Ivey et al. 2020). This shrub also facilitates arthropod communities due to the increased vegetation present below the shrub canopy (Braun et al. 2021). Its plants have either pollen or seed cones, of which the seed cones can be used as a food source by rodents and birds (Meyer 2008). *Larrea tridentata* provides a habitat for desert tortoises and kangaroo rats, under which they dig their shelters or make their dens (Baxter 1988, Monson and Kessler 1940). Its flowers produce both nectar and pollen, making it an important resource for pollinators (Simpson et al. 1977). It provides a food source for jackrabbits and desert woodrats through its seeds, foliage, and terminal twigs (Marshall 1995, Hoagland 1992, Meyer 1974). Both of these shrub species are important foundation species in their local ecosystems.

Foundation shrub species and their effects on local bird populations are not well-studied. Shrubs can act as thermal refuges for birds, which allow birds to live in hotter environments than they may otherwise (Carroll et al. 2015). Shrubs can provide a food source for birds through seed production (Londei 2021). They can provide a nesting habitat for some avian species (Kozma and Mathews 1997). Birds may use shrubs for perching to survey the surrounding habitat for resources (Milesi et al. 2008). Shrubs also foster local arthropod communities, which can be used by birds as a food source (Anderson and Anderson 1946, Maclean 2013). The density of foundation shrub species may facilitate a shift in the abundance and diversity of birds in an ecosystem.

Biodiversity and Ecosystem Stability

Ecosystem stability is important both ecologically and economically (Smith 1996). The stability of an ecosystem will determine how it responds to any environmental shifts (de Bello et al. 2021). These shifts can include extreme weather events such as heat waves and floods (Maxwell et al. 2019), or the introduction of invasive species to the ecosystem (Garcia et al. 2022). The ecosystem's resilience to these shifts will influence the ecosystem's ability to provide services and resources (Weise et al. 2020). Examples of ecosystem services include water purification, resistance to soil erosion, and carbon storage (Lal et al. 2013); these services all help to maintain the integrity of the ecosystem and are needed by many species, including humans.

The extent of an ecosystem's stability and resilience can be determined by its ability to return to a stable state after a perturbation (Holling 1973). These perturbations can include drought, abnormal amounts of precipitation, invasive species, or land management decisions (Mori 2011). If an ecosystem becomes unbalanced due to an external biotic or abiotic shift, the organisms within the ecosystem may be unable to maintain equilibrium (Montoya and Raffaelli 2010, Spence and Tingley 2020).

Habitat heterogeneity can increase biodiversity (Rotenberry and Weins 1980), which in turn benefits ecosystem stability. An indicator of ecosystem stability is whether an ecosystem has experienced a large shift in its characteristics over time, independent of an environmental perturbation. The occurrence of such a shift can indicate an unstable ecosystem (Gilbert and Levine 2017). Unstable ecosystems are characterized by a loss of biodiversity (Oliver et al. 2015). Reduced biodiversity, in turn, has implications for human health and may result in more rapid changes in climate (Keesing et al. 2010, Garcia et al. 2018).

Ecosystem stability is maintained through a network of species interactions (Loreau and de Mazancourt 2013). A fundamental ecological theory is that plant-animal interactions help to support ecosystem biodiversity (Peterson et al. 1998). The nature of these interactions can be positive, negative, or neutral (García-Callejas et al. 2018). There are several types of species interactions, including trophic, mutualistic, and competitive interactions (Landi et al. 2018). Each organism involved in an interaction may experience a positive, negative, or neutral effect as a result of that interaction, and the effect may be different for each organism involved. For example, a trophic interaction involves an organism feeding on another; this is directly positive for one organism and negative for the other. However, there may also be indirect effects occurring; for example, fruit consumption may result in seeds being dispersed in more distant locations. Further, because those seeds will be far from the original plant, no local resources will be diverted away from the original plant. This seed dispersal is a positive effect for the plant and is a neutral effect for the seed dispersing organism.

Interactions can be either symmetric or asymmetric (Landi et al. 2018). Working from the example above, the bird benefits more from the shrub than the shrub from the bird. The shrub underwent a negative effect (resources spent on seeds that got eaten) and a positive effect (seed dispersal), while the bird underwent a positive effect (energy from the seed) and a neutral effect (seed dispersal). Due to the nature of trophic interactions, not all interactions in an ecosystem will be symmetric. However, a stable ecosystem will remain in balance after accounting for these asymmetric interactions. A balanced ecosystem should be in equilibrium after accounting for the sum of the interactions occurring (Tschirhart 2000); this will allow the ecosystem to remain in a stable state over time.

Desert ecosystems are maintained through a network of biological interactions (Stachowicz 2001, Filazzola et al. 2017). The nature of these interactions can change as shifts in environmental stress occur (He et al. 2013) and may result in either more competition or facilitation (Miriti 2006). Examples of environmental stress in deserts are fluctuations in temperature and changes in water availability (Mirzabaev et al. 2022). Large or sudden changes in temperature or in the amount of water available can cause the collapse of local populations (Cruz-McDonnell and Wolf 2016). Another factor that can influence ecosystem stability is the presence of cattle in dryland ecosystems. Cattle have grazed on the Carrizo Plain for over a century. However, native California grassland species are less resilient to grazing pressures than other invasive grassland species (Kimball and Schiffman 2003). In desert ecosystems, this consistent grazing pressure has resulted in reduced biodiversity and a reduction in ecosystem resilience (Pelliza et al. 2020).

Birds: Indicator Species, Diversity, Functions

Birds are an integral part of many ecosystems. They can provide key functions to other plants and animals, including pollination, seed dispersal, insect control, scavenging, and ecosystem engineering (Whelan et al. 2008). Furthermore, most birds are more readily able to take advantage of irregular resource availability due to their ability to fly (Newton 2008). This mobility allows birds to access more resource-dense areas, rather than exhaust a single ecosystem's resources. This flexibility also improves birds' odds of survival in years with low resource availability resulting from environmental events such as droughts. As such, bird populations can be more dynamic with regards to habitat location and resource selection, while their overall populations can remain more stable (Catano et al. 2020).

Birds are more mobile than other species, and so they can respond quickly to any shifts in ecosystem health (Smits and Fernie 2013). Significant changes in local bird abundances may therefore help to alert of any ecosystem disruptions. If an ecosystem's resource availability changes, such as through increased food availability or a decrease in nesting locations, the local bird population will also shift accordingly (Li et al. 2022). Bird populations may not change evenly across species, as species will respond to disturbances differently (Scheele et al. 2017). Birds can be easily observed due to their size, abundance, and calls. Because of this, birds are often used as indicator species (Mekonen 2017). Which species are used as indicator species will vary based on location. Not all species present in a location may be useful or necessary as indicator species; instead, a smaller selection of species that encompasses all ecosystem niches may be sufficiently informative (Butler et al. 2012). Examples of bird species that are considered indicator species are Eurasian blackcaps, Blackbirds (Morelli et al. 2021), and Cactus wrens (Preston et al. 2022).

California is a major migratory hotspot, both for stopovers and as a wintering ground for many bird species (Carlisle et al. 2009, DeLuca et al. 2021). Because of this, bird populations and diversity fluctuate throughout the year (Norris and Mara 2007). Resource availability is an important determinant in stopover and wintering location selection (Throup et al. 2017) but it is not known to what extent shrub density and aridity affect bird diversity and abundance.

Citizen Science Data and eBird

Citizen science describes scientific work conducted by members of the general public (de Sherbinin et al. 2021). One of the most significant benefits of citizen science is its accessibility (NASEM 2018, Allf et al. 2022). While citizen science helps increase the accessibility of data collection and ease of access to data, it is difficult to use the data directly due to a lack of

standardization in data collection (Lukyanenko et al. 2016). While some data collection protocols can be implemented to help reduce this variability, the open-ended style of data collection does result in a large amount of unaccounted variation in the available data (Mair and Ruete 2016). Some key issues are a lack of repeatability and a lack of a baseline in observer experience, which can produce errors such as double counting and misidentification (McCaffrey 2005). However, the cost to citizens and researchers to produce and use this data is minimal and has the potential to provide data on a massive scale (Bonney et al. 2009).

Citizen science data is often incomplete or lacks independence; in particular, sampling efforts are inconsistent and lack replication, which makes deriving statistically significant results from the data challenging (Kamp et al. 2016). While some statistical models have been used to help account for some of these confounding factors, there remains an inherent difficulty in using these data (Walker and Taylor 2020).

eBird is a repository for bird observation data collected through citizen science (eBird 2021). An observer can input their location anywhere in the world, and in turn receives a checklist containing all species that have been observed at that location (LaSorte and Somveille 2019, eBird 2021). The observer is also assigned a number and can include notes about their trip when uploading the checklist. Researchers can access this database, which began recording data in 2002 (Wood et al. 2011, eBird 2021). eBird data is also available through database aggregators, such as GBIF (Amano et al. 2016). eBird data has been used to study regional and global trends in avian abundance and diversity (Bianchini and Tozer 2023). While eBird shows promise for determining trends at smaller spatial scales (Callaghan and Gawlik 2015), it has not yet been widely utilized for this purpose.

Research Objectives

The objective was to examine whether shrub density and aridity influence the diversity and abundance of avian communities. The primary objective was to test the hypothesis that the foundation shrubs *Ephedra californica* and *Larrea tridentata* are important predictors of bird abundance and diversity in desert ecosystems. The following predictions were examined:

1. Shrub density is relatively more important to birds in more arid sites than in less arid sites because the need for thermal refuges increases as aridity increases. In very arid sites there will be a greater increase in bird abundance/diversity as shrub density increases because thermal refuges can help to mitigate the effects of very arid climates.
2. Shrub density will vary in importance to birds depending on their use of shrubs. Bird taxa that directly benefit from shrubs (seed-eating granivores, raptors that use shrubs for perches) will show a strong relationship between abundance/diversity and shrub density. Bird taxa that do not directly benefit from shrubs will not show a similarly strong relationship between abundance and diversity and shrub density.
3. Shrub density is more important to birds in the winter because the presence of migratory birds will increase total bird abundance, which will in turn increase demand for resources. Resources provided by shrubs will become more important as demand for resources increases.

I predict that avian abundance will increase as shrub density increases, and that this increase will be relatively greater at high aridity levels (more arid sites) than at low aridity levels (less arid sites). I predict that when shrub density is high, there will be a greater abundance of birds belonging to functional groups that rely heavily on shrubs compared to bird species that rely less on shrubs. I predict that bird abundance will be greater in the winter, and that as

shrub density increases, a greater number of birds will rely on shrubs in the winter than in the summer. These predictions are illustrated below (Figure 1).

