

The importance of native shrubs on the distribution and diversity of reptiles and amphibians in the central deserts of California

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Abstract

Conservation and management of drylands is a global challenge. Key attributes of these ecosystems, such as dominant vegetation including shrubs, can provide a crucial mechanism to inform conservation strategies. The shrub species *Ephedra californica* and *Larrea tridentata* are common native shrub species within the deserts of California and frequently benefit other plant and animal species. Here, we tested the hypothesis that shrubs support reptile and amphibian communities through relative increases in available habitat, estimated through increasing shrub densities at the site level. Reported occurrence data from the Global Biodiversity Information Facility (GBIF) and high-resolution satellite images were used to test for local-to-regional patterns in reptile and amphibian distribution and diversity by shrub densities at sites. A total of 71 reptile and amphibian species were present regionally. Increases in shrub density across sites positively influenced the relative abundance and richness of reptiles and amphibians observed. Moreover, increasing shrub density also had a positive influence on species evenness. Aridity did not significantly influence the relationship between shrub density and herptiles suggesting the relationship is robust. This study highlights the importance of foundational shrub species in supporting reptile and amphibian communities in arid and semi-arid regions supporting better understanding of large-scale patterns of biodiversity supported by positive ecological interactions in the context of global change.

Introduction

Predicting responses to climate change is a global priority as many species are threatened by the projected increases in global temperatures. Reptile and amphibian species are disproportionately threatened by anthropogenic climate change due to their need to thermoregulate (Aragón et al., 2010; Sunday et al., 2014; Vicente Liz et al., 2019; Gaudenti et al., 2021). Responses of ectotherms to climate change require an understanding of the evolutionary, ecological, behavioral, and physiological factors that drive where a species can occur or inhabit (Diaz & Cabezas-Diaz, 2004; Ferreira et al., 2016; Soares & Brito, 2006; Stewart et al., 2018; Sunday et al., 2014). Most reptiles and amphibians that occur in desert ecosystems face the primary thermal challenge of keeping cool at extremely high temperatures (Gaudenti et al., 2021; Sunday et al., 2014; Zuliani et al., 2023b). The ability of ectotherms to alter their seasonal activity and reproduction is a key adaptation (Ivey et al., 2022; Zuliani et al., 2023b). Nonetheless, availability of fine-scale habitat such as that provided by vegetation for cover, influences the capacity of these species to take advantage of shade and thermal refuges (Stewart et al., 2019; Gaudenti et al., 2021). These habitats are also important for foraging and other behaviors in deserts (Sinervo et al., 2010; Westphal et al., 2018; Ivey et al., 2021). Hence, vegetation can be a key factor and mediate the extent that climate warming affects thermoregulating ectotherms (Kearney et al., 2009; Westphal et al., 2018). Links between the ecology and associations between reptiles and amphibians and vegetation are thus needed to advance ecological theory (Lortie et al., 2015; Filazzola et al., 2017; Zuliani et al., 2023a) including facilitation (i.e., positive interactions) (Bertness & Callaway, 1994; Schemske & Horvitz 1988; Żywiec et al., 2019) in order to support future conservation practices.

Temperature is a key factor for many animal species in deserts. Heliothermic (sun-basking) reptiles and amphibians that live in desert ecosystems are constrained by the extreme temperatures of their environment and are vulnerable to climate warming because of direct exposure to extreme heat (Mosauer, 1936; Sinervo et al., 2010). In high-stress environments such as deserts, shelter is critical for these species (Fisher 2007; Westphal et al., 2018). Shrubs and vegetation are important contributors to habitat heterogeneity by providing reptiles and amphibians with a mosaic of microclimates for effective thermoregulation (Filazzola et al., 2017; Lortie et al., 2022b; Westphal et al., 2018; Ivey et al., 2022; Zuliani et al., 2023). A foundation species is defined as a species that supports ecological processes that shape community assembly and diversity patterns, despite not necessarily being common within a region (Ellison et al., 2005; Ellison, 2019; Lortie et al., 2018; Schöb et al., 2012). In order to mitigate the effects of climate change, foundation species, such as shrubs, are needed as a buffer from extreme temperatures and aridity (Basson et al., 2017; Barrows, 2011). Refuges and shelter from climate can also provide protection from predation (Dutra et al., 2011; Westphal et al., 2018) in addition to providing foraging and mating habitats (Basson et al., 2017; Goller et al., 2014, Lortie et al., 2022b). However, we also need to deepen the extent that site-level variation in the foundation species, such as shrubs, collectively influence animals, such as reptiles and amphibians. Single or fewer shrubs at a site can provide some of the benefits needed to support a diverse animal population; however, if individual animals need to forage widely, defend territories, or seek mates, then the density and general availability of shrubs within a site relevant to animals can be a key measure as well (Ivey et al., 2021; Zuliani et al., 2023b). The benefits of foundation species are well established, but the extent that population level density estimates of desert shrubs support animals warrants additional research, likely at local-to-regional scales (Filazzola et al., 2017; Lortie et al., 2015; Noble et al., 2016; Zuliani et al., 2023b).

Shrubs are often the dominant vegetation in deserts and semi-arid mixed grasslands. In the central deserts of California, Mormon tea (*Ephedra californica*) and creosote bush (*Larrea tridentata*) are two widely distributed species of native shrubs (Braun et al., 2021; Lortie et al., 2017; Schafer et al., 2012). Foundation species can create complex structures that provide diverse microhabitat availability, and if this fine-scale heterogeneity is relevant to reptiles and amphibians in deserts, then increases in shrub densities across sites within the region should increase the likelihood that these animal populations are more abundant and the communities more diverse (Zuliani et al., 2021 and 2023a). Increases in the density of native shrubs have been shown to increase the likelihood of relocations in telemetry studies for the endangered species *Gambelia sila* in this region (Ivey et al., 2021; Zuliani et al., 2023b). Here, we extend this prediction that increases in the resident population density native shrubs benefits many reptiles and amphibians within the region. First, benefits can be positive and linear as increasing shrub density increases shelter and refuge access within a site. However, if a site is relatively large for the animal species it supports or if the site overlaps with the home range and activity use patterns of the species (Ivey et al., 2021; Gaudenti et al., 2021), then it is likely that the benefits of shrub density will reach an asymptote as the diversity of the animal communities plateau when an adequate number of shrubs to support species is reached (Zuliani et al., 2023b). Relatively high densities of shrubs or shrub encroachment with changing climate (Loera et al., 2012) can also have negative effects on other plants

and animals by decreasing diversity of resources provided by other plant species (Germano et al., 1994; Sinervo et al., 2010) or in increasing predation of reptiles and amphibians through challenges to mobility (Westphal et al., 2016; Zuliani et al., 2023b). Facilitating the growth of native annual plants does increase habitat heterogeneity and species diversity across different sites (Holzapfel & Mahall, 1999; Lucero et al., 2020) provided there is a mosaic of light and temperature at sites (Lucero et al., 2021; Pulsford et al., 2017). Reptiles and amphibians rely on *E. californica* and *L. tridentata* for shelter in Central California deserts (German et al., 2019; Ivey et al., 2020; Westphal 2018; Zuliani et al., 2023b), for protection from predation (Germano et al., 2019; Ivey et al., 2022; Zuliani et al., 2021), and for direct micro-environmental amelioration (Lortie et al., 2017; Ivey et al. 2020). There is also significant variation in shrub densities regionally (Filazzola et al., 2020) and the region supports a diversity of reptile and amphibian species (Stewart et al., 2019).

