Shrub density effects on the structure and composition of a desert animal community.

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Abstract

Positive interactions between shrubs and animals are frequent in desert ecosystems. Shrub canopies can provide refuge to some animal species from predators and shelter from stressful environmental conditions by ameliorating high temperatures. Consequently, there have been many contrasts of shrub versus open effects, however, I extend this approach further by testing these effects on a gradient of shrub densities in a region of the Carrizo National Monument, California. I tested the hypothesis that shrub density is a landscape-level predictor of vertebrate community composition and structure. I used camera traps, transects, and focal observations to estimate animal density and composition, and temperature sensors were also deployed. Plots were established within shrub patches ranging from 0 to 12 shrubs per 20m area. Plots with relatively higher shrub densities had increased abundance and richness of vertebrates. Temperature and residual dry matter were important mediators of animal density and richness.

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Introduction

Positive interactions between plant and animal species are a central focus of community ecology. These positive interactions are defined as non-trophic interactions between species, where at least one of these interacting individuals benefit, while the other is either unaffected or also benefits in the process (Bertness & Leonard 1997; Gross 2008; Montenegro et al. 2016; Kéfi et al. 2016; Grinath et al. 2012). Facilitation is defined as a form of positive interaction when one of the interacting species benefits while the other species either benefits or is unaffected (Filazzola et al. 2017; Dangles et al. 2018). Commensalism is a type of facilitative interaction where one of the interacting species benefits while the other receives no benefit nor experiences as cost or negative effect from the interaction, and typically the main type of interaction focused on in facilitation studies (Araújo & Rozenfeld 2013). Understanding the relative importance of facilitation or positive interactions between shrubs and other taxa has been proposed as an important means to better understand community function in high-stress ecosystems (Lortie et al. 2016; Dangles et al. 2018). Desert shrubs and animals interact in a variety of ways. Specifically, in arid/semi-arid ecosystems, it has been proposed that positive plant-plant, plant-animal, and animal-animal interactions often occur more frequently than in mesic systems and are crucial for mutual species survival (Holzapfal & Mahall 1999; Stachowicz 2001; Bertness & Callaway 1994). Facilitation is the term used to describe interactions where at least one interacting species benefits from another (Holzapfel & Bruce 1999; Kefi et al. 2016; Kikvidze & Callaway 2009). Desert shrubs can facilitate animals by providing shade that ameliorates stressful abiotic conditions such as extreme temperature (Lortie et al. 2016; Westphal et al. 2018; Bart et al. 2016; Moore et al. 2018). Shrub species in arid ecosystems are frequently reported to facilitate plants and animals and have been termed foundation species (Bertness & Leonard 1997;

Bortolus et al. 2002; Lortie et al. 2016). A foundation species typically facilitates local communities and maintain habitats that are beneficial for other species (Bittick et al. 2019, Lortie et al. 2020). This is different from keystone species that are disproportionately greater in their abundance and they maintain habitat and species diversity (Bond 1994; Soulé et al. 2005). Indirect effects of shrubs can include microclimatic buffering that allows for some animal species to take refuge from the harsh arid conditions of the California deserts (Hanley 1978; Holzapfel & Mahall 1999; Fillazola et al. 2017), resulting in higher animal densities being observed under shrub canopies than in open spaces with no cover (Hanley 1978; Koyama et al. 2015). For instance, *Gambilia sila* uses shrub canopies to reduce its body temperature during peak times in the day (Noble et al. 2016; Westphal et al. 2018; Ivey et al. 2020). Shrubs can also provide refuge for some desert animal species from predators (Lortie et al. 2016; Milchunas & Noy-Meir 2002) by reducing predation risks for kit foxes (Nelson et al. 2007), and by acting as cover for some kangaroo rat burrows (Edelman 2011). Shrubs can augment resources for animals by trapping seeds consumed by small mammals (Bullock & Ibby 2004; Giladi et al 2013) or directly producing resources such as fruit consumed by birds (Hertel et al. 2018). Nonetheless, there can also be negative interactions between animals mediated by shrubs including competition (Bachelot et al. 2015). Consequently, the net outcome of interactions between shrubs and animals, and interactions with other animals, can thus be a product of positive and negative effects. Therefore, these shrub species can act as foundation species in arid environments by positively influencing the structure and composition of local animal communities.

Density is a fundamental concept in community ecology. Density itself is a relatively simple measure that has been well established in competition theory in plants (Antonovics &

Levin; 1980; Zand & Tielbörger 2020), animals (Adams & Walters 1995; Nilsson 2001), and in trophic interactions (Lamb et al. 2017; McPeek 2019), but less so in facilitation studies. Density of non-mobile species, such as vegetation and shrubs, is typically determined by counting the number of individuals within a defined area (Lyon 1968; Nath et al. 2010). This is different for estimations of animal densities which have to use different means of measuring density since these species are mobile. These methods can include telemetry (Westphal et al. 2018), camera traps (Noble et al 2016), or through species specific cues like passive acoustics (Marques et al. 2013). These methods are typically used for determining vertebrate animal densities. In order to quantify the invertebrate densities in an ecosystem, pitfall traps (Liu et al. 2017), sweep netting (Scrimgeour et al. 1993), or malaise traps (Campbell & Hanula 2007) can be used to name a few. In the context of plant-animal facilitation in deserts, the density of plants can influence the net outcome of interactions with animals (Springer et al. 2003; Tietje et al. 2008). Some animal species disproportionately occupy shrub canopies over open areas because they provide better microhabitats and movement trails (Stapp & Van Horne 1997). However, there have been no studies conducted on the shrub and animal density correlations, particularly in arid ecosystems. With a varying shrub-density gradient, if more shrubs cause increasing animal densities and the diversity of species present within the community, then the likelihood for more direct and indirect interactions between animals increases (Hassell 1975; Adams & Walters 1995) and also potentially generates more complex trophic structures (Polis 1991; Schneider et al 2016). Understanding how shrub and animal densities covary is essential to understanding the dynamics of association in desert ecosystems and how a gradient of shrub densities within a region influence the animal community and the relative effect of shrub canopies to open-gap plots. Furthermore, it is important to evaluate density-dependent associations among multiple animal

and shrub species simultaneously, because animals and shrubs interact directly and indirectly in complex species assemblages in nature. Since animal densities respond to variations in shrubs (Skarpe 1990) and to habitat stressors (Filazzola et al. 2018), then with these changes in facilitation, shrub densities would have an impact on animal densities.

An effective method to estimate associations between animal and shrub species is camera traps deployments in different contexts. Camera traps automatically take images of animals when the passive infrared sensor detects a change in temperature or movement in the background (O'Connell et al. 2011; Meek et al. 2014; Noble et al. 2016). These devices are typically used to determine the presence or absence of species in an ecosystem (O'Connell et al. 2011; Rovero et al. 2013; Noble et al 2016); however, the use of camera traps have been increasingly used to estimate animal density, overall species abundance, and habitat occupancy (Meek et al. 2014; Burton et al. 2015). Using camera traps is a beneficial method for measuring density that offers minimal overall disturbance to a study area (Gompper et al. 2006; Noble et al. 2016) and continuously runs in the study area, making them more effective at detecting species (Silveira et al. 2003; Gompper et al. 2006). Since a digital observation is produced by camera traps, it is considered to be more advantageous than just physically observing an animal as it provides quantitative evidence and digital recordings of the observations. (O' Connell et al. 2011; Noble et al 2016). With this, researchers are able to observe animal species at all time periods as well as their association with the ecosystem, and potentially gain data on rare species who are more difficult to observe (Noble et al. 2016) Unfortunately, when using camera traps the possibility for observer bias and effects still exists including disturbance to set up. In addition, some brands of camera traps can emit a sound or light detectible by some animal species that changes movement, but this does not usually impact the animals being detected by the camera (Meek et

al. 2014). Therefore, camera traps could prove to be a valuable tool in recording animal density, abundance, community composition as they are able to collect useful imagery data at all times of the day.

High-stress environments have proven to be a large obstacle in the survival of both plant and animal species. Many of the species living in these harsh ecosystems rely on the amelioration of high-stressor abiotic conditions through interaction with others, such as the use of canopy to escape high-temperature periods of the days (Ivy et al. 2020; Lortie et al. 2016; Westphal et al. 2018). This gave rise to the Stress-gradient hypothesis, where high stressor environmental situations, such as temperature, nutrient levels, and soil moisture, will alter the overall facilitative interaction (Bertness & Callaway 1994; Butterfield et al. 2016). Abiotic factors such as accessibility to shade, soil composition, water availability, and daily temperatures have been seen to impact species, leading to their interactions with others to alleviate the negative repercussions associated with these abiotic impacts (Bertness & Callaway 1994; Turner et al. 1966). With the increase in these abiotic stressors, plant and animal species tend to rely on one another to reduce this stress by increasing facilitative interactions (Callaway et al. 2002; Dangles et al. 2018). Since climate is a high impact abiotic factor on ecosystems, many studies have focused on how the facilitative interactions between plant species are able to ameliorate the associated negative impacts of increasing temperatures (Brooker et al. 2007; Dangles et al. 2018). On the other hand, many studies have been conducted to see how the Stress-Gradient Hypothesis could be applied to animal communities. Studies conducted on these animal species suggests that even a reduction in the overall negative interactions between individuals will decrease, where species begin to opt for more positive interactions, in order to reduce their overall stress (Bertness & Leonard 1997; Fugère et al. 2012; Hart & Marshall 2013; Dangles et

al. 2013). With these abiotic factors influencing the positive interactions between plant and animal species. Aside from abiotic stressors, biotic stressors such as residual dry matter could also act as a way to estimate net primary production (NPP) and thus is a component of the annual plant community in grasslands (Bartolome et al. 2002; Smart et al. 2017). Residual Dry Matter (RDM) is a standard measurement used by land management agencies for assessing an ecosystems health (Bartolome et al. 2002; Filazzola et al 2017) and net primary production (NPP) which is defined as the rate which plant matter converts CO_2 and water into dry matter (Ito & Oikawa, 2002; Smart et al. 2017). Residual dry matter is typically the plant matter left on the ground from both previous seasons and the current season (Bartolome 2002). Large abundances of plant matter in a given area can impact animal species ability to forage, move, and escape predation (Vasquez 2002) that can have a negative impact on shrub-animal associations. Hence, it can be used as a proxy for the annual plant biomass in grasslands (Vasquez 2002; Filazzola et al. 2017), and here it is used as a means to estimate the indirect effects of shrubs on animals through vegetation. This study examines the relationship between animals and the densities of foundation shrub species including potential indirect effects from associated vegetation.

