CAUSES AND CONSEQUENCES OF DESERT ANT COMMUNITY ASSEMBLY

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Abstract

Understanding the mechanisms that maintain species coexistence and determine patterns of community assembly are fundamental topics of community ecology. This dissertation examines the drivers of ant community assembly mechanisms along environmental stress gradients in dryland ecosystems. This work positions facultative mutualisms and positive interactions alongside competition as key drivers of community structure. To start, I used experimental resource addition to show that the identity of mutualist ant defenders on silver cholla is a consequence of coexistence processes (here, resource partitioning of individual plants based on EFN resource availability). Investment into EFN resources is worthwhile for plants because ant defense benefits silver cholla; however, this investment is mediated by competition within the ant community. I then examined the importance of the EFN-bearing plant community for ant community assembly at macroecological scales using stacked species distribution models. The EFN-bearing plant community predicted the geographic distribution and diversity of the nectar-feeding ant community. However, interactions between the groups are vulnerable to climate change because of the predicted decrease in geographic overlap between ant-EFN-bearing plant pairs under future climate scenarios. I then examined the relative importance of environmental and biotic assembly mechanisms for ants along a desert stress gradient. The functional structure of the ant community was significantly more diverse than expected which is consistent with the mechanisms of limiting similarity and suggests the importance of competition to ant community structure. The strength of this mechanism decreased with increasing stress, demonstrating that environmental and biotic assembly mechanisms jointly and non-independently structure the ant community. Finally, I asked if environmental filtering on the functional trait composition of the plant and granivorous ant communities scales to shape ant-seed interactions. Ant functional traits responded to both environmental stress and to the functional traits of the plant community. However, seed size-dependent foraging choices arose from ant population size and not the functional structure of either community. This work showed that ant-plant interactions are integral to community assembly for both dryland communities.

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Chapter 1: General Introduction

Understanding the mechanisms that maintain species coexistence and determine patterns of community assembly are fundamental topics of community ecology (Weiher and Keddy 1995, HilleRisLambers et al. 2012, Mittelbach and Schemske 2015). This dissertation examines the drivers of ant community assembly mechanisms along environmental stress gradients in dryland ecosystems. I explore how these mechanisms also shape ant-plant interactions and scale to several aspects of community structure. Here, I begin by introducing community assembly, ant-plant mutualisms, the study of extrafloral nectary bearing plants in deserts, stress gradients, and end by summarizing the aims and scopes of this work.

Community assembly

Assembly processes are the set of processes that determine which species are found within a given community. Community ecologists primarily conceptualize these processes using the niche-based "pool-filter-subset' metaphor (Weiher et al. 2011). Species are hypothesized to belong to a regional species pool whose composition is determined through historical processes, including evolution (Vellend 2010, HilleRisLambers et al. 2012, Mittelbach and Schemske 2015). A subset of these species is capable of dispersing to the local community, first passing through a set of abiotic and biotic filters (Gotzenberger et al. 2012). Environmental filtering structures communities by only allowing organisms capable of surviving local conditions to establish and persist within the local species pool, i.e., the fundamental niche (Keddy 1992, Vellend 2010, Kraft et al. 2015). Biotic filtering restricts species to those able to coexist with the rest of the community, i.e., the realized niche (Vellend 2010). Modern coexistence frameworks explain the maintenance of diversity as the outcome of local processes such as resource partitioning and niche differentiation, as well as interspecific interactions within differing environments (Chesson 2000, Chase and Leibold 2009) and biogeographical processes, including dispersal and local extinction (Kneitel and Chase 2004). However, assembly processes can also be explained independently of the niche of the species. Neutral theory is built on the hypothesis of 'functional equivalence' between species, i.e., species on the same trophic level have identical fitness and demographics (Hubbell 2005). Neutral theory proposes that the differences between species are not relevant for explaining community dynamics and that these dynamics can be explained through stochastic processes, including ecological drift and dispersal (Weiher et al.

2011). Neutral theory is controversial because it is built upon clearly untrue premises; however, it can also be quite successful in explaining community structure (Hubbell 2005). Thus, the current approach to understanding assembly is a synthesis created through the lenses of modern coexistence, niche and neutral theories (Cody et al. 1975, Ricklefs and Schluter 1993, Hubbell 2011). At this time, community assembly processes can be considered a conceptual framework for community ecology because it is concerned with both the creation and maintenance of communities themselves (HilleRisLambers et al. 2012).

Diamond proposed that competition was the primary driving force of community assembly on islands, following assembly rules that led to predictable patterns in species co-occurrence (Diamond 1975). These assembly rules were controversial, in part because the co-occurrence patterns could also be generated by null models (Connor and Simberloff 1979). There is support for the existence of the patterns themselves across many taxa*,* i.e., fewer co-occurrences than expected; however, the processes that generate the patterns are wide-ranging (Gotelli and McCabe 2002, Brazeau and Schamp 2019, Blanchet et al. 2020). Negative co-occurrences are not the rule and in some systems, such as harsh environments, positive co-occurrences can be more common (Gotzenberger et al. 2012, Bar-Massada 2015). "Assembly rules" are no longer an active part of assembly theory vocabulary because a broader concept of assembly is now widely accepted (Weiher et al. 2011). This competition-based paradigm has been expanded to include the full range of interspecific interactions including facilitation (Lortie et al. 2004), mutualisms (HilleRisLambers et al. 2012, Ponisio et al. 2019), predation (Larios et al. 2017) and herbivory (Pearson et al. 2018). There has also been a growing interest in how multitype interactions, for instance, the combined roles of trophic and mutualistic interactions, fit into our understanding of assembly processes, (Barbier et al. 2018, Yeakel et al. 2020). Communities are networks of interacting species, with key groups such as ecosystem engineers and foundation plants playing central roles in their assembly (Schöb et al. 2012, Yeakel et al. 2020, Priest et al. 2021). Understanding the role of these key groups in multitype interactions is a valuable contribution to community theory because they can capture community complexity in a tractable way.

The little interactions that run the world

E.O. Wilson called insects 'the little things that run the world' because of their outsized influence on food webs and ecosystem services (Wilson 1987). Ants are one of the most numerically

dominant insect groups in terrestrial ecosystems, often representing 10 – 15% of animal biomass (Beattie and Hughes 2002). In deserts, many ant species are keystone taxa due to their ecosystem engineering influence on soil properties, which includes soil cycling and modification of water infiltration (Whitford 2000). For instance, the harvester ant *Pogonomyrmex rugosus* enhances water infiltration into the ground and alters overland flows because its nests have a different conductivity than the surrounding area (James et al. 2008). Ants also strongly impact most ecological processes, in part because they engage in diverse interactions with many species of plants and act as important plant defenders, seed dispersers, pollinators and herbivores (Hölldobler and Wilson 1990, Rico-Gray and Oliveira 2007). Ant-plant interactions may be particularly strong in deserts because the dietary expansion from only predation to using plant-related foods facilitated ants' evolutionary expansion into xeric ecosystems (Wilson and Hölldobler 2005). Several ant genera are granivorous, an ecological trait that is almost completely restricted to arid environments but is present all over the world (Rico-Gray and Oliveira 2007). The trait evolved independently in different desert regions, suggesting a strong role for aridity in shaping desert ant-plant interactions (Kusnezov 1956). Studying the ecology of ant-plant interactions provides insight into two of the most successful biological communities and therefore interspecific interactions in general (Rico-Gray and Oliveira 2007).

Ant-plant interactions are also a model system for understanding mutualisms. One of the first experimental papers on mutualisms was Janzen's work on swollen-thorn acacias and the ant species *Pseudomyrmex ferruginea* (Janzen 1967). He showed that the plant provides sugar from foliar nectaries, proteins from Beltian bodies and hollows used as nesting sites to ants in return for protection, and that restricting ants from the plants caused an increase in damage to the plants (Janzen 1967). The *Acacia-Pseudomyrmex* system was described as obligate, i.e., a specialized relationship between interaction partners (Janzen 1967). This system spurred both interest in ant-plant interactions and mutualistic interactions, contributing to the traditional view of mutualisms that they primarily occur between pairs of closely coevolved species and are consistently beneficial for both interacting species (Bronstein 1994, Stanton 2003). However, most ant-plant interactions are facultative and non-specialized, such that a given ant or plant species can interact with a guild of functionally similar species (Stanton 2003, Rico-Gray and Oliveira 2007). Even in the obligate domatia nesters within Pseudomyrmecinae, the specialist ants can use a variety of plant species (Davidson and McKey 1993, Beattie and Hughes 2002). Ant-plant interactions and

protective mutualisms in particular have contributed to the idea that mutualisms tend to be more context-dependent than other interactions (Chamberlain and Holland 2009, Chamberlain et al. 2014). Recognizing and describing the drivers of context-dependence gives deeper insights into ecological processes and improves predictive understanding across ecology (Catford et al. 2022).

The surprisingly recent study of EFN in deserts

Extra-floral nectaries (EFN) are defined ecologically rather than anatomically; nectar-secreting glands in plants not involved in pollination. EFN have been reported in 3941 species of plants within 108 families and have evolved 457 times independently (Weber and Keeler 2013) suggesting that this trait is beneficial to plants in a wide range of environments. Even within Cactaceae, the EFN are morphologically similar in *Cylindropuntia* and *Ferocactus* but arose independently (Mauseth et al. 2016). EFN-ant interactions are a model system for evolutionary study globally (Heil and McKey 2003) but are not well studied in deserts (Aranda-Rickert et al. 2014). Historically, botanists believed that xerophytic plants lacked EFN as a rule because of the water required (Pemberton 1988). Before Pemberton's Mojave Desert survey, only a single native species (*Helianthella californica*) had been reported in California (Keeler 1981), while other sources report that they are completely absent (Buckley 1982). Pemberton found that the northern slopes of the Granite Mountains in the Mojave Desert have some of the highest cover recorded of EFN-bearing plants so far (24-28%) in temperate areas, and that EFN-bearing plants are abundant across the Mojave and Colorado deserts (1982). Now, more than 30 EFN-bearing genera have been reported in the neighbouring Sonoran Desert (Marazzi et al. 2013, Franklin et al. 2016). There are many species of Cactaceae with EFN, but they are still very poorly studied (Mauseth et al. 2016). There are likely many more species of cacti that have EFN than are currently described because EFN are often located in non-modified spines or foliage leaves with no way of distinguishing them from non-secreting parts (Mauseth et al. 2016). In *Cylindropuntia imbricata*, they are vascularized and can provide water to the EFN even during drought periods (Ávila-Argáez et al. 2019). EFN nectar production can be costly for plants in deserts (Leal and Peixoto 2017). Therefore, EFN are likely a key trait that improves survival in these harsh conditions because they are found in many desert species despite their cost.

Stress gradients in stressful environments

Stressors are any environmental factors that reduce species' fitness in terms of survival, growth or reproduction (Grime 1989, Lortie and Pugnaire 2010). Environmental gradients are directional, spatially consistent changes in community composition and environmental factors (Lortie and Pugnaire 2010). Environmental factors that are not limiting are not stress (Underwood 1989). Thus, the key difference between environmental gradients and stress gradients is that species abundances/performance will always decrease along a stress gradient but can vary in different ways along environmental gradients (He and Bertness 2014). Extreme stress is defined as a condition where 80% of a species' success (independent of interactions) is impaired by stress (Lortie and Pugnaire 2010). Stressors can also be biotic, such as resource gradients; however, most of the literature focuses on environmental stress gradients. Most models of coexistence have focused on the impacts of lethal stress instead of species adapted to stressful environments (Kim and Ohr 2020). Under these models, only a few species can tolerate the very harsh conditions which leads to low diversity. Yet, deserts globally are home to incredible diversity. The Mojave Desert is home to at least 1680 species of vascular plants, many endemic (Rundel and Gibson 2005). Drylands in Australia have far higher ant diversity than expected, for instance, some semi-arid regions have upwards of 120 species of ant per hectare and some desert-adapted genera have over 300 species within them (Andersen et al. 2015, Andersen 2016). Species can respond to or cope with long-term abiotic stress by evolving different locally adapted strategies (Calow 1989). Stress gradients within stressful environments provide an opportunity to better understand the drivers of desert diversity.

A key application of stress gradient research is climate change prediction. Spatial gradients are one of the most used approaches to studying ecosystem-level responses to climate change (Dunne et al. 2004). Species have critical thermal and drought tolerance limits that constrain where they can be found along gradients (Diamond et al. 2012, Parr and Bishop 2022). Interactions between species can be strong and are not necessarily correlated with climate which can reduce the predictability of responses if not considered (Dunne et al. 2004). Changes to species interactions can cause losses to ecosystem functioning before stress levels hit certain thresholds (Walther 2010). For these reasons, studying whole community responses to stress can complement manipulative, experimental approaches to better understand when natural

complexity or emergent properties of whole ecosystems hinder our predictive ability. Climate vulnerability is the degree of threat due a changing climate to a community or ecosystem (Kling et al. 2020) and variation in vulnerability arises from the amount of climate change itself (exposure), the amount of detrimental change from a given amount of exposure (sensitivity) and the ability of an ecosystem to adapt or reorganize following these changes (Dawson et al. 2011, Kling et al. 2020). Stress gradients are natural laboratories for quantifying these metrics. Studying community changes along stress gradients can help us to understand the thresholds at which ecosystem functioning and ecosystem services (the subset of function relative to us) are impacted by environmental stress arising from a changing climate.

Aim and scope of current work

This work centers facultative mutualisms and positive interactions alongside competition as key drivers of community structure. I extend community ecology theory to study interactions on multiple trophic levels enabling a deeper understanding of complex ecological dynamics.

How plant investment into EFN nectar translates into partner identity, and thus defensive quality, is a fundamental question in facultative mutualisms because plants cannot restrict visitation to only the most effective mutualist. Chapter 2 proposes that the identity of ant defenders is a consequence of coexistence processes (here, resource-partitioning of individual plants based on EFN-resource availability). I used experimental resource addition alongside the natural variation in EFN resources on silver cholla (*Cylindropuntia echinocarpa*) to test if the quality of ant defense is determined by competition hierarchies within the ant community. By manipulating the sugar resources available to ants this chapter aims to demonstrate a causal relationship between EFN resource availability and the associated ant communities with consequences for herbivore reduction and plant fitness. This chapter also contributes to the growing body of literature establishing the importance of EFN-mediated ant defense for Cactaceae because these interactions have not been tested in silver cholla, a widespread and common EFN-bearing foundation species of the Mojave Desert, California.

Chapter 3 evaluates the contribution of the EFN-bearing plant community for ant community assembly at macroecological scales. I built stacked species distribution models (s-SDMs) of the EFN-bearing plant and nectar-feeding ant communities of the Mojave and Colorado deserts under current and two future climate scenarios. I examined if adding the EFN-bearing plant

community to ant species distribution models improves their predictive accuracy. I also quantified the proportion of the diversity of the ant community arising from the EFN-bearing plant community diversity and the proportion arising from shared climate preferences with the EFN-bearing plant community. Ants and plants are obviously different physiologically and may have different climate niches and, therefore, different responses to climate change. Chapter 3 also examines the extent of this variation in climate sensitivity, and consequently, the future capacity for ant–plant interactions in the Mojave and Colorado deserts. This chapter contributes to our understanding of the biotic drivers of species distributions and assembly patterns, as well as the drivers of diversity and the consequences of climate change for two important Mojave Desert communities.

Chapter 4 provides a comprehensive assessment of the relative importance of environmental and biotic filtering for desert ant community assembly. Two major hypothesized deterministic processes predict contrasting but non-exclusive patterns in the trait distributions of coexisting species. Environmental filtering can lead to a convergence in traits among coexisting species (Weiher and Keddy 1995). In contrast, limiting similarity suggests that dissimilarity in traits among ecologically similar species can promote coexistence through reducing competition and partitioning resources and the environment (Abrams 1983, Gotzenberger et al. 2012). The stress-dominance hypothesis of community assembly predicts that environmental filtering should be stronger in more stressful environments and that competition is stronger in benign environments (Grime 1977, Weiher and Keddy 1995, Swenson and Enquist 2007). Thus, functional similarity should increase with increasing environmental stress. To test these predictions, I used population-level morphological trait measurements (i.e., mean values per species per site) to study the functional structure of ant communities along a regional-scale environmental stress gradient across the San Joaquin Desert. Though not the primary focus of this chapter, I also compared assembly patterns estimated from functional traits to patterns estimated from phylogenetic relationships. Second, I compared climatic niche overlap to trait dissimilarity for the species collected to describe patterns at the scales of species distributions across North America. The results from this chapter improve our ability to generalize when predicting the outcome of environmental change.

Seed removal by ants is part of desert ecosystem function because granivorous ants can collect large quantities of seeds which influences plant abundance, diversity and seed bank densities (Brown et al. 1979, MacMahon et al. 2000, Johnson 2001, DeFalco et al. 2009). Chapter 5 aimed to show how environmental filtering on ant and annual plant functional traits translates into seed removal rates. This chapter used functional traits and gradients to understand the consequences of increasing aridity on community composition, and to gain a mechanistic understanding of how these shifts can impact interactions and therefore ecosystem functioning.

Collectively, this dissertation contributes to an understanding of how ant communities are assembled in deserts and explores the consequences of ant-plant interactions on several aspects of community structure.

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Chapter 2: Experimental resource supplementation shifts ant-mediated defense on silver cholla

Citation

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Data availability statement

All data is published: https://doi.org/10.5281/zenodo.17185793 Statistical analyses and figures are available in a reproducible document: https://jennabraun.github.io/ant-cactus_interactions/

Authorship statement

JB conceived of the study, JB and CJL designed the survey, JB collected the data and designed the analysis, JB wrote the manuscript and CJL critically edited the manuscript.

Abstract

1. Extra-floral nectaries (EFN) often mediate facultative mutualisms between plants and ants. Ants obtain a nutrient-rich food source from plants in exchange for defending the plant from herbivores. Ant species can differ in effectiveness as plant defenders and compete for access to mutualism partner resources. The partitioning of mutualist-provided resources between ant species can have important implications for both ant coexistence and plant fitness. How plant investment into defensive traits translates into partner identity, and thus defensive quality, is a fundamental question in facultative mutualisms because plants cannot restrict visitation to only the most effective mutualist.
2. We conducted an artificial nectar supplementation experiment in the Mojave Desert using a population of the EFN-bearing cactus species silver cholla (*Cylindropuntia echinocarpa*), replicated over two spring growing seasons. We measured the response of the ant community to supplemented and natural EFN resources and evaluated the effectiveness of ant defense against herbivores and for plant fitness.
3. Resource availability, both natural and experimental, impacted the abundance and identity of ants associated with silver cholla. Experimentally increasing sugar resources disrupted the existing resource partitioning between ant species. Cactus coreid (*Chelinidea vittiger*) abundance on unsupplemented silver cholla increased over the study period but not on resource-supplemented plants. The most important mutualist was *Crematogaster depilis*, at least during the early spring, because this species was associated with lower herbivore abundance and increased seed set.
4. This trend suggests that increases in EFN resources provided by plants directly translate to increased services from mutualists. Collectively, these results suggest that the energetic investment into EFN is beneficial to silver cholla, but the return on investment is mediated by competition hierarchies between mutualists.

Synthesis: The partitioning of EFN resources between ant species influences defense and subsequent fitness effects on silver cholla.

Introduction

Facultative mutualisms involve guilds of interacting species and are more common than one-to-one relationships (Stanton 2003). Facultative mutualisms are often consumer-resource relationships, where resources are exchanged from one partner to the other in return for services (MacArthur and Levins 1967, Holland and DeAngelis 2010). However, resource provisioning is costly and there is a risk if the resources are provided to partners that do not reciprocate (Bronstein 2001a). The maintenance of facultative mutualisms can be challenging to explain because mutualism partners often differ in the benefit they provide to their partners (Bronstein 2001a, 2001b, Miller 2007a). This variation in benefit can shift the interaction from mutualism to commensalism to parasitism (Klironomos 2003). When the costs of mutualism outweigh the benefits, there should be selection against the costly mutualism traits, potentially leading to the loss of the traits. Examining the drivers of variation in facultative mutualisms is key to understanding the evolution of positive interactions and will provide insight into the vulnerability of mutualisms to future collapse.

Indirect plant defense mutualisms are complex yet tractable model systems to examine how partner investment structures the dynamics of multi-trophic systems. Defense mutualisms are often mediated by extra-floral nectaries (EFN), wherein ants and other predatory arthropods defend plants from herbivores in return for a food source rich in carbohydrates, water, lipids and other nutrients secreted by the plant's EFN (Heil and McKey 2003, Koptur 2005, Rico-Gray and Oliveira 2007). These facultative mutualisms are maintained by the resource investment by plants but are prone to context-dependence; however, quantitative syntheses have demonstrated that these interactions are on average beneficial for the plants (Heil and McKey 2003, Rosumek et al. 2009, Chamberlain and Holland 2009, Trager et al. 2010, Leal and Peixoto 2017). The quantity and quality of the EFN resources provided by plants can directly impact defensive efficacy by influencing the foraging activity and aggressiveness of associated ant species (Ness et al. 2006, 2009, Miller 2014, Fagundes et al. 2017). Defense efficacy varies between ant species (Ness et al. 2006, Fagundes et al. 2017) and increases in EFN availability do not always translate to enhanced defense (e.g. Chinarelli et al. 2022, Souza et al. 2022). How EFN

availability shapes partner identity is a fundamental question, as plants can't limit visits to only the most effective mutualists.

Competition among ant species can provide a mechanistic explanation for the variation in the partner identity in mutualisms. Typically, the most competitive and dominant ant species is expected to monopolize the best resources, displacing subordinate species to lower quality resources (Blüthgen and Fiedler 2004a, Cerdá et al. 2013). This raises the question of how mutualist guild diversity is maintained in the face of intense competition (Palmer et al. 2003). The classic coexistence mechanisms are forms of niche partitioning within heterogeneous environments (Chesson 1991, Palmer et al. 2003). Ants partition resources through foraging at different times, temperatures, and within specific territories (Savolainen et al. 1989, Albrecht and Gotelli 2001, Wittman et al. 2010, Perfecto and Vandermeer 2013). Recent theoretical models have demonstrated that partitioning partner-related resources can mediate stable competitive coexistence among consumers in a consumer-resource mutualism (Lee and Inouye 2010, Johnson and Bronstein 2019). Thus, intraspecific variation in EFN resource availability may have important implications for ant species coexistence which, in turn, impacts plant fitness. Studies that manipulate EFN resource availability (through augmentation or induction, for example) have demonstrated that ants respond directly to resource variation (e.g. Pacelhe et al. 2019, Calixto et al. 2021a). However, few have related the response to ant competition and partner identity in natural systems (but see Palmer et al. 2002). Relating resource partitioning to defense efficacy is a key step to a deeper understanding of indirect defense systems.

We conducted an artificial nectar augmentation experiment in the Mojave Desert repeated over two spring seasons using a population of silver cholla *Cylindropuntia echinocarpa* **(**Engelm. & J.M. Bigelow), an EFN-bearing shrub in the Cactaceae. Cactaceae, and the opuntiads particular are emerging as model systems for studying the function of EFN in arid environments though only a small proportion of species have been studied (e.g. Pickett and Clark 1979, Miller 2014, Mauseth et al. 2016, Sandoval-Molina et al. 2018, Ávila-Argáez et al. 2019). Ant defense has not been studied in the Mojave Desert even though the northern slopes of the Granite Mountains have some of the highest percent cover of EFN-bearing plants outside the tropics (around 22-24%) (Pemberton 1988). We examined the hypothesis that EFN resource availability influences the quality of ant defense through resource partitioning within the ant guild. We tested the

following predictions: 1) Resource supplementation alters ant assemblages through species-specific increases in ant attendance and abundance on silver cholla; 2) Ant species differ in their defensive abilities in terms of reductions in herbivore abundance and effects on plant fitness; 3) Ant species partition silver cholla individuals on the basis of natural EFN availability and 4) The ant species that dominates the supplemented plants will also dominate plants with the greatest natural EFN resource availability. This study addresses how investment into defensive traits translates into defensive quality through partner identity and provides insight into the capacity to use EFNs as a tool to index mutualistic association patterns in a harsh ecosystem relatively unexplored for plant-ant mutualisms.

Methods

Study Species

Silver cholla (*Cylindropuntia echinocarpa*) is a common EFN-bearing cholla cactus native to the Southwest United States. Silver cholla's range spans the Mojave and Colorado deserts between elevations of 300 – 1400 m (Pemberton 1988, Baldwin 2002). Silver cholla has a shrubby habit with a short main trunk and main spreading branches that curve upwards (Baldwin 2002). It has cylindrical segments 2-3 cm in diameter and with 6 - 15 mm tubercles and spines (Baldwin 2002). Silver cholla flowers from April to May and sets seed in the early summer. The fruits are dry and also have spines and tubercles (Baldwin 2002). The mean crown diameter of the focal silver chollas at the study site was 55 cm and the mean height was 53 cm (Figure A1).

Silver cholla's EFNs are located within areoles, small flat highly modified spine bearings areas that are the only new growth sites (Figure 2.1). Therefore, EFNs are limited to developing vegetative segments and reproductive structures (flower buds and, later, ripening fruits) (Mauseth et al. 2016). Active EFNs are associated with both reproductive and vegetative growth (authors, pers. obs). EFNs are active even on sites of very early growth and appear to continue nectar secretion throughout fruit production (authors, pers. obs). Silver cholla reproduce primarily through seeds; however, some asexual vegetative reproduction occurs through the rooting of detached stem segments but at much lower rates than other cholla species (Bobich and Nobel 2001, Ebert 2006). The *Cylindropuntia* genus contains species without EFN (Baldwin 2002), suggesting that this trait may be evolutionary labile (Miller 2007b).

Figure 2.1: Blue arrows point towards locations of extra-floral nectaries (EFN) within areoles of silver cholla (*Cylindropuntia echinocarpa*). Photographs panels show areoles with EFNs (upper), growth habits of silver cholla (lower left) and *Crematogaster depilis* foraging on silver cholla (lower right).

Study Location

The study was conducted in Sunset Cove at the University of California's Sweeney Granite Mountains Desert Research Center (GMDRC) within the Mojave National Preserve in California on the eastern slopes of the Granite Mountains (34°46′26.5″N, 115°39′31.3″W, 1280 MASL). Mean annual precipitation is 217 mm but is highly variable (WRCC 2024). The diverse shrub and cactus community includes *Larrea tridentata*, *Acamptopappus sphaerocephalus*, *Ambrosia salsola*, *Eriogonum fasciculatum* and *Cylindropuntia ramossima*. Silver cholla is the most

abundant EFN-bearing species at the site; other EFN-bearing species include *Opuntia basilaris* and *Cylindropuntia acanthocarpa*. All fieldwork took place on GMDRC property with permission from the GMDRC's director; no permits were required. No ethics approval was required for this study.

Data collection

Resource supplementation

The resource supplementation experiment was run between April and May 2023 and again in April and May 2024 with another set of plants. Sixty focal silver plants were used in 2023 and 80 were chosen in 2024 within a spatial extent of 280 × 165 m. Individual plants were selected by walking in a line starting in different quadrants of the site and choosing plants with both new vegetative and reproductive growth. We created a high-value resource by filling 15 ml centrifuge tubes with 20 Brix honey water and providing unlimited access to the artificial nectaries with cotton watering wicks (Figure 2.2). We were not able to successfully measure the natural sugar concentration due to the inability to reliably restrict arthropods from the EFN. Additionally, sugar concentration can vary throughout the day in arid environments due to environmental conditions. The honey water's concentration approximates a general range of common nectar concentrations and was achieved using a refractometer (Eclipse low volume). Honey solutions have been used in other studies to experimentally recruit ants (e.g. Del-Claro and Oliveira 1993), including within arid ecosystems (Lanan and Bronstein 2013, Flores-Flores et al. 2018). Each artificial nectary was placed within a 50 ml centrifuge tube to prevent vertebrate access (Figure 2.2). Every other focal plant was 'treated' by wiring one artificial nectary tube per cholla individual among new growth near the top of the plant. The tubes were kept filled with the honey water solution and the wicks were replaced weekly.

Figure 2.2: Artificial nectaries were created by filling 15 ml centrifuge tubes with 20 Brix honey water. Unlimited access was provided to the artificial nectaries with cotton watering wicks. Each artificial nectary was placed within a 50 ml centrifuge tube to prevent vertebrate access.

Surveys

In EFN-bearing cholla, EFN are restricted to areoles which are the only sites of new growth (Mauseth et al. 2016). To estimate the quantity of EFN resources available from each plant in 2023, we counted the number of segments bearing areoles with active new growth, new growth nodes (both vegetative and reproductive) and the number of flower buds. The number of new growth nodes was strongly correlated with the number of segments bearing areoles with active new growth (Pearson's = 0.9, $t = 15.9$, $df = 59$, $p < 0.001$). Therefore in 2024, we estimated EFN resources using only the number of segments bearing areoles with active new growth and flower buds because they are simpler to estimate on dense plants. In both years, new growth segments, new growth nodes and the number of flower buds were quantified as total counts per plant. We measured the cholla's width at the widest horizontal axis and height to estimate plant size. We also counted the number of EFN-bearing plants growing within a 1.5 m radius of the focal plant.

To measure the ant and herbivore community responses to supplemented and natural EFN resources, we conducted repeated surveys of all focal plants each season. During each survey, we

recorded the abundance and identity of ants and all other arthropods on the plants visually. Only adult Hemiptera were included to facilitate accurate identifications. We collected representative specimens using an aspirator to aid species-level identifications. Survey times varied throughout the day but typically took place in mid-morning or early evening (Table A1). A total of five surveys were conducted in 2023 and seven surveys were conducted in 2024, both one week after resource supplementation began (Table A1). During the final survey each season, we counted cactus coreid bug (*Chelinidea vittiger*) eggs on the plant and the number of aborted flower buds.

Ant community sampling

We used arboreal pitfall traps as an additional approach to measuring the ant communities associated with cacti (Figure A2). We also measured the ant communities associated with two additional co-occurring cholla species. Buckhorn cholla (*C. acanthocarpa*) has EFN but flowers later than silver cholla, and pencil cholla (*C. ramosissima*) does not have EFN. Buckhorn cholla's stem nectaries are not active during the spring, whereas the flower buds are (Pickett and Clark 1979). The pitfalls were 50 ml centrifuge tubes containing a 50% mixture of propylene glycol and water, baited with sardine oil and honey, and attached to a main stem or branch for 72 hours. The traps were deployed after the final visual survey. Each year, 30 of the focal control silver chollas and 30 buckhorn chollas were sampled. A total of 20 pencil cholla were sampled in 2023 and 30 were sampled in 2024. The width and height of each buckhorn and pencil cholla individual, and the number of segments bearing new growth, buds, and EFN-bearing neighbours with 1.5 m were recorded in the same way as the silver chollas.

Ants were first identified to genus and then to species using keys (Fisher and Cover 2007, AntWiki 2021).

Plant fitness estimation

Silver cholla fitness was estimated in late June of each year. Up to three fruits per focal silver plant were harvested and the number of seeds per fruit was counted. Only seeds with developed endosperms were considered viable. 161 fruits were collected in 2023 and 216 in 2024, a total of 377.

Analyses

We used patterns of abundance and occupancy to infer ant numerical dominance (Andersen 1992, Cerda et al. 1997). Numerical dominance is an effective method of inferring the outcomes of competition when the goals are to assess which species dominates resources rather than how they dominate (Andersen 1992, Dáttilo et al. 2014). This method is widely used in ant community studies because it is strongly related to behavioral dominance (Parr 2008, Parr and Gibb 2012). Cholla are relatively long-lived, and we rarely observed multiple species on the same plant individual. Therefore, it is not likely that we would observe competition occurring in the field i.e., the 'ghost of competition past' (Connell 1980, Dáttilo et al. 2014).

To analyze the response of ant abundance and occupancy to natural EFN and supplemented resources, we fit generalized linear mixed models (GLMM) (package: glmmTMB, Brooks et al. 2017) to the visual survey data. Ant abundance per plant per survey was used as the response variable, and the number of segments with new growth, the width of the plant and the number of EFN-bearing neighbours were used as predictors, as well as the interaction between treatment (supplementation or control) and the number of days since treatment. Plant width and height were correlated, therefore we included only width in the final models because shrub height is not an estimate of canopy cover (Zamora 1981). A negative binomial error distribution was used because overdispersion was detected in the models (package: performance, Lüdecke et al. 2020). The unique identifier for each plant individual was included as a random effect to account for the repeated measurements. The study year was also included as a random effect. A logistic model was fit using ant presence as the response and the same predictors and random effects as the abundance model. We tested for species-specificity to resource supplementation by fitting an additional set of models including the ant species identity as an interaction term. The binomial presence response model was not tractable with the same set of covariates as the abundance model, so only the species by treatment contrast was included. We verified the results by fitting individual presence models with the full set of covariates for the two most abundant ant species, *C. depilis* and *S. xyloni*. The significance of the pairwise contrasts was determined using emmeans (Lenth et al. 2018).

We evaluated the ant community compositional responses to natural EFN and supplemented resources using a used a model-based approach to analyzing multivariate abundance data implemented in the mvabun R package (Wang et al. 2012). This approach fits separate GLM to

each species using a common set of explanatory variables and then accounts for the correlations between species which improves the robustness of the significance testing over alternative multivariate techniques. Additionally, this method allows for the use of negative binomial distributions to better handle dispersed count data. Treatment, the number of segments with new growth, plant width and the study year were used as predictors. A negative binomial error distribution was used. Significance was assessed using resampling within blocks based on the plant's identifier to account for the repeated measures.

Herbivore reduction was used as an estimate of ant defensive efficacy. While reduction is a frequently used metric (Chamberlain and Holland 2009) it does not directly capture behavioural dynamics. However, reduction captures both the outcome of herbivore removal as well as the outcome of indirectly deterring herbivores from foraging (i.e., trait-mediated indirect interactions). The latter can also be important in ant defense systems (e.g., Dáttilo et al. 2016, Parmentier et al. 2018). We fit GLMMs using 1) herbivore abundance and 2) only the most abundant herbivore, *Chelinidea vittiger* (cactus coreid) as response variables. For each response, we fit two sets of models: one including ant presence and one including abundance as predictor variables. We also included an interaction term between treatment and days since treatment to test for the change in response over the study period. We used emtrends to test for the difference between slopes on the significant interaction. The abundance of other predators detected during the survey was also included as a predictor. To test for species-specificity in ant defense, we fit additional models using the presence of the two most abundant ants as predictors (*C. depilis* and *S. xyloni*). A Poisson error distribution was used, and the individual plant identifier and study year were included as random effects.

We evaluated the evidence for EFN resource-based partitioning between the three most abundant ant species: *Crematogaster depilis*, *Solenopsis xyloni* and *Myrmecocystus flaviceps*. We considered an individual silver cholla plant to be used by a species of ant if that species of ant was observed on an individual silver cholla during any of the surveys. A single plant individual could be used by multiple species of ants. We tested whether the silver cholla individuals used by each ant species differed significantly in terms of traits related to EFN resource availability. We fit GLMM using the EFN resources as the response variable (package: glmmTMB). The interaction between the ant species and the treatment variable was included to test if the

differences in resource use between ant species were altered by experimental resource supplementation. A negative binomial error distribution was used because overdispersion was detected in the model.

We tested for the net effect of ant attendance on silver cholla by estimating plant fitness in terms of seeds per fruit and fruit per plant. For the seeds per fruit model, we included fruits that were empty of seeds as zeroes. We fit a series of GLMMs using ant presence, *C. depilis* presence or *S. xyloni* presence as a predictor. Treatment (resource supplemental or control), the number of segments with new growth and plant width were included in all models. The plant identifier and study year were included as random effects. For the fruit per plant model, we included the number of flower buds instead of the number of segments with new growth.

Using the pitfall trap data, we tested for differences in the ant communities associated with silver cholla, buckhorn cholla, and pencil cholla. We fit GLMM with the abundance of ants caught within the pitfall trap as the response and the plant species as a predictor. The study year was included as a random effect and a negative binomial error distribution was used.

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

Results

A total of eight ant species were recorded foraging on or near the EFN of silver cholla (Figure 2.3). 1337 ants were observed across the visual surveys in total. *Crematogaster depilis* and *Solenopsis xyloni* were the most frequently observed ant species (Figure 2.3). Of the 140 silver cholla plants, 38.6 % (54, 24 in 2023 and 30 in 2024) were tended by *C. depilis* at some point over the study period. Over the two years, 19.2% (27) were attended by *S. xyloni*. At least one individual ant was detected during 28% of surveys (241 of 860 observation periods). Typically, only a single species was observed foraging at a single time; however, two species were detected on the same plant 10 times (5 times in 2023 and 5 times in 2024). Over both years, 50 plants were never attended by any ants during any observation period.

At least one herbivore was observed during 50% (431) of observation periods, and herbivores were present on 90% (126) of plant individuals during at least one observation period. 76% (643) of the 842 herbivores observed were adult cactus coreid bugs, *Chelinidea vittiger*, a significant pest of *Opuntia* cacti across the southwestern United States (Mann 1969). A total of 11 herbivore

morphospecies were observed on silver cholla and 22 predatory or parasitoid morphospecies were observed (Table A2)

Ant responses to resource availability

Resource supplementation increased the abundance and shifted the species composition of ants on silver cholla (Table 2.1, Figure 2.3). Across species, the probability of ant presence increased over the study period on the supplementation plants only (Table 2.2). Ant abundance also increased over the study period on both supplementation and control plants; however, abundance increased significantly more strongly on the supplementation plants (Table 2.2). Ants showed species-specific responses to resource supplementation. *Solenopsis xyloni* and *Myrmecocystus flaviceps* were significantly more abundant and more likely to be present on supplementation plants (Figure 2.3, Table A3, A4, A5). There was no impact of resource supplementation on *Crematogaster depilis*, one of the most frequently observed ant species (Figure 2.3, Table A3, A4, A5).

Table 2.1: Results from generalized linear mixed models and multivariate GLM testing for differences in ant communities in response to resource supplementation (treatment and control) and natural variation in EFN resources. Plant width (cm) and the number of days from the beginning of the supplementation treatment were included as covariates in ant presence and abundance models. The study year was included as a random intercept in the presence and abundance models, and as a factor in the composition model. The individual plant identifier was included as a random intercept to account for the repeated visual surveys. Significant values are shown in bold.

	Ant Presence		**Ant Abundance**		**Ant Community Composition**	
Predictor	Coef	p-value	Coef	p-value	Predictor	p-value
Treatment (Supplementation)	-2.01	**0.005**	-1.25	**0.046**	Treatment (Supplementation)	**0.009**
EFN Resources	0.03	**0.004**	0.034	**0.002**	EFN Resources	**0.044**
Plant width (cm)	-0.04	**0.01**	-0.037	**0.01**	Plant width (cm)	**0.006**
Days since treatment	0.01	0.65	0.1	**0.01**	Year	**0.002**
Treatment*Days since treatment		**0.0002**		**<0.001**		

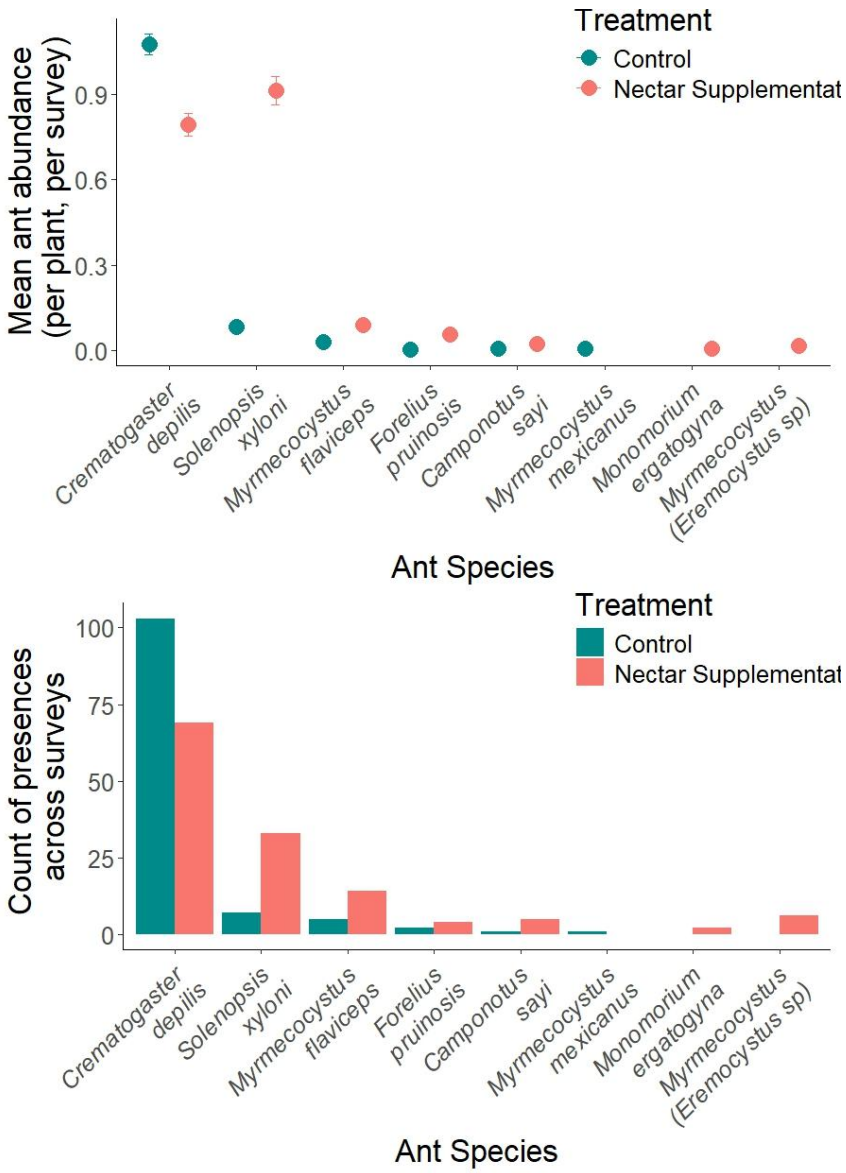

Figure 2.3: Species-specific ant responses to experimental resource supplementation on silver cholla. The upper figure shows mean (±SE) abundance per plant, per survey and the lower figure shows the total count of ant presences across all plants and surveys.

