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The shrub density effect: unraveling vertebrate community dynamics along an aridity gradient in Southern California

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Foundational shrub species can support vertebrate communities within desert ecosystems. These shrubs provide thermal refuge to aid in temperature amelioration and to escape predation. Within Southern California, USA, harsh abiotic conditions influence the frequency of these shrub-animal interactions. We tested the hypothesis that increasing shrub density will positively influence local vertebrate communities across a variety of arid ecosystems within Southern California. We used a combination of camera trapping and temperature pendants across a 2-year field study to assess the effects of shrub density and near-surface air temperature on vertebrate community composition. Sites were established across Southern California, each consisting of four 20 m radius microsites, with shrub densities ranging from 0 to 14 individuals. Increasing shrub densities significantly increased the frequency of observation and richness of local vertebrate communities. Relatively higher near-surface air temperatures (NSAT) significantly decreased vertebrate observations, richness, and evenness. Sites with relatively higher annual aridity negatively influenced vertebrate species observations and richness, but could be offset by increasing shrub densities. While shrub encroachment in many ecosystems may have negative impacts on species biodiversity, our findings suggest that increasing densities of foundational shrub species positively influences vertebrate community measurements and composition across varying arid ecosystems. Understanding how these foundational shrub species can be used to assess vertebrate communities can provide key insight into vertebrate-shrub interactions and how these densities can shape the biodiversity of an ecosystem.

KEYWORDS

aridity, community, density, facilitation, shrub, temperature

Introduction

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

Given that foundational shrubs positively influence local animal communities, increasing the number of shrubs available should provide more opportunities for facilitative associations. In terms of plant-animal interactions, the density of shrubs can influence the net outcome of animal interactions while also influencing the local community composition (Springer et al., 2003; Zuliani et al., 2021). As shrub density increases within an ecosystem, vertebrate species are given more opportunities to benefit from the facilitative associations, such as having more areas to thermoregulate (Milling et al., 2018; Zuliani et al., 2023b). For instance, the federally endangered species *Gambelia sila*, the Blunt-Nosed Leopard Lizard, uses shrubs within the desert of Southern California to thermoregulate, and has been predicted to have higher abundances as shrub densities increase (Ivey et al., 2020, Ivey et al., 2022; Zuliani et al., 2023b). While shrub cover is more commonly measured when assessing plant communities (Lortie et al., 2020), it can be used in tandem with shrub density to predict animal abundances (Van Auken, 2009; Zuliani et al., 2023a).

While foundational shrubs can positively influence animal communities, desert and grassland ecosystems globally are experiencing shrub encroachment, a phenomenon where woody shrub species increase in density, contributing to significant changes in vegetation cover (Van Auken, 2009; Losapio et al., 2024). Shrub encroachment has complex and sometimes contradictory effects on ecosystem health and biodiversity with traditional perspectives viewing shrub encroachment negatively, as it can increase desertification and reduce diversity in desert and grassland ecosystems (Van Auken, 2009; McCleery et al., 2018). For example, high densities of woody shrubs can negatively affect avian species distribution and diversity (Andersen and Steidl, 2019). However, recent studies have revealed that increasing shrub cover can also benefit wildlife, though these effects are highly context and species dependent (Stanton et al., 2021). In North American arid ecosystems, studies have documented positive relationships between increasing shrub densities and associated species (Stanton et al., 2018; De Souza et al., 2022). Vertebrate species that associate with foundational shrubs generally benefit from encroachment through increased abundance and richness (Zuliani et al., 2023a; Owen et al., 2024). Some Southern California ecosystems, such as the Carrizo Plain National Monument, exemplify these benefits as encroachment can reconvert arid grasslands back into a shrubland (Browning et al., 2008). Increases in shrub density and cover, particularly of foundational species, can promote facilitative associations that positively influence vertebrate abundance and richness (Whitford, 1997; Eldridge and Soliveres, 2014; Schooley et al., 2018; Zuliani et al., 2024). Understanding how changing shrub densities influence animal community provides valuable insights for assessing community composition and informing conservation practices.

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

As the frequency of these mega-drought events increase in Southern California, ecosystems will become more arid (Germano et al., 2011; Abella et al., 2012; Marengo and Bernasconi, 2015). Increasing aridification of dryland ecosystems is causing a dynamic shift in the structure of ecosystems as plant and animal communities adjust to new conditions (Hacker and Gaines, 1997; James and Tallis, 2019). Across Southern California, there is an increasing aridity gradient in dryland ecosystems, suggesting that local species utilize ecosystem resources differently to reduce harsh abiotic conditions (Welles and Funk, 2021). As these ecosystems become more arid, the negative impacts on plant and animal communities become more prevalent (Lucero et al., 2020). Within animal communities, aridity can have negative impacts on their associations, becoming more reliant on ecosystem resources, such as shrubs, which are more readily available at higher densities (Tews et al., 2004; Zuliani et al., 2021). Furthering the knowledge of how variations in aridity influence local animal species, and how these species utilize ecosystem resources to ameliorate these stressors, can increase our understanding of how these conditions alter environmental processes and community associations.

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

1) Shrub Density at Microsite Level
   a. Increasing shrub density will increase the total frequency of observations, richness, and evenness of vertebrate species at the microsite level.
   b. The effects of increasing shrub densities at microsite level will positively influence vertebrate community composition.
2) Temperature at Microsite Level
   a. Increasing near-surface air temperature will decrease the total observations, richness, and evenness of vertebrate communities.
3) Shrub density & Aridity at Site Level
   a. The positive effects of site-level estimates of shrub density on animal communities will increase with increasing relative aridity between sites.

