



Non-trophic interactions in deserts: Facilitation, interference, and an endangered lizard species

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Abstract

Research on plant–animal interactions has been focused on direct consumer interactions (*i.e.* plants as resources), but non-trophic interactions including providing shelter or interference with movement can also affect the fine-scale distribution of animals. In particular, non-trophic interactions that are positive could support threatened animal populations. Positive interactions have been used in the restoration of plant communities, but have not yet been extended to the management of animal habitat. In this study, we tested the hypothesis that non-trophic interactions influence the occurrence of an endangered lizard species in an arid shrub-annual system. At a location known to have a population of blunt-nosed leopard lizards (*Gambelia sila*), we geotagged 700 shrubs, measured shrub morphometric traits, collected biomass samples, and surveyed for lizard presence using scat detection dogs over two years. Relative to 2014, in 2013 plant productivity was high and lizard scats were found more frequently in areas with low invasive grass cover (*i.e.* residual dry matter, RDM). In 2014, plant productivity was low because of an extreme drought year, and lizard scats were more frequently observed under shrub canopies, particularly those with relatively dense cover. These findings support the novel theory that positive non-trophic interactions are a critical form of plant–animal interactions in addition to consumption. Dominant shrubs can act as a foundation species by functioning as a basal node in structuring both plant and animal communities through a network of interactions. Managing dominant plants, in addition to habitat, is therefore important for conserving animal species in arid ecosystems.

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Introduction

Positive interactions are important in resource-limited ecosystems. In deserts, dominant shrubs are a common benefactor to many other species, particularly plant species within

their canopy (Flores & Jurado 2003). Positive shrub interactions in these systems have been shown to directly and indirectly influence animals at nearly an equivalent rate (Lortie, Filazzola, & Sotomayor 2015). Shrubs can positively influence animals directly by providing food resources, such as seeds (Hansen, Kiesb y, Jones, & M ller 2007; Valido & Nogales 1994), or indirectly by facilitating a prey species (Parmenter & MacMahon 1983). Desert shrubs can

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also influence animals by providing thermal shelters for thermoregulation (Bauwens, Hertz, & Castilla 1996; Parmenter & MacMahon 1983) or by acting as a refuge from predators (Milchunas & Noy-Meir 2002). In addition, shrubs can play a more passive role by acting as a physical designation of territory (Muller 1998) or as a perching site for birds (Aukema & Martínez del Río 2002). Consequently, animal species associate with shrubs more than open spaces because the shrub fulfils a critical functional role (Lortie et al. 2015). Plants are a form of habitat, but their effects on animals can extend much further through indirect pathways. It is thus reasonable to propose that explicitly examining the positive effects of shrubs on animals in deserts will inform our understanding of ecosystem structure and provide an estimate of plant–animal interactions. Moreover, examination of positive non-trophic interactions of shrubs on animals could have management implications in support of species that are threatened.

Non-trophic interactions are any non-consumptive interactions between two species that are characterised by their mechanism, sign (positive, neutral or negative), and strength. Non-trophic interactions between shrubs and lizards in deserts are novel and advances ecological theory because these interactions are described as a habitat requirement. Deserts are high-stress ecosystems and positive interactions are more frequent in these systems (Filazzola & Lortie 2014). However, trophic interactions, such as herbivory, can be less important or infrequent given the relatively low productivity of arid systems (Crain 2008; Howard, Eldridge, & Soliveres 2012). Research has explored lizard adaptations to environmental extremes that include altered behaviour in favour of specific habitat characteristics (Kearney, Shine, & Porter 2009; Sunday et al. 2014). For example, the habitat of desert lizards is commonly characterised by a combination of vegetation composition, availability of animal burrows for refuges, and food resources (Grillet et al. 2010; Souter, Bull, Lethbridge, & Hutchinson 2007). Burrows and shrubs are also important shelters for lizards (Milne, Bull, & Hutchinson 2003; Sunday et al. 2014) because they provide refuges from predators and relief from extreme temperatures for ectotherms (Milne & Bull 2000; Milne et al. 2003). There can also be negative non-trophic interactions of plants on lizards in desert systems. For example, dense annual cover has been shown to increase predation risk (Vásquez, Ebensperger, & Bozinovic 2002), inhibit movement (Newbold 2005) and reduce foraging ability for animals (Castellano & Valone 2006). Therefore, the distribution of a desert animal species within a landscape is not only determined by vegetation composition, burrow availability, and food resources but also the interaction among these factors. Identifying these non-trophic interactions will provide more realistic descriptions of lizard habitat with which to inform conservation (Barrows, Preston, Rotenberry, & Allen 2008). Positive non-trophic interactions mediated by dominant, ‘nurse’ plants can provide the means to couple plant–animal theory with practice in deserts.

Herein, we measured the fine-scale association patterns of an endangered species, *Gambelia sila*, with the dominant shrub *Ephedra californica* and invasive annual grasses. We used highly trained dogs to survey for lizard scat as a proxy for *G. sila* occurrence because this technique rapidly detects animal presence and accounts for biases in visual surveys (Woollett (Smith), Hurt, & Richards 2014). The hypothesis that non-trophic interactions influence the occurrence of an endangered lizard species in an arid shrub–annual system was tested. Shrubs potentially provide benefits to lizards directly by ameliorating the microclimate, increasing visual cover from predators, and indirectly by increasing habitat availability through burrows (Prugh & Brashares 2012). Conversely, shrubs can indirectly impact lizards negatively by increasing invasive grass cover that interferes with movement increasing susceptibility to predation. These predictions were tested to examine the following mechanisms:

1. Shrubs reduce temperature and relative humidity under their canopy (direct benefit), increase relative plant cover (indirect benefit from reduced potential predation), and support higher burrow densities (indirect benefit) relative to paired open microsites.
2. Lizard scat is more frequently observed under shrubs (proxy to estimate plant–animal facilitation).
3. Lizard scat is more frequently observed with relatively lower cover of annual grasses (indirect cost via interference effects).