Table 2.2: Posthoc contrasts for significant interactions in generalized linear mixed models testing for differences in ant communities in response to resource supplementation (treatment and control). Emtrends trends were calculated for factor (treatment)-covariate (days since treatment) interactions and estimates the slopes of the covariate trends at each factor level. Overall model results are presented in Table 2.1. Significant values are shown in bold

	Treatment	Days since treatment slope ± SE	p-value
Ant Presence	Control	0.012 ± 0.03	0.65
	Nectar Supplementation	0.15 ± 0.02	**<0.0001**
Ant Abundance	Control	0.05 ± 0.02	**0.011**
	Nectar Supplementation	0.17 ± 0.02	**<0.0001**

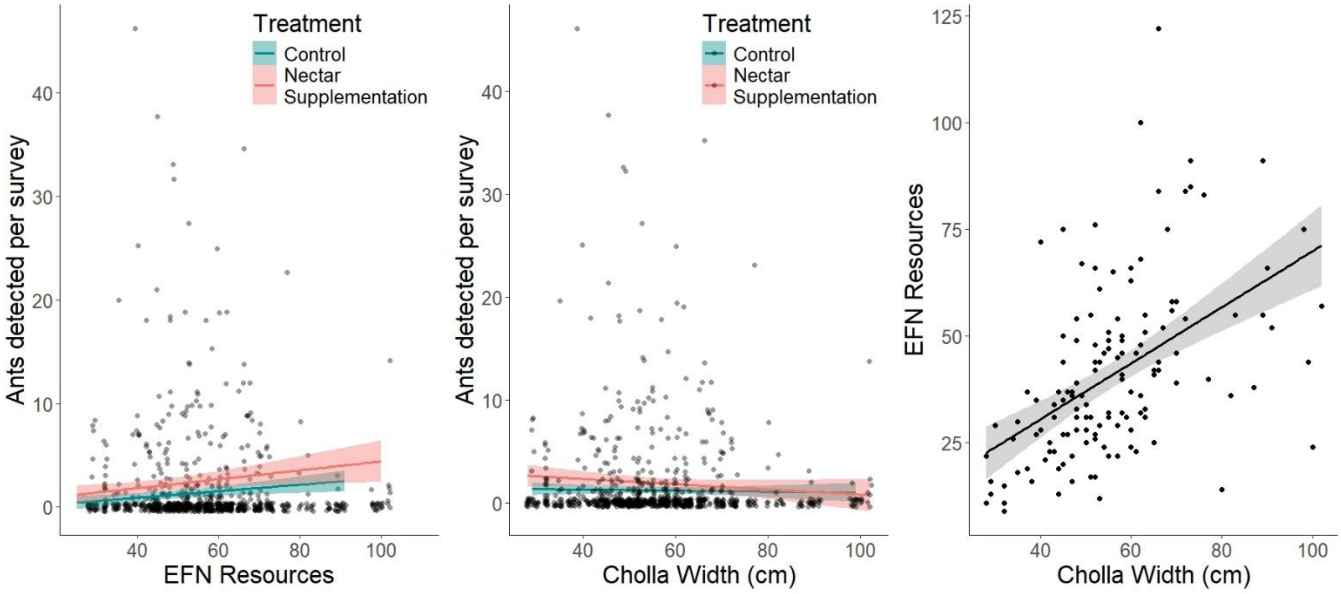

Figure 2.4: Responses of the ant community to EFN resource availability and silver cholla size. Black points represent observation periods (left, centre) or silver cholla individuals (right). There is a jitter applied to the points of (left, centre) for visibility. EFN resources were estimated as the count of segments with new growth per plant individual. The bands around the trendlines represent the 95% confidence interval

Natural variation in resource availability was also an important driver of the ant communities found on silver cholla. Both the presence of ants and the abundance of ants on silver cholla

increased with increasing EFN resources (segments bearing new growth) (Table 2.1, Figure 2.4). The quantity of EFN resources per cholla significantly increased with plant size; however, the ant community showed an inverse response to plant size. Ant presence and abundance decreased with increasing plant size (Table 2.1, Figure 2.4). Ant species composition was also influenced by the availability of natural resources (Table 2.1, Figure 2.4). There was no impact of the density of EFN-bearing neighbours on ant abundance or probability of presence (GLMM: abundance, coef = -0.35, z - -0.76, p = 0.44; presence, coef = -0.47, z = -1.02, p = 0.31).

Neither resource supplementation nor natural EFN resources influenced the number of species associated with an individual silver cholla (i.e., the difference between having 1, 2 or 3 partners) over the study period (GLMM, treatment: coef = 0.19, p = 0.3; EFN: coef = 0.003, p = 0.53; width: coef = 0.001, p = 0.885).

Niche partitioning by ants

The three most abundant ant species (*S. xyloni*, *C. depilis* and *M. flaviceps*) used control silver cholla with significantly different quantities of natural EFN resources (Figure 2.5, GLMM: Chisq = 11.31, p = 0.0014). However, resource supplementation altered the partitioning of EFN resources as the differences were not present on supplementation plants (GLMM: Chisq = 6.37, p = 0.041). Of the three species, *Solenopsis xyloni* used cholla with the largest quantities of EFN resources, *M. flaviceps* used the least, and *C. depilis* was intermediate (Figure 2.5, Table A6).

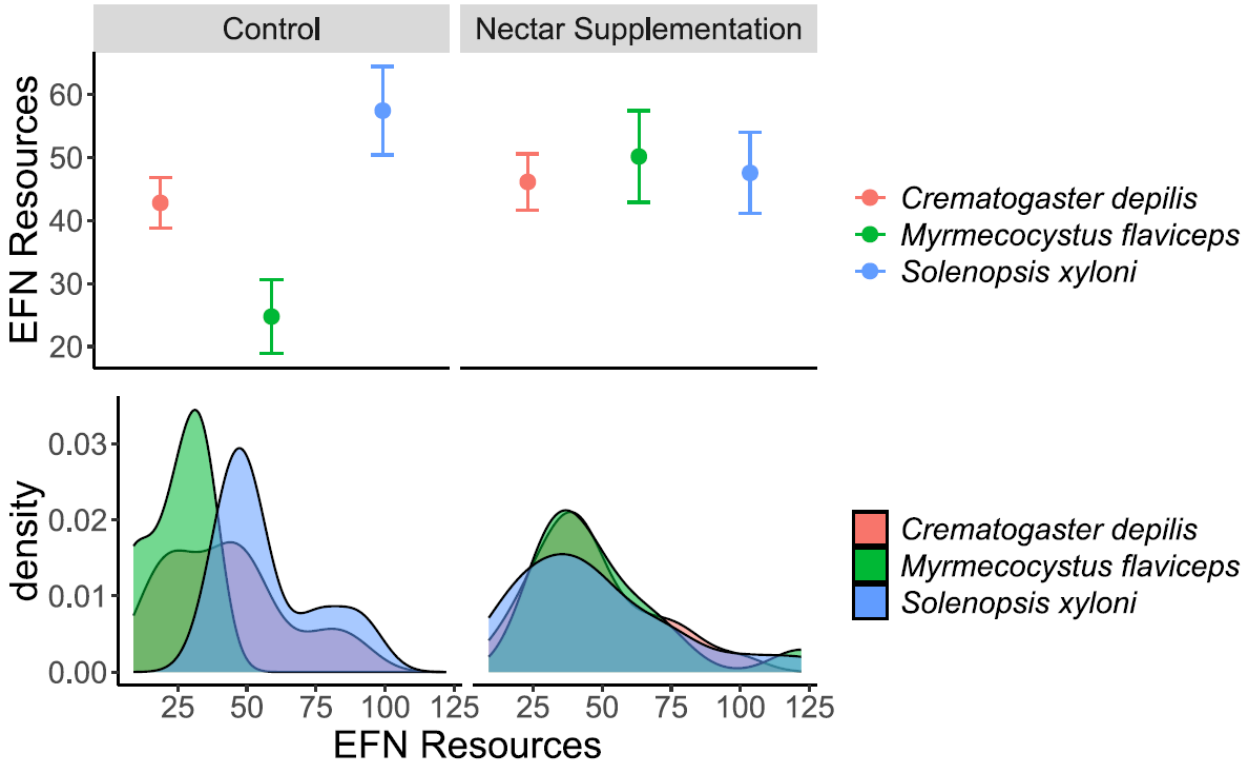

Figure 2.5: Means ± SE (upper) showing the differences in silver cholla EFN resource use (number of segments bearing new growth) between the three most abundant ant species on silver cholla. Density plots (lower) showing the distribution and overlap of EFN resource use (number of segments bearing new growth) between the three ant species. Both plots are facetted by resource supplemented plants and control plants.

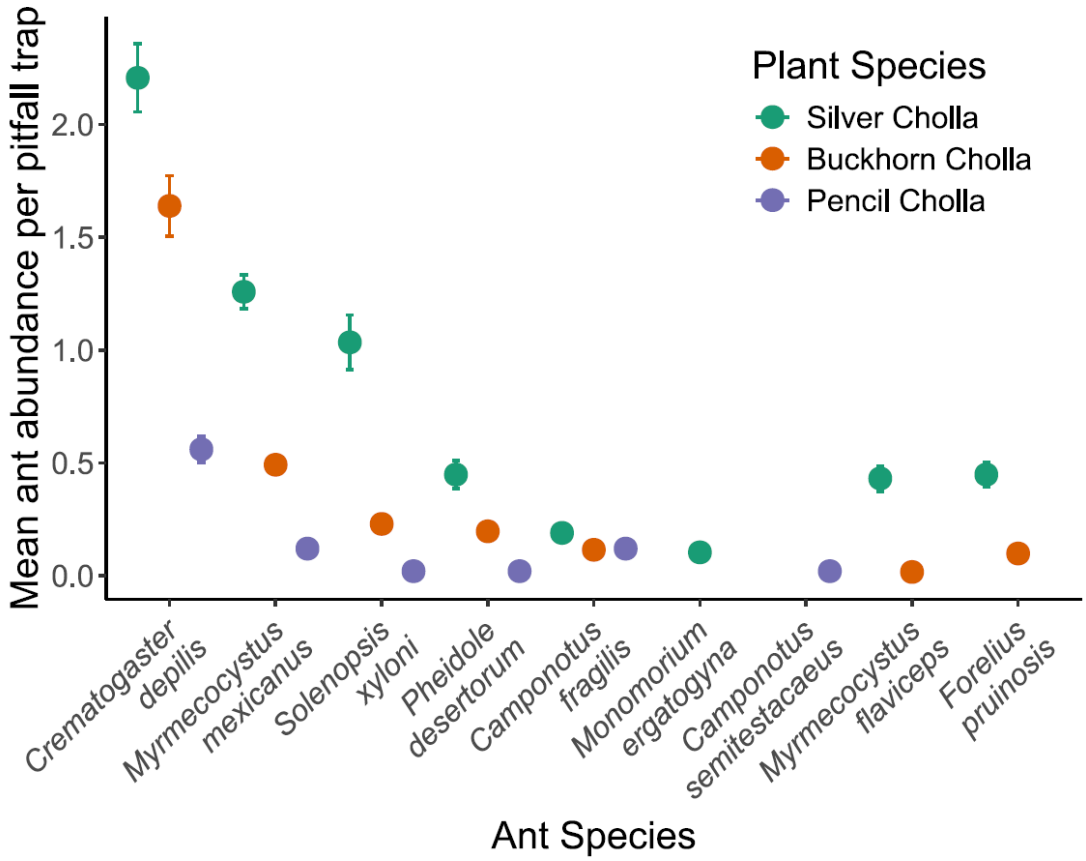

Figure 2.6: Mean abundance of each ant species caught within pitfalls traps on silver cholla (*C. echinocarpa*, buckhorn cholla (*C. acanthocarpa*) and pencil cholla (*C. ramossima*).

Differences between cholla species

On silver cholla, two additional nocturnal ant species were caught within pitfall traps: *Pheidole desertorum* and *Camponotus fragilis* (Figure 2.6). Additionally, the nocturnal *Myrmecocystus mexicanus* was frequently caught within the pitfall traps but observed rarely during visual surveys (Figure 2.6). Ant abundance within pitfall traps differed significantly between the three cholla species tested (Figure A3, GLMM: Chisq = 22.03, $p < 0.001$). Ant abundance was significantly lower on pencil cholla than both silver cholla and buckhorn cholla (emmeans, pencil-silver: est = -1.72, $p < 0.001$, pencil – buckhorn: est = -1.32, $p = 0.001$) but did not significantly differ between silver cholla and buckhorn cholla (emmeans, buckhorn – silver, est = -0.4, $p = 0.18$). However, when plant size was accounted for in the models, the buckhorn – silver contrast neared significance (emmeans, est = -0.68, $p = 0.059$).

Ant-mediated plant defense

On average across species, the presence of ants reduced the abundance of herbivores and cactus coreids found on silver cholla during the surveys (Table 2.3). There was species-specificity in ant efficacy; the presence of *C. depilis* significantly reduced herbivore abundance but the presence of *S. xyloni* did not have the same impact (Table A7). There was no independent impact of resource supplementation on herbivore and coreid abundances (Table 2.3); however, the abundance of cactus coreids significantly increased over the study period on control plants (emtrends: coef = 0.02 ± 0.01, p = 0.03) but not on resource supplementation plants (emtrends: coef = -0.012 ± 0.01, p = 0.25). For the whole herbivore community, the trends over time were not significant but the divergence between the slopes due to supplementation was significant with supplementation having a steeper slope (emtrends: estimate = 0.027 ± 0.01, p = 0.039). The abundance of other predators on silver cholla did not influence herbivore abundance (Table 2.3). All results were similar for models including ant abundance in place of ant presence (GLMM, herbivores: coef = -0.02, p = 0.052; coreid: coef = -0.03, p = 0.04; Table A8).

Table 2.3: Results from GLMM using herbivore and cactus coreid (*Chelinidea vittiger*) abundance as a response. The presence of ants, predator abundance, the number of segments with new growth and the interaction between experimental treatment and the number of days since treatment were included as predictors. The study year and individual plant identifier were included as random effects. Significance at the $p < 0.05$ level is represented in bold.

	Herbivore abundance			**Cactus coreid abundance**		
Predictor	Coef	Chisq	p-value	Coef	Chisq	p-value
Ant presence	-0.24	6.55	**0.01**	-0.27	6.17	**0.03**
Supplementation	0.32	1.79	0.18	0.40	0.82	0.15
Days since treatment	0.02	3.00	0.08	0.02	0.69	**0.03**
Predator abundance	-0.11	2.34	0.13	-0.04	0.23	0.63
Segments with new growth	0.017	27.6	**<0.001**	0.018	22.5	**<0.001**
Supplementation*Days since treatment		4.35	**0.037**		5.44	**0.019**

Silver cholla attended by *Crematogaster depilis* had significantly more seeds per fruit (GLMM: coef = 0.23, Chisq = 5.65, p = 0.017). However, this impact was not detected for the full ant community (GLMM: coef = 0.14, Chisq = 1.82, p = 0.177). There was no impact of resource supplementation on seed set (Crematogaster GLMM: coef = -0.11, Chisq = 1.43, p = 0.23, whole community GLMM: coef = -0.15, Chisq = 2.75, p = 0.097). The number of seeds per fruit also did not vary with the amount of natural EFN resources on the plant (Crematogaster GLMM: coef

= -0.001, Chisq = 1.43, p = 0.23). The mean number of seeds per fruit was 34.5 ± 16.9 SD. There was no difference in seeds per fruit between the study years (2023: 35.8, 2024: 33.62).

The silver cholla plants produced an average of 19.98 fruits per plant. Neither attendance by *C. depilis* nor the whole ant community impacted the number of fruits produced per plant (Crematogaster GLMM: coef = 0.03, Chisq = 0.06, p = 0.8; Ant community GLMM: coef = -0.07, Chisq = 0.321, p = 0.57). The number of buds was a significant predictor of fruit set per plant (GLM: coef = 0.016, Chisq = 61.15, p < 0.001)

Discussion

Plant traits related to nectar resource availability influenced the quality of ant defense through resource partitioning within the ant guild. There was evidence that the ant community reduces the abundance of herbivores on silver cholla, including an important pest, *Chelinidea vittiger*. Over the study period, the abundance of *C. vittiger* was also reduced by experimentally increasing sugar-rich resources but this effect was not observed for the entire herbivore community. The most important ant mutualist, at least during the early spring, was *Crematogaster depilis* because this species was associated with lower herbivore abundance and increased seed set. Resource availability, both natural and experimental, impacted the abundance and identity of ants associated with silver cholla. Ant abundance also differed between EFN-bearing and non-EFN-bearing species of co-occurring cholla cacti. Collectively, these results suggest that the energetic investment into EFN is worthwhile for silver cholla because ant-mediated defense benefits this species. Our study demonstrated that experimental resource supplementation disrupts the existing partitions of resources between ant species. Supplementation changed the composition of the ant communities associated with silver cholla, primarily attracting the native fire ant *Solenopsis xyloni*, a more competitive but less effective mutualist in terms of plant fitness effects. Therefore, the return on investment for silver cholla is mediated by competition hierarchies between mutualists.

Solenopsis xyloni responded strongly to the resource supplementation and used silver cholla individuals with relatively more EFN resources than those used by the two other most frequently observed ant species. *Solenopsis xyloni* is highly competitive, and behaviourally and numerically

dominant due to both its high abundance and aggressive behaviour (Andersen 1992, 1997, Braun et al. 2021a). A common expectation is that aggressive, dominant ants are better defenders than subordinate ants because the same traits that make them good competitors make them good defenders (Ness et al. 2006, Parr 2008). However, the benefits of highly aggressive defenders are typically demonstrated through reductions in herbivores rather than changes to plant fitness (Leal et al. 2023). Increasingly, there is the recognition that highly aggressive ants can also lead to a reduction in fitness through interference with pollinators (Nogueira et al. 2021, Calixto et al. 2024). For example, *Solenopsis xyloni* is the highest quality defender for the barrel cactus *Ferocactus wislenzi* in the Sonoran desert; however, there are trade-offs involved with this ant species because *S. xyloni* also interferes with pollinator visitation (Ness 2006). Our experiment focused on bud development and many of the *S. xyloni* may have left after the supplementation ended. Therefore, the most competitive mutualist may not always be the best mutualist because ant species may differ in their benefits at different times and stages of plant development.

Cactus coreid abundance on unsupplemented silver cholla increased over the study period but did not increase on resource-supplemented plants. This trend suggests that increases in resources provided by plants can directly translate into increased services from ant mutualists. Ant species turnover occurred only 21 times over the study periods; thus, the increase in service likely resulted from the increased ant recruitment to the plants over the study period and/or behaviour changes. Increasing carbohydrate availability has been shown to increase the aggressiveness of desert ant defenders against herbivores (Ness et al. 2009). The silver cholla population was not saturated by ants, and plants with more EFN were more likely to have ant defenders, raising the possibility that there is intraspecific competition between plants for plant defenders. Our results suggest that silver cholla is likely under selective pressure by ants to increase investment into EFN resources. Over longer timelines, EFN nectar can improve colony growth and survival by providing important sugar and water resources, reinforcing the mutualism (Byk and Del-Claro 2011, Calixto et al. 2021b). However, there are limits to investment by desert plants due to low water availability in arid ecosystems. On cholla, new bud and branch segments grow from areoles on older segments (Mauseth et al. 2016), thus older plants tend to be larger and have more EFN. For example, *Cylindropuntia imbricata* has more EFN with increasing age and size, and older, larger *C. imbricata* are better defended by ants (Miller 2014). In contrast, we found that ants were choosing plants with relatively more EFN regardless of size; however, there was

an inverse relationship between ant attendance and plant size. If ants are foraging optimally (Pyke et al. 1977), then changes to EFN density may be a strategy to increase the attractiveness of a plant to ants while avoiding major increases in EFN investment.

Experimental resource supplementation altered the existing partitions of silver cholla individuals by the ant community. This shows that the ant-EFN associations are dynamic and can change over short time periods leading to chains of indirect interactions. Interaction chains emerge when pairwise competitive interactions are embedded within a larger interaction network (Levine et al. 2017). The communities can harm each other through depleting and dominating resources, but they are supporting the same species of mutualists and so engaging in indirect positive interactions with each other (Johnson and Bronstein 2019). Positive, indirect interactions can stabilize multi-species assemblages and promote and maintain diversity (McIntire and Fajardo 2014). We found partitioning of partner-related resources between ant species; therefore, our results provide support to the models demonstrating competitive coexistence between consumer species within a consumer-resource mutualism (Johnson and Bronstein 2019). Thus, variation in silver cholla traits may contribute to the coexistence of ant mutualists.

Water gained from herbivory is a critical resource for many animal communities within arid environments. The water within EFN secretions is known to play a role in attracting ants to *Ferocactus* in the Sonoran (Ruffner and Clark 1986). Our experimental design does not permit us to conclude if the observed disruption to niche partitioning was driven mainly by the sugar or water content of the honey water. The relative importance of sugar and water resources to mutualists likely varies throughout the year and with environmental conditions, in addition to species-specific needs and colony age (Blüthgen and Fiedler 2004b). EFN nectar concentration and volume can vary throughout the day due to strong evapotranspiration in arid environments leading to variation in ant attendance (Oliveira et al. 1999 p. 199, Rico-Gray and Oliveira 2007, Flores-Flores et al. 2018). Thus, our artificial nectar may have had a higher water content than the natural EFN nectar at times. Nonetheless, the artificial nectar attracted ants and reduced *C. vittiger* abundance over the study period, shifting the composition of ants on silver cholla. Future work is needed for a more nuanced understanding of the relationship between investment into key nutrients and the efficacy of the mutualism.

The costs and benefits of mutualisms can be more intense and more important ecologically in harsh environments, where there are limited resources and at times highly limiting abiotic conditions. Ant-mediated plant defense tends to increase in importance in arid environments even after accounting for the increased herbivore pressures in these systems (Leal and Peixoto 2017). Globally, surveys of EFN-bearing plants are missing from arid environments, though the few that exist show that these plants are common (Pemberton 1988, Marazzi et al. 2013, Aranda-Rickert et al. 2014). This lack of information is likely a legacy of the historical belief by botanists that EFN are too costly for desert plants (Pemberton 1988). The importance of ant defense is likely underestimated in these systems as well. While our study is the first report of ant defense for the Mojave Desert and in silver cholla, this work contributes to a growing body of research demonstrating the importance of ant defense for EFN-bearing cacti. For example, in the Sonoran and Chihuahuan deserts, ants reduce herbivory on the common cacti species *Ferocactus wislizeni*, *Cylindropuntia acanthocarpa* and *C. imbricata* (Pickett and Clark 1979, Miller 2007b, Ness et al. 2009). *Crematogaster opuntiae* is an effective defender of *C. acanthocarpa* against *C. vittiger*, the same abundant herbivore that was reduced by the presence of *C. depilis* in our study. Understanding the benefits of these mutualisms despite the resource cost to the plant in harsh environments can help describe the potential selective pressures that maintain these costly traits despite the harsh environments. In the Mojave Desert, EFN-bearing species are mainly perennials with shrub habits (Pemberton 1988). In deserts, perennial shrubs are foundation species that benefit associated plant and arthropod communities through multiple mechanisms, including stress amelioration and increased nutrient and water availability (Filazzola and Lortie 2014). These positive effects increase local biodiversity; higher annual and arthropod abundance and diversity is typical for the understory of desert shrubs e.g. (Filazzola et al. 2019, Braun and Lortie 2020, Braun et al. 2021b, 2025). The mutualisms that support these foundation species, including ant defense, therefore also support ecosystem function more broadly.

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Chapter 3: Projected climate change scenarios spatially decouple desert extrafloral nectary bearing plant-ant interactions.

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Data availability statement

The Github repository containing statistical workflows, data and code has been published publicly to Zenodo with DOI (https://doi.org.10.5281/ zenodo.14920272). Reproducible document containing analyses and main figures is additionally available: https://jennabraun.github.io/desertantplantdistributions/

Authorship statement

JB conceived of the study, JB and CJL designed the survey, JB collected the data and designed the analysis, JB wrote the manuscript and CJL critically reviewed and edited the manuscript.

Abstract

Aim: Climate change is altering species distributions globally, but predicting the impacts on assemblages and their spatial overlaps under future scenarios remains an ongoing challenge. Here, we explore how climate change influences distributions among two interacting 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 the nectar-feeding ant community and projected these models under two future climate scenarios. To assess the robustness of interactions between these communities 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 the distribution of both the plant and ant communities, as well as their responses to future climate change. We then explored whether climatic niche breadth and phylogeny could account for the differential responses of species 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 climatic 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 the geographic distribution and diversity of the nectar-feeding ant community. More climatically generalized ant species benefit from the changing climate, whereas the EFN-bearing plants are uniformly and negatively impacted, despite climate breadth. Despite the range increase of some ant species across the Mojave and Colorado Deserts, interactions between the groups 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 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 positive interactions i.e., species have flexible interactions with multiple partners, are expected to be more resilient to climate change than specialized interactions, 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 positive interactions 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 positive interactions.

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 (Rico-Gray and Oliveira 2007). The outcomes of these interactions are prone to context-dependence; however, quantitative syntheses have demonstrated that these interactions are on average beneficial for the plants (Heil and McKey 2003, Rosumek et al. 2009, Chamberlain and Holland 2009b, Trager et al. 2010, Leal and Peixoto 2017). 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 for plants increases with decreasing precipitation (Leal and Peixoto 2017). However, ants and plants are different physiologically and may have different climate niches and, therefore, different responses to climate change. However, if both taxa are well adapted to arid conditions, their distributional shifts might still be parallel, allowing interactions to persist. The extent of this variation in climate sensitivity, and consequently, the future capacity for ant-plant interactions, remains untested. Therefore, understanding how ant and plant distributions will shift is critical research to understanding the vulnerability of these communities, as well as their interactions, in the face of a dramatically changing climate.

Species distribution models (SDMs) are powerful tools for predicting shifts in species distributions under a changing climate. 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). By linking aspects of species biology to predicted distribution shifts, we can gain generalizable insights into how communities will respond to climate change. For example, if there is a phylogenetic signal in species shifts, then climate responses can be generalized to other closely related species (Buckley and Kingsolver 2012). Species with broader climatic niches are expected to be more resilient to changes; however, empirical evidence remains limited (Thuiller

et al. 2005, Shay et al. 2021). 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 EFN-bearing plant and nectar-feeding ant communities in the Mojave Desert and Colorado Deserts using s-SDMs. We tested the hypothesis that EFN-bearing plant and ant communities are coupled in space but become decoupled due to climate change. To address the first part of the hypothesis, we evaluated evidence for present-day spatial relationships between ant and plant distributions. We predicted that including the EFN plant community in the SDMs for ant species improves the ant model's predictive accuracy relative to climate-only SDMs. We also predicted that species richness between the two communities is correlated beyond that expected from similar climate needs, i.e., variation in the EFN plant community richness explains variation in ant richness independent of covariation that arises from shared climate suitability. To address the second part of the hypothesis, we quantified the shifts in geographic overlap between EFN-bearing plant and ant species under two future climate scenarios. We compared the major environmental gradients influencing the distribution of both communities. If ant and plant communities differ in their environmental drivers, then we expect a decrease in overlap between the two guilds in the future, which would reduce the future capacity for positive interactions between them. Finally, we conducted post hoc analyses to explore the differing responses of species to climate change by relating two frequently invoked explanations, phylogeny and climate breadth, to future suitability. A phylogenetic signal i.e., when closely related taxa are more similar than expected in terms of climate responses, indicates that responses are phylogenetically conserved. We expect that species with a larger climate niche breadth will do better under future scenarios than relatively more specialized species. 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 2009a).

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 2009a) 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 3.1). 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 3.1). 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.

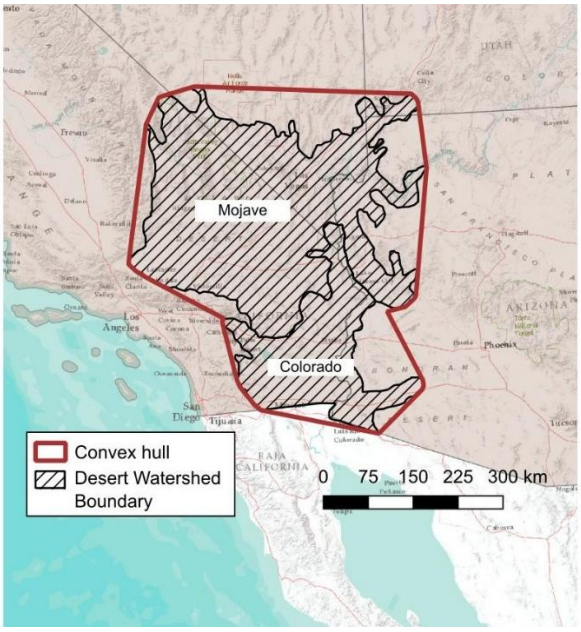

Figure 3.1: Map of the Southwestern USA showing the Mojave and Colorado Deserts. The primary study area used was the watershed boundary as defined by the United States Geological Survey (USGS).

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).

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 and to characterize the major environmental gradients within the study area (Harrell 2001, Dormann et al. 2013). The use of PCA-derived variables avoids the negative impacts of collinearity and is an objective solution for variable selection when dealing with multiple species with differing responses to environmental variables (De Marco and Nóbrega 2018).

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 (Figure B1 and B2).

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; hereafter named as mild scenario) and SSP3-7.0, the middle of road baseline outcome if no changes are made to global climate policy; hereafter named as severe scenario) (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 using the Maxent algorithm implemented within 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, Van Proosdij et al. 2016). 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 the probability of presence instead of the estimates that can only be interpreted as relative 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 retained species with at least 15 occurrences within the MCP area as focal species, for a total of 11 EFN-bearing plant species (Table 3.1) and 15 ant species (Table 3.2).

We generated pseudo-absences by randomly sampling 10000 points from across the study area ('randompoints()', 'dismo' package (Hijmans et al. 2017). We used cross-validation to assess the predictive performance of each model, using random *k* folds at a value of five to determine which partitions to hold back for model testing. We repeated models for each species 40 times each with different subset randomization. For each model run, we calculated 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 testing AUC >= 0.7 across replicates were retained in the stacked SDMs (Table B1 and Table 3.2, *Forelius pruinosis* was thus excluded due to low AUC. All EFN-bearing plant species tested were retained).

Table 3.1: 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 3.2: 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

We applied the framework of van Proosdij et al. (2016) to robustly assess if the sample size of 15 was adequate to model species distributions in this study area. This method uses simulated data to identify the minimum sample size required to generate accurate SDMs. Using the R code provided by van Proosdij et al (2016), we created artificial species distributions using our environmental rasters with differing levels of prevalence and assessed how minimum sample size impacts model performance at each prevalence level. Since we do not know the true prevalence of our focal species, we assessed minimum sample sizes at 0.1, 0.3 and 0.5 prevalence levels (i.e., narrow to widespread). We found that our sample size of 15 produced high-performing models (AUC > 0.9) across all tested prevalence levels (Figure B3).

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 LMMs for ants and plants (glmmTMB, Brooks et al. 2017) each with the scenario (present, mild and severe) 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 climatic niche breadth.

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

We first asked if phylogeny explains the variation in 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 3.2). 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 (Figure B4). For EFN-bearing plant species, we used the species-level vascular plant mega-tree backbone (i.e., GBOTB) provided in the R package 'V.Phylomaker'(Figure B5, Jin and Qian 2019). We tested for a phylogenetic signal in plant and ant distribution changes by calculating Blomberg's K using the change in environmental suitability for each 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).

Niche breadth is the diversity of environmental conditions that can support a species (Carscadden et al. 2020). We calculated Levins' (1968) B2 metric of niche breadth (here, the spatial heterogeneity of the distribution of species probability scores) from the present scenario SDM output rasters ('raster.breadth', ENMtools, Warren et al. 2021). A species that is more climatically generalized would have higher probability scores across a wide range of the climatic conditions present within the study area and a more specialized species would have higher scores associated with a narrower band of conditions. We then calculated Pearson's correlation between niche 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 niche breadth for the ant and plant communities.

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

Results

Study area current climate and changes

The primary environmental gradient (PC1) was an aridity gradient, ranging from cooler and wetter to hotter and drier (Figure B1 and B2), and explained 54% of the variance in climate across the study area. The bioclimatic variables with the largest impact on the PC1 gradient were related to temperature and precipitation (e.g., Maximum temperature of the warmest month, mean temperature of the warmest quarter, annual precipitation, precipitation of the driest quarter; see Figure B1 and B2). The second most important climate gradient was a seasonality gradient (PC2, accounting for 19% of the variance); positive values corresponded to a higher range of annual temperatures and a decrease in precipitation variation. 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, Figure B1 and B2). PC3 was dominated by isothermality and mean diurnal range (11% explained); here, positive values correspond to decreased variation within a day. PC4 was dominated by the mean temperature of the wettest quarter (typically the winter months) and the precipitation of the warmest quarter (the summer months), accounting for 7% of the variance. Maps of each gradient are provided in Figure B6.

Aridity (PC1 gradient) increases under both future climate scenarios across the Mojave and Colorado Deserts (Figure 3.2, Figure B7 and B8). There was an increase in temperature variability, accompanied by a decrease in precipitation variability (Figure 3.2, Figure

B6). Combined with the warming trend, this suggests an increase in extreme heat events and the decrease in precipitation variability suggests that it will become more uniformly dry. The shift in the isothermality gradient increased in the southeast quadrant of the study area (Figure B7 and B8), with no shift or a small increase in the rest of the study area.

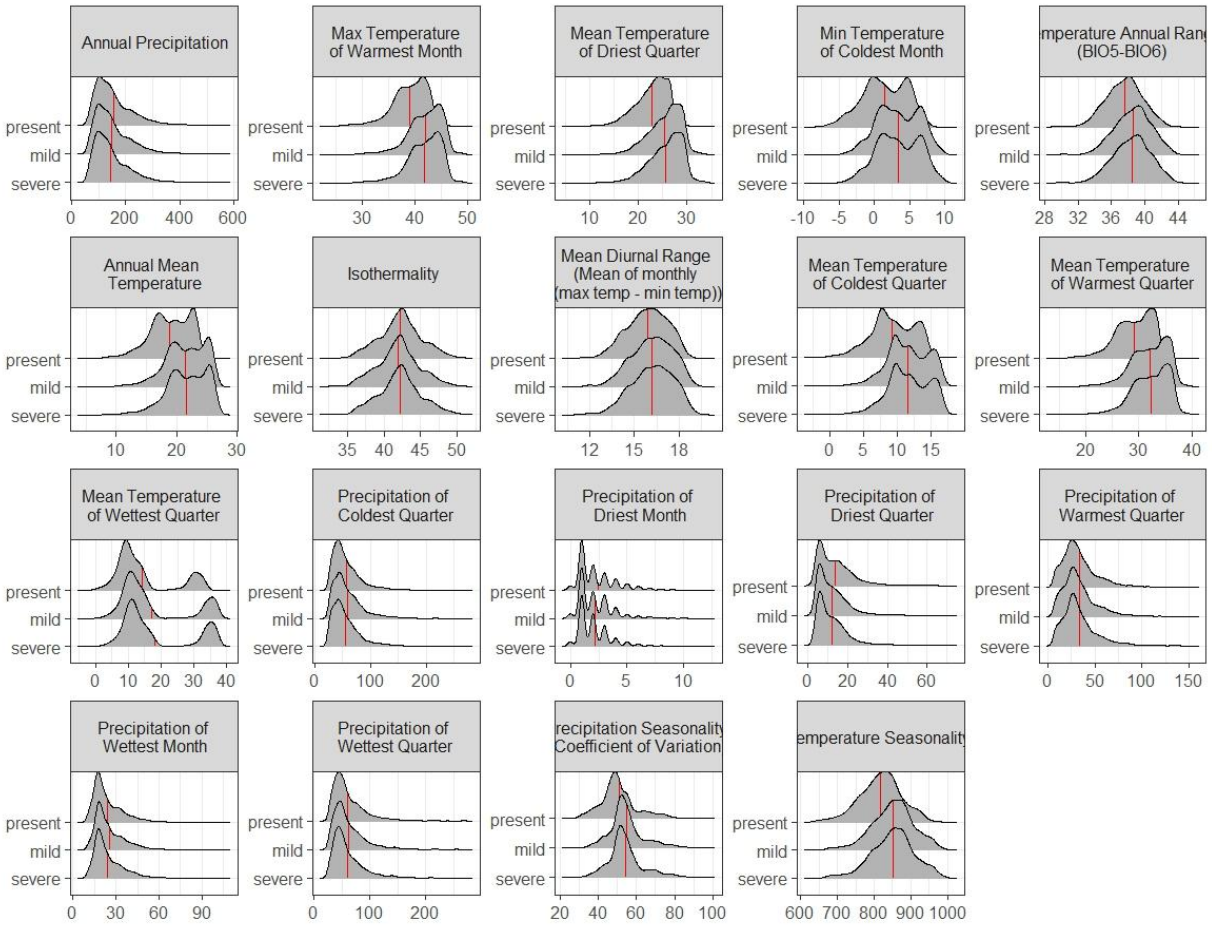

Figure 3.2: The distribution of each of the 19 bioclimatic variables (Worldclim 2) for present climate conditions (1970-2000) and two future scenarios (mild and severe, 2041-2060) across the Mojave and Colorado deserts. Vertical red lines represent mean values.

Comparison of the major environmental drivers for each community

The relative importance of the climatic predictors differed between the ant and plant communities. The aridity gradient (PC1) 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 seasonality gradient (PC2) 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).

Consequences of climate change for EFN plant and ant communities

EFN plant and ant species richness were both projected to decline across the Mojave and Colorado Deserts due to a changing climate (Figure 3.3, Figure B10, GLMM: Chisq = 2115, $p < 0.001$, emmeans, present – mild: est = 0.036, $p < 0.001$; severe: est = 0.039, $p < 0.001$). Richness declines were significantly greater under the severe scenario (i.e., SSP3-7.0) than the mild scenario (i.e., SSP2-4.5) 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 3.3) was predicted to gain both EFN plant and ant species. These increases are due to the area's relatively small increase in suitability for six ant species (*Solenopsis xyloni*, *Dorymyrmex bicolor*, *D. insanus*, *Camponotus fragilis*, *Myrmecocystus kennedyi*, *M. flaviceps*, SI Fig. 10). For EFN-bearing plants, the increases in suitability for the western part are for *Senegalia greggi*, *Fouquieria splendens, Chilopsis linearis, Cylindropuntia bigelovii* and *Prosopsis juliflora* (Figure B11). Distribution maps for each ant and plant species with occurrence points overlaid are available in Figure B12 and B13.

The responses of individual ant species 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 (Table B3). Suitability for *Myrmecocystus kennedyi, M. mimicus and Forelius mccooki* increased the most. *Myrmecocystus testaceus* and *Camponotus ocreatus* were most negatively impacted. In contrast, mean environmental suitability decreased for all EFN plant species except for *Prosopis juliflora* (Table B4). *Prunus fasciculata* was the most negatively impacted, followed by *Cylindropuntia echinocarpa* and *Opuntia basilaris* (Table B4).

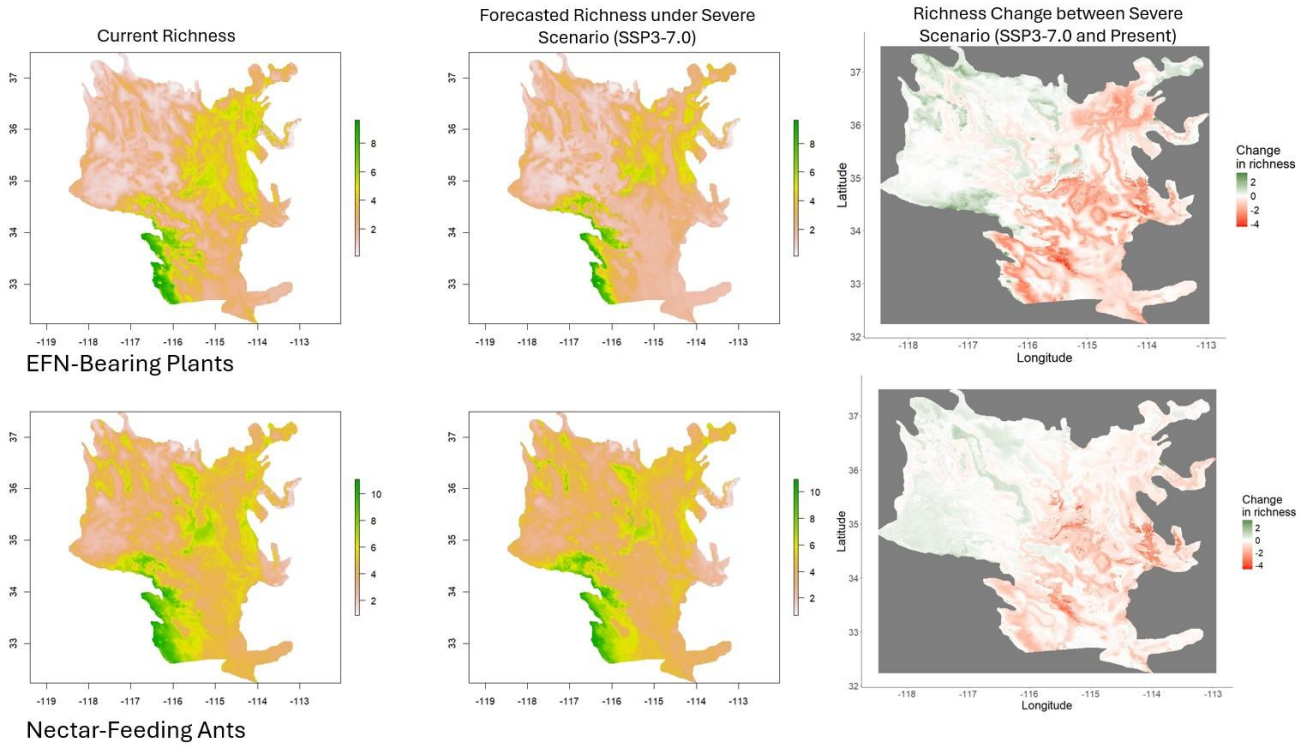

Figure 3.3: Current and forecasted species richness of EFN-bearing plants (top row) and their associated ant species (bottom row) across the Mojave and Colorado deserts, as well as the predicted change in richness. The maps of forecasted richness under the mild scenario (SSP2-2.5) are very similar and provided in the supplemental information.

Ant species with broader climatic niches tended to have increased environmental suitability in the future. The mean difference in suitability across the study site between the future scenarios and the present was significantly correlated with niche breadth (Figure 3.4, mild: Pearson's r = 0.61, df = 12, p = 0.019; severe: Pearson's r = 0.598, df = 12, p = 0.024). However, this relationship was absent within the EFN plant community (Figure 3.4, mild: Pearson's r = 0.12, df = 9, p = 0.73; severe: Pearson's r = 0.095, df = 9, p = 0.78). There was no significant difference in mean niche 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 niche breadth (Blomberg's K = 0.56, p = 0.3) nor for the mean change in suitability for ants (mild: Blomberg's K = 0.61, p = 27; severe: Blomberg's K = 0.59, p = 0.28). There was also no phylogenetic signal detected for EFN-bearing plant niche

breadth (Blomberg's K = 0.17, p = 0.43) or the mean change in suitability (mild: Blomberg's K = 0 0.43, p = 0.2; severe: Blomberg's K = 0.4, p = 0.18).

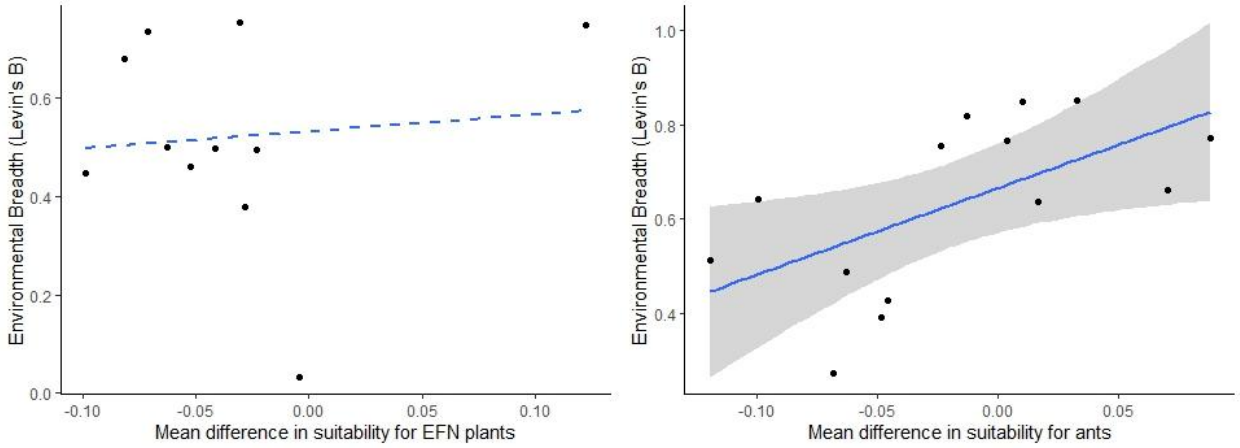

Figure 3.4: Correlations between environmental breadth and suitability changes between the present and severe future climate scenarios for the EFN plant and ant communities of the Mojave and Colorado deserts. The solid trendline denotes a significance at the $p < 0.05$ level, and the dashed line denotes an insignificant relationship.

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 r = 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 B14, 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 B14, GLMM: coef = -0.04 ± 0.003 SD, z = -13.04, p > 0.001). The EFN-only models were not tractable for three ant species and were therefore not compared (*C. fragilis*, *F. mccooki* and *M. testaceus*).

Mean pair-wise geographic overlap between ant and EFN-bearing plant species was 0.57 ± 0.18 SD and ranged from 0.1 to 0.87. In all scenarios, *Prunus fremonti* overlaps the least with ants;

this plant species has the smallest distribution of the plant species and is restricted to a relatively small area in the southwest part of the study area (Figure B13).

