

**AN EXAMINATION OF FACILITATIVE INTERACTIONS BETWEEN SHRUBS AND  
LOCAL DESERT ORGANISMS WITHIN THE DESERT ECOSYSTEMS OF  
SOUTHERN CALIFORNIA**

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## ABSTRACT

In recent decades, facilitative interactions have been the focus of ecological studies, specifically those with foundational shrubs within drylands. However, little has been done to analyze how the density of shrubs influence the frequency of these interactions. Here, I aim to establish shrub density as a crucial measure in ecology and facilitative interactions.

I begin with a systematic review and meta-analysis (Chapter 2) to quantify the current understanding of shrub density on local animal abundance. A full text review of shrub density and animal abundance was conducted with 113 unique observations utilized in the meta-analysis. Shrub density positively predicted animal abundance, specifically within grassland and desert ecosystems.

I conducted a greenhouse experiment to examine the effects of temperature on native and invasive plant species germination (Chapter 3). Temperatures were manipulated to simulate cooler microclimates and high temperature extremes. Increasing temperatures reduced germination, establishment, and biomass of all plant species, with the invasive species suffering more than natives.

I conducted a telemetry experiment to determine the effects of shrub densities on an endangered species (Chapter 4). Telemetry data was combined with satellite-based counts of shrub density. Increasing shrub densities positively predicted the presence of *G. sila* individuals above ground.

A field experiment comparing high and no shrub densities across aridity ecosystems in Southern California was conducted (Chapter 5). Camera traps were used at distinct ecosystems across southern California to determine vertebrate association. Areas of high shrub density

influenced the richness and evenness of vertebrate species, while increasing temperatures negatively impacted vertebrate abundance, richness, and evenness.

Finally, I tested if facilitative associations could be replicated with artificial structures (Chapter 6). Mimics were deployed within California drylands. Camera traps were utilized to estimate vertebrate communities, with temperature pendants used to contrast microclimates. Shrubs and mimics had similar microclimates, reducing the temperature underneath their canopy. Mimics displayed a higher vertebrate abundance and richness than open areas.

These findings illustrate that facilitation between shrubs and dryland communities are crucial interactions. These findings suggest that shrub density is a critical measure, increasing the likelihood of interactions and possible benefits associated with shrubs.

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## CHAPTER 1: GENERAL INTRODUCTION

### 1.1: FACILITATION BETWEEN PLANT AND ANIMAL SPECIES

The biodiversity of ecosystems can be significantly influenced by plant-animal interactions. These interactions can enhance the overall natural system through beneficial ecological functions (Tilman et al. 2014, Lortie et al. 2021), or may have negative impacts such as the enhancement of invasive species (Lucero et al. 2019). Plant-animal interactions are evident globally in all ecosystems ranging from interactions where all participating individuals benefit to those with mixed net effects. However, within dryland ecosystems, facilitative interactions are more frequently observed. Facilitation, which can also be known as commensalism, is defined as non-trophic interactions between individuals where one of the interacting species has a positive benefit, while the other remains unaffected (Bertness & Callaway 1994; Kikvidze & Callaway 2009; Kéfi et al. 2016; Molina-Montenegro et al. 2016). In dryland ecosystems, these types of interactions often occur at higher frequencies as the associated benefits increase species survival (Holzaphel & Mahall 1999, Stachowicz 2001). It has been proposed that without these interactions, harsh conditions within an ecosystem can have detrimental effects on both plant and animal survival (Holzaphel & Mahall 1999; Lortie et al. 2016). In addition, the increasing severity of climate events, such as mega-droughts, can further the reliance on these facilitative interactions within harsh dryland ecosystems (Callaway et al. 2002; Westphal et al. 2016; Dangles et al. 2018). Understanding the relative importance of these facilitative interactions between species can provide meaningful insight into the community composition and distribution within ecosystems.



## 1.2: FOUNDATIONAL SPECIES

Within these dryland ecosystems, some species can provide these facilitative interactions at a much higher frequency. These species that provide facilitative benefits are known as foundational species. Classifying a species as foundational requires several criteria including: (1) they both abundant and comprise most biomass in an ecosystem, (2) they are at or near the base of interactions, and (3) have an abundant connection to several other plant and animal species (Ellison 2019). In the desert ecosystems of Southern California, the shrub species *Ephedra californica* acts as a foundational species that mediates positive interactions (Lortie et al. 2016; Filazzola et al. 2017). *Ephedra californica* is the dominant foundational plant species in several dryland ecosystems across Southern California (Figure 1.1; Lortie et al. 2018, Filazzola et al. 2018). These shrubs act as keystone species, species that are in high abundance within an ecosystem aiding in the maintenance and biodiversity of the habitat, allowing for facilitative interactions to occur (Bond 1994; Soulé et al. 2005; Filazzola & Lortie 2014; Lortie et al. 2018). Direct positive interactions from these shrubs influence animal communities through various mechanisms including acting as a food source (Parmenter & MacMahon 1983; Auger et al. 2016), providing shelter from potential predators (Greenfield et al. 1989, Vázquez et al. 2009, Lortie et al. 2018), and aiding thermoregulation (Noble et al. 2016, Westphal et al. 2018; Ivey et al. 2020; Zuliani et al. 2023). Specifically, the microclimate under these foundational shrubs is more advantageous for proper thermoregulation and provides thermal refuge from harsh abiotic conditions (Ivey et al. 2020, Zuliani et al. 2021). These mechanisms can drastically impact the survival of a species and influence local animal associations, thus impacting local community composition (Hughes 2012, Rey et al. 2018). These shrub species can provide critical resources

within dryland ecosystems, acting as foundational species and positively influencing the structure and composition of both plant and animal species.



**Figure 1.1:** *Ephedra californica* individual within the Carrizo Plain National Monument, California, USA.

### 1.3: UTILIZATION OF FOUNDATIONAL SHRUBS BY PLANT AND ANIMAL SPECIES

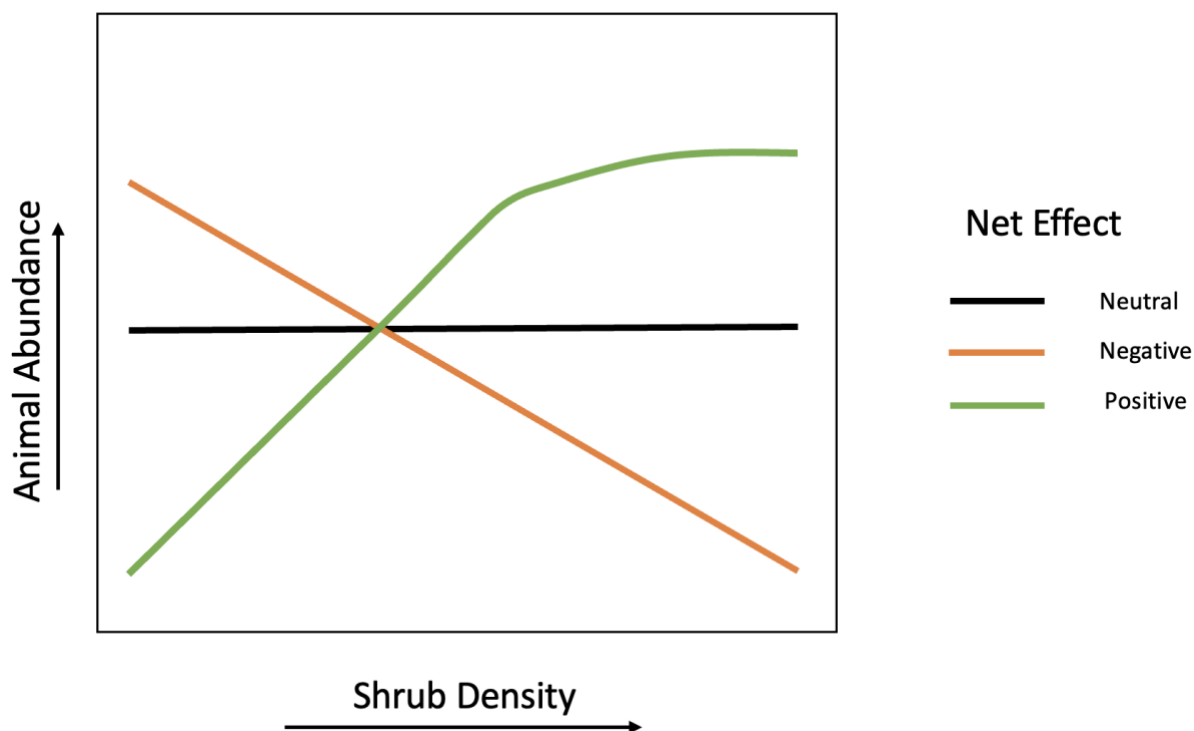
Federally endangered species, such as *Gambelia sila*, the blunt-nosed leopard lizard, utilize these positive associations with shrubs to increase their survival. These benefits are then indirectly reciprocated by animal species through the dispersal of seeds and consumption of species that are harmful to shrubs (Vázquez et al. 2009, Lortie et al. 2016). This endangered species utilizes these shrubs to reduce harsh abiotic conditions during peak seasons and as a hunting ground for herbivorous invertebrate and vertebrate species (Ivey et al. 2020; Zuliani et al. 2023). These shrubs also benefit native and invasive plant species under their canopies through reducing heat stress by shading and increasing soil moisture (Badano et al.2016;

Filazzola et al. 2018; Lucero et al. 2019; Filazzola et al. 2020). Invasive plant species, such as *Bromus rubens*, *Bromus hordeaceus*, and *Schismus barbatus*, positively associate with foundational shrub species, while negatively impacting annual communities by outcompeting for resources (Lucero et al. 2019). In particular, *B. rubens* is a highly invasive species that is able to quickly outcompete most annual plant species. This species rapidly invades large portions of the Southern California deserts, such as the Carrizo Plain National Monument, quickly dominating local plant communities, outcompeting them for nutrients and light, while also altering microhabitats (Abella et al. 2012). The benefits seen with facilitative interactions promote the success of these invasive species showing the potential dark side of this type of interaction (Simberloff 2006; Lucero et al. 2019). However, these foundational shrubs provide the same direct benefits to native plant communities through temperature amelioration, seed trapping, and herbivory protection, thus increasing the biomass of understory vegetation (Bullock & Moy 2004; Lortie et al. 2018, Filazzola & Lortie 2014). The positive benefits experienced by local animal and plant species are directly linked with the density-dependent associations seen with *E. californica* individuals.

#### 1.4: DENSITY AS A TOOL FOR ECOLOGICAL ASSESSMENT

Density is a simple measure well established in competition theory with plants (Antonovics & Levin; 1980) and animal species (Adams & Walters 1995), however, it is typically under-reported, if not completely overlooked in facilitation studies. Shrub density itself is defined as the number of woody shrub individuals within a specified area, such as the number of shrubs within a 20 m radius (Martínez-Cabrera et al. 2009; Zuliani et al. 2021). Shrub density can influence inter and intraspecific interactions between plant and animal communities

(Springer et al. 2003; Tietje et al. 2008; Zuliani et al. 2021). Since foundational shrub species interact with local plants and animal species (Hughes 2012), the density of these shrubs can influence local population dynamics. This increase in shrub density can be utilized to predict the presence of organisms while also increasing the probability of facilitative interactions (Zuliani et al. 2023). Within shrub-animal and shrub-plant interactions, the density of these foundational shrub species can positively influence the net outcome of interactions with other species (Figure 1.2; Springer et al. 2003; Tietje et al. 2008). Over time, areas with a relatively low number of shrub individuals will increase in density and overall shrub size (Musick et al. 1998). This phenomenon is known as shrub encroachment, where there is an increase in woody and/or shrub plants resulting in significant changes in total vegetation cover (Van Auken 2009; Eldridge & Soliveres 2015). While this increase in shrub vegetation is beneficial for woody plant species, typically the herbaceous layer of the ecosystem is negatively impacted by a decrease in abundance (Van Auken 2009; Maestre et al. 2016). Shrub encroachment typically has negative impacts on an ecosystem (Van Auken 2009), however, this increase in shrub density in shrublands can enhance these ecosystems by increasing the likelihood of facilitative interactions (Van Auken 2009; Eldridge & Soliveres 2015). Several ecosystems within Southern California benefit from this encroachment as it is reconverts arid grasslands back into their original shrubland ecosystems (Browning 2008). This reversion to shrubland can increase the abundance and richness of species as the total density of these facilitative shrubs increase (Browning 2008; Zuliani et al. 2021).

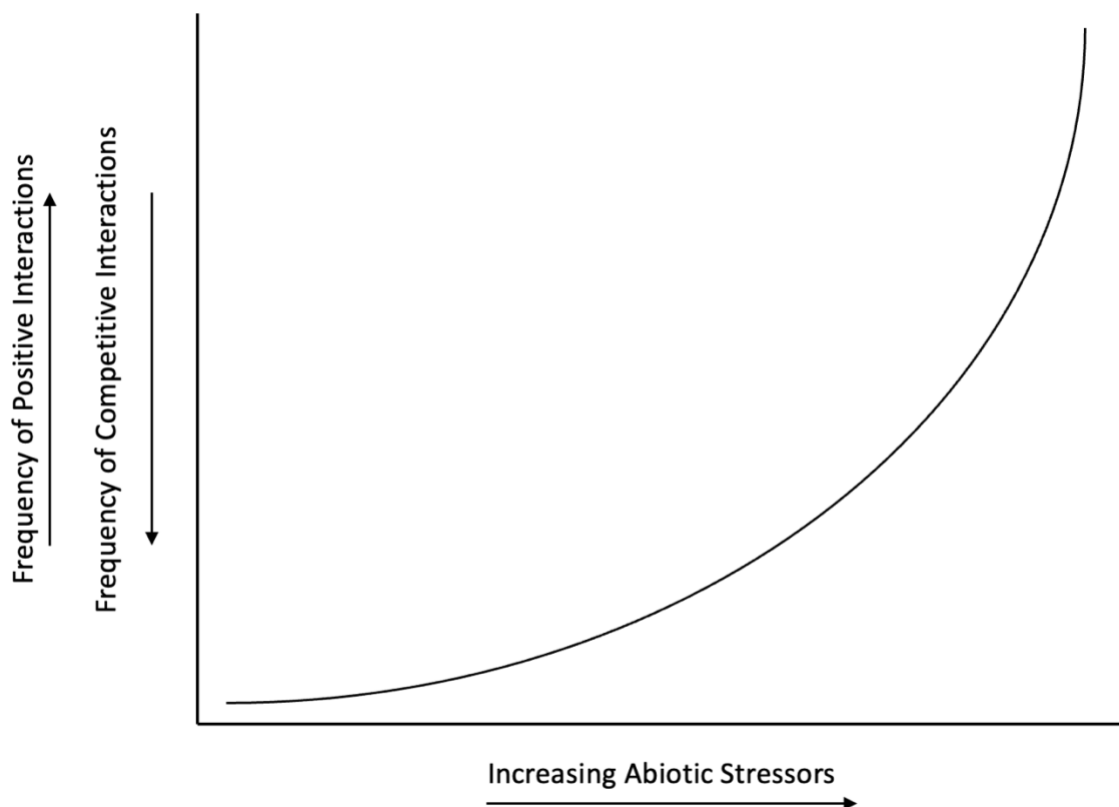


**Figure 1.2:** The proposed theoretical outcomes for increasing shrub density on animal abundance. Three possible net effects are proposed; 1) as shrub density increases within an ecosystem, animal abundance remains unaffected, 2) as shrub density increases within an ecosystem, animal abundance begins to decrease, 3) as shrub density increases within an ecosystem, animal abundance will begin to increase and eventually reach a critical threshold before leveling off.

### 1.5: ABIOTIC STRESSORS WITHIN DESERT ECOSYSTEMS

Abiotic environmental stressors negatively impact both plant and animal species within their respective ecosystems. These stressors are typically defined by abiotic features of an ecosystem, such as extreme temperatures, total precipitation, wind speed, and UV intensity (Lortie et al. 2016; Westphal et al. 2018; Moore et al. 2018). These conditions in high-stress environments have substantial impacts on the survival and behaviour of species. Many local desert species rely on the amelioration of these high-stress conditions through facilitation interactions with foundational species (Ivy et al. 2020). This concept of organisms utilizing more beneficial interactions is one of the primary concepts associated with the Stress Gradient

Hypothesis, SGH (Bertness & Callaway 1994). According to this hypothesis, when high-stress environmental factors are present, species will alter the behaviour and interactions between organisms (Bertness & Callaway 1994; Butterfield et al. 2016). In these situations, there will be a decrease in competitive interactions, while positive interactions, such as mutualism, commensalism, and facilitation, will increase in frequency (Figure 1.3; Turner et al. 1966; Bertness & Leonard 1997). However, with this reduction in competition and increase in positive interactions, the overall biomass and productivity of organisms will decrease as the total amount of resources utilized by individuals is reduced from these positive interactions (Bertness & Leonard 1997; Hart & Marshall, 2013; Dangles et al. 2013). While these individuals may have reduced biomass and productivity, their overall survival will be much higher as they are now depending on both inter and intraspecific interactions to survive (Bertness & Leonard 1997). Since climate is a high-impact abiotic stressor on ecosystems, greater emphasis has been placed on facilitative interactions that could aid both plant and animal communities (Brooker et al. 2007; Dangles et al. 2018).



**Figure 1.3:** A theoretical representation of the stress gradient hypothesis in terms of increasing positive interactions. As harsh abiotic conditions become more frequent and intense, both plant and animal species become reliant on positive interactions such as facilitation, mutualism, and commensalism. However, once the high abiotic stressors are reduced or are less frequent, more competitive interactions are observed.

#### 1.6: CURRENT WORK: ASSESSING THE POTENTIAL IMPORTANCE OF SHRUB DENSITY WITHIN ECOLOGICAL STUDIES

While measurements, such as shrub cover, are predominantly utilized in ecological assessments, the total number of available resources is typically under-reported or completely ignored. Shrub density can prove to be a vital measurement in ecological assessments for predicting animal presence, determining community composition, and in restoration practices. To address this gap in knowledge, this dissertation comprises a substantial examination of the importance of foundational shrub species, and also how the density of these species can have vital impacts on local desert communities. I begin with a systematic review and meta-analysis to

investigate the potential use of shrub density as a predictive measurement for animal abundance (Chapter 2). This review provides the foundation for the studies that follow as it sets the framework that shrub density can be utilized in ecological assessments. Within this meta-analysis, I found evidence that suggests shrub density influences animal abundance within dryland ecosystems, particularly those designated as desert and grasslands.

Building on the insights gained from the review, Chapter 3 presents an empirical greenhouse germination study, which simulated the cooler temperatures, as experienced under shrub canopies, and high temperature extremes of open areas. This chapter emphasizes that increasing cover, and increasing shrub density, provides cooler microclimates that would be more beneficial for early-life stage processes of desert annual species. Chapter 4 continues to build on the concept of shrub density by utilizing it as a tool to predict the presence of an endangered species of lizard, *Gambelia sila*. Utilizing a combination of radio telemetry and satellite data, a relationship between shrub density and *G. sila* presence was determined. Continuing previous work from 2021 (Zuliani et al. 2021), Chapters 5 and 6 were conducted in-field to determine if shrub density would influence desert animal communities. Chapter 5 primarily focused on assessing the differences between high shrub density and no density plots across several dryland ecosystems in Southern California. Areas of higher shrub density displayed significantly higher vertebrate abundance, richness, and evenness compared to areas with no shrubs. In chapter 6 I furthered this idea by introducing artificial shrubs to dryland ecosystems across Southern California to determine if these structures could ‘mimic’ the facilitative effects of foundational shrubs at areas of varying shrub densities. Artificial shrubs displayed similar microclimates to foundational shrubs and had significantly higher abundance, richness, and evenness of vertebrate species.



**CHAPTER 2: A META-ANALYSIS OF SHRUB DENSITY AS A PREDICTOR OF ANIMAL ABUNDANCE**

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## 2.1 ABSTRACT

Facilitative interactions between shrub and animal species influence the structure and composition of communities. The benefits associated with woody shrub species can critically influence local animal populations, in particular. Here, I tested the relative importance of the density of shrub species on the local abundance of animal populations using a meta-analysis. Full-text review for shrub density, animal abundance or density, and sampling effort, resulted in a total of 113 independent observations that reported both shrub density and animal abundance. A meta-regression of shrub density on animal density with feeding functional group of the animal species as a moderator was used to test the predictive capacity of this simple vegetation measure on animal populations. Shrub density positively predicted animal abundance in these studies – particularly in deserts and grasslands. Shrub and woody plant density can thus be used as a potential rapid proxy for habitat in predicting local animal abundances. This method can support restoration and conservation of resident animal species in impacted ecosystems structured by woody shrubs globally.

## 2.2 INTRODUCTION

The measure of animal abundance in ecological studies is a fundamental tool used both at local and landscape levels. Many ecological disciplines strive to create models and frameworks to better understand and predict the abundance-environment relationship (Lancaster and Belyea 2006). There are several different characteristics that ecologists can use to describe the population dynamics, including abundance-environment relationship (Ferguson et al. 2000; Lancaster and Belyea 2006; Walker 2011). There are several different characteristics that ecologists can use to describe population dynamics (Ferguson et al. 2000; Walker 2011).

Density is a direct measure that can be used to predict the net abundance of a species in many ecosystems. In ecology, density is defined as the number of organisms per unit area (Lyon 1968), whilst abundance is defined as the number of animals in a reported study (Lawton 1993). Unlike density, abundance does not include a measure of the species' geographic area but that does not mean it is independent of the size of the area where species are recorded (Lawton 1993). The practice to use density has previously been used to determine community structure in population-based studies (e.g., Antonovics & Levin, 1980; Adams & Walters 1995). Many ecological frameworks use density as a measure to describe the relationship between the abundance and distribution of species relative to physical and abiotic environmental variables (Brown 1984). Often with ecological studies involving telemetry and cam trapping, abundance but not density is reported because the spatial extent of site sampled is not generally provided. Density can also provide insight into trophic interactions (e.g., Nilsson 2001; Laundré & Hernández 2003; McPeck 2019). The density of both plant and animal species directly relates to density-dependent associations which have been shown to regulate population growth rates (Ray & Hastings 1996; Jenkins et al. 1999). In plant-animal associations, plant density can further influence the net outcome of animal associations from positive to negative thereby shaping community composition across different ecosystems (Springer et al. 2003). In arid ecosystems such as scrublands, increasing levels of shrub density has a net positive influence on species abundance because relatively smaller animals use these areas for habitat and shelter from predation (Nelson et al. 2007; Filazzola et al. 2017; Lortie 2020), as a refuge (Valone & Balaban-Feld 2019), as a food source (Lortie 2020), and reduce harsh abiotic conditions (Ivey et al. 2020). In ecosystems characterized by relatively stressful environmental factors, these

shrubs can support behavioral thermoregulation of individual animals (Westphal et al. 2018; Ivey et al. 2020). With higher shrub densities, the frequency that animals use these shrubs has been shown to increase as the associated benefits through facilitative interaction become more prevalent in arid and semi-arid ecosystems (Zuliani et al. 2021). This has a positive contribution to the overall health of the ecosystem through the reversal of desertification (Maestre et al. 2009; Sirami et al. 2009). Variation in shrub densities will thus impact local animal species in ecosystems supporting a more diverse set of trophic and non-trophic interactions.

Interacting individuals can experience both negative and positive associations with other organisms. These positive associations are typically the main focus of many plant-plant studies (Stachowicz 2001; Kikvidze & Callaway 2009; Van der Merwe et al. 2021); however, positive plant-animal associations are more recently being examined (Vázquez et al. 2015; Westphal et al. 2018; Zuliani et al. 2021). Facilitation is a non-trophic interaction between species where one individual benefits, while the other is unaffected (Montenegro et al. 2016). Shrub species, such as *Ephedra californica* (Mormon tea) and *Caragana korshinskii* (Korshinski pea shrub), can act as foundational species as they are the source of beneficial interactions with both plant and animal species (Bittick et al. 2019, Lortie et al. 2020). The density of shrub species can influence the associations seen by animal species (Zuliani et al. 2021), increasing both direct and indirect associations (Adams & Walters 1995), allowing for more complex trophic interactions and influencing overall animal abundance (Schneider et al. 2016). These facilitative interactions play a defining role in various ecosystems worldwide (Callaway 2007; Verwijmeren et al. 2013), as they provide environmental benefits through microclimatic buffering (Kefi et al. 2008), providing refuge for animals during extreme conditions by lowering

the amplitude of environmental variation (Holzapfel & Mahall 1999; Fillazola et al. 2017). With the importance of shrub density and their corresponding facilitative interactions playing a crucial role in community composition, this variable can be used as a potential predictor of animal density and abundance in varying ecosystems.

In this study, I conducted an in-depth systematic review and meta-analysis of the peer-reviewed literature to test if shrub density can directly predict or influence reported animal abundance. I also propose that this relationship between density and animal abundance is ecosystem-specific. The purpose of this review is to connect shrub density to animal abundance, as it could prove to be a key tool for managers and conservation specialists who work to preserve animal populations in distributed regions.

## 2.3 METHODS

### *Literature Review*

To explore the use of shrub density as an indicator for animal abundance and density, I surveyed the literature using a combination of the keywords: 1) “density”, “abundance”, “facil\*”, “shrub”, AND “animal”, 2) “density”, “facil\*”, “abundance”, AND “shrub”, 3) “density”, “abundance”, “shrub”, in the Web of Science database (Web of Science 2021). I used these combinations of keywords to conduct an additional search on Google Scholar to validate listed articles from Web of Science in June 2021. A total of 532 articles were screened for their potential inclusion in our meta-analysis. A PRISMA diagram was generated to illustrate the inclusion process (Moher 2009) (Appendix A Figure A1). The main text of the articles was screened using the following criteria: (1) interaction between shrub species and local animals reported, (2) sample area(s) were defined, (3) shrub density and animal abundance reported,

and (4) total study duration reported. Studies that included all criteria with the exception of a recorded shrub density or animal abundance were not included in this review as they did not provide any quantifiable data that could be used. Nonetheless, all relevant studies that examined this topic directly were summarized (Appendix A; Table A1). Techniques listed were categorized based on the type of experimental procedure outlined within the literature. Studies that used a combination of techniques were categorized as methodological.

Densities were recorded for all woody shrubs and animal species. A common unit of shrub density was derived by converting all observations into one common unit (number of individuals per km<sup>2</sup>). Animal abundance was recorded for each incorporated study as the number of individuals per unit area. The method used to determine shrub density and animal abundance for each candidate study was recorded (Appendix A; Table A1). Reported animal species were then also classified into feeding functional groups (FFG) based on a specific diet of the species (Cummings et al. 2005; Sundstorm et al. 2012; Nash et al. 2015). Categories included detritivore, omnivore, carnivore, insectivore, herbivore, and nectarivore (although sensitivity to both simpler classification schemes and more complex ones were also tested). Each reported observation of both shrub density and animal abundance was then recorded as an independent observation. The identity of the focal shrub and animal species was recorded from each instance. The total duration of the study (number of days) was also recorded. Studies reporting the number of years conducted were converted into days. The ecosystem of each study was recorded for all studies summarized in the systematic and in studies that reported quantitative data amenable for the meta-analysis. All collected systematic review data is available at Figshare (Zuliani et al. 2022).

### *Meta-Analysis*

All statistical analyses were done using R version 4.2.1 (R Core Team, 2022). Data are available on The Knowledge Network of Biocomplexity (Zuliani 2021). Effect sizes were calculated using the reported density of target shrub species and overall animal abundance, each acting as an independent variable. The *escalc* function from the *metafor* package was used to estimate the incidence rates by dividing the shrub densities by the number of days (Viechtbauer 2010). The *metafor* package was also used to conduct a random-effect meta-regression to analyze estimated values of the animal abundance and shrub density (Viechtbauer 2010). The meta-regression was weighted by the duration of each study (number of days), and feeding functional group was included as a moderator /covariate in meta-analysis. The Maximum likelihood (ML) method was used to estimate the animal abundance in relation to shrub density, in combination with a Knapp-Hartung Method (KNHA) test, with ecosystem set as a moderator (Hartung & Knapp, 2001). The heterogeneity of all models was examined using Cochran's Q test (Cochran 1950) to ensure that the variance in data was not a result of inflation from grouping (Langan et al. 2019; Page et al. 2021).

## 2.4 RESULTS

### *Systematic Review*

A total of 753 articles were obtained through the search of the previously outlined keywords (Appendix A, Figure A1). After a full-text review, a total of 113 unique observations including shrub density and animal abundance were extracted. The most common ecosystem

recorded amongst collected studies was desert at 75% of the observations, and grassland comprised the remaining 25% of observations. Amongst the 45 studies included in the systematic review, 82% recorded indirect interactions between shrubs and animals while 18% recorded direct interactions (Appendix A; Table A1). The systematic review of all relevant studies showed that the technique used to estimate the shrub densities in this body of literature included the following: telemetry, survey, experimental, methodological, and restoration (Appendix A; Table A1). Methodological was defined as studies that used a combination of 2 or more techniques. These techniques associated with ecosystem classification varied in frequency. Visual surveys were commonly used in deserts but were also used in alpine and savanna ecosystems (Appendix A; Figure A2). Studies within forest ecosystems used 4 of the 5 techniques with the exclusion of restorative practices (Appendix A; Figure A2). Studies in alpine, grassland, and mixed ecosystems used a variety of sampling techniques to observe facilitative associations (Appendix A; Table A1; Figure A2). Three unique shrub species were observed for their effects on animal abundance including; *Ephedra californica*, *Caragana korshinskii*, and *Caragana microphylla* (Table A1). All recorded animal species were native to the ecosystems tested.

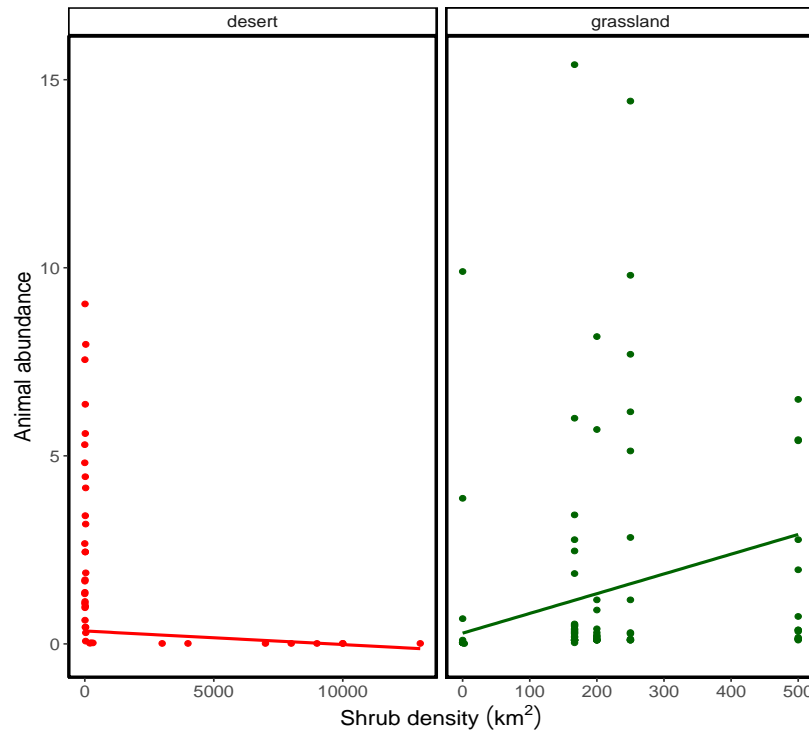
### *Meta-Analysis*

Shrub density positively predicted the incidence rate of animal abundances in meta-regression (Figure 2.1; Estimate =  $1.97 \pm 0.28$ ,  $df = 108$ ,  $p < 0.0001$ ), and feeding functional group was a significant moderator (Appendix A; Figure A3;  $R^2 = 23.01$ ,  $p < 0.001$ ). The identity of shrub species was also important in this synthesis ( $F = 18.61$ ,  $df = 3$ ,  $p < 0.0001$ ). The shrub species *Caragana korshinskii* had positive effects on animal population densities while *Ephedra*

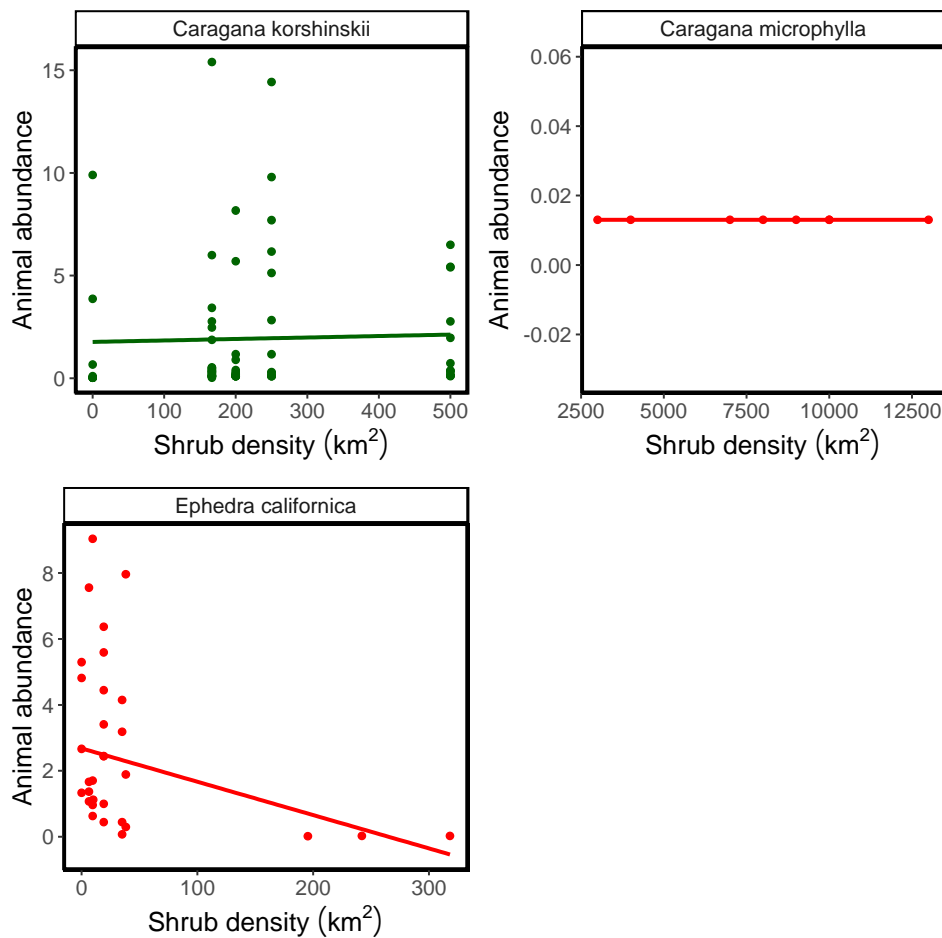


*californica* negatively impacted animal abundances (Figure 2.2; heterogeneity  $p < 0.0001$ ).