Relationship between Shrub Density and Bird Counts

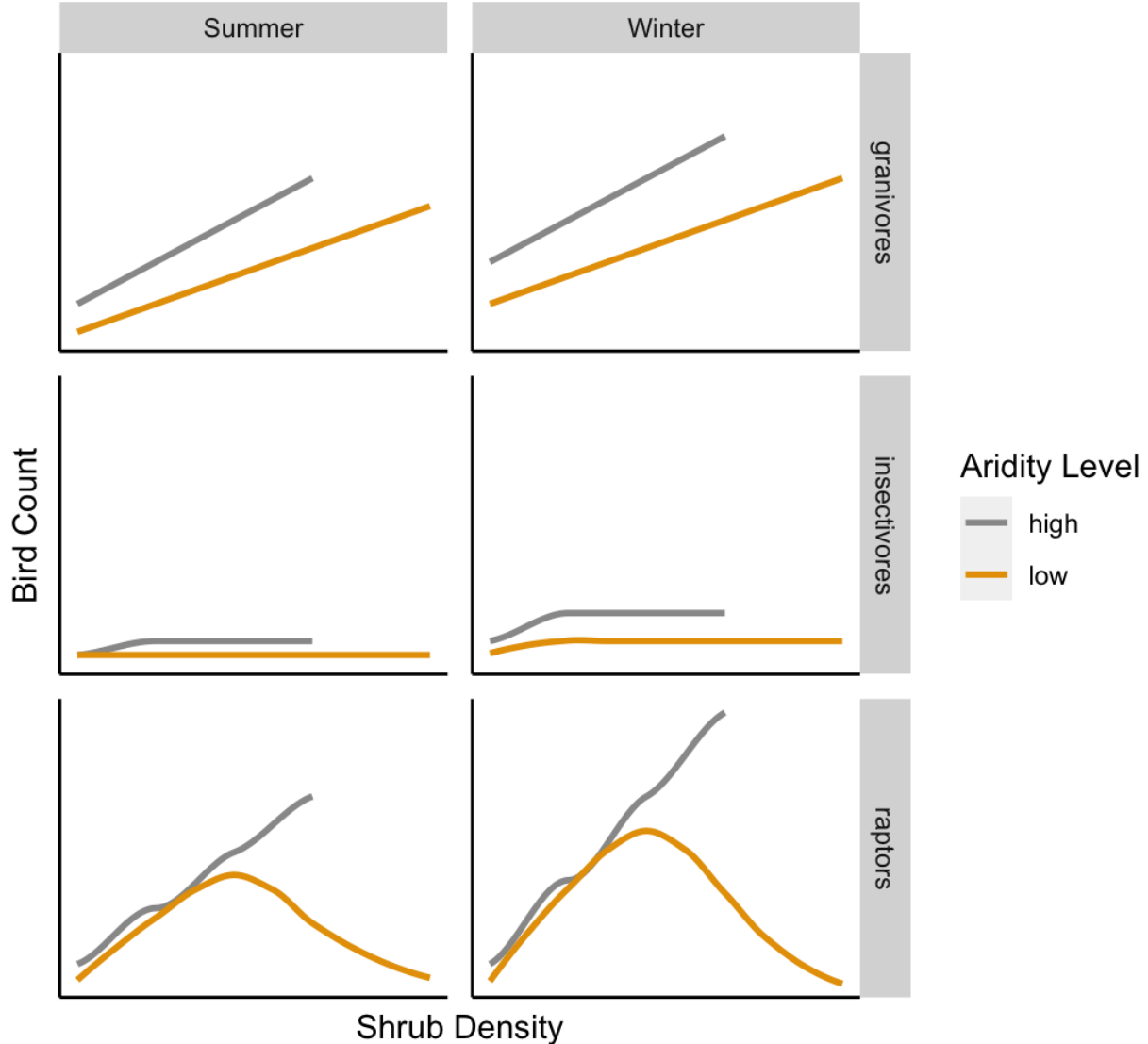


Figure 1. The predicted associations between avian communities and shrubs by local aridity. Overall avian abundances are estimated to be greater in the winter season than in the summer season. Avian abundances are estimated to be greater when the aridity level is higher when sites have greater shrub density. The relative importance of shrub density will be greater in the winter than in the summer. Different species will use and rely on shrubs differently, and so the relative importance of shrub density will vary by species.

Answering the above ecological questions over large spatial scales requires multi-year data on bird diversity and abundance, which was not feasible to acquire through direct field surveys as this would have required extensive field work and human resources. In addition, travel to California was not possible due to the covid pandemic. This study set out to use publicly available citizen science data, specifically eBird, to obtain the bird data at the study site level with which to test the predictions. eBird data have been used extensively on large spatial scales to predict how a species' abundance, or bird diversity overall, will vary with climate and environmental variables over large geographical areas, but has rarely been used to estimate bird data for pre-defined study sites (Callaghan and Gawlik 2015). Thus, my other research objective was to evaluate (i) the extent to which eBird can provide good quality bird survey data at the site level and therefore (ii) the extent to which eBird can be a tool for answering site-level ecological questions.

Methods

Study Sites

Study sites were located throughout the Central California desert (Fig. 1). Sites were primarily located in either the San Joaquin Desert or the Mojave Desert. Due to the distribution of the sites, several were located either within or adjacent to the Mojave National Preserve, Death Valley National Park, or the Carrizo Plain National Monument. Other site locations included those either by or within the Semitropic Ecological Reserve and the Panoche Hills Ecological Reserve.

The Mojave National Preserve was established in 1994. It covers an area of 6,474km² and is located primarily within the Mojave Desert; however, it also covers some of the Great Basin and Sonoran Deserts. It is governed by the National Park Service. It contains basin and range topography, which is characterized by a pattern of mountains and flatlands; geographical features such as lava beds, sand dunes, and cinder cones are also present. Its elevation varies from between 270m to 2,417m. Annual precipitation ranges from 86mm to 230mm, and temperatures can exceed 41 °C. Its status as a national preserve ensures that development will not occur within the borders, though some resource-extractive activities such as hunting and mining are permitted (National Park Service 2013).

Death Valley National Park was established in 1994 and is located between the Great Basin and Mojave Deserts. It is characterized by basin and range topography, with an elevation that ranges from -86m in the Badwater Basin to 4,421m at Mount Whitney. It is governed by the National Park Service. It covers an area of 13,757.167 km², of which close to 92% is designated wilderness and thus contains no roads. Its annual precipitation ranges from 49mm to 380mm; higher elevations receive a greater amount of precipitation, while the Badwater Basin

receives the least. Its status as a national park ensures that both development and resource-extractive activities are not permitted (National Park Service 2017).

The Carrizo Plain National Monument is governed by the United States Bureau of Land Management, the California Department of Fish and Game, and The Nature Conservancy. It was established in 2001 and spans an area of 836.22km². It contains part of the Carrizo Plain, the largest single native grassland in California. It is also the largest protected habitat along the Pacific Flyway, a migratory route for birds (The Nature Conservancy 2023). Its status as a national monument allows for resource-extractive activities such as grazing, though development is not permitted. It is characterized by series of mountain ranges and valleys and contains features such as the San Andreas Fault as well as Soda Lake, an alkaline lake (Bureau of Land Management 2010).

The Semitropic Ecological Reserve spans approximately 60km² and is located in Kern County, California. It was established by the California Fish and Game Commission in 2007, as a way to offset habitat loss in the San Joaquin Valley. It contains several sensitive species. It is currently managed passively as natural lands; thus, the land is unable to be used for purposes other than wildlife habitat (CDFW 2023).

The Panoche Hills Ecological Reserve covers an area of 2.4km² and is located in Fresno County, California. It is primarily a shrub grassland. The California Fish and Game Commission established the reserve in 1990. The goal in establishing the reserve was twofold: to acquire a section of private land located within federal land boundaries, and to allow public access to federal lands via the purchased lands. Hunting is permitted within the reserve (CDFW 2023).

I had access to shrub and climate data for 43 sites. The area of each site was determined by creating spatial polygons using the site perimeters; these polygons were generated using

Google Earth satellite imagery (Zuliani and Lortie 2022). Shrub count data were collected using satellite imagery via Google Earth and geolocating each shrub within the boundaries of the site polygons (Zuliani and Lortie 2022). Satellite images used for geolocation were dated between 2019-2021. Shrub density was then calculated by dividing the number of shrubs by the site area and converted to shrubs per square metre.

I took the centroid of each site polygon and added a 10km buffer around the centroid of each site. I chose to use a 10km buffer because this yielded a greater number of bird observations. Adding these buffers helped to account for differences in size and area between sites that were present in the site polygons. The shrub sites are not necessarily in locations that are accessible to birdwatchers, such as off of main roads (Zuliani and Lortie 2022, Cooke et al. 2019) or on property that was since privately sold; as a result, some of the sites had no bird observations recorded within the original site area (Hillier-Weltman *et al.* 2023). Since birds are not static and may both utilize the shrubs within the site polygon as well as venture beyond those borders when foraging or nesting, adding buffers to the sites is unlikely to significantly influence the true diversity and abundance of bird observations in that location (Rechetelo et al. 2016). Further, adding a buffer helps to account for the lack of precision that can occur while birdwatching; for example, if an observer sees a bird flying, determining the exact geolocation of that bird is unlikely (Johnston et al. 2020). In this case, the buffer may provide more accurate data by accounting for the variance in skill between observers (Kelling et al. 2015). Finally, since microclimates are unlikely to change in a small area such as that used for the buffered sites, bird populations are unlikely to vary significantly between the true site area and the buffered sites (Barnagaud et al. 2012). Adding a buffer does allow for a greater range of topographical features to be included, such as nearby hills and mountains, which may influence bird habitats (Iknayan

and Beissinger 2018, Anderle et al. 2022). However, as the overall size of the buffered sites is small, any effect of shrub density or aridity on birds is unlikely to change significantly due to the buffer.

As some sites are located near others, and in some cases are adjacent to other sites, I selected sites in part based on the amount of overlap between sites. Any site that overlapped more than 25% after buffering was removed from the dataset in order to minimize duplicate observations.

eBird Data

I used bird observation data from eBird (eBird Basic Dataset 2022). This is an open-source database that contains semi-structured bird observation data. I used the R package *auk* to filter the dataset down to only include observations that occurred within a polygon encompassing all sites within California, and to only include complete checklists (eBird Basic Dataset 2013). Checklists are filled out by observers when they go to eBird to record their observations, and a checklist is a list that includes all of the species that might be observed at a given location. A complete checklist is when an observer notes that they included all birds they observed- from this, we can derive pseudoabsence data- it's implied that the observer did not see the other species on the list. I zero-filled the checklists to create presence-absence data for all checklists using the *auk_zerofill* function. From there, I spatially joined the observation data to the buffered sites. To ensure no duplicates were present in the dataset, I used the *st_difference* function in the *sf* package in R (Pebesma 2018).

To account for uneven sampling efforts between sites but ensure an adequate sample size, I filtered out sites that had fewer than 6 checklists per season per year. In cases of multiple sites that overlapped, I selected whichever site had the largest number of eBird checklists. These two

steps yielded 10 sites with the required number of checklists. I chose to use fewer years of data to try and avoid confounding effects like drought (Dong et al. 2019). I also selected sites to ensure an even distribution of microclimates across the aridity gradient. I defined seasons by time of year in an effort to encompass shifts in bird populations due to migratory species (Eyres *et al.* 2020, Somveille *et al.* 2013). I defined the summer season as occurring between March and August and the winter season as occurring between September and February (Lack 1968). I then further filtered the data to 10 surveyors or less, durations of 5 hours or less, travel distances of 85km or less, and to protocol types “stationary” and “traveling” (Feng and Che-Castaldo 2021); this minimized the variation between checklists due to differences in sampling method (Strimas-Mackey et al. 2020, Bianchini and Tozer 2023). All of these filters also help reduce the likelihood of including double counts of birds (Stoudt et al. 2022). I removed any observations that were non-numeric. I also removed any observations that occurred for a duration of one minute or less; this allowed me to later add in log time as an effort variable. I removed any checklist that only contained a count for a single species, as this can indicate a targeted search; the checklist may therefore be inaccurately labelled as complete (Walker and Taylor 2017). The final dataset contained observation data from ten sites located across the Central California desert, from the years 2018-2021.

Aridity Indices

The aridity index is a measure of dryness- that is, the difference between precipitation and evapotranspiration in a given location (Barrow 1992). To determine aridity, I used precipitation and evapotranspiration data from TerraClimate. This dataset contains monthly precipitation and evapotranspiration data for global terrestrial surfaces at an approximately 4km spatial resolution (Abatzoglou *et al.* 2018). The data are updated annually and date back to 1958.

I collected this aridity data using a bounding box that contained all of the site locations. I calculated mean annual values of precipitation and evapotranspiration for every data point within the bounding box. To calculate the aridity indices, I divided the mean annual precipitation value by the mean annual evapotranspiration value for each point within the bounding box. I spatially joined the aridity dataframe to the sites dataframe using the *sf* package in R (Pebesma 2018). I removed any point that did not fall within a site boundary; for those sites that contained multiple aridity data points, I calculated the average aridity index across these points and used that mean value as the site's aridity index value. Aridity is a long-term climactic feature (IPCC 2022), and so I did not consider site-specific aridity on an annual basis. Instead, I averaged the aridity indices across years for each site to produce one average value per site. The product was a dataframe that contained one average aridity index per site.

