THE RELATIVE IMPORTANCE OF MICROCLIMATIC HETEROGENEITY ON PLANT AND ANIMAL COMMUNITIES IN DESERTS OF SOUTHERN CALIFORNIA, U.S.A

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ABSTRACT

This dissertation examines the intricate relationships between facilitation, environmental heterogeneity, and artificial habitat constructions in arid ecosystems, focusing on plant-animal and plant-plant interactions. By leveraging ecological principles, it explores the role of foundation plant species like *Ephedra californica* and *Larrea tridentata* in fostering ecosystem resilience and biodiversity under adverse conditions due to climate change, land use, and desertification.

The study starts with an overview of facilitation theory, highlighting its importance in mitigating the negative effects of abiotic stressors in arid and semi-arid regions. It highlights the Stress Gradient Hypothesis (SGH) as a framework for understanding how competitive interactions can shift towards facilitation under harsh conditions, thus promoting the survival of diverse flora and fauna. The dissertation then delves into environmental heterogeneity, explaining its complex influence on ecosystem dynamics, species composition, and microclimatic regulation.

Chapter 2 provides a detailed analysis of camera trapping techniques, offering optimal sampling design strategies for accurately estimating vertebrate abundance and richness. Chapter 3 examines the effects of artificial canopies on microclimate regulation. This chapter evaluates various eco-friendly fabrics, such as natural burlap, cotton, and nursery seedling fabric, in buffering microclimate through lab experiments measuring understory temperature, relative humidity, and radiation.

Chapters 4 and 5 investigate how climatic variations and vegetation structure contribute to spatial and environmental heterogeneity, shaping flora and fauna diversity and abundance. A key aspect of the study is evaluating the effectiveness of artificial habitat construction as a conservation and restoration strategy in arid landscapes. Field experiments assess the microclimatic buffering capabilities of artificial shelters compared to natural vegetation in supporting vertebrate populations amid desertification in the Southwestern U.S.A.

Overall, this dissertation enhances our understanding of the complex interplay between facilitation, environmental heterogeneity, and habitat modification in arid ecosystems. By uncovering the mechanisms behind these ecological processes, it provides valuable insights for conservation, management, and restoration efforts in regions vulnerable to anthropogenic disturbances and climate change.

DEDICATION

"To the people whose labors go beyond ideas into the realm of 'real materials'- to the dry-land ecologists, wherever they may be, in whatever time they work, this effort at prediction is dedicated in humility and admiration."

— Frank Herbert

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CHAPTER 1: GENERAL INTRODUCTION

1.1: PLANT-ANIMAL AND PLANT-PLANT FACILITATION

Facilitation is a non-trophic interaction that is widely studied in community ecology (Brooker et al., 2007). Facilitation is defined as an interaction where one species called the *benefactor* provides benefits to one or more species referred to as *beneficiaries* while none are harmed (Bertness & Callaway, 1994). Generally, competitive interactions tend to become facilitative in the face of harsh abiotic conditions, and the magnitude of this interaction also increases. This is referred to as the Stress Gradient Hypothesis (SGH; Figure 1.1) and is widespread in many dryland ecosystems where harsh abiotic conditions pose a threat to many animals and plants (Lortie et al., 2020; Lortie, Filazzola, et al., 2022; Westphal et al., 2018). Because facilitation is common along a gradient of high abiotic stress as opposed to more benign conditions (Maestre et al., 2009), many studies of positive interactions have focused on harsh environments, including arid and semi-arid ecosystems (Lu et al., 2018; Synodinos et al., 2015). Plant-animal interactions are widespread in many ecosystems and foundation species (a species with a strong role in community structuring) can benefit animals via mechanistic pathways that include, but are not limited to, seed trapping, abiotic stress amelioration, herbivore protection, increasing pollination services, facilitation-mediated secondary seed dispersal, and soil modification (Filazzola & Lortie, 2014; Lortie et al., 2016). Similarly, plant-plant interactions also center around benefits such as increased nutrient availability, increased soil moisture, and buffering of abiotic stress (Brooker et al., 2007). The pivotal role of facilitation is more clear today than ever before given the current paradigm of anthropogenic disturbances, including climate change, extreme weather events, and the increased frequency of mega-droughts in deserts (Bachelet et al., 2016; Finch, 2012; Williams, 2014). Hence, it is important

to understand how the theory of facilitation can be used to advance conservation, management, and restoration efforts in arid and semi-arid regions.

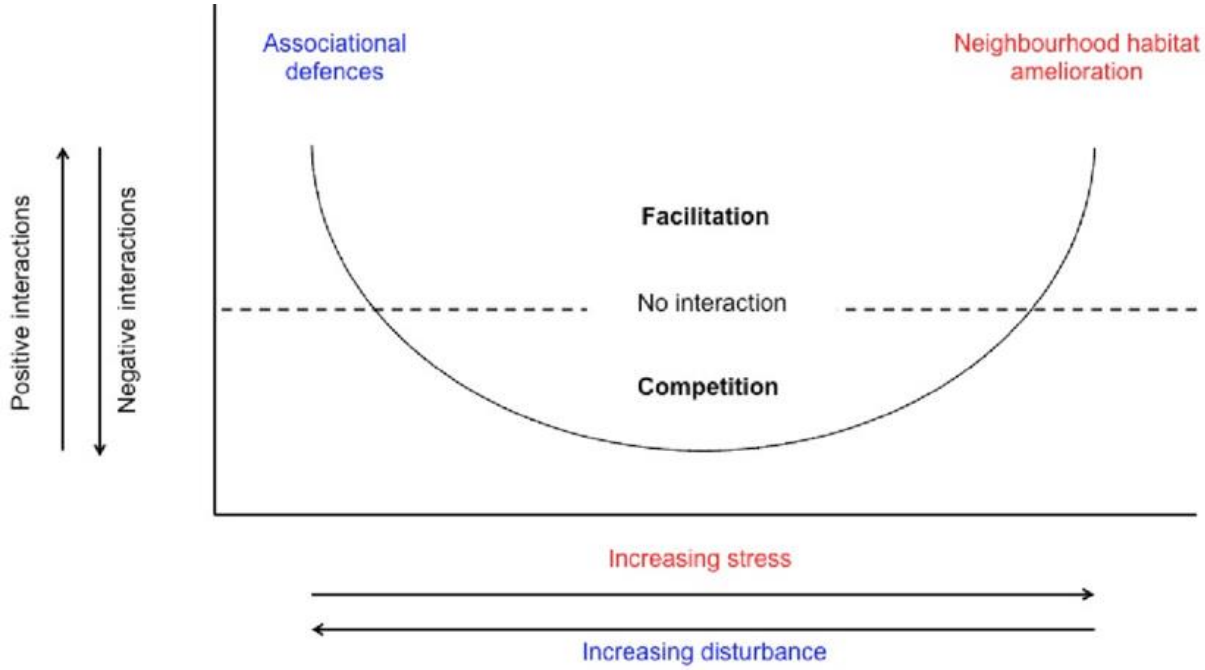

Figure 1.1: The Stress Gradient Hypothesis (SGH) is the shift in abiotic interactions along stress and disturbance gradients. Competitive interactions become facilitative under stressful abiotic conditions. This is evident in many arid and semi-arid regions of Southern California. Adapted from *Al Hayek, (2014).*

1.2: FOUNDATION PLANT SPECIES

Vegetation is an integral component of all ecosystems globally. Similar to a keystone species, a foundation species can occupy a lower trophic level but create locally stable conditions required by other species (Attum & Eason, 2006). Unlike keystone species, however, foundation species are generally plants that are locally abundant and encompass the greatest biomass in an ecosystem (Ellison et al., 2005). *Ephedra californica* (Mormon Tea) is a dominant or co-dominant native foundation shrub occurring with *Larrea tridentata* (Creosote Bush) in the Southwestern regions of California (Figure 1.2 and 1.3; Sawyer et al., 2009). This key foundation plant plays a pivotal role

in the facilitation of dryland ecosystems in California (Liczner et al., 2016; Lortie et al., 2020) acting as a structural agent of facilitation providing shelter and acting in thermoregulation (Gaudenti et al., 2021; Ivey et al., 2020; Vázquez et al., 2009). *Larrea tridentata* (Creosote bush) is also a dominant or co-dominant flowering shrub that is often found in the sandy soils, desert pavements, and well-developed cryptogram layer of the Mojave Desert (Braun et al., 2021; Stuart & Sawyer, 2001). *Larrea tridentata's* association is well-explored concerning pollinators but not vertebrate species (Braun & Lortie, 2019). Foundation plants are important at fine scales because they lower temperature, elevate humidity, create a windbreak, and reduce exposure to direct sunlight, and at coarse scales because they increase spatial connectivity and environmental heterogeneity (Sanczuk et al., 2023). Foundation shrubs provide critical resources to both resident flora and fauna of a given region and positively influence community structure and assemblage.

Figure 1.2: *Ephedra californica* commonly referred to as Mormon Tea is a yellow-flowering shrub within the Carrizo Plain National Monument, California, U.S.A. Photograph is courtesy of *Calflora* (https://www.calflora.org/app/taxon?crn=2972).

Figure 1.3: *Larrea tridentata* or Creosote Bush is a dominant or co-dominant shrub within the Mojave Desert, California, U.S.A. Photograph is courtesy of *Calflora* (https://www.calflora.org/app/taxon?crn=4573).

1.3: ENVIRONMENTAL HETEROGENEITY AND CLIMATE

One of the main goals of ecology is understanding the effects of environmental heterogeneity on diversity, disturbance, ecosystem services, and ecosystem resilience. Environmental heterogeneity (EH) is broadly defined as, "non-uniformities in physical and ecological landscape characteristics" (Dronova, 2017). Spatial EH encompasses horizontal habitat variation (variation through space) and complexity in the vertical components such as vegetation (Grelle, 2003). Spatial EH can be divided into five main subject areas including two biotic components: land cover, and vegetation, and three abiotic components: climate, soil, and topography (Stein et al., 2014; Stein & Kreft, 2015). Broadly speaking, climate varies by latitude, which influences temperature and moisture (Turner & Gardner, 2015). Though latitude and continental position are important, finer-scale heterogeneity can be dictated locally by topography (Bailey, 2009). Thus, climatic EH can be

defined using latitude (i.e. relative closeness to the poles) and topography (i.e. elevation). Climate or 'macroclimate' is measured as the long-term averages of the suit of meteorological variables such as temperature, precipitation, humidity, and wind (Turner & Gardner, 2015). 'Microclimate' is an exceptionally complex, non-linear phenomenon that involves interplay between local and global processes (Zanchi et al., 2023). Microclimate is the climate experienced in the lower 2m of the atmosphere and the upper 0.5-1m of the soil (Stoutjesdijk & Barkman, 2014). Thus, microclimate involves local variabilities in climate due to landscape heterogeneity, such as temperature under a tree canopy versus in the open. Climatic changes are expected to modify the type and distribution of ecosystems around the globe (Moritz & Agudo, 2013). Climate can impact plant community assembly by dictating species range shift and composition (Feeley et al., 2020), as well as phenological activities such as fruiting and flowering (Panchen, 2016). Monitoring the rapid change in climate over the upcoming years and how it influences heterogeneity through impacting 1) which species can localize which areas and 2) the distribution of plants and animals will be key to wildlife conservation and management.

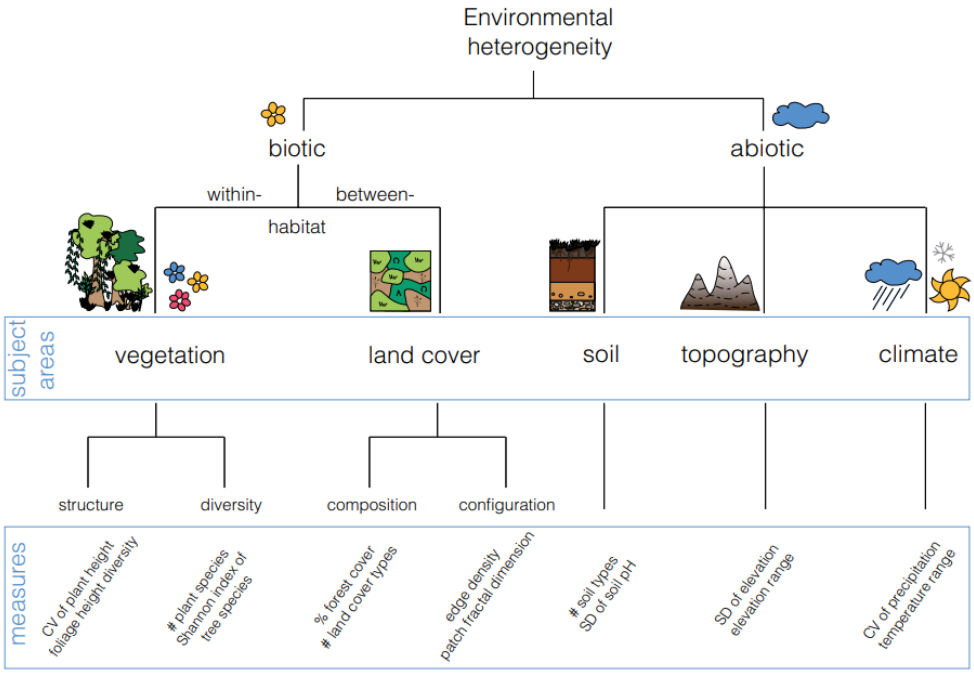

Figure 1.4: Abiotic and biotic components of Environmental Heterogeneity (EH) are shown. Abiotic components include soil, topography, and climate, and biotic components are vegetation and land cover. The most common measure(s) for each component are listed. Adapted from *Stein and Kreft (2015)*.

1.4: ENVIRONMENTAL HETEROGENEITY AND PLANTS

Vegetation is a widely studied aspect of heterogeneity because the type of vegetation can directly affect both the local animal and plant species' composition and abundance. Vegetation EH is defined using two different criteria: the taxonomic profile of plants (i.e. diversity), and measures of the physical structures such as foliage height diversity and trunk diameter (Stein & Kreft, 2015). Vegetation heterogeneity is associated with diversity in resources, shelter, roosting, and breeding and oviposition sites for resident species (Kissling et al., 2007; Tews et al., 2004). Diversity in the 3-D structure of plants is important because it controls the transfer and interception of solar radiation, productivity, nutrient cycling, and sequestering of atmospheric carbon dioxide (Dronova, 2017). For instance, shrub canopies create micro-environmental benefits including increasing shade, reducing radiation load, increasing night-time winter temperature, and increasing soil moisture, and canopy

structure plays an important role in differences observed in these microclimatic parameters (Jankju, 2013). In deserts, microclimatic variability by shrubs can contribute to the overall EH (D'Odorico et al., 2010). Because EH provides small niches where species can continue to persist, we must examine the interplay of plant structure in creating such niches.

1.5: ARTIFICIAL HABITAT CONSTRUCTION

Artificial shelters and refuges are commonly present today for conservation, restoration, and habitat enhancement purposes (Liberman et al., 2024; Watchorn et al., 2024). Like natural vegetation, artificial infrastructure can alter and buffer the surrounding microclimate and impact species' behavioural and physiological regulations (Ghazian et al., 2020b; Liberman et al., 2024; Yu et al., 2022). To a certain extent, they can mitigate the impacts of global warming and promote processes such as hatchling production (Esteban et al., 2018; Reboul et al., 2021). Species can use artificial structures for thermoregulation (Lelièvre et al., 2010) and perching (Athiê & Dias, 2016). However, to ensure artificial construction is not used as an improper biodiversity offset, it is crucial that they are monitored across pertinent ecological geographical and temporal scales and that their effects are compared to suitable controls (Watchorn et al., 2023). Shelters constructed from biodegradable lignocellulosic fabrics are an ecologically viable option that aids in buffering microclimate in drylands (Ghazian, MacDonald, et al., 2024). It is essential that their effects are tested in the field to better understand their influence on local species abundance and diversity and thus their use in wildlife conservation.

1.6: CAMERA TRAPPING IN ECOLOGY AND WILDLIFE BIOLOGY

Animal observation is an important form of behavioural and ecological research in many ecosystems. Camera traps provide a mechanism to collect observation data on animals in their natural habitat and interactions with their environment with relatively limited human disturbance (O'Connell et al., 2011a). Besides their use in wildlife viewing, camera traps have been used in studies that focus on nest ecology, detection of rare species, estimation of population size and species richness,

behavioural studies, habitat use, and occupation of human-built structures (Cutler & Swann, 1999; O'Connell et al., 2011b). One of the major uses of the device, particularly in ecology, has been to record vertebrate activity patterns used to determine parameters such as occupancy, abundance, and diversity (Karanth et al., 2004; Kelly, 2008). Perhaps the greatest advantage of this sampling method as opposed to other efforts is that it can record accurate data without the animal being captured or the researcher being present. As such, camera traps allow for a versatile method that can be employed for the monitoring of wildlife but also enable the evaluation of conservation and management actions.

1.7: CURRENT WORK: EXAMINING THE IMPACT OF MICROCLIMATIC HETEROGENEITY AND ARTIFICIAL SHELTERS ON DESERT VERTEBRATES AND PLANTS

There is widespread evidence that plants like foundation species can support related species through various mechanistic pathways (Filazzola & Lortie, 2014). Despite this, microclimatic facilitation by vegetation is largely ignored (Brigham & N. Suding, 2023). The importance of vegetation's 3-D structure, such as canopy volume and area, in creating microclimatic heterogeneity is often overlooked. Additionally, natural vegetation's microclimatic buffering abilities are seldom compared to eco-friendly artificial structures intended for conservation, and their associations with resident fauna are not well-explored. The purpose of this dissertation is to address such gaps in the facilitation literature. To do this, I begin with a systematic review and meta-analysis of camera traps to evaluate the minimum sampling effort required to accurately estimate animal abundance and richness in a given area (Chapter 2). The findings suggested that deploying more cameras for a shorter number of days provides the most effective estimates of vertebrate abundance and richness for a region. I used these findings to create a more effective experimental design for evaluating the association of vertebrates with artificial shelters and shrubs in my final chapter (Chapter 5).

Further to this, I continued from my previous work (Ghazian et al., 2020b), to test the impacts of artificial canopies in buffering microclimate (Chapter 3). I tested lignocellulosic, eco-friendly

fabrics, including natural burlap, cotton, and nursery seedling fabric, and tested their impact on understory temperature, relative humidity, and radiation. This chapter demonstrated that natural fabrics influence microclimate differently and their selection and use in the field ultimately depends on which parameters you are trying to control. Nonetheless, it showed that eco-friendly, biodegradable fabrics offer immense potential for artificial habitat construction in drylands.

In my next chapter, I investigated the relationship between *E. californica's* 3-D canopy volume and understory microclimate, and the impact of microclimate on the understory plant abundance and richness (Chapter 4). Canopy volume was a weak predictor of microclimate, demonstrating that even small, low-stature shrubs can uphold positive interactions. Shrub cover also had positive effects on the understory plant abundance due to increasing EH but not plant richness. This suggested that plant-plant interactions and their responses to climate can be more complex than formerly thought.

In my final chapter, I extend the findings of Chapter 2 by testing artificial shelters in the field (Chapter 5) during a 'dry' and a 'wet' year. I tested two types of artificial shelters (square and triangle) with burlap as covering. Vertebrate abundance and richness exhibited higher numbers at foundation shrubs and artificial shelters compared to the open gap likely due to the microclimatic buffering abilities of these microsites.

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CHAPTER 2: FINDING THE SWEET SPOT IN CAMERA TRAPPING: A GLOBAL SYNTHESIS AND META-ANALYSIS OF MINIMUM SAMPLING EFFORT

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2.1: Chapter Summary

Camera traps are one of the most common tools in wildlife and conservation biology. Sampling can document and measure animal presence and activity. Captures can be used to estimate population parameters such as presence, abundance, habitat suitability, and resident species richness of specific populations. Effective camera trapping is relevant to conservation for many reasons. For instance, they can be used to inform pre and post-restoration efforts, monitor the use of artificial structures by species and assess behaviours like predator-prey interactions. This sampling approach can aid in assessing diversity change, habitat change, pre- and post restoration efforts, artificial structure effects, species presence, and animal behaviour. We reviewed the literature to collect data and estimate incidence effect size measures for both vertebrate abundance and vertebrate richness to examine the relative efficacy of deploying more camera traps for a given period in different ecosystems. Increasing sampling effort through an increased number of cameras significantly increased net positive abundance detection rates in grasslands and mixed ecosystems. Net richness detection rates in mixed, tropical, deciduous, and grassland ecosystems similarly increased with the number of cameras deployed. The total number of days however was not a significant predictor of abundance or richness rates detected in any ecosystem. These findings suggest that deploying relatively more cameras for relatively fewer days provides the most effective estimates of vertebrate abundance and richness for a region.

2.2: Implications for Managers

- Camera traps are an extremely useful tool in wildlife research. Upon reviewing the literature, we have concluded that to obtain accurate estimates of animal abundance and richness, managers should opt for deploying more cameras systematically rather than for longer periods.
- Our results show that the ecosystem of study is an important factor in deciding how many camera traps you need and for how long, and the predicted Minimym Trapping Effort (MTE)

suggests that it is important to take deployment into account differentially within a site or region.

- Although purchasing more camera traps requires more initial funding, the cost is offset by the low maintenance required and the results obtained are comparable to those of live traps.

2.3: Introduction

Monitoring and measuring the number of animals and diversity of animal communities in terrestrial ecosystems comprises an important set of methods in ecology and evolution. Camera traps are frequently a primary tool to survey wildlife and their interactions with the surrounding environment. These survey devices normally record animal presence via a triggered passive, infrared motion sensor (Rowcliffe et al., 2011). They are one of the most popular survey tools in current wildlife research, particularly in the domain of terrestrial vertebrate biology (Meek et al., 2014). Cameras can record activity patterns and be used to infer occupancy, abundance, and species diversity (Kelly, 2008; O'Connell et al., 2011b). Camera traps have also been used in studies to examine behaviour (Rowcliffe et al., 2014), habitat use (Rovero et al., 2014), detection of rare species in a community (Thomas et al., 2020), estimation of population size and species richness (Whytock et al., 2021), and occupation of human-built structures (Table 2.2) (O'Connell et al., 2011). Thus, camera trap data can be used to quantify many ecological parameters and help advance theories such as niche partitioning, habitat use, as well as various behavioural models (Frey et al., 2017; Smith et al., 2020). They are also a fundamental species monitoring tool in higher conservation value ecosystems such as the Serengeti (Swanson et al., 2015) and the Amazon Basin (Trolle, 2003). These data can then be used to evaluate the efficacy of survey designs (Kays et al., 2020) to support management.

Various factors can influence the number of species detected by camera traps, as well as the trapping rate (ratio of photographs of particular individuals of a species to camera trapping duration) (Rovero & Marshall, 2009). The camera model, placement and orientation, temperature differentials,

and species' behavioural responses are some of the factors that impact the collected data (Meek et al., 2015). Thus, study design decisions include camera model, number of cameras, duration, and placement within a system. The factors above can be summarized as trapping effort and trapping design, which can influence abundance and diversity estimates (Wegge et al., 2004; Yasuda, 2004). Trapping rate is a useful index for abundance and diversity estimates (Rovero and Marshall 2009; Rowcliffe et al., 2008; Silveira et al., 2003). Minimum trapping effort (MTE) is another important factor for population estimates (Table 2.3) (Si et al., 2014). MTE refers to the number of camera trap days required to record species of interest in an area and varies extensively across studies (Si et al., 2014). Sampling design decisions can be directly related to factors such as funding that can affect detection probabilities and impact the strength of population estimates (Foster & Harmsen, 2012). The interplay amongst these factors provides us with an excellent opportunity to explore the relationship between trapping duration, number of cameras, and richness and abundance estimates across the literature, worldwide.

Globally, many species are threatened by anthropogenic challenges such as climate change, pollution, habitat loss, and hunting. The capacity of camera traps shows that this simple technology if effectively deployed can be used in directing conservation actions including when and where species are doing well or declining and what factors are different between these stations (Wich & Piel, 2021). In addition, it can show us to the extent that species diversity is changing (Rich et al., 2017). Camera trapping in different habitats can be used to identify species' habitat preferences, niche models, and range models (Wich & Piel, 2021) such that biologists can inform assessments of the effectiveness of different potential management strategies. For example, the distribution patterns of secretive mammals, such as the bushy-tailed mongoose (*Bdeogale crassicauda*) in Tanzania, were documented using camera traps (Pettorelli et al., 2010). This species was detected at higher rates in national park areas than in-game reserves. Spatial comparison using camera traps can also serve as a

threat assessment (de Oliveira et al., 2020). In a private reserve in Africa, camera trap imagery demonstrated that trophy hunting of leopards contributed to the fall of the population size below carrying capacity (Chapman & Balme, 2010). The implementation of cameras for conservation is thus varied and there are many other implications and uses (Table 2.2). As such, camera trapping not only allows for the monitoring of wildlife, but also enables the evaluation of conservation actions.

The TEAM project is an excellent example of a partnership between various organizations that conducts standardized camera trapping of 17 protected areas worldwide (Fegraus et al., 2011). In one of their studies, this partnership examined the protection of threatened mammal populations by comparing and contrasting poorly-protected forest sites and reserve sites in Tanzania. They found a reduction in species richness, community structure, and species-specific occupancy in unprotected sites (Oberosler et al., 2020). This partnership has also shown that a ban on anthropogenic threats, such as firewood, can positively affect animal communities. Wildlife biologists commonly rely on camera trap studies for conservation. Synthesis of the effectiveness of experimental deployments of camera traps thus falls at the heart of informing conservation.

We used a meta-analysis to evaluate the relationship between sampling effort (number of cameras, days of trapping) and abundance and richness estimates. Previous methods such as rarefaction curves and extrapolations developed by Chao et al., (2014) do provide us with the means to quantify the relationship between sampling effort and estimates of richness and abundance; however, herein we developed two incidence effect size measures used in other fields (Ilies et al., 2003; X. Li et al., 2018) to evaluate the relationship between abundance and richness by sampling effort when you do not have diversity or population estimate data from the field. We hypothesized that sampling size can be used to inform us of the optimal way of allocation sampling effort. Furthermore, we estimated the inflection points (Goshu, 2013) for both net abundance and net richness indices to obtain the MTE required for abundance per camera and richness per camera. The

importance of these critical design decisions was also assessed for different ecosystems. Given that camera traps are increasingly used in ecology and evolution (Tabak et al., 2019), this synthesis provides an insight into the 'sweet spot' for potential optimal sampling before one begins a field study in any ecosystem. The capacity for this method to provide meaningful and sufficient animal data will better inform conservation efforts and fundamental theory.

2.4: Methods

Literature review

We reviewed the literature to obtain data for a measure of richness or diversity, the number of captures (abundance), and the duration of camera trapping (i.e. days), and the number of cameras. We conducted a systematic review using the terms camera trap* and richness*, or diversity*, and camera* trap* and rarefaction* curve* in ISI Web of Science (WoS) (*Web of Science.*, 2021) as two searches. These searches were done in the latter quarter of 2021. Additionally, we conducted supplemental searches in book chapters and Google Scholar to validate the publication coverage of WoS. This process resulted in a total of 557 publications, once duplicates were removed, spanning the years 2001-2021. A PRISMA diagram illustrates the exclusion and review process (Moher et al., 2009) (Appendix A; A). We used best practices to ensure that workflow and synthesis were reproducible and transparent (Bayliss & Beyer, 2015). We screened the abstracts (summaries) and excluded papers based on relevance, whether they were a review, opinion, or idea paper, focused on aquatic ecosystems, were not written in English (or the English text version was unavailable), were qualitative, did not examine vertebrate species, and if they focused on one species or a group of animals (such as wild cats) and ignored other observed animals. A total of 292 full-text articles were reviewed for a measure of richness or diversity, the number of captures, and/or duration of camera trapping (i.e. days) of which 149 full-text articles had viable data and were included in the final analysis. Data were extracted from article text or tables. Variables such as the location of the study, number of cameras, sites, and ecosystem were also recorded.

Meta-Analyses

All meta-statistical analyses were performed in R version 4.2.2 (R Development Core Team, 2023). Effect sizes were calculated using the number of species and the number of animals (captures) using the incidence rates in the package *metafor* version 3.0-2 (Viechtbauer, 2010). The incidence rates for the effect size measure were calculated by dividing the number of animals or the number of species against the total number of cameras by the total number of study days (Higgins et al., 2021). These indices are defined as net abundance and net richness detection rates. Random-effects models (*rma)* were used to model estimated indices and their standard errors with 'Ecosystem' serving as moderator. This was done to model the effects of deploying more cameras on net abundance and net richness and see estimated significance. 'Ecosystems' were extracted from the studies and later narrowed down to six main ecosystems, including coniferous, deciduous, tropical, grassland, mixed, and desert. Mixed ecosystem referred to any ecosystem that was a combination of two or more ecosystems listed in the analyses. Weighted regression models were applied to analyze estimated values for abundance per camera and richness per number of cameras over the total number of days to correct for heteroscedasticity (Kutner et al., 2005). In this procedure, more weight is given to observations with smaller variances to provide more reliable information about the regression function than those with large variances (Kutner et al., 2005). Heterogeneity in all models was examined to ensure that variance was not unduly inflated from grouping similar measures into the random-effect models (Langan et al., 2019). Heterogeneity was tested by examining Cochran's Q statistic (Bowden et al., 2011). Publication bias was tested using Egger's regression test (Egger et al., 1997).

2.5: Results

A total of 149 articles were included in the meta-analysis comprising 3428 unique sites. The supporting R scripts are published on Zenodo (Ghazian and Lortie, 2021), and data are published on Knowledge Network for Biocomplexity (KNB) (Ghazian & Lortie, 2021). The most common

ecosystems for the studies were tropical (38) and deciduous forest (25 studies). Observed vertebrates were small and large mammals, birds, and reptiles. The number of study days varied between 163-426,250 days.

Net abundance detection rate estimates resulted in an asymmetric funnel plot, suggesting systematic differences between the studies (Appendix A; B, heterogeneity $p<0.0001$). Ecosystem was a significant moderator in the model for net abundance detection rates ($F = 4.8830$, $p = 0.0003$, $df = 6$). The effect of deploying more cameras was significantly positive in grassland and mixed ecosystems (Figure 2.1 and Table 2.1). Systematic differences between studies were also shown in funnel plots of net richness detection rates (Appendix A; C, heterogeneity $p<0.0001$). Ecosystem was a significant moderator in the model ($F = 14.79$, $p<0.0001$, $df = 6$). Furthermore, the net effect of deploying more cameras was positive in mixed, tropical, deciduous, and grassland ecosystems (Figure 2.1, Table 2.1). Abundance per camera regressed against the total number of days showed significant heterogeneity between groups (Figure 2.2, $R^2 = 0.0\%$, heterogeneity $p<0.0001$). This was also shown for richness regressed against the number of days (Figure .32, $R^2 = 0.73\%$, heterogeneity $p<0.0001$). The MTE for abundance per camera was 3236 days and 855 days for richness per camera was calculated based on inflection when the rate was convex (Goshu, 2013). There was no effect of increasing the duration of the study (i.e. total number of days) on abundance per camera deployed ($F = 0.0037$, $p<0.952$, $df = 1$), or richness per camera ($F = 0.3698$, $p<0.545$, $df = 1$).

Table 2.1: Mixed-effect model estimates and standard error (SE) for net abundance detection rate (number of animals/number of cameras/number of days) and net richness detection rate (number of species/number of cameras/number) are given. Ecosystem served as a moderator in the model. Significant p-Values are bolded.

Detection Rate	***Ecosystem***	***Estimate***	***SE(±)***	***t-Value***	***95% CI.lb***	***95% CI.ub***	***p-Value***
Abundance	***Coniferous***	0.1417	2.6849	0.0528	-5.2057	5.4891	0.9580
Abundance	***Deciduous***	1.0125	0.7594	1.3333	-0.5000	2.5250	0.1864
Abundance	***Desert***	1.1951	2.1922	0.5452	-3.1710	5.5612	0.5872
Abundance	***Grassland***	2.9580	1.3424	2.2035	0.2843	5.6317	**0.0306**
Abundance	***Mixed***	6.8013	1.5501	4.3876	3.7139	9.8886	**<0.0001**
Abundance	***Tropical***	1.0870	0.6160	1.7647	-0.1398	2.3138	0.0816
Richness	***Coniferous***	0.0018	0.0063	0.2825	-0.0108	0.0144	0.7784
Richness	***Deciduous***	0.0104	0.0018	5.8472	0.0069	0.0140	**<0.0001**
Richness	***Desert***	0.0069	0.0052	1.3454	-0.0033	0.0172	0.1826
Richness	***Grassland***	0.0086	0.0034	2.5522	0.0019	0.0153	**0.0127**
Richness	***Mixed***	0.0153	0.0036	4.2010	0.0081	0.0226	**<0.0001**
Richness	***Tropical***	0.0077	0.0014	5.3384	0.0048	0.0106	**<0.0001**

Table 2.2: A summary of ways camera trap data uses that can be incorporated in directing management actions. Implications and descriptions, as well as examples from the literature, are presented.

Use in management	***Implication***	***Description***	***Illustrative Studies***
Examining the types of species living in a region.	**Diversity change**	Monitor the extent of species diversity change to direct conservation action.	Rich et al. 2017
Observing the impacts of changes in spatial and temporal dynamics of an ecosystem.	**Habitat change**	Examine habitat change, such as changes in vegetation dynamics, to make better-informed management decisions.	Sun et al. 2021
Examining wildlife parameters in areas before and after restoration.	**Pre/post-restoration**	Compare and contrast protected and unprotected sites to examine species richness and community dynamics.	Littlewood et al. 2021 Oberosler et al. 2020
Gathering information about how species in a region interact with artificial structures.	**Artificial structure**	Monitor the use of artificial construction such as electric fences and trenches, wildlife corridors, and acoustic, light-based, and agricultural deterrents that reduce human-wildlife conflict.	Green et al. 2018 Shaffer et al. 2019
Assessing if threatened species have ceased or continue to exist in a given region.	**Presence/absence**	Assess the presence and absence of endangered or hard-to-identify species using camera traps.	Burns et al. 2017
Gathering information about what animals are doing on a daily or in specific situations such as respond to stimuli.	**Animal behaviour**	Assess behaviour such as predator-prey interactions to guide future management efforts of endangered species.	Linkie and Ridout 2010

Table 2.3: A definitions table for key terminologies.

Terminology	*Definition*
Abundance (captures)	Number of individual animals in a particular ecosystem. In this study, we used the number of captures and abundance interchangeably.
Richness/diversity	The number of different species present in an ecological community.
Minimum Trapping Effort (MTE)	The number of camera trap days required to record species of interest in an area
Trapping Rate	The number of photographs, of usually a particular species, over the duration of camera trapping in a particular area.
Detection Rate	The probability that a given individual will encounter a camera per unit of time.
Incidence Rate Ratio	An effect size measure consisting of the ratio of two rates. The first is a count in a particular parameter such as abundance or richness divided by sampling effort in terms of the number of cameras. Then, you divide the first rate by the total number of days the study was done to incorporate time into the effects size estimate.
Net Abundance Detection Rate	An incidence rate effect size measure calculated using species abundance per total number of cameras by total number of trapping days.
Net Richness Detection Rate	An incidence rate effect size measure calculated using species richness per total number of cameras by total number of trapping days.