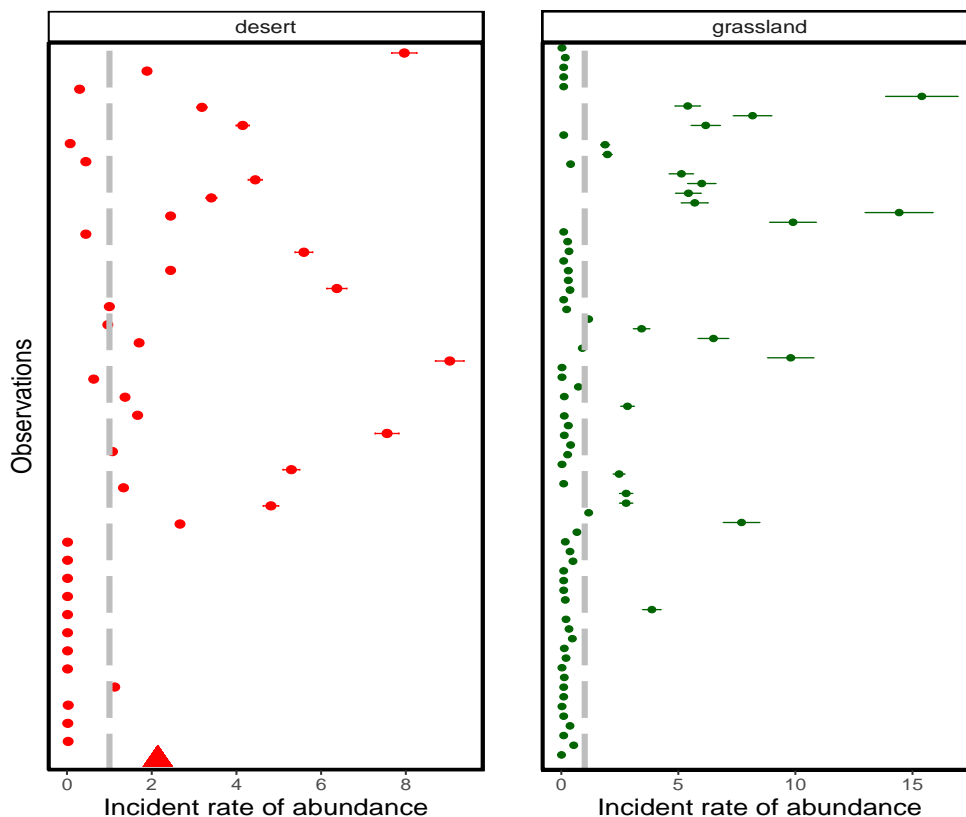
Ecosystem was a significant moderator of animal abundance (Figure 2.3;  $F = 24.66$ ,  $df = 2$ ,  $p < 0.001$ ). Specifically, shrub density positively influences reported animal abundance in grasslands, but negatively influenced animals in deserts (Figure 2.1;  $p < 0.0001$ ).



**Figure 2.1:** Meta-regression plot depicting the relationship between shrub density (individuals/km<sup>2</sup>) and animal abundance (number of individuals) in 2 different ecosystems. Smooth conditional means are fitted using a random-mixed model using the method maximum likelihood and are weighted by the number of days.



**Figure 2.2:** A meta-regression depicting the relationship between shrub density (individuals/ $\text{km}^2$ ) and animal abundance (number of individuals) amongst 3 different shrub species. Colored points represent the ecosystem with green depicting grasslands and red depicting deserts.



**Figure 2.3:** Forest plot showing the estimated effect size from random-mixed model outputs for animal abundance/number of days in 2 different ecosystems of study. Triangles represent the grand mean for each ecosystem. Colored dots represent meta-analytic mean while lines represent the 95% confidence interval.

## 2.5 Discussion

The use of woody plant densities as a predictor of animal abundance can be a critical tool in simply estimating the habitat relevant to the density of resident, native animals in many ecosystems. In this synthesis, shrub species, ecosystem, and feeding functional group of animals were all relevant moderators of this measure of habitat. Nonetheless, shrubs are crucial resources within desert and grassland ecosystems in describing a key habitat proxy. The shrub species *Caragana korshinski* and *Ephedra californica* significantly influence animal

abundance within their ecosystems further depicting the relationship between shrubs and local animal communities.

Studies used in this meta-analysis, such as Westphal et al. (2018) and Zuliani et al. (2021) test if shrub species in arid ecosystems have an impact on animal associations by examining overall shrub density. The keywords included in both systematic review and meta-analysis were specific to better support evidence-based conservation with woody shrubs. Therefore, with the limited studies, this may be an emerging field of study that will further develop. Nonetheless, the techniques used in these types of studies varied depending on the taxa of the target species. Studies focusing on vertebrate species exclusively, used techniques, such as telemetry and surveys (Filazzola et al. 2017; Westphal et al. 2018). The use of telemetry tracking and animal surveying methods allows for aid in the determination of species abundance, distribution, and habitat utilization (Westphal et al. 2018; Lortie et al. 2020). Studies that used a combination of camera traps and transects to record species abundance are likely a next-generation approach to estimating species abundance and overall density within an ecosystem (Lancaster & Belyea 2006; Iijima 2020; Zuliani et al. 2021). Specifically, the use of camera traps as a means of recording the abundance of unmarked animals has become increasingly useful and prevalent in recent years (Gilbert et al. 2020; Bengsen et al. 2022; Haucke et al. 2022). These methods are typically used to determine the mean number of individuals for many species within an ecosystem whilst also providing insight into the local community composition through inferences of species co-occurrence patterns when deployed at specific habitats (Gilbert et al. 2020; Zuliani et al. 2021). Often when density of shrub species is examined associating animal species are unreported, the abundance of animal individuals is

not listed, and sampling extent is not evident in the study. These are critical research gaps in shrub-animal associations that will better inform conservation and restoration practices if reporting practices are improved.

While these methods would be ideal for recording vertebrate species abundance, only a generalized estimate of invertebrate abundance can likely be determined. In order to properly estimate invertebrate abundance, a combination of methodologies including, pitfall traps, pan traps, and sweep netting, are used (Corti et al. 2013; Spafford & Lortie 2013). Studies such as Liu et al. (2017), included in this meta-analysis, using a methodological technique including pitfall traps to best estimate the overall abundance of invertebrate individuals in shrubbed areas. It is therefore critical for the appropriate techniques to be used when recording species abundance based on the phylum of that species.

The beneficial associations between shrub species and local animal communities suggest that interactions occur at higher frequencies in areas with a higher shrub density than in areas with little to no individuals (Zuliani et al. 2021). This higher frequency of interactions will allow for more beneficial associations to occur and thus will positively impact both plant and animal species. Many of the studies used in this meta-analysis show foundational shrub species and various animal species that associate with them (Westphal et al. 2018; Zuliani et al. 2021). These foundational plant species are individuals who play a pinnacle role in the association of animal species and can support various ecosystem functions (Filazzola et al. 2020, Zuliani et al. 2021). Foundational shrub species, such as *Ephedra californica*, facilitate these beneficial interactions with various species (Westphal et al. 2018; Braun et al. 2020), while also buffering extreme environmental conditions such as solar radiation, temperature, and wind

(Pugnaire 2010; Ivey et al. 2020). While these foundational plant species can prove to be beneficial for native communities, the promotion and growth of various invasive species can occur, thus potentially degrading local ecosystems and negatively impacting native species (Lortie et al. 2021). Invasive species, such as *Bromus rubens*, positively benefit from foundational shrub species which can exacerbate biological invasion (Lucero et al. 2019; Lortie et al. 2021). The promotion of invasive species through these positive associations can potentially lead to natives being outcompeted for habitat and resources (Lortie et al. 2021). With the influence foundational plants have on both plant and animal species, it can be extrapolated that the density of these shrub species could have a potential role in both native and invasive succession in arid ecosystems. Therefore, shrub density can allow for these associations to occur, while also serving as a potential proxy for predicting animal abundance.

Associations between foundational species with local plant and animal individuals can be seen through various direct and indirect mechanisms. In particular, facilitative interactions can play a pinnacle role in various ecological communities, thus influencing the overall composition of local animal species. This association could be explained by several mechanisms associated with foundational species. These shrub species can positively associate with animals through; acting as a refuge (Valone & Balaban-Feld 2019), temperature amelioration (Westphal et al. 2018; Ivey et al. 2020), predation avoidance (Filazzola et al. 2017), augmentation of resources through seed trapping (Bullock & Moy 2004), and production of fruit (Hertel et al. 2018). Having a higher availability of shrub species in an area can further amplify these benefits to animals as these resources are made more abundant and accessible (Auger et al. 2016; Zuliani et al. 2021). However, the utilization of these shrubs varies depending on the specific

taxa a target species belongs to. Invertebrate species, specifically herbivores, use these benefits both by consuming shrubs and understory vegetation (Derraik et al. 2005). Some vertebrate species, specifically small rodents, have been observed to consume seeds from shrub species, further suggesting that the overall availability and abundance of resources can influence animal association (Auger et al. 2016; Valone & Balaban-Feld 2019). Vertebrate and invertebrate individuals that use shrubs to forage or provide thermal refuges would be more likely found in these high shrub density areas as shrubs serve as key habitats. Nonetheless, diet and foraging preferences for the animal species must be examined as this was a key moderator in this synthesis study. Furthermore, it is important to evaluate these density-dependent associations among multiple animal and shrub species simultaneously, while using the appropriate technique, as these individuals interact both directly and indirectly in various complex assemblages in nature. While the species that associate with these foundational shrub species may directly benefit, the probability of more complex trophic interactions increases due to the variation in community composition (Van der Putten et al. 2004). Numerous indirect feedbacks may also result from this positive association including varying foraging herbivores (Kotler et al. 1991) as well as the association of predator species (Carbone et al. 2011). Predator species, such as *Crotalus oreganus* (Northern Pacific Rattlesnake), consume smaller vertebrates (Holding et al. 2018) which use shrub species as a refuge from predators, thus impacting community composition and association. These multitrophic interactions will produce richer and more diverse associations than those seen through a single trophic level (Duffy et al. 2007). Hence, I suggest that studies looking at associations between shrub and animal species consider the density of these shrub species in their studies as it has the potential to act as a direct indicator

for animal abundance, while also influencing both trophic interactions and community composition.

## 2.6: STUDY IMPLICATIONS

This meta-analysis quantitatively supports that shrub density can predict local animal abundance in varying arid ecosystems. Specifically, shrub density should be considered when conducting ecological studies focusing on the abundance of a target animal species, and those that observe local community compositions, as it is a relatively simple variable to record and can be used to directly analyze animal associations. The feeding functional group of a species is likely relevant to how animals utilize and interact with local shrubs and other woody plant species in many ecosystems. With the current increase in desertification of arid ecosystems impacting at-risk and endangered species, the implications of shrub density on both animal associations and environmental health can prove to be a vital tool in conservation and restoration. With the decline of ecosystem health, the connection between density and animal abundance can guide restoration work by emphasizing simple ecosystem resources utilized by animal species. Studying factors influencing animal associations with shrubs can provide key insight into the restoration of these ecosystems. Our results provide new and novel insights into the use of density as it has the potential to be used for restorative and conservative practices. Based on our observations, it is evident that shrub density should be further reported in plant-animal interaction studies. It is evident from our findings that density of shrub species is not considered when observing animal abundance in the ecological literature, thus posing a major research gap. I recommend that these studies, focusing on animal abundance in arid ecosystems, consider reporting the overall density of shrub species to strengthen our current



understanding of density and its implications. In addition, our study was not meant to imply that animal species require shrub species to survive, rather it is meant to show that shrub species can be of use to local animal populations. Future research can potentially continue observing these associations to further support this theory that shrub densities can be used as a potential means to predict animal abundance.

**CHAPTER 3: A CONTROLLED TEMPERATURE CONTRAST ON THREE CALIFORNIA NATIVE AND A  
HIGHLY INVASIVE PLANT SPECIES**

Currently Under review at: Plos One

### 3.1: ABSTRACT

Plant responses to changes in temperature can be a key factor in predicting and managing invasive plant species and conserving resident native plant species in dryland ecosystems. Climate can influence germination, establishment, and seedling biomass of both native and invasive plant species. I tested the hypothesis that common native and an invasive plant species in dryland ecosystems in California respond differently to increasing temperatures. These species are widely distributed and often associated with native shrub species in dryland ecosystems. To test this, I examined the microclimatic effects of temperature on germination, establishment, and seedling biomass of three native and one invasive plant species in 6 week growth trials in a controlled greenhouse. Higher relative temperatures reduced the germination, establishment, and seedling biomass of all tested plant species. However, germination and establishment of the invasive species *Bromus rubens* was significantly reduced relative to the native species. This invasive species can often outcompete natives, but temperature can potentially shift the balance in germination and establishment. A warming climate will however negatively impact most native annual plant species in California because increasing temperatures can co-occur with drought. This study shows that native annual plant species have potential resilience to relatively significant increases in temperature and this can favor natives relative to at least one highly noxious invasive plant species.

### 3.2: INTRODUCTION

Dryland ecosystems including shrublands, deserts, and grasslands are essential to plant communities globally. These ecosystems support endemic species and thus influence global biodiversity (Sharafatmandrad & Khosravi Mashizi 2021; Lucero et al. 2022). With increasing

abiotic stressors in these ecosystems causing severe degradation (King & Hobbs 2006; Huang et al. 2020), it is imperative to determine the impacts these conditions will have on dryland plant communities. Increasing environmental abiotic stressors, such as temperature (Shah et al. 2011), drought events (Niu et al. 2006; Verwijmeren et al. 2019), and other abiotic disturbances (Potts et al. 2012), have overall negative impacts on many plant species, but can particularly tip the balance between native and invasives in dryland ecosystems. (Niu et al. 2006; Cowles et al. 2018; Moore et al. 2018). Ecosystems, such as those found in the Carrizo Plain National Monument (35.11982, -119.62853) in Southern California are highly invaded (Lucero et al. 2019), and subject to extreme weather conditions (Westphal et al. 2016; Lortie et al. 2021). The mean annual precipitation within this region can reach 25 mm, however this area can experience extensive periods of extreme drought (Prugh et al. 2018). The variation in temperatures across dryland ecosystems can strongly influence plant establishment, germination, productivity (in the form of biomass, fruiting, and flowering), and overall survival (Rivas-Arancibia et al. 2006; Ebrahimi & Eslami 2012; Hatfield & Prueger 2015). For instance, plant species can experience thermoinhibition, defined as the inability for seeds to germinate at high temperatures (Vleeshouwser et al. 1995; Hills & van Staden 2003; Toh et al. 2012), which can increase seed dormancy, preventing the initial stages of germination. This thermoinhibition gives species with larger temperature niches a significant advantage in terms of germination and establishment, by delaying germination of potential competitors (Toh et al. 2012; Silva et al. 2017). Understanding how these constantly changing dryland ecosystems influence plant species can provide key insights into community compositions and the establishment of individuals.

Most plant species' relative growth rates differ and respond uniquely to key environmental factors that signal when to grow and at what rate (Bareke 2018). There are several early life-stage performance measures associated with plant species including: germination—the appearance of an embryo through the surrounding structure (Nonogaki et al. 2010), establishment—seedlings are established typically at 2-3 weeks for most semi-arid annuals (Aronson et al. 1992; Pik et al. 2020), and seedling biomass—a proxy for future individual performance (Licznar et al. 2019; Pik et al. 2020). Temperature can influence all early-life stage measures, likely increasing all factors initially, provided there is sufficient soil moisture and nutrients. However, higher temperatures can become a stressor depending on the climate envelope of each species (Vázquez-Ramírez & Venn 2021). To ameliorate these high abiotic stressors, such as extreme temperatures, areas with more favorable microclimatic conditions, such as shrub canopies and artificial structures that provide shade, can influence plant association and establishment (Filazzola et al. 2019; Roque Marca et al. 2021; Zuliani et al. 2024). Foundational shrubs within these dryland ecosystems can act as buffers for plant species richness, reducing high temperature conditions, specifically within dryland ecosystems (Lortie et al. 2024). This suggests that plant species, within dryland ecosystems, favor conditions not directly exposed to high temperatures and can thrive in more favorable conditions (Pugnaire et al. 2024). These opportunities for stress amelioration are utilized by both native and invasive plant species (Lucero et al. 2019) and can provide more favorable early-life stage growing conditions for these species.

Invasive plant species are defined as non-native species that establish in natural ecosystems, inducing a change that threatens native biodiversity (Szumańska et al. 2021). These

species can influence the structure and composition of plant communities in ecosystems globally (Laughlin & Abella 2007; Flory & Clay 2009; Pik et al. 2020). These invasive plant species disrupt local communities through the decline and degradation of biodiversity, while negatively impacting ecosystem functions including soil fertility and water availability (Grice 2006; Maestre et al. 2016; Milanović et al. 2020). The negative impacts of invasive plants can also extend to animal communities by displacing habitats (Beck et al. 2008), reducing foraging behavior of both livestock and wildlife (Brunson & Tanaka 2011), and impeding the movement of some animal species (Stewart et al. 2021). Some invasive species are resilient to high temperatures (Clements & Ditommaso 2011) including many species in the genus *Bromus*. In dryland ecosystems, invasive plants can show resilience to drought-like conditions, displaying higher performance than native species (Ali & Bucher 2022). This extended climate envelope for some invasives can help them to outcompete natives as they have a higher probability of establishing successful populations (Bradley et al. 2013; Hou et al. 2014). Temperature changes in semi-arid ecosystems, alongside increasing drought frequency (Abatzglou & Kolden 2011; Cherwin & Knapp 2012), suggests that we need to better understand species-specificity in response to changes in temperature (Parmesan & Hanley 2015). This is important at local and regional sites in predicting if species will spread or invade into other regions when temperatures increase (Wallingford et al. 2020; Ali & Bucher 2022). Further understanding how these invasive species are impacted by their climate will provide valuable insight both for the management of these species and for predicting potential scenarios for community assembly of native versus invasive with a changing climate.

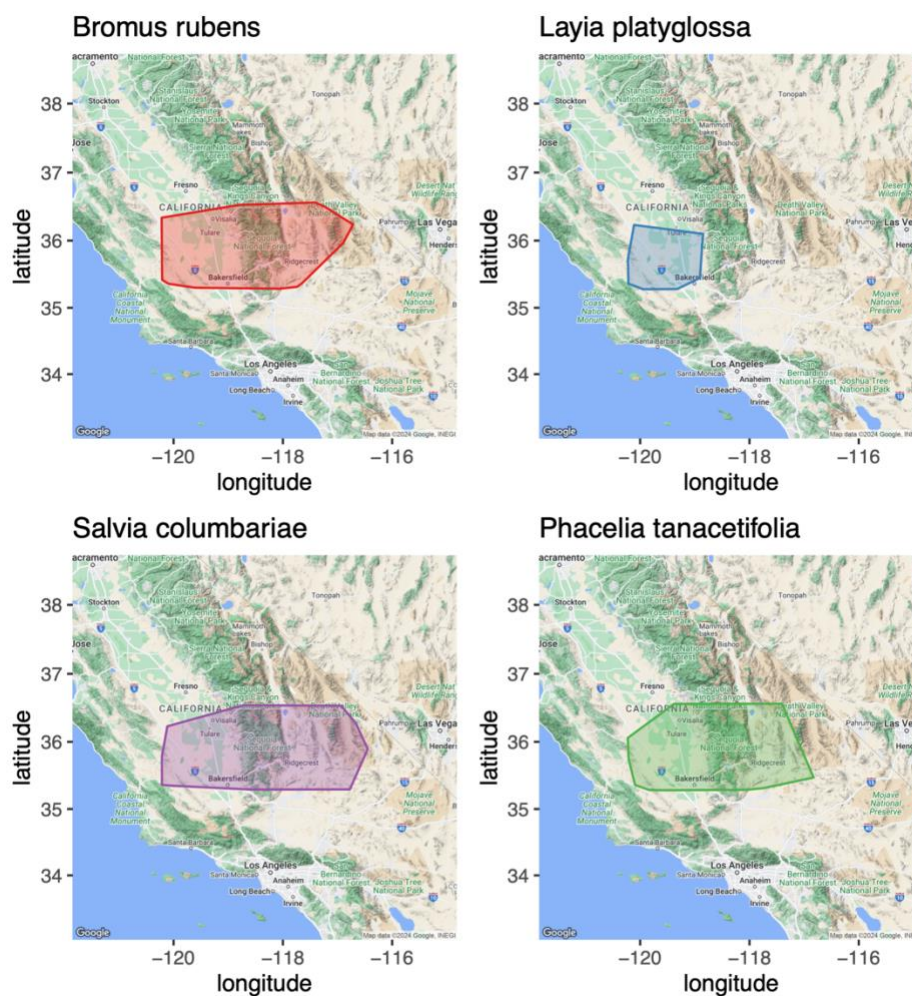
The purpose of this study is to determine if increasing temperatures influence key early life-stage plant performance measures of native and invasive plant species local to the arid/semi-arid ecosystems of Southern California. Our main semi-arid region of interest within Central and Southern California is both highly invaded and comprised of a high diversity of native species—thus understanding how variations in temperature influence these communities is key to conservation information (Lucero et al. 2022). To test this, I used a controlled greenhouse to conduct temperature trials to explore performance differences between three natives and the highly invasive species *Bromus rubens* within the region. I examined the hypothesis that temperature will directly influence key early-life stage performance measures in these semi-arid annual plant species, with their responses being highly species-specific. I tested the following predictions:

- 1) Increasing temperatures will negatively impact all plant species because higher temperatures will likely exceed their respective current climate envelopes.
- 2) The invasive brome species tested is most likely to benefit from increasing temperatures because this species has a higher temperature envelope.
- 3) Early-life stage performance for all species will be negatively impacted by high temperature exposure.

### 3.3: METHODS

A series of controlled temperature trials were conducted to test the impacts of increasing temperatures on early-life stage performances of Southern California plant species. A total of three native and one highly invasive plant species were tested independently for the duration of six weeks to determine if increasing climatic temperature would negatively influence the

germination, establishment, and seedling biomass of all individuals. GBIF data were compiled for each species located within the central drylands of Southern California to determine the climate envelope for these species from reported occurrences (Figure 3.1; Gbif.org 2023; Zuliani et al. 2024b).



**Figure 3.1:** Maps of GBIF data for each tested species across drylands within Southern California. All species tested in the greenhouse trials were selected and reported observations mapped. Colours for each species are consistent through all figures. The map was generated utilizing the R package ggmaps and images of sites were taken via satellite imagery from Google Earth TM.



### *Study Species*

*Bromus rubens* (*Poaceae*) is an annual grass species native to regions of Southern Europe, Southeast Asia, and Northern Africa (Rauber et al. 2014). *Bromus rubens* is a highly invasive species in Southern California because it is rapidly invading large portions of the Mojave, Sonora, and Great Basin Deserts, as well as semi-arid grasslands, such as the Carrizo Plain National Monument (Ogle et al. 2003; Abella et al. 2012; Curtis & Bradley 2015). This invasive species can quickly dominate local plant communities, outcompeting them for nutrients and light, while also altering microhabitats (Hamilton et al. 1999; Brooks 2000; Gioria & Osborne 2014). *Bromus rubens* typically grow to heights of 16 – 40 cm tall with a red coloration to the upper most seed-dense head and have a seed viability of approximately 95 % (Wu & Jain 1978; Jurand et al. 2013). This species germination rate is more rapid than native annuals in dryland ecosystems, as a small amount of precipitation can awaken seeds from dormancy (Salo 2004). *Bromus rubens* can survive at temperature extremes ranging from 10 – 36°C (Bykova & Sage 2012; Bykova 2014).

*Layia platyglossa* (*Asteraceae*), *Phacelia tanacetifolia* (*Boraginaceae*), and *Salvia columbariae* (*Lamiaceae*), are three native species common in various arid and semi-arid regions within Southern California (Buck-Diaz & Evens 2011). *Layia platyglossa*, also known as tidy tips, ranges in size from 45 – 60 cm, and has a blooming season ranging from March to June with temperatures ranging between 21 – 40 °C, with a potential seed viability of more than 80% (Hobbs & Mooney 1985; Christensen 2000; Marty & BassiriRad 2013). *Phacelia tanacetifolia* has an average plant height of around 42 cm and can survive late spring and early summer temperatures, having an optimal growth temperature of around 30 °C, (Yildiz 2022). *Phacelia*

species typically display a seed viability of approximately 98 % (Cavieres & Arroyo 2000). The height of *S. columbariae* ranges from 10 – 50 cm, while surviving at temperatures ranging from 20 – 35 °C, with related *Salvia* species having a seed viability of approximately 98% (Adams et al. 2005; Al-Turki & Baskin 2017; Grimes et al. 2020). These species commonly co-occur with *B. rubens* in North America (Horn & St.Clair 2017). They are of particular interest as they can be used for the restoration of other native species that have been disrupted by the invasion of *B. rubens* (Liczner et al. 2019; Arroyo et al. 2021). *Layia platyglossa*, *P. tanacetifolia*, and *S. columbariae*, are essential resources for both herbivorous species and native pollinators (Ferrero et al. 2013; Braun & Lortie 2019; Bishop et al. 2020) and may compete with *B. rubens* (Pik et al. 2020). *Bromus rubens* seeds were collected in the field within Southern California at the Wind Wolves Preserve (34.9929, -119.1832) within a 1.6 km radius. All native California seeds were purchased through Outsidepride where seeds are produced in a greenhouse setting. All seeds were ordered as needed and received within 2 days of conducting each species' seed trials. Seeds were stored in Ziplock bags and boxed to avoid direct sunlight exposure and reduce humidity exposure (Suma et al. 2013). Seeds were then kept at a constant temperature of around 8 °C. While all species tested can be found in areas outside of the drylands of Southern California, determining how increasing temperatures, in these specific ecosystems, influence early-life stages can provide insight on these species' ability to establish in more arid conditions.

### *Experimental Design*

Temperature trials were done in a climate-controlled facility in Toronto, Canada. The effects of increasing temperatures on the germination, establishment (the successful

germination and growth of an individual), and seedling biomass (the total weight of individual plants) of three California Native plant species (*S. columbariae*, *L. platyglossa*, *P. tanacetifolia*) and one invasive plant species (*B. rubens*) were tested for 6-week trials. Here, germination is defined as the visible emergence of early-stage seed development of 0.1 mm (Porceddu et al. 2013). Species were tested in 10 cm diameter pots (1400 cm<sup>3</sup> in soil volume). A total of 40 seeds for each species were sown independently approximately 5 - 10 cm below the soil surface (Lortie et al. 2022). To approximate the soil of California arid/semi-arid ecosystems, I mixed “Miracle Grow” potting soil with coarse sand at a 1:1 ratio (Pik et al. 2020). Once seeds were sown, each pot was watered once every two weeks with approximately 50 – 75 mL of water. Large heat lamps (Simple Deluxe 2017) and Garpsen 315 LED Plant Lights (Kingbo 2019) were positioned to fully cover the pots. Heat lamps at each table consisted entirely of either 40, 60, or 100 Watt incandescent lights for a variation of temperature while UV and light were kept constant. These heat lamps produced temperatures ranging from 17 °C at lower wattages to 34 °C at higher wattages. All temperature and heat lamps were set on a 12 hour timer to simulate light/dark cycles. An LI-250A light meter was used to measure the light intensity of all lightbulbs in  $\mu\text{mol}/\text{m}^2\text{s}$ . Local ambient temperature was recorded using a total of 9 OMEGA pendant loggers suspended 10 cm on a stake in a pot chosen at random (<https://www.omega.ca/en/data-acquisition/data-loggers/temperature-and-humidity-data-loggers/om-90-series/p/OM-92>). Germination measurements were taken weekly to determine the number of seedlings that had emerged. Proportion of germinated seeds were calculated as the number of germinated seeds divided by the total number of sown seeds per pot (Pik et al. 2020). Establishment measurements were recorded as the total number of individual seedlings

present per pot at the end of 6 weeks. Proportion established was calculated as the number of established seedlings divided by the total number of sown seeds per pot (Pik et al. 2020). All seedlings in each pot were dried in a Yamato Mechanical Convection Oven DKN900 for 72 hours and subsequently weighed to measure total seedling dry biomass per pot. Per capita biomass was calculated as the total biomass divided by the total number of established individuals per pot (Pik et al. 2020). Any seeds that did not germinate during their 6 week trial were not included in this biomass estimate.

### *Temperature Validation*

The temperatures used to conduct the greenhouse trials were selected based on the temperatures associated with the reported occurrences for each species within the region of Southern California. The Global Biodiversity Information Facility (GBIF) was used to secure the occurrence data for all four species tested in this study (Gbif.org 2023). Climatic data were then gathered from WorldClim with a 0.5 minute resolution (~1 sq-km). The climatic data taken from WorldClim was cropped to correspond to the GBIF data including the minimum and maximum observed latitudes and longitudes reported for each species (Latitude: 35.28531 – 36.56198, Longitude: -120.2184 – -116.7162). Climatic and occurrence data were then combined to both validate the temperature used in the greenhouse trials to estimate the current climatic niche of each species (Pender et al. 2019). Mean monthly temperatures were then derived from the WorldClim data to match the extent of the spatial occurrences of each species (Pearson et al. 2001). These estimates were used to infer the climate niche for each species (<https://github.com/RS-eco/climateNiche>; Schweiger et al. 2014). Pseudo-absences were then generated from pixels using the WorldClim raster data that did not already include data, using

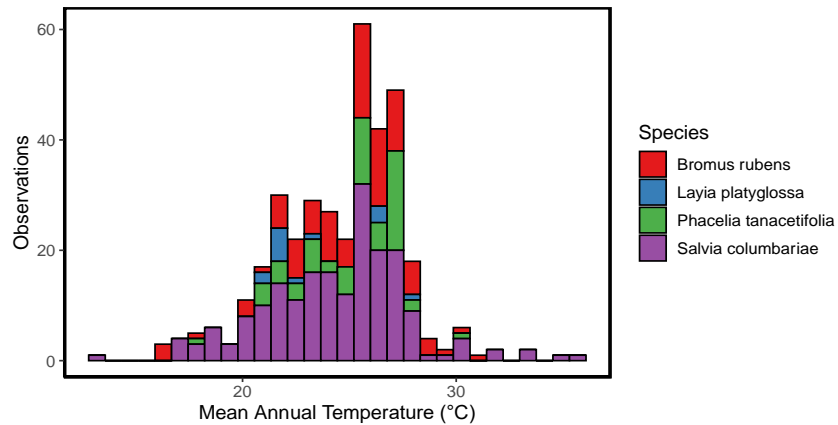
the biomod2 package in R (Thuiller et al. 2023). The number of pseudo-absences chosen was 3 times the number of presences per species (Barbet-Massin et al. 2012). The increasing increments of 1.5 – 3°C was thus consistent with current models projecting the mean annual temperature projections by 2050 and were utilized only for GBIF models (Shackell et al. 2014). These data were used to generate distribution climate occurrences for each species independently.

### *Statistical Analysis*

All statistics and models were done using the programming language R version 4.2.1 (R core team 2023). A general linear mixed model (GLMM) was used to test temperature effects using the glmmTMB package. All temperature data were compared with light treatment (40, 60, or 100-Watt lights) and OMEGA pendant ID as a random factor. Generalized linear models (GLMs) were then used to estimate the proportion germinated, proportion established, and per capita biomass of each species. Mean treatment temperature and species were treated as factors.  $R^2$  values were generated as an effect size for species establishment (Low-Décarie et al. 2014). Proportion germinated and proportion established were treated as a quasi-binomial (Warton & Hui 2011), while per capita biomass (g) was fitted to a gaussian distributions (Granados et al. 2017). Overdispersion was checked before selecting a gaussian fit for the models (Harrison et al. 2018). Comparisons between species and treatments were done using the emmeans package (Lenth 2023) for both the GLMMs and GLMs. WorldClim and GBIF data were fitted to a GLM with a binomial distribution to estimate predicted values for climate envelopes of each plant species independently.