Materials and methods

Study site

All surveys were conducted at the Panoche Hills Management Area located on the western margin of the San Joaquin Valley, California (Bureau of Land Management; 36°41.78'N, 120°47.89'W at 650 m. a.s.l.). The region has an arid climate with the majority of precipitation in the late fall and winter months (October–March). The average annual precipitation is 22.9 cm with mean monthly temperatures of 7.6 °C in January and 25.8 °C in July as recorded at Los Banos weather station, CA (37°03.30'N, 120°51.00'W; <http://www.usclimatedata.com/>). During 2013 and 2014, Panoche Hills experienced below-average rainfall levels receiving 18.35 cm and 12.65 cm respectively (<http://www.usclimatedata.com/>).

The vegetation at Panoche Hills is characterised by an *Ephedra californica* scrubland that is heavily invaded by Mediterranean annual grasses and forbs including red brome (*Bromus madritensis* ssp. *rubens*, hereafter *B. madritensis*), *Bromus hordeaceus*, *Erodium cicutarium* and *Schismus barbatus*. The native community is significantly underrepresented but nonetheless includes *Phacelia tanacetifolia*, *Amsinckia grandiflora* and *Monolopia congdonii*. The shrub *E. californica* is dominant (>80% cover) (Hawbecker 1951).

Frequently observed herbivores are rodents such as the desert cottontail (*Sylvilagus audubonii*), the black-tailed jackrabbit (*Lepus californicus*), and the kangaroo rat (*Dipodomys heermanni*) (Hawbecker 1951). The lizard species found in the area include blunt-nosed leopard lizard (*G. sila*) and side-blotched lizard (*Uta stansburiana*).

Study species

The blunt-nosed leopard lizard (*G. sila*) is a federally listed Endangered species in the U.S.A. and an IUCN Red Listed (EN) species found in Southern California within habitats typically characterised as semi-arid scrub (USFWS 2010). *G. sila* is the largest lizard within the San Joaquin Valley with cryptic colouration on the back alternating dark brown and beige and a uniformly white underside (Stebbins & McGinnis 2012). The diet of *G. sila* consists mostly of arthropods (~97%) and less frequently (~3%) of smaller lizard species such as *U. stansburiana* (Germano, Smith, & Tabor, 2007). The *G. sila* arthropod diet is generally (>70%) Coleoptera and Orthoptera (Germano et al. 2007). Adult *G. sila* become active above ground in April and remain active until July when they go below-ground and are replaced by juveniles until November (Germano & Williams 2005). Most *G. sila* lizards live for 2 years (Germano & Williams 2005). This species was previously widely distributed throughout the San Joaquin Valley and surrounding foothills (Montanucci 1965); however, *G. sila*'s original range has been reduced by nearly 85% because of increased agriculture and industrialization (Germano, Rathbun, & Saslaw 2001; Supplementary Appendix A: Fig. 1). *G. sila* is found in association with the vegetation alliances of Mormon tea (*E. californica*) or Salt-bush (*Atriplex* spp.) and typically in areas with low vegetation cover (Germano et al. 2001). *G. sila* is dependent on burrows within their habitat that are typically created by kangaroo rats. The last 50 years of management techniques have not change the status of *G. sila* from Endangered (USFWS 2010).

Scat surveys

In April/May 2013, a study area including 700 *E. californica* shrubs was delineated based on previous road-side surveys of *G. sila* conducted at the Panoche Hills plateau between 2010 and 2014 (Supplementary Appendix A: Fig. 2). The total survey area was 32.3 hectares including all 700 surveyed shrubs and a 50m buffer around the outermost perimeter shrubs. Two scat detection dogs from Working Dogs for Conservation (<http://wd4c.org>) were used to detect lizard faecal pellets (hereafter termed scat). The use of dogs to detect scat has been used previously with species such as San Joaquin kit fox (*Vulpes macrotis mutica*), black bear (*Ursus americanus*), fisher (*Martes pennanti*), bobcat (*Lynx rufus*), and North Atlantic right whale (*Eubalaena glacialis*) (e.g. Long, Donovan, Mackay, Zielinski, & Buzas, 2007; Rolland et al., 2006; Smith et al., 2003). However, to our knowledge

this is the first instance of this protocol on lizard scat. Dogs were trained using sample specimens in a four-step protocol to ensure accurate identification (Supplementary Appendix B). The two dogs were used for two weeks at the end of April and beginning of May between the morning hours of 06:00 and 09:00 to reduce heat stress on the dogs and to optimise olfactory detection capability (MacKay, Smith, Long, & Parker 2008; Smith et al. 2003). Dogs were directed by their handlers to survey around the entire perimeter of each shrub or designated open microsites. Scat identified by the dogs was visually confirmed by the handler and a second lizard expert for consistency with voucher specimens of *G. sila* scat. Typically, *G. sila* scat will have a more cylindrical shape than that of a rodent and will be fairly large when compared to *Uta* spp. scat (Supplementary Appendix B: Fig. 2). In 2013, scat surveys were conducted on the 700 shrubs only, and in 2014, the surveys included 287 shrub and open pairs (574 total microsites). Surveys in 2013 targeted shrub only to establish a study site and focus on particular shrub traits. In 2014, the intended focus was for differences between shrub and open microsites. Open surveys were conducted two metres to the north of surveyed shrubs in a flagged circular plot that was representative of the average shrub area (3 m²).