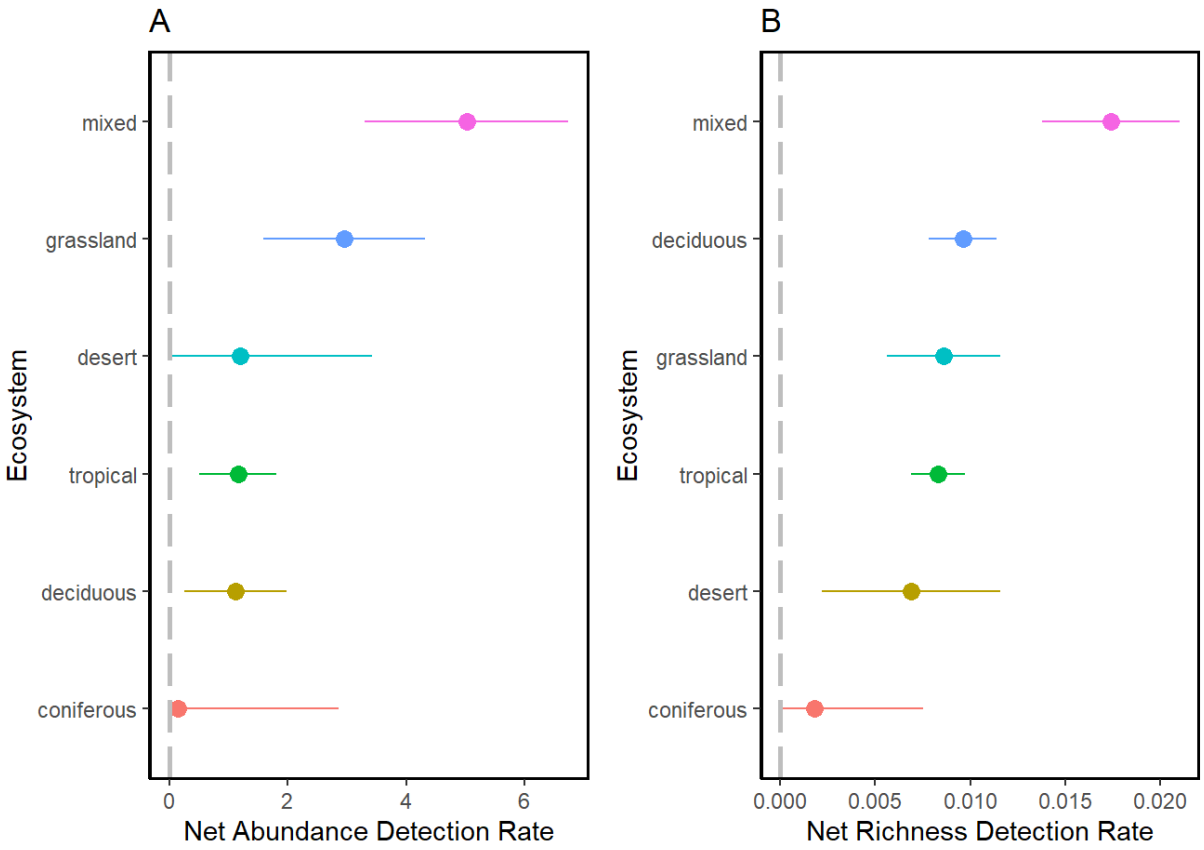

Figure 2.1: Forest plots showing estimated effect sizes from random-mixed model output for net abundance detection rate (A, animals/camera•day) and net richness detection rate (B, richness/camera•day) in 6 different ecosystems of study. Dots represent the meta-analytic mean and dashed lines represent the 95% confidence intervals.

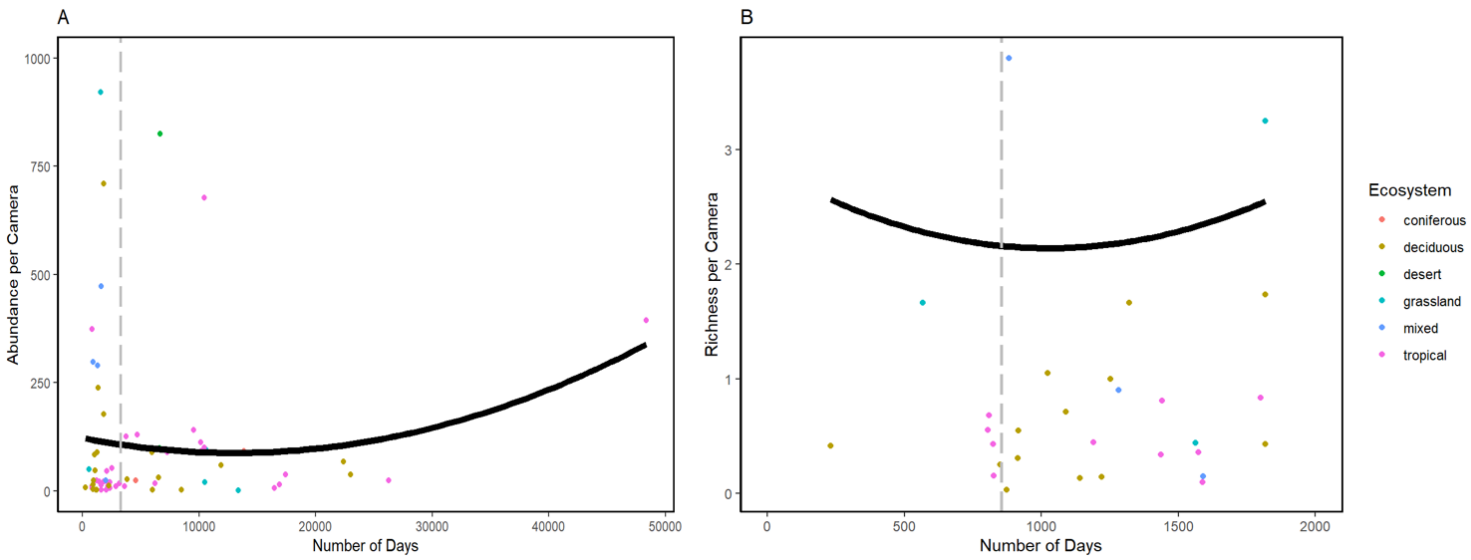

Figure 2.2: Weighted regression plot showing the relationship between the number of animals per camera (A) and the number of species per camera (B) throughout the duration of the study (days), weighted by the variation in abundance or richness. Coloured dots represent the ecosystem of study. Black line represents smooth conditional mean and grey dashed line represents Minimum Trapping Effort (MTE).

2.6: Discussion

The conservation and restoration of the world's ecosystems ultimately depend on the ability to identify wildlife and estimate biodiversity effectively. The hypothesis that sampling size can be used to inform us of the optimal way of allocating sampling effort was supported here. Deploying more camera traps, but not necessarily for more days, is likely the most effective ecological tool to estimate abundance in grassland and mixed ecosystems, as well as local species richness in all but coniferous forests and deserts. 'Ecosystem' was relevant and some systems require additional study. The estimated MTE does not necessarily mean per study but does suggest that within a site or region, it is valuable to consider deployment differently. Our study showed that deploying more cameras versus longer for the same sample is better for estimating abundance in grassland and mixed ecosystems and richness in all ecosystems, except for deserts and coniferous forests. Thus, it is important to frame quantitative expectations based on the returns published in similar studies or summarized in syntheses like this study.

Camera traps effectively estimate population parameters in many different ecosystems worldwide. Herein, we examined the net abundance detection rate and net richness detection rate. Examining both these indices, we found evidence that richness and abundance were influenced by the number of cameras deployed at a site or region. The primary finding of this synthesis is that success in detecting species in a given system was highly dependent on the number of cameras. This is aligned with the findings of Ferreras et al. (2017) which suggests that for effective detection, it is more efficient to deploy more camera traps for a shorter duration rather than to deploy fewer camera traps for a longer period. Although the number of cameras is important, there are at least two other design decisions associated with camera deployment: placement and habitat type. The number of cameras is not independent of camera deployment because more cameras can increase the likelihood of overlap and sampling more environmental heterogeneity. To increase sampling effort through more cameras, a systematic trap placement design or a design suited to that particular habitat is

essential if the primary goal of the survey is population parameter estimation, such as richness (O'Brien, 2008). To limit the chance of missing species, camera traps should not be too close together and maximize the total area covered (O'Connell et al., 2011). If multiple cameras are placed in one site, placement should be systematic and cameras should have different fields of view to maximize the detection of animals (Pease et al., 2016). Random and systematic (grid) camera setups can both result in similar estimates of species richness and group size, but differ in estimates of abundance and activity pattern (Tanwar et al., 2021). Sampling effort is also a critical design topic in all of ecology and evolution (Albert et al., 2010; Hamel et al., 2013), particularly in field studies. In this study, we found that increasing the number of trapping days is not a significant predictor of increased capacity for cameras to detect more animals neither in abundance, nor diversity. This is directly related to MTE (Si et al., 2014) because MTE is the number of camera trap days required to detect a terrestrial species of interest in an area record. The interdependence of camera trap placement and the number of cameras is not a hypothesis explicitly tested in this meta-analysis. However, it is integral in maximizing the potential of camera traps for wildlife monitoring. Understanding how many cameras are needed for how long, and how far apart they need to be placed relative to the particular ecosystem of study will ensure more precise data are obtained for species diversity and habitat change, behaviour, and use of artificial structures, which is critical for conservation.

It was striking that increasing the number of cameras significantly increased the net abundance detection rate in only grasslands and mixed ecosystems. One reason that animal abundance was higher in grasslands, as opposed to other arid lands, may be due to the abundance of prey, such as mice or birds, alongside the natural grass and vegetation. This in turn attracts more mid-size or larger mammals that feed on these small animals (Silveira et al., 2005) that can be easily detected by cameras. Vegetation can augment the abundance of prey and predators, hence increasing the total observed animal abundance in the area (Barbosa & Castellanos, 2005). Furthermore, mixed

systems support relatively higher habitat diversity because they are comprised of many different types of plant species (Felton et al., 2010). It is likely that this heterogeneity supports a greater number of animals because of resources and habitats (MacArthur & MacArthur, 1961). Net richness detection rate did not significantly increase with the number of cameras. Arid and semi-arid systems are globally threatened by increased rates of anthropogenic changes, such as climate and land-use changes (Mahmoud and Gan 2018), and species in these regions face extensive ecological shifts (Barrows 2011; Bachelet et al. 2016). Hence, the reason why species diversity may not increase with more camera trap sampling may be due to the fact diversity in animal communities is declining in drylands (Maestre et al., 2016). Landscape-level differences influence animal assemblage in different ecosystems and offer us valuable insight into the utility of camera traps in different regions.

2.7: Implications for Optimal Camera Trapping

This synthesis provides both a critical insight into experimental design considerations associated with sampling efforts and the relative efficacy of camera traps as a tool in monitoring changes in wildlife populations in different ecosystems. Across the same sample size, deploying more camera traps over a shorter duration, with appropriate placement, is the most effective strategy as estimated from the relevant published scientific literature to date – across studies. This trend is likely relevant within studies at a specific site or region. Increasing camera traps is certainly a more effective sampling strategy, in general, to increase relative sampling effort spatially. Purchasing more cameras is a more efficient strategy for conservation biology and stakeholders, including land owners and nature conservancies in the area. We understand that camera trapping generally requires a large sum of initial funding, but this funding is offset by the low efforts required for camera trapping fieldwork (Lamelas-López & Salgado, 2021). Cameras are more affordable than intensive sampling via direct observational survey because over time hiring people to do fieldwork takes more funding than the initial cost of camera traps. Results of population estimates from camera trapping sampling compare favourably with those of traditional live trapping techniques, and funds saved from not

doing live trapping can be invested in purchasing camera traps (De Bondi et al., 2010). Of course, the recommendation is not to replace researchers with cameras because nonetheless photos captured by cameras still need to be processed; however, despite greater initial costs, camera traps are a more reliable monitoring tool to identify species since species identification in live surveys is highly-dependent on the person's confidence of species identification (Roberts, 2011). We do suggest however that with the increase in the number of cameras, the setting and programming be as simple as possible to allow workers with varying degree of field experience to effectively conduct trapping without errors (Rovero et al., 2013). Furthermore, we understand that seasonality can impact species detection because of migration and hibernation (Kays et al., 2020; Tape & Gustine, 2014); thus, sampling may need to be done in all seasons, and for long-term monitoring, repeated visits/continuous sampling may be necessary. Our results direct us towards the necessity to better examine survey efforts, experimental design, and camera trap placement to increase detection probabilities of wildlife to ensure good data for management to make better-informed restoration and conservation decisions.

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2.10: Author's Contributions

NG and CJL designed the study and methodologies; NG wrote the manuscript; NG and CJL analyzed the data; CJL thoroughly edited the manuscript and contributed critically.

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CHAPTER 3: AN EXPERIMENTAL TEST OF LIGNOCELLULOSIC FABRICS FOR POTENTIAL USE IN ARTIFICIAL HABITAT CONSTRUCTION IN DESERTS

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3.1: Chapter Summary

Climate change has profound effects on drylands, where vegetation like shrubs provide microclimatic refugia for animals. However, prolonged drought and higher temperatures are reducing the resilience of vegetation. Artificial habitat constructions, such as shelters, may function similarly to shrubs in providing climatic refuge. Natural fabrics, including lignocellulosic fabrics, have gained popularity in conservation due to their biodegradability, lightweight, and strength. In this study, we tested the effects of natural fabric canopies on key desert microclimatic variables, including temperature, relative humidity (RH), and light intensity/radiation to select the best-suited fabric for microclimatic amelioration of resident fauna in future field experiments. We used 0.45m^2 microsites of burlap, canvas, and nursery fabrics angled to the ground at three repetitions per fabric and paired them with data loggers for 30 days to record near-surface air temperature, RH, and radiation. We compared uncovered and similarly illuminated 0.45m^2 areas to serve as the control. We saw that the control was consistently the warmest microsite, while burlap and cotton canvas were the coolest. However, burlap offered a lower amplitude of temperature variation compared to cotton canvas. The lowest mean radiation was experienced under burlap and it functioned similarly to cotton canvas when controlling light regimes. We found that nursery fabric showed the highest humidity levels with the lowest variation, while cotton canvas had the lowest humidity and the highest variation. Yet, the high variation in temperature for nursery fabrics suggests it is not ideal for deployment in the field for sheltering resident fauna. Natural fabrics for small shelters could support conservation and management, as they can be deployed, are ecologically friendly, and serve as a stop-gap solution for early restoration efforts in sites while vegetation is re-established post-disturbance.

3.2: Introduction

The pressures of anthropogenic change are becoming stronger and more frequent in all ecosystems around the world. Some of these changes include, but are not limited to, fragmentation

due to agriculture and urbanization, the spread of invasive species, and most notably, climate change (Elmqvist, 2013; Irwin et al., 2010; Nopper et al., 2018). Human activities increase atmospheric carbon dioxide levels, mainly through the burning of fossil fuels, which in turn heat up both land and oceans (Redlin & Gries, 2021). In deserts, many species are not only sensitive to large-scale changes but also small, fine-scale fluctuations (Hadley, 1970; Shrode & Gerking, 1977). This is important because deserts support a high level of endemism and are thus key for the sustainability of global biodiversity (Davies et al., 2012). Climate stability is key to the continuity of plant endemism in deserts including phylogenetic endemism of vascular plants (Sosa et al., 2020). The scale at which climate is assessed is critical for the survival of species because variation in microclimates is a small-scale change that may affect species' day-to-day survival, while long-term climate patterns can influence reproduction and distribution (Bellard et al., 2012; Walther, 2010). “Microclimate” is the climate experienced in the lower 2m of the atmosphere and the upper 0.5-1m of the soil, while “Macroclimate” or simply climate is defined as the atmospheric situation over long periods occurring independently of local topography, soil type, and vegetation (Stoutjesdijk & Barkman, 2014). Climatic heterogeneity is an important component of environmental heterogeneity (EH), with (EH) being defined as the non-uniformities in physical and ecological landscape characteristics (Dronova, 2017). Climatic heterogeneity is crucial in deserts because these areas are shown to buffer harsh temperatures and create “tiny niches” that would enable species to behaviourally adapt (Brooker et al., 2018). Hence, the scale at which climate is assessed is critical for the survival and persistence of many species. Capacity to adapt to a changing climate is finite (Visser, 2008) and we must actively examine effective restoration and management methods that go beyond restoring the natural landscape to incorporate and directly address microclimatic challenges.

Vegetation is an integral component of many dryland ecosystems. Foundation plants including shrubs that are not necessarily always locally abundant are critical for community structure

and diversity of plants and animals in many dryland ecosystems (Ivey et al., 2019; Zuliani et al., 2021). However, increased mean temperatures, extreme variability in precipitation and temperature, as well as extended drought periods, are limiting the ecological resilience of vegetation and leading to vegetation loss (Lortie et al., 2022). Restoration and management of key vegetation species are crucial to the well-being of drylands, but it is also important to examine short-term, stop-gap solutions while new vegetation grows and recovers post-disturbance. Shelters and natural or human-made architecture, are often used in deserts and are significant for a variety of ecological interactions. Furthermore, even in planting seedlings and germination trials, shelters and protective structures are often used (Oliet et al., 2012; Prinsley, 1993). Shelters or artificial structures can aid in increasing environmental heterogeneity locally. For instance, simulated solar panels have been shown to create altered microhabitats in desert landforms in turn influencing plant richness and abundance (Tanner et al., 2020). Artificial habitat structures with the aim of conservation are habitat structures that are usually deployed in degraded, disturbed, or modified environments to maintain or improve the state of individuals or populations, including their survival, growth, reproduction, and abundance (Watchorn et al., 2022). Some snakes use artificial structure to thermoregulate (Lelièvre et al., 2010), while certain birds use them for perching (Athiê & Dias, 2016). Artificial structures can be constructed in the form of shelter, such that they reduce direct solar radiation, provide more consistent temperatures throughout the day, and function similarly to natural vegetation (Ghazian et al., 2020). For instance, artificial shade can be used to reduce the nest temperature for the incubation of sea turtles, in turn mitigating the impacts of global warming and ensuring hatchling production (Esteban et al., 2018; Reboul et al., 2021). It is important however that artificial structures are monitored across relevant ecological spatial and temporal scales, and that their effects be compared to appropriate controls such that they do not serve as a greenwashing mechanism or inappropriate biodiversity offset (Watchorn et al., 2023). Thus, artificial shelters can potentially provide refuge to

larger, non-burrowing animals during the hottest hours of the day, in addition to creating small or ‘tiny niches’ of microclimatic heterogeneity, which can allow animal species to behaviourally adapt and persist given the current paradigm of land use and changes in climate (Brooker et al., 2018). However, their effective testing and monitoring both in the field and in lab is key.

The focus of this study is a preliminary in-lab trial of different eco-friendly fabrics for later use in an artificial habitat construction experiment in drylands. Shelters built with eco-friendly covers, such as natural burlap or cotton, can be beneficial because they reduce artificial debris (waste left behind from some manipulative scientific experiments). This is a problem present in many scientific fields including astronomy (Šilha, 2019), and can apply to the field of ecology. Natural burlap or jute fibers are biodegradable and are generally treated to resist decay (Kuhns, 1997). Herein, it is important to define the term ‘biodegradability’. The mechanisms of biodegradation, although important, are not the major concern of this term, instead, biodegradability refers to the environmental fate and effects of a material (Table 3.3) (Swift, 1992). Natural fibers are made up of repeating units called monomers, which when assembled turn into bigger compounds called oligomers, and eventually larger compounds referred to as polymers. For a material to be considered environmentally biodegradable, it must be able to completely break down (be mineralizable) or leave no harmful residues in the environment (Swift, 1992). When we discuss biodegradability in relation to fibers and fabrics, ‘mineralization’ refers to when the oligomers and monomers assimilated within the cells of a fabric are broken down and converted to CO_2 and H_2O (aerobic), and CO_2, CH_4, and H_2O (anaerobic) (Zambrano et al., 2020). In general, biologically synthesized polymers are readily biodegradable in natural environments, though the accessibility of the structure for moisture and enzyme diffusion and the capacity of the microbes and fungi in the environment to assimilate the final monomers are also important factors to consider (Arshad & Mujahid, 2011; Zambrano et al., 2020).

Most natural fabrics are made up of lignocellulosic materials, unlike synthetic fabrics which are made up of man-made materials. Lignocellulosic materials come from natural resources, such as the stems and roots of trees, and woody plants consisting of brittle and fibrous tissues and are made up of polymers of cellulose, hemicellulose, and lignin (Chen, 2015). Since cellulose is the primary carbohydrate that plants generate, it is the most prevalent organic polymer found in nature and is used in a wide range of products, including textiles and paper (Arshad & Mujahid, 2011). Lignocellulosic materials, including fibers, are degraded biologically because organisms reorganize the carbohydrate polymers in the cell wall, and have specific enzyme systems capable of hydrolyzing these polymers into digestible units (Ramamoorthy et al., 2019). For instance, cotton (canvas' base fiber) is a fiber made of the plant from the genus *Gossypium*, belonging to the family *Malvaceae* (Weigmann, 2023). This fiber is composed of ~87-90% cellulose, ~5-8% water, and ~4-6% natural impurities (Weigmann, 2023). The cuticle, which encircles the principal wall of the cotton fiber and is mostly made of cellulose, pectin, waxes, and proteinaceous material, is the outermost layer of the fiber (Yafa, 2005). The secondary wall, which is separated into multiple parallel layers, makes up the interior portion of the cotton fiber (Yafa, 2005). The cellulose in cotton makes it a sturdy option for short-term field studies because the fabric decays over time when subjected to tension, humidity, temperature fluctuations, and UV irradiation (Nechyporchuk et al., 2017). Biodegradable nursery fabrics are used to increase the rates of seedling establishment because they retain moisture and humidity (Wightman et al., 2001). Nursery bags are part of 'agrotextiles,' a term used to categorize the woven, nonwoven, and knitted fabrics, mesh or foil used for growing, harvesting, and storage of either crops or animals, livestock protection, shading, weed, and insect control, and extension of the growing season (Sharma et al., 2022). Non-woven, biodegradable nursery fabrics like burlap, are generally made from jute (Marasović & Kopitar, 2019). Jute comes from the jute plant consisting of cellulose and lignin coming from a few different varieties of species,

including *Corchorus olitorius* (white jute), and *Corchorus capsularis* (tossa jute) (Sewport, 2023). Jute is a long, soft, shiny plant fiber from which we can spin coarse and strong threads (Arshad & Mujahid, 2011). Jute's roughness and durability make it ideal for industrial applications (Sewport, 2023). Biodegradable fibers including the ones listed above and others, are ecologically harmless, relatively strong and lightweight, low-cost, highly hydrophilic, and capable of acting as both substrate and humidity-sensitive material, and have shown great potential as structural components in automobiles, aerospace, construction, and buildings (Huang et al., 2023; Rangappa et al., 2022). Furthermore, they are generally harmless if ingested by animals as long as they are appropriately cleaned (Fynn et al., 2021).

Our objective was to quantify the extent to which cotton canvas, burlap, and nursery fabric could ameliorate, and reduce the amplitude of variation in near-surface air temperature, RH, and radiation in a lab setting, with the goal of using these data to select the best-suited fabric for shelter construction for fauna in the field in a follow-up study. We hypothesized that the lignocellulosic fabric barrier would lower the relative variation in microclimate, including near-surface temperature, relative humidity, and radiation/light intensity. We predicted that 1) the three fabrics would have different light absorption and dappling effects because of their chemical makeup, leading to different radiation regimes (Jiang et al., 2022), 2) temperature and radiation have a direct, inverse relationship, and 3) an artificial canopy increases relative humidity compared to the paired-lab control by acting as a windbreak and creating a boundary layer (Cleugh & Hughes, 2002). These in-lab trials serve as a basis for future field experiments, which are key for the effective testing of human-made constructions with the aim of conservation of endangered fauna.

3.3: Materials and Methods

Microsite deployment

Trials were conducted under controlled lab conditions at York University, Toronto, ON (43.7730, -79.5036). In this experiment, one edge of the fabric was taped to a table and the other

edge was taped to the ground such that there was a 45º angle horizontal shade created. Each fabric was approximately 0.45m^2. We tested three environmentally-friendly fabrics including natural burlap (The Felt Store, 2021), 100% cotton canvas (Trimaco, 2021), and non-woven, biodegradable seedling nursery fabric (Endpoint, 2021), and tested their impact on understory climatic parameters. In order to create the 0.45m^2 nursery fabrics, we had to glue smaller nursery seedling bags together to achieve the desired dimension. There were three replicates for each fabric and the adjacent open microsite, for a total of six microsites. The open was defined as the 0.45m^2 area directly beside the angled shade. Fabrics were each tested for 30 days (one 30 day trial for each fabric triplet); however, the entire duration of the study was between March 13th – October 13th, 2021.

Abiotic measurements

Data loggers were attached to pegs using zip ties (to ensure ambient and not ground climatic parameters were recorded, they were placed ~10 cm above ground) and placed in 250mL cups filled to ¾ with play sand (*Quickrete*, 2021). We placed the cups under each fabric and in the open to measure RH (%), radiation (lum/ft^2), and near-surface temperature (used interchangeably with temperature) (°C) at 1-hour intervals. OMEGA OM-91 pendant loggers were used to measure RH and temperature (OMEGA Engineering, 2021). Onset HOBO Temperature/Light Pendant (64K) loggers were used to record solar radiation and temperature (Hoskin Scientific, 2021). 150 LED chip, 70-watt lamps provided UV for a total of 12 hours/day (suggested in the manual for dryland vegetation, Likesun 2021). 60-watt heat lamps were used to create artificial heat to match the warm, dry conditions experienced in our designated dryland site in California, U.S.A during the spring-summer period, which has a mean average range of 19-32 ºC between May and June ("Carrizo Plain National Monument," 2023). We made sure the heat lamps were set such that the temperature was always greater than 20ºC. Humidity was not manipulated; however, by increasing temperature, we decreased relative humidity considering there is a direct, inverse relationship between these two variables (*Britannica*, 2023). The U.S Fish and Wildlife Service Recovery Plan for Upland Species

of the San Joaquin Valley (semi-arid grassland) names three key recovery sites, the largest of which is the Carrizo Plain National Monument (D. F. Williams et al., 1998). The composition and structure of the vegetation, which have been drastically impacted by land conversion, invasive non-native plant species, and shifts in shrub and herb coverings due to inter-annual climatic oscillations, have a considerable impact on local species (Stout et al., 2013). These local species include but are not limited to, the Blunt-nosed Leopard Lizard (*Gambelia sila*; federally listed as endangered (Ivey et al., 2020)), the Giant Kangaroo Rat (*Dipodomys ingens*), Kit Fox (*Vulpes macrotis*), and the San Joaquin Antelope Squirrel (*Ammospermophilus nelson*) (Zuliani et al., 2021a).

Statistical analyses

All statistics were performed using R version 4.2.2 (R Development Core Team, 2022). Code is openly published on Zenodo (Ghazian 2022) and data are openly published on the Environmental Data Initiative (EDI) (Ghazian et al., 2022). Q-Q plots were used to examine the distribution of data and to check for normality and homoscedasticity (Schützenmeister et al., 2012). The relationship between temperature and radiation was examined using Kendall's rank correlation (non-parametric, continuous data) (Abdi, 2007). Furthermore, the relationship between temperature and RH was also examined using Kendall's rank correlation (non-parametric, continuous data). Generalized Linear Models (GLM) were used to compare temperature, RH, and radiation by microsite (Nelder & Wedderburn, 1972). GLM dispersion parameters with AIC scores were used to compare and select the appropriate family to fit models (Richards et al., 2011). Post-hoc tests were done using the function *emmeans* (Estimated Marginalized Mean) from the emmeans R package (Lenth & Herve, 2019). We explored relative variation in histograms by examining variance and used Levene's Test to check the heterogeneity of variances for temperature, RH, and radiation across microsites (Schultz, 1985). The coefficient of variation (CV) was also calculated for each shelter type and controls for each abiotic variable (Brown, 1998). The CV estimates were contrasted with the equality package

(Marwick & Krishnamoorthy, 2019) using the *Asymptotic test for the equality of coefficients of variation from k populations* by Feltz and Miller (1996), often regarded as the 'gold test' when comparing multiple CVs.

3.4: Results

Near-surface air temperature effects

Near-surface air temperature significantly and positively increased with radiation at all microsites (Kendall's tau= 0.342, $p<0.001$; Appendix B; G and H). Overall, there was a significantly, positive relationship between temperature and humidity at microsites (Kendall's tau= 0.0125, p= 0.00992; Appendix B; I and J) except for the control. The control was consistently the warmest microsite (Estimated Marginalized Mean (EMM) 21.98 ± 0.0081 ºC; Table 3.1, Figure 3.1, Appendix B; A and B), while nursery fabric and canvas were the coolest microsites (EMM 21.46 ± 0.014 ºC and 21.68 ± 0.015 ºC, respectively). Calculated variances in temperature were significantly different between the microsites (Levene's F-value= 219.16, $p<0.001$; Figure 3.2; Appendix B; F). There were significant differences between the CV calculated for near-surface air temperature for the various microsites (Asymptotic Test= 4858.663, $p<0.001$). The lowest CV in temperature calculated was under burlap (1.81%; Table 3.2), while the highest was under nursery fabric (5.39%).

Light intensity and humidity effects

Not to our surprise, the control microsites experienced the greatest light radiation effects (EMM 18.20 ± 0.155 lum/ft^2; Table 3.1, Figure 3.1, Appendix B; A) and were significantly brighter than all canopied microsites (post-hoc $p<0.001$; Appendix B; D). The lowest mean radiation was experienced under burlap (EMM 1.96 ± 0.261 lum/ft^2; Table 3.1, Figure 3.1; Appendix B; D). Burlap was significantly more shaded than nursery fabric, (post hoc p= 0.0005; Figure 3.2) but not canvas. Variances in light radiation were significantly different between microsites (Lavene's test F-value= 838.07, $p<0.001$; Figure 3.2; Appendix B; F). There were significant differences between the CV calculated for radiation at the various microsites (Asymptotic Test= 297.4007, $p<0.001$). The

coefficient of variation for radiation was the lowest for nursery fabric (103%; Table 3.2) and burlap (116%).

The most humid microsite was the nursery fabric (EMM 55.2 ± 0.305 %; Table 3.1, Figure 3.1) and the control (EMM 43.4 ± 0.166 %). The lowest humidity was recorded under canvas (EMM 38.4 ± 0.280). Pairwise comparisons of all microsites showed to be significantly different (post-hoc $p<0.001$; Appendix B; C). Variances in relative humidity were significantly unequal between the microsites (Lavene's F-value= 838.07, $p<0.001$; Figure 3.2; Appendix B; F). Calculated CVs for humidity across microsites were significantly different (Asymptotic Test= 2137.138, $p<0.001$). The greatest variation was under canvas (46.5%; Table 3.2), while the lowest CV was recorded under nursery fabric (14.2%).

Table 3.1: A summary of the GLM output for near-surface air temperature (ºC), humidity (%), and radiation (lum/ft^2). Significant p-values are bolded, standard errors (SD) are given and confidence intervals (CI) provided are at the 95% level.

	Predictors	***Estimates***	***SD (±)***	***CI***	***p-value***
Temperature (ºC)	Intercept	21.83	0.0136	21.80-21.85	**0.001**
	as.factor Microsite [canvas]	-0.15	0.0206	-0.19- -0.11	**0.001**
	as.factor Microsite [control]	0.15	0.0158	0.12-0.18	**0.001**
	as.factor Microsite [nursery]	-0.37	0.0196	-0.41- -0.33	**0.001**
Observations	19110				
Null Deviance	12938				
df	19019				
Humidity (%)	Intercept	40.87	0.280	40.32-41.41	**0.001**
	as.factor Microsite [canvas]	-2.43	0.396	-3.21- -1.66	**0.001**
	as.factor Microsite [control]	2.52	0.326	1.88-3.16	**0.001**
	as.factor Microsite [nursery]	14.38	0.414	13.57-15.19	**0.001**
Observations	18987				
Null Deviance	5473500				
df	18986				
Radiation (lum/ft^2)	Intercept	1.96	0.261	1.45-2.47	**0.001**
	as.factor Microsite [canvas]	0.60	0.394	-0.18-1.37	0.130
	as.factor Microsite [control]	16.24	0.304	15.64-16.83	**0.001**
	as.factor Microsite [nursery]	1.48	0.376	0.74-2.22	**0.001**
Observations	19110				
Null Deviance	5646019				
df	19109				

Table 3.2: The coefficients of variation are given as a percentage for each microsite for each climatic parameter including near-surface air temperature (ºC), humidity (%), and radiation (lum/ft^2).

Microsite	CV Temperature (%)	CV Humidity (%)	CV Radiation (%)
burlap	1.81	42.3	116
canvas	1.91	46.5	174
control	1.84	39.2	116
nursery	5.39	14.2	103

Table 3.3: Keywords and definitions about materials used in this study, as well as some illustrative studies from the literature, and where the materials were purchased (if applicable).

Keyword	*Description*	*Illustrative Studies*	*Where Purchased*
Biodegradability	The ability of a material to be mineralizable (naturally break down) into its components, including CO_2 and H_2O (aerobic), and CO_2, CH_4, and H_2O (anaerobic) when exposed to moisture, enzymes, microbes, and fungi in the environment.	*Swift, 1992; Zambrano et al., 2020; Arshad and Mujahid, 2011*	NA
Lignocellulose	Materials that come from natural resources, such as the stems and roots of trees, and woody plants consisting of brittle and fibrous tissues are made up of polymers of cellulose, hemicellulose, and lignin. These materials are naturally biodegradable because organisms reorganize the carbohydrate polymers in them and can digest them.	*Chen, 2015; Ramamoorthy et al., 2019*	NA
Agrotextile	A term used to categorize the woven, nonwoven, and knitted fabrics, mesh or foil used for growing, harvesting, and storage of either crops or animals, livestock protection, shading, weed, and insect control, and extension of the growing season.	*Sharma et al., 2022*	NA
Cotton	The base for canvas, this biodegradable fiber is made of the plant from the genus *Gossypium*, belonging to the family *Malvaceae*. The cuticle, which encircles the principal wall of the cotton fiber and is mostly made of cellulose, pectin, waxes, and proteinaceous material, is the outermost layer of the fiber, while the secondary wall, which is separated into multiple parallel layers, makes up the interior portion of the cotton fiber.	*Weigmann, 2023; Yafa, 2005*	Trimaco, 2021
Burlap	A non-woven fabric made from a biodegradable fiber jute. Jute comes from the jute plant consisting of cellulose and lignin coming from a few different varieties of species,	*Marasović & Kopitar, 2019; Sewport, 2023; Arshad*	The Felt Store, 2021

	including *Corchorus olitorius* (white jute), and *Corchorus capsularis* (tossa jute). Jute is a long, soft, shiny plant fiber from which we can spin coarse and strong threads.	*& Mujahid, 2011*	
Nursery Fabric	A type of non-woven biodegradable agrotextile generally used to increase the rates of seedling establishment because they retain moisture and humidity. They are used in germination trials to increase seedling establishment.	*Sharma et al., 2022; Schmal et al., 2007*	Endpoint, 2021

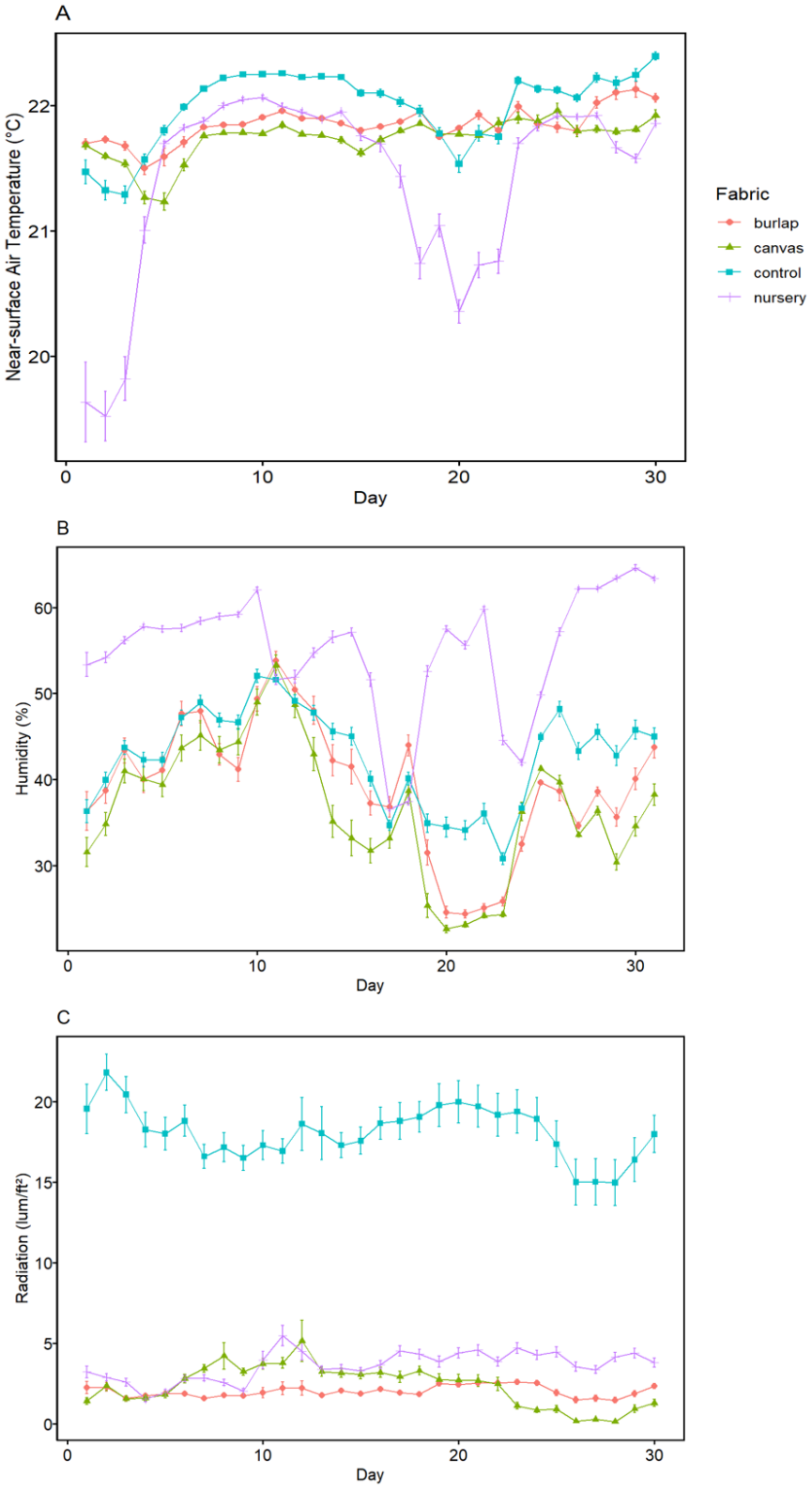
A
Near-surface Air Temperature (°C)
22
21
20
0
10
20
30
Day
Fabric
burlap
canvas
control
nursery
B
Humidity (%)
60
50
40
30
0
10
20
30
Day
C
Radiation (lum/ft²)
20
15
10
5
0
0
10
20
30
Day

Figure 3.1: Mean daily near-surface air temperature (ºC) (A), humidity (%) (B), and radiation (lum/ft^2) (C) over the course of the 30-day study period recorded at each fabric and control using data loggers. Point shapes represent different microsites. Solid lines connect daily means. Errors bars are standard error (SE).