### 3.4 RESULTS

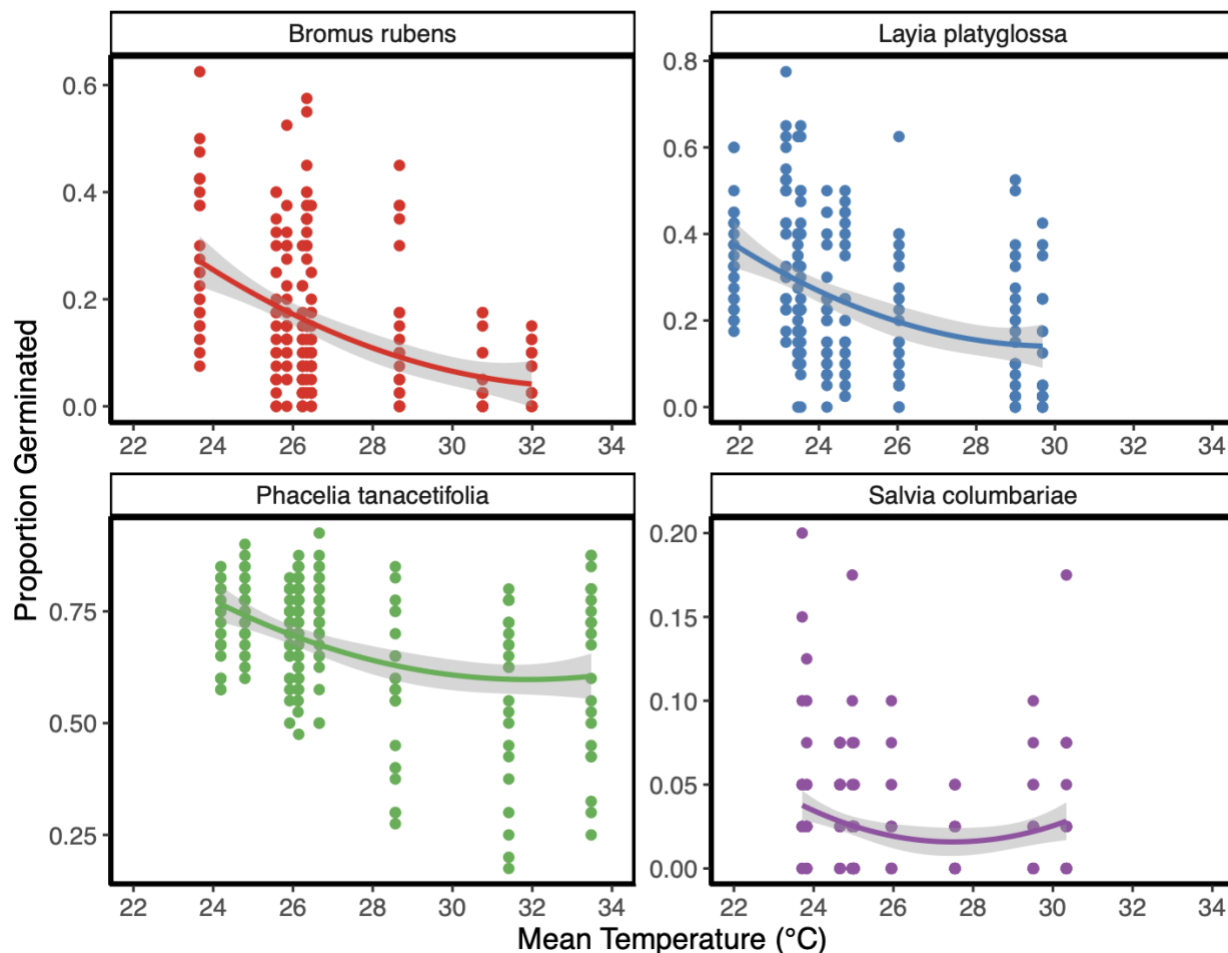
The temperature treatments across varying heat lamps were significantly different between all tested levels (GLMM,  $\chi^2 = 524$ ,  $df = 12$ ,  $p\text{-value} < 0.001$ ). Light intensity significantly differed amongst varying heat lamp bulbs, with higher wattage bulbs yielding a significantly higher light intensity (ANOVA,  $df = 1$ ,  $F\text{-value} = 2228$ ,  $p\text{-value} < 0.001$ ). The tested temperature positively correlated with light intensity (Correlation = 0.77,  $df = 838$ ,  $t = 35.55$ ,  $p\text{-value} < 0.001$ ). WorldClim data suggested no significant differences in reported observations between native and invasive species, as they all occur around the same mean temperatures (Figure 3.2; ANOVA,  $F_{(56.153, 3405)}$ ,  $p = 0.11$ ).



**Figure 3.2:** The relative effects of temperature on the total observations of native and invasive plant species in Southern California. Temperature data were extracted from WorldClim and combined with reported observations for each species from GBIF.

Increasing temperature significantly reduced the total germination of all tested plant species (Figure 3; Table 3.1). At relatively higher temperatures, the germination of *B. rubens* was significantly lower than *P. tanacetifolia* (Figure 3.3; Table 3.2). *Bromus rubens* was

significantly higher than *S. columbariae* (Figure 3.3; Table 3.2) and was not significantly different from *L. platyglossa* (Figure 3.3; Table 3.2).



**Figure 3.3:** The relative effects of temperature on the overall germination of native and invasive Southern California plant species. Germination trials were conducted for each species independently for 6 weeks. Points indicate the total number of successfully germinated plant individuals per pot for each temperature replicate. Shaded areas show a 95% confidence interval band for the lines of best fit.



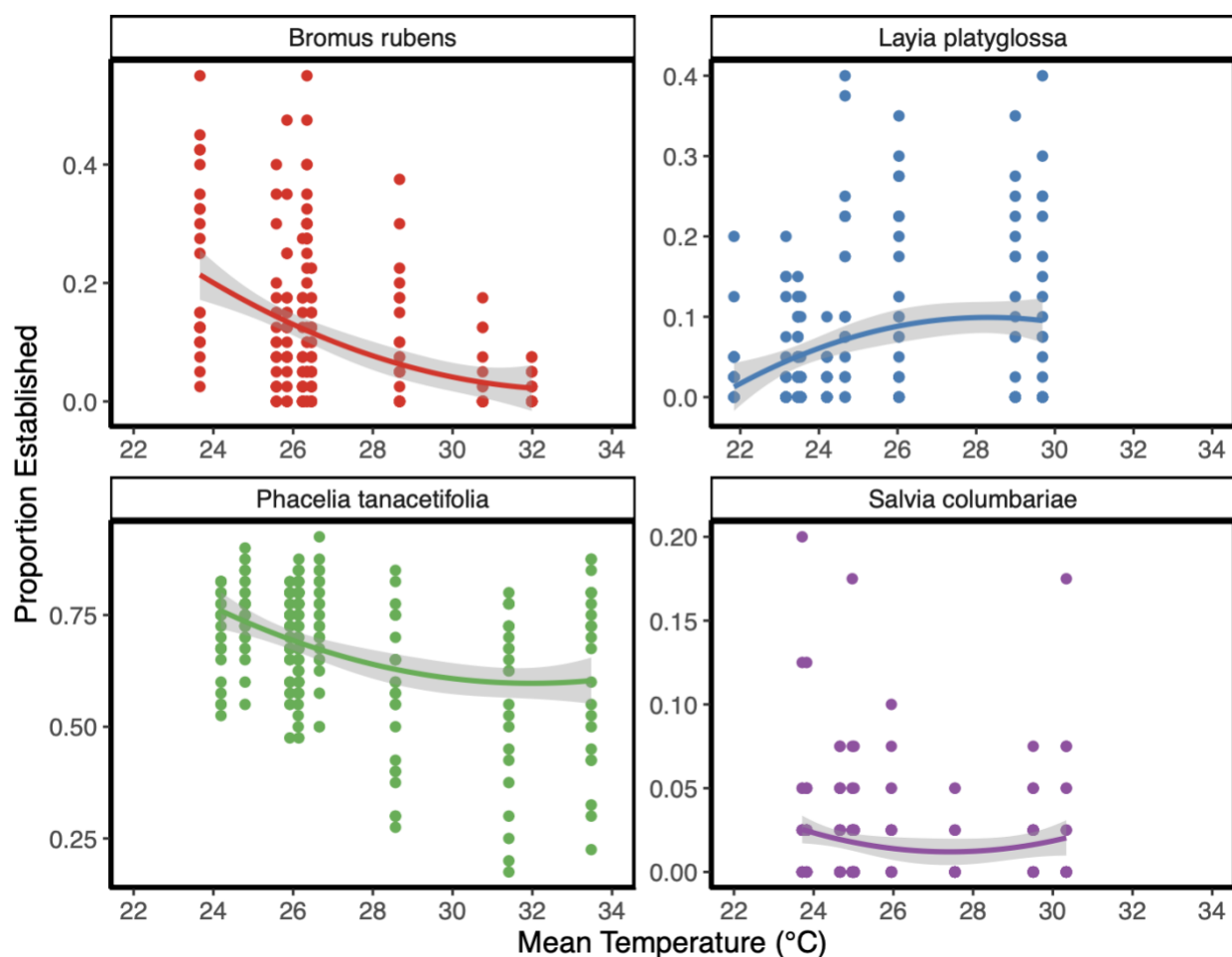
**Table 3.1:** Generalized linear models for the effects of temperature on proportion germinated, proportion established, and per capita biomass (g). The following Southern California plant species included *Bromus rubens*, *Layia platyglossa*, *Phacelia tanacetifolia*, and *Salvia columbariae*.

<b>Response Variable</b>	<b>Factor</b>	<b>df</b>	<b>Deviance</b>	<b>df residual</b>	<b>Deviance residual</b>	<b>p-value</b>
Proportion Germinated	Temperature	2	3.092	837	358.76	< 0.001
	Species	3	274.344	834	84.33	< 0.001
	Temperature X Species	6	2.502	827	81.15	< 0.001
Proportion Established	Temperature	2	8.87	837	407.67	< 0.001
	Species	3	324.67	834	82.99	< 0.001
	Temperature X Species	6	8.56	827	73.71	< 0.001
Per Capita Biomass	Temperature	2	0.05518	572	2.2846	< 0.001
	Species	3	0.39188	569	1.8927	< 0.001
	Temperature X Species	6	0.07429	562	1.8067	< 0.001

**Table 3.2:** Emtrends contrast on the effects of temperature on the proportion germinated, proportion established, and per capita biomass (g) on all tested annual plant species. Trends were generated as a pairwise function with species set as a factor and mean temperature as the main variable. Each species was contrasted to one another to compare the effects of temperature across each pair of individuals.

Factor	Contrast	Estimate	SE	df	t.ratio	p-value
Proportion Germinated	Brome – Layia	-0.3405	0.1231	827	-2.479	0.0632
	Brome-Phacelia	-2.498	0.0984	827	-25.381	<b>&lt; 0.001</b>
	Brome – Salvia	2.229	0.2803	827	7.954	<b>&lt; 0.001</b>
	Layia – Phacelia	-2.193	0.1086	827	-20.199	<b>&lt; 0.001</b>
	Layia – Salvia	2.535	0.2834	827	8.943	<b>&lt; 0.001</b>
	Phacelia – Salvia	4.728	0.2745	827	17.225	<b>&lt; 0.001</b>
Proportion Established	Brome – Layia	0.0685	0.194	827	0.352	0.9850
	Brome-Phacelia	-2.8020	0.106	827	-26.534	<b>&lt; 0.001</b>
	Brome – Salvia	2.2440	0.321	827	6.984	<b>&lt; 0.001</b>
	Layia – Phacelia	-2.8705	0.175	827	-16.379	<b>&lt; 0.001</b>
	Layia – Salvia	2.1756	0.347	827	6.265	<b>&lt; 0.001</b>
	Phacelia – Salvia	5.0460	0.313	827	16.127	<b>&lt; 0.001</b>
Per Capita Biomass	Brome – Layia	0.00782	0.01073	562	0.729	0.8856
	Brome-Phacelia	0.00531	0.00761	562	0.698	0.8978
	Brome – Salvia	-0.07737	0.01305	562	-5.929	<b>&lt; 0.001</b>
	Layia – Phacelia	-0.00251	0.01003	562	-0.250	0.9945
	Layia – Salvia	-0.08519	0.01448	562	-5.885	<b>&lt; 0.001</b>
	Phacelia – Salvia	-0.08268	0.01263	562	-6.549	<b>&lt; 0.001</b>

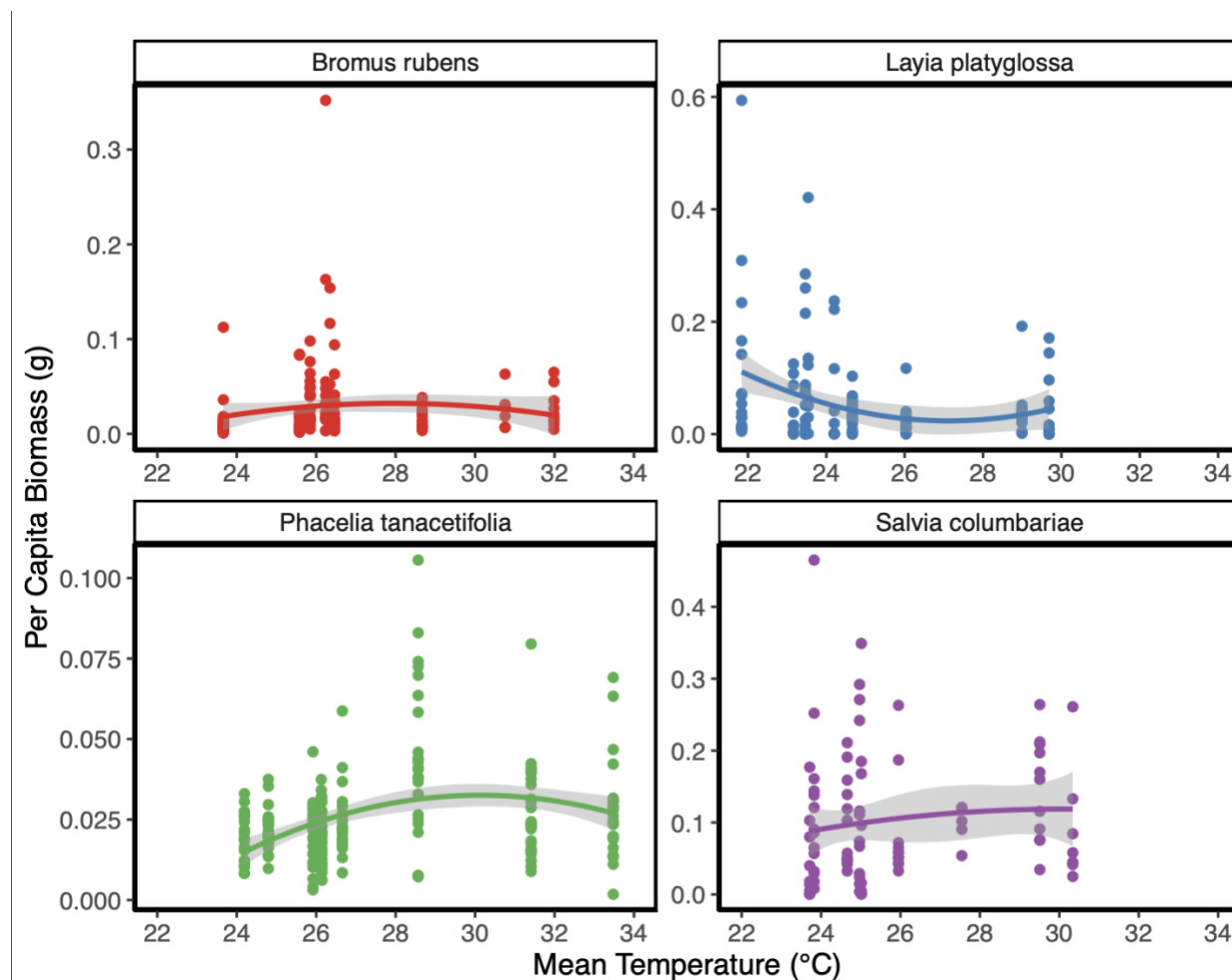
Increasing temperature significantly reduced plant species establishment (Figure 3.4; Table 1). *Bromus rubens* was affected by temperature significantly more than *S. columbaria* (Appendix B Figure B1). At relatively high temperatures, the establishment of *B. rubens* was significantly lower than *P. tanacetifolia* (Figure 3.4; Table 3.2), was significantly higher than *S. columbariae* (Figure 4; Table 3.2) and was not significantly different from *L. platyglossa* (Figure 3.4; Table 3.2).



**Figure 3.4:** The relative effects of temperature on the proportion established of native and invasive Southern California plant species. Trials were conducted for each species independently for 6 weeks. Points indicate the total number of successfully established

individuals for each temperature replicate. Shaded areas show a 95% confidence interval band for the lines of best fit. See Table 1 for complete statistics.

Increasing temperature significantly reduced the seedling biomass of all species (Figure 3.5; Table 3.1). Seedling biomass of *B. rubens* was significantly lower than *S. columbariae* (Figure 3.5; Table 3.2) with no significant difference between *B. rubens*, *P. tanacetifolia*, and *L. platyglossa* (Figure 3.5; Table 3.2).



**Figure 3.5:** The relative effects of temperature on the total biomass of native and invasive Southern California plant species. Trials were conducted for each species independently for 6 weeks. Points indicate the total number of successfully germinated individuals for each temperature replicate. Shaded areas show a 95% confidence interval band for the lines of best fit. See Table 1 for complete statistics.

### 3.5 DISCUSSION

The effects of temperature on both native and invasive plant species will enhance both current empirical models for community assembly and advance plant-interaction theory in the context of a changing climate. In dryland ecosystems in particular, temperature can alter the composition of plant communities, creating conditions more favorable for invasive plants to establish populations. I found support for the hypothesis that temperature will directly influence key early-life stage performance measures in common dryland plant species. Their responses were species-specific with differences in provenance relevant to climate sensitivity. Increasing temperature significantly influenced the germination, establishment, and seedling biomass of all native and invasive plant species. Specifically, I determined that the early-life stage processes of the invasive species *B. rubens* were more negatively impacted than the native species *P. tanacetifolia*, but less so when compared to *S. columbariae*. I also found that increased temperature within the niches of these species within Southern California did not influence the total number of reported observations. These findings support our first prediction, when temperatures reached each species' upper envelope, there were significant decreases in their early-life stage processes. I did not find support for our second prediction as increasing temperature negatively influenced all early-life stage performance measures of *B. rubens*. Finally, I found support for our third prediction as higher temperatures negatively impacted all early-life stage processes. These findings suggest that increasing temperature can influence key early-life stage measures or performance and thus can be used to assess plant health and community composition.

Increasing temperature is one critical component of a changing climate, particularly in dryland ecosystems. In this study, I utilized temperature extremes to simulate intense climatic events, as many dryland regions within Southern California are experiencing increasingly harsh and frequent drought-like events (Renwick et al. 2018; Scholes 2020). An increasing frequency of these higher temperatures can result in more drought events, subsequently resulting in a higher rate of water loss both at an ecosystem and species level (Reynolds et al. 1999; Farooq et al. 2009). The negative impact of temperature on plant germination suggests thermoinhibition may be an important part of the lifecycle of these species. Thermoinhibition was not directly tested in this study, however it could be a possible explanation as to why higher temperatures resulted in lower germinations of all tested plant species. Thermoinhibition of ungerminated seeds can result in dormancy, reducing both the biodiversity and richness of ecosystems (Silva et al. 2017). However, this inhibition can be reversed once more favorable conditions for the target species are reached (Guo et al. 2020). In dryland ecosystems, such as the deserts of Southern California, the conditions that induce thermoinhibition can become more common as increasing drought events and temperature extremes become more frequent (Potts et al. 2012; Duffenbaugh et al. 2015), making thermoinhibition an important strategy for the long-term persistence of these species. Increasing temperatures not only influenced the germination of plant species but also influenced their per capita seedling biomass. During the growth of many plant species, higher temperatures can significantly reduce their overall yield, including flowering, grain production, and fruiting (Boek 2008; Hatfield & Prueger 2015). This can subsequently influence reproductive stages, as a lower yield of these attributes can decrease their ability to reproduce while also reducing plant-pollinator interactions (Hatfield & Prueger 2015; Descamps et al. 2018). Reductions in per capita seedling biomass with increasing temperatures leads to decreases

in photosynthesis and chlorophyll content (Descamps et al. 2018). This reduction in photosynthesis can influence the establishment of Southern California plant species (Hamerlynck et al. 2000). In addition, the increase in temperature can have drastic impacts on the soil moisture available for plant species (Flanagan & Johnson 2005). It is possible that during our study, trials of higher temperature could have reduced the overall availability of water within each pot, thus reducing plant species germination, establishment, and seedling biomass. In addition, light intensity can have a direct impact on the early-life stages of plant development and typically displays a positive correlation with temperature (Forde et al. 1975; Yan et al. 2013). A positive correlation was shown between light intensity and temperatures utilized in this study, emphasising the relationship between these variables. However, for the premise of this experiment, I focused primarily on temperature extremes that would more likely be experienced in drylands as all of the tested species can establish populations in these ecosystems. At the current rate of climate change, local plant species may be greatly hindered in their ability to mitigate these increasing temperatures, thus reducing their ability to establish in these ecosystems (Sosa et al. 2020). These increasing temperatures influencing germination, establishment, and seedling biomass in tandem with one another can impact the overall structure and biodiversity of dryland ecosystems.

Understanding key traits of invasive species in all ecosystems is crucial to inform conservation and management. These invasive plant species can outcompete native species as they possess key traits that help them quickly and effectively establish a population, including rapid growth rate, high reproduction, high dispersal rate, and wide tolerance to environmental conditions (Mathakutha et al. 2019). Here, I tested only temperature as a proxy for a changing climate within dryland ecosystems. The simple climate niche estimates I derived from the

WorldClim data suggests that there is a maximum temperature that will impact the ability of *B. rubens* to germinate and establish in an ecosystem. If this invasive species was able to survive at temperatures higher than its estimated niche, then it may easily outcompete natives in these ecosystems. However, our findings suggest that higher temperatures reduced the germination, establishment, and per capita seedling biomass of *B. rubens*. Despite the widespread distribution of *B. rubens* across Southern California, this invasive species is not resistant to an increasingly warming climate. *Bromus rubens* was negatively impacted by increased temperatures, suggesting an increased sensitivity to high temperatures. Since its introduction into North America, this species has rapidly invaded and established populations in several arid ecosystems, negatively affecting the local biodiversity of both plant and animal species through alterations in microhabitat, increased nutrient competition, and altering fire regimens (Bossard et al. 2000; Hamilton et al. 1999; Brooks 2000; Freeman et al. 2014). Within these dryland ecosystems, invasive species may be reliant on facilitation from foundational species in order to successfully establish their populations because of this increased temperature sensitivity. These foundational shrub species facilitate local communities (Lortie et al. 2020; Zuliani et al. 2021), providing benefits to both plant and animal species within Southern California through reducing heat stress by shading and increasing soil moisture (Prieto et al. 2010; Filazzola et al. 2018; Filazzola et al. 2020). However, there is evidence which suggests that as the aridity of these ecosystems further increases, invasive species will no longer be able to benefit from the facilitative effects of shrubs due to global climate change and increased drought events, while native plant species continue to experience these benefits (Lucero et al. 2022). In addition to temperature, light intensity and density-dependent interactions can influence the overall establishment of *B. rubens* (Pik et al. 2020). Our findings suggest that if increasing temperatures reduce the overall germination and



abundance of these invasive plant species more so than native species, then native species may have a competitive advantage over invasive species like *B. rubens* at high temperatures. Several studies have tested the relationship between the native plant species and the invasive *B. rubens* species (Pik et al. 2020; Ghazian et al. 2021; Braun et al. 2023). In studies that tested the impacts of light, seed density, and water level, the native annual species *P. tanacetifolia*, outcompetes *B. rubens*, reducing their germination, establishment, and per capita seedling biomass (Pik et al. 2020; Ghazian et al. 2021; Braun et al. 2023). This suggests that the native annual species *P. tanacetifolia* can be utilized for restoration, particularly in areas dominated by *B. rubens*, as this species is more resilient in harsher abiotic conditions (Braun et al. 2023).

Hence, I suggest that studies focusing on the effects of abiotic conditions on dryland plant communities assess the composition of these species and the relative impacts abiotic factors can have on the germination, establishment, and seedling biomass of invasive and native species. Nonetheless, this study shows that temperature, in isolation, can potentially become a limitation to the early-life stage processes of *B. rubens*, suggesting relatively warmer sites within a region might favor natives.

### 3.6 IMPLICATIONS

With the increasing frequency of climatic events and invasions by exotic plant species, understanding at least one component of climate change—temperature—can provide valuable information for conservation in dryland systems. Previous studies focusing on early-life performance of dryland native and invasive species have yielded similar results as our study. Research conducted have tested the effects of light (Pik et al. 2020), seed aggregation (Ghazian et al. 2021), and water level (Braun et al. 2023) on native and invasive plant growth. Our findings, as well as the findings from these previous studies, suggest that the native species *P.*

*tanacetifolia* can outcompete *B. rubens*. However, there are other factors that can be tested to further enhance the growing body of literature to support better restoration practices, in the context of highly invasive plant species in dryland ecosystems. Further analysis of these species and the relative importance of temperature and other drivers of change, such as timing of events and rainfall, will provide more robust predictive models. I conducted a 6 week study to directly assess only early-stage development of these plant species. However, many of these species can survive for longer periods of time after germination and can germinate in ecosystems outside drylands. Focusing on the effects of increasing temperatures on already established seedlings could provide more insight into their resilience and adaptation to their changing environment. These species typically do not exist independently in nature and experience interspecific interactions. For the purposes of this study, I chose to test temperature independently to remove the effects of these interspecific interactions that could impact the early-life stages of these plant species. Our findings can guide conservation through highlighting future habitats that may be favored more by natives than invasive species. With the decline in dryland ecosystem health and increase in global temperature and aridity, it is essential to study abiotic factors that can impact plant communities. Future research should continue observing the impacts of temperature on dryland plant communities by conducting *in situ* multi-year observational studies.

**CHAPTER 4: SHRUB DENSITY AFFECTS THE PRESENCE OF AN ENDANGERED LIZARD OF THE  
CARRIZO PLAIN NATIONAL MONUMENT, CALIFORNIA**

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#### 4.1: ABSTRACT

Positive associations between animals and foundational shrub species are frequent in desert ecosystems for shelter, resources, refuge, and other key ecological processes. Herein, I tested the impact of the density of the shrub species *Ephedra californica* on the presence and habitat use of the federally endangered lizard species, *Gambelia sila*. To do this, I used a 3-year radio telemetry dataset and satellite-based counts of shrub density across sites at the Carrizo Plain National Monument in San Luis Obispo County, CA. The effect of shrub density on lizard presence was contrasted with previous shrub cover analyses to determine whether measures of shrub density were superior to shrub cover in predicting lizard presence. Increasing shrub density increased lizard presence. As shrub density increased, lizards were located more frequently “aboveground” versus “belowground” in burrows. Male lizards had significantly larger home ranges than females, but both sexes were similarly associated with increasing shrub densities. Shrub density and shrub cover models did not significantly differ in their prediction of lizard presence. These findings suggest that both habitat measures are effective analogs and that ecologically, both cover and the density of foundation shrub species are key factors for some desert lizards.

#### 4.2: INTRODUCTION

Repopulation and protection of endangered species are driving factors for many restoration and conservation practices globally. For successful habitat protection and restoration, I must understand 1) species distribution within suitable habitat and 2) how that habitat is utilized – daily as well as seasonally (Guisan & Thuiller 2005; Elith et al. 2006; Eyre et

al. 2022). The relationship among animal species and their interactions with plants provides key insights into how managing plant communities can better support animal species (Zwolak et al. 2022). In arid/semi-arid deserts and scrublands, animal species experience greater stress due to extremes in temperature and precipitation (Barrows 2011; Van de Ven et al. 2020). Refuge from abiotic (Filazzola et al. 2018; Ivey et al. 2020), and biotic stressors primarily drive the dependency of organisms on ecosystem resources (Milchunas & Noy-Meir 2002; Nelson et al. 2007). Physiologically, reptilian species are highly dependent on thermoregulatory processes using exterior resources as they cannot maintain their internal temperature through metabolic heat (Sunday et al. 2014; Ivey et al. 2020). Thermoregulating reptile species such as lizards and snakes overtly exhibit this dependency, as extreme temperatures can only be avoided by seeking refuge aboveground in/under vegetation or belowground in burrows, thus making these excellent species to study how resources are used within an ecosystem (Sunday et al. 2014; Urban 2015; Germano et al. 2019; Ivey et al. 2020; Dematteis et al. 2022).

Significant research has been done on the endangered blunt-nosed leopard lizard, *Gambelia sila*, including examining how this species uses the arid shrublands they inhabit (Westphal et al. 2016; Westphal et al. 2018; Germano et al. 2019; Ivey et al. 2020; Lortie et al. 2020, Gaudenti et al. 2021). This breadth of research has informed numerous conservation planning efforts (Kelsey et al. 2018; Stewart et al. 2019; Bryant et al. 2020) and has begun to inform land acquisitions and restoration efforts (Kelsey et al. 2018; Butterfield et al. 2021). *G. sila* thermoregulates by basking in direct sunlight (Westphal et al. 2018; Ivey et al. 2020; Ivey et al. 2022, Gaudenti et al. 2021). *G. sila* activity, “aboveground” and “belowground”, changes as temperatures increase from spring to early summer (Germano et al. 1994). However, as

ambient temperatures seasonally increase above certain thresholds (25°C - 30°C) (Ivey et al. 2020), these individuals are forced to take refuge, either in underground burrows or in areas above ground with higher shrub cover (Germano 2019; Ivey et al. 2020; Lortie et al. 2020). The home range for *G. sila* varies depending on the sex of the lizard but can range between 4 - 6ha for males and 1 - 8ha for females (Germano & Rathbun 2016; Westphal et al. 2018). These home ranges are typically influenced by the presence and number of shrubs, suggesting that there may be an optimal number of shrub individuals that is sufficient for *G. sila* habitats (Westphal et al. 2018). With a higher number of shrubs within these areas, there is more opportunity for this species to thermoregulate as well as find food and shelter from predation (Westphal et al. 2016; Westphal et al. 2018). However, previous work by Germano and Rathbun (2016) suggests that while the home ranges of *G. sila* contain more shrub habitat, it is still possible for this species to travel and establish home ranges in the absence of shrubs. Challenges to thermoregulation – and dependency on the local environment for refuge – for lizards, including *G. sila*, are becoming more acute as global temperatures and the likelihood of drought events increases (Sinervo et al. 2010; Dell et al. 2014; Westphal et al. 2016; Lortie et al. 2020).

Lortie et al. (2020) found that there was a significant association between increasing shrub cover, the Normalized Difference Vegetation Index (NDVI) and *G. sila* presence - i.e., an individual observation of each individual during data collection. To build off that work and to further examine the relationship between shrub density and lizard presence (Germano et al. 2011), I examined here whether shrub density could also be used, in addition to cover, to predict *G. sila* presence. Shrub density was selected for this study to further build on the finding

previously reported by Zuliani et al. (2021) and (2023), that shrub density influences the abundance and richness of local desert species while acting as an indicator for overall animal abundance. Here, I hope to extend these findings to a federally endangered species and show that shrub density is easier – and thus potentially cheaper and more cost effective for rapid range-wide surveys – to measure, both in the field and with satellite-based data.

While studies have evaluated the importance of shrub density on other vertebrate species within arid ecosystems (Zuliani et al. 2021; Zuliani et al. 2023), previous studies evaluating the importance of shrub density on *G. sila* presence relied on observational data (Westphal et al. 2018) and thus were not broadly applicable. To address these deficiencies and to increase the potential for an approach that could be more easily scaled across *G. sila*'s range, I developed methodology that uses radio telemetry and other *G. sila* presence data previously collected by Westphal et al. (2016) and Lortie et al. (2020) together with novel satellite-based shrub density measurements to test the potential of free, easily accessible satellite data for predicting *G. sila* presence across large suitable landscapes. In this paper, I specifically examined the following questions:

- 1) Does *G. sila* presence increase with shrub density?
- 2) Do shrub density and cover similarly predict *G. sila* presence?
- 3) Is *G. sila* more likely to be observed above ground than below ground as shrub density increases?
- 4) Do home range and mean annual travel distance differ between male and female *G. sila*?

#### 4.3: METHODS

##### *Study Species*

*Ephedra californica* is the dominant shrub species within the Elkhorn Plain in the Carrizo Plain National Monument in San Luis Obispo County, CA, USA (35.11982, -119.62853) (Lortie et al. 2021). *E. californica* can reach heights of up to one meter and typically takes 5 to 10 years to reach 0.5m in size, suggesting that its cover and density changes over a longer period (Cutler 1939; Filazzola et al. 2020). With numerous twigs and needle-like leaves, this species possesses unique characteristics of both gymnosperms and angiosperms, making it well-adapted to its native semi-arid and arid environments (Loera et al. 2012). *E. californica* is considered a foundational shrub species because it plays a disproportionately large role in structuring the system (Hawbecker 1951; Westphal et al. 2018; Zuliani et al. 2021). This shrub species provides several unique resources to local lizard populations, including as a refuge from predators and as a place for thermoregulation (Lortie et al. 2018; Ivey et al. 2020; Gaudenti et al. 2021; Braun et al. 2021; Zuliani et al. 2021).

Within the Carrizo Plain National Monument, *G. sila* are found in both shrubbed and open areas in isolated populations (Westphal et al. 2018; Lortie et al. 2020; Gaudenti et al. 2021). Male *G. sila* individuals are territorial, minimally overlapping with other males (Westphal et al. 2018; Germano 2019). *G. sila* are mainly insectivores, however, they may consume smaller lizard species (Warrick et al. 1998; Westphal et al. 2018; Germano 2019). The active season for *G. sila* adults lasts only ~3 months in the late spring to early summer, after which they transition into hibernation (Germano et al. 1994; Ivey et al. 2020). *G. sila* associate with shaded areas under shrub species and in underground burrows (Lortie et al. 2020), which they



use as an additional way to thermoregulate (Germano 2019; Ivey et al. 2022, Gaudenti et al. 2021). *G. sila* will spend nights within burrows and may return to these burrows during the day when temperatures become too high (Warrick et al. 1998; Westphal et al. 2018).

