

Research

Modelling the niche space of desert annuals needs to include positive interactions

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The niche is a necessary consideration when estimating habitable area and geographic range of a species. Modellers often examine the fundamental niche and the environmental requirements for plant species, ignoring interactions among species. In deserts, positive plant interactions are important drivers of biodiversity and structure communities through many mechanistic pathways including modifying environmental conditions. Thus, we tested the hypothesis that desert shrubs increase the geographical extent of some annual species because, through modifying the microclimate, they match the niche requirements of beneficiary species. We used the database of the Global Biodiversity Information Facility to construct MaxEnt species distribution models (SDM) with and without reported benefactor species within the Mojave Desert in California. We chose 20 annual species to be modeled including 10 species that had been previously reported in the literature as being facilitated (beneficiary) and 10 that had no record of being facilitated (unreported). Beneficiary annuals co-occurred significantly more with benefactor shrubs than the unreported annual species. The inclusion of shrubs into SDMs significantly improved model predictability and geographic range for all the beneficiary annual species, but not for the unreported annual species. Thus, positive interactions are species specific and it is possible to determine annual species dependency on benefactor shrubs at the regional scale. The co-occurrence of benefactor shrubs and annual species can be used as a proxy for facilitation and recent developments in SDM techniques encourage the inclusion of biotic interactions. Species distribution models should include estimates of facilitation because biotic interactions determine the niche of species and can have implications with a changing climate.

Introduction

Positive interactions can influence the niche space of responding species, but this relationship has been understudied when examined empirically. The ecological niche for a species is typically defined by its abiotic requirements and by limitations associated with negative interactions, such as parasitism or consumer pressure (Pearman

et al. 2008). However, this definition neglects the effects of positive interactions (Bruno et al. 2003, Stachowicz 2012). Facilitation is recognized as an important driver that structures many ecological communities (Bruno et al. 2003, Brooker et al. 2008, McIntire and Fajardo 2014) especially in high-stress systems, such as deserts, where shrubs can facilitate communities of annuals within their understorey (Franco and Nobel 1988, Flores and Jurado 2003, Filazzola and Lortie 2014). This is because positive interactions in plant communities can provide suitable habitat for beneficiary species in landscapes with characteristics outside of their strict physiological tolerance limit (Bruno et al. 2003, Cavieres and Badano 2009). In deserts, shrubs increase the microscale heterogeneity (i.e. fine spatial extents of < 1 m) in a landscape by modifying the microclimate within their canopy relative to an open space (Gómez-Aparicio et al. 2005, Pescador et al. 2014). Additionally, positive interactions can reduce biotic pressures such as competition from neighbors or consumer pressure (He and Bertness 2014, Michalet et al. 2015, Sotomayor and Lortie 2015). In these cases, facilitation is either increasing the geographical area that matches a beneficiary species' fundamental niche or counteracting the negative interactions that restrict the species realized niche (Rodríguez-Cabal et al. 2013). Positive interactions can expand the suitable area a beneficiary species can inhabit and this represents an important research gap in ecology and niche theory.

Recent development of modelling tools has increased interest in estimating species occurrence in response to climate. Species distribution models (SDMs) are one example of these approaches and typically consider the environmental variables that predict species occurrence; however, the biotic interactions from co-occurring species are often neglected (Pollock et al. 2014). SDMs are empirical models relating field observations to a set of environmental predictors that are derived from climate data resources, such as WorldClim (Guisan and Thuiller 2005, Phillips et al. 2006, Elith et al. 2011). Thus, an integral concept in SDMs is the niche (Guisan and Zimmermann 2000) because SDMs assume that the fundamental niche for a given species is determined by its tolerances to multiple abiotic variables (Hutchinson 1965). However, species do not exist in isolation with climate and instead co-exist with other species (Hirzel and Le Lay 2008). Consequently, these other species can alter the niche space of one another, reducing the predictability of SDMs that examine only abiotic factors (Pearson and Dawson 2003). Some recent studies have included biotic interactions such as competition from invasive species (Kulhanek et al. 2011, Pollock et al. 2014), but positive interactions in SDMs have been tested infrequently (but see Wisz et al. 2013, Afkhami et al. 2014). It is therefore imperative to include positive interactions when modeling SDMs because of their role in defining geographic extent particularly in resource limited or high-stress environments where positive interactions are more common (He et al. 2013). Hence, positive interactions are an integral and important

set of drivers for community composition that should also be included in SDMs.