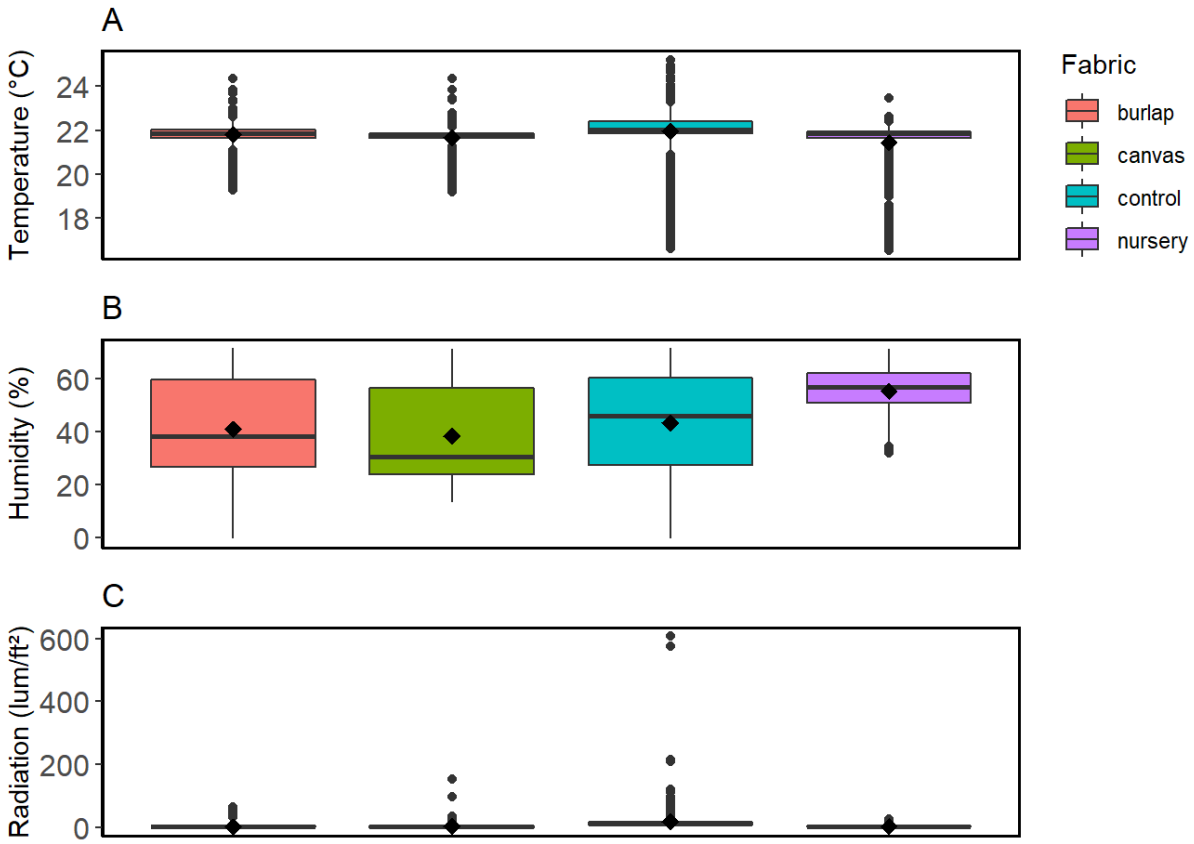

Figure 3.2: Boxplots showing near-surface air temperature (°C), humidity (%), and radiation (lum/ft^2) at each fabric and control. Solid middle lines show the median of the data, whilst whiskers show 1.5 standard deviation. Solid dots are outliers >1.5 interquartile range (IQR). Diamond dots represent the mean

3.5: Discussion

In drylands, heterogeneity in microclimates is important because it provides species with a variety of climatic profiles for refuge and movement (Ma et al., 2023). Critically, it is these fine-scale environments that most species experience that are inherently variable in deserts (Kotzen, 2003; Shenbrot et al., 2002) and with a changing climate even more so (Li et al., 2019). In this study, we tested the impact of natural fabrics on the understory microclimate for future use in artificial shelter construction in deserts for ecological conservation of resident animal species (Ghazian et al., 2020). The hypothesis that natural fabrics can both provide refuge from extremes and also decrease relative variation in key arid microclimatic drivers was tested. We found that microsites with fabric were significantly cooler and had a lower relative variation compared to the open controls supporting this idea that even modest, relatively small shelters can generate meaningful heterogeneity relevant to many plants and animals in deserts. Nursery fabric was often much more humid, which could benefit vegetation and mitigate against desiccation and plant death. Nursery seedling bags are generally used in germination trials because they moderate moisture and improve germination and seedling establishment (Schmal et al., 2007). Water as well as air circulate fairly well within these agrotextiles and temperatures can get really hot at times; thus, a reason for the big temperature variation may be due to the inherent nature of this fiber (Marasović & Kopitar, 2019). Hence, non-woven, biodegradable nursery fabrics may be ideal for seedling germination experiments in the field, with possible herbivore exclusion, but perhaps not for artificial habitat construction for resident fauna, which is the aim of our follow-up in field study. The goal is not necessarily to provide the coolest shelter for mobile animals but instead a place where extremes in physical and abiotic conditions can be avoided (Schwarzkopf & Alford, 1996). This type of refugia is especially important for thermoregulatory species like lizards that now have to tolerate even longer periods of higher ambient temperature given the current paradigm of climate change (Ivey et al. 2022). In recent years, there has been increased interest in the use of biodegradable polymers that minimize the issues caused by

the disposal of synthetic polymer bags (Bilck et al., 2014). In our study, we used a biodegradable nursery fabric to minimize ecological impacts and observed that it was in fact the best fabric at moderating relative humidity; however, the large spread in variation observed in temperature makes it a less-than-ideal candidate for use in artificial shelters for ecological conservation of dryland animals because you want to offer a consistency in the microsite's microclimate. Furthermore, biodegradable non-woven nursery fabrics are not available in large dimensions because they are designed for seedling germination as small bags originally (seeds are relatively small); hence, it is not optimal for shelter constructions even for small to medium-scale conservation.

Recently, ecological and environmental concerns have initiated the use of natural fibers in green technology. Despite their use in reinforced engineering, all-natural fibers have different surface morphologies and physical/chemical properties (Pai & Jagtap, 2015). Burlap is generally made from jute and hemp and is considered a 'bast' fiber (from the phloem of the plant) while canvas is made from cotton seeds (Pai & Jagtap, 2015). Because of their location of origin on the plant, these fabrics differ in properties including density, moisture content, and elongation capacity. Most natural fibers are lignocellulosic (Satyanarayana et al., 2009) and are hydrophilic, meaning they have high moisture absorption profiles (Jawaid and Abdul Khalil 2011). In this study, we observed that burlap was more hydrophilic in profile in terms of relative humidity compared to cotton canvas and its canopy was on average more humid than canvas with less variation in humidity experienced. This property of this cellulosic fiber makes it an ideal candidate for dryland studies in the context of refugia for animals, given the prolonged periods of drought and low precipitation experienced in these regions and that drylands are mediated by rainfall (Bachelet et al., 2016). Lower near-surface air temperatures with less variation were also recorded under burlap, which many desert animals may find important for thermoregulation. Some animals may even use these shelters diurnally for their windbreak properties (Baker et al., 2021). Cellulosic fibers are relatively strong, lightweight, harmless to human health

and the environment, and biodegradable (Rangappa et al., 2022). Recent advances in lignocellulosic research and our findings demonstrate their significant potential as structural components in construction.

The type of canopy impacts the quantity, quality, and distribution of the incoming light. Light is a fundamental force in nature, impacting many interactions such as predator-prey interactions (Spinner et al., 2013), thermoregulation for some species (Refsnider et al., 2018), as well as helping animals navigate their environment and interact with other organisms using eyes/light-sensitive organs (Palmer et al., 2018). Natural fibers have complex profiles consisting of cellulose, hemi-cellulose, lignin, pectin, and other proteins, waxes, and organic molecules (Truss et al., 2016). The quality and quantity of incoming light (red shift or blue shift) can be impacted through the availability of hydrogen bonds (Yamaki et al., 2005), which in turn can influence light-dappling regimes. Our data suggest that if your main goal is humidity and moisture retention for plant growth in deserts, nursery fabric is the superior option. However, for constructing artificial shade for animals while minimizing both the variation experienced in temperature and solar radiation under the shelter canopy, while controlling for moisture, then burlap is the ultimate choice. In our study, the lowest mean light intensity was measured under burlap. Burlap also showed the lowest variance for light intensity. This is important as it implies that burlap canopy can offer more consistent light regimes and thus provide more stable refugia for resident animals. The light regime measured under the burlap canopy was no different than canvas, suggesting both fabrics function similarly in controlling light variation.

3.6: Implications

Microclimatic variability in drylands is a critical issue because the rate of global desertification is steadily increasing. Many desert species have limited plasticity to buffer further warming (Gunderson & Stillman, 2015), hence, management actions can mitigate the potential for species loss including restoration, translocation, refuges, and seeding. Environmental heterogeneity

augments the ability of organisms to inhabit different microsites (Lundholm, 2009). However, it is also likely that we need to protect abiotic heterogeneity in deserts because of increasing temperatures and decreasing precipitation (Li et al., 2019). At least in desert environments, shelters can serve a similar purpose to plants in some ways, increasing the thermal heterogeneity within the ecosystem. According to Bishop et al. (2019), ecological communities and wildfire regimes in California are changing as a result of climate change. In addition to the fact that post-disturbance vegetation recovery can take decades (Berry et al., 2016), other obstacles impeding the recruitment of native vegetation include competition and non-native invasion (Bowman et al., 2009, 2011). Artificial shelters can thus act as a stop-gap and as at least transient mechanisms to protect and even increase the microclimatic heterogeneity at fine scales in deserts (Ghazian et al., 2020). Of course, our suggestion is not to use artificial shade as a replacement for natural vegetation but instead, we argue that shelters like the ones discussed here are portable, affordable, and fill in small, critical spatial gaps locally, while natural vegetation re-grows post-disturbance. Shrubs are also under threat (García-Guzman et al., 2012) so augmenting support for animals is key because vegetation can take decades to recover post-disturbance (Berry et al., 2016) and artificial shade can mitigate the challenges that accompany re-establishment and recruitment for a short period of time. Natural fibers offer viable constituents for shelters and they can also reduce the environmental impacts of debris when damaged and are relatively low-cost to construct. The results of our study demonstrate that lignocellulosic fibers have immense potential for ecological management and conservation efforts.

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3.8: Author's Contributions

N.G, C.J.L, and S.E.M designed the study; N.G collected data; N.G performed statistical analyses; N.G wrote the manuscript; C.J.L offered input for statistical analyses; C.J.L and S.E.M thoroughly edited the manuscript and offered valuable insight.

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CHAPTER 4: THE MICROCLIMATIC EFFECTS OF THE NATIVE SHRUB *EPHEDRA CALIFORNICA* (MORMON TEA) IN CALIFORNIA DRYLANDS

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4.1: Chapter Summary

The impacts of climate change can be profound in many ecosystems worldwide, including drylands such as arid and semi-arid scrublands and grasslands. Foundation plants such as shrubs can provide microclimatic refuges for a variety of taxa. These shrubs can directly influence micro-environmental measures, and indirectly increase the local environmental heterogeneity as a result. We examined the hypothesis that, in comparison to an open gap, foundation shrubs improve the microclimate beneath their canopy and that microclimate is in turn a significant predictor of annual vegetation. The following predictions were made: 1) mean air temperature (NSAT), ground temperature (SGT), and vapour pressure deficit (VPD) will be significantly lower under the shrubs than in the open microsites; 2) shrub canopy size predicts microclimate; 3) site-level aridity estimates and percent shrub cover influence annual plant abundance and richness; and 4) the site-level mean of NSAT and VPD predict annual plant abundance and richness. Our study took place in Southwestern California, U.S.A. We used a handheld device with a probe to measure microclimatic variables such as near-surface air temperature (NSAT), near-surface relative humidity (NSRH), and surface ground temperature (SGT) at the shrub species *Ephedra californica* and in the open gap, across six sites in California, United States. Air temperature and RH were then used to calculate VPD. The mean number of vascular plant species across each site was also recorded. Only SGT was significantly reduced under shrub canopies. Canopy volume was not a significant predictor of all three microclimatic variables, demonstrating that even small, low-stature shrubs can have facilitative effects. Furthermore, total shrub cover and aridity at sites significantly predicted mean plant richness and abundance. There were significantly more plants associated with shrubs and there were significantly more species associated with the open. Mean air temperature and VPD at the site-level significantly predicted vegetation abundance and richness, though microsite-level differences were only significant for richness. Foundation shrubs are a focal point of resiliency in dryland ecosystems.

Understanding their impact on microclimate can inform us of better management, conservation, and restoration frameworks.

4.2: Introduction

Facilitation, defined as an interaction where one or more species (beneficiary) benefit from another species (benefactor) while none are harmed (Bertness & Leonard, 1997), is well-studied in community ecology (Brooker et al., 2007; McIntire & Fajardo, 2014). This interaction is often present in relatively high-stress environments, such as drylands, and generally, the magnitude of this interaction also increases with an increase in abiotic pressures (Bertness & Callaway, 1994). Foundation species like shrubs can act as structural agents of facilitation through many mechanistic pathways, one of which is microclimatic amelioration (Filazzola et al., 2017). Shrub understories provide more favourable environments for plants and animals by buffering against extreme temperatures, offering refuge from direct solar radiation, and increasing soil moisture (Filazzola & Lortie, 2014; Flores & Jurado, 2003; Holzapfel & Mahall, 1999). Thus, foundation shrubs are critical for community structure and diversity in many dryland ecosystems (Ivey et al., 2020; Zuliani et al., 2021).

Foundation shrubs are key components of environmental heterogeneity. Foundation shrubs physically ameliorate the understory microclimate compared to the open gap (Anthelme et al., 2014; Filazzola et al., 2017; Zuliani et al., 2021); thus, resulting in environmental heterogeneity as a byproduct of this microclimatic difference. Environmental heterogeneity (EH), defined as non-uniformities in physical and ecological landscape characteristics (Dronova, 2017), can be divided into many subcomponents including climatic, vegetation, land cover, soil, and topography heterogeneity (Stein & Kreft, 2015). ‘Microclimate’ is the climate experienced in the lower 2m of the atmosphere and the upper 0.5-1m of the soil and is dependent on local topography, soil type, and vegetation (Stoutjesdijk & Barkman, 2014). Foundation plans provide resilience and microclimatic

heterogeneity in drylands (Lortie et al., 2022), where elevated mean temperatures, fluctuations in temperature and precipitation, and prolonged drought episodes are on the rise (Maestre et al., 2021). Resiliency is a concept that refers to the ability of a system to resist changes in response to perturbations (Van Meerbeek et al., 2021). Plants can buffer perturbations that are the result of harsh climatic conditions (De Frenne et al., 2019). The impacts of plants in buffering climate have been primarily tested through landscape-level analyses, such as NDVI (Normalized Difference Vegetation Index) or vegetation land cover (Bagley et al., 2017); however, the structure of foundation species offers significant ecological functions that are crucial for offering climatic refuge at finer scales (Milling et al., 2018).

Like plant canopies in other systems, shrub canopies can, directly and indirectly, buffer climatic regimes. Plant canopies offer mediation from harsh climates by increasing environmental heterogeneity and cover (De Frenne et al., 2019). The quantity, quality, and temporal distribution of incoming sunlight are governed by the canopy's structure, which also affects air movement, which in turn affects temperature and precipitation regimes via boundary layer effects (S. B. Jennings et al., 1998). Shrub volume is directly associated with micro-environmental conditions, with larger shrubs showing a greater environmental heterogeneity in their understory (Alday et al., 2014). Similar to other studies with plants (Yang et al., 2017), this is likely due to the greater heterogeneity of conditions beneath larger plant canopies. Many dryland organisms are vulnerable to small, fine-scale oscillations in addition to large-scale changes (Shrode and Gerking 1977; Hadley 1970), which can further push species past the point of no return. Thus, foundation shrubs, including *Ephedra californica*, can help facilitate some of these species (Lortie et al., 2018) through small-scale climatic amelioration. The idea of vegetation and microclimate in arid systems is well-explored (El-Bana et al., 2002; Jankju, 2013; Xue et al., 2019) but not necessarily concerning the size of the foundation species at multiple arid sites. Shrub volume measured and reported to such an extent at multiple arid

sites in addition to its impact on annual plant richness and abundance is where the novelty of this study lies.

Ephedra Californica (Mormon Tea) is a foundation shrub native to the Southwestern regions of California that can occur dominantly or co-dominantly with *Larrea tridentata* (Sawyer et al., 2009), a flowering shrub that is often found in sandy soils, desert pavements, and the well-developed cryptogram layer of the Mojave (Braun et al., 2021; Sawyer et al., 2009). In this study, we measured microclimatic variables, including near-surface air temperature (NSAT), near-surface relative humidity (NSRH), and surface ground temperature (SGT) using a handheld device across six sites in California. NSAT is a point-station, air temperature measure that differs from a direct land surface measure of temperature and is a critical factor in the process of energy exchange between the land and the atmosphere (Xu et al., 2012). SGT (also referred to as Land Surface Temperature in the literature) is the measure of temperature directly on land as opposed to NSAT (Good et al., 2017). Similar to NSAT, NSRH refers to the measurement of the air moisture content near the surface (Pfahl & Niedermann, 2011). We used NSAT and NSRH to calculate vapour pressure deficit (VPD). We tested the hypothesis that foundation shrubs ameliorate the microclimate underneath their canopy relative to the open gap and that microclimate is a significant predictor of annual vegetation. The following predictions were made: 1) mean air temperature (NSAT), ground temperature (SGT), and vapour pressure deficit (VPD) will be significantly lower under the shrubs than in the open microsites; 2) shrub canopy size predicts microclimate; 3) site-level aridity estimates and percent shrub cover influence annual plant abundance and richness; and 4) the site-level mean of NSAT and VPD predict annual plant abundance and richness. Shrubs and vegetation improve microclimate and can thus provide key environmental heterogeneity that is crucial to the persistence of many dryland species given the current trajectory of climate change.

4.3: Materials & Methods

Site description

We surveyed a total of six sites across arid and semi-arid areas during the winter of 2023 (Table 4.1). The sites were located in Southwestern California, United States, and divided into two main ecological areas: Cuyama Valley and Carrizo Plain National Monument. The surveys took place between February 13 and 23, 2023. We surveyed a total of three sites in Cuyama Valley and three sites in the Carrizo Plain. Sites were always surveyed in the morning at approximately 9:00 AM. The year this study took place was considered a high precipitation year, characterized by a 'superbloom' and winter rainfall exceeding the long-term means by ≥70% (W. B. Jennings & Berry, 2023). We chose this study period because the early species of annuals normally begin germinating in March (W. B. Jennings & Berry, 2023), but because of the superbloom and high rainfall periods, they germinated earlier in late January (W.B. Jennings, 2001). We retrieved daily min and maximum temperatures (F) and precipitation (in) for each day of the study period from the National Oceanic and Atmospheric Administration (NOAA) (https://www.noaa.gov/; Appendix C; C) using the nearest satellite located in New Cuyama, Cuyama Valley. Moreover, site-level mean annual temperature (MAP) and mean annual precipitation (MAP) were obtained from WorldClim (https://www.worldclim.org/data/index.html) at a 1km resolution. We further calculated DeMartonne's aridity values using the following formula: aridity = $P/(T + 10)$ where P = annual precipitation and T = mean annual temperature and classified the climate gradient according to Croitoru et al. (2013).

Vegetation sampling & microclimate

We selected 30 pairs of shrub-open microsites at each study site. *Ephedra californica* was the dominant shrub across all these sites and there were no other dominant or co-dominant shrub species present. The length (at longest axis), width (perpendicular to length), and height to the tallest vegetation branch that had green tissue (Mormon tea is a shrub with many branches) were measured

for every shrub (Lortie et al., 2018). We used the equation for the volume of a hemisphere ($v = \frac{2}{3}\ \pi r^3$) to calculate canopy volume and the equation for the area of a circle ($a = \ \pi r^2$) to calculate the canopy area (Liczner et al., 2016; Lortie et al., 2018). We recorded the percent shrub cover at each site within a 20m radius at the centre of the site via *Google Earth* composite satellite images at a spatial resolution of 30cm (Hestrio et al., 2021; Owen et al., 2024). Within each circular plot (20m in radius), the length at the longest axis of every shrub was measured and used to calculate the individual shrub cover area using a formula of a circle (Liczner et al., 2016; Lortie et al., 2018). Shrub covers were then summed and divided by the total area of the circular plot to produce percent shrub cover estimates of each site (Appendix C; D and L).

We used the Mengshen Digital Temperature and Humidity Meter (*Mengshen*, 2023) to record near-surface air temperature (NSAT, ºC) and near-surface relative humidity (NSRH, %). To record these microclimatic variables, the handheld probe was positioned at approximately ~10-15cm above the soil at the north side of the shrub, immediately within the canopy dripline (inside), and 1m away from a shrub in the adjacent, interstitial open area (outside). We used a cover to stop direct sunlight on the probe bulbs when air temperature and RH were being recorded. Furthermore, we also used the Etekcity Laser Thermometer Gun (*Etekcity*, 2023) to record surface ground temperature (SGT, ºC) both underneath the shrub canopy at the north side of the shrub, and in the open area located adjacently 1m away from a shrub. We then used air temperature and RH to calculate the vapour pressure deficit (VPD) as vegetation structure and microtopography, directly and indirectly, impact this measurement (Novick et al., 2024). We used the following equation: $VPD = SVP * (1 - \frac{RH}{100})$ where saturation vapour pressure (SVP) is the maximum amount of water vapour that air can hold as a certain recorded temperature and RH = relative humidity.

To further explore if microclimate changes depending on the site-level differences in vegetation, we conducted vegetation surveys in shrub and open microsites at each study site. We

identified all vascular plant species present in four paired 1 m^2 quadrats at each microsite (8 total per site). In shrub microsites, one of the paired quadrats was placed under the drip line of randomly selected shrubs on the south-facing side and the paired open quadrat was placed due south with 1m spacing between the two quadrats. In open microsites, each pair of quadrats was randomly placed in what we deemed as the center of the site. We summarized the results of the eight plots to determine the mean annual plant abundance and richness.

Statistical analyses

All statistical analyses were done using R version 4.3.1 (R Core Team, 2024). Data and codes are publicly available on Zenodo (Ghazian & Lortie, 2023). Data distribution was examined using Q-Q plots, and homoscedasticity and normality were tested (Schützenmeister et al., 2012). The relationship between NSAT, SGT, NSRH, and VPD was examined using Pearson's correlation (Benesty et al., 2009). The relationship between canopy area and volume was also examined using Pearson's correlation, as well. We fit Generalized Linear Models (GLM) to test for differences in shrub volume and its effects on air temperature, VPD, and ground temperature for the open versus the shrub. GLM dispersion parameters with AIC scores were used to compare and select the appropriate family to fit to models (Richards et al., 2011). Post-hoc tests were done using the function *emmeans* from the emmeans R package (Lenth & Herve, 2019). We then used Generalized Linear Mixed Models (GLMM) to model shrub volume as a predictor of each microclimatic variable, with microsite nested in site to serve as a covariate. We further explored if mean plant richness and abundance were predicted by percent shrub cover, aridity, mean NSAT, and mean VPD using GLMs. We included predictors in these models by testing multicollinearity using the *Performance* package and excluded those that lead to high variance inflation factors (VIF) (Daoud, 2017), and hence high collinearity (Appendix C; A and B).

4.4: Results

A total of 180 shrub-open microsites were surveyed for microclimatic measures (n = 180). Mean shrub volume and area for *E. californica* were 39.64 ± 27.80 m^3 and 37.16 ± 22.06 m^2, respectively (Appendix C; F). Shrub area and canopy volume were significantly, and positively related (Pearson's product-moment correlation = 0.92, $p<0.01$; Appendix C; G); thus, we used shrub volume as a proxy for size in all our models. Percent shrub cover at study sites ranged from 6.68-31.18% (Appendix C; D). Table 4.3 provides the mean air temperature and VPD under the shrub and in the open at each site. The lowest mean air temperature was recorded in the open at Carrizo_soda_shrub (15.06 ± 3.48 ºC) and the lowest mean VPD was recorded under the shrub (0.55 ± 0.16 kPa) in Cuyama_3. Figure 4.2 depicts the frequency distribution of change in air temperature between the open and the shrub in Kelvin. Mean ground temperature was the only microclimatic parameter significantly lower under the shrub than in the open (Estimated Marginalized Mean (EMM) 13.5 ± 0.39 ºC, $p<0.01$; Figure 4.1).

Overall, shrub volume did not have a significant effect on air temperature in fixed-effect models (GLMM estimated $\beta = 0$; Table 4.2). The same was observed for VPD (GLMM estimated ($\beta = 0$) and ground temperature (GLMM estimated $\beta = -0.01$). The confidence intervals for all three estimates were also narrow, which further confirms the weak effects of shrub volume on these microclimatic variables.

A total of 27 different annual plant species were found under shrubs and in the open (Appendix C; E). *Bromus madritensis rubens* (red brome) was the most abundant species observed under the shrubs, while *Lasthenia gracilis* (needle goldfield) was the most abundant species in the open. *Astragalus lentiginosus nigricalycis* (spotted locoweed), *Brassica nigra* (black mustard), *Lactuca serriola* (prickly lettuce), *Lupinus microcarpus* (chick lupine) were the equally the least abundant species under the shrub. *Lupinus microcarpus* (chick lupine) was also the least abundant

species in the open. There were four species exclusively found under shrubs, including *Brassica nigra* (black mustard), *Eremalche exilis* (white mallow), *Lactuca serriola* (prickly lettuce), *Pholistoma membranaceum* (white fiesta flower). Both site-level shrub cover and aridity were significant predictors of plant abundance and richness (Figure 4.3 and Table 4.4). Mean plant abundance was significantly greater under the shrubs (EMM 23 ± 1.82, $p<0.01$), while mean richness was significantly greater in the open (EMM 6.82 ± 0.16, $p<0.01$). Site-level mean air temperature and mean VPD were significant predictors of plant richness both under the shrub and in the open, but not abundance (Figure 4.4 and Table 4.5).

Table 4.1: Sites List of study sites in California, United States surveyed for this study and their respective geographical coordinates. Mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted from WorldClim and used to calculate DeMartonne's aridity index.

Site Code	*Semi-arid Region*	*Latitude*	*Longitude*	*MAT (ºC)*	*MAP (mm)*	*Aridity*	*Regional Gradient Classification*
Cuyama_1	San Joaquin	34.849	-119.483	14	136	5.67	Arid
Cuyama_2	San Joaquin	34.854	-119.486	14.1	137	5.69	Arid
Cuyama_3	San Joaquin	34.938	-119.481	14.2	139	5.74	Arid
Carrizo_3	San Joaquin	35.163	-119.675	14.5	149	6.08	Arid
Carrizo_4	San Joaquin	35.116	-119.621	14.7	147	5.95	Arid
Carrizo_soda_shrub	San Joaquin	35.119	-119.629	14.7	148	5.99	Arid

Table 4.2: Model Summary I Contrast of microclimatic measurements estimated using Generalized Linear Mixed Models (GLMM). Microsite was nested within the site code. Significant p-values are in bold. CI represents the 95% confidence interval.

	Predictors	***Estimates***	***CI***	***p-value***	***Standard Error (SE)***
NSAT (℃)	**(Intercept)**	16.44	12.82-20.07	**0.01**	1.85
	shrub_volume	0	-0.01-0.02	0.57	0.0059
	Number of Observations: 180 Marginal R^2: 0 N_{sites}: 6				
VPD (kPa)	**(Intercept)**	1.43	1.06-1.80	**0.01**	0.19
	shrub_volume	0	-0.01-0.04	0.59	0.001
	Number of Observations: 180 Marginal R^2: 0 N_{sites}: 6				
SGT (℃)	**(Intercept)**	14.09	10.5-17.67	**0.01**	1.83
	shrub_volume	-0.01	-0.03-0.01	0.17	0.01
	Number of Observations: 180 Marginal R^2: 0.005 N_{sites}: 6				

Table 4.3: Air Temperature & VPD Summary Mean near-surface air temperature (NSAT) and vapor pressure deficit (VPD) with their standard deviations are provided across each site, under the shrub, and in the open.

Site Code	*Semi-arid Region*	*Microsite*	*Mean ± SD NSAT (ºC)*	*Mean ± SD VPD (kPa)*
Cuyama_1	San Joaquin	open	29.14 ± 2.59	1.67 ± 0.41
Cuyama_1	San Joaquin	shrub	19.73 ± 1.98	1.59 ± 0.25
Cuyama_2	San Joaquin	open	20.78 ± 1.32	1.76 ± 0.22
Cuyama_2	San Joaquin	shrub	21.08 ± 1.69	1.81 ± 0.23
Cuyama_3	San Joaquin	open	8.46 ± 1.91	0.56 ± 0.18
Cuyama_3	San Joaquin	shrub	8.45 ± 1.97	0.55 ± 0.16
Carrizo_3	San Joaquin	open	17.24 ± 1.21	1.66 ± 0.16
Carrizo_3	San Joaquin	shrub	17.62 ± 1.40	1.70 ± 0.19
Carrizo_4	San Joaquin	open	17.34 ± 0.54	1.62 ± 0.08
Carrizo_4	San Joaquin	shrub	17.33 ± 1.10	1.61 ± 0.13
Carrizo_soda_shrub	San Joaquin	open	15.06 ± 3.48	1.35 ± 0.34
Carrizo_soda_shrub	San Joaquin	shrub	15.12 ± 3.74	1.39 ± 0.38

Table 4.4: Model Summary II Analysis mean annual plant richness and abundance are shown using a Generalized Linear Model (GLM). Significant p-values are bolded. Given model has the lowest AIC for the family of fit.

	Predictors	***df***	***Deviance Residuals***	***df residuals***	***Residual Deviation***	***p-value***
Mean richness	**NULL**			107	227.87	
	shrub_cover	1	35.57	106	192.30	**0.01**
	microsite	1	8.89	105	183.4	**0.01**
	aridity	1	66.72	104	117.13	**0.01**
Mean abundance	**NULL**			107	51383	
	shrub_cover	1	20589.9	106	30793	**0.01**
	microsite	1	1633.3	105	29160	**0.01**
	aridity	1	6803.6	104	22356	**0.01**

Table 4.5: Model Summary III Analysis mean annual plant richness and abundance are shown using a Generalized Linear Model (GLM). Significant p-values are bolded. Given model has the lowest AIC for the family of fit.

	Predictors	***df***	***Deviance Residuals***	***df residuals***	***Residual Deviation***	***p-value***
Mean richness	**NULL**			107	227.87	
	mean_NSAT	1	9.75	106	218.12	**0.01**
	microsite	1	9.15	105	208.96	**0.01**
	mean_VPD	1	38.31	104	170.65	**0.01**
Mean abundance	**NULL**			107	51383	
	mean_NSAT	1	14719.1	106	36664	**0.01**
	microsite	1	419.5	105	36244	0.08
	mean_VPD	1	21743.3	104	14501	**0.01**

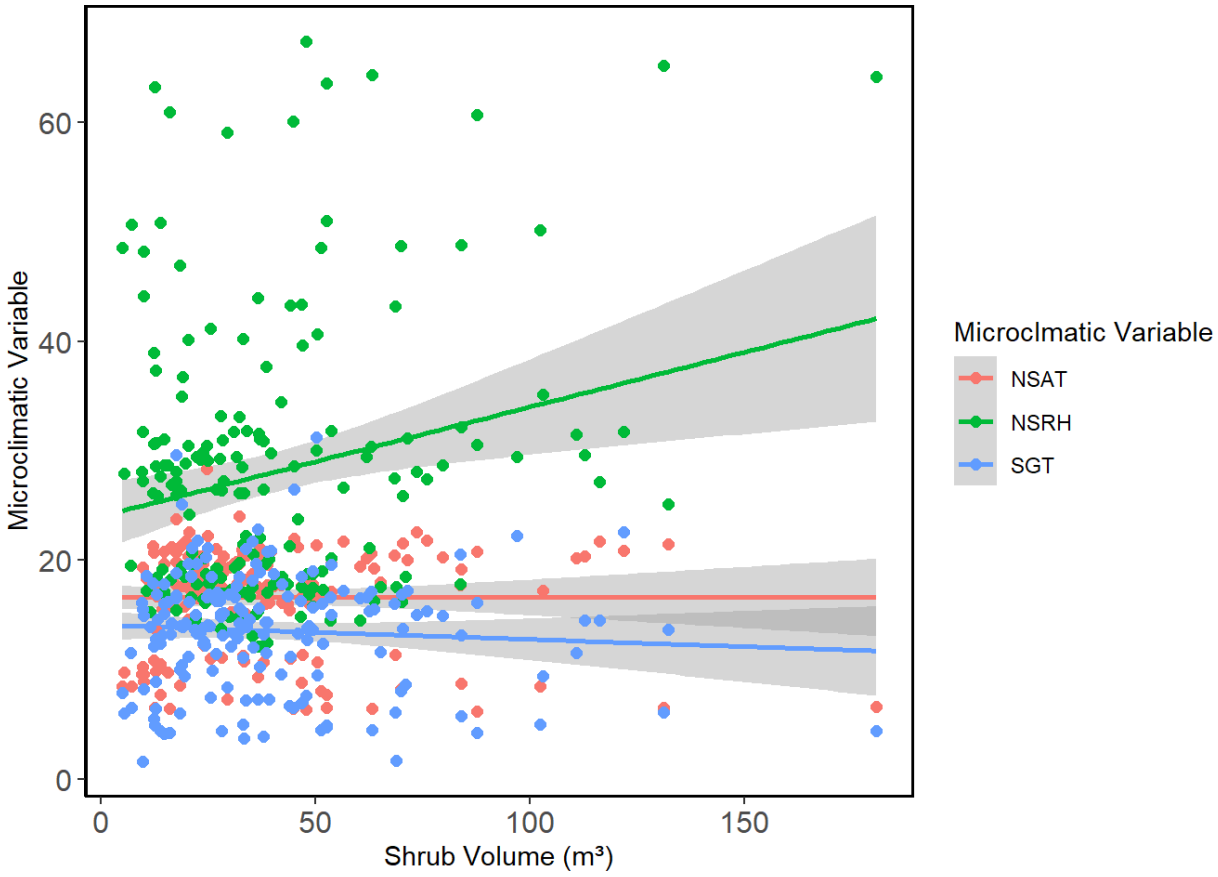

Figure 4.1: Shrub Volume vs. Microclimatic Measures The relationship between shrub volume (m^3) and microclimatic measures including NSAT (ºC), NSRH (%), and SGT (ºC) are presented using points. Smoothed means are fitted using the linear method. Colours represent the different key microclimatic variables.