Geographic overlap between ants and plants (Shoener's D) significantly decreases under both climate change projections for future distributions (Figure 3.5 and 3.6, Figure B15, mild paired t-test: mean difference = 0.03, t = 6.24, df = 153, $p < 0.001$; severe: mean difference = 0.03, t = 6.7, df = 153, $p < 0.001$). In terms of proportional changes, approximately 25% of species pair overlaps decrease by 10% or more, whereas only 7% increase by 10% or more. 70% of shifts were negative and the decreases in overlap were observed across a range of plant and ant species. In contrast, increases in overlap were primarily driven by specific pairs of species. Mean pairwise overlap with plants increased for three ant species: *Camponotus semitestaceous*, *Liometopum luctuosum* and *Myrmecocystus testaceus*) with the most significant increase was with *Fouquieria splendens* and *Cylindropuntia bigelovii* (Figure 3.6). However, the average overlap with ants by *C. bigelovii* was still, on average, negative.

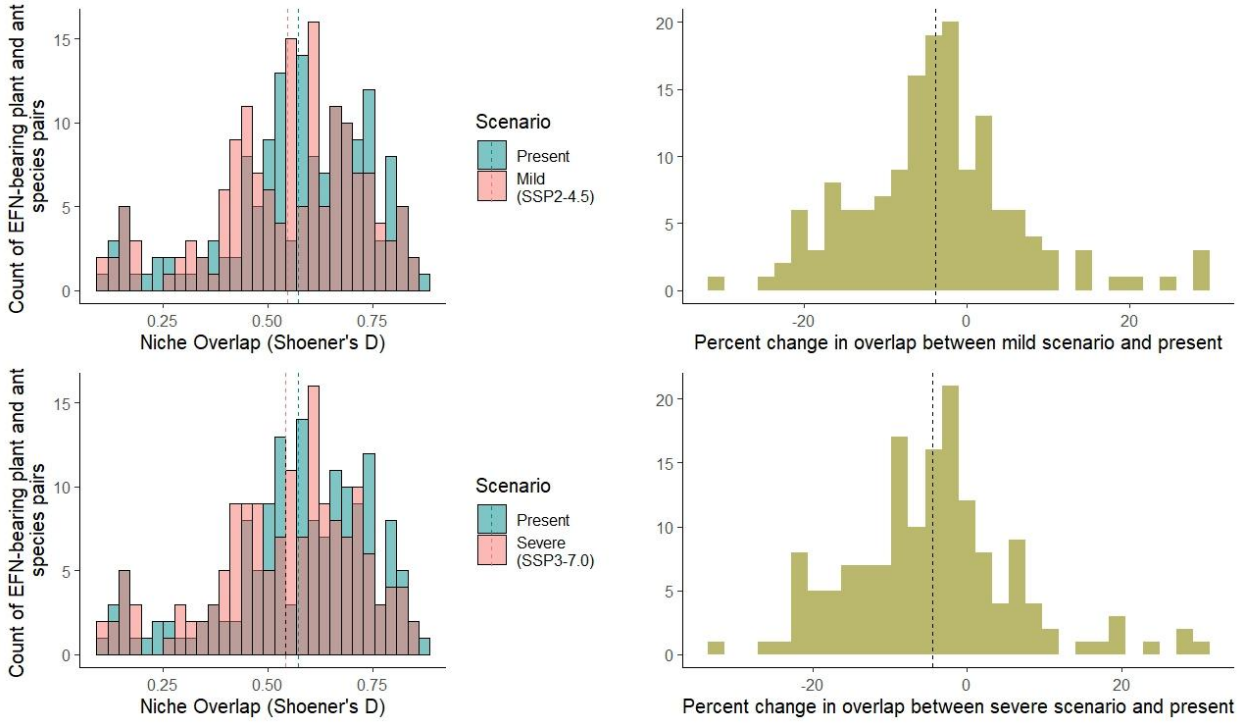

Figure 3.5: Histograms showing the in interspecific overlap of distribution ranges (Schoener's D niche overlap index) between EFN-bearing plant and ant species under present (1970-2000) and two future climate scenarios (mild and severe, 2041-2060).

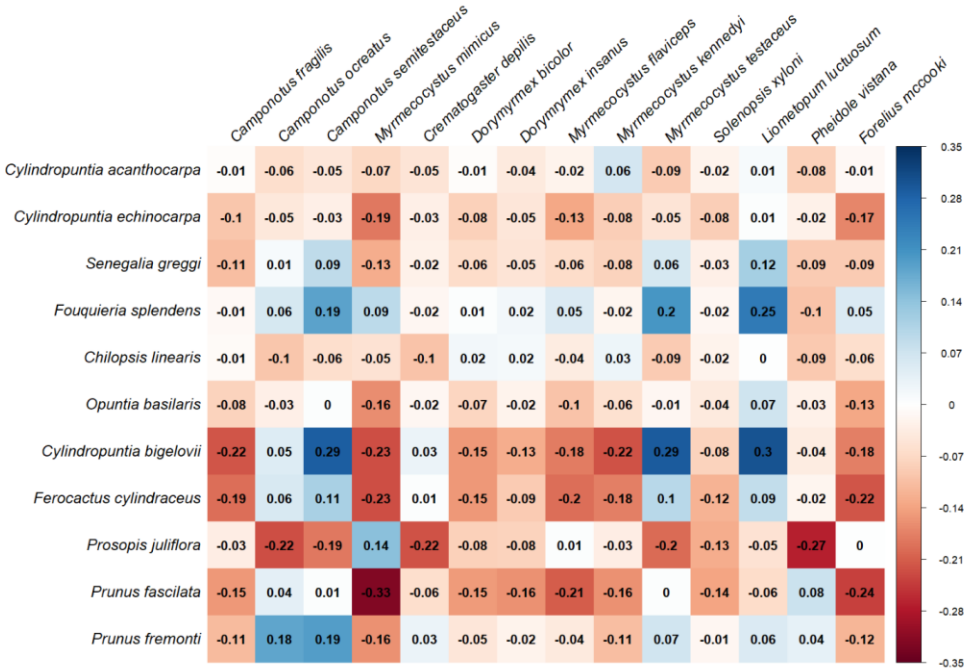

Figure 3.6: Proportional change in interspecific overlap of distribution ranges (Schoener's D niche overlap index) between the periods 1970-2000 and 2041-2060 for severe (SSP3-7.0, right). SSP 245 is very similar (within 1% for most species) and the figure is in SI Fig 15. Negative values in red indicate 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. Relative change was calculated as the percent change: ((future overlap – present overlap)/present overlap).

Discussion

In this study, we analyzed the climatic factors that drive the current and potential future distributions of two associated desert species guilds. 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 are expected to increase for 42% of the ant species. Pairwise geographic overlap between ant and EFN-bearing plant species is expected to decrease though the magnitude of this shift averaged over all species-pairs is relatively small. However, a substantial subset of species pairs exhibit more pronounced declines in overlap, indicating that while most interactions persist across the study site, some pairs may be at greater risk of more widespread decoupling under future climate scenarios. This

suggests that the observed pattern reflects species-pair level mismatches rather than a widespread decoupling of interactions at the community level. Some species such as *Cylindropuntia bigelovvi* have both substantial decreases and increases in overlap with ant species, indicating that even though net overlap changes can be low that there can still be a reshuffling of co-occurring partners across space. The EFN-bearing plant species have relatively low dispersal capacities (Martínez-Berdeja, 2015), making it unlikely that these plants will be able to migrate outside the desert study area within the projected time frame. Consequently, the potential for some interactions to persist under climate change will decrease due to this spatial mismatch, as well as the limited capacity of many species to adjust to shifting climates.

Species with broader climatic niches are generally better equipped to cope with a changing climate as they possess greater ecological tolerance than those with narrower niches (Thuiller et al. 2005, Carscadden et al. 2020). This synthesis revealed that ant species with broader niches benefit from the changing climate, whereas the EFN-bearing plants are negatively impacted more uniformly despite similar environmental generalization. Plants and vertebrate animals have similar niche breadths (Liu et al. 2020), and previous studies have shown that niche breadth confers protection to climate change across plant taxa (Thuiller et al. 2005). However, climate niche breadth may not provide advantages if species are already near their limits. Precipitation frequency and seasonality is a key environmental driver for desert plant communities (Reynolds et al. 2004). We found that seasonality (PC2 gradient) was a significantly more important driver of plant distributions than ant distributions, suggesting that this is a key constraining factor for future EFN-bearing plants. We found that the climate niche breadth of these ant and plant 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 these desert communities.

Positive interactions between species can cause correlations in species richness between communities (Gaston 1996) and 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, a large component of the covariation between the communities was independent of their shared environmental needs. 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 of the nectar-feeding ant community but climate-based SDMs are suitable to model the distribution of these ant communities. Globally, EFN-bearing plant diversity clusters with ants in several biogeographic regions and is attributed in part to mutualistic interactions between the guilds (Rico-Gray and Oliveira 2007, Luo et al. 2023). Ant defense improves at least two of the included plant species' fitness: *Cylindropuntia echinocarpa* and *C. acanthocarpa* (Braun and Lortie 2025, Pickett and Clark 1979); however, the outcomes of association have not yet been broadly studied for most of the pairs of species in our study. Direct assessments of ant-EFN plant associations remain limited in deserts because there are relatively few surveys of EFN plant diversity in deserts. However, studies have demonstrated the ecological importance of EFN resources for ants in these environments (Lanan and Bronstein 2013, Aranda-Rickert et al. 2014, Valdez-Ojeda et al. 2025). In addition to defense mutualisms, non-trophic positive interactions may couple these groups together. For example, *Crematogaster depilis* nests in the base of cholla and shrubs in addition to using EFN resources (AntWiki 2021). Both *C. depilis* and *Myrmecocystus kennedyi* are associated with desert shrubs (Braun et al. 2021). Both trophic and non-trophic positive interactions may shape ant community dynamics even in arid ecosystems where EFN-bearing plant diversity is relatively low.

Macroecological approaches provide broad insights into biodiversity patterns and interactions, but they also come with limitations, especially when dealing with ecological interactions that are highly context-dependent and flexible. A key limitation of the study is that does not fully capture the spatial and temporal variability of ant–plant interactions. Understanding the relationships between local and macroecological patterns in ant-plant interactions is a underdeveloped area of research (Juárez-Juárez et al. 2023), but exploring how biotic interactions scale to larger patterns has been increasing (Kissling and Schleuning 2015). Some locally co-occurring pair of species will not interact due to differences in phenology or competitive abilities. Therefore, at local scales, interactions are likely more limited than at the scale of our study and this study may underestimate the consequences for species-pairs overlap shifts at local scales.

The consequence for species shifts and the reshuffling of co-occurring partners across space will vary with the traits of the species. Increases in environmental suitability did not tend to coincide

with increased overlap with species in the other guild. Suitability increases for *Myrmecocystus mimicus* and *M. kennedyi* were relatively larger than for other ant species; however, the relative decreases in overlap are negative. *Myrmecocystus* species (honeypot ants) rely on stored nectar to survive in the desert. Therefore, these species that can potential expand due to increased climatic suitability would experience a decrease in available food resources. *Forelius mccooki* also increases in range across the study area. This species has a high thermal tolerance and nests in open areas (Holway et al. 2002). Forelius species are subdominant and poor competitors relative to more aggressive ants (Andersen 1997). As ant species vary in their defensive quality (e.g., Miller 2007), changes to identity of ants making up assemblages can impact the outcome of interactions for plants due to changes in competition intensity.

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 (SI Fig. 14). The variation among species suggests ant species respond differentially to climatic and food resources. Generalized interactions are expected to be more resilient to climate change because species can switch interaction partners. However, the capacity for the generalized nature of this interaction to buffer is constrained by the climatic responses of its participant species.

Literature Cited

Chapter 4: Environmental filtering mediates desert ant community assembly at two spatial scales

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Data availability statement: All data and reproducible documents have been published to Zenodo with DOI: 10.5281/zenodo.7644251. Each specimen record in BOLD is accompanied by photographs of the voucher specimen and collection date, locality, geographic coordinates, voucher depository, and barcode sequence. All records are publicly available through the BOLD system (https://www.boldsystems.org) in the “DS-ANTSSJD” dataset. Statistical analyses are available here: https://jennabraun.github.io/ant_habitat_coexistence/

Authorship statement

Ant specimens were collected as part of a larger BLM-funded arthropod barcoding and distribution project. JB was the principal investigator on that project and lead federal contractor in the contract. JB designed the field surveys and trained the field technicians.

Conception and study design: MW, AF, MS, JB, and CL; field data collection: MW, MG, KP, KR, JEnglish, and JEvans, specimen identification and management: JB, data analysis: JB, first draft: JB, revision: all authors. *Published:* Braun, Jenna, Michael Westphal, Marina Goldgisser, Kevin Padula, Kathryn Ramirez, John English, Jason Evans, Mark Statham, Amy Fesnock, and C. J. Lortie. "Environmental drivers of arthropod communities across the endangered predator *Gambelia sila's* current and historic range." *Conservation Science and Practice* 7, no. 1 (2025): e13288.

For Chapter 4:

JB conceived of the study, JB and CJL designed the study, JB did ant identification, lab work and trait measurements, JB designed the analysis, JB wrote the manuscript and CJL critically reviewed and edited the manuscript.

Abstract

Understanding the mechanisms that maintain species coexistence and determine patterns of community assembly are fundamental goals of ecology. Quantifying the relationship between species traits and stress gradients is a necessary step to disentangle assembly processes and to be able to predict the outcome of environmental change. We examined the hypothesis that desert ant communities are assembled by niche-based processes i.e., environmental filtering and limiting similarity. First, we used population-level morphological trait measurements to study the functional structure of ant communities along a dryland environmental stress gradient. Second, we developed species distribution models for each species to quantify large-scale climatic niche overlap between species. Body, femur, antennal scape and head lengths were correlated with environmental gradients. Regionally, the ant community was significantly and functionally overdispersed in terms of morphological traits which suggests the importance of competition to ant community structure. Ant community assembly was also strongly influenced by environmental factors as the degree of functional trait divergence, but not phylogenetic divergence, decreased with increasing environmental stress. Thus, environmental stress likely mediates limiting similarity in these desert ecosystems. Species with lower climatic niche overlap were more dissimilar in morphological traits. This suggests that environmental filtering on ant functional traits is important at the scale of species distributions in addition to regional scales. This study shows that environmental and biotic filtering (i.e., niche-based assembly mechanisms) are jointly and non-independently structuring the ant community.

Introduction

Understanding the contributions of niche-based processes to community assembly is a central topic in ecology. Trait-based approaches explain assembly processes through the mechanistic link between functional traits of organisms and their environments and are generalizable because by examining common traits even communities with no species in common can be compared (McGill et al. 2006). Two major hypothesized deterministic processes predict contrasting but non-exclusive patterns in the trait distributions of coexisting species. Environmental filtering impacts community structure by allowing only organisms capable of surviving local conditions to persist within the local species pool (Keddy 1992, Lortie et al. 2004, Vellend 2010). Environmental filtering can therefore lead to a convergence in traits among coexisting species (Weiher and Keddy 1995). In contrast, the concept of limiting similarity suggests that dissimilarity in traits among ecologically similar species can promote coexistence through reducing competition and partitioning resources and the environment (Abrams 1983, Gotzenberger et al. 2012). Limiting similarity can therefore lead to trait divergence amongst coexisting species (Weiher and Keddy 1995). Trait convergence can also result from competition if specific traits lead to competitive dominance (Chesson 2000, HilleRisLambers et al. 2012). Therefore, trait similarity is not enough evidence to infer environmental filtering from observational data. It is necessary to also demonstrate that trait convergence relates to environmental heterogeneity (Cadotte and Tucker 2017). Examining community-level trait-environment associations along gradients is valuable to understanding processes of community assembly (HilleRisLambers et al. 2012).

The relative importance of environmental and biotic filtering mechanisms can change along environmental stress gradients. The stress-dominance hypothesis of community assembly predicts that environmental filtering should be stronger in more stressful environments and that competition is stronger in benign environments (Grime 1977, Weiher and Keddy 1995, Swenson and Enquist 2007). Thus, functional similarity should increase with increasing environmental stress. These predictions are in part derived from the stress gradient hypothesis (SGH) plant ecology theory that has shown decreasing competition intensities with increasing relative

environmental stress (Grime 1977, Bertness and Callaway 1994). There is extensive empirical support for the SGH in plant communities (Lortie and Callaway 2006, He et al. 2013), however, in animal communities, tests are rare (but see Dangles et al. 2018). Consequently, most research in community assembly along stress gradients has focused on plant communities which limits the capacity to generalize to other trophic levels.

Ants are a model animal system to study assembly processes along stress gradients because ant communities are often strongly structured by abiotic environmental conditions (Retana and Cerdá 2000, Gibb et al. 2015) and competition (Camarota et al. 2016), though the latter is the subject of continuing debate (Andersen 2008, Cerdá et al. 2013, Tschinkel and King 2017). Ants are one of the most dominant insect groups in terrestrial ecosystems, and in deserts, many species are keystone taxa through their strong influence on most ecological processes (Whitford 2000). While an increasing number of studies have been published linking ant morphological traits, environmental characteristics and ecological function (Kaspari and Weiser 1999, Weiser and Kaspari 2006, Gibb and Parr 2010, Yates et al. 2014, Gibb et al. 2018), relatively few include intraspecific variation into their estimate of functional community structure (but see Ibarra-Isassi et al. 2022). Most functional ecology papers use traits measured at the species level (de Bello et al. 2021), however, intraspecific trait variability can be extensive due to local adaptations and phenotypic plasticity (Kawecki and Ebert 2004, Des Roches et al. 2017). Traits measured at the population level can better detect assembly processes such as environmental filtering (Jung et al. 2010, Violle et al. 2012, Wong and Carmona 2021). Incorporating intraspecific variation into ant trait-based ecology is an important step to creating generalizable, mechanistic explanations of the processes that generate and maintain biodiversity.

We studied desert ant community assembly across the San Joaquin desert of California. The region has significant ecological value due to habitats that sustain populations of endemic and endangered species, however, it has lost 90% of its natural areas to agriculture, industry and urbanization (Williams 1997, Germano et al. 2011, Lortie et al. 2018). The remaining habitat fragments have been further impacted by drought, climate change and invasive species (Westphal et al. 2016, Williams et al. 2020, 2022, Lucero et al. 2021). These pressures are facing dryland ecosystems across the world (Winslow et al. 2011), therefore evaluating community assembly mechanisms in these systems is important for understanding the complex impacts of

these changes. We examined the hypothesis that desert ant communities are assembled by niche-based processes i.e., environmental filtering and limiting similarity. First, we used population-level morphological trait measurements (i.e., mean values per species per site) to study the functional structure of ant communities along a dryland environmental stress gradient. Though not the primary focus of this study, we compared assembly patterns estimated from functional traits to patterns estimated from phylogenetic relationships. Second, we compared climatic niche overlap to trait dissimilarity for the species collected to describe patterns at the scales of species distributions across North America.

The following predictions were tested: (1) There will be evidence for regional environmental filtering on ant communities through the following responses: a) species richness and beta diversity will be correlated with the environmental gradient, b) trait convergence i.e., mean effect size of functional dispersion across the region will be less than zero, c) the effect size of functional trait dispersion of co-occurring ants will decrease with increasing environmental stress and d) individual trait by environment interactions will be present i.e., community weighted mean trait values will be correlated with environmental gradients. (2) Climatic environmental niche overlap between species will be related to traits (large-scale environmental filtering). The first set of predictions provide a comprehensive assessment of the relative importance of environmental filtering and limiting similarity along stress gradients at regional scales. The second, larger-scale analysis explores whether traits are related to the overall distribution overlap between species.

Methods

Field collection

Ant communities were sampled using pitfall traps at nine sites in the San Joaquin Valley, California, USA that span ~200 km from north to south (Figure C1). Sites were located on US Bureau of Land Management lands within California. Each site was sampled once per month between July and September 2020 for a total of 27 sampling events (Table C1). A different location within the study site was sampled each month to avoid repeated measures. The shrub species *Ephedra californica* (Ephedraceae) or *Atriplex* sp. (Chenopodiaceae) were the dominant woody species at six of the sites (shrub sites) and the remaining three sites are relatively open with few shrubs (open sites). Most herbaceous vegetation present at the sites were grasses in the

form of residual dry matter which is the dried persistent standing plant biomass that results from the slow decomposition of plant matter in ecosystems with limited precipitation (Bartolome et al. 2002). Soils are well-drained, low in organic matter and range from sandy to gravelly (Arroues 2006, Germano et al. 2011). Vegetation and ground substrate characteristics were measured at each of the 27 sampling locations by placing 0.5 m quadrats every 4 m along ten 25 m transects distributed around the site. The percent cover of ground-covering vegetation was estimated within the quadrat and vegetation height was measured at the center of the quadrat (Table C2). We calculated site-level vegetation cover and height as the mean values of the 40 quadrats, and calculated variation in vegetation cover as the standard deviation of cover within the quadrats.

White plastic drink cups (12.4 cm tall, 9 cm diameter) were placed with the top of the cup flush with the ground. To prevent vertebrate bycatch, 0.5-inch hardware cloth was placed horizontally within the trap and a piece of aluminum flashing was elevated three cm above the trap. The traps were filled to a depth of 3 cm with 100% propylene glycol. Propylene glycol is a biodegradable, non-toxic preservative that does not evaporate and preserves DNA (Nakamura et al. 2020). At shrub sites, traps were placed at 12 pairs of shrub/open microsites, and pairs were located at least 10 m apart. Shrub microsites were located beneath the canopy of a foundation shrub at the center of a 0.5 m quadrat placed just inside the dripline of the shrub. Open microsites were located randomly at least 2 m away from shrub microsites. At sites without shrubs in collections areas (i.e., within 500 - 1000 m of collections), pitfalls traps were deployed every 10 m in open areas along two transects located at least 10 m apart (Figure C2). 24 pitfall traps were deployed continuously for 72 hours per sampling event. Throughout the season, 648 traps were deployed totaling 46656 trap-hours.

Trait measurements

Ants were first identified to genus using Fisher & Cover (2007) and to species using AntWiki keys (www.antwiki.org). Representative individuals of each species were also barcoded by the Canadian Centre for DNA Barcoding (CCDB). The resulting COI sequences were compared to existing BINs in the BOLD system. Two singletons, *Solenopsis molesta* and *Solenopsis aurea* were excluded from analyses.

Morphometric traits have been widely used to study community assembly and trait-environment relationships (Schofield et al. 2016, Parr et al. 2017, Guilherme et al. 2019, Ibarra-Isassi et al.

2022). In addition to single functional trait – ecological function relationships, when used multidimensionally, morphometric traits can predict ant niches across lineages (Sosiak and Barden 2021). Morphometric traits are straightforward to accurately measure from local populations and therefore provide a high-resolution method to relate intraspecific variation with local environmental conditions. We measured each of the seven traits (Table 4.1) in up to six individuals per species, per site (262 individual ants). For this study, we defined a population as the members of a species present at a single site. Thus, up to nine populations per species were possible. We dissected each ant and affixed them to microscope slides using Elmer's glue. We placed each ant mount slide on top of a stage micrometer slide and took focus-bracketed photographs using a Canon 60D DSLR camera with a 60 mm macro lens and Canon EF 25 II extension tube. Helicon Focus software was used to combine the focus stacks into single images. We imported each composite image into ImageJ software (Schneider et al. 2012) and used the micrometer divisions within the image to calibrate the measurement scale within the software and then measured each trait using the software. We divided the six non-body size traits by Weber's body length to remove the impact of body size (Table 4.1). Only minor caste workers were measured.

Table 4.1: List of morphometric traits examined in the study with their ecological relevance and key citations.

Morphometric Trait	**Function**	**Citation**
Weber's body length (longest diagonal on the thorax)	Measure of overall worker body size	Brown, 1953
Femur length	Foraging ability in complex environments and thermoregulation	Feener Jr. et al 1988, Sarty et al 2006, Sommer and Wehner 2012
Mandible length	Foraging behaviour and diet	Gibb 2015
Head length	Foraging behaviour and diet	Weiser and Kaspari, 2006
Head width	Foraging behaviour and diet	Weiser and Kaspari, 2006; Gibb 2015
Scape length	Chemosensory ability	Jelley and Barden 2021; Weiser and Kaspari, 2006
Eye length	Foraging behaviour	Weiser and Kaspari, 2006

Environmental gradient

We extracted the mean annual precipitation, mean annual temperature and maximum annual temperature for each sampling location from WorldClim (Fick and Hijmans 2017). We extracted NDVI (normalized difference vegetation index) from EVIIRS (USGS EROS Visible Infrared Imaging Radiometer Suite). EVIIRS has a 375 m spatial resolution, and 7 and 14-day temporal resolution (USGS, 2021). We used the NDVI measurement collected from the date closest to the field sampling date (Table C4). NDVI is often used as an estimate of plant productivity within animal ecology (Pettorelli et al. 2011). We also extracted two below-ground measures from a recently published dataset of global soil temperature: mean annual soil temperature and the annual range of soil temperatures, both at the 5cm to 15 cm depth (Lembrechts et al. 2022).

We combined the environmental variables (mean annual precipitation, mean annual temperature and maximum annual temperature, NDVI, mean annual soil temperature, the annual range of soil temperatures, mean percent vegetation cover, variation in vegetation cover and mean annual vegetation height) into a composite environmental gradient using PCA (Figure 4.1). Before the PCA all variables were standardized to a mean of zero and unit variance (decostand(), 'vegan' package, Oksanen et al. 2010). All analyses used R version 4.1.0 (R Core Team 2022).

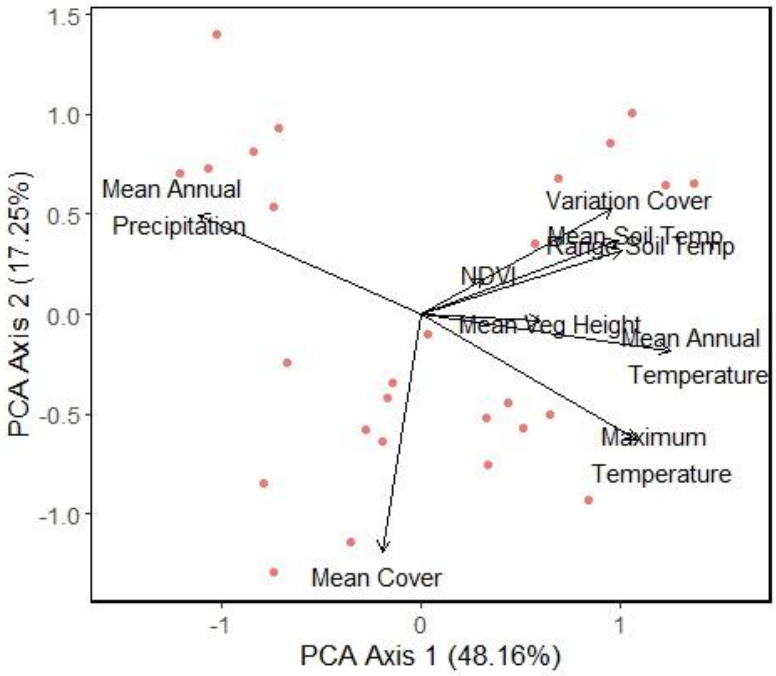

Figure 4.1: Biplot showing the relationship among environmental variables. Principal components analysis was used to combine environmental variables into a composite environmental gradient. The gradient ranges from relatively hot and dry to cooler and wetter.

Taxonomic diversity analyses

To describe general taxonomic diversity patterns, we fit a Poisson generalized linear mixed model (GLMM) with species richness as the response and the PC1 and PC2 axes as continuous predictors and the study site as a random intercept ('glmmTMB' package, Brooks et al. 2017). We modelled species richness at the level of the sampling location by pooling data from pitfall traps (n = 27). We created species accumulation curves to assess sampling completion by resampling without replacement for all sites pooled together and each of the nine sites individually (Gotelli and Colwell 2001).

Ants forage socially and this leads to the clustering of individuals from the same colony (Longino and Coddington 2002). We converted the ant data from abundance to occupancy i.e., the proportion of pitfall traps at the sampling location where each ant species was detected. We calculated taxonomic beta diversity as Bray-Curtis dissimilarity ('betapart' package, Baselga and Orme 2012, Baselga 2013). To test if beta-diversity were correlated with the environment, we calculated the Euclidean distance between sampling locations using the standardized

environmental matrix i.e., the same nine-variable matrix as the PCA input, and then used Mantel tests to test for correlations.

Functional and phylogenetic dispersion calculations

We characterized the functional structure of the ant communities by calculating functional dispersion (FDisp) for each of the 27 sampling locations using the population-level trait means ('dbFD()', 'FD' package, Laliberté et al. 2014). Fdisp is the weighted average distance of species to the centroid in multivariate trait space and a measure of multivariate dispersion (Laliberté et al. 2014). We used occupancy as an estimate of abundance for this and all subsequent community-level functional trait calculations.

To test if the observed communities were functionally clustered or dispersed, we compared the observed communities to a null model. We generated 1000 random communities using the 'independent swap' algorithm, which holds rows sums i.e. species richness and column sums i.e. occupancy/abundance of each population constant while randomizing ('RandomizeMatrix(), 'picante' package, Kembel et al. 2010). Fdisp was calculated for each of these 1000 matrices. Standardized effect size (SES) was then calculated for each sampling location using the following formula: (Obs – MeanRandom)/SD Random) (Swenson 2014). Positive values of SES indicate that a community is functionally dispersed, whereas negative values indicate functional trait clustering (de Bello et al. 2021).

The evolutionary history shared by species can influence functional trait variation among species in addition to ecological factors (Harvey and Pagel 1991). By comparing functional and phylogenetic responses to environmental gradients, we examine the role of environmental filtering on ant communities regardless of how community relationships are estimated (Cadotte et al. 2019). A complete species-level phylogenetic tree for ants is still lacking. We used the tree created by Moreau and Bell 2013. In our study, seven genera contained a single species. We pruned the tree to a single species for each of these genera. The two remaining genera in our collection each contained two species. One species per genera matched a species on the tree, and we included an additional random cogener to the tree and pruned the remaining species for a total of 11 tips. We calculated phylogenetic dispersion by computing the SES of mean phylogenetic distance (MPD) ('picante', Kembel et al. 2010) using the independent swap algorithm.

Assembly patterns

To determine if environmental filtering impacts functional dispersion along the environmental gradient and the direction of the relationship, we fit linear mixed models using the SES functional dispersion scores as responses. The first and second axes of the PCA (PC1 and PC2), and SES phylogenetic dispersion were included as predictors. We included the study site as a random effect in the model; however, the random effects explained 2.8% of the model variation. Thus, a one-sample t-test was used to determine if the mean value of SES across all the sites was significantly different than zero i.e., clustered or dispersed (de Bello et al. 2021). To determine if phylogenetic dispersion is related to the environmental gradient, we fit LMM using the SES phylogenetic dispersion as the response, and the PC1 and PC2 gradients as predictors and study site as a random effect.

Multiple ecological processes can confound trait-dispersion analyses that use only observational data (Cadotte and Tucker 2017). Relating environmental heterogeneity to trait dispersion using variance partitioning methods can disentangle abiotic, biotic and neutral effects on trait variation in communities (Gotzenberger et al. 2012, de Bello et al. 2021). We used variance partitioning to quantify the independent contribution of environmental factors, pure space i.e., dispersal limitations and history, phylogeny, and the joint contributions of the environment, space and phylogeny on variation in SES functional dispersion. We converted the WGS 1984 site coordinates to cartesian coordinates ('geoXY()', 'SoDA' package, Chambers 2020). We then created Moran's eigenvector maps (MEMs) from the cartesian coordinates ('dbmem()', 'adespatial' package, Dray et al. 2018). We used the SES functional dispersion values as the response, and the standardized environmental variable matrix i.e., the same nine-variable matrix as the PCA input, the three MEM axes and SES phylogenetic dispersion as predictors ('varpart()', 'vegan' package, Oksanen et al. 2010).

Drivers of individual trait variation

To test for individual-trait environment relationships, we calculated the community-weighted mean (CWM) trait values for each trait at each of the 27 sampling locations ('dbFD()', 'FD' package, Laliberté et al. 2014). To test if the mean value of each trait was correlated with the environmental gradient, we fit a series of linear mixed models ('glmmTMB', Brooks et al, 2017)

with the CWM for each trait as the response and each of the PC1 and PC2 axes as single predictors, and the study site as a random intercept.

To determine if intraspecific trait values are relevant for these ant communities compared with interspecific trait values, we quantified the relative contribution of intraspecific trait variability to overall trait variability based on the decomposition of sum of squares (De Bello et al. 2011, de Bello et al. 2021). We used a series of ANOVA with each individual-level trait measurement as a response (n = 262 individual ants) and species identity (n = 11 species) as a predictor. We compared the sum of squares due to species identity (between-factor variability) to the residuals (within factor variability).

Phylogenetic signal is the tendency for closely related species to resemble each other in terms of traits (Blomberg et al. 2003). We tested for phylogenetic signal for each of the seven traits by calculating Blomberg's K using the species-level trait values ('phytools', Revell 2012). This method permutes trait values among the tips of the phylogenetic tree and compares the values to those from a Brownian motion model of trait evolution (the variance in the trait values is proportional to the tree branch length) (Münkemüller et al. 2012). We also tested for a multivariate trait signal (K_{mult}) using R-code provided by (Adams 2014).

Large-scale environmental niche overlap analyses

We conducted an additional set of analyses to examine the relationship between overall climatic niche overlap and trait similarity. We extracted occurrence data from the Global Ant Biodiversity Informatics (GABI) database (Guenard et al. 2017) for each of the 11 ant species in our study. We excluded the Brazilian occurrence points for *Dorymyrmex insanus* because they were the only points south of Panama and they are likely *D. pyramicus* (Cuezzo and Guerrero 2012). For each species, occurrence points were thinned to one point per raster cell to reduce spatial bias. We generated pseudo-absences by randomly sampling 10000 points ('randompoints()', 'dismo' package, Hijmans et al. 2017). For each species, the background sampling area was determined by buffering the minimum convex hull of the occurrences by 100 km. This step was done to ensure that the background points were relevant to the range of each species. Mean annual temperature, maximum annual temperature and mean annual precipitation rasters from Worldclim and mean and range of annual soil temperature rasters were used as input into species distribution models (SDMs). The two soil rasters were resampled using bilinear interpolation to

match the climate rasters. The rasters were clipped to the following extent: -140, 7; -70, 50. Thus, the area used to generate pseudoabsences was unique for each species and the area used for prediction i.e., the extent of the rasters was identical for all species to allow for the comparison of model predictions. We created SDMs for each of the ant species using the MaxEnt algorithm implemented by the 'ENMeval' package (Muscarella et al. 2017). The approach used by ENMeval runs a series of models in succession, using different combinations of tuning parameters to avoid overfitting while maximizing goodness of fit. We used random *k* folds at a value of five to determine which partitions to hold back for model validation. We chose models from the range of candidate models by using the one with the lowest AIC value. 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 an AUC values > 0.7 are considered good (Phillips and Dudík 2008).

For the resulting SDM prediction rasters, we calculated Schoener's D i.e. climatic niche overlap for each pair of species ('calc.niche.overlap()', 'ENMeval' package, Muscarella et al. 2017). We converted Shoener's D to a dissimilarity index by subtracting each value from one. We then computed Gower dissimilarity for all seven traits together ('gowdis()', 'FD' package, (Laliberté et al. 2014) for each pair of species using the species level mean trait values. We used a Mantel test ('vegan' package, Oksanen et al. 2010) to test if the dissimilarity in traits is correlated with the dissimilarity in climatic niche overlap between species. Significance was assessed using 999 permutations.

Results

A total of 15 519 individual ants from 11 species were collected and identified, not including the two excluded singletons. All species were native to California. The most abundant species were *Solenopsis xyloni*, the native southern fire ant, and *Pheidole hyatti*, the big-headed ant. Mean species richness per site was 4.1 ± 1.4 SD and ranged from a minimum of two species to a maximum of eight species. Species accumulation curves revealed that sampling was adequate to measure species richness (Figure C3).

Environmental gradient

The first PCA axis (PC1) explained 48.17% of the environmental variation (Figure 4.1). Mean annual precipitation, mean and maximum annual temperature, mean annual soil temperature, annual range of soil temperatures and variation in ground covering vegetation were the largest environmental contributors to the PC1 axis. The composite environmental gradient was therefore cooler, wetter sites (negative PC1 values) to hotter, drier sites (positive PC1 values). The second PCA axis explained 17.3 % of the environmental variation. The largest contributor to PC2 was mean percent cover of ground covering vegetation.

Taxonomic diversity patterns

Species richness was not significantly predicted by PC1 (Table 4.2). Taxonomic beta diversity (mean Bray-Curtis: 0.48 ± 15 SD) was significantly correlated with environmental distance (Mantel statistic r: 0.262, p = 0.003).

Table 4.2: Results from linear and generalized linear mixed models testing for the response of ant species richness and standardized effect sizes of functional and phylogenetic dispersion to the composite environmental gradients (PC1 and PC2). Phylogenetic dispersion was included as a predictor in the functional dispersion model. We included the study site as a random intercept in the models. R^2 quantifies the proportion of variation explainable by the fixed effects in the model, and the intraclass correlation coefficient (ICC) quantifies the proportion explainable by the random effects.

Response	**Predictor**	**Estimate ± SE**	**z-value**	**P**	**R^2 marginal**	**ICC**
Species Richness	PC1	-0.164 ± 0.125	-1.32	0.187	0.114	0
	PC2	0.144 ± 0.125	1.15	0.250		
SES Functional Dispersion	SES Phylogenetic Dispersion	0.27 ± 0.114	2.36	**0.018**	0.381	0.028
	PC1	-0.53 ± 0.18	-2.91	**0.004**		
	PC2	-0.23 ± 0.20	-1.14	0.25		
SES Phylogenetic Dispersion	PC1	0.36 ± 0.41	0.88	0.37	0.23	0.43
	PC2	-0.07 ± 0.44	-0.18	0.86		

Assembly patterns

Regionally, there was significant trait divergence because the mean SES functional dispersion was greater than zero (one-sample t-test: mean = 0.58, 95% CI[0.24 – 0.92], t = 3.54, df = 26, p = 0.002). The degree of functional trait divergence ($SESf_{disp}$) significantly decreased as PC1 increased (Figure 4.2) but not PC2 (Table 4.2). The degree of phylogenetic divergence (SES_{MPD}) was not related to the environmental gradient (Figure 4.2, Table 4.1) but was a significant influence on SES_{Fdisp} (Figure 4.2, Table 4.2). The degree of functional trait divergence (SES_{fdisp}) was not significantly different between sites with large foundation shrubs and sites comprised primarily of open areas (LMM: coef = -0.06 ± 0.41 SE, z = -0.16, p = 0.88, open sites: mean 0.625 ± 0.841 SD, shrub sites: mean 0.562 ± 0.892 SD).

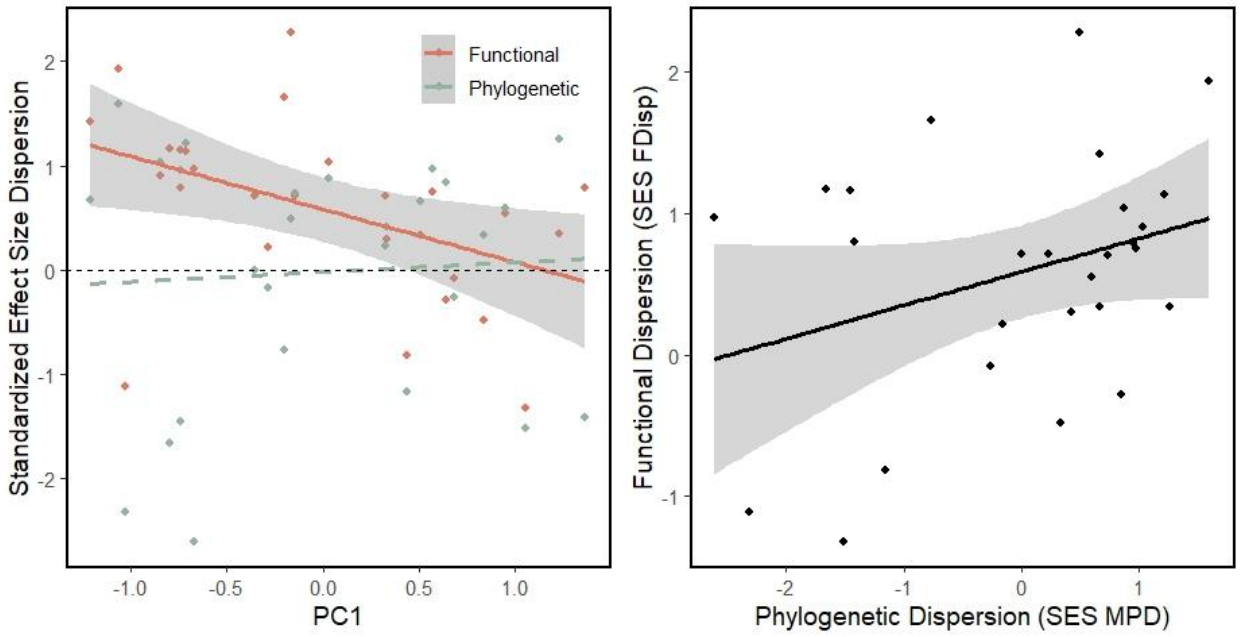

Figure 4.2: Linear regressions between A) the standardized effect size of functional dispersion and the composite environmental gradient (PC1), and B) the standardized effect size of functional dispersion and the standardized effect size of phylogenetic dispersion (mean pairwise distances). Solid lines represent significant linear relationships ($p < 0.05$), and dashed lines represent insignificant linear relationships ($p > 0.05$). The shaded gray band represents the 95% confidence interval. The points represent sampling instances.

Environmental predictors independently explained 25% of the variation in the degree of trait dispersion (i.e., $SES_{fdisp)}$. Space and environmental factors jointly explained 33% of the variation in trait dispersion. The purely spatial component of variation independently contributed 19% of the variation the trait dispersion scores. The degree of phylogenetic dispersion (i.e., SES_{MPD}) independently contributed 33%. There was no shared variation explained by SES_{MPD} and the environment, or SES_{MPD} and pure space. Total variation explained by the variance partitioning model was 85% (SS = 19.198). Residual variation that remained unexplained by environment and space was 15%.

Drivers of individual trait variation

Two traits, Weber's body length and relative femur length, were significantly and negatively correlated with the PC1 gradient (Figure 4.3, Table 4.3). The remaining traits were not significantly related to the PC1 gradient. Relative femur length was significantly and positively related to the PC2 gradient, and relative head and scape length were significantly and negatively to the PC2 gradient (Figure 4.4, Table 4.3). There was a significant multi-trait phylogenetic signal present as well as for the individual trait relative head width (Table 4.4). Blomberg's K was significantly lower indicating that closely related species had lower than expected trait similarity relative to a null model of Brownian trait evolution.

Table 4.3: Results from linear mixed models testing for relationships between the community weighted mean of each trait and each environmental composite gradient. The study site was included as a random intercept in the models. R^2 quantifies the proportion of variation explainable by the fixed effects in the model, and the intraclass correlation coefficient (ICC) quantifies the proportion explainable by the random effects.