Positive interactions can increase the suitable habitat of a beneficiary species and this is one of the potential mechanisms associated with increasing geographic extent. However, the spatial extent of these increases has not been examined because it is difficult to estimate positive interactions at a regional scale. Herein, we use the co-occurring density of shrubs previously identified as facilitators as a proxy for positive interactions. This is a coarse estimate that allows for usage of open access databases of species occurrences in large regional areas. We hypothesized that desert shrubs increase the geographical extent of some annual species because through microclimate amelioration they match the niche requirements of beneficiary species. We infer facilitation of desert shrubs reported as benefactors and estimate annual species extent using SDMs recognizing that not all annual species are necessarily facilitated. Therefore, we selected annual species that have been previously reported as facilitated (beneficiaries) and that have no record as being facilitated (unreported). We tested the prediction that SDMs for previously reported beneficiary species are improved and estimate larger spatial extents with the inclusion of shrub density than with climate alone. We also predicted that SDMs for the unreported annual species within the same region are not improved by the inclusion of shrubs into the models (i.e. the null model). Positive interactions may be a significant factor in determining the geographic extent of desert annual species and estimating this effect can support previous research suggesting facilitation as a driver of biodiversity at a regional scale (McIntire and Fajardo 2014, Afkhami et al. 2014).

Methods

Species database

Plant species lists for the Mojave Desert were extracted from the Global Biodiversity Information Facility database (GBIF; www.gbif.org/). An extensive list of native Mojave Desert species was obtained from the literature for 61 shrubs and annual plants. This list was generated from four papers and a review on plant interactions in the Mojave Desert (Cody 1993, Brittingham and Walker 2000, Brooks 2003, Flores and Jurado 2003, Miriti 2006). The dominant Mojave shrub species *Ambrosia dumosa*, *Artemisia tridentata*, *Ephedra nevadensis* and *Coleogyne ramosissima* were selected from the list of Mojave Desert species because they have been previously examined for facilitative effects (Franco and Nobel 1988, Cody 1993, Brittingham and Walker 2000, Brooks 2003, Miriti 2006). These shrub species were frequent in the Mojave Desert (> 300 occurrences) and do not have any reported allelopathic effects such as with the common Mojave shrub *Larrea tridentata* (Mahall and Callaway 1992). In total, 4269 occurrences of these four shrub species were collected

from the GBIF (Filazzola et al. 2016: <<https://dx.doi.org/10.6084/m9.figshare.3586065.v1>>). From the initial plant list and using a random number table, we randomly selected ten annual species that were previously reported as beneficiary species by the identified benefactor shrubs (Flores and Jurado 2003), and we further selected another ten annual plants that have not been reported previously as beneficiaries, hereafter ‘unreported’ (Table 1). All twenty annual plant species are commonly observed in the Mojave Desert with at least 100 occurrences listed within GBIF (Filazzola et al. 2016: <<https://dx.doi.org/10.6084/m9.figshare.3586065.v1>>). These species occupy similar ecological requirements within desert shrublands at elevations less than 1800 m. Only species records with GPS coordinates were extracted for further analysis. The shrub, beneficiary, and unreported datasets were reviewed to check for duplicates and inconsistencies with species name. Sub-species were classed as the same species.

The survey area was defined as the Mojave Desert within the political boundary of Southern California. The extent was restricted to include the western most portion of the Mojave Desert, including Antelope Valley (latitude: 34.79°, longitude: -118.7°). The southern, eastern and northern boundaries were restricted based on the political boundaries with Mexico, Arizona and Nevada respectively (latitude: 32.7° to 37.0°; longitude: -118.5° to -114.5°). We chose to restrict our study on the Mojave to within California because there are large collaborative efforts within the state that contribute to plant occurrences such as, Calflora (<www.calflora.org/>) and the Californian Native Plant Society (<www.cnps.org/>), that are included in the GBIF database. This defined study area, hereafter referred to as Southern California, includes a total land area of 173 894 km².

Table 1. Annual species chosen from the literature on plant interactions in the Mojave Desert.

Species name	Family	Beneficiary
<i>Camissonia claviformis</i>	Onagraceae	yes
<i>Caulanthus cooperi</i>	Brassicaceae	yes
<i>Chaenactis fremontii</i>	Asteraceae	yes
<i>Delphinium parishii</i>	Ranunculaceae	yes
<i>Descurainia pinnata</i>	Brassicaceae	yes
<i>Lepidium lasiocarpum</i>	Brassicaceae	yes
<i>Malacothrix glabrata</i>	Asteraceae	yes
<i>Phacelia distans</i>	Boraginaceae	yes
<i>Rafinesquia neomexicana</i>	Asteraceae	yes
<i>Sphaeralcea ambigua</i>	Malvaceae	yes
<i>Acmispon brachycarpus</i>	Fabaceae	unreported
<i>Cryptantha intermedia</i>	Boraginaceae	unreported
<i>Eremalche exilis</i>	Malvaceae	unreported
<i>Gilia minor</i>	Polemoniaceae	unreported
<i>Layia glandulosa</i>	Asteraceae	unreported
<i>Linanthus dichotomus</i>	Polemoniaceae	unreported
<i>Lupinus sparsiflorus</i>	Fabaceae	unreported
<i>Oxytheca perfoliata</i>	Polygonaceae	unreported
<i>Plantago ovata</i>	Plantaginaceae	unreported
<i>Salvia columbariae</i>	Lamiaceae	unreported