Methods

Study sites

Our study was conducted across arid ecosystems in Southern California for 30-days between May and June 2022 and 2023. Six study sites were divided within the Carrizo Plain National Monument (35.11566, -119.62069), the Cuyama Valley (34.848726, -119.48312), and the Mojave Desert (35.851515, -116.18671; Figure 1). At each study site, four microsites were established, approximately 100 m away from each other, ranging from no shrubs to relatively high densities (the densest shrub patches within a site) (n = 24). To establish each microsite, a random centroid was selected to act as the middle of the 20 m radius microsite. To calculate shrub density, the number of shrubs within the 20 m radius was counted. Shrub cover was measured for each

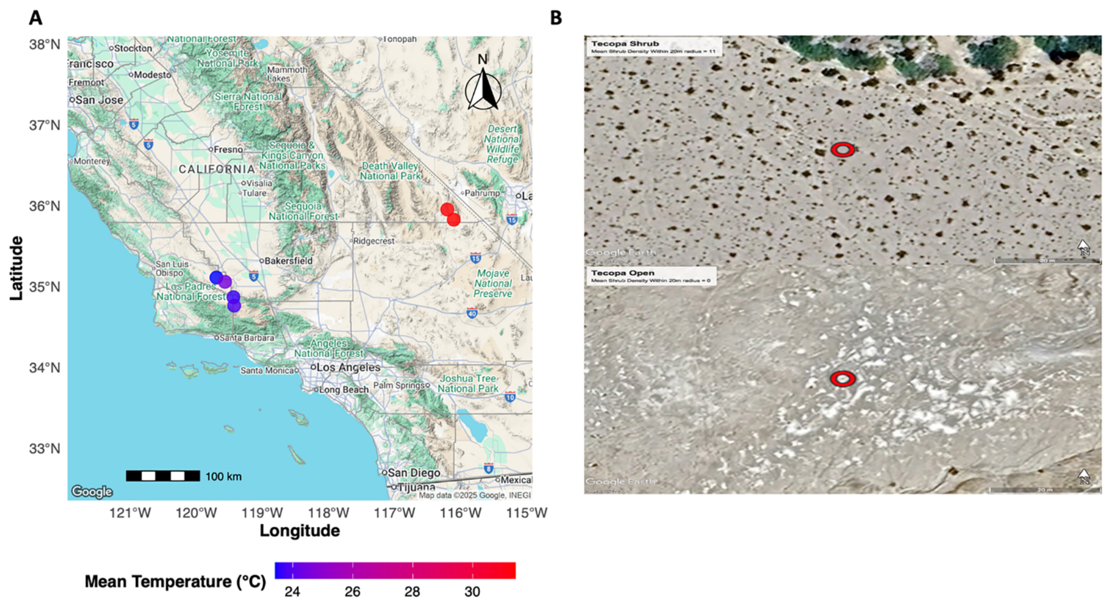

FIGURE 1
A map **(A)** of study sites sampled across Southern California. Average temperatures were recorded per study site and displayed using a blue-red color gradient. Images **(B)** of high and low shrub densities were included to better illustrate the contrast between sample sites. Centroids of the sites are indicated by red open circles. Sites were selected based on the presence of the foundational shrub species *Ephedra californica*. The map was generated utilizing the R package ggmaps and images of sites were taken via satellite imagery from Google Earth TM.

shrub within a microsite by taking the longest dimensional width of the shrub, the perpendicular length, and the height to the highest living tissue (Filazzola et al., 2017; Zuliani et al., 2021). Shrub canopy cover was then estimated by calculating the volume of the shrub individual using the formula of a sphere (Zuliani et al., 2021).

Study species

Ephedra californica is one of the most common native woody plant species within Southern California. *Ephedra californica* typically grows 0.25–1 meter in height with a similar spread within a 5–10-year period, forming dense, rounded canopies with distinctive jointed, photosynthetic stems that lack true leaves (Sawyer et al., 2009; Whitford and Steinberger, 2020; Braun et al., 2021). *Ephedra californica* is a flowering shrub species with a blooming season from March to May, is typically found in sandy soils and the well-developed cryptogram layer of the Mojave Desert (Sawyer et al., 2009; Braun et al., 2021). This is a vital foundation species in California desert ecosystems as it is one of the most common facilitative species in these regions and is at the base of interactions with both plant and animal communities (Lortie et al., 2018; Filazzola et al., 2017). *Ephedra californica* is resilient and can survive severe abiotic stressors, such as drought, extreme heat, and lack of nutrition, while also surviving mechanical damage, such as branch breaking or herbivory (Lortie et al., 2018). *Ephedra californica* is used by several species of vertebrates including the Blunt-Nosed Leopard Lizard, Giant Kangaroo Rat, and San Joaquin Jack Rabbits (Prugh and Brashares, 2010; Noble et al., 2016). One frequently observed species at our study sites was *Dipodomys heermanni* (Heermann's Kangaroo Rat). This is a small nocturnal rodent species present in relatively high abundances within Southern California and is known for creating interconnecting burrows throughout these arid ecosystems (Prugh and Brashares, 2010). This species consumes the seeds found underneath shrub canopies, resulting in them showing high associations to foundational shrub species. *Lepus californicus* (Black-tailed Jackrabbit), is a large species active both during the day and at night, is frequently found in the Carrizo Plain and Cuyama Valley, and is commonly detected using camera traps. It typically consumes vegetation in open areas and under shrub canopies (Johnson and Anderson, 1984).