Global change is occurring at large scales. Testing for changes in both patterns in biodiversity regionally and key ecological interactions can preserve species at large scales within ecological regions. Here, we hypothesize that foundational shrub species *E. californica* and *L. tridentata* positively influence reptile and amphibian communities at different sites across an aridity gradient in the drylands of central California. The following predictions were tested:

1. Increasing shrub density at sites increases the relative abundance and diversity of reptiles and amphibians.
2. The evenness and community-level similarity in reptile and amphibian communities between sites is increased by increasing shrub densities because shrubs provide both increased micro-environmental heterogeneity and more stability in the system both environmentally and ecologically (Wilby and Shachak, 2004)
3. Increasing aridity at sites increases the benefits provided by shrubs because of the importance of thermal refuges for reptiles and amphibians within the region (Lortie et al., 2022b).

Methods

Study Sites

The study was done within the central drylands of California (Fig. 1). The most northern extent of region sampled included the Panoche Hills Management Area—which is a range of hills located in San Benito County, California, United States. The Panoche Hills—located in a semi-arid region—receive an average annual precipitation of around 250–300 mm per year and regularly experience summer temperatures exceeding 38°C (Filazzola et al., 2017). The Panoche Hills are a shrubland dominated by *E. californica* (Braun et al., 2021). Similarly, the Carrizo Plain is a slightly more arid region that experiences summer temperatures greater than 38°C (Prugh & Brashares 2010) and receives an average annual precipitation of around 230–250 mm within the central region studied here (Westphal et al., 2016; Zuliani et al., 2023b). This landscape is also primarily dominated by native *E. californica* (Loera et al., 2012; Zuliani et al., 2021). The Mojave Desert is a vast desert region located in Southeastern California, United States and

comprises the southernmost extent of this study. The Mojave Desert is the most arid of the three regions with an average annual precipitation of less than 150 mm in most areas and summer temperatures that can exceed 49°C (Brooks and Minnich, 2006). Although both *E. californica* and *L. tridentata* can be present at various sites within the Mojave Desert, *L. tridentata* is the dominant species of shrub across much of this arid landscape (Braun et al., 2021; Ruttan et al., 2016). Consequently, two native shrub species comprise the dominant vegetation within these arid lands that can support animal species regionally.

Study Species

E. californica is a branching shrub species capable of reaching heights greater than 1 meter with extensive branching (Cutler 1939; Loera et al., 2012). *L. tridentata* is a prominent drought-tolerant evergreen shrub species capable of attaining heights of over 2 meters with well-developed canopies (Franco et al., 1994; Sternberg, 1976). Both shrub species facilitate local annual plant and animal communities and can play a significant role on the structure and function of an ecosystem (Angelini et al., 2015; Braun et al., 2021; Filazzola et al., 2019; Lortie et al., 2017; Ruttan et al., 2016; Zuliani et al., 2023a). There are many species of reptiles and amphibians found across the broad region of the San Joaquin Desert and Mojave Desert (Germano et al., 2011; McGinnis & Stebbins, 2018; Stewart et al., 2019). There are also many endemic and federally listed species including *Gambelia sila* (blunt-nosed leopard lizard), *Uma inornata* (Coachella fringe-toed lizard), *Masticophis flagellum ruddocki* (San Joaquin coachwhip), *Masticophis lateralis euryxanthus* (Alameda striped racer), *Gopherus agassizii* (desert tortoise), *Batrachoseps sp.* (slender salamander) (Barrows, 1997; Germano et al., 2011; Mitrovich et al., 2018; Nussear et al., 2009; Richman., 1973).

Shrub density and site-level climate data

Site-level shrub densities were determined using composite, high-resolution satellite imagery acquired from Google Earth (Google LLC, 2022). Digital images were compiled of stacked images from 2022 (Zuliani et al., 2023b). Shrub density was calculated by dividing the total shrubs at a site by the site's total area (Lortie et al., 2022a). All shrubs at each study site were geotagged to within 1m. Shrub data (e.g., shrub counts, density, and size) was then ground-truthed *in situ* in Spring 2023 to confirm the geolocated shrub densities. Long-term climate data for every site was derived at 1km scale (Fick & Hijmans, 2017; Lortie & Haas-Desmarais, 2023). Mean annual temperature and mean annual precipitation were used to calculate aridity for each site with shrub point counts. Aridity was quantified using the de Martonne index, which is the ratio of the mean annual precipitation and mean annual temperature plus 10°C (Botzan et al., 1998; Pellicone et al., 2019) Thus, lower values of the de Martonne index correspond with relatively more arid sites.

Reptile and amphibian occurrence data were retrieved from the Global Biodiversity Information Facility. Georeferenced occurrence data were compiled for reptile and amphibian species across the entire region from January 1st, 1700, to December 30th, 2022. A total of 127 datasets were retrieved resulting in

729,581 occurrences for the region. Occurrence data were then joined to the centroids of the site level shrub data at a scale of 10,000 m for the 43 distinct sites with discrete shrub-point count data.

Data Analysis

Data retrieval, data processing, statistical analysis, and visualizations were conducted using R version 4.2.2 (R Core Team, 2022). The 'glmmTMB' package was used to fit Generalized Linear Mixed Models (GLMMs) to examine the relationship between shrub density and reptile and amphibian class on community measures including abundance, richness, and evenness (v1.1.7-1; Brooks, 2023). The GLMMs were fitted to a quasi-Poisson distribution to account for over-dispersion in the data. The 'emmeans' package was used to compute contrasts of estimated marginal means (v1.8.4-1; Lenth, 2022). WorldClim data were retrieved using the R package 'raster' (Fick & Hijmans., 2017; v3.6-20; Hijmans, 2023). Aridity was tested as a covariate in models for abundance and richness. For each species of reptile and amphibian, we calculated a Bray-Curtis dissimilarity value by comparing the proportions of shrub density to those of reptile and amphibian class (Oksanen et al., 2019) using the R package 'vegan' (v2.6-4; Oksanen, 2022). Generalized Linear Mixed Models were checked for heteroskedasticity (Bolker et al., 2009). Linearity of fit curves versus curvilinear fits were done postdoc regression tests and AIC scores were used to contrast and identify best fit lines in terms of parsimony (and in variation explained) (Mangan et al., 2017). Aridity was modeled as a covariate in shrub density tests. The sensitivity of models by shrub species was examined, and all models were robust. The independence between sites in reptile and amphibian reported occurrences was also examined using the physical distances between sites as a covariate calculated using the 'sf' package in R (Edzer Pebesma & Bivand, 2023).

Results

A total of 71 different species of reptiles and amphibians were reported within the region sampled. The class Reptilia consisted of 47 unique species—comprising 29 different genera. Some of the most abundant species of reptiles included *Uta stansburiana* (Common-side blotched lizard), *Gambelia sila* (blunt-nosed leopard lizard), and *Crotalus oreganus* (Western rattlesnake). The class Amphibia contained a total of 24 species—comprising 10 different genera—and the most abundant amphibians were *Anaxyrus woodhousii* (Woodhouse's toad), *Anaxyrus boreas* (Western toad), and *Pseudacris regilla* (Pacific tree frog). The top ten most abundant species of reptiles and amphibians were compiled and accounted for a total of 2425 and 254 observations, respectively—indicating reptiles were observed on a more frequent basis (Fig 2). The highest number of reported occurrences were from *Uta stansburiana*, a reptile species with 710 occurrences. The least frequently reported was *Batrachoseps attenuates* (California slender salamander), a species of amphibian with only 6 occurrences. *Uta stansburiana* accounted for 29.2% of the reptile class, and *Anaxyrus woodhousii* accounted for 18.7% of the amphibian class.

