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

Mario Zuliani, Nargol Ghazian and Christopher J. Lortie

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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 through lowering the amplitude of variation. Consequently, there have been many contrasts of shrub versus open effects; however, we extend this approach further by testing these effects on a gradient of shrub densities in the Carrizo National Monument, California. We tested the hypothesis that shrub density is a landscape-level predictor of vertebrate community composition and structure. We used camera traps, transects and focal observations to estimate animal density and composition, alongside the deployment of temperature sensors. Plots were established within shrub patches ranging from 0 to 12 shrubs per 10 m radius. Plots with relatively higher shrub densities had increased abundance and richness of vertebrate animal species. Temperature and residual dry matter were also important mediators of animal density and richness. Shrub cover was also an important driver of animal communities but we propose that shrub density is a more rapid proxy for vegetation effects in deserts relevant to wildlife conservationists, and managers.

Keywords: arid, community composition, conservation, density, desert, foundation species, landscape ecology, plant–animal interactions, semi-arid, shrubs, vertebrate animals

Anthropogenic changes are impacting arid/semi-arid ecosystems globally, driving these areas closer to desertification. These anthropogenic changes are mainly caused by factors including water availability and increasing temperatures (Burrell et al. 2020). Local animal species exposed to these changes rely on interactions with one another to reduce the adverse effect experienced (Bertness and Callaway 1994, Dangles et al. 2013). To ameliorate the stressors associated with these changes, positive interactions between these local animal species and foundational shrubs have been reported (Lortie et al. 2016, Dangles et al. 2018). 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 and Leonard 1997, Molina-Montenegro et al. 2016). This is more formally defined as facilitation (Filazzola et al. 2017, Dangles et al. 2018). Understanding the relative importance of facilitative interactions between

shrubs and other taxa has been proposed as an important means to understand community function in high-stress ecosystems since these interactions are common in these systems (Lortie et al. 2016, Dangles et al. 2018).

Vegetation is a key aspect of any landscape. In drylands, shrubs can facilitate animals through direct and indirect mechanisms such as providing shade from their canopy that ameliorates temperature extremes (Lortie et al. 2016, Moore et al. 2018, Westphal et al. 2018). A foundation species typically facilitates local communities and maintains habitats that are beneficial for other species (Bittick et al. 2019, Lortie et al. 2020). Since these shrub species are frequently reported to facilitate plant and animal species they have been termed foundation species (Bertness and Leonard 1997, Bortolus et al. 2002, Lortie et al. 2016). Foundational shrub species provide benefits through indirect mechanisms such as microclimatic buffering that allows for some animal species to take refuge from the harsh arid conditions of the California deserts (Holzapfel and Mahall 1999, Filazzola et al. 2017), by lowering temperature extremes, resulting in higher animal densities being observed under shrub canopies than in open spaces (Koyama et al. 2015). For instance, *Gambelia sila* uses shrub canopies to reduce its body temperature during peak times in the day (Noble et al. 2016, Westphal et al.

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2018, Ivey et al. 2020). These foundational shrubs also influence the total vegetation cover underneath their canopy (Bartolome et al. 2002). These abundances of plant matter under shrub canopies can impact animal species' ability to forage, move and escape predation (Vasquez et al. 2002) that can have a negative impact on shrub–animal associations. In addition, shrubs increase vertebrate species abundance in arid ecosystems, showing that these shrubs play a pinnacle role in the ecosystem (Germano and Lawhead 1986). Other indirect mechanisms provided by these shrubs include acting as a refuge for some desert animals from predators (Milchunas and Noy-Meir 2002, Lortie et al. 2016) by reducing predation (Nelson et al. 2007) and acting as cover burrows (Edelman 2011). Shrubs can augment resources by trapping seeds consumed by small mammals (Bullock and Moy 2004) and by producing resources such as fruit (Hertel et al. 2018). Nonetheless, 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 measure that has been well established in competition theory in plants (Antonovics and Levin 1980), population studies in animals (Adams and Tschinkel 1995, Nilsson 2001), and in trophic interactions (McPeck 2019). In the context of plant–animal facilitation in deserts, the density of plants can influence the net outcome of animal interactions with shrubs (Springer et al. 2003). Shrub cover is an important component of plant communities relevant to animals as smaller vertebrate individuals utilize areas of cover as habitats and shelter from predators (Schooley et al. 1996, Lortie et al. 2020). Shrub density was selected as the main measure of this study as it is a more tractable measure than shrub cover. Positive correlations between shrub cover and density imply that density can be used as a proxy for shrub cover, thus acting as a more direct measure (Roques et al. 2001). Both landscape management and species-specific restorations focus primarily on plant species densities as a possible restorative practice (Westphal et al. 2018). Several biodiversity benefits have been identified with the conduction of shrub-based planting such as; reduction in harmful incursions from other areas, supplementation of core habitat species, and increase in habitat connectivity (Collard and Fisher 2010). Some animal species disproportionately occupy shrub canopies over open areas because they provide better microhabitats and movement trails (Stapp and Van Horne 1997). If more shrubs individuals result in increased animal abundance and diversity within the community, then the likelihood for more direct and indirect interactions between animals also increases (Adams and Tschinkel 1995); thus, potentially generating more complex trophic structures (Polis 1991, Schneider et al. 2016). 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. Shrub encroachment is a common phenomenon where an increase in both woody and shrub plants is observed in drylands contributing to vast changes in shrub and vegetation cover (Knapp et al. 2008, Van Auken 2009). Though, in areas such as the Carrizo Plain National Monument, foundational shrub species such as *Ephedra californica* are responsible for returning this ecosystem from an arid grassland back into shrubland