Camera trapping

VIKERI Model A1 camera traps were used to sample animal communities at each site during the day and night (Noble et al., 2016). No flash was emitted by cameras to ensure that there were no disturbances to interacting animal species. Two camera traps were deployed on 20 cm stakes driven in the ground, facing each other at the edge of each 20 m radius microsite. A total of 48 camera traps were deployed across all microsites (6 sites, 4 microsites, 2 cameras per site). Each camera trap was set to medium sensitivity with a 1-minute delay to minimize the number of misfired photos taken from background activity (Tourani et al., 2020; Zuliani et al., 2021; Mashintonio et al., 2022; Leorna and Brinkman, 2024). Camera traps were checked approximately every four to five days to ensure proper function for the 30-day field study between May and June 2022 and 2023. Camera locations were not food-baited. The images were saved on 24 GB SD cards as Joint Photographic Export Group (JPEG) files and examined during data extraction. Each photo was taken as a new species instance with photo ID, site, year, date, camera number, shrub density, presence or absence of animal, species of animal, and camera trap timestamp all recorded. Independent photos were defined as when the individual animal was not observed at the same position within the 1-minute lag-time (Lepard et al., 2018; Zuliani et al., 2021). Camera trap rate of capture was calculated per year by taking the difference between the number of new species instances, with the total number of observations for the 30-day duration (Noble et al., 2016; Zuliani et al., 2021). All data taken from camera traps each year were then combined into one density datasheet.

Species validation

Identification of vertebrate individuals to the species level via camera traps is challenging as the exact physiological characteristics can be difficult to distinguish (Dorning and Harris, 2019). For example, differentiating between *Dipodomys merriami* and *Dipodomys microps* is dependent on coloration and variations in length (Sjoberg et al., 1984; Siciliano-Martina et al., 2023). Vertebrate species observations through camera trap photos were validated using a combination of Wildlife Insight (Vélez et al., 2023) and the iNaturalist application (Unger et al., 2021; iNaturalist). Combining both applications for species validation provided the most plausible identification for images with species present and were further validated by individual observers. Unknown animals detected in images were labeled as 'unknowns' and were later excluded from the community composition data. Images were saved as JPEG files on hard drives for data analysis.

Microclimatic microsite level measures

Near-surface air temperature for each site was recorded using OMEGA USB loggers, suspended approximately 20 cm above ground on a wooden stake (Ashcroft, 2018; Terando et al., 2018). At shrub density microsites, two loggers were placed under random shrub canopies, while at open microsites two loggers were placed next to camera traps. These loggers remained within the shrub and open microsites for the duration of the field experiment. Hourly near-surface air temperatures were logged (°C) and used to calculate the daily means.

Site-level climate measures

The annual aridity of each region was estimated utilizing the De Martonne Aridity Index equation $AI = P/(MAT + 10)$, where P is the total annual precipitation in mm, and MAT is the Mean Annual Temperature in °C (Zomer et al., 2008; Gebremedhin et al., 2018; Rafiq et al., 2023). Site-level temperature and precipitation data were collected and compiled from local weather stations within 1–5 km of the study sites (Zuliani et al., 2024).

Statistical analysis

All statistical analyses were conducted in R version. 4.3.1 (R Core Development Team, 2024). A Pearson's correlation test was used to determine the relationship between shrub density and cover and to test if density could be used as a proxy for shrub cover. Density and cover were significantly correlated (r = 0.749, p-value < 0.001) and had moderate to high degree of multicollinearity in GLMs (Supplementary Table S1). Therefore, only density was used for GLMs. A Pearson's correlation test was used to test for a relationship between temperature and humidity and to determine if temperature could be used as a proxy for humidity in the GLMs. Temperature and humidity at microsites were significantly correlated (Supplementary Figure S1; r = -0.91, p-value < 0.001). Thus, temperature was used in GLMs to represent the microclimate of microsites. The number of individual animal observations (henceforth termed "observations"), species richness, and evenness of vertebrate species was tested at the fine-scale to determine the influence of shrub density within a 20-meter radius and near-surface air temperature. Second degree general linear mixed models (GLMMs) were used to examine these relationships in Southern California for each year independently, with shrub density and near-surface air temperature set as factors and nested within site. Collinearity between shrub density and cover for observations, richness, and evenness was tested in each model using the function 'check_collinearity' from the *performance* R package (Lüdecke et al., 2021). Multiple linear and non-linear models for observations, richness, and evenness, were tested with the models yielding the lowest AIC scores being used for all statistical analyses (Supplementary Table S2; Portet, 2020). Total animal observations and richness were treated as a Poisson distribution, while evenness was treated as a Gaussian distribution. Site-level analysis was conducted utilizing a second degree general linear mixed model with total shrub density and site level aridity as factors. Site-level statistical analyses were conducted with observations and richness treated as a Poisson distribution, while evenness was treated as a Gaussian distribution. All site-level models had shrub density and aridity as covariate. Multivariate analysis of composition was tested using the vegan package (Oksanen et al., 2022). Principle Coordinate Analyses (PCOAs) compared the different vertebrate communities at both shrub and open microsites and to assess whether the composition of the communities varied at increasing shrub density and open microsites within Southern California (Dray et al., 2006).

Results

Shrub density

A total of 250,000 photos was taken, with 2022 yielding 58,000 photos and 2023 yielding 192,000 photos. Models testing vertebrate observations, richness, and evenness showed high collinearity between shrub density and cover (Supplementary Table S1). In 2022, increasing microsite level shrub density positively influenced vertebrate observations, but did not influence richness and evenness (Figure 2; Table 1). In 2023, vertebrate observations and richness significantly increased with increasing microsite level shrub density, while evenness had no effect (Figure 2; Table 1).

Near-surface air temperature

In 2022, vertebrate observations and richness significantly decreased with increasing near-surface air temperatures, while evenness was unaffected (Figure 3; Table 1). In 2023, vertebrate observations significantly decreased with increasing near-surface air temperatures, while evenness significantly increased (Figure 3; Table 1).

