Projected climate change scenarios spatially decouple desert EFN-ant mutualisms.

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Abstract

Aim: Climate change is changing species distributions globally, but predicting these impacts on assemblages and their spatial overlaps under future scenarios is an ongoing challenge. Here, we explore how climate change influences distributions among two mutualistic assemblages.

Location: The Mojave and Colorado Deserts, California, United States

Methods: We developed stacked species distribution models for the community of extrafloral nectar (EFN)-bearing plants and their mutualistic ant community and projected these models under two future climate scenarios. To assess the vulnerability of this mutualism due to spatial mismatches, we examined potential shifts in geographic overlap between the EFN-bearing plants and ant species under both scenarios. We analyzed the bioclimatic factors influencing species richness and distribution in both the plant and ant communities, as well as their responses to future climate change. We also tested whether environmental breadth and phylogeny could predict the responses of ants to climate change. Lastly, we evaluated the significance of the EFN community on ant species distributions by determining whether the inclusion of EFN plants in ant distribution models enhances their predictive accuracy.

Results: The species richness of both the EFN-bearing plant communities and ant communities decreased under both predicted climate change scenarios. The geographic overlap between EFN plants and ants significantly decreased under both future scenarios. The response of different ant species to climate change varied based on their environmental generalization but not their evolutionary relationships. Including the EFN plant community as a predictor in the species distribution models for ants improved their predictive performance.

Main conclusions: The EFN plant community is an important driver of their ant mutualists' geographic distribution and diversity. More environmentally generalized ant species benefit from the changing climate, whereas the EFN-bearing plants are uniformly and negatively impacted despite their environmental generalization. Despite the range increase of some ant species across

the Mojave and Colorado Deserts, these mutualisms are vulnerable to climate change because of the decrease in geographic overlap between pairs of ant and EFN-bearing plant species.

Introduction

Climate change is profoundly changing the diversity and distribution of species globally. The responses of individual species to a changing climate can decrease or increase their range size, as well as causing spatial shifts leading to changes in the spatial overlap of species (Thomas 2010, Lenoir and Svenning 2015). Spatial overlaps play a key role in biotic interactions, and thus, climate change impacts the capacity for interactions in addition to the species themselves (Walther 2010, Gómez-Ruiz and Lacher 2019). The loss of the interaction partners resulting from the spatial reorganization of communities can decrease the delivery of ecosystem services, as well as reducing ecosystem functioning and stability (Walther 2010, Pyke et al. 2016). Generalized mutualisms i.e., species have flexible interactions with multiple partners, are expected to be more resilient to climate change than specialized mutualisms i.e., species rely on specific partners for interactions, because having flexibility in interaction partners buffers the interaction to species loss (Toby Kiers et al. 2010). However, generalized mutualisms can also be vulnerable if one community spatially shifts much more than the other, leading to potential declines in both participant species and the ecosystem services that they respectively provide. Many recent biogeographic studies look at future changes in species distributions and biodiversity (e.g., Tovar et al. 2022, Biber et al. 2023); however, relatively few of these examine interacting mutualistic communities on different trophic levels (but see Vasconcelos et al. 2017, Morales-Linares et al. 2021, Adedoja et al. 2024). Anticipating the impacts of climate change on spatial overlaps at the community level is a necessary step for predicting and mitigating the consequences of these shifts for mutualism.

Ant-plant interactions are a model for understanding the ecology and evolution of generalized mutualisms (Heil and McKey 2003). These include ant defense mutualisms; ants obtain a nutrient-rich food nectar secreted from extrafloral nectaries (EFNs) by plants in exchange for defending the plant from herbivores, improving plant fitness (Heil and McKey 2003, Rico-Gray and Oliveira 2007, Rosumek et al. 2009). EFNs have been reported in 3941 species of plants within 108 families and have arisen 457 times independently, indicating that this trait is adaptive in a wide range of systems (Weber and Keeler 2013). Global biogeographic studies have documented many positive correlations between ant diversity and EFN plant diversity and that they are also often mediated by climate (Luo et al. 2023). Ant-EFN interactions may be fundamental to the persistence of plants in arid ecosystems because the effectiveness of ant defense mutualisms for plants increases with decreasing precipitation (Leal and Peixoto 2017). However, ants and plants are different physiologically and likely have different climate niches and, therefore, different responses to climate change. The extent of this variation in climate sensitivity and, consequently, the future capacity of this mutualism is untested. Therefore, understanding how ant and plant distributions will shift is critical research to understanding the vulnerability of these interactions in the face of a dramatically changing climate.

Species distribution models (SDMs) are powerful tools for predicting species distribution shifts under a changing climate. By linking aspects of species biology, such as phylogeny and environmental breadth, to predicted distribution shifts, we can gain generalizable insights into how communities will respond to climate change. Understanding and predicting assemblage-level responses to climate change have been proposed as critical components of ecological forecasting, yet these remain challenging tasks due to incomplete field sampling of assemblages (Suding et al. 2008, Walther 2010, Urban et al. 2016). One solution is to use stacked species distribution models (s-SDMs), which extend the functionality of SDMs from understanding the distribution of single species to understanding the distribution of communities (Del Toro et al. 2019). When stacked, the models can provide both species richness and composition for a given area (Dubuis et al. 2011). S-SDMs stacked using probabilities provide richness estimates comparable to macroecological models (MEMs), i.e., models that statistically relate species richness to environmental variables, while avoiding the issues of overestimation associated with thresholded s-SDM (Gould 2000, Dubuis et al. 2011). An advantage of s-SDMs is that they can be developed using presence-only data, allowing researchers to leverage public biodiversity data clearinghouses such as the Global Biodiversity Information Facility (GBIF) (GBIF 2022). With climate change occurring now and limited time to study each community in the field, these tools can provide valuable support.

Here, we conduct a synthesis to explore the role of current and future climate on the geographic distribution of two mutualistic guilds. We tested the hypothesis that EFN mutualisms couple plant and ant communities together in space but become decoupled with climate change. We modelled the distributions of the EFN-bearing plant and their mutualistic ant communities of the Mojave Desert and Colorado Deserts using s-SDMs. We tested for shifts in geographic overlap between EFN-bearing plant and ant species under two different future scenarios to evaluate the impacts on the potential for this mutualism to occur. We contrasted the environmental drivers of species richness and distributions between the plant and ant communities, and their responses to future climate change. We then tested if environmental breadth and phylogeny predict individual ant species' responses. Finally, we evaluated evidence for the importance of EFN plants on the distribution of mutualistic ants by testing the following predictions: 1) Including the EFN plant community into the SDMs for ant species will improve the ant model’s predictive accuracy; 2) Variation in the EFN plant community richness explains variation in ant richness independent of covariation that arises from shared climate needs. This synthesis contributes to our understanding of the biotic drivers of species distributions, as well as the drivers of diversity and the consequences of climate change for two important Mojave Desert communities.

Methods

Species data collection

A species list of EFN-bearing plants of the Mojave and Colorado deserts was created from the paper by Pemberton (1988) that documented the percent ground cover of EFN-bearing plants using field surveys. A more exhaustive list of all EFN-bearing species of the area has not been published and the surveys covered the major plant communities of the area (Pemberton 1988). Additionally, these EFN-bearing species have been reported to be used by ants within the Mojave, Colorado or Sonoran deserts (Pemberton 1988, Chamberlain and Holland 2009). Ant defense improves at least two of the included plant species’ fitness: *Cylindropuntia echinocarpa* and *C. acanthocarpa* (Braun and Lortie, unpub, Pickett and Clark 1979).

We created a list of ant species found within the Mojave and Colorado deserts that use EFN nectar, honeydew or have been reported to interact with EFN-bearing plants from published species lists. We used the Mojave National Preserve ant species list (Ikeda and des Lauriers 2008) and ant species from a published Sonoran ant-EFN interaction network (Chamberlain and Holland 2009) that are also found within the Mojave desert.

The boundaries of the Mojave and Colorado deserts were defined as the watershed boundary delineated by the USGS (USGS 2006, Figure 1). We used the minimum convex polygon (MCP) around the watershed boundary map as the study boundary for extracting occurrences to increase the sample size for several ant species with low sample sizes (Figure 1). We used species occurrences and environmental data from within the MCP to include within the species distribution models but clipped out model outputs to the study area boundary.

Occurrences for plant and ant species were extracted from the Global Biodiversity Information Facility database (GBIF, www.gbif.org) using the rgbif package (Chamberlain et al. 2022). We supplemented the GBIF occurrences with occurrences extracted from the Global Ants Biodiversity Informatics databased (GABI) (Guenard et al. 2017). We retained species with at least 10 occurrences within the MCP area as focal species, for a total of 11 EFN-bearing plant species (Table 1) and 16 ant species (Table 2).

Environmental variables

We used 19 bioclimatic variables from WorldClim Version 2 global climate gridded data at a resolution of 30 seconds (~1 km^2) (Fick and Hijmans 2017). The bioclimatic variables represent climate averages for the years 1970-2000. We used PCA for dimension reduction to eliminate correlations between the variables objectively (Harrell 2001, Dormann et al. 2013). The PCA was done using 100 000 random points sampled across the study area, and the bioclimatic variables were centred and scaled prior to analysis. We retained rasters for the first four PCA axes, accounting for 90% of the variation within the climate data (SI Fig 1 and SI Fig 2).

The CNRM-CM6-1 model is a widely used and well-validated climate model. It is a fully coupled atmosphere-ocean general circulation model developed by Centre National de Recherches Météorologiques (CNRM) for the sixth generation of the IPCC Coupled Model Intercomparison Project 6 (CMIP6) (Eyring et al. 2016, Voldoire 2019). We used two future CNRM-CM6-1 models for the same 19 bioclimatic variables at the same 30-second resolution for the years 2041-2060 obtained from WorldClim 2.1 (Fick and Hijmans 2017, Voldoire 2019). Shared Socioeconomic Pathway (SSP) models are updates to the previous RCP models. Of the five possible pathways, we chose the following two scenarios: SSP2-4.5 (optimistic, some effort is made to limit warming to around 3 degrees, closest to RCP 4.5) and SSP3-7.0, the middle of road baseline outcome if no changes are made to global climate policy) (Eyring et al. 2016, O'Neill et al. 2017).

We then applied the PCA model to each of the two future datasets and again retained the first four rasters for analysis. All future climate rasters were masked using the watershed boundary of the Mojave and Colorado deserts (USGS 2006).

Distribution models

We built SDMs for each plant and ant species using the R package SDMtune (Vignali et al. 2020). We used Maxent because it is suitable for use with presence-only data and because it has been shown to work well with even small datasets (Hernandez et al. 2006).We used the Maxnet method of Maxent as described in Philips et al (2017), which improves previous versions of Maxent by implementing a complementary log-log (clog-log) transformation to produce an estimate of occurrence instead of the estimates of habitat suitability produced by the exponential method because this method models species occurrences as an inhomogeneous Poisson process (IPP) (Phillips et al. 2017).