### *Radio Telemetry*

I used *G. sila* location data previously collected using radio telemetry at the Carrizo Plain National Monument from 2016 to 2018 (Noble et al. 2016; Westphal et al. 2018; Lortie et al. 2020; Zuliani et al. 2021). *G. sila* location data was collected on a total of 62 individuals, 36 males and 26 females. *G. sila* individuals were tracked for three months (May-July) each year (2016-2018) during the time period of greatest activity for this species (Westphal et al. 2018; Lortie et al. 2020). Holohil model BD-2 tags were attached to *G. sila* individuals using a small beaded chain, jewelry wire, and epoxy (Westphal et al. 2018). Collar weight (with the tag) ranged from 1.6 - 2.2g, ensuring that the weight did not exceed between 5% and 10% of the lizard's body mass (Westphal et al. 2018). Each instance of *G. sila* presence was geolocated. Individual characteristics such as an individual's sex were also collected during the initial capture. Individuals located above ground and active were designated as "aboveground", while individuals judged to be below ground were designated as "belowground". At each location, the presence of shrubs was recorded. *G. sila* association with a shrub individual or in open areas was then recorded as microsite. Within the 3 years of observations, a total of 3553 *G. sila* observations were recorded with 1502 aboveground and 2051 belowground (Westphal et al. 2016; Lortie et al. 2020). *E. californica* is a long-lived, slow growing shrub species and will thus not change in size and density over three years of continuous sampling (Bowers et al. 1995), allowing us to compare lizard presence and shrub density data from slightly different time periods. Additional details on the telemetry procedures can be found in Westphal et al. (2018).

Capture, collaring, and monitoring of *G. sila* was authorized by the United States Fish and Wildlife Service via permits TE166383-4 (MFW), a Memorandum of Understanding issued to the California Department of Fish and Wildlife, and by the California Department of Fish and Wildlife via Scientific Collecting Permit SC-2925 (MFW). The transportation, care, and use of lizards were in accordance with the Animal Welfare Act (7 U.S.C. 2131 et. seq.) which guides U.S. government use of vertebrates. I ameliorated any suffering of captured animals by allowing only trained personnel to handle them, and by limiting handling and housing time to the minimum necessary.

#### *Shrub density data collection and ground truthing*

*E. californica* density data were derived from Google Earth using composite satellite imagery— digital images comprised of elements from several different images – from 2021. Composite imagery was developed using Landsat/Copernicus satellite data, with a 30m spatial resolution. Satellite imagery was obtained for the same locations as the lizard telemetry tracking data within the Carrizo Plain National Monument, with an area of 6,613,399m<sup>2</sup>. Each individual shrub located within the telemetry field site was geolocated and given a unique identification marker. Once all *E. californica* individuals were marked, Keyhole Markup Language (kml) files containing shrub locations were extracted and converted into a useable Comma-Separated Values (csv) file. Each shrub individual was given a unique latitude and longitude value corresponding to their location within the field site. I used R version 4.2.1 (R Core Team 2022) to determine the density of *E. californica* individuals within a 20m radius of each *G. sila* presence. A total of 200 random shrub locations were then selected and ground-truthed in the field to determine the accuracy of our satellite imagery-based shrub density measurements. *In situ* shrub density was determined by locating each of the randomly selected

200 shrubs and measuring the number of shrubs within a 20m radius. Shrub cover, measured as percent cover within a 20m radius, was extracted from shrub cover data previously collected via Landsat 8 by Lortie et al. (2020). I also resampled NDVI data at a 20m radius, similar to what Lortie et al. (2020) did with their investigation of shrub cover and lizard presence. NDVI was calculated as  $NDVI = (NIR - RED)/(NIR + RED)$  (Zaitunah et al. 2018) and was included here as it is known to be a strong predictor of vegetation greenness and primary production (Butterfield and Malmström 2009; Ju & Masek 2016) and is therefore commonly used to quickly identify vegetated areas (Zaitunag et al. 2018). NDVI and shrub density were then both used to determine if these factors influenced *G. sila* presence. All data are publicly published and available on the Knowledge Network of Biodiversity (KNB) (Zuliani et al. 2022).

### *Statistical Analysis*

All statistics and models were done in R 4.2.1 (R core team 2022). The *ResourceSelection* R package (Subhash et al. 2019) was used to model *G. sila* shrub use based on density and cover (Lortie et al. 2020). The *distinct* function was used in base R 4.2.1 to remove any duplicates within the lizard presence data. Data were filtered and compared based on similarity of latitude, longitude, lizard identification, year, and microsite. Individuals with identical latitude and longitude coordinates within the same year were removed to minimize the probability of duplication. In addition, individuals who were located at the same latitude and longitude associating with the same microsite were also filtered. I also tested the effects of rounding the latitude and longitude to 4 and 3 decimal points on lizard duplicate removal. Rounding the lizard geolocations to 4 decimal places reduces the distance of each coordinate by 11m while rounding the geolocations to 3 decimal places reduces the distance of each coordinate by

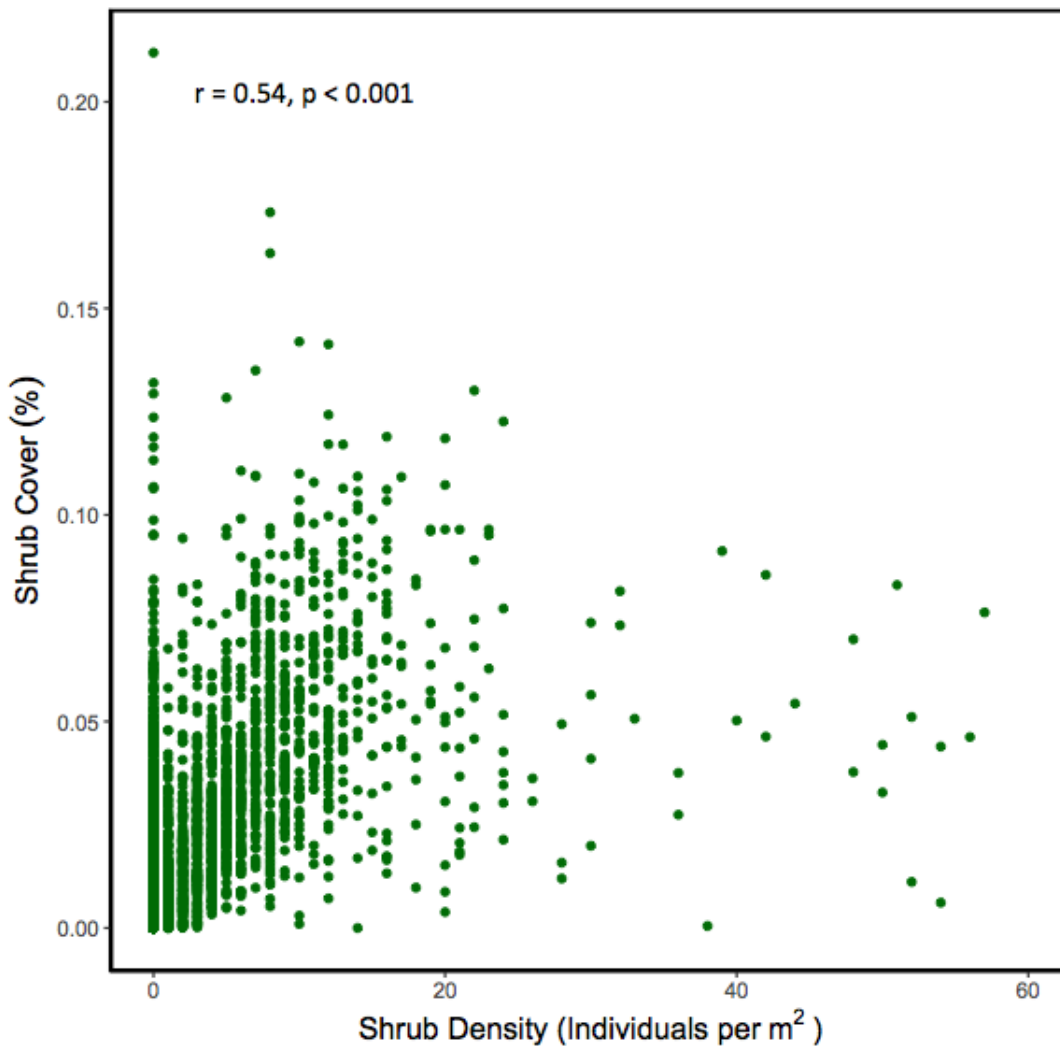
111m. This was conducted in a variety of combinations and compared to the raw data. The SF package was used to calculate the mean annual distance travelled by individual lizards using three different duplication removal methods (Appendix C Table C1; Pebesma 2018). These methods were selected as they provided the most meaningful data after filtering for possible duplicates. 1000 pseudo-absence data points were then generated using the dismo R package to simulate areas where *G. sila* individuals were not located (Hijmans et al. 2022). The resource selection probability function (rspf) was used to estimate the probability of a lizard individual at shrubbed areas (Lele et al. 2013; Roberts et al. 2017). In addition, sex and year were used as a factor with shrub density to estimate the resource selection of shrub density between male and female individuals across three years of telemetry data. This function estimates the frequency of occurrence of a species for a specific factor such as shrub density and cover (Roberts et al. 2017). AIC (Akaike Information Criterion) scores were generated for both shrub density and shrub cover models and compared as both strongly correlated with lizard shrub use (Lele et al. 2013; Roberts et al. 2017; Lortie et al. 2020). The scores determined which model best suited the data – based on a lower AIC score. Pearson’s Product-Moment Correlation was used to determine the strength and directions of the relationship between shrub density and cover. An approximation of second derivative for the data points for the mean fitted use by shrub density curve was used to determine the inflection point of fit (Christopoulos 2014). Maximum likelihood estimates were used with shrub density, shrub cover, and ground use (above vs. below) as predictor variables. Shrub density and cover were analyzed against lizard presence to depict their relationship. Home range sizes were then calculated using 95% and 100% minimum convex polygon (MCP) areas, using the adehabitatHR package (Mohr 1947; Calenge 2006). Both

male and female *G. sila* home ranges were calculated and compared across the three years of telemetry data. General linear models (GLM) were then used to compare shrub density and shrub cover use by both male and female *G. sila* individuals.

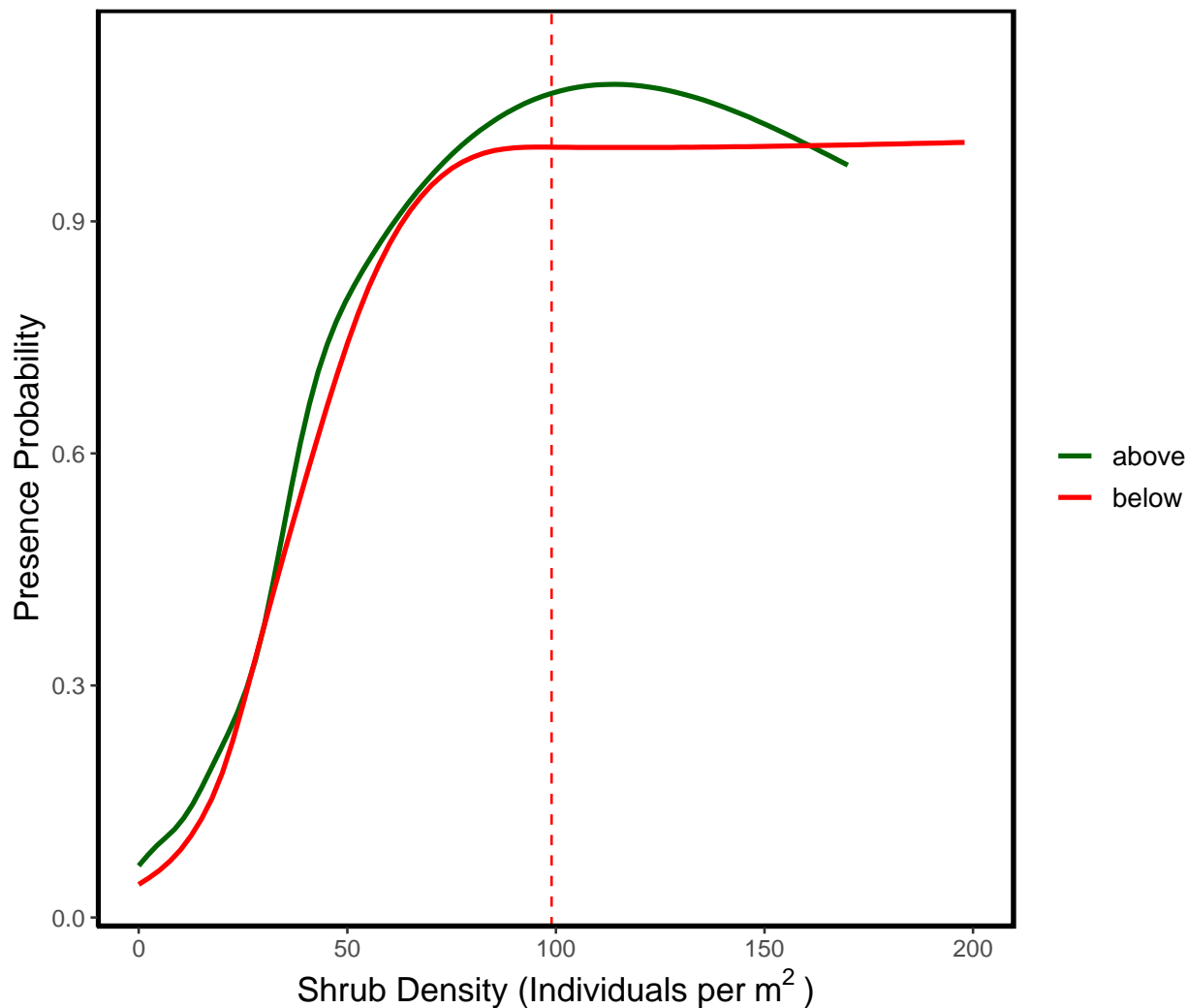
#### 4.4: RESULTS

There were no statistically significant differences between the geolocated shrub density estimates and the ground-truthed shrub density counts in the field (Paired t-test,  $t = -0.048$ ,  $df = 389.41$ ,  $p = 0.962$ ). Shrub cover and density were positively correlated (Figure 4.1, Pearson's Product-Moment Correlation, estimate = 0.369,  $t$ -value=23.761,  $df = 3571$ ,  $p < 0.001$ ). The AIC score for the shrub density rsf model was lower than the shrub cover model suggesting that density is a more parsimonious model fit for presence data (Snipes & Taylor 2014) (Appendix C Table C2; AIC scores density = 11253.37, cover = 11257.06). Shrub density significantly predicted the presence of *G. sila*, for both the aboveground and belowground categories (Figure 4.2, AIC = 11289.36, Estimate = 0.088  $\pm$ 0.006,  $p < 0.001$ ). The inflection point of the predicted use curve for lizards by shrub density was 99 shrubs per 20m radius plot (or about 100 shrubs per 20m<sup>2</sup>) (Figure 4.2). Lizard presence was significantly greater aboveground at higher shrub densities (Figure 4.2, rspf Estimate = -0.380  $\pm$ 0.083,  $p < 0.001$ ). The removal of *G. sila* presence duplicates had no impact on model outcomes (Appendix C Table C3). NDVI positively correlated with lizard presence (Appendix C Table C3). Mean annual distance traveled by *G. sila* individuals was significant across all duplicate removal methods (Appendix C Table C1;  $t = 19.026$ ,  $df = 215$ ,  $p < 0.001$ ). Mean annual distance traveled was significantly different across all duplicate removal methods except between methods 2 and 3 (Tukey, estimate = -9.8,  $t$ -value = -1.457,  $p = 0.3139$ ). Shrub density significantly predicted the presence of male (rspf Estimate =

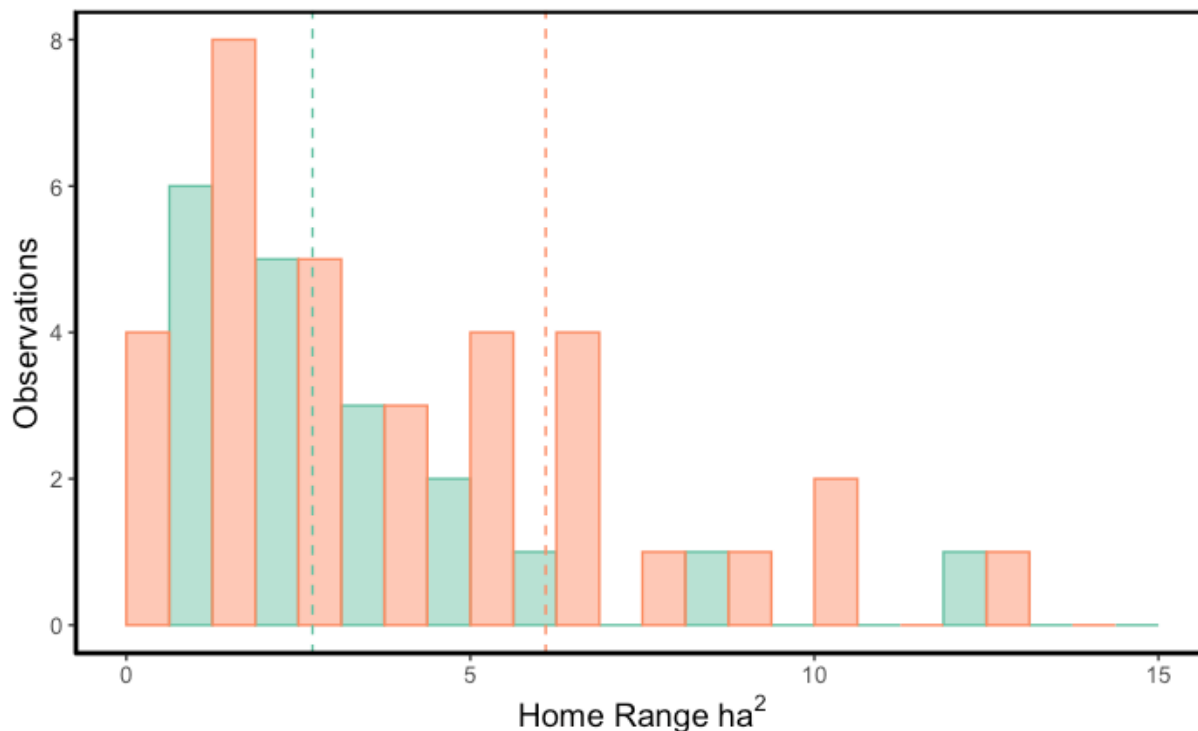
0.06851 ± 0.0118,  $p < 0.001$ ) and female *G. sila* individuals (rspf Estimate = 0.06538 ± 0.0071,  $p < 0.001$ ). Male *G. sila* had significantly greater home range sizes in 2018 sampling (Figure 4.3; Appendix C Table C4; t-test = -2.318.  $df = 56$ ,  $p = 0.0241$ ).



**Figure 4.1:** The relationship between shrub density (number of *E. californica* individuals per 20m<sup>2</sup> radius) and shrub cover for *Ephedra californica* within the Carrizo Plain National Monument study site. Total shrub density was joined with estimate shrub cover from imagery data to test for a correlation ( $r = 0.54$ ,  $p$ -value  $< 0.001$ ).



**Figure 4.2:** The relative effects of shrub density (number of *E.californica* individuals per 20m<sup>2</sup> radius) on *Gambelia sila* presence probability above and “belowground” for each individual presence. Radio telemetry data were joined with geolocated shrub data to estimate the shrub density within a 20m radius of each *Gambelia* observation. The data were then grouped by above and “belowground”. Shaded areas show a 95% confidence interval band for the lines of best fit.



**Figure 4.3:** The relative home range of *Gambelia sila* individuals (ha<sup>2</sup>) across 3 years of radio telemetry tracking. Home range sizes were calculated using the `adehabitatHR` package in R 4.2.1. Individuals were separated based on lizard sex with blue representing females and red representing males. Dashed lines represent the average home range of male and female individuals independently.

#### 4.5: DISCUSSION

The major finding of this study is that presence of *G. sila* individuals increased with higher shrub density, up to a plateau, which I identified was 100 shrubs per 20 m<sup>2</sup>, or 25% shrub cover (Lortie et al. 2020). Higher shrub densities were also associated with increased likelihood of lizard presence “aboveground” versus “belowground”. Measurements of NDVI in our shrub density models positively predicted the presence of *G. sila* individuals, similar to conclusions drawn from previous work by Lortie et al. (2020) which showed that both shrub cover and NDVI positively predicted lizard presence. Male lizards had larger home ranges than female individuals for the 2018 sampling season only. Males were frequently associated with higher density shrub areas, but the predicted habitat use was not significantly different between lizard



sexes, suggesting that shrub density and cover are important as potential resources for both male and female *G. sila* (Lortie et al. 2020; Ivy et al 2022). Increasing shrub densities increases the likelihood that a lizard will encounter and interact with a shrub (Zuliani et al. 2021), providing stopping points or distributed refuges for individuals as they move within their home range.

Landscape features and various natural resources are important factors to consider in ecological surveys that observe associations. Typically, in arid/semi-arid ecosystems, shrub species provide benefits to local animal communities through buffering climatic extremes, acting as refuges from potential predation, and other abiotic and biotic conditions (Bruno et al. 2003; Noble et al. 2016; Eldridge & Soliveres 2014; Filazzola et al. 2017; Westphal et al. 2018; Ivey et al. 2022). Areas with higher shrub cover allow for lower thermal amplitudes, while areas with higher density can consist of smaller shrubs utilized for abiotic stress amelioration, which provides multiple areas for individual utilization (Holzapfel & Mahall 1999; Filazzola et al. 2017). This behavior extends beyond *G. sila* as several other reptile species utilize shrub cover and density to ameliorate abiotic stressors. For instance, *Psammodromus algirus*, the Algerian sand racer, utilizes shrubs within the Tajo Basin of Spain (Diaz & Carrascal 1991; Zamora-Camacho et al. 2016) for thermoregulation, predator avoidance, and movement minimization (Diaz & Carrascal 1991). These facilitative associations, in which one species benefits while the other is unaffected (Molina-Montenegro et al. 2016), can be subdivided into facultative, (being able to live with the presence or absence of an environmental condition), and obligate, where one species requires the benefits from another to exist (Butterfield 2009). The relationship observed in our study is more facultative than obligate, as *G. sila* will utilize shrubs when

present; however, if absent, individuals can still be present within a site. With more shrubs, there are likely more opportunities for positive associations as even relatively small shrub individuals provide benefits (Lortie et al. 2018; Gaudenti et al. 2021; Zuliani et al. 2021).

Shrubs can provide refuge for lizards to thermoregulate and escape harsh abiotic conditions, such that they might stay above ground even when below ground temperatures are more optimal (Gaudenti et al 2021). Shrub cover and density therefore potentially provide crucial opportunities for lizard thermoregulation and can be utilized to predict the frequency of individual lizard observations (Filazzola et al. 2017; Lortie et al. 2020; Zuliani et al. 2021). This contrasts with lizard individuals in open or relatively shrub-free habitats which are more reliant on burrows to reduce their body temperature, similar to other desert species (Bean et al. 2014; Germano & Rathbun 2016; Ivey et al 2020, Gaudenti et al 2021). Males also generally extended their home ranges in this ecosystem suggesting that refuge provided by foundational plant species can be important stopping or foraging points (Ivey et al. 2020; Ivey et al. 2022). While female *G. sila* individuals similarly utilize these areas for foraging points, a large portion of their active season is spent underground while breeding (Germano 2019; Ivey et al. 2020). The influence of shrub density on the thermoregulation, behavior, and associations of blunt-nosed leopard lizards with habitat further illustrate how these resources are beneficial to this endangered species and how important relevant associations are to their conservation and restoration.

#### 4.6: CONCLUSIONS

Shrub density can be utilized to predict the presence of *G. sila* individuals within arid California ecosystems. This can guide species conservation and restoration efforts through both the preservation of shrubbed – and likely suitable and occupied habitat – landscapes and the restoration of areas that could be suitable if shrubs were planted. Shrub density was positively correlated with shrub cover suggesting that both are viable measures that can be used to predict lizard presence. However, I suggest measures of shrub density are easier to collect in the field and are thus easier and cheaper to collect across large areas. Restoring areas with *E. californica* or preserving already established areas can benefit *G. sila* populations as these areas can act as distributed refuges for these individuals. There is a significant current opportunity to retire and restore agricultural land within the San Joaquin Valley in Southern California (Kelsey et al. 2018; Bryant et al. 2020; Butterfield et al. 2021). Restoring these ecosystems could lead to *G. sila* – as well as more than 20 other threatened and endangered species – recovery. Our findings can help guide these restoration efforts, identifying specific density and cover thresholds that will provide the best potential habitat for *G. sila* individuals.

**CHAPTER 5: THE SHRUB DENSITY EFFECT: UNRAVELLING VERTEBRATE COMMUNITY  
DYNAMICS ALONG AN ARIDITY GRADIENT IN SOUTHERN CALIFORNIA**

Currently under review at Ecosphere

## 5.1: ABSTRACT

Foundational shrub species can support vertebrate communities within desert ecosystems. These shrubs provide thermal refuge to aid in temperature amelioration and to escape predation. Within Southern California, USA, harsh abiotic conditions influence the frequency of these shrub-animal interactions. I tested the hypothesis that increasing shrub density will positively influence local vertebrate communities across a variety of arid ecosystems within Southern California. I used a combination of camera trapping and temperature pendants across a 2-year field study to assess the effects of shrub density and near-surface air temperature on vertebrate community composition. Six sites were established across Southern California, each consisting of four 20 m radius plots, with shrub densities ranging from 0 to 14 individuals. Increasing shrub densities significantly influenced the visitation, richness, and evenness of local vertebrate communities. Relatively higher near-surface air temperatures (NSAT) significantly reduced vertebrate visitation, richness, and evenness. Site-level aridity estimates showed that increasing aridity has negative effects on vertebrate species, but increasing shrub densities can offset these negative effects. These findings suggest that increasing densities of foundational shrub species positively influences vertebrate community measurements and composition across varying arid ecosystems. Understanding how these foundational shrub species can be utilized to assess vertebrate communities can provide key insight into both restoration and management practices.

## 5.2: INTRODUCTION

Within the last decade, Southern California has experienced increasingly harsh climatic conditions, with a combination of record low rainfall and temperature highs resulting in extended drought events (Mann & Gleick 2015). With these increasing anthropogenic changes, animal species have become dependent on both inter- and intraspecific interactions to reduce potential adverse effects (Dangles et al. 2018; Rahman & Candolin 2022). To reduce these harsh conditions, animals will associate with foundational species (Westphal et al. 2018; Ellison 2019). These foundational species often exhibit facilitative associations with animals, as one interacting species benefits while the other is unaffected (Noble et al 2016; Dangles et al. 2018). These positive associations are observed in both plant and animal communities (Callaway & D'Antonio 1991; Lortie et al. 2016; Lortie et al. 2018; Lucero et a. 2020). Foundational species define ecosystems by shaping the biodiversity of associating species and mitigating ecosystem processes (Ellison 2019). Within the deserts of Southern California, shrubs will act as these foundational species, providing several benefits to both plant and animal communities (Lortie et al. 2016; Zuliani et al. 2021). Vertebrate species are reliant on foundational shrub species (Pugnaire et al. 1996; Braun et al. 2021; Zuliani et al. 2023) as they are utilized to escape predation (Filazzola et al. 2017; Salido & Vincente 2019), thermoregulate (Ivey et al. 2020; Gaudenti et al. 2021; Zuliani et al 2023b), and as a food source (Lortie et al. 2020). Further understanding the facilitative associations between foundational shrubs and vertebrate species can provide key insight into how these environmental resources are utilized both by vertebrate individuals and communities.

With foundational shrubs positively influencing local animal communities, the number of shrubs available allow for more opportunities for these facilitative associations. In terms of plant-animal interactions, the density of shrubs can influence the net outcome of animal interactions while also influencing the overall local community composition (Springer et al. 2003; Zuliani et al. 2021). Density is measured as the number of individuals within a given sample area (Bonham 2013). As density increases within an ecosystem, vertebrate species are given more opportunities to benefit from the facilitative associations, such as having more areas to thermoregulate (Milling et al. 2018; Zuliani et al. 2023b). For instance, the federally endangered species *Gambelia sila*, the Blunt-Nosed Leopard Lizard, uses shrubs within the desert of Southern California to thermoregulate, and has been predicted to have higher abundances as shrub densities increase (Ivey et al. 2020; Ivey et al. 2022; Zuliani et al. 2023b). While shrub cover is more commonly used with plant communities (Lortie et al. 2020), it can be utilized in tandem with shrub density to predict animal abundances (Van Auken 2009; Zuliani et al. 2023). However, desert and grassland ecosystems globally are experiencing a phenomenon referred to as shrub encroachment, where woody shrub species are increasing in density, contributing to significant changes in both shrub and vegetation cover (Van Auken 2009). This is typically seen as negative as it directly relates to ecosystem desertification (Van Auken 2009). However, several ecosystems within Southern California, such as the Carrizo Plain National Monument, benefit from this encroachment as it is reconverting arid grasslands back into a shrubland (Browning 2008). This increase in shrub density, specifically of foundational species, can also promote more facilitative associations, as shrub encroachment can positively influence vertebrate abundance and richness (Whitford 1997; Eldridge & Soliveres 2014; Schooley et al.

2018). Further analyzing how these increasing shrub densities influence animal communities can provide insight to assess community composition and for conservation practices.

Desert ecosystems in Southern California are experiencing higher frequencies of mega-droughts (Reynolds et al. 1999; Kogan & Guo 2015; Gols et al. 2021). As temperatures increase within deserts, vertebrate associations change to promote activities that are more suitable for thermoregulation and reduce abiotic stressors (Moore et al. 2018). High near-surface air temperatures (NSAT) will influence species at both an individual and community level (Newbold 2018). These increasing temperatures will cause a significant decline in vertebrate communities by reducing migration patterns and behavior (Newbold 2018; Riddell et al. 2021). However, the effects increasing temperatures have on vertebrates are species dependent and can be mediated through ecosystem resources, such as the presence of burrows and shrubs (Pike & Mitchell 2013; Riddell et al. 2021; Zuliani et al. 2021). Within desert environments, high temperatures are associated with reduction in both humidity and precipitation (Walker & Landau 2018). Under these high abiotic conditions, the regions within southern California are classified as arid or semi-arid (Abella et al. 2012; Marengo & Bernasconi 2015). As global temperatures increase, vertebrate species will continue to depend on ecosystem resources, including shrubs, to ameliorate harsh abiotic conditions.

As the frequency of these mega-drought events increase in Southern California, ecosystems will become more arid (Germano et al. 2011; Abella et al. 2012; Marengo & Bernasconi 2015). This increasing aridity contributes to the aridification of dryland ecosystems while also causing a dynamic shift in the structure of ecosystems as plant and animal communities adjust to new conditions (Hacker & Gaines 1997; James & Tallis 2019).



Across Southern California, there is an increasing aridity gradient in dryland ecosystems, suggesting that local species utilize ecosystem resources differently to reduce harsh abiotic conditions (Welles & Funk 2019). As these ecosystems become more arid, the negative impacts on plant and animal communities become more prevalent (Lucero et al. 2020). Within animal communities, aridity can have larger impacts on their associations, becoming more reliant on ecosystem resources, such as shrubs, as they are more readily available at higher densities (Tews et al. 2004; Zuliani et al. 2021). Furthering the knowledge of how variations in aridity influence local animal species, and how these species utilize ecosystem resources to ameliorate these stressors, can increase our understanding of how these conditions alter environmental processes and community associations.

Determining the effects of shrub density on vertebrate community composition can further the current understanding of facilitative associations and provide insight on how this ecosystem resource is utilized in dryland ecosystems. Here, I conducted a 2-year study at six different sites across Southern California. I tested the hypothesis that increasing shrub density will positively influence vertebrate communities within Southern California. In this study, I tested the following predictions:

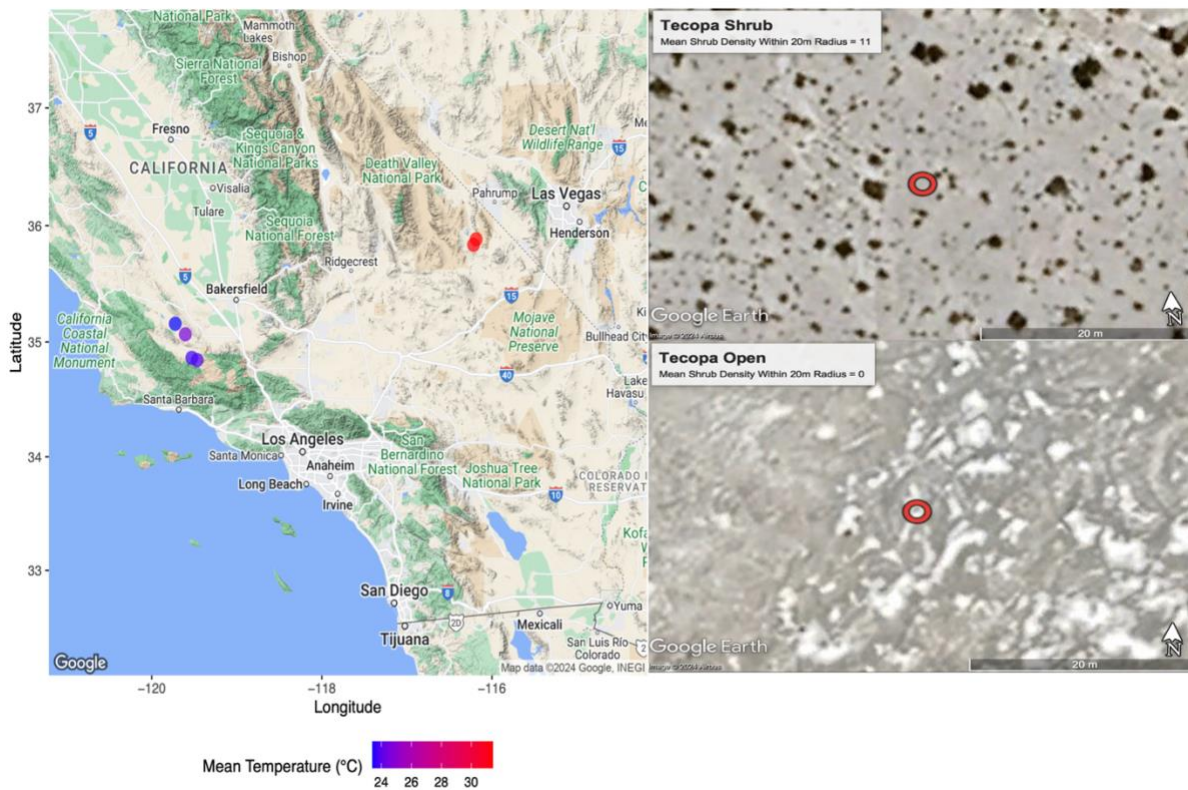
- 1) Increasing shrub density will positively influence the visitation, richness, and evenness of vertebrate species.
- 2) Increasing near-surface air temperature will negatively influence the visitation, richness, and evenness of vertebrate communities.
- 3) The effects of increasing shrub densities can influence vertebrate community composition.