Research Objectives

The objective was to examine whether shrubs and increasing density of shrubs positively influences key measures of animal communities. Specifically, I tested the hypothesis that shrubs and a shrub-density gradient will influence the structure and composition of the local animal community. The following predictions were examined:

1) Shrub and animal densities are positively related.

2) Increasing shrub density also positively predicts animal species composition.

3) Local differences in microclimate between shrub and open microsites have a negative indirect effect through residual dry matter on the soil surface mediates shrub-animal associations.

Methods

Study Site

This study was conducted in the Elkhorn Plain of the Carrizo Plain National Monument (CNM, 35.11982, -119.62853; Figure 1). The average temperature and precipitation for the site was taken from the nearest weather station in Cuyama using the California Irrigation Management Information System (https://cimis.water.ca.gov/Default.aspx). The plain sits at an elevation of 2697ft with an average temperature of 14.7 and 21.7 Celsius in the months of May and June. Average precipitations for these months are extremely low with only the month of May experiencing 0.17 centimeters of rain (Table 1). The study site is dominated by the shrub *Ephedra californica*. The flora of the Elkhorn Plain is composed primarily of native species (http://www.rareplants.cnps.org/advanced.html), but the invasive grass species *Bromus madritensis ssp. rubens, Bromus hordeaceus,* and *Schismus barbatus* are present and associated positively with *E. californica* (Lucero & Callaway 2018; Lucero et al. 2019).
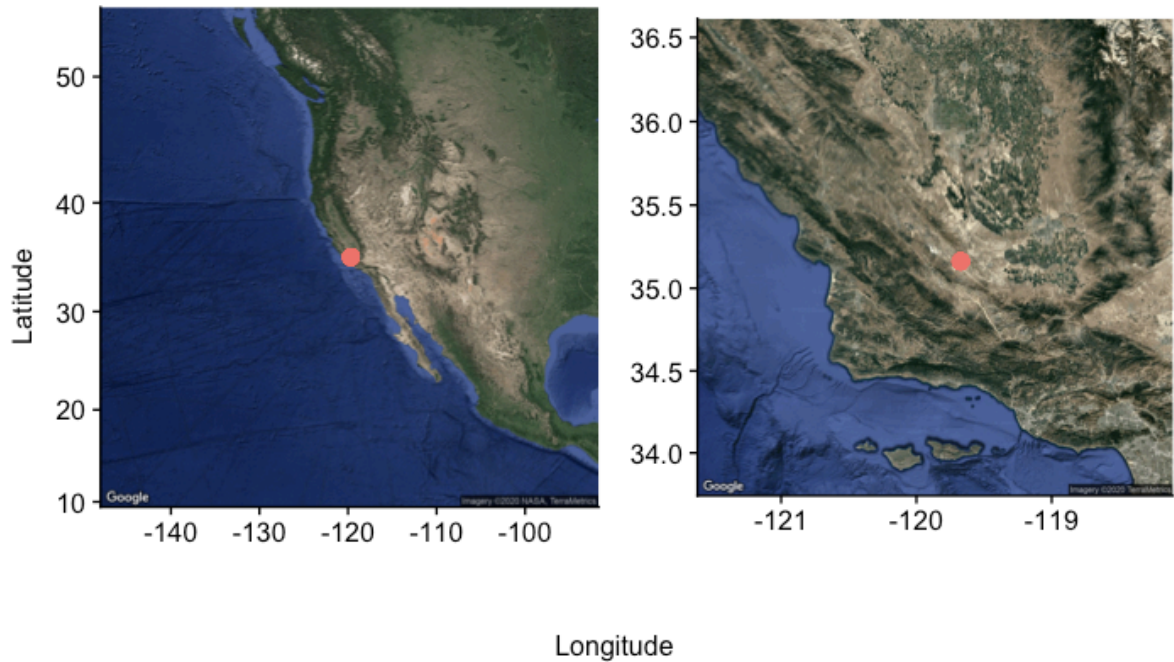
Figure 1: GPS location of the field site in the Carrizo Plain National Monument, California, US (35.1899, -119.8633) indicated with a red circle.

Table 1: Climate and temperature data for the Carrizo Plain National Monument, CA, including; total precipitation, average max/min air temperature, average air temperature, average relative humidity, average wind speed and average soil temperature(https://cimis.water.ca.gov/Default.aspx)

Month-Year	Total Precipitation(in)	Avg Max Air Temp (F)	Avg Min Air Temp (F)	Avg Air Temp (F)	Avg Relative Humidity (%)	Avg Wind Speed (mph)	Avg Soil Temp (F)
May-2019	0.07	74.1	44.7	58.4	60	5.3	71.5
June-2019	0	92	52.4	71.0	40	5.2	84.6

I established a shrub gradient along the Elkhorn Road in the CNM (Figure2). The shrub density at plot scales was assessed using imagery and field surveys (Lortie & Zuliani 2020; Zuliani & Lortie 2020; Zuliani & Lortie 2020). Over 80 sites were randomly satellite located where the average number shrubs in a 10m radius were recorded. The mean estimate shrub densities were not significantly different between these estimates and the min was 0 and max as 12 (ANOVA, $F = 9.319$, $p < 0.001$ df = 2). A better understanding of the maximum, minimum and average number of shrub individuals possible per plot for the field site was obtained. A total of 8 circular plots, each 10m in radius, were established to capture the range of shrubs present in the region from entirely shrub free up to 12 shrubs per plot. The total number of the *Ephedra Californica* individuals per site were recorded, each shrub georeferenced, and total individual canopies measured. Shrub canopy measurements included width at longest axis from above shrub, perpendicular measure of width to the longest axis, and height of each individual shrub to live vegetation (Lortie et al. 2018). Areas in established plots under shrub canopy were denoted as shrub microsites, while areas outside the canopy were considered open microsites. The animal community was measured using 3 different techniques; camera traps, transects, and focal observations. Abundance and species composition were recorded using each method. Once each method was complete, all camera traps, transects and focal observations data were aggregated into a compiled estimated density dataset with sample units being at the plot level (i.e. N = 8, but data for plots with shrub were compiled to shrub and open estimates per plot). A microsite is defined here as a 0.5m scale measure of animal association patterns with a specific shrub individual or open patch, and a plot is defined at the scale of 10m radius (Figure 3) encompassing a range from 0-12 shrub individuals. Distance between plots were150m while distance between transects was 30m.
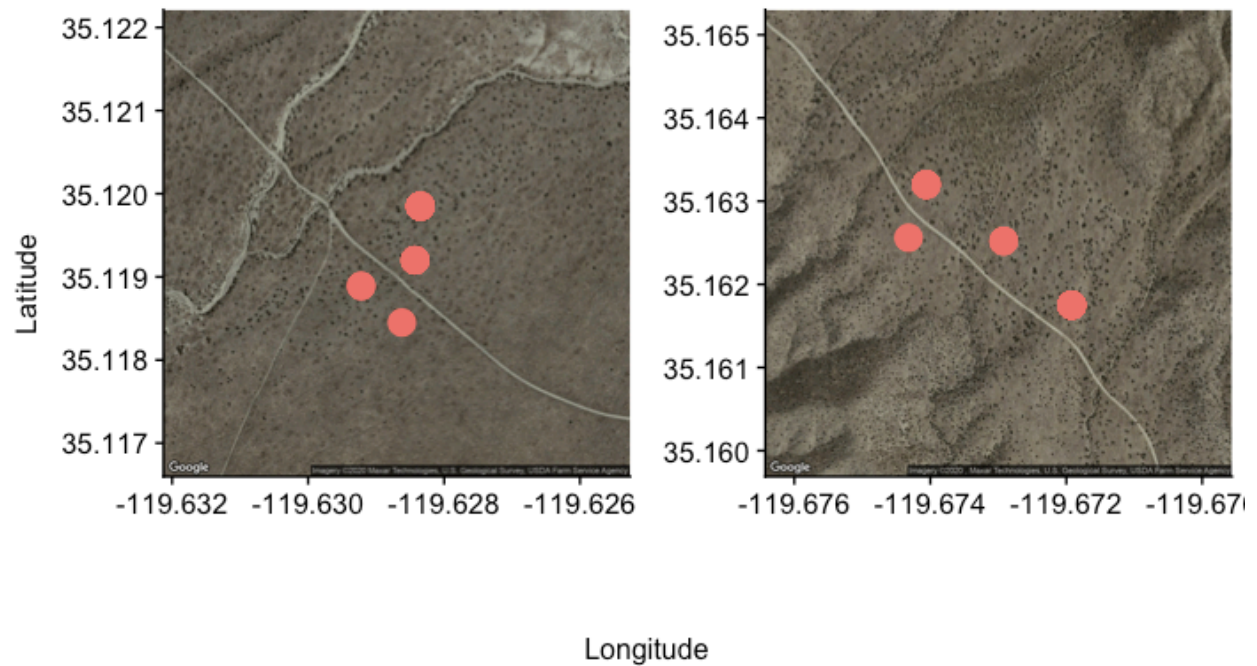
Figure 2: GPS location of *Ephedra californica* plots in the Carrizo Plain National Monument, California, US (35.1899, -119.8633). Red dots indicate a measure 10m radius plot. Two separate maps were generated due to the distance between established shrub plots.
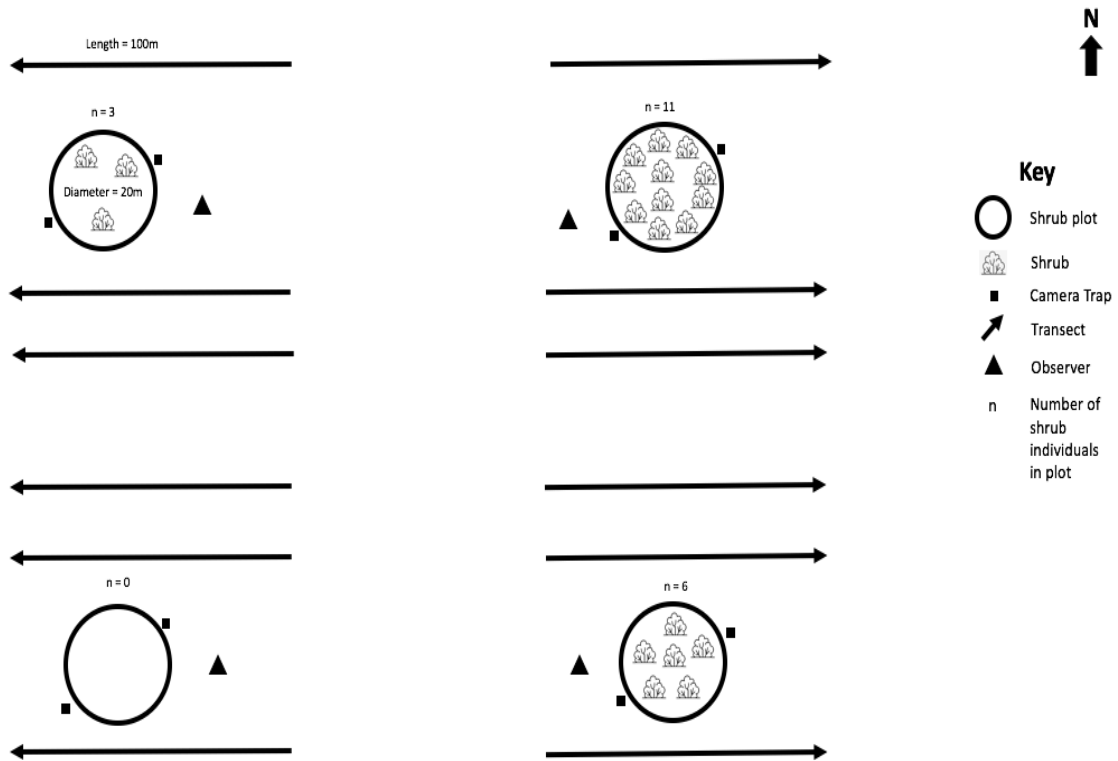
Figure 3: A schematic displaying the relationship of shrub density plots to one another and relative relation to transects and focal observation. Distance between plots was approximately 150-200m while distance between transects was approximately 30m. Shrub icon in plot denoting shrub microsite while remaining uncovered are representing open microsite.