Sampling Effort and Bias

Bias from sampling efforts is introduced by observer effort when producing estimates of relative abundance and diversity (Zhang 2020, Strimas-Mackey et al. 2020). At the checklist level, I divided each total number of birds observed per checklist by the duration in minutes of that checklist; I used this when determining avian abundance. I then averaged this rate for all checklists across each site by dividing the overall rate by the number of checklists collected for that site. When applicable, I produced a seasonal rate by grouping site checklists by season. The result for bird abundance after accounting for sampling effort was a rate of birds observed per minute per checklist per site, which I then used as a proxy for relative abundance.

Bird Species Diversity

To calculate bird diversity, I took the number of species observed on a checklist and divided that by the total number of species known to occur at that site. The total number of

species known to occur at a site does not take season into consideration and is based off of observer data (Sullivan et al. 2014). The number of species observed per checklist and divided by the number of known species in that site yielded a proportion of species observed for each checklist. I divided this proportion by the log of the checklist duration in minutes. I used log minutes because observations of species increase logarithmically, not linearly (Verberk 2011). I averaged this rate for all checklists across each site by dividing the total rate of species observed over time by the number of checklists collected for that site. When applicable, I produced a seasonal rate of species observed over time by grouping site checklists by season. The result for bird diversity after accounting for sampling effort was a rate of proportion of species observed per minute per checklist per site. I used this rate of species observed as a proxy for relative diversity.

I used the Shannon index as a further measure of diversity. The Shannon index uses the number of species and the proportion each species is of the number of individuals when computing an index value (Nolan and Callahan 2006). I divided all observation counts by the log time of its checklist to account for observer sampling effort. I computed the diversity index value for each checklist and then calculated an average index value for each site. This method took both species proportion and relative abundance into account and so provided another method to determine species diversity.

Statistical Analyses

The data did not meet the assumptions of a normal distribution and variance. I used a Kruskal-Wallis test to determine if there was a significant difference in relative bird abundances between species. I used Dunn's test to compare the species to determine which differed from each other. I used generalized linear models with a Gaussian distribution to determine if shrub

density or aridity was a significant predictor of bird relative abundance for each species. I used generalized linear models with a quasibinomial distribution to determine if shrub density or aridity was a significant predictor in bird diversity. I used generalized linear models with a quasipoisson distribution to determine if shrub density or aridity was a significant predictor in diversity as measured by the Shannon index.

I modeled the effects of aridity and shrub density on avian abundance and diversity using the ggplot2 package in R (Wickham 2016). I added trend lines using the stat_smooth function. These helped to visualize the overall trends occurring within the data.

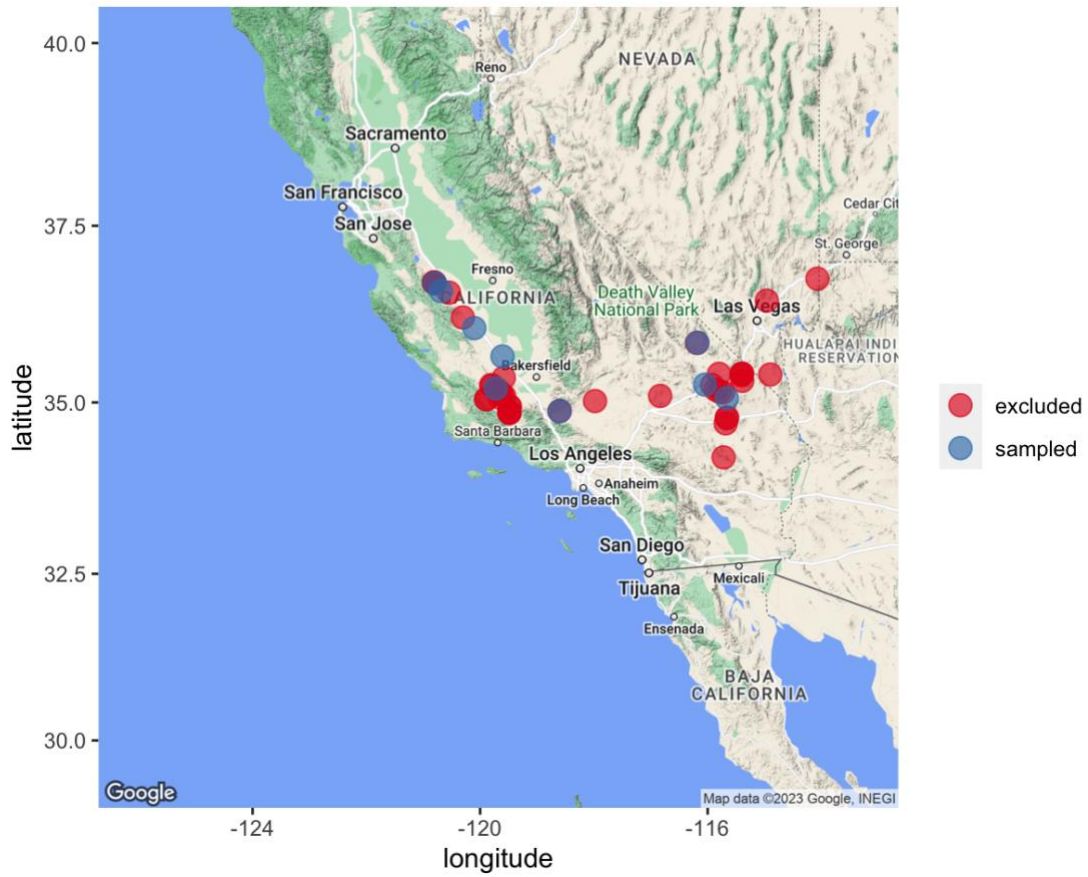


Figure 2. Map of desert sites. Sites indicated by blue circles were retained and sampled, while those indicated with red circles were excluded from the dataset.

Table 1. Aridity index values and climate classification. Drylands are defined by the United Nations Environment Program as tropical and temperate areas with an aridity index of less than 0.65 (UNEP 1992).

Aridity index (AI) values	Climate classification
AI < 0.05	Hyper-arid
0.05 < AI < 0.2	Arid
0.2 < AI < 0.5	Semi-arid
0.5 < AI < 0.65	Dry sub-humid
0.65 < AI < 0.75	Humid
AI > 0.75	Hyper-humid

Results

Evaluation of e-Bird data by Site

Sampling effort varied between sites. Some sites were more heavily sampled overall, and sites were sampled differently in summer and winter (Fig. 3). The cumulative number of species observed also varied between sites. Number of species observed within a site will increase as sampling effort increases (Bean *et al.* 2012, Shen *et al.* 2023); as a result, the total number of species that may be present in a site is not fully reflected in the eBird data. As sampling effort increases, the cumulative number of species present is expected to level off, as is seen with species accumulation curves (Kelling *et al.* 2015).

The maximum possible number of observable species varied between sites' checklists. Using the proportion of species observed, rather than the total number of species, helped to account for this disparity (Fig. 4). Taking the mean proportion across checklists and within a site helps account for the sampling effect discussed above- namely, that more checklists will increase the number of species observed within a site. Overall, the mean proportion of species observed within sites was fairly constant across years and seasons. Of note is that the mean proportion of species observed was very low, with between 0-1% of species observed. This may indicate that the overall amount and quality of data available is low due to low overall sampling effort.

Bird abundance was calculated as a rate of birds observed per minute per checklist and averaged for sites and seasons. This helps to control for sampling effort, since cumulative observation counts increase with survey duration and number of checklists (Callaghan *et al.* 2019). Bird abundance varies substantially both between sites and within sites and across seasons (Fig. 5). Some sites have twice as many birds encountered per minute during eBird surveys than other sites.

Bird abundance also varied greatly among common species. Common species were present across all of the sampled sites and were also relatively abundant across sites. The species used were selected based on their likelihood of shrub interactions, in addition to being common across all sites. The most common and abundant species were *Zonotrichia leucophrys*, *Passer domesticus*, and *Agelaius tricolor* (Table 2, Fig. 6). All of these species are likely to be shrub dependent and are common across seasons (Meese 2017, Porzig *et al.* 2018, Hanson *et al.* 2020).

The Shannon Index is a measure of species diversity (Shannon 1948). The Shannon index was calculated for each checklist and averaged across all checklists within each site (Fig. 7). This plot takes the checklist duration into account. Shannon index values show low-to-moderate species diversity across sites.

Cumulative Number of Checklists and Species per Site

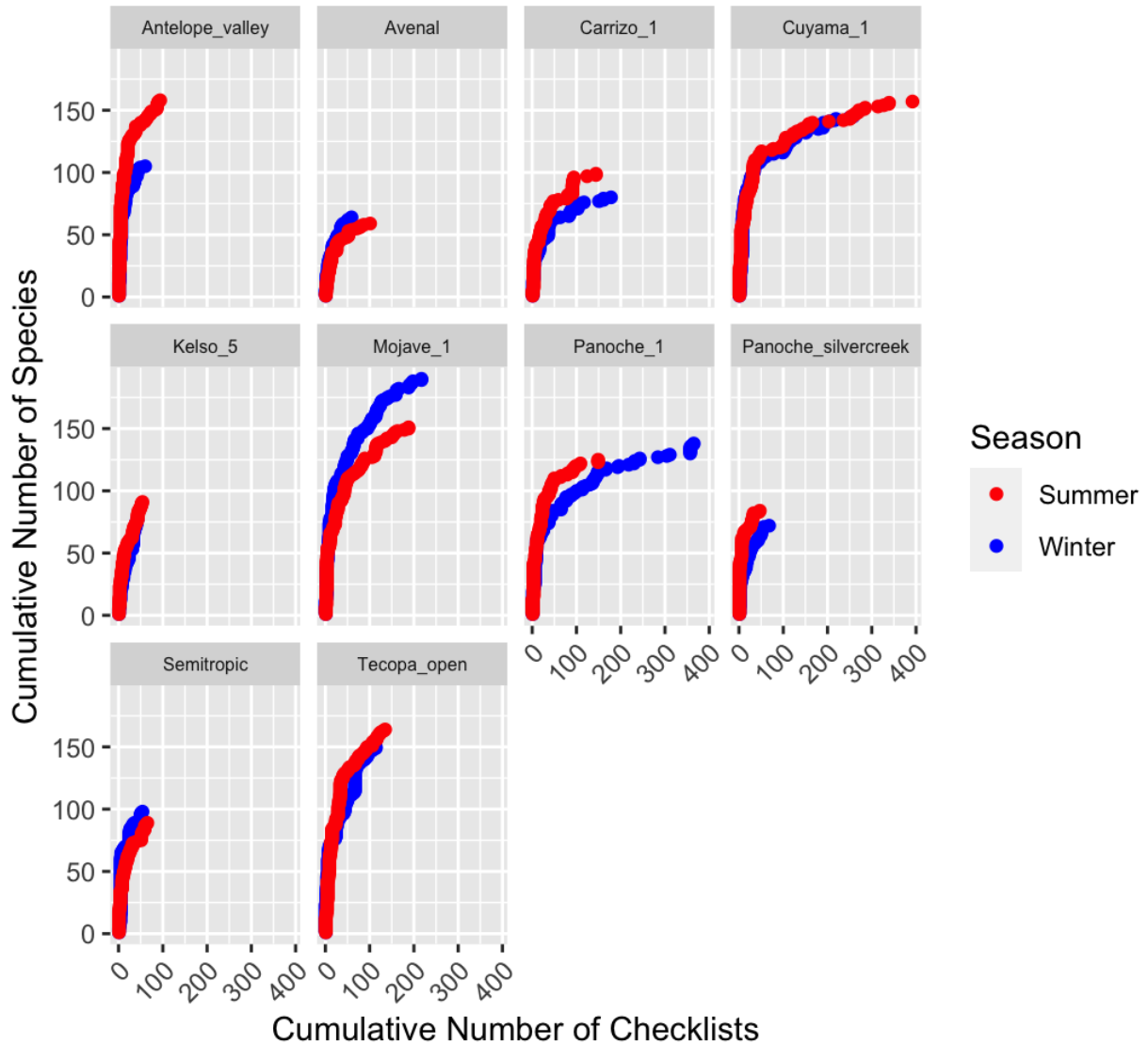


Figure 3. Cumulative number of checklists and species by site and by season. Number of checklists is associated with sampling effort in each site. Sampling effort is uneven across sites.