(Buffington and Herbel 1965, Browning et al. 2008). Shrub encroachment is typically negative because it is associated with desertification of arid ecosystems (Van Auken 2009). However, encroachment may not necessarily reduce these shrub functions and evidence further suggests that encroachment can enhance these ecosystems (Eldridge and Santiago 2015). Specifically, in arid scrubland, this increase in density can positively influence species abundance and richness and potentially play a key role in the reversal of desertification (Maestre et al. 2009, Sirami et al. 2009). In addition, encroachment can be linked to the enhancement of vascular plant richness and is linked with greater soil fertility (Maestre et al. 2009). These changes in shrub densities will impact local animal species due to the importance of these facilitative interactions.

Understanding the importance of shrubs as foundational species can provide insight into the facilitative interactions associated with populations of local animal species. Here we examined whether shrubs and increasing density of shrubs positively influence key measures of animal communities. We tested the hypothesis that a shrub-density gradient will influence the structure and composition of the local animal community. The following predictions were examined:

- 1) Increasing shrub densities positively influence the abundance and composition of the animal community locally.
- 2) The effects of shrub density on a gradient from low to high densities can influence the animal community and the responses by these animals are species-specific.
- 3) Direct effects of the shrub canopies include temperature amelioration and indirect effects include impacts through understory vegetation differences relative to the open such as residual dry matter (i.e. plant litter under the canopies).

## Methods

### Study site

This study was conducted in the Elkhorn Plain of the Carrizo Plain National Monument (CNM, 35°07'11.352"N, 119°37'42.707"W; Fig. 1). The average temperature and precipitation for the site were 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 approximately 822.05 m asl, with an average temperature of 14.7 and 21.7°C in the months of May and June respectively. Average precipitations for these months are extremely low with only the month of May experiencing 0.17 cm of rain (Supporting information). The study site is dominated by the shrub *Ephedra californica*. The flora of the Elkhorn Plain is composed primarily of native species (<[www.rare-plants.cnps.org/advanced.html](http://www.rare-plants.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 and Callaway 2018, Lucero et al. 2019).

We established a shrub gradient along the Elkhorn Road in the CNM (Supporting information). The shrub density at plot scales was assessed using imagery (ArcGis) and field

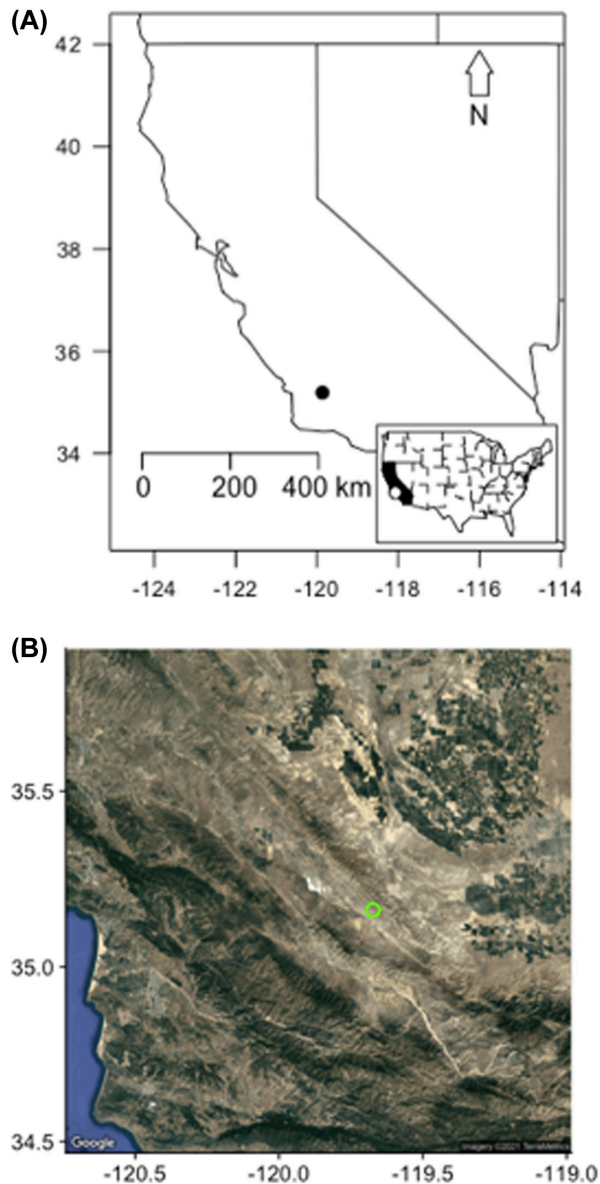


Figure 1. A set of maps displaying different scales of study site. (A) depict the general location of sampling area specific to study. (B) depicts the location of the field site in the Carrizo Plain National Monument, California, US (35°11'23.64N, 119°51'47.879"W) indicated with a green circle. All maps were generated using the R package *ggmap* (Kahle and Wickham 2013) on 5 June 2019.