Biotic variables

Online herbaria data suffer from sampling bias, and consequently, we used geographic filtering for the initial raw occurrences (Varela et al. 2014). We subsampled using a grid across an x-y layer and discarded multiple instances within a radius of 3 arc minutes (~ 5 km). This geographical filtering of occurrences was conducted for all plant species modeled. We calculated a two-dimensional kernel density estimate using the coordinates of the geographically filtered occurrences for the shrub and annual species evaluated on a square grid (function *kde2d*, package MASS). The density rasters for each of the three species groups (shrub, beneficiary and unreported) were resampled (function *resample*, package raster) using the nearest neighbor method to have the same resolution as WorldClim data (30 arc-second or ~1 km²) and cropped to match the extent of Southern California. To test if shrub density predicted annual plant density, we fitted a model with each beneficiary and unreported plant density as a response variable and shrub density as the predictor. A random set of 1000 geographic points (*randomPoints* function; *Dismo*) was extracted for each of the three rasters (shrub, beneficiary, and unreported). We then used f-tests to determine whether the effect of shrub density on each annual plant group was significantly different from zero. We also tested for underlying differences between the beneficiary and unreported groups to ensure the chosen species had similar niche overlaps (Supplementary material Appendix 1). Using a random set of geographic points we compared the densities of beneficiary and unreported plant groups with a Pearson’s correlation. All analyses and data extraction were conducted in R ver. 3.2.3 (<www.r-project.org>).

Environmental variables

Eight bioclimatic variables (Supplementary material Appendix 1; Hijmans et al. 2005) and also elevation with 30-second (~ 1 km) spatial resolution were downloaded from the WorldClim dataset (<www.worldclim.org>). These eight variables were selected because they are strongly associated with winter-annual germination and productivity (Beatley 1974). To check for collinearity among these bioclimatic variables we extracted climate data from 1000 randomly chosen points in Southern California and performed a correlation matrix. We removed correlated bioclimatic variables at $r > 0.6$ (Dormann et al. 2013). Precipitation seasonality was maintained despite having a strong correlation ($r > 0.6$) with other bioclimatic variables because deserts systems are extremely sensitive to precipitation frequency (Reynolds et al. 2004). Therefore, the chosen bioclimatic variables were elevation, temperature during the wettest quarter, precipitation during the wettest quarter, and precipitation seasonality.

MaxEnt models

MaxEnt (‘maximum entropy’) is a powerful technique for modeling species distribution and the environmental niche

using presence only data (Phillips et al. 2006, Merow et al. 2013). MaxEnt has two distinct advantages over other techniques, such as GARP, in that it produces a more detailed prediction and increases the contrast of the predicted occurrence (Phillips et al. 2006). Hence, we used MaxEnt to predict the habitat suitability for each of the 20 species using environmental predictors only (m_{env}) versus environmental predictors plus shrub density ($m_{shrub.env}$). MaxEnt models were run in R (*maxent* function, package *dismo*), and a total of 20% of the occurrence data were withheld as a testing to evaluate the predictive ability of the models (Phillips and Dudík 2008). We repeated models on each species 40 times each with a different subset randomization and reported aggregate means of the output statistics across all models to account for uncertainty of SDM predictions (Syfert et al. 2013). The maximum number of background points used was set to 10 000 to accurately capture the ambient variation in climate (Yang et al. 2013). The area under the receiving operator curve (AUC) statistic is an estimate of model performance compared to null expectations where 1 represents a perfect prediction and values of 0.5 or lower are attributed to chance (Merow et al. 2013). We compared AUC values between the beneficiary and unreported species groups using a Student's two-sample t-test.

To account for unequal survey effort of plant species from GBIF we used both a restriction of the background data and incorporation of a survey bias dataset (Phillips et al. 2009, Kramer-Schadt et al. 2013). We manipulated the background area by creating a 10 km buffer around each occurrence for Southern California. The resulting polygon was used to extract the background climate data. A survey bias dataset was generated using the initial list of Mojave Desert plant species identified from the literature. The occurrences for each of the 61 species were checked for duplicates or inconsistencies and a density estimate was calculated in the same manner as for the other biotic rasters (i.e. shrub, beneficiary and unreported species groups). A bias file for a large number of species approximates the survey effort for a subset species of that dataset and is often used in MaxEnt modelling (Elith et al. 2010, Fourcade et al. 2014). Thus, the bias file was used in all MaxEnt models within this study. A workflow of the species selection, model inputs, and adjustments of survey bias can be found in the Supplementary material Appendix 2.