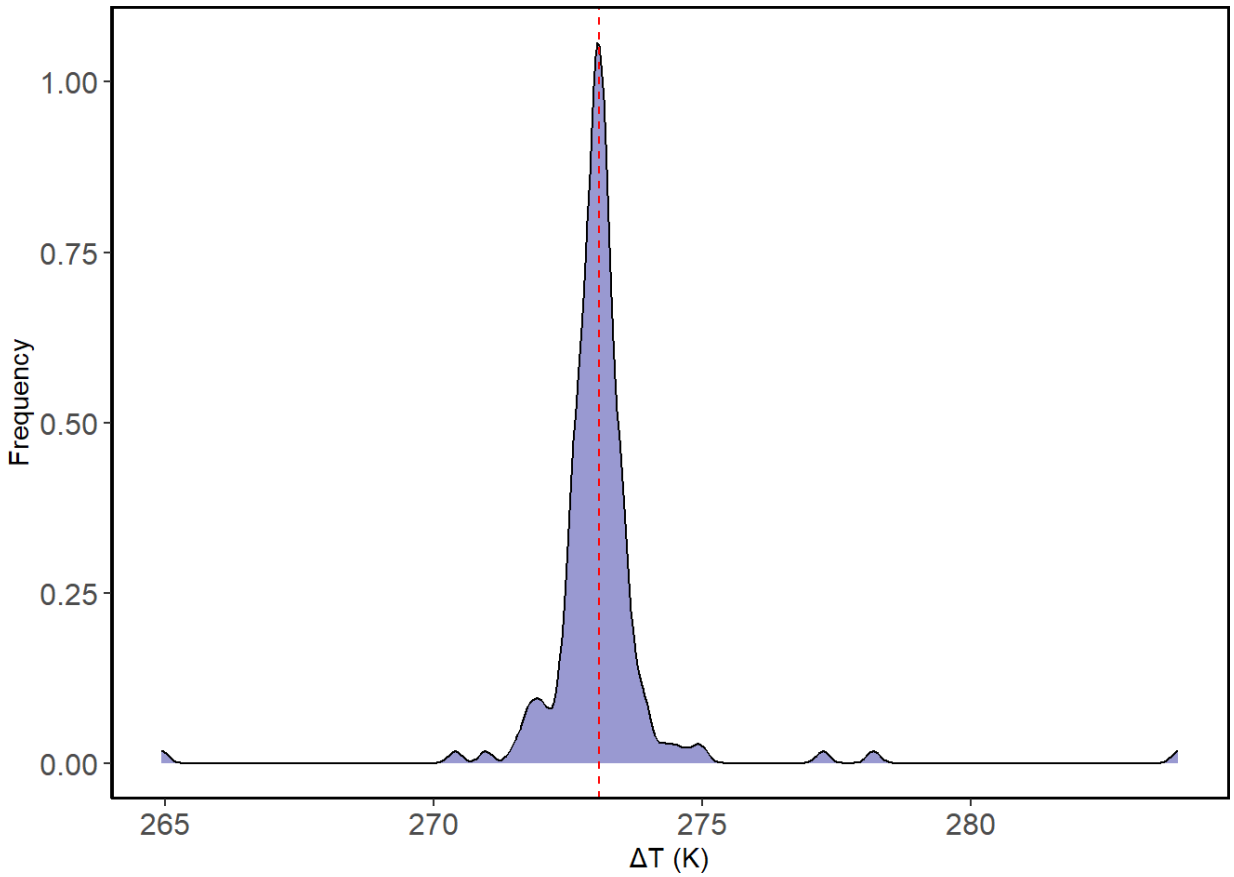

Figure 4.2: Frequency Distribution The frequency distribution of temperature differences between the open and shrub is presented. The x-axis represents the difference in temperature in Kelvin while the y-axis represents the particular frequency ΔT that was observed. Dashed red line is the mean of temperature changes.

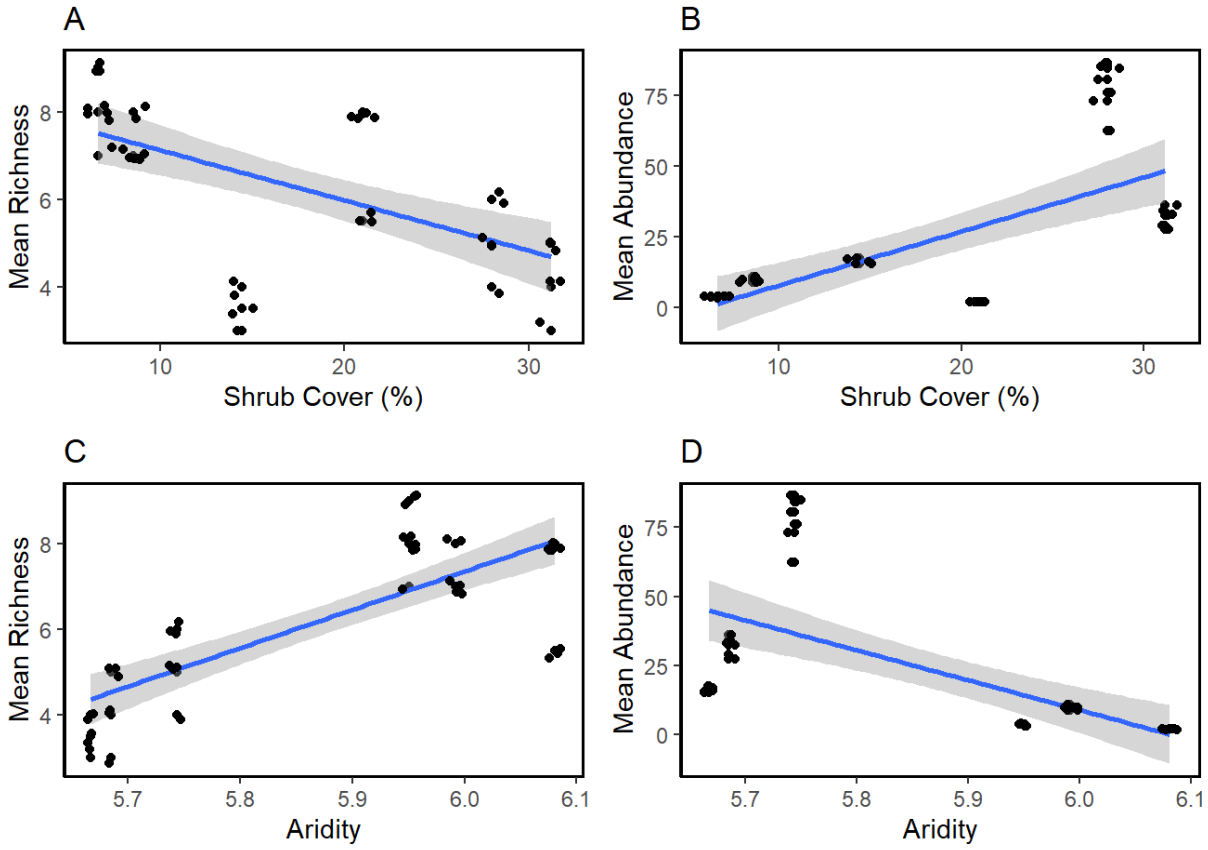

Figure 4.3: Vegetation Measures I Mean plant abundance and richness regressed against percent shrub cover (%) (A and B) and aridity (C and D). Smoothed means are fitted using the linear method.

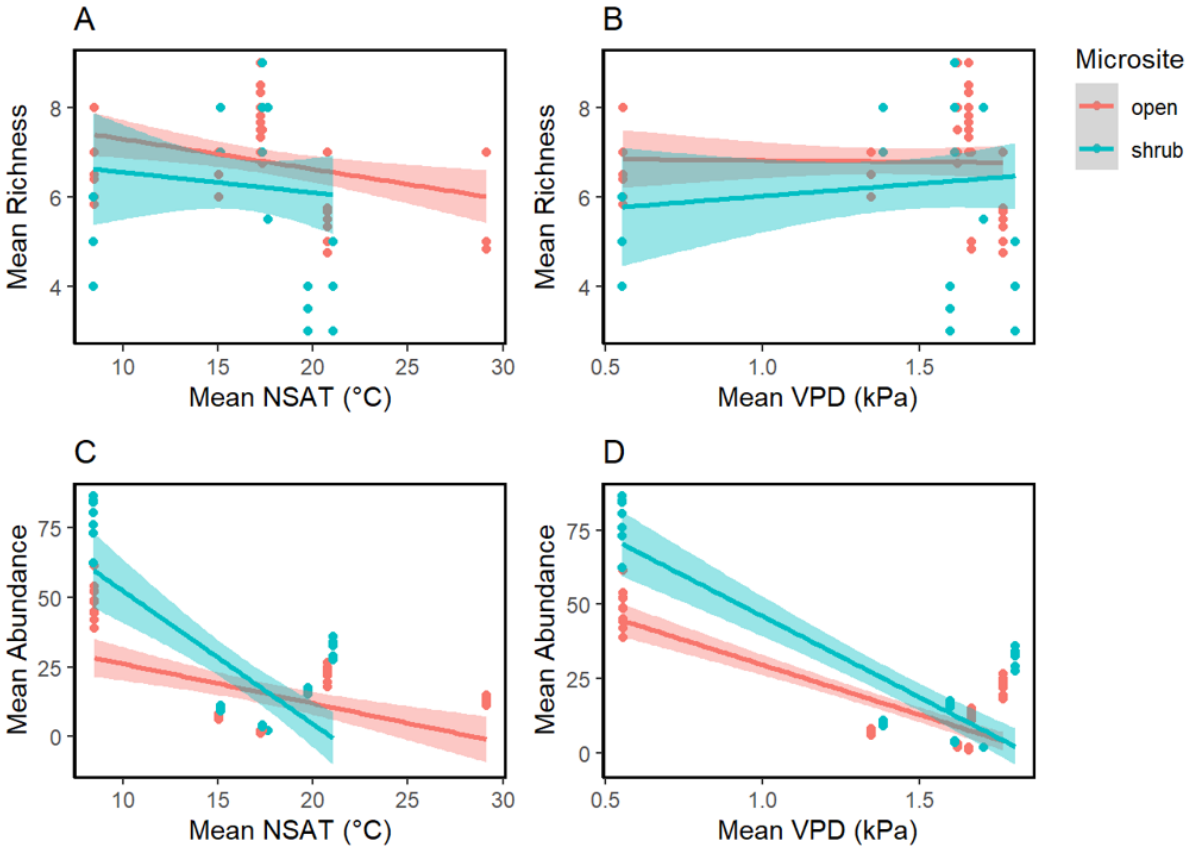

Figure 4.4: Vegetation Measures II Mean plant abundance and richness regressed against mean NSAT (ºC) (A and C) and mean VPD (kPa) (B and D). Smoothed means are fitted using the linear method. Color represents the microsite.

4.5: Discussion

Abiotic amelioration via foundation shrubs is a key component of many dryland ecosystems. Herein, we examined the microclimate of the foundation shrub species, *Ephedra californica* in order to determine the relative significance of shrub volume on microclimate and the role of microclimate in predicting vegetation richness and abundance. These were tested across six sites in the drylands of California. We hypothesized that, in comparison to an open gap, foundation shrubs improve the microclimate beneath their canopy and that microclimate is in turn a significant predictor of annual vegetation. Despite our prediction that all microclimatic variables under the shrub would be significantly lower than in the open, we only observed significantly lower ground temperature under the shrub. Shrub volume was not a significant predictor of air temperature, ground temperature, and VPD. Thus, we propose that *E. californica* is a good benefactor species when it comes to facilitating some micro-environmental measures compared to the open gap; though, its role in microclimatic amelioration is weakly dependent on size. Furthermore, we concluded that site-level percent shrub cover and aridity are significant predictors of vascular plant abundance and richness. Mean air temperature and VPD at the site level significantly predicted vegetation richness and abundance, however, microsite-level differences were only significant to plant richness. Mean plant abundance was greater under shrubs suggesting that shrub cover has an impact on microclimate, and the environmental heterogeneity induced by shrubs that may act on different spatial scales, hence altering the dynamics of distribution and establishment of the herbaceous plant community (Madrigal et al., 2008). We suggest that one factor may be microclimatic amelioration, such as cooler ground temperatures, by foundation species that allow for the presence of species that would otherwise be absent. This is consistent with the results of Soliveres and Maestre (2014) who observed 29% more species associated with shrubs in drylands compared to the open. Furthermore, we observed that mean plant richness was higher in the open. We believe that this may be due to the fact some shrubs restrict the establishment and survivorship of certain annual plants because the reduction of light by

shrub canopy can limit the photosynthetic activity of annuals (Swank & Oechel, 1991). Semi-arid annual plants attain high net photosynthetic rates by having very high light saturation levels (Werk et al., 1983). A reduction in radiation by shrubs can reduce resource acquisition (Jackson & Caldwell, 1992). Thus, we suggest that plant-plant interactions and their responses to ongoing climate change are more complex than previously thought (Seiferling et al., 2014), but these interactions are nonetheless crucial in maintaining biodiversity in dryland ecosystems, particularly given the number of species that exclusively associate with shrubs. Though beyond the scope of our study, we suggest that future experiments consider plant traits as a tool to understand why some species are more benefited than others.

More than 30% of the total land area in California is defined as a semi-arid ecoregion (Syphard et al., 2022). Shrubs create heterogeneity in these regions by creating variation in physical structure and thus provide a generalized facilitation function of ameliorating microclimate (Braun et al., 2021). Shrub canopies create micro-environmental benefits including increasing shade, reducing radiation load, increasing night-time winter temperature, and increasing soil moisture, and canopy structure play an important role in differences observed in these micro-environmental parameters (Jankju, 2013). In this study, we observed the facilitative effects of *E. californica* are not dependent on size. This shows that even the canopy of smaller, low-stature, long-lived ancient shrubs can nonetheless provide fine-scale climatic refuges for other species (Ivey et al., 2020; Lortie et al., 2018, 2020). Maintaining the biodiversity of semi-arid regions is crucial as it translates to the overall biodiversity of the entire region of California. There is a direct relationship between environmental heterogeneity (EH) and biodiversity, with species richness increasing with greater EH (Agra et al., 2021). Maintaining *E. californica* presence and promoting its persistence in the region through conservation, restoration, and management will result in greater heterogeneity in the region and thus higher regional biodiversity. Shrubs and annual plants enable small areas in the species niche that

can allow species persistence in a shifting climate (Brooker et al., 2018). Thus providing animal species with the option to move around and behaviourally mitigate climate change effects. Hence, management and restoration efforts need to focus on not only protecting existing shrub species but also restoring and managing disturbed scrubland and they are key to the persistence of biodiversity. Supporting the persistence of other taxa through foundation shrubs like *E. californica* that both directly and indirectly influence microclimatic heterogeneity is crucial in the future well-being of dryland ecosystems under the current climate change paradigms.

4.6: Acknowledgments

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4.7: Author's Contributions

N.G, M.Z, C.J.L designed the study; N.G and R.K collected data; N.G performed statistical analyses; N.G wrote the manuscript; C.J.L and R.K offered input for statistical analyses; M.Z, R.K, and C.J.L thoroughly edited the manuscript and offered valuable insight.

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CHAPTER 5: ARTIFICIAL SHELTERS PROVIDE MICROCLIMATIC REFUGES FOR RESIDENT VERTEBRATE ANIMAL SPECIES FROM INCREASING DESERTIFICATION

Currently under review at *Ecological Evidence and Solutions*.

5.1: Chapter Summary

Climate change and anthropogenic disruptions are significantly impacting deserts, which cover 41% of the Earth's surface and are prone to further desertification. The purpose of this study was to examine whether eco-friendly artificial shelters can replicate the microclimatic benefits of foundation shrubs to support vertebrate abundance and richness in North American deserts. Vertebrate surveys were conducted at four desert sites in Southwestern California (2022-2023). Camera traps were used to record vertebrate abundance, richness, and evenness, and microdata loggers were used to record microclimatic variables, including temperature, humidity, and solar radiation at shrubs (*Ephedra californica* and *Larrea tridentata*), open areas, and artificial shelters (square and triangle). Surveys were conducted during the spring and winter seasons. Statistical analyses, including Generalized Linear Models and an effect size measure, the Relative Interaction Index (RII), were used to assess the impact of microsites on vertebrate community dynamics. Eighteen vertebrate species were documented across all seasons. Vertebrate abundance, richness, and evenness were higher at artificial shelters and shrubs compared to open areas. Yearly variation influenced these metrics, with more vertebrates associating with shelters and shrubs in the dry ‘year’ (2022) compared to the ‘wet’ year (2023) when they associated more with the open areas. This supports the main prediction that the relative importance of and need for shelters for animals will increase with desertification. In the winter, vertebrates were almost always entirely associated with the open areas when it was relatively cooler than the spring temperatures. Artificial shelters provided similar microclimatic benefits to foundation shrubs in that they also increased vertebrate abundance and richness. These results suggest that eco-friendly shelters can support resident biodiversity in degraded desert ecosystems, and can offer a viable short-term solution for vertebrate conservation in the context of increasing desertification.

5.2: Introduction

The impacts of anthropogenic change are profound in deserts and desert scrublands. North American deserts are expected to warm up faster than other regions because of climate change (Stahlschmidt et al., 2011). Climate estimates from multiple sources suggest that temperatures in the deserts of southern California will rise by almost 2 °C by the mid-century (Bachelet et al., 2016). Furthermore, in the desert regions of North America, precipitation is infrequent and changes over shorter (seasonal) and longer (decade) time scales (Stahlschmidt et al., 2011). This variability in precipitation and extended drought and mega-droughts pose limitations to ecological resilience for both plants and animals (Cook et al., 2010; Lortie, Ghazian, et al., 2022). Deserts cover 41% of the Earth's surface and they are thus critically important ecosystems. However, deserts are at risk of further degradation and expansion (Vendruscolo et al., 2021) typically termed desertification and defined as "land degradation in arid, semiarid, and subhumid areas, resulting from various factors including climatic variations and human activities" (Orr et al., 2017). There are at least four dominant forms of desertification, "vegetation loss due to agriculture, vegetation loss due to changes in climate or land use, invasion of woody vegetation into perennial grassland, and invasion of exotic grasses into desert scrubland, in turn replacing woody vegetation" (Okin et al., 2009). Whatever the form, desertification impacts biodiversity dynamics (Bestelmeyer, 2005; Whitford, 1997). Desertification diminishes the biological potential of land and can lead to more desert-like conditions (Mabbutt, 1986). If current trends continue, resident species will likely not be able to behaviourally mitigate climatic and land use changes like urbanization and desert agriculture (Germano et al., 2011) or further degradation. Although most desert plants and animals can withstand extremely high temperatures, some may be getting close to their physiological threshold (Smit et al., 2016). Even though temperature-driven mortality may not rise in some species, it may nevertheless have an impact on their ability to survive (Serra-Diaz et al., 2014). Due to the relative climate envelopes, changes in the environment at fine scales can drive species beyond the point of no return and result

in local extirpations (Ivey et al., 2020, 2022; Vickers et al., 2011), impacting the species' ability to adapt to climate change (Bauwens et al., 1996; Visser, 2008), or to migrate (Lennox et al., 2016; Seebacher & Post, 2015). Likewise, higher temperatures can negatively impact the vigour of hatchlings and the sex determination of eggs deposited by species such as desert tortoises (Bachelet et al., 2016). Long-term climate patterns can affect reproduction and distribution, but at fine scales, microclimate has an instantaneous impact on survival (Parmesan, 2006; Walther, 2010). Thus, considering the scale at which climate is measured is key to effective biodiversity planning and development.

To help decision-makers develop effective land rehabilitation plans and combat global desertification, it is crucial to assess how climate change and human activities influence desertification globally (Huang et al., 2020). Climate can serve as an indirect desertification indicator and assessment of desertification trends through an integration of the effects of several contributory phenomena, or their scale effects across an area (Mabbutt, 1986). ‘Microclimate’ is the climate at the lower 2m of the atmosphere and the upper 0.5-1m of the soil while ‘macroclimate’ or simply climate is the atmospheric condition over long periods occurring without the interference of local topography, soil type, and vegetation (Stoutjesdijk & Barkman, 2014). Microclimate is an exceptionally multifaceted, non-linear phenomenon that comprises an interplay between local and global processes (Zanchi et al., 2023). Environmental heterogeneity (EH) is described as non-uniformities in physical and ecological characteristics of the landscape, and climatic heterogeneity is a significant component of EH (Dronova, 2017; Stein & Kreft, 2015). The importance of microclimates in predicting species responses to climate change is becoming more important (Brigham & Suding, 2023). Regions with greater microclimatic heterogeneity have an overall greater environmental heterogeneity and thus greater species richness (Agra et al., 2021) as they provide “tiny niches” that allow species to persist in a shifting climate (Brooker et al., 2018). Species’ ability

to adjust to a changing climate is relatively limited and variable depending on the extent of capacity for a given species to shift with or adapt to changes. Hence, we need to actively look into key restoration and conservation practices that take microclimatic issues into account and directly treat them in restoring the natural landscape. Ecological solutions are well-established in deserts (Zhang et al., 2023), and here we explore this opportunity directly at the scale of microclimatic mitigation for wildlife.

There is widespread evidence that plants can moderate the microclimate to support related species. Foundation plants often include shrubs and other dominant perennials with a canopy that can serve as an agent of facilitation (Aguirre et al., 2021; Bernath-Plaisted et al., 2023; Liancourt & Dolezal, 2021). Facilitation is defined as an interaction where one or more species (beneficiaries) benefit from another species (benefactor) while none are harmed (Bertness & Callaway, 1994; Bertness & Leonard, 1997). At fine scales, facilitative plants ameliorate abiotic conditions via their canopy by lowering temperature, elevating humidity, creating a windbreak, and reducing exposure to direct sunlight (Filazzola et al., 2017; Filazzola & Lortie, 2014; Holzapfel & Mahall, 1999). Furthermore, foundation shrubs offer microclimatic benefits regardless of their canopy size or stature (Ghazian et al., 2024). Despite their demonstrated importance, microclimatic facilitation by vegetation is largely overlooked (Brigham & Suding, 2023). In desert ecosystems, variability in the microclimate created by natural shrubs can contribute to the overall environmental heterogeneity (D'Odorico et al., 2010). Shrub density and total shrub cover can provide benefits to interacting species (Crofts et al., 2018; Zuliani et al., 2023). Foundation shrubs can positively influence the abundance, richness, and distribution of vertebrate species within desert ecosystems (Owen et al., 2024; Westphal et al., 2018; Zuliani et al., 2021, 2023). To further our knowledge of these facilitative interactions, we must understand the interplay between climate and species associations to enhance our understanding of community assembly and dynamics.

One short-term solution to offset potential desertification effects is the use of artificial habitat structures that can be placed in degraded, disturbed, or altered environments to aid conservation efforts. (Watchorn et al., 2022). For instance, some snakes use artificial structures to thermoregulate (Lelièvre et al., 2010), and certain bird species use them for perching (Athiê & Dias, 2016). In deserts, shelters, and human-made architecture are important for a range of ecological interactions (Ghazian et al., 2020; Ghazian, MacDonald, et al., 2024; Zuliani et al., 2024). Artificial habitat constructions and infrastructure can alter the surrounding microclimate (Ghazian et al., 2020; Tillman et al., 2021; Yu et al., 2022) and directly affect the physiological and behavioural regulation of certain species, such as reptiles (Yu et al., 2022). In addition to providing safety and shelter, the covers can create a microhabitat for reptiles and amphibians that can improve the temperature and moisture levels necessary for their physiology and behaviour (Liberman et al., 2024). Likewise, by lowering the nest temperature during sea turtle incubation, artificial shade can help mitigate the effects of global warming and ensure hatchling production (Esteban et al., 2018; Reboul et al., 2021). Artificial shelters can be used as a restorative solution, particularly if the canopy is made from more eco-friendly materials. However, to ensure that artificial structures do not act as an ecological trap or an inappropriate biodiversity offset, it is crucial that they are monitored across pertinent ecological geographical and temporal scales and that their effects are compared to suitable controls (Watchorn et al., 2023). Artificial shelters and refuges are now commonly used in conservation (Watchorn et al., 2024) and so there is a pressing need to assess their impact on microclimatic heterogeneity and thus the facilitation of resident species.

The purpose of this study was to test if eco-friendly, artificial shelters can influence vertebrate community composition and dynamics. We used camera traps to record vertebrate species at microsites, including shelters, shrubs, and open areas. Additionally, we used microdata loggers to record temperature, humidity, and solar radiation at these microsites. We tested this conservation tool at different sites within

Central California deserts in a relatively hot, drought year (2022) and again in a wetter, cooler year (2023). We also tested this tool once during the winter season when temperatures were relatively cooler than the spring periods. Here, we have thus both variations in space, season, and two representative desert years to test the importance of shelter for animals. We hypothesized that artificial shelters provide refuge for desert vertebrates through microclimatic facilitation similar to the native shrub species. We tested the following predictions:

1) Microsite type has a direct, positive influence on vertebrate species abundance, richness, and evenness, and these measurements are similar between shelters and shrubs and different from the open microsites.
2) Vertebrates are more associated with shrubs and shelters in dry, warm years (positive effect size value), and less in cool, wet years, or colder seasons (negative effect size values).
3) Microclimate predicts the relative association patterns of species with shrubs and shelters within these tested habitats.

5.3: Materials & Methods

Sites description

We surveyed a total of four sites across desert and semi-desert deserts of Southwestern, California, USA (Figure 5.1; Appendix D; A). The annual aridity of each site was estimated using the De Martonne's Aridity Index using the equation A= P/(MAT+10), where P is the total annual precipitation and MAT is the Mean monthly Annual Temperature (Croitoru et al., 2013). We chose these sites because of their distinct differences in aridity and whether they had foundation shrubs or were completely open. We conducted a total of three surveys between 2022-2023, one during the spring of each year and one in the winter of 2023. Each census was composed of microclimate and vertebrate surveys. The first spring census (a) took place from May 11th to June 6th, 2022. The winter census (b) took place from February 12th to March 13th, 2023. The second spring census (c) took

place from April 19th to May 22nd, 2023. While 2022 was considered a 'dry' year, 2023 was considered a high precipitation year, characterized by a superbloom and winter rainfall exceeding the long-term averages by ≥70% (Jennings & Berry, 2023).

Study species

Ephedra californica (Mormon Tea) is a dominant or co-dominant foundation shrub native to the Southwestern regions of California (Sawyer et al., 2009). This key foundation plant plays a pivotal role in the facilitation of desert ecosystems in California (Liczner et al., 2016; Lortie et al., 2018; Zuliani et al., 2021). *Ephedra californica* is a structural agent of abiotic amelioration, providing shade from direct sunlight and cooler temperatures under its canopy (Filazzola et al., 2017). This foundation shrub can reach heights of over 1m tall, typically taking 5-10 years to grow 0.5m (Lortie et al., 2018). In the Carrizo Plain National Monument, *E. californica* is the dominant, or co-dominant shrub with saltbush (genus *Atriplex*) (Noble et al., 2016). Furthermore, this species is used by various vertebrates such as the Blunt-Nosed Leopard Lizard (*Gambelia sila*) (Gaudenti et al., 2021; Lortie et al., 2020), and the Giant Kangaroo Rat (*Dipodomys heermanni*) (Prugh & Brashares, 2010).

Larrea tridentata (Creosote bush) is also a dominant or co-dominant flowering shrub that is often found in the sandy soils, desert pavements, and well-developed cryptogram layer of the Mojave Desert (Braun et al., 2021; Sawyer et al., 2009). Even in situations with extreme heat and limited water potential, this foundation plant can continue to perform photosynthesis (Barbour et al., 2007). The association of *L. tridentata* is well-explored regarding pollinators (Braun & Lortie, 2019, 2020) but not vertebrate species.

Microsite deployment & abiotic measurements

Shelters were constructed using a previously developed protocol (Ghazian et al., 2020) with natural burlap for covering. The use of natural fabrics in conservation has gained popularity due to

their lightweight, biodegradability, and strength (Rangappa et al., 2022). We selected burlap rather than other natural, lignocellulosic fabrics because of its ability to lower the amplitude of temperature variation and control light regimes efficiently (Ghazian, MacDonald, et al., 2024). We selected a total of five microsites: *E. californica*, *L. tridentata*, open, square, and triangle. In both spring seasons, we had eight microsite triplets, which included a square and triangle shelter, and a shrub (species depended on the site) at each shrubbed site. In each open site, we had a total of eight open microsites with four squares, and four triangles (Appendix D; N). In the winter season, we conducted a mini survey that included two shrubs, two squares, and two triangles at the shrubbed sites, in addition to two opens, two squares, and two triangles in the open sites. We georeferenced all microsites. Because many animals associate with shrubs, we had more microsites in the shrubbed areas because we wanted to maximize vertebrate species detection by having more camera traps rather than leaving the cameras for a longer period as this has proven to be a more effective survey technique (Ghazian & Lortie, 2023).

Temperature (ºC), relative humidity (RH, %), and solar radiation (lum/ft^2) were recorded at each shelter, open, and shrub using microdata loggers in both spring seasons. In the winter season, only temperature and solar radiation were recorded due to supply chain issues with the humidity loggers. Onset HOBO Temperature/Light Pendant (64 K) pendants were used to measure temperature and solar radiation (Hoskin Scientific, 2021). In the spring of 2022, OMEGA OM-91 pendants were used to measure relative humidity (OMEGA Engineering, 2021); however, in the spring of 2023, Elitech RC-51H USB humidity loggers were used instead (Elitech, 2024). Data loggers were attached to pegs using zip ties and placed ~10 cm above ground. This was done to ensure ambient and not ground microclimate was recorded. Microdata loggers were set to record abiotic measurements at 1-hour intervals.

Camera trapping & Species validation

Vikeri A1 model camera traps were used to sample vertebrate communities (Vikeri, 2024). Cameras were attached to stakes using zip ties and the stakes were driven into the ground until cameras were flush to the ground. Cameras were set up ~ 1.5-2 m away facing the shrub, shelter, or open microsite and they were spatially paired with loggers. Cameras were set to survey communities night and day. No flash was emitted by the cameras to ensure that animals were not disturbed. Cameras were set to medium sensitivity with a 1-minute delay to minimize instances of false positives when the camera fired but no animal was present (Kolowski & Forrester, 2017; Lepard et al., 2019; Zuliani et al., 2021). This also reduced the rapid triggers of the same animal. Photos were defined as independent when individual animals were not seen at the same position within the 1-minute delay period. This was done to ensure vertebrate abundance can be effectively measured as opposed to visitation rates (Krauss et al., 2018). Cameras were unbaited and were maintained every four to five days to ensure proper functioning. During each maintenance, the images were saved onto 24 GB SD cards and saved as Joint Photographic Export Group (JPEG) files. The JPEG files were then examined and used to extract data, including photo ID, site, microsite, year, date, rep, camera number, presence/absence of animal, and species binomial name. Species composition data and hourly microclimatic measurements were joined by taking the mean average of each abiotic measurement by microsite, site, and year.

Vertebrate animals were validated using a mixture of *Wildlife Insight* (Vélez et al., 2023) and *iNaturalist* (Unger et al., 2021). For photos containing species, both applications offered the most likely identification and were then confirmed by expert researchers of the region. After being classified as unknowns, questionable photos were later removed from the community composition data. Capture efficiency was calculated by dividing the number of photos with vertebrate species by the total number of photos taken (Noble et al., 2016).

Statistical analyses

All statistical analyses were performed using R version 4.4.0 (R Core Team, 2024). Code is published at *Zenodo* (Ghazian, Zuliani, et al., 2024) and all data are published on *Figshare* (Ghazian, lortie, et al., 2024). Q-Q plots were used to examine the distribution of microclimatic data and to check for normality and homoscedasticity (Schützenmeister et al., 2012). Evenness was calculated using the Shannon-Weaver (or Weiner) diversity index based on obtained richness values (Stirling & Wilsey, 2001). Principle Coordinate Analysis (PCOA) was conducted to compare the vertebrate community composition between each shrub and shelter type, and the open microsites. Generalized Linear Models (GLM) were used to test if vertebrate abundance, richness, and evenness are predicted by microsite nested in site, year as a fixed effect factor (in spring models only) (Firebaugh et al., 2013), and microclimatic variables as covariates. We created separate models for the different seasons to account for differences in the spring and winter. AIC (Akaike Information Criterion) scores were used to choose the family that best suited the data (Richards et al., 2011). All reported models are the ones with the lowest AIC scores. As well, we checked overdispersion using the *performance* package when selecting the family fit. Post-hoc tests were done using the function *emmeans* (Estimated Marginalized Mean) from the emmeans R package (Lenth & Herve, 2019). A Principle Component Analysis (PCA) was conducted for microclimatic variables to reduce the number of variables to one dimension based on the most important variable (Tadić et al., 2019). However, only 74.1% of the variation was explained by the data and all of the PC1 or PC2 eigenvalues were <1, and deemed not useful for use in models (Tadić et al., 2019). Instead, we included microclimatic predictors in the microclimate models by testing multicollinearity using the *Performance* package and excluded those that lead to high variance inflation factors (VIF) and thus high collinearity (Daoud, 2017)**.** Thus, all post-hoc analyses and final models were created using temperature as the only microclimatic covariate. Interaction among species is central to community ecology and testing these hypotheses requires a qualification of the magnitude of interaction between

species (Bruno et al., 2003; Goldberg et al., 1999). The Relative Interaction Index (RII) is an effect size that measures plant interaction with defined limits of [-1, +1] (Armas et al., 2004). In this study, the index was calculated by taking vertebrate metrics values at a shrub or shelter and comparing them to the open values in the same area as follow:

$$\mathrm{RII} = \frac{A_s - A_o}{A_s + A_o}$$

Where A_s and A_o are the values for the particular animal measurement under the shelter or shrub and the open microsite. Positive values of this index denote facilitation or the association of vertebrates with shrubs and shelters. Negative values indicate that the vertebrate animal is more often found in the open as opposed to the shrub or shelter. A neutral interaction is indicated by zero.

5.4: Results

Vertebrate community composition

The total number of animals observed at each year, census, and site is summarized in Table 5.1. We observed a total of 18 different vertebrate species across all sites in the spring and winter (Figure 5.3; Appendix D; M). Commonly observed vertebrate species included *Dipodomys heermanni* (Heerman's Kangaroo Rat), *Lepus californicus* (Black-tailed Jackrabbit), and *Dipodomys ingens* (Giant Kangaroo Rat) (Figure 5.3). Vertebrate community composition differed significantly between the microsites in spring 2022 (PPERMANOVA, F-value = 6.82, p-value <0.01; Appendix D; B, C, and D) and in winter 2023 (PPERMANOVA, F-value = 7.174, p-value <0.01; Appendix D; E, F, and G). Specifically, significant differences in vertebrate composition were detected between *L. tridentata* and *E. californica* (post-hoc p-value <0.01), *L. tridentata* and the open (post-hoc p-value <0.01), *L. tridentata* and square (post-hoc p-value <0.01), and *L. tridentata* and triangle (post-hoc p-value <0.01).

Vertebrate associations

Differences in microsite varied by year, and microsite was a significant predictor of vertebrate abundance, richness, and evenness (p-value <0.01; Table 5.2). An increase in temperature was a significant covariate in determining species abundance, richness, and evenness in the spring (p-value <0.01; Table 5.2). Specifically, the highest relative abundance of vertebrate animals was observed at the triangle shelter in spring 2022 (Figure 5.2). The greatest species richness and species evenness were recorded at the square shelter, also in spring 2022 (Figure 5.2). Post-hoc analyses showed greater species richness at triangle and square shelters compared to *E. californica* in 2023 (post-hoc p-value <0.01; Appendix D; P). The same was observed for species evenness (post-hoc p-value <0.01).

In the winter, microsite significantly predicted both vertebrate abundance and richness (p-value <0.01; Table 5.3). A temperature increase was shown to be a significant covariate in determining both abundance and richness (p-values <0.01; Table 5.3). In particular, the greatest relative abundance of vertebrate animals was observed at *E. californica* in the winter (Figure 5.2). The highest richness and evenness were recorded at triangle shelters in the winter (Figure 5.2). Species richness was significantly greater at the triangle shelter compared to *E. californica* during the winter (post-hoc p-value <0.043; Appendix D; R).

In spring 2022, which was classified as a ‘dry’ year, RII effect size measure values for vertebrate abundance, richness, and evenness were mostly positive or neutral at shrubs and shelters (Figure 5.4). In 2023 however, which was a ‘wet’ year, the RII values were mostly negative or neutral. RII values for vertebrate abundance, richness, and evenness were almost exclusively negative across all microsites in the winter (Figure 5.4).

Table 5.1: Summary of the total number of animals detected at each site by sampling year and season. Census abbreviations are also provided.