surveys (Lortie and Zuliani 2020, Zuliani and Lortie 2020a, b). Over 80 sites were randomly located from satellite images through the use of the R program *ggmap* (Kahle and Wickham 2013) and the mean number of shrubs in a 10 m radius were recorded. A total of eight circular plots, each 10 m in radius, were established randomly stratified from south to north to ensure independence and to capture the range of shrubs present in the region from entirely shrub free up to 12 shrubs per plot. The mean estimate shrub densities via satellite imagery were significantly different, where the min was 0 and max was 12 (ANOVA,  $F=9.319$ ,  $p < 0.001$ ,  $df=2$ ). The total number of the *Ephedra californica* individuals per site were recorded, each shrub georeferenced and the total individual canopy measured. Shrub canopy measurements

included width at longest axis from above shrub, a 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 three different techniques including 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 dataset with sample units at the plot level (i.e.  $n=8$ , with shrub and open fine-scale data coded in plots with both habitat types). A microsite is defined here as a 0.5 m scale measure of animal association patterns with a specific shrub individual or open patch whilst a plot is defined at the scale of 10 m radius (Supporting information) encompassing a range from 0 to 12 shrub individuals. Distance between plots was 150 m while the distance between transects was 30 m.

### Study species

*Ephedra californica* (Supporting information) is the dominant plant species in the Elkhorn plain. Reaching heights of over 1 m, this species is native to the California Basin and Baja Mexico (Cutler 1939). Possessing unique characteristics of both angiosperms and gymnosperms, with numerous twig and needle like-leaves (Alfieri and Mottola 1983, Loera et al. 2012), this species is seen as a foundation species that are vital for the possible restoration of deserts in California (Filazzola et al. 2018, Lortie et al. 2018). The species interacts with other animal species within the Elkhorn plain including blunt-nosed leopard lizards (Westphal et al. 2018). Burrows are much more common under the *Ephedra* canopy and are used for refuge from predators (Hawbecker, 1951).

### Camera traps

Campark T70 camera traps were used to sample animals at each site during the day and night (O'Brien 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 (Supporting information). Each camera was set to medium sensitivity with a 1-min delay after each consecutive photo. Cameras were checked approximately every three to four days to ensure proper function for the duration of the 27 day field study. The images from SD cards were saved as Joint Photographic Export Group (JPEG) and examined for data extraction.

There was a total of 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, presence of absence of animal, 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 min lag-time. During focal sampling surveys by researchers, observers, positioned near camera traps during observations 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 (Noble et al. 2016). All data collected from camera traps were then combined with transect and focal observation data into a compiled density dataset.

## Transect

Transects were used to estimate the animal community through walk-through survey protocol, where any individual located within a 10 m radius from the transect was recorded (Sutherland 2006). We used three parallel 100 m transects located outside each of the established shrub plots. Each transect was measured and marked with flags at 25 m intervals. Each plot consisted of three transects, allowing for a total of 24 transects total. Researchers used the transects to visually spot animals every two to three 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 min. The observer was situated just outside the plot at a distance of 5 m 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 (Van Horn et al. 2018) during photo processing where the best estimation of the possible species was taken. In addition, camera trap data were validated by a second observer after recording. Uncertain images were classified as unknowns. Images were saved into a separate hard drive as Joint Photographic Experts Group (JPEG) 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 were then aggregated into a large community dataset, with total number of each individual recorded (Supporting information).

## Temperature measurement

Local measures of ambient temperature were recorded using HOBO pendant loggers, which were either suspended above ground approximately 20 cm on a stake or embedded in the soil (<[www.onsetcomp.com/files/manual\\_pdfs/9531-O%20UA-001%20Manual.pdf](http://www.onsetcomp.com/files/manual_pdfs/9531-O%20UA-001%20Manual.pdf)>). Twenty-eight loggers were deployed at varying plot densities in both shrub and open microsites for a total of 27 days. Hourly temperatures were logged (°C) by pendants and used to calculate daily mean and maxima (Supporting information).

## Dry matter

Residual dry matter (hereafter dry matter) is the measure of the total mass of varying grass and vegetation species in a given area (Bartolome et al. 2002, Filazzola et al. 2017). Dry matter was collected by placing a 20 × 20 cm square randomly at both shrub and open microsites at each shrub density plot. All grass within the indicated square was 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 six times where three samples were conducted under shrub canopy and three samples were taken in the open. Plots that did not contain three shrubs within were sampled at all possible shrub and open microsites. Data were compiled to a single plot-level estimate of dry matter for shrub and open microsites using R ver. 4.0.2 (<[www.r-project.org](http://www.r-project.org)>). Weight in grams, geo-tag location, microsite (shrub, open) and corresponding shrub density were recorded.

## Shrub cover

Shrub cover was determined by measuring the longest dimensional width of the shrub, the perpendicular length and the height to the highest living tissue (Filazzola et al. 2017). Canopy cover was estimated by calculating the volume of the shrub individual using the formula of a sphere. The relative importance of shrub cover and animal abundance was then examined (Supporting information).