Community contrasts

Dipodomys heermanni was the most observed vertebrate species observed with 2397 observations (Supplementary Table S3; Figure 3). The composition of vertebrate species communities did not significantly vary across shrub and open microsites (Figure 4; PERMANOVA, $F_2 = 0.2553$, $R^2 = 0.0294$, p – value = 0.6184). The composition of vertebrate species communities significantly differed across various sites (Figure 5; PERMANOVA, $F_2 = 3.736$, $R^2 = 0.0184$, p-value = 0.0409) with Carrizo sites having a significantly different community composition than Tecopa sites (Supplementary Figure S3; Observed p-value = 0.0166). Removal of *Dipodomys heermanni* observations resulted in no significant differences in vertebrate community composition ($F_2 = 0.975$, $R^2 = 0.0191$, p-value = 0.3938).

Site-level shrub density and aridity effects

In 2022, vertebrate observations and evenness significantly increased with higher total site-level shrub density, while in 2023, only vertebrate observations significantly increased (Table 2). In 2022, vertebrate observations and richness increased at higher aridity sites while evenness was unaffected (Figure 6; Table 2). In 2023, only vertebrate observations significantly decreased at higher aridity ecosystems (Figure 6; Table 2).

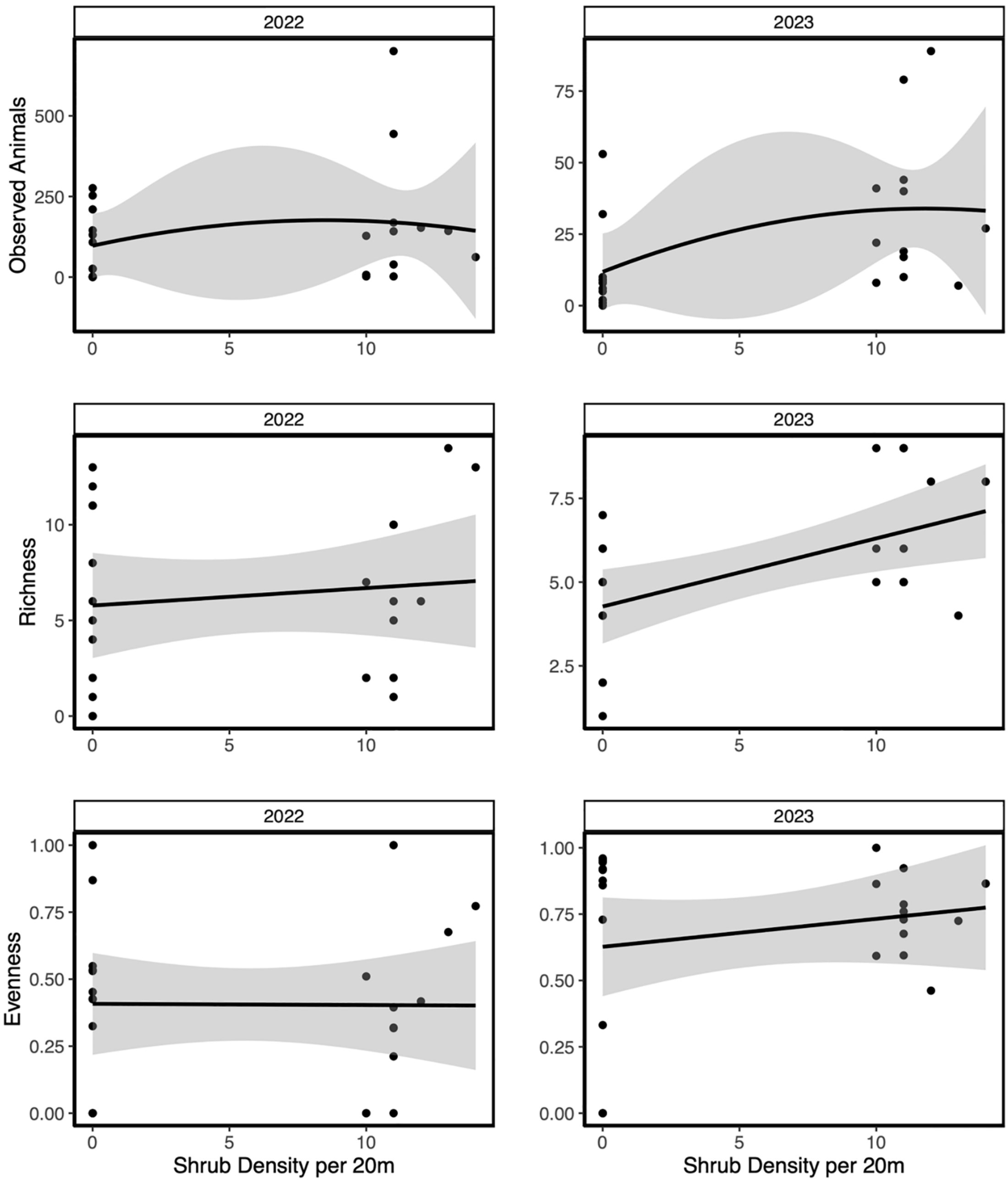

FIGURE 2
The relative effects of increasing shrub density across arid sites within Southern California. Data were collected from camera traps in 2022 and 2023 field seasons then split by year to display the variation in vertebrate community measurements including Observed animals, Richness, and Evenness. Shaded regions indicate 95% confidence intervals.

Discussion

In this study, we examined the effects shrub densities on the vertebrate community composition, individual observations, species richness, and evenness across ecosystems within Southern California. We found support for the hypothesis that increasing shrub density will positively influence vertebrate communities across ecosystems within Southern California. Shrub density positively influenced the observations and richness of vertebrate species. Fine-scale temperatures had a significant negative impact on individual observations and species richness in 2022 and a negative influence on individual observations and evenness in 2023. Sites were significantly more arid in 2022 than in 2023. Community compositions significantly varied between shrubs and open microsites, suggesting that shrubs promote vertebrate communities. Individual vertebrate observations and species

TABLE 1 Analysis of microsite-level vertebrate observations, richness, and evenness from general linear model for study period with shrub density and logger-temperature as factors.