Study Species

Ephedra californica (Figure 4) is the dominant plant species in the Elkhorn plain. This species is seen as a foundation species that are vital for the possible restoration of deserts in California (Lortie et al. 2018, Filazzola et al. 2018). The species interacts with other animal species within the Elkhorn plain including Blunt-nosed Leopard lizards (Noble et al. 2016), and Kangaroo rats (Prugh & Brashares, 2010). The Ephedra have positive interactions with many of the species in the Carrizo plain, primarily with the formation of burrows under its canopy cover, which are used for refuge from predators and as home burrows (Hawbecker, 1951). After mechanical damage (such as branch breaking or herbivory) is inflicted on the *Ephedra californica* species, it recovered even in periods of drought (Lortie et al. 2018). The interactions that are associated with this plant species, along with the population densities of the species that it interacts with, will be the major focus of the study.

Figure 4: *Ephedra californica* foundational shrub species. A native shrub species to Southern California and seen to provide numerous benefits to interacting animal species.

Camera Traps

Camera traps (Campark T70) were used to sample animals at each site during the day and night (https://www.campark.net/pages/campark-t70-trail-camera-user-manual) (O'Brien 2011; O'Connell et al. 2011; Noble et al 2016). No flash was emitted by cameras at night, preventing the disturbance of animals. Two cameras were deployed facing into the plots, at opposite ends resulting in a total of 16 camera traps being deployed (Appendix A, Figure S1). Each camera was set to medium sensitivity, to limit the total number of misfires caused by movement of vegetation. Cameras were set to photo with a 1-minute delay after each consecutive photo. Cameras were checked every 3-4 days to ensure that they had been constantly firing, had sufficient battery levels, and SD cards were replaced. The cameras remained deployed for a total of 27 continuous days before being removed. During each set of maintenance, all SD cards were labeled based on which camera they came from and their corresponding site density level. The data from these SD cards were then transferred to a larger hard drive for storage and then cleared for future use during the next maintenance period.

All camera trap capture data was recorded from the files including all misfired photos for a total of over 55,000 photos taken across all plots. Each photo was taken as an individual data point and recorded; the file name, date, rep, camera number, density level, if an animal was present, species of animal, observable behavior, and camera timestamp. All positive presence instances were validated by a second evaluator. New animal instances were defined when individuals were not observed in the same position within the 1 minute lag-time. During focal sampling surveys by researchers, observers, positioned near camera traps during observations (Figure 3), ensured that cameras that were triggered by a single individual multiple times were coded as a single animal. This was done by matching time stamped pictures to recorded time

from focal observations. Camera trap rate of capture was determined by taking the difference between total number of positive observation in a shrub plot by the total photos taken in the corresponding plot throughout the 27 day duration (O' Connell et al. 2011; Noble et al 2016). All data collected from camera traps were then combined with transect and focal observation data into a compiled estimated density dataset.

Transect

Transects were used to estimate the animal community through walk-through survey protocol, where any individual located within a 10m radius from the transect was recorded. I used 3 parallel 100m transects located outside each of the established shrub plots. Each transect was measured and marked with flags at 25m intervals. Each site had a total of 12 transects in it, 3 per shrub plot, allowing for a total of 24 transects. Researchers used the transects to visually spot animals every 2 to 3 days. In each instance, the distance on the transect was recorded, microsite (shrub, open), the corresponding shrub density, species of recorded animal, and time of recording.

Focal Observations

Daily observations were done at each shrub density plot for 30 minutes. The observer was situated just outside the plot at a distance of 5m and recorded the presence of any species entering or within the plots. The species of animal was recorded, behavior, time, and estimated distance to the nearest shrub within the plot (except the no density shrub plots).

Species Validation

Vertebrate and invertebrate species observations through camera traps were validated through the use of iNaturalist (https://www.inaturalist.org/) during photo processing where the best estimation of the possible species was taken. In addition, camera trap data was validated by

a second observer after recording. Uncertain images were classified as unknowns. Images were

saved into a separate hard drive and were later visually validated. Transect and focal

observations were validated using a combination of visual observations and iNaturalist in field.

Vertebrate and invertebrate species data was then aggregated into a large community dataset,

with total number of each individual recorded (Appendix C, Table S1).

Temperature Measurement

Local measures of ambient temperature were recorded using HOBO pendant loggers,

which were either suspended above ground or on a stake and embedded in the soil

(https://www.onsetcomp.com/files/manual_pdfs/9531-O%20UA-001%20Manual.pdf). A total of

28 loggers were deployed at varying plot densities in both shrub and open microsites for a total

of 27 days. These pendants recorded hourly temperatures which were then taken to find the mean

and maximum daily temperatures. The relationship between Maximum temperature and animal

abundance was then determined (Appendix B, Figure S2).

Residual Dry Matter

Residual Dry Matter (RDM) is the measure of the total mass of varying grass and

vegetation species in a given area (Bartolome 2002; Kurten & Carson 2015; Filazzola et al.

2017). RDM was collected by placing a 20cm x 20cm square randomly at both shrub and open

microsites at each shrub density plot. All grass within the indicated square were removed entirely

from the ground and weighed on a digital scale to determine the total mass of vegetation

growing. This estimate was done at each plot a total of 6 times where 3 samples were conducted

under as shrub canopy and 3 samples were taken in the open. Plots that did not contain 3 shrubs

within were sampled at all possible shrub and open microsites. Data were compiled to a single

plot-level estimate of RDM for shrub and open microsites. Weight in grams, geographical

location, microsite (shrub, open), and corresponding shrub density were recorded.

Shrub Cover

Shrub cover was determined by taking various dimensional measurements of shrub

individuals in a shrub plot. Length of the shrub, perpendicular length and height were taken to

determine the overall cover of the shrubs. The cover of all shrubs in an established plot was then

calculated, summed, and treated as a covariate. Relationship between shrub cover and animal

abundance was then determined (Appendix B, Figure S3).

Statistical Analysis

All statistical analysis was done using R version 4.0.0 (R Core Team, 2010), and code is

available at GitHub https://mariozuliani.github.io/Chapter-2/Index.html. Model selection was

determined by taking the lower Akaike Information Criterion (AIC) (Hurvich et al. 1998;

Johnson & Omland 2004). AIC scores are used to estimate if a particular model with a specific

set of parameters is a valid statistical fit (Snipes & Taylor 2014). General Linear Mixed Models

(GLMMs) were used to examine the relationship between shrub density, and phylum on animal

community measures. Residual dry matter, temperature, and shrub cover were then treated as

covariates. Total animal abundances were treated as a quasipoisson with animal presence as a

binomial. Shrub density was treated as a factor with microsite and phylum, while RDM,

temperature, and canopy cover were kept as covariates and fitted with a quasipoison. ANOVAs

with Chi-square tests were performed where variables in the models were shown to have

significance. Tukey tests were performed for post-hoc analysis of the GLMMs to test the

interactions (Russel 2019). Linear fits were chosen over others by first running linear fits and

then testing others and comparing the resulting AIC scores. Multivariate analysis of composition

was tested using the vegan package (Oksanen et al. 2018). Principle Coordinate Analysis (PCOA) were conducted to compare the abundances of different animal communities based on the number of shrubs present at a plot to assess whether composition varied between shrub and open gap sites, and between plots (Legendre & Anderson 1999). The PCOAs were conducted with vertebrates and invertebrates as separate factors. In addition, sensitivity analysis was conducted on the data both including and excluding camera traps to ensure that density estimates from cam trap observations did not introduce bias by key factors tested here (Cariboni et al. 2007).

Results

The above methods resulted in the establishment of the varying density plots (Figure 2) with a range of 0 to 12 total shrubs being observed. Camera traps proved an effective method of collecting animal interaction data (Appendix D; Figure S4) with this method yielding higher number of animal captures (GLM, p-value = 0.001; post-hoc, Estimated Marginalized Means (EMM) 2.339 ± 0.459, p-value < 0.0001) than transect and focal observations.

