EXAMINING MECHANISMS OF POSITIVE PLANT INTERACTIONS IN DESERTS

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Abstract

Deserts are ecologically important ecosystems that contain high levels of endemism and that are sensitive to global change. Positive interactions among plants have been cited as factors that support desert biodiversity by buffering against climate variability. However, there is limited understanding on the underlying mechanisms that determine positive plant interactions. Herein, we proposed a conceptual framework that describes multiple mechanisms of facilitation among plants. We then empirically tested in multiple deserts of California the different facilitation mechanisms in the context of extreme climate events, multiple stressors, and spatial gradients. We also conducted species distribution modelling to assess the role of positive interactions in expanding the niche and geographic range of beneficiary species. We expanded upon the previous literature by describing six mechanisms of facilitation and two meta-mechanisms. We found in experimentation that shrubs can buffer against extreme drought using the described mechanisms, but that facilitation effects are strongest at intermediate or low levels of abiotic stress. The shrub species used was found to deter herbivory and ameliorate abiotic stress, but not increase soil moisture. We also found shrub facilitation to be species specific and typically increased the biomass of plant species with more competitive traits. Consequently, non-native species were found to be frequently facilitated and shrubs were observed to have lower species richness. Positive interactions were determined to increase the geographic range of annual plant species that have been previously reported as facilitated in the literature. We challenged previous research that suggests positive interactions increase linearly with abiotic stress and that facilitation can buffer against climate variability. Shrubs were determined to be significant foundation species in these desert ecosystems supporting annual productivity and the unique occurrence of annual species. However, these interactions are more sensitive to global change than previously thought and could collapse at environmental extremes. The proposed framework and experiments provides better understanding into the predictability of positive plant interactions and an opportunity for future applied research into the restoration and conservation of desert ecosystems.

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Chapter 1

A systematic review and conceptual framework for the mechanistic pathways of nurse plants

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Abstract:

Aim - To conceptualize the mechanistic pathways of the nurse-plant syndrome by life form and to identify the implications of positive plant-plant interactions for landscape and evolutionary ecology.

Location - Global

Methods - We conducted a quantitative review examining 298 articles to categorize the nurse-plant ecological literature based on geographic region, mechanism of facilitation, ecological hypothesis, and nurse life form.

Results - A total of nine different nurse mechanisms were identified and two were classified as meta-mechanisms. We found that shrubs were the dominant nurse life form (46% of total studies) and that studies of positive plant interactions were most frequent in areas of high abiotic stress. Nurse-plant studies were also distributed unevenly around the globe with nearly a quarter in the South American Andes and Spain. Studies testing the direct nurse-protégé interactions were the most frequently studied including the ecophysiological responses of protégé species (32.2%). Research gaps identified in the nurse-plant literature included indirect interactions and seed trapping as well as the large-scale implications for landscape ecology and evolution.

Main Conclusions – Nurse plants are often considered keystone species because they commonly structure plant communities. This is an important confirmatory finding in many respects, but it is also novel in that it challenges traditional plant ecology theory and has important implications for landscape-level dynamics over time. The categorization of mechanisms proposed provides both a conceptual framework useful for organizing the research to date and can accelerate linkages with theory and application by identifying important connections. It is becoming

increasingly apparent that future studies of the nurse-plant syndrome must decouple and consider multiple mechanisms of interaction to explain the processes that influence community structure, particularly in high stress conditions, given a changing climate and potential shifts in biodiversity.

Introduction

The inclusion of facilitation into ecological theory has generated a paradigm shift that establishes positive interactions as pivotal in explaining many dynamics of ecosystems (Callaway, 1995; Bruno *et al.*, 2003). An apparent core concept used to examine facilitation is the nurse plant; these are species that benefit other plants or taxa through varied mechanisms (Gómez-Aparicio *et al.*, 2004; Brooker *et al.*, 2008) and are typically perennial species such as shrubs, trees, or cushion plants. With facilitation research increasing in scope and frequency (Bruno *et al.*, 2003; Brooker *et al.*, 2008), there is a growing need to clearly define nurse plants and the mechanistic pathways of their effects particularly on other plant species. The nurse-plant syndrome can in theory affect every life-history stage of another plant species including: (1) seed dispersal by increasing beneficiary species reproductive output, (2) seed arrival by functioning as a seed trap, (3) seedling establishment through substrate modification, (4) increased plant growth from reduction in herbivory or abiotic stress, and (5) increased survival and reproductive output. Consequently, the result of these positive interactions on individual plants can cause community-level changes in species composition (Cavieres & Badano, 2009). Both direct (nurse-protégé) and indirect (nurse-intermediary-protégé) pathways (Bruno *et al.*, 2003) can impact the various life stages and can shift in sign or magnitude with the ontogeny of a plant (Callaway and Walker 1997). In successional contexts, the pioneer plant may facilitate the development of others and eventually be replaced as it is exceeded by the increasing size of the benefactor species (Connell and Slatyer 1977). Though this is an excellent example of facilitation, it is not a typical nurse-protégé interaction used in the current literature as the nurse generally remains as a component of the ecosystem and the protégé is commonly (but not always) an annual plant species (Brooker *et al.*, 2008; McIntire & Fajardo, 2014). Nurse plants have also been tested as tools for restoration in disturbed landscapes (Zhao *et al.*, 2007; Gómez-Aparicio, 2009) and can interact with invasive plant species (Cavieres *et al.*, 2007). Nurse-plant studies have the capacity to inform both theoretical and applied plant ecology.

In a review conducted by Brooker *et al.*, (2008), six key facilitation concepts were identified, and we have expanded upon these to generate nine ecological hypotheses that are specifically tested using nurse plants (Table 1.1). These ecological hypotheses represent the scope of the current nurse-plant topics and simplify the broad facilitation literature into distinct disciplines including practices from theoretical, applied, and experimental ecology. Although positive plant interactions have been previously reviewed (Bruno *et al.*, 2003; Flores and Jurado, 2003; Callaway, 2007; Brooker *et al.,* 2008), further efforts are required to understand the ecosystem level implications of the nurse-plant syndrome. For instance, nurse plants are capable of driving biodiversity in multiple ecosystems (McIntire & Fajardo, 2014). There is also additional evidence of nurse plants as components of landscape-level processes such as ecological succession (Raffaele & Veblen, 1998), invasion biology (Cavieres *et al.*, 2007), and as a restoration tool (Gómez-Aparicio, 2009). Therefore, a formal review and conceptual framework is needed to quantitatively summarize the current state of research on nurse plants and to anchor the mechanistic pathways to global implications for ecology. Conceptual frameworks provide both a comprehensive understanding of the literature to date while setting an agenda for future avenues of research. By supplementing these frameworks with a systematic review, we provide a more robust synthesis that both highlights novel pathways and identifies research gaps.

Conceptual framework

Nurse plants can positively affect both members of the same species as well as other plant species through a suite of direct and indirect mechanisms (Callaway, 2007). Previous studies have categorized positive interactions into pathways between the benefactor and beneficiary (Anthelme & Dangles, 2012; McIntire & Fajardo, 2014). However, only one previous synthesis has examined the physical mechanisms underpinning plant-plant facilitation (Flores & Jurado, 2003). The nurse-protégé mechanisms were originally categorized into five pathways including seed trapping and safe sites for moisture, herbivory, nutrients, and physical support (Flores & Jurado, 2003). However, empirical research has since progressed to extend these mechanisms to include at least two primary and two ancillary mechanisms (Table 1.2). For example, the physical support safe site has been expanded here to consider all forms of substrate modification including root grafts, providing soil humus, and increasing soil microorganisms such as mycorrhiza (Cuenca & Lovera, 1992; Carrillo-Garcia *et al.*, 1999). The first additional primary nurse mechanism is the indirect facilitation of pollinator visitation by magnet species effects (Feldman *et al.*, 2004; Molina-Montenegro *et al.*, 2008). A nurse may sustain a population of pollinators or may function with protégé plants to jointly increase visitation of shared pollinators (Laverty, 1992; Moeller, 2004). The second additional mechanism is the amelioration of abiotic stress, such as protection from weather, heat, or cold extremes, particularly common in studies examining the stress gradient hypothesis (Bertness & Callaway, 1994; Maestre *et al.*, 2009; Holmgren & Scheffer, 2010). The remaining two additional pathways are best classed as meta-mechanisms because they are ancillary effects that function as responses to primary mechanisms. The first meta-mechanism is nurse-mediated distribution, which affects the spatial presence of protégé plants with more frequent occurrences of species or individuals under the nurse canopy versus open microsites (Franco-Pizaña *et al.,* 1995). Commonly, this pathway uses general association patterns and not formal spatial statistics (e.g. Carrillo-Garcia *et al.,* 2002; Yang *et al.*, 2010). The second meta-mechanism is nurse-mediated evolution resulting in changes to genetics (Liancourt *et al.*, 2012), ontogenic shifts (Armas & Pugnaire, 2009), or phylogenetic variation (Armas & Pugnaire, 2009; Valiente-Banuet & Verdú, 2007; Armas *et al.,* 2013). These nine mechanisms represent the entire documented contemporary scope of nurse-plant interactions with other plant species (Figure 1.1). Collectively, this framework organizes nurse-plant effects by life-stage because net interactions in plants often shift with plant development (Valiente-Banuet & Verdú, 2008). We summarize this framework as a clock wherein each independent notation in the ring represents a potential mechanistic pathway studied empirically, and the clockwise motion represents the progression of the protégé's life stages. The conceptual framework specifically lists key pathways of plant facilitation but also allows space for the incorporation of yet unexamined additional pathways.

In this study, we also conducted a formal systematic review to quantitatively describe the nurse-plant literature. The primary purpose of this review is to summarize, organize, and firmly link studies of the nurse-plant syndrome to ecosystem and evolutionary theory. We explored this topic by synthesizing the studies associated with the following objectives:

1) To assess the global extent of published nurse-plant effects and test whether there is a correlation between climate and the reported mechanisms.
2) To describe, contrast, and highlight research gaps for each nurse-plant mechanism and ecological hypothesis including differences in the nurse-plant life form.

3) To broaden and formalize the semantics of the nurse-plant syndrome by organizing all the studies and incorporating processes associated with evolution and macroecology (i.e., termed meta-mechanisms).

For simplicity, we assume that publication frequency is an indication of prevalence in natural systems, but we also recognize that there are legitimate biases in the study of an ecological process associated with the viability of studying particular places, species, and processes (Onwuegbuzie & Leech, 2007). We predict that resource-limited environments will have the greatest proportion of nurse studies because positive interactions have been shown to be greatest in conditions of high stress (Lortie & Callaway, 2006; Maestre *et al.*, 2009), but may collapse at gradient extremes (Michalet *et al.*, 2013a). Consequently, we predict that mechanisms associated with ameliorating abiotic stress and hypotheses testing it (i.e. the stress-gradient hypothesis) are more commonly studied and have been increasing in frequency recently. This does not necessarily imply relative importance, simply that nurse plants more commonly interact by these mechanisms. Some nurse life forms may be particularly associated with specific mechanisms, such as shrubs with seed trapping because xeric environments have fewer physical obstructions. We also predict that nurse-protégé interactions play a dominant role in shaping the ecosystems where they are present, but have been relatively understudied in aspects of landscape ecology and evolution. By better understanding nurse-plant interactions we are able to project ecosystem responses to landscape level changes and develop more effective land management practices.

Methods

Systematic Review

A systematic literature search was conducted using Web of Science from 1960-2014 with the following search terms: “nurse” and “plant*”. Topics unrelated to ecology were excluded such as substance abuse, virology, and biochemistry (Supplementary information, Figure A.1). The remaining 560 studies were individually reviewed for relevance and then categorized based on ecological hypothesis (Table 1.1) and nurse mechanisms (Table 1.2). Using the same criteria, a sub-set of the total 560 studies were examined and classified by an independent expert on plant interactions to ensure replicability (Côté *et al.*, 2013). Publications that tested more than one mechanism or hypothesis were independently classified, i.e. an article could be associated with multiple categories. Supplemental searches were conducted on Google Scholar and Scopus using the same search terms to ensure accurate capture of the nurse-plant literature.

The articles were then further reviewed for additional criteria that are common in nurse-plant studies, such as climate and nurse life form, to summarize the field of research. The climate for all the study sites were recorded for each paper and organized into six major environmental classes based on the Köppen climate classification: Tropical (megathermal), arctic-alpine, arid and semi-arid, Mediterranean (mesothermal), Temperate (microthermal) and other (Michalet *et al.*, 2013b). The "other" classification represents environments that belong to the previously mentioned climate categories but have been severely degraded from anthropogenic disturbances such as agricultural barrens or mining scrapes. Nurse plants were classified into the following life form groups: shrub, tree, cushion, other plant life form, and inanimate object. Geographical coordinates were also extracted from each study and mapped using ARCGIS 10 (ESRI, 2010).

Data Analysis

The relative frequency of each ecological hypotheses and nurse mechanism tested per study were compared using Pearson's chi-squared tests (*chisq.test* function) in *R* version 2.13 (R Development Core Team, 2011). Each nurse mechanism can function independently, meaning that we would expect that all should have equal relevance and similar numbers of associated studies. We also expect that the ecological hypotheses will favour theoretical based studies rather than applied. To contrast the frequencies of nurse mechanisms and ecological theories, we used a Pearson's chi-squared test and compared the proportion for each grouping to the resulting standardized residuals as post hoc tests (Coolidge, 2012). To compare how the frequency of studies has been changing over time, we plotted the number of nurse studies per year for the last 20 years. Additionally, we fit linear models with year as the predictor and each ecological hypothesis and nurse mechanisms as the response variable. We also separated the number of studies associated with each ecological hypothesis based on nurse life form and conducted a Kruskal-Wallis test followed by post hoc multiple comparisons tests (*pgirmess* package in *R*). To determine if the proportion of nurse life forms were similar between ecological hypotheses, each one was treated as percentages of total nurse-plant studies, and a one-way ANOVA was conducted between life forms. Tukey's HSD tests were used for these post hoc comparisons.

Results

A total of 298 papers explicitly reported testing for nurse-plant mechanisms (Supplemental material, Figure A.1). The largest proportion of studies (43.6%) were conducted in arid and semi-arid environments ($\chi^2 = 178.62$, $p < 0.001$, $n = 127$; Figure 1.2), and the study of nurse-plants was distributed broadly across the globe but not uniformly (Figure 1.3). Many studies were conducted in Spain and the Andes representing 14.1% and 9.1% respectively (Supplemental material, Figure A.2). A total of 57% of studies tested only one mechanism (χ^2 = 213.54, $p < 0.001$, $n = 171$), and only six articles examined four or more mechanisms. There were also significant differences in the frequency of study for each nurse mechanism (χ^2 = 164.68, $p < 0.001$, $n = 298$) or ecological hypothesis (χ^2 = 132.38, $p < 0.001$, $n = 298$). Abiotic stress amelioration was the most frequently documented mechanistic pathway (n = 118; Table A.2). Pollinator enhancement and evolutionary changes in protégés were rarely documented mechanisms and significantly understudied (Table A.2).

Hypotheses associated with documenting the direct effects of nurse-plant mechanisms were the most commonly studied (n = 96; Figure 4B; Table A.1). Indirect mechanisms of nurse plants were significantly understudied (Table A.1). Hypotheses associated with the effect of nurse plants on population dynamics and biodiversity (n = 73) and net interactions between nurse protégé depending on abiotic stressors (n = 62) were commonly studied collectively consisting of 45% of the total studies (Figure 1.4). The study of nurse mechanisms in general have been increasing dramatically in the last twenty years (mean effect ± SE = 2.27 ± 0.42, t_{19} = 5.37, $p <$ 0.001; Figure A.3), driven primarily by studies that examine the amelioration of abiotic stress, increases in soil moisture and favourably modification of soil nutrients (mean effect ± SE = 1.08 ± 0.26, t_{19} = 4.10, $p = 0.0006$; Figure A.3).

There was no trend observed between a particular nurse mechanism or ecological hypothesis and a nurse life form. Shrubs were the dominant life form in nurse-protégé interactions (46 % of the total studies) and most commonly examined for all nurse mechanisms and ecological hypotheses (χ^2= 17.4, $p = 0.001$; Figure 1.4). All other life forms of nurse plants were take into account in a similar number of studies including trees, cushions and inanimate objects ($p > 0.05$; Figure 1.4). The proportion of the nurse life forms associated with each ecological hypothesis differed significantly ($F_4 = 27.94$, post hoc contrasts, all $p < 0.001$).

Discussion

Nurse plants are important focal species for the study of plant-plant interactions, ecophysiology, restoration, and the ecology of dry land ecosystems. Not surprisingly, studies in arid and semi-arid environments comprised the bulk of the literature on nurse plants. There were also relatively high frequencies of arctic-alpine and Mediterranean studies that supported the stress gradient hypothesis. Herein, the nurse-plant literature was appropriately classified based on the mechanistic pathways and ecological hypothesis examined. Specifically, studies testing for the amelioration of abiotic conditions have been increasing steadily and significantly in the last two decades. The capacity for nurse plants to facilitate protégé plants through other mechanistic pathways, not associated with abiotic stress, is an important research gap for future research efforts. Shrubs are the most common life form tested to date, but there is also evidence accumulating that some tree species, inanimate objects, and cushion-forming alpine species may function similarly. Importantly, these findings suggest that the mechanisms associated with shrubs are applicable to other life forms. Lastly, recent studies have examined the role of nurse plants in the contexts of applied ecology and landscapes. This conceptual framework clearly illustrates that nurse-plant interactions can impact all plant life stages leading to community-level changes and that these ideas have been well documented in the literature but poorly integrated as related mechanisms. Thus, this synthesis provides a coherent and improved description of nurse mechanisms, hypotheses and empirical studies while introducing the potential macro-ecological significance of nurse-protégé interactions over evolutionary time.

Global distribution of nurse-plant studies

Specific land formations in the Western Hemisphere are particularly amendable to the study of nurse plants. This could either be due to the researchers/themes preferred in those regions or the ecology of those systems. For example, 40.1% of the alpine studies were conducted in the South American Andes. The coupled effects of high plant diversity, limited bio-geographical connectivity between mountains, and the harsh aridity gradient of this longitudinally spanning range (Arroyo *et al.,* 1988) provided ideal conditions to document nurse-plant interactions, i.e. similar to research reported at the edge of life (Michalet *et al.,* 2013a). These elements may be important in applying the nurse-plant methodology to the study of plant-plant interactions in other systems. These climate trends were similar to the synthesis by Flores & Jurado (2003) in that nearly half of all nurse-plant studies were conducted in arid and semi-arid environments. Although experiments in tropic and temperate climates collectively comprised 25% of all studies, both are extremely broad climatic categories including a diverse range of ecosystems such as coastal systems, grasslands, forests, and wetlands. Generally, nurse plant studies are most frequently reported in climates characterized by abiotic stress (Maestre *et al.,* 2009; Holmgren & Scheffer, 2010; Malkinson & Tielborger, 2010) or in degraded habitats for purposes of restoration (Gómez-Aparicio *et al.,* 2004; Padilla & Pugnaire, 2006). The nurse-plant syndrome can be generally restricted to resource limited environments though positive interactions between may diminish in areas of extreme stress (Maestre *et al.*, 2009). However, a recent study in Antarctica has also shown that facilitation was important even in extremely adverse systems (Molina-Montenegro *et al.*, 2012). The high frequency of nurse plant studies in stressful environments may explain the greater proportion of studies examining mechanisms of abiotic amelioration. Nurse plants may therefore be functioning as key drivers of community composition in these systems (Hacker & Gaines, 1997; McIntire & Fajardo, 2014). A global survey of positive interactions and climate in the alpine found that net interactions generally shifted from negative to positive with increasing altitude, but that different climatic regions did not always respond similarly (Michalet *et al.,* 2013b). Facilitation by drought-tolerant species in xeric climates increased at low altitudes thereby buffering the potential effects of climate change but in stress environments with moderate-severity, climate change could amplify the interplay between facilitation and competition increasing variability in community dynamics (Butterfield, 2009). In a related meta-analysis, He *et al.,* (2013) also detected a shift from negative to positive interactions globally with species richness and also found that the strength of interactions varied with climate. Consequently, expanded tests for nurse-plants on gradients and in more precise sets of climatic conditions are needed to better model the mediation effects of nurse-plants on communities. Alternative mechanistic pathways and interactions between the different species are also critical because each will respond differently to climatic perturbations.

Research gaps in the research on nurse-plant pathways

Though indirect nurse-effects are less extensively studied than direct mechanisms, they are still important pathways of facilitation. For instance, biotic ‘stress’ is a major driver of plant-plant interactions (Graff & Aguiar, 2011) and nurse plants can indirectly protect understorey plants from herbivory (Barbosa *et al.,* 2009). A nurse plant can reduce the likelihood of disturbance for neighbouring plant species through shared defences by either being unpalatable (Smit *et al.,* 2006; Bee *et al.,* 2009) or by physically obstructing large animals with thorns and branches

(Flores & Jurado, 2003; Callaway, 2007). More commonly, nurses act through associational resistance to reduce visibility to herbivores, thereby decreasing browsing events (Barbosa *et al.*, 2009). Nurse-effects on external species are not always negative and may act to increase visitation of favourable species for protégé plants. For example, pollination visitation can be indirectly increased when a nurse functions as a magnet species to protégé plants that are otherwise unattractive for pollinators (Laverty, 1992; Callaway, 1995). A nurse can also indirectly improve soil chemistry for the understorey community by facilitating mycorrhiza colonization (Cuenca & Lovera, 1992). Direct and indirect mechanistic pathways can also be specific to certain nurse species (Callaway, 1995) and not purely a physical effect such as trapping windborne seeds (Giladi *et al.*, 2013). For instance, apparent competition among annuals under a shrub canopy can sometimes be reduced by nurse effects (Soliveres *et al.*, 2011; McIntire & Fajardo 2014). Currently, these indirect pathways are ideal opportunities to better understand the impacts of intermediary species in nurse-protégé interactions. This will provide the capacity to construct interaction networks thereby advancing the development of ecological theory (Goudard & Loreau, 2008). Direct and indirect effects may function in concert, interact non-linearly, and influence more than one pathway simultaneously, but we commonly study only singular, direct effects in most instances.

Although not commonly associated with nurse-plant interactions, seed trapping is a mechanism that can positively affect seed arrival of dispersing plant species. Seed dispersal strongly influences population dynamics thereby affecting major ecological processes including biodiversity, plant invasion, and community composition (Myers & Harms, 2009). Nurse plants can increase seed arrival of protégé plants either directly, by nurses physically obstructing passing seeds (Groeneveld *et al.*, 2007; Giladi *et al.*, 2013), or indirectly through animal mediated transport such as bird perching sites (Debussche & Isenmann, 1994) and mammal caches (Vander Wall & Joyner, 1998). Although seed trapping increases seed arrival, it may not be commonly termed a nurse-plant mechanism because the net outcome of effects on seed success may not always be positive due to increased competition, pathogens, or granivory and because seed dynamics in the field are difficult to quantify (Howe & Smallwood, 1982; Lortie & Turkington, 2002). For seed trapping to be function as a nurse mechanism, the increased seed arrival must result in an increased spatial correlation between nurse and protégé (Cody, 1993), and this may occur if the nurse acts to reduce seed dormancy (Franco-Pizaña *et al.,* 1996), seed granivory (Munguia-Rosas & Sosa, 2008) or act as a "fertile island" by ameliorating abiotic conditions (Yang *et al.*, 2010; Wang *et al.*, 2011). Seed trapping is an under-examined mechanism because it is contingent on additional nurse effects to encourage positive spatial correlation between plant species (Cody, 1993; Cavieres & Arroyo, 2001). It is nonetheless a compelling and likely viable opportunity for increased precision in estimating annual plant dynamics in stressful arid and semi-arid systems that rely heavily on seedbanks.

Differences in nurse-plant life form on positive interactions

The life form classifications of nurse plants were not specifically related to any particular mechanism or ecological hypothesis. Nurse 'objects' were the least studied life form but often out-performed their live counter-parts likely because of an inherent lack of competition with the potential resource needs of protégé plants (Munguia-Rosas & Sosa, 2008; Peters *et al.,* 2008). It has been commonly observed that shorter seed dispersal occurs in more heavily vegetated areas (Bullock & Moy, 2004). Therefore, it was expected that shrubs are the dominant life form for seed trapping in xeric environments because the annual plants communities are often sparse and highly variable in cover (Caballero *et al.,* 2008). Unexpectedly, shrubs were not significantly more studied than other life forms as a seed trapping mechanism potentially because secondary dispersal from rainfall deposits seeds in the sediment flows of open areas in many arid systems thereby reducing direct shrub effects on seed movements (Aerts *et al.*, 2006). Shrubs however were the dominant life form for herbivory protection because their morphology (i.e. thorns, branching, woody) makes them conducive to deterring herbivores (Callaway, 2007). Trees, cushions, and other plant species may not be as physically repealing as shrubs but still deter herbivory from their neighbours through secondary compounds and reduced palatability (Smit *et al.,* 2006; Barbosa *et al.,* 2009; Bee *et al.,* 2009). The observed frequency of life forms, particularly the high proportion of nurse shrubs, is also a consequence of the climates used to study this form of plant facilitation. For example, cushions are more likely to be found in arctic-alpine climates while shrubs dominate Mediterranean, arid, and semi-arid climates. The climate rather than the mechanism most commonly predicts the life form of a nurse protégé interaction in the literature to date, but this does not preclude the possibility that many other plant species can function as nurse plants in other communities.

Inclusion of two meta-mechanisms and implications for applied ecology

The semantic work included in this review highlighted two previously undefined meta-mechanisms that should be considered in mainstream nurse-plant theories. The first meta-mechanism is nurse-mediated evolution that occurs when the selection pressures on protégé plants are changed by the nurse plant (Michalet *et al.*, 2011). Plant traits, such as biomass and fitness, can be increase in stressful environments by positive interactions (Callaway *et al.,* 2002). Nurse-effects are temporally dependent and may result in ontogenetic shifts from facilitation to competition as the protégé plant develops, especially with increasing phylogenetic relatedness of neighbours (Valiente-Banuet & Verdú, 2008; Armas & Pugnaire, 2009; Armas *et al.*, 2013). Positive interactions may also cause ecotypic differentiation wherein plants in an ameliorated nurse microclimate are selected for competitive traits while those in an open microclimate are selected for stress-tolerant traits (Liancourt & Tielbörger, 2011). In some instances, nurse plants may also alter evolution trajectories by increasing the phylogenetic diversity of plant communities through the facilitation of distantly related species (Soliveres *et al.*, 2012; Valiente-Banuet & Verdú, 2007; Lortie, 2007). These positive interactions between nurse-protégé can either encourage or hinder gene flow within a plant population, thereby impacting rates of ecological speciation (Liancourt *et al.*, 2012). The second described meta-mechanism is the nurse-mediated distribution of neighbouring plant species (Franco & Nobel, 1989; Franco-Pizaña *et al.*, 1995). In stressed environments, protégés may become associated with a specific nurse plant such that the area under the nurse acts as an "island" surrounded by an "ocean" of inhabitability (Walker *et al.*, 2001; Wang *et al.*, 2011). Consequently, many studies have shown that plant species are found positively correlated with a nurse-plant species (e.g. Franco-Pizaña *et al.*, 1995; Yang *et al.*, 2010; Wang *et al.*, 2011). This presents concern for biological conservation as some invasive species may use nurse plants as a pathway for invasion into stressful environments typically unavailable to them (Cavieres *et al.*, 2007). However, the spatial associations between nurse-protégé can also have positive implications by introducing a nurse species to increase succession of a deteriorated plant community (Lookingbill & Zavala, 2009). Nurse plants can also function as drivers of biodiversity by increasing niche availability and creating novel habitats (McIntire & Fajardo, 2014). The inclusion of these two meta-mechanisms, nurse-mediated evolution and dispersal, are a novel categorization of studies that extends the scope of positive plant interactions and establishes important linkages with evolutionary theory.

Nurse plants have restoration applications as well as global implications for conservation biology, but their capacity to do so has been poorly examined. Although the research on direct nurse-plant mechanisms and ecophysiology is by no means complete, additional attention needs to be focused on the practicality of nurses-protégé interactions. Overall, there are considerably fewer papers examining applied ecological practices such as restoration ecology and invasion biology. Nurse plants have been repeatedly used for restoration purposes in a variety of degraded habitats and ecosystems (e.g. Gómez-Aparicio *et al.,* 2004; Padilla & Pugnaire, 2006). Although nurse plants are commonly applied in the reforestation of the Mediterranean basin (Castro *et al.,* 2002), there are other potential areas applicable for landscape restoration including the lower subtropics, arid ecosystems, and peatlands. The widespread potential for nurse plants to be used for restoration applications strengthens their role in applied ecology.

Conclusions

A conceptual framework was proposed herein to organize nurse-plant mechanisms by the life-stages of protégé species with plant development as the most affected. The high frequency of studies in arid/semi-arid ecosystems is consistent with a former review on the topic and a clear signal that nurse-plants are important in these ecosystems. The dominant pathway studied is abiotic amelioration, but there is accumulating evidence for the role of nurses as seed traps or as refuges from consumers. There was no specific relationship between particular life forms and mechanisms or ecological hypotheses tested suggesting that the ecological relevance of nurses can be very broad. Climate classification was however an important factor in organizing the nurse-plant literature. Two novel meta-mechanisms are also proposed that describe and incorporate the emerging empirical research on distributions and evolutionary implications for protégé species. This conceptual framework by life-stage provides a unification of the nurse-plant literature to date and suggests that linkages between different mechanistic pathways will become increasingly important in facilitation studies. These nurse mechanisms may act independently or function in concert making it critical that future studies decouple the different pathways of facilitation when trying to understand the ecology of communities defined by nurse-protégé interactions.

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Tables

Table 1.1: A list of ecological hypotheses tested using nurse plant mechanisms. Each hypothesis is listed with their central concept, key associated paper and possible nurse mechanism that may be used. More than one hypothesis may be examined within a study at a time.

Hypotheses tested	**Applicable Nurse Mechanism**	**Key Paper(s)**
Mechanisms		
Nurse plants directly affect the fitness or productivity of plants in their vicinity	All	Flores & Jurado, 2003; Callaway, 2007
Nurse plants indirectly affect the fitness or productivity of plants in their vicinity through an intermediary species	Seed trapping, pollinator visitation and herbivore protection	Barbosa *et al.*, 2009; McIntire & Fajardo, 2014
Gradients		
Net interactions between nurse and protégé are dependent on abiotic stressors	Substrate modification, soil moisture retention, soil nutrient modification, abiotic stress amelioration	Bertness & Callaway, 1994; He *et al.*, 2013;
Plant interactions mediate consumer pressures	Herbivore protection	Smit *et al.*, 2006
Community assembly		
Nurse plants facilitate the development of community structure to increasing complexity	All	Hacker & Gaines, 1997; Raffaele & Veblen, 1998
Nurse plants alter spatial dynamics of plant communities and increase local diversity	All	Franco-Pizaña *et al.*, 1995; Soliveres *et al.*, 2012.
Nurse plants alter the evolution trajectories and phylogenetic history of beneficiary species.	All	Valiente-Banuet & Verdú, 2007
Applications		
Nurse plants are tools for restoration of native flora in degraded landscapes	All	Gómez-aparicio, 2009
Nurse plants mediate the invasion regimes of non-native plant species	All	Cavieres *et al.*, 2007

Table 1.2: A list of mechanisms associated with nurse plants. Five of the nurse-protégé interactions are from Flores & Jurado, 2003 (*) and the remainder proposed herein. Each nurse mechanism is listed with their facilitative effect, key associated paper and categorization as a meta-mechanism. A meta-mechanism is an effect that occurs as the result of another nurse mechanism.