Year	*Season*	*Census*	*Site*	*Total Number of Animals*
2022	**Spring**	**a**	Carrizo_4	1159
			Carrizo_soda_open	482
			Tecopa_shrub	29
			Tecopa_open	5
2023	**Winter**	**b**	Carrizo_4	100
			Carrizo_soda_open	39
			Tecopa_shrub	4
			Tecopa_open	0
2023	**Spring**	**c**	Carrizo_4	433
			Carrizo_soda_open	78
			Tecopa_shrub	201
			Tecopa_open	56

Table 5.2: Generalized Linear Models (GLM) Spring analysis of vertebrate abundance, richness, and evenness are shown for the spring sampling seasons. Microsite was nested in site and used as a predictor. Mean temperature (°C) was used as a covariate. Year was included as a fixed-effect factor. Significant p-values are bolded. Asterisk denotes an interaction term. Given models have the lowest AIC for the family of fit.

		df	***Deviance Residuals***	***df residuals***	***Deviance***	***p-value***
Abundance	**intercept**			126	500.48	
	year	1	40.906	125	459.57	**0.01**
	mean_temp	1	52.735	124	406.84	**0.01**
	microsite:site	11	94.912	113	311.93	**0.01**
	microsite:site*year	11	141.952	102	169.98	**0.01**
Richness	**intercept**			126	622.83	
	year	1	13.331	125	609.50	**0.01**
	mean_temp	1	82.683	124	526.82	**0.01**
	microsite:site	11	198.332	113	328.49	**0.01**
	microsite:site*year	11	101.636	102	226.85	**0.01**
Evenness	**intercept**			126	41.309	
	year	1	0.0621	125	41.247	0.548
	mean_temp	1	5.4774	124	35.769	**0.01**
	microsite:site	11	12.5584	113	23.211	**0.01**
	microsite:site*year	11	5.6145	102	17.596	**0.01**

Table 5.3:Generalized Linear Models (GLM) Winter analysis of vertebrate abundance, richness, and evenness are shown for the winter sampling season. Microsite was nested in site and used as a predictor variable. Mean temperature (°C) was used as a covariate. Significant p-values are bolded. Given models have the lowest AIC for the family of fit.

		df	***Deviance Residuals***	**df *residuals***	***Deviance***	***p-value***
Abundance	**intercept**			23	122.177	
	mean_temp	1	36.845	22	85.332	**0.01**
	microsite:site	11	34.214	10	31.822	**0.01**
Richness	**intercept**			23	60.894	
	mean_temp	1	10.823	22	50.072	**0.01**
	microsite:site	11	25.950	10	21.544	**0.01**
Evenness	**intercept**			23	5.4172	
	mean_temp	1	1.349	22	4.0674	**0.01**
	microsite:site	11	1.883	10	2.1298	0.577

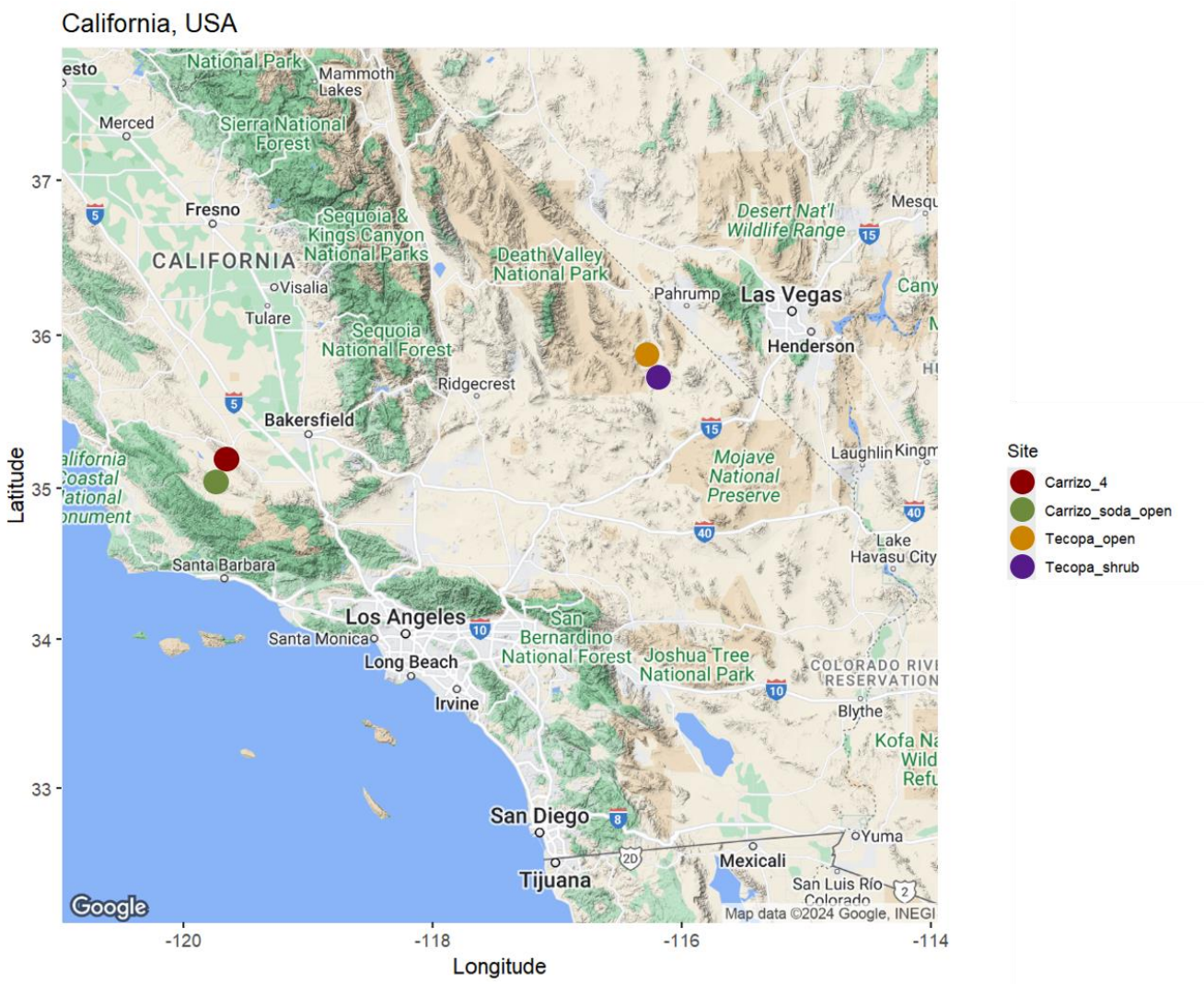

Figure 5.1: Map of Study Sites used to test the effects of shelters and shrubs on desert vertebrate communities. This map was generated on April 29th, 2024 using the R package *ggmap* (Kahle and Wickham, 2013) using a base layer provided by Google. Sites are represented using colours.

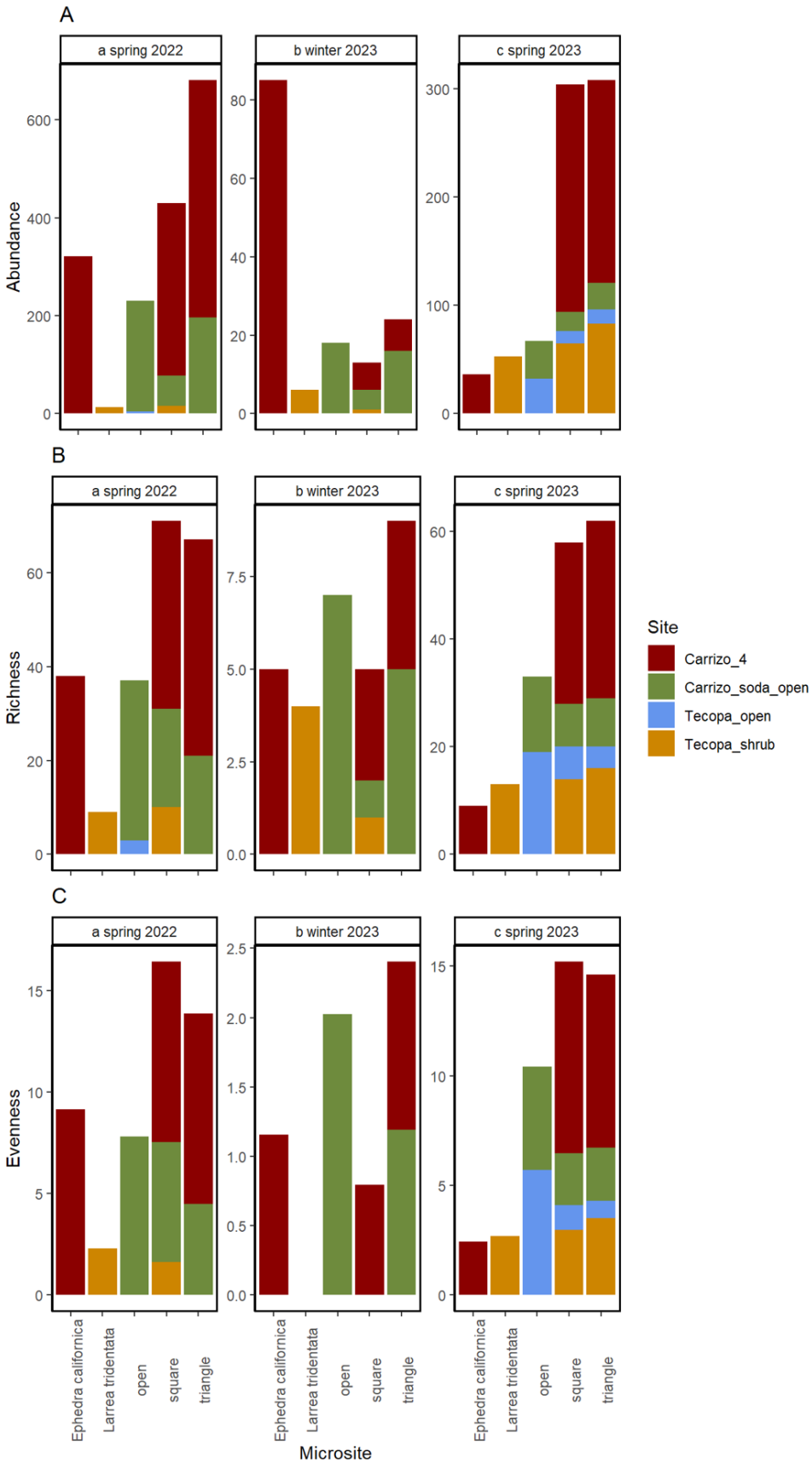
A
a spring 2022
b winter 2023
c spring 2023
Abundance
B
Richness
C
Evenness
Site
Carrizo_4
Carrizo_soda_open
Tecopa_open
Tecopa_shrub
Ephedra californica
Larrea tridentata
open
square
triangle
Microsite

Figure 5.2: Barplot Comparison of the effects of shelter and shrub microsites on vertebrate community abundance (A), richness (B), and evenness (C) is given for the three sampling censuses during spring 2022-2023, and winter 2023 (a, b. c). Colour represents vertebrate communities at each site sampled.

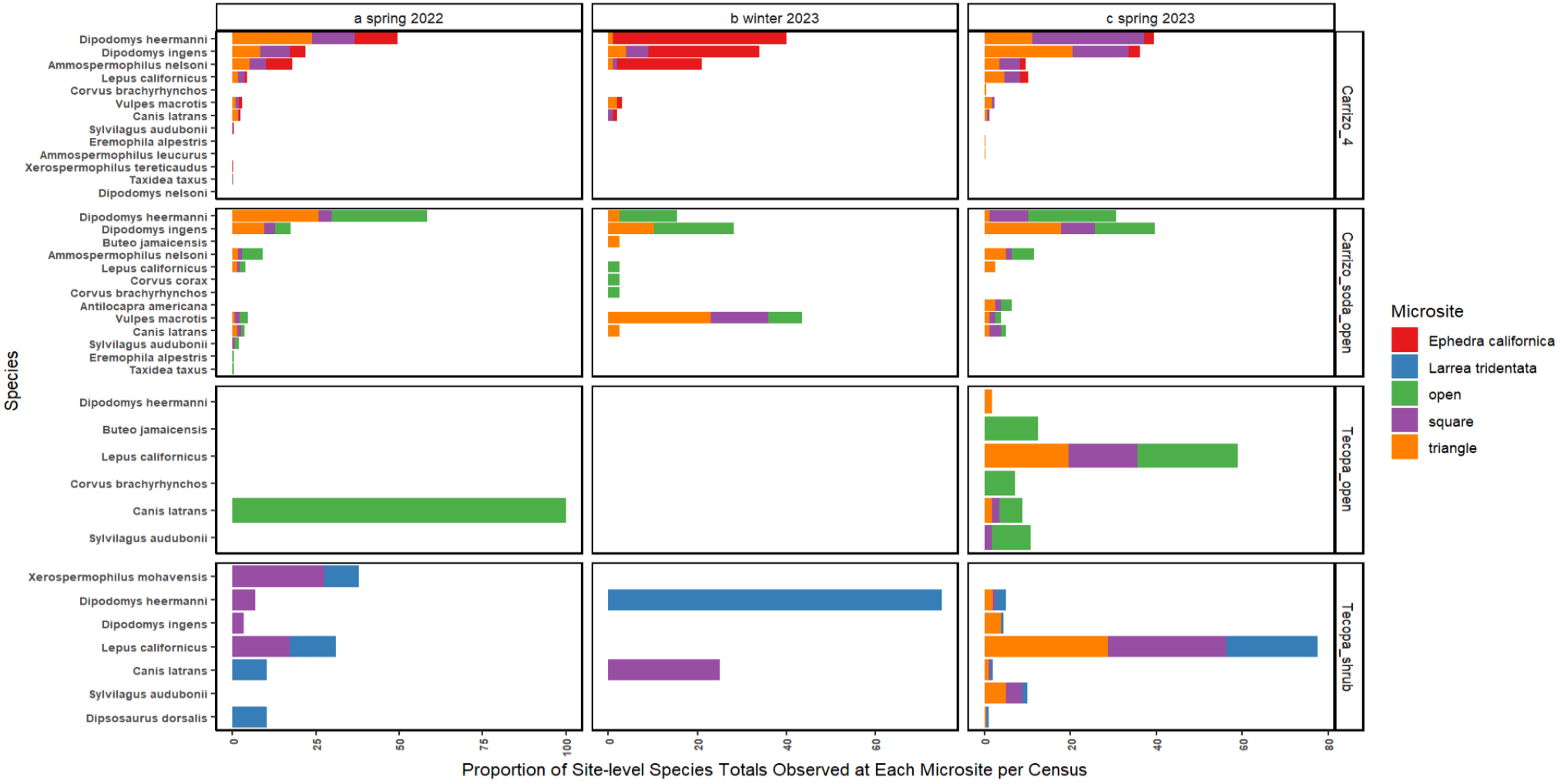
a spring 2022
b winter 2023
c spring 2023
Carrizo_4
Carrizo_soda_open
Tecopa_open
Tecopa_shrub
Species
Dipodomys heermanni
Dipodomys ingens
Ammospermophilus nelsoni
Lepus californicus
Corvus brachyrhynchos
Vulpes macrotis
Canis latrans
Sylvilagus audubonii
Eremophila alpestris
Ammospermophilus leucurus
Xerospermophilus tereticaudus
Taxidea taxus
Dipodomys nelsoni
Buteo jamaicensis
Corvus corax
Antilocapra americana
Xerospermophilus mohavensis
Dipsosaurus dorsalis
0
25
50
75
100
20
40
60
80
Proportion of Site-level Species Totals Observed at Each Microsite per Census
Microsite
Ephedra californica
Larrea tridentata
open
square
triangle

Figure 5.3: Species Proportion Totals are given across three sampling censuses during spring 2022-2023, and winter 2023 (a, b. c) at each site. The y-axis indicates the observed species' Latin binomial name. Colour indicates the microsite where the species was observed.

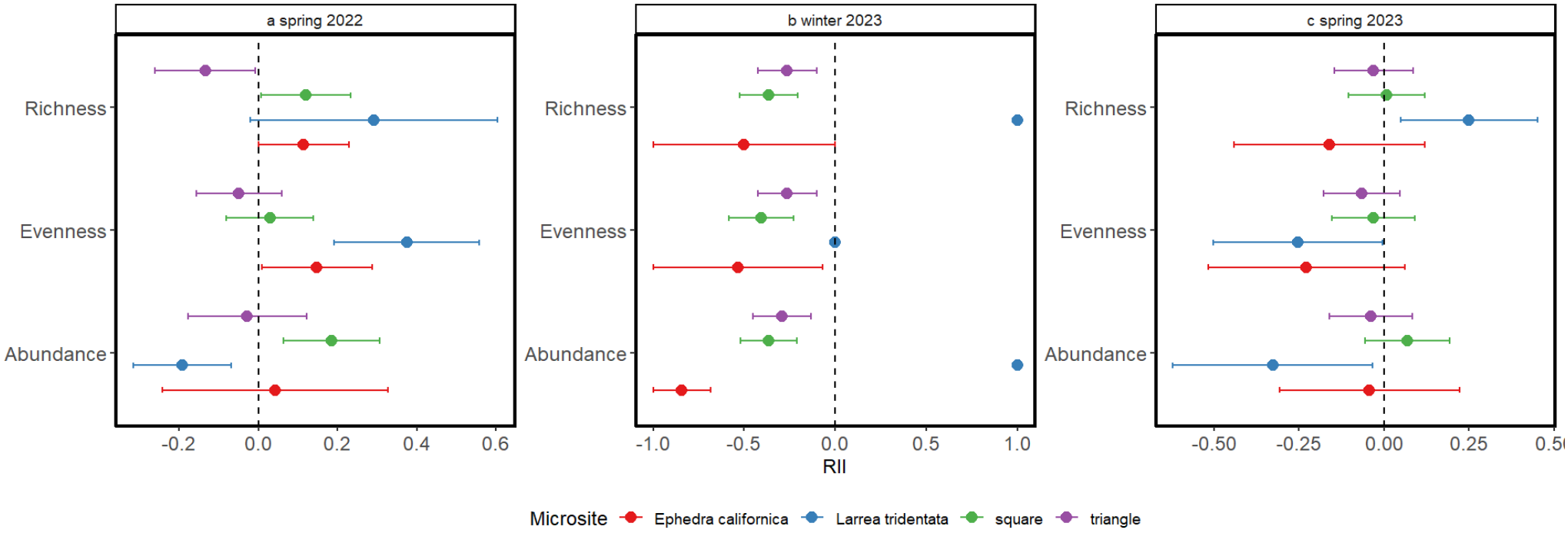
a spring 2022
b winter 2023
c spring 2023
Richness
Evenness
Abundance
-0.2
0.0
0.2
0.4
0.6
-1.0
-0.5
0.0
0.5
1.0
-0.50
-0.25
0.00
0.25
RII
Microsite
Ephedra californica
Larrea tridentata
square
triangle

Figure 5.4: Relative Interaction Index (RII) effect size measure for vertebrate abundance, richness, and evenness is shown for the three sampling censuses during spring 2022-2023, and winter 2023 (a, b. c). Colour indicates microsite. The relative interaction intensity effect size measure (RII) is reported with positive values representing facilitative or positive interactions at shelters and shrubs (Armas et al. 2004). Values overlapping 0 indicate neutral interactions. All values shown indicate means ± standard error (SE).

5.5: Discussion

Desertification is a widespread and critical issue that results in the degradation of North American deserts. Populations that depend on land resources are most severely impacted by climate change and land degradation in ecosystems that are experiencing drought and desertification (Reed, 2015). Microhabitat availability is a strong predictor of species habitat occupancy and thus management strategies (Sankararaman et al., 2021). Most species live in fine-scale habitats that are intrinsically variable in deserts (Kotzen, 2003; Shenbrot et al., 2002) and even more so with changes in climate (Li et al., 2019). As such, microclimatic heterogeneity is key for resident flora as provides a variety of microclimatic profiles for movement and refuge (Ma et al., 2023). In this study, we tested the impact of eco-friendly, artificial shelters on animal abundance, richness, and evenness across four sites in Southwestern California. We found support for the hypothesis that artificial shelters provide refuge for desert vertebrates through microclimatic facilitation similar to foundation shrub species. We observed that temperature was an important covariate moderating the association of vertebrates with shrub and shelter complexes both in the spring and the winter seasons. Specifically, the sampling year was a significant determinant of variation in observed vertebrate abundance, richness, and evenness. With increased temperatures, more species were associated with shrubs and shelters compared to the open areas. Most vertebrate animals were associated with shelters in spring 2022, which was a hot, dry year compared to the average. In the same census, shelters functioned similarly to foundation shrubs when influencing vertebrate community dynamics, and shelters and shrubs both positively influenced vertebrate abundance, richness, and evenness (positive RII values). The shelter that attracted the largest number of animals in the spring was triangle, but the square shelter attracted a greater array of vertebrate species. In spring 2023, which was a cooler, and wetter ‘superbloom’ year, shelters still positively influenced vertebrate communities at times (positive RII values), but animals were also found associating with the open occasionally (neutral RII values). In the same census, shelters worked even better than the shrub *E. califonica*. In the winter, animals

almost, always associated with the open areas (negative RII values). This implies that more vertebrates and a greater number of species are associated with the shelters and shrubs in the warm, drought years in comparison to the cool, wet years, or colder seasons when temperatures are relatively cooler.

The rate of global desertification is increasing, while the ability of desert species to withstand global warming is decreasing or limited (Gunderson & Stillman, 2015). Abiotic heterogeneity in deserts thus needs to be protected given the rise in temperature and decrease in precipitation (Li et al., 2019). Structural heterogeneity is the variation in physical structure in an area (Buhl-Mortensen et al., 2010) and foundation plants in deserts are one of the sources of structural heterogeneity (Cáceres et al., 2015; Zuliani et al., 2024), and thus the overall EH. Generally, an increase in the number of foundation shrubs positively influences structural heterogeneity and thus the vertebrate community of a given area (Lortie et al., 2020; Westphal et al., 2018; Zuliani et al., 2021). Shrub canopies create microclimatic benefits including increasing shade, reducing radiation load, increasing night-time winter temperature, and increasing soil moisture, and canopy structure plays an important role in differences observed in these microclimatic parameters (Jankju, 2013). *Ephedra californica* is a foundation shrub and a structural agent of facilitation whose canopy offers a cooler and moister microclimate compared to the open (Filazzola et al., 2017) regardless of its low stature or small size (Lortie et al., 2018; Lortie, Filazzola, et al., 2022). Shrubs increase the EH of an area, and EH and biodiversity are directly correlated with higher EH leading to higher species richness (Agra et al., 2021). This is consistent with our findings that foundation shrubs are vital to the vertebrate community's abundance and richness during warmer seasons of the year, including the spring, and they are especially crucial during the same seasons in hotter, drought/low precipitation years. Furthermore, in the winter when temperatures are generally cooler, more species were associated with the open areas, suggesting that microclimatic amelioration is less crucial during colder months

of the year. Thus the effective management and conservation foundation of plant species is key to the well-being of deserts in the current paradigm of anthropogenic disturbances, including climate change.

Nevertheless, there is widespread evidence that desertification is impacting vegetation loss through climate change (Khalaf & Al-Ajmi, 1993; Patrick Gonzalez, 2001). Due to changes in temperature, precipitation, wind, solar isolation, and other geographical and temporal patterns, desertification aggravates climate change, which in turn exacerbates climate change due to the release of CO2 from cleared land and dead vegetation (Patrick Gonzalez, 2001). Furthermore, desertification can replace woody vegetation in scrubland via biological invasion by exotic grasses (D'Antonio & Vitousek, 1992). Another disadvantage of native shrubs as a form of structural heterogeneity is that they can at times facilitate exotic annuals more strongly than native annuals in desert ecosystems (Lucero et al., 2019, 2022). Additionally, post-disturbance vegetation recovery can take decades (Berry et al., 2016). In this study, it was observed that vertebrate species positively associated with triangle and square shelters and that their abundance, richness, and evenness were highest at these microsites, especially in low precipitation, hot years. Given this, our findings suggest that artificial habitat constructions, including artificial shelters, can as act as a stop-gap and as at least a transitory mechanism to defend and even augment the microclimatic heterogeneity at fine scales in deserts (Ghazian et al., 2020; Yu et al., 2022). This suggests that artificial structures in deserts, including shelters and shrub mimics, generally have the potential to act as a proxy for foundation shrubs such as *E. californica* during post-disturbance recovery, or even whilst foundation shrubs are present. Of course, our suggestion is not to abandon the conservation and restoration of natural vegetation because plants play a critical role in various other trophic (Renner & Zohner, 2018) and non-trophic pathways (Ohgushi, 2008). However, we suggest that artificial shelters can positively influence vertebrate abundance and diversity in the absence of foundation species or the presence of

lower numbers caused by climate change and desertification. The selection of the shelter type will also depend on the goal. For instance, if the goal is to have the greatest number of vertebrates associated with a shelter for conservation purposes during warmer seasons, we suggest the use of triangle shelters. For aims targeting species diversity and richness, we suggest the implementation of square shelters. Ultimately, however, we suggest the use of both shelter types together for effective conservation and restoration of wildlife in the face of climate change and desertification.

5.6: Conclusion

Bare ground connectivity will inevitably increase as desertification dominates many desert and semidesert regions in the upcoming years (Fick et al., 2016). To counteract these effects, adaptation measures are desperately needed. Artificial habitat constructions could give conservationists a useful tool for preserving animal populations at lower spatial scales (Esteban et al., 2018). The survival, growth, reproduction, and abundance of individuals or groups can all be maintained or enhanced by artificial structures (Watchorn et al., 2022). Similar to natural vegetation, such structures can provide animals with climatic refuge and a place to thermoregulate (Esteban et al., 2018; Reboul et al., 2021; Watchorn et al., 2024; Zuliani et al., 2024) and even provide a small-scale-barrier mitigating desertification processes and enhancing plant recruitment in degraded ecosystems (Fick et al., 2016; Tang et al., 2016; Warneke et al., 2023). However, artificial structures must be carefully monitored and compared to suitable controls to avoid acting as an ecological trap. Ecological traps occur where sudden environmental change, including brood parasitism, predation, pesticide use, and human disturbance disrupt the cues individuals use to assess habitat quality from the real quality of the landscape or environment (Dwernychuk & Boag, 1972). Robertson and Hutto (2006) argue that ecological traps are created when the habitat alterations either 1) alter the cue set (increases in attractiveness) in the absence of change in its suitability, 2) decrease the suitability of the habitat without the loss of attractiveness, or 3) does both simultaneously. Herein, we avoided all

three scenarios by building artificial shelters that did not resemble natural shrubs in structure or colour to avoid confusing vertebrate animals in their habitat selection, and we evaluated the suitability of shelters as a form of microenvironmental facilitation. We used shelter coverings that were khaki coloured and blended in with the natural desert landscape, and we observed they performed similarly to natural shrubs in terms of facilitating microclimate. Additionally, we ensured that the shelters had multiple openings just like shrubs such that animals could easily get in or out at any given time. Hence, we conclude that these structures can help mitigate unfavorable conditions and thus provide optimism for the maintenance of biodiversity in the face of anthropogenic changes. Nevertheless, we suggest that future studies should not only evaluate the risk of artificial structures serving as traps at small-scale geographical patches but also in terms of their fitness population-level fitness effects across the landscape (Hale & Swearer, 2016), which is highly relevant for management practices.

5.7: Acknowledgments

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5.8: Author's Contributions

N.G, C.J.L, and S.E.M designed the study; N.G and M.Z collected the data; N.G and C.J.L performed statistical analyses; N.G wrote the manuscript; C.J.L, M.Z, and S.E.M thoroughly edited the manuscript and offered valuable insight.

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CHAPTER 6: GENERAL CONCLUSION

6.1: Conclusion

Positive interactions are the central theme of a growing body of literature and these interactions are especially important in resource-limited ecosystems such as deserts. Although positive trophic interactions are well-explored, non-trophic interactions have been explored to a lesser extent. This is particularly true for the effects of foundation plants on climate, and specifically, climate measured at finer scales. This is important because it is variability at these finer scales that species experience most, which can dictate their day-to-day survival. Microclimatic heterogeneity can create pockets of micro "niches" that can enable species to continue to exist. This is key considering higher temperatures and more frequency in drought events increase bare ground connectivity in deserts. Climate and land use changes also exacerbate plant loss and thus the release of higher amounts of greenhouse gases into the atmosphere. Thus, it is essential that we use empirical approaches to examine the impacts of artificial construction in mimicking the microclimatic profiles of foundation plants, and the associations of such constructs with resident animal communities for later use in conservation and management.

In this thesis, I examined the impacts of foundation plant species on microclimate across the Southwestern deserts of California and compared them to those of eco-friendly, artificial shelters. Firstly, I examined the camera trapping literature to test for sampling effort when measuring the abundance and richness of vertebrate communities (Chapter 2). The results showed that it is more effective to deploy more cameras as opposed to for more days to obtain more accurate estimates of community abundance and richness.

Then I conducted in-lab trials of eco-friendly, lignocellulosic fabrics to test their impact on understory microclimate (Chapter 3). Burlap had more stable temperatures and lower radiation than cotton canvas, with both materials controlling light similarly. Nursery fabric had the highest and

most stable humidity, while cotton canvas had the lowest and most variable humidity. Despite this, nursery fabric's high-temperature variation makes it unsuitable for field use to protect fauna.

Following this, I conducted a field experiment exploring the impacts of the structure (canopy volume and area) of foundation plants on microclimatic variables and thus their influence on understory plant abundance and richness compared to the open (Chapter 4). Canopy volume was shown to be a weak predictor of microclimatic variables, indicating that even small shrubs can have positive effects. Out of all microclimatic metrics, only surface ground temperature was significantly lower between under the shrub than in the open. Aridity and shrub cover were significant predictors of vascular plant abundance and richness. Shrubs facilitated a greater abundance of plants, but not a greater number of species.

Finally. I used all the knowledge gained from the previous chapters to conduct a two-year field study examining the impacts of foundation shrubs and artificial shelters on desert community vertebrates and microclimate (Chapter 5). This research demonstrated that desert vertebrates interact positively with eco-friendly, burlap-covered shelters, like foundation shrubs, in warm seasons, and especially in hotter, drought years, suggesting that artificial shelters can be used as a transient, stop-gap solution during and post-disturbance. In colder seasons and cooler and wetter seasons, these interactions were neutral to negative, suggesting that shelters and shrubs are always important, but even more so in harsh abiotic conditions.

6:.2: Future Directions

There is extensive evidence that plants can moderate microclimates; however, studies examining the microclimatic aspects of abiotic amelioration are underrepresented in biodiversity functioning literature (Guimarães-Steinicke et al., 2021). Both the canopy structure and diversity of the plants associated with the canopy are important drivers of energy fluxes between the plant and the environment, and hence the abiotic amelioration capabilities of plant canopies. Future directions should focus on examining canopy structure describing metrics, including Leaf Area Index (LAI)

and mean height, as well as canopy distribution (evenness), and biomass allocation along a stratum (centre of gravity) can provide us with in-depth information regarding the heterogeneous 'heat-scape' created by foundation plants in drylands. Furthermore, foundation plants can also at times facilitate the exotic plant communities more than the natives (Lucero et al., 2019, 2020). There are complex relations between annual plants, exotics, and animals and these interactions cannot be ignored. Examining horizontal plant metrics such as community stand gaps, canopy surface variation, and emergent flowers can also help us predict biodiversity effects on microclimate including surface temperatures. Further to this, we must examine the impacts of various lignocellulosic fabrics on plant abundance and richness, and extend this knowledge to the field to test for the relative impacts of artificial shelters on plant communities. Laser scanning and 3-D point clouds are proven methods for examining plant canopy structure, as well as horizontal metrics (Guimarães-Steinicke et al., 2021). Perhaps, a similar methodology can be used to examine artificial structures and their effects on climate and fine scales. There is widespread evidence that foundation shrubs support the native annual plant communities, (Castro et al., 2004; Filazzola & Lortie, 2014; Flores & Jurado, 2003), hence we must examine if the same holds for artificial habitat constructions. How artificial shelters impact energy fluxes between their canopy and the outside environment can tell us about their potential effects on annual plants and thus arthropod assemblages, and ultimately vertebrates. This will be crucial in furthering our knowledge of positive interactions in deserts.

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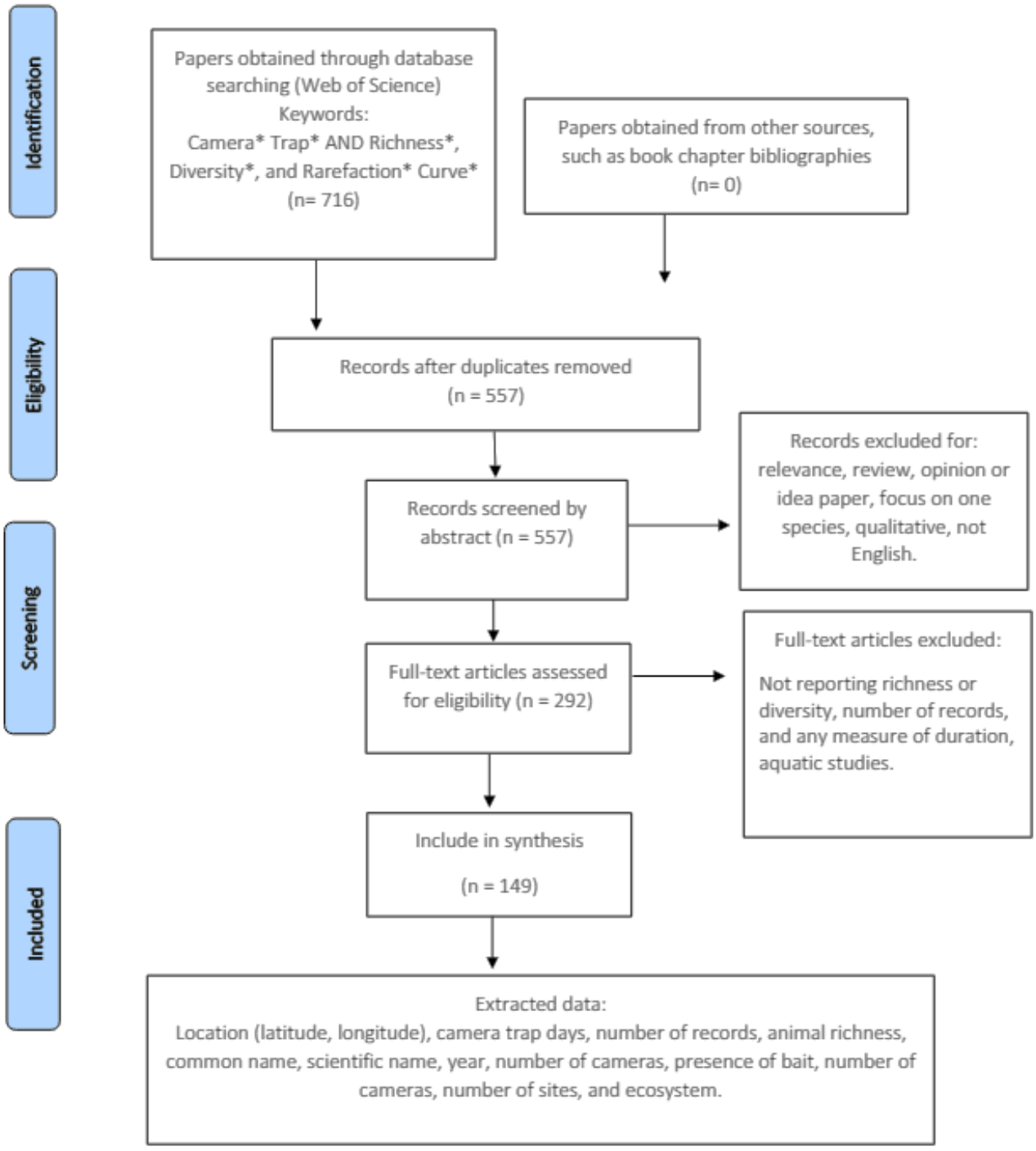
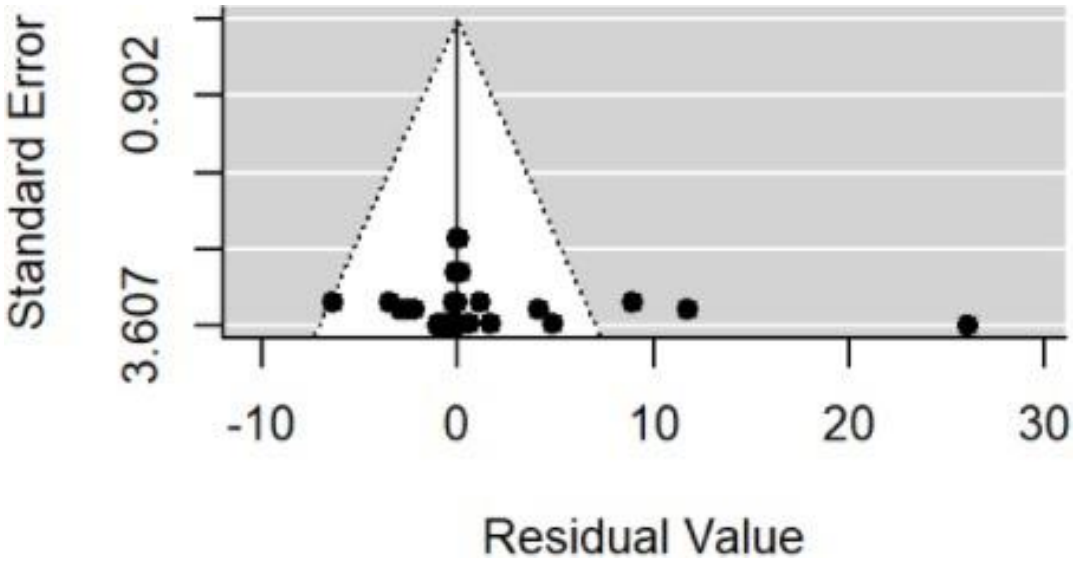
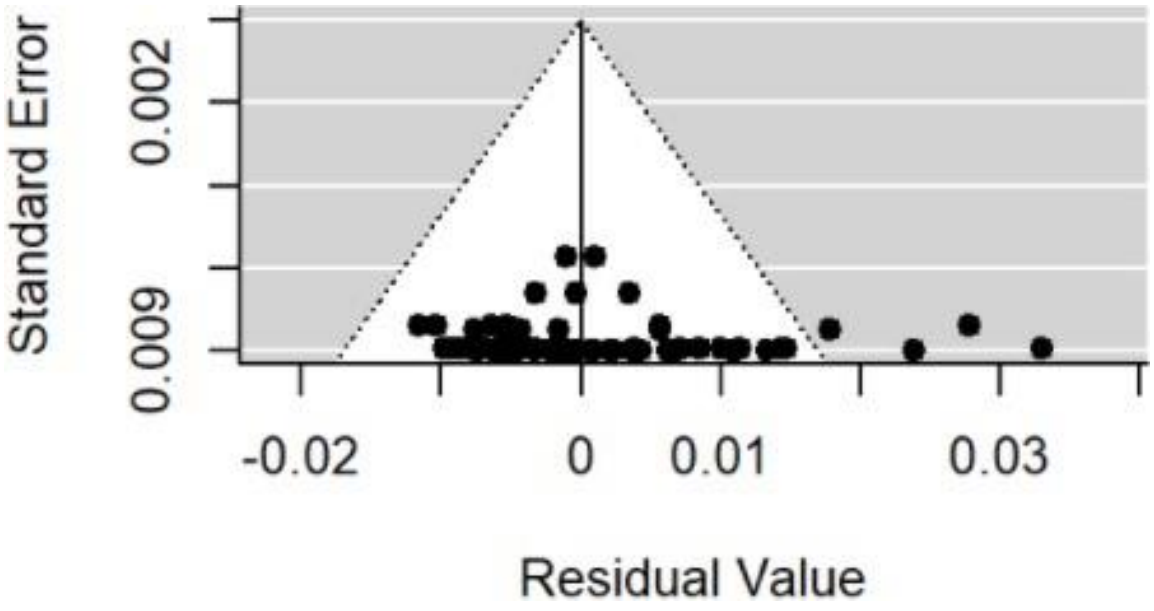
APPENDIX A


Identification
Eligibility
Screening
Included
Papers obtained through database searching (Web of Science)
Keywords:
Camera* Trap* AND Richness*, Diversity*, and Rarefaction* Curve*
(n= 716)
Papers obtained from other sources, such as book chapter bibliographies
(n= 0)
Records after duplicates removed
(n = 557)
Records screened by abstract (n = 557)
Records excluded for: relevance, review, opinion or idea paper, focus on one species, qualitative, not English.
Full-text articles assessed for eligibility (n = 292)
Full-text articles excluded:
Not reporting richness or diversity, number of records, and any measure of duration, aquatic studies.
Include in synthesis
(n = 149)
Extracted data:
Location (latitude, longitude), camera trap days, number of records, animal richness, common name, scientific name, year, number of cameras, presence of bait, number of cameras, number of sites, and ecosystem.