Occurrence points were thinned to one point per raster cell for each species to reduce spatial bias. We generated pseudo-absences by randomly sampling 10000 points from across the study area ('randompoints()', 'dismo' package (Hijmans et al. 2017). We used random *k* folds at a value of five to determine which partitions to hold back for cross-validation. We repeated models for each species 40 times each with different subset randomization. We assessed the predictive performance of each model using the area under the receiver operating characteristic curve (AUC). AUC ranges between 0 and 1, where 1 is perfect prediction and 0.5 is the baseline accuracy of a binary outcome. Models with AUC values >= 0.7 are considered good (Phillips and Dudík 2008). Only species with mean AUC >= 0.7 across replicates were retained in the stacked SDMs (SI Table 1 and Table 2, two species of ants were thus excluded due to low AUC: *Camponotus sayi* and *Forelius pruinosis*. All EFN-bearing plant species tested were retained).

We predicted each species' distribution across the study area and used the clog-log transformation to obtain a probability of presence between 0 and 1 for each of the 40 model runs. To account for the uncertainty of the SDM predictions, we took the aggregate mean of the 40 prediction rasters to form a consensus distribution raster for each species.

We then projected each of the 40 model runs for each ant and plant species onto both future climate scenarios. We again took the means of the resulting rasters to determine the final consensus distribution model for each species for each future climate scenario.

Stacking procedures

To create the plant and ant community richness rasters, we stacked the consensus rasters for each community and summed the continuous probabilities. This approach to creating stacked SDMs outperforms thresholded binary stacked SDMs and the output is equivalent to species richness (Dubuis et al. 2011, Calabrese et al. 2014, Zurell et al. 2020). We also created predicted future community richness rasters for each community under each future climate change scenario.

Distributional relationship between EFN plants and ants

We sampled 5000 random points from the plant and ant community stacked SDMs. We calculated Pearson's correlation coefficient to quantify the strength of the association between the species richness of the two communities.

Correlations in species richness between the two communities can arise from shared environmental preferences, thus we used variance partitioning to determine the independent and shared components of ant community richness variation explainable by EFN-bearing plant species richness and climate ('varpart', vegan package, Oksanen et al. 2010). The four PCA axes were used as the climate predictor matrix and EFN plant community richness was used as the second predictor.

We then evaluated if EFN plant richness influences ant species distributions by fitting two additional sets of SDM for each ant species: the first with the EFN plant community richness raster included as a predictor alongside the climate variables, and the second with the EFN plant community as the sole predictor. We followed all the same procedures as the climate-only models.

We tested for differences in the predictive performance of the three sets of models by fitting linear mixed models (LMM) using the test AUC as the response variable and the ant species as a random effect (glmmTMB, Brooks et al. 2017). We used the model type (climate, climate+EFN or EFN only) as the predictor. All model runs (40) for each ant species were included in the models and the species was included as a random effect.

Comparing environmental responses between ant and plant communities

We calculated the variable importance of each of the four climate predictors (PC1 through PC4) for each ant and plant species using 50 permutations (‘varimp’ function in SDMtune). The function randomly permutes one variable at a time and computes the decrease in training AUC. The result is normalized to percentages for each predictor variable (Vignali et al. 2020).

We tested for differences in ant and EFN plant environmental needs by contrasting the variable importance scores. For each climate variable (PC1 through PC4), we conducted a t-test between the ant species’ scores and the EFN plant species’ scores.

Understanding ant and plant community-level responses to climate change

To understand how climate change will impact future diversity patterns across the Mojave and Colorado deserts, we tested for shifts in ant and plant communities’ richness distributions for each future climate change scenario. These, and all subsequent analyses for future distributions used the climate-only SDMs. Using 5000 random points, we extracted the species richness for both communities under each scenario. We fit separate LMM for ants and plants each with the scenario (present, SSP 245 and SSP 370) as the predictor and species richness as the response. The pixel identifier was included as a random effect. We used emmeans (Lenth et al. 2018) to contrast the three scenarios.

To test if the plant and ant communities become mismatched due to species-specific differences in responses to climate change, we calculated the geographic overlap between each ant and plant species in the present and for both climate scenarios using Schoener’s D niche overlap index ('calc.niche.overlap', ENMeval package, Kass et al. 2021). We then used paired t-tests to test for differences in overlap between the present and each of the future scenarios.

Understanding species-specificity in response to climate change

We conducted a post hoc investigation to explain the observed variation in the responses of individual species to climate change. We chose two possible explanations for species-specific responses to the future climate scenarios: phylogeny and environmental breadth.

We individually quantified the change in mean environmental suitability across the study area for each ant and plant species by subtracting the present distribution from the future distribution and calculating the mean pixel value. Negative values represent an average decrease in suitability, and positive values represent an average increase in the study area's environmental suitability.

We first asked if phylogeny explains the variation in ant species' distribution shifts in response to climate change. A complete species-level phylogenetic tree for ants is still lacking. We used the tree created by Moreau and Bell (2013). In our study, five genera contained a single species (Table 2). We pruned the tree to a single species for each of these genera. For the remaining genera, we added the missing species as random congeners to the tree for a total of 14 tips (SI Fig 3) We tested for a phylogenetic signal in ant distribution changes by calculating Blomberg's K using the change in environmental suitability for each ant species ('phytools', Revell 2012). This method permutes values among the tips of the phylogenetic tree and compares the values to those from a Brownian motion model of evolution (the variance in values is proportional to the tree branch length) (Münkemüller et al. 2012).

Environmental breadth is the range of environmental conditions that a species uses (Sexton et al. 2017). Environmental breadth metrics measure the uniformity of the geographic distribution of environmental suitability scores for a species (Warren et al. 2021). We calculated Levins' (1968) metric of environmental breath i.e., the spatial heterogeneity of the distribution of suitability scores ('raster.breadth', ENMtools, Warren et al. 2021). We then calculated Pearson's correlation between environmental breadth and the difference in suitability under each climate change scenario for each species within the ant and plant communities. We additionally tested for phylogenetic signal in environmental breadth for the ant community.

All analyses were done using R version 4.3.1 (R Core Team 2023).

Results

Distributional relationship between EFN plants and ants

Ant species richness was positively correlated with EFN plant species richness across the Mojave and Colorado Deserts (Pearson's = 0.765, $p < 0.001$). Variance partitioning revealed that EFN plant species richness independently explained 50% of the variation in ant species richness.

Climate and EFN plant species richness jointly explained 20% of the variation in ant species richness, and climate explained 9% of the variation independently.

Ant species distribution models that included EFN richness as a predictor alongside climate performed significantly better in terms of test AUC than models built with only climate (Figure 2, GLMM: coef = 0.014 ± 0.003 SD, z = 5.18, $p < 0.001$). Climate-only ant SDMs outperformed models built using only EFN plant richness as a predictor (Figure 2, GLMM: coef = -0.04 ± 0.003 SD, z = -13.04, $p > 0.001$). The EFN-only models were not tractable for three ant species (*C. fragilis, F. mccooki* and *M. testaceus*). Distribution models for each ant and plant species with occurrence points overlaid are available in SI Fig 4 and 5.

Comparing environmental responses between ant and plant communities

The bioclimatic variables with the largest impact on the PC1 gradient were related to temperature and precipitation (e.g., Maximum temperature of warmest month, mean temperature of warmest quarter, annual precipitation, precipitation of driest quarter, SI Fig. 1 and 2). The PC1 gradient ranges from warmer/drier to cooler/wetter and can be characterized as an aridity gradient (SI Fig. 1 and 2). The major bioclimatic contributors to the PC2 gradient were related to the variation in temperature and precipitation (e.g., temperature annual range, precipitation seasonality and temperature seasonality, SI Fig. 1 and 2).

The relative importance of the climatic predictors differed between the ant and plant communities. The PC1 gradient made a significantly larger contribution to the ant species models than the plant species models (t-test, ant mean = 33.12, EFN mean = 13.45, t = 2.33, df = 17.2, p = 0.03). However, the PC2 gradient made a significantly larger contribution to the EFN plant species models (t-test, mean ants = 23.2, mean EFN plants = 43.57, df = 14.2, p = 0.018). Precipitation frequency is a key environmental driver for desert plant communities (Reynolds et al. 2004).

Consequences of climate change for mutualist communities

EFN plant and ant species richness were both projected to decline across the Mojave and Colorado Deserts due to a changing climate (Figure 3, GLMM: Chisq = 2115, $p < 0.001$, emmeans, present – SSP 245: est = 0.036, $p < 0.001$; SSP 370: est = 0.039, $p < 0.001$). Richness declines were significantly greater under the SSP 370 scenario, i.e., the more severe scenario, than the SSP 245 scenario for both communities (emmeans, plants: est = 0.03, t = 3.59, $p = 0.001$; ants: est = 0.038, t = 5.27, $p < 0.001$). The western part of the Mojave Desert (Figure 3) was predicted to gain both EFN and ant species; however, those areas had low species richness for both communities during the present scenario. Across the Mojave and Colorado Deserts, there was an increase in temperature variability with a decrease in precipitation variability (SI Fig 6). Combined with the warming trend, this suggests an increase in extreme heat events. The decrease in precipitation variability suggests that it will become more uniformly dry.

Geographic overlap between ants and plants (Shoener's D) significantly decreases under both climate change projections for future distributions (Figure 4, 245 paired t-test: mean difference = 0.03, t = 6.24, df = 153, $p < 0.001$; 370: mean difference = 0.03, t = 6.7, df = 153, $p < 0.001$).

Understanding species-specificity in response to climate change

The response of species within the ant community to future climate change were more variable than the responses of the EFN plant community. Mean environmental suitability of the Mojave and Colorado Deserts decreased for eight species of ants but increased for six (SI Table 3). In contrast, mean environmental suitability decreased for all EFN plant species except for *Prosopis juliflora* (SI Table 4).

More environmentally generalized ant species tended to have increased environmental suitability in the future. The mean difference in suitability between the future scenarios and the present was significantly correlated with environmental breadth (Figure 5, SSP 245: Pearson's cor = 0.61, df = 12, p = 0.019; SSP 370: Pearson's correlation = 0.598, df = 12, p = 0.024). However, this relationship was absent within the EFN plant community (Figure 5, SSP 245: Pearson's cor = 0.12, df = 9, p = 0.73; SSP 370: Pearson's cor = 0.095, df = 9, p = 0.78). There was no significant difference in mean environmental breadth between the EFN plant and ant communities (t.test: mean ants = 0.63, plants = 0.52, t = 1.37, p = 0.18).

There was not a phylogenetic signal for environmental breadth (Blomberg's K = 0.56, p = 0.3) nor for the mean change in suitability for ants (SSP245: Blomberg's K = 0.61, p = 27; SSP 370: Blomberg's K = 0.59, p = 0.28).

Discussion

In this study, we analyzed the climatic factors that drive the current and potential future distributions of two mutualistic species guilds. The hypothesis that EFN mutualisms couple plant and ant communities together in space but become decoupled with climate change was supported. We found that including the EFN-bearing plant community as a predictor, alongside climate, improved the predictive performance of SDMs for ants; however, the actual effect size was relatively small. Thus, the EFN-bearing plant community is an important driver of the geographic distribution and diversity of their mutualists, but climate-based SDMs are suitable to model the distribution of these ant communities. Our study highlights that climate change will negatively impact nearly all EFN-bearing plant species and approximately half of the associated ant communities of the Mojave and Colorado Deserts by reducing habitat suitability for both guilds. In contrast, environmental suitability and thus range size is expected to increase for 42% of the ant species. Nonetheless, pairwise geographic overlap between ant and EFN-bearing plant species is expected to decrease, demonstrating that the range increases of some species within the ant guilds do not compensate for the range losses of the plants. The dispersal capacities of these EFN-bearing species are relatively low (Martínez-Berdeja 2015) making it unlikely that these plant species can disperse beyond the desert study area in these timelines. Thus, the potential for this mutualism to persist under climate change will decrease because of this spatial mismatch as well as the capacity for either guild to respond to shifted climates in space.