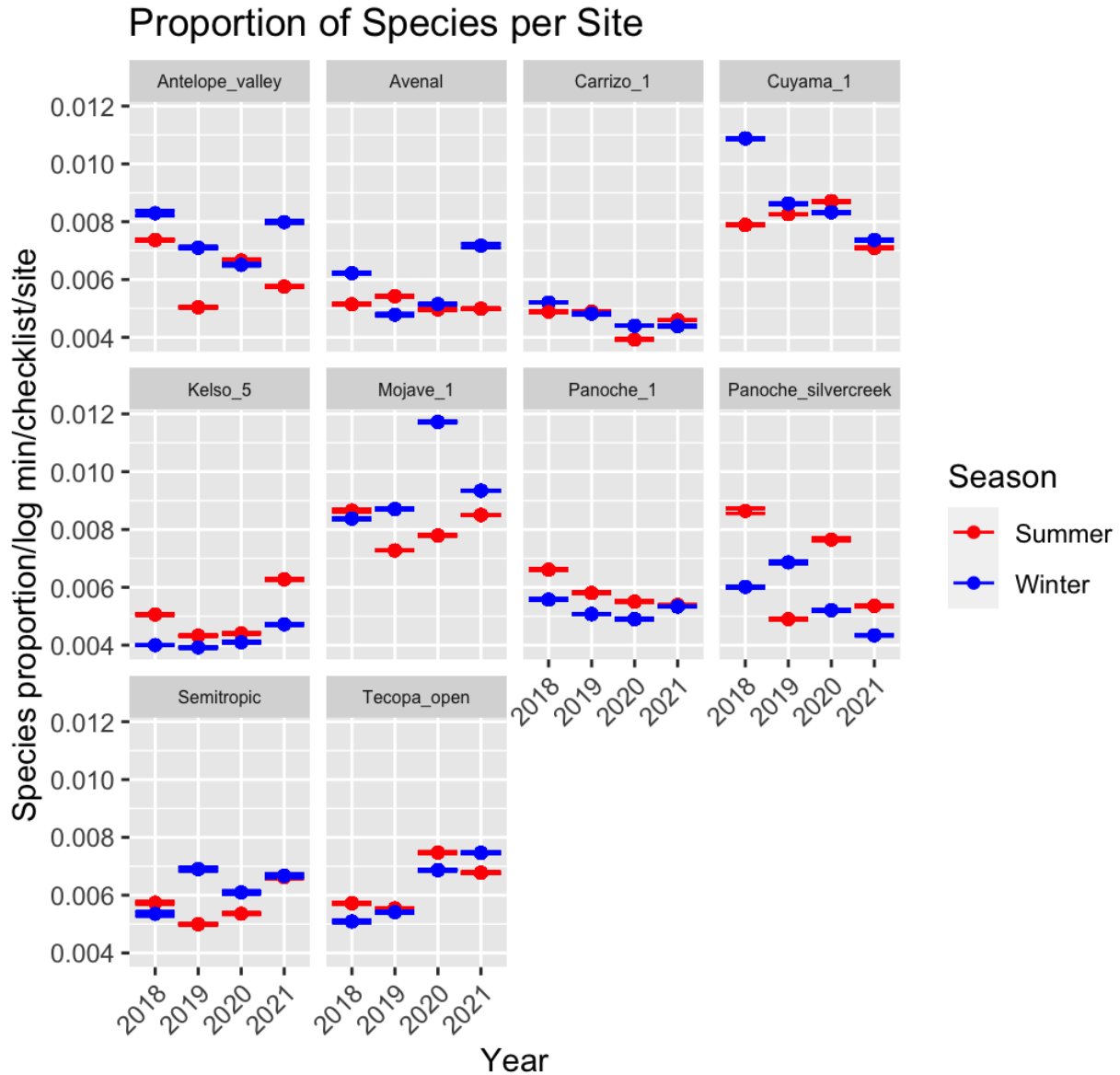


Figure 4. Mean proportion of species observed per log minute per site by season per year. The proportion of species is the number of species observed relative to the number of species expected to be in the area, according to eBird. The mean proportion is an average for each site. The total number of species expected to be in the area varies per site. This plot accounts for the total number of checklists per site and the time spent observing. Overall, the mean proportion of species observed was very low and ranged from approximately 0-1%.

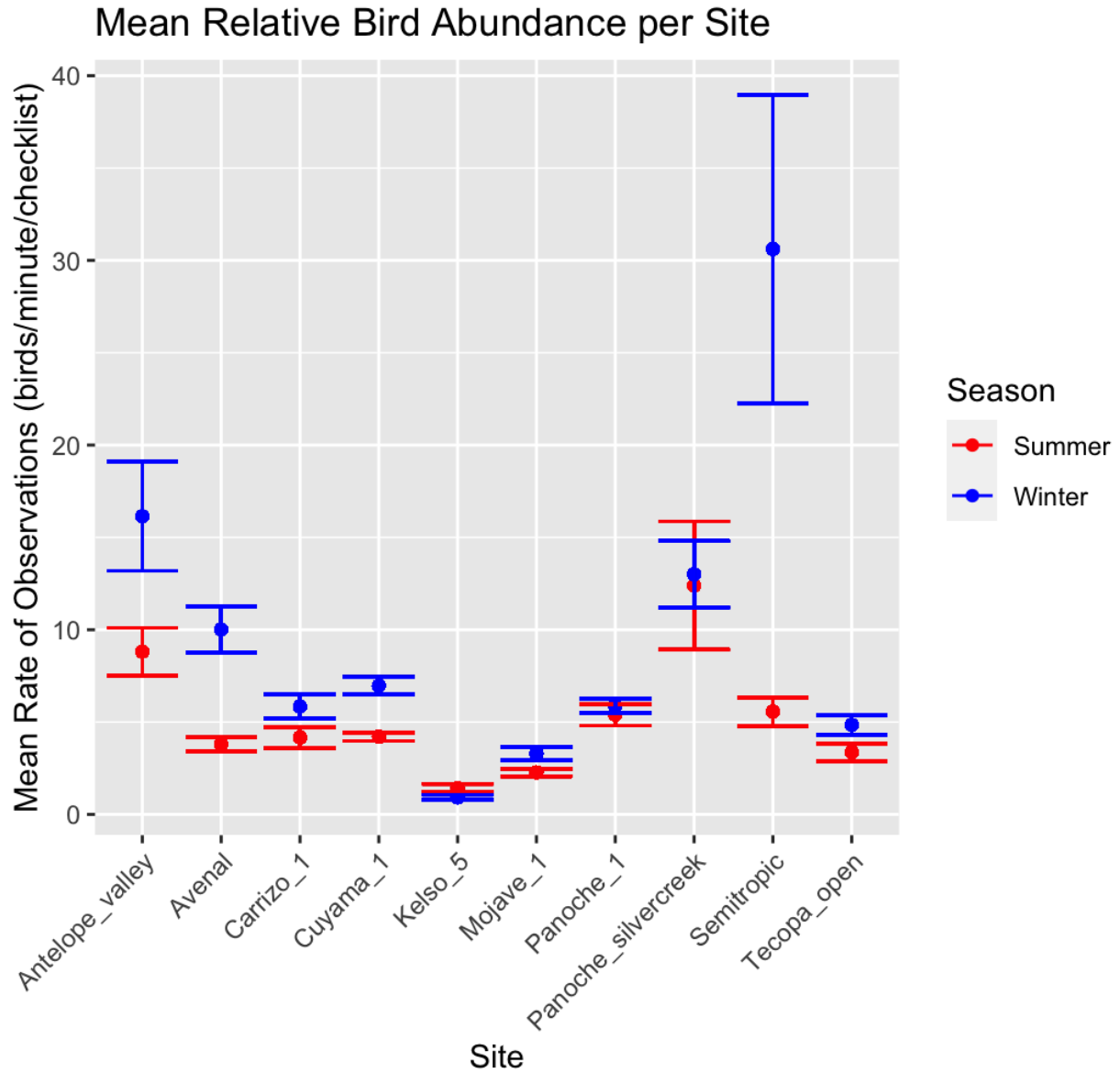


Figure 5. Mean relative number of birds observed per site by season. The mean rate of the number of birds per minute per checklist per site is used as a proxy for relative bird abundance.

Top Two Bird Species Across Sites per Season

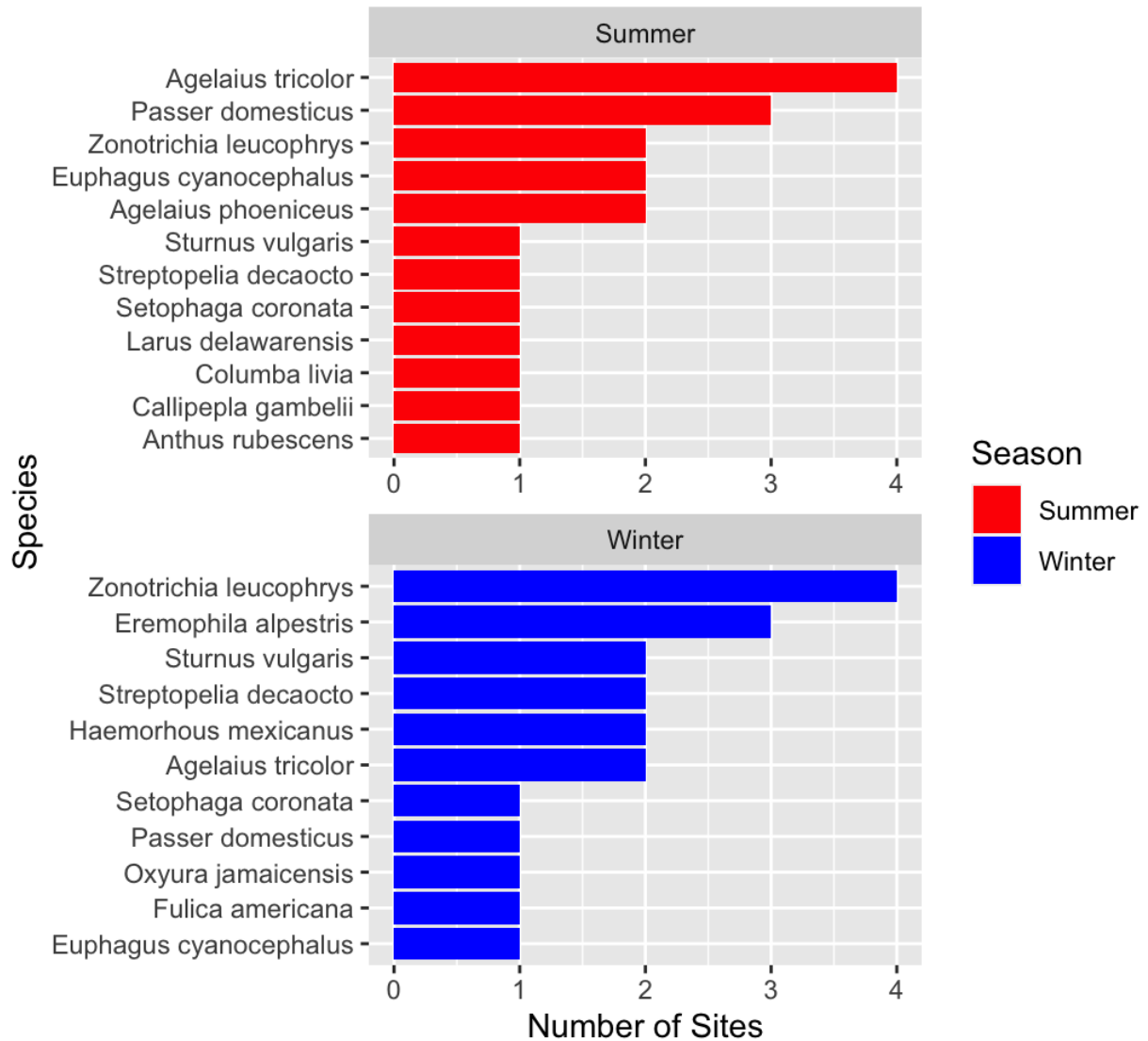


Figure 6. Cumulative abundance of top two bird species per site per season, across all checklists per site. The most common species across sites were *Zonotrichia leucophrys*, *Passer domesticus*, and *Agelaius tricolor*.