Nurse Mechanism	**Protégé response**	**Key Paper(s)**
Abiotic stress amelioration	Reduced environmental variability	Bertness & Callaway, 1994; Lortie & Callaway, 2006
Herbivore Protection*	Reduced browsing/trampling	Barbosa *et al.*, 2009; Smit *et al.*, 2006
Pollinator visitation	Increased pollination rate	Laverty, 1992
Substrate modification*	Physical assistance	Carrillo-Garcia *et al.*, 1999
Seed Trapping*	Increased seed arrival	Vander Wall & Joyner, 1998; Giladi *et al.*, 2013
Soil moisture retention*	Higher soil moisture	Maestre *et al.*, 2009
Soil nutrient modification*	Higher soil nutrient	Walker *et al.*, 2001
Nurse-mediated distribution (*meta-mechanism*)	Nurse association	Franco & Nobel, 1989; Franco-Pizaña *et al.*, 1995
Nurse-mediated evolution (*meta-mechanism*)	Altered genetics/phylogeny	Valiente-Banuet & Verdú, 2007

Figures

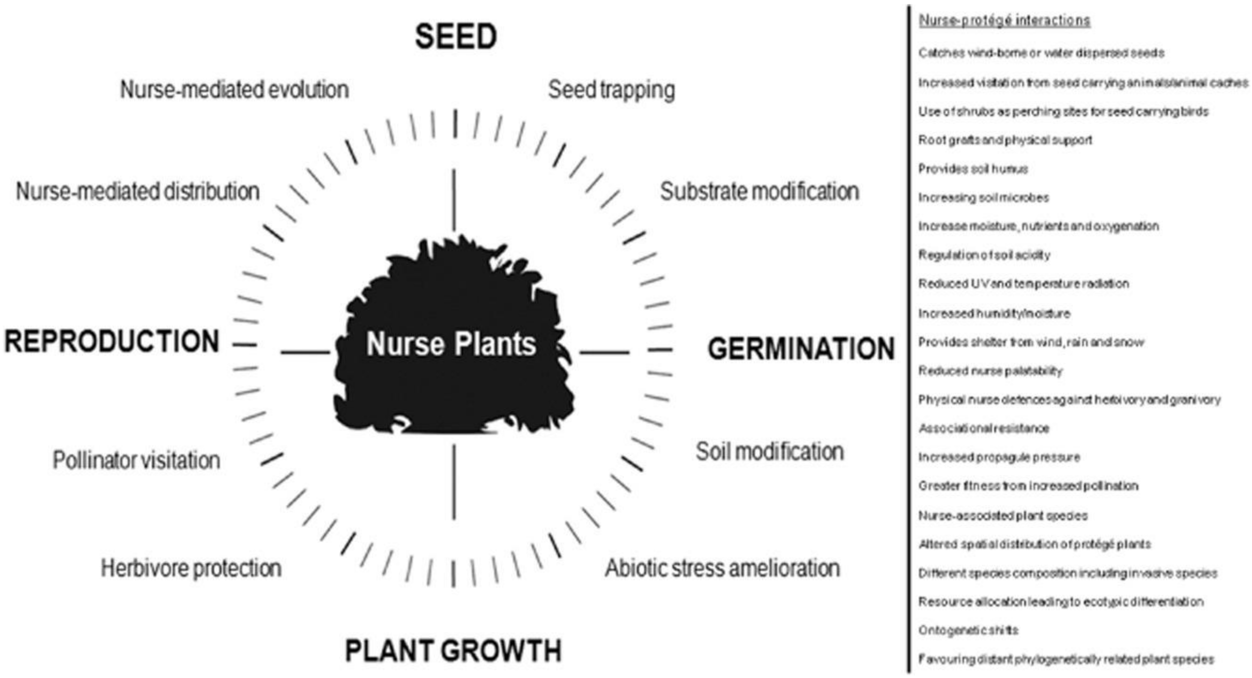

Figure 1.1: A conceptual framework for the abiotic and biotic mechanisms of nurse-plant effects studied in the ecological literature. Nurse mechanisms are ordered based on effect of protégé life-stage and the clockwise motion around figure represents the progression of a plant through its life history (i.e. Seed, seedling, plant/growth, reproduction). Listed to the right are possible nurse-protégé responses.

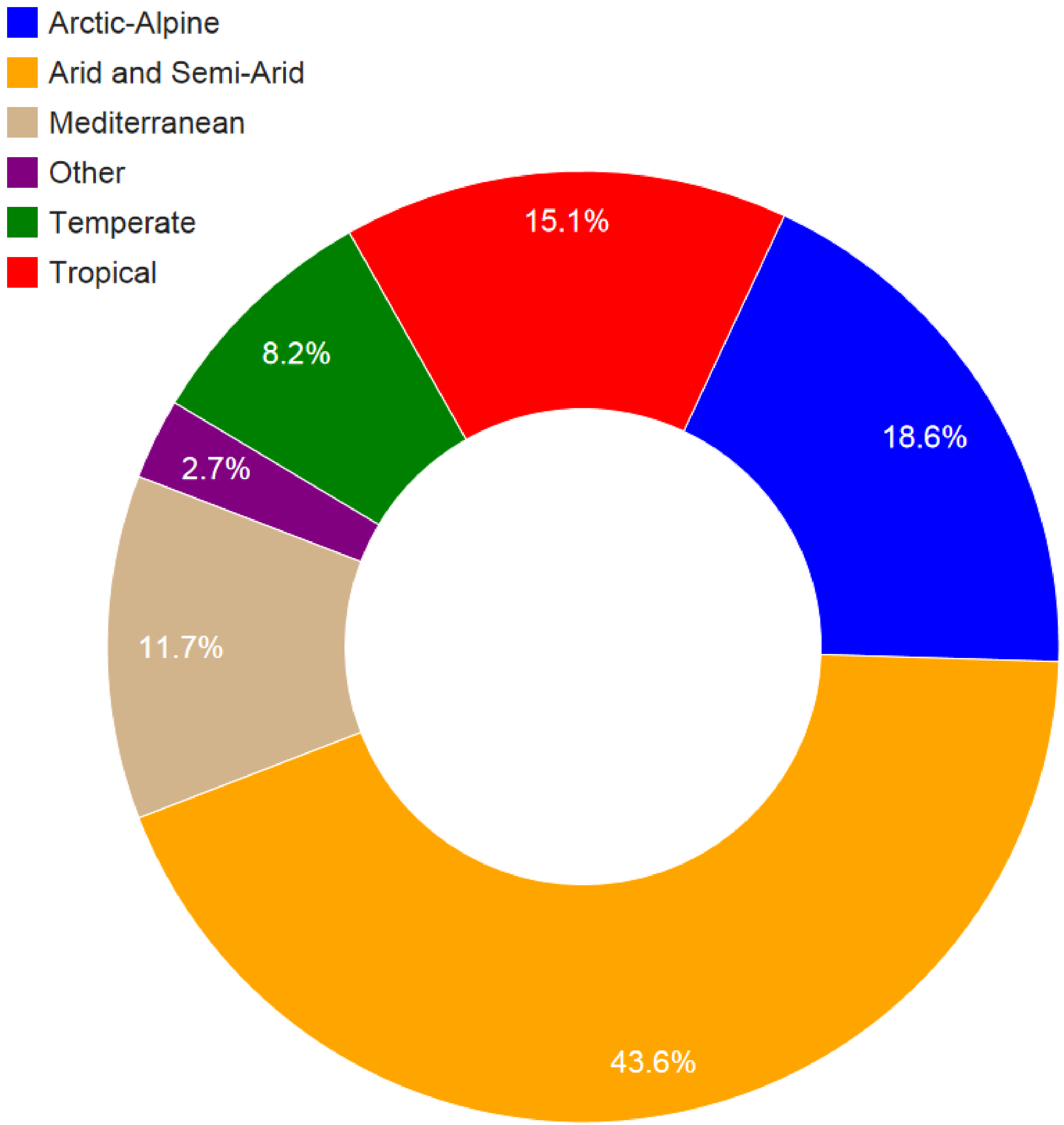

Figure 1.2: The percentage of nurse-plant studies conducted in each global climate.

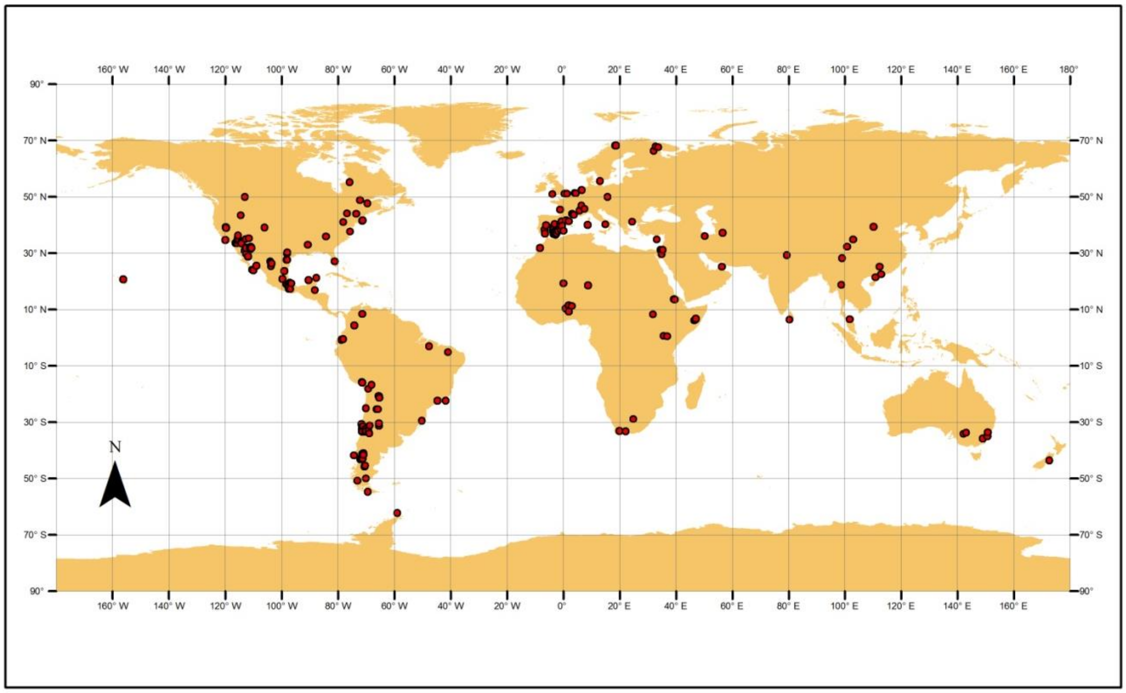

Figure 1.3: Geographical location of previous studies for nurse plants throughout the world

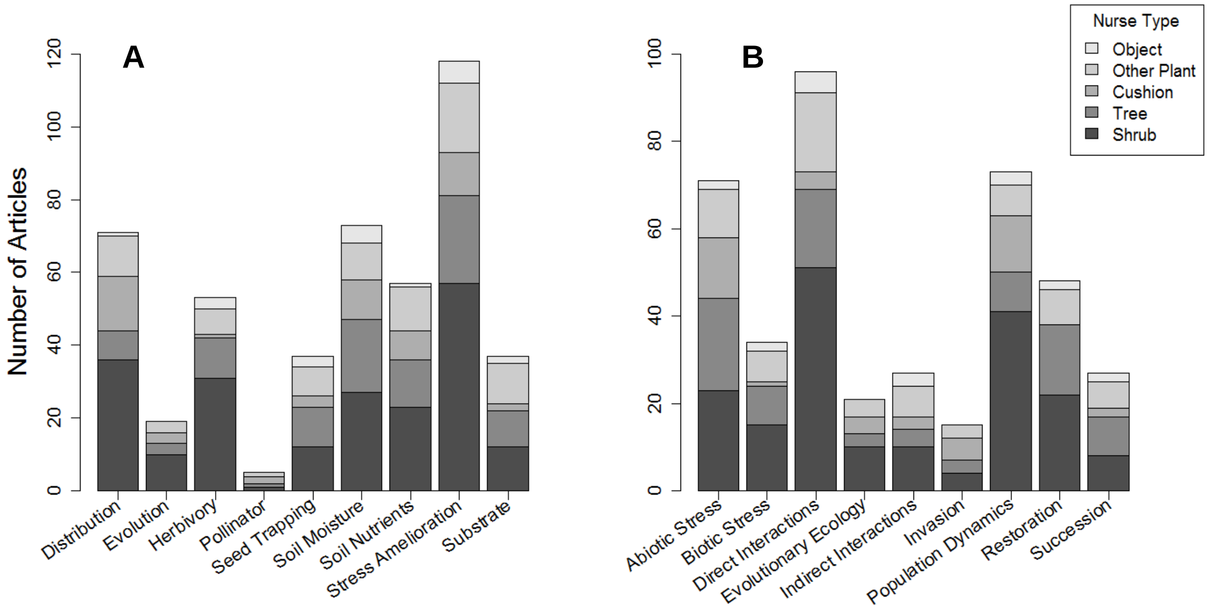

Figure 1.4: The number of associated studies based on nurse life form for each nurse mechanism (A) and each testable ecological hypothesis of facilitation (B).

Chapter 2

The effect of consumer pressure and abiotic stress on positive plant interactions are mediated by extreme climatic events

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Summary

Environmental extremes because of a changing climate can have profound implications for plant interactions in desert communities. Positive interactions can buffer plant communities from abiotic stress and consumer pressure caused by climatic extremes, but limited research has explored this empirically.

We tested the hypothesis that the mechanism of shrub facilitation on an annual plant community can change with precipitation extremes in deserts. During years of extreme drought and above-average rainfall in a desert, we measured plant interactions and biomass while manipulating a soil moisture gradient and reducing consumer pressure.

Shrubs facilitated the annual plant community at all levels of soil moisture through reductions in microclimatic stress in both years and herbivore protection in the wet year only. Shrub facilitation and the high rainfall year contributed to the dominance of a competitive annual species in the plant community.

Precipitation patterns in deserts determine the magnitude and type of facilitation mechanisms. Moreover, shrub facilitation mediates the interspecific competition within the associated annual community between years with different rainfall levels. Examining multiple drivers during extreme climate events is a challenging area of research, but it is a necessary consideration given forecasts predicting these events to increase in frequency and magnitude.

Introduction

Climate change is predicted to increase the variation in weather patterns, including the frequency of precipitation events (IPCC, 2014). In California, the climate has changed relative to historical patterns with an increased frequency of extreme drought followed by shorter periods of relatively higher rainfall (Pierce *et al.*, 2013; Griffin & Anchukaitis, 2014). Desert ecosystems are particularly vulnerable to changes in precipitation (Seager *et al.*, 2007; Thomey *et al.*, 2011) because their community assembly is determined by the frequency and magnitude of rain events (Reynolds *et al.*, 2004; Bates *et al.*, 2006; Holmgren *et al.*, 2006). For instance, some annual plants are absent in drought years but frequent in higher rainfall years and *vice versa*. This is because stress-tolerant species associate more with drought years while competitive or ruderal species associate more with relatively high precipitation years (Liancourt *et al.*, 2005; Holmgren *et al.*, 2006). Many species are also unable to adapt to extreme climate events (Seager *et al.*, 2007; Thomey *et al.*, 2011), but these species can adapt to changes in climate patterns over longer time frames (Jump & Penuelas, 2005). Additionally, extreme climate events can exceed particular climate parameters beyond critical thresholds, accelerating changes to community composition relative to gradual trends (Jentsch *et al.*, 2007).

In deserts, precipitation extremes can mediate both water availability and consumer pressure. During a drought, lower plant productivity can fail to support a full set of herbivore populations, and the plant community is thus regulated by bottom-up effects such as water availability (van de Koppel *et al.*, 1996; Kuijper & Bakker, 2005). Increasing precipitation can reduce resource limitations promoting productivity, but there can also be top-down regulation by herbivores and thus increased consumer pressure (van de Koppel *et al.*, 1996; Kuijper & Bakker, 2005). There are also non-resource based stressors in deserts that respond to weather including high temperatures and low humidity that limit plant growth (Michalet, 2007; Maestre *et al.*, 2009). Therefore, precipitation extremes in arid communities can be conceptually modelled as two ends of a larger, composite gradient that shifts from primarily abiotic (low precipitation, low productivity, reduced herbivore populations) to biotic (higher precipitation, higher productivity, increased consumer pressure). This model suggests that increase frequency of extreme climate events can lead to significant shifts in driver type and magnitude on desert communities.

Positive interactions among plants can buffer climate extremes, but the specific mechanism of facilitation responsible will change. For instance, the stress gradient hypothesis predicts that the frequency of positive plant interactions will increase with abiotic stress or consumer pressure (Bertness & Callaway, 1994) thereby considering both plant-plant and plant-plant-animal interactions (Lortie *et al.*, 2016). Support for the independent proposed predictions is equivocal because it depends on length of gradient and extent that different species are sensitive to the specific stressor or disturbance tested (Maestre *et al.*, 2006, 2009; Brooker *et al.*, 2008; He *et al.*, 2013; Michalet *et al.*, 2014). This debate is also likely because the effects of consumer pressure on positive plant interactions have been relatively understudied compared to studies on abiotic stress (Smit *et al.*, 2009; Soliveres *et al.*, 2012). In periods of high rainfall, shrubs can reduce consumer pressure (Holmgren & Scheffer, 2010; Graff & Aguiar, 2011) by physically obstructing consumers with thorns or dense branching (Smit & Ruifrok, 2011). Consumers respond to high levels of precipitation (Augustine & McNaughton, 2006; Wenninger & Inouye, 2008) and are known to be important drivers in drylands (Holmgren & Scheffer, 2010; Soliveres *et al.*, 2012). During drought, shrubs can ameliorate the microclimate below their canopy by reducing evapotranspiration and increasing soil moisture availability through hydraulic lift (Flores & Jurado, 2003; Espeleta *et al.*, 2004; Zou *et al.*, 2005). Thus, during both periods of extreme drought and relatively high rainfall, plant-plant interactions can remain positive in sign because the underlying facilitative mechanism changes from abiotic stress amelioration to protection from herbivores (Howard *et al.*, 2012). Therefore, co-occurring gradients of abiotic stress and consumer pressure can result in a substitution of facilitation pathways as a decrease in one driver can concurrently increase the other (Bertness & Callaway, 1994; Lortie, 2010). Plant communities in desert ecosystems naturally experience high levels of variation in rainfall that shifts the mechanism of facilitation and these shifts will become more common because climate change is expected to increase the amplitude of variation.

It is important that the mechanism of plant facilitation be further explored during extreme climate events because it is predicted that climate change will increase the frequency and severity of these events (Jump & Penuelas, 2005; Jentsch *et al.*, 2007). We experimentally tested the response of plant interactions to concurrent reductions in drought stress and consumer pressure in an arid shrubland during an extreme drought year in 2014 and in an above-average rainfall year in 2016. A gradient of soil moisture was experimentally introduced via a controlled watering-regime in each year, and exclosures were also erected to reduce sheep grazing. This design extends previous studies that have examined the effects of abiotic stressors on positive plant interactions in isolation (but see Soliveres *et al.*, 2012; Le Bagousse-Pinguet *et al.*, 2014), but have not tested for interactions with consumer pressure on co-occurring gradients (see theories proposed by Kawai & Tokeshi, 2007; Crain, 2007). Grazing is a form of consumer pressure and typically viewed as a disturbance (Grime, 1973) and/or stressor (Smit *et al.*, 2009). In this study, we conceptualize consumer pressure as a disturbance and a driver of plant community biomass, which can be reduced by positive plant interactions (Holmgren & Scheffer, 2010; Graff & Aguiar, 2011). We experimentally tested the hypothesis that the mechanism of plant facilitation provided by shrubs on the annual community can change with precipitation extremes in deserts to match the respective driver. We predicted that shrubs facilitate the annual plant community (i.e. abundance, richness, and biomass) by ameliorating the microclimate through reductions in temperature extremes and increases in relative humidity during the both years. We predicted that during the drought years, experimentally adding water would reduce the magnitude of positive interactions because the shrub is mechanistically increasing soil moisture availability for the annual community. In a year with above-average precipitation we expected animal exclosures to reduce the magnitude of positive interactions because the shrub is reducing consumer pressure on the annual community. Shrub facilitation on the annual community is expected under both drought and high rainfall conditions, but the mechanism of facilitation is predicted to change depending on the dominant driver of plant productivity that year (i.e. consumer pressure during the high rainfall year versus water availability during the drought year).

Methods

Study site and community composition

The study was conducted at Panoche Hills Ecological Reserve located in the hills west of the San Joaquin Valley, California (Bureau of Land Management; 36°41.776'N, 120°47.886'W at 650 m. a.s.l.). It has a semi-arid climate with the majority of precipitation occurring in the late fall and winter months (October to March). Therefore, we define a year within this study as the beginning of fall precipitation to the end of the growing season (i.e. October to April). Inter-annual rainfall varies dramatically; however, average annual precipitation is 25.5 cm with mean monthly temperatures of 8.9°C in January and 26.1 °C in July (Los Banos Weather Station data at 37°03.30' N, 120°51.00' W from U.S. Climate Data 2016). During the 2013-2014 growing season from October to April, rainfall within this region was classified as an exceptional drought (D4, the highest level) by the United States Drought Monitor (USDM 2014). The total amount of precipitation that fell during this period was approximately 8.5 cm and represents ~33% percent of the average annual precipitation (U.S. Climate Data 2014). During the 2015-2016 growing season an El Niño event brought high levels of precipitation to California and Panoche Hills received above average rainfall with approximately 30.5 cm of precipitation or 119% of the annual average (U.S. Climate Data 2016).

The dominant shrub at Panoche Hills is *Ephedra californica*. Other common perennials include *Marrubium vulgare, Juniperus californica and Eriogonum fasciculatum* (Hawbecker, 1951). *E. californica*, commonly referred to as Mormon Tea, is a member of the Gnetophyta division and produces cones during good rainfall years between May and June (Hickman, 1993). *E. californica* is native to southern and central California at elevations under 1000 m and often grows in arid shrublands (Hickman, 1993). The annual community is dominated by the following non-native species: Red Brome (*Bromus madritensis ssp. rubens,* hereafter *B. madritensis*), Soft Brome (*Bromus hordeaceus),* Red-stem Filaree *(Errodium cicutarium)* and common Mediterranean grass (*Schismus barbatus).* The native annual community is significantly underrepresented but included *Phacelia tanacetifolia, Amsinckia grandiflora* and *Monolopia lanceolata*. Frequently observed consumers include the desert cottontail (*Sylvilagus audubonii*), the black-tailed jackrabbit (*Lepus californicus*) and Heerman's kangaroo rat (*Dipodomys heermanni*) (Hawbecker, 1951). The full Panoche Plateau of 10,000 acres was grazed by 780 head of sheep in 2014 and 600 head of sheep in 2016 from mid-March until the time of biomass collection.

In May 2013, a total of 700 individual *Ephedra californica* shrubs were measured, geo-tagged, and labelled with metal number tags (Appendix B). Dimensions taken for the shrubs included diameter at the longest side (D1), the diameter immediately perpendicular to D1 (D2), and shrub height from basal stem to tallest branch (H). Shrub size was then calculated using the formula for volume of a semi-sphere ($1/3\pi r^3$). A visual estimate of shrub decadence on a Likert scale of 0-10 was also included with 0 indicating no foliage and a 10 indicating a full green canopy.

Water addition and animal exclosures

In January 2014, the soil moisture beneath all 700 shrubs was measured using a SM150 soil moisture sensor from Delta-T Devices (± 3.0%) (http://www.delta-t.co.uk/). A sub-sample of 120 shrubs were chosen using the following criteria: shrub volume within two standard deviations of the mean from shrub dataset, ambient soil moisture above 5% and the shrub canopy at 50% active/green. On the north side of each shrub, a 50 x 50 cm quadrat was marked using pin-flags and an open quadrat of equal size was replicated approximately two meters away from the target shrub. A watering regime was developed that applied six levels of water that represented a range of low rainfall years (cm): 0.0, 4.0, 6.5, 9.0, 11.5 and 14.0 (Geologica, 2010). Each water-level was randomly assigned to a set of 20 shrub/open pairs for a total of 240 quadrats. The total water was applied over five days between January 23rd and 31st, 2014. An additional five-shrub/open pairs from each watering-level were randomly selected and animal exclosures were constructed on March 30th after annual plant establishment using 21ga galvanized poultry netting buried 10 cm below ground and 1.2 meters above the surface (Figure B.3). Netting was secured around the sample quadrat at a diameter of 70.1 cm and extra care was taken to not disturb the surrounding vegetation. A 1.5 meter rebar post was hammered into the ground and secured to netting to prevent damage to exclosures from ungulates. As an additional herbivore reduction, an animal repellent (Deer Off®) was applied to the perimeter of each exclosure at the same time. In January 2016, 60 shrub-open pairs were selected to repeat the experiment, however, a two-level watering regime, 0.0 and 9.0 cm, was used to provide a clearer signal of water addition with the natural precipitation (Figure B.3). Exclosures were erected around 30 shrub-open pairs just after plant establishment. Quadrats were watered on January 16th, 2016 and exclosures were fully constructed by January 26th, 2016 to match precipitation patterns that year. Artificial watering was conducted in January which is typically the coldest and wettest part of the growing season for California. We chose January in both years because emergence was either very minimal or non-existent. Our intent was to initiate emergence with a single wetting event rather than extend the growing season at the end with further watering.

Abiotic measurements and plant surveys

We measured photosynthetically active radiation (PAR; 400-700 nm) in every quadrat on clear sunny days January 2014 during peak daylight hours (10:00 – 14:00) using a Licor line quantum sensor (Li-191SA, Li-COR Biosciences, Lincoln, NE) set to an average reading over 15 seconds to account for sun flecks. Soil moisture was measured twice with a SM150 soil moisture probe- once after watering (SWC_0) and again at the end of the growing season in April (SWC_t) in all plots. Onset HOBO Pro V2 loggers were deployed for air temperature and humidity under six pairs of shrub-open microsites on January 20th and collected May 2nd, 2014. In 2016, three pairs of loggers were placed under three pairs of shrub-open microsites November 1st 2015 and collected on April 1st 2016 (Filazzola *et al.* 2016; https://dx.doi.org/10.6084/m9.figshare.3486551.v1). The loggers were buried underground with the temperature and relative humidity sensor placed 2 cm above the soil surface on the north side of the shrub. The hourly average for the all loggers during the growing season was compiled for each microsite. The LiCor sensor, soil moisture probe and HOBO loggers were all placed within the canopy drip line on the north side of the shrub and adjacent open microsites.

Individual plants in each quadrat were identified to species level in April 2014 and 2016, and relative abundances were counted. A biomass sample was collected from the center of each quadrat using a 10 cm diameter ring. These samples were dried at 85°C for three days and weighed to the nearest 0.0001 gram.

Statistical Analyses

To compare the effects of shrubs on microclimate, we fit a model with temperature and relative humidity as the response variables and microsite and experimental year as factors. Temperature was normally distributed and was modelled using a general linear mixed model - LMM (function lmer, package lme4). We determined if microsite and experimental year significantly influenced temperature using F-tests with degrees of freedom calculated using Satterthwaite approximation (package lmerTest; Schaalje, McBride & Fellingham 2002). Relative humidity represents a percentage between 0-100%, and for this we used a generalized linear mixed model - GLMM (function glmer, package lme4) fitted to a binomial distribution with the logit link function. We determined if microsite and experimental year significantly influenced relative humidity using Z-tests fit by maximum likelihood Laplace approximation (Bolker *et al.*, 2009). Both models included logger replicate and day of the year as random effects. We also tested for differences in soil moisture (SWC_0 and SWC_t) among microsites and years using a general linear model. We used a t-test to compare differences in PAR between shrub and open microsites.

We tested if the shrub facilitation effect on biomass changed with water availability or reductions in consumer pressure using an Analysis of CoVariance (ANCOVA) with exclosure, microsite, and soil moisture (SWC_0) as the predictor variables and biomass as the response. All predictors were fully crossed. Biomass was adjusted using Box-Cox transformation to meet assumptions of normality (Osborne 2010).

We also determined if the frequency of positive interactions, consumer pressure, and water availability were species-specific by examining changes in community composition. The invasive grass *B. madritensis* was frequently observed as a dominant annual comprising more than 50% of the community composition for 70% of the quadrats. Therefore, we decided to fit models that separately test only *B. madritensis* abundance and the abundance of the remaining annual community (subordinates). We fitted models with *B. madritensis* and the subordinate abundance as the response variables and microsite, exclosure, and soil moisture gradient fully crossed as predictors for both 2014 and 2016. We also compared the shrub facilitation effect on the different species groups by fitting models with plant abundance as the response variable and microsite and species as the predictor variables for both years. The models were fitted with a negative binomial error distribution (glm.nb function, MASS library) because the abundance of the *B. madritensis* or the subordinate annual community represented discrete counts that are over-dispersed, i.e. variance exceeds the mean (Lindén & Mäntyniemi, 2011).We then used a z-test to determine whether the effects of *B. madritensis* or the subordinate annual community significantly differed from zero.

To compare if the mechanism of facilitation was related to consumer pressure, we examined differences in the effect size of shrub facilitation on biomass with and without consumers. We calculated effect size using the relative interaction index - *RII* (Eq. 1) because of its common usage in plant-interaction studies (Armas *et al.*, 2004; Cavieres *et al.*, 2014). It is symmetrical and bound between +1 (treatment effect - $biomass_t$) and -1 (control effect – $biomass_c$). We also compared the effects of consumer pressure, water addition, and shrub facilitation within the dry and wet years using *RII* calculated with and without treatment. In these instances, animal exclosures, water-addition plots, and shrub microsites were the treatments while ambient consumer pressure, no water added, and open plots were the controls.

$$RII = \frac{biomass_t - biomass_c}{(biomass_t + biomass_c)} \qquad \text{Eq. 1}$$

To compensate for variability when pairing, treatment and control quadrats were randomly subsampled for calculations of *RII* for 999 iterations and a mean was calculated (i.e. bootstrapping. Filazzola 2016; https://dx.doi.org/10.5281/zenodo.60810). The calculated means from the bootstrapped data were aggregated into a grand mean and 95% confidence intervals were obtained. These confidence intervals were used to determine if the treatments were significantly different from zero and to compare among treatments.

We used structural equation models (SEM) to test and quantify the effect of consumer pressure, soil moisture availability, and shrub facilitation on the annual community. A SEM was used because of its easy interpretation and because it implies correlation among the members of the annual community (Grace *et al.*, 2010). SEMs also assist in understanding how the responses of different components of the plant community are affected by multiple factors (Grace *et al.*, 2010). The SEM was modelled using the *lavaan* package in R (Rosseel, 2012). The annual community was specified as a latent variable composed of annual biomass, annual abundance, and *B. madritensis* dominance (i.e. percentage of the total plant abundance per quadrat). Soil moisture, microsite, and exclosures were fit as exogenous variables regressed upon the annual community. We developed models *a priori* and used two separate models for each year in order to best capture the differences in weather conditions. The SEM was evaluated using the Bollen-Stine bootstrapping method (R = 1000), as is typical of non-normal data (Rosseel, 2012).

Results

Micro-environmental differences

Temperature was significantly lower in the wet year than in the dry year (mean effect ± SE: -5.69 ± 0.56, $t = -10.1$, $p < 0.001$; Figures 2.1a, 2.1b) and it was also relatively cooler under shrubs compared to open microsites in both years (mean effect ± SE: -2.19 ± 0.16, $t = -13.6$, $p < 0.001$; Figures 2.1a, 2.1b). Relative humidity was significantly greater in the wet year than in the dry year (mean effect ± SE: 2.1 ± 0.11, $t = 18.8$, $p < 0.001$; Figures 2.1c, 2.1d) and it was relatively greater in the shrub microsite relative to open for both years (mean effect ± SE: 0.84 ± 0.03, $t = 27.5$, $p < 0.001$; Figures 2.1c, 2.1d). In both years, the open microsites had significantly higher soil moisture ($F_{356} = 37.2$, $p < 0.001$) and %PAR ($t_{239} = 15.6$, $p < 0.001$). There were no significant microsite by year interactions for all micro-environmental comparisons ($p > 0.05$).