## Statistical analyses

All statistical analyses were done using R ver. 4.0.2 (<[www.r-project.org](http://www.r-project.org)>), and code is available on GitHub (Zuliani 2020). Model selection was determined by taking the lower Akaike information criterion (AIC) (Johnson and Omland 2004). AIC scores are used to estimate if a particular model with a specific set of parameters is a valid statistical fit (Snipes and Taylor 2014). General linear mixed models (GLMMs) were used to examine the relationship between shrub density, and subphylum on animal community measures. Residual dry matter, temperature and shrub cover were then treated as covariates. Total animal abundances were treated as a quasi-poisson with animal presence as a binomial. Shrub density was treated as a factor with microsite and subphylum, while residual dry matter, temperature and canopy cover were kept as covariates and fitted with a quasipoisson. ANOVAs with  $\chi^2$  tests were performed where variables in the models were shown to have significance. Tukey tests were performed for posthoc analysis of the GLMMs to test the interactions. 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 and 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). The data was then used to generate several maps using the R package *ggmaps* (Kahle and Wickham 2013).

## Results

An effective shrub-density gradient was established ranging from 0 to 12 shrubs per 10 m radius plot (Supporting information). Camera displayed a high effectiveness in the collection of animal association (Supporting information) with this method yielding instances of animal captures (GLM,  $p\text{-value}=0.001$ ; post hoc, estimated marginalized means (EMM)  $2.339 \pm 0.459$ ,  $p\text{-value} < 0.0001$ ) than transect and focal observations.

### Shrub density effects on animal communities

The abundance and richness of animal species increased with increasing shrub densities at these scales (Table 1, 2, Fig. 2). The abundance (Table 1, GLM,  $p\text{-value}=1.34 \times 10^{-08}$ ; EMM  $-0.3490 \pm 0.104$ , post hoc,  $p\text{-value}=0.0008$ ) and richness (Table 2, GLM,  $p\text{-value}=1.22\text{e-}0.08$ ; EMM  $-0.2403 \pm 0.0876$ , post hoc,  $p\text{-value}=0.0061$ ) of vertebrate communities declined with shrub densities in the open microsites across the shrub-density gradient, while evenness (Table 3, GLM,  $p\text{-value}=0.3547$ ) was not significantly different between plots. Abundance (Fig. 2, Table 1; EMM  $-0.0772 \pm 0.134$ , post hoc,  $p\text{-value}=0.5644$ ), richness (Table 2, EMM  $-0.0949 \pm 0.1015$ , post hoc,  $p\text{-value}=0.3500$ ) and evenness (Table 3, EMM  $0.0265 \pm 0.0136$ , post hoc,  $p\text{-value}=0.0505$ ) of invertebrate species did not vary with the shrub densities tested here.

### Community contrasts

The most common vertebrate observed was *Dipodomys ingens* whereas the most commonly observed invertebrate species were *Oedaleonotus enigma* and *Icaricia acmon* (Fig. 3, Supporting information). The composition of the vertebrate species community did not significantly differ between shrub and open microsites (PERMANOVA,  $F_2=1.2960$ ,  $R^2=0.0840$ ,  $p\text{-value}=0.215$ ). The composition of the vertebrate communities significantly varied by shrub density

(Supporting information; PERMANOVA,  $F_2=3.3678$ ,  $R^2=0.21829$ ,  $p\text{-value}=0.012$ ). The invertebrate community composition significantly differed between shrub and open microsites (Supporting information; PERMANOVA,  $F_2=13.8373$ ,  $R^2=0.53146$ ,  $p\text{-value} < 0.001$ ), but it did not significantly vary by shrub density on the gradient tested (PERMANOVA,  $F_2=0.9143$ ,  $R^2=0.03512$ ,  $p\text{-value}=0.386$ ).

### Covariates

Dry matter was an estimate of indirect vegetation effects. There was significantly greater dry matter under shrubs than in open microsites (Fig. 4, GLM,  $p\text{-value}=0.01$ ; EMM  $-1.33 \pm 0.0878$ , post hoc,  $p\text{-value}=0.0239$ ). Dry matter did not vary across the shrub density gradient (GLM,  $p\text{-value}=4.823 \times 10^{-05}$ ; EMM  $0.0361 \pm 0.0207$ , post hoc,  $p\text{-value}=0.0813$ ). Dry matter significantly influenced the abundance (Fig. 4; GLM,  $p\text{-value}=0.044679$ ; EMM  $-1.20 \pm 0.263$ , post hoc,  $p\text{-value}=0.0001$ ), species richness (GLM,  $p\text{-value}=0.037954$ ; EMM  $-1.65 \pm 0.220$ , post hoc,  $p\text{-value}=0.0001$ ) and evenness (GLM,  $p\text{-value}=4.508 \times 10^{-13}$ ; EMM  $-0.921 \pm 0.468$ , post hoc,  $p\text{-value}=0.0489$ ) of vertebrate species showing a decline with increasing dry matter. Invertebrate species richness significantly increased (Fig. 4; GLM,  $p\text{-value}=0.037954$ ; EMM  $-1.94 \pm .848$ ,  $p\text{-value}=0.0221$ ) while evenness (GLM,  $p\text{-value}=4.508 \times 10^{-13}$ ) and abundance showed no significance (Fig. 4; GLM,  $p\text{-value}=0.044679$ ). Maximum temperature significantly mediated animal abundance (Table 1, Supporting information), richness (Table 2) and evenness (Table 3). Vertebrate abundance (Supporting information, Table 1; EMM  $-0.0557 \pm 0.0130$ , post hoc,  $p\text{-value} < 0.001$ ), richness (Table 2; EMM  $-0.0674 \pm 0.0292$ ,  $p\text{-value}=0.0211$ ) and evenness (Table 3; EMM  $-0.0733 \pm 0.0365$ , post hoc,  $p\text{-value}=0.0443$ ) significantly decreased with increasing temperature. In contrast, maximum temperature predicted invertebrate evenness (Table 3; EMM  $-0.0674 \pm .0156$ , post hoc,  $p\text{-value} < 0.0001$ ) while abundance (Supporting information, Table 1) and species richness were not significantly impacted (Table 2). Shrub cover did not predict overall animal abundance across the shrub-density gradient (Supporting information). Both vertebrate and invertebrate abundance (Table 1), species richness (Table 2) and evenness (Table 3) were unaffected by shrub cover.