Impact of Shrub Density on Animal Abundance, Richness and Evenness

The abundance and richness of animal species increased with increasing shrub densities (Table 2; Table 3; Figure 5). The abundance (Table 2, GLM, p-value = 1.34e-08; EMM -0.3490 ± 0.104, post-hoc, p-value = 0.0008) and richness (Table 3, GLM, p-value = 1.22e-0.08; EMM -0.2403 ± 0.0876, post-hoc, p-value = 0.0061) of vertebrate communities declined with shrub densities in the open microsites across the shrub-density gradient, while evenness (Table 4, GLM, p-value = 0.3547) was non-significant. Post-hoc analysis showed the abundance (Figure 5, Table 2; EMM -0.0772 ± 0.134, post-hoc, p-value = 0.5644), richness (Table 3, EMM -0.0949 ± 0.1015, post-hoc, p-value = 0.3500) and evenness (Table 4, EMM 0.0265 ± 0.0136, post-hoc, p-value = 0.0505) of invertebrate species had no significant relationship with shrub density

Community Comparison

The most common vertebrate observed was *Dipodomys ingens* whereas the most commonly observed invertebrate species were *Oedaleonotus enigma* and *Icaricia acmon* (Figure 6, Appendix C, Table S1). The composition of the vertebrate species community did not significantly differ between shrub and open microsites (PERMANOVA, F_2 = 1.2960, R^2 = 0.0840, p-value = 0.215). The composition of the vertebrate communities significantly varied by shrub density (Appendix E, Figure S5; PERMANOVA, F_2 = 3.3678, R^2 = 0.21829, p-value =

0.012). The invertebrate community composition significantly differed between shrub and open microsites (Appendix E, Figure S6; PERMANOVA, $F_2 = 13.8373$, $R^2 = 0.53146$, p-value < 0.001), but it did not significantly vary by shrub density on the gradient tested (PERMANOVA, $F_2 = 0.9143$, $R^2 = 0.03512$, p-value = 0.386).

Impact of Covariates on Data

Residual Dry Matter (RDM) was an estimate for indirect vegetation effects. There was significantly greater RDM under shrubs (Figure 7, GLM, p-value = 0.01; EMM -1.33 ± 0.0878, post-hoc, p-value = 0.0239). Post-hoc analysis determined that RDM did not vary across the shrub density gradient (GLM, p-value = 4.823e-05; EMM 0.0361 ± 0.0207, post-hoc, p-value = 0.0813). RDM significantly influenced the abundance (Figure 7; GLM, p-value = 0.044679; EMM -1.20 ± 0.263, post-hoc, p-value = 0.0001), species richness (GLM, p-value = 0.037954; EMM -1.65 ± 0.220, post-hoc, p-value = 0.0001) and evenness (GLM, p-value = 4.508e-13; EMM -0.921 ± 0.468, post-hoc, p-value = 0.0489) of vertebrate species showing a decline with increasing RDM at shrub and open microsites. Invertebrate species had an increase in richness (Figure 7; GLM, p-value = 0.037954; EMM -1.94 ± .848, p-value = 0.0221); however, evenness (GLM, p-value = 4.508e-13) and abundance was not significantly influenced by local RDM (Figure 7; GLM, p-value = 0.044679). Maximum temperature significantly mediated the influence of shrub microsites on animal abundance (Table 2; Appendix B, Figure S2) and richness (Table 3) and evenness (Table 4). Vertebrate abundance (Appendix B, Figure S2; Table 2; EMM -0.0557 ± 0.0130, post-hoc, p-value < 0.001) species richness (Table 3; EMM -0.0674 ± 0.0292, p-value = 0.0211) and evenness (Table 4; EMM -0.0733 ± 0.0365, post-hoc, p-value = 0.0443) were significantly decreased with increasing temperature. In contrast, maximum temperature predicted invertebrate evenness (Table 4; EMM -0.0674 ± .0156, post-hoc, p-value

< 0.0001) but not abundance (Appendix B, Figure S2; Table 2) and species richness (Table 3). Shrub cover did not predict overall animal abundance across the shrub-density gradient (Appendix B, Figure S3; Table 1). Both Vertebrate and invertebrate abundance (Table 2), species richness (Table 3) and evenness (Table 4) were unaffected by shrub cover.

Method of Measurement Comparison

Camera traps captured the highest number of animal observations when compared to transect and focal observations (Appendix D, Figure S4; GLM, p-value = 1.982e-09; EMM 2.339 ± 0.459, post-hoc, p-value < 0.001). Vertebrate and invertebrate species were detected more on camera traps than through transect (Appendix D, Figure S4; GLM, p-value = 0.001; EMM 1.55 ± 0.372, p-value = 0.001) and focal observations (GLM, p-value = 0.001; EMM 2.339 ± 0.459 post-hoc, p-value = 0.001). Both focal observations and transects showed no significant differences in observing vertebrate and invertebrate species (GLM, p-value = 0.001; EMM -0.784 ± 0.490, post-hoc, p-value = 0.2459). A sensitivity analysis of animal density without camera traps showed that both vertebrate and invertebrate species were observed at higher abundances (Appendix F, Figure S7; Table S2; EMM -1.01 ± 0.397, p-value = 0.0114). Capture rate for both vertebrates and invertebrates was determined to be unrelated to the shrub density gradient (Appendix G, Figure S8; GLM, p-value = 0.6767).
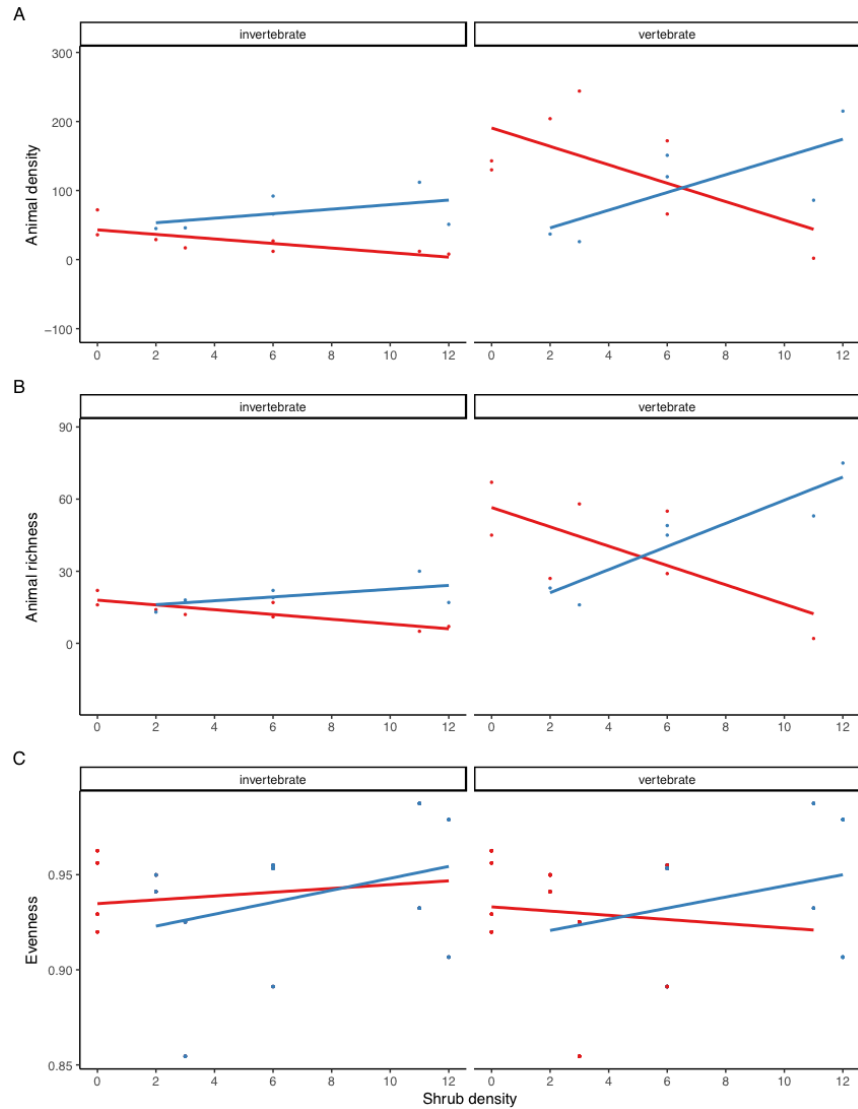
Figure 5: The relative effects of shrubs versus open gaps on a gradient of plot-level densities in a desert ecosystem. Data was combined from camera trap, transects and focal observations, then split by phylum to represent the relationship between shrub and animal densities (Panel A), shrub density and species richness (Panel B), and the relationship between shrub density and the evenness of animal species (Panel C). The blue line represents the trend for shrub microsites while the red line represents the trend for the open microsites. Shaded areas show 95% confidence interval associated with line of best fit.

Table 2: Analysis of animal abundance from general linear model for study period. Density, microsite and phylum were treated as fixed factors. All significant p-values (p < 0.05) are indicated in bold. Cover was defined as the total shrub canopy cover in a given plot while RDM was defined as the total mass of grasses within a 20cmx20cm square in a plot.

	DF	DEVIANCE	DF RESIDUAL	DEVIANCE RESIDUAL	PR(>CHI)
NULL			22	1389.49	
DENSITY	1	5.22	21	1.38E+03	0.5299373
MICROSITE	1	17.87	20	1.37E+03	0.2453242
PHYLUM	1	427.23	19	9.39E+02	**1.34E-08**
RDM	1	116.33	18	8.23E+02	**0.003032**
MAX_TEMP	1	283.43	17	539.41	**3.70E-06**
COVER	1	14.94	16	524.47	2.88E-01
DENSITY:MICROSITE	1	142.7	15	381.77	**0.0010257**
DENSITY:PHYLUM	1	22.8	14	358.97	0.1894213
MICROSITE:PHYLUM	1	152.64	13	206.34	**0.0006844**
DENSITY:MICROSITE:PHYLUM	1	41.57	12	164.77	0.0763625

Table 3: Analysis of animal richness from general linear model for study period. Density, microsite and phylum were treated as fixed factors. All significant p-values (p < 0.05) are indicated in bold. Cover was defined as the total shrub canopy cover in a given plot while RDM was defined as the total mass of grasses within a 20cm x 20cm square in a plot.