Table 2. List of bird species that were one of the top two most abundant species at each site across all checklists during summer or winter. See Fig. 6 for abundance values. Species selected for testing predictions are in bold; these were abundant and present in the greatest number of sites.

Species	Summer	Winter
<i>Agelaius phoeniceus</i>	Avenal, Semitropic	
<i>Agelaius tricolor</i>	Antelope Valley, Cuyama 1, Panoche 1, Panoche-Silvercreek	Cuyama 1, Panoche-Silvercreek
<i>Anthus rubescens</i>	Carrizo 1	
<i>Callipepla gambelii</i>	Tecopa-open	
<i>Columba livia</i>	Semitropic	
<i>Eremophila alpestris</i>		Antelope Valley, Carrizo 1, Mojave 1
<i>Euphagus cyanocephalus</i>	Panoche 1, Panoche Silvercreek	Avenal
<i>Fulica americana</i>		Semitropic
<i>Haemorhous mexicanus</i>	Panoche-Silvercreek	Antelope Valley
<i>Larus delawarensis</i>	Tecopa-open	
<i>Oxyura jamaicensis</i>		Semitropic
<i>Passer domesticus</i>	Avenal, Kelso 5, Mojave 1	Kelso 5
<i>Setophaga coronata</i>	Kelso 5	Tecopa-open
<i>Streptopelia decaocto</i>	Mojave 1	Kelso 5, Mojave 1
<i>Sturnus vulgaris</i>	Cuyama 1,	Avenal, Cuyama 1
<i>Zonotrichia leucophrys</i>	Antelope Valley, Carrizo 1	Carrizo 1, Panoche 1, Panoche-Silvercreek, Tecopa-open

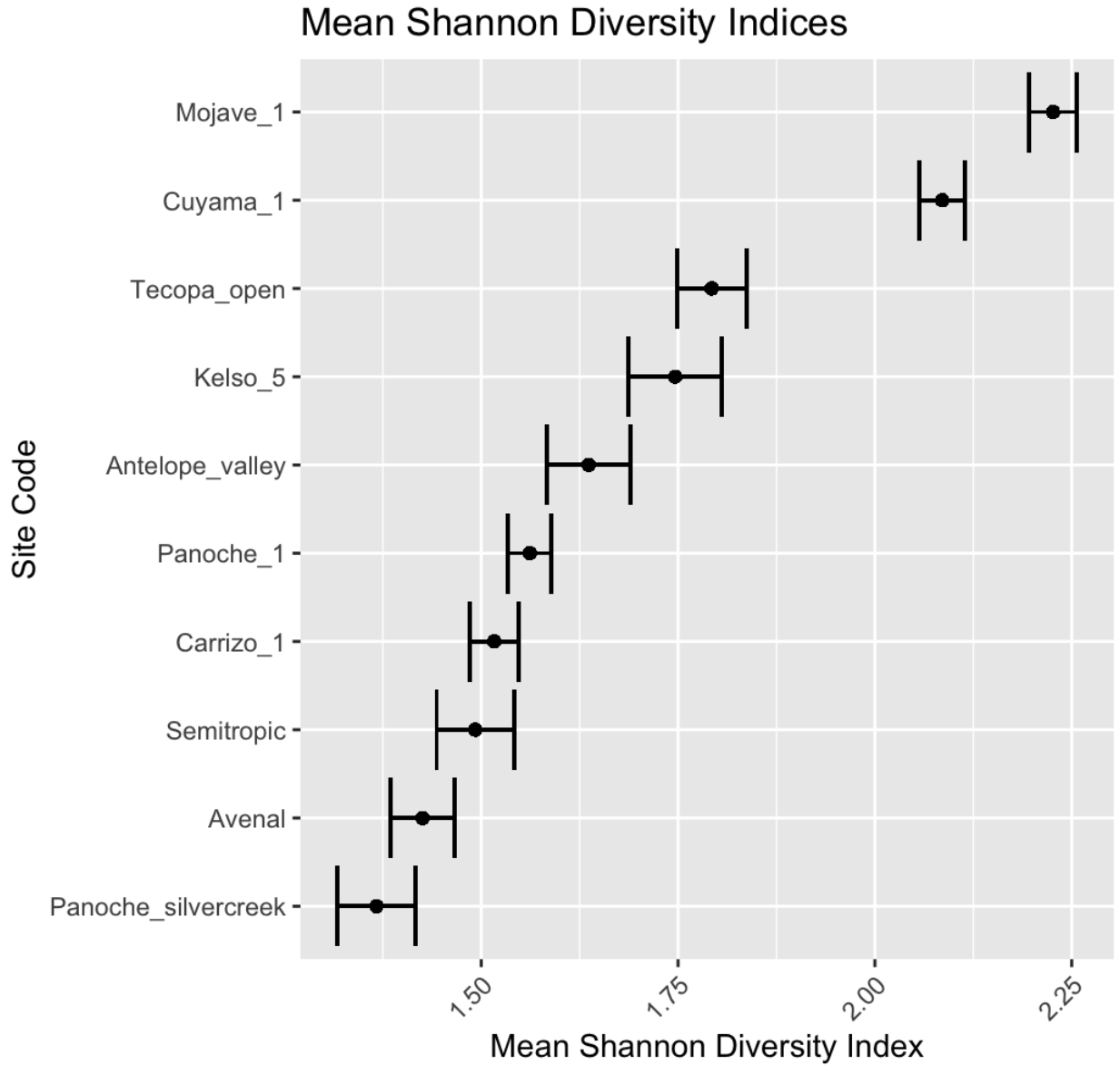


Figure 7. Mean Shannon Diversity Index values per site. The Shannon index, a measure of diversity, was calculated for each checklist and averaged per site. This plot does take duration of checklist into account; specifically, observation counts were divided by log time before calculating Shannon index values.

Results: Effects of aridity and shrub density on avian abundance and diversity

I tested (1) if highly arid sites have a lower abundance of birds and (2) if sites with high shrub density have a higher abundance of birds. For both tests I examined if there was an interaction effect between aridity and shrub density, as shrub density was predicted to have a stronger influence on birds in arid sites. I also tested if there was a seasonal effect on avian diversity or abundance. Species used for testing predictions are *Zonotrichia leucophrys*, *Passer domesticus*, and *Agelaius tricolor*. These species are all granivores, and so they are likely to benefit from shrubs as a seed source.

I compared the aridity index and the mean rate of bird observations by site and by season for these three common species (Fig. 8). I found that aridity was a significant predictor of relative abundance for *Zonotrichia leucophrys* and *Agelaius tricolor* (Table 5, 7). As aridity decreased (i.e., as sites became more arid), the relative abundance of these species increased.

Next, I compared shrub density and the mean rate of bird observations, for each of the three common bird species and by season (Fig. 9). Shrub density was taken as the number of shrubs per square meter within each site. Bird observation counts were grouped by species, site code, and season. The mean rate of bird observations was measured by calculating the number of birds of each species and dividing by time and by number of checklists. Each point represents the relative number of birds of a given site. I found that shrub density was a significant predictor of *Zonotrichia leucophrys* and *Agelaius tricolor* abundance (Table 5,7). As shrub density decreased, the relative abundance of these species increased. Shrub density alone therefore appears to have a negative effect on avian relative abundance.

I found that there was no effect of season on the relative abundance of any of the common species tested. Shrub density is therefore unlikely to be more important to birds in the winter.

I tested the effect of the interaction between shrub density and aridity on avian relative abundance for the three common species. I found that there was an interaction effect between these variables and the relative abundance of both *Zonotrichia leucophrys* and *Agelaius tricolor* (Table 5, 7). Because the interaction term was significant and positive while both aridity and shrub density alone were significant and negative, these two variables may be counteracting each other. Bird relative abundance may be greatest at neither extreme end of these variables. Shrub density may therefore be more important to bird abundance in more arid sites.

I tested if aridity or shrub density influenced bird diversity by examining (1) the proportion of species observed out of all species considered possible in the area by eBird (Fig. 10, 11) and (2) species diversity as measured by the Shannon Index (Fig. 12, 13). The proportion of species was calculated by dividing the number of species observed in each checklist by the total number of species listed on that checklist by the eBird app. The mean proportion is the average for each site. The total number of species per checklist varies based on location and season. This plot accounts for number of checklists within sites as well as time spent observing; the response variable is a rate of species observed.

I tested to see if aridity influenced the proportion of species observed within a site (Fig. 11). The proportion of species was calculated by dividing the number of species observed in each checklist by the total number of species listed on that checklist. The mean proportion is the average for each site. The total number of species per checklist varies based on location and season. This plot accounts for number of checklists within sites but not time spent observing. I

found that aridity was a significant predictor of species proportion (Table 3). As the aridity index increases (i.e., a site becomes less arid), the proportion of species increases.

Shrub density also has a positive effect on the proportion of species observed (Table 3). As shrub density increases, the proportion of species present also increases. This indicates that shrub density is an important predictor of bird diversity.

The interaction of shrub density and aridity was also significant (Table 3). The combined effect of shrub density and aridity had a negative effect on species proportion. Because the interaction term was significant and negative while both aridity and shrub density alone were significant and positive, these two variables may be influencing each other. The proportion of species present may be greatest when shrub density and aridity are either very high or very low. Shrub density may therefore be more important to bird diversity in very arid (low aridity index) locations, but it may become less important for bird diversity as sites become less arid.

I found that season had no significant effect on species proportion, which indicates that shrub density is not more important for bird species diversity in the winter than in the summer.

I tested the effect of aridity on species diversity (Fig. 12). A lower aridity index value indicates a drier, more arid site. The Shannon index, a measure of diversity, was calculated for each checklist and averaged per site. This plot does not take duration of checklist into account. Aridity was a significant predictor of the mean Shannon diversity index (Table 4). As the aridity index increases (i.e., a site becomes less arid), the mean Shannon index increases. Shrub density also has a positive effect on avian diversity (Table 4). As shrub density increases, the mean Shannon index increases (Fig. 13). The interaction of shrub density and aridity was also significant (Table 4). This indicates that as both shrub density and aridity increase, bird species

diversity also increases. The Shannon index is negatively biased at small sample sizes (Mouillot and Leprêtre 1999), which may account for the difference in directionality between these results and those obtained using species proportion as a measure of diversity. Season was also a significant predictor of species diversity (Table 4), with less avian diversity seen in the winter than in the summer.