Table 1. Analysis of animal abundance from general linear model for study period. Density, microsite and subphylum 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 dry matter was defined as the total mass of grasses within a 20 × 20 cm square in a plot.

	df	Deviance residual	df residual	Deviance	Pr (> $\chi$ )
Null			22	1389.49	
Density	1	5.22	21	$1.38 \times 10^{03}$	0.5299373
Microsite	1	17.87	20	$1.37 \times 10^{03}$	0.2453242
Phylum	1	427.23	19	$9.39 \times 10^{02}$	<b><math>1.34 \times 10^{-08}</math></b>
Dry matter	1	116.33	18	$8.23 \times 10^{02}$	<b>0.003032</b>
Max_temp	1	283.43	17	539.41	<b><math>3.70 \times 10^{-06}</math></b>
Cover	1	14.94	16	524.47	$2.88 \times 10^{-01}$
Density:Microsite	1	142.7	15	381.77	<b>0.0010257</b>
Density:PhylumM	1	22.8	14	358.97	0.1894213
Microsite:Phylum	1	152.64	13	206.34	<b>0.0006844</b>
Density:Microsite:Phylum	1	41.57	12	164.77	0.0763625

Table 2. Analysis of animal richness from general linear model for study period. Density, microsite and subphylum 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 dry matter was defined as the total mass of grasses within a 20 × 20 cm 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	<b>0.017671</b>
Phylum	1	122.179	19	152.874	<b>1.22 × 10<sup>-08</sup></b>
Dry matter	1	13.284	18	139.59	0.060314
Max_temp	1	42.77	17	96.82	<b>0.00075</b>
Cover	1	10.957	16	85.863	0.088003
Density:Microsite	1	27.062	15	58.801	<b>0.007337</b>
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

### Method of measurement comparison

Camera traps captured higher instances of animal when compared to transect and focal observations (Supporting information; GLM,  $p$ -value =  $1.982 \times 10^{-09}$ ; EMM  $2.339 \pm 0.459$ , post hoc,  $p$ -value < 0.001). Vertebrate and invertebrate species were detected more on camera traps than both transect (Supporting information; GLM,  $p$ -value = 0.001; EMM  $1.55 \pm 0.372$ ,  $p$ -value = 0.001) and focal observations (GLM,  $p$ -value = 0.001; EMM  $2.339 \pm 0.459$  post hoc,  $p$ -value = 0.001). Sensitivity analysis of animal abundance without camera traps displayed both vertebrate and invertebrate species were observed at higher abundances along the shrub-density gradient (Supporting information; EMM  $-1.01 \pm 0.397$ ,  $p$ -value = 0.0114). Capture rate of vertebrate and invertebrate species was not significantly different along the shrub-density gradient (Supporting information; GLM,  $p$ -value = 0.6767).

### Discussion

In this study we examined whether shrubs and an increasing shrub-density gradient positively influence key measures of animal composition. We found support for the hypothesis that a shrub-density gradient positively influences the structure and composition of the local animal community. Vertebrate species responded positively to the 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 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 may be an important form of habitat heterogeneity.

Structural landscape features are important in studies that observe species associations and interactions. Shrubs typically benefit animal communities in arid ecosystems through many mechanisms including acting as a refuge (Valone and Balaban-Feld 2019), escape from harsh temperature (Westphal et al. 2018, Ivey et al. 2020), acting as a food source for some small animals (Lortie et al. 2020), and predation

avoidance (Filazzola et al. 2017). The facilitative effects associated with *Ephedra californica* provide these necessary functions to animal species (Noble et al. 2016, Westphal et al. 2018). Small prey species such as *Uta stansburiana* use these shrubs as shelter from larger predatory animals (Greenfield et al. 1989). Our observation of *Dipodomys ingens* at higher abundance at shrub areas supports the hypothesis that smaller vertebrate species are reliant on shrubs for predator avoidance. 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, 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 (Westphal 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 foundational shrubs by animal species (Westphal et al. 2018, Ivey et al. 2020). This study found higher associations of animals near shrubs at peak times of day where the maximum temperature was experienced, suggesting thermal amelioration is a direct benefit to local animal communities. Animals favoring shrub microclimates as a means of escaping periods of intense heat has been supported through other studies that have been conducted in the Carrizo Plain National Monument such as the work by Ivey et al. (2020) where the use of foundational shrub canopies supported *Gambelia sila*. Since some species show associations between shrub and open microsites for activities, such as thermoregulation in desert ecosystems (Diaz and Cabeza-Diaz 2004, Ivey et al. 2020), shrubs may be fundamental in the thermal heterogeneity of ectotherms (Filazzola et al. 2017). With shrubs 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 in some instances shrub microsites were hotter than open microsites. In these cases, the abundance of animals decreased suggesting that individuals would seek cooler microclimates. Higher temperature recordings could be due to increasing land surface albedo (Ghulam et al. 2007) in