This synthesis revealed that more environmentally generalized ant species benefit from the changing climate, whereas the EFN-bearing plants are negatively impacted more uniformly despite their environmental generalization. Species with a broader environmental niche are generally expected to cope better with a changing climate because they possess greater ecological tolerance than those with narrower niches (Thuiller et al. 2005, Carscadden et al. 2020). Our results suggest that caution is needed when comparing environmental breadth across taxa on different trophic levels, as these groups often have distinct physiological strategies. We found that the environmental breadth of these ant species was unrelated to their phylogeny. While our results do not preclude the role of phylogeny at larger scales, they highlight the role of local adaptation within this desert ant community. While the PC1 and PC2 gradients decrease across the deserts, the PC4 gradient exhibits both increases and decreases in the future (see SI

Figure 6). The PC4 gradient is marked by increases in the mean temperature of the wettest quarter, precipitation during the warmest quarters, and isothermality (SI Fig 2). Most precipitation in the Mojave Desert occurs during the colder winter months (WRCC, 2024), which suggests that some environmentally generalized ant species may benefit from the warming winter temperatures.

Interactions between species can cause correlations in species richness between communities (Gaston 1996). The interactions between the ant species and EFN-bearing plants in our study were established a priori (e.g. Pemberton 1988, Chamberlain and Holland 2009); however, we found multiple lines of evidence for a relationship between the diversity of the two communities across the Mojave and Colorado Deserts. This includes a strong correlation between the diversity of the EFN-bearing plant community and the diversity of the ant community. Additionally, the variation in EFN-bearing plant community diversity explained a large component of the variation in the diversity of the ant community, independent of their shared environmental needs. Meta-analyses have shown that plant richness supports animal richness, and these relationships are stronger between trophically linked arthropods and plants (Castagneyrol and Jactel 2012) and plant-pollinator mutualisms (Kral-O'Brien et al. 2021). Globally, EFN-bearing plant diversity clusters with ants in several biogeographic regions (Luo 2022) but these relationships are not well studied in arid ecosystems because there are relatively few surveys of EFN plant diversity in deserts. Collectively, our results join those of the literature suggesting that the benefits of maintaining EFN-bearing plant diversity will extend beyond that focal community into their ant mutualists with implications for ecosystem functioning.

Considering interspecies dependencies is necessary when considering the full extent of climate change impacts. SDMs that contain species interactions can help identify which species rely more heavily on their partners for persistence within an ecosystem (Filazzola et al. 2018). Including the EFN plant community as a predictor into the ants' SDM improved their predictive performance on average; however, we used richness as the measure of the plant community and therefore our results reveal which species' distributions depend more strongly on the diversity of their mutualists (Figure 2). Generalized interactions are expected to be more resilient to climate change because species can switch interaction partners. However, we found that spatial overlap between mutualists decreases significantly in the future. Thus, the capacity for the generalized nature of this interaction to buffer it is constrained by the climatic responses of its participant species.

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Data availability statement

Statistical workflows and code will be published in reproducible documents along with the derived data.

Figures and Tables

Table 1: List of the 11 Mojave Desert EFN-bearing plant species included in this study.

Species name	Common names	Family
Cylindropuntia acanthocarpa	Buckhorn cholla	Cactaceae
Cylindropuntia echinocarpa	Silver cholla	Cactaceae
Senegalia greggii	Catclaw acacia	Fabaceae
Fouquieria splendens	Ocotillo	Fouquieriaceae
Chilopsis linearis	Desert willow	Bignoniaceae
Opuntia basilaris	Beavertail prickly pear	Cactaceae
Cylindropuntia bigelovii	Teddy-bear cholla	Cactaceae
Ferocactus cylindraceus	California barrel cactus	Cactaceae
Prosopis juliflora	Mesquite	Fabaceae
Prunus fasciculata	Desert almond	Rosaceae
Prunus fremonti	Desert apricot	Rosaceae

Table 2: List of 14 Mojave Desert EFN-associated ant species included in this study.

Ant species names	Subfamily
Solenopsis xyloni	Myrmicinae
Forelius mccooki	Dolichoderinae
Crematogaster depilis	Myrmicinae
Dorymyrmex bicolor	Dolichoderinae
Dorymyrmex insanus	Dolichoderinae
Camponotus fragilis	Formicinae
Camponotus ocreatus	Formicinae
Camponotus semitestaceus	Formicinae
Myrmecocystus kennedyi	Formicinae
Myrmecocystus testaceus	Formicinae
Myrmecocystus flaviceps	Formicinae
Myrmecocystus mimicus	Formicinae
Pheidole vistana	Myrmicinae
Liometopum luctuosum	Dolichoderinae

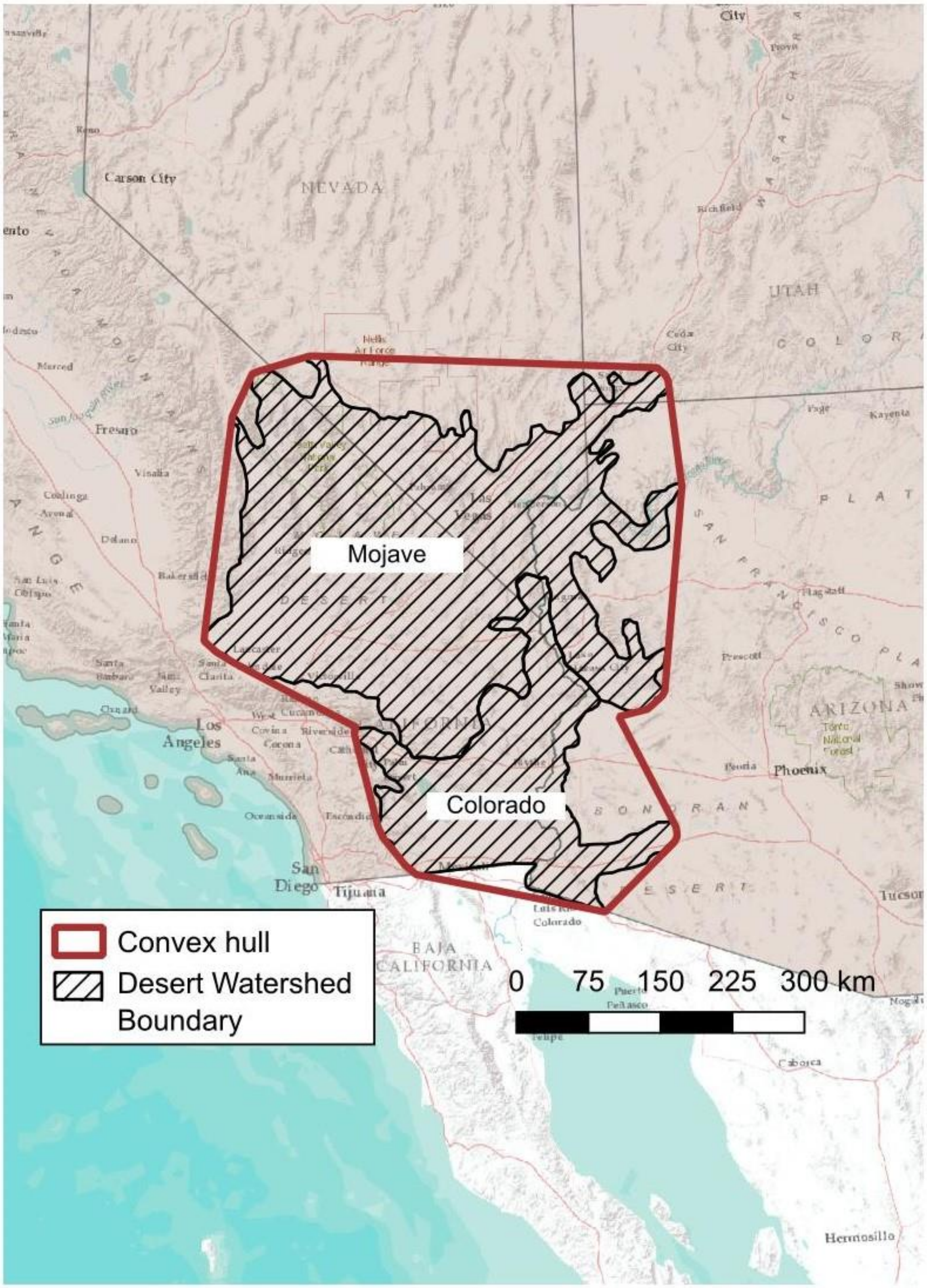


Figure 1: Map of Southwestern USA showing the Mojave and Colorado Deserts. The main study area used was the watershed boundary from the United States Geological Survey (USGS).