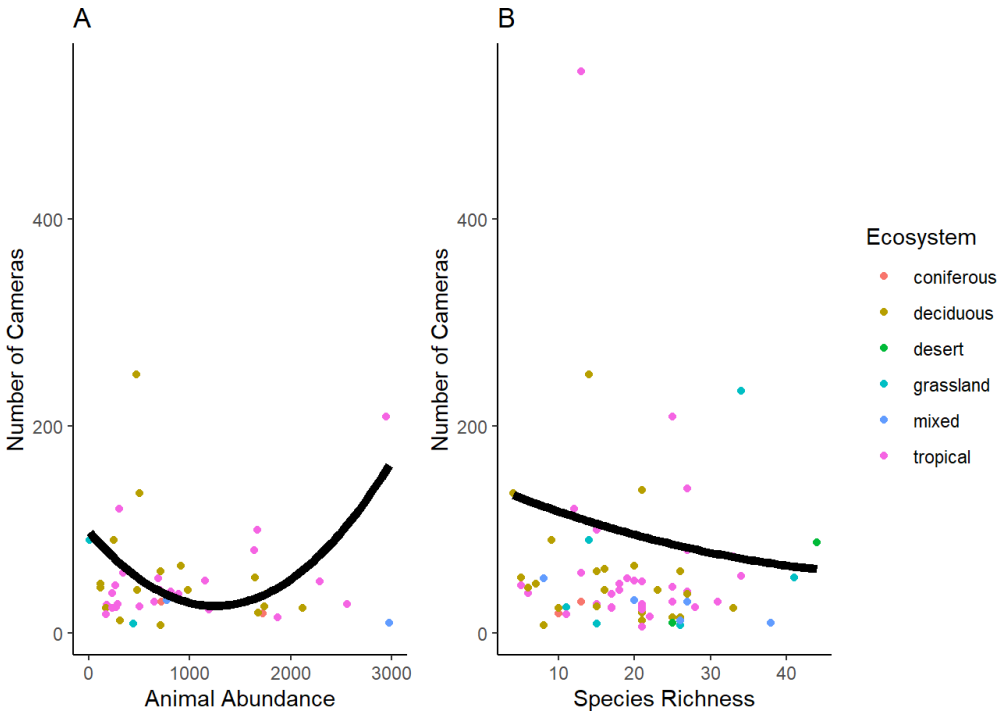
A: PRISMA diagram used for camera trapping effort systematic review (Moher et al. 2009). Search was done with keywords: Camera Trap* and Richness*, or Diversity*, and Camera* Trap* and Rarefaction* Curve* in July of 2021.



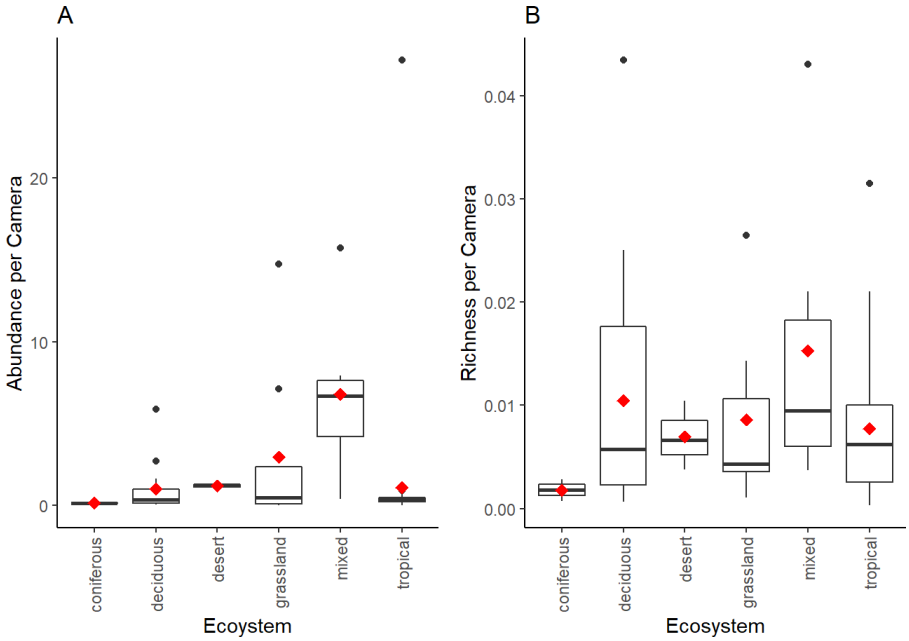
B: Residual funnel plot from random-effect model for net abundance detection rate estimates.



C: Residual funnel plot from random-effect model for net richness detection rate estimates.



D: Plot of animal abundance and richness by the number of cameras.



E: Box plot showing abundance per camera (A) and Richness per Camera (B) in each ecosystem. Solid middle lines shows the median of the data, whilst whiskers show 1.5 standard deviation. Solid dots are outliers >1.5 interquartile range (IQR). Red diamonds dots represent the mean.

APPRNDIX B

A: Estimated Marginalized Mean (EMM) and standard error (SE) are given for each fabric and the open gap based on the Generalized Linear Models (GLM) for near-surface air temperature (ºC), humidity (%), and radiation (lum/ft^2). Confidence interval used was 95%.

Measurement	*Microsite*	*emmean*	*SE (±)*	*Asymp.LCL*	*Asymp.UCL*
Temperature (ºC)	Control	21.98	0.010	21.96	21.99
	Burlap	21.83	0.013	21.80	21.85
	Canvas	21.68	0.015	21.65	21.71
	Nursery	21.46	0.014	21.43	21.48
Humidity (%)	Control	43.4	0.17	43.1	43.7
	Burlap	40.9	0.28	40.3	41.4
	Canvas	38.4	0.28	37.9	39.0
	Nursery	55.2	0.31	54.6	55.8
Radiation (lum/ft^2)	Control	18.20	0.16	17.89	18.50
	Burlap	1.96	0.26	1.45	2.47
	Canvas	2.56	0.30	1.98	3.14
	Nursery	3.44	0.27	2.91	3.97

B: Near Surface Temperature Post-hoc Contrast based on near-surface air temperature GLM. Standard error and p-values are provided. Significant p-values are bolded.

Contrast	*estimate*	*SE (±)*	*z.ratio*	*p-value*
burlap-canvas	0.15	0.021	7.19	**0.001**
burlap-none	-0.15	0.016	-9.32	**0.001**
burlap-nursery	0.37	0.020	18.91	**0.001**
canvas-none	-0.30	0.017	-16.98	**0.001**
canvas-nursery	0.22	0.021	10.70	**0.001**
none-nursery	0.52	0.016	31.84	**0.001**

C: Humidity Post-hoc Contrast based on humidity GLM. Standard error and p-values are provided. Significant p-values are bolded.

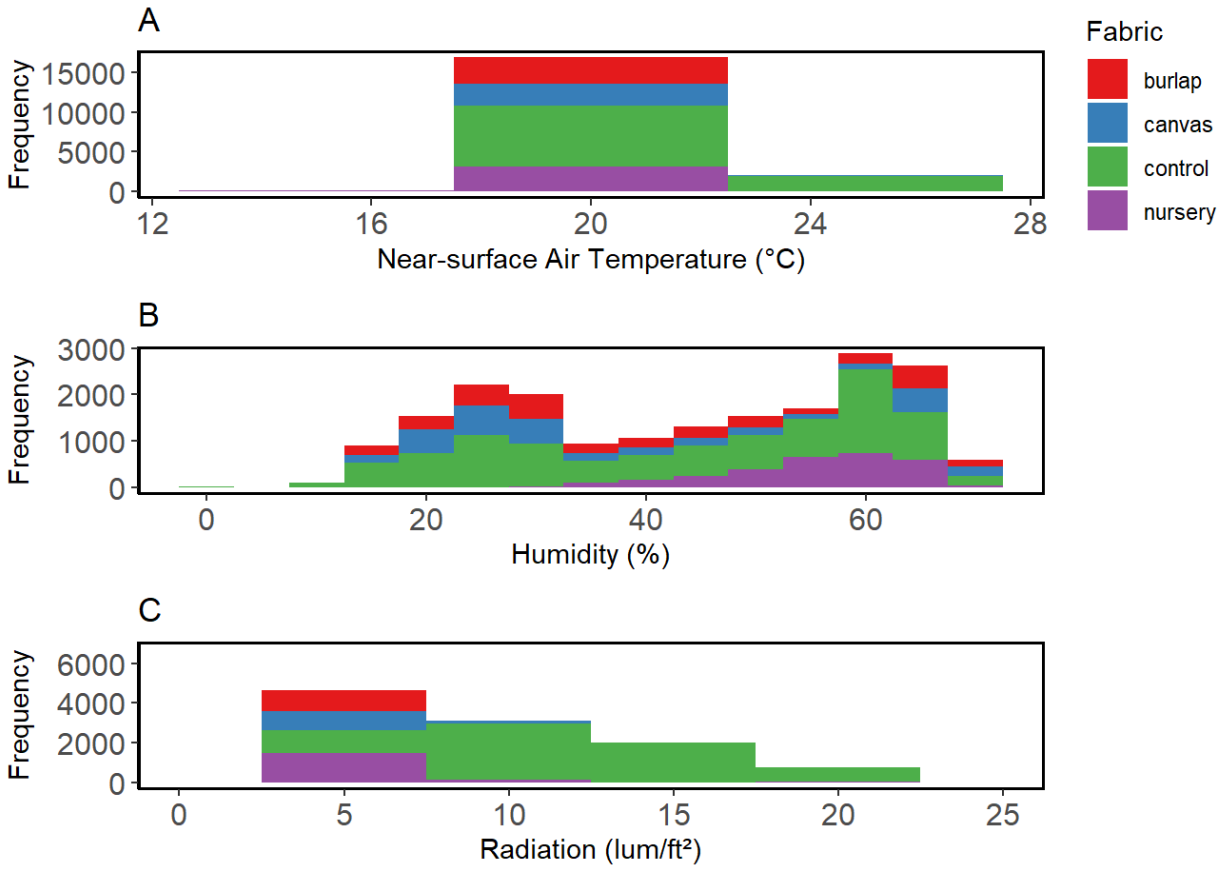
Contrast	*estimate*	*SE (±)*	*z.ratio*	*p-value*
burlap-canvas	2.43	0.40	6.15	**0.001**
burlap-none	-2.52	0.33	-7.73	**0.001**
burlap-nursery	-14.38	0.41	-34.74	**0.001**
canvas-none	-4.95	0.33	-15.21	**0.001**
canvas-nursery	-16.81	0.41	-40.64	**0.001**
none-nursery	-11.86	0.35	-34.16	**0.001**

D: Radiation Post-hoc Contrast based on radiation GLM. Standard error and p-values are provided. Significant p-values are bolded.

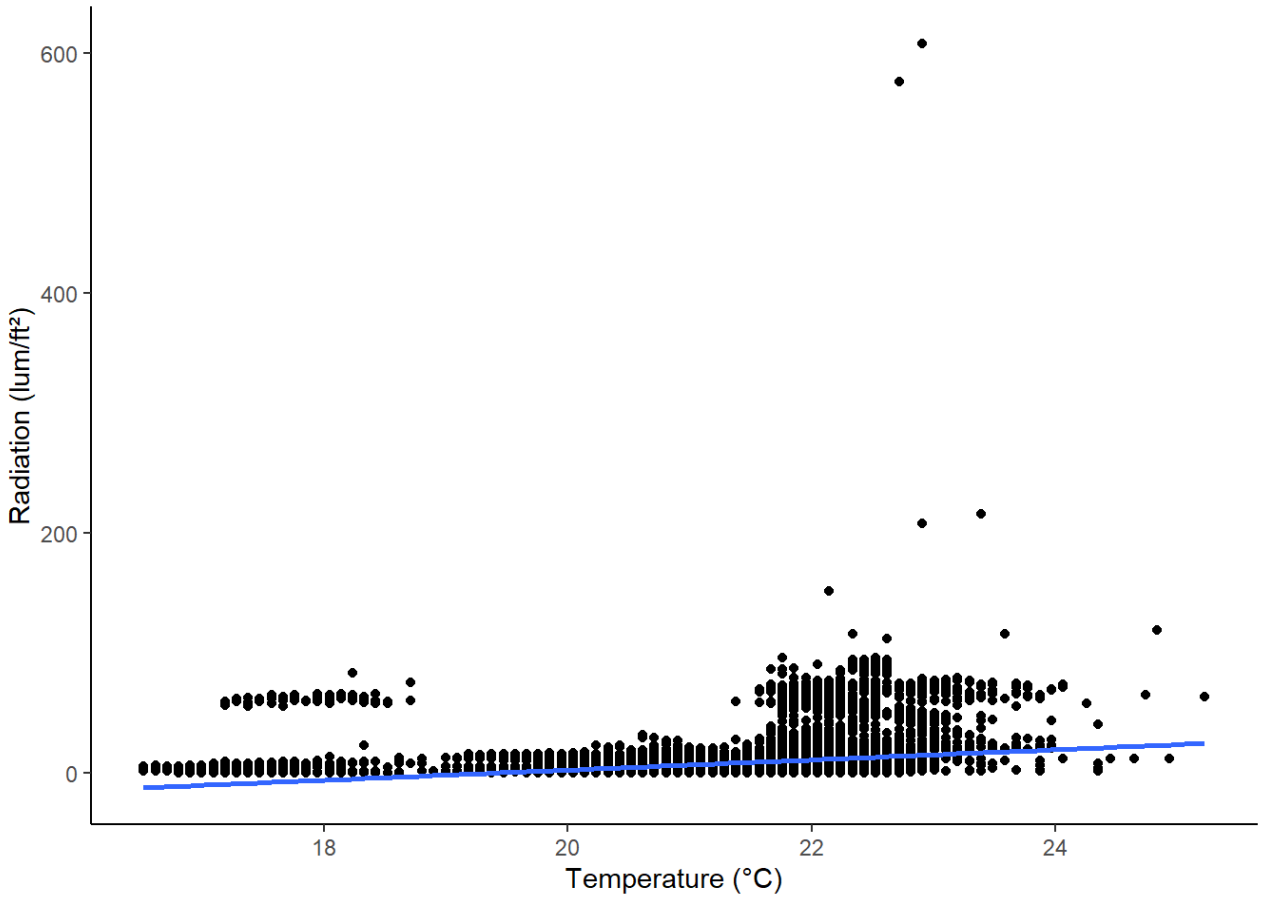
Contrast	*estimate*	*SE (±)*	*z.ratio*	*p-value*
burlap-canvas	-0.60	0.40	-1.52	0.4281
burlap-none	-16.24	0.30	-53.50	**0.001**
burlap-nursery	-1.48	0.38	-3.93	**0.0005**
canvas-none	-15.64	0.33	-46.94	**0.001**
canvas-nursery	-0.88	0.40	-2.20	0.1223
none-nursery	14.76	0.31	47.25	**0.001**

E: Variances Histogram spread for near-surface air temperature (ºC), humidity (%), and radiation (lum/ft^2) are given for each fabric and the open.

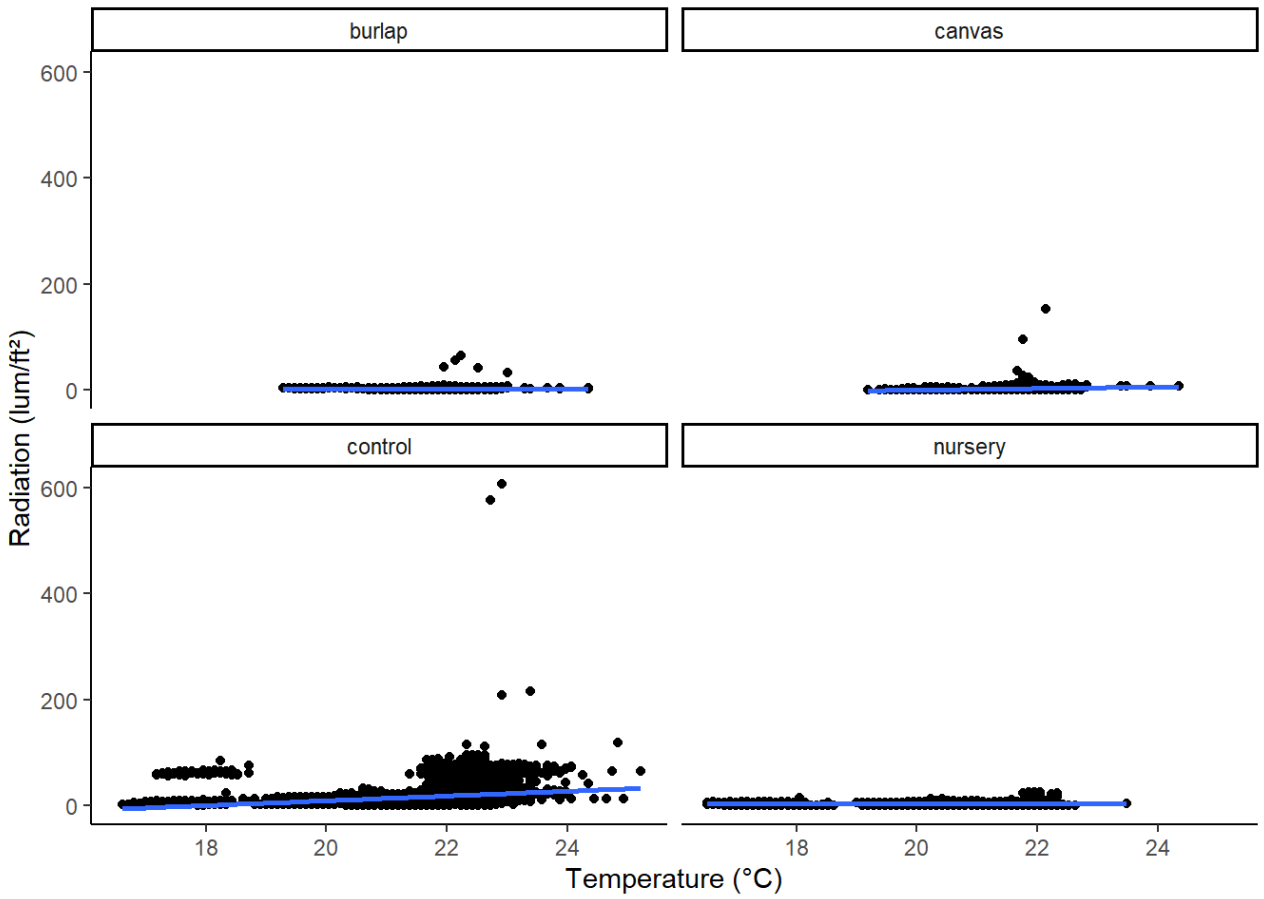
Microsite	*Variance Temperature (s^2)*	*Variance Radiation (s^2)*	*Variance Relative Humidity ($s^{2)}$*
control	1.33	458.49	274.46
burlap	1.29	4.90	275.10
canvas	0.16	19.56	305.98
nursery	1.33	12.70	61.97



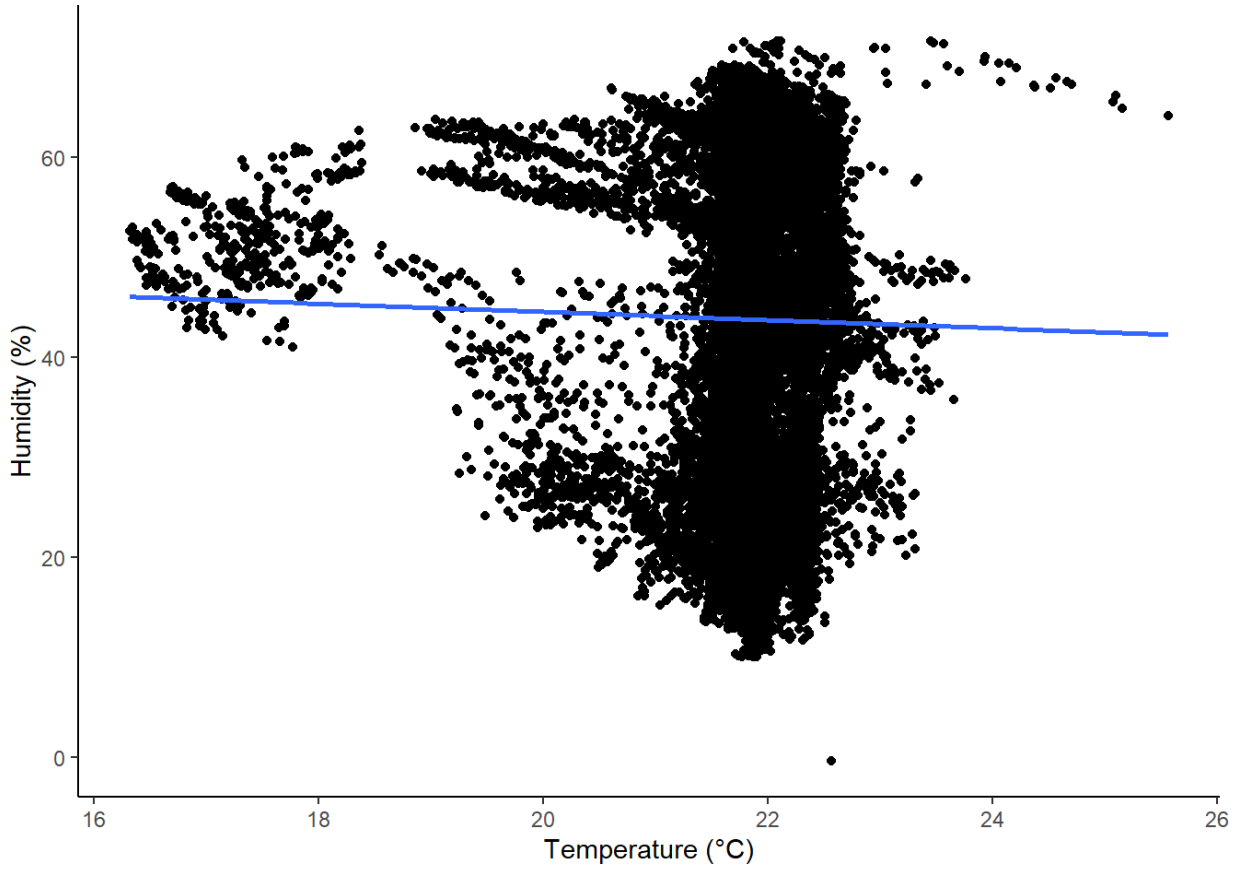
F: Frequency Histogram of near-surface air temperature (ºC) (A), humidity (%) (B), and light radiation (lum/ft^2) (C) recorded at each fabric and control using data loggers. Colours represent different microsites. Frequency represents how often the particular parameter was recorded at a specific measurement on the x-axis.



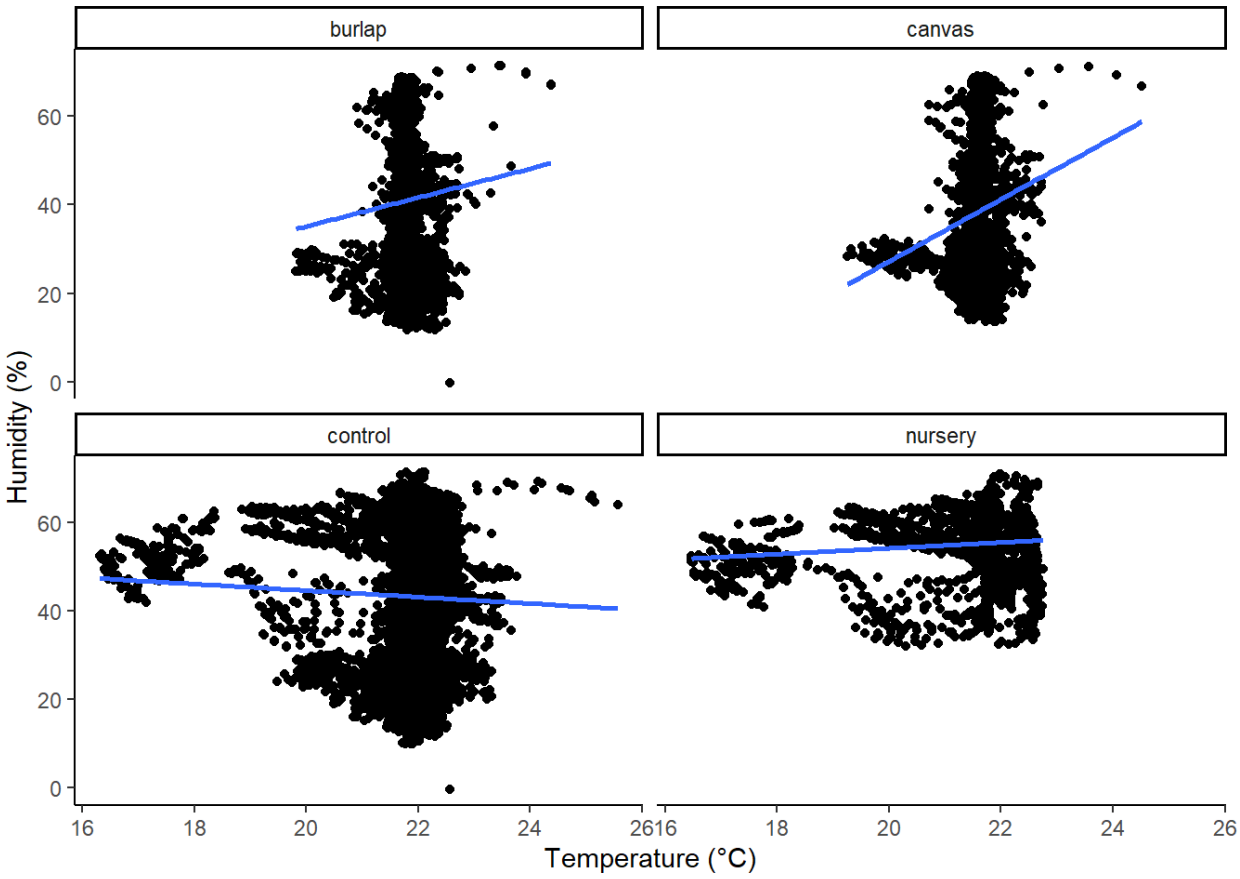
G: Near-surface Air Temperature v.s Radiation scatterplot depicting the overall relationship of radiation (lum/ft^2) and temperature (ºC) (Kendall's tau 0.342, p= 0.0001). Blue line represents the smooth conditional mean fitted using the method GLM.



H: Faceted Near-surface Air Temperature vs. Radiation Scatterplots depicting the overall relationship of radiation (lum/ft^2) and temperature (ºC) (Kendall's tau 0.342, p= 0.0001) faceted by fabric and the control. Blue lines represent the smooth conditional mean fitted using the method GLM.



I: Near-surface Air Temperature vs. Humidity Scatterplot depicting the overall relationship of humidity (%) and temperature (ºC) (Kendall's tau= 0.0125, p= 0.00992). Blue line represents the smooth conditional mean fitted using the method GLM.



J: Faceted Near-surface Air Temperature vs. Humidity Scatterplot depicting the overall relationship of humidity (%) and temperature (ºC) (Kendall's tau= 0.0125, p= 0.00992) faceted by fabric and the control. Blue lines represent the smooth conditional mean fitted using the method GLM. The relationship was positively linear in all microsites, except for the control.

APPENDIX C

A: Multicollinearity The variance inflation factors (VIF) for the GLMs where site level aridity and percent shrub cover are predictors of annual vegetation. VIFs <5 indicate low collinearity. CI is the 95% confidence interval.

Measure	*Term*	*VIF*	*CI*	*Standard Error*	*Tolerance*	*Tolerance CI*
Mean richness	shrub_cover	2.93	2.26-3.96	1.71	0.34	0.25-0.44
	microsite	1.01	1-4.84*10^8	1.00	0.99	0-1
	aridity	2.93	2.26-3.96	1.71	0.34	0.25-0.44
Mean abundance	shrub_cover	2.93	2.26-3.96	1.71	0.34	0.25-0.44
	microsite	1.01	1-4.84*10^8	1.00	0.99	0-1
	aridity	2.93	2.26-3.96	1.71	0.34	0.25-0.44

B: Multicollinearity The variance inflation factors (VIF) for the GLMs where mean near-surface air temperature (NSAT) and vapour pressure deficit (VPD) are predictors of annual vegetation. VIFs <5 indicate low collinearity. CI is the 95% confidence interval.

Measure	*Term*	*VIF*	*CI*	*Standard Error*	*Tolerance*	*Tolerance CI*
Mean richness	mean_NSAT	3.06	2.33-4.21	1.75	0.33	0.24-0.43
	microsite	1.05	1-3.94	1.02	0.96	0.25-1
	mean_VPD	3.03	2.31-4.16	1.75	0.33	0.24-0.43
Mean abundance	mean_NSAT	3.06	2.33-4.21	1.75	0.33	0.24-0.43
	microsite	1.05	1-3.94	1.02	0.96	0.25-1
	mean_VPD	3.03	2.31-4.16	1.75	0.33	0.24-0.43

C: Weather Data Daily maxima and minima for temperatures (F), as well as total precipitation (inches), were obtained from the National Oceanic and Atmospheric Association (NOAA) for the February 13th- 23rd, 2023 study period. The satellite station nearest to all six study sites was located in Cuyama Valley, New Cuyama, CA.

Year	*Month*	*Day*	*Max Temperature (F)*	*Min Temperature (F)*	*Mean Temperature (F)*	*Precipitation (in)*
2023	02	13	60	37	48.6	0
2023	02	14	47	23	46.5	0
2023	02	15	48	20	34	0
2023	02	16	55	26	40.5	0
2023	02	17	56	24	40	0
2023	02	18	57	26	41.5	0
2023	02	19	58	28	43	0
2023	02	20	67	31	49	0
2023	02	21	64	29	46.5	0.01
2023	02	22	44	26	35	0.01
2023	02	23	45	31	38	0.01

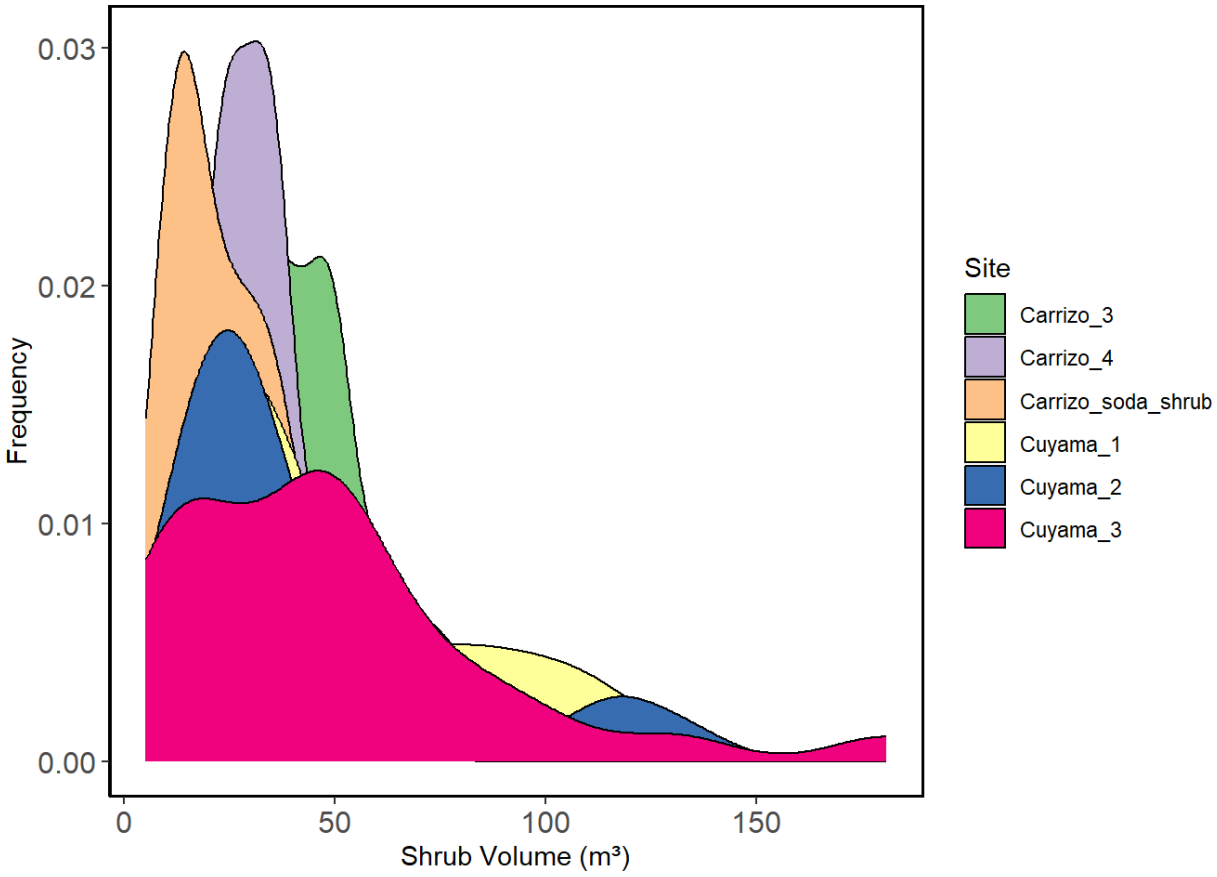
D: Shrub Cover Percent shrub cover within a 20m radius was estimated at the centre of each site using *Google Earth* composite satellite images at a spatial resolution of 30cm. The total number of shrubs within each radius is provided. All shrubs were geotagged and given a unique identifying number. Site coordinates are provided.