- 4) The positive effects of site-level estimates of shrub density on animal communities will increase with increasing aridity.

### 5.3: METHODS

#### ***Study Sites***

Six sites were selected across Southern California based on the presence or absence of foundational shrub species and variation in temperature (Figure 5.1). All sites were classified as arid/semi-arid ecosystems and are dominated by the foundational shrub species *Ephedra californica* (Filazzola et al. 2020; Braun et al. 2021; Zuliani et al. 2023b). Of the six sites established, two were located within the Carrizo Plain National Monument (35.11566, -119.62069), two within the Cuyama Valley (34.848726, -119.48312), and two within the Mojave Desert (35.851515, -116.18671). At each site, four plots were established, ranging from no shrubs to relatively high densities ( $n = 24$ ). To establish each plot, a random centroid was selected to act as the middle of the 20 m radius plot. To calculate shrub density, the number of shrubs within the 20 m radius plots was counted.



**Figure 5.1:** A map of study sites sampled across Southern California including images of high and low density shrub sites sampled. Centroids of the sites indicated by red open circles. Six sites were selected based on the presence of the foundational shrub species *Ephedra californica*. The map was generated utilizing the R package ggmaps and images of sites were taken via satellite imagery from Google Earth TM.

### **Study Species**

*Ephedra californica* is one of the most common woody plant species within Southern California. This is a vital foundation species that could play a major role in the restoration of desert ecosystems in California (Lortie et al. 2018, Filazzola et al. 2017). This species is resilient and can survive large abiotic stressors, such as drought, extreme heat, and lack of nutrition, while also surviving mechanical damage, such as branch breaking or herbivory (Lortie et al. 2018). This species is used by several species of vertebrates including the Blunt-Nosed Leopard Lizard, Giant Kangaroo Rat, and San Joaquin Jack Rabbits (Hawbecker 1951; Noble et al 2016).

One of the key species observed at these sites is *Dipodomys heermanni*, or Heerman's Kangaroo Rat. This is a small nocturnal rodent species present in relatively high abundances within Southern California and is known for creating interconnecting burrows throughout these arid ecosystems (Hawbecker 1951). This species consumes the seeds found underneath shrub canopies, resulting in them showing high associations to foundational shrub species. *Lepus californicus*, otherwise known as the Black-Tailed Jack Rabbit, is a large species active both during the day and at night. This species is frequently found in the Carrizo Plain and Cuyama Valley, and is most frequently observed through camera traps. It typically consumes vegetation in open areas and under shrub canopies (Johnson & Anderson 1984).

### **Camera Trapping**

VIKERI Model A1 camera traps were used to sample animal communities at each site during the day and night (Noble et al. 2016). No flash was emitted by cameras to ensure that there were no disturbances to interacting animal species. Two camera traps were deployed on 20 cm stakes driven in the ground, facing each other at the edge of each 20 m radius plot. A total of 48 camera traps were deployed across all 24 plots. Each camera trap was set to medium sensitivity with a 1-minute delay to minimize the number of misfired photos taken from background activity (Zuliani et al. 2021). Camera traps were checked approximately every four to five days to ensure proper function for the 30-day field study between May and June 2022 and 2023. Camera locations were not baited. The images were saved on 24GB SD cards as Joint Photographic Export Group (JPEG) files and examined during data extraction.

A total of 250,000 photos were taken with 2022 yielding 58,000 photos and 2023 yielding 192,000 photos. Each photo was taken as a new species instance with photo ID, site,

year, date, rep, camera number, shrub density, presence or absence of animal, species of animal, and camera trap timestamp all recorded. Independent photos were defined as when the animal individual was not observed at the same position within the 1-minute lag-time (Zuliani et al. 2021). Camera trap rate of capture was calculated per year by taking the difference between the number of new species instances with the total number of observations for the 30-day duration (Noble et al. 2016; Zuliani et al. 2021). All data taken from camera traps each year were then combined into one density datasheet.

### ***Species Validation***

Vertebrate species observations through camera trap photos were validated using a combination of Wildlife Insight (Vélez et al. 2023) and the iNaturalist application (Unger et al. 2021). Both applications provided the most plausible identification for images with species present and were further validated by individual observers. Uncertain images were labeled as unknowns and were later filtered from the community composition data. Images were saved as JPEG files on hard drives for data analysis. Since identifying unique individuals via camera trapping can be challenging independent identification were judged based on the ecology of each independent species and possible unique identifiers on individuals, while excluding possible duplicates (Choo et al. 2020).

### ***Microclimate Plot-level Measures***

Near-surface air temperature for each site was recorded using OMEGA USB loggers, suspended approximately 20 cm above ground on a stake (Ashcroft 2018; Terando et al. 2018). At shrub density plots, two loggers were placed under random shrub canopies, while at open plots two loggers were placed next to camera traps. These loggers remained within the shrub

and open plots for the duration of the field experiment. Hourly near-surface air temperatures were logged (°C) and used to calculate the daily means.

### ***Site-level Climate Measures***

The annual aridity of each region was estimated utilizing the De Martonne Aridity Index equation  $AI = P/(MAT + 10)$ , where P is the total annual precipitation in mm, and MAT is the Mean Annual Temperature in °C (Zomer et al. 2008; Gebremedhin et al. 2018; Rafiq et al. 2023). Site-level temperature and precipitation data were collected and compiled from local weather stations (Zuliani et al. 2024).

### ***Statistical Analysis***

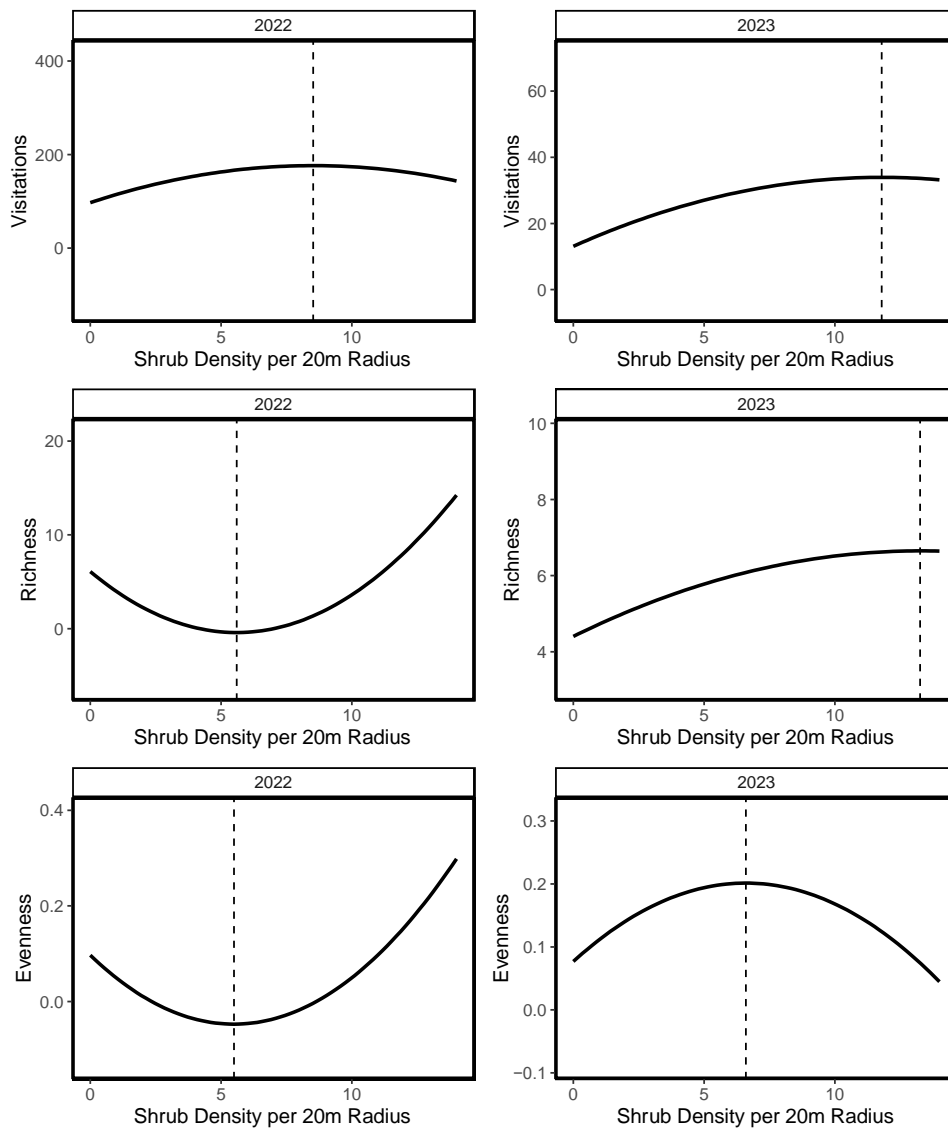
All statistical analyses were conducted in R version. 4.3.1 (R Core Development Team, 2024). A Pearson's correlation test was used to determine the relationship between temperature and humidity and to determine if one of these variables could be utilized as a proxy within the tested models. Temperature and humidity strongly correlated (Appendix D Figure D1;  $r = -0.91$ ,  $p\text{-value} < 0.001$ ), therefore, only one, temperature, was required for our models. Data were tested at the fine scale level for visitations, richness, and evenness of vertebrate species per shrub density within a 20 meter radius and near-surface air temperature. Second degree general linear mixed models (GLMMs) were used to examine these relationships in Southern California with shrub density and near-surface air temperature set as factors. Multiple linear and non-linear models were tested with the model yielding the lowest AIC score utilized (Portet 2020). Total visitations, richness, and evenness were treated as a Poisson distribution. Site-level analysis was conducted utilizing a second degree general linear mixed model with total shrub density and site level aridity as factors. Multivariate analysis of

composition was tested using the vegan package (Oksanen et al. 2022). Principle Coordinate Analyses (PCOAs) compared the different vertebrate communities at both shrub and open plots and to assess whether the composition of the communities varied at increasing shrub density and open plots within Southern California (Dray et al. 2006).

## **5.4: RESULTS**

### ***Shrub Density***

In 2022, vertebrate visitation, richness, and evenness significantly increased with increasing shrub densities (Figure 5.2; Table 5.1). Vertebrate visitation in 2022 significantly increased to a threshold of 8.5 shrubs per 20 m radius (Figure 5.2; Estimate = -0.042; p-value < 0.001), vertebrate richness declined until a threshold of 5.6 shrubs per 20 m radius (Figure 5.2; Estimate = 0.098; p-value = 0.05), and evenness declined with increasing shrub density until a threshold of 5.5 shrubs per 20 m (Figure 5.2; Estimate = 0.003; p-value = 0.002). In 2023, vertebrate visitation, richness, and evenness significantly increased with increasing shrub density (Figure 5.2; Table 5.1).



**Figure 5.2:** The relative effects of increasing shrub density across various arid sites within Southern California. Data was combined from camera traps utilized in 2022 and 2023 field seasons then split by year to display the variation in vertebrate community measurements including visitation, richness, and evenness. Critical thresholds are indicated by a black dashed line. Shaded regions indicate 95% confidence intervals.

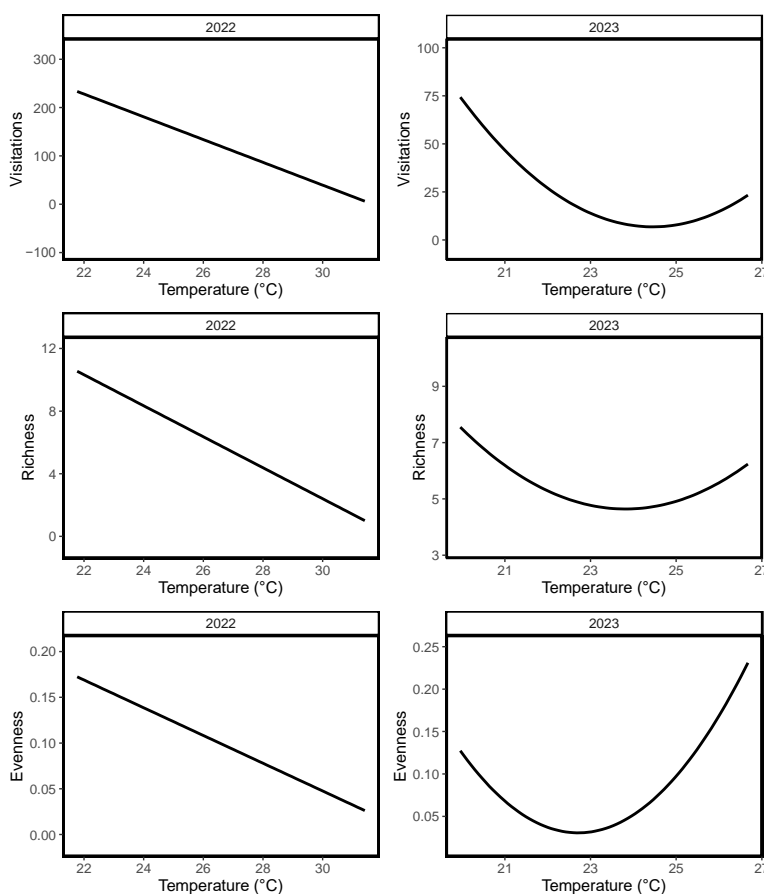


**Table 5.1:** Analysis of site-level vertebrate visitation, richness, and evenness from general linear model for study period with shrub density and logger-temperature as factors. All p-values that were significant at  $p < 0.05$  are indicated in bold.

Year	Factor	Variable	df	Deviance	Residual df	Residual Deviance	p-value
2022	Visitations	Null			23	4036.2	
		Shrub Density	2	227.94	21	3808.2	<b>&lt; 0.001</b>
		Temperature	1	2700.17	20	1108.0	<b>&lt; 0.001</b>
	Richness	Null			23	474.96	
		Shrub Density	2	112.38	21	362.10	<b>&lt; 0.001</b>
		Temperature	1	262.720	20	99.38	<b>&lt; 0.001</b>
	Evenness	Null			23	0.14552	
		Shrub Density <sup>2</sup>	2	0.06372	21	0.08180	<b>&lt; 0.001</b>
		Temperature	1	0.04971	20	0.03209	<b>&lt; 0.001</b>
2023	Visitations	Null			21	468.53	
		Shrub Density	1	101.012	19	367.52	<b>0.0490</b>
		Temperature	1	56.245	18	311.28	<b>&lt; 0.001</b>
	Richness	Null			21	95.318	
		Shrub Density	2	25.9015	19	69.417	<b>0.0337</b>
		Temperature	1	0.6475	18	68.769	0.6806
	Evenness	Null			21	0.16079	
		Shrub Density	2	0.033874	19	0.12692	<b>&lt; 0.001</b>
		Temperature	1	0.085588	18	0.04134	<b>&lt; 0.001</b>

### ***Near-surface Air Temperature***

In 2022, vertebrate visitation, richness, and evenness significantly decreased with increasing near-surface air temperatures (Figure 5.3; Table 5.2). Within 2023, visitation and evenness both significantly decreased with increasing near-surface air temperature, while richness showed no significance (Figure 5.3; Table 5.2).



**Figure 5.3:** The relative effects of near-surface air temperature across various arid sites within Southern California. Data was combined from temperature loggers utilized in 2022 and 2023 field seasons then split by year to display the variation in vertebrate community measurements including visitation, richness, and evenness. Shaded regions indicate 95% confidence intervals.

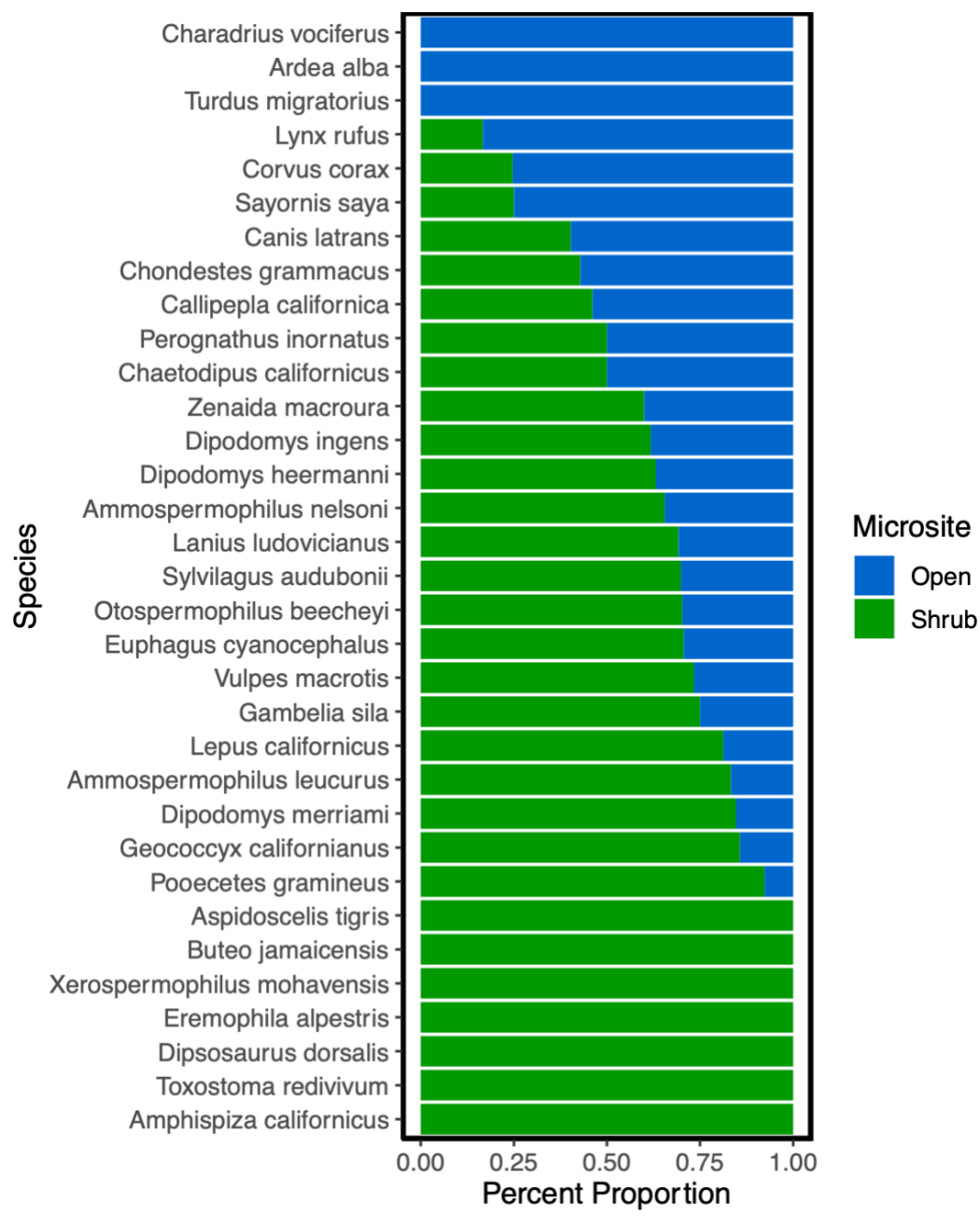
**Table 5.2:** Analysis of site-level vertebrate visitation, richness, and evenness from general linear mixed model for study period with shrub density and aridity as factors All p-values displaying significance ( $p < 0.05$ ) are indicated in bold.

Year	Factor	Variable	df	Deviance	Residual df	Residual Deviance	p-value
2022	<b>Visitations</b>	Null			23	3293.2	
		Shrub Density	2	2223.43	21	1069.8	< <b>0.001</b>
		Aridity	1	884.14	20	185.6	< <b>0.001</b>
		Shrub Density:aridity	2	185.64	18	0.00	< <b>0.001</b>
	<b>Richness</b>	Null			23	459.12	
		Shrub Density	2	293.998	21	165.21	< <b>0.001</b>
		Aridity	1	134.733	20	30.48	< <b>0.001</b>
		Shrub Density:aridity	2	30.477	18	0.00	< <b>0.001</b>
	<b>Evenness</b>	Null			23	0.1353	
		Shrub Density	2	0.0694	21	0.0659	< <b>0.001</b>
		Aridity	1	0.0385	20	0.0274	< <b>0.001</b>
		Shrub Density:aridity	2	0.0274	18	0.0000	< <b>0.001</b>
2023	<b>Visitations</b>	Null			21	277.313	
		Shrub Density	2	65.371	19	211.942	< <b>0.001</b>
		Aridity	1	121.606	18	90.336	< <b>0.001</b>
		Shrub Density:aridity	2	90.336	16	0.000	< <b>0.001</b>
	<b>Richness</b>	Null			21	8.569	
		Shrub Density	2	2.278	19	6.292	0.320
		Aridity	1	3.827	18	2.465	0.051
		Shrub Density:aridity	2	2.465	16	0.000	0.292

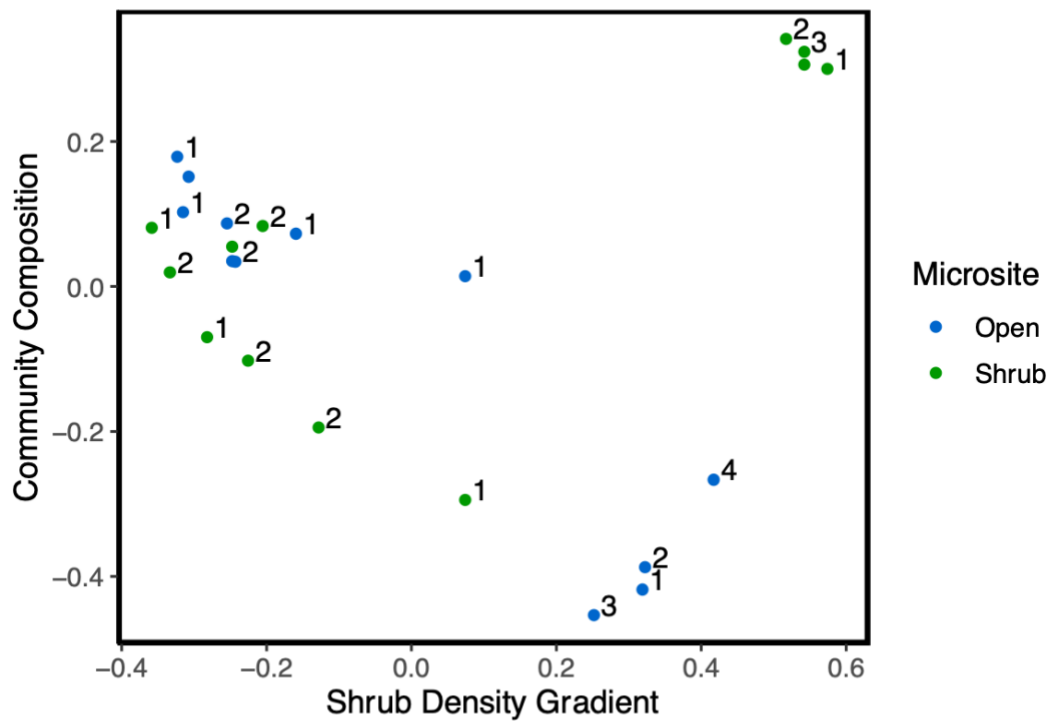
<b>Evenness</b>	Null			21	0.154	
	Shrub Density	2	0.138	19	0.016	< <b>0.001</b>
	Aridity	1	0.008	18	0.008	< <b>0.001</b>
	Shrub Density:aridity	2	0.008	16	0.000	< <b>0.001</b>

### **Community Contrasts**

*Dipodymus heermanni* was the most abundant vertebrate species observed with 2397 observations (Appendix D Table D1). The composition of vertebrate species communities did not significantly vary across shrub and open plots (Figure 5.4; PERMANOVA,  $F_2 = 0.2553$ ,  $R^2 = 0.0294$ , p-value = 0.6184). The composition of vertebrate species communities significantly differed across various sites (Figure 5.5; PERMANOVA,  $F_2 = 3.736$ ,  $R^2 = 0.0184$ , p-value = 0.0409) with Carrizo sites having a significantly different community composition than Tecopa sites (Appendix D Figure D2; Observed p-value = 0.0166).



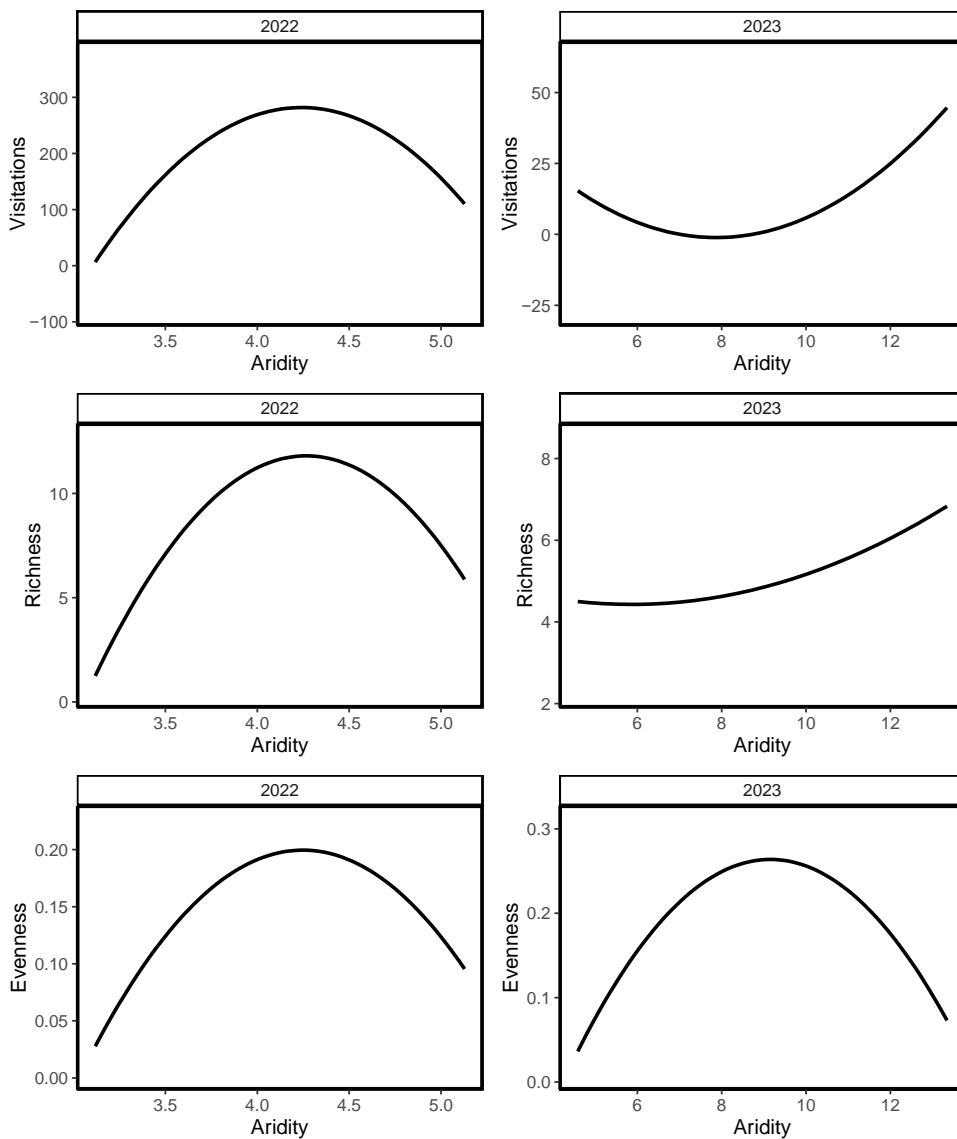
**Figure 5.4:** The relative proportion of vertebrate species across shrub and open sites across arid ecosystems within Southern California. X-axis displays the percent proportion (%) of individuals at both shrub and open plots. Y-axis displays the scientific names of each observed individual during both the 2022 and 2023 field seasons.



**Figure 5.5:** PCA figure displaying the relative similarity in community composition across a shrub density gradient. Data was combined from camera traps utilized in 2022 and 2023 field seasons then split by microsite to display the similarities between community compositions.

### ***Site-level Shrub Density and Aridity Effects***

In 2022, vertebrate visitation, richness, and evenness significantly increased with higher total site-level shrub density, while in 2023, only vertebrate visitation and evenness significantly increased with increasing shrub densities (Table 5.2). In 2022, vertebrate visitation, richness, and evenness increased at higher aridity sites, while in 2023, vertebrate visitation and evenness significantly decreased at higher aridity ecosystems (Figure 5.6; Table 5.2). The visitation, richness, and evenness of vertebrate species significantly increased with relatively higher shrub densities at higher aridity ecosystems in 2022 (Table 5.2). In 2023, visitation and evenness of vertebrate species significantly increased with relatively higher shrub densities at higher aridity sites (Table 5.2).



**Figure 5.6:** The relative effects of aridity across various arid sites within Southern California. Data was collected from weather stations located near each site. 2022 and 2023 field seasons were split by year to display the variation in vertebrate community measurements including visitation, richness, and evenness. Shaded regions indicate a 95% confidence interval.



## 5.5 DISCUSSION

In this study, I examined the effects of changes in shrub densities on the vertebrate community composition, visitation, richness, and evenness across ecosystems within Southern California. I found support for the hypothesis that increasing shrub density will positively influence vertebrate communities across ecosystems within Southern California. Shrub density positively influences the visitation, richness, and evenness of vertebrate species. Fine-scale temperatures had a significant negative impact on the visitation, richness, and evenness of species in 2022 and a negative influence on visitation and evenness in 2023. Sites were significantly more arid in 2022 than in 2023. Community compositions were significantly higher at shrub than at open plots, suggesting that shrubs promote vertebrate communities. Finally, the visitation and evenness of vertebrate species increased with relatively higher shrub densities at higher aridity sites in 2022.

In this study, I found that shrub density positively influences vertebrate species. Structural resources, both artificial and natural, are critical in studies that not only observe species associations, but also measure key structural components of an ecosystem. Globally, shrubs act as benefactor species (Ruttan et al. 2021) through temperature amelioration (Ivey et al. 2020; Zuliani et al. 2023), production of seeds and other food sources (Lortie et al. 2020), and refuge from predation (Filazzola et al. 2017). *Ephedra californica* also provides these facilitative effects that are necessary functions to vertebrate species (Westphal et al. 2018; Zuliani et al. 2021). Smaller vertebrate individuals including *Dipodomys heermanni*, *Gambelia sila*, and *Ammospermophilus leucurus*, utilize these shrubs to reduce predator-prey interactions (Longland & Dimitri 2021). Species that are reliant on these interactions tend to be in locations

where ecological resources, including shrub density and cover, are readily accessible and abundant (Zuliani et al. 2023). For instance, *Gambelia sila*, the Blunt-nosed Leopard Lizard, is known to utilize areas of high shrub density and cover to aid in thermoregulation (Ivey et al. 2020; Lortie et al. 2021; Zuliani et al. 2023b). Other desert species such as *Dipodomys ingens* (the Giant Kangaroo Rat) and *Lepus californicus* (the Black-Tailed Jack Rabbit) utilize these shrubs for foraging and protection from predation (Johnson & Anderson 1984; Prugh & Brashares, 2010). However, as shrub densities increase, shrub encroachment is more prevalent. This increase in shrub density will reconvert these ecosystems into shrublands (Browning 2008), while also enhancing ecosystem functioning through the reduction of desertification and microclimatic buffering (Eldridge & Soliveres 2014; Filazzola et al. 2017). However, the effects of shrub density reached critical points for visitation, richness, and evenness, suggesting that there is a potential limit to the effects shrub density has on these measures before the opposite effect are observed. However, the effects these shrubs have can be ecosystem specific, and have varying impacts on local animal communities. Understanding the importance of the direct interaction between these shrubs and local animal communities, across an increasing stress gradient, can provide insight into the local animal community composition and utilization of these shrubs.

The composition of these vertebrate communities, while not different between shrub and open plots, did differ across sites in Southern California. This suggests that while these sites have similar community compositions, the variation in their shrub density and temperature directly influences individual associations. Vertebrate species such as *Lepus californicus*, while found at all tested sites, were much more frequently observed at Cuyama and the Carrizo Plain

National Monument, than in Tecopa. This suggests that while some species are able to inhabit multiple ecosystems, sites with more favorable conditions are likely to be more suitable and preferred (Vale & Brito 2015). Several factors can cause this variation in community composition including elevation, temperature gradient, available vegetation, aridity, shrub cover and density, and water availability (Marengo & Bernasconi 2015; Welles & Funk 2019; Ivey et al. 2022). Directly analyzing the differences in these communities, in combination with multiple factors that can influence community composition, could further help explain not only the associations these vertebrate species have with foundational shrubs, but how the increasing aridity of Southern Californian deserts are altering these ecosystems.