Plant-community response

In both growing years, annual plant biomass and abundance were greater under shrubs, and species richness was lower (Table 2.1; Appendix C). Water addition did not change the relative frequency of positive interactions in either the dry or wet year (Table 1; Appendix E). Consumer pressure had no detectable effects in the dry year, however, in the wet year exclosures had significantly higher biomass relative to control quadrats (Table 2.1). The frequency of positive interactions decreased when consumer pressure was buffered by exclosures in the wet year (Table 2.1; Figure 2.2a). Soil moisture positively increased annual biomass, but there was no shrub by soil moisture interaction effect detected (Table 2.1). Shrub facilitation was the main driver of annual biomass in both years while the second relevant driver (as estimated by effect size magnitudes) switched from water addition in dry year to consumer pressure in the wet year (Figure 2.2b).

There was no change in the sign or frequency of interactions for *B. madritensis* or the subordinate annual species when consumer pressure was reduced or water was added (Table 2.2). *B. madritensis* was more abundant than the other subordinate plant species for dry year ($\chi^2 = 61.4$, $p < 0.001$) and 2016 ($\chi^2 = 31.3$, $p < 0.001$). The shrub microsite significantly facilitated *B. madritensis* abundance relative to open microsites and reduced the subordinate abundance in the dry year ($\chi^2 = 44.9$, $p < 0.001$; Figure 2.3a) and the wet year ($\chi^2 = 109.7$, $p < 0.001$; Figure 2.3b).

In the structural equation model we observed that shrub facilitation had the strongest effect on the composition of the annual community and this effect increased during the wet year (Figure 4). When considering the entire model, shrub facilitation supported annual biomass and plant abundance, but also the dominance of an exotic species, *B madritensis* (Figure 2.4). Consumer pressure did not affect annual composition in either year, and soil moisture was only relevant during the drought year (Figure 2.4a).

Discussion:

Positive interactions in desert ecosystems can be both directly and indirectly influenced by the large variation in precipitation patterns predicted to be caused by climate change (Reynolds *et al.*, 2004; Bates *et al.*, 2006; Metz & Tielbörger, 2016). Shrub facilitation was the most important driver of annual plant biomass in both years and this effect was greatest in the wet year. We also observed a switch in driver of annual biomass from water availability (bottom-up effects) in the dry year to consumer pressure (top-down regulation) in the wet year. However, our hypothesis was not supported that the facilitation mechanism will change at precipitation extremes to match these respective drivers. During the wet year, shrubs positively increased annual plant biomass by ameliorating the microclimate and by reducing consumer pressure. In the dry year, microclimate amelioration was the only mechanism of shrub facilitation. Experimentally adding water did not reduce the shrub facilitation effect in either year suggesting increasing soil moisture is not a significant mechanism of facilitation in this ecosystem. The presence of facilitation mechanisms are therefore related to the most limiting driver in the system (e.g. microclimatic stress within this study) and the facilitator's ability to ameliorate the stress or disturbance. The magnitude of positive interactions varies at environmental extremes because additional facilitative mechanism can become relevant, such as within this study. Positive interactions can buffer annual biomass in deserts from extreme climate events, underscoring the importance of future research using environmental extremes. Understanding factors that maintain productivity in arid ecosystems is critical for supporting ecosystem function globally particularly with a changing climate.

Positive interactions at environmental extremes

Precipitation can mediate the mechanistic pathway of plant facilitation in a given year. The shrubs within our study were found to consistently have a positive effect on the annual community in both a drought and high-rainfall year. Although shrubs in arid ecosystems have been found to provide hydraulic lift and reduce evapotranspiration (Zou *et al.*, 2005; Armas *et al.*, 2010), the shrubs within this study did not appear to increase soil moisture availability. Instead, the primary mechanism of facilitation was reducing non-resource based stress by ameliorating the shrub microclimate in both years (Michalet *et al.*, 2006; Howard *et al.*, 2012) and inhibiting consumers in the above-average rainfall year. This is supported by previous studies that found consumer pressure becomes relatively more important in determining plant interactions when productivity is high (Daleo & Iribarne, 2009; Graff & Aguiar, 2011). Therefore, positive interactions among plants occur through multiple mechanistic pathways (Smit *et al.*, 2009; Mod *et al.*, 2014) acting in concert, but the net effect is often determined by the most limiting factor. Multiple factors can also have interacting effects that are either synergistic or antagonistic (Crain *et al.*, 2008; Albert *et al.*, 2010). Thus, studying abiotic stress or consumer pressure independently that likely co-occur within a community limits our capacity to infer the relative importance of different mechanistic pathways and interactions among them (Flores & Jurado, 2003; Filazzola & Lortie, 2014). Multiple co-occurring factors and their associated mechanistic pathways are important topics for the development of more complex statistical models that pertain to research on climate variation.

Plant communities have evolved tolerance to the natural climate variation present in deserts (Tielbörger *et al.*, 2014). Desert annual species are tolerant to some inter-annual variability in climate through increased phenotypic plasticity (Aronson *et al.*, 1992). However, if climate variation is extreme, acclimatization is more difficult for individual plants (Gutschick & BassiriRad 2003; Jump & Peñuelas 2005). For instance, Jentsch *et al.* (2009) reported accelerated flowering times during an extreme drought while duration of flowering was reduced during heavy rainfall events. A prolonged extreme climate event, such as a multi-year drought, can have legacy effects on plant species in desert ecosystems (Reichmann *et al.*, 2013). Precipitation in California is predicted to become more variable in the future (Pierce et al. 2012) and therefore, positive interactions will become more important to maintain desert productivity. Ecological management plans will need to consider maintaining shrubs on arid rangelands to support ecosystem productivity through annuals for both native herbivores and livestock. Shrubs are thus foundation species for desert communities and positive interactions could be a component of community resilience to climate variation.

We detected a net positive effect of shrubs on the annual community in both years and at all levels of water addition and consumer pressure. However, the magnitude of effect was significantly lower in the extreme drought year. The facilitation effect of the shrub can shift from positive to negative as a result of increased resource competition, such as water availability, that exceeds the benefits of positive mechanisms (Bellot *et al.*, 2004; Noumi *et al.*, 2016). More extreme drought events could thus result in a neutral or negative shrub effect on the annual plant community (Michalet *et al.*, 2014). This suggests that shrubs could lose the ability to buffer the annual community at more extreme precipitation levels. Positive interactions extend the resilience of a plant community to extreme climate events, but these extremes could be exceeded with forecasts of climate change.

Facilitation effects on interspecific competition

An invasive grass species, *B. madritensis*, dominated the majority of the surveyed quadrats and was strongly correlated with soil moisture and the shrub facilitation effect. Positive interactions have been previously shown to facilitate the invasion of a non-native species into a habitat that is otherwise unsuitable for the invader species (Cavieres *et al.*, 2007). Though the effect of the shrub on the annual community was positive within this study, the ameliorated abiotic conditions may have altered interspecific competition within the community such as through increasing exploitative competition (Melgoza *et al.*, 1990; Tielbörger & Kadmon, 2000; Michalet *et al.*, 2015). Reduction in abiotic stress was positively related to *Bromus madritensis*, but negatively related to the remaining annual community likely because of increased competition from the exotic grass species (Abella *et al.*, 2011). For instance, shading and reduced temperature variation by the shrub *Atriplex vesicaria* in a semi-arid ecosystem increased the growth and establishment of an invasive succulent *Orbea variegata* because it was significantly more abundant within the shrub canopy (Lenz & Facelli, 2003). By removing resource limitations, competitive species can gain an advantage over stress-adapted species within the plant community (Callaway & Walker, 1997; Brooker & Callaghan, 1998; Liancourt *et al.*, 2005). Consequently, shrub facilitation can have effects on interspecific competition among the annual community and increase the dominance of another species (Tielbörger & Kadmon, 2000; Rodríguez-Buriticá & Miriti, 2009). Positive interactions in arid environments can also have indirect effects that are non-trophic on the annual plant community (Lortie *et al.*, 2016). Invasion by non-natives is increasingly becoming a critical issue even in relatively high-stress ecosystems (Rodríguez-Buriticá & Miriti, 2009; Abella *et al.*, 2011). Moreover, there is an increasing need to consider multiple factor when modeling interactions of native and exotic species with climate variation (Preston et al. 2008; Olden *et al.* 2010; Van Zuiden & Sharma 2016). Positive interactions can increase apparent competition in a changing climate, promoting shifts in species composition. Facilitation therefore may be a factor in the transition of arid and semi-arid ecosystems of California from native perennial bunchgrasses to exotic annuals (Orrock *et al.*, 2008; Abraham *et al.*, 2009). Surveys and manipulation of potential drivers of exotic success in deserts need to include positive interactions from shrubs.

Conclusions

Previous studies predict that positive plant interactions are more common with high levels of consumer pressure (Daleo & Iribarne, 2009; Graff & Aguiar, 2011) or abiotic stress (Callaway *et al.*, 2002; He *et al.*, 2013). Our support confirms these findings and suggests that precipitation extremes represent ends of biotic and abiotic gradients in desert ecosystems. We expected a switch in the mechanism of facilitation to match these different drivers, but this was not observed. Amelioration from abiotic stress was the dominant mechanism of facilitation in both years and also herbivore protection in the wet year only. The presence or absence of a facilitation mechanism is thus closely tied to the drivers in the community that are limiting and the facilitator's capacity for amelioration. Incorporating extreme climatic events into research on positive plant interactions is a difficult, yet important avenue of research as many communities may not be able to adapt to the climate extremes of the future. This is especially true with forecasts predicting greater climatic variability in the future (Stocker et al. 2013). Further research of positive interactions should include larger-scale gradients encompassing greater environmental extremes. Management and restoration of high-stress ecosystems also needs to incorporate multiple gradients and consider inter-annual variation as a potential mediator of any interventions.

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Tables

Table 2.1: Results from an ANCOVA testing for differences in the biomass of the plant community among, microsites (shrub and open), consumer pressure (ambient and reduced), and gradient of soil moisture. Separate ANCOVAs were conducted for a year of extreme drought (2014) and an above average rainfall year (2016). Significance at α < 0.05 is denoted by bolded values.

Effect	**Biomass 2014**			**Biomass 2016**		
	sign	*F*	*p*	sign	*F*	*p*
soil moisture	+	5.29	**0.022**	+	52.1	**< 0.001**
microsite	+	38.6	**< 0.001**	+	369	**< 0.001**
consumer pressure	0	0.054	0.82	-	6.36	**0.013**
microsite*soil moisture	0	0.088	0.77	0	2.61	0.11
microsite*consumer pressure	0	0.67	0.41	+	4.24	**0.042**
microsite*consumer pressure * soil moisture	0	0.55	0.46	0	0.10	0.75

Table 2.2: Results from GLMs testing for differences in *B. madritensis* abundance and the subordinate species abundance among, microsites (shrub and open), consumer pressure (ambient and reduced), and gradient of soil moisture. GLMs were conducted for a year of extreme drought (2014) and an above average rainfall year (2016). Significance at α < 0.05 is denoted by bolded values.

Effect	**2014**				**2016**			
	B. madritensis		subordinates		*B. madritensis*		subordinates	
	χ^2	*p*	χ^2	*p*	χ^2	*P*	χ^2	*p*
soil moisture	4.18	**0.041**	7.77	**0.0053**	2.85	0.091	1.37	0.24
microsite	34.9	**< 0.001**	13.6	**< 0.001**	100.7	**< 0.001**	40.2	**< 0.001**
consumer pressure	0.021	0.64	0.017	0.90	1.94	0.16	0.22	0.64
microsite*soil moisture	0.71	0.40	0.17	0.68	0.85	0.36	1.21	0.27
microsite*consumer pressure	0.17	0.68	0.020	0.89	0.057	0.81	1.84	0.17
microsite*consumer pressure * soil moisture	0.003	0.96	0.069	0.79	0.52	0.47	0.48	0.49

Figures

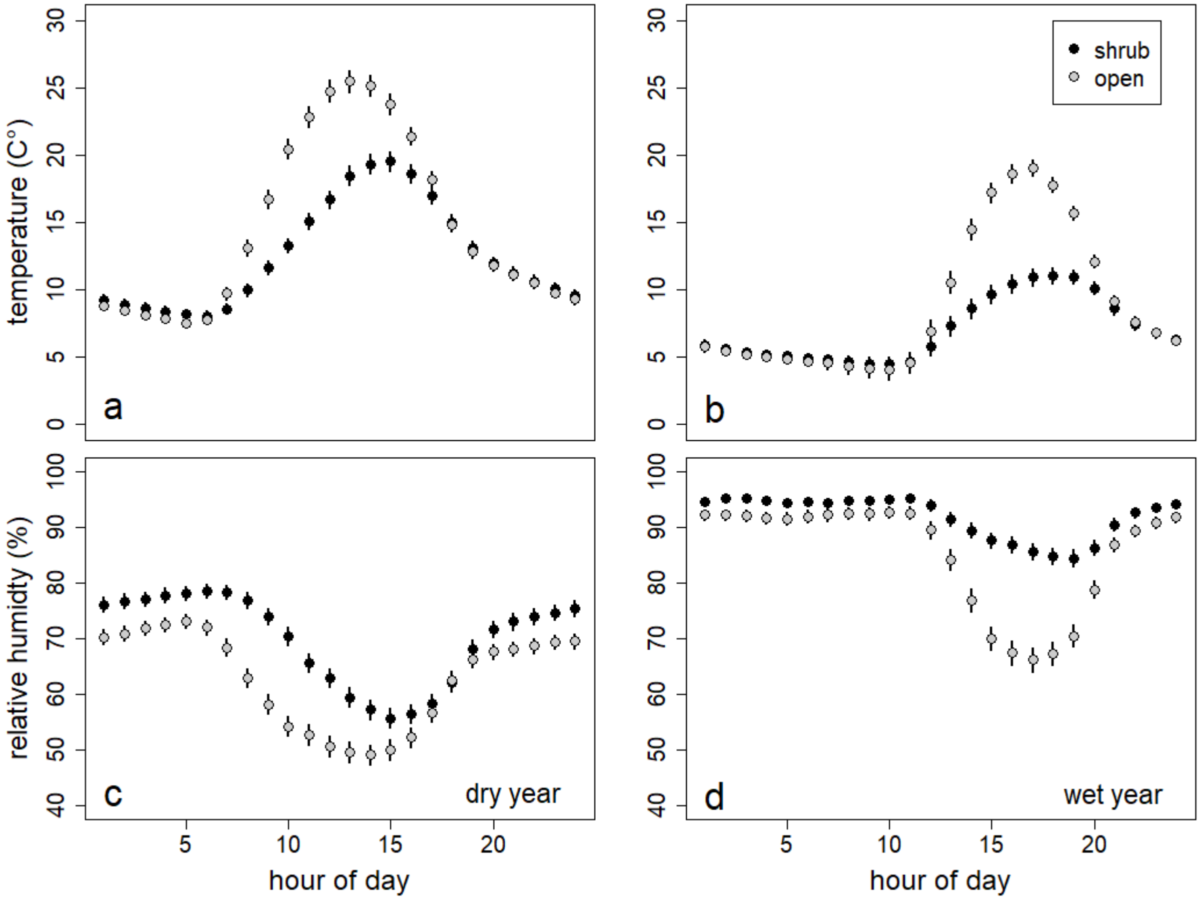

Figure 2.1: Average hourly temperature (C°) and relative humidity (%) for the growing season during the drought year (2014) and a year of above-average precipitation year (2016) for both shrub and open microsites. Error bars represent 95% confidence intervals.

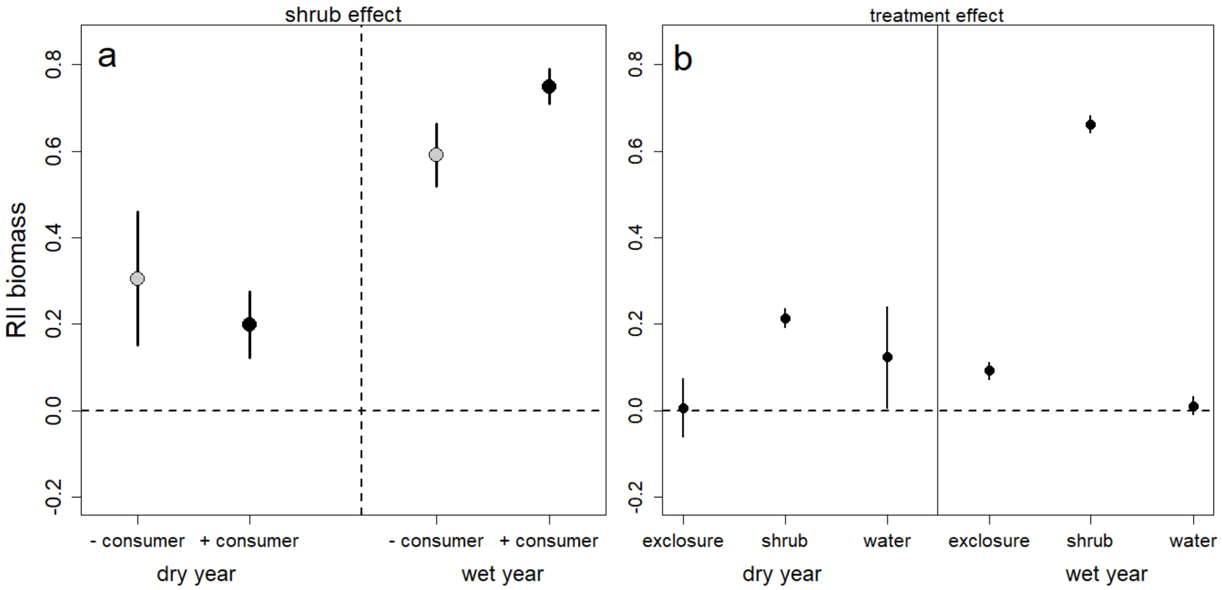

Figure 2.2: The shrub effect (**a**) and the effect of each treatment (**b**) on biomass compared using the relative interaction index (RII) in both the dry (2014) and wet (2016) years. Values for shrub effect are mean RII with error bars of 95% confidence intervals. The values for each treatment effect are bootstrapped RII (999 iterations) with 95% confidence intervals derived from the means of each iteration. Positive values represent a positive treatment effect and negative values represent negative treatment effect.

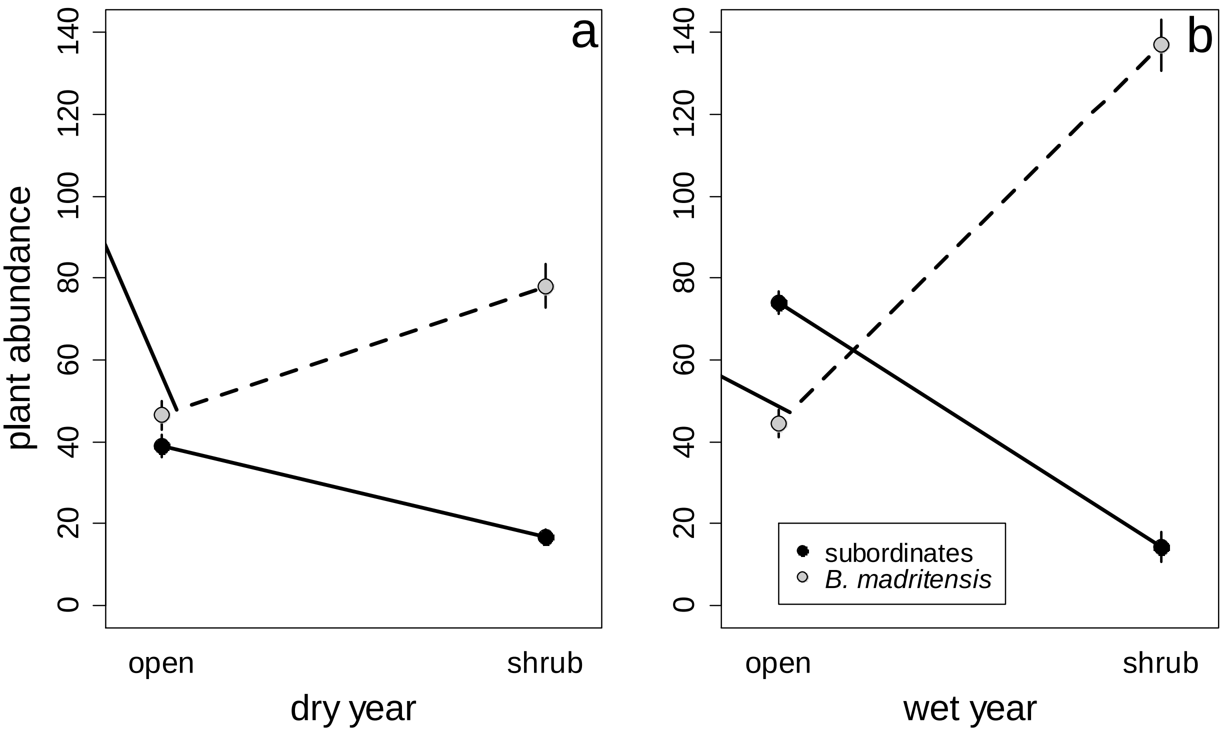

Figure 2.3: Plant abundance of *B. madritensis* and the subordinate species in shrub and open microsites during a drought year (2014) and a year of above-average rainfall year (2016). Error bars represent 95% confidence intervals.

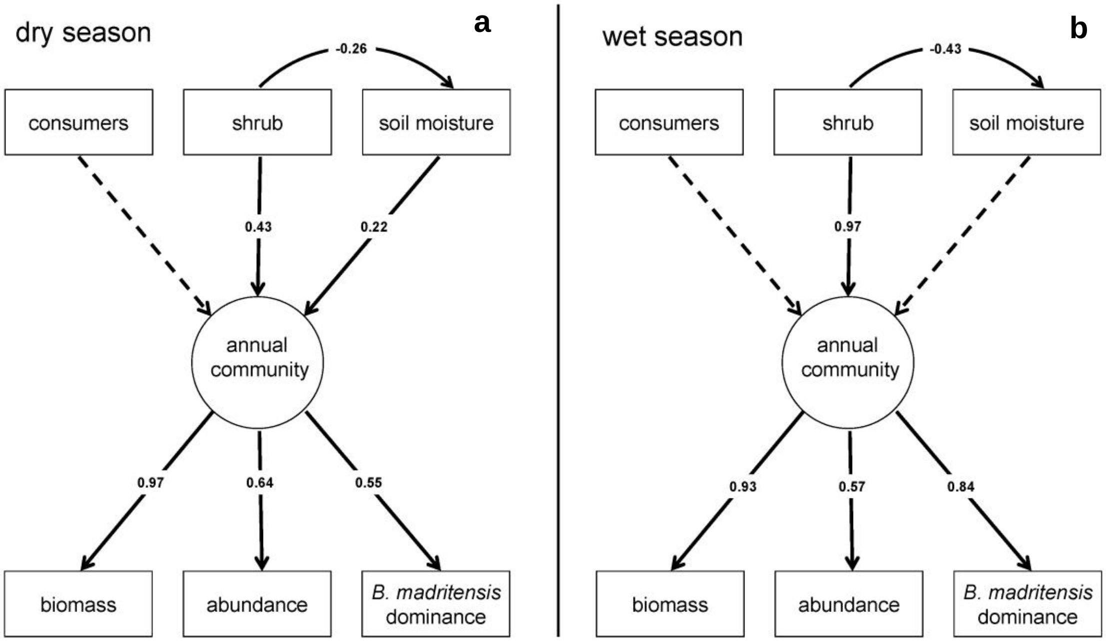

Figure 2.4: Structural equational modeling (SEM) results for the composition of the annual community in the dry and wet year. Black lines show relationships that were significantly different from zero ($\alpha = 0.01$), whereas dashed lines represent non-significant pathways. Annual community represents a latent variable that is composed of biomass, abundance and the percent dominance of *B. madritensis*. Models for the dry (**a**) and wet season (**b**) converged normally after 82 and 83 iterations respectively. Parameter estimates from the structural equation models are present within figure and Appendix D.

Chapter 3

Positive interactions among native species collapse at the extremes of an aridity gradient because of drought and indirect competition

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Summary

Deserts ecosystems are projected to be threatened by increasing aridity. Plant communities in deserts are particularly sensitive to shifts in precipitation patterns that can alter interactions among species. Shrubs often positively influence native plant communities through a series of mechanisms and can buffer against precipitation extremes. We examined the effects of shrub facilitation on plant community composition along a regional gradient of aridity. We selected seven sites located across three deserts in California with the common shrub species *Ephedra californica.* At each of these sites between 2015 and 2017, seeds of three phytometer species, all of them annual plants, were sown within thirty pairs of shrub-open microsites at each of the regional sites. We measured characteristics of the ambient plant community and each of the phytometers. Shrubs facilitated the biomass of the annual community but this effect collapsed with increasing aridity. Phylogenetic diversity and species richness decreased at the more mesic sites only in shrub microsite. There was significant turnover in the species composition of the ambient plant community along the aridity gradient, and the more mesic sites were also significantly invaded by non-native grass species. The response of the phytometers to shrubs varied among species and was determined by their respective traits. These results confirm previous research suggesting shrub-annual interactions are species-specific and challenges facilitation theory that proposes positive interactions should increase with aridity. We also propose an inverse relationship between abiotic stress and invasion that is mediated by shrub facilitation in deserts. Understanding positive interactions in the context of environmental gradients provide better insights into the expected changes in species compositions that will occur as a result of global change

Introduction

Deserts contain extremely high levels of endemism and are sensitive to shifts in precipitation patterns (Thomey et al. 2011; Baldwin et al. 2017). Climate change is predicted to globally increase desertification (IPCC 2014) and existing deserts, such as those in the Southwestern United States, are likely to become more arid in the future (Griffin & Anchukaitis 2014). Aridity threatens ecosystem health because it reduces the ability for plants to capture carbon dioxide or use soil moisture (Arnone III et al. 2008). Desert plant communities have some adaptations to inter-annual variability in climate and are dependent on pulse-events of high precipitation to support long-term persistence of the plant communities (Noy-Meir 1973; Ogle et al. 2004). However, prolonged drought may threaten the resilience of these systems to precipitation variability. Spatial gradients of aridity also represent long-term processes of community assembly and co-evolution among species that can be significantly disrupted by relative short shifts in precipitation patterns that can occur because of climate change (Sandel et al. 2010; Metz & Tielbörger 2016). Deserts are generally resource driven ecosystems with “bottom-up” regulation and drought effects on the plant community can have cascading impacts to the ecosystem as a whole (Báez et al. 2006). Exploring spatial gradients of aridity are thus crucial for ecologists because critical threshold of precipitations can be identified that sustain desert communities.

Shrubs in deserts can positively affect plant communities and buffer against precipitation extremes. However, there is continued debate as to the predictability of positive interactions along gradients of aridity (Michalet 2006; Maestre et al. 2009; Soliveres et al. 2015), and the sign and strength of interactions have been proposed to depend on scale, species identity, and mechanism of facilitation (Liancourt et al. 2005; Michalet 2007; Michalet et al. 2014; Soliveres

& Maestre 2014; Filazzola & Lortie 2014). For instance, studies that have examined plant interactions along large gradients including deserts and more mesic Mediterranean sites found that the frequency of facilitation responded linearly with aridity (Gómez-aparicio et al. 2004; Holzapfel et al. 2006; Armas et al. 2011). This is often cited as the Stress Gradient Hypothesis that predicts a linear response between positive interactions and abiotic stress (Bertness & Callaway 1994) . However, others have suggested that at environmental extremes, positive interactions can switch to negative interactions because of a scarcity of available resources (Davis et al. 1998; Tielbörger & Kadmon 2000; Maestre & Cortina 2004) and weakening of nurse effects (Michalet et al. 2006; Michalet et al. 2014). Inclusion of appropriate spatial scales in plant community interaction studies and in particular long gradients can help identify thresholds that shift the sign of interactions (Le Bagousse-Pinguet et al. 2014). The mechanism of facilitation is another consideration that affects the predictability of plant interactions. Shrubs can facilitate annual plants by ameliorating abiotic stress, increasing resource availability, or reducing consumer pressure (Mod et al. 2014; Butterfield et al. 2016; Zhang et al. 2017; Filazzola et al. 2018). Explicit testing for the mechanism of facilitation is important because the net interaction effect, when considered with competition for resources may not always be positive depending on the environmental gradient (Miriti 2006). Similarly, the consideration of multiple response variables in plant communities is necessary to estimate the overall net outcome of facilitation on a population or species along an environmental gradient (Lortie et al. 2016). Inclusion of species-specificity as a response variable is a notable example because species with different plant traits (e.g. competitive, stress tolerant) will have different optimal environmental conditions (Liancourt et al. 2005; Albert et al. 2010; Liancourt et al. 2017). Consequently, each species within a community will have different thresholds along a gradient of aridity that determines their relative presence or absence. Researchers must disentangle the species-specificity and mechanisms of interaction within desert plant communities along gradients of aridity to advance our theoretical understanding of facilitation and to provide evidence for applied predictions in response to climate change.

Nutrient availability in deserts supports ecosystem function and is related to precipitation patterns. Deserts are sensitive to nutrient availability relative to other ecosystems because low precipitation reduces rates of mineralization and production/release of organic matter (Marschner & Rengel 2007; He et al. 2015). Additionally, desertification typically reduces the fertility of some soils (Delgado-Baquerizo et al. 2013; Huang et al. 2016) and anthropogenic disturbance is increasing nitrogen deposition in others (Padgett et al. 1999; Tilman et al. 2001). Shrubs can increase soil nutrient content directly through nitrogen fixation via plants such as legumes(Gómez-Aparicio et al. 2005), and indirectly by creating a microclimate that favours nutrient cycling (Noumi et al. 2016; Abdallah et al. 2016) as well as by increasing the diversity of soil microbiota (Rodríguez-Echeverría et al. 2016). In arid ecosystems, shrubs can increase available potassium that is linked with better water-use efficiency in certain plant species during drought (Gómez-Aparicio et al. 2005). More often, annual species are unable to take advantage of increased nutrient availability because of limitations in water (Delgado-Baquerizo et al. 2013; Michalet et al. 2015). Increasing aridity under climate change can thus reduce the facilitative effects of shrubs through nutrients (Noumi et al. 2016). Understanding the spatial heterogeneity of soil nutrients and the response of the desert annuals along a gradient of aridity is necessary for developing strategies to mitigate species loss.

Examining plant interactions along gradients of aridity can also shed light on impacts of changing precipitation patterns on desert communities and the capacity for shrubs to mitigate biodiversity loss. Shrubs can facilitate annual plants through a series of mechanisms along a gradient of aridity that include increasing soil nutrients, increasing soil moisture, ameliorating temperature extremes, and providing a suitable substrate (Filazzola & Lortie 2014). A better understanding of plant community responses to environmental gradients can be obtained by examining both the individual species responses and the interactions among them (Lortie et al. 2004). Here, we examined the effects of a dominant shrub species, *Ephedra californica*, along a regional gradient of aridity spanning three deserts provinces in Southern California. We surveyed the ambient plant community, collected environmental data, and planted three phytometer species with different plant traits at seven sites across this regional gradient. Phytometers are plant species that are experimentally added to systems to identify between-site differences of a plant trait because of environmental conditions independent of other community assembly filters, such as dispersal and co-evolutionary history (Dietrich et al. 2013). The purpose of this study was to determine how a dominant shrub species mediates the composition of the annual plant communities along a gradient of aridity and to test for specificity using seeds of three annual plant species that are naturally present at all the sites. We addressed the following questions in response to the gradient of aridity:

1) What are the effects of shrubs on the environment along a gradient of aridity?
2) What are the species-specific responses of the annual plants to shrub facilitation?
3) How do positive interactions change along a gradient of aridity and what are the consequences for community composition

Understanding these questions can help resolve discrepancies in predictions of plant interactions along gradients of aridity and thus advance our ecological knowledge.