Site Code	***Semi-arid Region***	***Latitude***	***Longitude***	***Number of Shrubs (n)***	***Percent Cover (%)***
Cuyama_1	San Joaquin	34.849	-119.483	12	14.42
Cuyama_2	San Joaquin	34.854	-119.486	18	31.18
Cuyama_3	San Joaquin	34.938	-119.481	21	27.98
Carrizo_3	San Joaquin	35.163	-119.675	4	21.0
Carrizo_4	San Joaquin	35.116	-119.621	6	6.68
Carrizo_soda_shrub	San Joaquin	35.119	-119.629	21	8.55

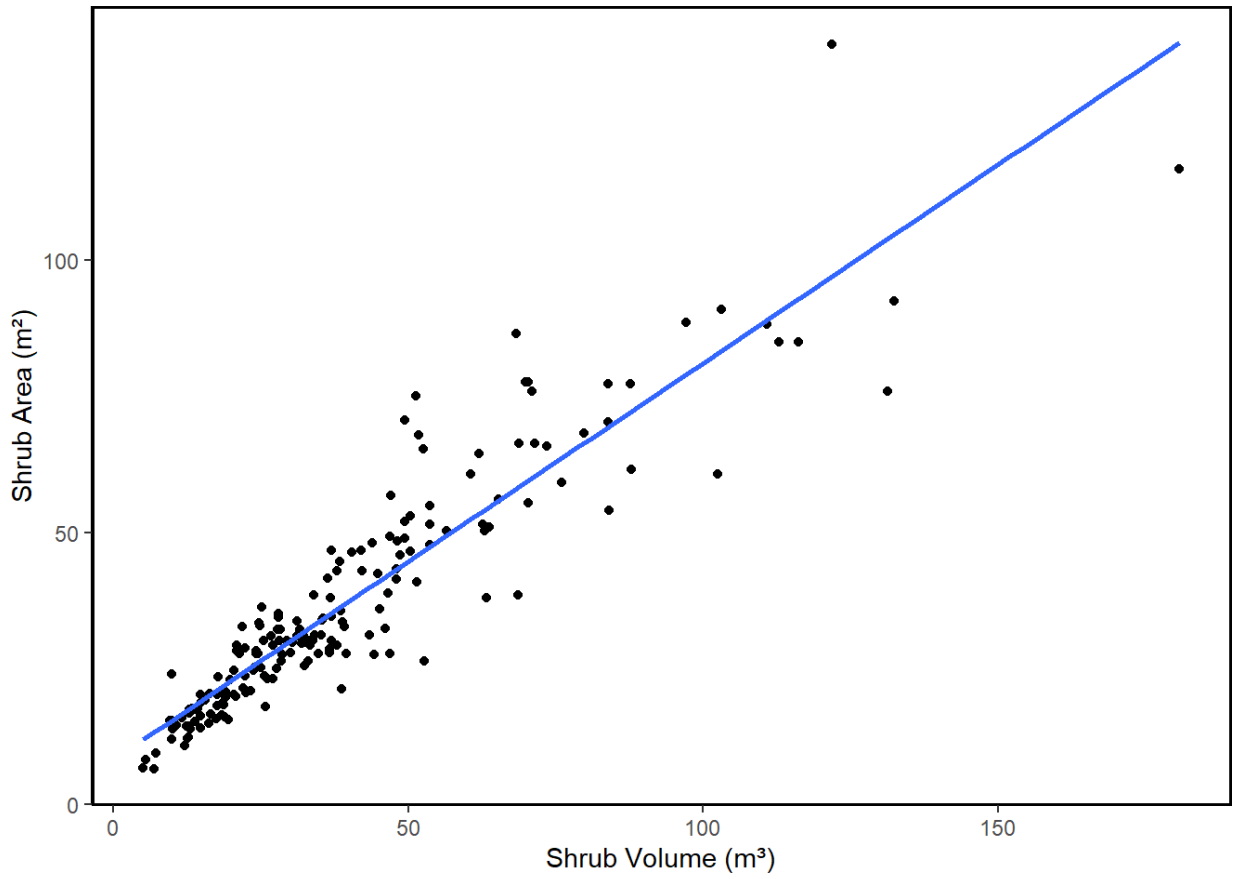
E: Plant List A list of all observed annual plant species' Latin binomial names are provided. Mean abundance values for each species are provided at both the shrub and open microsites.

Latin Binomial Name	*Microsite*	*Mean Abundance*
Acmispon wrangelianus	open	13.5
Acmispon wrangelianus	shrub	3.5
Agoseris grandiflora	open	3.33
Agoseris grandiflora	shrub	5
Allium peninsulare	open	40.25
Amsinckia intermedia	open	33.33
Amsinckia intermedia	shrub	49.5
Amsinckia tessellata	open	36.14
Amsinckia tessellata	shrub	6.57
Astragalus lentiginosus nigricalycis	open	3
Astragalus lentiginosus nigricalycis	shrub	1
Brassica nigra	shrub	1
Bromus madritensis rubens	open	116
Bromus madritensis rubens	shrub	81.58
Calandrinia menziesii	open	75.5
Calandrinia menziesii	shrub	9
Camissonia strigulosa	open	6.8
Caulanthus lasiophyllus	open	2
Caulanthus lasiophyllus	shrub	6
Eremalche exilis	shrub	25
Eriastrum densifolium	open	2
Erodium cicutarium	open	206.68
Erodium cicutarium	shrub	13.16
Gutierrezia californica	open	6
Lactuca serriola	shrub	1
Lasthenia gracilis	open	443.54
Lasthenia gracilis	shrub	4
Lepidium nitidum	open	72.42
Lupinus microcarpus	open	1
Lupinus microcarpus	shrub	1
Monolopia lanceolata	open	9.69
Monolopia lanceolata	shrub	2.75
Pectocarya penicillata	open	114
Pectocarya penicillata	shrub	10.2
Phacelia tanacetifolia	open	2
Phacelia tanacetifolia	shrub	25
Pholistoma membranaceum	shrub	2
Plagiobothrys arizonicus	open	36
Poa secunda	open	10
Schismus barbatus	open	262.89

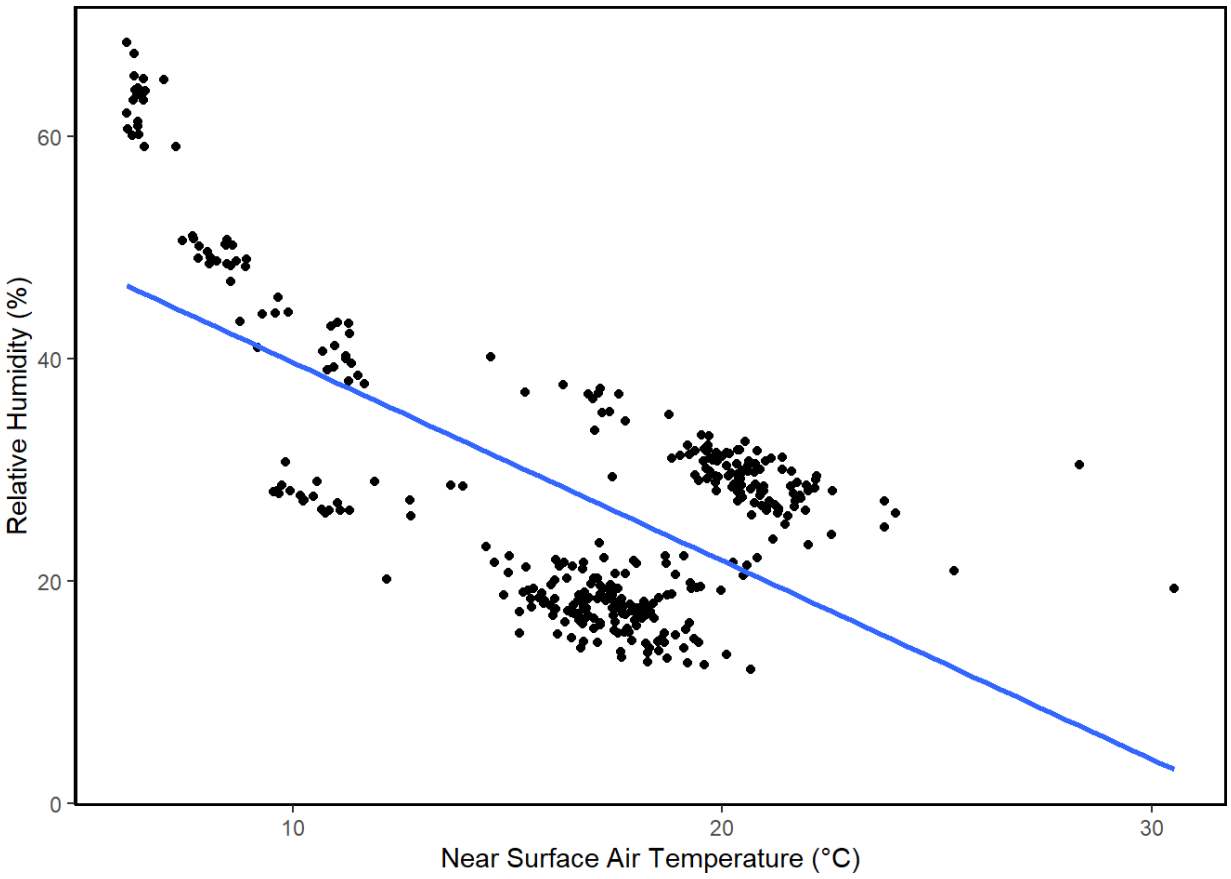
Schismus barbatus	shrub	28.38
Tropidocarpum gracile	open	10



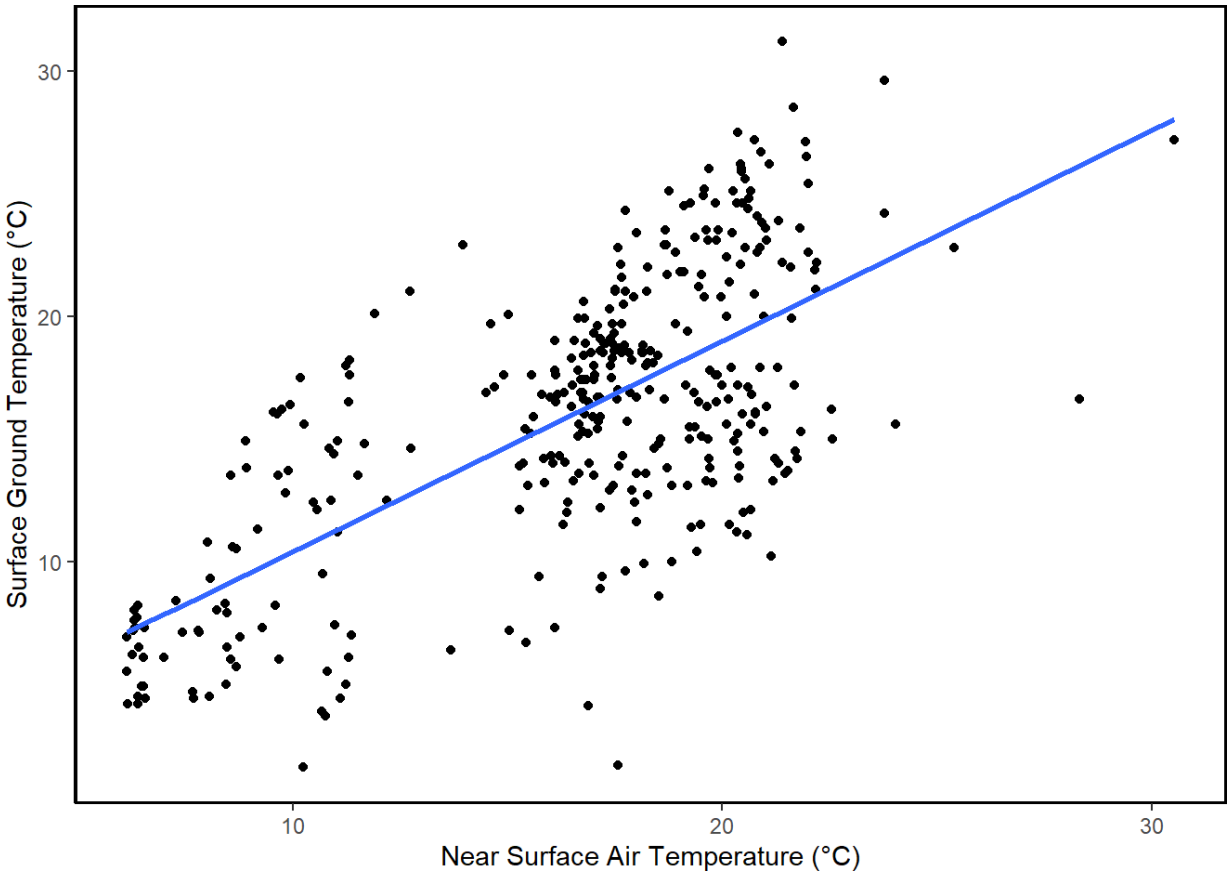
F: Frequency Distribution Density showing shrub volume (m^3) at each site on the x-axis. The y-axis represents the frequency at which the particular volume was found. Colour represents the site.



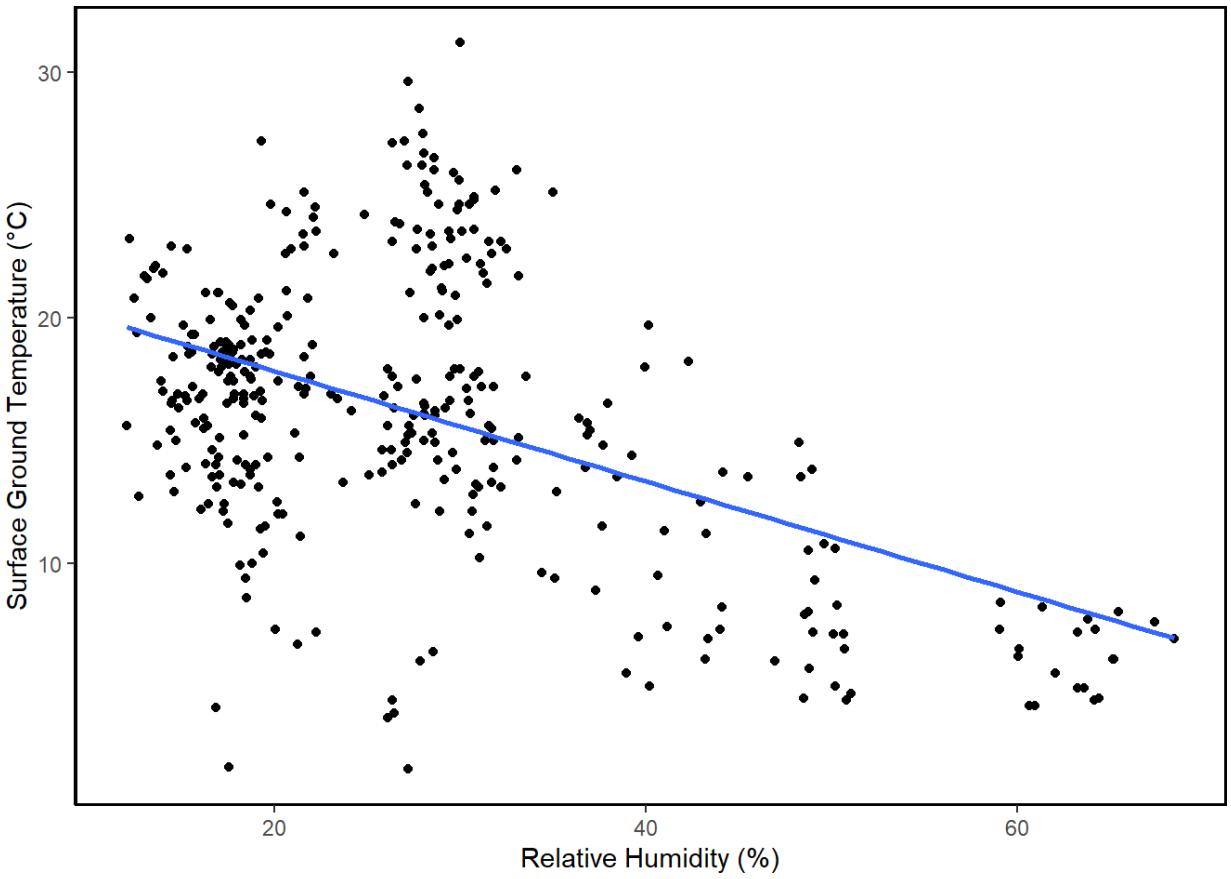
G: Shrub Volume vs. Shrub Area scatterplot depicting the overall relationship of shrub volume (m^3) and shrub area (m^2) (Pearson's product-moment correlation = 0.918, $p<0.001$). Blue line represents the smooth conditional mean fitted using the method GLM.



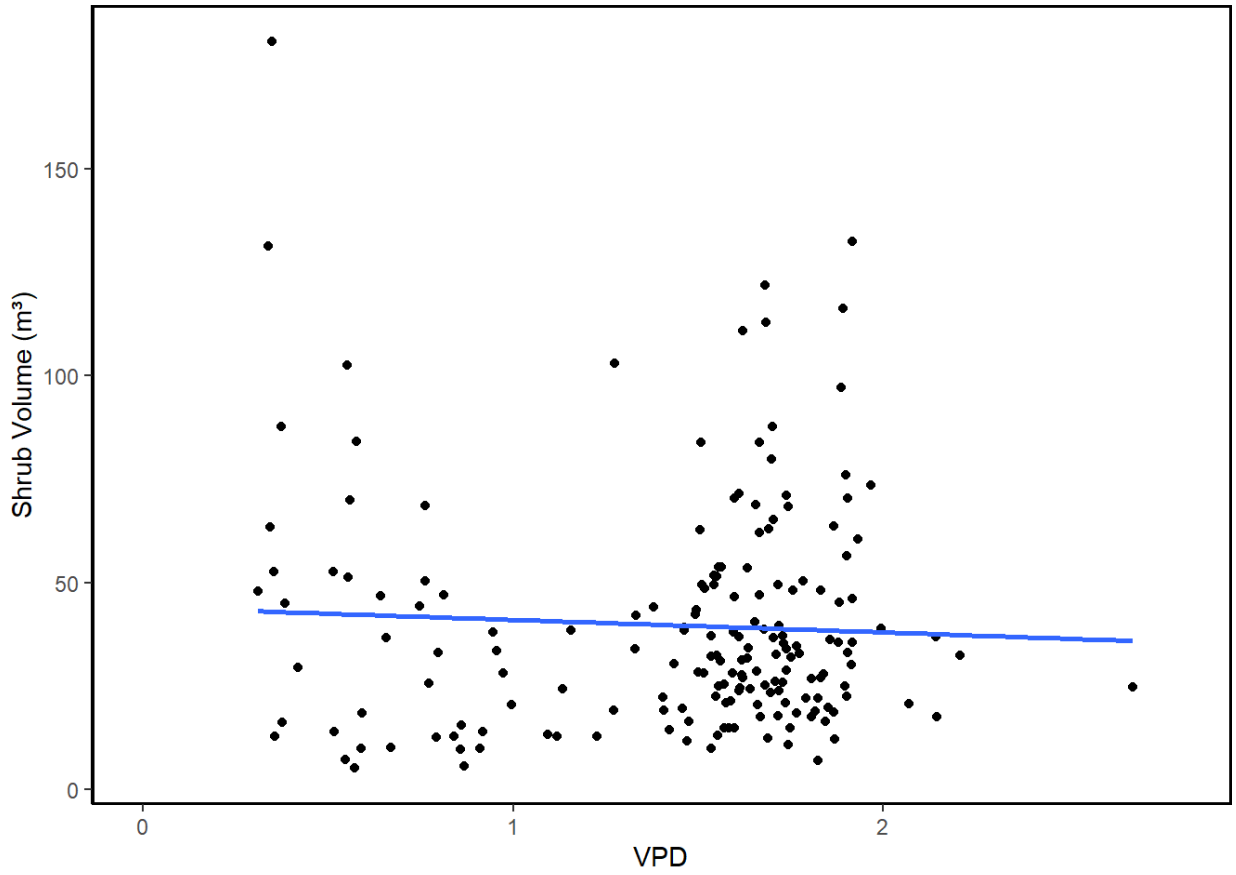
H: NSRH vs. NSAT scatterplot depicting the overall relationship between near-surface relative humidity (%) and near-surface air temperature (ºC) (Pearson's product-moment correlation = -0.652, $p<0.001$). Blue line represents the smooth conditional mean fitted using the method GLM.



I: SGT vs. NSAT scatterplot depicting the overall relationship between surface ground temperature (ºC) and near-surface air temperature (ºC) (Pearson's product-moment correlation = 0.679, $p<0.001$). Blue line represents the smooth conditional mean fitted using the method GLM.



J: SGT vs. NSRH scatterplot depicting the overall relationship between surface ground temperature (ºC) and near-surface relative humidity (%) (Pearson's product-moment correlation = -0.487, $p<0.001$). Blue line represents the smooth conditional mean fitted using the method GLM.



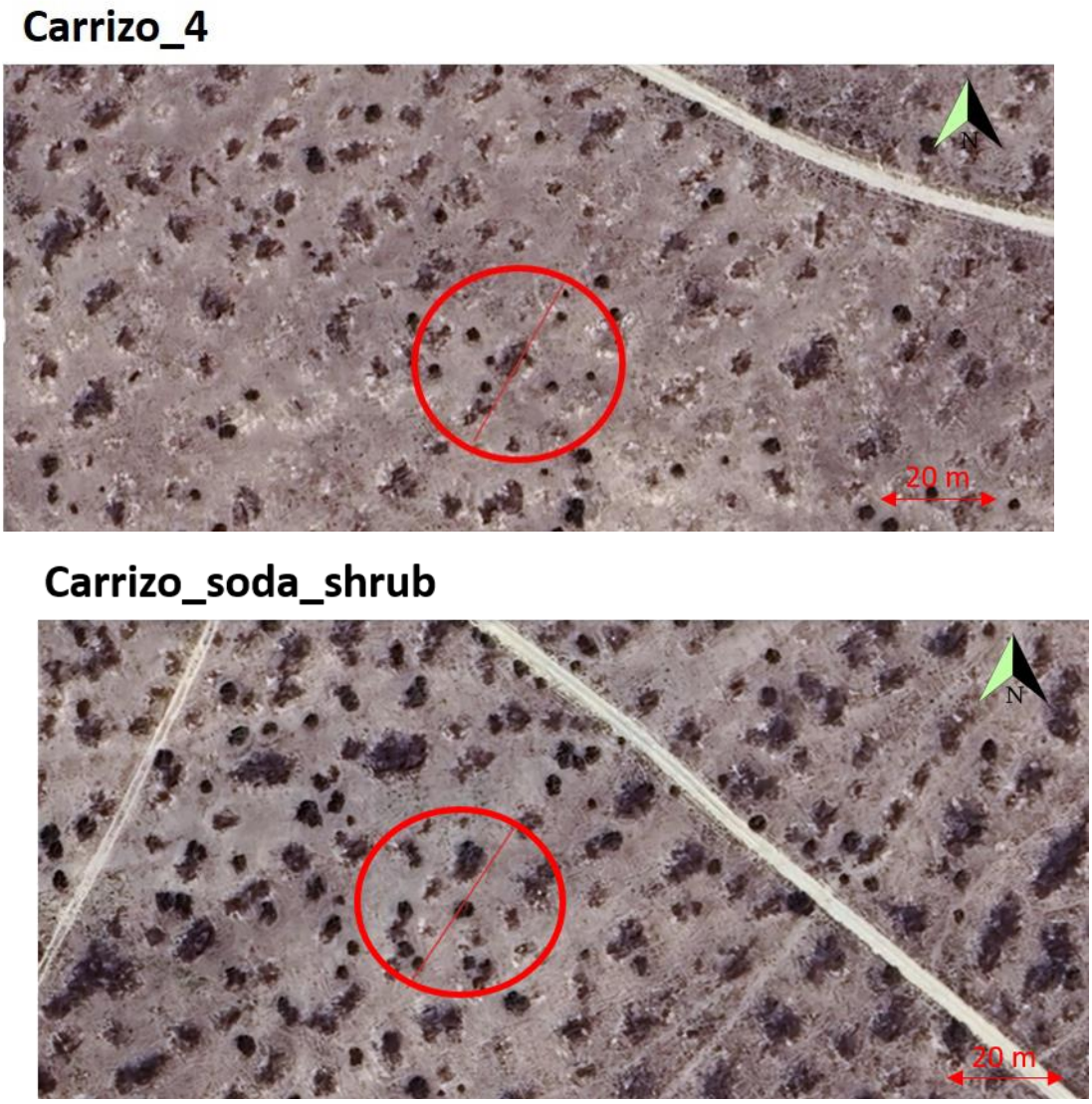
K: Shrub Volume vs VPD scatterplot depicting the overall relationship between shrub volume (m^3) and vapour pressure deficit (VPD) (Pearson's product-moment correlation = -0.0523, $p<0.485$). Blue line represents the smooth conditional mean fitted using the method GLM.

Cuyama_1

Cuyama_2

Cuyama_3

Carrizo_3



L: Satellite Imagery of Shrub Cover A circular plot with with a 40m diameter used on *Google Earth* composite satellite images provided by *Airbus* at a spatial resolution of 30cm is shown at each site. The zoom is set the same in each instance.

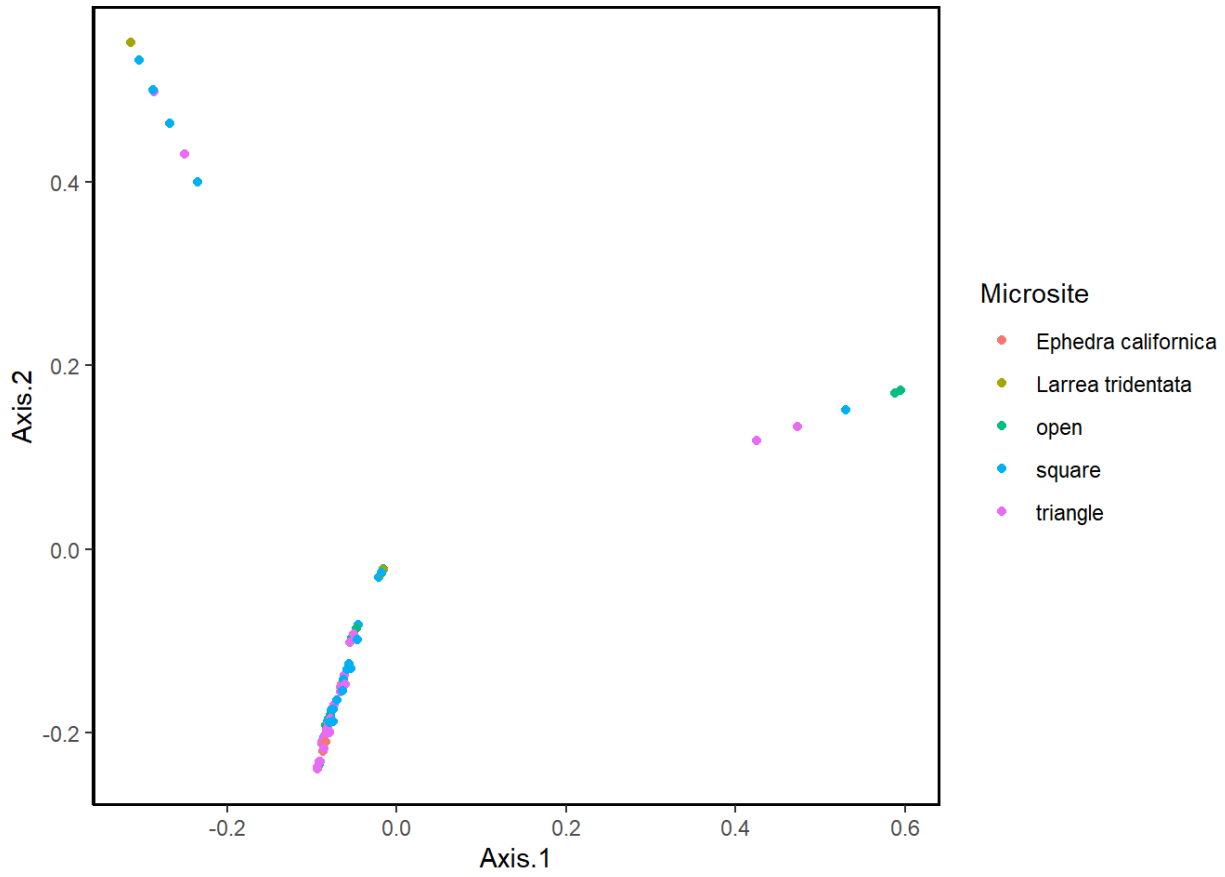
APPENDIX D

A: A summary of Site information, total annual precipitation (mm), mean monthly temperature (ºC), and aridity. Data were compiled from various weather stations and available on *Figshare* (https://doi.org/10.6084/m9.figshare.25115357.v3).

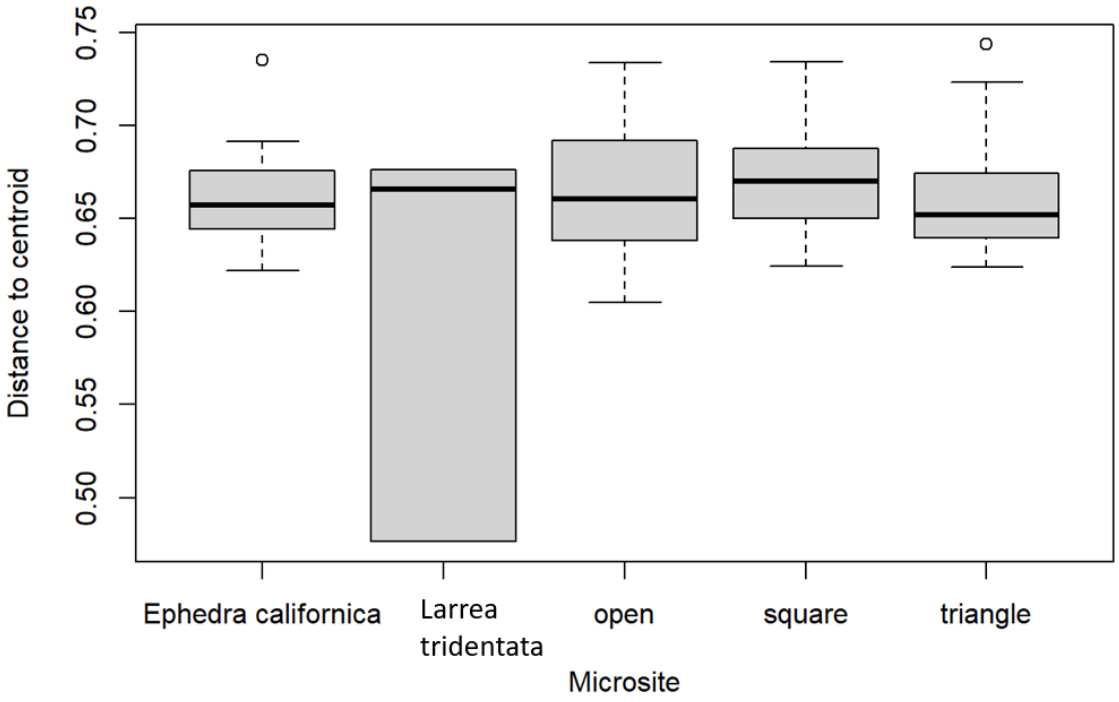
Site	*Lat*	*Long*	*Year*	*Total Annual Precipitation (mm)*	*Mean Monthly Temperature (ºC)*	*Aridity*
Carrizo_4	35.11566	-119.621	2022	143.256	17.935	5.128
Carrizo_4	35.11566	-119.621	2023	350.012	16.231	13.343
Carrizo_soda_open	35.09061	-119.577	2022	159.004	17.46	5.790
Carrizo_soda_open	35.09061	-119.577	2023	391.668	16.96	14.528
Tecopa_shrub	35.85152	-116.187	2022	85.598	17.454	3.118
Tecopa_shrub	35.85152	-116.187	2023	300.99	16.384	11.408
Tecopa_open	35.85474	-116.179	2022	85.598	17.454	3.118
Tecopa_open	35.85474	-116.179	2023	300.99	16.384	11.408

B: PERMANOVA Spring 2022 summary for community composition PCOA by microsite.

	df	*Sum of Squares*	*Mean of Squares*	*F. Model*	*Pr(>F)*
groups	4	0.031697	0.0070243	6.81	**0.01**
residuals	217	0.252507	0.001163		
number of permutations			999		



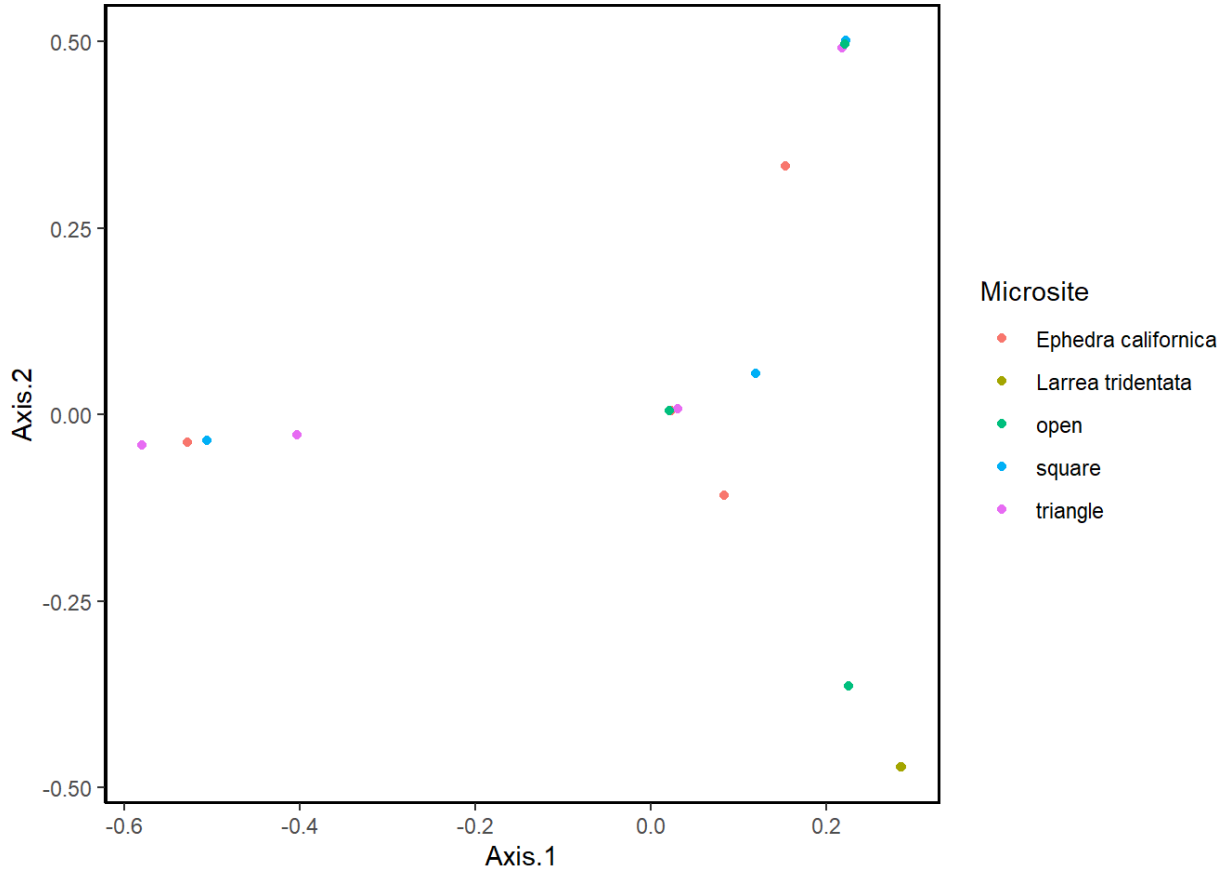
C: PCOA Spring 2022 figure displaying similarity in vertebrate animal compositions across the various microsites in Southern California. Analysis was conducted using the R package *Vegan*.