Response	**Predictor**									
	PC1					**PC2**				
	Estimate ± SE	Z	P	Marginal R^2	ICC	Estimate ± SE	Z	P	Marginal R^2	ICC
Weber's Body Length	-0.101 ± 0.032	-3.19	**0.001**	0.298	0.037	0.036 ± 0.04	0.934	0.35	0.038	0.32
Femur length	-0.026 ± 0.01	- 2.41	**0.016**	0.248	0.168	0.022 ± 0.01	2.02	**0.04**	0.142	0.576
Head length	-0.001 ± 0.007	-0.19	0.85	0.003	0.384	-0.011 ± 0.005	-2.04	**0.04**	0.156	0.385
Eye length	0.003 ± 0.005	0.63	0.53	0.028	0.458	0.0002 ± 0.003	0.06	0.956	<0.001	0.4420
Head width	-0.002 ± 0.01	-0.19	0.846	0.003	0.565	-0.0015 ± 0.008	-0.63	0.529	0.019	0.623
Scape length	-0.006 ± 0.02	-0.27	0.786	0.007	0.561	0.07 ± 0.014	1.94	**0.053**	0.109	0.757
Mandible length	-0.003 ± 0.006	-0.6	0.545	0.025	0.470	0.006 ± 0.005	1.39	0.166	0.1	0.33

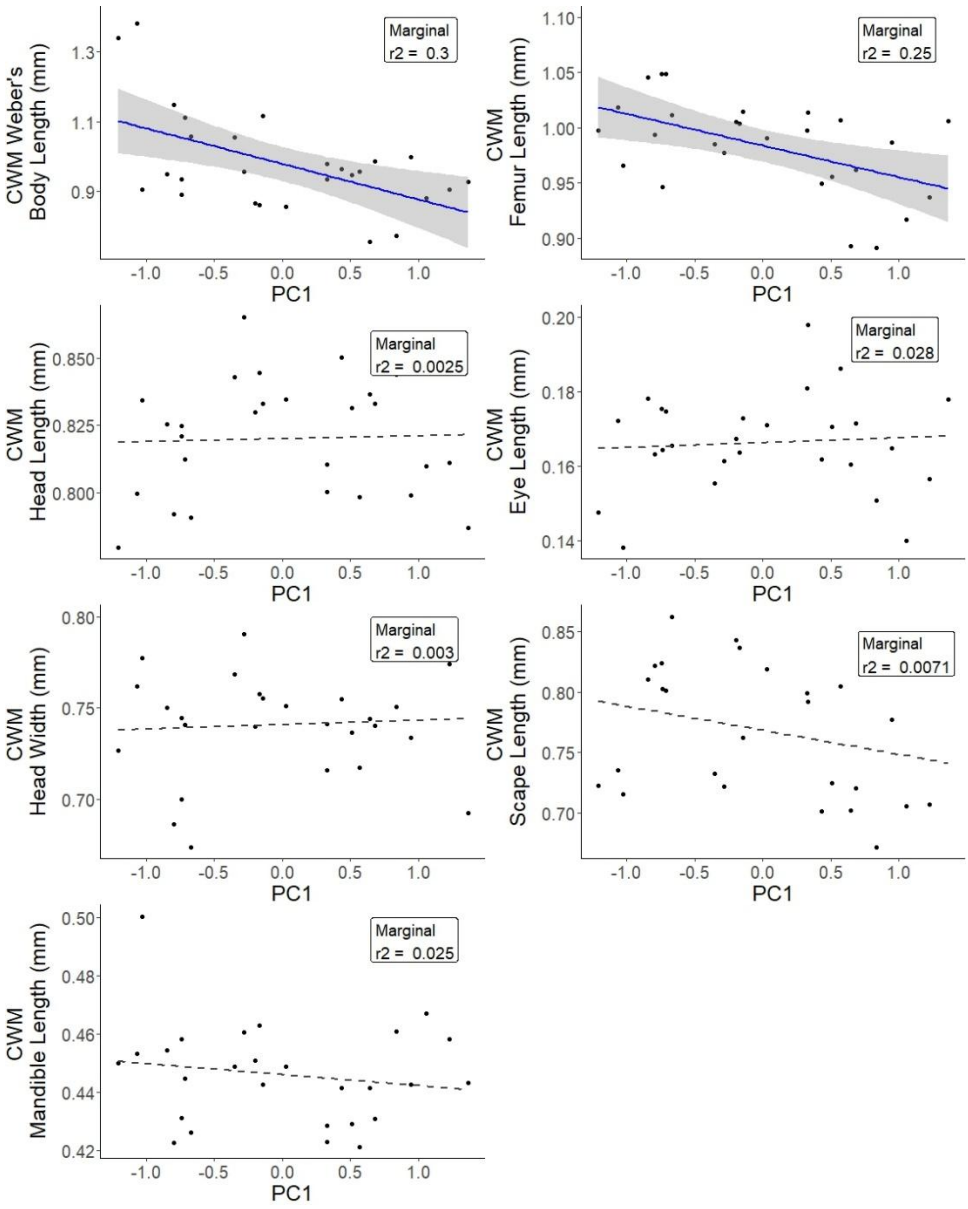

Figure 4.3: Linear regressions of community-weighted mean trait values and the composite environmental gradient (PC1). Sites with higher annual temperatures and lower annual precipitation are higher on the PC1 gradient. The shaded gray band represents the 95% confidence interval. Solid lines represent significant linear relationships ($p < 0.05$), and dashed lines represent insignificant linear relationships ($p > 0.05$).

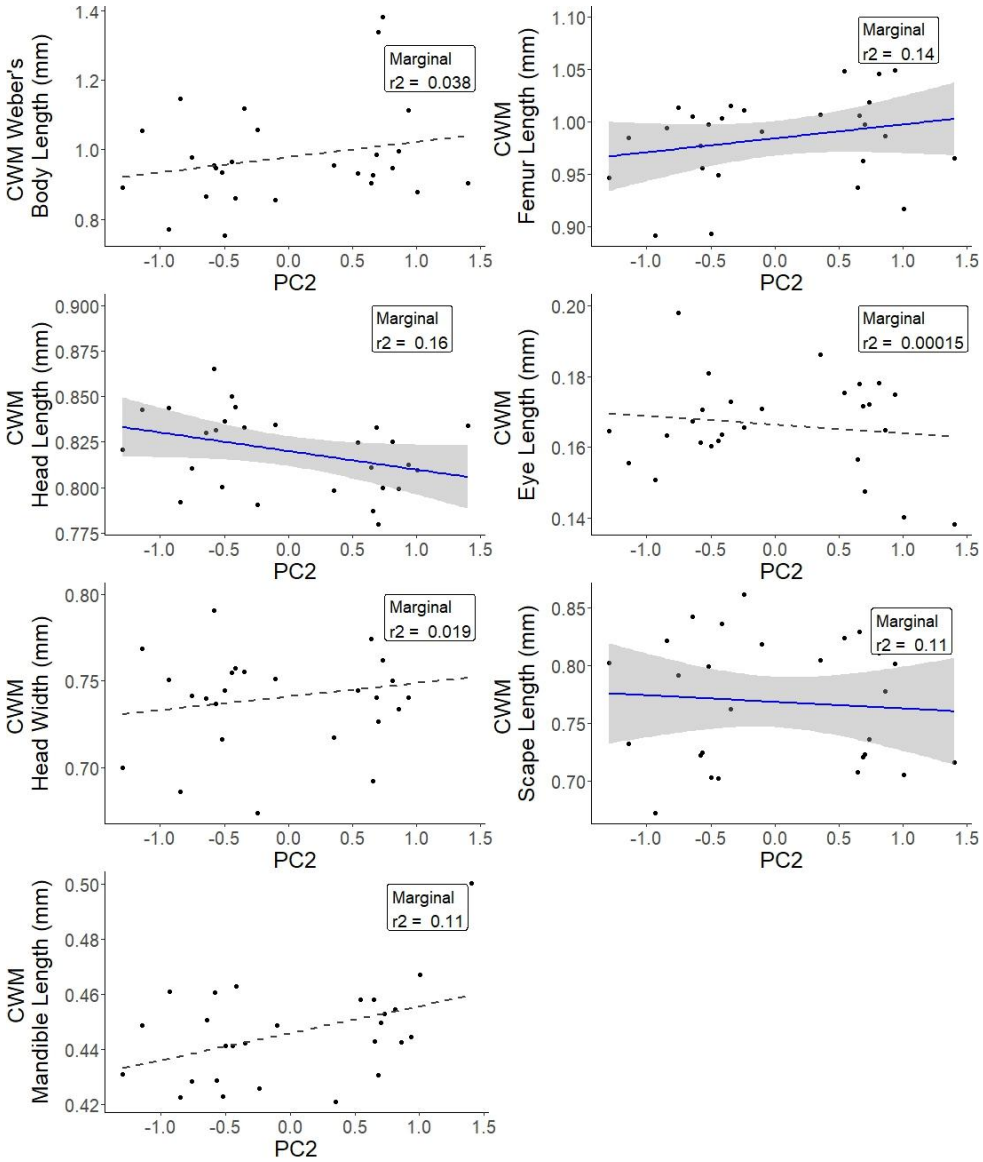

Figure 4.4: Linear regressions of community-weighted mean trait values and the second composite environmental gradient (PC2). The shaded gray band represents the 95% confidence interval. Solid lines represent significant, linear fits ($p < 0.05$), dashed lines represent insignificant linear relationships ($p > 0.05$).

Table 4.4: Results from permutation tests of phylogenetic signal (Blomberg's K) for all traits combined and for each trait individually. K > 1 indicates stronger phylogenetic conservatism than expected from a Brownian evolution model and K <1 indicates weaker phylogenetic conservatism than expected. Significance at $p < 0.05$ is indicated by bold.

Trait	K value	Z	P
Multi	0.47	N/A	**0.005**
Weber's body length	0.58	-0.89	0.163
Femur length	0.59	-0.86	0.145
Head length	0.51	-0.89	0.135
Head width	0.80	-0.91	**0.043**
Mandible length	0.51	-0.79	0.15
Scape length	0.50	-0.74	0.198
Eye length	0.25	-0.31	0.502

The extent of intraspecific trait variation depended on the trait (Figure 4.5). Species identity was significant in all models of trait variation (ANOVA, all $p < 0.001$, Table C3). Interspecific trait variation was larger than intraspecific trait variation for all traits tested and accounted for a mean of 71.1%. However, the relative contribution of intraspecific variability was non-negligible as the mean intraspecific trait variation across all seven traits was 28.9%.

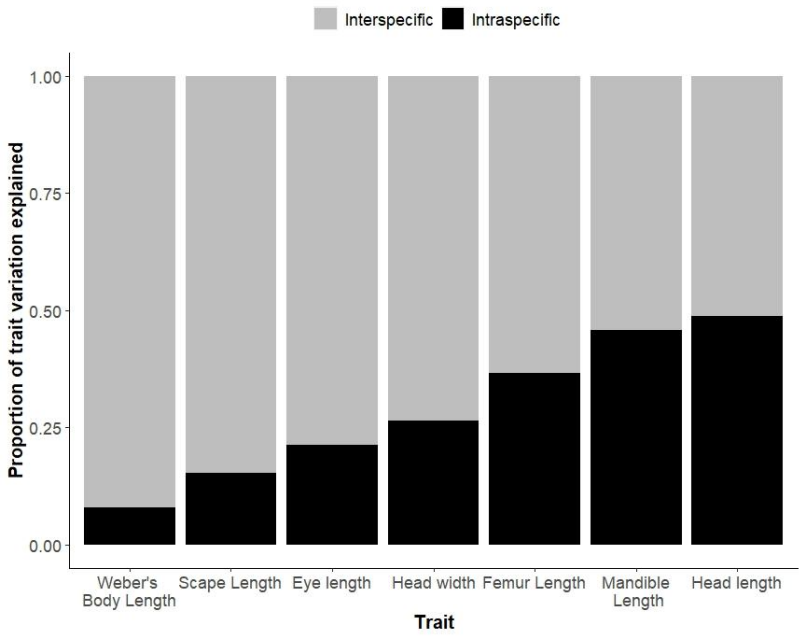

Figure 4.5: The percent contribution of intraspecific variation (grey) and interspecific variation (black) to overall trait variation for each of the seven morphological ant traits considered in this study. Proportions were obtained by variance partitioning through sum of squares decomposition.

Large-scale analyses

Dissimilarity in large-scale climatic niche overlap (complement of Shoener's D) was significantly correlated with species-level Gower dissimilarity in traits (Figure 4.6, Mantel statistic r: 0.378, p = 0.028). All SDMs had a good predictive performance of AUC > 0.7 (Table C4), except for *Dorymyrmex bicolor* (AUC: 0.691) and *Cyphomyrmex wheeleri* (AUC: 0.56). When *C. wheeleri* was excluded from this analysis the Mantel r value increased (Mantel statistic r: 0.466, p = 0.008) rather than decreased, suggesting that the poor predictive capacity of *C. wheeleri*'s SDM does not drive the statistical relationship between ant trait dissimilarity and large-scale climate niche overlap.

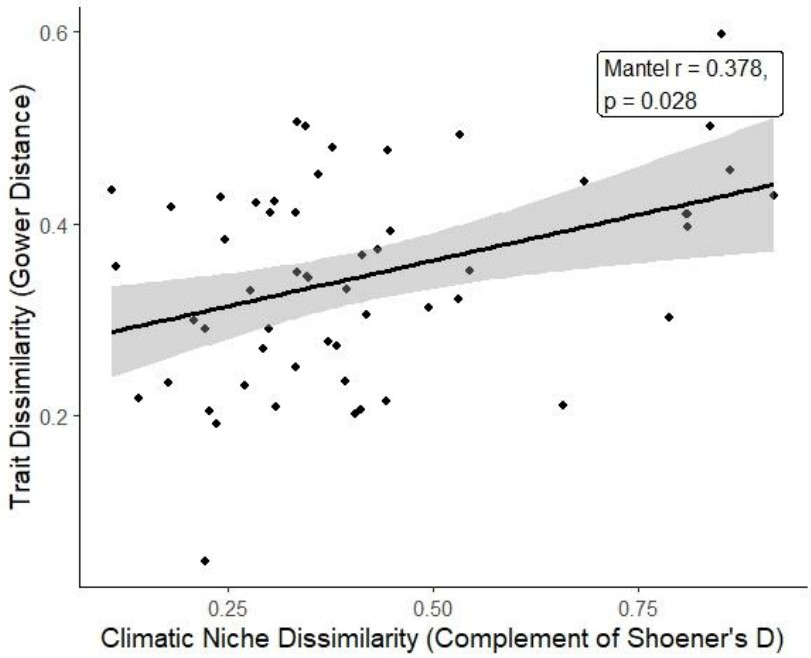

Figure 4.6: The relationship between climate niche dissimilarity (complement of Shoener's D) and species-level trait dissimilarity (Gower distance). Climate niche dissimilarity was obtained by modelling the distribution of each ant species and quantifying the environmental overlap. The shaded gray band represents the 95% confidence interval. Solid line represents a significant relationship estimated by a Mantel test ($p < 0.05$).

Discussion

Studying community assembly along environmental gradients advances our understanding of the mechanisms that generate and maintain biodiversity. Our results support the hypothesis that desert ant communities are assembled through niche-based processes. Regionally, the ant community was significantly and functionally dispersed in terms of morphological traits. Functional trait overdispersion is the signature of limiting similarity which suggests the greater importance of interspecific interactions, specifically competition and niche partitioning, in structuring the ant community (Weiher and Keddy 1995, Gotzenberger et al. 2012). However, ant community assembly was also strongly influenced by environmental factors. Environmental heterogeneity independently accounted for 25% of the variation in the degree of functional dispersion. The degree of functional dispersion was also significantly correlated with the environmental stress gradient showing that the importance of biotic filters is mediated through or dependent on the environmental conditions. Collectively, these results suggest that there is an important role of environmental stress in mediating limiting similarity in these desert ecosystems. Using environmental niche modelling, we found large-scale evidence consistent with the predictions of environmental filtering – species more dissimilar in environmental niches were also more dissimilar in morphological traits. This suggests that environmental filtering on functional traits is important at the large scale of species' overall distribution in addition to regional scales. Most frameworks of community assembly warn of the non-independence between filters (HilleRisLambers et al. 2012). This study shows that environmental and biotic filtering (i.e., niche-based assembly mechanisms) are jointly and non-independently structuring the ant community.

Local variation in climate can influence the relative importance of community assembly processes. Here, as sites became relatively more arid (hotter and drier), the ant community shifted from functionally dispersed to randomly assembled. Competition as the dominant force structuring ant communities has been an ongoing paradigm of ant community ecology (Cerdá et al. 2013). Our observation of regional trait overdispersion supports this paradigm, however the community response to stress is consistent with the predictions of the stress dominance hypothesis which predicts a breakdown in the importance of competition with increasing environmental stress (Swenson and Enquist 2007). One mechanistic explanation within deserts is

the trade-off between competitive ability and physiological heat tolerance observed within ant communities (Cerda et al. 1997, Cerdá et al. 1998). High heat tolerance allows less competitive species to avoid competition by foraging at temperatures that restrict the more competitive species (Cerda et al. 1997, Cerdá et al. 1998). Thus, the role of environmental stress on mediating interspecific interactions through physiological limitations and promoting coexistence merits further study because stress dominance assembly theory may generalize beyond plants to other trophic levels including ants.

The relationship between functional trait divergence and environmental factors was independent of phylogenetic divergence. Phylogenetic dispersion independently explained 33% of functional dispersion but failed to reveal the role of environmental factors on ant assembly. Phylogeny is frequently used as a proxy for functional traits or as a complementary diversity measure that can account for unmeasured traits (de Bello et al. 2015, Cadotte et al. 2019). However, these methods operate under the assumption that the unmeasured traits are evolutionary conserved (Pavoine et al. 2013). The traits used in our study were not phylogenetically conserved, rather, when all traits were considered together species were less similar than expected given their evolutionary relatedness. This result is relatively common, as phylogenetic signal test results frequently show that Blomberg's K values tend to be significantly weaker than expected (Cadotte et al, 2019). Understanding the strength of phylogenetic signal is useful for assembly studies because simulations have shown that under significantly low trait conservatism phylogenetic methods have low power to detect environmental filtering (Kraft et al. 2007). These results highlight that the functional structure of ant communities is a product of both evolutionary history and ecological factors.

We found evidence for community-wide relationships between individual traits and environmental gradients. Relative femur length and Weber's body length decreased with increasing environmental stress (PC1). Femur length has been shown to be negatively associated with temperature at the individual worker level along a climatic gradient across Quebec (Ibarra-Isassi et al. 2022). This trait also decreased in magnitude along our composite environmental gradient here in Californian drylands. However, in Mediterranean drylands, body size and femur length have been shown to increase with increasing aridity (Frasconi Wendt et al. 2020). Therefore, even similar environmental variables do not necessarily filter for identical ant traits

globally which demonstrates that specific trait-environment relationships can be regional. Variation and mean percent cover of ground vegetation were important contributors to the PC1 and PC2 gradients respectively. Leg length decreased as the variation and mean value of this environmental measure increased. Critically, some functional traits of ant assemblages may change under extreme global change, including body appendages (Parr and Bishop 2022). Indeed, other previous studies have also shown interesting patterns related to relative leg size and habitat use, as increased leg size allows some ant species to forage in hotter substrates (Sommer and Wehner 2012, Kaspari et al. 2015), which is supported by findings that ants from drier habitats tend to have longer legs (e.g., Nooten and Guénard 2022). Femur length can be related to habitat complexity because shorter legs allow ants to be more manoeuvrable in complex environments (Kaspari and Weiser 1999). Ants had relatively longer antennal scapes at sites with greater vegetation cover which may improve their chemosensory abilities in denser vegetation. Thus, vegetation structure may be acting as a filter on the ant community through impacts on ant movement and perception.

Conclusions

We identified multiple lines of evidence showing that desert ant communities are deterministically assembled. Functional traits were related to the environment even at large scales suggesting that integrating traits into species distribution models will be an important area for future research. Interspecific differences in trait variation were larger than intraspecific differences for each trait tested, however, intraspecific variation was non-negligible and differed in magnitude among individual traits. These results suggest that species-level trait analyses for desert ants are appropriate and useful, and that intraspecific variation can also contribute to trait variation and thus likely also contribute to community assembly processes. Due to the ecological importance of ants in arid ecosystems, understanding how their communities and overall distributions may change along climatic gradients is important to predicting the outcome of global change on these ecosystems.

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Chapter 5: The direct and indirect drivers of annual seed size, ant worker size and size-dependent seed removal rates along a desert climatic gradient.

Data availability statement

Data for this manuscript is available within this GitHub repo: https://github.com/jennabraun/stressgradient_ants_seeds and a reproducible document containing the analyses is available here: https://jennabraun.github.io/stressgradient_ants_seeds/.

Authorship statement

JB conceived of the study, JB and CJL designed the survey, JB collected the data and designed the analysis, JB wrote the manuscript and CJL critically reviewed and edited the manuscript.

Abstract

1. Granivorous ants facilitate ecosystem functioning in deserts by collecting and dispersing large quantities of seeds. Along desert stress gradients, environmental filtering selects species with traits that confer tolerance to local conditions such as body size and seed size. We asked if environmental stress shapes ant-seed interactions by filtering the functional trait composition of the ant and plant communities.
2. We examined the direct and indirect responses of annual seed size, ant worker size, and seed removal rates along a desert climatic stress gradient spanning two Californian deserts.
3. Environmental stress influenced the abundance, richness and the functional composition of both communities. Ant body size and annual seed size both increased with aridity. The size-matching relationship between annual seed size and ant body size was predominantly explained by their shared environmental responses to the aridity gradient. However, annual seed size made a unique contribution to ant body size, indicating a bottom-up constraint on the functional structure of ant communities.
4. In contrast, we found no evidence that ant body size predicted seed size, and seed size selectivity was also unrelated to ant body size. Instead, ant foraging choices were density-dependent, with removal rates for less-preferred seed sizes increasing with ant abundance. Productivity increased ant abundance but also decreased seed removal rates along the gradient. This pattern indicates that overall predation rates are influenced by plant productivity and that selectivity emerges from ant foraging behaviour. Ant foraging choices were therefore driven more by biotic drivers than environmental drivers.
5. The interdependence suggests that future increases in environmental stress may drive shifts in the functional composition of both ant and plant communities, with implications for ecosystem functioning and plant community assembly due to reductions in ant community abundances. Understanding these multi-trophic assembly processes is essential for predicting desert ecosystem reorganization under climate change.

Introduction

Stress gradients are widely used natural systems for understanding how abiotic factors structure community assemblages. Climate change is anticipated to result in more stressful conditions for many ecosystems. For instance, the Mojave Desert is projected to become hotter, drier and to experience an increase in extreme weather events (MacDonald 2007, MacDonald et al. 2016, Braun and Lortie 2025). This region is known for its relatively high species diversity and endemism but is highly vulnerable to the impacts of climate change because it is already water-limited (Sala 2000, Baldwin et al. 2017). Interactions between impacted species can be strong and are not necessarily correlated with climate, which can reduce the predictability of responses if not considered (Dunne et al. 2004). To improve our ability to predict how climate change will impact ecosystem function, we need to incorporate multiple levels of biological organization (Scheffers et al. 2016), multiple trophic levels (Rosenblatt and Schmitz 2014), as well as horizontal (i.e., competition and facilitation) alongside vertical interactions (i.e., predation) (Tylianakis et al. 2008). Recent work that focuses on key traits has helped provide a more mechanistic understanding of how community assemblages and thus ecosystem function may change (Schleuning et al. 2020). By examining how trait-mediated interactions change along stress gradients, we can better predict how ongoing environmental changes will reshape ecological communities and their interaction network structure.

In semi-arid and arid environments globally, harvester ants are ecosystem engineers through their direct and indirect impact on key ecosystem processes, such as food web dynamics and soil nutrient cycling (Whitford 2000, Uhey and Hofstetter 2022). Granivorous ants can collect large quantities of seeds, influencing plant abundance, diversity and seed bank densities (Brown et al. 1979, MacMahon et al. 2000, Johnson 2001, DeFalco et al. 2009). However, the net effects of seed predation are not necessarily negative because a limiting factor for annual plants in deserts is dispersal to suitable microsites (Venable et al. 2008). Granivorous ants can disperse seeds through dyzoochory, i.e., abandoning the seeds after moving them without consuming them (Azcárate et al. 2005, Arnan et al. 2012, García-Meza and Martorell 2022), and by transporting them to protected middens (Mull 2003). Due to the ecological importance and high biomass of this group, ant assemblages are important drivers of community dynamics. Seed-granivore

interactions have been identified as a key component of plant community assembly, but they are also still poorly integrated into plant community theory (Larios et al. 2017). Understanding granivorous ant and plant responses to increasing environmental stress is important because the environmental gradient affects multiple taxa and their respective connections.

Along stress gradients, environmental filtering selects species with traits that confer tolerance to local abiotic conditions. For instance, seed size tends to increase with aridity because higher seed mass and seed longevity increase the chances of survival and persistence under dry environments (Baker 1972, Metz et al. 2010, Volis and Bohrer 2013, Gremer and Venable 2014). Size-matching between seeds and harvester ant body size is frequently reported (Retana et al. 1994, Kaspari 1996, Pfeiffer et al. 2006). Body size is a morphological constraint on harvesting, since upper and lower limits to seed size exist, beyond which an ant cannot carry the seed. Therefore, the seed size of annuals can constrain the functional traits of granivorous ants (Silvestre et al. 2019). As stress gradients filter ant communities toward smaller or larger-bodied species (Frasconi Wendt et al. 2020, Braun and Lortie 2024), the resulting changes in seed size-dependent harvesting can potentially cascade to alter plant community composition. Selective harvesting by ants can lead to patterns in seed traits that strongly mimic those created by environmental filtering (Larios et al. 2017). Ants' foraging choices can depend on environmental conditions such as elevation, precipitation and plant productivity (Segev et al. 2014, Silvestre et al. 2019). For example, *Messor* ant colonies are more selective with the seeds they forage in higher resource, less arid sites (Segev et al. 2020). Therefore, stress has the capacity to influence ant-seed interactions through the functional composition of the ants and plant communities, and through changes to selective foraging.

A key mediator of environmental stress in harsh environments globally is foundation plants. Microclimate amelioration by shrubs is a well-established mechanism of facilitation that affects the survival, growth, and reproduction of annual plants, which often lead to concentrations of biomass beneath the shrub canopy (Flores and Jurado 2003, Filazzola and Lortie 2014, McIntire and Fajardo 2014). A growing body of evidence further demonstrates the importance of shrub canopy facilitation for arthropod communities in drylands (Liu et al. 2016, Braun et al. 2021, 2025). However, these direct and indirect effects of shrubs can change along stress gradients. The stress gradient hypothesis predicts increasing frequency of positive interactions between species

with stress due to climate amelioration (Bertness and Callaway 1994). Shrub canopy facilitation can increase in frequency along a stress gradient by providing relatively more stable microclimates (Pugnaire et al. 2011). However, how shrubs impact ant-plant interactions along stress gradients has not been tested. Comparisons of shrub and open spaces in the Negev desert found that there was higher seed predation by harvester ants in open areas (Wilby and Shachak 2000). Conversely, shrubs can negatively impact the interactions between insects and plants beneath their canopies, for example, through changes to pollinator visitation (Braun and Lortie 2020). If shrub amelioration leads to a concentration of granivore biomass beneath shrubs, then predation could also be relatively higher under shrubs.

We examined the direct and indirect responses of annual seed size, ant worker size, and seed removal rates along a desert climatic stress gradient. Here, we measured the diversity patterns and functional traits of two major desert assemblages: annual plants and granivorous ants, as well as their interactions with and without foundation shrubs along an aridity gradient from semi-arid to arid climates. We tested the hypothesis that environmental stress shapes ant-seed interactions by filtering the functional trait composition of the plant and ant communities. We tested the following predictions: 1) Environmental stress directly reduces ant and plant abundance and richness; 2) Foundation shrubs mediate the impact of environmental stress on ant and plant abundance and species richness; 3) Seed size and worker ant size (estimated by body length and relative mandible length) increase with environmental stress; 4) Seed removal rates by ants depend on environmental stress, foundation shrubs, ant abundance and bait seed size and 5) Seed size selection by ants is mediated by ant worker size (estimated by body length and relative mandible length) and mean annual seed size at the study site. We also measured if seeds were native or not. For predictions 3 and 5, we tested both the native and invasive plant communities to account for potential differences between the communities. This study uses functional traits and gradients to not only understand the consequences of increasing aridity on community composition but also to provide a mechanistic understanding of how these shifts can impact interactions and therefore ecosystem functioning.

Methods

Study sites

A total of seven sites spanning approximately 400 km were surveyed three times: in spring and summer 2023, and in spring 2024 (Table 5.1, Table D1). Sites were located on United States Bureau of Land Management lands, all within California, USA. The study sites form an aridity gradient across two deserts, ranging from semi-arid in the San Joaquin Desert to arid to hyper-arid in the Mojave Desert (Filazzola et al. 2020). The shrub species *Ephedra californica* (Ephedraceae) was the dominant perennial species at the semi-arid extents of the site gradient at Cuyama Valley within the San Joaquin Desert, and it is codominant with *Larrea tridentata* (Zygophyllaceae) at arid sites in the Mojave Desert. Mojave sites were sandy and typical for *L. tridentata* (Lei 1998). The sampling was stratified by shrub and open microsites because the arthropod and plant communities beneath the canopy of desert shrubs are typically distinct from open areas, even a short distance away (Liu et al. 2016, Braun and Lortie 2020, Braun et al. 2021). Shrub microsites were located beneath the canopy of a foundation shrub at the center of a 0.5 m quadrat placed just inside the dripline of the shrub. Open microsites were located randomly at least 2 m away from shrub microsites and not near any other shrub canopy.

Table 5.1: Locations and environmental characteristics of the seven study sites. Mean annual temperature (MAT) and mean annual precipitation (MAP) were obtained from Worldclim. Aridity is DeMartonne's Aridity Index; lower values correspond to higher environmental aridity.

Site	**Desert**	**Lat**	**Long**	**Elevation (m)**	**MAT**	**MAP**	**Aridity**
Tecopa	Mojave	35.85	-116.186	448.9	20.26	85	2.8
Barstow	Mojave	35.09	-116.835	589	19.93	82	2.74
Heart of Mojave	Mojave	34.69	-115.688	780	20	141	4.7
Sheephole Valley	Mojave	34.21	-115.719	559	20.8	113	3.65
Yucca Grove	Mojave	35.41	-115.798	1252	16.4	191	7.23
Cuyama 1	San Joaquin	34.85	-119.484	843	13.9	453	18.9
Cuyama 2	San Joaquin	34.85	-119.487	833	14.1	447	18.58

Site-level mean annual temperature and mean annual precipitation were obtained from World-Clim 2 at a 30s resolution (~ 1km^2, Fick and Hijmans 2017). DeMartonne's aridity values were calculated using the following formula: aridity = P/(T + 10), where P = mean annual precipitation and T = mean annual temperature. Worldclim's temporal range is 1970-2000 (Fick and Hijmans 2017).

We extracted NDVI (normalized difference vegetation index) from EVIIRS (USGS EROS Visible Infrared Imaging Radiometer Suite). EVIIRS has a 375 m spatial resolution, and a 7-day

and 14-day temporal resolution (USGS, 2021). We used the NDVI measurement collected from the date closest to the field sampling date (Table D2). NDVI is often used as an estimate of plant productivity within animal ecology (Pettorelli et al. 2011). NDVI and aridity overlap in terms of stress; low values of NDVI represent an immediate snapshot of plant stress, whereas aridity is a long-term measure of climate conditions because of their differences in temporal resolutions.

Plant assemblages

We focused on annual species for this study because they are a large part of dryland plant diversity (Noy-Meir 1973) and they play key roles in ecosystem function through energy flows and nutrient cycling (Maestre et al. 2016). Annuals have faster species turnover than perennials and therefore are more likely to also respond faster to environmental changes.

We measured species-level annual plant abundance within a 0.5 m by 0.5 m quadrat during the spring each year to coincide with peak blooming to help identify the plants. In 2023, 30 shrub/open pairs were measured, and in 2024, 40 shrub/open pairs were measured.

Seed weights were used as a proxy for seed size (Westoby et al. 1996). Mean seed weights (reported in g per 1000 seeds) were obtained from the Seed Information Database (Royal Botanic Gardens Kew 2022) and the TRY Plant Trait Database (Kattge et al. 2020). An independent literature search was conducted for the remaining seeds (Schiffman 1994, Liczner et al. 2017, Liczner and Lortie 2024, Grant n.d.). *Crypthantha augustofolia* and *Eremocarya* syn *Crypthantha micrantha* could not be consistently identified in the field, and thus we used the mean value of their seed weights as their trait values. Seed trait information was available for ~80% of species and 97% of individual annual plants.

Community weight mean (CWM) trait values are the average values of a trait across species within a community, weighted by abundance. We calculated CWM for seed size at both the quadrat level and the site level using the FD package (Laliberté et al. 2014). We also described the assemblages by abundance and species richness at the quadrat level and by mean abundance and richness at the site level.

We assigned the provenance of each species using Calflora (calflora.org) as native or invasive (Table D3). We then calculated the CWM seed size for invasives and natives at both the quadrat and site levels.

Ant assemblages

We measured the ant communities using pitfall traps (50 ml centrifuge tubes with 33 mm opening diameter) placed beneath shrubs and in open areas for 48 hours per visit. The traps were filled with a 50% propylene glycol and water solution with 2-3 drops of dish soap to break the surface tension. This size of pitfall is frequently used to target the ant communities (e.g., Gotelli and Arnett 2000, Bujan et al. 2022).

Ant community sampling took place alongside annual community sampling, with an additional sampling visit in the summer of 2023. A total of 561 traps was placed over the three visits (Table D4). After trap losses, there were 535 replicates.

Ants were first identified to genus using Fisher and Cover (2007) and to species using AntWiki keys (AntWiki 2021). We classed both harvester ants and omnivorous, seed-collecting species as granivorous (Table D5).

We estimated worker size using Weber's body length (alitrunk length from the anterior edge of the pronotum to the posterior edge of the propodeum). Weber's length is a general measure of body length (Brown 1953). We also measured mandible length and then divided it by Weber's body length.

We measured each trait in up to six individuals per species, per site (n = 155 individual ants). For this study, we defined a population as the members of a species present at a single site. Thus, up to seven populations per species were possible. We dissected each ant and affixed it to a microscope slide using Elmer's glue. We placed each ant mount slide on top of a stage micrometer slide and took focus-bracketed photographs using a Canon 60D DSLR camera with a 60 mm macro lens and Canon EF 25 II extension tube. Helicon Focus software was used to combine the focus stacks into single images. We imported each composite image into ImageJ software (Schneider et al. 2012) and used the micrometer divisions within the image to calibrate the measurement scale within the software, and then measured each trait using the software (as in Braun and Lortie 2024)

Ants forage socially and this leads to the clustering of individuals from the same colony (Longino and Coddington 2002). We converted the ant data from abundance to occupancy, i.e., at the pitfall trap level, presence-absence and at the site level, the proportion of pitfall traps at the sampling location where each ant species was detected.

The CWM trait value for Weber's body length and relative mandible length for the pitfall trap level and the site level were calculated. We used the population-level traits for the trait calculations. CWM reflects the dominant trait values within assemblages and is therefore robust to missed, rare species.

Seed removal rates

We estimated seed removal rates and tested for size preferences by offering seed baits in 6 cm diameter Petri dishes covered with a lid. We cut four 1 cm^2 holes in the sides using a soldering iron to permit ants to access the seeds while preventing access from larger animals (Figure D1). Pearl barley was milled and sieved into three sizes: whole barley (49 seeds per 2 g, 40.1 g per 1000 seeds), medium-sized (134 seeds per 2 g, 14.93 g per 100 seeds) and small (939 seeds per 2 g, 2.13 g per 1000 seeds). Pearl barley was chosen because it has been used in classic studies of desert ant-seed interactions (e.g. Davidson 1977). Pearl barley has had its seed coating removed, and therefore there is no difference in handling difficulty.

We weighed out 2 g of barley per seed depot and left them in the field for 48 hours before collecting the remaining barley to be weighed. The seed depots were placed in shrub/open microsites using the exact locations as the plant quadrats, but not the pitfalls, to avoid biasing the pitfall data. Across the seven sites, we placed 526 depots (Table D4) in 2023 (spring and summer) and 336 in 2024 (spring). After depot losses, there were 781 replicates.

Data analysis

We first examined the role of environmental stress in structuring annual plant and ant abundance and species richness. We fit generalized linear mixed models (GLMM) using the R package glmmTMB (Brooks et al. 2017) with Poisson error distributions for the richness models, and negative binomial distributions for the abundance models because we detected overdispersion ('performance' package, Lüdecke et al. 2020). For each model, microsite (shrub or open) was included as a factor and the study site was included as a random intercept. Aridity and NDVI

were included in the initial models as continuous predictors. While VIF was acceptably low (i.e., below 5) in all models, the two stress gradients were strongly related to each other. Therefore, we evaluated if non-significant predictors reduced model parsimony using AIC and removed them if they did. If both stress gradient variables were significant, we quantified the unique and shared components of explained variation using model-based variance partitioning ('glmmhp' package, Lai et al. 2022). Model-based partitioning adapts variance partitioning methods for mixed models and preserves the hierarchical structure in the data (Lai et al. 2022). The stress gradient hypothesis predicts that stress mediates interactions between species; thus, we included an interaction term between microsite and aridity, and microsite and NDVI.

We then fit GLMM examining the functional structure of each community using Gaussian error distributions. Quadrat-level log-transformed CWM native seed size and CWM invasive seed size, and pitfall trap level CWM Weber's length and CWM relative mandible length were the response variables. The same environmental variables were used as in the previous abundance/richness models. To the plant models, we added site-level CWM_{webers} as a predictor. To the ant CWM models, we added site-level CWM seed as a predictor and fit a separate model with both CWM natives and CWM invasives as predictors to the models. The trait values of each group are also responses to the environmental factors; thus, we used model-based variance partitioning to quantify the unique and shared contributions of each predictor to the response CWM (Lai et al. 2022).

We then fit GLMM to study the drivers of seed removal rates by ants. We used the weight of the barley remaining in the depot as the response variable. We included the study site and the study year as random intercepts. Microsite, aridity, NDVI, the size of the barley (small, medium or large), and mean ant abundance at the study site. To test for drivers of selectivity, we tested for interactions between the barley size and the other predictors. We also included ant body size, mandible length and seed size at the site level as interaction terms. However, we did not test the main effects of these drivers for lack of a reason. We only retained significant interactions in the final models. We used model-based variance partitioning on the final models to estimate the unique and joint effects of each predictor.

All analyses were conducted using R Version 4.3.1 (R Core Team, 2023)

Results

Of the 25 ant species collected, 13 were granivorous, or omnivorous seed collectors (Table D5). All ant species were native. A total of 85 species of annual plants was observed, comprising 73 native, nine invasive, and three unidentified species (Table D3). 52% (n = 25926) of individual plants were invasive species and 48% (n = 24090) were native.

Stress gradient impacts on annual plant and ant communities

Shrubs mediated the relationship between both annual plant species richness and abundance in relation to aridity (Table 5.2, Figure 5.1). Annual plant richness decreased with increasing aridity (i.e., lower values of the aridity index) more quickly in open areas than beneath shrub canopies (Figure 5.1, emtrends, richness: open–shrub = 0.03, $p < 0.001$; open slope = 0.05 ± 0.008, $p < 0.0001$, shrub slope = 0.02 ± 0.008, $p = 0.02$). Annual abundance decreased with aridity in open areas but not beneath shrubs (Figure 5.1, $p < 0.001$, open slope = 0.2 ± 0.04 SE, $p < 0.0001$, shrub slope = 0.013 ± 0.04, $p = 0.73$). Annual plant richness and abundance were greater in open areas at the semi-arid part of the gradient; however, at the arid part of the gradient, annual richness and abundance were greater beneath shrubs (Figure 5.1). Productivity (estimated by NDVI) was not a significant predictor of annual richness and reduced the fit of the models (Table D6). Shrubs also mediated the relationship between annual plant abundance and site-level productivity, the difference between shrub opens was greatest at the most productive side of the gradient and decreased (Figure D2, open trend = -0.0005 ± 0.0001 SE, $p < 0.001$, shrub trend = 0.0002 ± 0.0001 SE, $p = 0.002$). Aridity explained more variation in annual plant abundance than productivity; however, the contributions of aridity and productivity were mainly unique (glmm.hp, arid*microsite = 25%, ndvi*microsite = 5%, shared contribution = 1%).

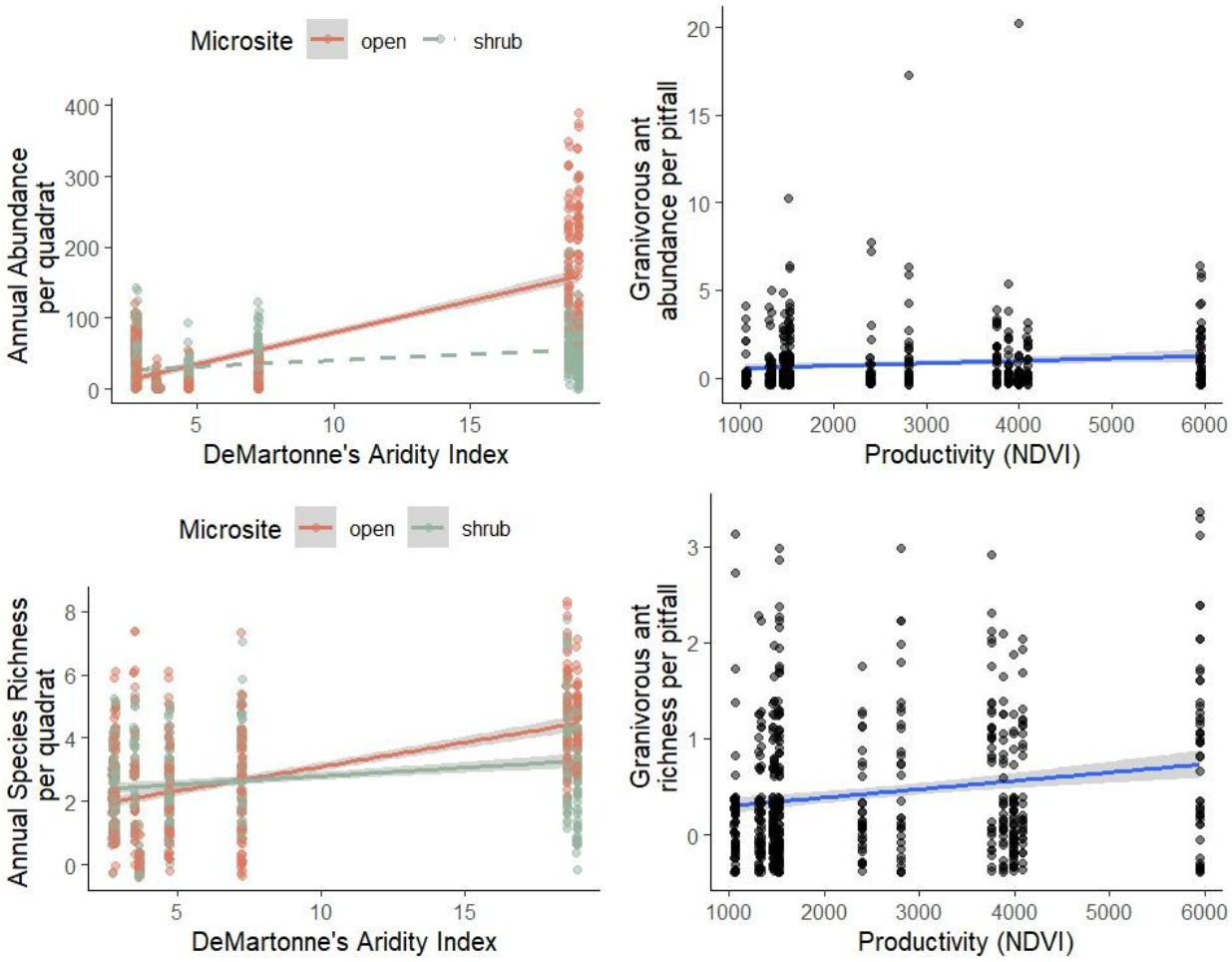

Figure 5.1: Linear regressions showing the response of the plant community to aridity and the granivorous ant community to productivity. Higher values of DeMartonne's Aridity Index correspond to lower aridity. Significance at $p < 0.05$ is represented by solid trendlines and non-significant relationships are represented by dashed trendlines.