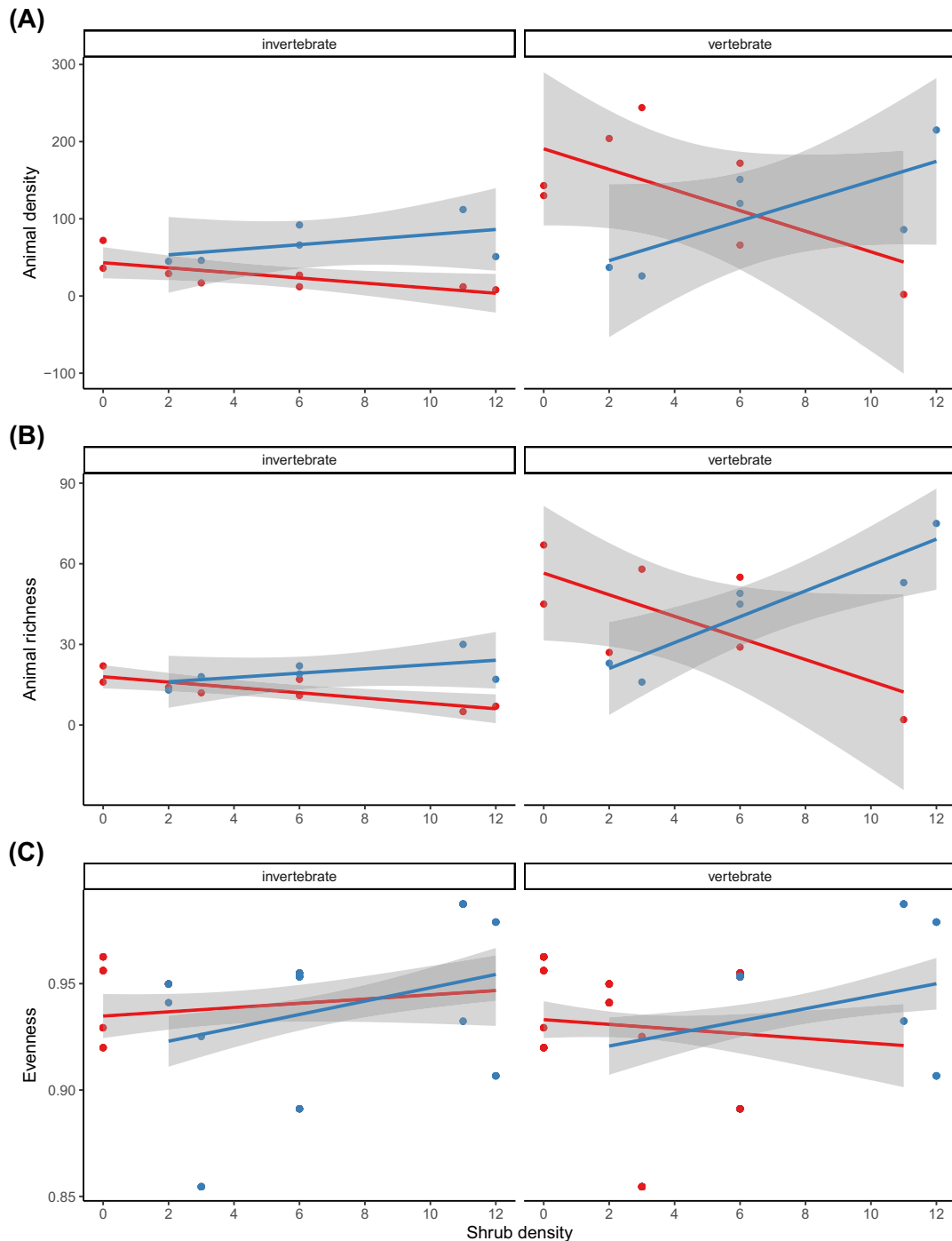


Figure 2. The relative effects of shrubs versus open gaps on a gradient of plot-level densities in a desert ecosystem. Data were combined from camera trap, transects and focal observations, then split by subphylum to represent the relationship between shrub and animal densities (A), shrub density and species richness (B) and the relationship between shrub density and the evenness of animal species (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.

desert ecosystems. 'Surface albedo' being the light reflected from a surface (Ghulam et al. 2007). Moreover, shrubs have been noted to reduce air velocity due to dense foliage, and generate a boundary layer, which increases microsite temperatures (Wezel et al. 2000). This could lead to HOBOPendants possibly recording higher temperatures under shrub canopies. Indirect effects from dry matter had negative impacts on vertebrate species abundance. Dense grass cover

impacts animal movement in similar systems (Vasquez et al. 2002, Filazzola et al. 2017). Vertebrate species avoided shrub microsites where a large abundance of grasses was present under the canopy. High grass abundance reduces the vigilance of an individual and the ability to escape predation, thus avoidance of these areas may serve as a beneficial survival technique (Vasquez et al. 2002). Closely examining the direct and indirect effects of animal species association



Table 3. Analysis of species evenness from general linear model for study period. Density, microsite and subphylum 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 dry matter was defined as the total mass of grasses within a  $20 \times 20$  cm square in a plot.