Methods

Study Sites

We selected seven sites with desert climates in Southern California, U.S.A. along a gradient of increasing aridity mostly driven by increasing distance from the ocean (i.e. continentality) and rainshadow effects (Figure F.1): Panoche Hills, Cuyama Valley, Tejon Ranch, Barstow/Ft. Irwin, Heart of the Mojave, Sheephole Valley Wilderness, and Tecopa (Table 3.1). The experiment was completed between October 2015 and May 2017. All the sites were located on Bureau of Land Management holdings with the exception of the Tejon Ranch, which is managed by the Tejon Ranch Conservancy. We chose sites that were similar in characteristics including soil substrate, elevation, and topography. The shrub species, *Ephedra californica*, composed at least 25% of the perennial plant community for each site. The sites range from semi-arid to arid climates with the majority of precipitation occurring in the late fall and winter months (October to March). However, the most eastern sites in the Mojave Desert can occasionally experience summer thunderstorms (Beatley 1974). Within this study, we defined the growing season from November 1st and ending May 1st. The 2016 year would therefore represent November 2015 until May 2016. The rainfall of the growing season is thus not the rainfall of the calendar year. Climate calculations were obtained from weather stations in closest proximity to the study sites (Appendix F).

All sites are considered desert communities and cross three desert vegetation provinces including the San Joaquin Desert, the Mojave Desert, and the Colorado Desert. Common shrub species at some of the sites included *Larrea tridentata*, *Atriplex californica*, *Artemisia spp*., and *Ambrosia dumosa*. Annual plant species varied at all sites, but common native annuals included *Phacelia tanacetifolia, Plantago insularis, Salvia columbariae, Amsinckia tessellata*, and *Chaenactis* *fremontii*. Common non-native species that were also present included *Bromus madritensis ssp. rubens, Erodium cicutarium*, and *Schismus barbatus*. Frequently observed herbivores present at all sites included the desert cottontail (*Sylvilagus audubonii*) and the black-tailed jackrabbit (*Lepus californicus*).

Aridity gradient

We calculated an aridity index for each of the sites in both years using Gams index of continentality (Gilles et al. 1996). California has multiple chains of mountain that contribute to the rainshadow effects that occur in the deserts. We thus used Gams index because elevation is correlated with precipitation and because the index has been previously observed to correlate with plant productivity in mountainous regions (Gilles et al. 1996). We used a modified version of Gams index (Eq. 1) calculated for each of the sites where P_t represents the total precipitation in millimeters in the wettest quarter (i.e. December, January, and February) of the respective growing season and A represents the elevation at that site in meters. Tejon Ranch was above 900 meters in elevation and required the original calculation of Gams index (Eq. 2). The Gams index decreases with water availability, where values approaching zero represent mesic sites and values that approach infinity are more arid. The Gams index of continentality was found to be significantly correlated ($R^2 = 0.55$) to a 30-year average of aridity calculated using a down-scaled modeling approach of climate variables to a 30 arc-second resolution (Zomer et al. 2008).

$$\cot(G) = \left(P_t - \frac{900 - A}{100} \times \frac{P_t}{10}\right) \times \frac{1}{A} \qquad \text{Eq. 1}$$

$$\cot(G) = \frac{P_t}{A} \qquad \text{Eq. 2}$$

Experimental design

In spring of 2015, thirty *Ephedra californica* shrubs were identified, geotagged, and physically tagged with unique metal tags at each of the seven sites. The dimensions of the shrubs were measured using the diameter of the longest side (D1), the side immediately perpendicular to D1 (D2), and the height of the shrub to the tallest branch. Shrub area and volume was then calculated using the formulas for a circle (πr^2) and semi-sphere ($1/3\pi r^3$) respectively. A visual estimate of shrub decadence on a Likert scale of 0–10 was also included, with 0 indicating no foliage and a 10 indicating a full green canopy. An adjacent open microsite was paired to every shrub that was approximately two metres away and one metre in diameter.

In October of 2015 and 2016, prior to the first rains of the growing season, three parallel plots 30 cm in length and 15 cm in width were delineated in each shrub and open plot. The plots had a 5 cm buffer between them. Plots in the shrub were placed on the north side of the shrub under the canopy. In each plot, the soil was removed to a depth of 5 cm, sieved with a 250 microns mesh to remove any ambient seedbank, and replaced back into the plot. In each of the three plots a randomized order of three phytometer species were planted. The species were *Phacelia tanacetifolia, Plantago insularis*, and *Salvia columbariae.* These species were chosen for presence throughout the entirety of the gradient and preference for specific regions within it (Appendix G). For each of the species, 0.3 grams of seed were sown into separate plots within each microsite. To create a fertilized treatment, in half of all shrub-open pairs 2.0 grams of Miracle Grow® Slow Release Plant Food were spread throughout the plots.

Abiotic measurements

We measured air temperature and humidity by deploying Onset HOBO ProV2 loggers in three paired shrub-open microsites at each of the sites along the aridity gradient. The loggers were deployed at the end of October and collected before May to capture the entirety of the growing season. The main unit of the logger was buried underground with only the temperature and relative humidity sensor exposed 2 cm above the surface of the soil. We placed loggers in the shrub microsite between the phytometer plots and the base stem of the shrub. We measured soil moisture within shrub and open microsites at the beginning of plant emergence (January) and end of the growing season (April) using a SM150 soil moisture sensor from Delta-T Devices (http://www.delta-t.co.uk/). We also measured soil compaction using a spring-operated penetrometer with an adapter foot when necessary in sandy soils. The penetrometer measures compressive strength of soil between 0 and 4.5 kg per square cm and increases in 0.25 increments.

We collected 400 gram soil samples from five shrub-open pairs that were randomly selected at each site in April 2016. Samples were excavated from three independent locations within each microsite to a depth of 20 centimeters. Each sample was air dried at 40 °C and ground to pass through a 2 mm sieve. The processed soil was then analyzed for soil fertility including soil nitrogen using the Extractable Ammonium-Flow Injection Analyzer Method (Hofer 2003), extractable phosphorus using the Olsen Method (Olsen & Sommers 1982), and exchangeable potassium using the Sulfuric Acid Extraction Method (Brown et al. 1973).

Plant surveys

We surveyed phytometer abundance during both seasons in January after plant emergence and at the end of the growing season in April. We also positioned a 50 cm x 50 cm quadrat adjacent to the phytometer plots to measure the ambient plant community composition and density. Individual plants in each plot were identified to species and counted. The total biomass of all three phytometer species and 20-cm diameter ring at the centre of the ambient plant quadrat was collected. These samples were dried at 85°C for 3 d and weighed to the nearest 0.0001 g. All sites were found to have reached an upper asymptote when species-accumulation curves were plotted (Appendix H).

Statistical analyses

We tested the relevant mechanism of shrub facilitation on the aridity gradient by comparing each of the abiotic variables in shrub and open microsites. We calculated site-level means for both microsites, at each of the seven sites along the gradient, and in both years (N = 28) in R 3.4.0 (R Core Team 2017). These site-level means were calculated for available soil nitrogen, percent soil moisture at emergence, and soil compaction. We also calculated site-level means for temperature, relative humidity, and temperature variation using the microenvironmental loggers for the entirety of both growing season. We fitted models with each of these response variables and the predictors aridity and microsite. Response variables were fitted with a polynomial as needed. We also compared the mean difference in the abiotic variables between microsites only using permutation anovas with 5,000 iterations (package *lmPerm*, function *aovp*).

To test for species-specificity in response to facilitation and aridity, we fitted models for each of the sown phytometer species. Each of the phytometer species had a high frequency of zero observations within plots, particularly at sites where that species is uncommon. To effectively capture trends within the zero-laden data we used a two-part model, i.e. hurdle model, that conducted a logistic regression for the presence/absence of the phytometer within a plot; and an ordinary linear regression for the biomass of plots that had at least one observation (Fletcher et al. 2005; Xu et al. 2015). These two models were fitted for each phytometer species with microsite, nutrient addition, and aridity gradient as the predictors. Year was treated as a random effect because sites were represented twice on the aridity gradient for each season and therefore were not independent observations. The mixed logistic regression was fitted using *glmer* (family binomial) in package *lme4* and the linear mixed model was fitted using *lmer* in package *lmerTest*. Biomass was log transformed to meet assumptions of normality.

We tested the response of the ambient plant community to the aridity gradient and shrub facilitation using linear mixed models. Site-level means were calculated for the following response variables of the plant community: annual biomass, annual plant abundance, annual species richness, plant abundance of native species, and plant abundance of non-native species. To test if the relation between species responds to facilitation or aridity, we also calculated the phylogenetic community dissimilarity of each plant community. The phylogenetic tree was produced using the Phylomatic software (http://phylodiversity.net) and the R-package *picante*. The annual species in each community were assigned to a respective node on the tree and branch length was calculated using Grafen's method (Grafen 1989). We then calculated the mean phylogenetic distance with abundance weighting (package *picante*, function *mpd*) (Nipperess et al. 2010). Phylogenetic dissimilarity, hereafter phylogenetic diversity, is a useful measure of community diversity that includes the evolutionary relationship of species and therefore their relatedness (Nipperess et al. 2010). We fitted models for each of these annual plant response variables and for the predictors aridity and microsite. The response variables were fitted with the inverse hyperbolic sin transformation (IHS) when necessary to meet assumptions of normality. The IHS transformation was used because of its tolerance of data with zeros and because of its similarity to a log transformation (Zhang et al. 2000). We also fitted a polynomial when appropriate to increase the coefficient of determination and reduce the model variation.

We compared shifts in the community composition of annual plants along the regional gradient of aridity and between microsites using a cluster analysis and correspondence analysis (CA). We used a CA instead of other ordination methods because the compositional data had a unimodal-based distribution based detrended correspondence analysis that determined the gradient axis length to be greater than 2: axis 1 = 3.45, axis 2 = 1.58, axis 3 = 1.03, axis 4 = 1.51 SD (Ter Braak & Prentice 1988). We calculated the total abundance of each species at the site and microsite level. A Hellinger transformation was applied to the data (package *vegan*, function *decostand*) to lower weight of rare species (Legendre & Gallagher 2001). To prepare the data for ordination analyses, we removed species with only one instance of occurrence and replaced outliers with mean species values (Zuur et al. 2007). Outliers were identified using dot plots when the maximum value was greater than four times the next highest value and there was no trend of significantly increasing values. We checked for co-linearity among species by calculating the variance inflation factor (package *usdm*, function *vifcor*) and excluding any highly correlated species when $\theta = 10$ (Naimi et al. 2014). A detailed description of the methodology and the species that were excluded can be found in the open access repository (https://afilazzola.github.io/ERG_2016-2017/). We conducted a correspondence analysis (package *vegan*, function *cca*) on the Hellinger transformed data. We also computed the dissimilarities indexes for the transformed community data (package *vegan*, function *vegdist*) using Bray-Curtis method (Legendre & Legendre 1998) and conducted a cluster analysis (package *vegan*, function *hclust*) using the squared version of Ward's hierarchical clustering method (Murtagh & Legendre 2014). We identified distinct groups within the cluster analysis and highlighted the clusters on the CA (Appendix I).

Results

Abiotic characteristics between microsites

The microclimatic environment and soil characteristics varied along the aridity gradient and microsites. Across all sites, shrub microsites had on average significantly greater nutrient content for nitrogen, potassium, and phosphorus, but lower air temperatures and soil compaction (Table 3.2). There was no significant difference between microsites for soil moisture and relative humidity (Table 3.2). In both shrub and open microsites, soil nitrogen increased with aridity, i.e. sites that were more arid had higher nitrogen ($F_2 = 25.8$, $p < 0.001$; Fig. 3.1A). However, there was a significant microsite by aridity interaction and slope was significantly lower in the open than in the shrubs ($F_2 = 13.5$; $p = 0.003$; Fig. 3.1A). Soil moisture was negatively related to aridity ($F_2 = 45.1$, $p < 0.001$; Fig. 3.1B) and there was no significant aridity by microsite interactions for soil moisture ($F_2 = 0.04$; $p = 0.96$). Temperature variation was positively related with aridity ($F_2 = 10.0$, $p < 0.001$; Fig. 3.1C) and was significantly lower in shrub microsites ($F_1 = 21.4$, $p = 0.001$; Fig. 1C), but there was no significant microsite by aridity interaction ($F_2 = 0.14$, $p = 0.87$). Log-transformed soil compaction was positively related to aridity ($F_1 = 13.2$, $p = 0.0046$; Fig. 3.1D) and there was a significant microsite by aridity interaction ($F_2 = 6.44$, $p = 0.029$; Fig. 3.1D).

Phytometer responses to aridity and microsites

Shrubs facilitated *P. tanacetifolia* and had no significant affect on *S. columbariae* or *P. insularis* in terms of biomass and probability of occurrence (Table 3.3; Fig. 3.2A). However, the biomass of *P. insularis* was more than two standard deviations lower in shrub than in the open microsites

(Fig. 3.2A) and there was also a significant microsite by aridity interaction for *S. columbariae* (Table 3.3; Fig. 3.2B). There were no other significant interactions among factors for phytometer occurrence (Table 3.3). The probability of occurrence for the phytometers varied between species with aridity: *P. insularis* increased with aridity and both *P. tanacetifolia* and *S. columbariae* had the highest occurrence at intermediate sites of aridity (Table 3.3; Fig. 3.2B). The addition of nutrients positively increased the biomass of all three phytometer species (Table 3.3; Fig. 3.2C) and had no effect on the occurrence (Table 3.3). The biomass of *S. columbariae* and *P. insularis* peaked at intermediate levels of aridity (Table 3.3; Fig. 3.2D). There were no significant interactions among factors for phytometer biomass except microsite and aridity for *P. tanacetifolia* (Table 3.3) The biomass of *P. tanacetifolia* was greatest at the mesic sites in shrub only and peaked at intermediate levels of aridity in the open microsites (Table 3.3; Fig. 3.2D).

Ambient plant community responses to aridity and microsites

Plant composition varied across the seven sites. In total, 40 different annual species were observed in both years. Species richness was greatest in open microsites ($F_1 = 8.76$, $p = 0.0031$; Fig. 3A) and at sites with intermediate levels of aridity ($F_2 = 69.9$, $p < 0.001$; Fig. 3.4A). Annual biomass decreased with greater aridity ($F_3 = 40.4$, $p < 0.001$; Fig. 3.3A) and was significantly higher in shrub microsites ($F_1 = 15.1$, $p = 0.001$, Fig. 3.3A). There was a significant microsite by aridity interaction ($F_2 = 74.2$, $p = 0.001$) and the shrub effect on biomass decreased at the most arid sites (Fig. 3.3B). The phylogenetic diversity of the plant communities increased was lowest in shrub microsites ($F_1 = 9.26$, $p = 0.0059$; Fig. 3.3C) and there was a significant microsite by aridity interaction ($F_1 = 7.52$, $p = 0.012$). The negative effect of shrubs on phylogenetic diversity decreased with aridity (Fig. 3.3C). Native plant abundance declined with aridity ($F_1 = 67.4$, p <

0.001) and was lowest in shrub microsites ($F_1 = 23.1$, $p < 0.001$). Non-native plant abundance also declined with aridity ($F_1 = 53.9$, $p < 0.001$), but was significantly higher in shrub microsites ($F_1 = 13.5$, $p < 0.001$). There was a significant microsite by aridity interaction for native plant abundance ($F_1 = 35.71$, $p < 0.001$; Fig 3.3D), but not for non-native plant abundance ($F_1 = 1.44$, $p = 0.23$; Fig 3.3D).

Our CA explained 62 percent of the variation in plant community composition (Fig. 3.4). The CA suggests that the observed plant communities represent a gradient of native species that expresses turn-over in composition towards the more arid sites (Fig. 3.4). We identified four unique groups in the cluster analysis for each of the 14 sites (two microsites and seven regional sites). There were greater similarities between regional sites than microsites in the more mesic deserts, such as Panoche Hills, Cuyama, and Tejon Ranch (Fig. 3.4). Conversely, at the other, drier desert, there were greater similarities between microsites than between regional sites (Fig. 3.4). In the more mesic sites the dominant non-native species (*Bromus madritensis* and *Schismus barbatus*) are responsible for the dissimilarities among regional and microsites (Fig. 3.4). The native species were diverse throughout the gradient and each site had relatively unique community assemblages. The plant species along CA1 shift from grasses and non-natives to native forbs (Fig. 3.4). The species along CA2 represent a gradient of different native species that are uniquely associated to the respective sites (Fig 3.4).

Discussion

Shrub facilitation can support desert productivity and biodiversity, but this effect is dependent on local precipitation patterns. Along a regional gradient of precipitation, we explored how shrub-annual interactions shift in facilitation mechanisms, species composition, and response variable. Shrub facilitation increased annual biomass at all sites except the driest along the gradient and this effect was driven by some, but not all, species within the plant community. Each of the three chosen phytometers responded uniquely to shrub interactions along the aridity gradient and therefore the predictability of shrub facilitation depends largely on the plant species. The annual community along the regional gradient shifted in composition at the more mesic sites to have higher plant abundance and lower native diversity. Shrubs further decreased the diversity of plant communities at the more mesic sites and were not significant drivers of other community-level estimates. Thus, shrubs likely indirectly increased competition within the annual community favouring the competitive non-native species. The relevant mechanism of shrub facilitation shifted along the gradient of aridity increasing soil nitrogen at the most arid sites, reducing soil compaction in the more mesic sites, and reducing temperature variation at all sites. This suggests that these shrubs do not increase soil moisture and that facilitation effects decrease with extreme aridity. The positive interactions of some benefactor species in deserts are thus dependent on precipitation patterns and context dependency, such as species identity and mechanism of facilitation, must be considered in modeling net outcomes of plant interactions in resource limited ecosystems.

Shrub effects on environmental variables

The dominant mechanisms of interaction shift along gradients of aridity. The shrubs ameliorated temperature variability at all sites, increased soil nitrogen in the driest sites, and reduced soil compaction in the more mesic sites. These findings support previous research that relevancy of different mechanisms of facilitation changes along environmental gradients (Bertness & Callaway 1994; Michalet 2007; Smit et al. 2009; Filazzola et al. 2018). Interestingly, shrubs were not found to increase soil moisture at any of the sites and this species is likely unable to mitigate aridity or reduce species loss from drought effects. The shrub canopy is thus a trade-off in environmental variables that are dependent on spatial gradients. Considering the mechanism of interaction between species as a result of the difference in environmental variables can help explain the discrepancy in correlating the response of plant interactions along spatial and temporal gradients of aridity, i.e. space-for-time (Metz & Tielbörger 2016). For instance, shrubs can facilitate the annuals through ameliorating temperature variation and the strength of this interaction increases proportionately with seasonal climate variation (Filazzola et al. 2018). However, shrubs effects on soil composition occur over longer timeframes because the effects are a consequence of soil weathering processing and therefore the strength of these interactions are dependent on long-term trends of aridity (Noumi et al. 2016; Abdallah et al. 2016). Relatively fast and permanent shifts in precipitation patterns due to climate change can thus cause a lag in the effects of shrubs on environmental variables that can have implications for the plant communities. Deserts may be more sensitive to shifts in precipitation patterns than previously thought because positive interactions cannot buffer against short-term shifts in aridity.

Nutrient availability in soils affects community biodiversity and can be mediated by shrubs. We observed increasing soil nitrogen with aridity that supports previous research that described higher nitrogen deposition in the Mojave Desert (Padgett et al. 1999), but this effect was only observed within shrub canopies. Shrubs can function as resource islands for nutrients in arid ecosystems (Whitford et al. 1997) and this is likely not an effect of nutrient deposition, but rather the long-term effects of shrubs on nutrient cycling that can increase with aridity (Michalet 2007). Each of the phytometer species benefited from the addition of fertilizer and thus nutrients are a limiting factor in these systems. However, *P. insularis* and *S. columbariae* did not have higher biomass in shrub microsites where nutrient content was greater, and sites where *P. tanacetifolia* was greatest in shrub canopies, there was no significant difference in nitrogen between microsites. This suggests that the benefits of increased nutrient availability are reduced by other limitations within the shrub canopy (e.g. net-negative interaction) and that nutrients other than nitrogen are the limiting factors in this system. For instance, available soil phosphorus has been described as a limiting nutrient in deserts that is strongly correlated with plant productivity and that decreases with aridity (He et al. 2015). Alternatively, the vertical distribution of nutrients within the soil could explain the difference observed between the nutrient addition that was on soil surface and deeper soil sampling. Shrub cover in deserts can increase nutrient uplift and thus nutrient content decreases with soil depth (Jobbagy & Jackson 2000). Aridity can further decrease the capacity for shrubs to uptake nutrients and alter the stratification of nutrient content along the gradient. Native desert annuals are also unable to exploit nutrient availability beyond the first few centimeters of the soil surface (DeFalco et al. 2003) and therefore can benefit from fertilizer applied to the surface, but not ambient nutrients deeper within the soil. Future research of shrub facilitation on annual plants through mediating nutrient availability must consider both the horizontal and vertical heterogeneity of the soil.

Species specificity

The sign of shrub-annual interactions is determined by the species traits. Advances to the stress Gradient Hypothesis (Bertness & Callaway 1994) propose that whether the responding species has competitive or stress tolerant traits can determine the sign of plant-plant interactions (Liancourt et al. 2005; Michalet et al. 2006; Saccone et al. 2009; Liancourt et al. 2017). We found support for these predictions within this study because the sign of interaction matched the species traits. The three species are found throughout the surveyed regions, but *Phacelia tanacetifolia* was more common in the mesic areas, *Plantago insularis* was more common in the arid areas, and *Salvia columbariae* was common throughout (Appendix B). Consequently, we can predict that *P. insularis* has stress-tolerant traits because of its preference for arid areas and this explains the association with open microsites rather than shrubs. The *Plantago* genus has been explored previously in shrub-annual interactions in the Atiquipa Desert and was found to have a neutral to negative association with woody perennials (Sotomayor et al. 2014). *P. tanacetifolia* was observed both in more mesic sites and in shrub canopies. It has been previously identified as a competitive species and one of the few remaining natives in California that can successfully compete with non-native species such as *B. madritensis* and *S. barbatus* (Brooks 2000). *P. tanacetifolia* can also have the largest leaf area and height relative to the other species when grown in optimal conditions further suggesting its competitive ability (Gaudet & Keddy 1988). *S. columbariae* is a widely-distributed species that expresses the phenotypic plasticity to exist both in shrub and open microsites. The predictability of shrubs to facilitate annual plant depends largely on responding species traits and whether it is capable of exploiting the differences in microclimatic conditions within the canopy. Researchers exploring plant interactions in deserts, especially for the purposes of using shrubs as tools for restoration, must therefore consider species specificity.

Native biodiversity decreased at the extremes of the aridity gradient. In the more mesic sites, shrubs facilitated non-native grass species that likely competed with and excluded native species (Eliason & Allen 1997). The first axis of the CA could be a gradient of stress tolerance from competitive, invasive species at the mesic sites at lower values along the axis and stress-tolerant natives at higher values. Additionally, the decrease in phylogenetic diversity at the mesic sites is attributable to the increase in the number of grass species, such as *Poa secunda* and the invasive grass species *B. madritensis* and *S. barbatus*. The annual species that therefore benefit most from shrub facilitation are likely exotics or introduced species that are not adapted to the respective environment and can take advantage of the ameliorated conditions within the shrub canopy. Facilitation of non-native grasses has been previously reported in the Mojave Desert and these species often have negative effects on shrubs by reducing water uptake and fitness (Holzapfel & Mahall 1999; Rodríguez-Buriticá & Miriti 2009). However, we observed the strongest effect of shrub facilitation on non-natives in the most mesic sites and that the invasibility of these species are limited by precipitation (Bradley et al. 2016). Projections of increased aridity for Southwestern North America suggest *B. madritensis* to shift from the Mojave Desert and replace *Bromus tectorum* in the Great Basin Desert (Bradley et al. 2016). Consequently, native shrubs in the Great Basin, such as sagebrush (*Artemisia spp.*), could facilitate the regime change in the relative density of *Bromus* species. Understanding the role of shrubs in mediating community composition in deserts is critical given predictions of a changing climate and emphasizes the need to include interactions, not just species, in conservation management.

Implications

Positive interactions decline at environmental extremes and will likely decrease with shifts in precipitation patterns. These findings challenge research on the Stress Gradient Hypothesis that suggests facilitation can buffer climate shifts. Our study highlights the pitfalls inherent in making generalizations about positive interactions along environmental gradients without considering context dependencies including the mechanism of facilitation, the species identity of benefactor/beneficiary, and the measured response variable. Specifically, the role positive interactions play in supporting the dominance of non-native species, and potentially competitive exclusion of natives, is a relatively underexplored consideration. These findings also demonstrate the importance of understanding the response of species interactions to climate change and further highlight the sensitivity of desert ecosystems to shifts in aridity. Aridity gradients at relatively large scales in a desert region are thus an important tool to explore net outcomes in plant communities. Projected changes in climate will likely have complex and non-linear consequences on desert plant communities that need to be considered in conservation planning.

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Tables

Table 3.1: Locations for each of the seven sites with their respective climate values for 2016 (top) and 2017 (bottom). Precipitation is the total volume of rain that fell during the growing season of the respective year.

ID	Site	Desert	Latitude	Longitude	Elevation (m)	Aridity	Mean T (C°)	Precipitation. (mm)
1	Panoche Hills	San Joaquin	36.7001	- 120.8010	656	62.7	11.4 ± 0.29	223
						49.5	10.9 ± 0.31	235
2	Cuyama Valley	San Joaquin	34.8552	- 119.4890	806	71.0	9.4 ± 0.30	119
						51.4	9.9 ± 0.29	211
3	Tejon Ranch	Mojave	34.8759	- 118.6020	1118	80.7	8.7 ± 0.36	72.1
						65.8	9.9 ± 0.32	130
4	Barstow / Ft. Irwin	Mojave	35.0940	- 166.8350	496	89.6	11.4 ± 0.40	9.3
						63.6	12.3 ± 0.38	104
5	Heart of the Mojave	Mojave	34.6982	- 115.6840	784	73.4	15.4 ± 0.41	17.0
						84.7	15.6 ± 0.40	83.4
6	Sheephole Valley Wilderness	Colorado	34.2057	- 115.7201	545	88.3	11.5 ± 0.40	26.4
						69.4	12.7 ± 0.39	68.0
7	Tecopa	Mojave	35.8515	- 116.1870	699	80.6	12.5 ± 0.43	53.8
						68.3	13.1 ± 0.46	87.3

Table 3.2: Results from linear permutation tests comparing differences in abiotic characteristics of shrub and open microsites. Significance was denoted at α = 0.05 and shown in bold. Permutations were set to a maximum of 5000 iterations.

	Mean shrub	**Mean open**	**p-value**
Nitrogen (ppm)	9.27	1.59	**0.0024**
Phosphorus (ppm)	10.1	6.37	**0.045**
Potassium (ppm)	231.6	141.4	**0.0067**
Soil compaction (kg/cm^2)	1.41	1.65	**0.0014**
Soil moisture (%)	10.7	11.2	0.28
Air temperature (°C)	9.44	11.1	**0.0014**
Relative humidity (%)	58.7	55.1	0.26

Table 3.3: Results from log-normal hurdle model testing for differences in the response variables of each phytometer species in response to microsite (shrub and open), nutrient addition (added and ambient), and aridity gradient. Presence of the phytometers was modeled with a generalized linear mixed model fit to a binomial distribution and log-transformed biomass of the phytometers was modeled with a linear mixed model. Year was treated as a random effect in both models. Significance was denoted at $\alpha = 0.05$ and shown in bold.

	P. tanacetifolia		*P. insularis*		*S. columbariae*	
Presence	χ^2 value	p – value	χ^2 value	p – value	χ^2 value	p – value
Microsite	**27.9**	**<0.001**	1.71	0.19	0.02	0.97
Nutrient	0.006	0.93	0.31	0.58	1.15	0.28
Aridity	**33.9**	< **0.001**	**17.9**	< **0.001**	**89.3**	< **0.001**
Microsite * Nutrient	1.78	0.18	1.94	0.16	3.44	0.063
Microsite * Aridity	4.71	0.095	5.41	0.067	**6.56**	**0.038**
Nutrient * Aridity	0.41	0.82	3.23	0.19	1.96	0.37
Microsite * Nutrient * Aridity	0.060	0.97	0.52	0.77	0.47	0.79
Biomass	F - value	p – value	F - value	p – value	F - value	p – value
Microsite	**12.2**	< **0.001**	0.51	0.47	0.20	0.65
Nutrient	3.15	0.077	**8.09**	**0.005**	**11.1**	< **0.001**
Aridity	**43.4**	< **0.001**	**16.3**	< **0.001**	**18.1**	< **0.001**
Microsite * Nutrient	0.043	0.83	0.10	0.53	0.23	0.63
Microsite * Aridity	**4.33**	**0.014**	0.39	0.68	0.38	0.68
Nutrient * Aridity	0.79	0.46	1.07	0.34	0.86	0.42
Microsite * Nutrient * Aridity	0.39	0.68	0.30	0.74	0.99	0.37

Figures

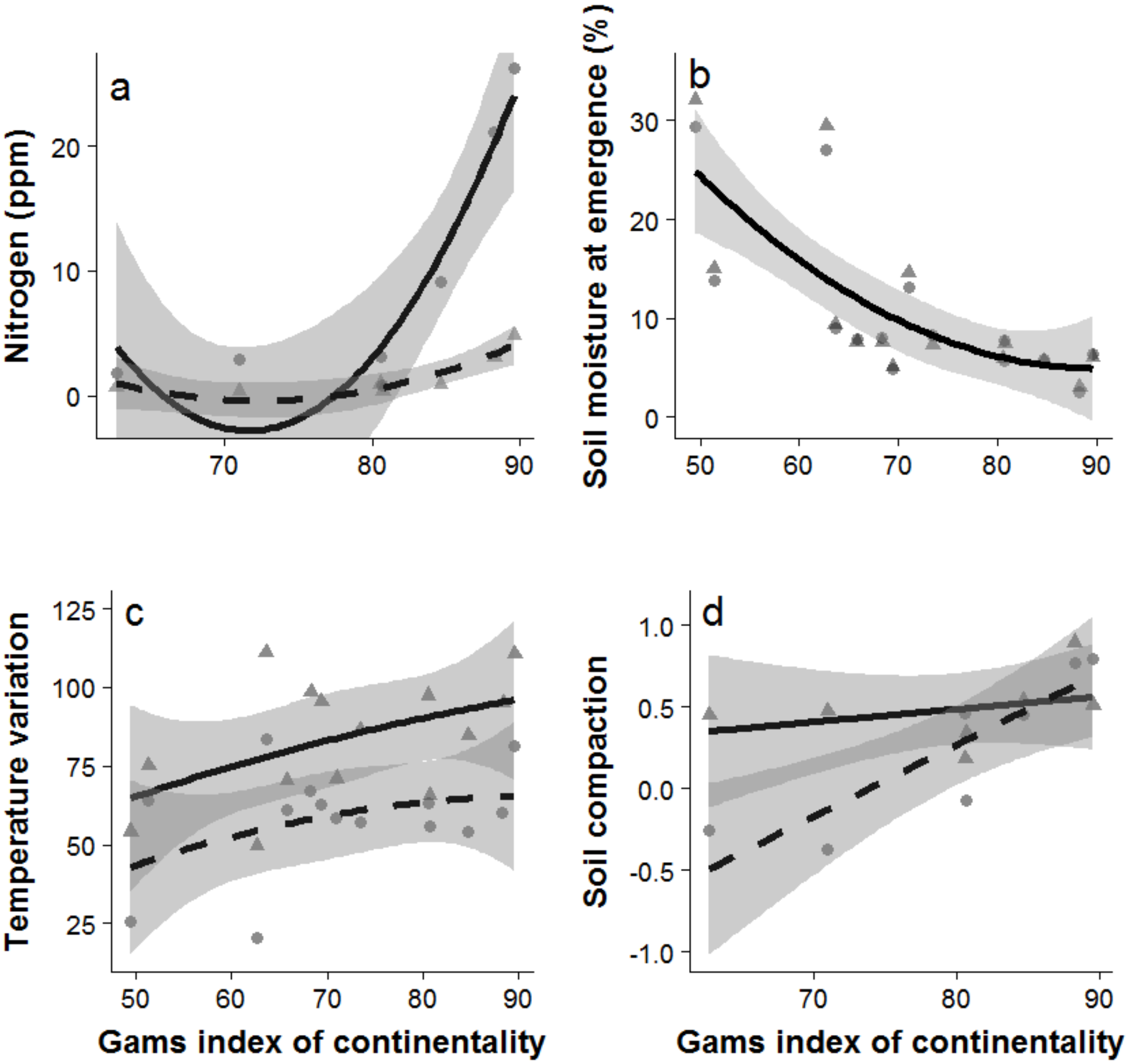

Figure 3.1: The relationship of abiotic characteristics in shrub (O) and open (Δ) microsites along a gradient of aridity. Solid lines represent mean model fit and shaded areas are 95% confidence intervals. Models with significant microsite by aridity interactions were plotted separately for shrub (solid line) and open (dashed line) microsites. The abiotic characteristics that were measured included a) soil nitrogen ($R^2 = 0.88$), b) soil moisture at emergence ($R^2 = 0.91$), c) temperature variation ($R^2 = 0.79$), and d) soil compaction ($R^2 = 0.63$).