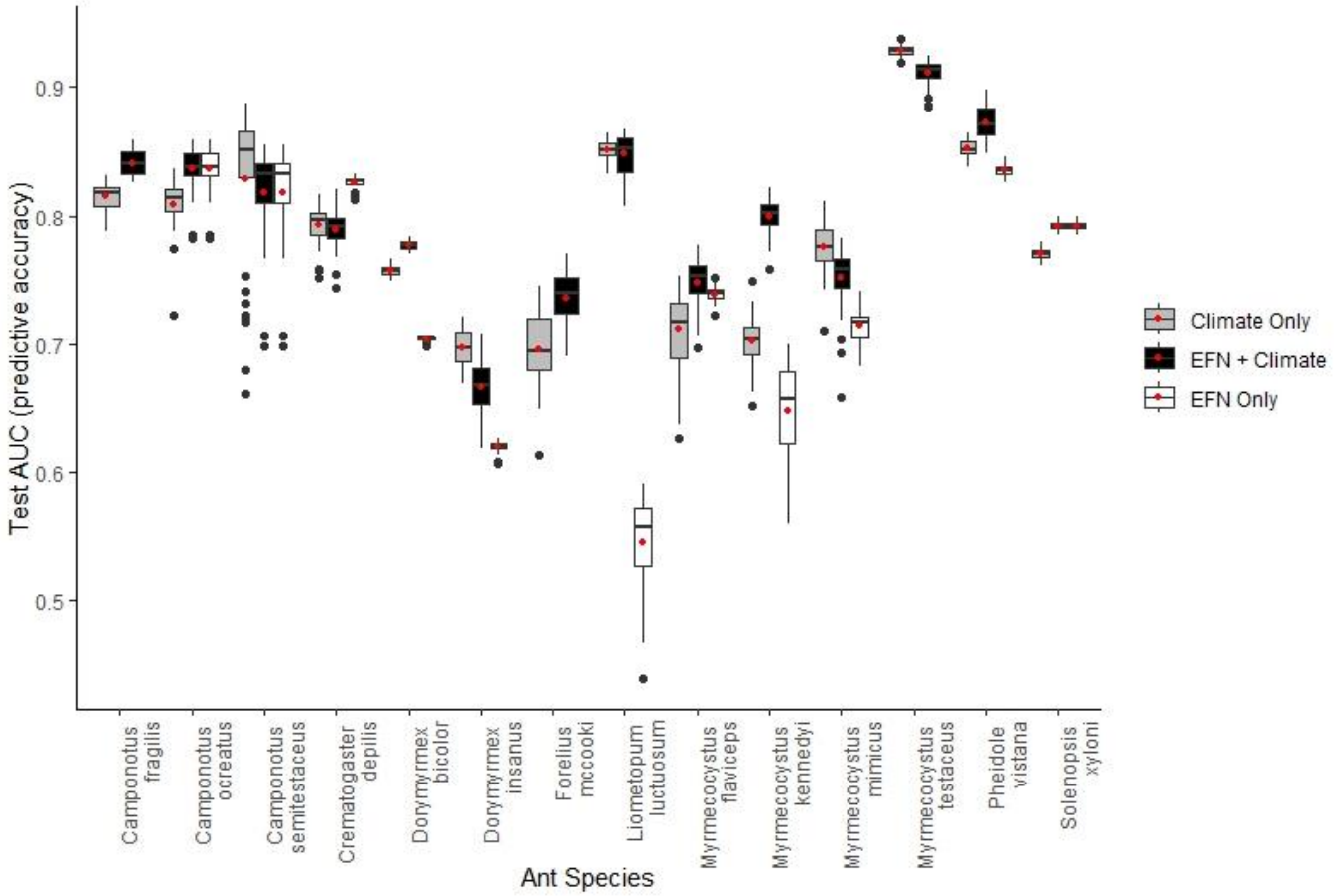


Figure 2: Boxplots comparing the predictive performance of ant species distribution models built using only climatic, climatic predictors or only extrafloral nectary (EFN) richness as a predictor. Lines on boxplots show median values, and the means are represented by the red diamonds. The variation in performance is summarized from 40 model runs per species, per set of predictors.

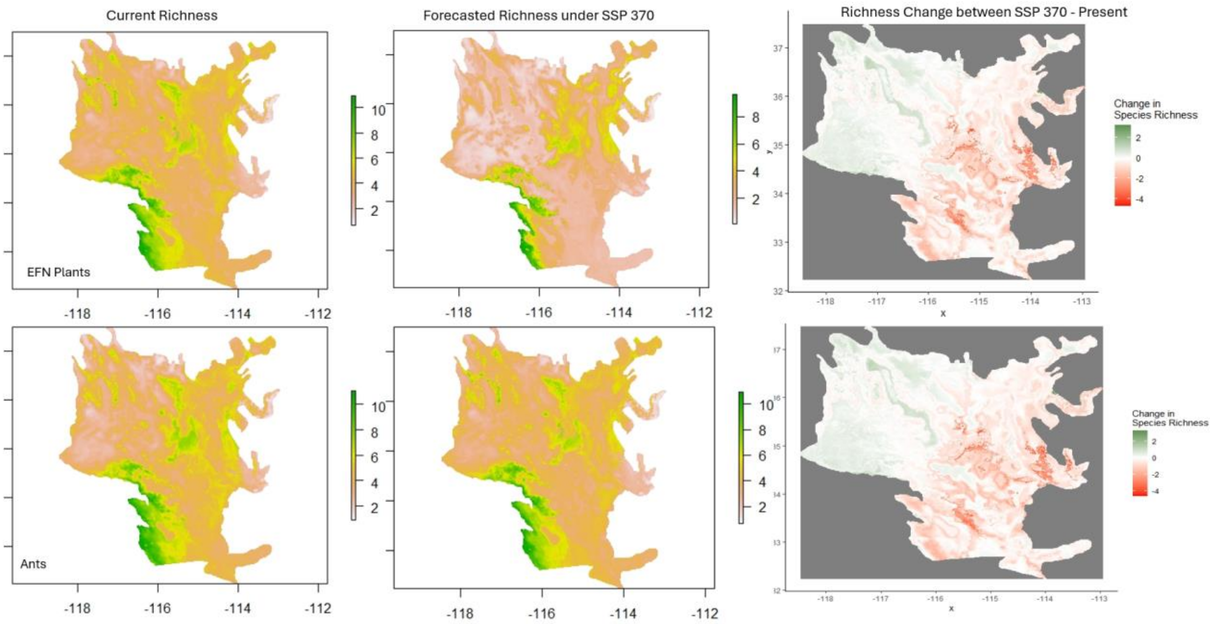


Figure 3: Current and forecasted species richness of EFN-bearing plants (top row) and their associated ant species (bottom row) across the Mojave and Colorado deserts, as well as the predicted change in richness.

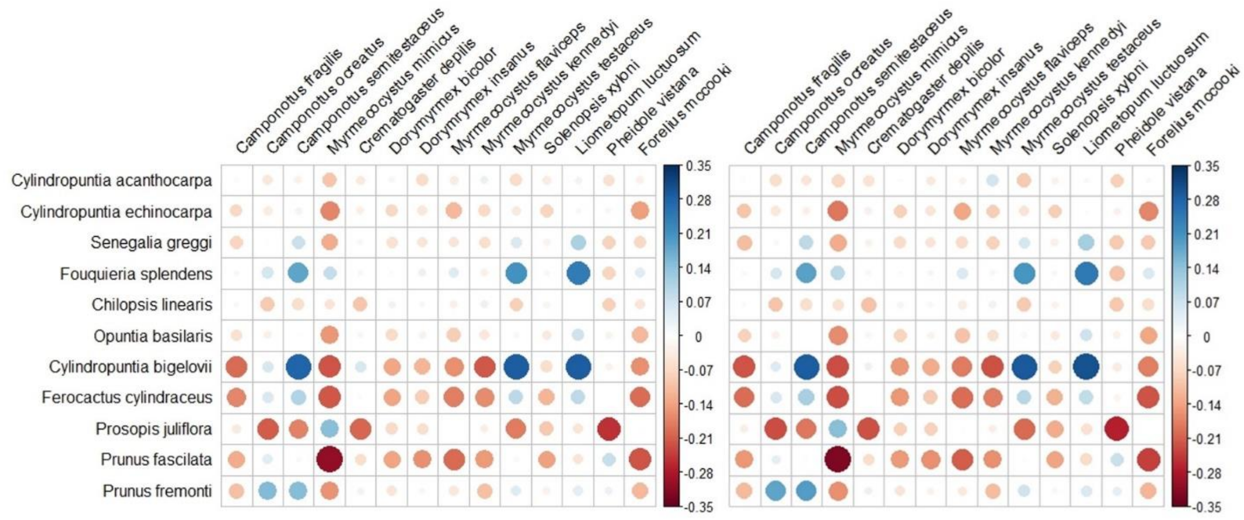


Figure 4: Proportional change in interspecific overlap of distribution ranges (Schoener's D niche overlap index) between the periods 1970-2000 and 2041-2060 for two climate scenarios: SSP 245 (left) and SSP 370 (right). Negative values in red indicate a decrease in range overlap between species over the time periods; blue indicates an increase in range overlap, and zero values in white indicate no changes to overlap.

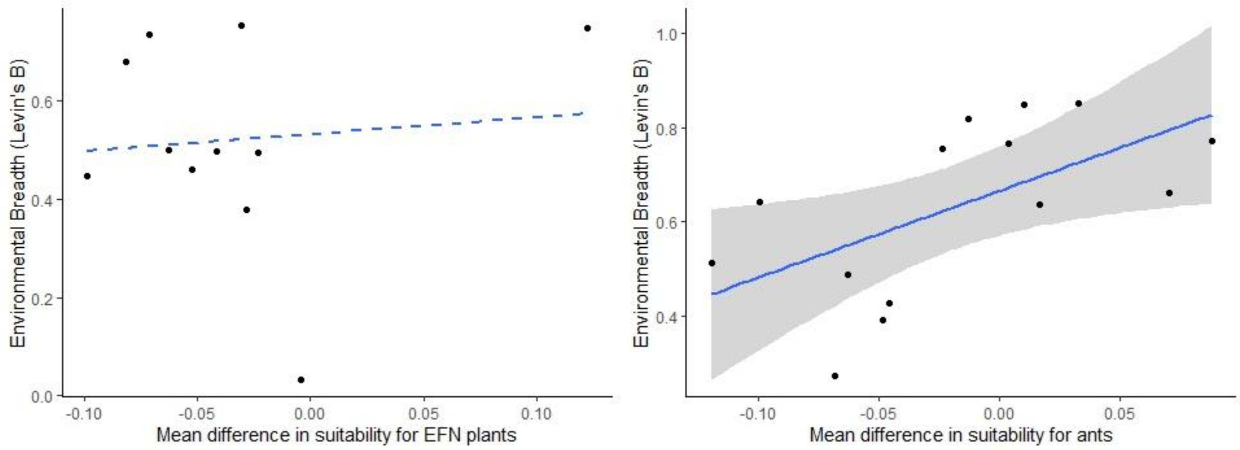


Figure 5: Correlations between environmental breadth and suitability changes for the EFN plant and ant communities of the Mojave and Colorado deserts. The solid trendline denotes a significance at the $p < 0.05$ level and the dashed line denotes an insignificant relationship.