	DF	DEVIANCE RESIDUAL	DF. RESIDUAL	DEVIANCE	PR(>CHI)
NULL			22	299.197	
DENSITY	1	2.955	21	296.242	0.375599
MICROSITE	1	21.189	20	275.053	**0.017671**
PHYLUM	1	122.179	19	152.874	**1.22E-08**
RDM	1	13.284	18	139.59	0.060314
MAX_TEMP	1	42.77	17	96.82	**0.00075**
COVER	1	10.957	16	85.863	0.088003
DENSITY:MICROSITE	1	27.062	15	58.801	**0.007337**
DENSITY:PHYLUM	1	0.499	14	58.303	0.715922
MICROSITE:PHYLUM	1	3.327	13	54.976	0.347164
DENSITY:MICROSITE:PHYLUM	1	6.157	12	48.819	0.200941

Table 4: Analysis of species evenness from general linear model for study period. Density, microsite and phylum were treated as fixed factors. All significant p-values (p < 0.05) are indicated in bold. Cover was defined as the total shrub canopy cover in a given plot while RDM was defined as the total mass of grasses within a 20cm x 20cm square in a plot.

	DF	DEVIANCE RESIDUAL	DF. RESIDUAL	DEVIANCE	PR (>CHI)
NULL			293	0.40214	
DENSITY	1	0.037918	292	0.36422	**1.08e-08**
MICROSITE	1	0.000213	291	0.36401	0.668368
PHYLUM	1	0.000993	290	0.36302	0.354794
RDM	1	0.000145	289	0.36287	0.724066
MAX_TEMP	1	0.018560	288	0.34431	**6.329e-05**
DENSITY:MICROSITE	1	0.010574	286	0.33374	**0.002534**
DENSITY:PHYLUM	1	0.001139	285	0.33260	0.321772
MICROSITE:PHYLUM	1	0.000596	284	0.33200	0.473303
DENSITY:MICROSITE:PHYLUM	1	0.000013	283	0.33199	0.916172
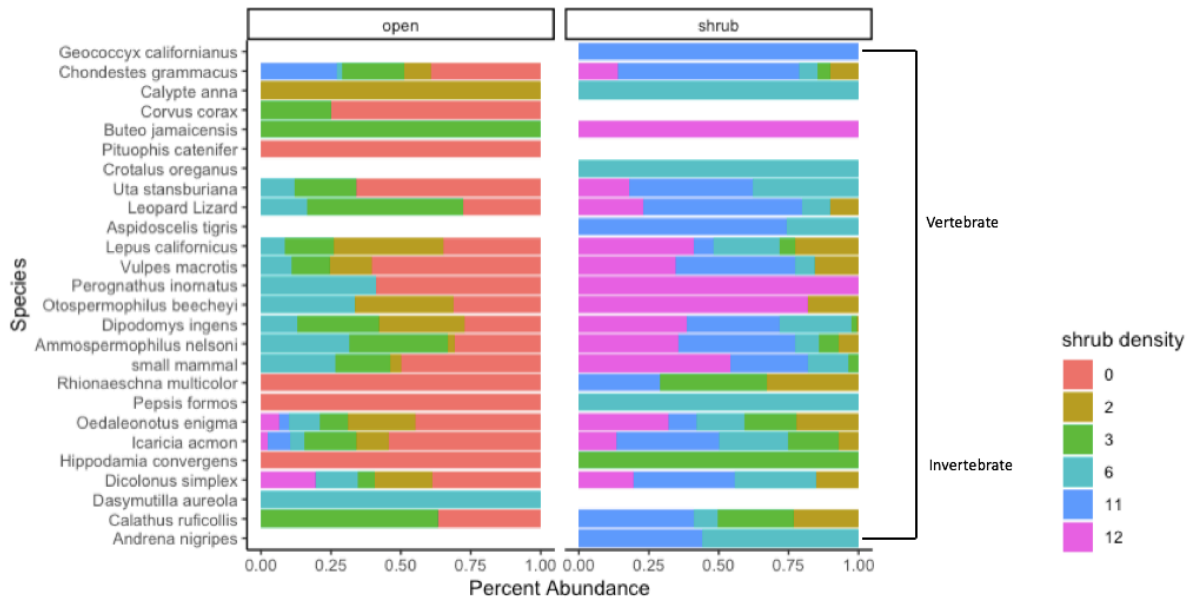
Figure 6: The relative proportion of total density of vertebrate and invertebrate species. The x-axis shows the percentage of the total number of individuals per density for each sample plot. Data were separated based on association with shrub/open microsite and by vertebrate/invertebrate species. Colors correspond to total number of shrubs in established plot.
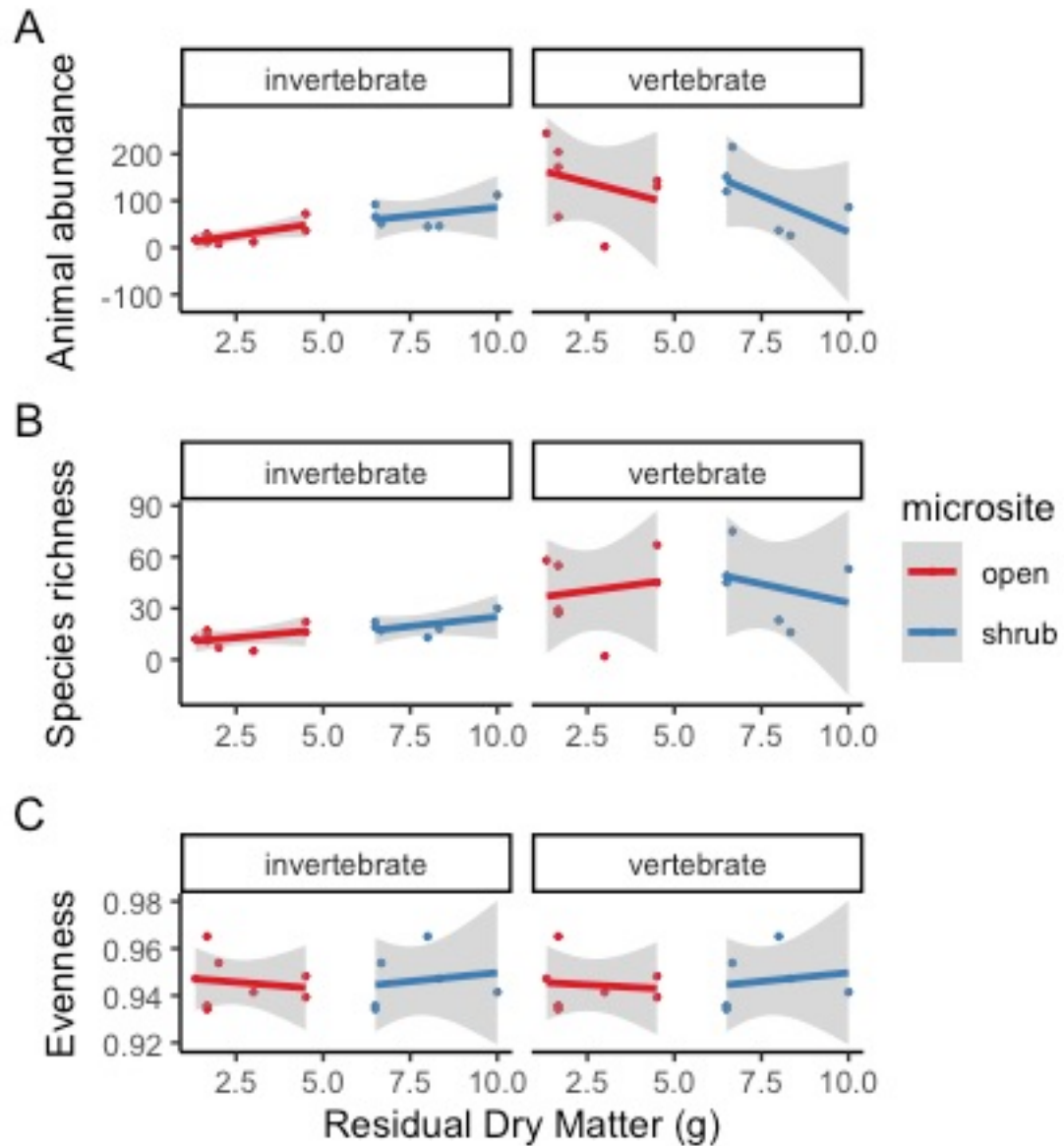
Figure 7: The relative effects of residual dry matter (RDM) on a gradient of plot-level densities in a desert ecosystem. The data was split by phylum to represent the relationship between RDM and animal densities (Panel A), RDM and species richness (Panel B), and the relationship between RDM and the evenness of animal species (Panel C). The blue line represents the trend for shrub microsites while the red line represents the trend for the open microsites. Shaded areas show 95% confidence interval associated with line of best fit.

Discussion

The purpose of this study was to examine whether shrubs and increasing density of shrubs positively influences key measures of animal composition. Within this study, I found support for the hypothesis that shrubs and a shrub-density gradient positively influences the structure and composition of the local animal community. Vertebrate species responded positively to the increasing shrub-density gradient while invertebrate species were unaffected. The composition of vertebrate species was positively influenced by the shrub-density gradient, while invertebrate communities were only influenced by shrub/open microsites. Residual dry matter indirectly decreased vertebrate abundance, richness, and evenness, while only decreasing invertebrate abundance. A shrub-density gradient in arid ecosystems having a positive impact on local animal species community assembly suggests that variation in foundation species density is an important form of habitat heterogeneity.

Mechanisms are important in studies that observe associations or interactions between different species. Shrubs typically benefit animal communities in arid ecosystems through many mechanisms including acting as a refuge (Valone & Balaban-Feld 2019), escape from harsh temperature (Westphal et al. 2018; Ivey et al. 2020), and acting as a food source (Parmenter & MacMahon 1983; Auger et al. 2016; Lortie et al 2020) for some small animals. Small prey species specifically use these shrubs as shelter from larger predatory animals. *Uta stansburiana* and various grasshopper species are reliant on the shelter provided by shrubs to act as a refuge from predation (Greenfield et al. 1989). Observations showing *Dipodomys ingens* as one of the species that associate with these shrubs, suggests that this species is the most reliant on this interaction for survival. Burrows located underneath the shrub canopy suggests that this species, and others, use these areas as a means of predator avoidance (Filazzola et al. 2017). The

facilitative effects associated with *Ephedra californica* provide these necessary mechanisms to animal species (Noble et al. 2016; Westphal et al. 2018). The established shrub-density gradient had a positive relationship with vertebrate species, driven by the positive effects associated with *E. californica* (Westphal et al. 2018), resulting in more vertebrate species being observed as the shrub-density gradient increased. As the shrub-density gradient increased, the richness of animal species associated with open microsites decreased, while an increased association with shrubs was observed. This displays avoidance of open microsites when there are more shrubs in a given area, suggesting that animal species opt to associate with these foundational shrubs when available (Wesphal et al 2018; Ivey et al. 2020). Thus, shrub association is a fundamental factor in increasing animal association.