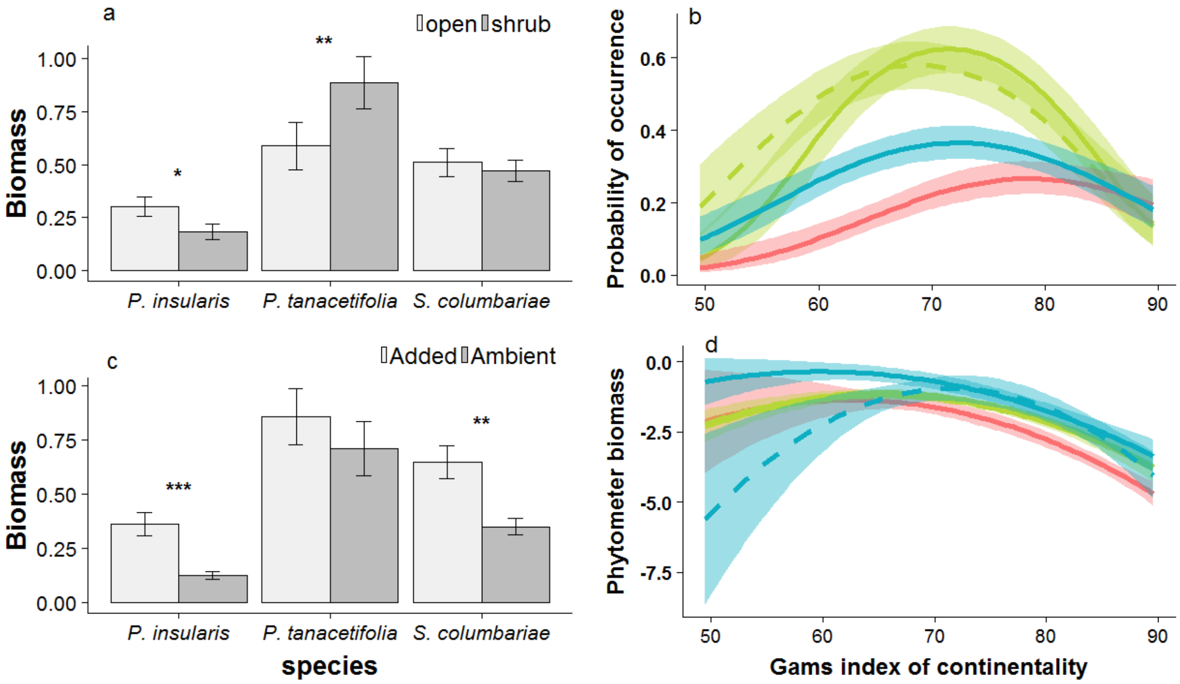

Figure 3.2: The effect of shrubs, nutrient addition, and the aridity gradient on the three phytometer species: *P. insularis* (red), *P. tanacetifolia* (blue), and *S. columbariae* (green). The mean biomass for each of the three phytometer species in shrub and open microsites (a) and with nutrient addition (c). Error bars represent 95% confidence intervals. Solid lines represent mean model fit and shaded areas are 95% confidence intervals. Models with significant microsite by aridity interactions were plotted separately for shrub (solid line) and open (dashed line) microsites.

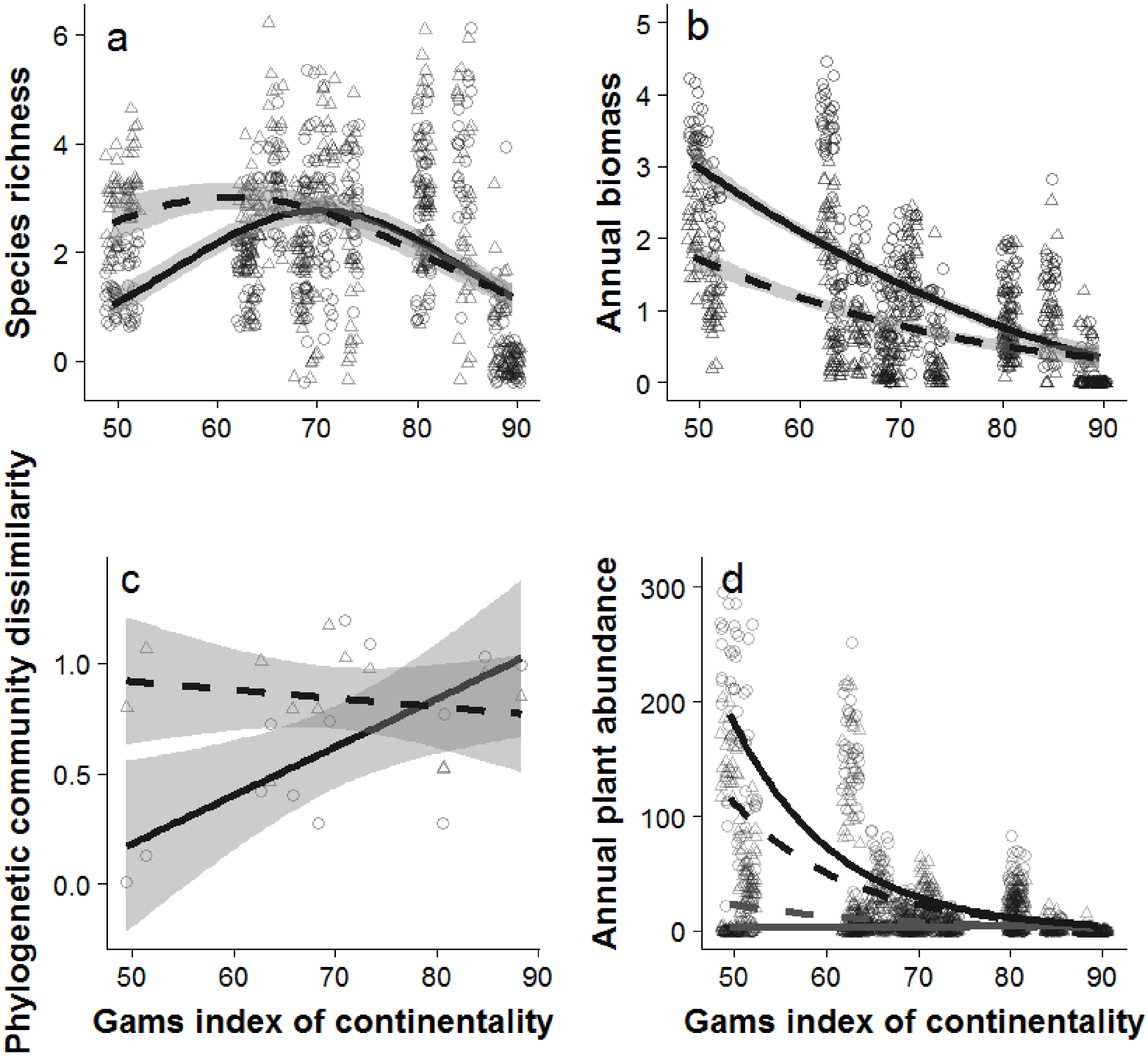

Figure 3.3: The effects of shrubs and the aridity gradient on community characteristics (shrub - O and open - Δ). Solid lines represent mean model fit and shaded areas are 95% confidence intervals. Models with significant microsite by aridity interactions were plotted separately for shrub (solid line) and open (dashed line) microsites. The community characteristics that were measured included a) annual species richness (pseudo-R^2 = 0.28), b) annual plant biomass - IHS transformed (R^2 = 0.23), c) mean phylogenetic community dissimilarity (R^2 = 0.38), and d) annual plant abundance for natives (grey; pseudo-R^2 = 0.73) and non-natives in black (black; pseudo-R^2 = 0.77).

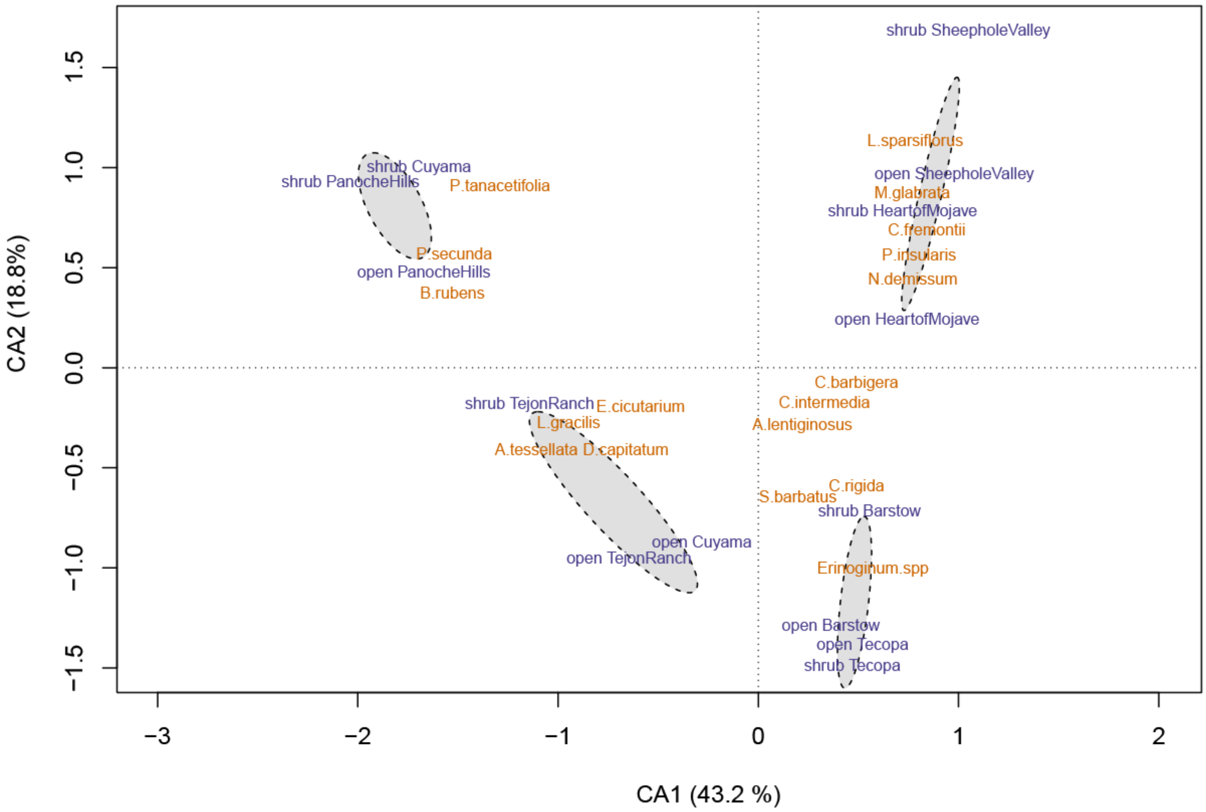

Figure 3.4: Correspondence analysis (CA) of plant community composition in each microsites and the seven sites along the gradient of aridity in Southern California. Only the first two axes are shown and explain 62% of the variation in the plant communities. The four groups identified from the cluster analysis are displayed as ellipses.

Chapter 4

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

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Abstract

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

Introduction

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

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

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

Methods

Species database

Plant species lists for the Mojave Desert were extracted from the Global Biodiversity Information Facility database (GBIF; http://www.gbif.org/). An extensive list of native Mojave Desert species was obtained from the literature for 61 shrubs and annual plants. This list was generated from four papers and a review on plant interactions in the Mojave Desert (Cody 1993, Brittingham and Walker 2000, Brooks 2003, Flores and Jurado 2003, Miriti 2006). The dominant Mojave shrub species *Ambrosia dumosa*, *Artemisia tridentata*, *Ephedra nevadensis*, and *Coleogyne ramosissima* were selected from the list of Mojave Desert species because they have been previously examined for facilitative effects (Franco and Nobel 1988, Cody 1993, Brittingham and Walker 2000, Brooks 2003, Miriti 2006). These shrub species were frequent in the Mojave Desert (>300 occurrences) and do not have any reported allelopathic effects such as with the common Mojave shrub *Larrea tridentata* (Mahall and Callaway 1992). In total, 4269 occurrences of these four shrub species were collected from the GBIF (Filazzola et al. 2016: https://dx.doi.org/10.6084/m9.figshare.3586065.v1). From the initial plant list and using a random number table, we randomly selected ten annual species that were previously reported as beneficiary species by the identified benefactor shrubs (Flores and Jurado 2003), and we further selected another ten annual plants that have not been reported previously as beneficiaries, hereafter "unreported" (Table 4.1). All twenty annual plants species are commonly observed in the Mojave Desert with at least 100 occurrences listed within GBIF (Filazzola et al. 2016: https://dx.doi.org/10.6084/m9.figshare.3586065.v1)**.** These species occupy similar ecological requirements within desert shrublands at elevations less than 1800 meters. Only species records with GPS coordinates were extracted for further analysis. The shrub, beneficiary, and unreported datasets were reviewed to check for duplicates and inconsistencies with species name. Sub-species were classed as the same species.

The survey area was defined as the Mojave Desert within the political boundary of Southern California. The extent was restricted to include the western most portion of the Mojave Desert, including Antelope Valley (Lat: 34.79°, Lon: -118.7°). The southern, eastern, and northern boundaries were restricted based on the political boundaries with Mexico, Arizona, and Nevada respectively (Lat: 32.7° to 37.0°; Lon: -118.5° to -114.5°). We chose to restrict our study on the Mojave to within California because there are large collaborative efforts within the state that contribute to plant occurrences such as, Calflora (http://www.calflora.org/) and the Californian Native Plant Society (http://www.cnps.org/), that are included in the GBIF database. This defined study area, hereafter referred to as Southern California, includes a total land area of 173,894 km^2.

Biotic variables

Online herbaria data suffer from sampling bias, and consequently, we used geographic filtering for the initial raw occurrences (Varela et al. 2014). We subsampled using a grid across an x-y layer and discarded multiple instances within a radius of 3 arc minutes (~ 5 km). This geographical filtering of occurrences was conducted for all plant species modeled. We calculated a two-dimensional kernel density estimate using the coordinates of the geographically filtered occurrences for the shrub and annual species evaluated on a square grid (function *kde2d,* package MASS). The density rasters for each of the three species groups (shrub, beneficiary, and unreported) were resampled (function *resample,* package raster) using the nearest neighbor method to the have the same resolution as WorldClim data (30 arc-second or ~1 km^2) and cropped to match the extent of Southern California. To test if shrub density predicted annual plant density, we fitted a model with each beneficiary and unreported plant density as a response variable and shrub density as the predictor. A random set of 1,000 geographic points (*randomPoints* function; *Dismo)* was extracted for each of the three rasters (shrub, beneficiary, and unreported). We then used f-tests to determine whether the effect of shrub density on each annual plant group was significantly different from zero. We also tested for underlying differences between the beneficiary and unreported groups to ensure the chosen species had similar niche overlaps (Appendix J). Using a random set of geographic points we compared the densities of beneficiary and unreported plant groups with a Pearson's Correlation. All analyses and data extraction were conducted in R version 3.2.3 (R Core Team 2016).

Environmental variables

Eight bioclimatic variables (Appendix J; Hijmans et al. 2005) and also elevation with 30-second (~ 1 km) spatial resolution were downloaded from the WorldClim dataset (www.worldclim.org). These eight variables were selected because they are strongly associated with winter-annual germination and productivity (Beatley 1974). To check for collinearity among these bioclimatic variables we extracted climate data from 1,000 randomly chosen points in Southern California and performed a correlation matrix. We removed correlated bioclimatic variables at $r > 0.6$ (Dormann et al. 2013). Precipitation seasonality was maintained despite having a strong correlation ($r > 0.6$) with other bioclimatic variables because deserts systems are extremely sensitive to precipitation frequency (Reynolds et al. 2004). Therefore, the chosen bioclimatic variables were elevation, temperature during the wettest quarter, precipitation during the wettest quarter, and precipitation seasonality.

MaxEnt models

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

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

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

$$HS_{diff} = \frac{\sum_n m_{shrub.env} - m_{env}}{n} \qquad \text{eq.1}$$

Phylogenetic analysis

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

Results

Shrub occurrence was positively related to with both the beneficiary species occurrence (mean effect ± SE = 0.77 ± 0.015; $p < 0.001$; Figure 4.1) and the unreported plant species occurrence (mean effect ± SE = 0.76 ± 0.031; $p < 0.001$; Figure 4.1). However, shrub occurrence more accurately predicted annual occurrence for the beneficiary species than for the unreported annuals ($R^2 = 0.72$; $R^2 = 0.38$, respectively).

Overall, all species were accurately predicted by the MaxEnt models (AUC > 0.70; Table 4.1). The AUC values of the beneficiary species were significantly increased by the inclusion of shrubs into the model ($t = -2.32$, $p = 0.033$; Figure 4.2), but AUC values were not significantly different for unreported species between models ($t = -0.73$, $p = 0.48$; Figure 4.2). Species distribution models for all beneficiary and unreported plant species were mapped (Appendix L) with two example species represented in Figure 4.3. Shrub MaxEnt models significantly increased the habitat suitability estimates (HS_{diff}) for the beneficiary species relative to unreported annuals ($W = 10$, $p = 0.0028$; Figure 4.3).

Plant species that are closely related were more likely to be classified together in either the beneficiary or unreported groups (Figure 4.4). For instance, plant species in the families Asteraceae and Brassicaceae were either classified as beneficiaries or had high HS_{diff} values while the Polemoniaceae family were classified as unreported and had low HS_{diff} values (Figure

4.4). There were two species in the unreported plant group, *Eremalche exilis* (Malvaceae) and *Layia glandulosa* (Asteraceae), that displayed model improvement with the inclusion of shrubs (Figure 4.2). These two species were closely related to other species classified as beneficiaries, such as *Sphaeralcea ambigua* (Malvaceae) and *Chaenactis fremontii* (Asteraceae) respectively (Figure 4.4). The Boraginaceae family was an exception because it had two closely related plant species, *Phacelia distans* and *Crypantha intermedia*, that had largely different trends in group classification and HS_{diff} values (Figure 4.4).

Discussion

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

Positive interactions on niche and range

There are two models for the effect of positive interactions on the fundamental niche of beneficiary species. The niche-construction model predicts that positive interactions increase the geographic area that corresponds to the fundamental niche of beneficiary plant species (Rodriguez-cabal and Barrios-garcia 2012, McIntire and Fajardo 2014). In this instance, benefactor plants increase the environmental heterogeneity of the landscape (Pescador et al. 2014) thereby providing a greater range of environmental conditions relative to open sites that meet species niche requirements (Rodriguez-cabal and Barrios-garcia 2012). The niche-expansion model is the second that proposes facilitation increases the realized niche to be greater than the fundamental niche (Bruno et al. 2003, Stachowicz 2012, He and Bertness 2014, Afkhami et al. 2014). There has been debate as to which model best describes the relationship between positive interactions and niche (e.g. Rodriguez-cabal and Barrios-garcia 2012, Stachowicz 2012), that has been revised to depend on context (Bulleri et al. 2016). However, we believe both models are possible depending on mechanism of interaction. Positive interactions can be divided into niche constructors, those that modify the environment to create suitable habitat, and niche expanders, those that modify the beneficiary species to tolerate the habitat. The shrubs within this study would be classified as niche constructors because they increase environmental heterogeneity to match niche requirements of the beneficiary species. Conversely, an example of a niche expander would be mutualistic endophytic fungi that increases the drought tolerance and geographic range of grass species, such as *Bromus laevipes* (Afkhami et al. 2014). Thus, there are at least two possible models that both describe how positive interactions modify the fundamental niche of a beneficiary species, and each has associated ecological theories and different implications.

Positive interactions and climate change

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

Species specificity

Positive interactions are species specific for both the benefactor and beneficiary species (Callaway 1998, Soliveres et al. 2012). Within this study, we found the inclusion of shrubs in SDMs improved model predictability for some, but not all tested species. For instance, models of beneficiary group and not the unreported group were improved with the inclusion of benefactor shrubs as a predictor. However, there were some species within the unreported group that displayed co-occurrence patterns with benefactor shrubs. We identified members of the family Asteraceae and Malvaceae as being improved with the inclusion of shrubs in both the beneficiary and unreported groups. Other studies have also identified Asteraceae species as being facilitated in deserts (Flores and Jurado 2003) and also in alpine ecosystems (Cavieres et al. 2006). This suggests that annual species within the Asteraceae family have traits that require the shrub microclimate. For instance, beneficiary species have been proposed to have more competitive life-history traits that benefit from the increased resource availability and the reduced abiotic stress found under benefactor shrubs (Maestre et al. 2009). However, empirical research has shown the relationship between desert shrubs and Asteraceae species to be because of stress-tolerant traits, such as lower light and soil moisture found under shrub canopies (Butterfield and Briggs 2011). SDMs that include positive interactions, such as the ones conducted here, can help identify species relatively more dependent on facilitation for persistence within an ecosystem (e.g. *Eremalche exilis* and *Layia glandulosa).* Positive interactions are species specific and these relationships can be identifiable at the macro-scale using co-occurrences, which can assist ecologist attempting to disentangle how these interactions will change through time.

Implications

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

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Tables

Table 4.1: Annual species chosen from the literature on plant interactions in the Mojave Desert.

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

Table 4.2: Summary statistics from MaxEnt models conducted on each of the annual species with predictors of environment only (m_{env}) and the environment with shrub ($m_{shrub.env}$). The number of occurrences and absences that were included in each model are represented as n.presence and n.absence respectively.

	m_{env}		$m_{shrub.env}$				
Species	**cor**	**AUC**	**cor**	**AUC**	**n.presence**	**n.absence**	**HS_{diff}**
Beneficiary							
Camissonia claviformis	0.15	0.71	0.18	0.75	69	1852	2.86
Caulanthus cooperi	0.16	0.77	0.2	0.81	60	1850	2.85
Chaenactis fremontii	0.3	0.79	0.37	0.84	150	1856	2.91
Delphinium parishii	0.23	0.78	0.3	0.83	119	1858	2.57
Descurainia pinnata	0.22	0.74	0.26	0.77	148	1855	2.67
Lepidium lasiocarpum	0.2	0.72	0.24	0.74	160	1855	2.61
Malacothrix glabrata	0.23	0.72	0.29	0.76	178	1855	2.94
Phacelia distans	0.3	0.75	0.32	0.77	260	1853	2.56
Rafinesquia neomexicana	0.27	0.79	0.32	0.82	126	1854	2.15
Sphaeralcea ambigua	0.28	0.75	0.31	0.77	220	1853	2.57
Unreported							
Acmispon brachycarpus	0.17	0.81	0.17	0.81	41	1865	1.23
Cryptantha intermedia	0.49	0.88	0.5	0.89	255	1862	1.07
Eremalche exilis	0.15	0.76	0.19	0.81	47	1867	2.79

Gilia minor	0.2	0.87	0.2	0.87	23	1862	1.3
Layia glandulosa	0.27	0.81	0.3	0.84	115	1863	2.14
Linanthus dichotomus	0.17	0.82	0.17	0.82	38	1860	1.26
Lupinus sparsiflorus	0.34	0.85	0.36	0.86	128	1861	1.63
Oxytheca perfoliata	0.15	0.83	0.15	0.84	25	1864	1.16
Plantago ovata	0.28	0.8	0.31	0.81	152	1867	1.46
Salvia columbariae	0.28	0.75	0.29	0.76	241	1862	2.04

Figures

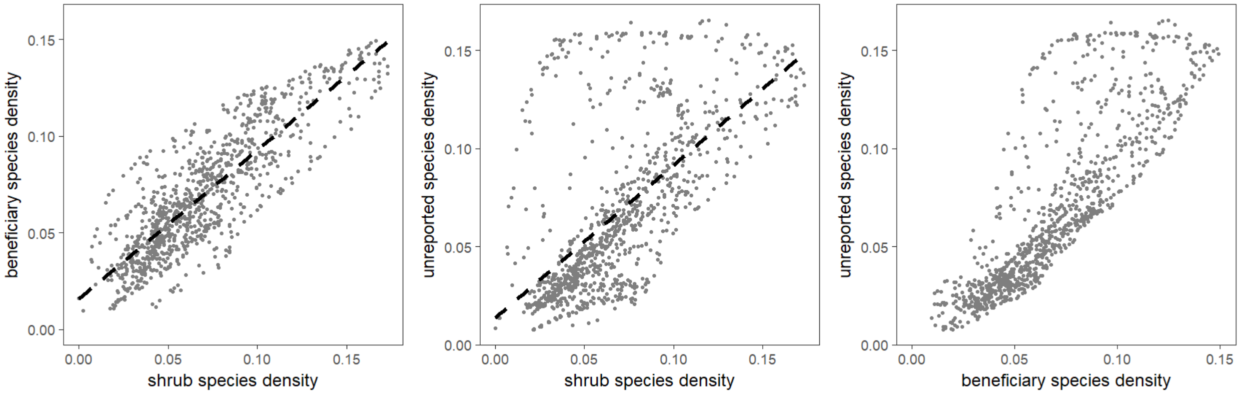

Fig. 4.1: Co-occurrence patterns of shrubs and annual plants species at 1000 random points within the Mojave Desert, California. The probability of shrub occurrence positively correlated with beneficiary occurrence probabilities ($R^2 = 0.42$, $p < 0.001$) and the occurrence of unreported annual species ($R^2 = 0.16$, $p < 0.001$). The probability of occurrence for beneficiary and unreported plant species were also correlated ($r = 0.85$).

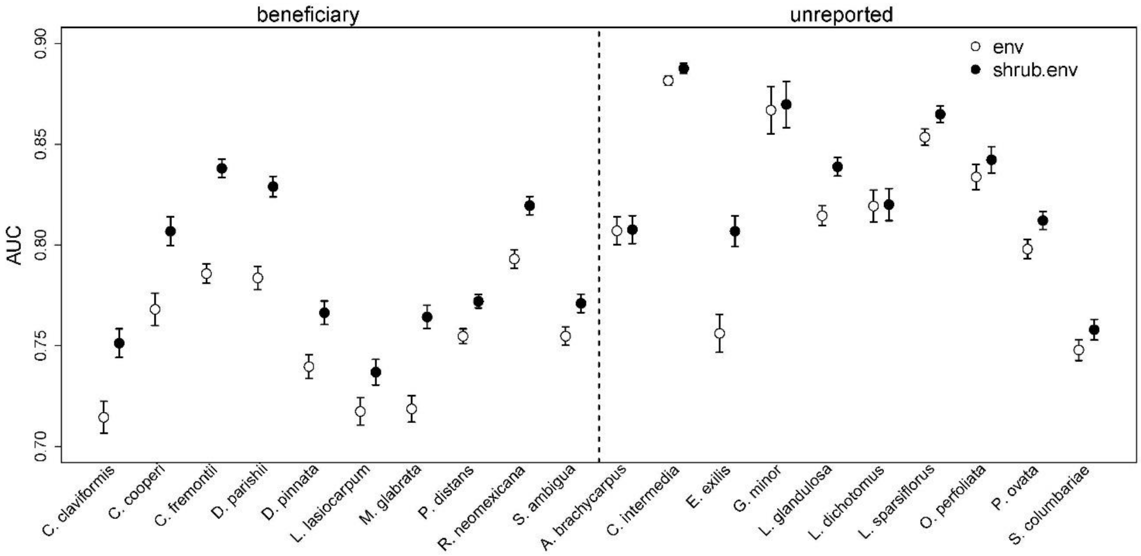

Fig. 4.2: MaxEnt models for each species trained and tested on occurrence only data from GBIF. AUC values were derived from average predictions of 40 runs with error bars representing 95% confidence intervals.

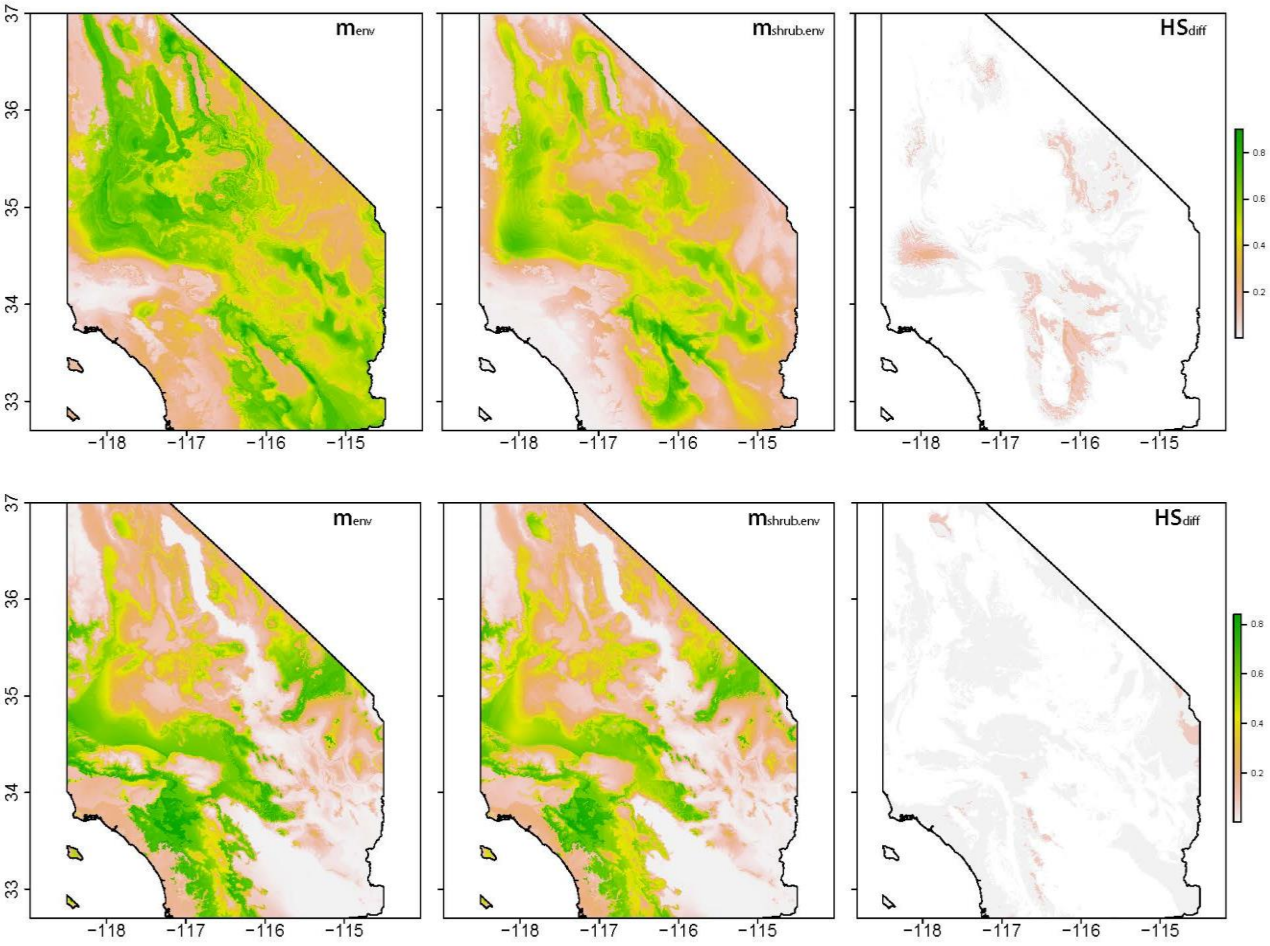

Fig. 4.3: A representative example of MaxEnt predictive models for the distribution of a known beneficiary species, *Camissonia claviformis* (top), and unreported species, *Acmispon brachycarpus* (bottom), with environmental predictors only (m_{env}) and environmental predictors with shrub density as a predictor ($m_{shrub.env}$). The shrub-based range expansion (HS_{diff}) represents the difference of prediction in $m_{shrub.env}$ and m_{env}.