The best fit curves were non-linear for all three reptile and amphibian responses tested in this study because of the lowest AIC scores and highest variance explained in each instance. The abundance of reptiles and amphibians significantly increased with increasing shrub density (Fig 3a, Table 1). Reptile

and amphibian abundance varied significantly between classes (Table 1). However, the interaction between shrub density and animal class was not significant suggesting that the positive effect of increasing shrub density was consistent for reptiles and amphibians within the region at this taxonomic resolution (Table 2). Reptile and amphibian species richness also significantly increased with increasing shrub density (Fig 3b, Table 1), the relationship between Reptilia and shrub density was more prevalent than the relationship between shrub density and Amphibia. Increasing shrub density positively influenced species evenness (Fig 3c, Table 1). Shrub density did not significantly influence the Bray-Curtis dissimilarity index, but there was a significant difference between the two classes with Amphibia being less similar between sites, i.e., higher scores (Table 1). Aridity did not significantly influence the shrub density effects (GLMs, $p < 0.05$ in all instances).

Discussion

Exploring the capacity for shrubs to support the distribution and diversity of sensitive, indicator species to changing climate in deserts is of fundamental ecological importance. Here, we tested this by examining the hypothesis that two native shrubs species function as foundation species for both amphibian and reptilian communities by enhancing their structure and composition across a large regional gradient. We selected sites with a difference in shrub density and aridity and, thus, used both a biotic shrub density gradient as a novel ecological tool to explore the relative importance of changes in positive plant-animal interactions in deserts and an abiotic environmental gradient. We found support for the hypothesis that increasing shrub density had a significant positive effect on reptile and amphibian abundance and richness. Shrub density did not, however, influence the community-level dissimilarity index, suggesting the species pool for reptiles and amphibians in this region is large and robust (Barrows & Allen 2010; Barrows et al., 2016) and that there can be significant variation or turnover in species between sites. Reptiles and amphibians responded positively to the biotic shrub density gradient. The prediction that variation in aridity between sites within the region was a significant covariate that mediated the positive influence of increasing shrub density was not supported. Even at relatively less arid sites, increasing shrub density positively influenced the reptile and amphibian communities. All significant trends were also non-linear suggesting that shrubs benefit the reptiles and amphibians regionally, but that from a conservation and restoration perspective, the mosaic of shrub and open, non-canopied sites is ideal (Ivey et al., 2021; Zuliani et al., 2023b). These two native shrubs species functioned as ecological foundation species supporting reptile and amphibian biodiversity within the region. Given that climate change is a large-scale factor and that stressors such as extended droughts or megadroughts are increasingly common (Fawcett et al., 2011; Stahle, 2020; Williams et al., 2020).

Density Effects

Density and animal abundance are important ecologically. Increasing shrub density positively predicted animal density for both reptiles and amphibians. These benefits were non-linear suggesting that there is likely an optimal number of shrubs that reptile and amphibian species prefer (Filazzola et al., 2017; Gaudenti et al., 2021; Zuliani et al., 2023a). Areas of higher shrub density provide the potential for these

reptile and amphibian species to utilize individual shrubs as refuges both from harsh abiotic conditions as well as from predation (Eldridge & Soliveres 2014; Noble et al., 2016). Areas with a higher number of shrubs are likely to have more structural resources available for reptiles and amphibians to utilize—potentially increasing the likelihood of positive plant-animal interactions (Bortolus et al., 2002; Schleuning et al., 2015; Zuliani et al. 2021). Species that depend on these shrubs to regulate their temperature would greatly benefit in areas with greater shrub density, even when shrub individuals are smaller in size, because shrubs provide multiple avenues for utilization (Holzaphel & Mahall 1999; Zuliani et al. 2023). Therefore, higher shrub densities can greatly impact both the association of reptiles and amphibians while also influencing both their behavior and interactions.

These findings are important as they provide realistic guidelines and goals for managers targeting reptilian and amphibian conservation. Shrub density predicted an increase in species richness for both reptiles and amphibians. Similarly, after a certain point, increases in shrub density had similar positive effects to reptile and amphibian abundance. The Bray-Curtis dissimilarity index revealed that no two sites shared all the same species for amphibians. The Bray-Curtis scores were low for reptiles indicating that many species are supported locally across all sites. Many factors can affect species richness including geographic (e.g., species pool dispersal), biotic (e.g., competition, predation, facilitation), and abiotic (e.g., resource availability, environmental heterogeneity, disturbance frequency and intensity) (Blakely & Didham. 2010; Brown et al., 2016). There was a negative relationship between shrub density and species evenness for both reptiles and amphibians. Many sites had low evenness, indicating that only a few species dominated these sites, which is not uncommon in desert animal communities (Chaves et al., 2021; Zeng et al., 2014). Desert ecosystems are difficult to colonize due to various environmental constraints, such as extreme temperatures and high aridity in addition to reptile and amphibian distributions being patchy. This combination of factors can result in sites that are comprised of a community that is dominated by only a couple species, as observed in the relative abundance of the top ten reptiles and amphibians (Fig. 2) (Barrows et al., 2010, 2016).

A fundamental step in conserving reptile and amphibian biodiversity in deserts is the ability to identify quality habitats needed to sustain populations of specific target species. The positive influence of shrub density on reptile and amphibian communities at high-aridity sites may be due to the provision of cover, food, and microclimatic conditions that support their survival and reproduction (Westphal et al. 2018; Ivey et al. 2020; Zuliani et al., 2021). Shrubs can benefit reptile and amphibian communities in arid ecosystems through many mechanisms including acting as a refugia to escape from harsh temperatures (Westphal et al. 2018; Ivey et al. 2020), acting as a food source for some herbivorous species (like *Gopherus agassizii*; Abella et al., 2016; Whitford & Bryant. 1979), and in ameliorating predation attempts (Filazzola et al. 2017; Lortie et al. 2020; Zuliani et al., 2023b). The benefits of shrub in desert regions are likely much more important to reptiles than amphibians since only a small fraction of amphibians, mainly anurans, occur in desert ecosystems. *Spea hammondi* (Western spadefoot toad) are a well-adapted amphibian species that occur in the region but displayed a low observation frequency in this study which could be explained by their nocturnal behavior and dependence on burrows as opposed to reliance on shrub cover to avoid desiccation during times of environmental stress (Baumberger et al., 2019). Desert

amphibian species rely on the formation of temporary ponds to successfully reproduce (Creusere & Whitford, 1976; Gilioli et al., 2018). The presence and duration of temporary water bodies are likely a more important limiting factor to the distribution and community structure of amphibians than shrub density (Dayton and Fitzgerald, 2006), which could explain the low occurrences of amphibians in this study. While the species that associate with these foundational shrub species may directly benefit, the probability of more complex trophic interactions increases due to the variation in community composition (Zuliani et al., 2021, 2023a). Indirect feedbacks may also result from this positive association including the association of predator species like *Crotalus oreganus* (Western rattlesnake) which consumes smaller species like *Gambelia sila* (blunt-nosed leopard lizard) that use shrubs as refuge from other predators, thus impacting community composition (Bailey and Germano, 2015; Germano. 2019; Zuliani et al., 2021 and 2023b). Reptiles and amphibians are important members of the food chain, but reptiles have a greater association with shrub presence, using a variety of mechanisms to not merely survive extreme heat and aridity but to thrive in extreme desert ecosystems.