Scat and other signs, such as tracks or burrows, for animal presence are well-established approaches in wildlife ecology to infer presence and sometimes density (Gompper et al. 2006; Long et al. 2007). Using scat for identification does have advantages over others methods, such as camera traps or artificial tracking surfaces which some target animals avoid (Gompper et al. 2006). However, these are indirect measures with some limitations. A caveat is that scat is a proxy for lizard occurrence and not equivalent to direct observation. Except defecation, behavior is not captured with this indirect measure. Presence and not density is best estimated using scat as an animal sign. To ensure we did not overestimate presence, we classed multiple instances of scat at the exact same location as single instances. Additionally, the scent cone of *G. sila* scat is small in comparison to other target species. Therefore, the dogs were kept on leash and specifically trained in a form of pressure-searching (Geneva International Centre for Humanitarian Demining 2004), where they moved slowly with their noses within a few inches of the surface of the area being searched. This highly detailed level of searching ensures full ground coverage and intense focus, and makes detection less susceptible to microclimate conditions. Hence, presence and not density is best estimated and focused searches reduces the likelihood of a missed detection of scat.

Shrub measurements

The dimensions of the 700 shrubs were measured, identified to shrub species, geotagged (*i.e.* latitude, longitude and elevation), and labelled with metal number tags (Supplementary Appendix: Fig. 2). Dimensions taken for the shrubs

Table 1. The mean values with standard error among shrub and open microsites located at the Panoche Hills plateau. Abiotic responses were compared using a t-test and biotic responses were compared using a Mann–Whitney U Test with microsite as the predictor. Significance at $\alpha < 0.05$ bolded values indicate significance.

| Response | Shrub | Open | Significance |
|--|-------------------|--------------------|---------------------|
| Abiotic | | | |
| Soil moisture (%) in May | 7.31 \pm 0.26 | 9.81 \pm 0.18 | p < 0.001 |
| PAR ($\mu\text{mol s}^{-1} \text{m}^{-2}$) | 402.2 \pm 37.9 | 1216.3 \pm 36.1 | p < 0.001 |
| Temperature ($^{\circ}\text{C}$) | 12.53 \pm 0.064 | 14.58 \pm 0.081 | p = 0.005 |
| Relative humidity (%) | 69.88 \pm 0.17 | 62.75 \pm 0.18 | p < 0.001 |
| Biotic | | | |
| Burrows | 2.50 \pm 0.12 | 1.17 \pm 0.082 | p < 0.001 |
| Trails | 3.71 \pm 0.14 | 2.24 \pm 0.084 | p < 0.001 |
| <i>G. sila</i> Scat | 0.10 \pm 0.018 | 0.014 \pm 0.0069 | p < 0.001 |

included diameter along the longest dimension (D1), the diameter immediately perpendicular to D1 (D2), and shrub height from basal stem to tallest branch (H). Shrub area was calculated using the average radius of D1 and D2 in the formula for the area of a circle (πr^2). To calculate shrub volume, the average radius of D1 and D2 with shrub height was used in the formula for the volume of a semi-sphere ($2/3\pi r^3$). A visual estimate of shrub decadence, hereafter shrub canopy, on a Likert scale of 0–10 was also measured. The number of burrows and animal trails present in each 287 shrub-open microsites were also surveyed in 2014. *G. sila* is known to use burrows and trails made by kangaroo rats for shelter and to move throughout the landscape (Germano et al. 2001).

Vegetation surveys

In 2013 and 2014 we randomly surveyed 45 pairs of shrub and open microsites with a 50 \times 50 cm quadrat. Shrubs were surveyed on the north side within the canopy dripline and open microsites were randomly placed 2 m north of the paired shrub. We surveyed the microsites for the abundance of plant individuals and number of different species. Surveys were conducted during April 22–25 for both years. In Septembers of both 2013 and 2014, residual dry matter (RDM) was collected within a 20 \times 20 cm square and weighed to the nearest gram for 1000 GPS points located in a grid pattern 10 m apart from each other and 10 m away from the gravel road (Fig. A.2). RDM is a measurement often used by land managers in California as a standard for measuring ecosystem health where 1 g per 400 cm^2 is estimated to be equivalent to ~ 20 kg of biomass per acre (Bartolome, Frost, McDougald, & Connor 2002).

Abiotic measurements

To measure differences in the microclimate between shrub and open microsites, we placed 12 Onset HOBO ProV2 data loggers in six shrub-open pairs. Each logger was buried with the sensor extended 5 cm above ground and set to measure

air temperature ($^{\circ}\text{C}$) and relative humidity (%) hourly. Loggers were placed out on January 20th and collected May 2nd in 2014 to represent the duration of the growing season and the beginning of lizard occurrence above-ground prior to scat surveys. The daily averages for all loggers were compiled for each microsite during the 102 days (Filazzola & Lortie 2014; <http://dx.doi.org/10.6084/m9.figshare.1375174>). A random subset of 120 shrub-open pairs was selected to measure soil moisture and solar radiation. Soil moisture was measured using a Delta SM150 soil moisture probe (<http://www.delta-t.co.uk/>) at the end of the growing season in April 2014. We also measured photosynthetically active radiation (PAR; 400–700 nm) in 120 shrub-open microsites on clear sunny days between January 12–15, 2014 during peak daylight hours (10:00–14:00). We recorded PAR using a Licor line quantum sensor (Li-191SA, Li-COR Biosciences, Lincoln, NE) using an average reading over 15 s to account for sun flecks.