Granivorous ant species richness and abundance increased with increasing productivity and decreased with aridity (Table 5.2, Figure 5.2, Figure D3); however, variance partitioning revealed that aridity made no unique contribution to species richness (glmm.hp: ndvi = 6%, aridity = 0%, shared component = .09%). The influence of aridity on species ant richness was therefore due to its shared component with productivity. Aridity contributed a very small unique portion to the variance of ant abundance (glmm.hp, ndvi = 5%, aridity = 0.4%, shared component = 0.1%). Shrubs did not mediate the relationship between productivity or aridity with ant species richness or abundance (Table 5.2).

Table 5.2: Results of generalized linear mixed models testing for the responses of granivorous ant and annual plant abundance and species richness to aridity and productivity (NDVI). Interactions were included with microsite (shrub or open) to test for mediation effects of shrubs.

		Abundance			Species richness		
Community	**Predictors**	**Coef**	**Chi**	**p-value**	**Coef**	**Chi**	**p-value**
Annual Plants	Arid	0.21	10.85	**< 0.001**	0.049	20.7	**< 0.001**
	Microsite (shrub)	-0.18	64.69	**< 0.001**	0.25	1.55	0.212
	Arid * Microsite	-0.194	228	**< 0.001**		30.9	**< 0.001**
	NDVI	-0.0004	13	**< 0.001**			
	NDVI * Microsite	0.0006	107	**< 0.001**			
Granivore Ants	Arid	-0.08	5.12	**0.024**	-0.07	4.72	**0.03**
	Microsite (shrub)	0.11	0.56	0.45	0.002	0.003	0.98
	NDVI	0.0004	10.26	**0.001**	0.0004	10.6	**0.001**

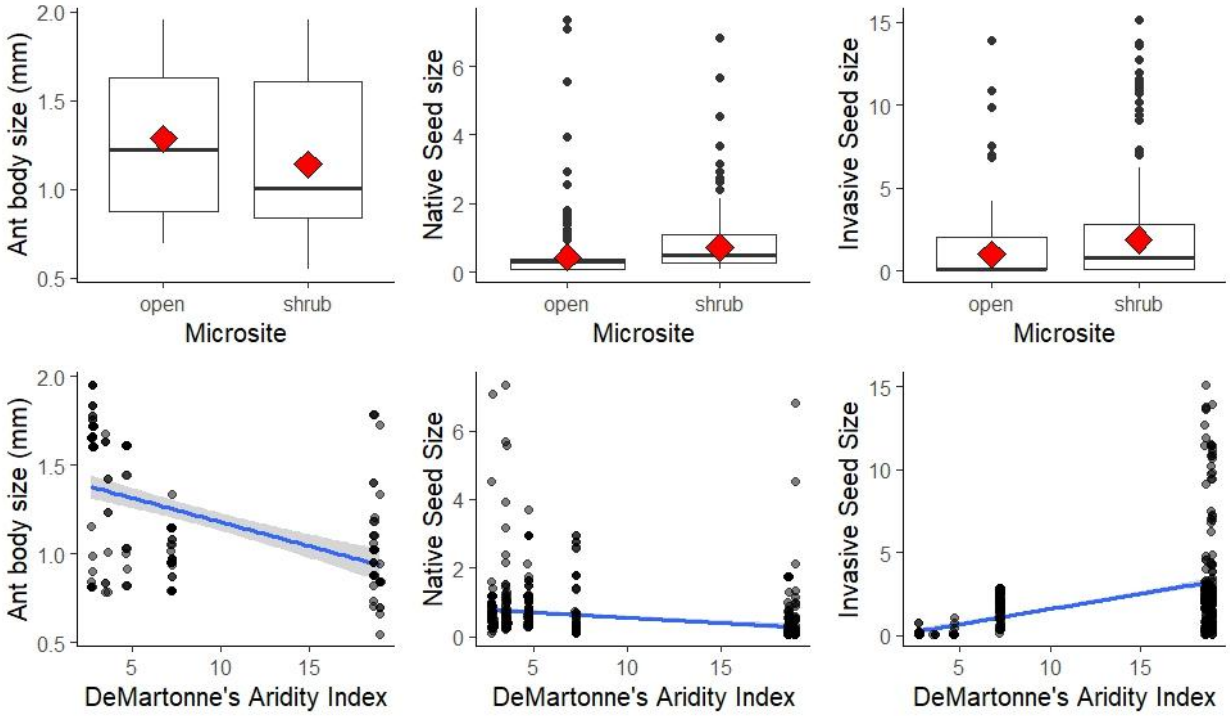

Figure 5.2: Responses of ant body, native seed size and invasive seed size to microsite (open or shrub) and DeMartonne's Aridity Index. Red diamonds on boxplots represent mean values. Higher values of DeMartonne's Aridity Index correspond to lower aridity.

Direct and indirect drivers of seed size and ant worker size

CWM seed size at the site level ranged from 0.085 to 2.21 g per 1000 seeds (mean = 0.79 ± 0.73 SD). Native assemblage CWM seed size ranged from 0.1 to 0.89 (mean = 0.48 ± 0.29 SD) and was smaller than invasive assemblages, which ranged from 0.07 to 3.74 (1.24 ± 1.47 SD).

Quadrat-level CWM seed size of the whole plant community was much more strongly correlated with invasive seed size (Pearson's $r = 0.9$, $p < 0.001$) than with the native community (Pearson's $r = 0.24$, $p < 0.001$). Seed size was significantly larger beneath shrub canopies for both native and invasive plant communities (Figure 5.2, Table 5.3). Native and invasive plants had contrasting aridity-seed size trends: natives increased in size with increasing aridity, while invasives decreased in size (Figure 5.2, Table 5.3). Site-level ant body size was not a significant predictor of native or invasive seed size (Figure 5.2, Table 5.3). NDVI was not a significant predictor of native seed size and reduced the fit of the models (Table D7). Most variation in

CWM invasive seed size was uniquely explained by aridity and productivity's contribution to the model was shared with aridity (glmm.hp, aridity = 59%, ndvi = 0%, shared component = 2%).

Ant communities beneath the canopy of shrubs were significantly smaller than those in open areas (Figure 5.2, Table 5.3). Ant body size increased with both increasing aridity and site-level CWM seed size (Table 5.3). However, when CWM invasive seed size and CWM native seed size were included as two separate predictors, neither was a significant influence on ant body size (GLMM, CWM invasive: coef = 0.03, p = 0.8; CWM native: coef = -0.38, p = 0.23). Variance partitioning showed that most of the relationship between ant body size and seed size was shared with aridity (Figure 5.2). Still, there was a unique contribution of seed size to ant body size (Figure 5.3). NDVI did not predict ant body size and reduced the fit of the model (Table D7). There were no significant relationships between CWM relative mandible length and any of the factors tested (Table 5.3).

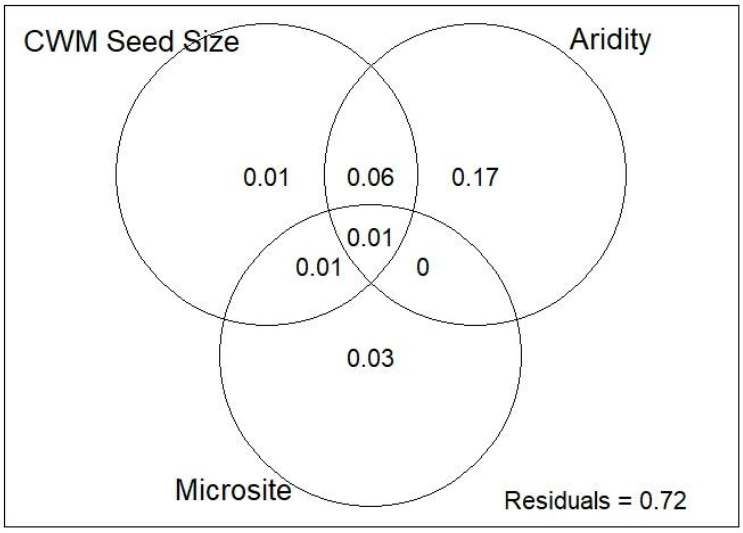

Figure 5.3: Venn diagram showing results of hierarchal variance partitioning of community-weighted mean annual seed size, microsite (shrub and open) and aridity on ant body size. Residuals refer to amount of variation not explained by the three variables.

Table 5.3: Results of generalized linear mixed models testing for the responses of community-weighted mean seed size (native and invasive plant communities) and ant size (Weber's body length and relative mandible length.

	CWM Native Plants			CWM Invasive Plants		
Predictors	**Coef**	**Chisq**	**p-value**	**Coef**	**Chisq**	**p-value**
Aridity	-0.09	31.06	< 0.001	0.23	18.7	< 0.001
NDVI	Na	Na	Na	-0.0002	13.84	0.0002
Microsite (shrub)	0.46	64.5	< 0.001	0.37	61.13	< 0.001
Ant body length	-0.26	0.79	0.37	0.009	0.001	0.97
Ant mandible length	-2.04	1.76	0.18	1.58	1.53	0.22
	CWM Weber's Body Length Ants			**CWM Relative mandible length ants**		
Aridity	-0.03	6.17	0.013	0.0016	2.03	0.154
Microsite (shrub)	-0.14	13.85	< 0.001	-0.005	0.77	0.38
CWM Annual Seed Size	0.17	5.83	0.016	-0.01	1.56	0.211

Seed removal rates and size preferences

Seed removal rates by ants decreased with increasing productivity (Table 5.4). Including both aridity and productivity in the model reduced its fit (Table D7) and the model containing only aridity had lower explanatory power (R^2c both 0.09, R^2c ndvi only = 0.21, R^2c arid only = 0.03). There was no influence of shrub microsite on seed removal rates (Table 5.4). The relationship between seed size and seed removal rates was mediated by ant abundance (Table 5.4). Small-sized seeds were removed at consistent rates independently of ant abundance (Figure 5.3, emtrends, trend = 1.87, p = 0.4), but medium and large seed removal rates increased with ant abundance at the site (Figure 5.3, emtrends, large trend = 9.19, p < 0.001, medium trend = 6.99, p = 0.004). Small seeds were removed at significantly higher rates than large seeds (emtrends, est = 7.32, p = 0.037). There was no relationship between seed size and the environmental predictors or ant traits (GLMM, all p > 0.05).

The largest size of pearl barley was larger than the heaviest annuals but approximates some shrub species present at the sites such as *Ephedra californica*. The medium-sized barley approximates some of the larger seed-grasses, including *Bromus diandrus* and *Hordeum murinum*. The small barley pieces approximate many herbs, such as *Aliciella leptomeria, Dalea mollissima, Erodium*

circicum, Phacelia tanacetifolia and *Salvia carduacea*. However, the mean seed size of native plants across the sites is smaller than the small barley bait size.

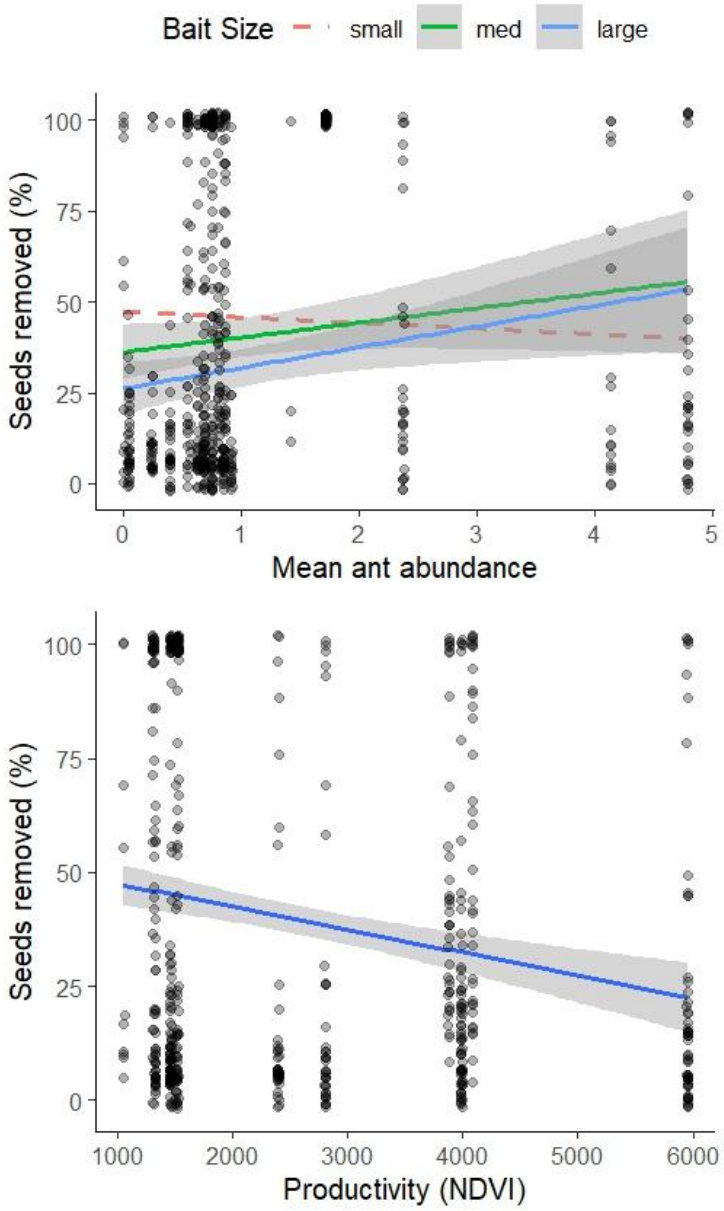

Figure 5.4: Regressions showing the response of seed removal rates to mean ant abundance at the site and the size of bait seeds offered (upper plot). Significance at $p < 0.05$ is represented by solid trendlines and non-significant relationships are represented by dashed trendlines. Lower plot shows the response of seed removal rates to productivity.

Table 5.4: Results of the generalized linear mixed model testing for the responses of seed removal rates (percent removed) of three sizes of bait barley (small, medium and large) to productivity (NDVI), microsite (shrub or open) and ant abundance.

Predictors	**Coef**	**Chi**	**p-value**
NDVI	-0.04	18.39	< 0.0001
Microsite	-1.74	0.39	0.53
Ant Abundance	9.33	18.61	< 0.0001
Seed Bait Size		14.15	< 0.001
Ant abundance * Bait Size		6.27	0.04

Discussion

Seed size, ant body size, and seed removal rates responded to the desert climatic gradient. We documented both bottom-up and top-down relationships between annual plants and ants. The size-matching relationship between annual seed size and ant body size was predominantly explained by their shared environmental responses to the aridity gradient. However, annual seed size made a unique contribution to ant body size, indicating a bottom-up constraint on the functional structure of ant communities. In contrast, we found no evidence that ant body size predicted seed size, and seed size selectivity was also unrelated to ant body size. Instead, ant foraging choices were density-dependent, with removal rates for less-preferred seed sizes increasing with ant abundance. Ant foraging choices were therefore driven more by biotic drivers than environmental drivers. Seed removal rates did not depend on the size of ants at the study sites. Seed removal rates decreased with increasing productivity along the gradient, a pattern consistent with previous Californian studies showing that seed production can outweigh seed predation (Brown and Human 1997). This pattern indicates that overall predation rates are influenced by plant productivity and that selectivity emerges from ant foraging behaviour. Since ants contribute significantly to seed bank dynamics through their selective predation (Crist and MacMahon 1992), our results demonstrate that biotic drivers are essential for community assembly in this desert system.

The physiological connection between ant body size and thermal tolerances likely explains the increase in assemblage-level ant body size with aridity. Large ants are expected to be able to move across hot surfaces better because they can lift their bodies above super-heated surfaces (Kaspari et al. 2015), run faster (Hurlbert et al. 2008) and tend to be more resistant to water loss

than smaller ants (Arnan and Blüthgen 2015). However, while the relationship between critical thermal maximums and body size tends to be positive, it can be inconsistent (Nascimento et al. 2022). For instance, *Forelius pruinosis* (the high noon ant) is very small, highly heat-tolerant, and an open area specialist (Fitzpatrick et al. 2014, Braun et al. 2021). In the San Joaquin Desert, assemblage-level body size has also been shown to decrease with increasing environmental stress (Braun and Lortie 2024). Therefore, while this trait clearly responds to macro and micro-climatic gradients across this system, the reason is more complex than simple thermal tolerances. Ant body size was also related to within-site microclimates, as the ant community associated with shrub canopies was significantly smaller than that of the open-area communities. Stress amelioration by shrubs may allow smaller-bodied ant species to persist beneath the canopy as it does for less stress-tolerant plant species (Holzapfel et al. 2006, Brooker et al. 2008). Thermal tolerances drive spatial and temporal partitioning between ant species (Lessard et al. 2009, Wittman et al. 2010). Thus, the microclimate heterogeneity created by shrubs may promote ant species coexistence.

Seed size is a key functional trait related to dispersal, persistence, germination timing and establishment of plants (Saatkamp et al. 2019). Seed sizes increase along Californian aridity gradients because large seed weights are an adaptation for droughts and aridity (Baker 1972). Our observation that this trend was reversed for invasive species is explained by the species identities of the most abundant invasives rather than a community-wide difference. The most abundant invasive species at the semi-arid sites are *Bromus* sp., which are some of the largest-seeded species across the sites. At the drier end of the gradient, *Schismus barbatus* was the most abundant invasive. These two highly abundant species had an overwhelming impact on the CWM seed size of invasives. Shrub facilitation in arid ecosystems leads to differences in the functional composition of the plant communities growing beneath shrubs and outside of them (Schöb et al. 2012). Both the native and invasive plant communities showed the same pattern of significantly larger seed sizes beneath shrub canopies. We found no evidence for shrub influence on seed removal rates nor selectivity by ants. A mechanism of shrub facilitation is seed trapping (Filazzola et al. 2019). Vegetation physically obstructs the dispersal of seeds, which increases their density in the seed bank (Bullock and Moy 2004). Numerous studies have demonstrated that seedbank density tends to be higher beneath shrubs in arid areas (e. g. Holzapfel et al. 2006,

Filazzola et al. 2019). While few have examined the size-dependency of this response, it has been reported in the Badain-Jaran Desert of China (Zhang et al. 2022).

Environmental stress influenced the abundance, richness and the functional composition of both communities. The relative importance of each gradient differed between the communities: aridity structured the annual community, and productivity structured the ant community. Thus, under the forecasted climate change scenarios that predict an increase in aridity in the area (Braun and Lortie 2025), there will likely be a decrease in the abundance and richness of annuals in this system. This change will lead to reduced overall plant productivity, thereby also impacting the size of the ant communities. The resulting decrease in ant abundance is expected to change size selectivity, leading to a reduction in predation and thus dispersal for larger seeds. The combination of aridity and shrub-created microclimates proved to be the most important predictor of functional composition in both communities. The interdependence suggests that future increases in environmental stress may drive shifts in the functional composition of both ant and plant communities, with implications for ecosystem functioning and resilience. The stress gradient hypothesis was supported for annual plants as a switch to facilitation by shrubs occurred about halfway through the aridity gradient. Maintaining shrub cover in arid environments is essential for supporting annual plant richness and abundance under increasing stress, and for preserving heterogeneity within sites to facilitate ant species coexistence.

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Chapter 6: General Discussion: A synthesis of ant-plant interactions and community assembly

This dissertation examined both the causes and consequences of ant community assembly mechanisms along environmental stress gradients in dryland ecosystems. Assembly mechanisms are often examined within communities on a single trophic level (Gotzenberger et al. 2012, Wong et al. 2019). However, interactions within and among trophic levels are key drivers of community structure. I extended community ecology theory to examine assembly and interactions on multiple trophic levels enabling a deeper understanding of complex ecological dynamics. My aim was to take a functional ecology approach to synthesize the study of ant-plant interactions from a community assembly perspective.

Summary of major findings

The overarching hypothesis that ant community assembly both drives and is an outcome of ant-plant interactions was supported. I started by conducting a manipulative field experiment (Chapter 2) to test if EFN resource availability influences the quality of ant defense through resource partitioning within the ant guild. I found that investment into EFN resources is worthwhile for plants because ant defense benefits silver cholla; however, this investment is mediated by competition within the ant community. I then examined the importance of the EFN-bearing plant community for ant community assembly at macroecological scales using stacked species distribution models (Chapter 3). I tested the hypothesis that EFN-bearing plant and ant communities are coupled in space but become decoupled due to climate change. The EFN-bearing plant community predicted the geographic distribution and diversity of the nectar-feeding ant community. However, interactions between the groups are vulnerable to climate change because of the predicted decrease in geographic overlap between ant-EFN-bearing plant pairs under future climate scenarios. I then examined the relative importance of environmental and biotic assembly mechanisms for ants along a desert stress gradient to test the hypothesis that desert ant communities are assembled by niche-based processes (Chapter 4). The functional structure of the ant community was significantly more diverse than expected which is consistent with the mechanisms of limiting similarity and suggests the importance of competition to ant community structure. The strength of this mechanism decreased with increasing stress,

demonstrating that environmental and biotic assembly mechanisms jointly and non-independently structure the ant community. Finally, I tested if environmental stress shapes ant-seed interactions by filtering the functional trait composition of the annual plant and granivorous ant communities (Chapter 5). Ant functional traits responded to both environmental stress and to the functional traits of the plant community. However, seed size-dependent foraging choices arose from ant population size and not the functional structure of either community.

Collectively, this dissertation contributes to an understanding of how ant communities are assembled in deserts and explore the consequences of ant-plant interactions on several aspects of community structure. This work demonstrates that ant-plant interactions are integral to community assembly for both dryland communities. Here, I discuss the major implications across chapters for community theory, stress gradient theory and of climate change in this system.

Implications for community theory

How functionally similar ant species that share the same host species are able to coexist is a fundamental question for the study of ant-plant interactions and community ecology (Heil and McKey 2003). Competition avoidance through niche-partitioning is an important mechanism that supports species coexistence (Chesson 2000). Recent theoretical models have extended Chesson's models to mutualisms, showing that stable competitive coexistence within a mutualistic guild is possible through the partitioning of a partner-provided commodity and another resource (Johnson and Bronstein, 2019). Chapter 2 demonstrated that ants partition silver cholla individuals based on EFN traits, i.e., a partner-provided commodity, and that the same ant guild uses more than one EFN-bearing species within the same study site (i.e., another resource). This demonstrates that the model's conditions are realistic within mutualisms in natural, complex communities. Plant exudates are a key dietary resource for many species of ants within the Mojave Desert and globally (Blüthgen and Fiedler 2004, Ikeda and des Lauriers 2008, Byk and Del-Claro 2011). The shift from pure predation to plant-based foods was a major reason that ants were able to spread and evolve in deserts (Wilson and Hölldobler 2005, Rico-Gray et al. 2007). Ant-plant mutualisms have contributed to the global diversification of ants and angiosperms through increased interdependence (Nelsen et al. 2018). Therefore, my findings in Chapter 3 that EFN-bearing plant richness predicts nectar-feeding ant community richness at macroecological

scales, even after shared climate responses are accounted for, may result from the increase of niche dimensions created by the EFN-bearing community. Due to the importance of EFN resources for ants, this variation in EFN traits likely facilitates ant species coexistence, and thus the maintenance of desert ant diversity more broadly.

This work revealed that non-trophic ant-plant interactions can also contribute to ant coexistence. The habitat heterogeneity created by the structural characteristics of plants shaped the functional structure of the ant community at small, micro-site scales (Chapter 5) and along regional gradients (Chapter 4, Chapter 5). Foundation shrubs in deserts create variation in micro-climates through shading, by increasing soil moisture through hydraulic lift and by increasing soil nutrients and organic matter in the understory (Filazzola and Lortie 2014). The granivorous ant communities associated with foundation shrubs were significantly smaller than those found in more open areas (Chapter 5). This pattern did not result from differences in species richness, suggesting highly localized, small-scale spatial partitioning mediated by trait differences. Three ant functional traits were related to vegetation gradients at regional scales (Chapter 4). Environmental heterogeneity, including vegetation structure, was significantly related to ant beta diversity but not to ant species richness. This suggests overall that the relationships between traits and vegetation contributed to the turnover of ant species along the regional gradient. The importance of biotic interactions for shaping large-scale distributions has often been ignored or dismissed (Wisz et al. 2013, Kissling and Schleuning 2015). However, the role of environmental filtering has likely been overstated because biotic interactions can actually give rise to many patterns seen (Kraft et al. 2015, Cadotte and Tucker 2017, Larios et al. 2017). The relationships between ant functional traits and these environmental and vegetation differences suggest that the variation created by plants contributes to niche differences and, thus, ant diversity.

Horizontal interactions, here, ant-ant interactions, cascaded to ant-plant interactions and plant herbivore interactions through ant-herbivore interactions (Chapter 2). Interaction chains emerge when pairwise competitive interactions are embedded within a larger interaction network (Levine et al. 2017). These chains have also been documented in ant dispersal systems with interspecific ant-ant interactions cascading through ant-plant interactions to affect the composition of the plant community (Prior et al. 2020). I showed that predation or dispersal risk for seeds of a certain size can depend on the abundance of species on another trophic level

(Chapter 5). Competition, or the 'ghost of competition past' (Connell 1980), may have caused ants to be displaced to less-preferred seed sizes as the community size increased. Thus, the outcome of ant-plant interactions is determined in part by the probability of interacting with a given ant species. Ant-plant interactions are famously context-dependent (Chamberlain and Holland 2009, Chamberlain et al. 2014). My research suggests that context dependency in ant-plant interactions can arise in part from predictable outcomes resulting from competitive hierarchies within the ant community. Mutualisms between guilds are mediated by competition within each side (Johnson and Bronstein 2019), but community ecology is dominated by concepts built from direct, pairwise interactions. This has resulted in the majority of empirical and theoretical work considering only two species at a time, e.g. (Holland et al. 2002). Network approaches have emerged as a method to quantify many interactions between many species or individuals, but often focus more on describing structure than understanding interaction outcome for species fitness (Delmas et al. 2019, but see Lázaro et al. 2020). My work bridges this gap in community ecology by demonstrating that field studies that incorporate interactions more widely across trophic levels can be tractable and explain interactions more completely than studies built only using species pairs.

Implications for stress gradient theory

The stress gradient hypothesis (SGH) explains a key aspect of context-dependence in harsh environments by explaining why interspecific interactions change along stress gradients (Bertness and Callaway 1994, Lortie and Callaway 2006). The SGH was explicitly tested in Chapter 5 and implicitly examined in Chapter 4. As predicted by the SGH, I found that the relationship between foundation shrubs and the annual plant community became more positive with increasing aridity (Chapter 5). In contrast, the relationship between shrubs and the granivorous ant community, at least in terms of abundance and species richness, was on average neutral and relatively invariant to stress. I have shown in my previous work that foundation shrubs of the Mojave and San Joaquin deserts facilitate both the annual plants and the ground-active arthropod community, but the SGH only applied to the plant community (Braun et al. 2021). The question of how well the SGH generalizes to taxa other than plants is ongoing (Adams et al. 2022). I found a decrease in the role of limiting similarity within the ant community with increasing stress, a pattern consistent with a decrease in the importance of

competition with stress and thus the SGH. Most support for the SGH in animals is based on animal-animal interactions, rather than animal-plant interactions (Fugère et al. 2012, Dangles et al. 2013, 2018). One possible explanation is that, because there is typically no competition between arthropods and plants, there is no competition to decrease. In terms of shrub facilitation along desert stress gradients, a strong mechanism of the SGH is that micro-climate amelioration becomes relatively more important as environmental harshness increases (Bertness and Callaway 1994). Facilitation of arthropods by desert shrubs has been repeatedly observed globally (e.g. Groner and Ayal 2001, Mazía et al. 2006, Liu et al. 2016, Braun and Lortie 2020, Braun et al. 2021). Understanding the context-dependence of these interactions under stress is critical for understanding the consequences of climate change because these drylands are expected to continue experiencing increasing aridity (Chapter 3, MacDonald et al. 2016).

A key gap in community assembly theory is understanding the relationships between biotic and abiotic filters and how this results in functional trait distributions (HilleRisLambers et al. 2012, Feng et al. 2025). The stress dominance hypothesis proposes that environmental filtering should be stronger in relatively harsher environments, leading to a decrease in the role of competition in determining functional traits and a convergence in traits within communities (Weiher and Keddy 1995, Swenson and Enquist 2007). Positive interactions, like those observed between shrubs and annuals (Chapter 4), and EFN-bearing plants and nectar-feeding ants (Chapter 3), often involve biotic factors modifying the environment (Bruno et al. 2003, Filazzola and Lortie 2014). This complicates the mechanisms of the stress dominance hypothesis in the presence of positive interactions. In plants, functional traits have been identified that increase the benefits of association with other species (Rolhauser and Pucheta 2016). At the community level, these traits would converge with increasing stress as the harsh environmental conditions select species with traits that allow them to coexist with foundation species. However, in the absence of the facilitating species, the traits wouldn't confer tolerance to the environment. This is a potential mechanism for biotic filtering masquerading as environmental filtering. Accurately portraying the relationship between the filters is important because trait-environment relationships are often used to predict the consequences of a changing climate (Heilmeier 2019, Green et al. 2022).

Implications of climate change for desert ant-plant interactions

Each chapter has implications for understanding how climate change will affect ant-plant interactions and ant community assembly in dryland systems. Climate vulnerability is the degree of threat due to a changing climate to a community or ecosystem and depends on the amount of exposure and sensitivity to a changing climate, as well as the community's ability to adapt to the changes (Dawson et al. 2011, Kling et al. 2020). My third chapter demonstrated that two desert-adapted communities differ in their vulnerability to climate change. Species richness of both the EFN-bearing plant and ant communities decreases across the Mojave and Colorado deserts under predicted climate change scenarios, despite the increase in suitability across the deserts for about 40% of the ant species (Chapter 3). Additionally, the decrease in spatial partner overlap between the communities outweighs the potential increases in overlap. Collectively, this suggests a high degree of vulnerability for these communities. Competitive ability in desert ants is traded off against stress tolerance (Andersen 1997, Bestelmeyer 2000). *Forelius* sp. have high thermal tolerances (Holway et al. 2002), and I found that the range of *F. mccooki* increases across the Mojave Desert (Chapter 3). *Forelius* species are behaviourally subdominant and poor competitors relative to more aggressive ants (Andersen 1997). *Forelius pruinosis* is one of the four main ant defenders of *Ferocactus*. However, it is the least effective defender and its per capita effectiveness less than a third of *Solenopsis xyloni*'s (Ness et al. 2006). *Solenopsis xyloni* is strongly competitive and was associated with silver cholla individuals with significantly more EFN resources than other co-occurring species (Chapter 2). However, *S. xyloni*'s range is predicted to decrease in the future under climate change (Chapter 3). These results suggest that subdominant species, such as *Forelius*, may increase in frequency in assemblages and interact with a wider range of EFN-bearing species and individuals due to competitive release from more dominant, but less stress-tolerant ant species. Since defense for silver cholla is mediated by ant competitive hierarchies, the quality of plant defense is likely to decrease due to increased contact with subdominant, poor quality defenders.

Studying whole community responses to stress can complement manipulative, experimental approaches to better understand when the natural complexity of whole ecosystems hinders our predictive ability. Seed removal rates were not directly tied to the aridity gradient; however, the predicted increases in aridity will alter seed removal rates because of its direct relationship with

seed size, and indirect relationship with ant abundance through productivity (Chapter 5). Together, these relationships predict a reduction in predation and thus dispersal for larger seeds. Large seed size is an adaptation to aridity and drought tolerance (Baker 1972); however, the reduction in dispersal services suggests that large-seeded plants may be more vulnerable to increased aridity than previously thought. Aridity strongly impacted community assembly processes for ant communities and functional trait diversity will likely decrease under increasing aridity (Chapter 4). Beta-diversity was related to the environmental gradient, but species richness was not. This means that species replacement with functionally similar species contributed to the observed community trait convergence with increasing aridity (Chapter 4). Therefore, changes to ant identity will precede changes to the functional structure of the ant community. Shifts in ant identity can cascade to the rest of the community through mutualistic partners (Chapter 2, Prior et al. 2020). Future research that partitions functional turnover from species turnover will further improve our ability to predict the role of species losses on the functional structure of communities.

Future directions

My dissertation increased our understanding of community theory by focusing on the relationship between community assembly and ant-plant interactions. Throughout this dissertation, I was able to manipulate the availability of plant resources (e.g. honey water and seed baits), but I could not manipulate the ant community. Mesocosm or artificial community experiments that control the identity and functional composition of mutualists would improve our understanding of the role of assembly mechanisms to ant-plant interactions. The inclusion of functional traits into SDMs is still fairly rare (but see Chapter 4); however, their inclusion can identify traits associated with climate change vulnerability. Unfortunately, these macroecological scale functional analyses are still strongly limited for arthropods by a lack of data on functional traits (i.e., Raunkiæran shortfall) (Wong et al. 2019, Gonçalves-Souza et al. 2023). Future community assembly developments, both empirical and theoretical, need to include multitype interactions and the dependencies between those interactions and the environment. For example, by explicitly including the indirect negative effects within the ant guild within ant-plant interactions and by including the biotic modification of the environment into trait-based

community assembly theory. These extensions to my work would further benefit community theory and our ability to predict the consequences of climate change at the community level.

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Appendix A: Supplemental Information for Chapter 2

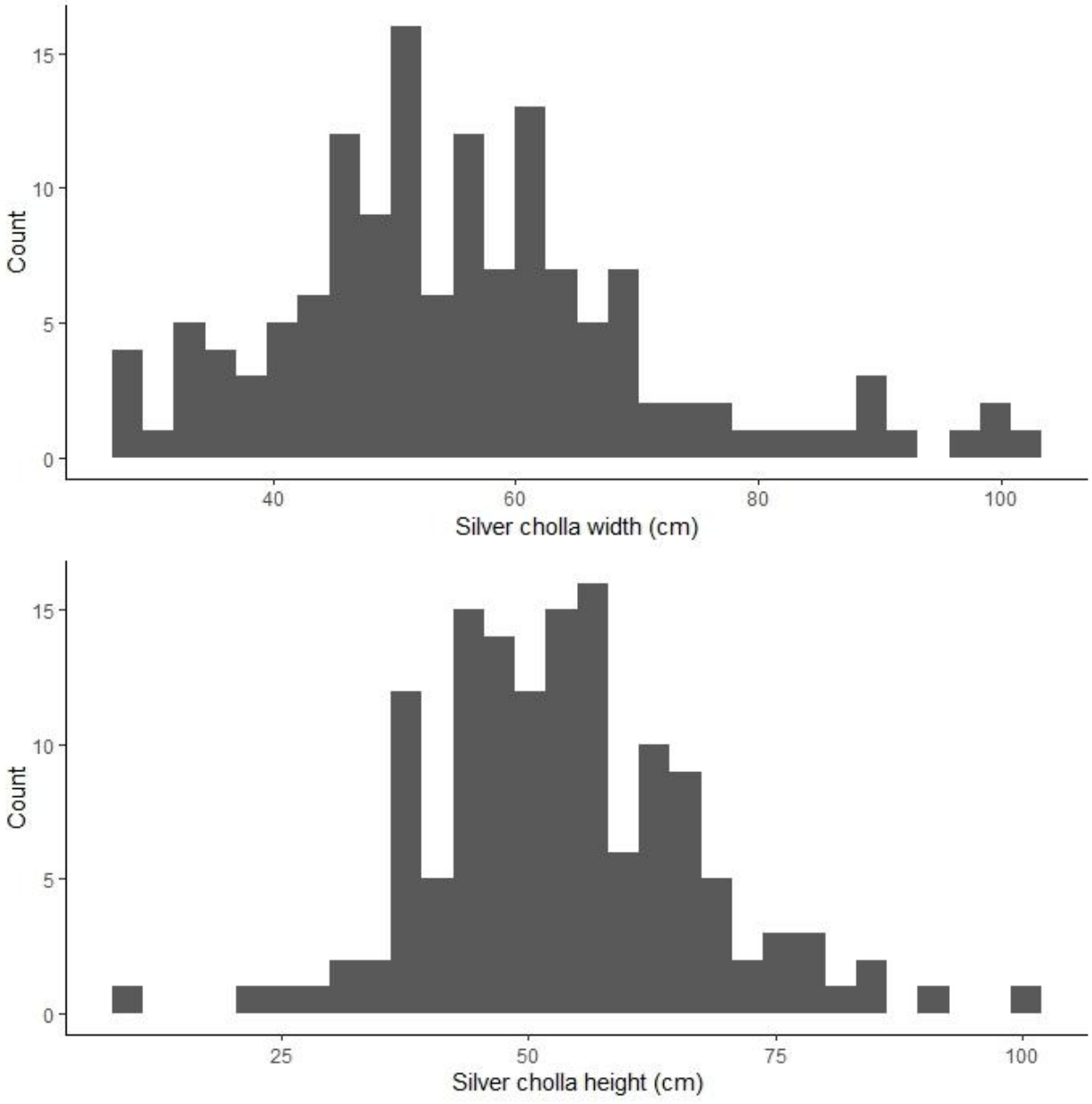


Figure A1: Histograms showing the distribution of silver cholla widths (left) and heights (right) in cm.

Table A1: Dates and times of visual surveys

Year	Date	Time	Survey Type	Days since treatment
2023	April 18	Morning	Visual	9
	April 21	Morning	Visual	12
	April 26	Morning	Visual	17
	May 1	Midday	Visual	22
	May 3	Afternoon	Visual	24
	May 3 – 6	72 hours	Pitfall	24-27
2024	April 19	Morning	Visual	7
	April 22	Evening	Visual	10
	April 24	Morning	Visual	12
	April 28	Morning	Visual	16
	April 29	Morning	Visual	17
	May 3	Afternoon	Visual	21
	May 4	Morning	Visual	22
	May 4 - 7	72 hours	Pitfall	22-25

Figure A2: Photo of arboreal pitfall trap used in this study. The pitfalls were 50 ml centrifuge tubes containing a 50% mixture of propylene glycol and water, baited with sardine oil and honey, and attached to a main stem or branch for 72 hours.

Table A2: Abundance and identity of herbivore and predator morphospecies observed on silver cholla.

	Common name	Scientific name	Observations across surveys
Herbivore			
	Cactus coreid	Chelinidea vittiger (Hemiptera:Coreidae)	643
	Leaf-footed cactus bug	Narnia sp. (Hemiptera:Coreidae)	93
	Picture-winged fly	Notogramma purpuratum (Diptera:Ulidiidae)	64
	Green stink bug	Hemiptera:Pentatomoidae	18
	California bordered plant bug	Largus californicus (Hemiptera: Largidae)	13
	Grass bug/Scentless plant bug	Arrhysus sp (Hemiptera: Rhopalidae)	3
	Leaf beetle	Coleoptera: Chrysomelidae	3
	Western leaf-footed bug	Leptoglossus.clypealus (Hemiptera: Coreidae)	2
	Green lygus bug	Lygus sp. (Hemiptera: Miridae)	1
	Caterpillar	Lepidoptera	1
	Stilt bugs	Hemiptera: Bertyidae	1
	Ornate checkered beetle	Trichodes ornatus (Coleoptera: Cleridae)	1
Predators			
	Big eyed bugs	Geocoris pallens/punctipes (Hemiptera: Geocoridae)	73
	Ladybug	Coleoptera (Coccinelidae)	36
	Jumping spider	Aranae:Salticidae	18
	Black parasitoid wasps	Hymenoptera: Apocrita	15
	Big eyed bugs	Isthmocoris sp. (Hemiptera: Geocoridae)	11
	Braconid wasps	Hymenoptera: Braconidae	9
	Green lacewing	Neuroptera: Chrysopidae	8
	Tiny wasp	Hymenoptera	7
	Spider wasps	Hymenoptera: Pompilidae	4
	Black big-eyed bug	Geocoris sp (black) (Hemiptera: Geocoridae)	4
	Other spiders	Aranae	3
	Wingless wasp	Gelis sp. (Hymenoptera: Ichneumonidae)	2
	Ichneumoid wasp	Ichneumoid (Hymenoptera: Ichneumonidae)	2
	Thread-waisted wasp	Hymenoptera:Sphecidae	2
	Assassin bug	Apiomeris sp. (Hemiptera:Reduviidae)	2
	Lynx spider	Aranae: Oxyopidae	1
	Crab spider	Aranae: Thomisidae	1
	Assassin bug	Zelus tetracanthus (Hemiptera: Reduviidae)	1
	Running crab spider	Aranae: Philodromidae	1
	Orb weaver spider	Araneus sp. (Aranae: Araneidae)	1

Table A3: Pairwise contrasts from emmeans for each ant species showing differences in abundance on resource supplemented (N) and control (C) silver cholla plants. Contrasts from ant species (factor) by treatment (factor) within a negative binomial generalized linear mixed model. Natural EFN resources and the study year were included as covariates in the model. The individual plant identifier was included as a random intercept to account for the repeated visual surveys.

Ant species	Contrast	estimate	SE	z.ratio	p-value
Camponotus sayi	C - N	-0.908	0.89	-1.017	0.3092
Crematogaster depilis	C - N	0.320	0.26	1.242	0.2142
Myrmecocystus flaviceps	C - N	-1.252	0.56	-2.219	**0.0265**
Myrmecocystus (Eremocystus)	C - N	22.538	87000.71	0.000	0.9998
Forelius pruinosis	C - N	-1.826	1.12	-1.635	0.1020
Monomorium ergatogyna	C - N	-16.739	2743.14	-0.006	0.9951
Myrmecocystus mexicanus	C - N	-18.791	4417.16	-0.004	0.9966
Solenopsis xyloni	C - N	-1.854	0.47	-3.950	**0.0001**

Table A4: Pairwise contrasts from emmeans for each ant species showing differences in presence on resource supplemented (N) and control (C) silver cholla plants. Contrasts from ant species (factor) by treatment (factor) within a binomial generalized linear mixed model. The individual plant identifier was included as a random intercept to account for the repeated visual surveys.

Ant Species	contrast	estimate	SE	z.ratio	p-value
Camponotus sayi	C - N	-1.069	9.10E-01	-1.174	0.2403
Crematogaster depilis	C - N	0.445	2.90E-01	1.513	0.1303
Myrmecocystus flaviceps	C - N	-1.431	5.90E-01	-2.420	**0.0155**
Myrmecocystus (Eremocystus)	C - N	23.426	1.47E+05	0.000	0.9999
Forelius pruinosis	C - N	-1.998	1.13E+00	-1.766	0.0774
Monomorium ergatogyna	C - N	-17.686	4.05E+03	-0.004	0.9965
Myrmecocystus mexicanus	C - N	-20.206	8.16E+03	-0.002	0.9980
Solenopsis xyloni	C - N	-2.028	5.00E-01	-4.049	**0.0001**

Table A5: Results from binomial GLMM for the presence of the two most frequently observed ant species on silver cholla.

	Crematogaster depilis presence		**Solenopsis xyloni presence**	
Predictor	Coef	p-value	Coef	p-value
Treatment (Supplementation)	-1.01	0.17	1.69	**0.001**
EFN Resources	0.06	**0.007**	0.023	**0.04**
Plant width (cm)	-0.07	**0.013**	0.01	0.53

Table A6: Pairwise contrasts from emmeans in EFN resource use between the three most frequently observed ant species on control plants.

Pair	Estimate	SE	p-value
Crematogaster depilis – Myrmecocystus flaviceps	0.636	0.293	0.076
Crematogaster depilis – Solenopsis xyloni	-0.374	0.159	**0.049**
Myrmecocystus flaviceps – Solenopsis xyloni	-1.009	0.32	**0.0045**

Table A7: Results from GLMM testing for the influence of the two most frequently observed ant species on the abundance of the herbivore community and cactus coreids. The presence of *C. depilis* or *S. xyloni*, predator abundance, the number of segments with new growth and the interaction between experimental treatment and the number of days since treatment were included as predictors. The study year and individual plant identifier were included as random effects.