Year	Factor	Variable	df	Deviance	Residual df	Residual deviance	p-value
2022	Observations	Null			23	4036.2	
		Shrub Density	1	205.26	22	3830.9	< **0.001**
		Temperature	1	2197.10	21	1633.8	< **0.001**
		Shrub Density * Temperature	1	30.56	20	1603.2	< **0.001**
	Richness	Null			23	73.099	
		Shrub Density	1	0.516	22	72.583	0.4725
		Temperature	1	58.223	21	14.36	< **0.001**
		Shrub Density * Temperature	1	0.247	20	14.113	0.619
	Evenness	Null			23	2.2424	
		Shrub Density	1	0.00015	22	2.2423	0.9715
		Temperature	1	0.27083	21	1.9714	0.0974
		Shrub Density * Temperature		0.00008	20	1.9714	0.9976
2023	Observations	Null			23	513.44	
		Shrub Density	2	131.337	21	382.10	< **0.001**
		Temperature	1	56.369	20	325.73	< **0.001**
		Shrub Density * Temperature	2	30.548	18	295.19	< **0.001**
	Richness	Null			23	29.2748	
		Shrub Density	1	7.3013	22	21.9735	**0.0069**
		Temperature	1	0.2204	21	21.7531	0.6387
		Shrub Density * Temperature	1	0.9602	20	20.793	0.3271
	Evenness	Null			23	2.23199	
		Shrub Density	1	0.08603	22	2.14596	0.2296
		Temperature	1	0.34360	21	1.80236	< **0.016**
		Shrub Density * Temperature	1	0.26824	20	1.5341	0.0615

Model selection was determined by comparing AIC scores of linear and nonlinear models (See Supplementary Table S2). All p-values that were significant at $p < 0.05$ are indicated in bold.

richness decreased at sites with lower aridity scores in 2022, while only individual observations decreased at more arid sites in 2023.

In this study, we found that shrub density positively influences animal vertebrate communities. Structural resources, both artificial and natural, are critical in studies that not only observe individual associations, but also measure key structural components of an ecosystem. Globally, foundational shrubs act as benefactor species (Ruttan et al., 2021) through temperature amelioration (Ivey et al., 2020; Zuliani et al., 2023a), production of seeds and other food sources (Lortie et al., 2020), and refuge from predation (Filazzola et al., 2017). However, the effects these foundational shrubs have on vertebrate communities may not have the same influence and can be context-dependent (Stanton et al., 2018). *Ephedra californica* provides these facilitative effects that are necessary functions for vertebrate species (Westphal et al., 2018; Zuliani et al., 2021). Smaller vertebrate species including *Dipodomys heermanni*, *Gambelia sila*, and *Ammospermophilus leucurus*, utilize these shrubs to reduce predator-prey interactions (Longland and Dimitri, 2021). Species that are reliant on these positive interactions tend to be in locations where ecological resources, including shrub density and cover, are readily accessible and abundant (Zuliani et al., 2023a). For instance, *Gambelia sila*, the Blunt-nosed Leopard Lizard, is known to use areas of high shrub density and cover to aid in thermoregulation (Ivey et al., 2020; Lortie et al., 2021; Zuliani et al., 2023b). Other desert species, such as *Dipodomys ingens* (the Giant Kangaroo Rat) and *Lepus californicus* (the Black-Tailed Jack Rabbit), utilize these shrubs not only for cooling but for foraging and protection from predation (Johnson and Anderson, 1984; Prugh and Brashares, 2010). However, as shrub densities increase, the effects of shrub encroachment may become more prevalent. This increase in shrub density will reconvert these ecosystems into shrublands (Browning