Anthropogenically driven climatic events, specifically drought and temperature extremes, will continue to increase the aridity of ecosystems across Southern California, influencing both vertebrate community measures and composition. In this study, I found that increasing near-surface air temperatures reduced abundance, richness, and evenness of vertebrate species. As these high temperatures become more prevalent and extreme, shelter via shrub canopies may be a crucial resource to ameliorate these abiotic conditions (Westphal et al. 2018; Ivey et al. 2020; Gaudenti et al. 2021). Previous studies conducted within the Carrizo National Monument showed a higher frequency of shrub-animal association during peak hours of the day when temperatures reached their maximums (Gaudenti et al. 2021; Zuliani et al. 2021; Ivey et al. 2022), suggesting that temperature amelioration is a direct benefit to local vertebrate communities. These shrub canopies generate shade, reducing both near-surface air and soil temperatures within their microclimate, minimizing the risks of overheating (Huxman et al. 2004). The area underneath these shrubs provides more hospitable

microclimates for vertebrate communities in an increasingly arid ecosystem. However, these climate extremes are increasing in intensity and are particularly driven by global warming, which is amplifying aridity through rising temperatures and altered precipitation patterns (Dai 2013). These increasing temperatures and reduced water availability directly contribute to the increased frequency and severity of mega-drought events (Kogan & Guo 2015; Mann & Gleick 2015). Furthering the current understanding on how these increasingly harsh climatic events impact vertebrate community measurements and composition can provide substantial insight into both the management of these ecosystems as well as the preservation of these vertebrate communities.

## **5.6: CONCLUSION**

Shrub density influencing the visitation, richness, and evenness of desert vertebrate species provides meaningful insight into resource selection and association. This suggests that the facilitative interaction between shrubs and desert vertebrate communities is critical for both community composition and structure. With temperatures continuing to rise and climatic extremes increasing in frequency, understanding these shrub-animal associations can guide the preservation and restoration of desert vertebrate communities by placing emphasis on facilitative interactions. Shrub density should be focused upon in ecological studies that aim to assess both the community composition and measurements within an ecosystem as it is a crucial resource utilized by all vertebrate individuals. Future studies focusing on how these shrubs are utilized, not only at the community level but also at a species and taxonomic level, may further enhance the understanding of these associations and the species-specific benefits associated with them. Focusing on how various taxonomic groups or specific species utilizes

these areas of high shrub densities can provide critical insight into community structure and behavior. Here, I advanced the current understanding of facilitative theory by focusing on the influence high densities of foundational shrubs have on local vertebrate communities. This outcome displays the benefits of utilizing an ecological facilitation approach towards community dynamics.

**CHAPTER 6: THE RELATIVE EFFECTS OF ARTIFICIAL SHRUBS ON ANIMAL COMMUNITY  
ASSEMBLY**

**Published as:**

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## 6.1: ABSTRACT

Facilitative associations between the foundational shrub species *Ephedra californica* and local vertebrate species can drive positive interactions within desert ecosystems that influence diversity and assembly processes. These foundational shrubs can contribute to the structural heterogeneity of ecosystems for plants and animals including variation in temperature profiles, refuge from predation, and habitat for foraging. Artificial structures can also influence fine-scale ecological and micro-environmental dynamics. I tested the hypothesis that artificial shrubs (mimics) positively influence desert vertebrate association through facilitative interactions, similar to foundational shrub species. Mimics were deployed at 4 distinct sites within the central deserts of Southern California. A combination of camera traps and temperature pendants were utilized to measure the association patterns of vertebrate species and the microclimatic variation at mimic, open, and shrubs. A total of 21 species were observed in this study. Mimics had a significantly higher vertebrate abundance and richness than open microsites and functioned similarly to shrubs. These findings suggest that mimics can be utilized as a stop-gap replacement for foundational shrub species as they can act as a novel fine-scale habitat for many desert vertebrate species.

## 6.2: INTRODUCTION

Understanding how positive interactions between foundational species and local vertebrate species influence overall community assemblage provides key insights into the community composition and dynamic of an ecosystem. This includes acting as an ecosystem engineer, acting as smaller habitats, and providing key food sources (Ellison et al. 2019). These foundational species structure ecological communities through direct interactions with both local plant and animal communities through the creation of physical structures and the mediation of ecosystem processes such as buffering abiotic stressors (Baiser et al. 2013; Van der Heide et al. 2021). In desert ecosystems, native shrubs act as foundational species providing several resources to local plant and animal communities including temperature amelioration (Ivey et al. 2022), food production (Whitford & Steinberger 2020), and refuge from predation (Westphal et al. 2018). These facilitative interactions drive the association between foundational shrubs and local plant and animal species, where shrub species remain unaffected while the interacting organism benefits (Zuliani et al. 2021). The association with foundational shrubs and their facilitative interactions becomes much more prevalent as local species become more reliant on these shrubs for survival (Michalet 2006). Shrub density and the total cover of these foundational shrubs can provide benefits to interacting species as both are directly associated with one another (Zuliani et al. 2023). The likelihood of these interactions begins to increase as the overall availability of these foundational shrubs increases (Zuliani et al. 2021). This increase in shrub density can positively influence the abundance and richness of vertebrate species within arid ecosystems as it allows more opportunities to benefit from the facilitative interactions (Zuliani et al 2023). With this increase in facilitative opportunities, the probability



for more complex trophic interactions to occur increases while influencing the overall abundance of local vertebrate species (Schneider et al. 2016). Furthering the understanding these facilitative associations between shrub and animal species can enhance our understanding of community dynamics, interactions, and assemblage.

Animal associations with foundational plant species increase substantially when an environment exhibits climatic extremes that require external methods for amelioration (Holmgren & Scheffer 2010). Arid desert ecosystems within Southern California span climatic extremes through frequent drought events in time and across space regionally with extremely low annual precipitation and relatively high temperatures (Reynolds et al 1999; Gols et al. 2021; González-Pérez et al. 2023). However, there are various microclimates within these arid ecosystems, such as those created by naturally occurring shrubs, that contribute to the environmental heterogeneity within an ecosystem (D'Odorico et al. 2010). Heterogeneity - defined as the non-uniformity in physical, ecological, and structural landscape characteristics - (Dronova 2017) at the micro-climatic level can aid not only in the amelioration of these harsh environmental conditions but can also contribute and maintain the biodiversity of species within an ecosystem (Ghazian et al. 2020; Cowan et al. 2021). This variation in micro-environments can substantially impact ectotherms as they provide cooler areas for thermoregulation (Gols et al. 2021). Artificial structures can also influence environmental factors at the micro-climatic level including temperature and relative humidity (Marion et al. 1997; Ghazian et al. 2020; Ghazian et al. 2023). Artificial structures present within ecosystems can lead to habitat fragmentation as seen through the increase in ambient temperature underneath solar farms (Grigorescu et al. 2019). However, some structures can also be utilized

in restoration and management practices by reducing harsh abiotic conditions, similar to foundational shrub species (Ghazian et al. 2020; Ghazian & Lortie 2023). Studies that focus on minimally invasive artificial structures that can provide benefits to both local plant and animal species range from structures that allow varying light permeability (Ghazian et al. 2020; Watchorn et al. 2022) to those that simulate the facilitative effects of shrub species (Holzaphel & Mahall 1999; Padilla & Pugniare 2009). While these artificial structures may take up space that may otherwise be used by naturally occurring structures and may also be comprised of material foreign to these ecosystems, the benefits associated with their microclimate production and animal association can be substantial (Smith et al. 1986). These artificial structures can provide simple resources for local species, such as telephone and other posts acting as perches for avian species (Chavez-Ramirez & Slack 1994; Urbanek et al. 2020). During growing seasons, artificial shrubs can aid both in the growth of plants (Holzaphel & Mahall 1999) and the association of animal species (Thompson 1982; Cobbold & Supp 2012). Utilizing artificial structures that best mimic naturally occurring woody shrub species may provide key insight not only in the facilitative associations between desert structures, shrubs in particular, and local vertebrate species, but also hold the potential to be a key tool utilized in land management and restoration practices.

The capacity for these artificial shrubs to be utilized as a means of species restoration and land management is a fundamental issue that needs further empirical research. *Ephedra californica* is the dominant and often foundational plant species in the region (Westphal et al. 2018; Zuliani et al. 2021). It has a relatively slow growth rate of 0.5 meters in height within a 5 – 10 year period (Lortie et al. 2018; Whitford & Steinberg 2020). Short-term recovery of these

foundational shrubs from fire, disturbances, or canopy loss could be supported through the implementation of artificial structures (Vasek et al. 1975; Lortie et al. 2018). These artificial structures that mimic shrubs provide shorter-term habitat facilitates and supports local vertebrate species until these foundational shrubs are either established or can develop canopies (Ghazian et al. 2020; Watchorn et al. 2022). Artificial structures deployed in areas of low shrub cover could augment resource selection by vertebrate species, influencing their interactions and associations both with local shrubs and between vertebrate populations (Schooley et al. 1996; Abella & Berry 2016; Lortie et al. 2020). The utilization of these artificial structures as a stopgap or short-term conservation and restoration tool can support local vertebrate species while more prominent solutions are developed or until natural shrubs recover from disruption.

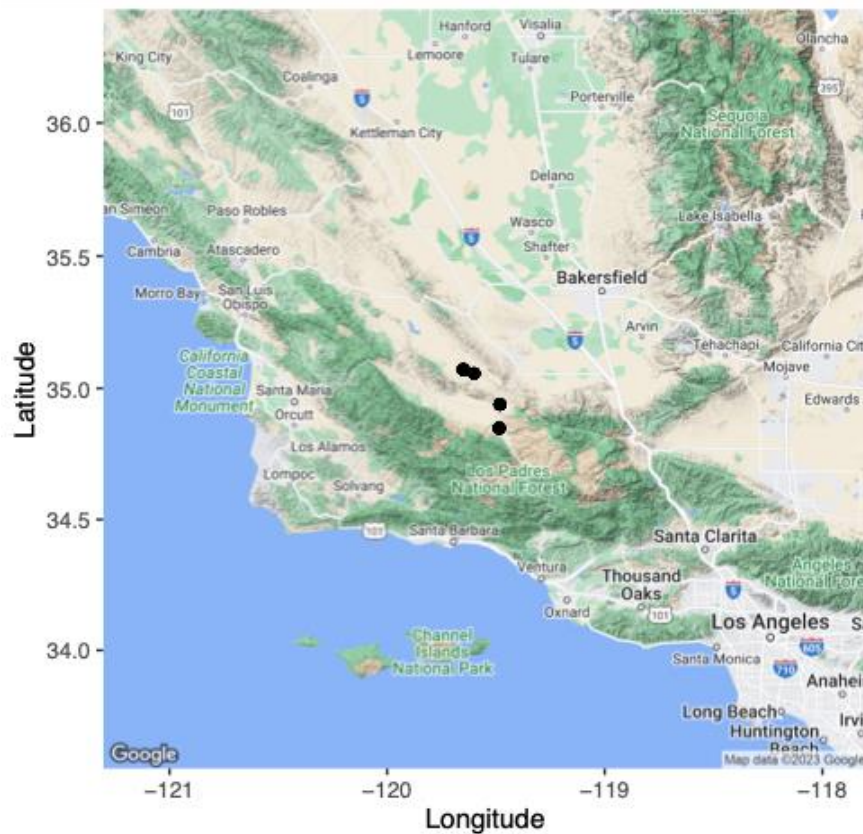
The purpose of this study was to test if shrub mimics, specifically those that closely resemble shrubs, can influence vertebrate community assemblage. I hypothesized that mimics would positively influence the association of desert vertebrate species and can provide facilitative effects similar to the native shrub species. I made the following predictions:

- 1) The reduced ambient and ground temperature under mimic canopies would be similar to that of native shrub species.
- 2) Vertebrate species abundance, richness, and evenness is greater near shrubs relative to open microsites, and the facilitative pattern will be similar with mimics.
- 3) Vertebrate species abundance, richness, and evenness will decrease with increasing ambient and ground temperature at all microsites.

- 4) Vertebrate species abundance, richness, and evenness will be higher at native shrubs as shrub density increases.
- 5) Vertebrate community composition will be significantly different at mimic and shrub microsites than open areas.

### 6.3: METHODS

In this study, the effects of mimics on vertebrate communities were investigated across four unique sites within Southern California (Figure 1). This region is dominated by the foundational shrub species *Ephedra californica*, with some species of salt bush (genus *Atriplex*) scattered throughout (Noble et al. 2016; Filazzola et al. 2017). This shrub species can reach heights of over 1m tall, typically taking 5-10 years to grow 0.5m (Lortie et al. 2018), and it is native to the California Basin (Cutler 1939; Lortie et al. 2018). This species is exceptionally adapted to surviving in the harsh arid condition of the California desert as its needle-like leaves give it characteristics of both angiosperm and gymnosperms (Loera et al. 2012; Di Stillo & Ickert-Bond 2021). This species can recover from full canopy damage within 2 years (Lortie et al. 2018).



**Figure 6.1:** The study sites used to test the effects of mimics on desert vertebrate communities. All maps were generated using the R package *ggmap* (Kahle & Wickham 2013) on November 30<sup>th</sup>, 2023, and the base layer is provided by Google.

The density of *E. californica* individuals at each site was estimated using satellite imagery from 2021. Composite satellite imagery was created using Landsat satellite data, at a 30m resolution (Zuliani et al. 2023b). Each shrub within the tested sites was marked and given a unique latitude and longitude value corresponding to its location (Zuliani et al. 2023b). R version 4.3.1 (R Core Team, 2023) was utilized to determine the average shrub density at each site per m<sup>2</sup>. The total density around each mimic, *E. californica*, and open area, was calculated within a 20m radius.

To assess the association of vertebrate species to these desert regions, I introduced artificial shrubs (mimics) to each site (Appendix Figure S1). These mimics were used to test if they could be utilized to facilitate the positive interactions reported for shrubs. Mimics were selected and purchased based on material, shape, and mean size. Mimics were constructed with large cement bases with plastic branches. Each mimic stood at approximately 1.2m with a mean width of 0.5m, best simulating the average height of *E. californica* individuals (Lortie et al. 2018). A total of 20 mimics was deployed evenly throughout 4 established sites within Southern California. Each mimic was securely dug into the ground, with the cement base flush with the soil surface. Mimics remained deployed at these sites for the 42-day field season and then were removed.

To estimate vertebrate community associations with treatments applied at these four sites, camera traps were deployed. Vikeri Model: A1 2020, with 20 megapixel photo and No-Glow infrared camera traps were utilized to sample vertebrate associations at shrub, mimic, and open microsites within both the Cuyama Valley and Carrizo Plain sites. Cameras were set up 1m from each mimic and shrub with another camera facing the opposite direction towards an open area. Each site consisted of 5 mimic cameras, 3 shrub cameras and 8 open cameras. Camera traps remained deployed for the duration of the 42-day field season taking photos both during the day and night (Noble et al. 2016). To prevent animal disturbance, no flash was set during night sampling. Each camera was set to medium sensitivity, with a 1-min photo delay to reduce the number of mis-fired recordings (Zuliani et al. 2021). Cameras were checked and maintained approximately every 4-5 days to ensure proper function for the duration of the 42-day field study. All images from SD cards were saved as Joint Photographic Export Group (JPEG)

and examined for data extraction. Each photo was taken as an individual datapoint and recorded; file name, rep, date, time, site, microsite, microsite number, presence of animal, scientific name of animal, and number of objects in photo. New animal individuals were defined as an individual that was not in the same location after the 1-min photo delay. Camera trap rate of captures were determined by taking the number of photos with an observable vertebrate individual by the total number of photos taken (Noble et al. 2016).

To gather local measures of ambient temperature and humidity, OMEGA compact portable temperature and humidity data loggers were suspended above ground by approximately 20cm (<https://www.omega.ca/en/data-acquisition/data-loggers/temperature-and-humidity-data-loggers/om-90-series/p/OM-91>). A pendant was placed at 3 randomly selected mimics, 3 randomly selected open areas, and 3 *E. californica* individuals at each site. A total of 33 data loggers were deployed across the 4 tested sites. These pendants remained deployed for the duration of the field experiment. Hourly temperatures (°C) were logged by the pendants and used to calculate the daily mean and maxima. Relative humidity (%) was recorded using a Mengshen hand-held humidity reader (<https://m.media-amazon.com/images/I/A1rsvBzcoNL.pdf>) at 5-day intervals. Ground temperature was recorded using a Etekcity Infrared Thermometer Digital Temperature Gun for all microsites. Ground temperature was measured every 5-6 days.

All statistical analyses were conducted using R version 4.3.1 ([www.rproject.org](http://www.rproject.org)). General Linear Models (GLMs) were used to test for a relationship between microsite and vertebrate abundance, richness, and evenness across all tested sites. Models included mean near-surface air temperature, ground temperature, and shrub density as factors. All models were fit to a

Poisson distribution. Linear fits were utilized over others by conducting Shapiro-Wilk tests. ANOVAs with  $\chi^2$  tests were utilized where variables in models showed significance. Post-hoc Tukey analyses were done using the function `emmeans` from the Estimated Marginal Means R package (Lenth 2023). Relative interaction indexes (RII) were generated to compare the effects of mimics and shrubs on animal community measures. RII was calculated using the equation  $RII = (A_s - A_o)/(A_s + A_o)$ , where  $A_s$  represents the parameter for temperature under shrub or mimic microsites, while  $A_o$  represents the temperature at the corresponding open microsites (Armas et al. 2004). Principle Coordinate Analysis (PCOAs) were conducted to compare the vertebrate community composition between mimic, shrub, and open microsites. The map was generated using the `ggmap` package and google imagery (Kahle & Wickham 2013; Wickham 2016).

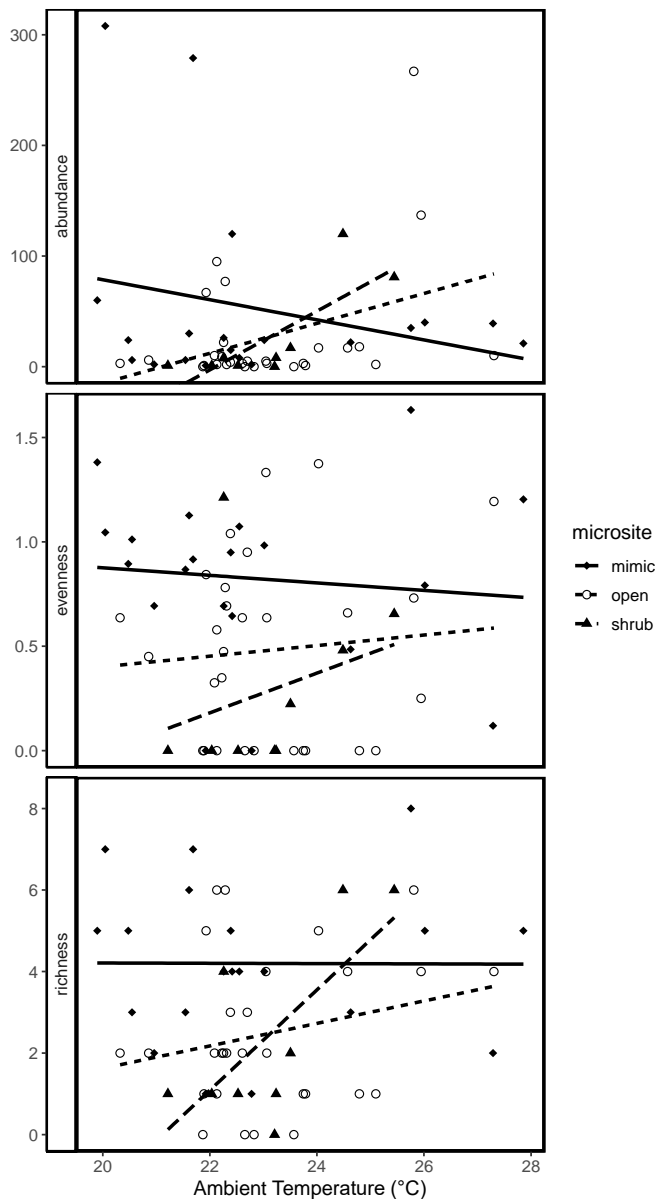
#### 6.4: RESULTS

A total of 425,464 photos were captured with all camera traps. There were 2,080 vertebrates positively identified, with a capture rate of 0.49%. Mean near-surface air temperatures did not significantly differ between microsites (Appendix E Figure E2; GLM,  $df = 3$ ,  $F = 0.21$ ,  $p$ -value = 0.81). Surface ground temperatures significantly varied (GLM,  $df = 3$ ,  $F = 26.56$ ,  $p$ -value < 0.001), and was significantly lower at shrubs relative to mimics (EMM  $11.44 \pm 1.78$ , post-hoc,  $p$ -value < 0.001) or open microsite (EMM  $11.94 \pm 1.7$ , post-hoc,  $p$ -value < 0.001).

While mean near-surface air temperatures did not significantly differ between the three microsites, increasing mean near-surface air temperatures predicted higher abundance (Figure 6.2; Table S1) and richness of vertebrate individuals (Figure 6.2; Table S1). There were



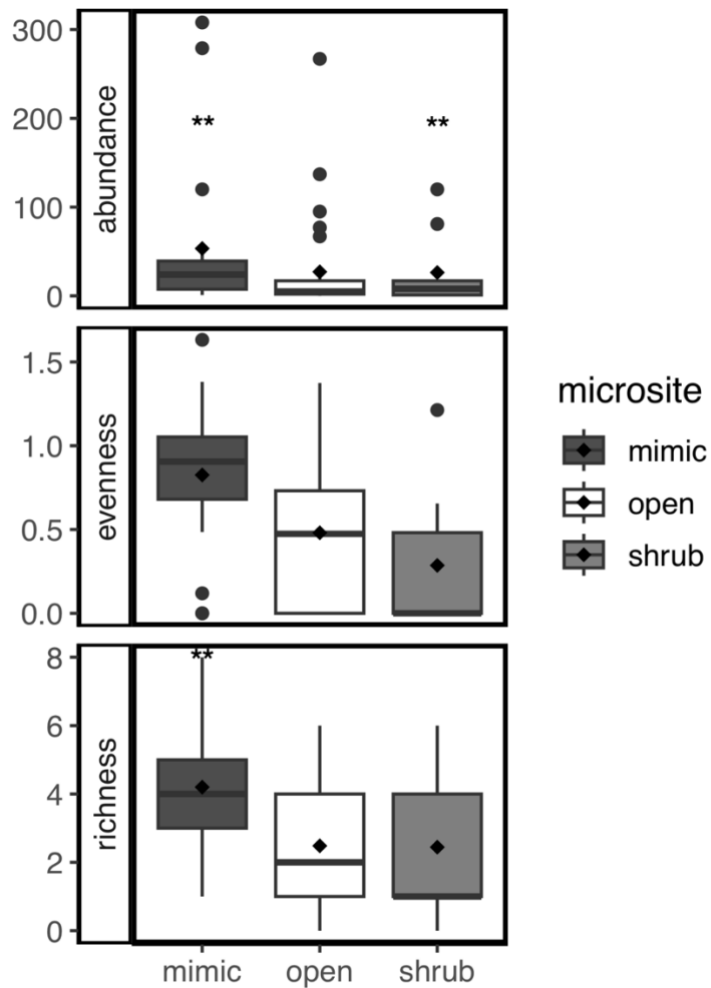
significantly more animals at mimics than in the open (EMM  $0.724 \pm 0.05$ , p-value  $< 0.001$ ) and shrub microsites (EMM  $0.773 \pm 0.122$ , p-value  $< 0.001$ ). Vertebrate richness was significantly higher at mimics than both open (EMM  $0.53 \pm 0.16$ , p-value  $< 0.01$ ) and shrubs (EMM  $0.669 \pm 0.28$ , p-value = 0.04). Increasing ground temperature significantly influenced the abundance of vertebrate species (Appendix E Figure E3; Table E1). Vertebrate abundance was significantly higher at mimic than open microsites (EMM  $0.302 \pm 0.07$ , p-value  $< 0.001$ ). There was no significant difference in vertebrate abundance between mimic and shrub (EMM  $-0.881 \pm 0.5409$ , p-value = 0.233), and shrub and open microsites (EMM  $-1.182 \pm 0.54$ , p-value = 0.07).



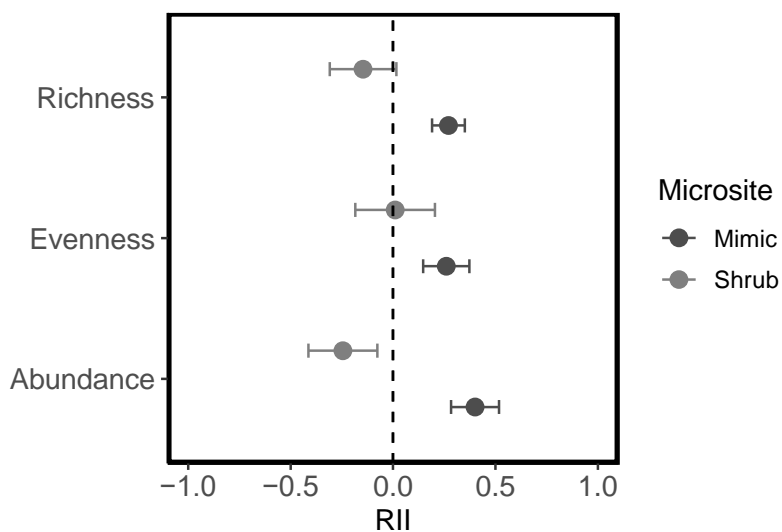
**Figure 6.2:** The relative effects of near-surface ambient air temperature on vertebrate species across all tested microsites. Shaded areas show a 95% confidence interval associated with each line of best fit.

The influence of microsite association on the abundance and richness of vertebrate species is evident, with significant variation observed across microsites (Figure 6.3; Table S1). Vertebrate abundance was significantly greater at mimic than open microsites (EMM  $0.578 \pm 0.05$ , p-value < 0.001) and at shrubs than in the open (EMM  $-0.473 \pm 0.08$ , p-value < 0.001).

Mimics and shrubs did not differ in abundances (EMM  $0.106 \pm 0.08$ ,  $p$ -value = 0.36). Vertebrate species richness was significantly higher only at mimic than open microsites (EMM  $0.5196 \pm 0.16$ ,  $p$ -value < 0.01). Mimic microsites had a positive mean effect on animal community measures (mean effect  $0.3103 \pm 0.1034$ ). Mimics were more beneficial to animal community abundance (Figure 6.4;  $t = 3.145$ ,  $df = 16.037$ ,  $p$ -value = 0.006) and richness (Figure 6.4;  $t = 2.302$ ,  $df = 12.068$ ,  $p$ -value = 0.04) but not evenness relative to shrub microsites (Figure 6.4;  $t = 1.112$ ,  $df = 13.656$ ,  $p$ -value = 0.2853).



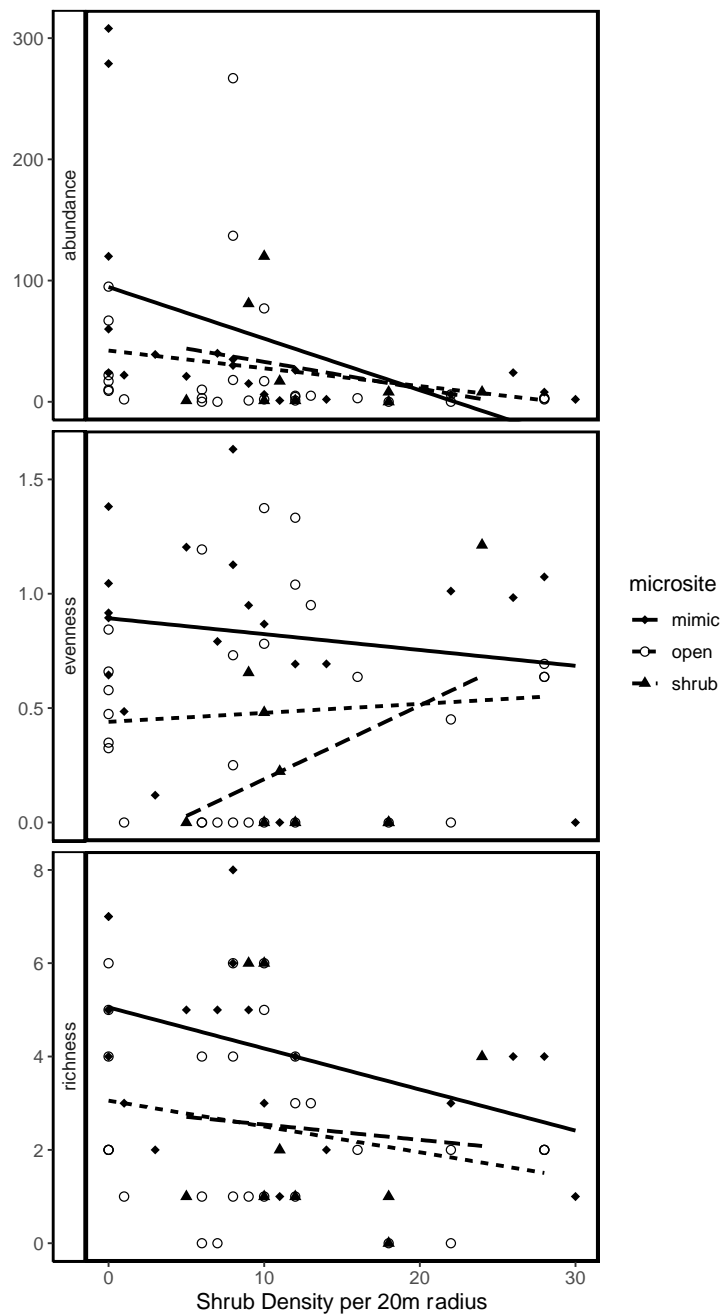
**Figure 6.3:** A comparison of the mimic, open, and shrub microsites on vertebrate community composition in Central California Deserts. Boxes represent the Interquartile Range (IQR), with medians indicated by a dark black line. Whiskers extend to 1.5x the IQR with points beyond these considered to be outliers. Black diamonds represent the mean values for each microsite. All significant relationships are indicated with black asterisks.



**Figure 6.4:** The relative association patterns of vertebrate abundance, richness, and evenness within Central California deserts, between paired shrub and open, and mimic and open microsites. The relative interaction intensity effect size measure (RII) is reported with positive values denoting facilitative or positive interactions and negative values denoting negative interactions (ranging from -1 to 1). Values overlapping 0 indicate neutral interactions. All values shown indicate means  $\pm$  95% confidence intervals.

There were significant reductions in both abundance and richness within 20m areas, while evenness remained unaffected (Figure 6.5; Table S1). Vertebrate abundance was significantly higher at mimics than open microsites as shrub density increased (EMM  $0.302 \pm$

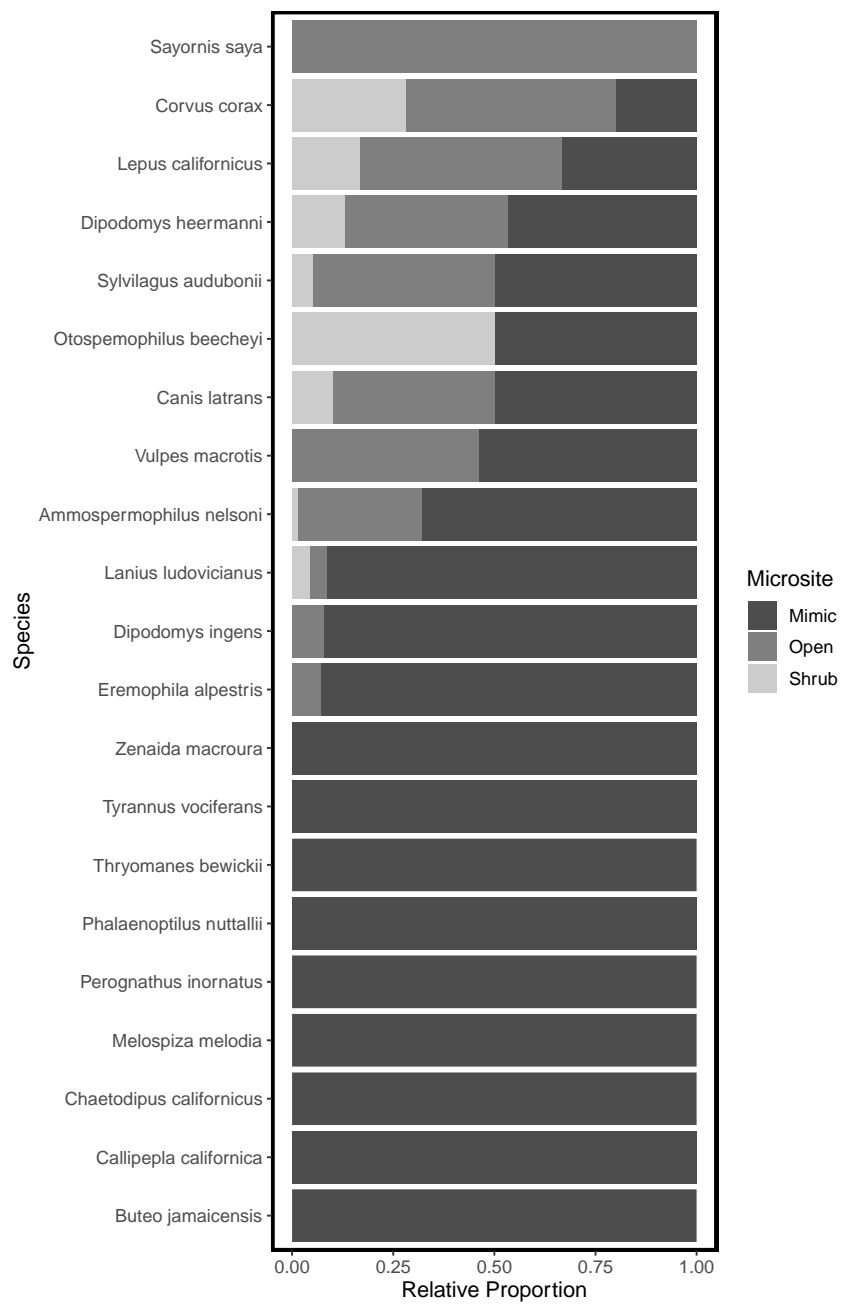
0.0739,  $p$ -value  $< 0.001$ ). There was no significant difference in abundance between mimics and shrub (EMM  $-0.881 \pm 0.54$ ,  $p$ -value = 0.234), and open and shrub microsites (EMM  $-1.182 \pm 0.54$ ,  $p$ -value = 0.073). Vertebrate species richness was significantly higher at mimics than in the open as shrub density increases (EMM  $0.473 \pm 0.198$ ,  $p$ -value = 0.044). There were no significant differences in vertebrate richness in the open and shrub (EMM  $0.34 \pm 1.46$ ,  $p$ -value = 0.97), and mimic and shrub microsites (EMM  $0.813 \pm 1.46$ ,  $p$ -value = 0.84).