Aridity and Mean Rate of Bird Observations

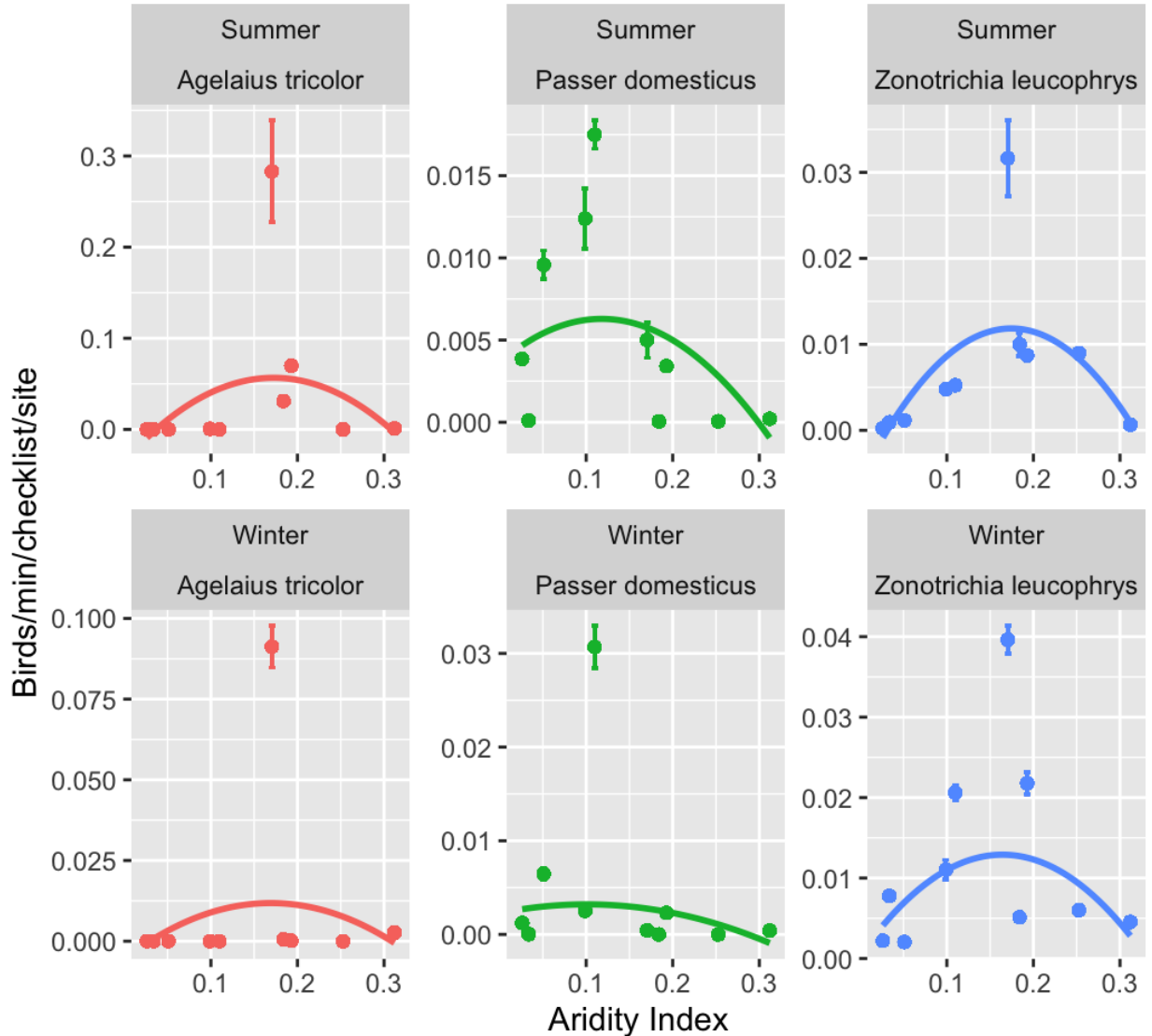


Figure 8. Aridity index and the mean rate of bird observations, per species and by season. The aridity index is a function of precipitation and evapotranspiration, and so a lower index value indicates a drier site location. Bird observation counts were grouped by species, site code, and season. The mean rate of bird observations was measured by calculating the number of birds of each species and dividing by time and by number of checklists. Each point represents the relative number of birds of a given site. Species used for testing predictions are *Zonotrichia leucophrys*, *Passer domesticus*, and *Agelaius tricolor*. Aridity was a significant predictor of *Zonotrichia leucophrys* and *Agelaius tricolor* abundance (Table 5, 7).

Shrub Density and Mean Rate of Bird Observations

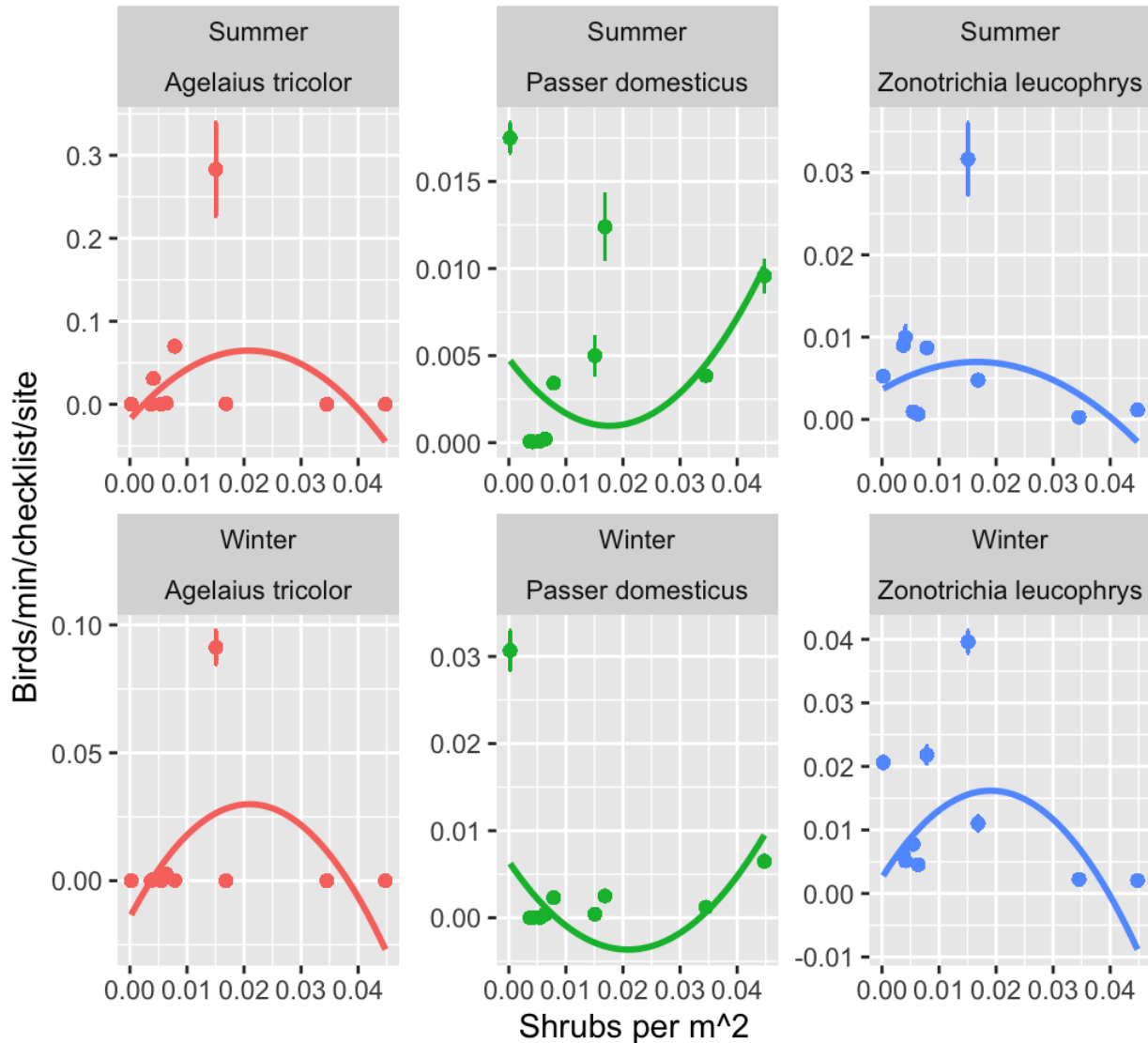


Figure 9. Shrub density and the mean rate of bird observations, per species and by season. Shrub density was taken as the number of shrubs per square meter within each site. Bird observation counts were grouped by species, site code, and season. The mean rate of bird observations was measured by calculating the number of birds of each species and dividing by time and by number of checklists. Each point represents the relative number of birds of a given site. Species used for testing predictions are *Zonotrichia leucophrys*, *Passer domesticus*, and *Agelaius tricolor*. I found that shrub density was a significant predictor of *Zonotrichia leucophrys* and *Agelaius tricolor* abundance (Table 5, 7).

Table 3. The relationship between proportion of species and shrub density, aridity, and the interaction of shrub density and aridity. Season was not found to be a significant predictor of species proportion. $R^2 = 0.240$.

Term	Estimate	Standard Error	Statistic (t value)	P-value (Pr(> t))
Intercept	-5.354	0.014	-365.427	< 2e-16 ***
Aridity_index	1.244	0.0827	15.038	< 2e-16 ***
Shrubs_m2	13.661	0.603	22.645	< 2e-16 ***
Season	0.0120	0.00771	1.567	0.117
Aridity_index*shrubs_m2	-31.772	9.565	-3.322	0.000906 ***

Table 4. The relationship between the mean Shannon index and shrub density, aridity, season, and the interaction of shrub density and aridity. $R^2 = 0.576$.

Term	Estimate	Standard Error	Statistic (t value)	P-value (Pr(> t))
Intercept	0.262	0.000454	577.14	< 2e-16 ***
Aridity_index	1.027	0.00278	369.07	< 2e-16 ***
Shrubs_m2	13.915	0.0190	732.41	< 2e-16 ***
Season	-0.0234	0.000189	-123.37	<2e-16 ***
Aridity_index*shrubs_m2	9.605	0.334	28.72	0.000906 ***

Table 5. The relationship between *Zonotrichia leucophrys* abundance and shrub density, aridity, season, and the interaction of shrub density and aridity. Season was not found to be a significant predictor of relative abundance. $R^2 = 0.322$.

Term	Estimate	Standard Error	Statistic (t value)	P-value (Pr(> t))
Intercept	0.0174	0.00505	3.453	0.000915 ***
Aridity_index	-0.111	0.0306	-3.637	0.000504 ***
Shrubs_m2	-1.088	0.218	-4.981	3.94e-06 ***
Season	0.00367	0.00311	1.180	0.242
Aridity_index*shrubs_m2	17.915	3.212	5.576	3.70e-07 ***

Table 6. The relationship between *Passer domesticus* abundance and shrub density, aridity, and the interaction of shrub density and aridity. Shrub density, season, and aridity index were not found to be significant predictors of relative abundance. $R^2 = 0.0855$.

Term	Estimate	Standard Error	Statistic (t value)	P-value (Pr(> t))
Intercept	0.0131	0.00358	3.654	0.000475 ***
Aridity_index	-0.0349	0.0217	-1.605	0.113
Shrubs_m2	-0.106	0.155	-0.687	0.494
Season	-0.00239	0.00221	-1.080	0.283
Aridity_index*shrubs_m2	-0.0558	2.283	-0.024	0.980

Table 7. The relationship between *Agelaius tricolor* abundance and shrub density, aridity, and the interaction of shrub density and aridity. Season was not found to be a significant predictor of relative abundance. $R^2 = 0.197$.