Landscape-level measurements

RDM values were measured within a grid formation with three survey points spaced 10 m apart on each side of the road that traverses the Panoche Hills plateau (Supplementary Appendix A: Fig. 2). To interpolate these values, ordinary kriging was conducted in ArcGIS using the Geostatistical Analyst package fitted to an exponential distribution (ESRI 2014). RDM values for each shrub were then extracted using interpolations from the kriging. Shrubs were predicted to increase biomass of associated plants and interpolated values from kriging would not accurately represent the potential values in between survey points. To address this, we included shrub density as an interacting factor for lizard scat. Shrub density was also calculated to the squared kilometre using the point density function in the spatial analyst package (ArcGIS). We compared the effects of inter-annual variability of rain on RDM using a Spearman's rank correlation in R and Mann–Whitney U test between values of 2013 and 2014.

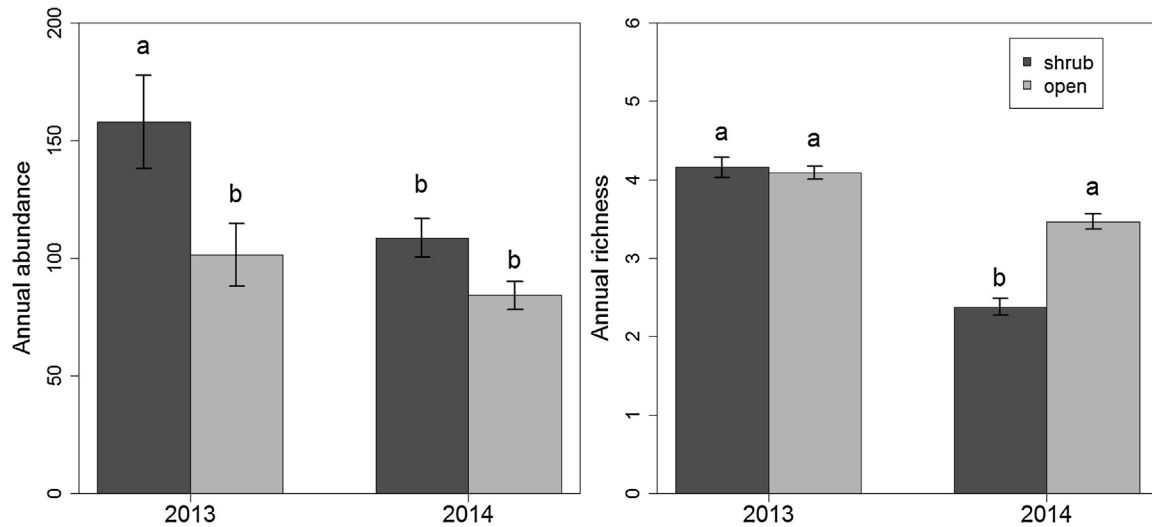


Fig. 1. Plant abundance and species richness measured among shrub and open microsites in 2013 and 2014. Error bars represent standard error.

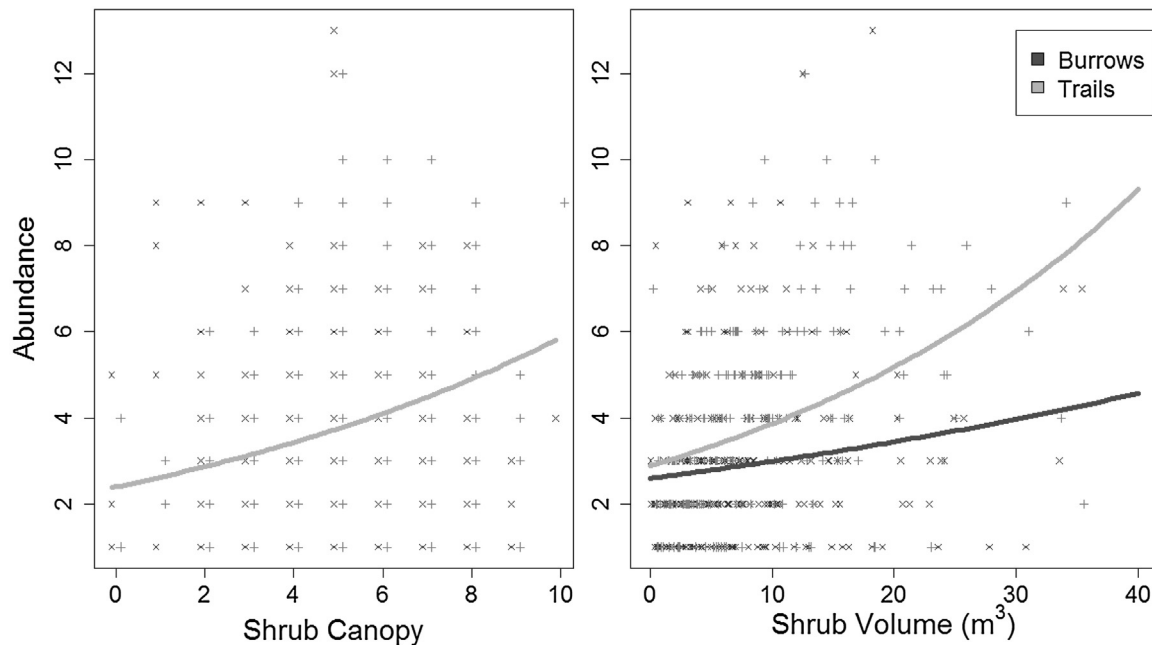


Fig. 2. Relationship of shrub canopy cover and volume on both burrows (x) and trails (+). Only significant relationships ($\alpha < 0.05$) are shown as curves.