	df	Deviance residual	df residual	Deviance	Pr ( $> \chi$ )
Null			293	0.40214	
Density	1	0.037918	292	0.36422	<b><math>1.08 \times 10^{-08}</math></b>
Microsite	1	0.000213	291	0.36401	0.668368
Phylum	1	0.000993	290	0.36302	0.354794
Dry matter	1	0.000145	289	0.36287	0.724066
Max_temp	1	0.018560	288	0.34431	<b><math>6.33 \times 10^{-05}</math></b>
Density:Microsite	1	0.010574	286	0.33374	<b>0.002534</b>
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

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, these small rodent species have been observed to consume seeds from desert shrub (Valone and Balaban-Feld 2019), suggesting that resource availability may be a driving factor in vertebrate association. The variation in shrub and open microsites is primarily driven by intraspecific associations between animal species. Species such as *Crotalus oreganus*, are seen to consume smaller vertebrate species (Holding et al. 2018) which in turn use shrub species as a refuge from predators, thus impacting community associations. 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. Direct analysis of 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. For instance, camera traps are typically used to collect data on vertebrate species and are more likely to detect large movement, as opposed to invertebrate species that may not trigger the camera (Meek et al. 2014, Noble et al. 2016). While the combination of our methodology is ideal for vertebrate species, it was likely only able to give us a coarse estimate of the local invertebrate community – particularly the relatively larger species that would trigger the camera trap. It is easier for observers to detect vertebrate species during transect and focal observations than invertebrate species which may go unnoticed (Nath et al. 2010). These observational challenges can be translated to both transect and focal observations as invertebrate species are more difficult to observe without the conduction of the appropriate trapping. A typical inverte-

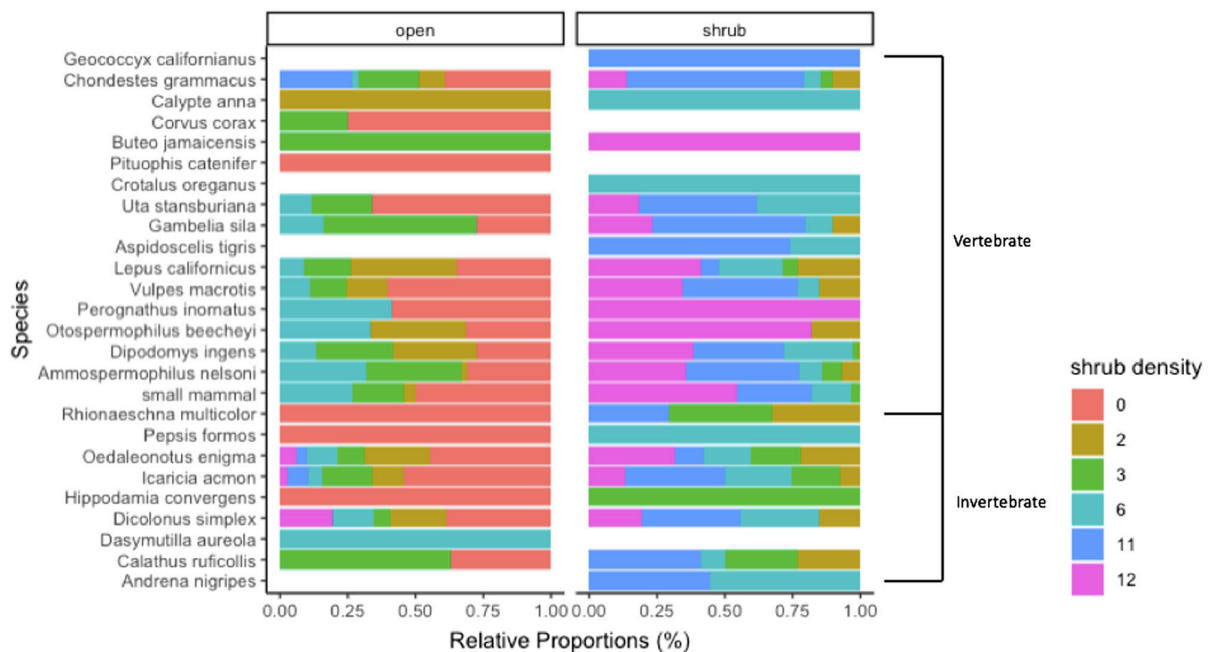


Figure 3. The relative proportion of total density of vertebrate and invertebrate species. The x-axis shows the percentage of the total number of individuals per density for each sample plot. Data were separated based on association with shrub/open microsite and by vertebrate/invertebrate species. Colors correspond to total number of shrubs in established plot.