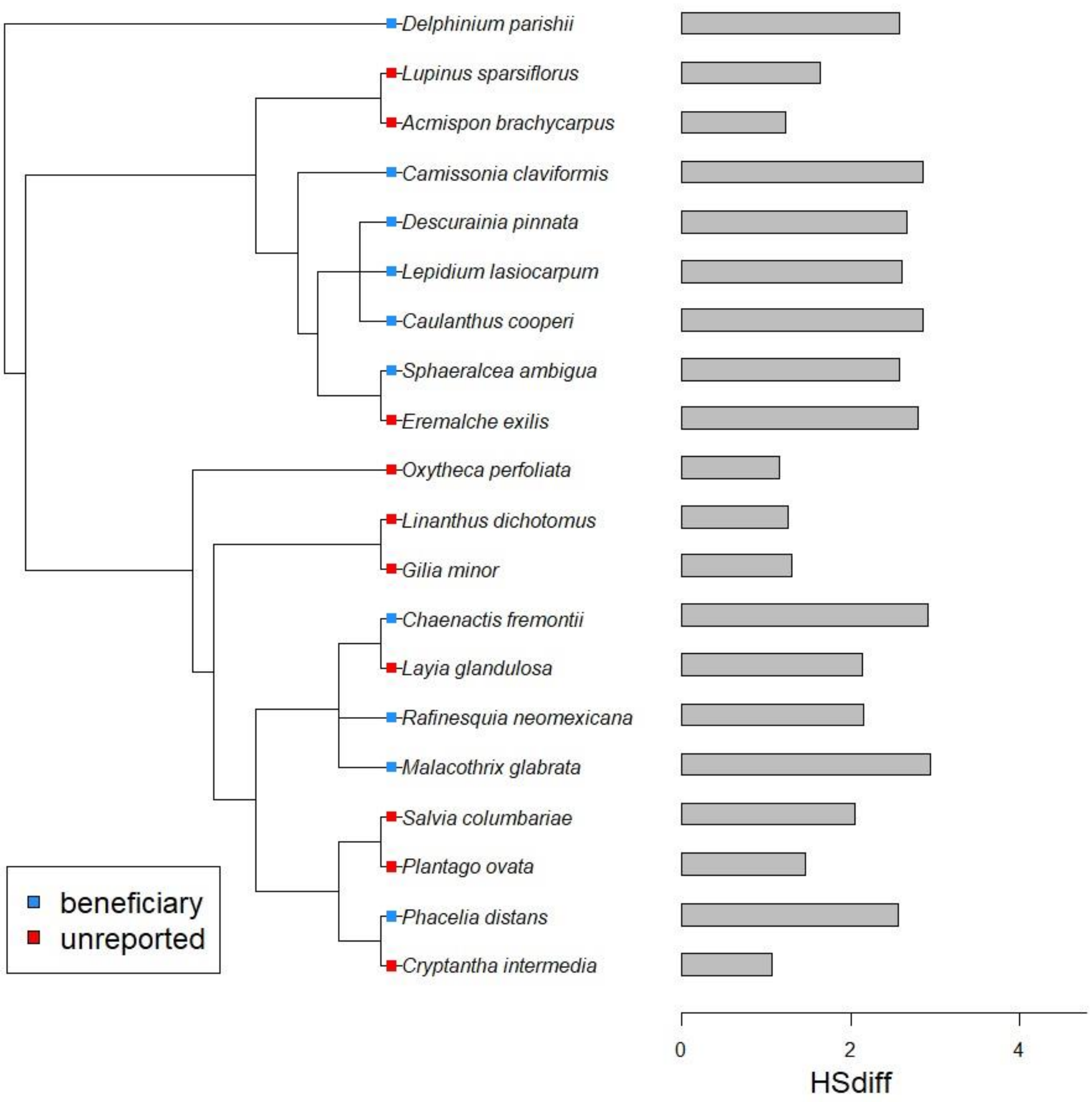

Fig. 4.4: A phylogeny of examined annual species and the associated range expansion effect from shrub facilitation (HS_{diff}).

Chapter 5

Synthesis: Re-thinking facilitation and ecological theory with mechanisms

Aim and over-arching hypotheses

Positive interactions support ecosystem function and this is especially true in resource limited environments such as deserts. Previous reviews of positive interactions have considered different ecological concepts, context dependencies, and predicted responses along environmental gradients (for examples, see Table 5.1). However, these reviews have focused on the interacting species or environmental factors and not considered the mechanisms underpinning the interactions. The purpose of this research program was to expand our ecological understanding of facilitation mechanisms in determining plant-plant interactions and the implications that these mechanisms have on community composition. We conducted a systematic review to describe and quantify the different mechanisms of facilitation that have been empirically tested (Chapter 1). The research gaps identified from the systematic review, such as the understudied mechanisms and testing multiple stressors, were a focus for this research program. Within the resource limited environment of Californian deserts (Figure 5.1), we experimentally tested the impact of abiotic and biotic stress on positive interactions during two extreme climate years (Chapter 2), and the mechanisms of facilitation in response to gradients of aridity (Chapter 3). We also conducted species distribution modelling to assess how these mechanisms of facilitation are responsible for extended the spatial distribution of beneficiary species (Chapter 4). We surveyed both a broad-range of environmental conditions within the deserts of California and a wide-range of plant species (for range map, Figure 5.1; for list of species, Appendix M). Each chapter thus explores the mechanisms of facilitation that we described (Chapter 1; Table 5.2). The mechanisms that were tested and the associated ecological hypothesis included:

i) Chapter 2: the mechanism of plant facilitation provided by shrubs on the annual community can change with precipitation extremes in deserts to match the respective stressor (herbivore protection, abiotic stress amelioration, and increasing soil moisture).

ii) Chapter 3: The relevant mechanism of facilitation and the response of positive interactions is determined by position along a gradient of aridity (substrate modification, increased soil nutrients, abiotic stress amelioration, and increased soil moisture).

iii) Chapter 4: desert shrubs alter the microclimate under their canopy to match the niche requirements of beneficiary species and this increases the geographical extent of those species (abiotic stress amelioration & nurse-mediated distribution).

The conceptual figure that we proposed in Chapter 1 allows for better predictions of positive interactions within different ecosystems and was used here as the unifying framework that structured this research program.

Summary of Major Findings

Positive interactions between plants can occur through a series of mechanistic pathways (Chapter 1). A previous review outlined some of the mechanistic pathways whereby shrubs positively influence other plant species including herbivore protection, seed trapping, and increases in resource availability (Flores and Jurado 2003). We expanded upon these mechanisms to include recent advances in the facilitation literature such as abiotic stress amelioration (non-resource based) and increasing pollinator visitation (Table 1.1). In addition to these mechanisms, the concept of a meta-mechanism was proposed that is an effect on the beneficiary species that is dependent on another mechanism. The proposed meta-mechanisms were benefactor-mediated distribution and benefactor-mediated evolution of the beneficiary species. Benefactor-mediated distribution is the extended geographic range as a result of positive interactions through one of the other facilitation mechanisms. Benefactor-mediated evolution is changes to the genetic population of a beneficiary species as a result of continued facilitation over time, such as ecotypic differentiation (Sotomayor et al. 2014; Liczner et al. 2017). These interactions occur in all ecosystems, but most commonly are observed in arid and semi-arid regions (Figure 1.2; Figure 1.3). There were also significant differences in the frequency each mechanism is being tested with increased pollinator visitation and seed trapping being among the least frequently studied (Figure 1.4). The conceptual framework and the definition of meta-mechanisms advances ecological theory and presented an opportunity to frame future studies in a similar context. The review also identified research gaps in the examination of certain mechanisms and highlighted important considerations that are typically not considered. For instance, one important consideration is the effect of multiple stressors on positive interactions that can be tested through the concurrent manipulation of multiple mechanisms. Given this research gap, we included this approach in the field experiments present in the other chapters.

Extreme climate events can act with stressor to determine the response of positive plant interactions (Chapter 2). Desert plant communities experience high variation in precipitation patterns, but climate change can further increase the amplitude of this variation and thus negatively impact plant communities (Seager et al. 2007; Jentsch et al. 2007; Thomey et al. 2011). We tested whether extreme climate events impact shrub facilitation on annual plant community by manipulation water availability and consumer pressure during an extreme drought year and a year of above-average rainfall. Shrubs were not found to have any effect on soil moisture, but did reduce temperature variation and consumer pressure on the annual plants (Table 2.1). These effects were significantly increased in the above-average rainfall year suggesting facilitation effects in this system are correlated with precipitation (Figure 2.2). Shrubs were also observed to increase the interspecific competition within the annual plant community by facilitating the dominance of a competitive invasive species, *Bromus madritensis* (Figure 2.3). This study contributed to an on-going discussion within the literature trying to predict the response of positive interactions to environmental variation, and supports the hypothesis that facilitation switches to negative or neutral interactions at extremes e.g. (Michalet et al. 2014).

The response of positive interactions along gradients of aridity is determined by the dominant mechanisms of facilitation (Chapter 3). Deserts are vulnerable to changes in precipitation patterns, and examining changes in plant interactions along aridity gradients can increase our understanding of how these communities will change with climate. We tested positive interactions at seven sites along an aridity gradient in Southern California and measured the differences in abiotic conditions within shrubs and open microsites. Our intent, was to determine the multiple mechanisms of facilitation that can be relevant at different points along a gradient of aridity. We also planted three phytometer species to better identify between-site differences that are not a consequence of factors other than climate (e.g. dispersal). We found significant differences in the abiotic conditions of shrub canopies relative to open microsites that favour annual plant growth including increased soil nitrogen in the arid sites, lower soil compaction at the mesic sites, and reduce temperature variation at all sites (Figure 3.1). Similarly, we did not find that shrubs increase soil moisture and this trend was consistent along the entirety of the aridity gradient (Chapter 2). In contradiction to our predictions, shrubs only facilitated the annual biomass of the ambient plant community and not species richness (Figure 3.2). The strength of facilitation on biomass also declined with aridity (Figure 3.2). At the more mesic sites, shrubs were found to decrease species richness and reduce phylogenetic diversity (Figure 3.2). Each phytometer species also had a unique response growing under a shrub canopy including *P. insularis* having decreased biomass, *P. tanacetifolia* having increased growth, and *S. columbariae* displaying no difference relative to an open microsite. These results confirm other studies that emphasize how facilitation is species specific (Liancourt et al. 2005; Michalet et al. 2006; Saccone et al. 2009; Liancourt et al. 2017) and suggests the response of these phytometers is largely determined by the ability of the species to utilize differences in environmental conditions. Controversially, this experiment rose concerns that positive interactions are decreasing biodiversity by favouring the invasion of non-native annual species. This study expanded the facilitation literature with empirical evidence on the importance of including mechanisms of interaction in studies and highlighted implications for climate change and invasion ecology.

Plant facilitation can alter the available niche for beneficiary plants and thus can mediate their distribution (Chapter 4). Research on niche theory has previously focused on negative interactions, but has recently expanded to include positive interactions (Bruno et al. 2003; Stachowicz 2012; McIntire 2014). However, there have been debates as to the correct definition of how positive interactions affect the niche (Rodriguez-cabal and Barrios-garcia 2012; Stachowicz 2012). There are two models relevant to this debate that include the niche-construction model where the benefactor species alters the microenvironment to match the niche characteristics of the beneficiary species (Rodriguez-cabal and Barrios-garcia 2012; McIntire 2014) and the niche-expansion model where the benefactor species reduces limitations or regulations that are inhibiting the beneficiary species survival. We resolve this debate by refer to the mechanism of facilitation that determines which of these models is relevant. For instance, niche-construction model occurs where a benefactor is ameliorating the microclimate to increase the survival of the beneficiary species, whereas the niche-expansion model occurs when a benefactor reduces regulation such as preventing herbivory on a beneficiary species. We use this framework to conduct species distribution modelling with desert benefactor shrubs and annual species that have either been previously reported as beneficiaries from the literature or unreported (Table 4.1). We found that beneficiary species were significantly correlated with benefactor shrubs and that their geographic distribution was significantly larger when shrubs were included as a predictor (Figures 4.1-4.3). Conversely, unreported species were weakly correlated with benefactor shrubs (Figures 4.1-4.3) and did not display an increase in geographic distribution. This study expanded our understanding of positive interactions in relation to niche theory and used species distribution modelling to apply the conceptual framework to estimate the increase in beneficiary species distribution.

Implications for theoretical ecology

The inclusion of facilitation mechanisms into theoretical ecology is both a novel and an important consideration. Controversies within the literature can be resolved by considering the mechanisms of interaction that are present within positive interactions. One of the more frequently discussed topics is the response of positive interactions along environmental gradients (Maestre et al. 2006; Lortie and Callaway 2006; Michalet 2006; Soliveres et al. 2015). A commonly tested concept from studies conducted along environmental gradients is the Defined Stress Gradient Hypothesis (SGH). SGH predicts that positive interactions increase with environmental stress or consumer pressure (Bertness and Callaway 1994). Revisions to the SGH posit that positive interactions collapse or become negative at environmental extremes (Michalet et al. 2014). However, this has been challenged by some authors that have found evidence of positive interactions in extreme environments (Dvorský et al. 2013; Pugnaire et al. 2015). We found evidence that the predictability of positive interactions along gradients is largely determined by the ability of the benefactor species to mitigate the environmental stress. For example, the strength of positive interactions was greater during an above-average rainfall year rather than during an intense drought (Chapter 2). We observed this trend because the benefactor shrub species ameliorated temperature variation and reduced consumer pressure that benefits annual plants only when the more limiting driver, water availability, was increased. However, other shrub species that increase soil moisture within their canopies display stronger facilitation effects during drought (Zou et al. 2005; Soliveres and Maestre 2014). When examined along a gradient of aridity, we observed that the response of positive interactions was largely determined by the species of the beneficiary species and whether their trait set allows them to utilize the environmental differences in shrub canopies (Chapter 3). In desert ecosystems, the availability of water is often the most limiting resource and the response of facilitation is determined by the capacity of the benefactors to increase soil moisture (Butterfield et al. 2016). The mechanism of interaction is thus integral to relationship of positive interactions along environmental gradients. We also advanced our conceptualized of facilitation in relation to niche theory by defining the niche-construction and niche-expansion models (Chapter 4). Here, the consideration of the facilitation mechanism can be used to explain some of the contradictory observations and conclusions that are present within the literature. We encourage ecologists to frame their future experiments on plant-plant interactions by testing the relevant mechanisms of facilitation that can assist in predicting responses of positive interactions along environmental gradients and drawing conclusions about the traits of the interacting species. It is critical for ecologists to understand the niche requirements of species and this includes their interactions with other species.

Implications for biological conservation

The effects of positive interactions on biodiversity are more context dependent than previously thought. Benefactor plants increase the spatial heterogeneity of the landscape and this has consequences for increasing the plant biodiversity (McIntire and Fajardo 2014; Pescador et al. 2014). Cushion plants in alpine environments around the globe have been observed to increase phylogenetic diversity of plant communities by facilitating less stress-tolerant species and species that are distantly related (Valiente-Banuet and Verdú 2007; Butterfield et al. 2013). However, we observed the opposite trend in desert ecosystems, where benefactor shrubs decreased phylogenetic diversity, facilitated closely related species, and had lower species richness relative to open microsites (Chapters 2-4). This can be explained by the difference in stress type for desert and alpine environments. Desert ecosystems are most limited by resource based stress (e.g. water & nutrients) and thus the capacity of shrubs to facilitate is determined by whether species can increases these resources and precipitation patterns (Zou et al. 2005; Pugnaire et al. 2009; Soliveres and Maestre 2014). Alpine environments are most limited by non-resource based stress (e.g. extreme cold, snow cover, and substrate) and thus the facilitation effects of cushions can be more predictable based on temperature. The differences in life-forms of cushion and shrubs also suggest difference in trait sets, such as shrubs competing for light with the understorey annuals while cushions do not. Restoration programs that utilized benefactor plants as tools for facilitating native recruitment (Gómez-Aparicio 2009) need to consider the trait set of the species and whether it can reduce the dominant stress in the system

(Maestre et al. 2009). The effects of positive interactions on local biodiversity are largely determined by the facilitation mechanisms of the benefactor plants.

Effects of facilitation on ecosystem function are not necessarily positive. Facilitation of species that are less stress-tolerant has negative impacts on biodiversity by increasing the invasion of non-natives into areas where the species would typically be uncommon. For instance, common dandelion has been observed to invade high-altitudes in the Chilean Andes where it is not-native (Cavieres et al. 2007). In Californian Deserts, grasses from the European Mediterranean are more frequent and have higher productivity in shrub canopies relative to open desert areas (Holzapfel and Mahall 1999; Rodríguez-Buriticá and Miriti 2009). Within our studies we observed that shrubs increased the dominance of non-native grass species, such as the *B. madritensis* and *S. barbatus* (Chapter 2, 3). Benefactor plants thus act as pathways of invasions into high-stress environments by acting as resource islands. However, shrubs can have positive effects on other components of ecosystem function such as productivity in deserts that is frequently observed to be facilitated (Chapters 2, 3).

There are also some species that are uniquely associated with shrub species that contribute to the total biodiversity present within a desert site (Chapter 2, 3). Most importantly, shrubs are foundational species in ecosystems supporting other plant species and animals through a network of interactions (Angelini et al. 2011; Lortie et al. 2016). We observed *E. californica* having facilitating effects on endangered lizard species by ameliorating temperature variation (Filazzola et al. 2017) and that other desert shrubs increase insect biodiversity (Ruttan et al. 2016). Shrub facilitation may not necessarily increase diversity within their canopy relative to open microsites, but play a larger role in ecosystem health in desert ecosystems by supporting animals and specific plant species.

Implications for climate change

Positive interactions reduce high abiotic stress and thus are cited as potential buffer for climate change (Callaway et al. 2002; Pennings et al. 2003). Extreme climate events are predicted to increase in intensity, duration, and frequency (IPCC 2014). Therefore, we tested the response of plant interactions to extreme climate events and observed significantly lower strength of facilitation during an extreme drought relative to an above-average rainfall year (Chapter 2). This suggests that positive interactions are negatively correlated to extreme climate events, but does not necessarily preclude facilitation as a buffer against climate variability. Positive interactions were still observed during the extreme drought when biomass was significantly lower and therefore can be sustaining ecosystem function (Chapter 2). The most commonly observed mechanism of facilitation within this research program was the amelioration of the microclimate, such as reducing temperature variability, increasing relative humidity, and intercepting solar radiation (Chapter 2, 3). We can expect these mechanisms to reduce the effects of climate variability on plant communities (Chapter 2-4) and have evidence that these mechanisms also extend to plant-animal interactions (Lortie et al. 2016; Ruttan et al. 2016; Filazzola et al. 2017). Although it has been identified that there are significant impacts of extreme climate events on species interactions, studies to date have been limited (Ogilvie et al.). To our knowledge, this is the first test of positive interactions in relation to extreme climate events (but see, (Ogilvie et al.; Jentsch et al. 2007). There is a need to better model, separate, and understand climate extremes relative to shifts in mean climate values (Jentsch et al. 2007; Smith 2011). Future research testing positive plant interactions should include tests of extreme climate events.

It has been suggested that tests of positive interactions along environmental gradients can be used as proxies for climate change. Modelling the effects of shrub facilitation on annual plants in the Mojave Desert, we estimated a significantly larger distribution of annuals than in the absence of facilitation (Chapter 4). Other studies that have observed increases in the strength of facilitation along gradients of aridity suggest these interactions can help mitigate impacts of climate change (Ziffer-Berger et al. 2014; López et al. 2016). However, a study by (Metz and Tielbörger 2016) challenged that spatial and temporal aridity gradients provide poor proxies of positive interactions in response to climate change. The authors highlight the challenges in using correlative approaches only and the necessity in conducting long-term experiments (Metz and Tielbörger 2016). Within this research program, we have addressed some of these concerns by conducting manipulations to better estimate the underlying mechanisms of interaction among species (Chapter 2, 3). We determined that shrub effects on environmental variables that support plant communities, such as soil nitrogen, are relatively slow processes in deserts and that the effect of positive interactions can lag behind changing precipitation pattern (Chapter 3). We thus challenged the current literature that suggests positive interactions are buffers of climate change, and suggest that deserts are more sensitive to shifts in climate patterns than what is expected (Chapter 2, 3). Ecologists intending on conserving biodiversity must expand beyond the species-loss paradigm and consider the mechanisms of interaction that are present within communities (Valiente-Banuet et al. 2015). The effects of positive interactions in response to climate are largely unknown or misunderstood and thus this is a critical research gap that can be address through examining of facilitation mechanisms through manipulative experiments that are long-term.

Future Research

Global change, either through anthropogenic disturbance or climate change, is the biggest threat to biodiversity and it is important to better understand the interactions that occur within deserts if management strategies are to be developed. Within this research program we provided a conceptual framework and validated it through empirical studies to allow future researchers better understanding of the drivers in plant-plant interactions. We also extended this research to have broader implications to include different species, life-stages, and trophic levels (Table 5.3). Importantly, we identified the implications that these findings have towards restoration strategies that are currently a major topic of concern for deserts in Southern California (Germano et al. 2011; Soulard and Wilson 2015; Westphal et al. 2016; Hanak et al. 2017). For example, we determined the facilitation of seed arrival and pollinators are significantly understudied (Chapter 1) although these could be crucial components that support desert biodiversity. In a study currently under review, we described and tested the multiple indirect pathways that benefactor plants can indirectly increase seedbank densities of other species, such as through trapping or facilitation seed production (Table 5.3). These mechanisms highlight benefactor species as significantly important for ecosystem health because of the indirect effects they have on the plant community (Angelini et al. 2011). Additionally, we have shown that shrubs increase the diversity and abundance of insect communities (Ruttan et al. 2016), but it is still unknown the effect this has on the pollination rate of the annual community. Finally, we have evidence that shrubs have potential as tools for restoration by increasing the recruitment rate of native plant species and supporting endangered animal species (Table 5.3). However, we have also discovered that shrub facilitation can affect non-native species and this can have reciprocal costs including reduced recruitment of native shrub seedlings (Chapter 2; Table 5.3). The role of non-native species in disrupted desert plant communities was not a primary focus of research, but was a common theme share in each chapter. These interactions cannot be ignore and are likely disrupted interactions between shrubs and native annuals that are already under threat from anthropogenic disturbance and climate change. It is necessary to better understand the relationship between native shrubs and non-native annuals because shrub facilitation is increasing their proliferation in desert, which can have negative effects on the shrub species that can cascade to other species.

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Tables

Table 5.1: Reviews of positive interactions and their associated themes in ecological theory over the past 25 years.

Title	Authors	Topic
Ecological concepts		
Inclusion of facilitation into ecological theory	Bruno et al. 2003	Niche concept, density dependence, and community invisibility.
Facilitation in plant communities: the past, the present, and the future	Brooker et al. 2008	Advances in ecological theory in the context of positive interactions.
Facilitation as a ubiquitous driver of biodiversity	McIntire & Fajardo 2013	The role of positive interactions in support biodiversity and ecosystem function.
Facilitation among plants in alpine environments in the face of climate change	Anthelme et al. 2014	Facilitation in response to climate change
Functional assessment of animal interactions with shrub-facilitation complexes: a formal synthesis and conceptual framework	Lortie et al. 2016	Benefactor species as the foundation for communities through direct and indirect pathways.
Context dependencies		
Competition and facilitation: a synthetic approach to interactions in plant communities	Callaway & Walker 1997	Positive interactions are determined by gradients, plant life-stages, densities, and are species specific.
Do biotic interactions shape both sides of the humped-back model of species richness in plant communities	Michalet et al. 2006	Revisions of Grime’s 1973 model of plant life strategies.
Inclusion of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis	Smit et al. 2009	The predictability of positive interactions is determined by life strategies of the species and inclusion of consumer pressure.
Refining the stress-gradient hypothesis for competition and facilitation in plant communities	Maestre et al. 2009	The traits of the benefactor or beneficiary species determine the predictability of positive interactions.
Moving forward on facilitation research: response to changing environments and effects	Soliveres et al. 2013	Reconciling controversies about the predictability of positive interactions by considering species-specificity,

on the diversity, functioning and evolution of plant communities		stress type, and scale of interest.
Environmental Gradients		
Positive interactions in communities	Bertness & Callaway 1994	Stress Gradient Hypothesis – Positive interactions increase with abiotic stress or consumer pressure.
Strong facilitation in mild environments: the stress gradient hypothesis revisited	Holmgren & Scheffer 2010	Facilitation can be common in environments that are not resource limited.
Global shifts towards positive species interactions with increasing environmental stress	He et al. 2013	The response of positive interactions to different types of stress.
Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition	Michalet et al. 2014	The response of positive interactions along environmental gradients is unimodal (i.e. parabolic).

Table 5.2: A summary of the studies examining the mechanisms of positive interactions within this research program.

Chapter	Predictions	Findings
1	To assess the global extent of facilitation studies and test whether there is a correlation between climate and the reported mechanisms	Positive interactions are present in every ecosystem, but are more common in regions of high abiotic stress and resource-limited environments (e.g. deserts and alpine).
1	To describe, contrast and highlight research gaps for each nurse-plant mechanism and ecological hypothesis including differences in the life-form of benefactor plants	Pollinator visitation and seed trapping were relatively understudied to other facilitation mechanisms. There were also other research gaps identified for the inclusion of positive interactions into the invasion literature and consideration of multiple stressors.
1	To broaden and formalize the semantics of the nurse-plant syndrome by organizing all the studies and incorporating processes associated with evolution and macroecology	The creation of two “meta-mechanisms” that describe the distributional and evolutionary effects of positive interactions on beneficiary plants.
2	Shrubs facilitate the annual plant community by ameliorating the microclimate through reductions in temperature extremes and increases in relative humidity during the both years	Shrubs were found to ameliorate the microclimate and increase relative humidity in both years. This effect was greater in the above-average rainfall year.
2	During a drought year, experimentally adding water would reduce the magnitude of positive interactions because the shrub is mechanistically increasing soil moisture availability for the annual community	There was no shrub effect on soil moisture and water addition did not reduce positive interactions.
2	In a year with above-average precipitation we expected animal exclosures to reduce the magnitude of positive interactions because the shrub is reducing consumer pressure on the annual community	Shrubs were found to reduce consumer pressure and animal exclosures reduced this effect.
3	What are the effects of shrubs on the environmental conditions along a gradient of aridity	Shrubs increase nutrients and reduce temperature variability throughout the aridity gradient.
3	What are the species-specific responses of the annual plants to shrub facilitation	Shrubs facilitate relatively competitive species and have a negative effect on more stress-tolerant species.
3	How do positive interactions change along a gradient of aridity and what are the effects on community composition	Shrub facilitate collapses at the extreme ends of the aridity gradient because of low water availability at the driest end and increased competition within the annual community at the mesic end.
4	The species distribution modelling for previously reported beneficiary species are improved and estimate larger spatial extends with the inclusion of shrub density than with climate along	Beneficiary annual species were found to be correlated with shrubs. These species were also found to have improved model fit and spatial distribution with the inclusion of shrubs

4	The species distribution modelling for unreported annual species are not improved by the inclusion of shrubs into the models (i.e. the null model	Unreported annual species were found to be weakly correlated with shrubs. These species were not found to have improved model fit or spatial distribution with the inclusion of shrubs

Table 5.3: The supporting studies that were conducted in addition to this project and that are either prepared or published manuscripts.

Authors	**Title**	**Purpose/Findings**	**Status**
Filazzola, A., Liczner, A., Westphal, M.F., & Lortie, C.J.	Direct and indirect shrub facilitation increases the spatial heterogeneity of desert seedbanks	Shrubs can facilitate seedbank densities through increasing annual seed production and trapping wind-dispersed seeds	*In review, Journal of Vegetation Science*
Filazzola, A., Westphal, M.F., & Lortie, C.J.	Cost of facilitation: invasive grasses limit recruitment of benefactor shrubs	Shrubs facilitate non-native grass densities and this can have a negative effect of the recruitment of native species	*In prep.*
Filazzola, A., Westphal, M.F., Powers, M., Liczner, A., Woolett, Johnson, B., & Lortie, C.J.	Non-trophic interactions in deserts: Facilitation, interference, and an endangered lizard species	Shrubs provide a thermoregulation refuge for an endangered species and invasive grass densities threatens the lizard's survival.	*Published, Basic and Applied Ecology*
Liczner, A., Filazzola, A., Westphal, M., & Lortie, C.J.	Shrubs facilitate the establishment of native forbs with reductions in non-native competition, but not consumer pressure, in an invaded arid shrubland	Grazing can limit the recruitment of native species into an invaded desert and shrubs can inhibit herbivory providing an opportunity for successful restoration	*In prep.*
Liczner, A., Sotomayor, D., Filazzola, A., & Lortie, C.J.	Germination response of desert annuals to shrub facilitation is species specific but not ecotypic	Shrubs increase the germination rate and speed of some species but this does not have consequence on the genetics of the beneficiaries	*Published, Journal of Plant Ecology*
Lortie, C., Filazzola, A., Sotomayor, D.A., Liczner, A., & Ruttan, A.	A contrast of the specificity of shrub species effects within the San Joaquin Desert region	A long-term study comparing the facilitation effects of shrub species in a highly degraded desert and a relatively undisturbed desert	*In prep.*
Lortie, C., Filazzola, A., Welham, C., & Turkington, R.	A cost–benefit model for plant–plant interactions: a density-series tool to detect facilitation	A methodology to determine the net effect of plant-plant interactions	*Published, Plant Ecology*
Lortie, C.J., Filazzola, A., & Sotomayor, D.A.	Functional assessment of animal interactions with shrub-facilitation complexes: a formal synthesis and conceptual framework	Shrubs act as foundation species through facilitation networks of the neighbouring community, both directly and indirectly.	*Published, Functional Ecology*
Lortie, C.J., Filazzola, A., Kelsey, R., Hart, A., & Butterfield, H.S.	A review of the evidence supporting strategic retirement and restoration of agricultural land for endangered species	A developed strategy for retiring agricultural land and restoring it in support of three endangered species of the San Joaquin Desert	*In review, Ecospheres*

Ruttan, A., Filazzola, A., & Lortie, C.J.	Shrub-annual facilitation complexes mediate insect community structure in arid environments	Shrubs can facilitate the insect community and supports theories that plant-plant facilitation extends to other trophic levels	*Published*, *Journal of Arid Environments*

Figures

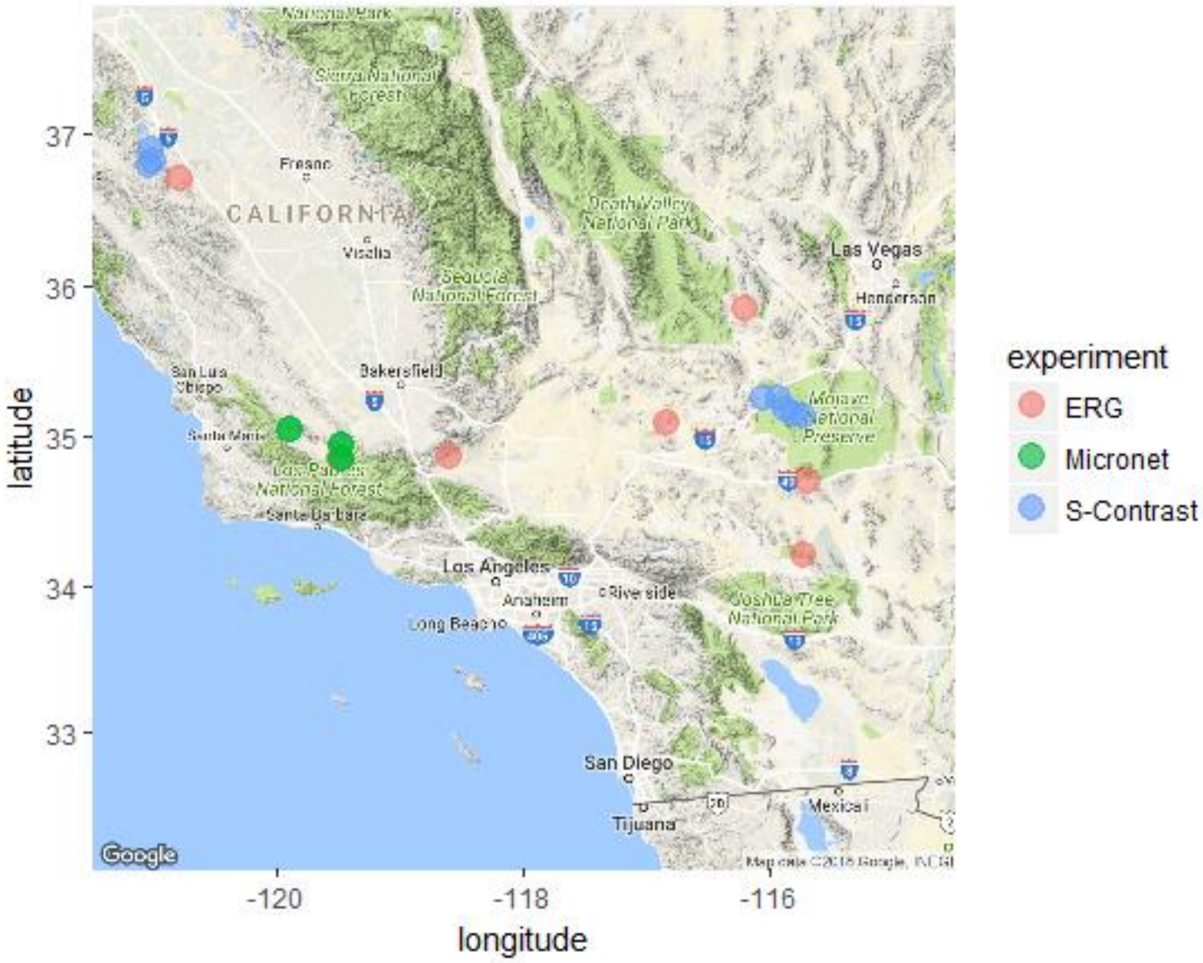

Figure 5.1: Location of the study sites used both directly for this project and other supplemental experiments.