The species distribution models for each species were mapped with values of 0 representing inhabitable and values of 1 representing suitable habitat. This estimate of habitat suitability was calculated using the *predict* function (package *dismo*), which created a raster based of the output of each MaxEnt model. To identify geographic areas, where shrubs are associated with habitable area, we subtracted the habitat suitability of m_{env} from $m_{shrub.env}$ and averaged the difference in habitat suitability for each raster cell (n) in the sampled region, hereafter HS_{diff} (Eq. 1). We tested if the HS_{diff} was different between beneficiary and unreported species using a Wilcoxon sign-ranked test (function *wilcox.test*) with the species group as the predictor. We did not compare the converse where the environmental-only model predicts areas of habitat

suitability because the inclusion of additional variables within any MaxEnt model will often better predict habitat suitability and produce a smaller predicted area. Consequently, the difference between these models would not be informative except for model determination.

$$HS_{diff} = \frac{\sum_n m_{shrub.env} - m_{env}}{n} \quad (1)$$

Phylogenetic analysis

We tested if closely related species were more likely to be facilitated by creating a phylogenetic tree of each tested plant species and comparing the HS_{diff} values. The phylogenetic tree was produced using the Phylomatic software (<<http://phylodiversity.net>>) and the R-package *picante*. The beneficiary and unreported species groups were assigned to each respective node on the tree. Models were run for 999 randomizations using a null model that randomized across all species within the data matrix.

Data deposition

Data available from the Figshare repository: <<https://doi.org/10.6084/m9.figshare.3586065.v2>> (Filazzola et al. 2016).

Results

Shrub occurrence was positively related to with both the beneficiary species occurrence (mean effect \pm SE = 0.77 ± 0.015 ; $p < 0.001$; Fig. 1) and the unreported plant species occurrence (mean effect \pm SE = 0.76 ± 0.031 ; $p < 0.001$; Fig. 1). However, shrub occurrence more accurately predicted annual occurrence for the beneficiary species than for the unreported annuals ($R^2 = 0.72$; $R^2 = 0.38$, respectively).

Overall, all species were accurately predicted by the MaxEnt models (AUC > 0.70; Table 2). The AUC values of the beneficiary species were significantly increased by the inclusion of shrubs into the model ($t = -2.32$, $p = 0.033$; Fig. 2), but AUC values were not significantly different for unreported species between models ($t = -0.73$, $p = 0.48$; Fig. 2). Species distribution models for all beneficiary and unreported plant species were mapped (Supplementary material Appendix 3) with two example species represented in Fig. 3. Shrub MaxEnt models significantly increased the habitat suitability estimates (HS_{diff}) for the beneficiary species relative to unreported annuals ($W = 10$, $p = 0.0028$; Fig. 3).

Plant species that are closely related were more likely to be classified together in either the beneficiary or unreported groups (Fig. 4). For instance, plant species in the families Asteraceae and Brassicaceae were either classified as beneficiaries or had high HS_{diff} values while the Polemoniaceae family were classified as unreported and had low HS_{diff} values (Fig. 4). There were two species in the unreported plant group, *Eremalche exilis* (Malvaceae) and *Layia glandulosa* (Asteraceae), that displayed model improvement with the inclusion of shrubs (Fig. 2). These two species were closely related to other species classified as beneficiaries, such

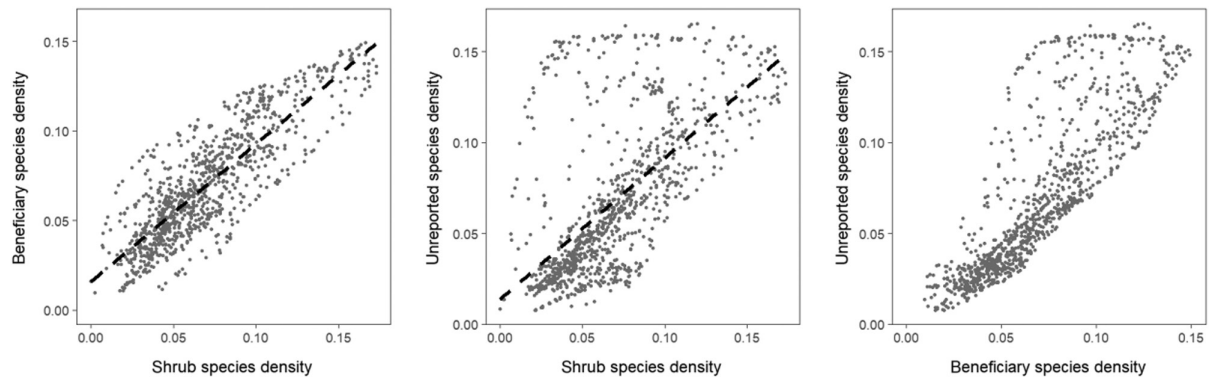


Figure 1. Co-occurrence patterns of shrubs and annual plants species at 1000 random points within the Mojave Desert, California. The probability of shrub occurrence positively correlated with beneficiary occurrence probabilities ($R^2 = 0.42$, $p < 0.001$) and the occurrence of unreported annual species ($R^2 = 0.16$, $p < 0.001$). The probability of occurrence for beneficiary and unreported plant species were also correlated ($r = 0.85$).

as *Sphaeralcea ambigua* (Malvaceae) and *Chaenactis fremontii* (Asteraceae) respectively (Fig. 4). The Boraginaceae family was an exception because it had two closely related plant species, *Phacelia distans* and *Cryptantha intermedia*, that had largely different trends in group classification and HS_{diff} values (Fig. 4).