Shelter from intense temperatures is one of the main uses of these foundational shrubs by animals (Westphal et al. 2018, Ivey et al. 2020). This study supported this trend because at peak times of day where the maximum heat was experienced, animals favored using shrub microclimates as a means of escaping periods of intense heat. This means local temperature in desert ecosystems can have direct effects on the local animal community, particularly at peak times of the day. This idea has been supported through other studies that have been conducted in the Carrizo Plain National Monument, such as the work by Westphal et al. (2018), where the use of foundational shrub canopies formed a facilitative interaction with *Gambilia sila*. Since some species show associations between shrub and open microsites for activities, such as thermoregulation in desert ecosystems (Diaz & Cabeza-Díaz 2004; Ivey et al. 2020), shrubs are fundamental in the thermal heterogeneity of ectotherms (Filazzola et al. 2017). Shrubs acting as a shelter from peak local temperatures can explain why the patterns in abundance of vertebrate species increase with the shrub-density gradient (Díaz & Cabeza-Díaz 2004; Filazzola et al.

2017), because they buffer the intense climate by creating more shade and reducing the overall heat experienced by animal species. With shrub canopies providing cooler microclimates for species at higher temperature periods of the day, animals favored shrub association, whereas during lower temperatures periods animals associated more with open microsites. Our findings showed that some instances shrub microsites were hotter than open microsites. In these cases, the abundance of animals decreased suggesting that individuals would seek cooler microclimates to escape harsher temperatures. It is possible that higher temperature recordings could be due to increasing land surface albedo (Ghulam et al. 2007) in desert ecosystems. Surface albedo being the light being reflected from a surface (Ghulam et al. 2007). In addition, shrubs have been noted to reduce air velocity due to dense foliage, and generate a boundary layer, which could increase microsite temperatures (Michels 1994; Wezel et al. 2000). This could lead to HOBO pendants possibly recording higher temperatures under shrub canopies. Indirect effects from RDM had negative impacts on vertebrate species abundance. Dense grass cover impacted animal movement in similar systems (Vasquez 2002; Filazzola et al. 2017). Vertebrate species avoided shrub microsites where a large abundance of grasses covered under the canopy. Since high grass abundance reduces the vigilance of a species and the ability to escape predation, avoidance of these specific areas served as a beneficial survival technique (Vasquez 2002). Closely examining the direct and indirect effects of animal species association with shrubs might better determine the effects of these associations.

The composition of animal communities responded to variation in shrub densities. Vertebrate species such as *Dipodomys ingens* have a higher association at open areas than invertebrate species. However, small rodent species such as *D. inguns* have been observed to consume seeds from desert shrub species (Valone & Balaban-Feld 2019; Whitford & Steinberger

2020), suggesting that resource availability may be a driving factor in vertebrate association with shrubs. The variation in vertebrate shrub and open association is primarily driven by the association between other species. With species such as *Crotalus oreganus*, known to consume smaller vertebrate species (Holding et al. 2018) being recorded in this ecosystem, the use of these shrub species can act as a refuge from predators, thus impacting community association with shrub and open areas. Invertebrate species, such as *Oedaleonotus enigma,* consume foliage of shrub species and some native grasses (Greenfield et al. 1989), suggesting that the association of invertebrates with an increasing shrub-density gradient is driven by herbaceous behavior. Directly analyzing the differences between community compositions in desert ecosystems could further help explain their association with the shrub-density gradient and the impact facilitative shrubs have on vertebrate and invertebrate species.

There are caveats to consider when conducting observational experiments to examine vertebrate and invertebrate community composition. Sampling bias is when nonrandomly selected samples are used to estimate variable relationships which can result in missing data (Heckman 1979; Fournier et al. 2019). For instance, camera traps are typically used to collect data on vertebrate species and are more likely to pick up on large movement, as opposed to invertebrate species that may not trigger the camera (Meek et al. 2014; Noble et al. 2016). This would result in lower total invertebrate observations and would could potentially not properly sample invertebrate species. It is typically easier for observers during transect and focal observations to observe vertebrate species due to their size. Since invertebrate species are much smaller and harder to observe, their presence may go unnoticed (Silveira et al 2003; Nath et al. 2010). Similarly to the challenges experienced with camera traps, missing invertebrate species

when conducting transect and focal observations would produce a sample bias and impact the invertebrate community composition data.

Implications:

Globally, the overall health of arid ecosystems is currently at risk due to stressful ecological conditions (Padilla et al. 2009) which could impacts the overall survival of various animal species. Restoration of both plant and animal species in arid ecosystems has been the topic of discussion for decades (Padilla et al. 2009), mainly focusing on improving the overall health of these environments can be used in the conservation of associated plant and animal species (Porensky et al. 2014; Ivey et al. 2020). One of the main themes for deserts is to focus on facilitative interactions that primarily impact desired species (Abella & Chiquoine 2019). Species such as *Gambilia sila* are listed as endangered in California at this specific site, and it is dependent upon these facilitative interactions (Westphal et al. 2018). It is because of this decline in desert health that it is essential to study factors influencing association of animal species with foundational shrubs, as it could prove to play a key role in the potential restoration of these types of ecosystems.

Conclusion

This study focused on facilitative shrub species and how a shrub-density gradient could positively correlate with animal species communities. Camera traps, transects, and focal observations displayed higher abundances of vertebrate species with an increasing shrub-density gradient. Species richness at these plots increased along the shrub-density, while evenness of vertebrate and invertebrate species was unaffected. Maximum daily temperature had a direct negative impact on animal association with shrub and open microsites, suggesting that at higher temperatures, animals will opt to interact with foundational shrubs rather than stay in open areas.

Residual Dry Matter (RDM) decreased the abundance, richness, and evenness of animal species, suggesting that local animal communities are deterred from areas with higher abundances of grasses. Vertebrate species communities were similar in composition to one another as the shrub-density gradient increased, while invertebrate species composition differed at the microsite level. A future study could potentially use larger and more numerous plots of varying shrub density over a longer period of time to gather further information on animal abundance, richness and evenness. This would allow for a better statistical significance while also obtaining a higher sample size. In addition, conducting this study at varying times of the year could potentially yield additional data. Conducting the study during colder seasons could potentially support the evidence that animal species are more associated with higher shrub areas due to higher temperatures. As more studies arise focusing on the relationship between shrub and animal species in arid ecosystems, data will continue to build on the evidence suggesting that these animal species are reliant on facilitative shrub species to survive harsh arid environments.

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Appendices

**Appendix A:** Establishment of Shrub Density Plots and Experimental Set-up

Figure S1: Left-establishment of a camera trap located at the outer edge of one of the microsites. Cameras were secured onto pegs with zip ties and then driven into the soil until the bottom of the camera came into contact with ground. Right-displays the entirety of the open microsite within the 20meter area. Both cameras set up facing each other into the site.

Appendix B: Analysis of Temperature and Canopy Cover on Animal Abundance
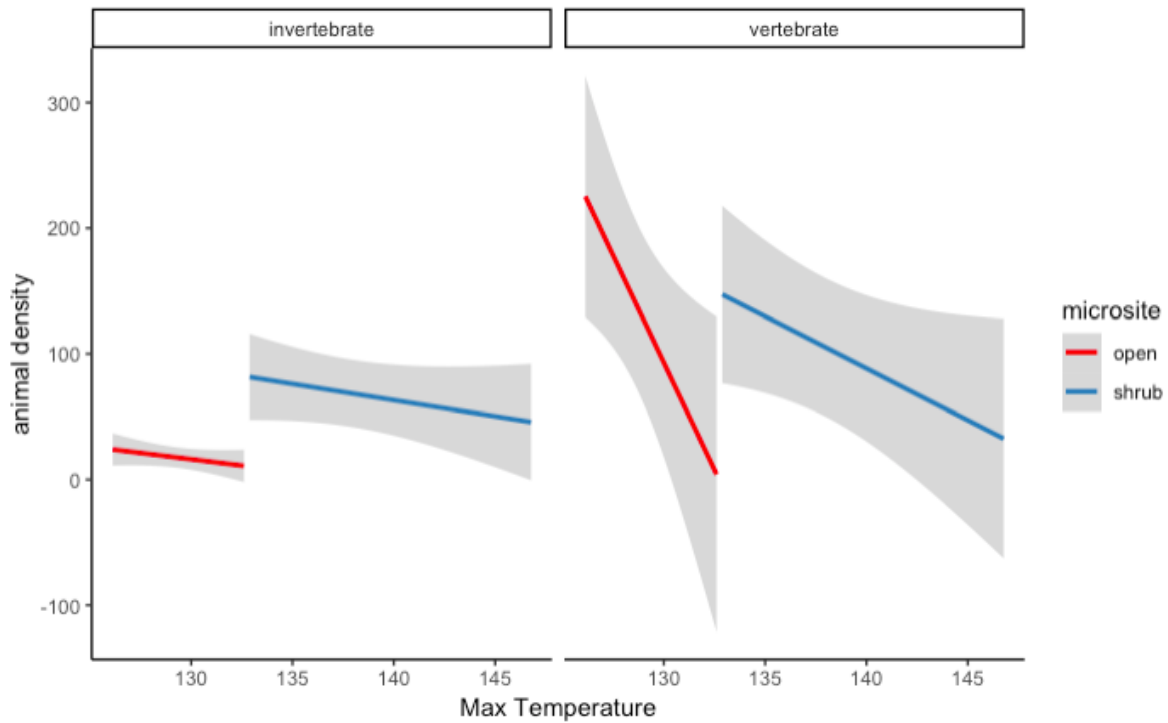
Figure S2: Animal density (number of individuals) and maximum temperature recorded (ºF). The blue line represents the trend for shrub microsites while the red line represents the trend for the open microsites. Shaded areas indicate the standard error of the data.
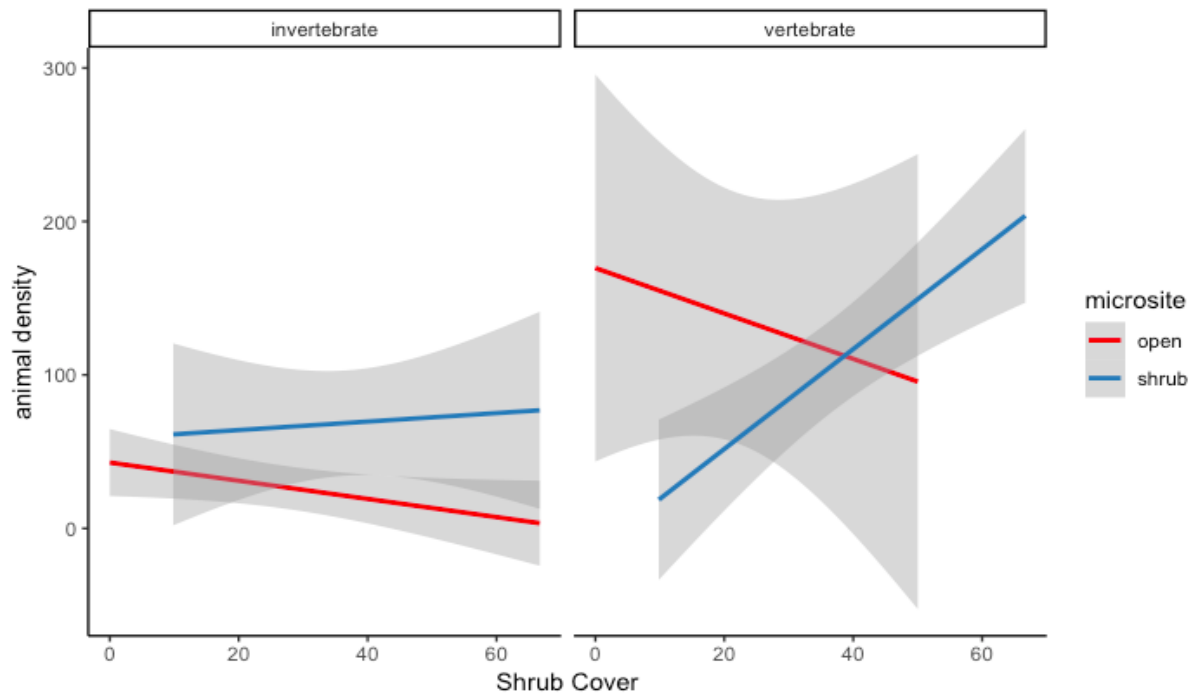
Figure S3: Animal density (number of individuals) and shrub cover (cm/area). The blue line represents the trend for shrub microsites while the red line represents the trend for the open microsites. Shaded areas indicate the standard error of the data.