Statistical analyses

We examined how the shrub modifies the microsite within the shrub canopy compared to an open microsite using t-tests in *R* (R Development Core Team 2014) with temperature and relative humidity as the response variables and microsite as the predictor for the growing season. Shrub and open microsites were each treated independently for all analyses. We also conducted t-tests with PAR and soil moisture content (%) as the responses and microsite as the predictor. To determine if there were differences in animal activity between shrub and open microsites, we used Mann–Whitney U (*wilcox.test* function) tests with burrows, trails and lizard

scat as the responses and microsite as the predictor. We compared the difference in the annual plant community among shrub and open microsites for both years by fitting a Generalized Linear Model (GLM) with abundance and richness as the response variables and microsite and year as the predictors. The models were fitted with a negative binomial error distribution (*glm.nb* function, *MASS* library) because both plant responses represented a discrete count that is over-dispersed, i.e. variance exceeds the mean (Lindén & Mäntyniemi 2011). We used least-squares means (*lsmeans* function, *lsmeans* library) for post-hoc comparisons of the generalised models (Lenth 2016). We also tested if shrub traits predicted mammal activity by fitting a GLM with negative binomial error

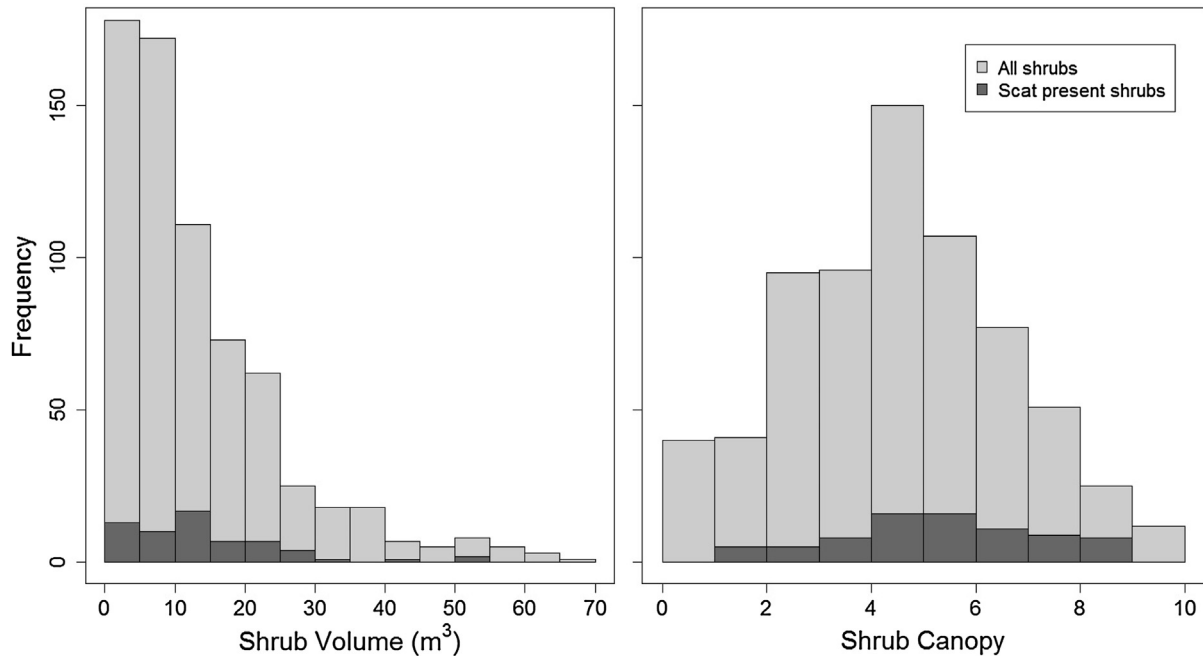


Fig. 3. Histograms of shrub canopy and volume for all shrubs at the Panoche Hills plateau ($n = 700$) and scat present ones in both years ($n = 78$).

distribution with shrub canopy and volume as the predictor variables and the number of burrows and trails as the response variables.

To determine the factors that best predict the occurrence of lizard scat, we used best subsets models for 2013 and 2014. The best subsets selection process considers all models of a response variable predicted by many factors and chooses the most parsimonious, usable model (Mac Nally 2000). Best subsets (*bestglm* function; package *bestglm*) was used rather than other selection processes because it can be used effectively with a binary response variable such as lizard scat occurrence (Hosmer, Jovanovic, & Lemeshow 1989; McLeod & Xu 2010). The factors that were considered included: shrub height, shrub area, shrub volume, shrub canopy, RDM in both years, shrub density, average distance between the three closest shrubs, number of burrows, and number of trails. Multicollinearity was assessed between predictors using correlation tests to remove any collinear variables (threshold of $r = 0.50$; Graham 2001). Models were chosen based on the smallest Akaike information criterion (AIC) and least amount of predictor variables (Hosmer et al. 1989).

To determine the landscape factors that predicted scat occurrence and the potential optimal lizard habitat, spatial associations were explored with additional analyses. These spatial analyses identify areas of conservation concern for *G. sila* at the Panoche Hills plateau and identify patterns of occurrence for individuals within this population. Higher probability areas of lizard occurrence either currently support *G. sila* abundance or can be suitable habitat if lizards are currently not present. The radii of *G. sila* home ranges are approximately 140 m for females and 200 m for males, but

only females have non-overlapping home ranges (Warrick, Kato, & Rose 1998). Consequently, we assumed the occurrence of scat to be less spatially associated only after the threshold of 140 m had been exceeded (*i.e.* zone of indifference, Maciel et al. 2010). Spatial correlation and clustering of scat occurrences was determined using Moran's *I*. Subsequently, we conducted a Getis-Ord cluster analysis correcting for false discovery rate to identify areas of the Panoche Hills plateau that would have high or low probabilities of lizard occurrence. These probabilities were based on 95% confidence or greater probability of occurring – “hotspots” and not occurring – “coldspots” (Getis & Ord 1996). Cluster analyses were conducted for 2013 and 2014 shrubs only. There were not enough scat occurrences in open microsites for cluster analyses.