Discussion

Positive plant interactions can provide favourable habitat for a responding species and this has implications for increasing the geographic extent of that species. We found support for our prediction that SDMs of beneficiary plant species were

improved with the inclusion of shrubs and that they had an increased geographical extent. Our prediction that the unreported species would not be improved with the inclusion of shrub in SDMs was also supported. Benefactor occurrence was thus successfully used as a proxy for positive interactions to test for increases in niche geographic extent in this study. This is a novel approach because previous studies of niche modelling were conducted mostly with abiotic variables. The more species we classify and test as beneficiaries the more likely we are to be able to build better SDMs in general and model the responses of desert communities to climate change. Where species are found likely has both an abiotic and biotic component and estimating co-occurrence patterns will more effectively predict how a species distribution will change over time.

Table 2. Summary statistics from MaxEnt models conducted on each of the annual species with predictors of environment only (m_{env}) and the environment with shrub ($m_{shrub,env}$). The number of occurrences and absences that were included in each model are represented as n.presence and n.absence respectively.

Species	m _{env}		m _{shrub.env}		n.presence	n.absence	HS _{diff}
	cor	AUC	cor	AUC			
Beneficiary							
<i>Camissonia claviformis</i>	0.15	0.71	0.18	0.75	69	1852	2.86
<i>Caulanthus cooperi</i>	0.16	0.77	0.2	0.81	60	1850	2.85
<i>Chaenactis fremontii</i>	0.3	0.79	0.37	0.84	150	1856	2.91
<i>Delphinium parishii</i>	0.23	0.78	0.3	0.83	119	1858	2.57
<i>Descurainia pinnata</i>	0.22	0.74	0.26	0.77	148	1855	2.67
<i>Lepidium lasiocarpum</i>	0.2	0.72	0.24	0.74	160	1855	2.61
<i>Malacothrix glabrata</i>	0.23	0.72	0.29	0.76	178	1855	2.94
<i>Phacelia distans</i>	0.3	0.75	0.32	0.77	260	1853	2.56
<i>Rafinesquia neomexicana</i>	0.27	0.79	0.32	0.82	126	1854	2.15
<i>Sphaeralcea ambigua</i>	0.28	0.75	0.31	0.77	220	1853	2.57
Unreported							
<i>Acmispon brachycarpus</i>	0.17	0.81	0.17	0.81	41	1865	1.23
<i>Cryptantha intermedia</i>	0.49	0.88	0.5	0.89	255	1862	1.07
<i>Eremalche exilis</i>	0.15	0.76	0.19	0.81	47	1867	2.79
<i>Gilia minor</i>	0.2	0.87	0.2	0.87	23	1862	1.3
<i>Layia glandulosa</i>	0.27	0.81	0.3	0.84	115	1863	2.14
<i>Linanthus dichotomus</i>	0.17	0.82	0.17	0.82	38	1860	1.26
<i>Lupinus sparsiflorus</i>	0.34	0.85	0.36	0.86	128	1861	1.63
<i>Oxytheca perfoliata</i>	0.15	0.83	0.15	0.84	25	1864	1.16
<i>Plantago ovata</i>	0.28	0.8	0.31	0.81	152	1867	1.46
<i>Salvia columbariae</i>	0.28	0.75	0.29	0.76	241	1862	2.04