Supplementary Information

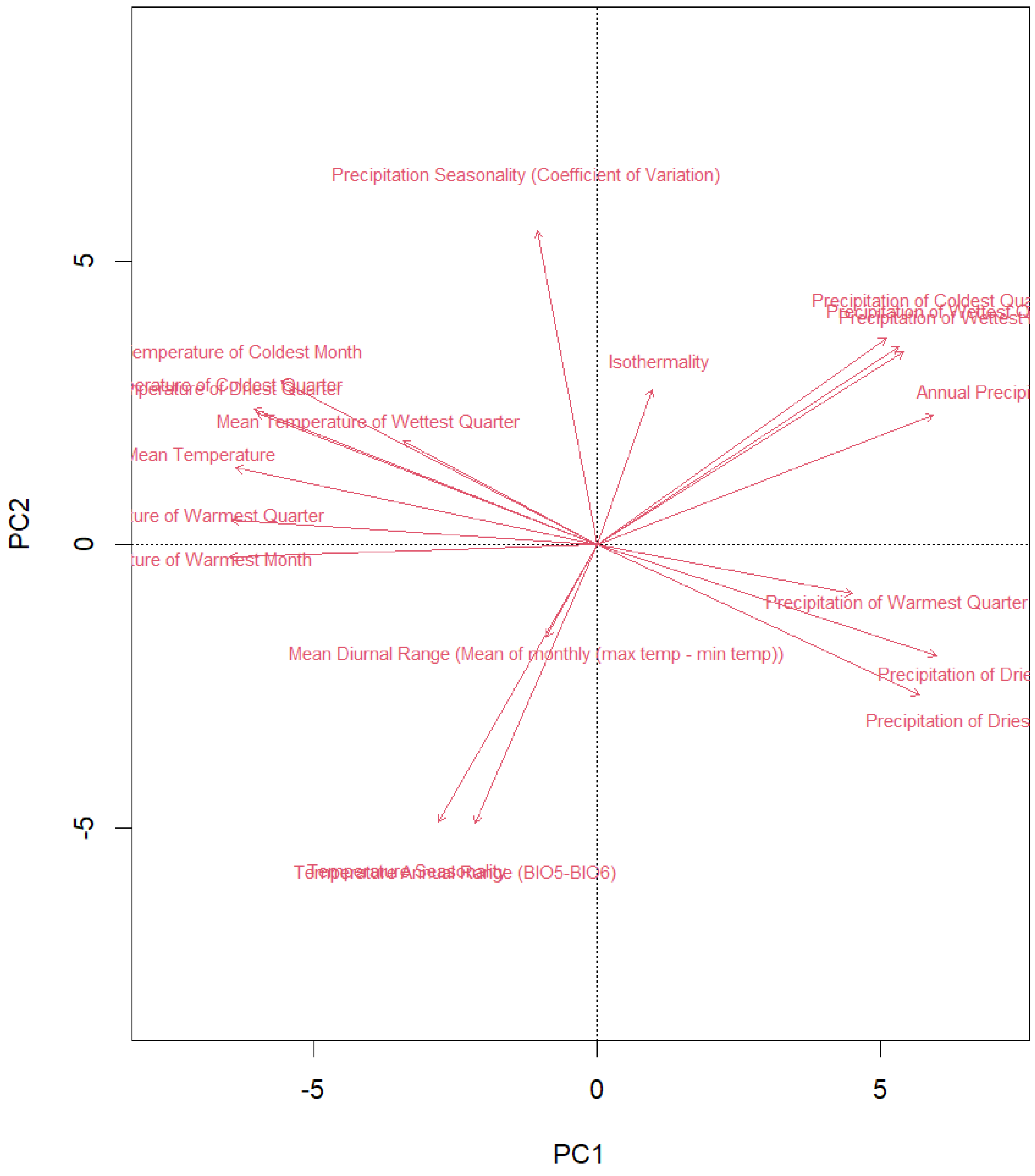
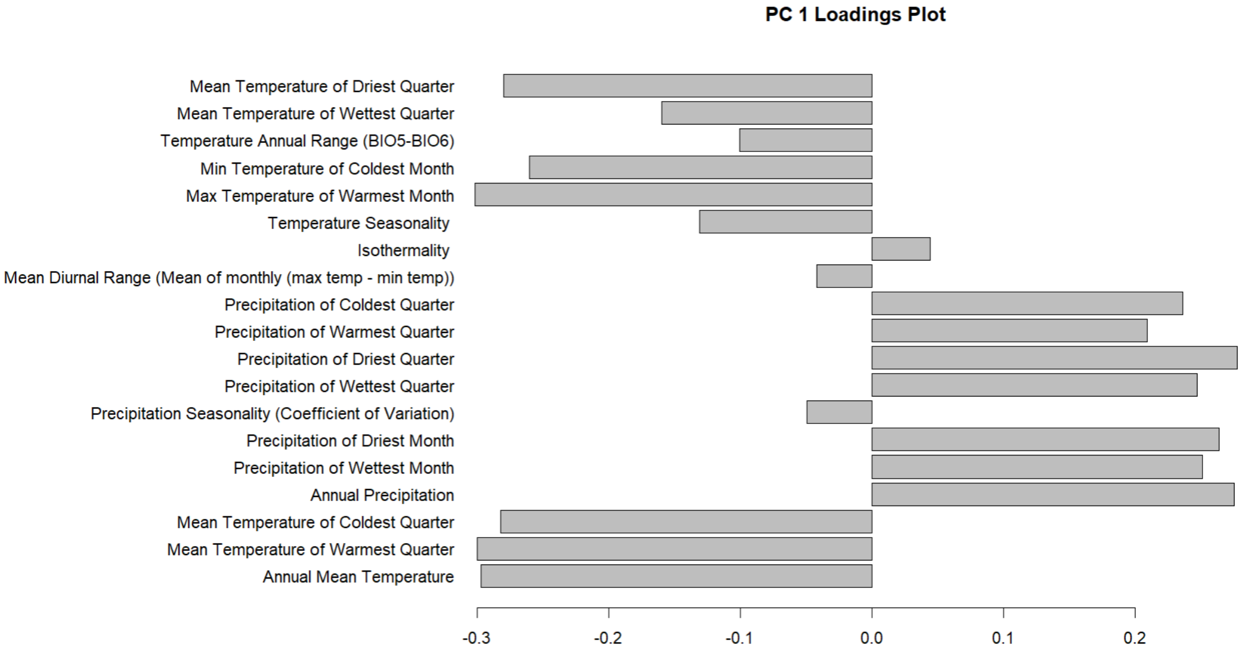
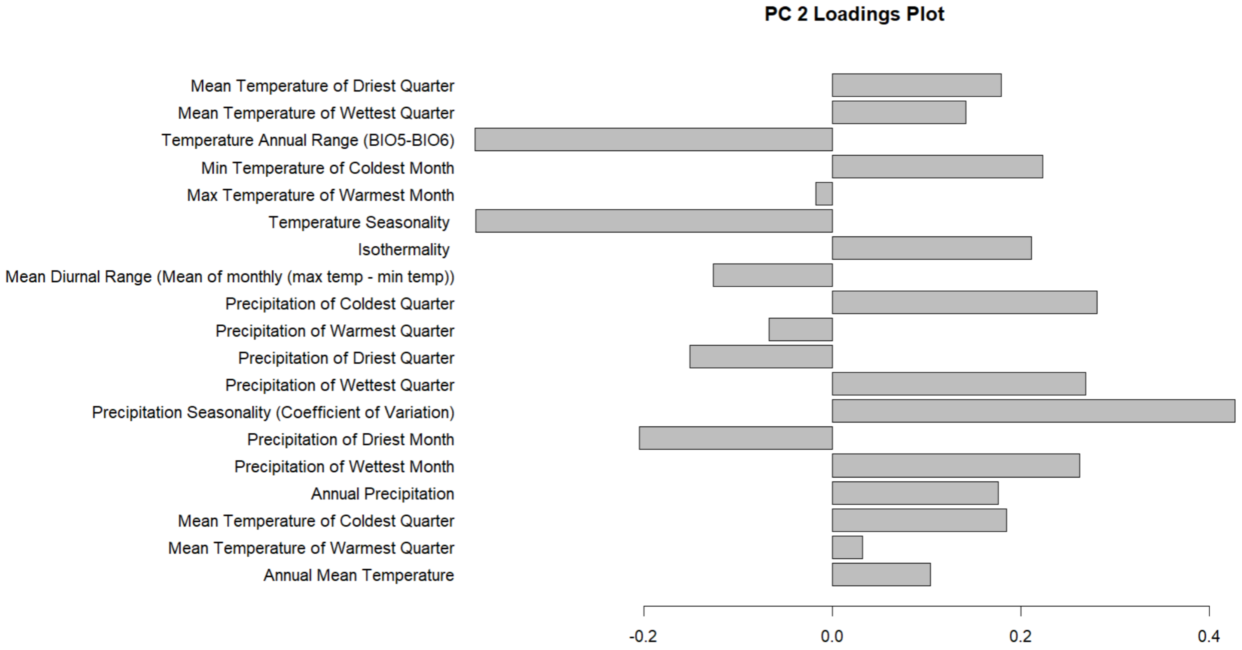


Figure 1: PCA of the 19 bioclimatic variables across the Mojave and Colorado deserts. The first four PCA axes explained 90% of the total bioclimatic variation.


PC 1 Loadings Plot
Mean Temperature of Driest Quarter
Mean Temperature of Wettest Quarter
Temperature Annual Range (BIO5-BIO6)
Min Temperature of Coldest Month
Max Temperature of Warmest Month
Temperature Seasonality
Isothermality
Mean Diurnal Range (Mean of monthly (max temp - min temp))
Precipitation of Coldest Quarter
Precipitation of Warmest Quarter
Precipitation of Driest Quarter
Precipitation of Wettest Quarter
Precipitation Seasonality (Coefficient of Variation)
Precipitation of Driest Month
Precipitation of Wettest Month
Annual Precipitation
Mean Temperature of Coldest Quarter
Mean Temperature of Warmest Quarter
Annual Mean Temperature
-0.3
-0.2
-0.1
0.0
0.1
0.2


PC 2 Loadings Plot
Mean Temperature of Driest Quarter
Mean Temperature of Wettest Quarter
Temperature Annual Range (BIO5-BIO6)
Min Temperature of Coldest Month
Max Temperature of Warmest Month
Temperature Seasonality
Isothermality
Mean Diurnal Range (Mean of monthly (max temp - min temp))
Precipitation of Coldest Quarter
Precipitation of Warmest Quarter
Precipitation of Driest Quarter
Precipitation of Wettest Quarter
Precipitation Seasonality (Coefficient of Variation)
Precipitation of Driest Month
Precipitation of Wettest Month
Annual Precipitation
Mean Temperature of Coldest Quarter
Mean Temperature of Warmest Quarter
Annual Mean Temperature
-0.2
0.0
0.2
0.4

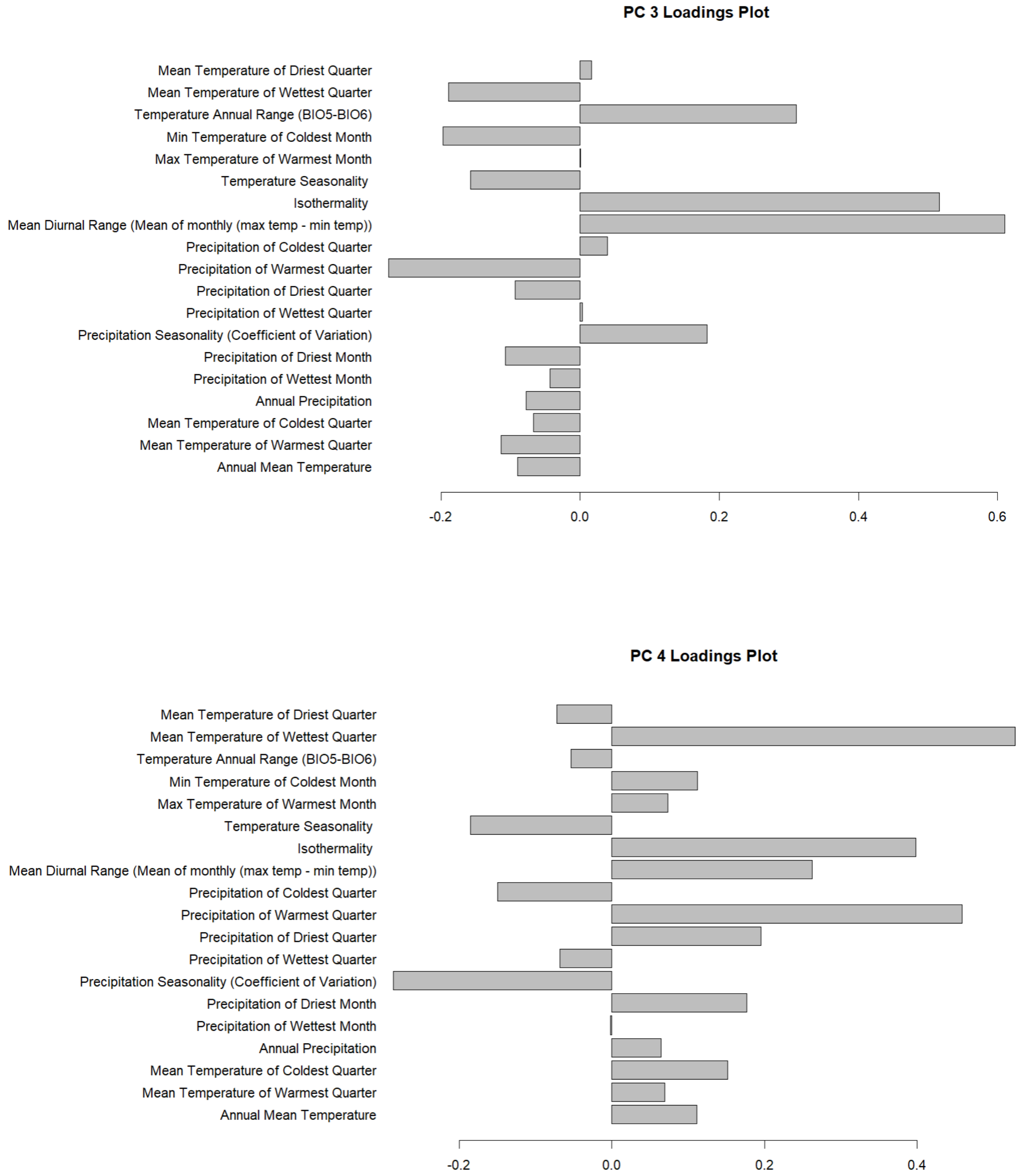


Figure 2: Loadings for each of the four PCA axes in the study.