Term	Estimate	Standard Error	Statistic (t value)	P-value (Pr(> t))
Intercept	0.0738	0.0452	1.632	0.107
Aridity_index	-0.629	0.274	-2.296	0.0245 *
Shrubs_m2	-5.521	1.956	-2.822	0.00611 **
Season	-0.0410	0.0279	-1.472	0.145
Aridity_index*shrubs_m2	113.208	28.780	3.934	0.000185 ***

Shrub Density and Proportion of Species Observed

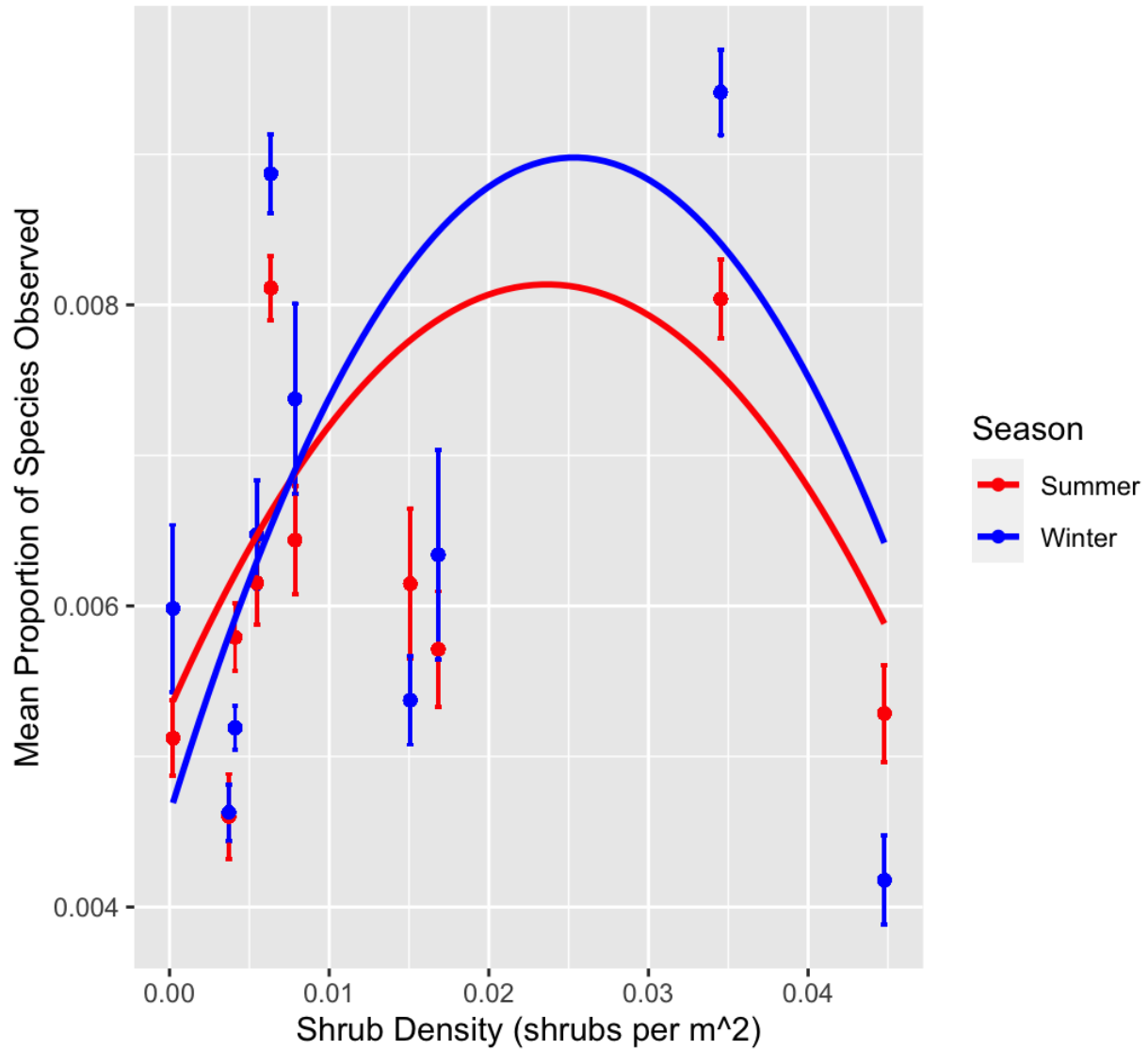


Figure 10. Shrub density and proportion of species observed. Shrub density values are specific to each site. The proportion of species was calculated by dividing the number of species observed in each checklist by the total number of species listed on that checklist and by the log time of checklist duration in minutes. The mean proportion is the average for each site, with standard error shown. The total number of species per checklist varies based on location and season. Shrub density has a positive effect on the proportion of species observed (Table 3).

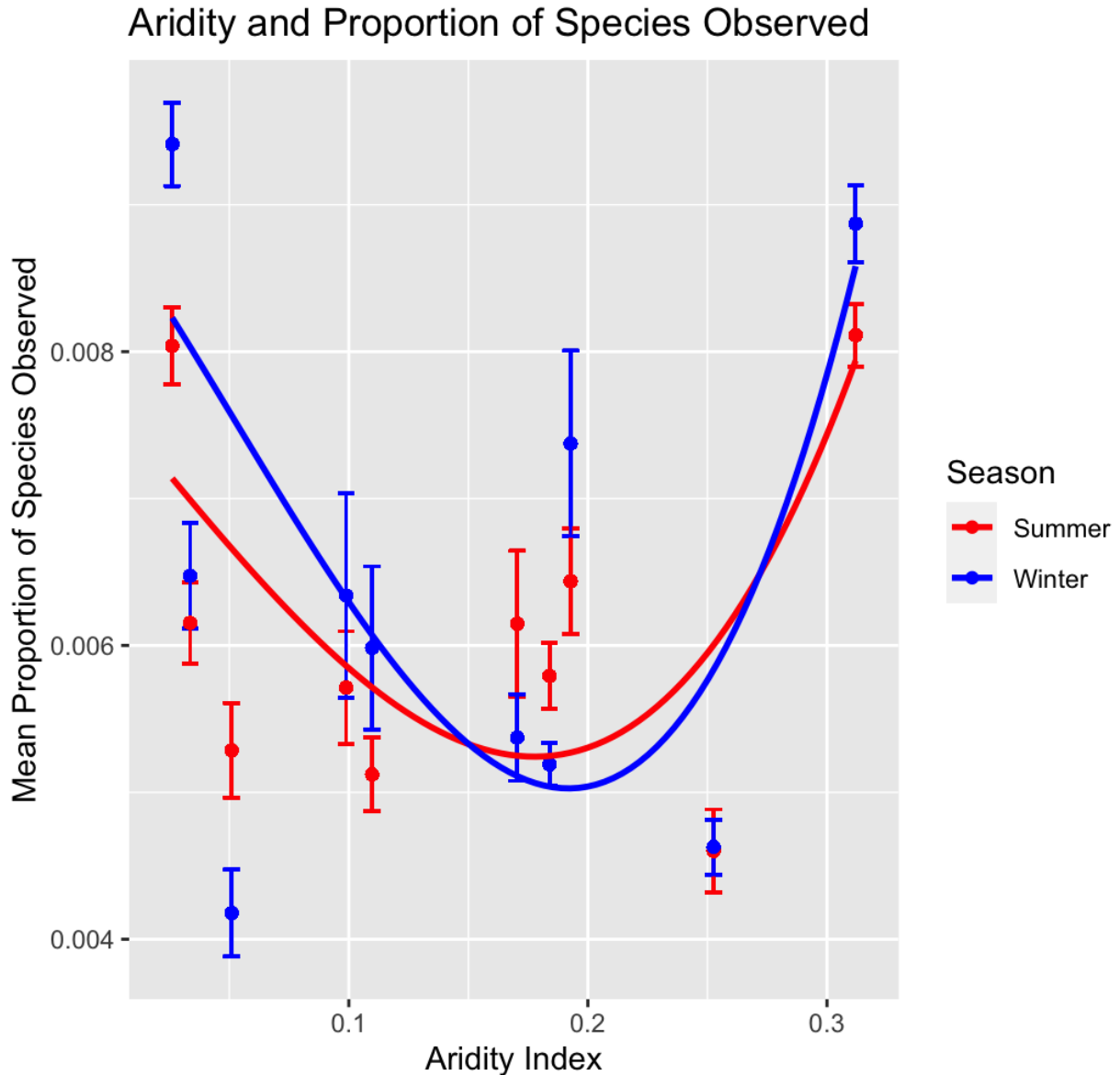


Figure 11. Aridity and proportion of species observed. Aridity was a significant predictor of the proportion of species observed (Table 3). Higher aridity index value indicates a less arid site. The proportion of species was calculated by dividing the number of species observed in each checklist by the total number of species listed on that checklist and by the log time of checklist duration in minutes. The mean proportion is the average for each site, with standard error shown. The total number of species per checklist varies based on location and season.

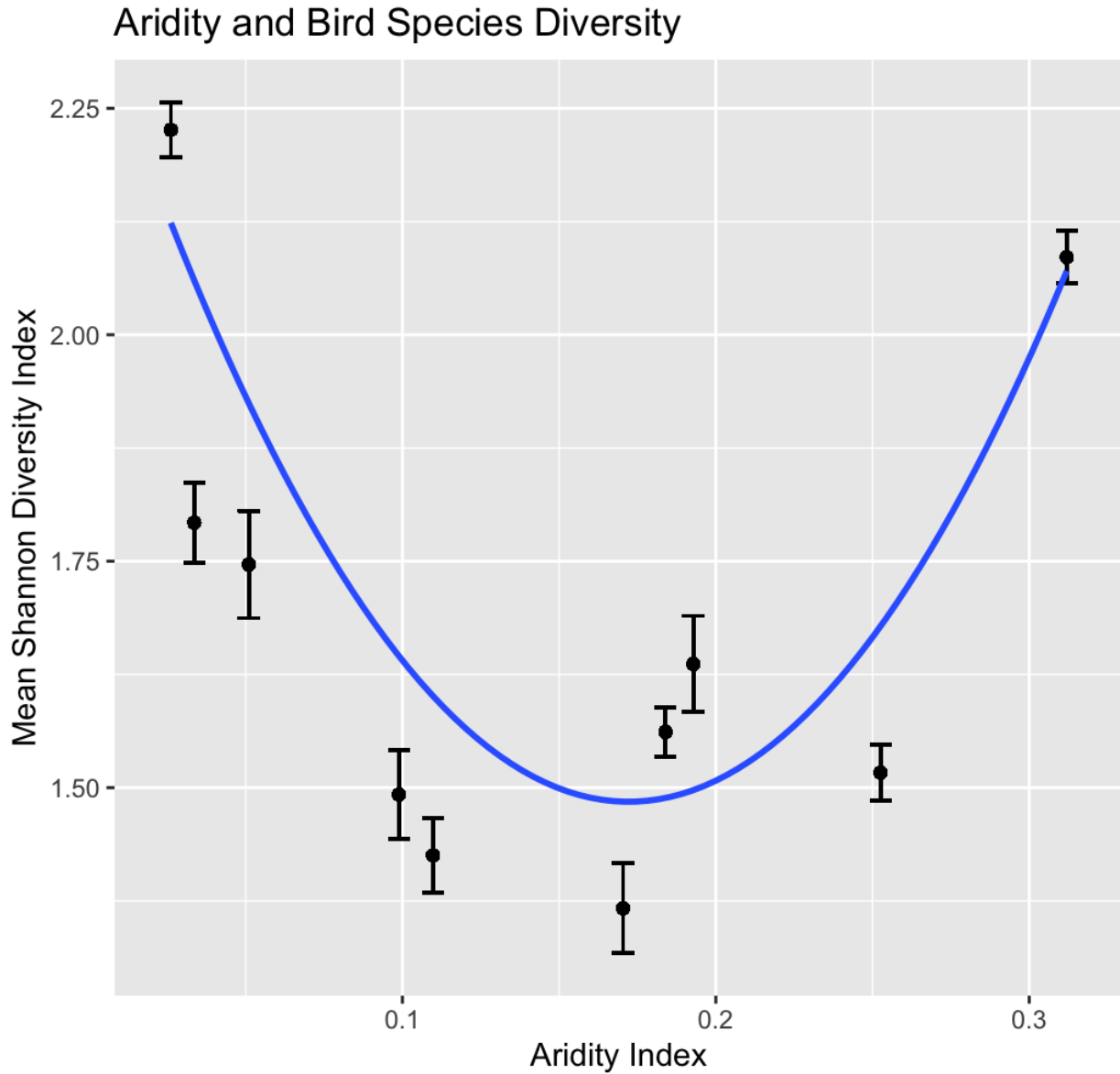


Figure 12. Aridity indices and mean Shannon diversity indices. Lower aridity indicates a drier, more arid site. The Shannon index, a measure of diversity, was calculated for each checklist and averaged per site. This plot does take the duration of each checklist into account. Aridity is a significant predictor of species diversity (Table 4).