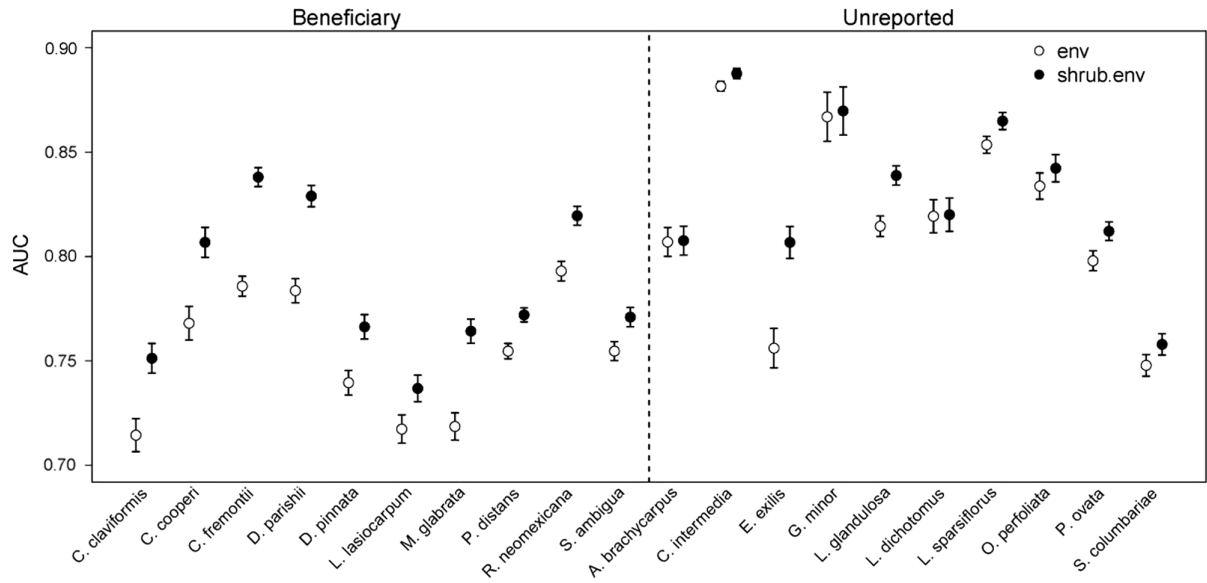


Figure 2. MaxEnt models for each species trained and tested on occurrence only data from GBIF. AUC values were derived from average predictions of 40 runs with error bars representing 95% confidence intervals.

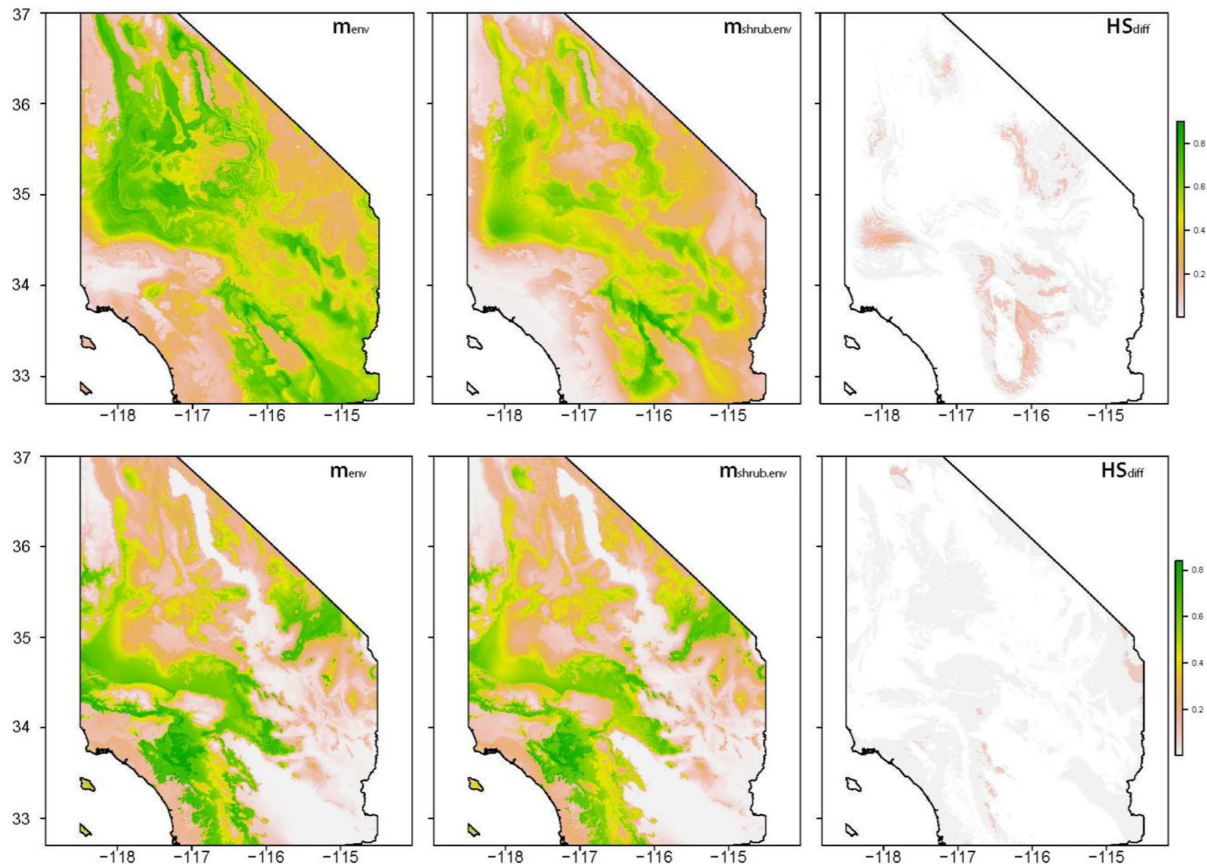


Figure 3. A representative example of MaxEnt predictive models for the distribution of a known beneficiary species, *Camissonia claviformis* (top), and unreported species, *Acmispon brachycarpus* (bottom), with environmental predictors only (m_{env}) and environmental predictors with shrub density as a predictor ($m_{shrub.env}$). The shrub-based range expansion (HS_{diff}) represents the difference of prediction in $m_{shrub.env}$ and m_{env} .