**Figure 6.5:** The relative effects of shrub density on vertebrate species abundance, richness, and evenness across all tested microsites. Data across all sites were combined by microsite to illustrate the effects of shrub density on microsite association. Shaded areas show a 95% confidence interval associated with each line of best fit.

The analysis of vertebrate species distribution showed that *Dipodomys heermanni*, Heerman's Kangaroo Rat, was the most prevalent species observed with 15550 unique pictures (Appendix E Table E2). Heerman's Kangaroo Rat was most frequently associated with mimics and shrubs rather than with open areas (Figure 6.6). The comparison of the vertebrate communities did not significantly vary across mimic, shrub, and open microsites (Appendix E Figure E4, Figure E5; PERMANOVA,  $F_2 = 1.17$ ,  $R^2 = 0.04$ , p-value = 0.28).





**Figure 6.6:** The relative proportion of observed vertebrate species across tested microsites. The x-axis indicates the relative proportion in decimal form of the total number of individuals at each microsite, while the y-axis indicates the scientific name of the observed species.

## 6.5: DISCUSSION

In this study, I examined the effects of mimics on vertebrate community assemblage and composition compared to naturally occurring shrubs and open areas. I found support for the hypothesis that mimics will positively influence the association of desert vertebrate species. I found that the air temperature under mimics was similar to shrubs while the ground temperature was significantly lower under naturally occurring shrubs. Vertebrate abundance and richness were significantly higher at mimic and shrub microsites when compared to open microsites. As near-surface air temperatures increased, mimics become more important for animals than shrubs and open areas. Increasing ground temperatures significantly influenced the abundance of vertebrate species at mimics compared with the open microsites. As shrub density increased, the abundance and richness of vertebrate species was reduced. However, with increasing shrub densities, the abundance and richness of vertebrates were higher at mimics than in the open microsites.

Biological structures, specifically within deserts, can influence the overall abundance and diversity of local species community composition and trophic interactions (Buhl-Mortensen et al. 2010; Stevens & Tello 2011; Ghazian et al. 2020). Having a diverse array of structures can influence both the resource and structural heterogeneity of these ecosystems (Ribas et al. 2003; Stevens & Tello 2011). Resource heterogeneity indicates variation in the available number of resources including size and quality of food sources, total shaded cover, and nutrient abundance (MacArthur & MacArthur 1961; Stevens & Tello 2011), while structural heterogeneity is seen as the variation in physical structures (Buhl-Mortensen et al. 2010; Stevens & Tello 2011; Hovick et al. 2014). Areas with larger and more numerous structures

contribute to a wider array of heterogeneity as it provides variation in plants, topography, and microclimate (Kappes et al. 2009; Oliver et al. 2010). Within desert ecosystems, foundational shrubs are the largest contributors to both resource and structural heterogeneity (Cáceres et al. 2015). When the density of these foundational shrubs increases, the frequency of association increases, supporting the theory that areas with more structural heterogeneity positively influence species (Wiens & Rotenberry 1981; Zuliani et al. 2021). Our findings suggest that the introduction of new structures, in the form of mimics or simple shelters with a canopy, could strongly contribute to the structural heterogeneity of desert ecosystems, and positively influence vertebrate communities. While these structures do not necessarily provide resources such as food, they are able to provide cover and protection from harsh abiotic factors (Lemm & Tobler 2021). In addition, these structures can provide refuges for invertebrates that many animals do eat, thus indirectly increasing prey item availability (Price et al. 1980). Although not measured here, these interactions can result in trophic cascades across multiple levels of interactions promoting local vertebrate communities (Hambäck et al. 2004). Thus, these artificial structures can enhance both resource and structural heterogeneity similarly to the way that naturally occurring shrubs influence their environment.

*Ephedra californica* also have the potential to act as foundational species within these ecosystems. These foundational species typically exert facilitative interactions with both plant and animal communities (Brewer et al. 2021; Lortie et al. 2021; Zuliani et al. 2021; Zuliani et al. 2023a). Foundational shrub species promote the recruitment and association of vertebrates primarily through temperature amelioration, as several species within desert ecosystems will utilize the microclimate produced by shrub canopies to thermoregulate (Attum et al. 2013; Ivey

et al. 2020; Ivey et al. 2022; Zuliani et al. 2023b). Previous work on *Gambelia sila* has supported this concept, with individuals associating more frequently with foundational shrubs (Westphal et al. 2018; Ivey et al. 2020; Ivey et al. 2022; Zuliani et al. 2023b). Our study showed that mimics provide consistent benefits to all three animal community measures, and outperformed shrubs in two instances. The net positive effects of mimics on animal community abundance and richness suggests that animals benefit from these associations and that mimics can act as foundation species, similar to naturally occurring shrubs. It is possible that these mimics could be utilized as a temporary means of species recruitment and conservation, especially in areas that have experienced severe weather or climate changes. The overall availability or density of these mimics may also influence the net interactions and associations of local vertebrate communities. In areas of increasing shrub density, these facilitative effects are much more frequent resulting in a higher association of vertebrate species in these areas (Zuliani et al. 2021). This higher frequency in possible facilitative associations can lead to more frequent and larger benefits for interacting species (Zhang & Tielbörger 2020; Zuliani et al. 2023a). Our findings suggest that mimics can imitate shrub canopy microclimates and could potentially be used by managers as a temporary replacement. Specifically, our findings showed areas with low densities of foundational shrubs had more vertebrates associating with mimics. However, as the density of foundational shrubs increased, mimics were utilized to a lesser extent. This suggests that these mimics have the potential to act as a proxy for these foundational shrub species for areas void of shrubs, while still having benefits when foundational shrubs are present. This is not to say that shrubs can be replaced by mimics as they still regulate several processes within desert ecosystems including acting as a food source (Lortie et al. 2020),

promoting native plant communities (Filazzola et al. 2020), and by acting as ecosystem engineers (Cushman et al. 2010). Our findings also showed that mimics had greater vertebrate abundance at increasing temperatures than in the open, suggesting that the necessary benefits needed by these species can be provided by artificial structures in the absence of naturally occurring shrubs. Further understanding the benefits associated with artificial structures, in particular those that mimic naturally occurring shrubs, can provide key information for restoration and conservation.

## 6.6: CONCLUSION

Mimics significantly influence the abundance and richness of vertebrate species as near-surface air temperature, ground temperature, and shrub density increase. This suggests that these structures have the potential to be utilized as a temporary replacement for foundational shrub species. These foundational shrubs, specifically *E. californica*, are extremely resilient to abiotic factors within these arid environments (Lortie et al. 2018). This species has a lifespan of over 100 years, however, the growing period for this species is relatively slow (Bowers et al. 1995). The utilization of these mimics, even as a temporary replacement for shrubs, could be greatly beneficial to local vertebrate communities. These mimics could potentially aid in the restoration and management of endangered or threatened vertebrate communities as they are able to mimic some of the key microclimatic variation that shrubs provide. Endangered species, such as *Gambelia sila*, are reliant on shrub microclimates to thermoregulate (Gaudenti et al. 2021), thus mimics could act as a valuable resource, or temporary solution, in the management of these types of species. However, these facilitative interactions associated with the foundational shrub species *E. californica* can in theory promote the growth and establishment of invasive annual species,

such as *Bromus rubens* (Lucero et al. 2020; Lucero et al. 2021). Further studies can assess the impacts that these mimics could have on desert plant communities. Changes in the plant community composition to favor invasive plant species can be tested through time under canopies, artificial and natural, relative to open microsites. A possible negative impact from these mimics is the introduction of microplastics into desert ecosystems. Since these structures are primarily composed of plastic material, there is a likelihood for microplastics to enter the environment (Manzoor et al. 2022). However, relatively shorter deployment could limit microplastic effects into the environment. Nonetheless, as plastic structures were utilized by vertebrate species, there is a possibility for smaller plastic portions to become present within the food chain (Li et al. 2022). Future studies could focus on utilizing biodegradable material that similarly mimic the benefits of foundational shrub species, such as burlap or cotton canvas (Kuhns 1997; Ghazian et al. 2020; Ghazian et al. 2024). With the current decline in desert health and decline in local species, it is imperative to understand how resources, both natural and artificial, can be utilized to not only preserve communities, but also aid in the restoration of individuals that have been negatively impacted. Ideally, nature-based solutions that use native plants to support local vertebrate populations are developed to reduce the impacts of natural hazards (Keesstra et al. 2018; Debele et al. 2023). The use of artificial structures, such as shrub mimics, is therefore a useful steppingstone to enable persistence whilst dryland restoration and conservation practices are further advanced. In this study, I show that mimics are effective at supporting local vertebrate communities. However, new research should explore the best context to deploy this solution.

## Chapter 7: GENERAL CONCLUSION

In these studies, I utilized the concept of shrub density to test if this naturally occurring resource can be utilized by other dryland species. I examined current facilitation literature to determine the reported effects of shrub density on animal species abundance (Chapter 2). I also tested if alterations in temperature, as seen under shrub canopies and in open areas, affect the early-life stages of dryland plant species (Chapter 3). I further emphasized the importance of shrub density by utilizing this measure to predict the presence of the endangered species *G. sila* (Chapter 4). I also examined the effects of high shrub density on vertebrate community composition (Chapter 5). Finally, I examined the effects of artificial shrubs on vertebrate community composition at sites with varying densities of foundational shrub species (Chapter 6). Until this point, shrub cover was considered to be the fundamental measure utilized when analyzing facilitative associations. However, these studies suggest that facilitative associations can also be analyzed by shrub density.

In Chapter 2, I found that shrub density could significantly predictor animal abundance, acting as a simpler estimate than shrub cover. These results were ecosystem specific, with shrub density having positive effects in grasslands but negative effects in deserts. These effects were also specific to the associated shrub species with *Caragana korshinkii* positively influencing animal populations. In Chapter 3, I found that increasing temperatures significantly reduced plant germination, establishment and overall biomass. However, the invasive species *B. rubens* seemed to suffer the most out of the four tested species. *Phacelia tanacetifolia* performed significantly better than the invasive *B. rubens* species, suggesting that promoting this particular native annual could be a potential tool in reducing invasive species populations. In Chapter 4, shrub density and cover positively correlated suggesting that both resources can be used to

estimate *G. sila* populations. This chapter also showed that shrub density can be used to predict the presence of *G. sila* individuals, both above and below ground, up to a critical point of around 99 shrubs per 20m radius. Shrub density significantly predicted the presence of male *G. sila*, suggesting that male individuals will be more frequently found at areas with more shrubs. In Chapter 5, shrub density significantly influenced vertebrate species abundance, richness, and evenness both in 2022 and 2023. The vertebrate community composition across tested sites significantly varied suggesting that each tested site had unique vertebrate communities. Increasing near-surface air temperatures significantly reduced the abundance, richness, and evenness of vertebrate species across all tested sites. Finally, vertebrate species abundance, richness, and evenness increased at sites with lower aridity scores, suggesting that as a site becomes more arid, vertebrate species become more reliant on facilitative associations with shrubs. In Chapter 6, I found that there was a higher abundance and richness of vertebrate species at both shrub and mimics microsites than in the open, suggesting that these artificial structures could provide similar benefits to that of natural shrubs. The density of shrubs around each microsite significantly influenced the abundance and richness of vertebrate species, further suggesting that shrub density is an important measure in facilitative studies. Finally, vertebrate community composition did not vary across shrub, mimic and open microsites.

A key innovation in my studies was utilizing the concept of shrub density in both analyzing the effects of facilitative associations and community composition. Shrub density is typically not measured, while shrub cover or percent cover is utilized both in estimating density and to analyze shrub-animal associations. However, I have shown that utilizing shrub density to assess facilitative associations, predict species presence, and analyze community composition, can be a much simpler in-field measure and act as a proxy for shrub cover (Zuliani et al. 2021;



Zuliani et al. 2023; Zuliani et al. 2024). This is not to say that shrub cover is not an important measure in facilitative studies, but that both shrub cover and density can be assessed to determine the effects of foundational shrubs on dryland ecosystem communities. A larger focus should be placed on shrub density in ecological studies that aim to assess community composition and measurements within dryland ecosystems, as these resources are utilized by both plant and animal communities to ameliorate high abiotic stressors. These resources can be utilized for conservation and restoration practices for endangered plant and animal species, as shrub density can increase the frequency of facilitative associations, thus further aiding benefactory species (Gaudenti et al. 2021; Zuliani et al. 2023).

Future studies focusing on facilitative associations between foundational shrubs and local plant and animal communities should assess the net impacts of these associations in terms of shrub density. Understanding how the availability of these resources shape community composition, behaviour, measurements, and distribution, can provide key insight into ecosystem functions and both intra and interspecific interactions. Focusing on how various taxonomic groups utilize both individual foundational shrubs and areas of varying shrub density can provide critical insight into community structure and behaviour. In addition, focusing on species specific responses to shrub density, like Chapter 4, can provide insight into species-specific utilization of foundational shrub species. Within this dissertation, I have provided a significant enhancement in the current understanding of facilitative theory by focusing on the influence shrub density can have at multiple ecosystem levels. These outcomes display the benefits of highlighting such an important resource for communities and suggest that shrub density should be a critical measure in dryland studies.

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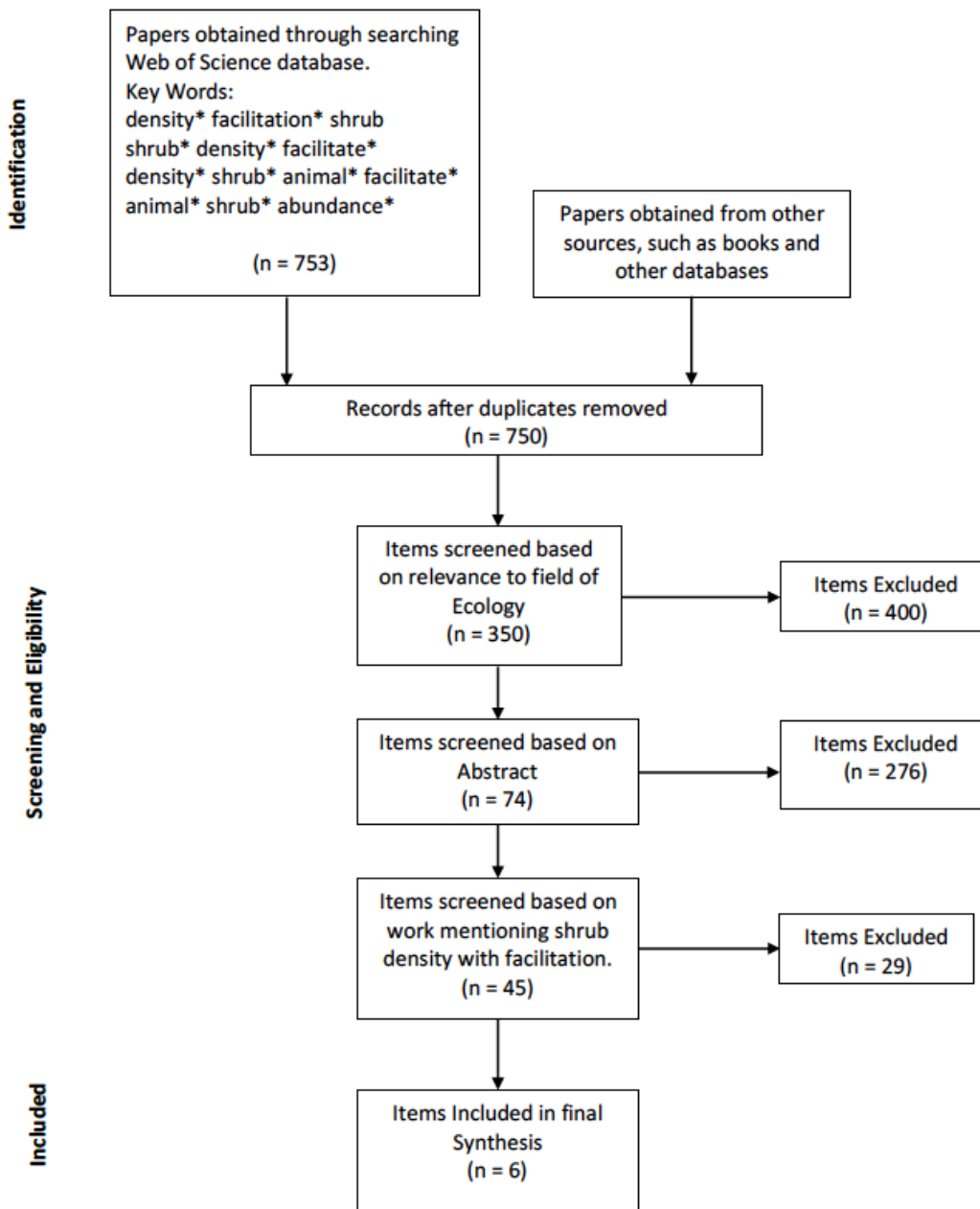
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## APPENDIX A:

**Figure A1:** Prisma diagram used for shrub density review (Moher et al. 2009). Keywords include: 1) density\*, shrub\*, facil\*, 2) density\*, shrub\* facil\*, animal\* 3) density\*, shrub\* animal\* facilitate\*, AND 4) animal\*, shrub\*, abundance\* in March 2022.



**Table A1:** A list of studies in a systematic review of shrub-animal association patterns that examined density directly. Data were extracted from each paper including title, year of publication, shrub species, and technique used in each study.

Title	Year	Shrub Species	Technique	Ecosystem	Animal Diversity	Focal Animal Species	Interaction	Key Findings
A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard	2018	<i>Ephedra californica</i>	Telemetry	Desert	1	<i>Gambelia sila</i>	direct	A dominant shrub species influenced the abundance and distribution of <i>Gambelia sila</i> .
Accuracy of space-for-time substitution for vegetation state prediction following shrub restoration	2016	<i>Caragana microphylla</i>	Restoration	Desert	various	community-level	indirect	Restoration of four dominant shrub species were identified as foundation species that likely support local animal populations in deserts.
Arid old-field restoration: Native perennial grasses suppress weeds and erosion, but also suppress native shrubs	2014	<i>Atriplex canescens</i>	Survey	Desert	various	community-level	indirect	Replanting of 4 native plant species can enhance animal population distribution within arid old fields
Canopy gaps facilitate establishment, growth, and reproduction of invasive <i>Frangula alnus</i> in a <i>Tsuga canadensis</i> dominated forest	2010	<i>Tsuga canadensis</i>	Model	Forest	various	community-level	indirect	Clearing to promote native shrub recruitment will influence positive plant and animal dynamics locally.

Canopy manipulations of exotic Bitter Willow ( <i>Salix elaeagnos</i> ) forest for indigenous seedling recruitment: A pilot study	2017	<i>Salix elaeagnos</i>	Survey	Forest	various	community-level	indirect	Shrub density influenced the association of exotic grasses and provided suitable structure for local bird species.
Characteristics of the boreal mixedwood forest associated with the use of subnivean access points by American martens	2013	Not specified	Telemetry	Forest	1	<i>Martes Americana</i>	direct	Presence of deciduous shrub species can facilitate <i>Martes americana</i> activity.
Characterizing <i>Betula litwinowii</i> Seeding Microsites at the Alpine-Treeline Ecotone, Central Greater Caucasus Mountains, Georgia	2009	<i>Rhododendron caucasicum</i>	Survey	Alpine	various	community-level	indirect	Higher densities of shrub individuals can influence both local plant and animal communities.
Cross-spatial-scale patterns in the facilitative effect of shrubs and potential for restoration of desert steppe	2010	<i>Caragana microphylla</i>	Survey	Desert	various	community-level	indirect	Transplant shrubs at higher densities can improve the succession of vegetation and indirectly influence local animal associations.

Demographic consequences of drought in the herbaceous perennial <i>Cryptantha flava</i> : Effects of density, associations with shrubs, and plant size	1996	<i>Juniperus osteosperma</i>	Model	Grassland	various	community-level	indirect	Drought does not have an impact on the facilitative effects of shrub individuals thus allowing animal associations.
Does size matter? Ontogenetic responses of an Andean shrub to conspecific density-dependence	2017	<i>Croton wagneri</i>	Survey	Alpine	various	community-level	indirect	Shrub interactions can influence the spatial structure of local plant communities and indirectly influence animal associations.
Early ecological succession on landslide trails, Hong Kong, China	2018	Not specified	Survey	Shrubland	various	community-level	indirect	Establishment of pioneer shrubs can aid in early ecological succession by facilitating local plant communities and providing bird perches.
Effects of drought and slope aspect on canopy facilitation in a mountainous rangeland	2016	<i>Astragalus meschedensis</i>	Experimental	Grassland	various	community-level	indirect	Shrubs can influence local ecosystem factors such as nitrogen fixation, which can indirectly influence the association of local herbivore species to understory plant matter.

Effects of exotic and endogenous shrubs on understory vegetation and soil nutrients in the south of Tunisia	2015	<i>Retama raetam</i>	Experimental	Desert	various	community-level	indirect	Local shrub individuals can positively influence understory plant community thus recruiting local herbivore species.
Effects of intraspecific and community density on the lifetime fecundity of long-lived shrubs	2013	<i>Protea repens</i>	Experimental	Forest	various	community-level	indirect	Shrub density can influence the association of generalized animal pollinators at the community level.
Effects of Sagebrush Restoration and Conifer Encroachment on Small Mammal Diversity in Sagebrush Ecosystem	2019	<i>Juniperus osteosperma</i>	Experimental	Desert	10	<i>Peromyscus maniculatus</i> <i>Reithrodontomys megalotis</i> <i>Tamias dorsalis</i> <i>Peromyscus truei</i> <i>Microtus montanus</i> <i>Microtus longicaudus</i> <i>Perognathus mollipilosus</i> <i>Lemmings curtatus</i>	direct	Sagebrush restoration can have high-intensity influence on small mammalian species.
Empirical evaluation of directed dispersal and density-dependent effects across successive recruitment phases	2012	<i>Ochradenus baccatus</i>	Survey	Desert	various	community-level	indirect	Shrub density effects can influence the distribution of seeds via animal species and other mechanisms.



Facilitation among plants: A strategy for the ecological restoration of the high-andean forest (Bogota, DC-Colombia)	2013	<i>Lupinus bogotensis</i>	Experimental	Forest	various	community-level	indirect	General benefit to animal populations proposed with native plant restoration.
Facilitation among woody plants establishing in an old field	1998	<i>Symphoricarpos occidentalis</i>	Experimental	Grassland	various	community-level	indirect	Shrub density can shelter nutrient-depositing animals.
Facilitation and edge effects influence vegetation regeneration in old-fields at the tropical Andean forest line	2015	<i>Baccharis prunifolia</i>	Survey	Forest	various	community-level	indirect	Facilitation and edge effects influence vegetation regeneration, thus indirectly recruiting herbivore species.
Facilitation of Nothofagus antarctica (Fagaceae) seedlings by the prostrate shrub Empetrum rubrum (Empetraceae) on glacial moraines in Patagonia	2005	<i>Empetrum rubrum</i>	Experimental	Alpine	various	community-level	indirect	Presence of shrub species facilitate the establishment of local plant species thus indirectly influencing herbivore species.
Focusing on individual species reveals the specific nature of assembly mechanisms in a tropical dry-forest	2018	Not specified	Experimental	Forest	various	community-level	indirect	Shrub facilitation can influence the recruitment of neighbor plant species thus influencing herbivore species.

Germination response of desert annuals to shrub facilitation is species specific but not ecotypic	2016	<i>Larrea tridentata</i>	Model	Desert	various	community-level	indirect	Shrub facilitation can influence seed recruitment and germination thus influencing granivore and herbivore communities.
Ground-active arthropod recovery in response to size of shrub plantations in a desertified grassland ecosystem	2017	<i>Caragana korshinskii</i>	Survey	Grassland	35	invertebrate species community	direct	Shrub density can influence terrestrial arthropod diversity recovery.
Intraspecific competition replaces interspecific facilitation as abiotic stress decreases: The shifting nature of plant-plant interactions	2013	<i>Hormathophylla spinosa</i>	Model	Alpine	various	community-level	indirect	Inter and intra-species plant-plant interactions are relevant to local animal populations.
Models of reforestation productivity and carbon sequestration for land use and climate change adaptation planning in South Australia	2016	Not specified	Model	Agriculture	various	community-level	indirect	Shrub and plant density can be used in reforestation models, which will influence local animal communities.

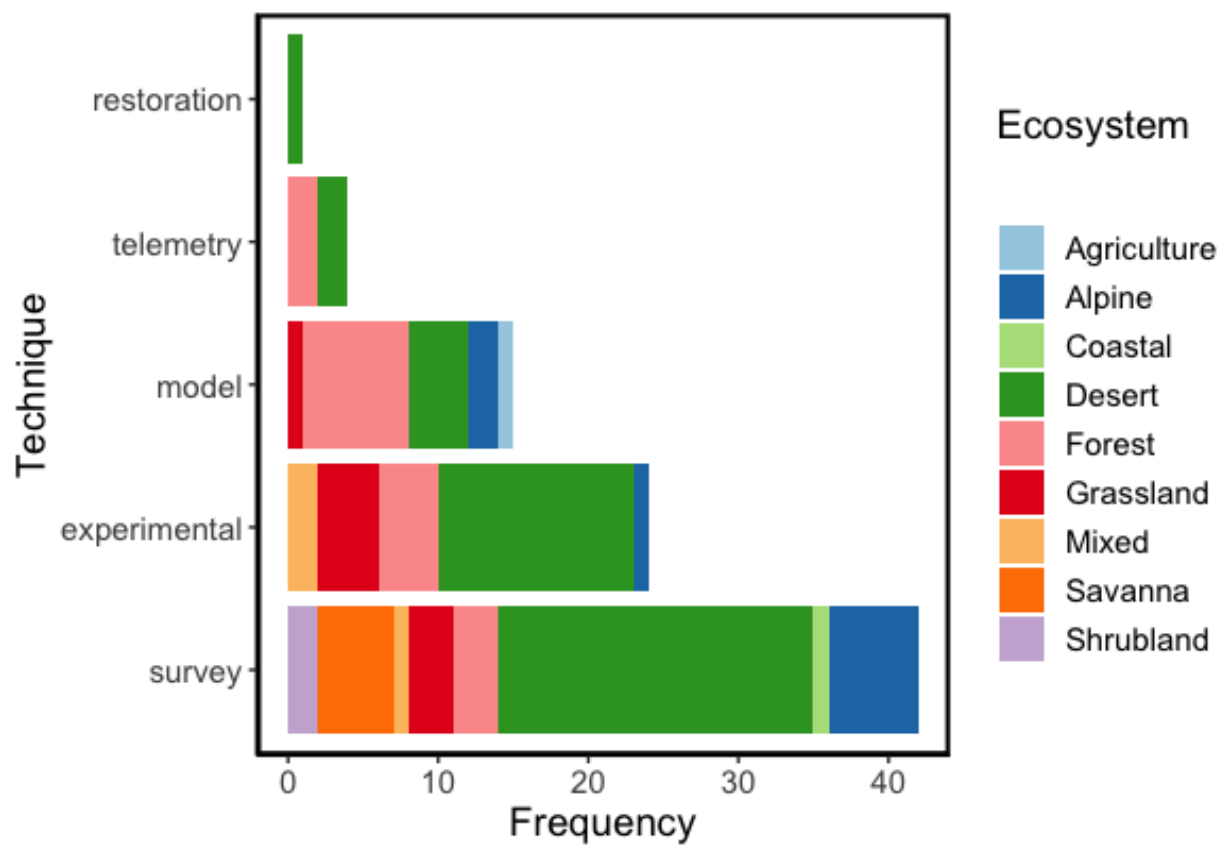
Mowing Wyoming Big Sagebrush Communities With Degraded Herbaceous Understories: Has a Threshold Been Crossed?	2012	<i>Artemisia tridentata</i>	Experimental	Desert	various	community-level	indirect	Sagebush communities with degraded understories can limit exotic annuals, promote perennial herbaceous vegetation which indirectly recruits herbivore species.
Multiscale assessment of woody species recruitment in Mediterranean shrublands: facilitation and beyond	2017	<i>Retama sphaerocarpa</i>	Survey	Shrubland	various	community-level	indirect	Shrub density can aid in the colonization of shrublands but may be weaker with higher levels of herbivory.
Neighbourhood interactions and environmental factors influencing old-pasture succession in the Central Pyrenees	2004	<i>Buxus sempervirens</i>	Model	Forest	various	community-level	indirect	Interactions between native and invasive shrub species reflect asymmetric interspecific competition.
Positive ecosystem engineering effects of the ant <i>Atta vollenweideri</i> on the shrub <i>Grabowskia duplicata</i>	2010	<i>Grabowskia duplicata</i>	Survey	Savanna	1	<i>Atta vollenweideri</i>	direct	<i>Atta vollenweideri</i> facilitate shrub recruitment through ecosystem engineering.
Recreational trails as a source of negative impacts on the persistence of keystone species and facilitation	2015	<i>Epacris gunnii</i>	Survey	Alpine	various	community-level	indirect	Shrub density positively influence local plant communities thus influencing local herbivore species.

Regeneration beneath a dioecious tree species ( <i>Spondias purpurea</i> ) in a Mexican tropical dry forest	2014	Not specified	Experimental	Forest	various	community-level	indirect	Shrub species positively associate with zoochorous species.
Resource partitioning and interactions enable coexistence in a grass-shrub steppe	2010	<i>Mulinum spinosum</i>	Experimental	Grassland	various	community-level	indirect	Shrub-grass coexistence with an ecosystem can indirectly influence local animal communities.
Rodent mounds facilitate shrubs and shrubs inhibit seedlings in the Mojave Desert, USA	2015	<i>Coleogyne ramosissima</i>	Model	Desert	various	rodent species community	direct	Shrub seedling establishment at open mounds have long-term influence on shrub density and influence local rodent species populations.
Shrub and vegetation cover predict resource selection use by an endangered species of desert lizard	2020	<i>Ephedra californica</i>	Telemetry	Desert	1	<i>Gambelia Sila</i>	direct	Shrub cover predicts resource selection by a single lizard species.
Shrub cover regulates population dynamics of herbaceous plants at individual shrub scale on the Mongolian steppe	2015	<i>Caragana microphylla</i>	Survey	Desert	various	community-level	indirect	Shrub density can influence the recruitment of local plant species and influence the local herbivore communities.