Shrub Density and Bird Species Diversity

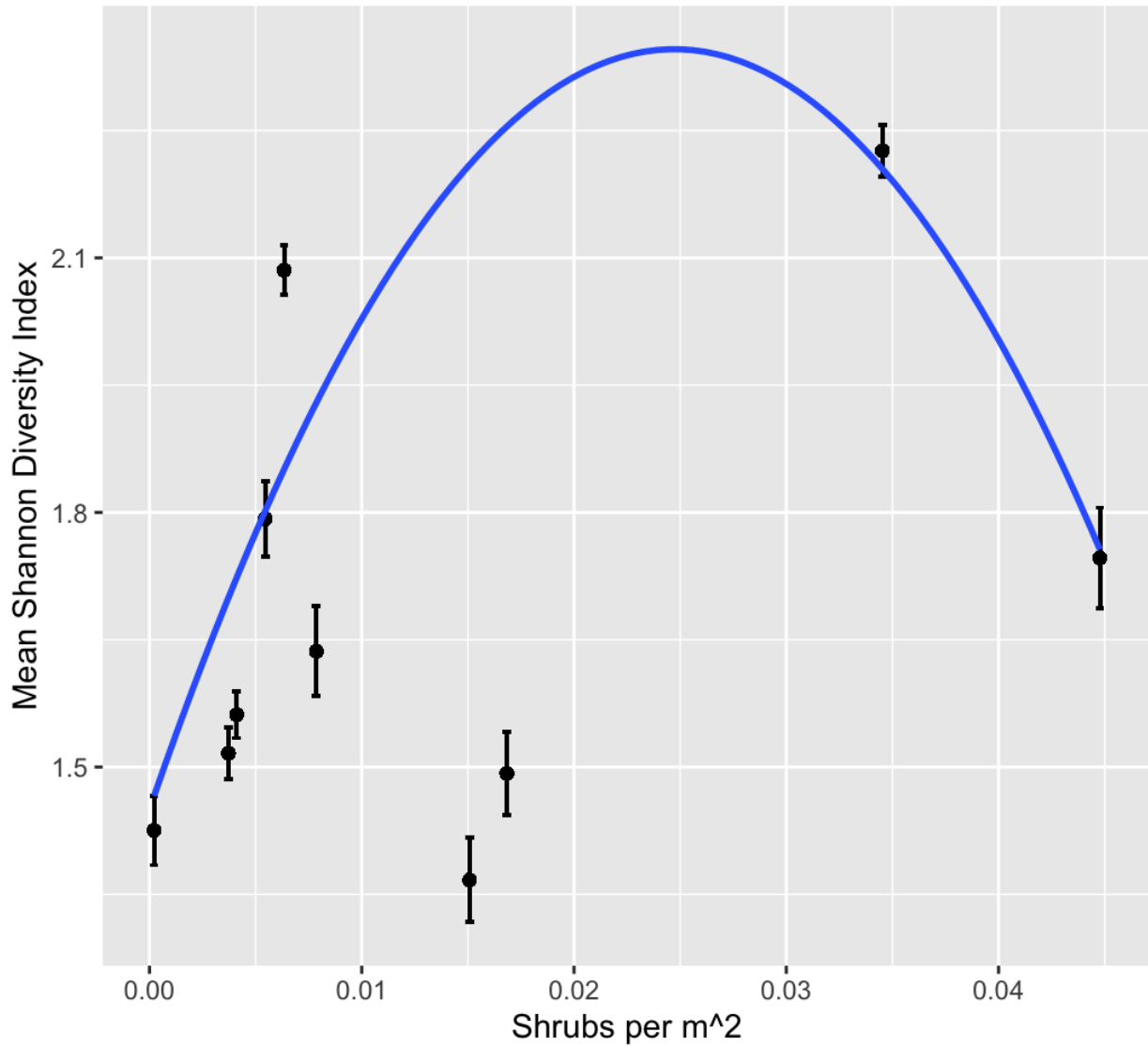


Figure 13. Shrub density and mean Shannon diversity indices, with standard error shown. The Shannon index, a measure of diversity, was calculated for each checklist and averaged per site. Shannon index values were produced by taking the index value for each checklist per site and calculating a mean index per site. This plot does take the duration of each checklist into account. Shrub density is a significant predictor of species diversity (Table 4).

Discussion

Drylands are subject to global anthropogenic changes (Mirzabaev et al. 2022). Avian communities are an important form of biodiversity and are useful for measuring and inferring the effects of these changes. Using citizen science data such as eBird for testing ecological hypotheses at a small spatial scale (e.g., the site level) could be an efficient and affordable means to quickly identify environmental variables that predict avian abundance and diversity in deserts.

The purpose of this study was two-fold, first to determine if eBird can be used to test ecological predictions at the site level and second to determine if shrub density and aridity influence the abundance and diversity of avian communities. I found that eBird has many limitations for site-level questions and that the hypothesis of shrub density influencing bird diversity and abundance was supported. I found that the prediction of greater bird abundance with increasing shrub density was supported, but that the strength of the response was mixed due to small sample sizes across sites.

While eBird data is readily available and abundant, its use for answering questions on small spatial scales is still limited. According to Callaghan and Gawlik (2015), eBird has potential for use at finer spatial scales. They noted that this would depend on survey coverage and whether assumptions and limitations are matched to the scale of inferences. Through my own research, I found that eBird survey coverage alone was an insufficient indicator of data availability and quality. While I began with a large amount of data initially, most of that data was pseudoabsence data derived from the zero-fill process used in marking checklists as complete. Many sites had insufficient eBird data to estimate avian abundance or diversity and so statistical power for hypothesis testing was low, and there were insufficient bird data to test predictions for different groups of birds (e.g., granivore, raptors, insectivores). Future studies instead may

consider selecting locations based on the availability of standardized survey data (e.g., Breeding Bird Survey, Breeding Bird Atlas) in addition to eBird data. Location selection should also consider a site's remoteness and its proximity to major cities or thoroughfares, and the region's overall participation rate in eBird data collection. Though eBird data is designed to minimize integrity problems through various quality filters, the additional use of data collected following a standardized protocol reduces sampling error and allows for replication (Dennis et al. 2010).

I accounted for the effect of time by constraining the data to only a few consecutive years of observations. This minimized the effect of droughts or other climactic factors that may influence bird abundance and diversity (Albright et al. 2010). However, it is worth noting that the COVID-19 pandemic occurred during the observation period, from 2020-onwards. As a result, there was more available data for the years 2020 and 2021 than in previous years (Hillier-Weltman *et al.* 2023). eBird does not test observer skill (Sullivan et al. 2009), and there is a noted effect of skill on bird observations: less experienced observers are more likely to overcount common and easily identifiable birds, undercount rare or difficult to identify birds, and misidentify bird species (Fitzpatrick et al. 2009, Kelling et al. 2015). Though it is difficult to account for observer skill when using citizen science data, future studies conducted at finer spatial scales may require greater precision and therefore greater observer skill than eBird data may provide.

I tested the predictions that shrub density is relatively more important to birds in high aridity sites than in low aridity sites; that shrub density will vary in importance to birds depending on their use of shrubs; that shrub density is more important to birds in the winter; and that overall bird abundance is greater in the winter. I found that there was an effect of the interaction between shrub density and aridity on both avian abundance and diversity. Shrub

density may help to offset the effect of aridity in very dry sites, though a comparison of shrubbed and non-shrubbed sites at various aridity indices would offer more insight into the relative importance of shrubs. I found that shrub density is a predictor of bird diversity but that avian abundance is not consistently influenced by shrub density. *Passer domesticus* is not endemic to California (Moulton et al. 2010); as such, it may be less reliant on ecosystem features such as shrubs. Shrub density may be more important for species that are endemic and non-migratory. Testing the prediction that shrubs are more important to birds in the winter proved difficult due to limitations within the dataset; however, there appeared to be no consistent effect of season on avian abundance or diversity.

Determining seasonal bird abundance on a multi-species scale is difficult because many populations of birds vary in their migratory habits. While most of a species may migrate biannually at regular intervals, not every population of that species will migrate (Ellis and Collins 2019). This was an important consideration, as the total population of *Zonotrichia leucophrys* that I looked at consisted of both migratory and nonmigratory sub-populations; the resident birds were mainly constrained to the location of my study sites, while the overall region was considered part of the migratory population's range (Udvardy and Ferrand 1994). Further, some species may conduct range migrations, where they move to the warmer and colder extents of their ranges; this can influence bird abundance and diversity, as the numbers of these species may not be accounted for with the seasonal division used in this study (Waller et al. 2018).

One factor that may have influenced the outcome of this study are anthropogenic influences such as agriculture, habitat encroachment, and urbanization (Matuoka et al. 2020). Some sites were located adjacent to farms, while others were very far from any urban centres. Anthropogenic factors can both positively and negatively influence birds, depending on their

feeding, breeding, and nesting habits and requirements (Lim et al. 2023, Rodriguez et al. 2017, Jagiello et al. 2022). As a result, species diversity may be lower in urbanized areas, while avian abundance may be higher or lower (Clergeau et al. 1998). Future studies may consider comparing sites that have less variation in their proximity to anthropogenic factors.

A point that could be explored in future studies is whether shrub size or the combination of shrub size and shrub density influences bird abundance and diversity; and whether shrub size is inversely correlated or not with shrub density. In the study sites, shrub size decreased as aridity increased. However, larger shrubs may be able to provide more and possibly more varied resources for a larger number of birds (Smallwood and Wood 2023). Because of this, the benefit of shrubs to birds may be more constrained by aridity rather than by their value to birds; in this case, shrub density may be a mitigating factor in the negative direct and indirect effects of aridity on birds (Rodriguez-Ramirez et al. 2017). Shrub coverage may be correlated with shrub size; as such, the potential benefit of shrubs as thermal refuges may be influenced by shrub coverage as well as by shrub density (Milling et al. 2018).

Groundwater reserves may influence shrub density, abundance, distribution, and size. Desert shrubs have root systems that can utilize groundwater from underground aquifers, but that can also make use of some surface level rainfall (Ng et al. 2015, Amundson et al. 1994). Shrub distribution can influence the amount of groundwater that is absorbed and retained in aquifers (Schreiner-McGraw et al. 2020). In turn, the amount of available groundwater can influence the number and size of shrubs in a site (Elmore et al. 2006). Site geography influences the amount of groundwater that is absorbed into the ground versus the amount captured by shrubs. Hilly landscapes are able to direct a greater amount of water runoff into streambeds when a moderate number of shrubs are present on the hillside, whereas hills with very high or very low shrub

density are less able to channel as much rainfall into streambeds (Schreiner-McGraw et al. 2020). Streambeds transport water more efficiently into groundwater stores due to the increased porosity of their soils, and so an increase in the amount of water they receive will allow for more water to reach underground aquifers (Shanafield et al. 2020). Understanding the relationship between shrub density and rainfall absorption and how shrub distribution may be influenced by groundwater availability is worth further consideration.

Determining the effect of aridity on migratory and resident bird populations may be a valuable next step. If some sites are more or less habitable to larger numbers of migratory species, determining if aridity plays a role in a site's habitability would help determine what factors increase the value of these sites to those species. This could be important for making conservation decisions, as the viability of some sites may strongly influence seasonal diversity, while protecting other sites may provide more benefit to the stable resident population. The importance of each of these types of sites would vary based on conservation goals.

The sites I used comprise a gradient of aridity and of shrub density. Understanding if species distributions change across these gradients, and how and why they might change, could be beneficial. In this case, considering any changes in abundance of indicator species may be worthwhile. As both shrub density and aridity do not change much per year in a given location, this would provide useful insight as to how species respond to immediate weather events such as annual droughts, and how shrub density may help to mitigate the impacts of these events.

Species diversity and abundance are important factors to consider for landscape conservation. Desert ecosystems are extreme environments that are rich in biodiversity. In a changing climate, factors such as species diversity and abundance become even more crucial to

an ecosystem's survival. Maintaining landscape diversity and stability is an important step in ensuring the long-term success of these desert ecosystems.

Implications

The results of my research have implications for future studies of avian desert ecology and the use of citizen science and eBird for testing hypotheses. Desert ecosystems are ecologically valuable, but are also vulnerable to climate change and habitat loss. Desert bird populations are diverse and abundant even in very arid habitats. However, they may be unable to adapt to the rapid increase in climactic events that include prolonged megadroughts and flooding. Understanding how ecosystems maintain stability through network interactions and the use of foundation species will help to inform conservation strategies to preserve desert ecosystems and biodiversity. While citizen science is a valuable resource due to its accessibility and ease of use, its quality and consistency is variable. The use of eBird in answering ecological questions at a fine spatial scale is promising, but its robustness is highly location dependent. As such, eBird data may complement data produced by structured surveys, but is not yet sufficient to be used as a sole data source.

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