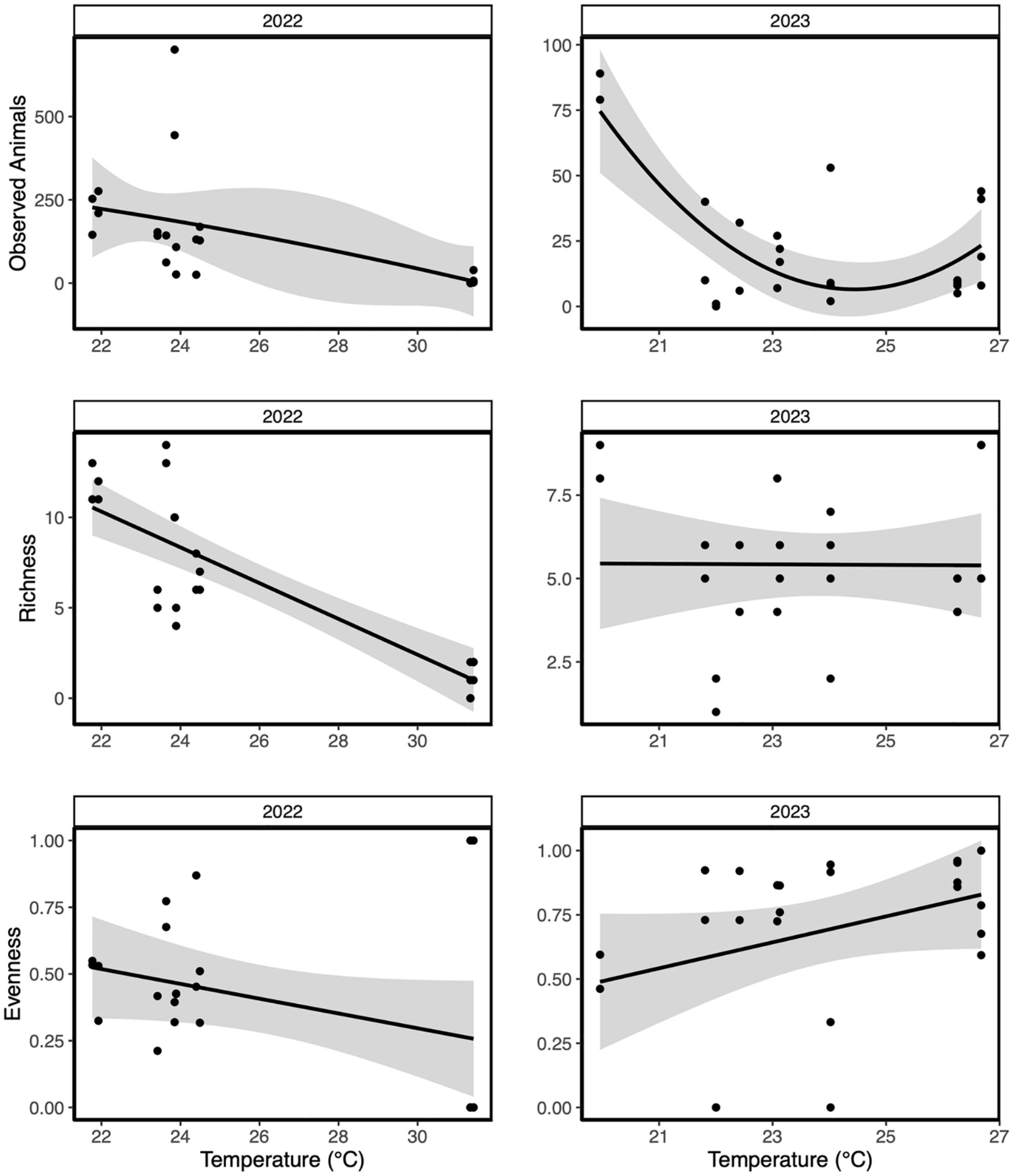

FIGURE 3
The relative effects of near-surface air temperature across arid study sites within Southern California. Data were combined from temperature loggers used in 2022 and 2023 field seasons then split by year to display the variation in vertebrate community measurements including Observed Animals, Richness, and Evenness. Shaded regions indicate 95% confidence intervals.

2008), while also enhancing ecosystem functioning through the reduction of desertification and microclimatic buffering (Eldridge and Soliveres, 2014; Filazzola et al., 2017). However, the effects these shrubs have are ecosystem specific, and have varying impacts on local animal communities. Understanding the importance of the direct interaction between these shrubs and local animal communities, across an increasing stress gradient, can provide insight into the local animal community composition and utilization of these shrubs.

The composition of these vertebrate communities, while not different between shrub and open microsites, did differ across sites in Southern California. This suggests that while our study sites have similar community compositions, the variation in their shrub density and temperature directly influences individual associations. Vertebrate species, such as *Lepus californicus*, while found at all tested sites, were much more frequently observed at Cuyama and the Carrizo Plain National Monument than in Tecopa. This suggests that while some species are able to inhabit multiple ecosystems, sites with more

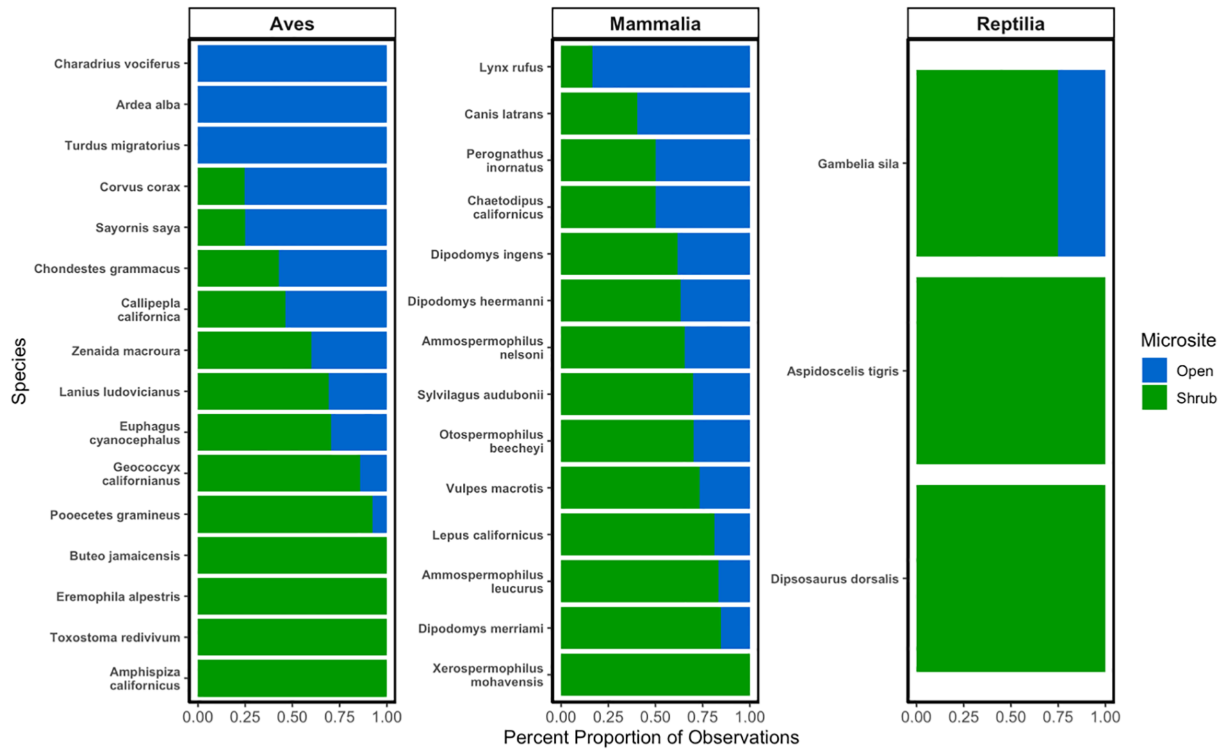

FIGURE 4
The relative percent proportion of vertebrate species observations across shrub and open microsites across arid ecosystems within Southern California. X-axis displays the percent proportion (%) of individuals at both shrub and open microsites. Y-axis displays the scientific names of each observed individual during both the 2022 and 2023 field seasons. More details on each species can be found in the Supplementary Table S3.