Implications

Anthropogenic climate change will exacerbate the already hot climate in the desert ecosystems and negatively impact most organisms—particularly reptiles and amphibians (Hinderer et al., 2020; Ivey et al., 2020). Higher shrub density has been shown to have a positive impact on the abundance and diversity of reptile and amphibian species. This study provides further evidence that studies testing for associations between shrubs and reptile and amphibian species should consider the density of these shrubs in their studies as it has the potential to act as a direct indicator for reptile and amphibian abundance while also influence both trophic interactions and community composition. More generally, the relative importance of vegetation for key animal species within deserts that influence persistence through refuges is crucial research (Filazzola et al., 2017; Ivey et al., 2020; Lortie et al., 2015; Zuliani et al., 2021). The design of habitats for conservation and restoration efforts, especially in arid ecosystems that are at risk of desertification and endangering animal species, needs simple and direct interventions—such as adding a set number of shrubs for providing key habitats. By understanding the important relationship between shrubs and reptile and amphibian species, restoration efforts can focus on preserving these foundational shrubs to restore the health of these ecosystems. Research that directly examines causation and mechanisms, in addition to correlation, is needed to better describe the key features of these habitats and benefits that shrub provided for reptiles and amphibians. Shelter is likely the major benefit, however resources, and other indirect positive interactions developed in the conceptual underpinnings here must be tested. Conservation is a multi-species endeavor, but here we show using a novel biotic, shrub density gradient as an excellent starting point that benefits many species of reptile and amphibian can be realized with protection and perhaps addition of two shrub species.

Declarations

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Author Contributions:

EO, CJL, and MZ conceptualized and designed the methodology; EO and MG generated detailed maps and acquired data; EO and CJL conducted formal analysis and visualization of the data; EO and CJL generated the original version of the manuscript; EO, CJL, MZ, and MG thoroughly reviewed and edited the manuscript.

Data Availability:

Data are available from, doi:10.5063/F18914BJ; <https://doi.org/10.15468/dl.5jhd82>

References

1. Abella, S. R., & Berry, K. H. (2016). Enhancing and restoring habitat for the desert tortoise. *Journal of Fish and Wildlife Management*, 7(1), 255–279. <https://doi.org/10.3996/052015-jfwm-046>
2. Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P., Smolders, A. J., & Silliman, B. R. (2015). Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States Salt Marshes. *Proceedings of the Royal Society B: Biological Sciences*, 282(1811), 20150421. <https://doi.org/10.1098/rspb.2015.0421>
3. Bailey, C. V., & Germano, D. J. (2015). Probability of occupancy of; blunt-nosed leopard lizards on habitat patches of various sizes in the San Joaquin Desert of California. *Western Wildlife*, 2, 23–28.
4. Barrows, C. W. (1997). Habitat relationships of the Coachella Valley fringe-toed lizard (*Uma inornata*). *The Southwestern Naturalist*, 42(2), 218–223. <https://www.jstor.org/stable/30055264>
5. Barrows, C. W., & Allen, M. F. (2010). Patterns of occurrence of reptiles across a sand dune landscape. *Journal of Arid Environments*, 74(2), 186–192. <https://doi.org/10.1016/j.jaridenv.2009.09.005>
6. Barrows, C. W. (2011). Sensitivity to climate change for two reptiles at the Mojave–Sonoran Desert interface. *Journal of Arid Environments*, 75(7), 629–635. <https://doi.org/10.1016/j.jaridenv.2011.01.018>
7. Barrows, C. W., Hoines, J., Vamstad, M. S., Murphy-Mariscal, M., Lalumiere, K., & Heintz, J. (2016). Using citizen scientists to assess climate change shifts in desert reptile communities. *Biological Conservation*, 195, 82–88. <https://doi.org/10.1016/j.biocon.2015.12.027>
8. Basson, C. H., Levy, O., Angilletta, M. J., & Clusella-Trullas, S. (2017). Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. *Functional Ecology*, 31(4), 856–865. <https://doi.org/10.1111/1365-2435.12795>

9. Baumberger, K. L., Eitzel, M. V., Kirby, M. E., & Horn, M. S. (2019). Movement and habitat selection of the western spadefoot (*Spea hammondi*) in southern California. *PLOS ONE*, 14(10), e0222532. <https://doi.org/10.1371/journal.pone.0222532>
10. Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
11. Blakely, T. J., & Didham, R. K. (2010). Disentangling the mechanistic drivers of ecosystem-size effects on species diversity. *Journal of Animal Ecology*, 79(6), 1204–1214. <https://doi.org/10.1111/j.1365-2656.2010.01729.x>
12. Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
13. Bortolus, A., Schwindt, E., & Iribarne, O. (2002). Positive plant-animal interactions in the high marsh of an Argentinean coastal lagoon. *Ecology*, 83(3), 733. <https://doi.org/10.2307/3071877>
14. Botzan, T. M., Mariño, M. A., & Nacula, A. I. (1998). Modified de Martonne aridity index: application to the napa basin, California. *Physical Geography*, 19(1), 55–70. <https://doi.org/10.1080/02723646.1998.10642640>
15. Braun, J., Westphal, M., & Lortie, C. J. (2021). The shrub *Ephedra californica* facilitates arthropod communities along a regional desert climatic gradient. *Ecosphere* 12(9): e03760. <https://doi.org/10.1002/ecs2.3760>
16. Brooks, M. L., & Minnich, R. A. (2006). Southeastern deserts bioregion. in N. Sugihara, fire in California's ecosystems (pp. 391–414). University of California Press. <https://doi.org/10.1525/california/9780520246058.003.0016>
17. Brown, R. L., Reilly, L. A., & Peet, R. K. (2016). Species richness: Small scale. *ELS*, 1–9. <https://doi.org/10.1002/9780470015902.a0020488.pub2>
18. Callaway, R. M. (1994). Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology*, 75(3), 681–686. <https://doi.org/10.2307/1941726>
19. Chaves, J. E., Aranibar, J. N., & Gatica, G. N. (2021). Species and functional plant diversity enhance ecosystem functions in the central Monte desert. *Journal of Vegetation Science*, 32(1). <https://doi.org/10.1111/jvs.12952>
20. Creusere, F. M., & Whitford, W. G. (1976). Ecological relationships in a desert anuran community. *Herpetologica*, 32(1), 7–18. <https://www.jstor.org/stable/3891893>
21. Cutler, H. C. (1939). Monograph of the North American Species of the Genus *Ephedra*. *Annals of the Missouri Botanical Garden*, 26(4), 373. <https://doi.org/10.2307/2394299>
22. Dayton, G. H., & Fitzgerald, L. A. (2006). Habitat suitability models for desert amphibians. *Biological Conservation*, 132(1), 40–49. <https://doi.org/10.1016/j.biocon.2006.03.012>
23. Diaz, J. A., & Cabezas-diaz, S. (2004). Seasonal variation in the contribution of different behavioral mechanisms to lizard thermoregulation. *Functional Ecology*, 18(6), 867–875. <https://doi.org/10.1111/j.0269-8463.2004.00916.x>