Table 1: Maxent species distribution model performance measures for each EFN bearing plant species used in the study and the number of occurrences after thinning included in the model. Area under the curve (AUC) ranges between 0 and 1, where 0.5 is the baseline performance.

Latin binomial	Occurrences after thinning	AUC (Mean ± SD)
Cylindropuntia acanthocarpa	1563	0.86 ± 0.000
Cylindropuntia echinocarpa	3243	0.79 ± 0.000
Senegalia greggii (previously *Acacia)*	1747	0.87 ± 0.000
Fouquieria splendens	2298	0.83 ± 0.000
Chilopsis linearis	1220	0.79 ± 0.001
Opuntia basilaris	4666	0.78 ± 0.000
Cylindropuntia bigelovii	125	0.87 ± 0.002
Ferocactus acanthodes syn cylindraceus	3166	0.86 ± 0.000
Prosopis juliflora	21	0.73 ± 0.03
Prunus fasciculata	798	0.84 ± 0.001
Prunus fremontii	437	0.97 ± 0.000

Table 2: Maxent species distribution model performance measures for each ant species used in the study and the number of occurrences after thinning included in the model. Area under the curve (AUC) ranges between 0 and 1, where 0.5 is the baseline performance. Species with a score of N/A had too few occurrences to model. Two species, Camponotus sayi and Forelius pruinosis were excluded due to poor predictive performance.

Ant Species	Occurrences after thinning	AUC (Mean ± SD)
Brachymyrmex depilis	4	N/A
Camponotus sayi	14	*0.6 ± 0.04 - Excluded*
Lasius californicus	5	N/A
Liometopum luctuosum	26	0.85 ± 0.01
Myrmecocystus mimicus	23	0.78 ± 0.02
Pheidole vistana	27	0.85 ± 0.01
Pseudomyrmex apache	10	N/A
Psedumomyrmex gracilis	0 on gbif	N/A
Pseudomyrmex pallidus	11	N/A
Solenopsis xyloni	191	0.77 ± 0.00
Forelius pruinosis	78	*0.62 ±0.02 - Excluded*
Forelius mccooki	27	0.7 ±0.03
Crematogaster depilis	38	0.79 ± 0.02
Dorymyrmex bicolor	172	0.76 ± 0.00
Dorymrmex insanus	42	0.7 ± 0.01
Camponotus fragilis	32	0.81 ± 0.01
Camponotus semitestaceus	15	0.83 ± 0.06
Camponotus ocreatus	45	0.81 ± 0.02
Myrmecocystus kennedyi	30	0.7 ± 0.02
Myrmecocystus testaceus	15	0.93 ±0.00
Myrmecocystus flaviceps	26	0.71 ± 0.03

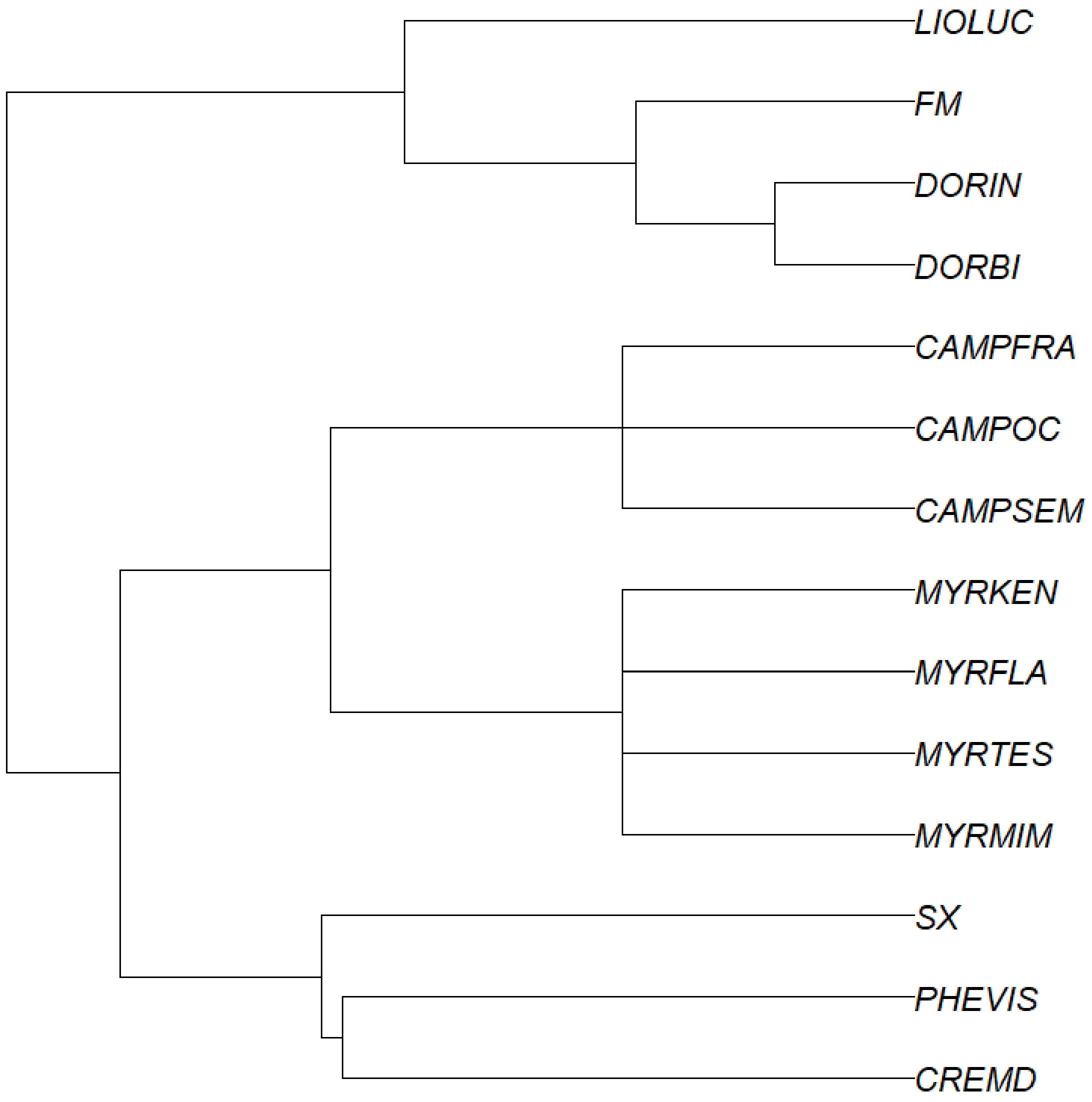
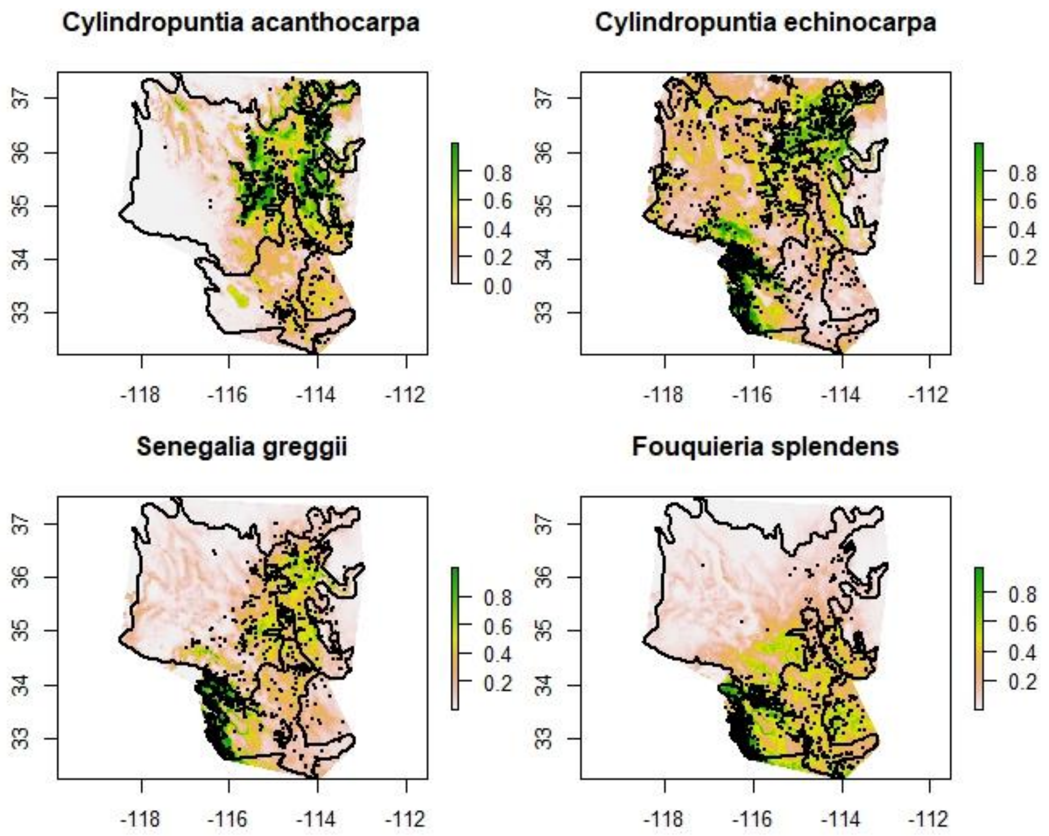


Figure 3: Pruned phylogenetic tree of ant species based on Moreau and Bell 2013.