# Appendix C: Species Identification and Total Plot Interactions

Table S1: Table displaying varying species recorded at The Carrizo Plain National Monument, CA, and the corresponding abundance associated with individual observations of each.

Species Name	Common Name	Taxa	Number Recorded
Ammospermophilus nelsoni	San Joaquin Antelope Squirrel	Vertebrate	132
Andrena nigripes	Big-headed Andrena	Invertebrate	4
Aspidoscelis tigris	Western Whiptail	Vertebrate	6
Buteo jamaicensis	Red-tailed hawk	Vertebrate	2
Calathus ruficollis	Ground Beetle	Invertebrate	8
Calypte anna	Anna's Hummingbird	Vertebrate	2
Chondestes grammacus	Lark Sparrow	Vertebrate	71
Corvus corax	Northern Raven	Vertebrate	4
Crotalus oreganus	Northern Pacific Rattlesnake	Vertebrate	1
Dasymutilla aureola	Velvet ant	Invertebrate	1
Dicolonus simplex	Robber Fly	Invertebrate	40
Dipodomys ingens	Giant Kangaroo Rat	Vertebrate	1014
Geococcyx californianus	Roadrunner	Vertebrate	1
Hippodamia convergens	Ladybug	Invertebrate	2

|			
Icaricia acmon	**Acmon Blue Butterfly**	**Invertebrate**	**294**
Gambilia sila	**Blunt-nosed Leopard Lizard**	**Vertebrate**	**48**
Lepus californicus	**Black-tailed Jackrabbit**	**Vertebrate**	**170**
Oedaleonotus enigma	**Valley Grasshopper**	**Invertebrate**	**307**
Otospermophilus beecheyi	**California Ground Squirrel**	**Vertebrate**	**9**
Pepsis formos	**Spider Wasp**	**Invertebrate**	**3**
Perognathus inornatus	**Salinas Pocket mouse**	**Vertebrate**	**25**
Pituophis catenifer	**The Great Basin Gophersnake**	**Vertebrate**	**2**
Rhionaeschna multicolor	**Blue-eyed Darner**	**Invertebrate**	**8**
Small mammal	**Small mammal**	**Vertebrate**	**78**
Uta stansburiana	**Side-blotched Lizard**	**Vertebrate**	**13**
Vulpes macrotis	**Kit Fox**	**Vertebrate**	**21**

# Appendix D: Comparison of Methods Used to Estimate Animal Abundance
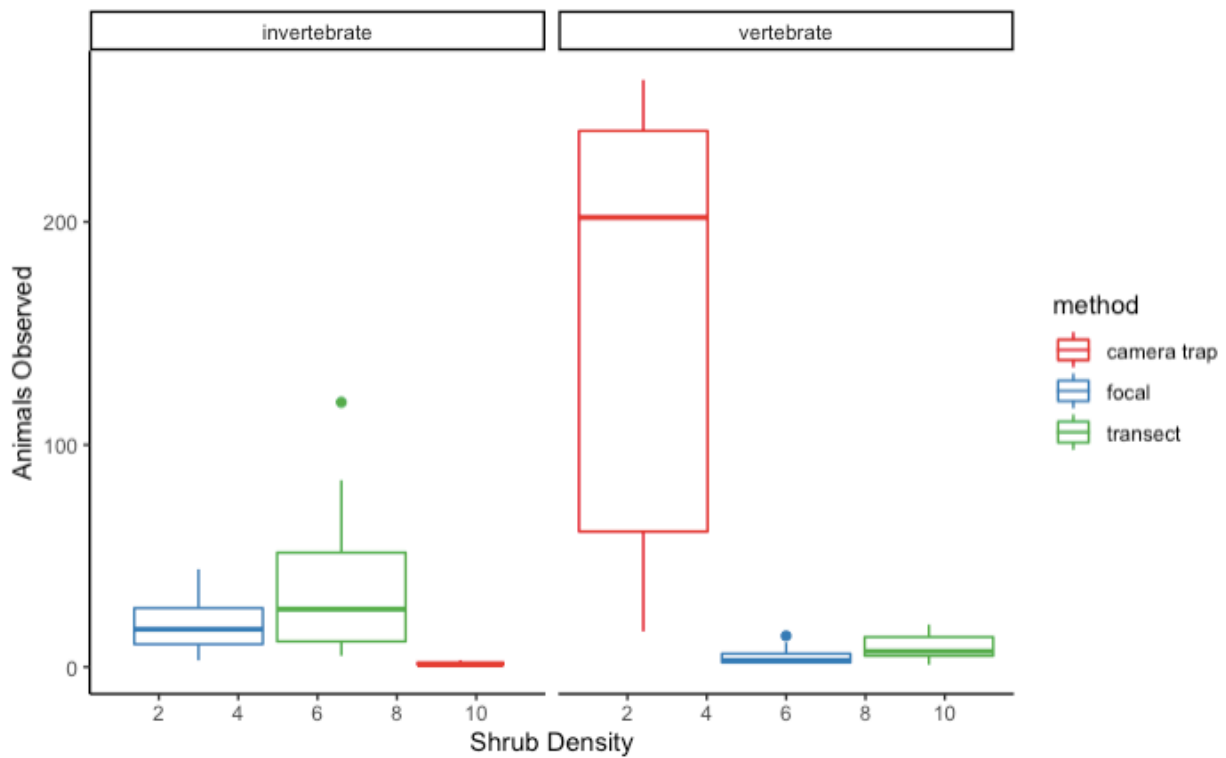
Figure S4: Boxplot showing the relationship between shrub density and animal abundance for each method of sampling. Solid middle lines show the median of the data while whiskers display standard deviation.