24. Dutra, H. P., Barnett, K., Reinhardt, J. R., Marquis, R. J., & Orrock, J. L. (2011). Invasive plant species alters consumer behavior by providing refuge from predation. *Oecologia*, 166(3), 649–657. <https://doi.org/10.1007/s00442-010-1895-7>
25. Edzer Pebesma, & Bivand, R. (2023). Spatial Data Science. <https://doi.org/10.1201/9780429459016>
26. Eldridge, D. J., & Soliveres, S. (2014). Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. *Australian Journal of Botany*, 62(7), 594. <https://doi.org/10.1071/BT14137>
27. Ellison, A. M. (2019). Foundation species, non-trophic interactions, and the value of being common. *IScience*, 13, 254–268. <https://doi.org/10.1016/j.isci.2019.02.020>
28. Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K. J., Ford, C. R., Foster, D. W., Kloeppel, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J. E., Orwig, D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. A., Swan, C. M., Thompson, J., Von Holle, B., & Webster, J. R. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3(9), 479–486. [https://doi.org/10.1890/1540-9295\(2005\)003](https://doi.org/10.1890/1540-9295(2005)003)
29. Fawcett, P. J., Werne, J. P., Anderson, R. R., Heikoop, J. M., Brown, E. T., Berke, M. A., Smith, S. M., Goff, F., Donohoo-Hurley, L., Cisneros-Dozal, L. M., Schouten, S., Damsté, J. S. S., Huang, Y., Toney, J. L., Fessenden, J., Wolde-Gabriel, G., Atudorei, V., Geissman, J. W., & Allen, C. R. (2011). Extended megadroughts in the southwestern United States during Pleistocene interglacials. *Nature*, 470(7335), 518–521. <https://doi.org/10.1038/nature09839>
30. Ferreira, D., Mateus, C., & Santos, X. (2016). Responses of reptiles to fire in transition zones are mediated by bioregion affinity of species. *Biodiversity and Conservation*, 25(8), 1543–1557. <https://doi.org/10.1007/s10531-016-1137-3>
31. Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
32. Filazzola, A., Westphal, M., Powers, M., Liczner, A. R., (Smith) Woollett, D. A., Johnson, B., & Lortie, C. J. (2017). Non-trophic interactions in deserts: Facilitation, interference, and an endangered lizard species. *Basic and Applied Ecology*, 20, 51–61. <https://doi.org/10.1016/j.baae.2017.01.002>
33. Fisher, M. W. (2007). Shelter and welfare of pastoral animals in New Zealand. *New Zealand Journal of Agricultural Research*, 50(3), 347–359. <https://doi.org/10.1080/00288230709510303>
34. Franco, A. C., de, G., Virginia, R. A., Reynolds, J. F., & Whitford, W. G. (1994). Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*. *Oecologia*, 97(2), 171–178. <https://doi.org/10.1007/bf00323146>
35. Gaudenti, N., Nix, E., Maier, P., Westphal, M. F., & Taylor, E. N. (2021). Habitat heterogeneity affects the thermal ecology of an endangered lizard. *Ecology and Evolution*, 11(21), 14843–14856. <https://doi.org/10.1002/ece3.8170>
36. GBIF.org (21 September 2022) GBIF Occurrence Download <https://doi.org/10.15468/dl.5jhd82>

37. Germano, D. J., Williams, D. F., & Ill, W. T. (1994). Effect of drought on blunt-nosed leopard lizards (*Gambelia sila*). *Northwestern Naturalist*, 75(1), 11. <https://doi.org/10.2307/3536555>
38. Germano, D. J., & Williams, D. F. (2005). Population ecology of blunt-nosed leopard lizards in high elevation foothill habitat. *Journal of Herpetology*, 39(1), 1–18. <https://www.jstor.org/stable/4092945>
39. Germano, D. J., Rathbun, G. B., Saslaw, L. R., Cypher, B. L., Cypher, E. A., & Vredenburg, L. M. (2011). The San Joaquin Desert of California: Ecologically misunderstood and overlooked. *Natural Areas Journal*, 31(2), 138–147. <https://doi.org/10.3375/043.031.0206>
40. Germano, D. J., & Rathbun, G. B. (2016). Home range and habitat use by blunt-nosed leopard lizards in the southern San Joaquin Desert of California. *Journal of Herpetology*, 50(3), 429–434. <https://doi.org/10.1670/15-006>
41. Germano, D. J. (2019). Predation of the endangered blunt-nosed leopard lizard (*Gambelia sila*) in the San Joaquin Desert of California. *The Southwestern Naturalist*, 63(4), 276. <https://doi.org/10.1894/0038-4909-63-4-276>
42. Gilioli, K. C., Kéry, M., & Guimarães, M. (2018). Unraveling fine-scale habitat use for secretive species: When and where toads are found when not breeding. *PLOS ONE*, 13(10). <https://doi.org/10.1371/journal.pone.0205304>
43. Goller, M., Goller, F., & French, S. S. (2014). A heterogeneous thermal environment enables remarkable behavioral thermoregulation in *Uta stansburiana*. *Ecology and Evolution*, 4(17), 3319–3329. <https://doi.org/10.1002/ece3.1141>
44. Haas-Desmarais, S., & Lortie, C. J. (2023). Direct and indirect interactions between shrubs and the flowering annual community in an arid ecosystem. *Flora*, 298, 152202. <https://doi.org/10.1016/j.flora.2022.152202>
45. Hinderer, R. K., Litt, A. R., & McCaffery, M. (2020). Habitat selection by a threatened desert amphibian. *Ecology and Evolution*, 11(1), 536–546. <https://doi.org/10.1002/ece3.7074>
46. Holzapfel, C., & Mahall, B. E. (1999). Bidirectional facilitation and interference between shrubs and annuals in the mojave desert. *Ecology*, 80(5), 1747. <https://doi.org/10.2307/176564>
47. Ivey, K. N., Cornwall, M., Crowell, H., Ghazian, N., Nix, E., Owen, M., Zuliani, M., Lortie, C. J., Westphal, M., & Taylor, E. (2020). Thermal ecology of the federally endangered blunt-nosed leopard lizard (*Gambelia sila*). *Conservation Physiology*, 8(1). <https://doi.org/10.1093/conphys/coaa014>
48. Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences*, 106(10), 3835–3840. <https://doi.org/10.1073/pnas.0808913106>
49. Lenth, R. (2020). emmeans: Estimated marginal means, aka least-squares means. R package version 1.5.4. <https://CRAN.R-project.org/package=emmeans>
50. Loera, I., Sosa, V., & Ickert-Bond, S. M. (2012). Diversification in North American arid lands: Niche conservatism, divergence and expansion of habitat explain speciation in the genus *Ephedra*. *Molecular Phylogenetics and Evolution*, 65(2), 437–450. <https://doi.org/10.1016/j.ympev.2012.06.025>