favorable conditions are likely to be more suitable and preferred (Vale and Brito, 2015). Several factors can cause this variation in community composition including elevation, temperature gradient, available vegetation, aridity, shrub cover and density, and water availability (Marengo and Bernasconi, 2015; Welles and Funk, 2021; Ivey et al., 2022; Hillier-Weltman et al., 2025). Previous studies found that kangaroo rat species like *Dipodomys heermanni* forage more actively in open areas than in woody shrub habitats, which initially appears to contrast with our findings that shrub density increases vertebrate observations (Daly et al., 1992; Upham and Hafner, 2013). However, this difference likely reflects the distinction between foraging behavior and overall habitat use, as our camera traps captured all vertebrate activities including sheltering and thermoregulation rather than just active foraging. Additionally, moonlight can significantly alter the activity and frequency of observations of these nocturnal rodent species (Upham and Hafner, 2013). The presence of moonlight may influence the foraging behavior and observations of kangaroo rat species as they shift their activity from open areas to those with more cover (White and Geluso, 2007). While our study did not measure moonlight, future studies could take this into consideration when assessing nocturnal animal community composition. Directly analyzing the differences in these communities, in combination with multiple factors that can influence community composition, could further explain not only the associations these vertebrate species have with foundational shrubs, but how the increasing aridity of Southern California deserts is altering these ecosystems.

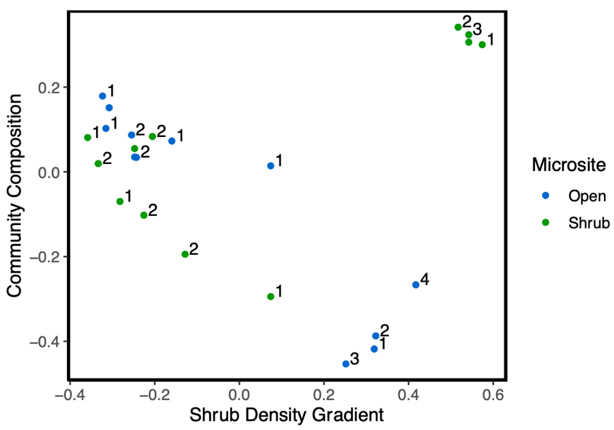

FIGURE 5
PCOA figure displaying the relative similarity in community composition across a shrub density gradient. Data were combined from camera traps used in 2022 and 2023 field seasons then split by microsite to display the similarities between community compositions.

Anthropogenically driven climatic events, specifically drought and temperature extremes, will continue to increase the aridity of ecosystems across Southern California, influencing both vertebrate community measures and composition. In this study, we found that increasing near-surface air temperatures reduced observations,

TABLE 2 Analysis of site-level vertebrate observations, richness, and evenness from general linear mixed model for study period with shrub density and aridity as factors.

Year	Factor	Variable	df	Deviance	Residual df	Residual deviance	p-value
2022	Observations	Null			5	3253.5	
		Shrub Density	1	11.48	4	3242.1	**< 0.001**
		Aridity	1	2538.28	3	703.7	**< 0.001**
		Shrub Density * Aridity	1	463.85	2	0239.9	**< 0.001**
	Richness	Null			5	21.7887	
		Shrub Density	1	1.5749	4	20.2139	0.2095
		Aridity	1	16.2061	3	3.9538	**< 0.001**
		Shrub Density * Aridity	1	0.4082	2	3.5456	0.5229
	Evenness	Null			5	0.2158	
		Shrub Density	1	0.12326	4	0.0926	**< 0.003**
		Aridity	1	0.04824	3	0.0444	0.0709
		Shrub Density * Aridity	1	0.02502	2	0.0193	0.1078
2023	Observations	Null			5	147.90	
		Shrub Density	2	56.357	4	91.54	**< 0.001**
		Aridity	1	17.020	3	74.52	**< 0.001**
		Shrub Density * Aridity	2	74.520	2	0	**< 0.001**
	Richness	Null			5	5.2135	
		Shrub Density	1	2.278	4	2.9738	0.1345
		Aridity	1	3.827	3	2.7295	0.6212
		Shrub Density * Aridity	1	0.008	2	2.7211	0.9269
	Evenness	Null			5	0.0823	
		Shrub Density	2	0.0169	4	0.0652	0.6728
		Aridity	1	0.0225	3	0.0427	0.3048
		Shrub Density * Aridity	2	0.0427	2	0	0.7845

Model selection was determined by comparing AIC scores of linear and nonlinear models (See Supplementary Table S2). All p-values displaying significance ($p < 0.05$) are indicated in bold.

richness, and evenness of vertebrate species. As these high temperatures become more prevalent and extreme, shelter via shrub canopies may be a crucial resource to mitigate these abiotic conditions (Westphal et al., 2018; Ivey et al., 2020; Gaudenti et al., 2021). Previous studies conducted within the Carrizo National Monument showed a higher frequency of shrub-animal association during peak hours of the day when temperatures reached their maximums (Gaudenti et al., 2021; Zuliani et al., 2021; Ivey et al., 2022), suggesting that temperature amelioration is a direct benefit to local vertebrate communities. These shrub canopies generate shade, reducing both near-surface air and soil temperatures within their microclimate, minimizing the risks of overheating (Huxman et al., 2004). The area underneath these shrubs provides more hospitable microclimates for vertebrate communities in an increasingly arid ecosystem. However, these climate extremes are increasing in intensity and are particularly driven by global warming, which is amplifying aridity through rising temperatures and altered precipitation patterns (Dai, 2013). These increasing temperatures and reduced water availability directly contribute to the increased frequency and severity of mega-drought events (Kogan and Guo, 2015; Mann and Gleick, 2015). Furthering the current understanding of how these increasingly harsh climatic events impact vertebrate community measurements and composition can provide substantial insight into both the management of these ecosystems as well as the preservation of these vertebrate communities.