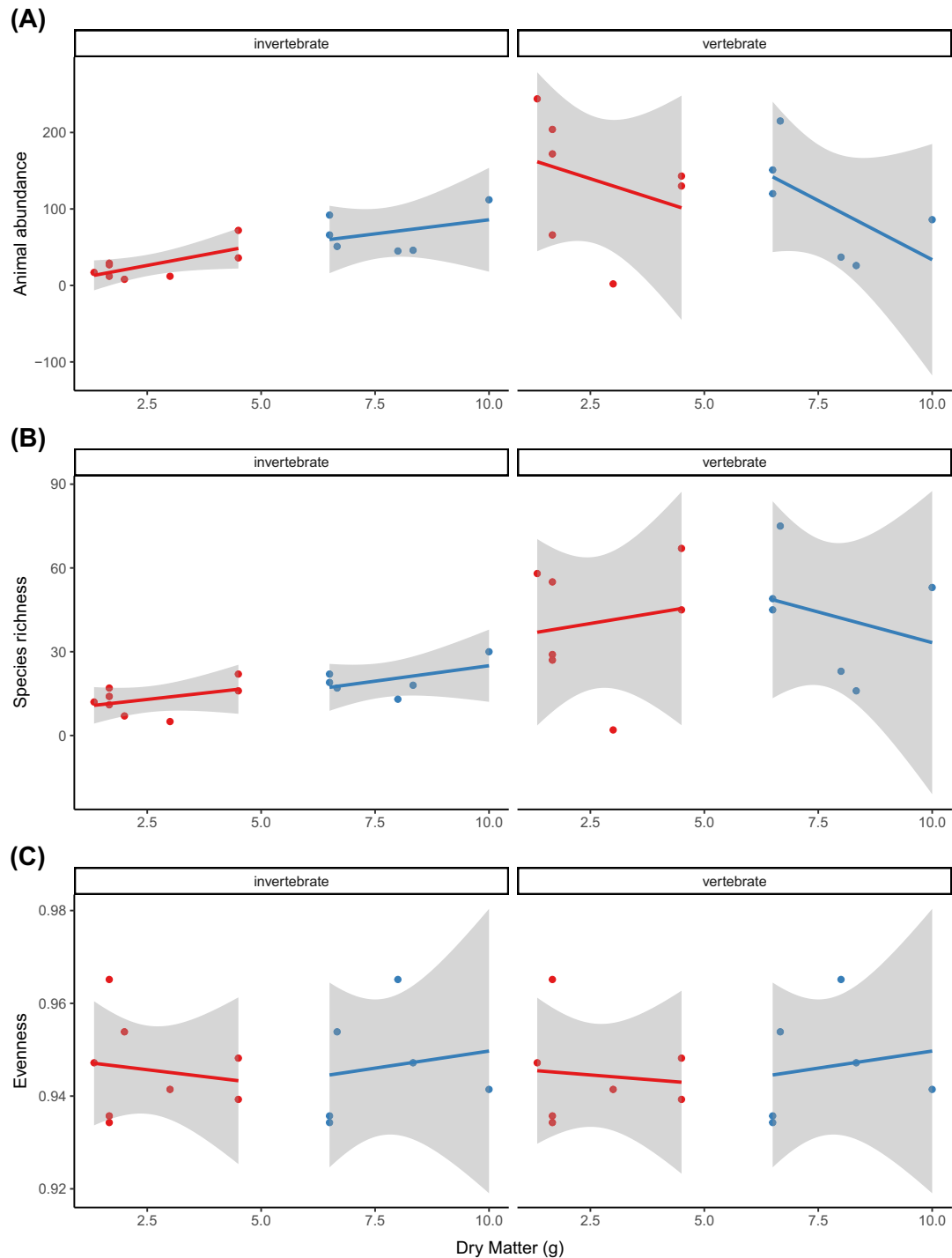


Figure 4. The relative effects of dry matter on a gradient of plot-level densities in a desert ecosystem. The data were split by subphylum to represent the relationship between dry matter and animal densities (A), dry matter and species richness (B) and the relationship between dry matter and the evenness of animal species (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.

brate species census consists of a combination of sweep netting (Scrimgeour et al. 1993), pitfall traps (Liu et al. 2017) and/or malaise traps (Campbell and Hanula 2007). Spatial home ranges and seasonal activity of species could play a role in their overall observation. The home ranges of several of these vertebrate species vary from a few hectares to over 100 km and are seasonally dependent (Westphal et al. 2018, Lortie et al. 2020). Species such as *Dipodops ingens* are

seen to alter their home ranges based on ecological characteristics of the environment, such as changes in seasonal temperature, thus altering the spacing between individuals (Cooper and Randall 2007). To counteract this, we conducted our study during the months of May and June, which are reported to be the peak activity months for several local species (Lortie et al. 2020). This is a local survey of animal communities that observes associations of animal

species at a specific site in the Carrizo Plain National Monument. Conducting this experiment encompassing several hectares of the Carrizo Plain could potentially capture the home range distributions of these vertebrate species and translate these observations into regional findings. Furthermore, conducting this survey for a longer duration and over multiple seasons could potentially display variation in shrub associations as the home ranges of vertebrate species are dependent on changing ecological characteristics of the environment (Cooper and Randall 2007). Future experiments can address these caveats to potentially expand our findings from a local landscape community, to one encompassing an entire region.

## Conclusion

A shrub-density gradient displayed that shrubs provide benefits to local vertebrate and invertebrate species, thus providing guidance for habitat preservation and restoration designs. With the desertification of arid ecosystems impacting at risk and endangered species, these findings may guide preservation work by placing emphasis on the importance of the facilitative interactions between these foundational shrubs and target animal species. It is because of this decline in desert health that it is essential to study factors influencing association of animal species with foundational shrubs because they play a key role in the potential restoration of these types of ecosystems. We advanced the methodology of facilitation theory by focusing on overall individual densities of facilitative shrub species. In addition, our study was not meant to test the hypothesis that these local animal species require shrub individuals to survive, rather we designed this study to ask whether these shrubs provide a benefit to local animal species and found evidence to support our hypothesis. This outcome demonstrates the benefits of taking an ecological facilitation approach toward animal community dynamics.

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.b2rbnzsdt>> (Zuliani et al. 2021).

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