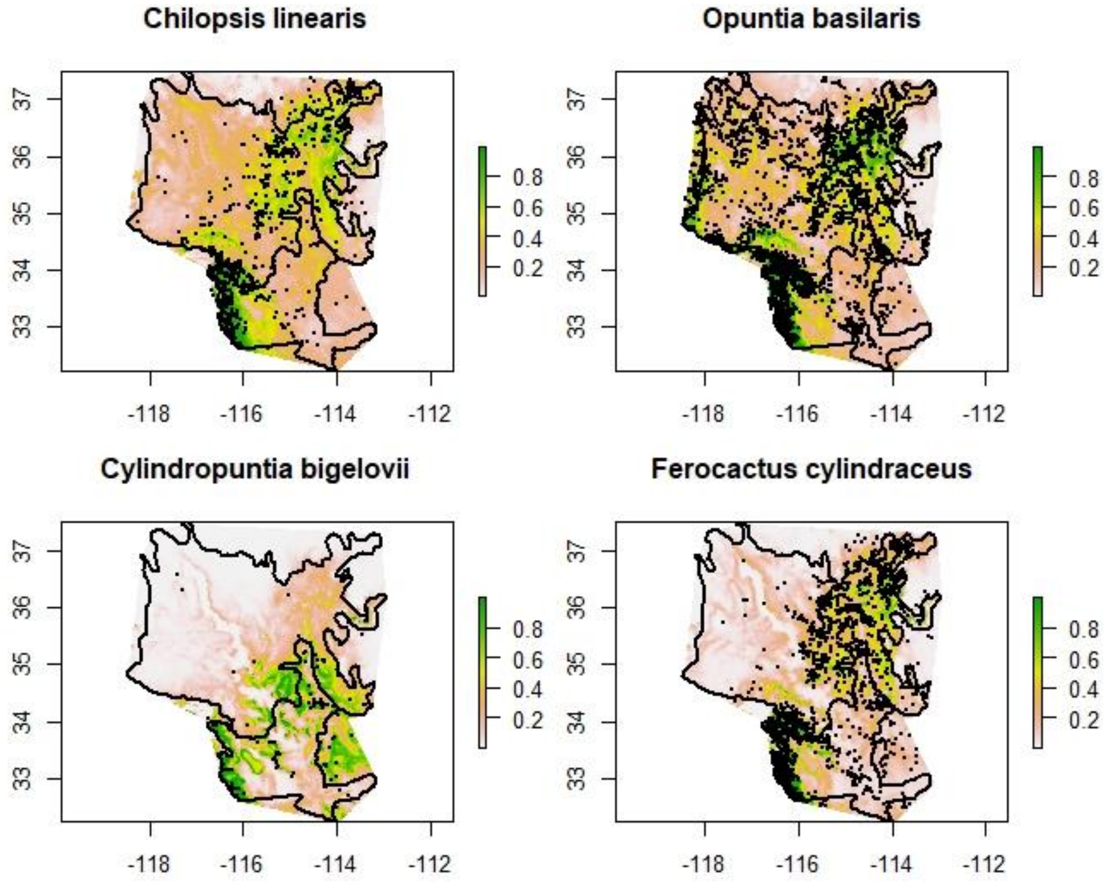


Cylindropuntia acanthocarpa

Cylindropuntia echinocarpa

Senegalia greggii

Fouquieria splendens



Chilopsis linearis

Opuntia basilaris

Cylindropuntia bigelovii

Ferocactus cylindraceus

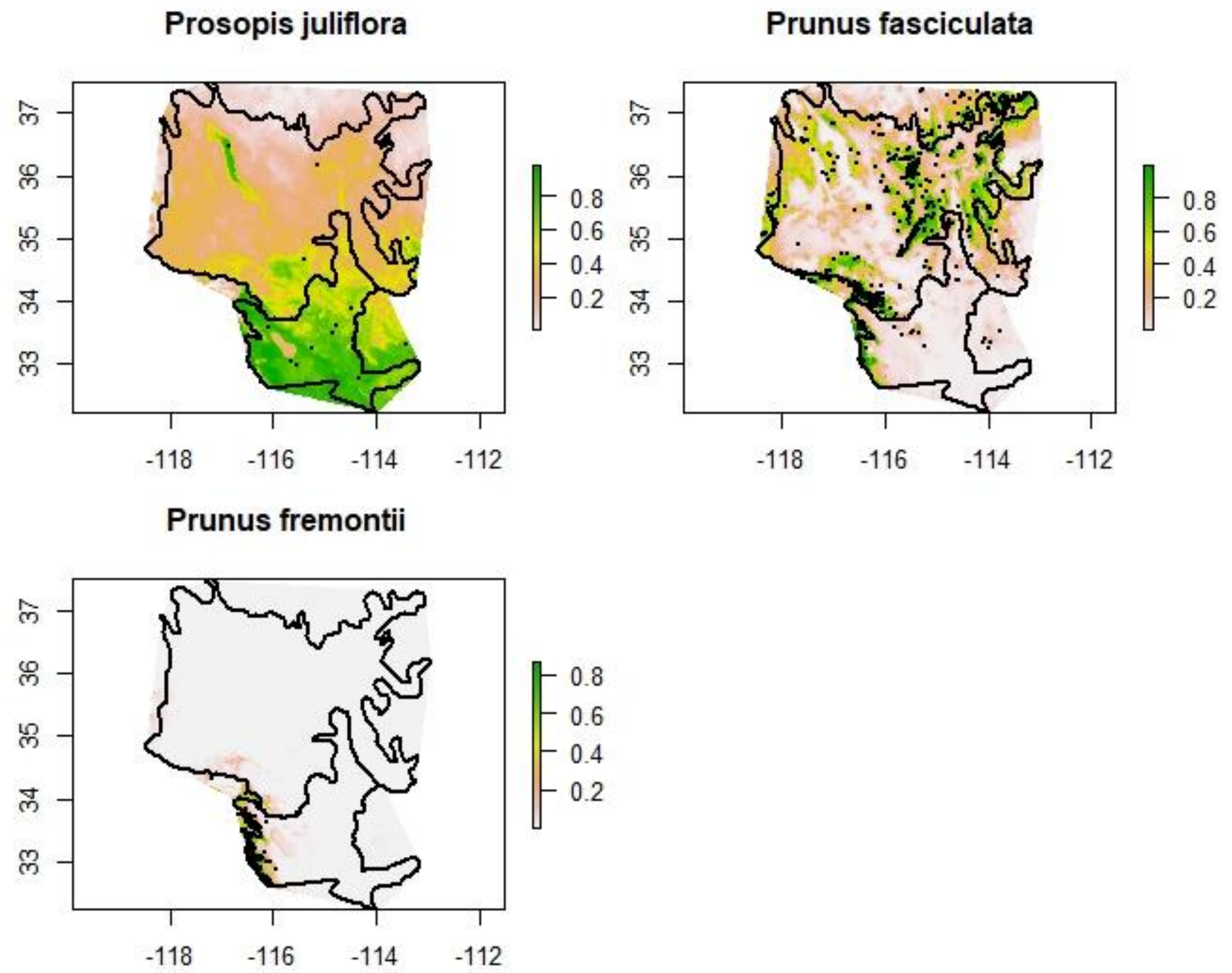
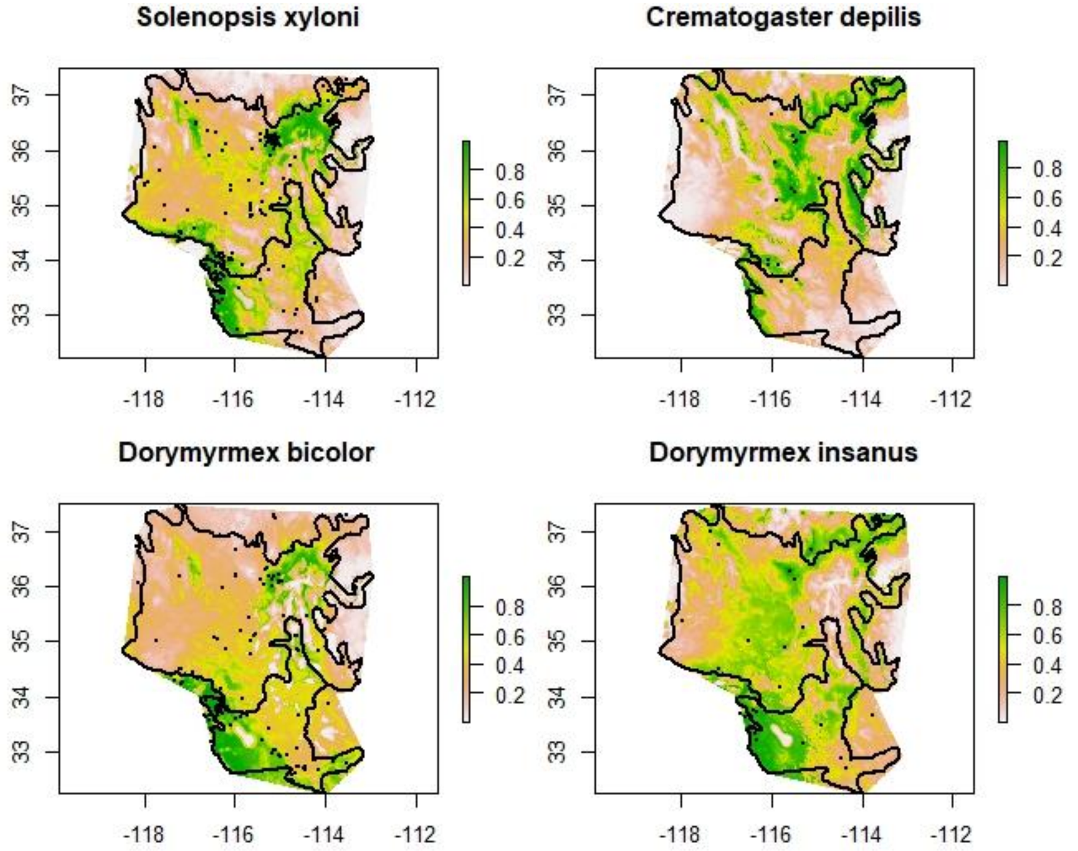
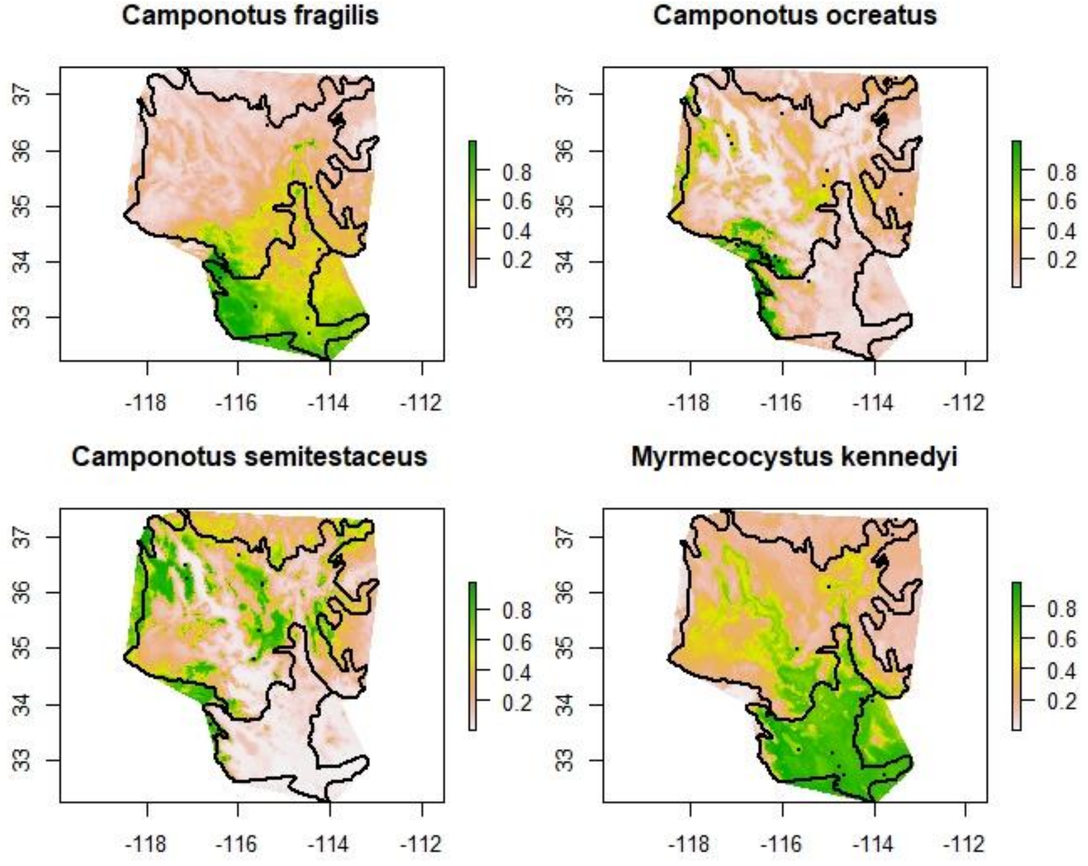


Figure 4: Consensus prediction maps for EFN-bearing plant species of the Mojave and Colorado deserts. Points are the thinned occurrences extracted from GBIF and the boundary file is the watershed boundary from USGS.