51. Lortie, C. J., Filazzola, A., & Sotomayor, D. A. (2015). Functional assessment of animal interactions with shrub-facilitation complexes: A formal synthesis and conceptual framework. *Functional Ecology*, 30(1), 41–51. <https://doi.org/10.1111/1365-2435.12530>
52. Lortie, C. J., Filazzola, A., Kelsey, R., Hart, A. K., & Butterfield, H. S. (2018). Better late than never: a synthesis of strategic land retirement and restoration in California. *Ecosphere*, 9(8), e02367. <https://doi.org/10.1002/ecs2.2367>
53. Lortie, C. J., Braun, J., Westphal, M., Noble, T., Zuliani, M., Nix, E., Ghazian, N., Owen, M., & Butterfield, H. S. (2020). Shrub and vegetation cover predict resource selection use by an endangered species of desert lizard. *Scientific Reports*, 10(1). <https://doi.org/10.1038/s41598-020-61880-9>
54. Lortie, C. J., Filazzola, A., Westphal, M., & Butterfield, H. S. (2022a). Foundation plant species provide resilience and microclimatic heterogeneity in Drylands. *Scientific Reports*, 12(1). <https://doi.org/10.1038/s41598-022-22579-1>
55. Lortie, C. J., Zuliani, M., Ghazian, N., Braun, J., & Haas, S. (2022b). A list of ecological study sites within Central California Drylands. Knowledge Network for Biocomplexity. <https://doi.org/10.5063/F18914BJ>
56. Lortie, C. J., & Haas-Desmarais, S. (2023). Climate data for Central California Dryland ecology sites [Data set]. figshare. <https://doi.org/10.6084/m9.figshare.22196149.v2>
57. Lucero, J. E., Callaway, R. M., Faist, A. M., & Lortie, C. J. (2021). An unfortunate alliance: Native shrubs increase the abundance, performance, and apparent impacts of *Bromus tectorum* across a regional aridity gradient. *Basic and Applied Ecology*, 57, 41–53. <https://doi.org/10.1016/j.baae.2021.09.001>
58. Lucero, J. E., Seifan, M., Callaway, R. M., & Lortie, C. J. (2020). Positive associations with native shrubs are intense and important for an exotic invader but not the native annual community across an aridity gradient. *Diversity and Distributions*, 26(9), 1177–1197. <https://doi.org/10.1111/ddi.13111>
59. Marina Goldgisser, Ethan Owen, Mario Zuliani, & CJ Lortie. (2023). GBIF data for all herptile species within Central California Deserts, USA. Knowledge Network for Biocomplexity. doi:10.5063/F1ZP44KT
60. McGinnis, S. M., & Stebbins, R. C. (2018). Peterson field guide to western reptiles and amphibians. Houghton Mifflin Harcourt Company.
61. Noble, T. J., Lortie, C. J., Westphal, M., & Butterfield, H. S. (2016). A picture is worth a thousand data points: An imagery dataset of paired shrub-open microsites within the Carrizo Plain National Monument. *GigaScience*, 5(1). <https://doi.org/10.1186/s13742-016-0145-2>
62. Nussear, K. E., Esque, T. C., Inman, R. A., Gass, L., Thomas, K. A., Cynthia S.A. Wallace, Blainey, J. B., Miller, D., & Webb, R. M. (2009). Modeling habitat of the desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran Deserts of California, Nevada, Utah, and Arizona. <https://doi.org/10.3133/ofr20091102>
63. Prugh, L., & Brashares, J. (2010). Basking in the moonlight? Effect of illumination on capture success of the endangered giant kangaroo rat. *Journal of Mammalogy*, 91(5), 1205–1212.

<https://doi.org/10.1644/10-MAMM-A-011.1>

64. Pulsford, S. A., Driscoll, D. A., Barton, P. S., & Lindenmayer, D. B. (2017). Remnant vegetation, plantings and fences are beneficial for reptiles in agricultural landscapes. *Journal of Applied Ecology*, 54(6), 1710–1719. <https://doi.org/10.1111/1365-2664.12923>
65. R Core Team. (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
66. Richman, J. B. (1973). A range extension for the Tehachapi Slender Salamander, *Batrachoseps stebbinsi*. *HISS News-J*, 1, 97.
67. Ruttan, A., Filazzola, A., & Lortie, C. J. (2016). Shrub-annual facilitation complexes mediate insect community structure in arid environments. *Journal of Arid Environments*, 134, 1–9. <https://doi.org/10.1016/j.jaridenv.2016.06.009>
68. Schemske, D. W., & Horvitz, C. C. (1988). Plant-animal interactions and fruit production in a neotropical herb: a path analysis. *Ecology*, 69(4), 1128–1137. <https://doi.org/10.2307/1941267>
69. Schafer, J. L., Mudrak, E. L., Haines, C. E., Parag, H. A., Moloney, K. A., & Holzapfel, C. (2012). The association of native and non-native annual plants with *Larrea tridentata* (creosote bush) in the Mojave and Sonoran Deserts. *Journal of Arid Environments*, 87, 129–135. <https://doi.org/10.1016/j.jaridenv.2012.07.013>
70. Schleuning, M., Fründ, J., & Garcia, D. F. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography*, 38(4), 380–392. <https://doi.org/10.1111/ecog.00983>
71. Schöb, C., Butterfield, B. J., & Pugnaire, F. I. (2012). Foundation species influence trait-based community assembly. *New Phytologist*, 196(3), 824–834. <https://doi.org/10.1111/j.1469-8137.2012.04306.x>
72. Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F., Ibargüengoytia, N., Puntriano, C. A., Massot, M., ... Sites, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328(5980), 894–899. <https://doi.org/10.1126/science.1184695>
73. Soares, C., & Brito, J. C. (2006). Environmental correlates for species richness among amphibians and reptiles in a climate transition area. *Biodiversity and Conservation*, 16(4), 1087–1102. <https://doi.org/10.1007/s10531-006-9070-5>
74. Stahle, D. W. (2020). Anthropogenic megadrought. *Science*, 368(6488), 238–239. <https://doi.org/10.1126/science.abb6902>
75. Sternberg, L. (1976). Growth Forms of *Larrea Tridentata*. *Madroño*, 23(8), 408–417. <https://www.jstor.org/stable/41413979>
76. Stewart, J. A., Butterfield, H. S., Richmond, J. Q., Germano, D. J., Westphal, M. F., Tennant, E. N., & Sinervo, B. (2018). Climatic niche contraction, habitat restoration opportunities, and conservation biogeography in California's San Joaquin desert. <https://doi.org/10.7287/peerj.preprints.26758v1>

77. Stewart, J. A., Butterfield, H. S., Richmond, J. Q., Germano, D. J., Westphal, M. F., Tennant, E. N., & Sinervo, B. (2019). Habitat restoration opportunities, climatic niche contraction, and conservation biogeography in California's San Joaquin Desert. *PLOS ONE*, 14(1).
<https://doi.org/10.1371/journal.pone.0210766>
78. Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, 111(15), 5610–5615.
<https://doi.org/10.1073/pnas.1316145111>
79. Westphal, M. F., Stewart, J. A. E., Tennant, E. N., Butterfield, H. S., & Sinervo, B. (2016). Contemporary drought and future effects of climate change on the endangered blunt-nosed leopard lizard, *Gambelia sila*. *PLOS ONE*, 11(5), e0154838. <https://doi.org/10.1371/journal.pone.0154838>
80. Westphal, M. F., Noble, T., Butterfield, H. S., & Lortie, C. J. (2018). A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard. *Ecology and Evolution*, 8(23), 12153–12162.
<https://doi.org/10.1002/ece3.4673>
81. Whitford, W. G., & Bryant, M. (1979). Behavior of a predator and its prey: The horned lizard (*Phrynosoma cornutum*) and harvester ants (*Pogonomyrmex* spp.). *Ecology*, 60(4), 686–694.
<https://doi.org/10.2307/1936605>
82. Wilby, A., & Shachak, M. (2004). Shrubs, granivores and annual plant community stability in an arid ecosystem. *Oikos*, 106(2), 209–216. <https://doi.org/10.1111/j.0030-1299.2004.13085.x>
83. Williams, A. M., Cook, E. R., Smerdon, J. E., Cook, B. I., Abatzoglou, J. T., Bolles, K., Baek, S. W., Badger, A. M., & Livneh, B. (2020). Large contribution from anthropogenic warming to an emerging North American megadrought. *Science*, 368(6488), 314–318. <https://doi.org/10.1126/science.aaz9600>
84. Zeng, Z., Bi, J., Li, S., Chen, S., Pike, D. A., Gao, Y., & Du, W. (2014). Effects of habitat alteration on lizard community and food web structure in a desert steppe ecosystem. *Biological Conservation*, 179, 86–92. <https://doi.org/10.1016/j.biocon.2014.09.011>
85. Zuliani, M., Ghazian, N., & Lortie, C. J. (2021). Shrub density effects on the community structure and composition of a desert animal community. *Wildlife Biology*, 2021(1), 1-12.
<https://doi.org/10.2981/wlb.00774>
86. Zuliani, M., Nargol Ghazian, & Lortie, C. J. (2023a). A meta-analysis of shrub density as a predictor of animal abundance. *Wildlife Biology*, 2023(3). <https://doi.org/10.1002/wlb3.01042>
87. Zuliani, M., Ghazian, N., Owen, M., Westphal, M. F., Butterfield, H. S., & Lortie, C. J. (2023b). Shrub density effects on the presence of an endangered lizard of the Carrizo Plain National Monument, California. *Ecology and Evolution*, 13(5). <https://doi.org/10.1002/ece3.10128>
88. Żywiec, M., Fedriani, J. M., Kurek, P., & Holeksa, J. (2019). Non-trophic plant–animal interactions mediate positive density dependence among conspecific saplings. *Oikos*, 128(7), 1041–1050.
<https://doi.org/10.1111/oik.06071>

Tables

Table 1 General linear models testing the relationship between animal abundance, species richness and species evenness with, shrub density per 1000 m² and animal class (reptilia and amphibia). All significant p-values (p < 0.05) are indicated in bold.