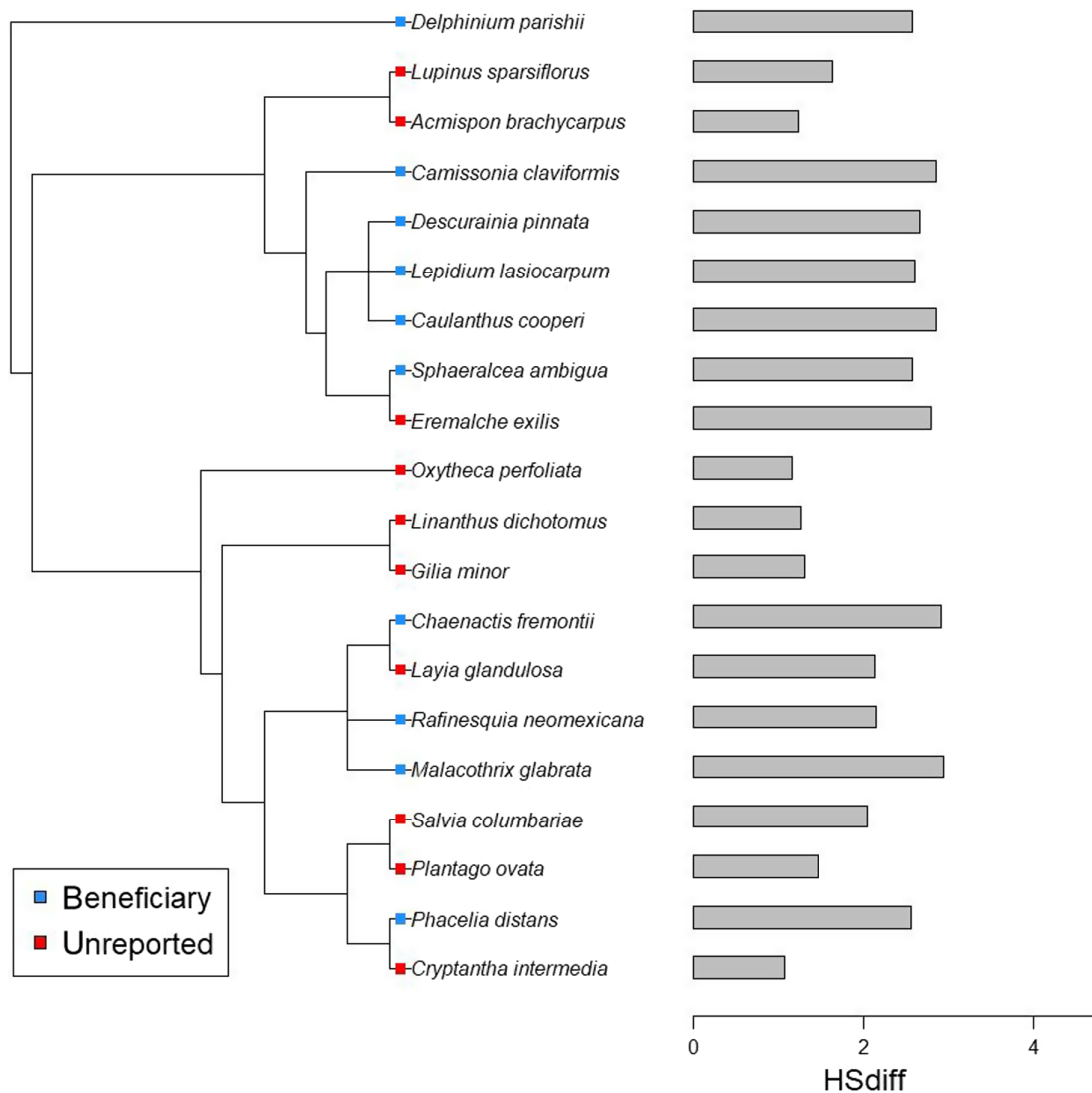


Figure 4. A phylogeny of examined annual species and the associated range expansion effect from shrub facilitation (HS_{diff}).

Positive interactions on niche and range

There are two models for the effect of positive interactions on the fundamental niche of beneficiary species. The niche-construction model predicts that positive interactions increase the geographic area that corresponds to the fundamental niche of beneficiary plant species (Rodriguez-Cabal et al. 2013, McIntire and Fajardo 2014). In this instance, benefactor plants increase the environmental heterogeneity of the landscape (Pescador et al. 2014) thereby providing a greater range of environmental conditions relative to open sites that meet species niche requirements (Rodriguez-Cabal et al. 2013). The niche-expansion model is the second that proposes facilitation increases the realized niche to be greater than the fundamental niche (Bruno et al. 2003, Stachowicz 2012, He and Bertness 2014, Afkhami et al. 2014). There has been debate as to which model best describes the relationship between positive interactions and

niche (Rodriguez-Cabal et al. 2013, Stachowicz 2012), that has been revised to depend on context (Bulleri et al. 2016). However, we believe both models are possible depending on mechanism of interaction. Positive interactions can be divided into niche constructors, those that modify the environment to create suitable habitat, and niche expanders, those that modify the beneficiary species to tolerate the habitat. The shrubs within this study would be classified as niche constructors because they increase environmental heterogeneity to match niche requirements of the beneficiary species. Conversely, an example of a niche expander would be mutualistic endophytic fungi that increases the drought tolerance and geographic range of grass species, such as *Bromus laevipes* (Afkhami et al. 2014). Thus, there are at least two possible models that both describe how positive interactions modify the fundamental niche of a beneficiary species, and each has associated ecological theories and different implications.