Appendices

Appendix A – Supplemental data for systematic review

Table A.1: The proportion of studies associated with each ecological concept. Standardized residuals greater than the ±1.96 confidence interval (α = 0.05) were considered significant. The majority of studies examine the direct mechanisms behind nurse-plant interactions, while few look at the consequences of biotic pressures or the practical applications of facilitation.

Hypothesis	**Number of Studies**	**Proportion of Studies**	**Standardized Residual**	**Frequently Studied?**
Mechanism testing				
Nurse plants directly affect the fitness or productivity of plants in their vicinity	96	32.2 %	8.12	Yes
Nurse plants indirectly affect the fitness or productivity of plants in their vicinity through an intermediary species	27	9.1 %	-2.82	No
Gradient testing				
Net interactions between nurse and protégé are dependent on abiotic stressors	62	20.8 %	2.73	Yes
Plant interactions mediate consumer pressures	34	11.4 %	-1.71	N.S.
Theoretical ecology				
Nurse plants can facilitate the development of community structure to increasing complexity	27	9.1 %	-2.82	No
Nurse plants affect population dynamics and the biodiversity of a community	73	24.5 %	4.47	Yes
Nurse plants alter the evolution trajectories and phylogenetic history of benefactor species.	21	7.1 %	-3.77	No
Applied Ecology				
Nurse plants are tools for restoration of native flora in degraded landscapes	48	16.1 %	0.51	N.S.
Nurse plants mediate the invasion regimes of non-native plant species	15	5.0 %	-4.72	No

Table A.2: The proportion of studies associated with each nurse mechanism. Standardized residuals greater than the ±1.96 confidence interval (α = 0.05) were considered significant. Abiotic stress amelioration was the most examined mechanism while pollinator visitation, substrate modification and seed trapping were all significantly understudied. Between the two meta-mechanisms, nurse-mediated distribution was significantly studied while nurse-mediated evolution was not.

Nurse Mechanism	**Number of Studies**	**Proportion of Studies**	**Standardized Residual**	**Frequently Studied?**
Abiotic stress amelioration	118	39.6 %	9.65	Yes
Herbivore Protection	53	17.8 %	0.11	N.S.
Pollinator visitation	5	1.7 %	-6.93	No
Substrate modification	37	12.4 %	-2.23	No
Seed Trapping	37	12.4 %	-2.23	No
Soil moisture retention	73	24.5 %	3.05	N.S.
Soil nutrient modification	57	19.1 %	0.70	N.S.
Nurse-mediated distribution	71	23.8 %	2.76	Yes
Evolutionary changes	19	6.4 %	-4.88	No

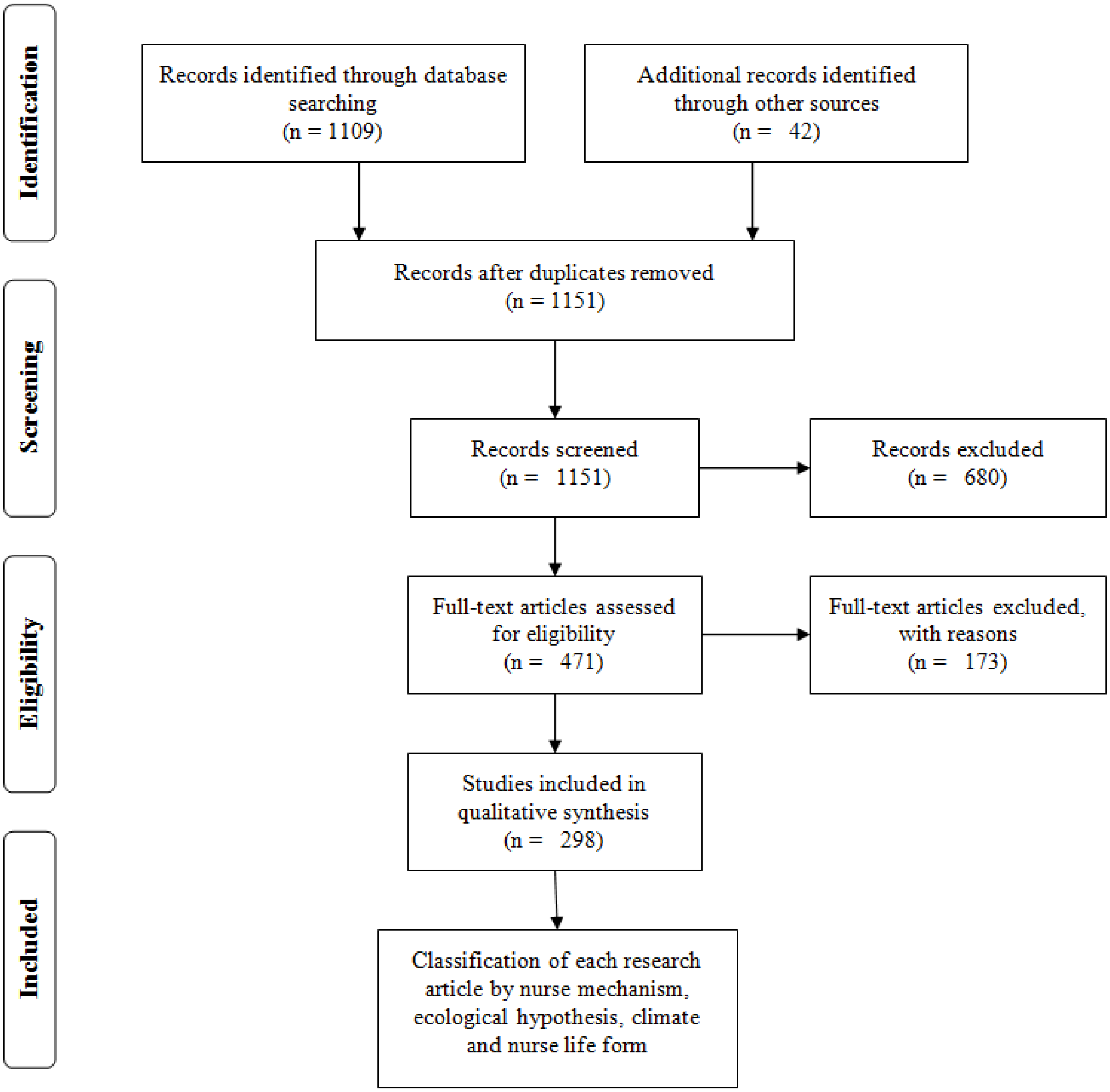

Figure A.1: The PRISMA diagram describing the search protocol used for systematic review to refine articles those that are relevant. Search was conducted with Web of Science on February 10st, 2014 with subsequent searches on Google Scholar. Non-relevant subjects (such as drug abuse or oncology) were excluded and further refinement was made for only plant-plant interactions.

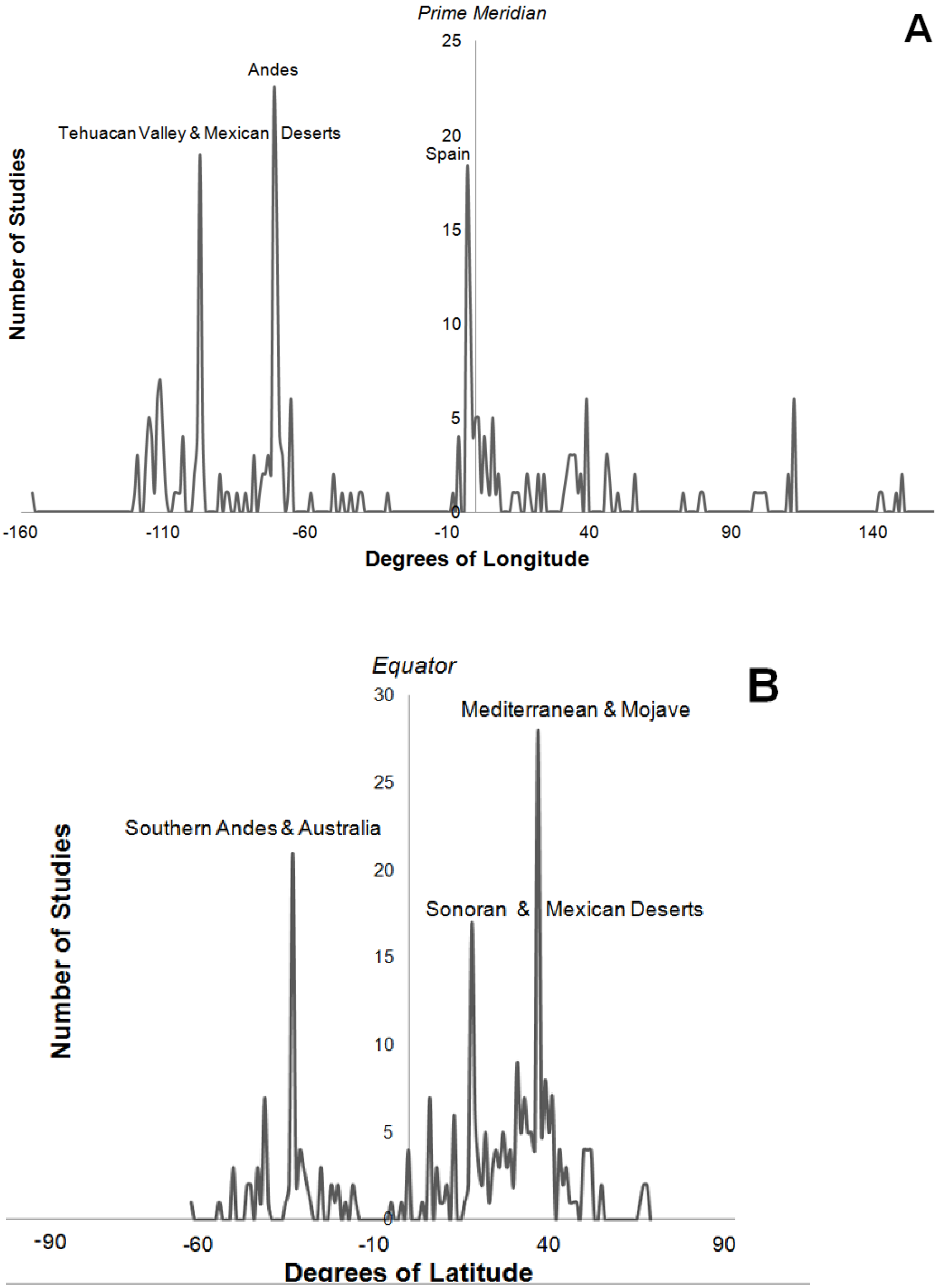

Figure A.2: Frequency of previous studies for nurse plants based on degrees of longitude (A) and latitude (B).

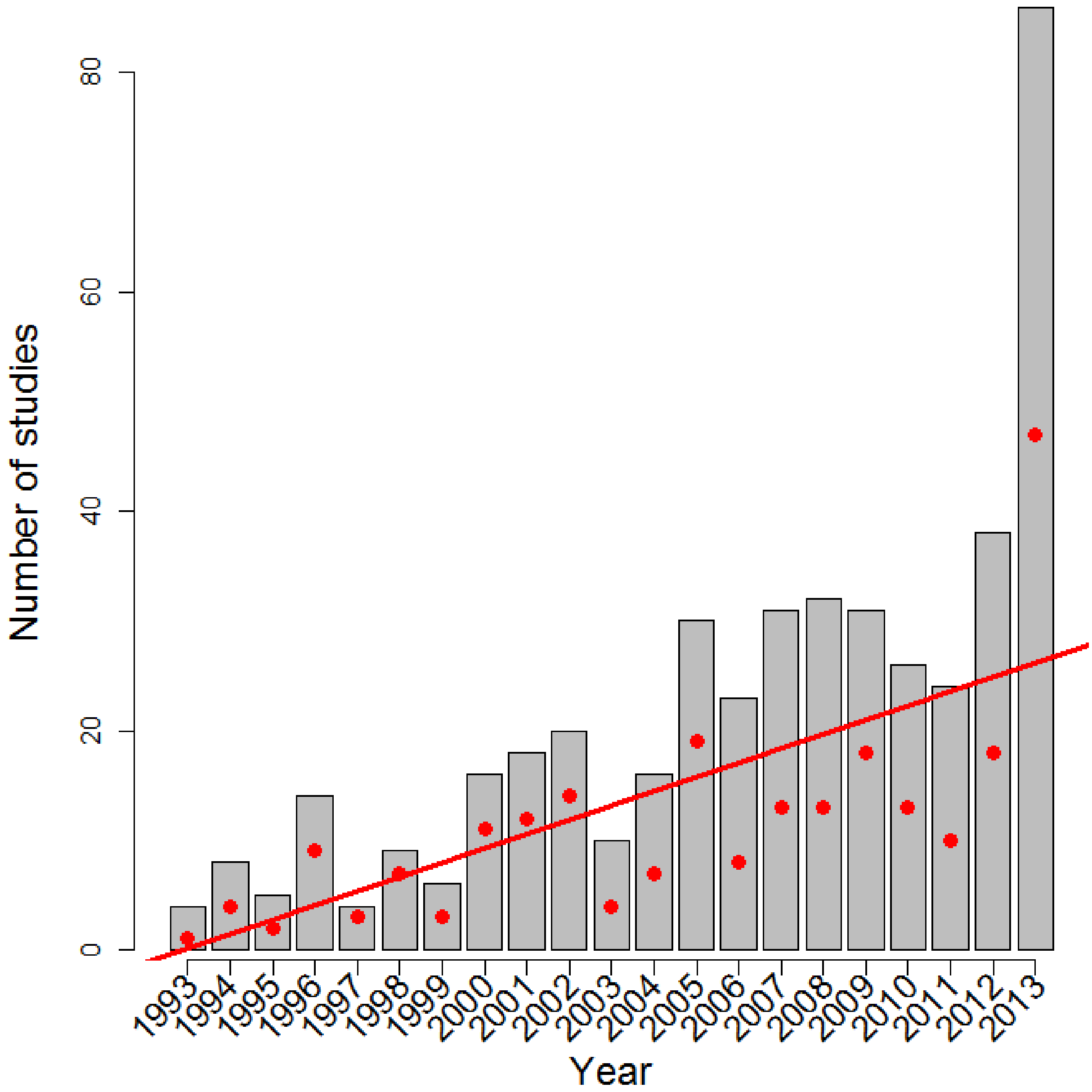

Figure A.3: The total number nurse studies conducted in the last 20 years. Red solid line is mean model fit for number of studies of nurse plants that favourable increase abiotic conditions for the last twenty years: Abiotic = -0.71 + 1.08*t*; model fit, $R^2 = 0.44$, p = 0.0006.

Appendix B- Location of Panoche Hills

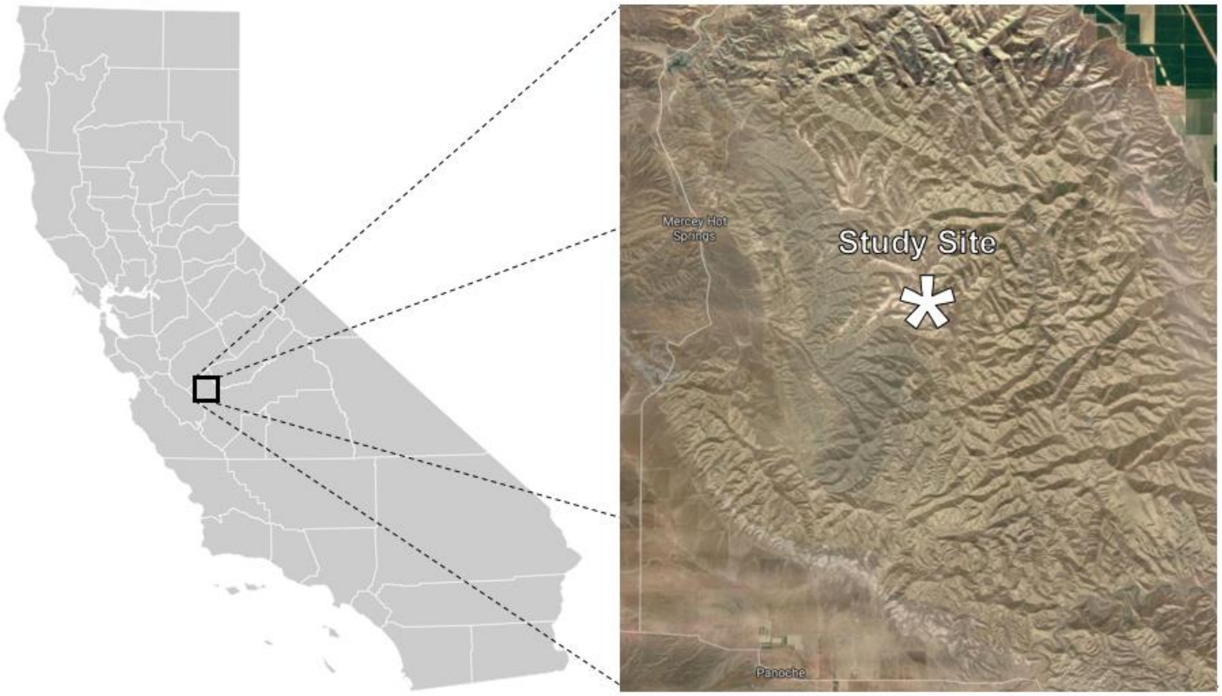

Figure B.1: Google Earth (2016) map of the study site location at Panoche Hills, Fresno County, California, USA **(**36°41.776'N, 120°47.886'W at 650 m).

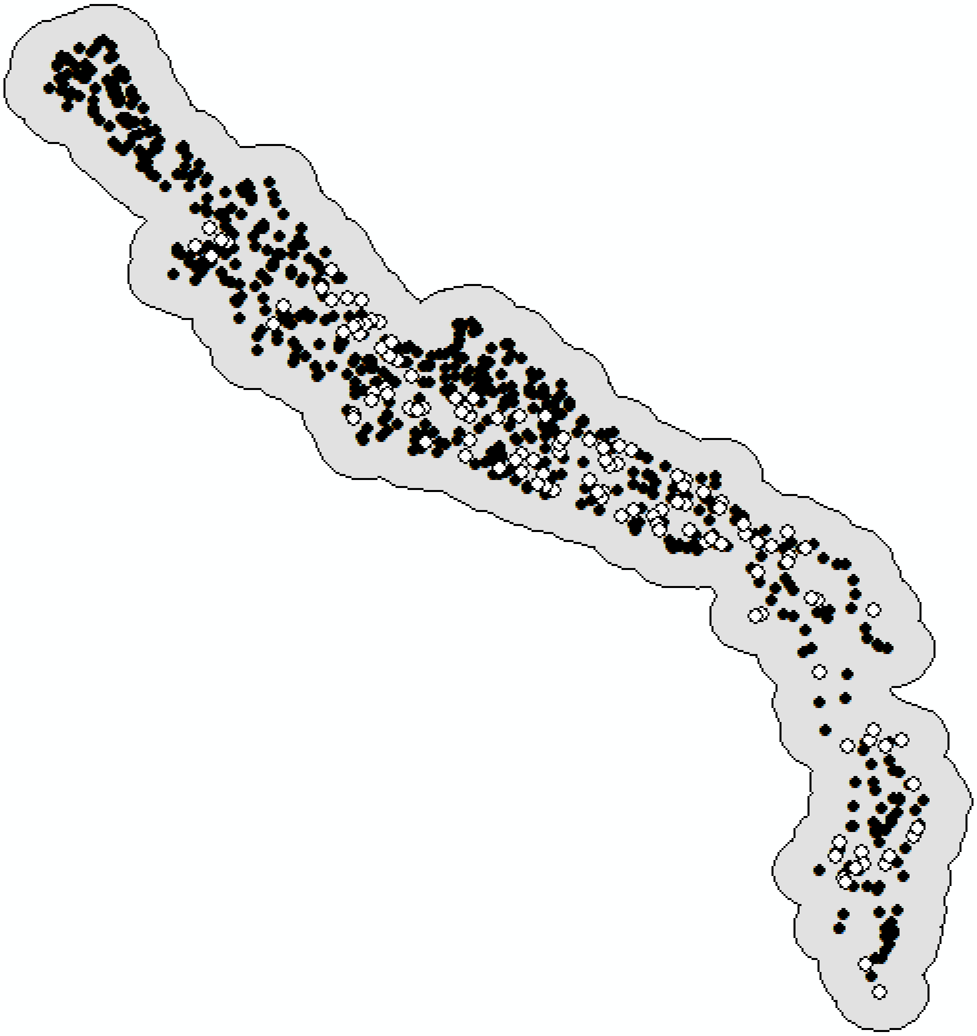

Figure B.2: GPS location of the 700 shrubs that were measured in 2013 are shown in black. Shrubs used in the experiment for both the 2014 and 2016 seasons are shown in white.

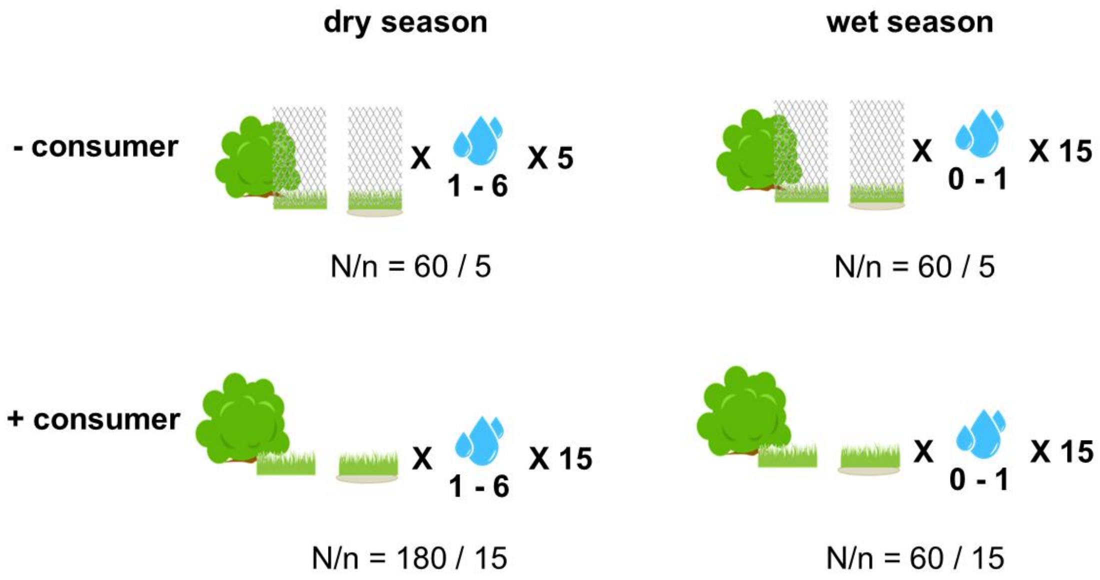

Figure B.3: Experiment design for watering levels and exclosures in the dry and wet seasons.

Appendix C – Models of extreme climate events and shrub facilitation on plant abundance

We tested if shrub facilitation, water availability and reductions in consumer pressure affected plant abundance or species richness of the annual plant community. We fitted models with abundance and richness as the response variables and microsite, exclosure, and SWC0 as the predictors for both seasons. The models were fitted with a negative binomial error distribution (glm.nb function, MASS library) because the abundance and species richness represented a discrete count that is over-dispersed, i.e. variance exceeds the mean (Lindén & Mäntynieme, 2011). We then used a z-test to determine whether the effects of annual abundance or species richness significantly differed from zero.

Table C.1: Results from GLMs testing for differences in plant abundance and species richness of the plant community among, microsites (shrub and open), consumer pressure (ambient and reduced), and gradient of soil moisture. GLMs were conducted for a year of extreme drought (2014) and an above average rainfall year (2016). Significance at α < 0.05 is denoted by bolded values.

Effect	**2014**				**2016**			
	abundance		richness		abundance		richness	
	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*
soil moisture	12.8	**< 0.001**	0.51	0.48	4.13	**0.042**	0.051	0.82
microsite	5.65	**0.017**	4.92	**0.026**	25.3	**< 0.001**	10.2	**0.0014**
consumer pressure	0.24	0.62	0.41	0.52	8.54	**0.0035**	2.07	0.15
microsite*soil moisture	2.66	0.10	0.002	0.96	1.75	0.19	0.32	0.57
microsite*consumer pressure	0.39	0.53	0.53	0.46	2.31	0.13	0.24	0.62
microsite*consumer pressure * soil moisture	0.058	0.81	0.17	0.68	5.43	**0.020**	0.007	0.93

Appendix D – Paramter estimates of SEM

Table D.1: Parameter estimates for structural equation models during the dry season (2014). SEM converged normally after 82 iterations and was estimated using Maximum likelihood with a Bollen-Stine bootstrapping method (p = 0.063). The minimum function test statistics was 19.2 on six degrees freedom. Significance at α < 0.05 is denoted by bolded values.

	Mean effect	**SE**	**Z-value**	**p**
Latent Variables				
annual community =~				
biomass	1.66	0.18	9.21	**<0.001**
abundance	23.8	3.16	7.52	**<0.001**
B. madritensis dominance	0.17	0.015	11.7	**<0.001**
Regressions				
annual community ~				
consumer pressure	0.17	0.17	1.02	0.31
microsite	0.95	0.15	6.36	**0.001**
soil moisture	0.036	0.011	3.15	**0.002**
Variances				
biomass	0.25	0.43	0.58	0.56
abundance	989.4	138.9	7.12	**<0.001**
B. madritensis dominance	0.082	0.007	11.6	**<0.001**

Table D.2: Parameter estimates for structural equation models during the wet season (2016). SEM converged normally after 83 iterations and was estimated using Maximum likelihood with a Bollen-Stine bootstrapping method (p = 0.12). The minimum function test statistics was 18.5 on six degrees freedom. Significance at α < 0.05 is denoted by bolded values.

	Mean effect	**SE**	**Z-value**	**p**
Latent Variables				
annual community =~				
biomass	2.55	0.49	5.19	**<0.001**
abundance	8.14	1.66	4.90	**<0.001**
B. madritensis dominance	0.11	0.02	6.08	**<0.001**
Regressions				
annual community ~				
consumer pressure	0.41	0.29	1.34	0.17
microsite	5.08	1.57	3.24	**0.001**
soil moisture	0.069	0.04	1.71	0.087
Variances				
biomass	7.16	2.87	2.5	**0.012**
abundance	962.3	145.6	6.61	**<0.001**
B. madritensis dominance	0.034	0.009	3.72	**<0.001**

Appendix E – Frequency of positive interactions

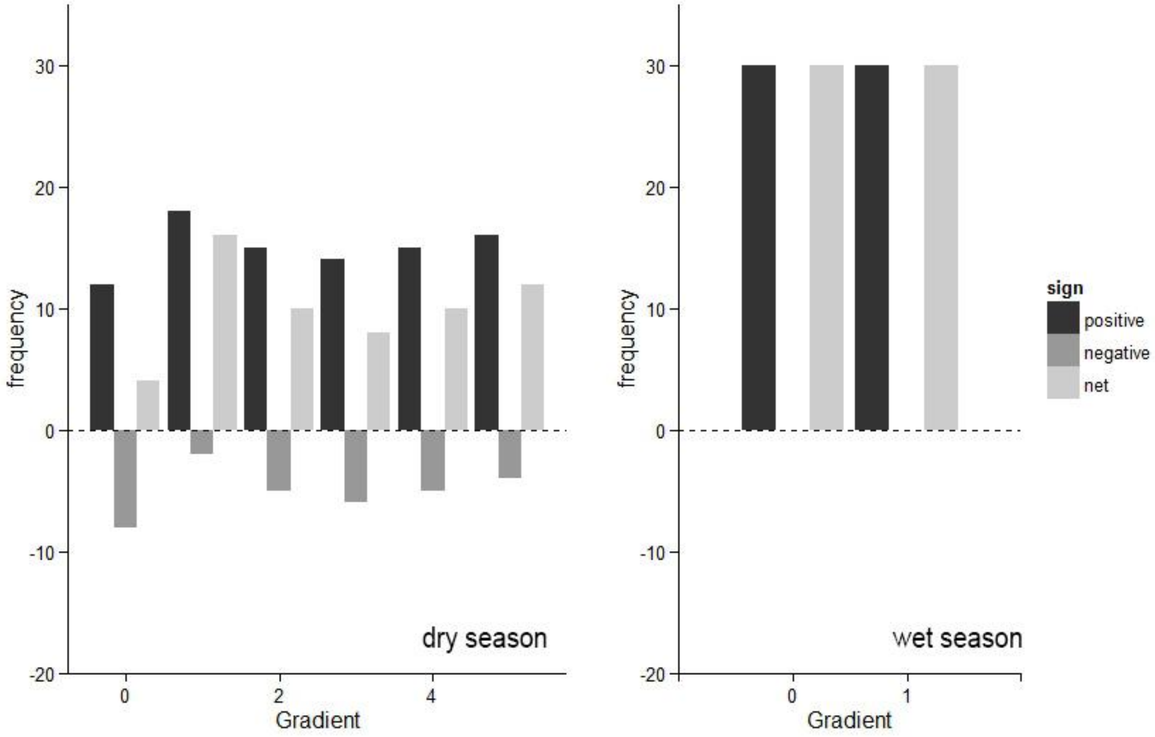

Figure E.1: Frequency of the sign of interactions among plots in each water level for the dry and wet seasons.