	Herbivore abundance			**Cactus coreid abundance**		
Predictor	**Coef**	**Chisq**	**p-value**	**Coef**	**Chisq**	**p-value**
Crematogaster presence	-0.33	8.28	0.004	-0.34	6.89	0.009
Supplementation	0.37	0.83	0.36	0.44	1.18	0.28
Days since treatment	0.016	0.006	0.93	0.02	0.2	0.65
Segments with new growth	0.017	27.38	<0.0001	0.02	22.2	<0.0001
Predator abundance	-0.12	2.52	0.11	-0.04	0.24	0.62
Supplementation*Days since treatment		6.06	0.014		7.07	0.009
Solenopsis presence	-0.12	0.39	0.53	-0.06	0.09	0.77
Supplementation	0.39	0.47	0.11	0.47	0.9	0.36
Days since treatment	0.016	0.05	0.07	0.02	0.3	0.59
Segments with new growth	0.017	26.76	<0.001	0.017	21.76	<0.001
Predator abundance	-0.11	2.39	0.12	-0.04	0.21	0.64
Supplementation*Days since treatment		5.72	0.017		6.86	0.009

Table A8: Results from GLMM with herbivore and cactus coreid abundance as a response. The abundance of ants, predator abundance, the number of segments with new growth and the interaction between experimental treatment and the number of days since treatment were included as predictors. The study year and individual plant identifier were included as random effects.

	Herbivore abundance			Cactus coreid abundance		
Predictor	Coef	Chisq	p-value	Coef	Chisq	p-value
Ant abundance	-0.02	3.75	0.052	-0.025	4.03	0.04
Supplementation	0.36	0.43	0.5	0.44	0.74	0.11
Days since treatment	0.07	0.23	0.62	0.02	0.87	0.02
Segments with new growth	0.017	28.3	<0.001	0.017	23.2	< 0.001
Predator abundance	-0.11	2.45	0.11	-0.042	0.27	0.6
Supplementation*Days since treatment		4.97	0.03		6.07	0.01

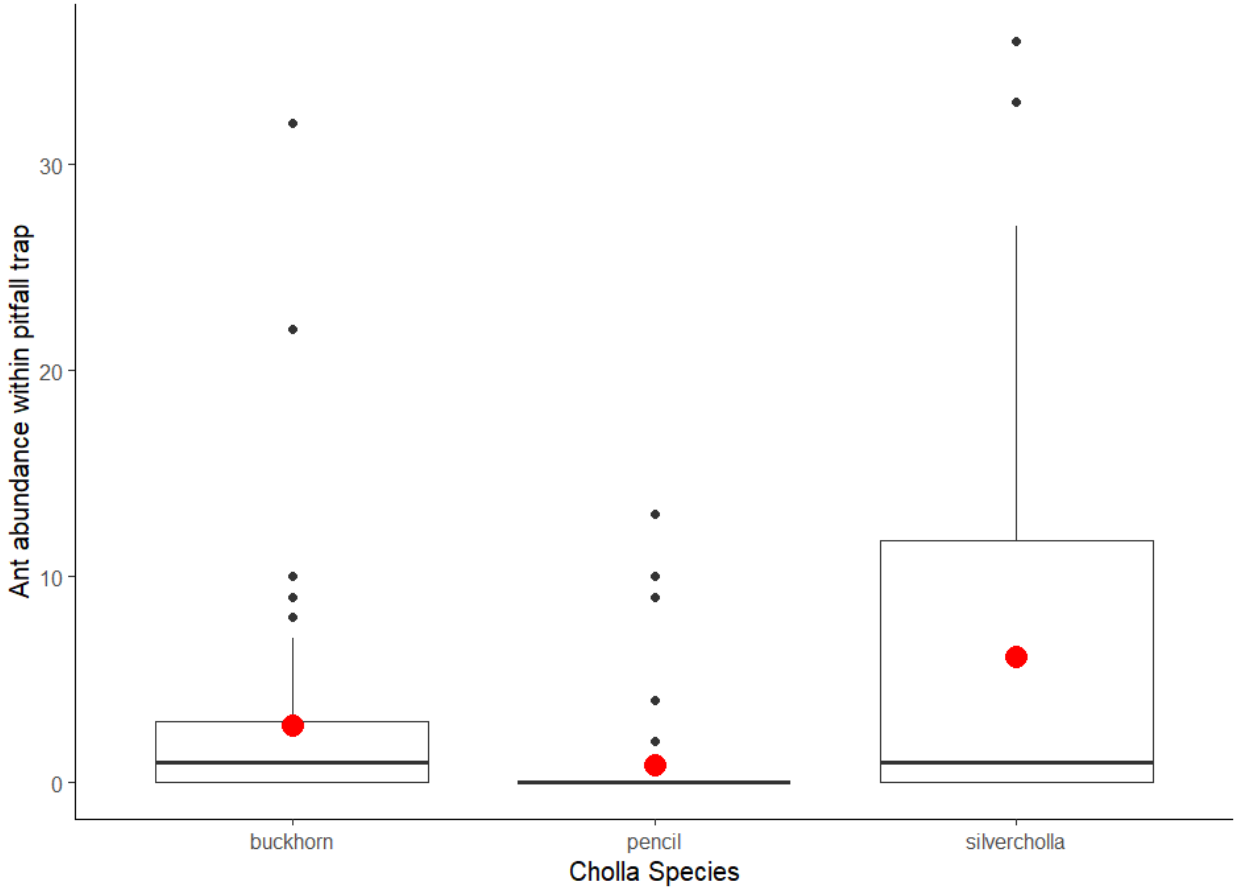


Figure A3: Boxplots showing the difference in ant abundance caught within pitfall traps between three species of cholla: Buckhorn cholla, pencil cholla and silver cholla. Mean abundances are indicated by black diamonds; median responses are indicated by the center horizontal black line

Appendix B: Supplementary Information for Chapter 3

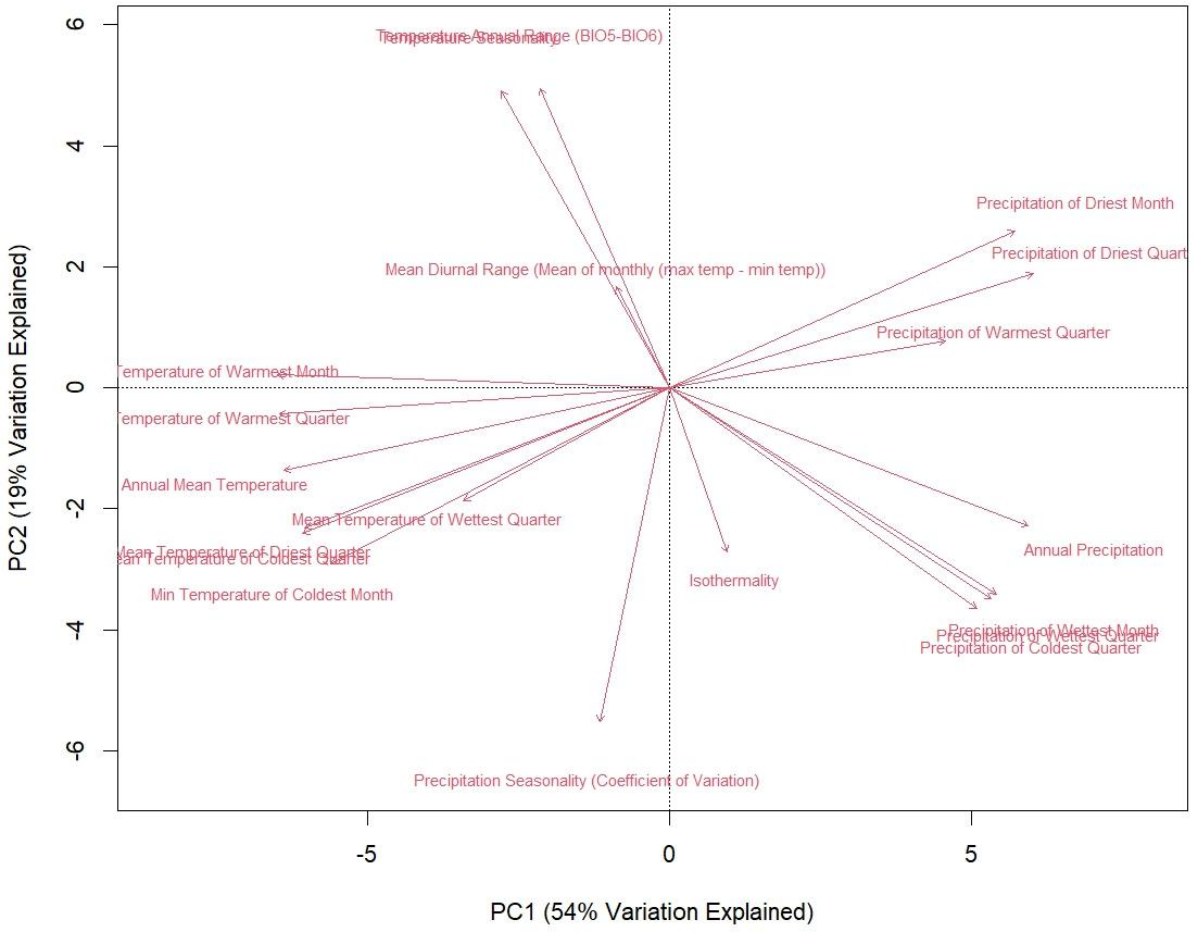
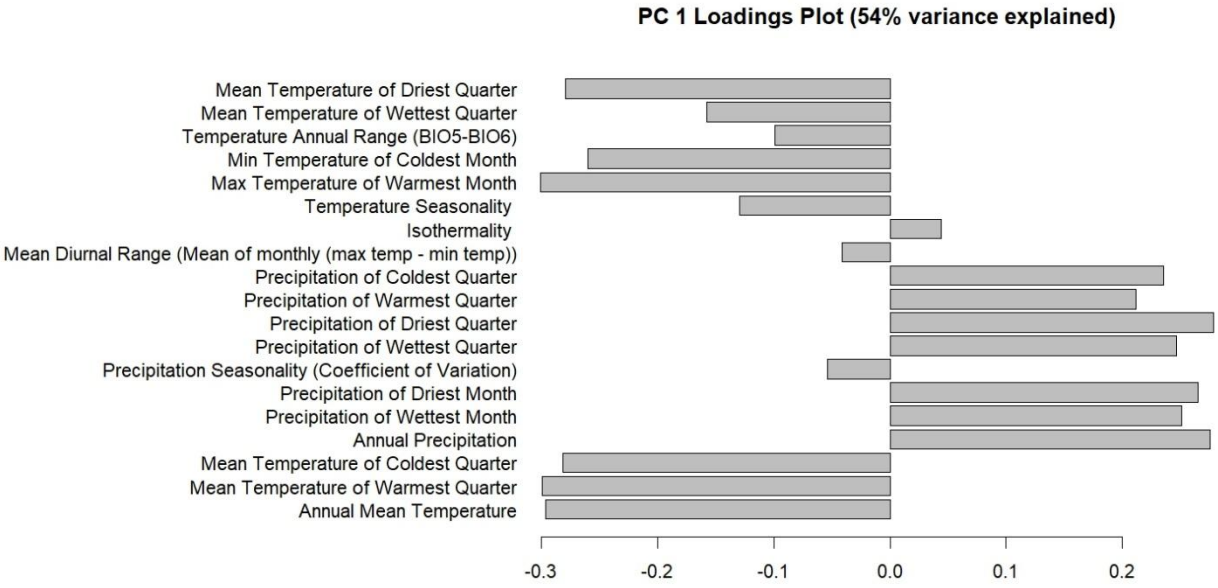
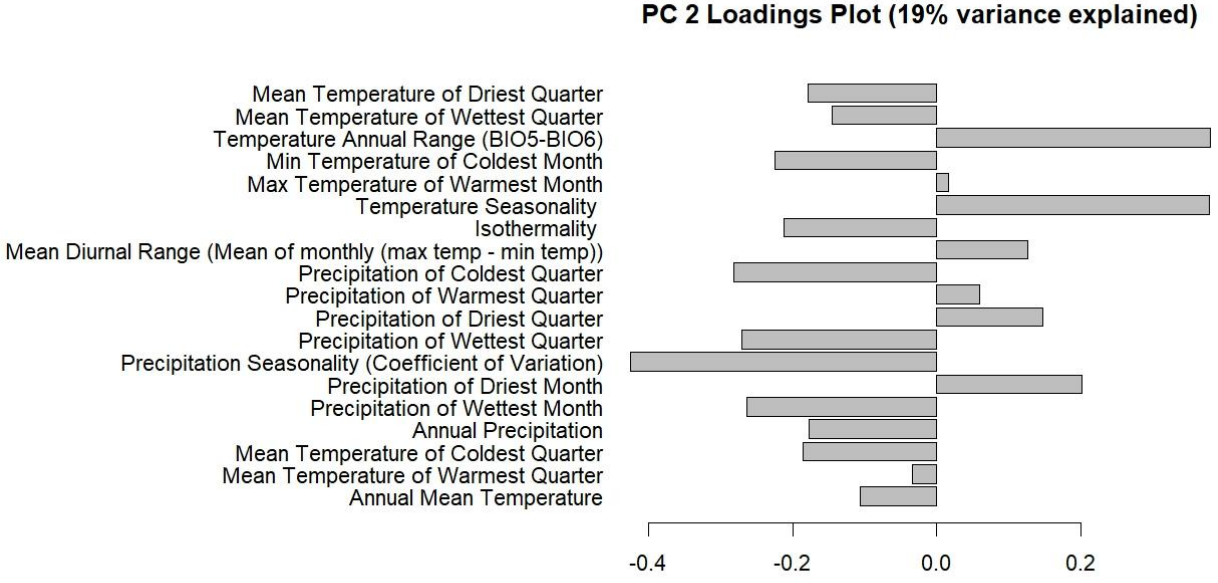


Figure B1: PCA of the 19 bioclimatic variables across the Mojave and Colorado deserts. The first four PCA axes explained 90% of the total bioclimatic variation. The bioclimatic variables were extracted from Worldclim 2.


PC 1 Loadings Plot (54% variance explained)
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 (19% variance explained)
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
-0.4
-0.2
0.0
0.2

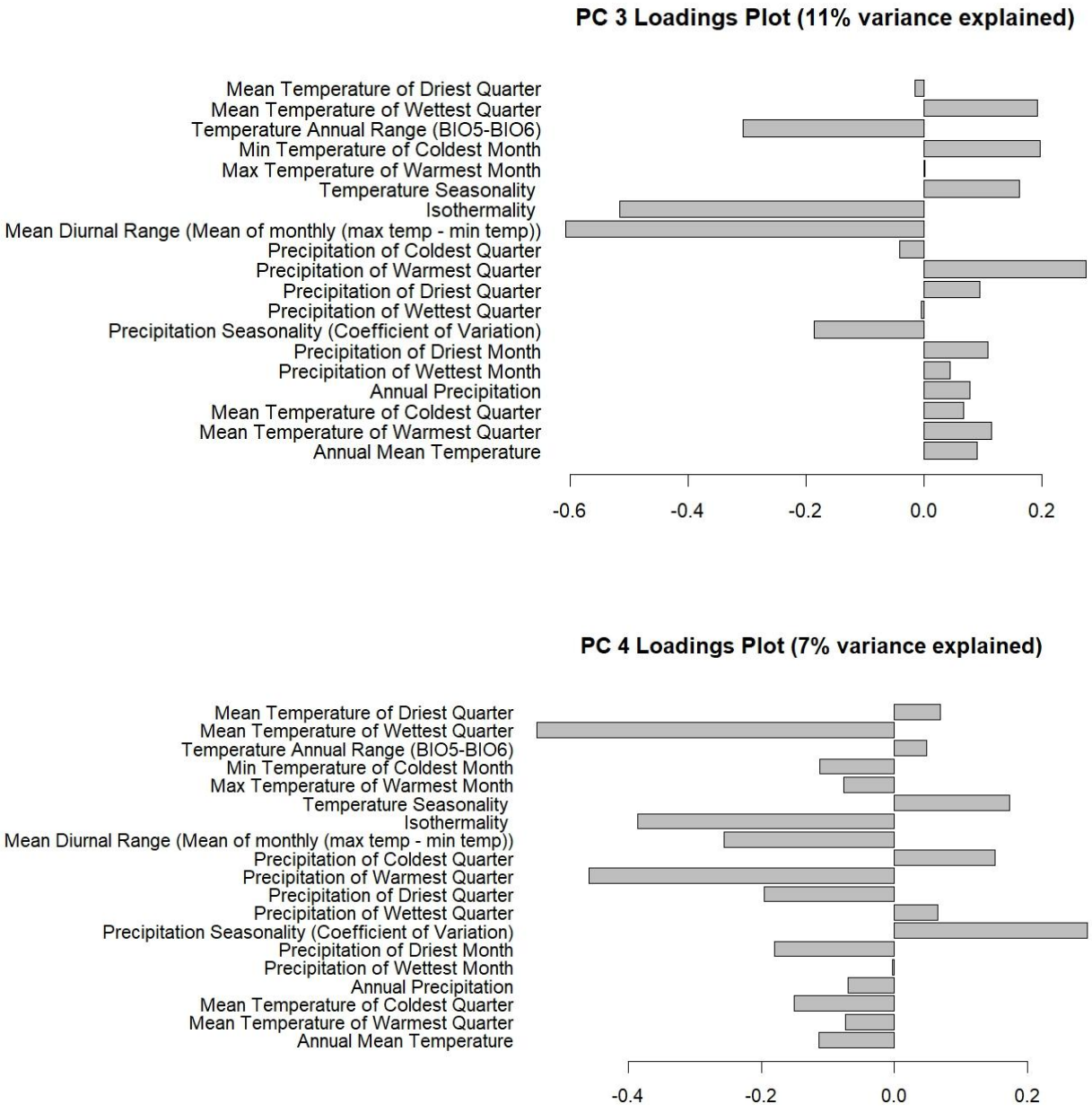


Figure B2: Loadings for each of the four PCA axes in the study.

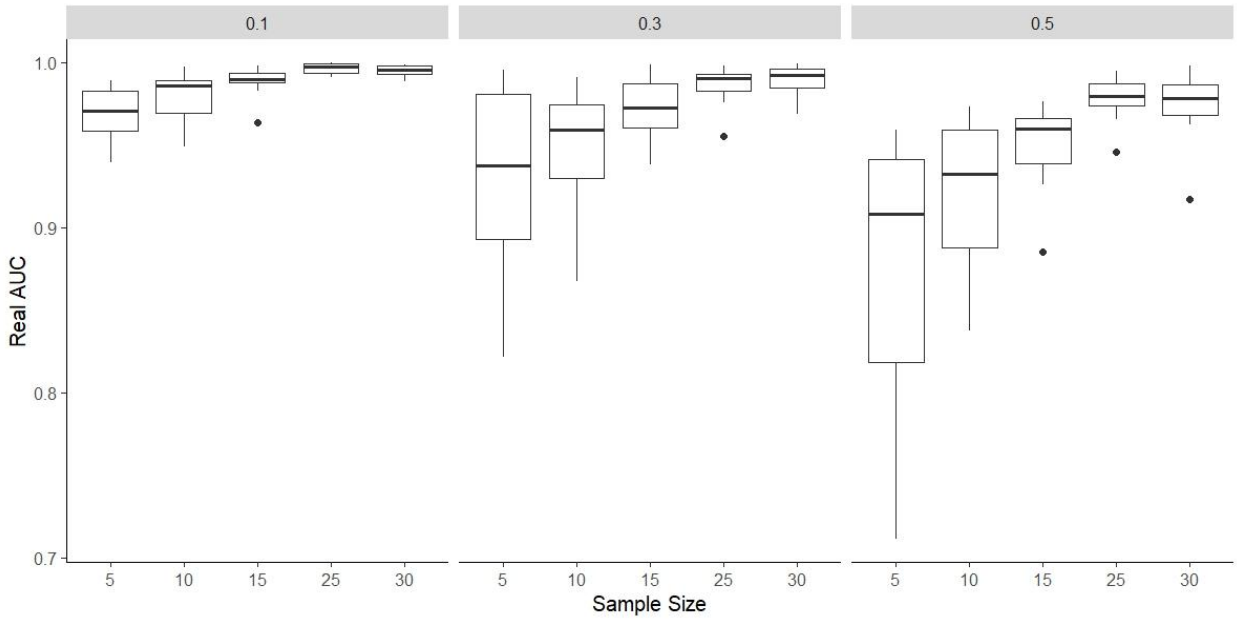


Figure B3: Results from applying van Proosdij (2015) framework for determining the minimum required sample size. Three prevalence levels were tested: 0.1, 0.3 and 0.5.

Table B1: 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 B2: 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. *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

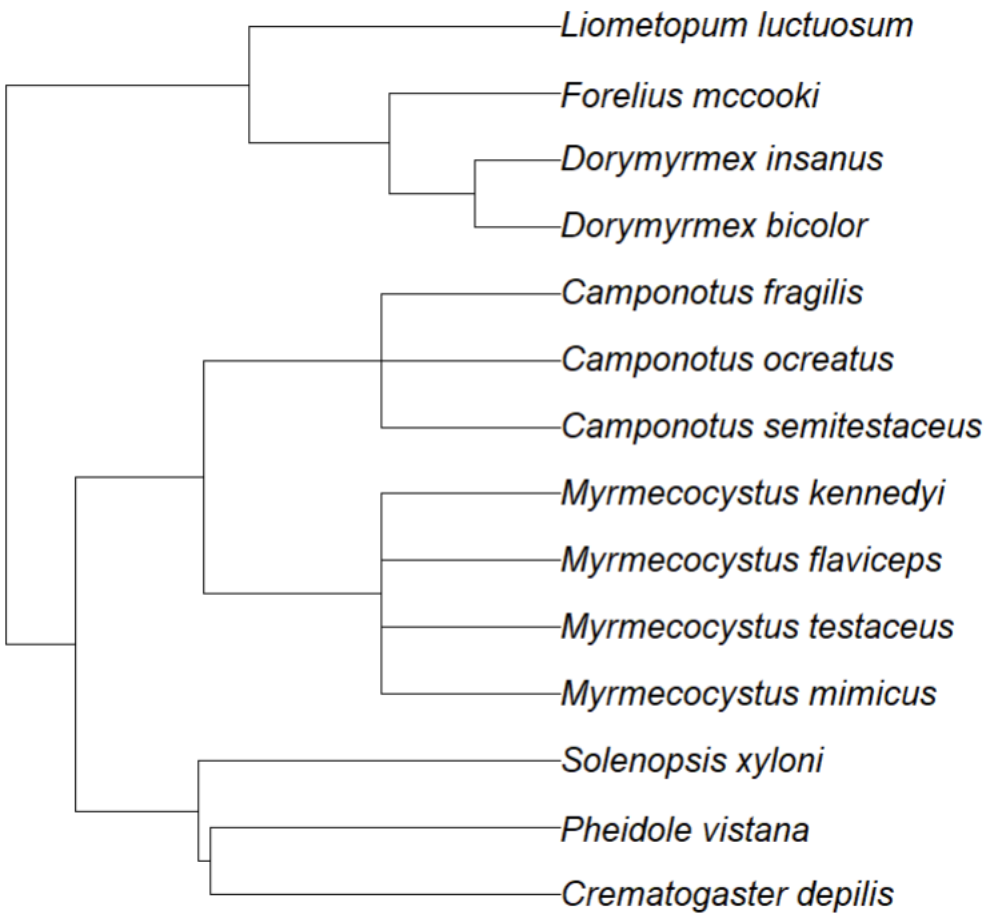


Figure B4: Pruned phylogenetic tree of ant species based on Moreau and Bell 2013.

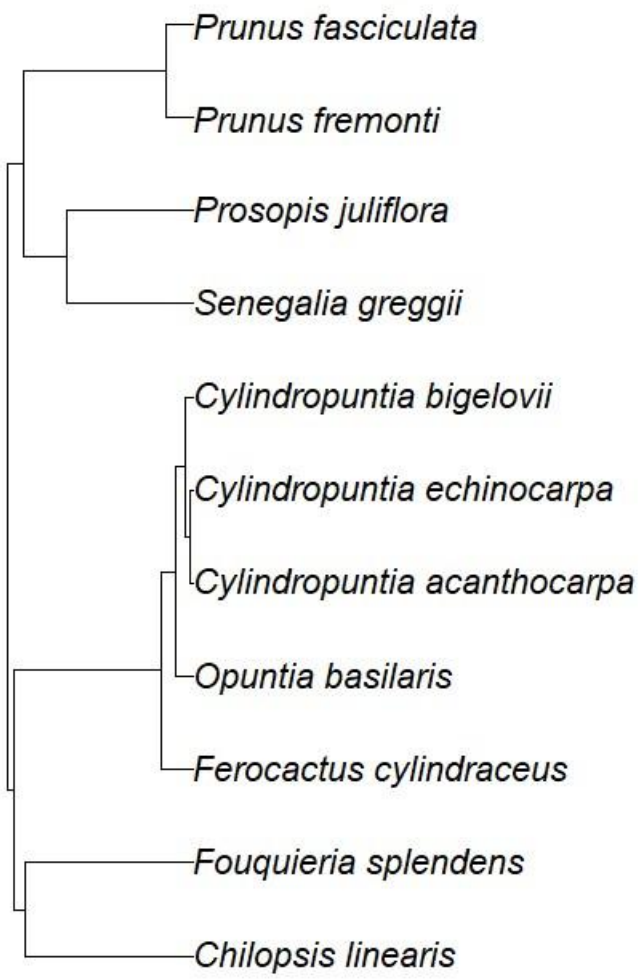


Figure B5: Pruned phylogenetic tree of EFN-bearing plant species created using the V.Phylomaker R package.

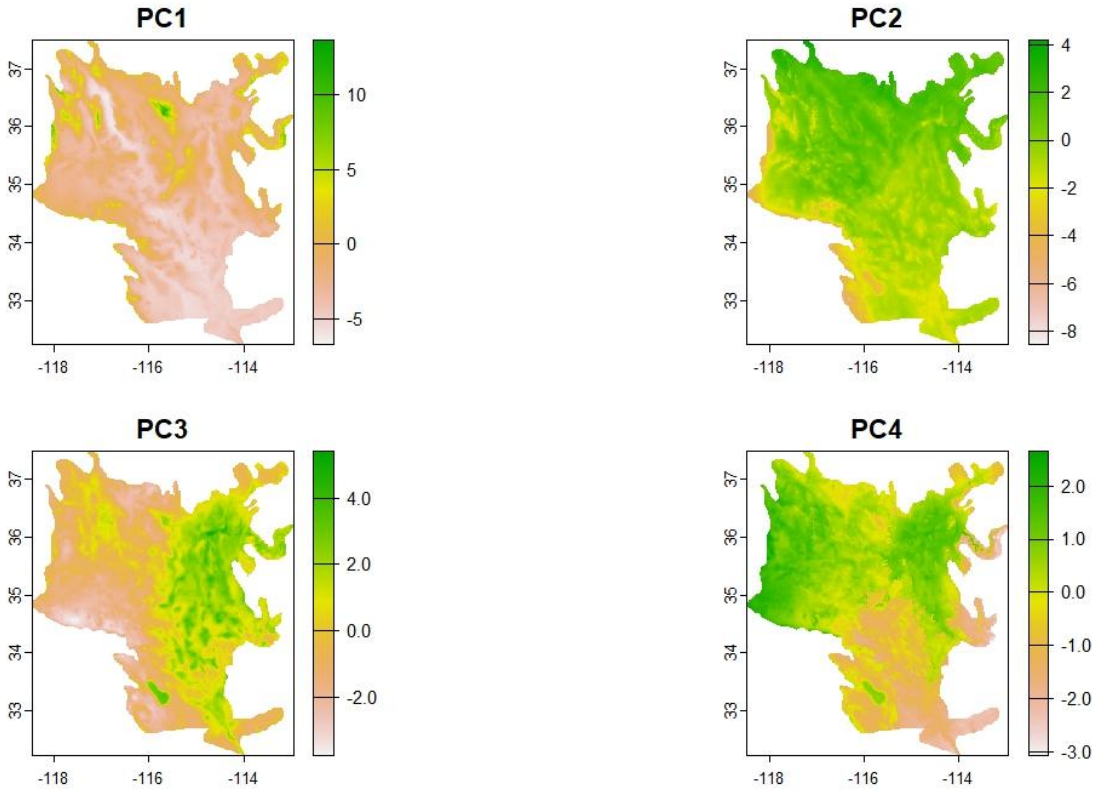


Figure B6: The current distribution of each of the four major environmental gradients considered in this study. PC1 can be characterized as an aridity gradient where positive values correspond to higher aridity (i.e. higher temperatures and lower precipitation). PC2 is a seasonality gradient; positive values correspond to a higher range of annual temperatures and a decrease in precipitation variation. PC3 is an isothermality gradient; here, positive values correspond to decreased variation within a day. PC4 corresponds to mainly to winter temperatures and summer precipitation.

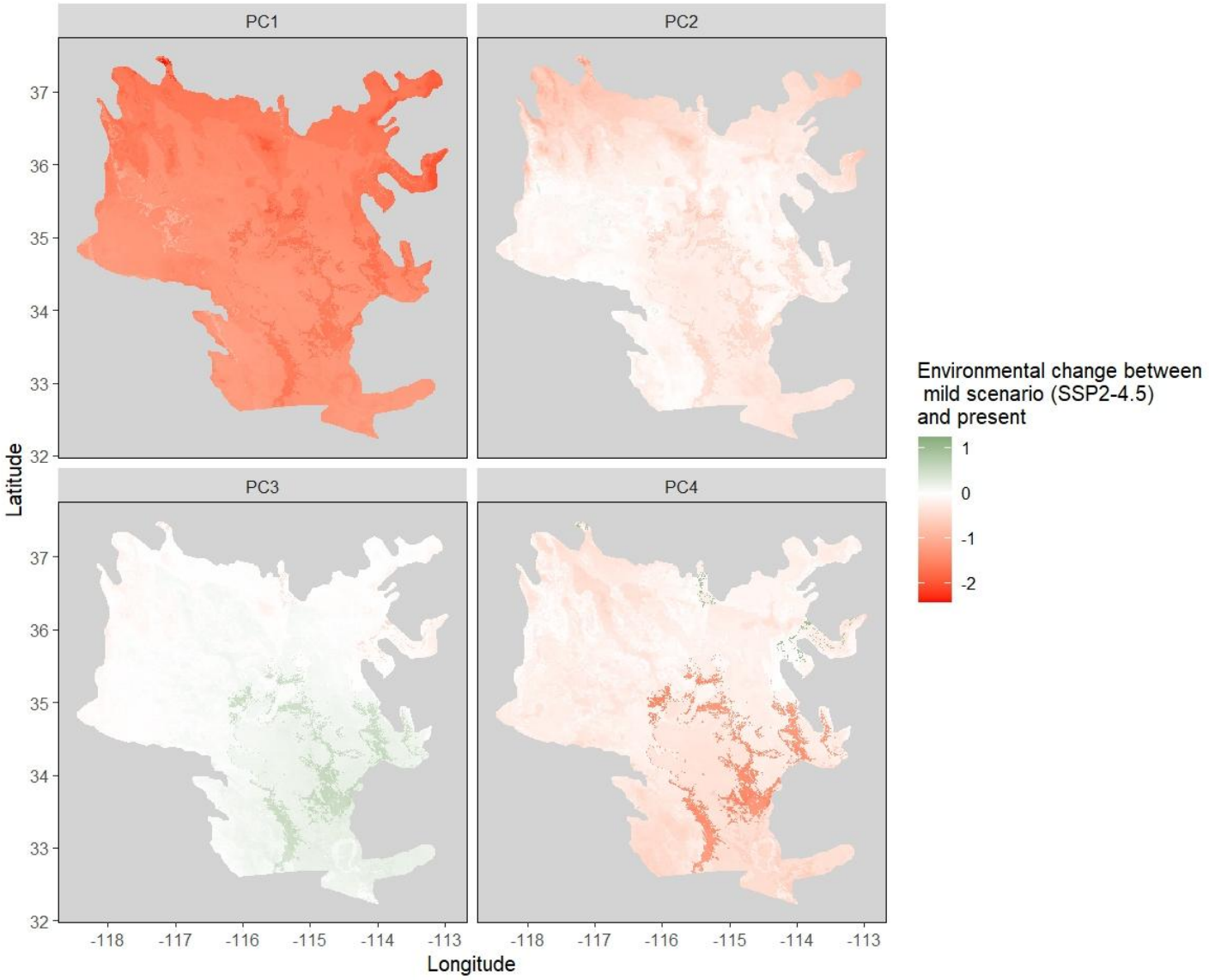


Figure B7: Shifts in the four main environmental gradients between the mild scenario (SSP2-4.5) and present conditions. The maps were obtained by subtracting current conditions from the future conditions.

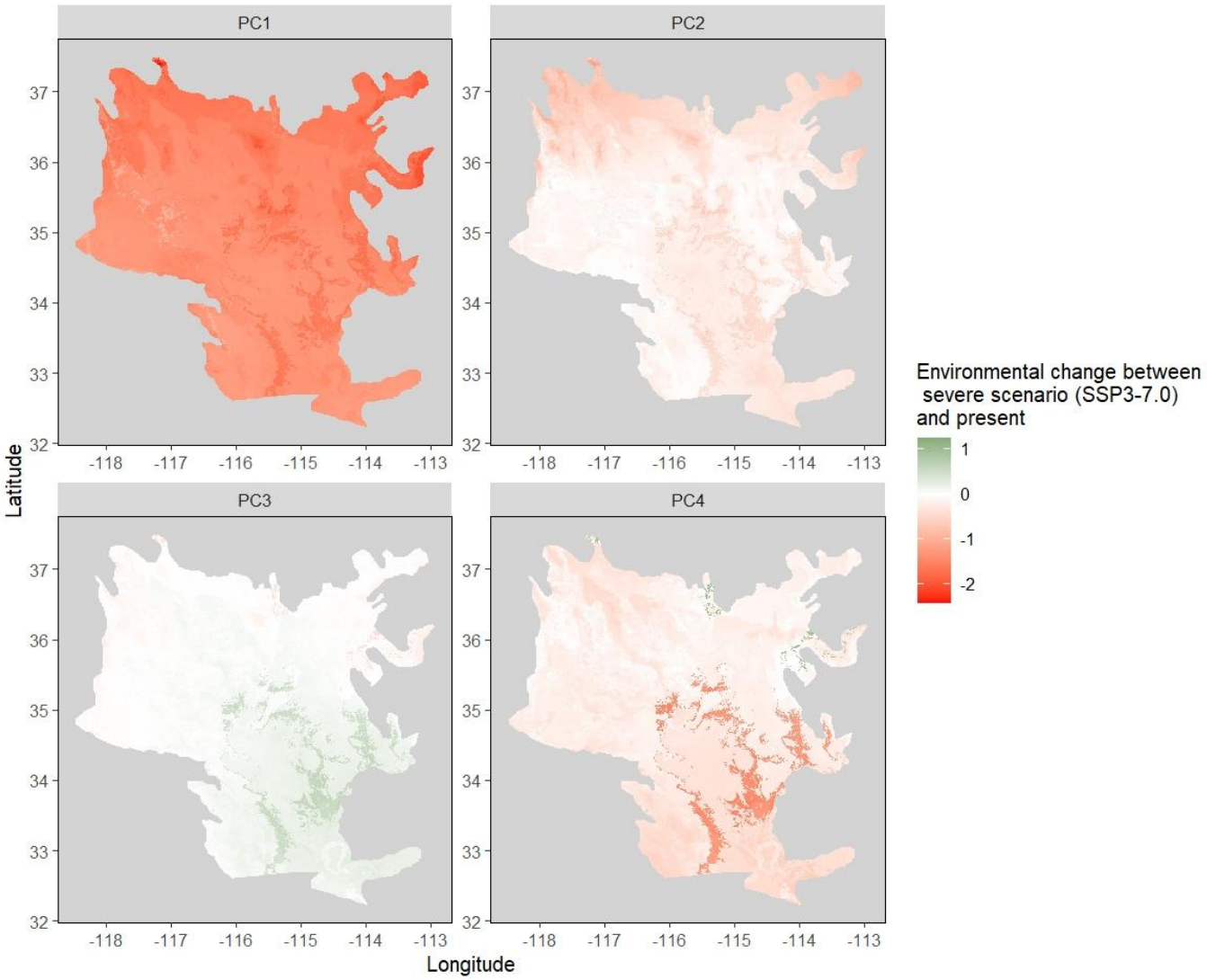


Figure B8: Shifts in the four main environmental gradients between the severe scenario (SSP3-7.0) and present conditions. The maps were obtained by subtracting current conditions from the future conditions.

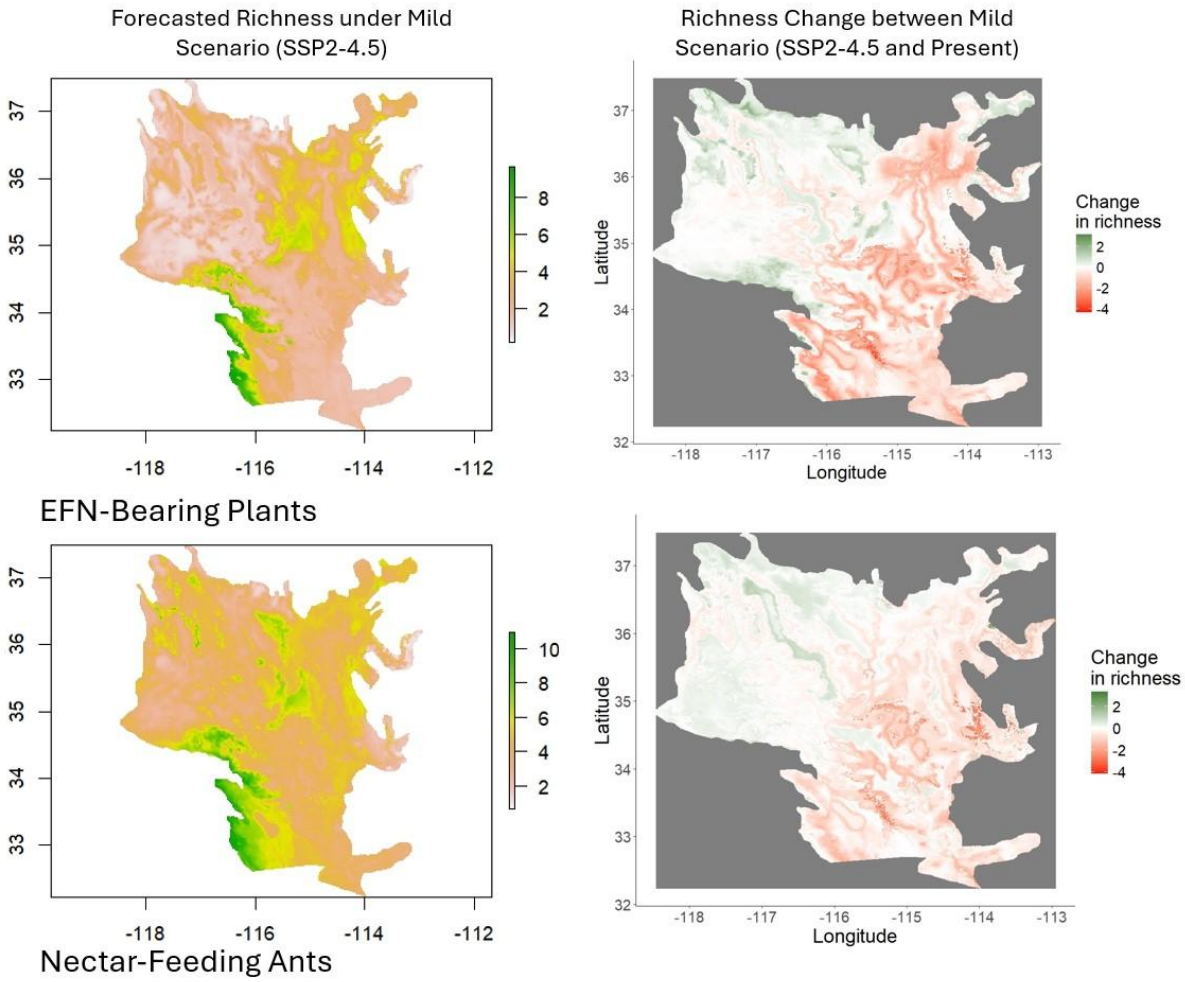
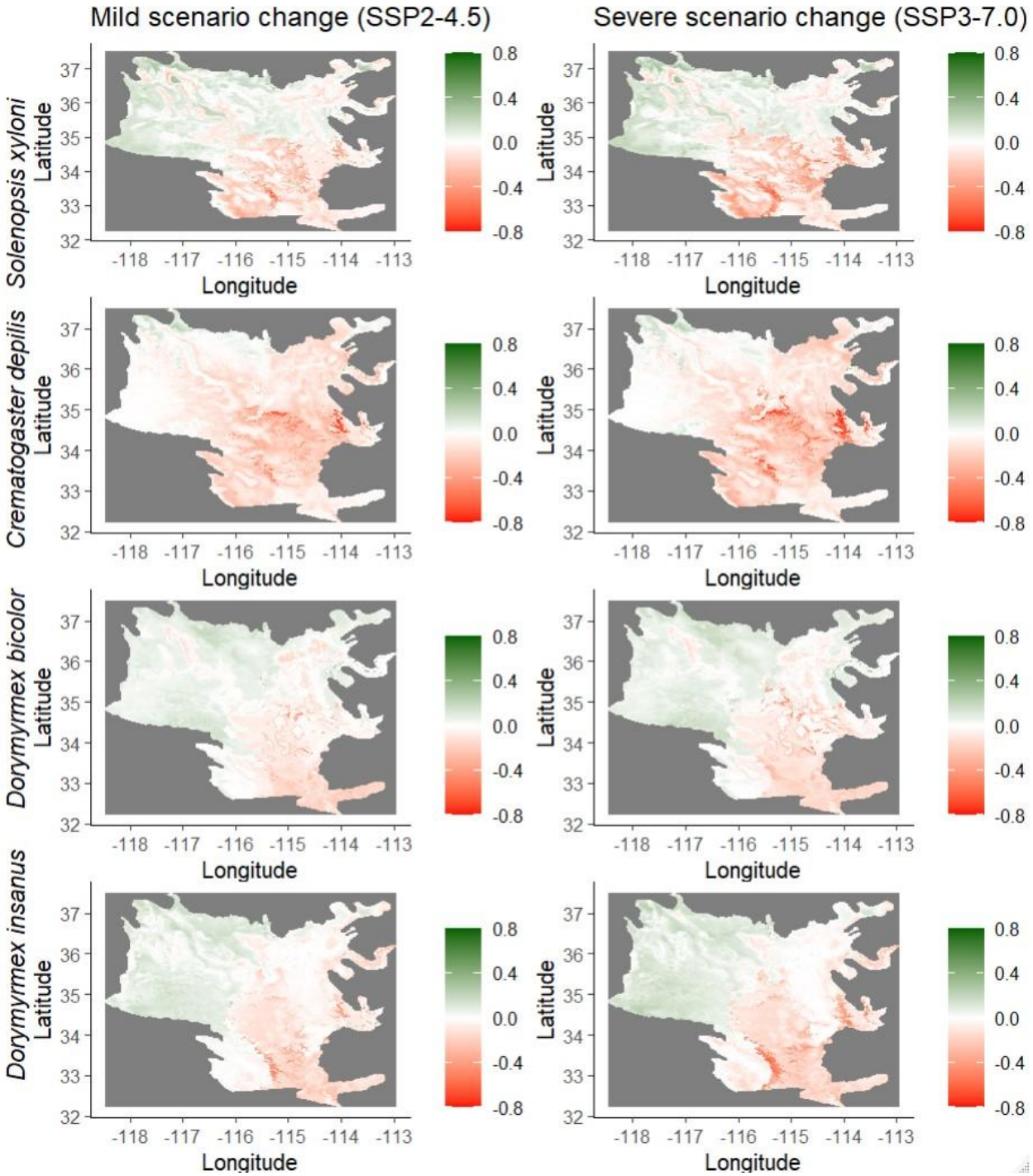
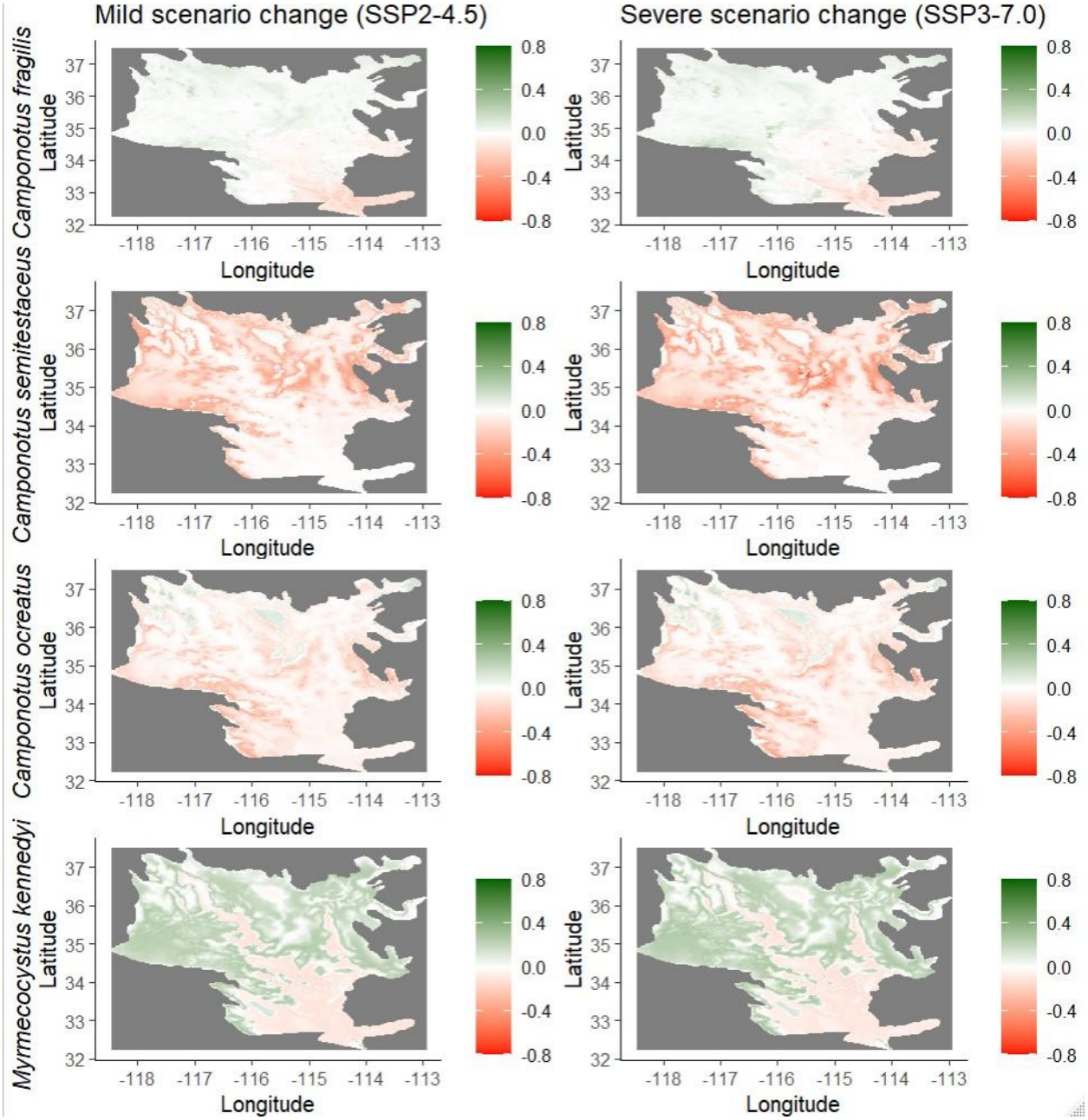
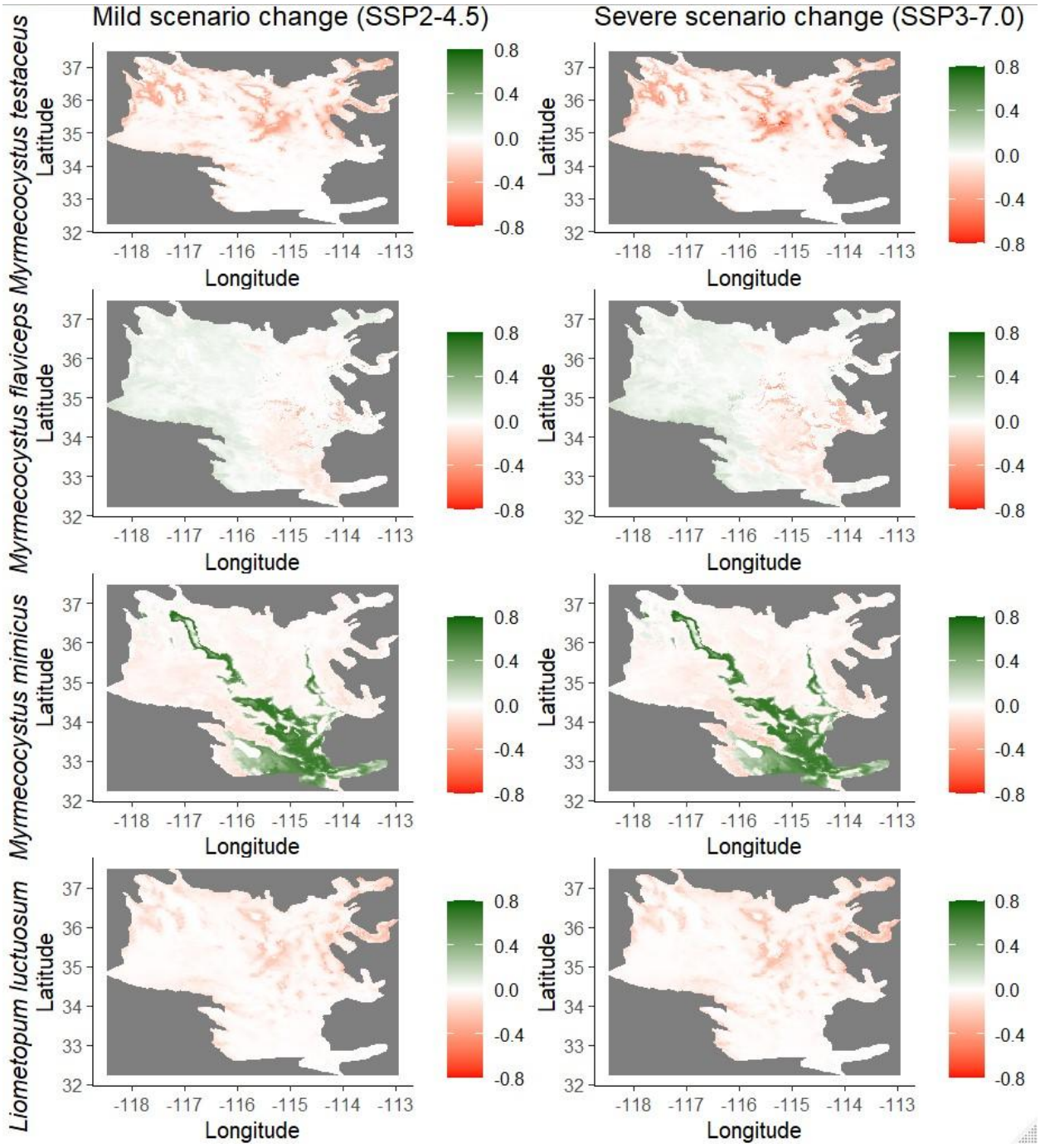