Conclusions

Our study demonstrates that shrub density strongly and consistently influences vertebrate observations and richness

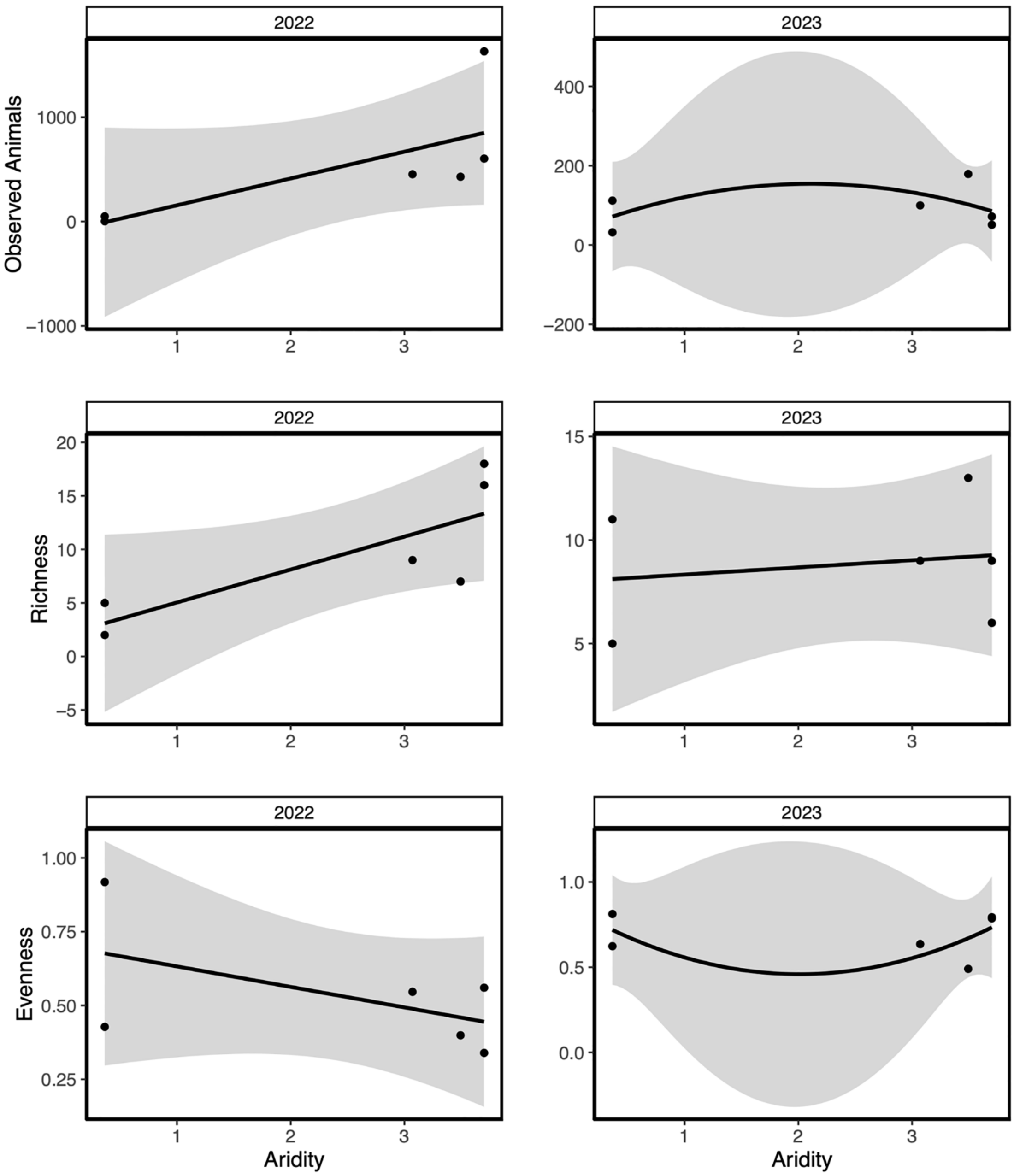

FIGURE 6
The relative effects of aridity across various arid sites within Southern California. Data were collected from weather stations located near each site. 2022 and 2023 field seasons were split by year to display the variation in vertebrate community measurements including Observed Animals, Richness, and Evenness. Shaded regions indicate a 95% confidence interval.

across Southern California desert ecosystems, providing compelling evidence for facilitative interactions between foundational shrubs and vertebrate communities. Microsite-level shrub density emerged as a robust predictor of vertebrate activity, with positive effects across both study years despite varying climatic conditions. Conversely, increasing near-surface air temperatures consistently reduced vertebrate observations and richness, emphasizing the critical role of shrub-mediated thermal refugia in these arid systems. These findings have significant implications for desert conservation under accelerating climate change. As temperatures continue to rise and drought events intensify in Southern California, protecting shrub densities will be essential for maintaining vertebrate diversity and community stability. Our results suggest that conservation strategies should prioritize the preservation of foundational shrub species like *E. californica*, as they serve as key facilitators supporting vertebrate communities through multiple mechanisms including thermal buffering, predator refuge, and resource provisioning during increasingly harsh climatic conditions.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: doi:10.5063/F1B856K9.

Author contributions

MZ: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. NG: Methodology, Visualization, Writing – review & editing. SM: Conceptualization, Methodology, Resources, Supervision, Validation, Visualization, Writing – review & editing. CL: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1648121/full#supplementary-material

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