Results

Shrub microsite effects

Shrubs significantly modified the microclimate during the plant growing season. Shrub microclimates were significantly cooler with higher relative humidity (Supplementary Appendix C), lower soil moisture, and lower solar radiation relative to adjacent open microsites (Table 1). Shrubs facilitated plant abundance ($\chi^2 = 11.9$, $p < 0.001$; Fig. 1), but not species richness ($\chi^2 = 3.34$, $p < 0.067$; Fig. 1) of the annual plant community. Plant abundance ($\chi^2 = 18.5$, $p < 0.001$; Fig. 1) and species richness ($\chi^2 = 7.18$, $p < 0.007$; Fig. 1) were significantly lower in 2014 than in 2013. There

Table 2. Best subsets logistic regression of factors determining scat occurrence at the landscape and microsite level for 2013. The interaction column identifies the type of effect from the plant factor on *G. sila* (direct, indirect, or both). Significance at $\alpha < 0.05$ bolded values indicate significance.

| Level | Factor | Interaction | Effect size | p-Value |
|-----------|---------------|-------------|-------------|------------------|
| Landscape | RDM (g) | Indirect | $z = -4.86$ | <0.001 |
| Landscape | Shrub density | Both | $z = -2.32$ | 0.021 |
| Microsite | Canopy | Both | $z = 3.38$ | <0.001 |
| Microsite | Shrub height | Both | $z = 2.53$ | 0.011 |

was no microsite by year interaction effect for plant abundance ($\chi^2 = 0.77$, $p = 0.44$) or species richness ($\chi^2 = -0.76$, $p = 0.45$). However, the effect of shrub facilitation was different between years. Plant abundance was greater in the shrub for 2013 (post-hoc $p = 0.0015$), but plant abundance was the same in both microsites in 2014 (post-hoc $p = 0.32$; Fig. 1). Conversely, species richness was greater in the open for 2014 (post-hoc $p = 0.014$), but richness was similar in both microsites for 2013 (post-hoc $p = 0.99$; Fig. 1).

Animal activity including burrows, trails, and *G. sila* scat were all higher under the canopy of shrubs (Table 1). The density of the shrub canopy was positively related to the number of animal trails (mean effect \pm SE = 0.089 ± 0.01 , $z_{235} = 4.52$, $p < 0.001$; Fig. 2), but it was not statistically related to the number of burrows ($z_{235} = -1.41$, $p = 0.16$; Fig. 2). Shrub volume was positively related to both the number of burrows (mean effect \pm SE = 0.01 ± 0.005 , $z_{235} = 2.75$, $p = 0.16$; Fig. 2) and number of animal trails (mean effect \pm SE = 0.03 ± 0.003 , $z_{235} = 8.05$, $p < 0.001$; Fig. 2).

Predictors of scat occurrence

Lizard scat was present in 8.9% of the total 700 surveyed shrubs in 2013 and 9.6% of all shrubs in 2014 (Fig. 3). Typically, only one scat was observed per survey point, but a maximum of seven scat pellets were found at one microsite (mean = 1.87; SE = 0.26). In 2013, the following predictor variables were included in the best subset model: shrub height, shrub area, shrub canopy, RDM, and shrub density. Shrub canopy and shrub height were both positively related with scat occurrence (Table 2). However, RDM and shrub density were negatively correlated with scat occurrence in 2013 (Table 2; Figs. 4 and 5). In 2014, predictor variables included in the best subset model were shrub area, shrub canopy, and animal burrows. Shrub area and shrub canopy were both positively related to scat occurrence (Table 3). Scat occurrence was spatially auto-correlated and clustered (Figs. 4 and 5, Moran's $I = 0.037413$, $z = 10.1$, $p < 0.001$). Trails were negatively correlated with scat occurrence, and there was no significant relationship of scat with any landscape factors such as RDM or shrub density (Table 3; Figs. 4 and 5). RDM values at the same location between years were significantly correlated with

Table 3. Best subsets logistic regression of factors determining scat occurrence at the landscape and microsite level for 2014. The interaction column identifies the type of effect from the plant factor on *G. sila* (direct, indirect, or both). Significance at $\alpha < 0.05$ bolded values indicate significance.

| Level | Factor | Interaction | Effect size | p-Value |
|-----------|--------|-------------|-------------|--------------|
| Microsite | Area | Both | $z = 2.46$ | 0.014 |
| Microsite | Canopy | Both | $z = 3.29$ | 0.001 |
| Microsite | Trails | Indirect | $z = -2.86$ | 0.004 |

each other ($r_s = 0.64$, $p < 0.001$), however, RDM in 2014 was significantly lower than RDM of 2013 ($RDM_{2013} = 7.04$, $RDM_{2014} = 3.65$; $p < 0.001$). This corresponds to the reduced precipitation of the 2014 drought.