Figure B9: Changes to EFN-plant and ant richness patterns across the Mojave and Colorado deserts between present and future scenario (mild, SSP2-4.5).


Mild scenario change (SSP2-4.5)
Severe scenario change (SSP3-7.0)
Solenopsis xyloni
Crematogaster depilis
Dorymyrmex bicolor
Dorymyrmex insanus
Latitude
Longitude
37
36
35
34
33
32
-118
-117
-116
-115
-114
-113
0.8
0.4
0.0
-0.4
-0.8


Mild scenario change (SSP2-4.5)
Severe scenario change (SSP3-7.0)
Camponotus fragilis
Camponotus semitestaceus
Camponotus ocreatus
Myrmecocystus kennedyi
Latitude
Longitude
37
36
35
34
33
32
-118
-117
-116
-115
-114
-113
0.8
0.4
0.0
-0.4
-0.8


Mild scenario change (SSP2-4.5)
Severe scenario change (SSP3-7.0)
Myrmecocystus testaceus
Myrmecocystus flaviceps
Myrmecocystus mimicus
Liometopum luctuosum
Latitude
Longitude
37
36
35
34
33
32
-118
-117
-116
-115
-114
-113
0.8
0.4
0.0
-0.4
-0.8

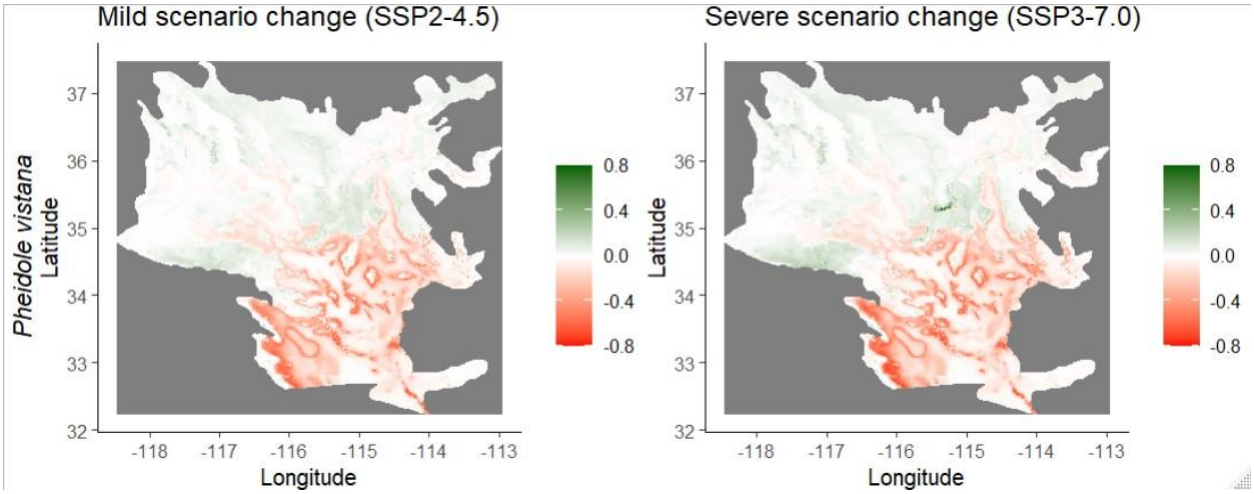
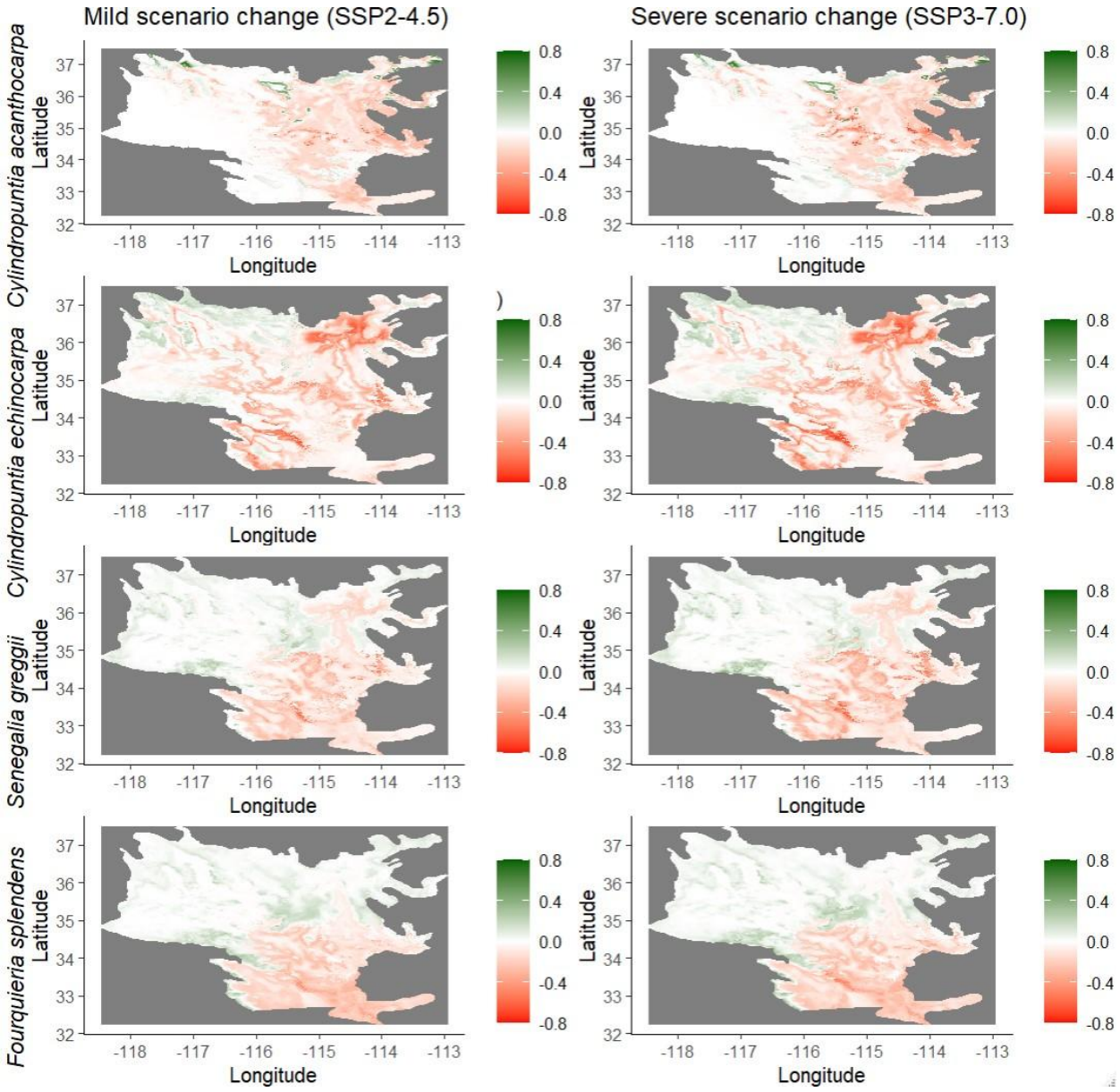


Figure B10: Relative changes in study area climatic suitability for each ant species.


Mild scenario change (SSP2-4.5)
Severe scenario change (SSP3-7.0)
Cylindropuntia acanthocarpa
Cylindropuntia echinocarpa
Senegalia greggii
Fourquieria splendens
Latitude
Longitude
37
36
35
34
33
32
-118
-117
-116
-115
-114
-113
0.8
0.4
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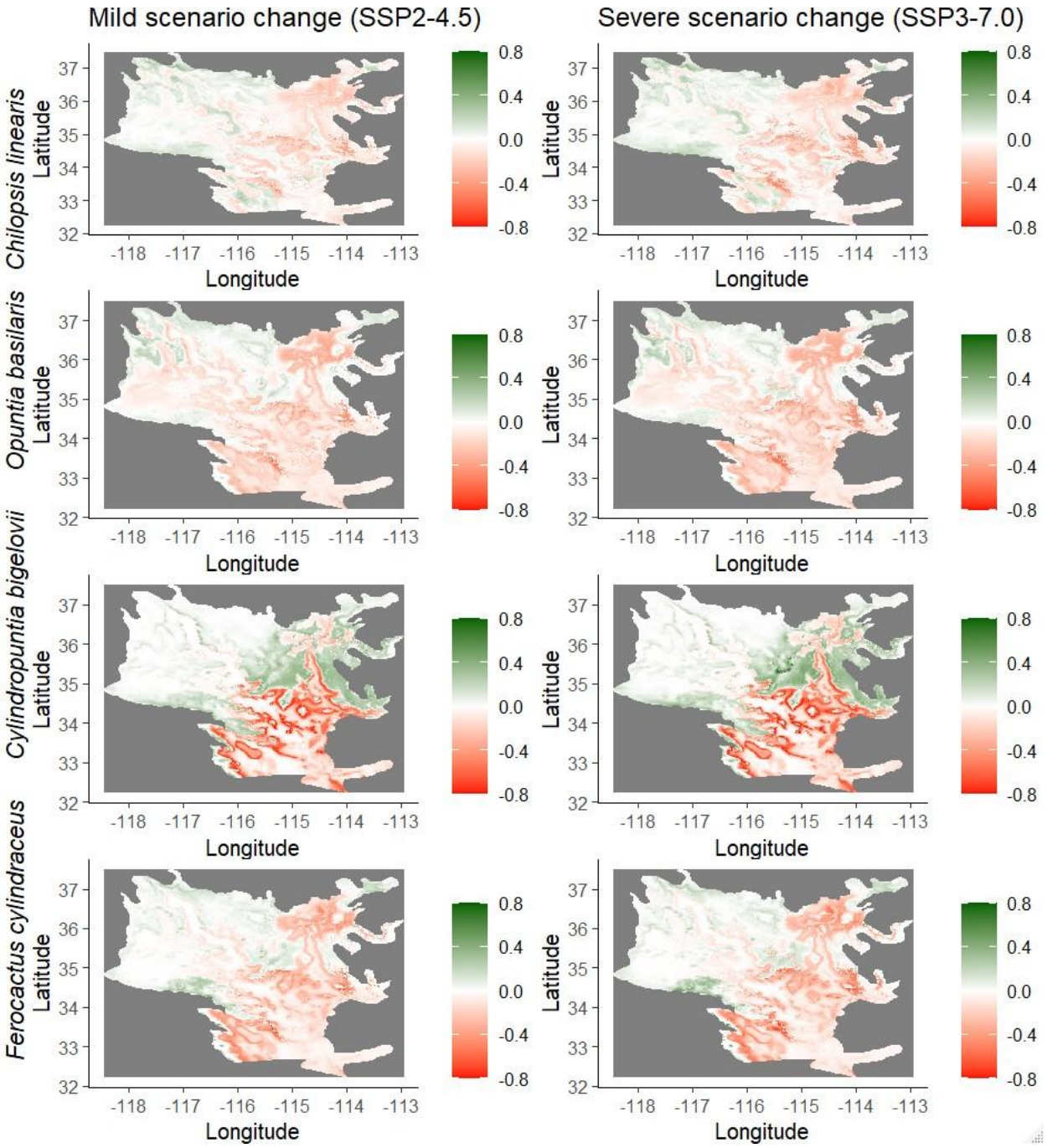
-0.8


Mild scenario change (SSP2-4.5)
Severe scenario change (SSP3-7.0)
Chilopsis linearis
Opuntia basilaris
Cylindropuntia bigelovii
Ferocactus cylindraceus
Latitude
Longitude
37
36
35
34
33
32
-118
-117
-116
-115
-114
-113
0.8
0.4
0.0
-0.4
-0.8

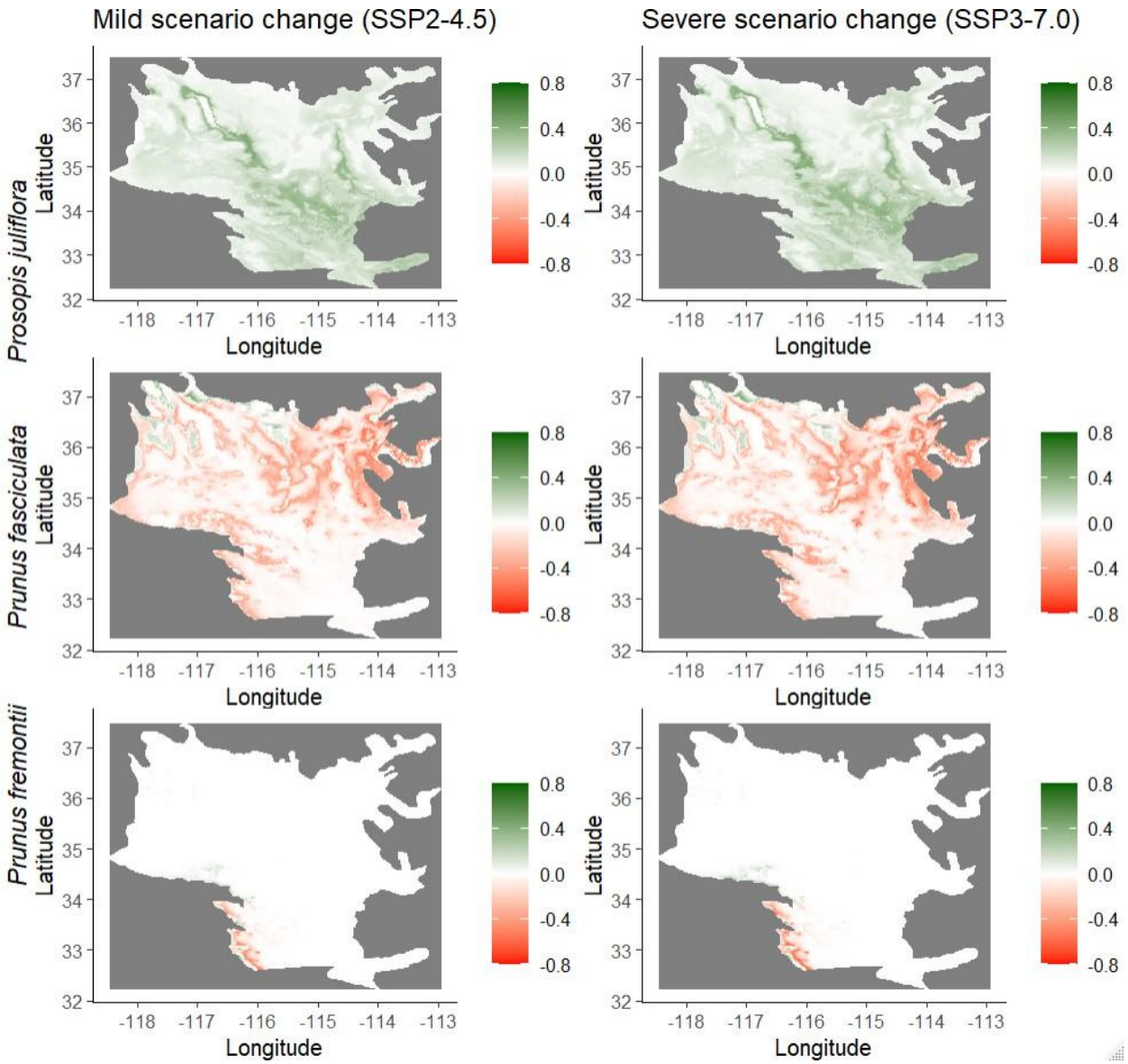
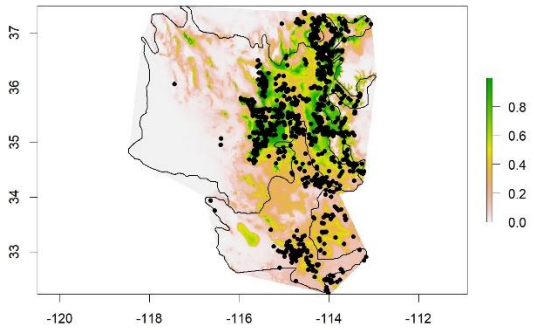
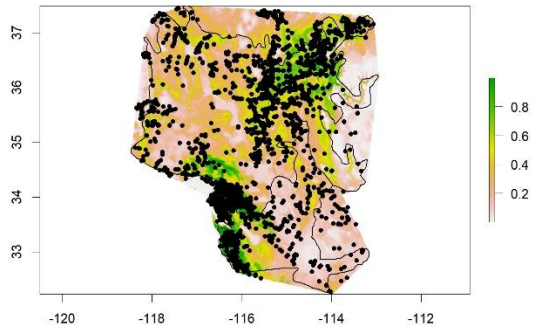


Figure B11: Relative changes in study area climatic suitability for each EFN-bearing plant species.

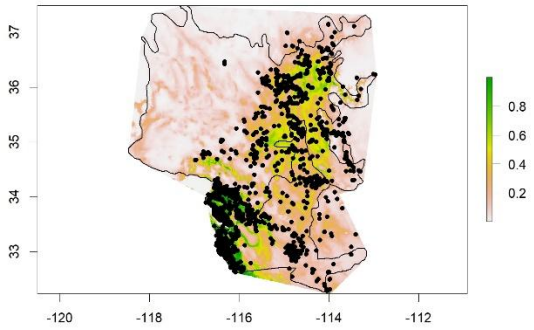
Cylindropuntia acanthocarpa



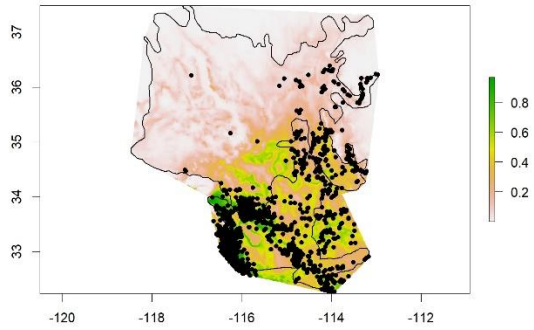
Cylindropuntia echinocarpa



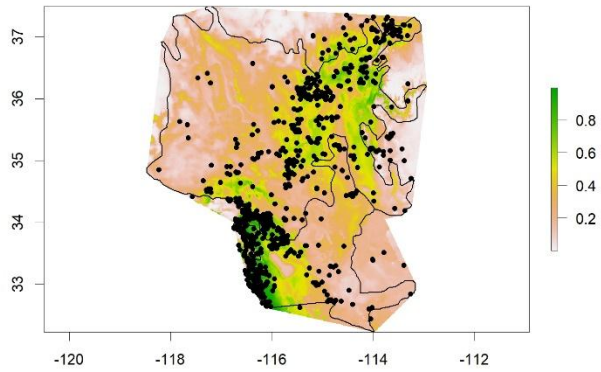
Senegalia greggii



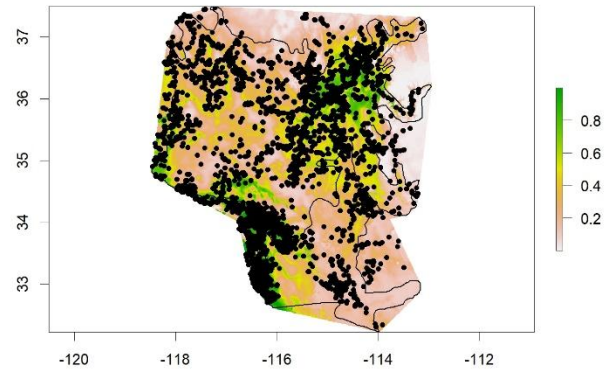
Fouquieria splendens



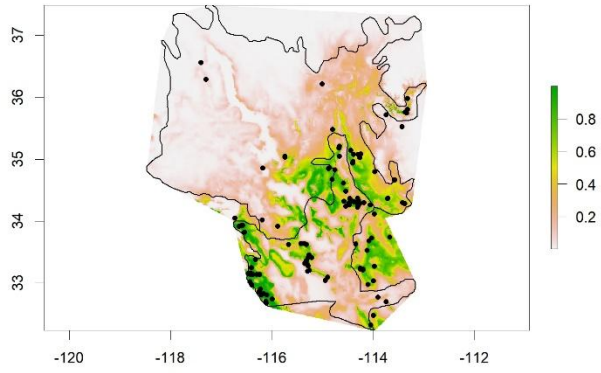
Chilopsis linearis



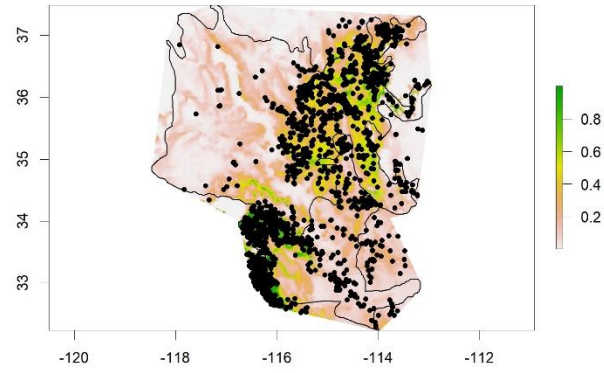
Opuntia basilaris



Cylindropuntia bigelovii



Ferocactus cylindraceus



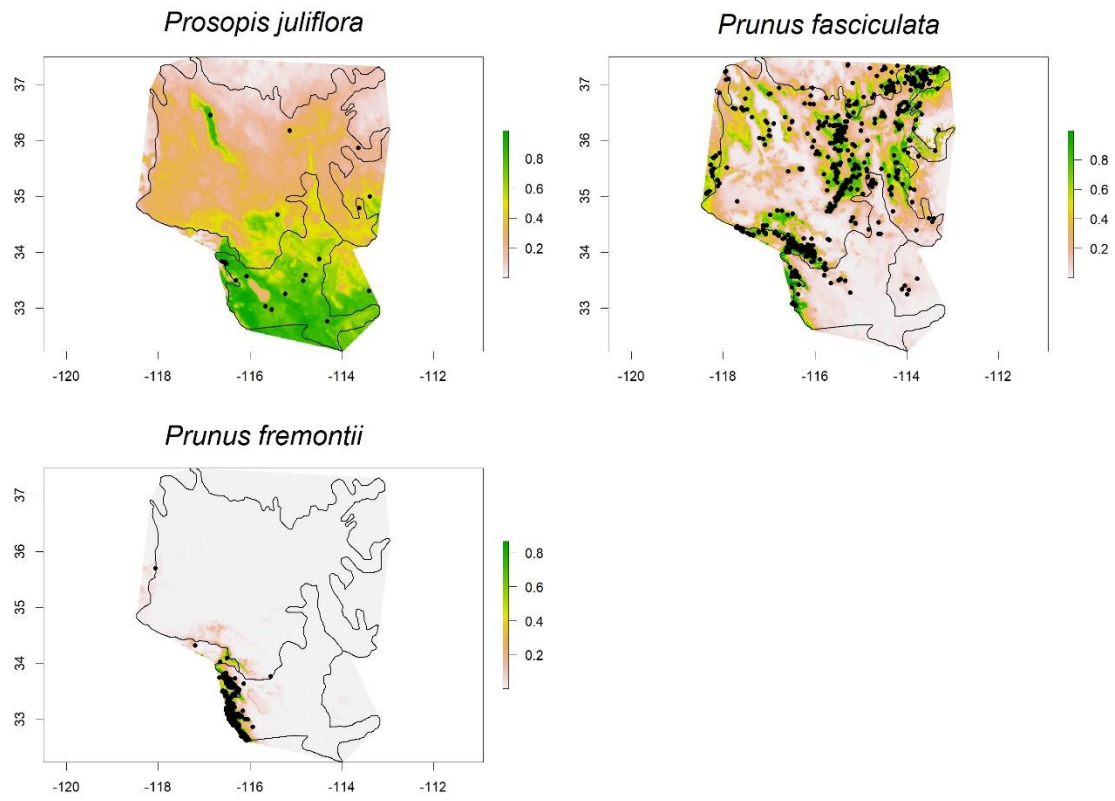
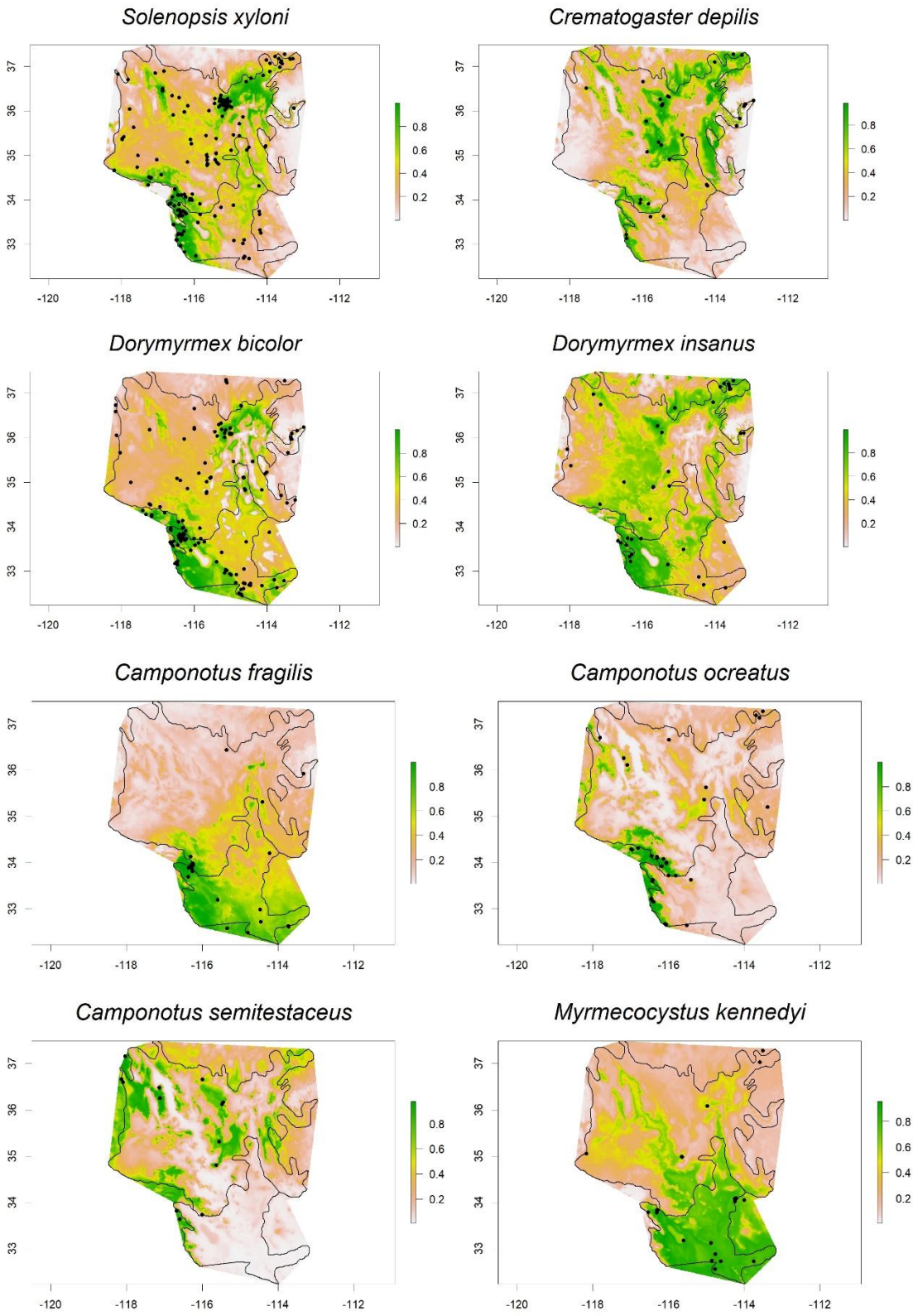


Figure B12: Consensus prediction maps for EFN-bearing plant species of the Mojave and Colorado deserts. Points are the thinned occurrences extracted from GBIF and the boundary file is the watershed boundary from USGS.


Solenopsis xyloni
Crematogaster depilis
Dorymyrmex bicolor
Dorymyrmex insanus
Camponotus fragilis
Camponotus ocreatus
Camponotus semitestaceus
Myrmecocystus kennedyi
-120
-118
-116
-114
-112
33
34
35
36
37
0.2
0.4
0.6
0.8

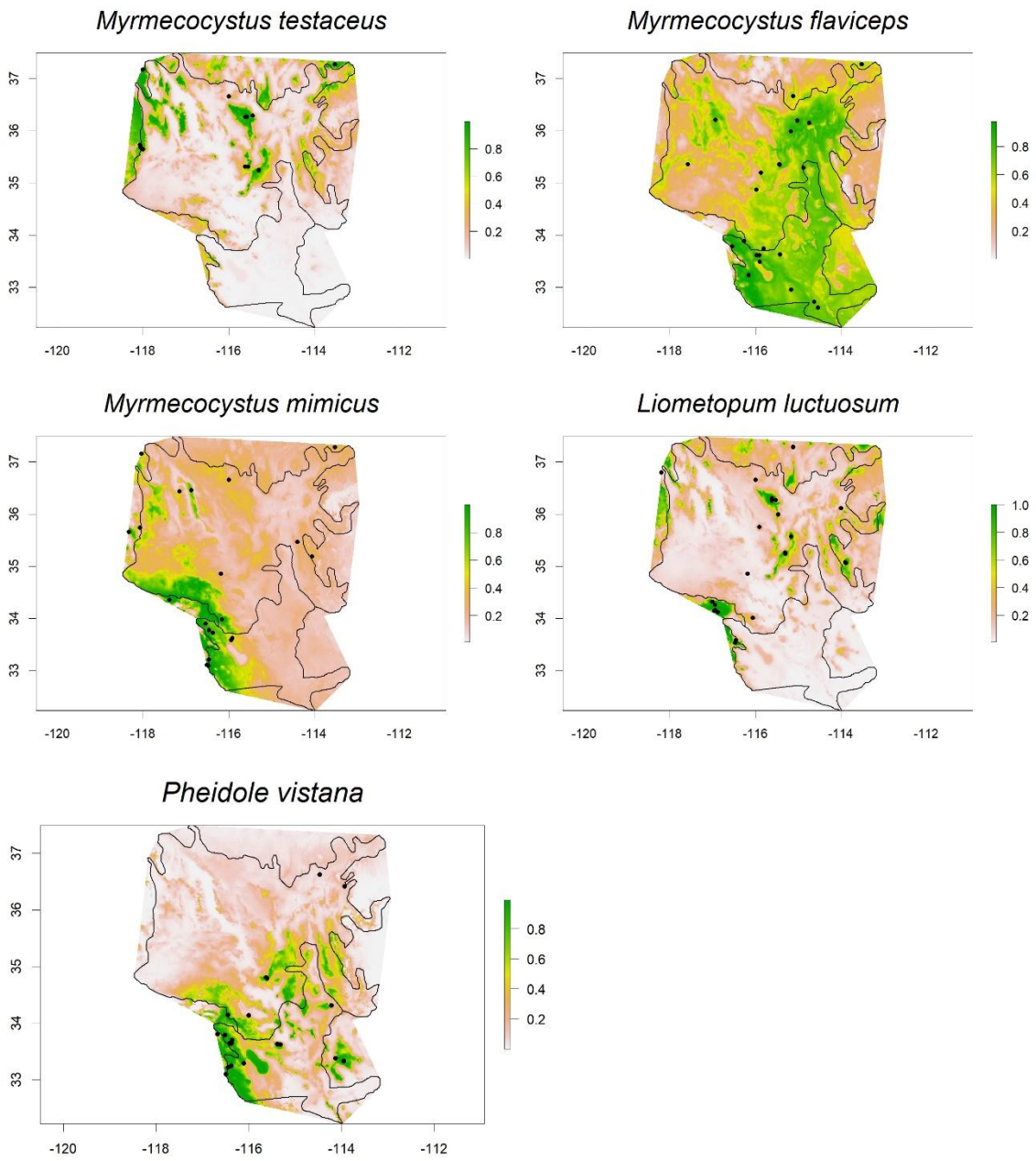


Figure B13: Consensus prediction maps for ant species of the Mojave and Colorado deserts. Points are the thinned occurrences extracted from GBIF and GABI, and the boundary file is the watershed boundary from USGS.

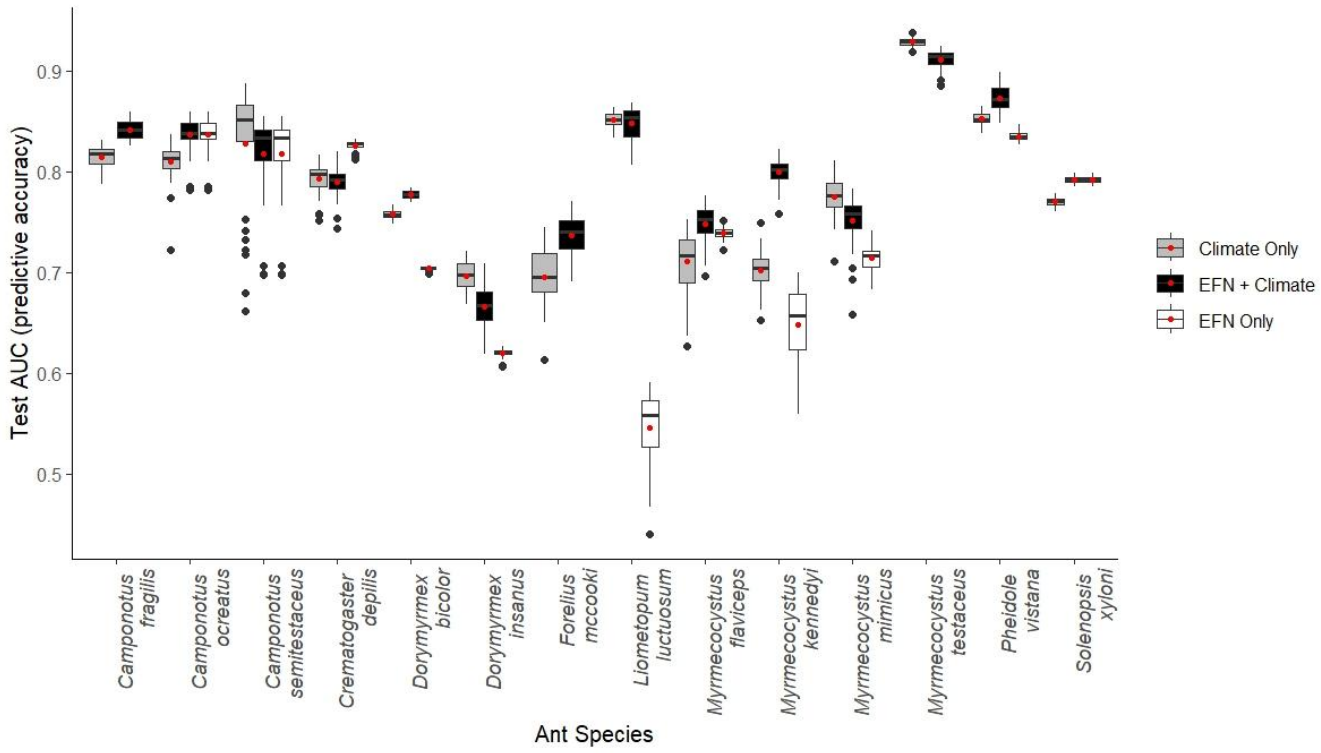


Figure B14: Boxplots comparing the predictive performance of ant species distribution models built using only climatic, climatic predictors or only extrafloral nectary (EFN) richness as a predictor. Lines on boxplots show median values, and the means are represented by the red diamonds. The variation in performance is summarized from 40 model runs per species, per set of predictors.