Appendix E: PCOA Comparison of Vertebrate and Invertebrate Species at Varying Shrub Densities
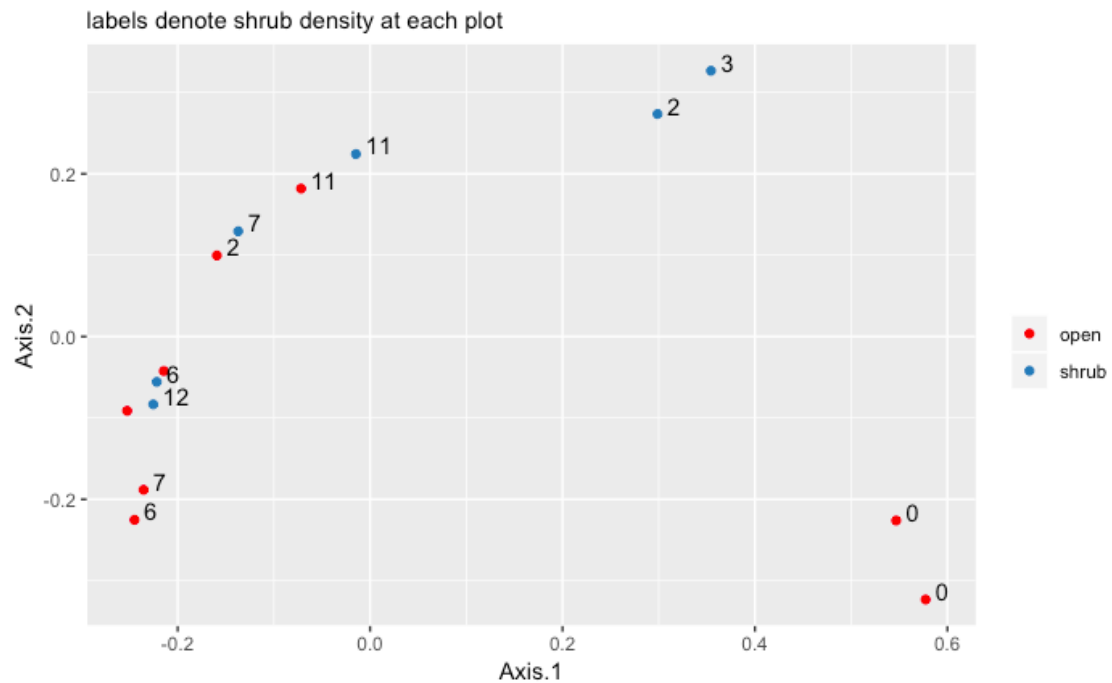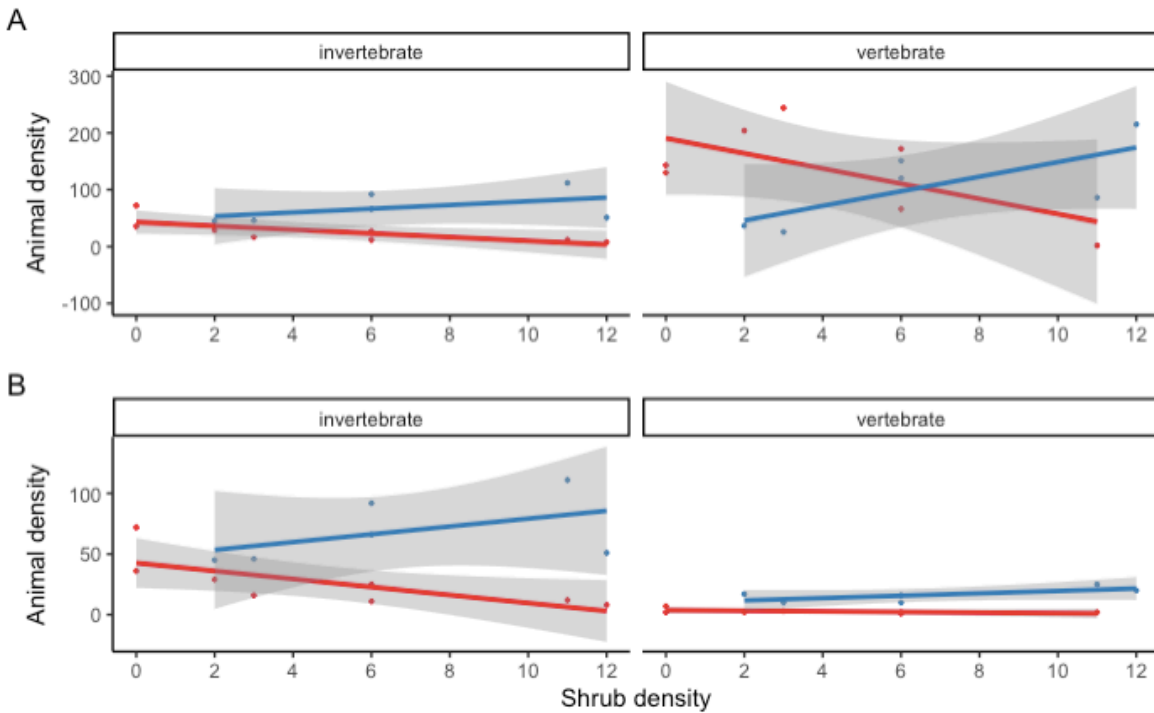

Figure S5: PCOA comparison of vertebrate species based on total *Ephedra californica* individuals and interacting species.
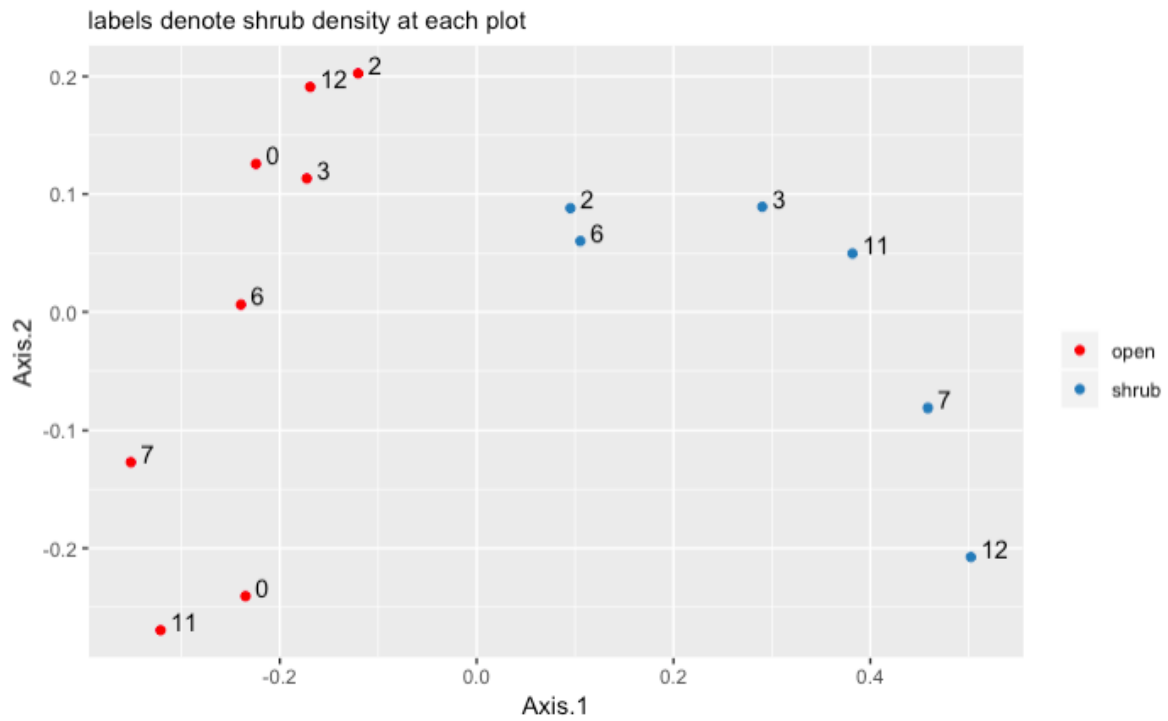
Figure S6: PCOA comparison of invertebrate species based on total *Ephedra californica* individuals and interacting species.

Appendix F: Analysis of Animal Density Including and Excluding Camera Trap Data


Figure S7: Analysis of shrub density against animal abundance both including camera trap data (A) and excluding camera trap data (B). The blue line represents the trend for shrub microsites while the red line represents the trend for the open microsites. Shaded areas show 95% confidence interval associated with line of best fit.

Table S2: Analysis of animal abundance from General linear model (GLM) with absence of camera trap data. Microsite and phylum were treated as factors. All significant p-values (p < 0.05) are indicated in bold. RDM was defined as the total mass of grasses within a 20cmx20cm square in a plot.

	DF	DEVIANCE RESIDUAL	DF. RESIDUAL	DEVIANCE	PR (>CHI)
NULL			293	0.40214	
DENSITY	1	0.037918	292	0.36422	**1.080e-08**
MICROSITE	1	0.000213	291	0.36401	0.668368
PHYLUM	1	0.000993	290	0.36302	0.354794
RDM	1	0.000145	289	0.36287	0.724066
MAX_TEMP	1	0.018560	288	0.34431	**6.329e-05**
DENSITY:MICROSITE	1	0.010574	287	0.33374	**0.002534**
DENSITY:PHYLUM	1	0.001139	286	0.33260	0.321772
MICROSITE:PHYLUM	1	0.000596	285	0.33200	0.473303
DENSITY:MICROSITE:PHYLUM	1	0.000013	284	0.33199	0.916172

Appendix G: Camera Trap Rate of Capture per Established Plot
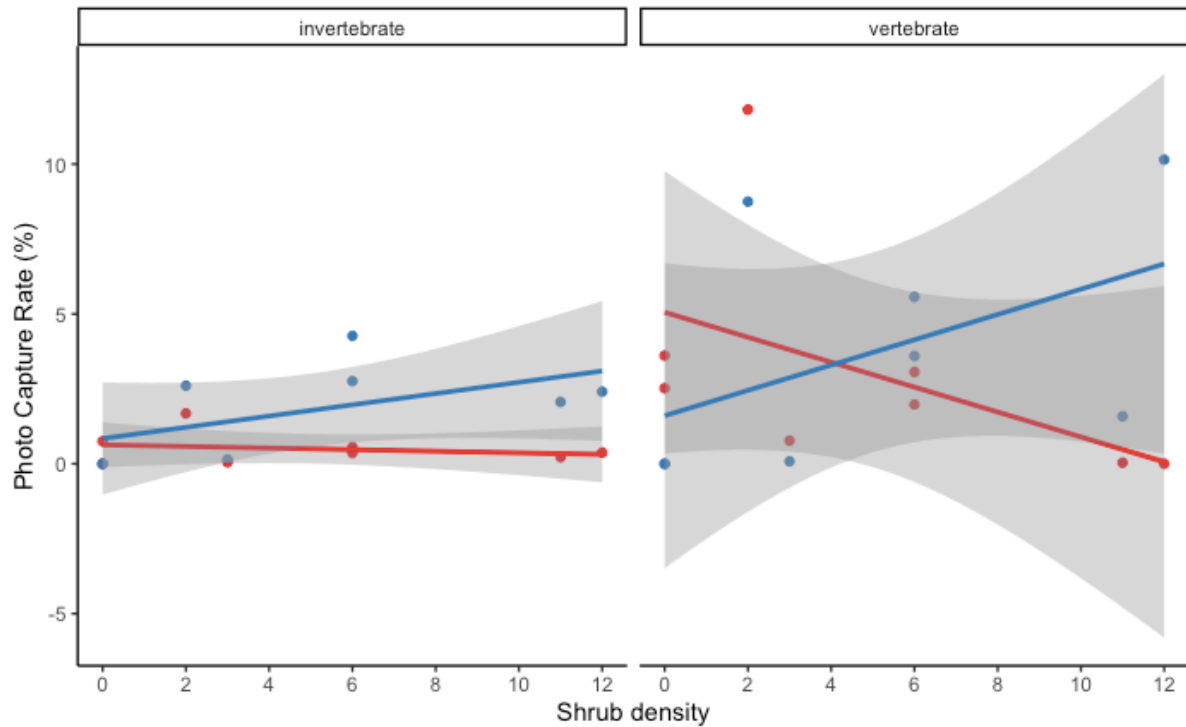
Figure S8: Shrub density and camera trap capture rate where data is split by phylum The blue line represents the trend for shrub microsites while the red line represents the trend for the open microsites. Shaded areas show 95% confidence interval associated with line of best fit.