	DF	DEVIANCE RESIDUAL	DF RESIDUAL	DEVIANCE	PR(>CHI)
<i>ABUNDANCE</i>					
NULL			71	3491.000	
SHRUB DENSITY)	2	195.160	69	3295.800	<0.001
CLASS	1	2171.380	68	1124.500	<0.001
SHRUB DENSITY * CLASS	2	81.990	66	1042.500	0.072
<i>RICHNESS</i>					
NULL			71	399.520	
SHRUB DENSITY)	2	49.610	69	349.910	<0.001
CLASS	1	276.430	68	73.480	<0.001
SHRUB DENSITY * CLASS	2	7.460	66	66.020	0.022
<i>EVENNESS</i>					
NULL			71	0.317	
SHRUB DENSITY	2	0.080	69	0.237	<0.001
CLASS	1	0.002	68	0.235	0.470
SHRUB DENSITY * CLASS	2	0.007	66	0.228	0.459

Table 2 Statistical findings of GLMs analyzing the Bray-Curtis dissimilarity index between shrub density per 1000 m² and animal class (reptilia and amphibia). Aridity was tested as a covariate in GLMS for animal abundance and species richness. All significant p-values (p < 0.05) are indicated in bold.

	DF	DEVIANCE RESIDUAL	DF RESIDUAL	DEVIANCE	PR(>CHI)
<i>BRAY - CURTIS</i>					
<i>NULL</i>			71	0.809	
<i>SHRUB DENSITY</i>	2	0.019	69	0.789	0.106
<i>CLASS</i>	1	0.493	68	0.296	<0.001
<i>SHRUB DENSITY * CLASS</i>	2	0.006	66	0.289	0.488

Figures

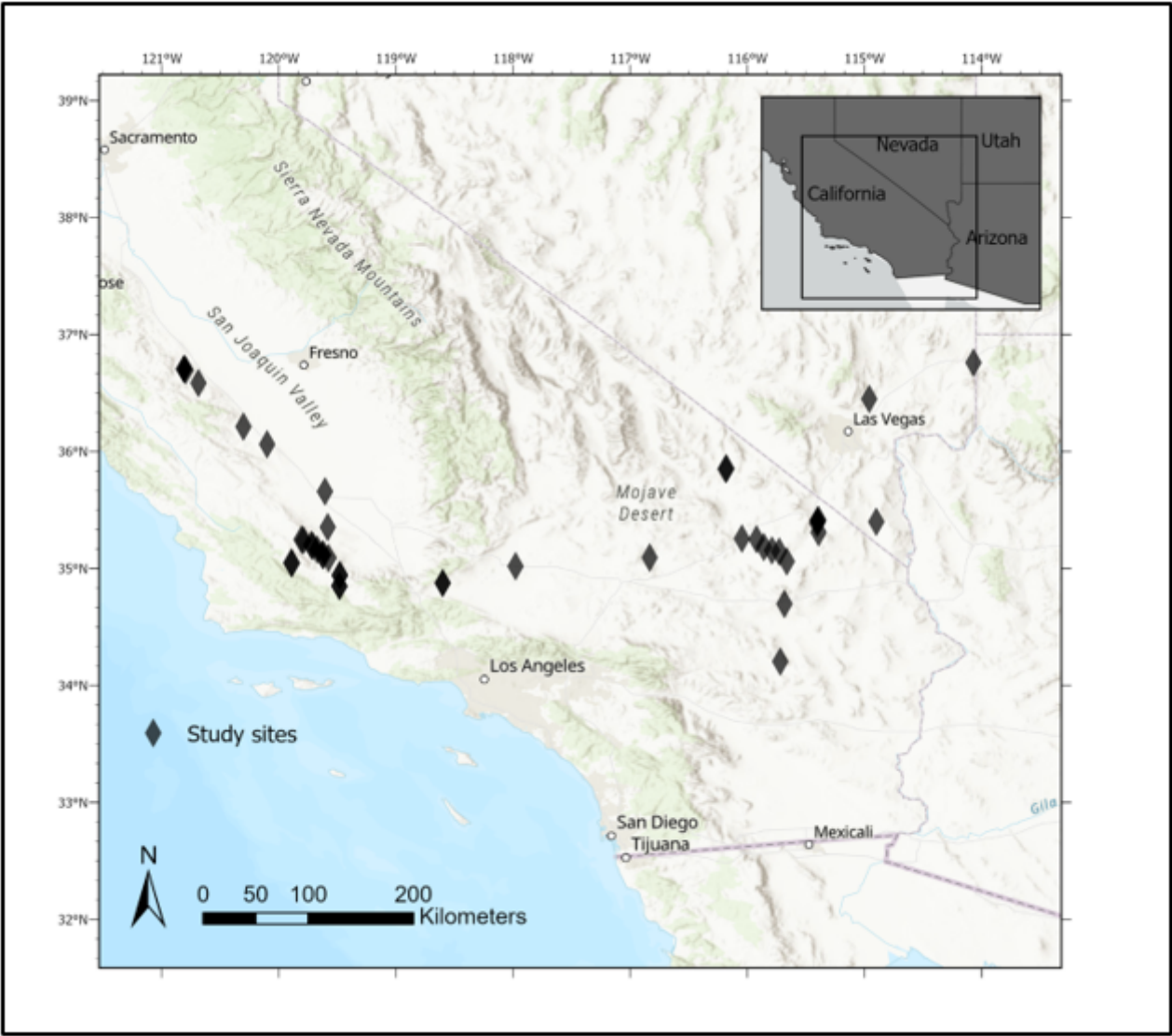


Figure 1

Map of 43 distinct study sites across the southwestern portion of the United States of America. Sites range from Southern California to Western Nevada. The greater the shrubs density present at the site

equates to the size of the point (larger point = higher shrub density). The level of shade in each point equates to concentration of sites within that area (darker point = more sites).