Discussion

We demonstrate here that non-trophic interactions among plants and animals are important for an endangered animal species. Planting shrubs could be a viable restoration strategy in deserts if shrubs *de facto* bring with them the direct micro-environmental conditions that animals need and the indirect benefits such as providing a refuge from predation. Within this study, we found support for the hypothesis that non-trophic plant–animal interactions are critical in a high-stress ecosystem for a federally listed lizard species within the USA. The shrub species tested here can directly provide a microclimatic shelter, indirectly provide burrows, and likely provide a predator refuge. Lizard scat was detected more frequently under shrubs suggesting that at least one of these mechanistic pathways is relevant to *G. sila* in the region. Furthermore, dense canopy cover increased the likelihood of lizard scat suggesting that direct effects associated with shrub cover magnifies their benefit to animals. We also found support for the prediction that lizard scat is negatively correlated with cover of invasive grasses. Dense grass cover has been found to interfere with animal movement in similar systems (Newbold 2005; Vásquez et al. 2002). Scat is a proxy for lizard presence and does not include estimates of animal behaviour or density, but it was nonetheless a rapid, effective technique within this desert landscape to estimate presence (Gompper et al. 2006). Mutual effects between plants and animals in deserts are critical measures needed to frame conservation and ecosystem function within networks and not specific taxon conservation efforts. Ecological network theory is also rapidly evolving and studies such as this one advance novel and extended tests of plant–animal interactions.

Shrub-shelter effects

G. sila was positively associated with the shrub species *E. californica*. This association may have been driven by shelter effects from temperature extremes because of the

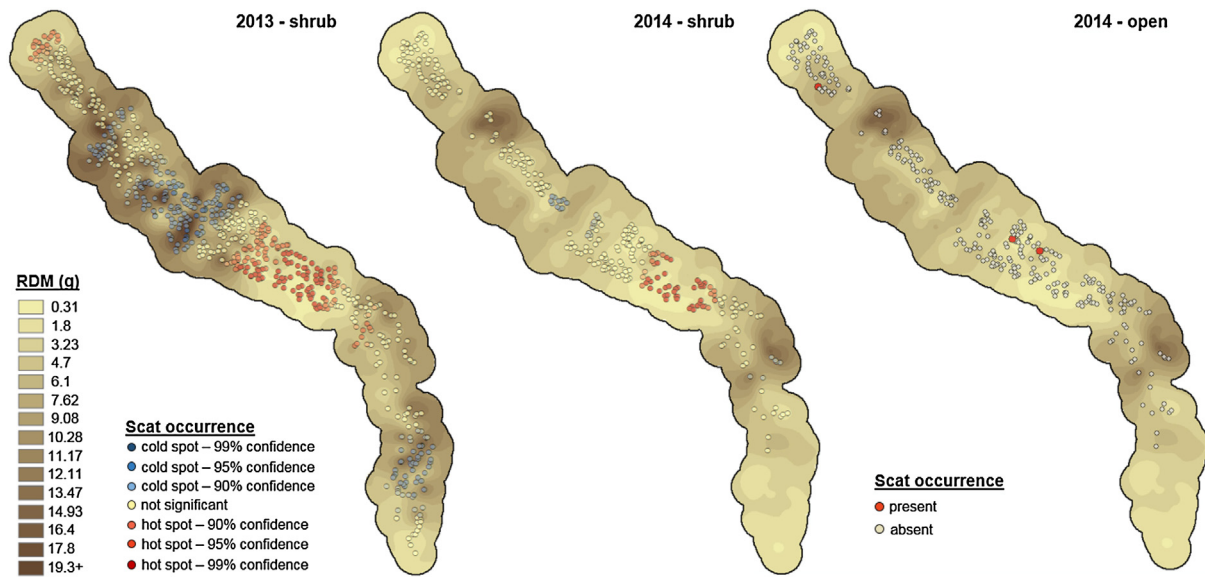


Fig. 4. Kriged residual dry mass (RDM) values for the Panoche Hills plateau with observed instances of lizard scat for 2013, 2014 shrubs only and 2014 open microsites. Confidence intervals from a Getis-Ord cluster analysis of observing a lizard scat at the shrubs within the Panoche Hills plateau in 2013 and 2014 (Red representing 95% or greater chance of occurrence and blue representing 95% or greater chance of no occurrence). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

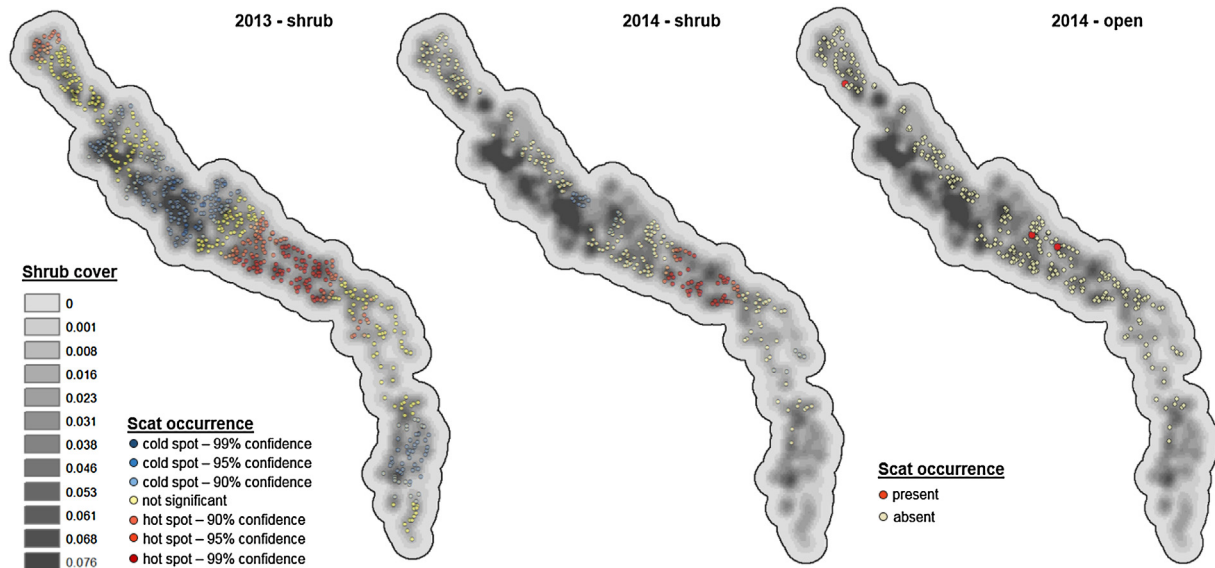


Fig. 5. Kriged shrub cover based on density of shrubs multiplied by area of shrub for the Panoche Hills plateau with observed instances of lizard scat for 2013, 2014 shrubs only and 2014 open microsites. Confidence intervals from a Getis-Ord cluster analysis of observing a lizard scat at the shrubs within the Panoche Hills plateau in 2013 and 2014 (Red representing 95% or greater chance of occurrence and blue representing 95% or greater chance of no occurrence). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