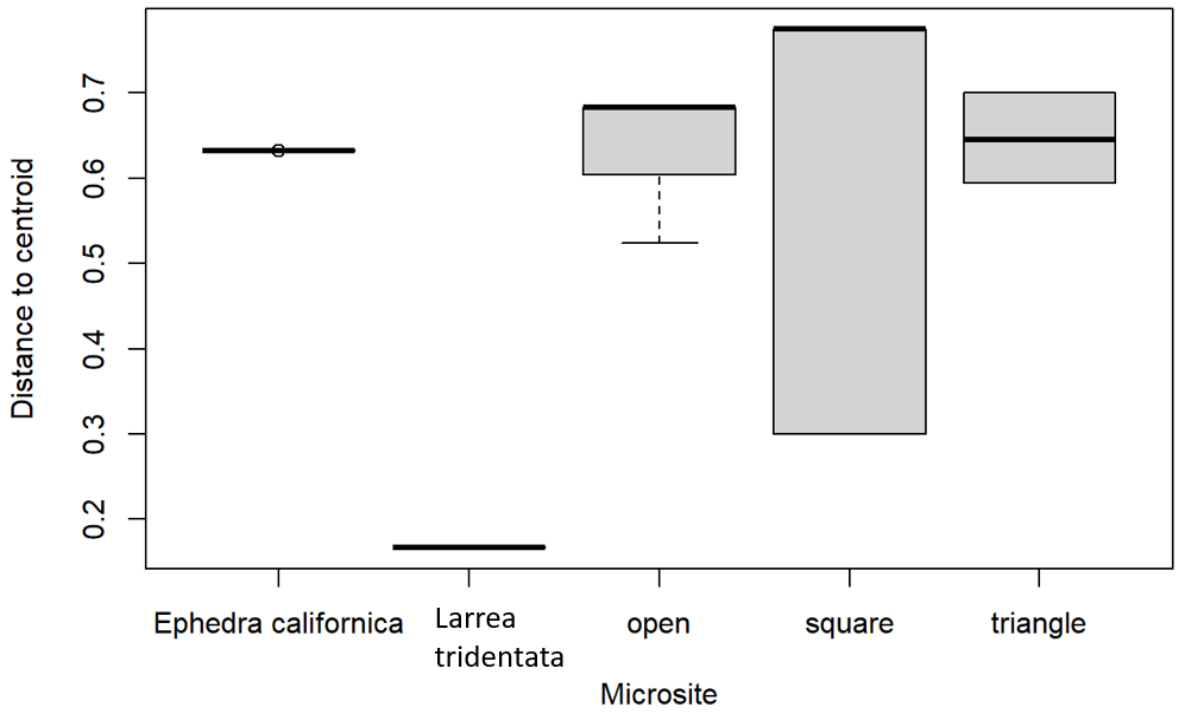
D: Distance to Centroid Boxplot Spring 2022 showing the variation in centroid distance among the microsites tested for spring 2022 census. Solid middle lines show the median of the data, whilst whiskers show 1.5 standard deviation. Dots are outliers >1.5 interquartile range (IQR). Significant differences were observed between *Larrea tridentata* and the other microsites, including *Ephedra californica*, square, triangle, and the open (post-hoc $p < 0.01$).

E: PERMANOVA Winter 2023 summary for community composition PCOA by microsite.

	df	*Sum of Squares*	*Mean of Squares*	*F. Model*	*Pr(>F)*
groups	4	0.40636	0.101591	7.1741	**0.01**
residuals	23	0.32570	0.014161		
number of permutations			999		



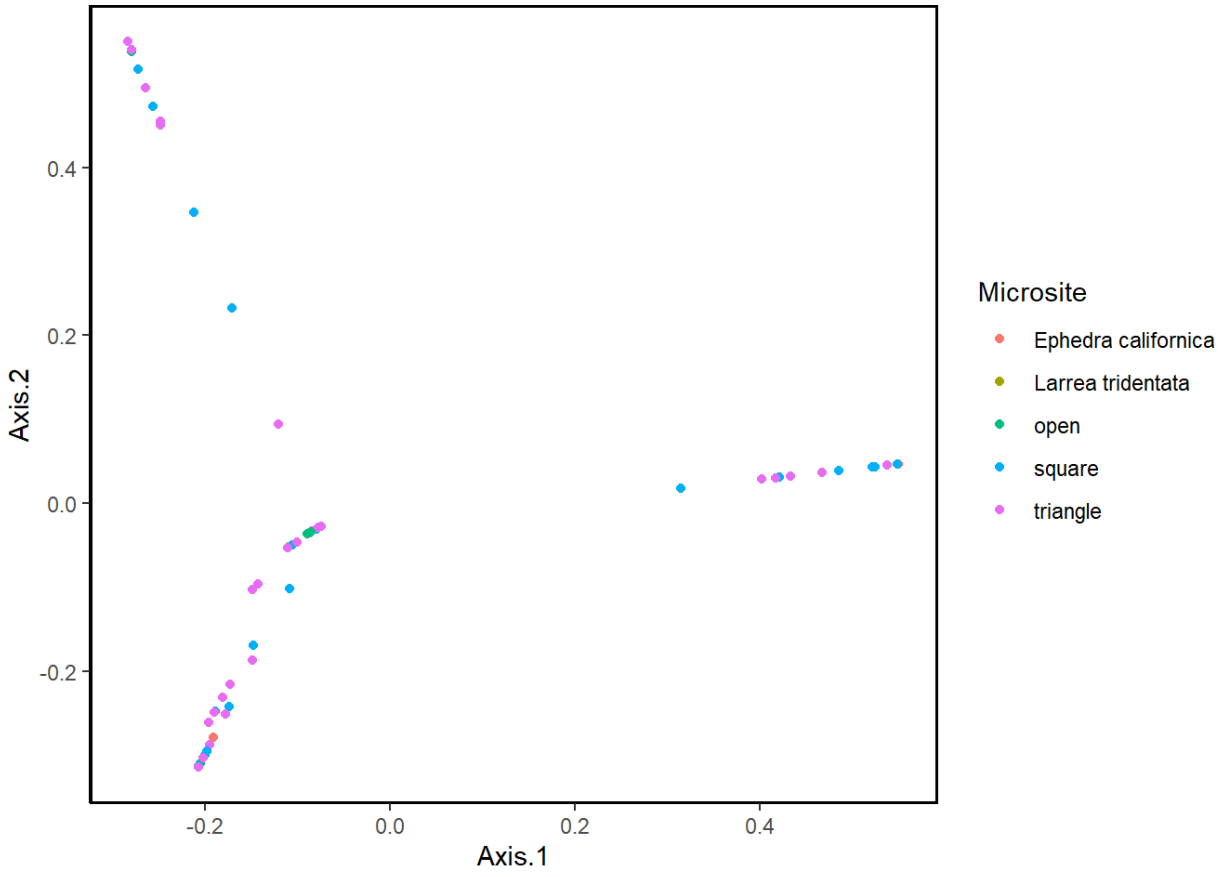
F: PCOA Winter 2023 figure displaying similarity in vertebrate animal compositions across the various microsites in Southern California. Analysis was conducted using the R package *Vegan*.



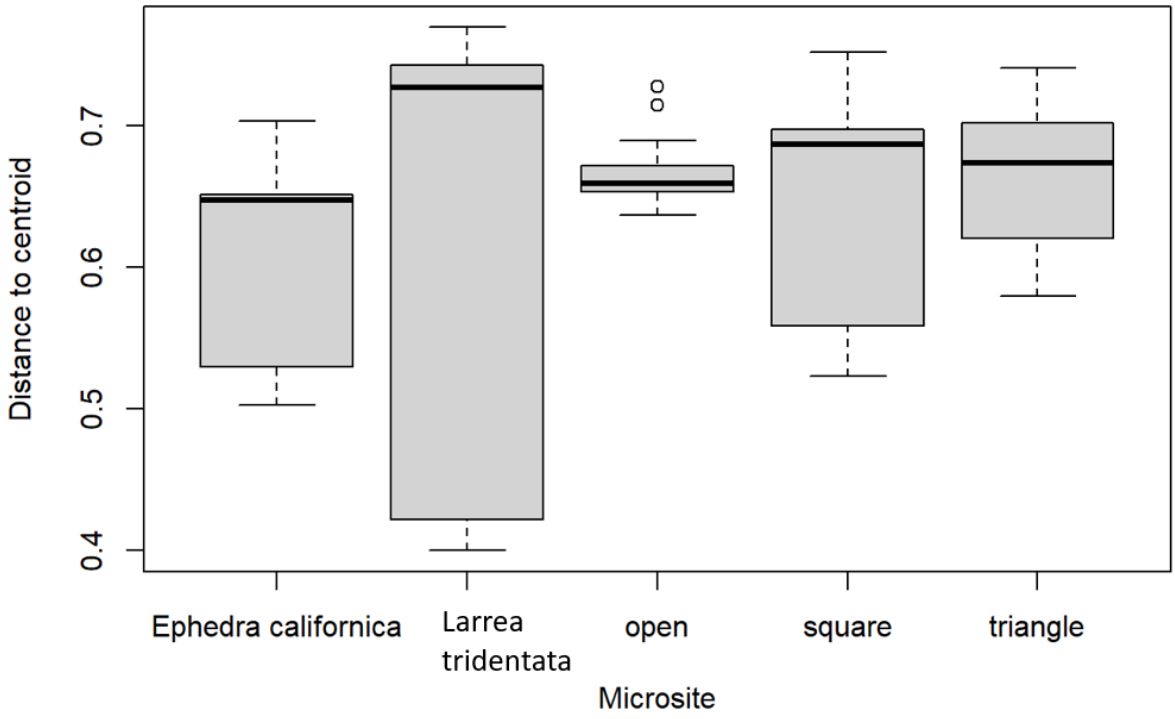
G: Distance to Centroid Boxplot Winter 2023 showing the variation in centroid distance among the microsites tested for winter 2023 census. Solid middle lines show the median of the data, whilst whiskers show 1.5 standard deviation. Dots are outliers >1.5 interquartile range (IQR). Significant differences were observed between *Larrea tridentata* and the other microsites, including *Ephedra californica*, square, triangle, and the open (post-hoc $p < 0.01$).

H: PERMANOVA Spring 2023 summary for community composition PCOA by microsite.

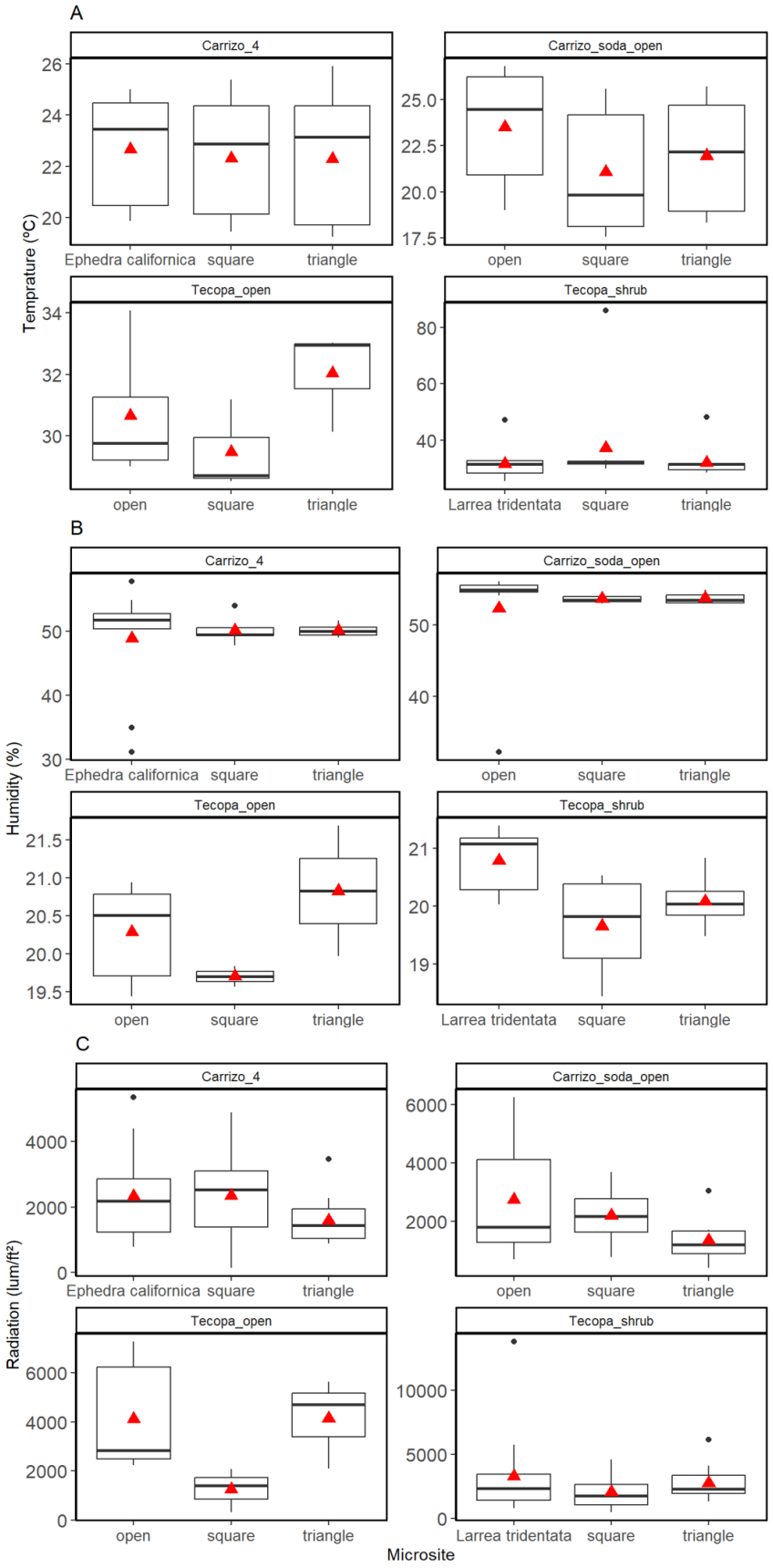
	df	*Sum of Squares*	*Mean of Squares*	*F. Model*	*Pr(>F)*
groups	4	0.04274	0.01068	2.1901	0.0721
residuals	170	0.82936	0.0048786		
number of permutations			999		



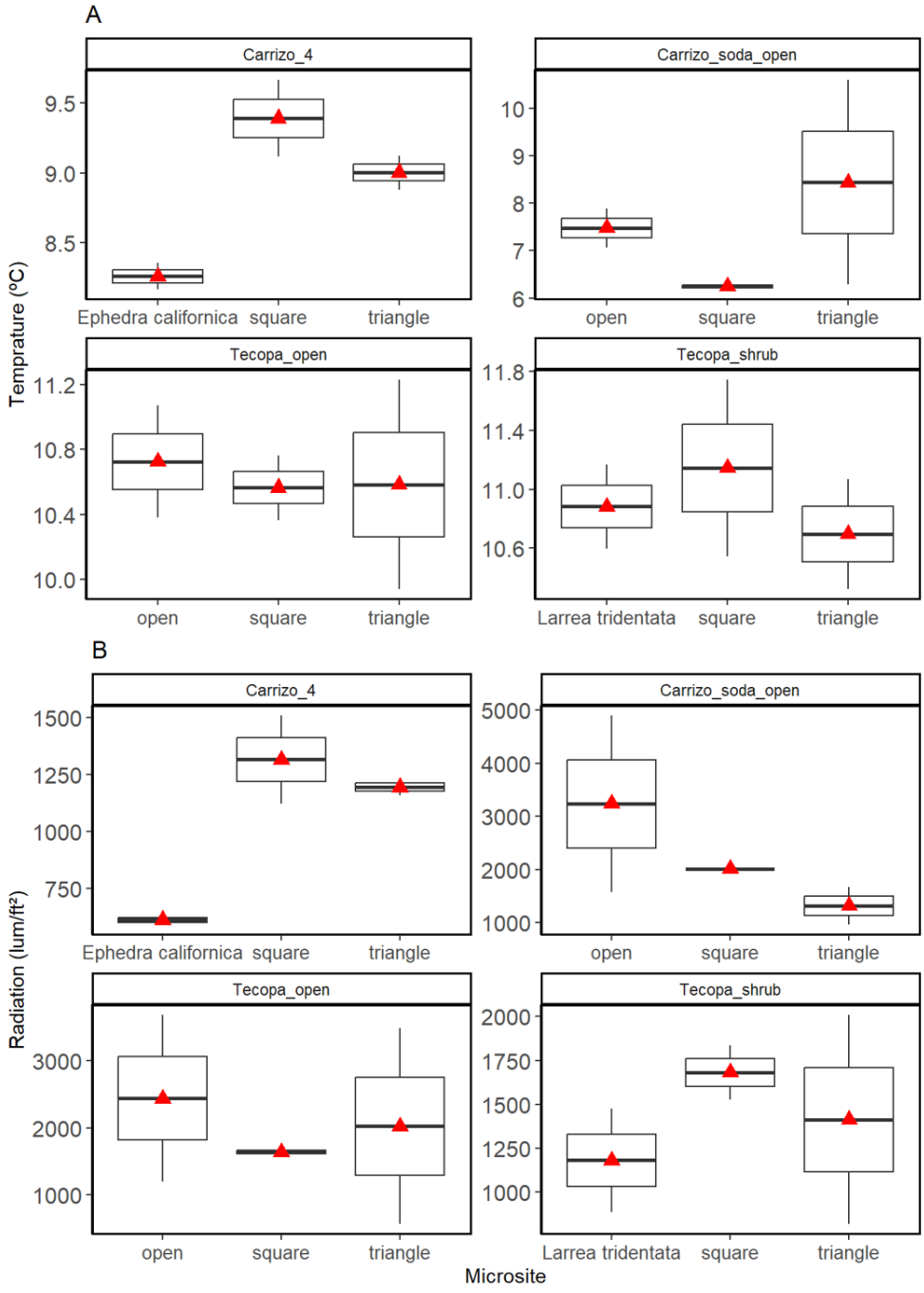
I: PCOA Spring 2023 figure displaying similarity in vertebrate animal compositions across the various microsites in Southern California. Analysis was conducted using the R package *Vegan*.



J: Distance to Centroid Boxplot Spring 2023 showing the variation in centroid distance among the microsites tested for spring 2023 census. Solid middle lines show the median of the data, whilst whiskers show 1.5 standard deviation. Dots are outliers >1.5 interquartile range (IQR).


A
Carrizo_4
Carrizo_soda_open
Tecopa_open
Tecopa_shrub
Temprature (ºC)
Ephedra californica
Larrea tridentata
open
square
triangle
B
Humidity (%)
C
Radiation (lum/ft²)
Microsite

K: Spring Microclimate Boxplot of temperature (°C, A), relative humidity (%, B), and solar radiation (lum/ft^2, C) are shown at each shrub and shelter, at each site for the 2022 and 2023 spring censuses. Solid middle lines show the median of the data, whilst whiskers show 1.5 standard deviation. Solid dots are outliers >1.5 interquartile range (IQR). Red triangles represent the mean.



L: Winter Microclimate Boxplot of temperature (°C, A) and solar radiation (lum/ft^2, B) are shown at each shrub and shelter, at each site for the winter 2023 census. Solid middle lines show the median of the data, whilst whiskers show 1.5 standard deviation. Solid dots are outliers >1.5 interquartile range (IQR). Red triangles represent the mean.

M: Vertebrate Species List for animals observed during all three censuses, including spring 2022-2023, and winter 2023.

Scientific Name	***Common Name***	***Total Captures***
Ammospermophilus leucurus	White-tailed Antelope Squirrel	1
Ammospermophilus nelsoni	Nelson's Antelope Squirrel	323
Antilocapra americana	Pronghorn	5
Buteo jamaicensis	Red-tailed Hawk	8
Canis latrans	Coyote	77
Corvus brachyrhynchos	American Crow	7
Corvus corax	Common Raven	1
Dipodomys heermanni	Heerman's Kangaroo Rat	1112
Dipodomys ingens	Giant Kangaroo Rat	582
Dipodomys nelsoni	Nelson's Kangaroo Rat	1
Dipsosaurus dorsalis	Desert Iguana	5
Eremophila alpestris	Horned Lark	3
Lepus californicus	Black-tailed Jackrabbit	315
Sylvilagus audubonii	Desert Cottontail	40
Taxidea taxus	American Badger	4
Vulpes macrotis	San Joaquin Kit Fox	89
Xerospermophilus tereticaudus	Red-tailed Ground Squirrel	11
Xerospermophilus mohavensis	Mojave Ground Squirrel	2

N: Design Reps showing the microsite type, site, season, and year, and the number of microsites that were deployed.

Year	*Season*	*Site*	*Microsite*	*Reps*
2022	**spring**	Carrizo_4	Ephedra californica	8
2022	**spring**	Carrizo_soda_open	Ephedra californica	0
2022	**spring**	Tecopa_shrub	Larrea tridentata	8
2022	**spring**	Tecopa_open	Larrea tridentata	0
2022	**spring**	Carrizo_4	open	0
2022	**spring**	Carrizo_soda_open	open	8
2022	**spring**	Tecopa_shrub	open	0
2022	**spring**	Tecopa_open	open	8
2022	**spring**	Carrizo_4	square	8
2022	**spring**	Carrizo_soda_open	square	4
2022	**spring**	Tecopa_shrub	square	8
2022	**spring**	Tecopa_open	square	4
2022	**spring**	Carrizo_4	triangle	8
2022	**spring**	Carrizo_soda_open	triangle	4
2022	**spring**	Tecopa_shrub	triangle	8
2022	**spring**	Tecopa_open	triangle	4
2023	**spring**	Carrizo_4	Ephedra californica	8
2023	**spring**	Carrizo_soda_open	Ephedra californica	0
2023	**spring**	Tecopa_shrub	Larrea tridentata	8
2023	**spring**	Tecopa_open	Larrea tridentata	0
2023	**spring**	Carrizo_4	open	0
2023	**spring**	Carrizo_soda_open	open	8
2023	**spring**	Tecopa_shrub	open	0
2023	**spring**	Tecopa_open	open	8
2023	**spring**	Carrizo_4	square	8
2023	**spring**	Carrizo_soda_open	square	4
2023	**spring**	Tecopa_shrub	square	8
2023	**spring**	Tecopa_open	square	4
2023	**spring**	Carrizo_4	triangle	8
2023	**spring**	Carrizo_soda_open	triangle	4
2023	**spring**	Tecopa_shrub	triangle	8
2023	**spring**	Tecopa_open	triangle	4
2022	**winter**	Carrizo_4	Ephedra californica	2
2022	**winter**	Carrizo_soda_open	Ephedra californica	0
2022	**winter**	Tecopa_shrub	Larrea tridentata	2
2022	**winter**	Tecopa_open	Larrea tridentata	0
2022	**winter**	Carrizo_4	open	0
2022	**winter**	Carrizo_soda_open	open	2

2022	**winter**	Tecopa_shrub	open	0
2022	**winter**	Tecopa_open	open	2
2022	**winter**	Carrizo_4	square	2
2022	**winter**	Carrizo_soda_open	square	2
2022	**winter**	Tecopa_shrub	square	2
2022	**winter**	Tecopa_open	square	2
2022	**winter**	Carrizo_4	triangle	2
2022	**winter**	Carrizo_soda_open	triangle	2
2022	**winter**	Tecopa_shrub	triangle	2
2022	**winter**	Tecopa_open	triangle	2

O: Emmeans Abundance Contrast Spring Estimated Marginalized Means (EMM) and standard errors (SE) are given for species abundance Generalized Linear Model (GLM) for the spring 2022 and 2023 censuses. Microsite nested in site and year were used as predictors. To reduce collinearity in microclimatic variables of the model, only temperature served as a covariate. Post-hoc p-values are given.

Site	*Year*	*Microsite*	*Contrast*	*emmean*	*SE (±)*	*asymp .LCL*	*asymp .UCL*	*p-Value*
Carrizo_4	2022	Ephedra californica		**3.66**	0.30	2.68	4.63	
Carrizo_4	2022	square		**3.74**	0.28	2.83	4.65	
Carrizo_4	2022	triangle		**4.07**	0.28	3.16	4.97	
Carrizo_soda_open	2022	open		**3.32**	0.29	2.37	4.27	
Carrizo_soda_open	2022	square		**2.56**	0.49	0.94	4.18	
Carrizo_soda_open	2022	triangle		**3.86**	0.41	2.51	5.22	
Tecopa_open	2022	open		**0.59**	0.69	-1.69	2.87	
Tecopa_open	2022	square		**-17.74**	4952.79	-16258.07	16222.59	
Tecopa_open	2022	triangle		**-17.30**	3350.27	-11002.90	10968.30	
Tecopa_shrub	2022	Larrea tridentata		**0.59**	0.44	-0.86	2.03	
Tecopa_shrub	2022	square		**0.76**	0.41	-0.60	2.12	
Tecopa_shrub	2022	triangle		**-17.70**	1748.51	-5751.10	5715.70	
Carrizo_4	2023	Ephedra californica		**1.71**	0.41	0.37	3.04	
Carrizo_4	2023	square		**2.53**	0.35	1.40	3.67	
Carrizo_4	2023	triangle		**3.18**	0.34	2.08	4.28	
Carrizo_soda_open	2023	open		**1.52**	0.38	0.27	2.78	
Carrizo_soda_open	2023	square		**1.40**	0.51	-0.28	3.07	
Carrizo_soda_open	2023	triangle		**1.72**	0.49	0.10	3.34	
Tecopa_open	2023	open		**1.38**	0.41	0.04	2.71	
Tecopa_open	2023	square		**1.41**	0.69	-0.85	3.67	
Tecopa_open	2023	triangle		**1.83**	0.90	-1.13	4.80	
Tecopa_shrub	2023	Larrea tridentata		**2.08**	0.36	0.89	3.27	
Tecopa_shrub	2023	square		**2.48**	0.88	-0.41	5.37	
Tecopa_shrub	2023	triangle		**2.59**	0.35	1.43	3.75	
Carrizo_4	2022		Ephedra californica - square	-0.09	0.40	-1.41	1.24	0.975

Carrizo_4	2022		Ephedra californica - triangle	-0.41	0.41	-1.77	0.94	0.577
Carrizo_4	2022		square - triangle	-0.33	0.41	-1.66	1.01	0.701
Carrizo_soda_open	2022		open - square	0.76	0.57	-1.11	2.63	0.375
Carrizo_soda_open	2022		open - triangle	-0.54	0.50	-2.18	1.10	0.521
Carrizo_soda_open	2022		square - triangle	-1.30	0.64	-3.40	0.79	0.102
Tecopa_open	2022		open - square	18.33	4952.79	-16222.00	16258.66	1
Tecopa_open	2022		open - triangle	17.89	3350.27	-10967.71	11003.49	1
Tecopa_open	2022		square - triangle	-0.44	5979.50	-19607.37	19606.50	1
Tecopa_shrub	2022		Larrea tridentata - square	-0.17	0.59	-2.09	1.75	0.952
Tecopa_shrub	2022		Larrea tridentata - triangle	18.28	1748.51	-5715.11	5751.68	0.999
Tecopa_shrub	2022		square - triangle	18.46	1748.51	-5714.94	5751.86	0.999
Carrizo_4	2023		Ephedra californica - square	-0.83	0.49	-2.43	0.78	0.209
Carrizo_4	2023		Ephedra californica - triangle	-1.47	0.49	-3.08	0.13	0.007
Carrizo_4	2023		square - triangle	-0.65	0.45	-2.11	0.82	0.315
Carrizo_soda_open	2023		open - square	0.13	0.59	-1.81	2.07	0.974
Carrizo_soda_open	2023		open - triangle	-0.19	0.58	-2.09	1.71	0.940
Carrizo_soda_open	2023		square - triangle	-0.32	0.66	-2.48	1.84	0.876

Tecopa_open	2023	open - square	-0.03	0.80	-2.65	2.58	0.999
Tecopa_open	2023	open - triangle	-0.46	0.98	-3.68	2.76	0.887
Tecopa_open	2023	square - triangle	-0.43	1.13	-4.13	3.28	0.924
Tecopa_shrub	2023	Larrea tridentata - square	-0.39	0.95	-3.50	2.71	0.908
Tecopa_shrub	2023	Larrea tridentata - triangle	-0.51	0.50	-2.15	1.13	0.564
Tecopa_shrub	2023	square - triangle	-0.12	0.91	-3.12	2.88	0.991

P: Emmeans Richness Contrast Spring Estimated Marginalized Means (EMM) and standard errors (SE) are given for species richness Generalized Linear Model (GLM) for the spring 2022 and 2023 censuses. Microsite nested in site and year were used as predictors. To reduce collinearity in microclimatic variables of the model, only temperature served as a covariate. Post-hoc p-values are given.

Site	*Year*	*Microsite*	*Contrast*	*emmean*	*SE (±)*	*asymp .LCL*	*asymp. UCL*	*p-value*
Carrizo_4	2022	Ephedra californica		**4.77**	0.53	2.97	6.56	
Carrizo_4	2022	square		**5.02**	0.53	3.22	6.81	
Carrizo_4	2022	triangle		**5.77**	0.53	3.97	7.56	
Carrizo_soda_open	2022	open		**4.26**	0.53	2.47	6.04	
Carrizo_soda_open	2022	square		**4.68**	0.86	1.77	7.60	
Carrizo_soda_open	2022	triangle		**5.27**	0.75	2.74	7.79	
Tecopa_open	2022	open		**0.96**	0.87	-1.99	3.91	
Tecopa_open	2022	square		**-0.03**	1.49	-5.07	5.02	
Tecopa_open	2022	triangle		**-0.23**	1.36	-4.81	4.35	
Tecopa_shrub	2022	Larrea tridentata		**1.08**	0.56	-0.80	2.95	
Tecopa_shrub	2022	square		**1.22**	0.54	-0.61	3.04	
Tecopa_shrub	2022	triangle		**-0.05**	0.55	-1.91	1.82	
Carrizo_4	2023	Ephedra californica		**1.54**	0.63	-0.58	3.67	
Carrizo_4	2023	square		**3.76**	0.59	1.77	5.75	
Carrizo_4	2023	triangle		**4.62**	0.59	2.63	6.61	
Carrizo_soda_open	2023	open		**2.04**	0.59	0.07	4.02	
Carrizo_soda_open	2023	square		**2.06**	0.78	-0.56	4.67	
Carrizo_soda_open	2023	triangle		**2.30**	0.77	-0.30	4.90	
Tecopa_open	2023	open		**2.48**	0.61	0.42	4.55	
Tecopa_open	2023	square		**1.49**	1.06	-2.07	5.05	
Tecopa_open	2023	triangle		**0.98**	1.49	-4.06	6.02	
Tecopa_shrub	2023	Larrea tridentata		**1.50**	0.61	-0.56	3.55	

Tecopa_shrub	2023	square		1.30	1.29	-3.07	5.66	
Tecopa_shrub	2023	triangle		2.32	0.61	0.25	4.38	
Carrizo_4	2022		Ephedra californica - square	-0.25	0.75	-2.77	2.27	0.939
Carrizo_4	2022		Ephedra californica - triangle	-1.00	0.75	-3.52	1.52	0.376
Carrizo_4	2022		square - triangle	-0.75	0.75	-3.27	1.77	0.576
Carrizo_soda_open	2022		open - square	-0.43	1.01	-3.84	2.98	0.906
Carrizo_soda_open	2022		open - triangle	-1.01	0.91	-4.09	2.08	0.513
Carrizo_soda_open	2022		square - triangle	-0.58	1.14	-4.43	3.26	0.865
Tecopa_open	2022		open - square	0.99	1.72	-4.83	6.80	0.834
Tecopa_open	2022		open - triangle	1.19	1.53	-3.99	6.37	0.717
Tecopa_open	2022		square - triangle	0.21	1.98	-6.47	6.88	0.994
Tecopa_shrub	2022		Larrea tridentata - square	-0.14	0.75	-2.67	2.38	0.981
Tecopa_shrub	2022		Larrea tridentata - triangle	1.12	0.75	-1.40	3.64	0.293
Tecopa_shrub	2022		square - triangle	1.26	0.75	-1.26	3.78	0.213
Carrizo_4	2023		Ephedra californica - square	-2.22	0.83	-5.02	0.58	**0.023**
Carrizo_4	2023		Ephedra californica - triangle	-3.08	0.83	-5.88	-0.27	**0.01**
Carrizo_4	2023		square - triangle	-0.86	0.80	-3.55	1.83	0.530
Carrizo_soda_open	2023		open - square	-0.01	0.94	-3.18	3.15	0.999
Carrizo_soda_open	2023		open - triangle	-0.26	0.94	-3.42	2.90	0.958
Carrizo_soda_open	2023		square - triangle	-0.24	1.05	-3.81	3.32	0.971

Tecopa_open	2023		open - square	0.99	1.22	-3.12	5.11	0.693
Tecopa_open	2023		open - triangle	1.50	1.61	-3.93	6.94	0.620
Tecopa_open	2023		square - triangle	0.51	1.83	-5.66	6.68	0.958
Tecopa_shrub	2023		Larrea tridentata - square	0.20	1.42	-4.60	5.00	0.989
Tecopa_shrub	2023		Larrea tridentata - triangle	-0.82	0.86	-3.73	2.09	0.607
Tecopa_shrub	2023		square - triangle	-1.02	1.40	-5.75	3.71	0.746

Q: Emmeans Abundance Contrast Winter Estimated Marginalized Means (EMM) and standard errors (SE) are given for species abundance Generalized Linear Model (GLM) for the winter 2023 census. Microsite nested in site was used as a predictor. To reduce collinearity in microclimatic variables of the model, only temperature served as a covariate. Post-hoc p-values are given.

Site	*Microsite*	*Contrast*	*emmean*	*SE (±)*	*asymp. LCL*	*asymp. UCL*	*p-value*
Carrizo_4	Ephedra californica		**2.91**	0.80	0.45	5.37	
Carrizo_4	square		**1.33**	0.76	-1.00	3.66	
Carrizo_4	triangle		**1.04**	0.78	-1.37	3.45	
Carrizo_soda_open	open		**1.09**	1.06	-2.18	4.36	
Carrizo_soda_open	square		**-1.16**	1.56	-5.96	3.63	
Carrizo_soda_open	triangle		**0.43**	1.21	-3.30	4.15	
Tecopa_open	open		**-17.97**	6307.64	-19433.45	19397.51	
Tecopa_open	square		**-18.06**	6337.90	-19526.67	19490.54	
Tecopa_open	triangle		**-18.09**	6196.99	-19092.97	19056.80	
Tecopa_shrub	Larrea tridentata		**2.04**	0.99	-0.99	5.07	
Tecopa_shrub	square		**0.45**	1.47	-4.08	4.99	
Tecopa_shrub	triangle		**-17.99**	6299.03	-19406.96	19370.98	
Carrizo_4		Ephedra californica - square	1.58	1.09	-1.76	4.93	0.313
Carrizo_4		Ephedra californica - triangle	1.87	1.03	-1.31	5.05	0.166
Carrizo_4		square - triangle	0.29	1.08	-3.05	3.63	0.961
Carrizo_soda_open		open - square	2.25	1.17	-1.36	5.86	0.133
Carrizo_soda_open		open - triangle	0.66	1.06	-2.61	3.93	0.806
Carrizo_soda_open		square - triangle	-1.59	1.24	-5.41	2.23	0.406
Tecopa_open		open - square	0.10	8941.77	-27523.66	27523.46	1
Tecopa_open		open - triangle	0.12	8842.46	-27217.99	27217.75	1

Tecopa_open		square - triangle	0.02	8864.06	-27284.35	27284.39	1
Tecopa_shrub		Larrea tridentata - square	1.59	1.55	-3.19	6.37	0.561
Tecopa_shrub		Larrea tridentata - triangle	20.03	6299.03	-19368.94	19409.00	1
Tecopa_shrub		square - triangle	18.44	6299.03	-19370.53	19407.41	1

R: Emmeans Richness Contrast Winter Estimated Marginalized Means (EMM) and standard errors (SE) are given for species richness Generalized Linear Model (GLM) for the winter 2023 census. Microsite nested in site was used as a predictor. To reduce collinearity in microclimatic variables of the model, only temperature served as a covariate. Post-hoc p-values are given and bolded if significant.

Site	Microsite	Contrast	emmean	SE (±)	asymp .LCL	asymp. UCL	p-value
Carrizo_4	Ephedra californica		**1.29**	0.15	0.82	1.75	
Carrizo_4	square		**1.56**	0.13	1.16	1.97	
Carrizo_4	triangle		**1.73**	0.12	1.35	2.11	
Carrizo_soda_open	open		**1.22**	0.15	0.77	1.68	
Carrizo_soda_open	square		**1.25**	0.22	0.57	1.93	
Carrizo_soda_open	triangle		**1.41**	0.19	0.83	1.99	
Tecopa_open	open		**0.63**	0.24	-0.10	1.37	
Tecopa_open	square		**-0.04**	0.58	-1.82	1.74	
Tecopa_open	triangle		**-1.64**	1.07	-4.94	1.66	
Tecopa_shrub	Larrea tridentata		**0.17**	0.24	-0.57	0.91	
Tecopa_shrub	square		**0.04**	0.32	-0.95	1.03	
Tecopa_shrub	triangle		**-0.09**	0.27	-0.92	0.75	
Carrizo_4		Ephedra californica - square	-0.28	0.19	-0.86	0.31	0.3170
Carrizo_4		Ephedra californica - triangle	-0.44	0.18	-1.01	0.13	**0.0432**
Carrizo_4		square - triangle	-0.17	0.17	-0.68	0.35	0.576
Carrizo_soda_open		open - square	-0.02	0.26	-0.82	0.77	0.995
Carrizo_soda_open		open - triangle	-0.18	0.23	-0.90	0.53	0.707
Carrizo_soda_open		square - triangle	-0.16	0.28	-1.03	0.70	0.832
Tecopa_open		open - square	0.67	0.62	-1.25	2.59	0.527
Tecopa_open		open - triangle	2.27	1.09	-1.07	5.61	0.09
Tecopa_open		square - triangle	1.60	1.21	-2.13	5.32	0.384
Tecopa_shrub		Larrea tridentata - square	0.13	0.38	-1.04	1.31	0.0937
Tecopa_shrub		Larrea tridentata - triangle	0.26	0.36	-0.84	1.36	0.0748
Tecopa_shrub		square - triangle	0.13	0.40	-1.11	1.36	0.945