Positive interactions and climate change

Predicting how species respond to climate change is a significant challenge for ecologists and conservationists. Current SDMs already incorporate environmental change in forecasts of projected climate change (Elith and Leathwick 2009), but this approach neglects the co-occurring species and their potential positive effects. Here we have shown that benefactor co-occurrence can be used as a proxy for positive interactions and it may be possible to model changes to this association through time using updated species occurrence data. This is important to consider because the sign and magnitude of plant interactions are dependent on climate and likely to change over time (Callaway et al. 2002, Sthultz et al. 2007). For instance, positive interactions can buffer communities from species loss at environmental extremes, but are less relevant in mild environments (Callaway et al. 2002, Cavieres et al. 2014). Thus, current 'climate-only' models are assuming the effect of positive interactions is consistent in modelling scenarios when this is likely not the case due to large-scale natural gradients (Butterfield et al. 2016, Metz and Tielbörger 2016). In any scenario, the loss of dominant plants and the associated positive interactions would then reduce an ecosystem's resistance to stressors resulting in additional species loss (Smith and Knapp 2003). Additionally, increases in dominant plants in other systems, such as shrub encroachment, could have profound effects on plant communities (Maestre et al. 2016). By increasing the environmental heterogeneity of the landscape, greater niche space is provided that was previously non-existent. It is important to determine how the effects of biotic interactions, such as facilitation, respond to a changing climate because species co-occurrence patterns are likely to be non-random and provide an opportunity to improve climate only models (Klanderud and Totland 2005). Inclusion of positive interactions in SDMs can provide a tool to make more informed decisions for conservation management in a changing climate.

Species specificity

Positive interactions are species specific for both the benefactor and beneficiary species (Callaway 1998, Soliveres et al. 2012). Within this study, we found the inclusion of shrubs in SDMs improved model predictability for some, but not all tested species. For instance, models of beneficiary group and not the unreported group were improved with the inclusion of benefactor shrubs as a predictor. However, there were some species within the unreported group that displayed co-occurrence patterns with benefactor shrubs. We identified members of the family Asteraceae and Malvaceae as being improved with the inclusion of shrubs in both the beneficiary and unreported groups. Other studies have also identified Asteraceae species as being facilitated in deserts (Flores and Jurado 2003) and also in alpine ecosystems (Cavieres et al. 2006). This suggests that annual species within the Asteraceae family have traits that require the

shrub microclimate. For instance, beneficiary species have been proposed to have more competitive life-history traits that benefit from the increased resource availability and the reduced abiotic stress found under benefactor shrubs (Maestre et al. 2009). However, empirical research has shown the relationship between desert shrubs and Asteraceae species to be because of stress-tolerant traits, such as lower light and soil moisture found under shrub canopies (Butterfield and Briggs 2011). SDMs that include positive interactions, such as the ones conducted here, can help identify species relatively more dependent on facilitation for persistence within an ecosystem (e.g. *Eremalche exilis* and *Layia glandulosa*). Positive interactions are species specific and these relationships can be identifiable at the macro-scale using co-occurrences, which can assist ecologist attempting to disentangle how these interactions will change through time.

Implications

Positive interactions, niche, and geographic extents can be linked and examined through SDMs. The inclusion of positive interactions in SDMs is an effective and novel means to explore ecological contexts without experimentation within the framework of niche theory by using existing open data and the ecological literature. Ecologists will need to continue to innovate and reuse scientific research at regional and larger scales to explore the potential importance of local interactions (Mouquet et al. 2003). Recently, SDMs have been used to model a target species in conjunction with other dominant species to provide better predictions of occurrence and available niche space (Wonham et al. 2013, Pollock et al. 2014). More comprehensive MaxEnt models or disaggregating the environmental effect and examining residual correlations among shrubs and the annual species are at least two additional opportunities for future studies (Pollock et al. 2014). Hierarchical modelling of species communities (HMSC) is another recent tool that models community interactions at different spatial or temporal scales (Ovaskainen et al. 2017). Detailed reporting of how species interact, positively or negatively, within ecological research that can be synthesized for macro-scale models would be a powerful asset for ecological modelers. Moreover, additional models could assess the mechanism of facilitation (e.g. cooler temperatures, higher soil moisture, less herbivory) rather than the more phenomenological method of modelling co-occurrences that were examined here. Modelling mechanisms could provide a more direct assessment of the processes that are likely to change with climate, such as drought events. Further modeling of positive interactions is crucial for species in high-stress environments and necessary consideration when predicting responses to climate.

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Supplementary material (available online as Appendix oik-04688 at <www.oikosjournal.org/appendix/oik-04688>). Appendix 1–3.