micro-environmental differences recorded within the shrub. Lizards alternate between shaded and sunny microsites for thermoregulation in deserts (Díaz & Cabezas-Díaz 2004; Huey 1974) suggesting that shrubs are vital components that increase the thermal heterogeneity of the landscape for ectotherms. Shelter for thermoregulation may also explain why scat was observed more frequently in shrubs with denser canopy cover (Díaz & Cabezas-Díaz 2004; Huey 1974) as they are creating more shade. Indirectly, shrubs can affect *G.*

silva by providing a predator refuge or by facilitating rodent burrowing (Fields, Coffin, & Gosz 1999). Shrubs have been shown to affect predation of rodents in arid ecosystems by providing protection from raptors, however, the relationship between predation risk and shrubs has not been examined for lizards (Castellano & Valone 2006; Vásquez et al. 2002). Facilitation of annuals around the shrubs is well established (Filazzola & Lortie 2014) and further increases these shelter effects. Rodent burrows are an alternative escape mecha-

nisms for *G. sila* (Hansen, Montanucci, & Switak, 1994). Higher burrow densities were also associated with shrubs in this desert landscape. Previous research has shown that desert lizards typically associate with specific burrow characteristics such as size, depth, and densities (Grillet et al. 2010; Milne & Bull 2000). Finally, shrubs could also provide shelter for *G. sila* prey items including other smaller lizards *Uta* spp. or grasshoppers (Greenfield, Shelly, & Gonzalez-Coloma 1989). Careful examination is required to separate the specific mechanisms responsible for lizards positively associating with shrubs in desert systems because each mechanism has different management implications. For instance, if shrubs are providing a shelter for thermoregulation, lizards may be expected to frequent shrubs more often given a changing climate (Kearney et al. 2009). Direct examination of lizard behaviour in addition to scat detection might better determine the non-trophic mechanism responsible for the shrub association.

Annual-interference effects

Invasive plant species are a threat to most terrestrial ecosystems globally. Invasive grasses can interfere with *G. sila* movement and thus reduce available habitat. Dense cover negatively impacts lizard behaviour by restricting movement even in years of low precipitation and plant productivity (Germano et al. 2001). The dominant grass within this study, *B. madritensis*, can interfere with lizard movement following senescence because it leaves a dense residual thatch that remains until the next year (Salo 2004). In the Great Basin Desert, *Bromus tectorum* (Cheatgrass) is also an invasive grass that has been shown to interfere with movement and speed of horned lizards (Newbold 2005). Reduced movement increases predation risk and also makes thermoregulation more challenging for these lizard species (Newbold 2005). Dense invasive grass cover has been shown to reduce rodent species richness (Rieder, Newbold, & Ostojá 2010) which lizards rely on to create burrows (Germano et al. 2001; Warrick et al. 1998). *B. madritensis*, is also fire-adapted while the native plant community is not (D'Antonio 2000), thus increasing susceptibility of the system to a catastrophic burn scenario (Salo 2005) or through increased competition (Abella et al. 2011; Rodríguez-Buriticá & Miriti 2009). The highly competitive invasive grasses can also limit the recruitment of shrubs (Rodríguez-Buriticá & Miriti 2009). The current shrub populations could be living relicts (Young, Petersen, & Clary 2005) whose inevitable loss through slow attrition can cascade to extirpation of *G. sila* from this region. Thus, negative non-trophic interactions extend beyond the direct impact on the target species, and indirect effects on benefactor species such as shrubs change and likely simplify the entire community structure. Managing for invasive plant species is therefore crucial in these ecosystems.

Implications

Non-trophic interactions among shrubs, invasive grasses, and lizards have important implications for conservation. Lizard density can correlate with precipitation (Ryan et al. 2015; Westphal, Stewart, Tennant, Butterfield, & Sinervo 2016), but high precipitation results in higher plant productivity that hinders the lizard populations (Germano & Williams 2005). Thus, lizards in California can experience a scenario wherein both drought and above-average precipitation negatively impact population densities. Predictions of increased drought events for California (Cook, Woodhouse, Eakin, Meko, & Stahle 2004; Griffin & Anchukaitis 2014) and estimates that lizards in California are reaching the extent of their thermal range (Cayan, Maurer, Dettinger, Tyree, & Hayhoe 2008; Sinervo et al. 2010) suggest that these species are at high risk of loss regionally. Lizards may also be over-expending energy when trying to thermoregulate with the changing climate (Vickers, Manicom, & Schwarzkopf 2011). Shrub addition would increase the available thermal heterogeneity for lizard populations (Díaz & Cabezas-Díaz 2004; Kerr & Bull 2004). Conversely, loss of shrubs in deserts would likely result in a bottom-up trophic cascade (Kagata & Ohgushi 2006). A clear implication here is that non-trophic interactions connect to a much larger web of interactions and that these cascades are not only a novel theory, but a viable process for conservation use.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baec.2017.01.002>.

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