Table B3: 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 B4: 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

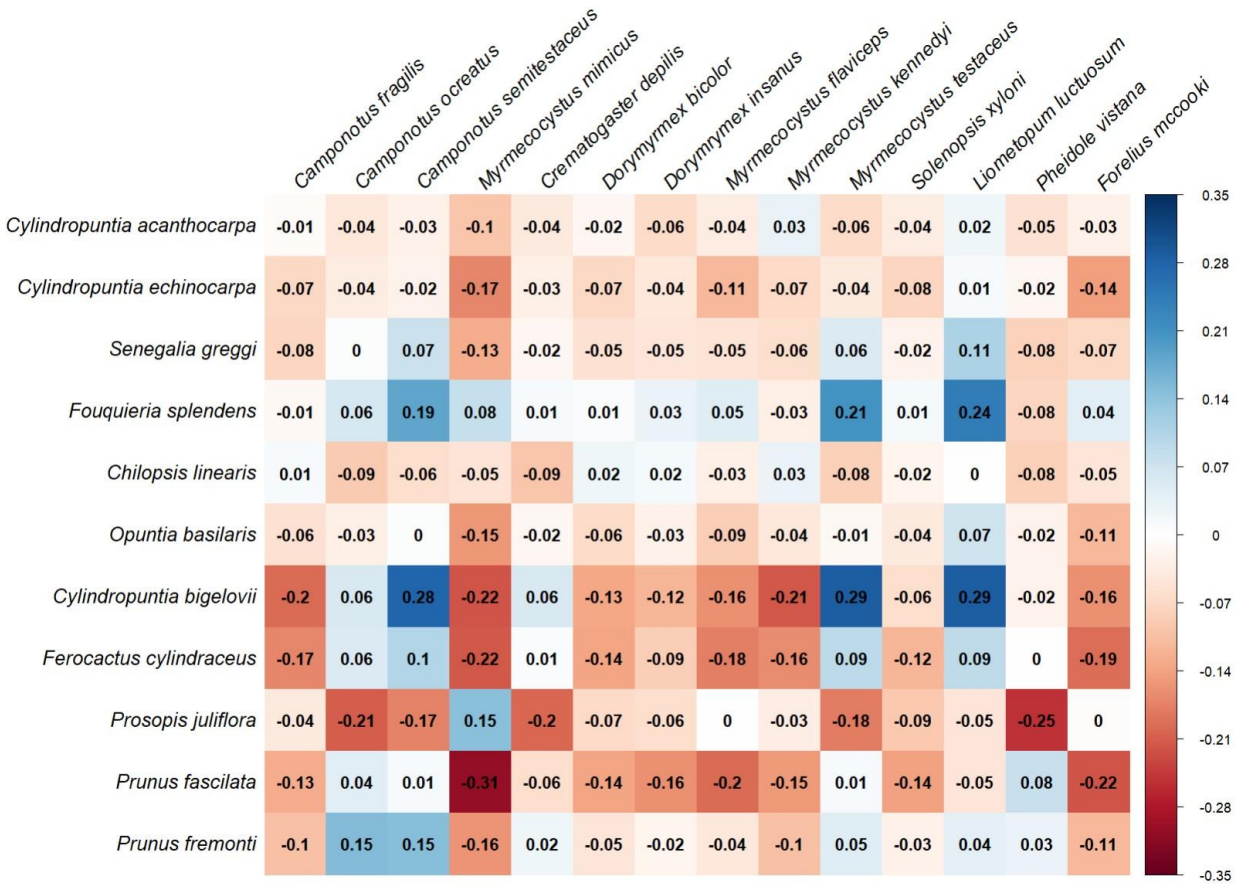


Figure B15: Proportional change in interspecific overlap of distribution ranges (Schoener's D niche overlap index) between the periods 1970-2000 and 2041-2060 for mild (SSP2-4.5, right). values in red indicate a decrease in range overlap between species over the time periods; blue indicates an increase in range overlap. Relative change was calculated as the percent change: ((future overlap – present overlap)/present overlap).

Table B5: Mean pairwise overlaps for each species considered in this study under present and two climate change scenarios.

Plant species	Mean present day overlap	Mean overlap in mild scenario (SSP2-4.5)	Mean overlap in severe scenario (SSP3-7.0)
Senegalia greggii	0.6084101	0.588058	0.583621
Cylindropuntia acanthocarpa	0.5159684	0.49978	0.5003954
Cylindropuntia echinocarpa	0.6741099	0.6296099	0.6214121
Chilopsis linearis	0.7094033	0.686453	0.6820951
Ferocactus cylindraceus	0.6174999	0.5736934	0.5679272
Fouquieria splendens	0.5674665	0.5893447	0.5870035
Opuntia basilaris	0.6893529	0.6575472	0.6527021
Cylindropuntia bigelovii	0.4926864	0.4676578	0.4613845
Prunus fasciculata	0.5808966	0.5303604	0.5250631
Prunus fremonti	0.1749034	0.1727441	0.1741508
Prosopis juliflora	0.6546372	0.6071884	0.6017142
Ant species	Mean present day overlap	Mean overlap in mild scenario (SSP2-4.5)	Mean overlap in severe scenario (SSP3-7.0)
Camponotus fragilis	0.619743	0.5756058	0.5659089
Camponotus ocreatus	0.5656658	0.5592065	0.557599
Camponotus semitestaceus	0.48501	0.4971635	0.4971031
Crematogaster depilis	0.6207882	0.5976977	0.5919752
Dorymyrmex bicolor	0.6067095	0.5698493	0.5648179
Dorymyrmex insanus	0.5876336	0.5583153	0.5568333
Forelius mccooki	0.6373011	0.5810691	0.5742354
Liometopum luctuosum	0.4942561	0.523624	0.5222831
Myrmecocystus flaviceps	0.6380384	0.5907397	0.5857541
Myrmecocystus kennedyi	0.5538195	0.5188198	0.516601
Myrmecocystus mimicus	0.5589826	0.4977958	0.4952755
Myrmecocystus testaceus	0.3926719	0.3972982	0.3945408
Pheidole vistana	0.6095381	0.5793642	0.5713161
Solenopsis xyloni	0.6293589	0.5929164	0.5879899

Appendix C: Supporting Information for Chapter 4

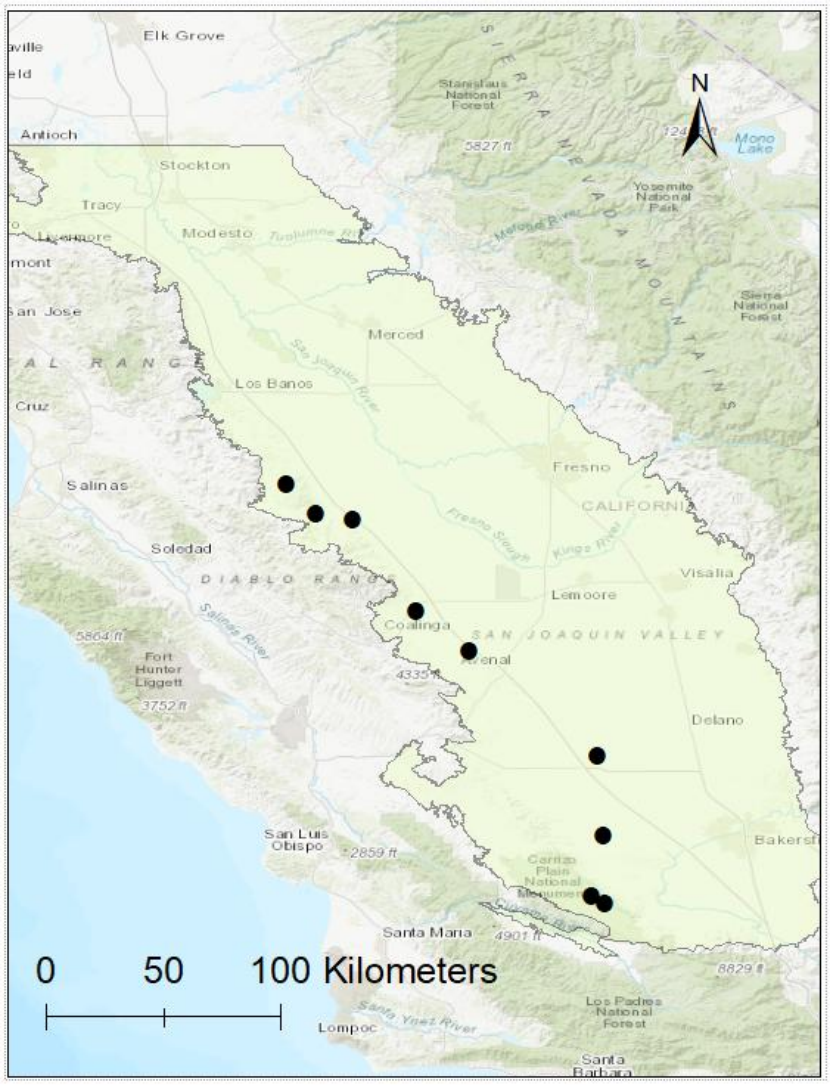


Figure C1: A map of the nine study areas within the drylands of Central California, USA. The San Joaquin Valley is shown in light green and study areas are in black points.

Table C1: Summary of ant sampling dates and site locations within the deserts of Central California, USA.

Site Name	Pitfall Trap Sampling dates	Coordinate of site centroid	
CaS	July 10 - 13	35.11995	-119.6283
	Aug 2 - 5	35.12000	-119.6280
	Sept 18 - 21	35.11600	-119.6240
CaSl	July 9 - 12	35.09	-119.574
	Aug 2 - 5	35.089	-119.576
	Sept 18 - 21	35.065	-119.539
SemiT	July 15 - 18	35.658	-119.612
	Aug 6 - 9	35.658	-119.612
	Sept 24 – 27	35.658	-119.61
Lokern	July 14 - 17	35.354	-119.584
	Aug 3 - 6	35.354	-119.584
	Sept 23 - 26	35.355	-119.588
PaPl	July 23 - 27	36.698	-120.799
	Aug 12 - 15	36.696	-120.795
	Sept 10 -13	36.7	-120.801
Aven	July 21 - 24	36.094	-120.197
	Aug 8 - 11	36.088	-120.19
	Sept 6 - 9	36.0878	-120.1912
Mov	July 28 - 31	36.563	-120.547
	Aug 13 - 16	36.562	-120.545
	Sept 12 - 16	36.561	-120.548
SiCr	July 20 - 23	36.586	-120.687
	Aug 12- 15	36.586	-120.686
	Sept 12 - 16	36.586	-120.688
Coal	July 16 - 19	36.213	-120.305
	Aug 8 - 11	36.212	-120.304
	Sept 6 – 9	36.213	-120.303

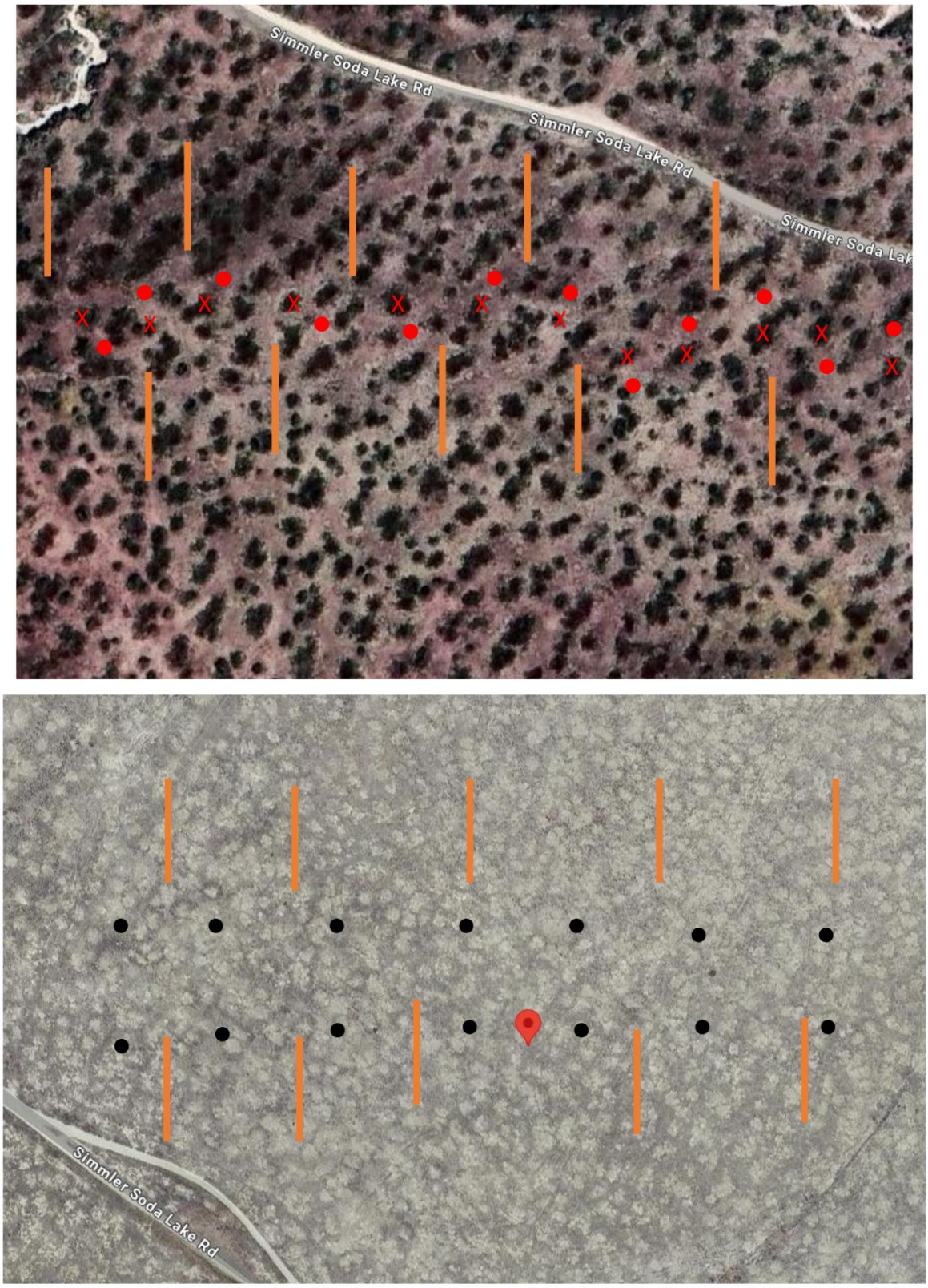


Figure C2: A graphical representation of sampling design. Example of field sampling at sites with foundation shrubs. At sites with foundation shrubs (top), pitfall traps were placed beneath the canopy of shrubs (red X), and beneath open sites at least 1.5 m away from shrubs (red circles). At sites without foundation shrubs (bottom), the pitfall traps (black circles) were placed at least 10 m apart along two parallel transects. The orange lines represent 25 m transects used

for ground vegetation estimation. Quadrats were placed every 4 m along the transects to measure the vegetation.

Table C2: Vegetation and climate characteristics of the study sites, along with the PC1 and PC2 axis values that represent the composite environmental gradients.

month	Site	Mean vegetation cover	Variation in vegetation cover	Mean vegetation height	Mean annual temperature	Mean annual precipitation	Max temp	Foundation species	NDVI	Mean annual soil temp (5 to 15 cm depth)	Annual range soil temp (5 to 15 cm depth)	SES Fdisp	PC1	PC2
		Percent within a quadrat	SD of mean cover	cm	Celsius* 10	mm	Celsius * 10			Celsius	Celsius			
Mean across sites		58.37	924.55	15.15	159.11	283.44	354.85		2350.22	18.44	17.71	0.58	0.00	0.00
Minimum across sites		23.73	167.87	7.47	141.00	170.00	320.00		1581.00	15.00	13.90	-1.32	-1.21	-1.30
Maximum across sites		92.60	1807.17	26.50	174.00	508.00	378.00		2878.00	21.40	20.60	2.27	1.36	1.40
Aug	Aven	61.00	1270.10	17.47	174.00	196.00	378.00	atriplex	2028.00	19.40	18.40	-0.28	0.64	-0.50
Sept	Aven	80.92	768.62	20.13	174.00	196.00	378.00	atriplex	2440.00	19.30	18.40	-0.48	0.84	-0.93
July	Aven	42.23	1807.17	26.50	174.00	196.00	378.00	atriplex	2783.00	19.30	18.40	0.79	1.36	0.66
Aug	CaS	53.90	732.23	13.98	150.00	442.00	330.00	ephedra	2327.00	17.00	16.90	0.79	-0.74	0.54
Sept	CaS	48.90	725.92	17.59	145.00	480.00	325.00	ephedra	2290.00	17.00	16.90	0.90	-0.84	0.81
July	CaS	44.85	992.10	9.63	150.00	442.00	330.00	ephedra	2438.00	16.90	16.60	1.13	-0.71	0.94
Aug	CaSl	54.50	613.47	9.67	141.00	508.00	320.00	open	2183.00	16.50	16.80	1.42	-1.21	0.70
Sept	CaSl	23.73	338.44	16.32	143.00	491.00	321.00	open	2354.00	16.60	16.70	-1.11	-1.03	1.40
July	CaSl	60.43	780.42	9.72	141.00	508.00	320.00	open	2383.00	16.90	16.80	1.93	-1.07	0.73
Aug	Coal	44.38	1552.00	18.07	166.00	235.00	371.00	open	2504.00	18.70	17.50	0.75	0.57	0.35
Sept	Coal	75.63	916.61	17.05	166.00	235.00	371.00	open	2571.00	18.70	17.50	0.30	0.33	-0.76
July	Coal	70.07	1172.17	13.30	166.00	235.00	371.00	open	2444.00	18.70	17.50	0.71	0.33	-0.52
Aug	Lok	73.42	679.50	21.42	168.00	200.00	359.00	atriplex	2164.00	20.70	20.50	0.34	0.51	-0.57
Sept	Lok	67.90	647.58	17.67	168.00	200.00	359.00	atriplex	2090.00	20.70	20.50	-0.81	0.43	-0.44
July	Lok	35.35	1096.16	19.92	168.00	200.00	359.00	atriplex	2258.00	20.70	20.50	-0.08	0.68	0.68
Aug	Mov	58.07	291.89	10.50	160.00	220.00	360.00	open	2280.00	18.70	17.50	0.22	-0.28	-0.58
Sept	Mov	58.98	650.49	8.98	160.00	220.00	360.00	open	2651.00	18.70	17.50	0.70	-0.14	-0.34

July	Mov	79.83	352.95	7.47	160.00	220.00	360.00	open	2280.00	18.70	17.50	0.71	-0.35	-1.14
Aug	PaPl	92.60	167.87	20.07	145.00	358.00	354.00	ephedra	2522.00	15.00	13.90	1.15	-0.74	-1.30
Sept	PaPl	56.88	582.68	17.63	145.00	358.00	354.00	ephedra	2124.00	15.00	13.90	0.97	-0.67	-0.24
July	PaPl	79.17	508.21	15.20	145.00	358.00	354.00	ephedra	2558.00	15.10	13.90	1.17	-0.80	-0.85
Aug	SemiT	36.63	1458.00	10.05	171.00	170.00	366.00	atriplex	2332.00	21.40	20.60	0.55	0.95	0.86
Sept	SemiT	50.75	1578.50	20.51	171.00	170.00	366.00	atriplex	2878.00	21.40	20.60	0.34	1.23	0.64
July	SemiT	35.45	1714.59	11.77	171.00	170.00	366.00	atriplex	2359.00	21.40	20.60	-1.32	1.06	1.01
Aug	SiCr	72.67	1070.16	9.20	158.00	215.00	357.00	atriplex	2217.00	18.50	17.40	1.65	-0.20	-0.64
Sept	SiCr	60.03	1217.66	13.58	158.00	215.00	357.00	atriplex	1581.00	18.50	17.40	2.27	-0.17	-0.42
July	SiCr	57.60	1277.40	15.65	158.00	215.00	357.00	atriplex	2417.00	18.50	17.40	1.03	0.03	-0.10

Table C3: Scene ID and satellite data collection metadatafor NDVI. All data was obtained using the USGS Earth Explorer.

Site Name	Site Name	Entity/Scene ID	NDVI Value	Path End Date	Path Start Date
CaS	July	EVUSS20200707202007136	2438	2020-07-13	2020-07-07
	Aug	EVUSS20200728202008106	2327	2020-08-10	2020-07-28
	Sept	EVUSS20200915202009216	2290	2020-09-21	2020-09-15
CaSl	July	EVUSS20200707202007136	2383	2020-07-13	2020-07-07
	Aug	EVUSS20200728202008106	2183	2020-08-10	2020-07-28
	Sept	EVUSS20200915202009216	2354	2020-09-21	2020-09-15
SemiT	July	EVUSS20200714202007206	2359	2020-07-20	2020-07-14
	Aug	EVUSS20200728202008106	2332	2020-08-10	2020-07-28
	Sept	EVUSS20200922202010056	2878	2020-10-05	2020-09-22
Lokern	July	EVUSS20200714202007206	2258	2020-07-20	2020-07-14
	Aug	EVUSS20200728202008106	2164	2020-08-10	2020-07-28
	Sept	EVUSS20200922202010056	2090	2020-10-05	2020-09-22
PaPl	July	EVUSS20200721202007276	2558	2020-07-27	2020-07-21
	Aug	EVUSS20200811202008176	2522	2020-08-17	2020-08-11
	Sept	EVUSS20200908202009146	2124	2020-09-14	2020-09-08
Aven	July	EVUSS20200721202007276	2783	2020-07-27	2020-07-21
	Aug	EVUSS20200728202008106	2028	2020-08-10	2020-07-28
	Sept	EVUSS20200901202009076	2440	2020-09-07	2020-09-01
Mov	July	EVUSS20200728202008036	2280	2020-08-03	2020-07-28
	Aug	EVUSS20200728202008106	2280	2020-08-10	2020-07-28
	Sept	EVUSS20200908202009146	2651	2020-09-14	2020-09-08
SiCr	July	EVUSS20200721202007276	2417	2020-07-27	2020-07-21
	Aug	EVUSS20200811202008176	2217	2020-08-17	2020-08-11
	Sept	EVUSS20200908202009146	1581	2020-09-14	2020-09-08
Coal	July	EVUSS20200714202007206	2444	2020-07-20	2020-07-14
	Aug	EVUSS20200728202008106	2504	2020-08-10	2020-07-28
	Sept	EVUSS20200901202009076	2571	2020-09-07	2020-09-01

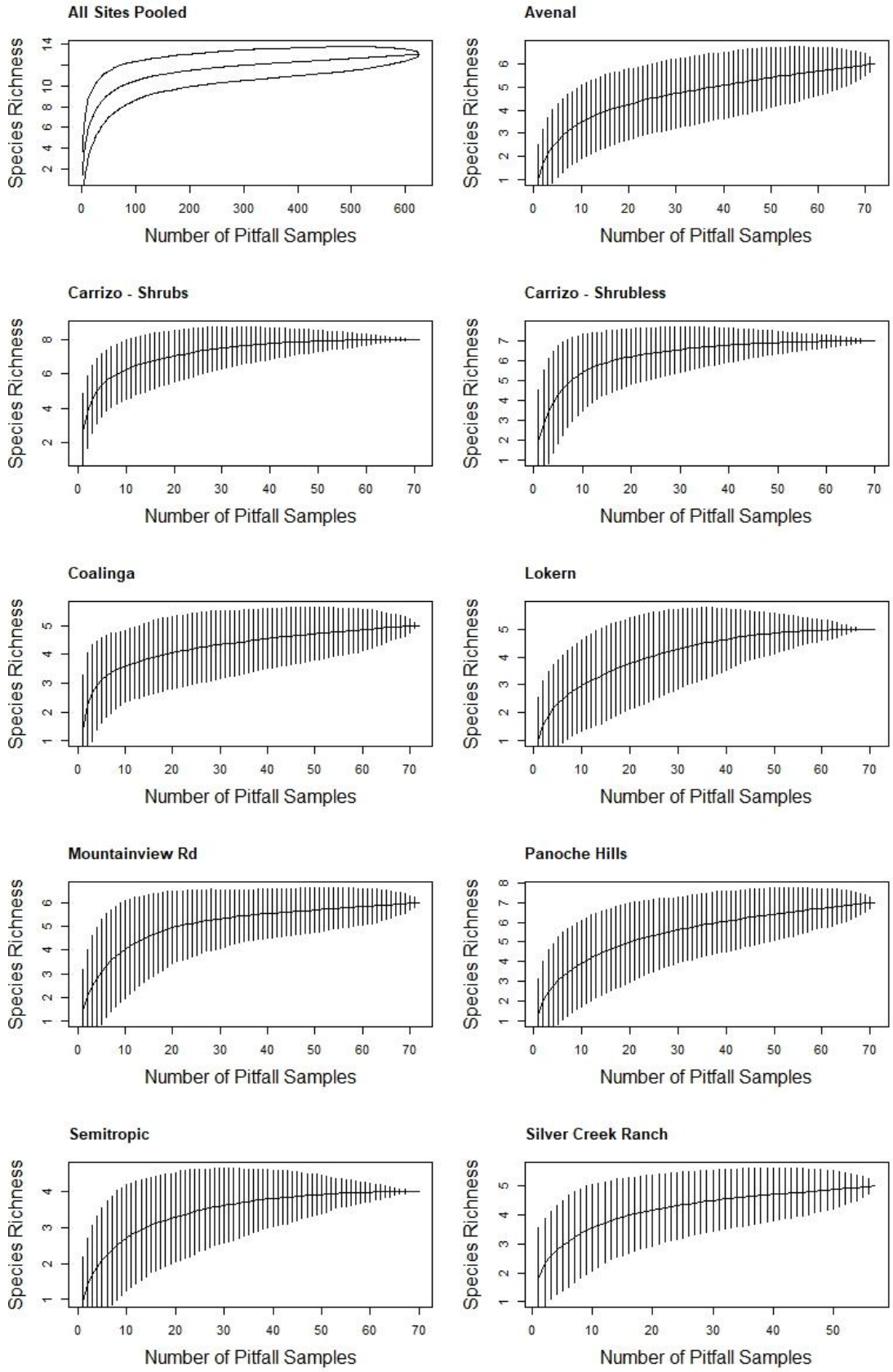


Figure C3: Rarefaction curves for each of the nine study sites and also all sites pooled together. The method used was 'random' which estimates the species accumulation curve without replacement (Gotelli and Colwell, 2008).

Table C4: Statistical output from variance partitioning on the standardized effect size of functional dispersion. Three matrices were used as predictors: the nine environmental variables, the three MEM axes and the effect size of phylogenetic dispersion.

Non-independent fractions: The non-independent influence of the environment is the independent influence of the envirment (a) + the shared influence of environment and space (d) + the shared influence of environment and phylogeny (f) + the shared influence of environment, space and phylogeny (g).

	df	R.square	Adj.R.square
[a+d+f+g] = environment	9	0.677992	0.507517
[b+d+e+g] =space	3	0.39711	0.318472
[c+e+f+g] = phylogeny	1	0.116762	0.081433
[a+b+d+e+f+g] = environment + space	12	0.73989	0.516938
[a+c+d+e+f+g] = environment + phylogeny	10	0.793616	0.664626
[b+c+d+e+f+g] = space + phylogeny	4	0.658164	0.596012
[a+b+c+d+e+f+g] = All	13	0.925135	0.85027

Independent fractions: The influence of each fraction while controlling for the influence the other fractions.

	df	R.square	Adj.R.square
[a] = environment	9	NA	0.254258
[b] = space	3	NA	0.185644
[c] = phylogeny	1	NA	0.333333
[d] shared environment + space	0	NA	0.328935
[e] shared environment + phylogeny	0	NA	-0.17622
[f] shared	0	NA	-0.05579
[g] shared	0	NA	-0.01988

[h] = Residuals	NA	NA	0.14973

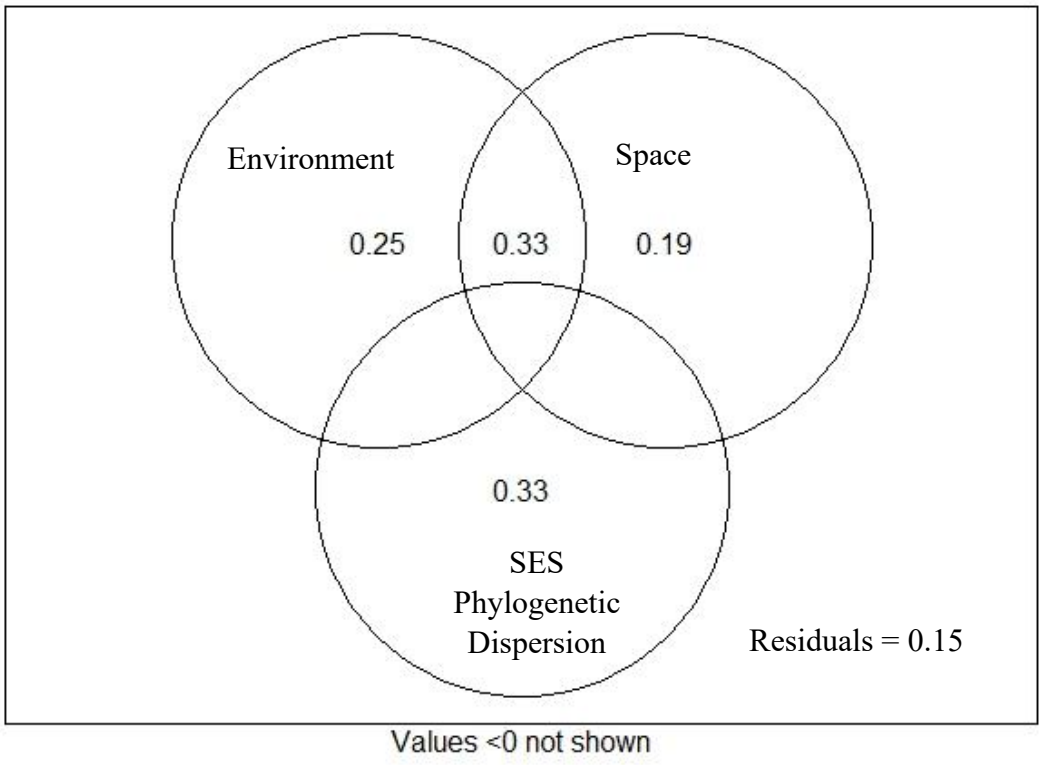


Figure C4: A Venn diagram showing the shared and independent partitions output from variance partitioning on the standardized effect size of functional dispersion. Three matrices were used as predictors: the nine environmental variables, the three MEM axes and the effect size of phylogenetic dispersion.

Table C5: Output from anova tests using each trait as a response and specifies identity as a predictor.

Trait	Variable	Sum of Squares	Df	N	F value	p
Weber's body length	Species	52.89	10	263	295.8	P < 0.001
	Residuals	4.51	252			
Femur length	Species	2.085	10	262	43.24	P < 0.001
	Residuals	1.208	251			
Scape length	Species	3.926	10	262	136.6	P < 0.001
	Residuals	0.706	251			
Mandible length	Species	0.412	10	262	29.74	P < 0.001
	Residuals	0.3478	251			
Eye length	Species	0.244	10	262	92.42	P < 0.001
	Residuals	0.066	251			
Head width	Species	1.393	10	262	70.1	P < 0.001
	Residuals	0.4988	251			
Head length	Species	0.775	10	262	26.34	P < 0.001
	Residuals	0.7387	251			

Table C6: Maxent model specifications and performance measures. We used regularization values between 1 and 5, as well as the following feature classes: linear, linear + quadratic, hinge, linear + quadratic + hinge, corresponding to typical settings (Muscarella et al. 2017).

Ant Species Name	**Tuning Arguments**	**AUC**
Solenopsis xyloni	fc.LQH_rm.1	0.7457032
Pheidole hyatti	fc.H_rm.1	0.7322713
Dorymyrmex bicolor	fc.LQ_rm.1	0.6912878
Cyphomyrmex wheeleri	fc.H_rm.2	0.5621083
Dorymyrmex insanus	fc.H_rm.1	0.7080344
Myrmecocystus kennedyi	fc.LQ_rm.1	0.745587
Pogonomyrmex hoelldobleri	fc.LQ_rm.2	0.7483136
Temnothorax andrei	fc.LQH_rm.1	0.8435886
Forelius pruinosus	fc.LQH_rm.1	0.7738061
Veromessor andrei	fc.H_rm.4	0.7674637
Veromessor pergandei	fc.LQH_rm.1	0.8185405

Appendix D: Supplemental Information for Chapter 5

Table D1: Pitfall installation dates and seed depot experiment dates

Site	Date	Season
Tecopa	April 11, 2023	Spring
Barstow	April 15, 2023	Spring
HOM	April 20, 2023	Spring
Yucca	April 17, 2023	Spring
Cuyama 1	April 28, 2023	Spring
Cuyama 2	April 28, 2023	Spring
Sheephole	April 20, 2023	Spring
Cuyama 1	June 28, 2023	Summer
Cuyama 2	June 28, 2023	Summer
Yucca	July 4, 2023	Summer
Barstow	July 5, 2023	Summer
Hom	July 6, 2023	Summer
Tecopa	July 8, 2023	Summer
Sheephole	July 9, 2023	Summer
Barstow	April 15, 2024	Spring
Tecopa	April 16, 2024	Spring
Cuyama 1	April 30, 2024	Spring
Hom	April 25, 2024	Spring
Yucca	April 21, 2024	Spring
Cuyama 2	April 30, 2024	Spring
Sheephole	April 20, 2024	Spring

Table D2: Scene ID and satellite data collection metadata for NDVI. All data was obtained using the USGS Earth Explorer.

Scene ID	Coordinates	Path End Date	Path Start Date
EVUSS20230418202305011	38.73687 , -97.20	2023-05-01	2023-04-18
EVUSS20240423202404291	38.736867 , -97.20	2024-04-29	2024-04-23

Table D3: Annual species, native or invasive, and their lifeform.

species	prov	lifeform
Achyronychia.cooperi	native	forb
Acmispon.strigosus	native	forb
Acmispon.wrangelianus	native	forb
Aliciella.leptomeria	native	forb
Allium.nevadense	native	forb
Amsinckia.tesselata	native	forb

Astragalus.didymocarpus	native	forb
Astragalus.lentigonsus	native	forb
Astragalus.nuttallianus	native	forb
Brassica.tournefortii	invasive	forb
Bromus.diandrus	invasive	grass
Bromus.rubens	invasive	grass
Bromus.tectorum	invasive	grass
Calyptridium.monandrum	native	forb
Camissonia.campestris	native	forb
Castilleja.exserta	native	forb
Caulanthus.lasiophyllus	native	forb
Chaenactis.carphoclinia	native	forb
Chaenactis.fremonti	native	forb
Chorizanthe.brevicornu	native	forb
Chorizanthe.rigida	native	forb
Chylismia.brevipes	native	forb
Chylismia.caliviformis	native	forb
Cryptantha.nevadensis	native	forb
Cryptantha.sp	native	forb
Dalea.mollissima	native	forb
Dasyochloa.pulchella	native	forb
Delphinium.parishii	native	forb
Descurainia.pinnata	native	forb
Ditaxis.lanceolata	native	forb
Eleymus.glaucus	native	grass
Eremalche.parryi	native	forb
Eremothera.boothi	native	forb
Eriastrum.diffusum	native	forb
Eriastrum.eremicum	native	forb
Eriogonum.gracillimum	native	forb
Eriogonum.reniforme	native	forb
Eriogonum.trichopes	native	forb
Eriophyllum.pringlei	native	forb
Eriophyllum.wallacei	native	forb
Erodium.cicutarium	invasive	forb
Eschscholzia.glyptosperma	native	forb
Eschscholzia.minutiflora	native	forb
Festuca.microstachys	native	grass
Festuca.octoflora	native	grass
fuzzypinnatecuy2 NA		
Gilia.clokeyi NA	native	forb
Globemallow. like bells	native	forb
Herniaria.cinerea	invasive	forb

Hordeum.murinum	invasive	grass
Lastarriaea.coriacea	native	forb
Lasthenia.californica	native	forb
Lepidium.lasiocarpum	native	forb
Leptosiphon.liniflorus	native	forb
Linanthus.demissis	native	forb
Loeseliastrum.schotti	native	forb
Logfia.depressa	native	forb
Lupinus.arizonicus	native	forb
Lupinus.flavoculatus	native	forb
Lupinus.microcarpus	native	forb
Malacothrix.glabrata	native	forb
Menzelia.sp	native	forb
Monoptilon.bellioides	native	forb
Nama.demissa	native	forb
Nemacladus.sp	native	forb
Oenothera.cespitosa	native	forb
Oxytheca.perfoliata	native	forb
Pectocarya.sp	native	forb
Phacelia.fremontii	native	forb
Phacelia.ramossima	native	forb
Phacelia.tanacetifolia	native	forb
Pholistoma.membranaceum	native	forb
Plantago.ovata	native	forb
Poa.secunda	native	grass
Rafinesquia.californica	native	forb
Rafinesquia.neomexicana	native	forb
Salvia.carduacea	native	forb
Salvia.columbariae	native	forb
Schismus.barbatus	invasive	grass
Sisymbrium.altissimum	invasive	forb
spikygren.CUY1 NA		forb
Stephanomeria.exigua	native	forb
Stipa.pulchra	native	grass
Stylocline.micropoides	native	forb
unknownallgreenCUY1 NA		forb

Table D4: A description of sampling intensity.

Sampling activity	Dates	Reps
Measured annual plants	Spring 2023	30 under shrubs and 30 in open areas per site, N = 420
	Spring 2024	40 under shrubs and 40 opens, N = 560
Pitfall traps	Spring 2023	12 shrub and 12 open per site, N = 168
	Summer 2023	12 shrub and 12 open per site, N = 168
	Spring 2024	16 shrub and 16 open per site, N = 168
Measured seed removal rates	Spring 2023	36 depots per site, N = 252
	Summer 2023	36 depots per site , N = 252
	Spring 2024	48 depots per site , N = 336

Table D5: A list of ant species collected and their diet classifications.

Species	Diet Classification
Aphaenogaster megommata	granivore
Crematogaster depilis	other
Dorymyrmex insanus	omni
Forelius mccooki	omni
Forelius pruinosis	omni
Leptothorax	other
Messor pergandei	granivore
Monomorium ergotyna/minima	other
Myrmecocystus ewarti	other
Myrmecocystus flaviceps	other
Myrmecocystus kennedyi	other
Myrmecocystus lugubris	other
Myrmecocystus mexicanus	other
Myrmecocystus semirufus	other
Myrmecocystus tenuinodis	other
Myrmecocystus testaceus	other

Myrmecocystus yuma	other
Pheidole desertorum	omni
Pheidole hyatti	granivore
Pheidole vistana	omni
Pogonomyrmex sp.	granivore
Pogonomyrmex californicus	granivore
Pogonomyrmex rugosus	granivore
Solenopsis molesta	omni
Solenopsis xyloni	omni

Figure D1: Seed baits were offered in 6 cm diameter Petri dishes with 1 cm^2. *Pogonomyrmex* sp. harvester ant removing a barley bait (large size bait shown here).

Table D6: AIC and BIC comparisons of models. Chosen model is shown in bold text.

	Candidate Models	AIC	BIC
Annual Richness	Arid * microsite + ndvi	3523	3552
	Arid * microsite	3521	3545
Annual Abundance			
	Arid * microsite + ndvi	8689	8723
	Arid * microsite	8717	8747
	Arid*microsite + ndvi*microsite	8587.57	8626

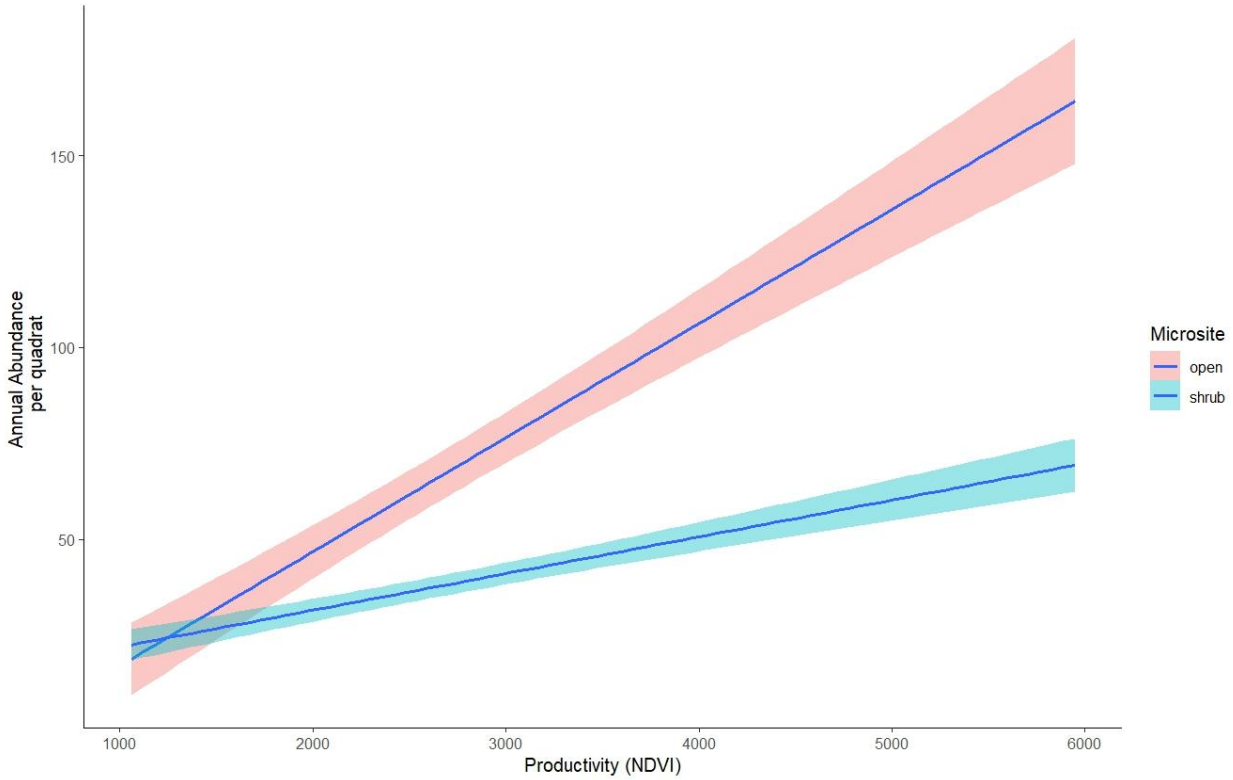


Figure D2: Relationship between productivity and annual plant abundance mediated by shrub microsites.

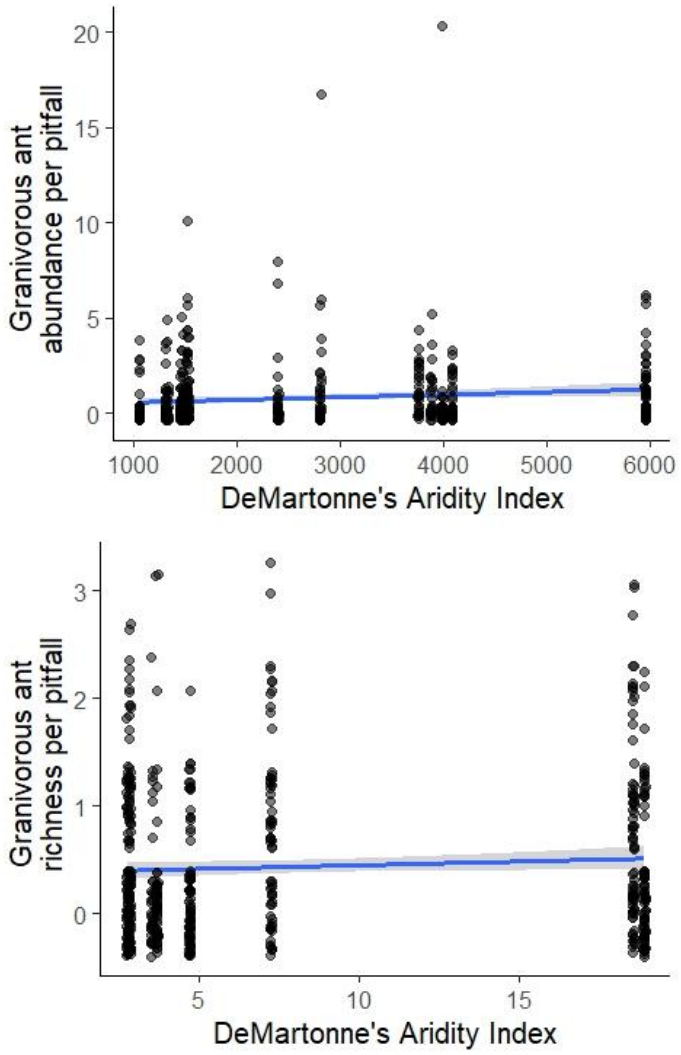


Figure D3: The response of ant abundance and ant richness in response to DeMartonne's Aridity Index. Higher values of DeMartonne's Aridity Index correspond to lower aridity.

Table D7: AIC and BIC comparisons of seed size, ant size and removal rate models.

	Candidate Models	AIC	BIC
Log Native Seed Size	Arid + Microsite + Webers + Mandible + NDVI	1592	1628
	Arid + Microsite + Webers + Mandible	1592	1620

Log Invasive Seed	Arid + Microsite + Webers + Mandible + NDVI	1603	1641
	Arid + Microsite + Webers + Mandible	1615	1648
Weber's Body Length	cwm.site + arid + Microsite + ndvi	49.75	72.06
	cwm.site + arid + Microsite	47.75	66.88
Seed removal rates	Microsite + mn.gr.abun*Size + arid	5924	5968.46
	Microsite + mn.gr.abun*Size + ndvi	5903.01	5946.9
	Microsite + mn.gr.abun*Size + arid + ndvi	5901.3	5949