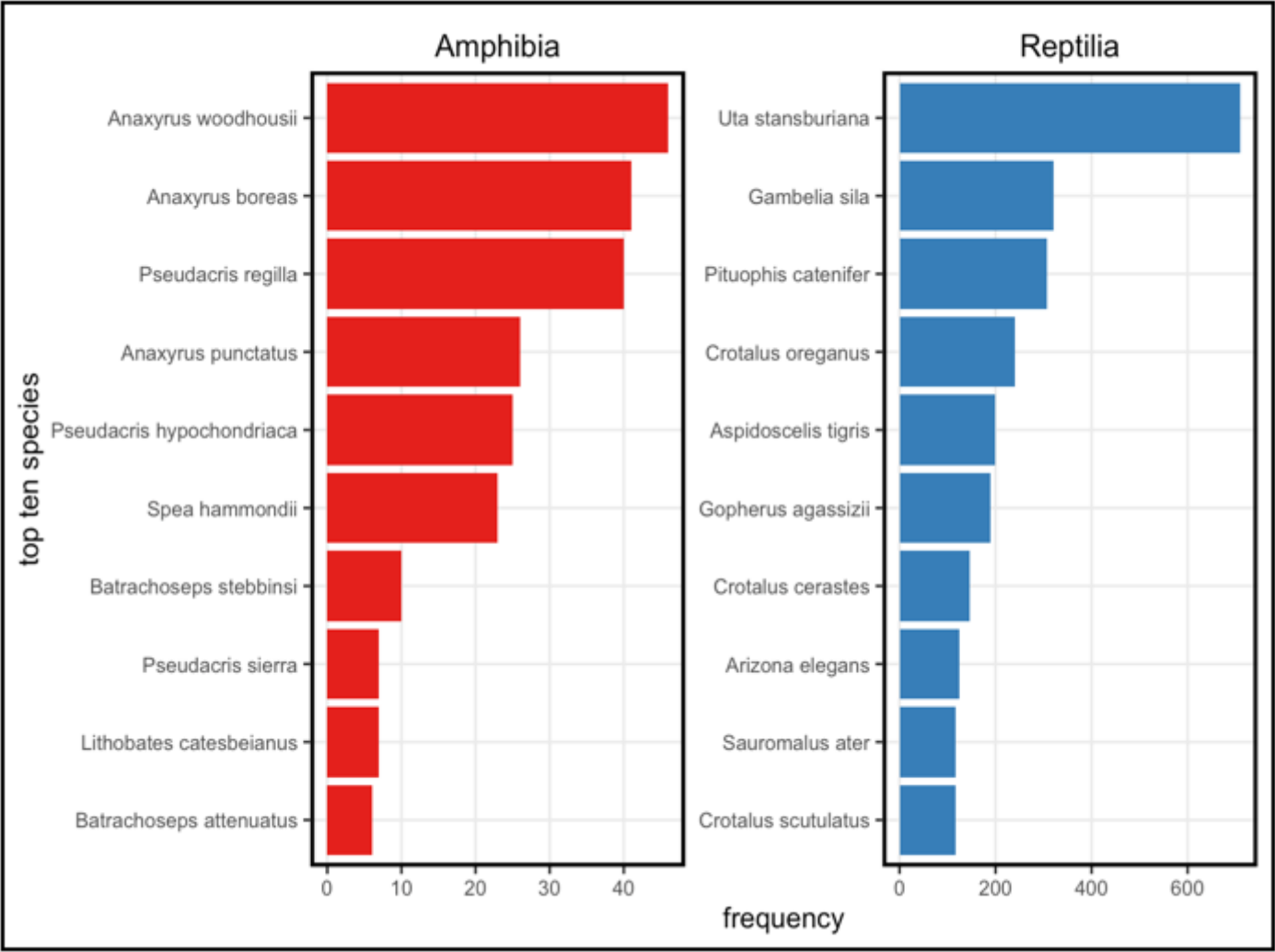


Figure 2

Relative abundance of the top ten amphibian (left panel; red) and reptilia (right panel; blue) species in Southwestern California based on GBIF occurrence data. The bars on the chart indicate the total number of occurrences of each species across all 43 study sites with species listed on the y-axis.

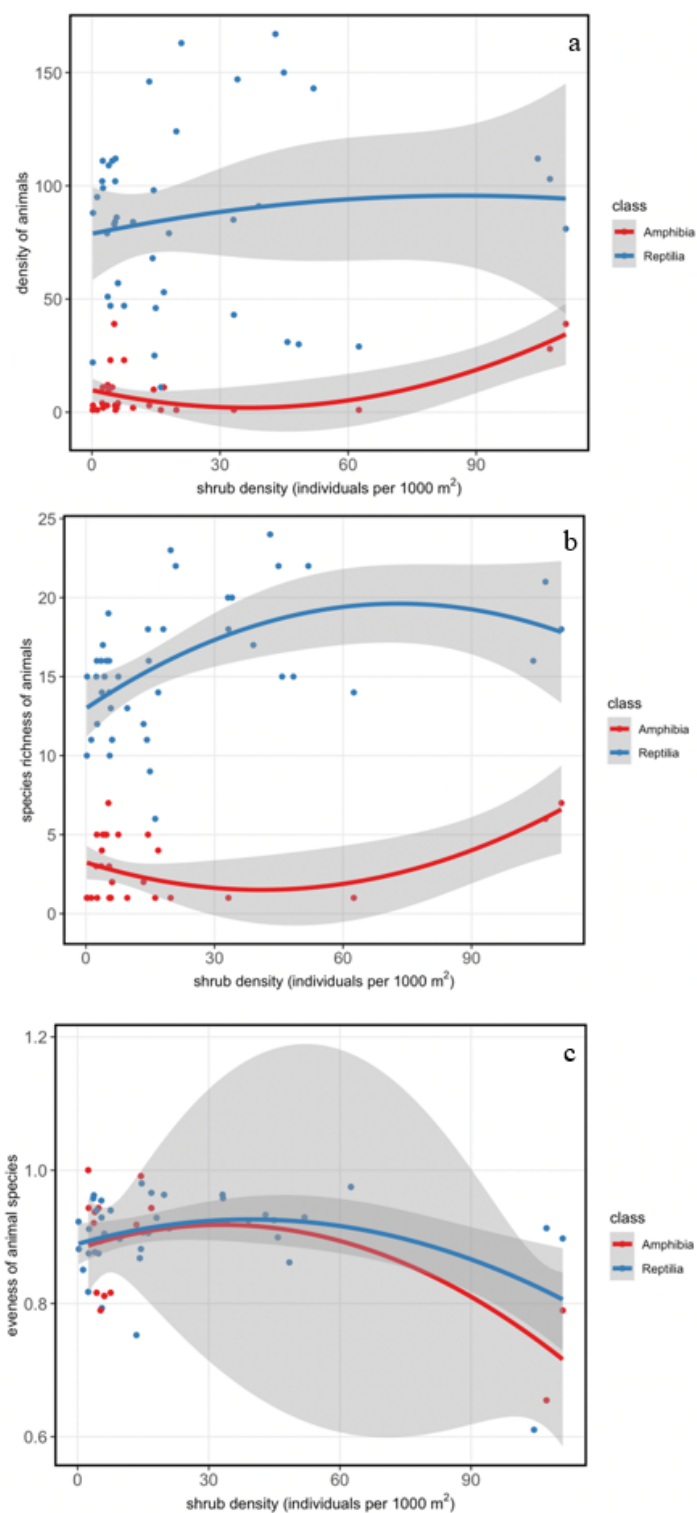


Figure 3

a) The relative effects of shrub density on Amphibia and Reptilia abundance. The blue line represents the trend for the class Reptilia while the red line represents the trend for the class Amphibia. Shaded areas show 95% confidence interval associated with line of best fit. b) The relative effects of shrub density on Amphibia and Reptilia richness. The blue line represents the trend for the class Reptilia while the red line represents the trend for the class Amphibia. Shaded areas show 95% confidence interval associated with

line of best fit. c) The relative effects of shrub density on Amphibia and Reptilia evenness. The blue line represents the trend for the class Reptilia while the red line represents the trend for the class Amphibia. Shaded areas show 95% confidence interval associated with line of best fit.