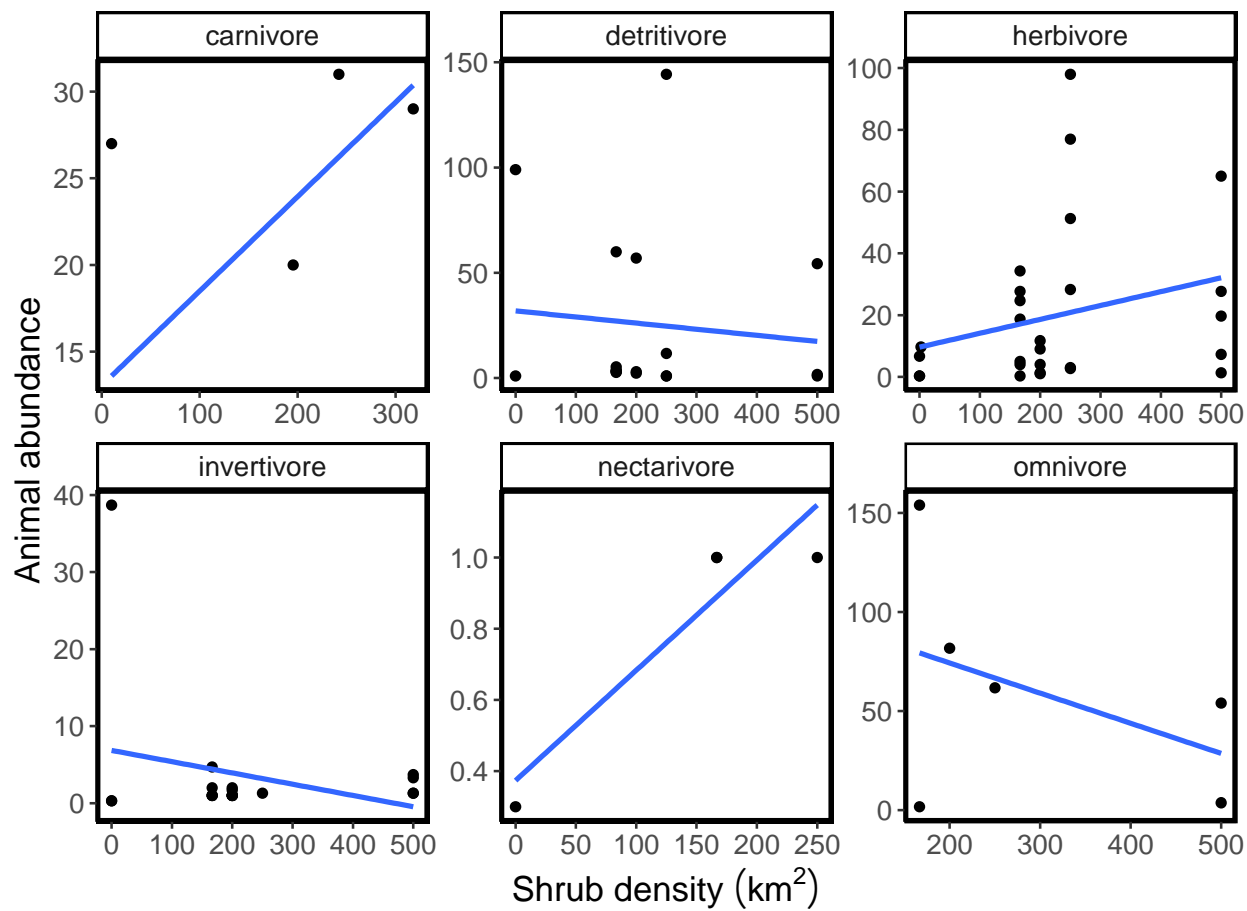
Shrub density effects on the community structure and composition of a desert animal community	2021	<i>Ephedra californica</i>	Survey	Desert	26	community-level	direct	Shrub density can influence the association and composition of local animal communities
Shrub effects on herbaceous vegetation vary with growth stages and herb relative location	2014	<i>Reaumuria soongorica</i>	Experimental	Desert	various	community-level	indirect	Shrubs can influence local plant species, thus influencing local herbivore communities
Shrub-ephemeral plants interactions in semiarid north-central Chile: Is the nurse plant syndrome manifested at the community level?	2016	<i>Porlieria chilensis</i>	Model	Forest	various	community-level	indirect	Shrubs can influence local plant species, thus influencing local herbivore communities
Spatial relations between shrubs and prosopis-glandulosa canopies	1995	<i>Prosopis glandulosa</i>	Experimental	Desert	various	community-level	indirect	Shrub density can influence further increases in shrub density and local animal communities.
The complex nature of headland shrub encroachment: The case of Headland Zieria ( <i>Zieria prostrata</i> )	2017	<i>Zieria prostrata</i>	Survey	Coastal	various	community-level	indirect	Encroachment of shrub species can impact ecosystem functionality and animal communities.
The Groot Effect: Plant facilitation and desert shrub regrowth following extensive damage	2018	<i>Ephedra californica</i>	Experimental	Desert	various	community-level	indirect	The resilience of foundational shrub species can aid in the recruitment and establishment of local animal communities

Tree-shrub interactions during early secondary forest succession in Uganda	2003	Not specified	Model	Forest	various	community-level	indirect	Facilitation during early succession by tree and shrub individuals can influence the recruitment of local animal communities.
Vegetation recovery and plant facilitation in a human-disturbed lava field in a megacity: searching tools for ecosystem restoration	2013	<i>Ageratina glabrata</i>	Survey	Mixed	various	community-level	indirect	Shrub facilitation of plant communities and influence recruitment of local animal communities.
Vegetation, Hydrologic, and Erosion Responses of Sagebrush Steppe 9 Yr Following Mechanical Tree Removal	2019	<i>Artemisia spp</i>	Experimental	Mixed	various	community-level	indirect	Native shrubs can influence various ecosystem functionalities affecting local animal communities.
Woody dominance in a semi-arid savanna rangeland - Evidence for competitive self-thinning	2012	<i>Acacia spp</i>	Survey	Savanna	various	community-level	indirect	Shrubs can impact long-term stability of savanna plant and animal communities.

**Figure A2:** Survey methods and frequency used from reviewed facilitation literature. Each technique was described within the corresponding literature. Frequency shows the total number of studies that utilized a specific technique across varying ecosystems.



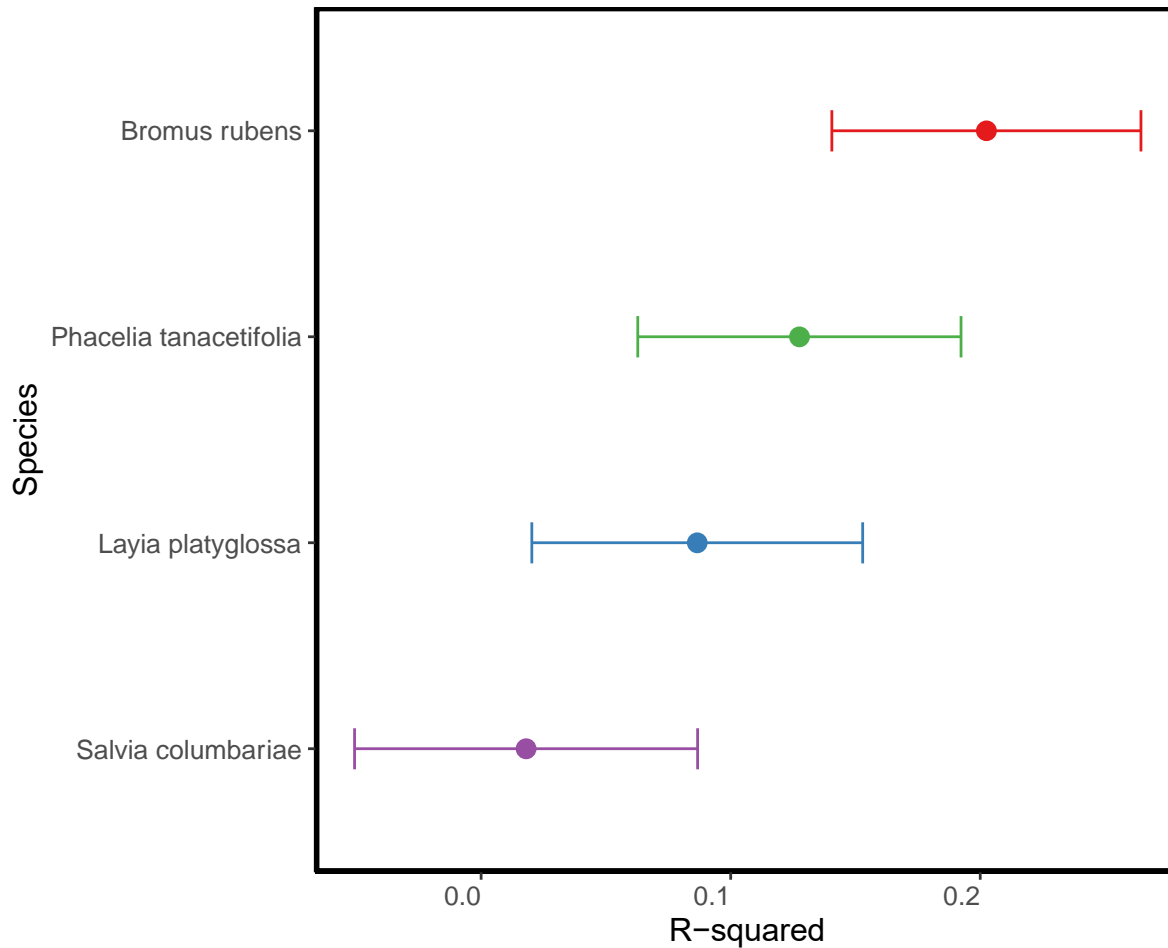
**Figure A3:** A meta-regression of shrub density (shrubs per km<sup>2</sup>) on the incidence rates of reported animal abundances by the feeding functional group.





**APPENDIX B:**

**Figure B1:** The  $R^2$  values for the establishment of Southern California plant species with increasing temperatures. All values were derived from greenhouse trial data for each species. Whiskers indicate standard error (SE) of each  $R^2$  value.



**APPENDIX C:****Table C1:** Mean annual traveled distance (m) by *G. sila* individuals across 3 years within the Carrizo Plain National Monument, after duplicate removal. Data was calculated using the sf package in R 4.2.1.

method	dataframe	year	mean annual distance (m)	standard error
1	distinct()	2016	22.55	2.63
		2017	31.88	4.61
		2018	33.84	3.82
2	distinct(year, lizard, lat, long)	2016	74.84	11.15
		2017	58.44	4.91
		2018	99.65	9.84
3	distinct(year, lat, long, microsite)	2016	59.05	7.23
		2017	56.48	5.67
		2018	90.18	10.44

**Table C2:** Akaike's information criterion (AIC) and related measures used for model selection of variables, based on the resource selection probability function (rspf). Models comparing shrub cover and density were used to determine which can be used to predict *G. sila* presence.

Model	k	AIC	$\Delta$ AIC	$\omega$
Density	7	11253.37	0.00	0.864
Cover	7	11257.06	3.69	0.136

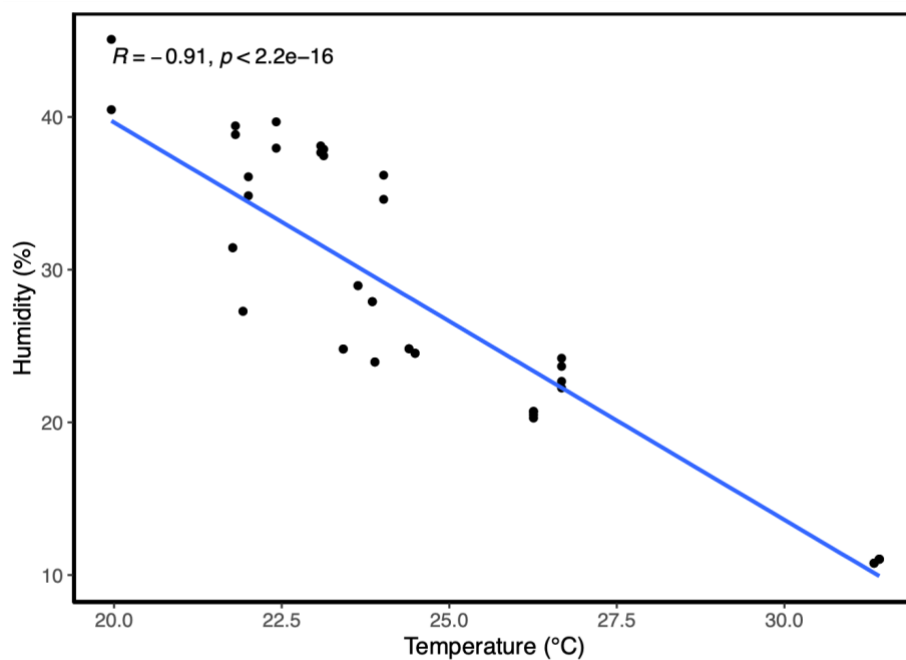
**Table C3:** The effects of duplicate removal on *G. sila* presence and rspf estimates. Data was filtered using the distinct() function in base R 4.2.1. Data were filtered based on unique values across key factors including; latitude, longitude, lizard identification, year, and microsite.

dataframe	n	predictor	estimate	std.error	z value	p-value
all relocations	9307	density	0.107967	0.002296	47.033	< 0.001
		NDVI	8.474163	0.784914	10.796	< 0.001
		ground	0.041556	0.032654	1.273	0.203
distinct()	8006	density	0.112317	0.002496	44.992	< 0.001
		NDVI	11.24338	0.826968	13.596	< 0.001
		ground	0.073399	0.037035	1.982	0.0475
distinct(year, lizard, lat, long)	4690	density	0.082796	0.005537	14.952	< 0.001
		NDVI	13.892995	1.441683	9.637	< 0.001
		ground	-0.627815	0.072326	-8.68	< 0.001
Rounded 4 decimal (within ~11m)	4690	density	0.082796	0.006648	12.455	< 0.001
		NDVI	13.892995	1.539875	9.022	< 0.001
		ground	0.627815	0.062725	-10.009	< 0.001
Rounded 3 decimal (within ~111m)	3532	density	0.085484	0.008311	10.286	< 0.001
		NDVI	11.023229	2.841259	3.88	< 0.001
		ground	-0.546276	0.117606	-4.645	< 0.001
distinct(year, lat, long, microsite)	4508	density	0.087971	0.005717	15.388	< 0.001
		NDVI	13.31861	1.605133	8.298	< 0.001
		ground	-0.64207	0.06684	-9.794	< 0.001

**Table C4:** The minimum convex polygon (MCP) area estimates for male and female *G. sila* individuals across 3 years of radio telemetry tracking at the Carrizo Plain National Monument. All individuals with 5 or more presences were included. Estimates were compiled using the adehabitatHR package in R 4.2.1.

Year	Sex	n	Home Range (ha)	Standard Error
2016	F	10	1.70	0.458
2016	M	11	4.76	2.047
2017	F	5	1.08	0.297
2017	M	10	1.82	0.406
2018	F	11	4.36	1.082
2018	M	15	9.93	2.601

## APPENDIX D:

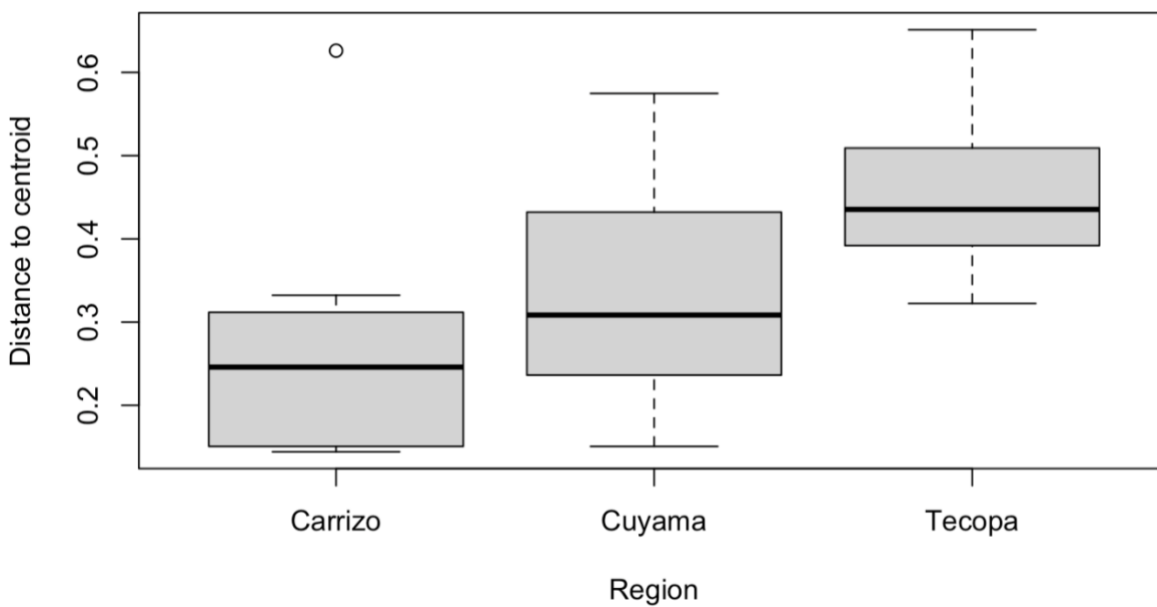


**Figure D1:** Relationship between near-surface air temperature (°C) and relative humidity (%) across all tested sites within a 2-year study period. A Pearson's correlation test was utilized to determine the relationship between these variables ( $r = -0.91, p < 0.001$ ) and to determine which variables would be utilized within main models.

**Table D1:** Total observations of all vertebrate organisms identified via camera trap deployments. All confirmed observations were compiled as independent photos.

Common Name	Scientific Name	Total Independent Photos
Heerman's kangaroo Rat	<i>Dipodomys heermanni</i>	2397
Black-Tailed Jackrabbit	<i>Lepus californicus</i>	357
California Ground Squirrel	<i>Otospermophilus beecheyi</i>	232
Nelson's Antelope Squirrel	<i>Ammospermophilus nelson</i>	171
Coyote	<i>Canis latrans</i>	134
Common Raven	<i>Corvus corax</i>	81
Giant Kangaroo Rat	<i>Dipodomys ingens</i>	68
Desert Cottontail	<i>Sylvilagus audubonii</i>	63
Desert Iguana	<i>Dipsosaurus dorsalis</i>	47
California Quail	<i>Callipepla californica</i>	26
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	17
San Joaquin Kit Fox	<i>Vulpes macrotis</i>	15
Loggerheaded Shrike	<i>Lanius ludovicianus</i>	13
Merriam's Kangaroo Rat	<i>Dipodomys merriami</i>	13
Vesper Sparrow	<i>Poocetes gramineus</i>	13
Greater Roadrunner	<i>Geococcyz californianus</i>	7
Lark Sparrow	<i>Chondestes grammacus</i>	7
Mojave Ground Squirrel	<i>Xerospermophilus mohavensis</i>	7
Bobcat	<i>Lynx rufus</i>	6
White-tailed Antelope Squirrel	<i>Ammospermophilus leucurus</i>	6
Mourning Dove	<i>Zenaida macroura</i>	5
Blunt-Nosed Leopard Lizard	<i>Gambelia sila</i>	4
California Pocket Mouse	<i>Chaetodipus californicus</i>	4
Salinas Pocket Mouse	<i>Perognathus inornatus</i>	4

Say's Pheobe	<i>Sayornis saya</i>	4
California Thrasher	<i>Toxostoma redivium</i>	3
Horned Lark	<i>Eremophila elpestris</i>	3
American Robin	<i>Turdus migratorius</i>	1
Black-throated Sparrow	<i>Amphispiza californicus</i>	1
Great White Egret	<i>Adrea alba</i>	1
Killdeer	<i>Charadrius vociferus</i>	1
Red-tailed Hawk	<i>Buteo jamaicensis</i>	1
Western Whiptail	<i>Aspidoscelis tigris</i>	1



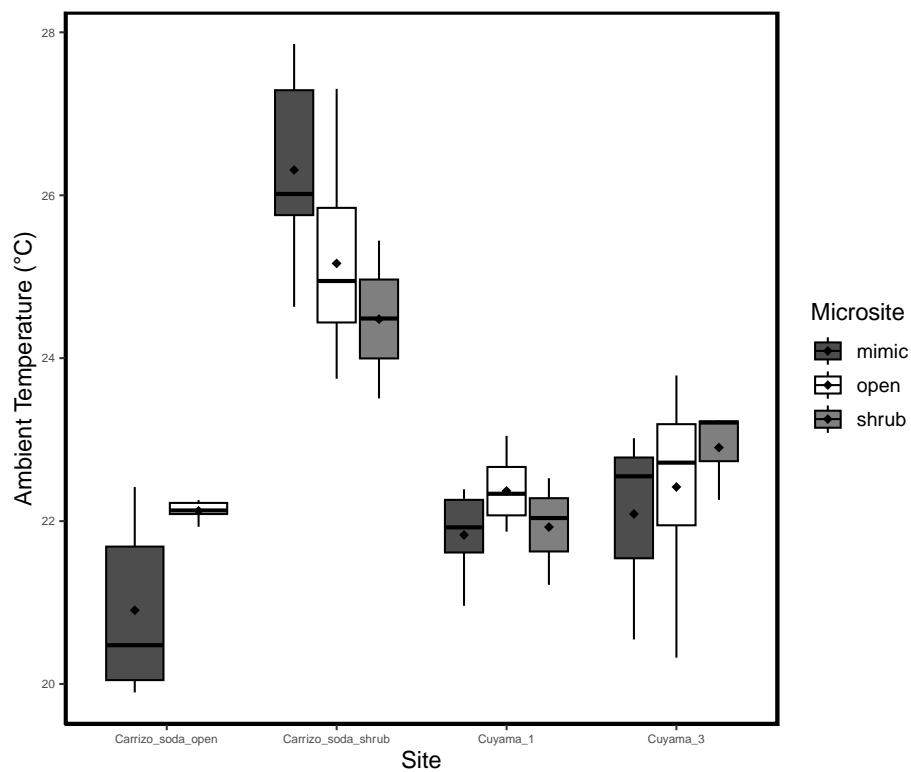
**Figure D2:** Boxplot illustrating the variation in centroid distance among the 3 tested sites. Y-axis represents the centroid distance while the x-axis indicates the tested site in Southern California. Boxes show the interquartile range (IQR), with medians indicated as horizontal lines inside each box. Whiskers extend to the maximum and minimum values within 1.5 times the IQR. Outliers beyond this range are represented as individual points. Analysis indicated significant differences in centroid distance between Carrizo and Tecopa.



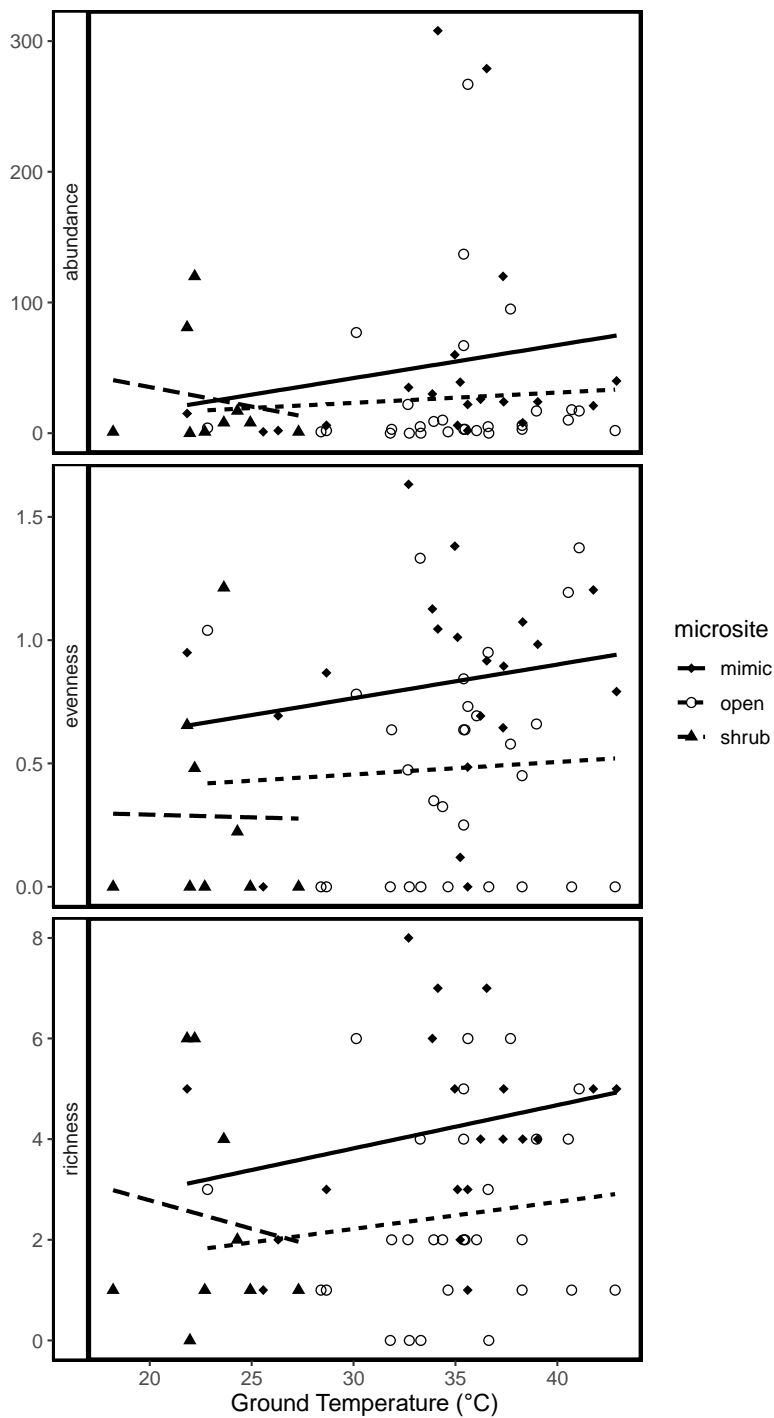
## APPENDIX E



**Figure E1:** An example of the shrub mimics deployed at both the Cuyama Valley and Carrizo Plain National Monument sites. A total of 20 shrub mimics were deployed evenly across all tested sites with a camera trap deployed approximately 1m away. Temperature loggers were deployed underneath each shrub mimic canopy to measure local ambient temperature.



**Figure E2:** Boxplot comparison of tested mimic, open, and shrub microsites, and recorded ambient temperature (°C) across all tested sites. Boxes represent the Interquartile Range (IQR), with medians indicated by a dark black line. Whiskers extend to 1.5x the IQR with points beyond these considered to be outliers. Black diamonds represent the mean value for each microsite.



**Figure E3:** The relative effects of ground temperature on vertebrate species abundance, richness, and evenness across all tested microsites. Data across all sites were combined by microsite to illustrate the effects of the ground temperature under each tested area. Shaded areas show a 95% confidence interval associated with each line of best fit.

**Table E1:** Analysis of vertebrate abundance, richness, and evenness from general linear models from study period. Microsite, Ambient Temperature, and Shrub Density were treated as factors within the models. P-values < 0.05 are indicated in bold. Shrub Density was defined as the total number of individuals within a 20m radius.

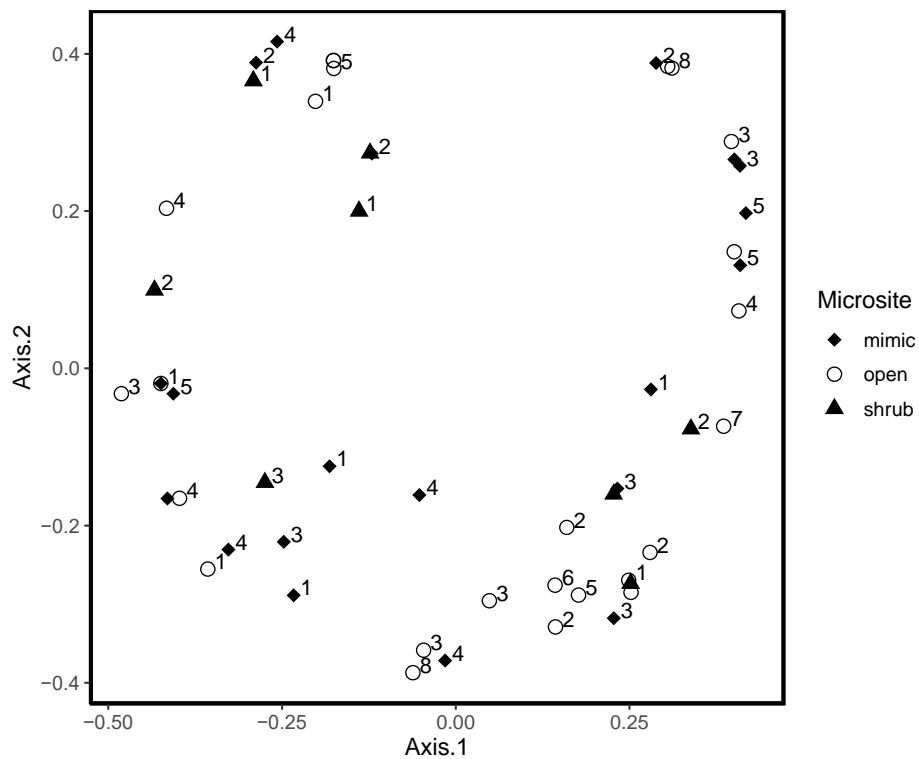
	df	Deviance residuals	df residuals	Deviance	Pr (>c)
<b>Abundance</b>					
Null			57	4372.1	
Microsite	2	241.77	55	4130.4	< <b>2.2 x 10<sup>-16</sup></b>
Ambient Temperature	1	14.07	54	4116.3	< <b>0.0001</b>
Ground Temperature	1	47.39	53	4068.9	< <b>0.0001</b>
Shrub Density	1	1005.41	52	3063.5	< <b>2.2 x 10<sup>-16</sup></b>
Microsite:Ambient Temperature	2	701.70	50	2361.8	< <b>2.2 x 10<sup>-16</sup></b>
Microsite:Ground Temperature	2	248.43	48	2113.4	< <b>2.2 x 10<sup>-16</sup></b>
<b>Richness</b>					
Null			57	93.497	
Microsite	2	12.1743	55	81.322	<b>0.0022</b>
Ambient Temperature	1	1.8426	54	79.840	0.1746
Ground Temperature	1	0.4189	53	79.061	0.5174
Shrub Density	1	5.7626	52	72.388	<b>0.0173</b>
Microsite:Ambient Temperature	2	7.6318	50	65.756	<b>0.0220</b>
Microsite:Ground Temperature	2	0.3744	48	65.382	0.8293
<b>Evenness</b>					
Null			57	29.230	

Microsite	2	4.0028	55	22.227	0.1351
Ambient Temperature	1	0.0103	54	25.216	0.9190
Ground Temperature	1	0.1296	53	25.087	0.7189
Shrub Density	1	0.0098	52	25.077	0.9211
Microsite:Ambient Temperature	2	0.5663	50	24.511	0.7534
Microsite:Ground Temperature	2	0.0653	48	24.445	0.9679

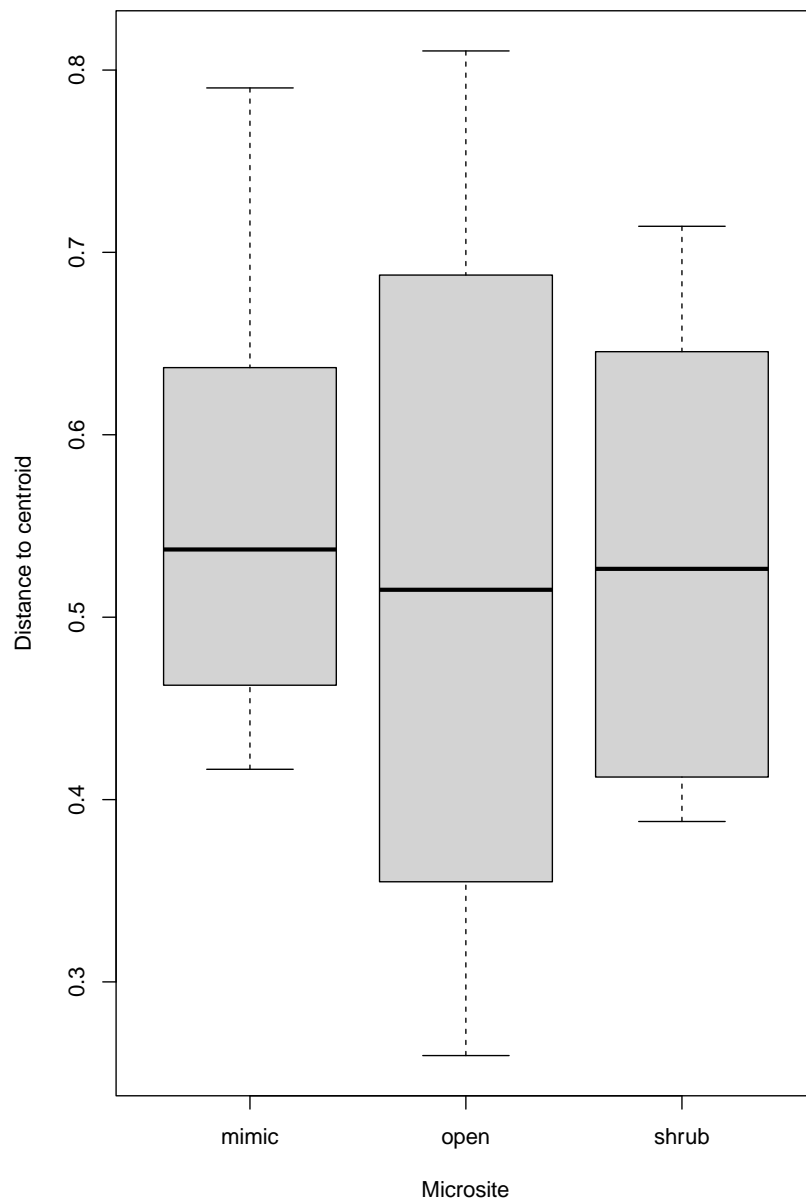
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**Table E2:** Total observations of all vertebrate organisms identified via camera trap deployments. All confirmed observations from mimic, open, and shrub microsites were compiled into “Total Observations”.

<i>Common Name</i>	<i>Scientific Name</i>	<i>Total Observations</i>
<i>Heermann's Kangaroo Rat</i>	<i>Dipodomys heermanni</i>	1550
<i>Nelson's Antelope Squirrel</i>	<i>Ammospermophilus nelsoni</i>	218
<i>Loggerhead Shrike</i>	<i>Lanius ludovicianus</i>	70
<i>Black-tailed Jackrabbit</i>	<i>Lepus californicus</i>	54
<i>Common Raven</i>	<i>Corvus corax</i>	50
<i>Kit Fox</i>	<i>Vulpes macrotis</i>	39
<i>Coyote</i>	<i>Canis latrans</i>	30
<i>Desert Cottontail</i>	<i>Sylvilagus audubonii</i>	20
<i>Horned Lark</i>	<i>Eremophila alpestris</i>	14
<i>Giant Kangaroo Rat</i>	<i>Dipodomys ingens</i>	13
<i>California Quail</i>	<i>Callipepla californica</i>	10
<i>Mourning Dove</i>	<i>Zenaida macroura</i>	4
<i>Salinas Pocket Mouse</i>	<i>Perognathus inornatus</i>	4
<i>California Pocket Mouse</i>	<i>Chaetodipus californicus</i>	3
<i>Red-tailed Hawk</i>	<i>Buteo jamaicensis</i>	3
<i>California Ground Squirrel</i>	<i>Otospermophilus beecheyi</i>	2
<i>Cassin's Kingbird</i>	<i>Tyrannus vociferans</i>	2
<i>Song Sparrow</i>	<i>Melospiza melodia</i>	2
<i>Bewick's Wren</i>	<i>Thryomanes bewickii</i>	1
<i>Common Poorwill</i>	<i>Phalaenoptilus nuttallii</i>	1
<i>Say's Phoebe</i>	<i>Sayornis saya</i>	1



**Figure E4:** PCOA figure displaying the vertebrate community composition across mimic, open, and shrub microsites through the Cuyama Valley and Carrizo Plain National Monument. Analysis was conducted using the *Vegan* package in R version 4.3.1.



**Figure E5:** Boxplot illustrating the variation in centroid distance amongst 3 microsites. Y-axis represents the centroid distance while the x-axis indicates the tested microsite within Southern California. Boxes represent the Interquartile Range (IQR), with medians indicated by a dark black line. Whiskers extend to 1.5x the IQR with points beyond these considered to be outliers.