Solenopsis xyloni
Crematogaster depilis
Dorymyrmex bicolor
Dorymyrmex insanus
37
36
35
34
33
-118
-116
-114
-112
0.8
0.6
0.4
0.2


Camponotus fragilis
Camponotus ocreatus
Camponotus semitestaceus
Myrmecocystus kennedyi
37
36
35
34
33
-118
-116
-114
-112
0.8
0.6
0.4
0.2

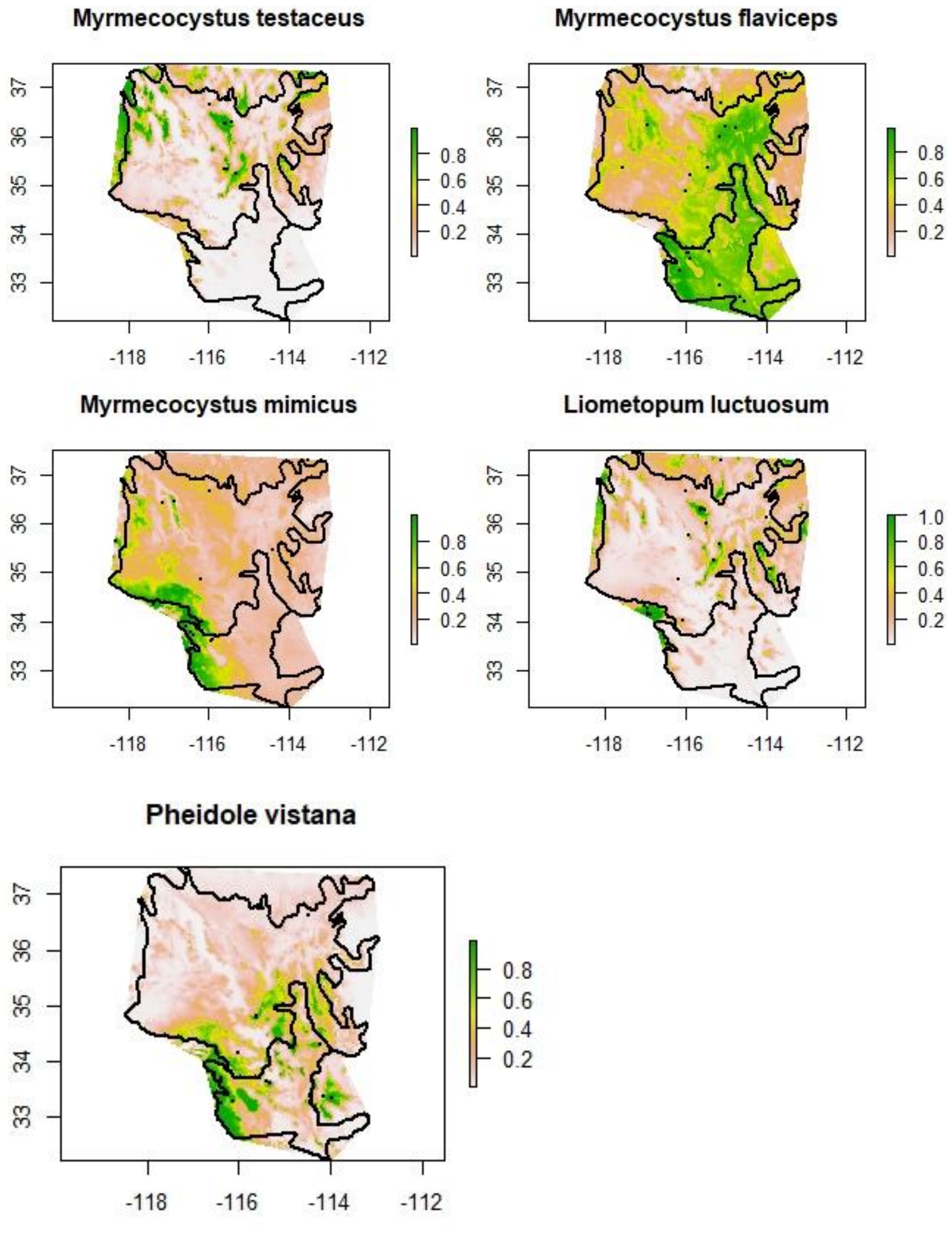


Figure 5: Consensus prediction maps for ant species of the Mojave and Colorado deserts. Points are the thinned occurrences extracted from GBIF and GABI, and the boundary file is the watershed boundary from USGS.

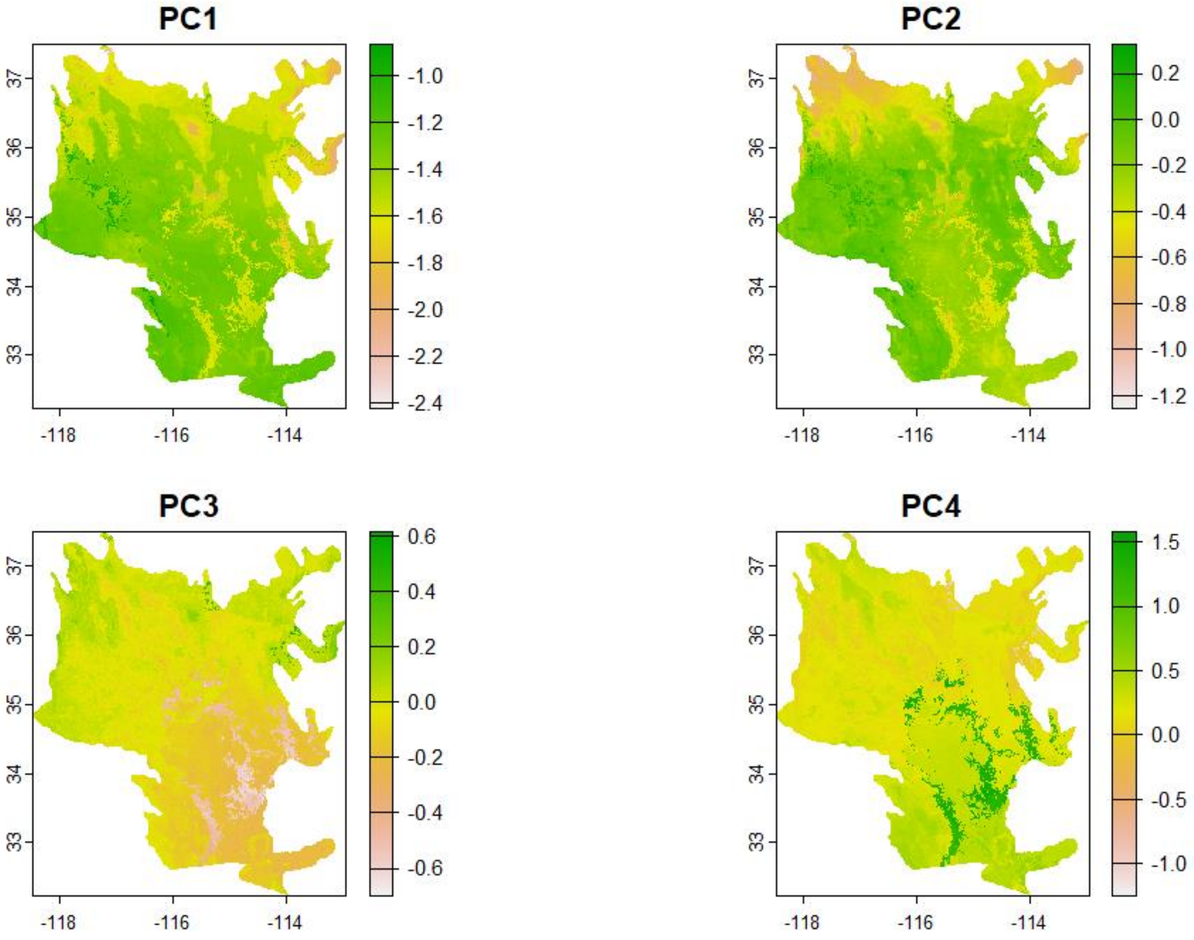


Figure 6: Shifts in the four main environmental gradients between SSP 370 and present conditions.

Table 3: Mean change in environmental suitability for individual ant species.

Ant species names	**Mean difference in future suitability under 245**	**Mean difference in future suitability under 370**
Solenopsis xyloni	-0.012	-0.02
Forelius mccooki	0.027	0.0327
Crematogaster depilis	-0.09	-0.1
Dorymyrmex bicolor	0.004	0.004
Dorymyrmex insanus	-0.009	-0.013
Camponotus fragilis	0.011	0.017
Camponotus ocreatus	-0.058	-0.062
Camponotus semitestaceus	-0.108	-0.11
Myrmecocystus kennedyi	0.081	0.088
Myrmecocystus testaceus	-0.062	-0.068
Myrmecocystus flaviceps	0.015	0.01
Myrmecocystus mimicus	0.066	0.07
Pheidole vistana	-0.042	-0.046
Liometopum luctuosum	-0.045	-0.048

Table 4: Mean change in environmental suitability for individual EFN-bearing plant species

Species name	**Mean difference in future suitability under 245**	**Mean difference in future suitability under 370**
Cylindropuntia acanthocarpa	-0.049	-0.052
Cylindropuntia echinocarpa	-0.074	-0.082
Senegalia greggii	-0.03	-0.04
Fouquieria splendens	-0.02	0.023
Chilopsis linearis	-0.025	-0.031
Opuntia basilaris	0.06	-0.071
Cylindropuntia bigelovii	0.03	-0.028
Ferocactus acanthodes syn cylindraceus	-0.057	-0.062
Prosopis juliflora	0.11	0.122
Prunus fasciculata	-0.09	-0.099
Prunus fremonti	-0.003	-0.004