Appendix F – Weather station locations along gradient

Table F.1: Locations of the weather stations used that were closest in proximity to the study sites. The same weather station was used for both years and climate data that were collected included, mean air temperature (°C) and daily precipitation (mm). The climate networks that were used included the California Irrigation Management Information System (CIMIS) and the Community Environmental Monitoring Program (CEMP).

id	Site	Weather station	Network	Initialization Date	Lat	Lon
1	Panoche Hills	Panoche.A	CIMIS	01-Jan-95	36.8900°	-120.7314°
2	Cuyama Valley	Cuyama	CIMIS	01-Jan-90	34.9425°	-119.6738°
3	Tejon Ranch	Palmdale	CIMIS	01-Jan-05	34.6149°	-118.0324°
4	Barstow / Ft. Irwin	Newberry Springs II	CIMIS	25-Feb-15	34.8834°	-116.8102°
5	Heart of Mojave	Cadiz Valley	CIMIS	28-Oct-10	34.5136°	-115.5106°
6	Sheephole Valley Wilderness	Joshua Tree	CIMIS	16-Nov-11	34.1381°	-116.2131°
7	Tecopa	Tecopa/Shosone	CEMP	01-Jan-08	35.9483°	-116.3495°

Appendix G – Phytometer species characteristics

The chosen phytometer species within this study were *Phacelia tanacetifolia*, *Plantago insularis*, and *Salvia columbariae*. These three species are desert annual plants in the Boraginaceae, Plantaginaceae, and Lamiaceae families respectively. *P. tanacetifolia* grows 15 to 100 cm in height, has leaves between 2 and 20 cm in length, and has purple flowers (Walden et al. 2013). *P. tanacetifolia* is widely distributed throughout California and in parts of Nevada and Arizona (Walden et al. 2013). However, it is more commonly found in the western portion of the state in the San Joaquin Valley and the mountains at the south of the Valley (Figure B.1). *Plantago insularis* has multiple alternate names and is also commonly referred to as *Plantago ovata. P. insularis* has small leaves between 2 and 17 cm and has white flowers (Rosatti 2012). *P. insularis* is widely distributed in southern California and throughout the Mojave Desert, but is generally absent from the San Joaquin Valley except on south-facing slopes (Figure B.1). *S. columbariae* grows 10 to 50 cm in height, has leaves between 2 and 10 cm in length and has flowers that are purple and white (Averett 2012). *S. columbariae* is widely distributed in California and neighbouring areas, especially on mountains at elevations less than 2,500 meters (Figure B.1).

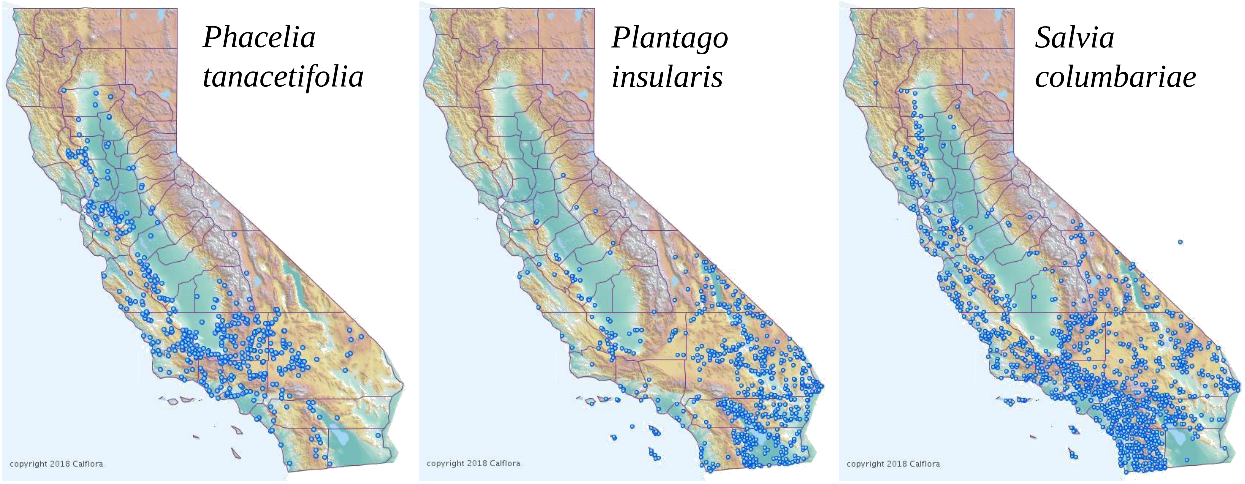

Figure G.1: Recorded observations of each phytometer species in California from the last 100 years (CalFlora 2018).

References:

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CalFlora (2018). Calflora: Information on California plants for education, research and conservation, with data contributed by public and private institutions and individuals, including the Consortium of California Herbaria. [web application]. Berkeley, California: The Calflora Database [a non-profit organization]. Available: http://www.calflora.org/ accessed on March 05, 2018.

De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. Oikos, 119, 1674-1684.

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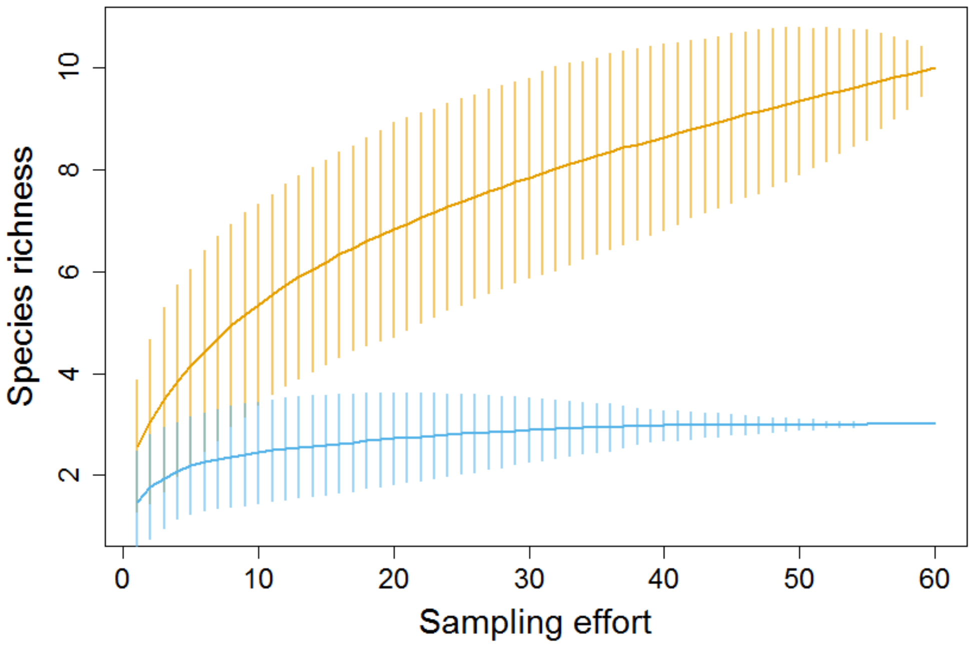
Walden, G.K., Patterson, R., Garrison, L.M. & Hansen, D.R. (2013). *Phacelia tanacetifolia*, in Jepson Flora Project (eds.) Jepson eFlora, Revision 1, http://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=37579, accessed on March 05, 2018.

Appendix H – Species accumulation curves along aridity gradient

We determined if the species we surveyed were a representative example of the species at each site by performing species-accumulation curves. We conducted species-accumulation curves (package *vegan*, function *specaccum*) separately for shrub and open microsites. The mean number of species obtained and the standard deviation was calculated from 999 random permutations of the data using sub-sampling without replacement (Gotelli & Colwell 2001). We also determined if certain species were significantly associated with a specific microsite within each site by using multi-level pattern analysis (library *indicspecies*, function *multipatt*). We conducted an indicator species analysis by using all possible combinations of groups of plots and calculating an indicator value to distinguish specific species to respective groups (Cáceres et al. 2010). We obtained p-values from the best matching pattern using permutation tests.

All sites were found to have reached an upper asymptote when species-accumulation curves were plotted (Figure C.1). Panoche Hills had a faster rate of species accumulation in open microsites relative to shrubs, but no other site had significantly different accumulation rates between microsites (Figure C.1). There were certain species that were significantly associated to a particular microsite depending on the location along the aridity gradient (Figure C.1).

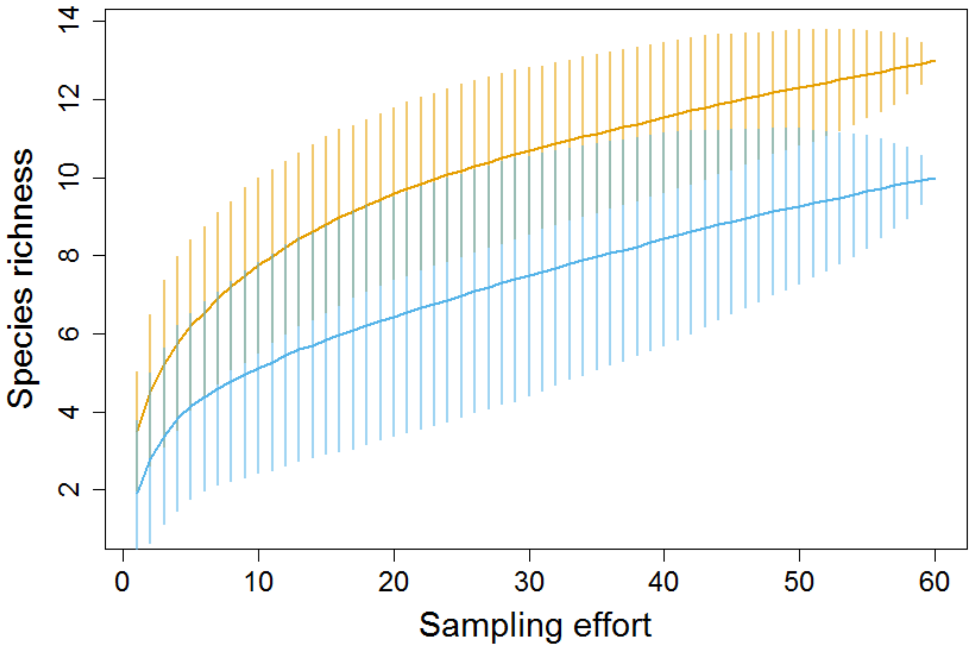


Panoche Hills

Shrub
None

Open

E. cicutarium
A. wrangelianus
A. grandiflora

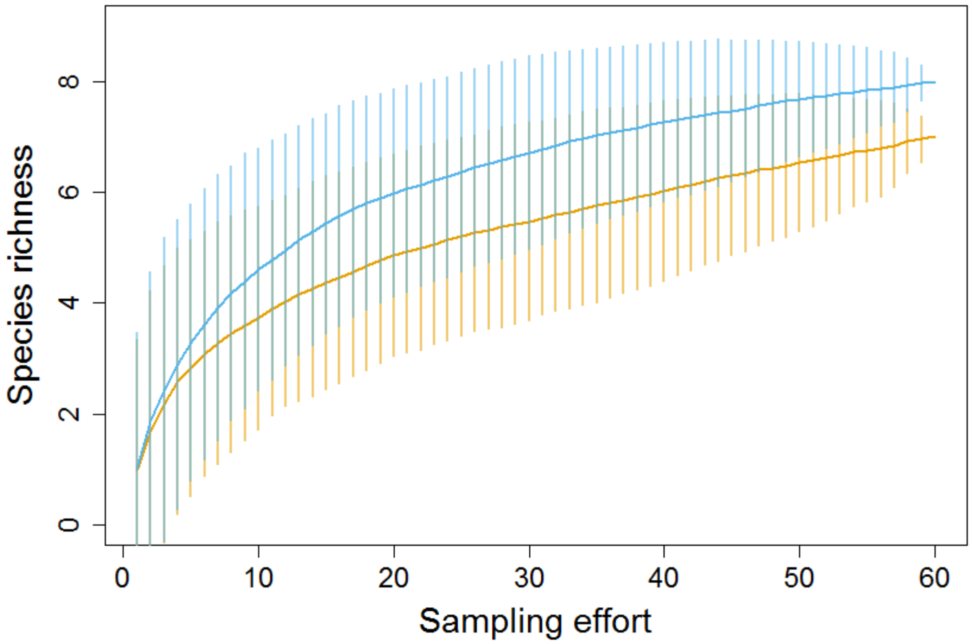


Cuyama Valley

Shrub
B. rubens
P. tanacetifolia

Open

E. cicutarium
L. gracilis
S. barbatus
C. barbigera
C. brevipes



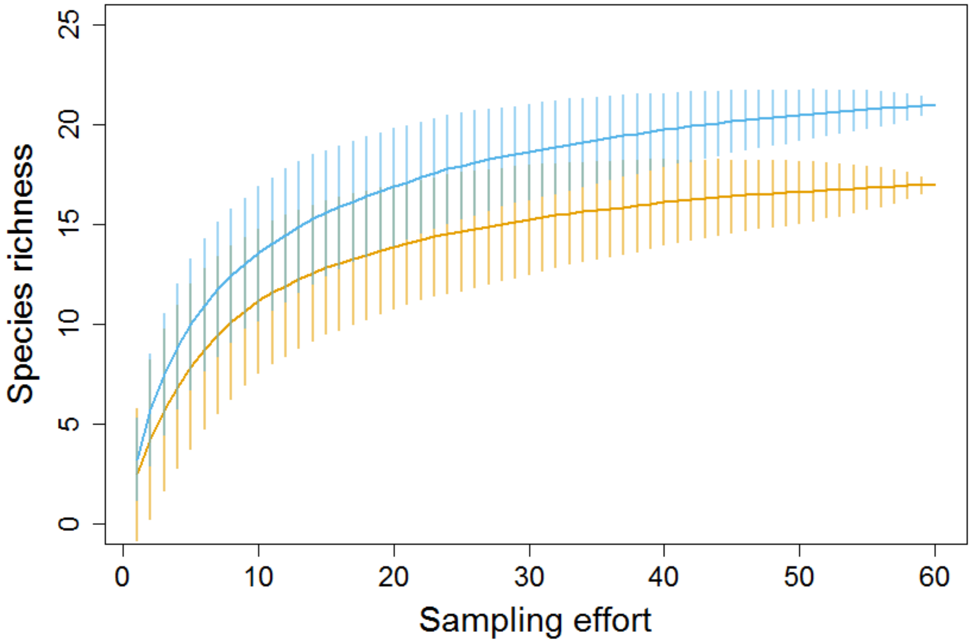
Barstow / Ft. Irwin

Shrub
C. fremontii
M. glabrata

Open

C. rigida

Heart of the Mojave



Shrub

C. fremontii

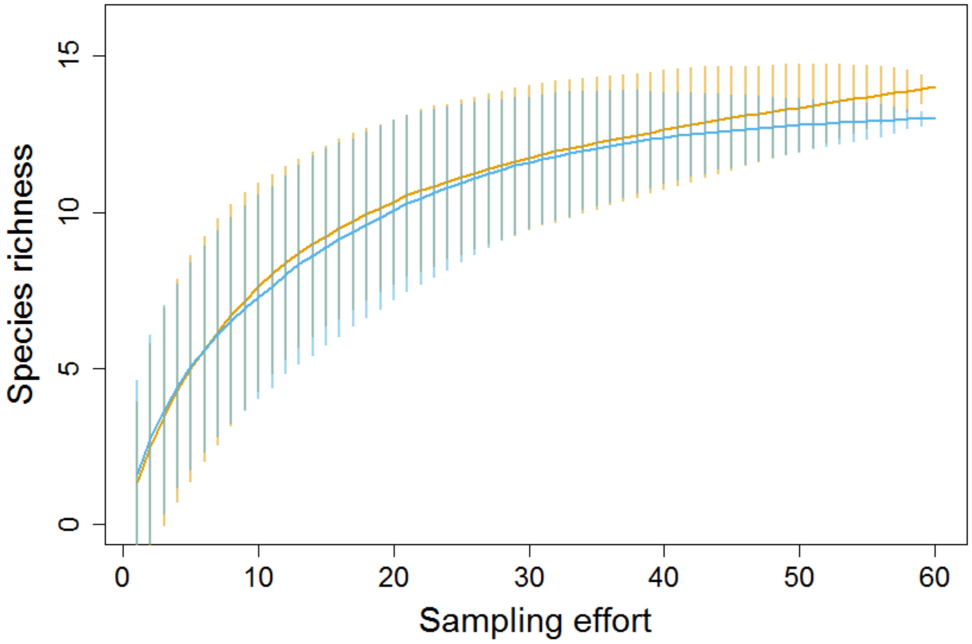
Pectocarya spp.

E. nitidum

Open

E. wallacei

Sheephole Valley Wilderness



Shrub

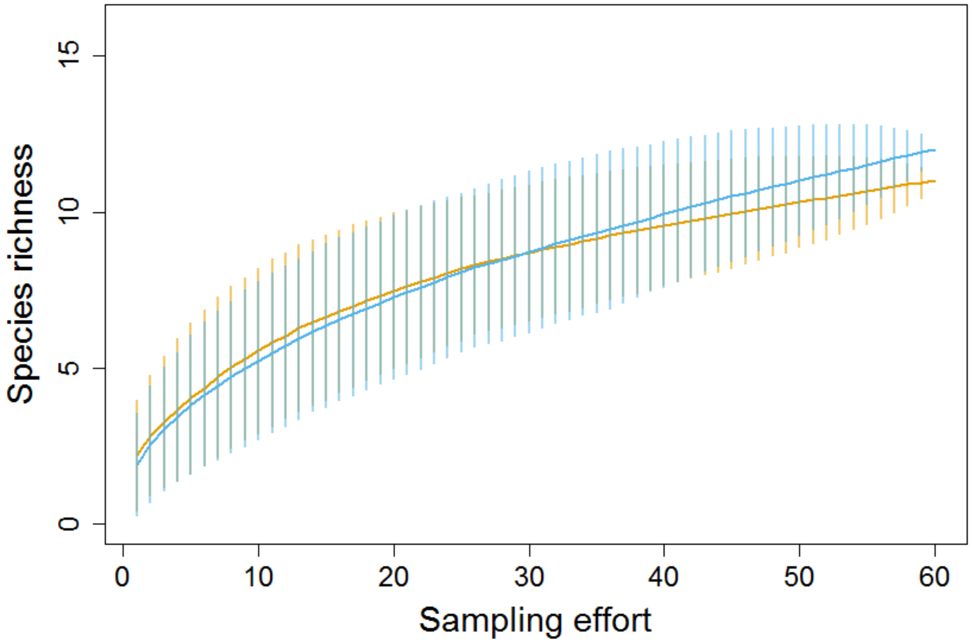
C. fremontii

M. glabrata

Open

None

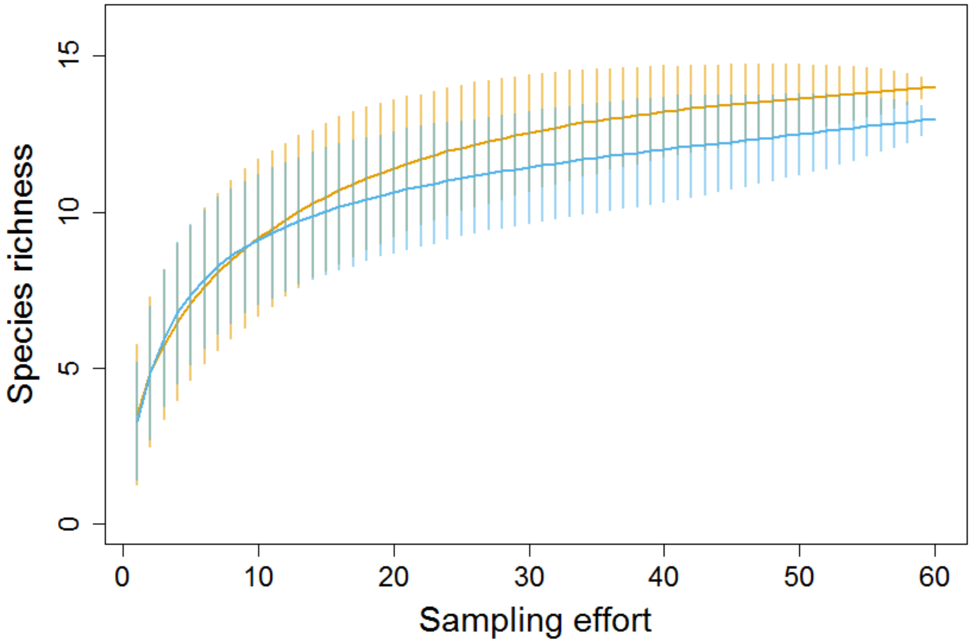
Tecopa



Shrub
None

Open
None

Tejon Ranch



Shrub
A. tessellata
B. nigra
M. affinis

Open
Boraginaceae sp.

Figure H.1: Species accumulation curves for shrub (blue) and open (orange) microsites at each of the seven sites along the gradient of aridity. Results from the indicator species analysis are shown on the right panel for species that significantly associated with specific microsites. Significant determined at α = 0.05.

Appendix I – Cluster analysis of communities

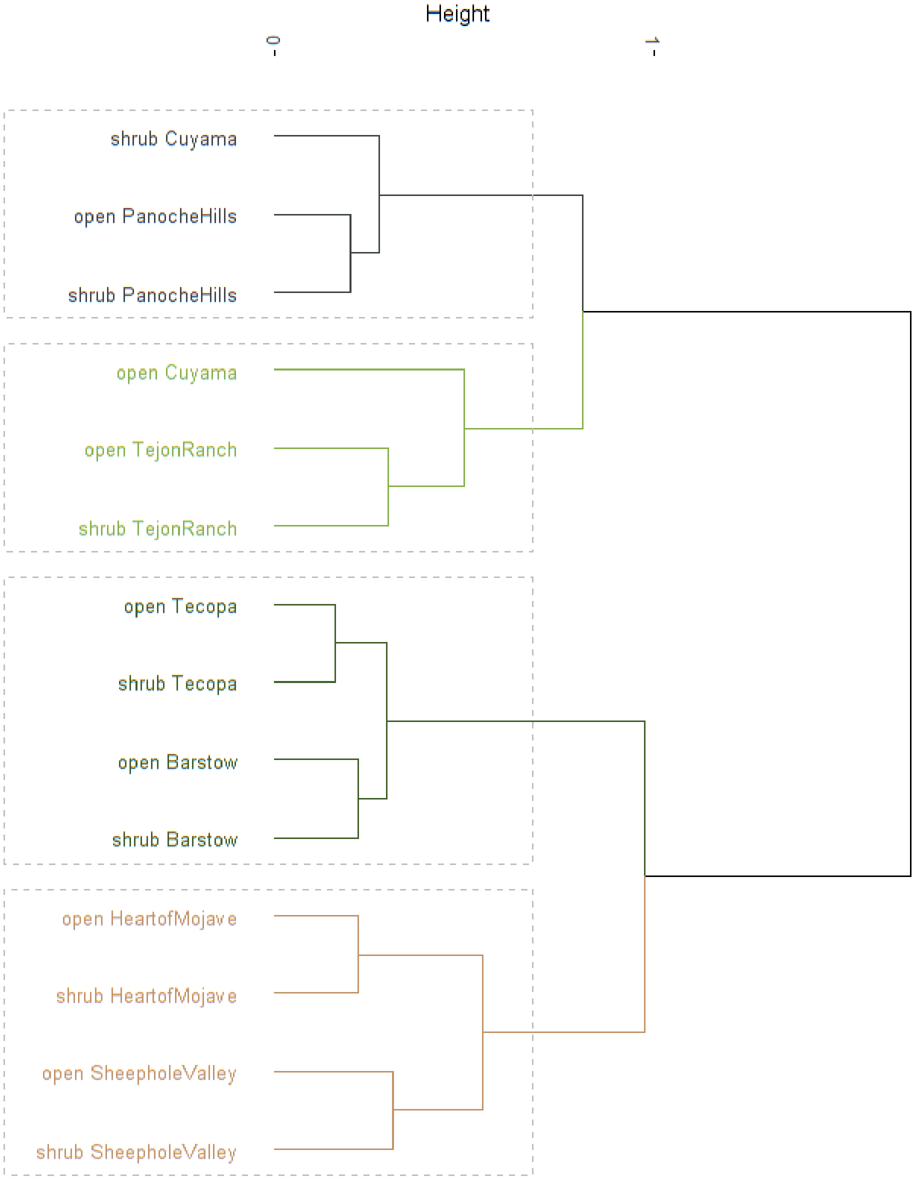


Figure D.1: Clustered dendrogram of each site based on the community dissimilarity. Community dissimmilarity calculated using Bray-Curtis and clustering calculated using Ward's minimum variance method squared. Four unique clusters were indentified.

Appendix J - BIOCLIM variables responsible for plant occurrence.

We used principal component analysis (PCA) to determine the BIOCLIM variables that explained annual occurrence using the *base* and *vegan* package in R (R Development Core Team 2016). For each occurrence of the facilitated and unreported plant species, four BIOCLIM variables were extracted for Southern California. These variables were elevation, temperature during the wettest quarter, precipitation during the wettest quarter, and precipitation seasonality. We then used PCA, which identifies orthogonal axes that best explain variation in environmental variables that linear and normally distributed. The four chosen bioclimatic variables explained ~97% of the environmental variation. PC1 represented differences in elevation and PC2 represented aridity (increasing temperature, decreasing precipitation) throughout the Mojave Desert in California (Figure 1).

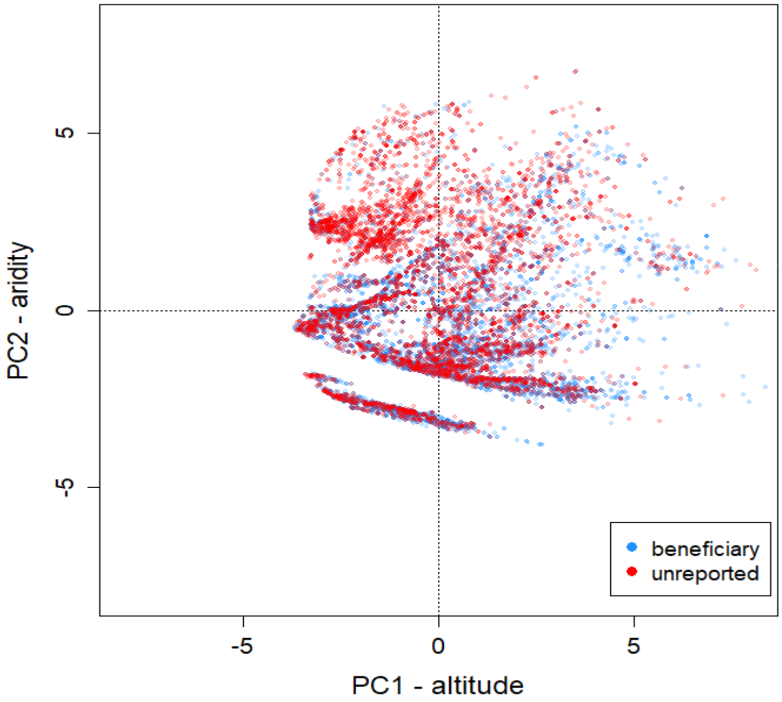


Figure J.1: The beneficiary and unreported plant species groups occupy similar climatic niches based a Principal Component Analysis of four bioclimatic variables at each plant occurrence.

Table J.1: Correlation matrix of environmental variables for 10,000 background points in Southern California.

Correlation	**Elevation**	**Annual Temp**	**Temp Seasonality**	**Temp wettest QR**	**Annual precip**	**Precip seasonality**	**Precipt wettest QR**
Elevation	1						
Annual Temp	-0.91	1					
Temp Seasonality	-0.05	0.39	1				
Temp wettest QR	-0.61	0.74	0.26	1			
Annual precip	0.59	-0.76	-0.69	-0.50	1		
Precip seasonality	0.014	-0.34	-0.81	-0.31	0.65	1	
Precipt wettest QR	0.49	-0.70	-0.74	-0.49	0.99	0.74	1

Table J.2: Best subset results for variables that predict annual plant occurrence. Fit to a binomial distribution with pseudo-absences generated from background climate data.

BIOCLIM variable	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Facilitated species				
(Intercept)	-22.3	1.16	-19.2	<0.001
Elevation	0.005	0.0004	12.3	<0.001
Annual Temp	0.099	0.006	16.8	<0.001
Temp Seasonality	-0.0005	0.00007	-7.6	<0.001
Temp wettest QR	-0.009	0.0005	-18.4	<0.001
Annual precip	0.18	0.003	6.17	<0.001
Precip seasonality	0.067	0.005	12.4	<0.001
Precipt wettest QR	-0.036	0.0053	-6.7	<0.001
Unknown species				
(Intercept)	-14.9	9.8	-15.25	<0.001
Elevation	0.003	0.0003	7.25	<0.001
Annual Temp	0.061	0.005	11.8	<0.001
Temp Seasonality	-0.0003	0.00005	-5.11	<0.001
Temp wettest QR	-0.0041	0.0004	-9.98	<0.001
Annual precip	0.0083	0.003	3.30	0.009
Precip seasonality	0.054	0.0048	11.2	<0.001
Precipt wettest QR	-0.016	0.005	-3.40	<0.001

Appendix K - Workflow of Model Inputs for MaxEnt

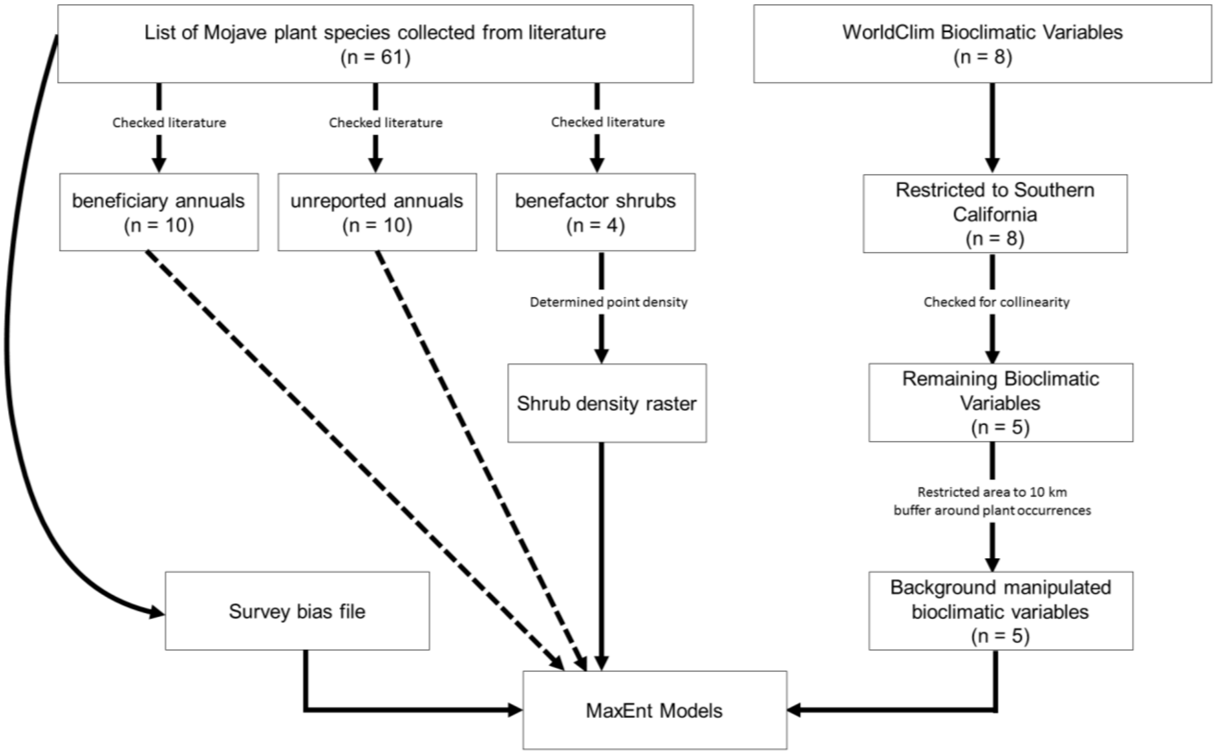
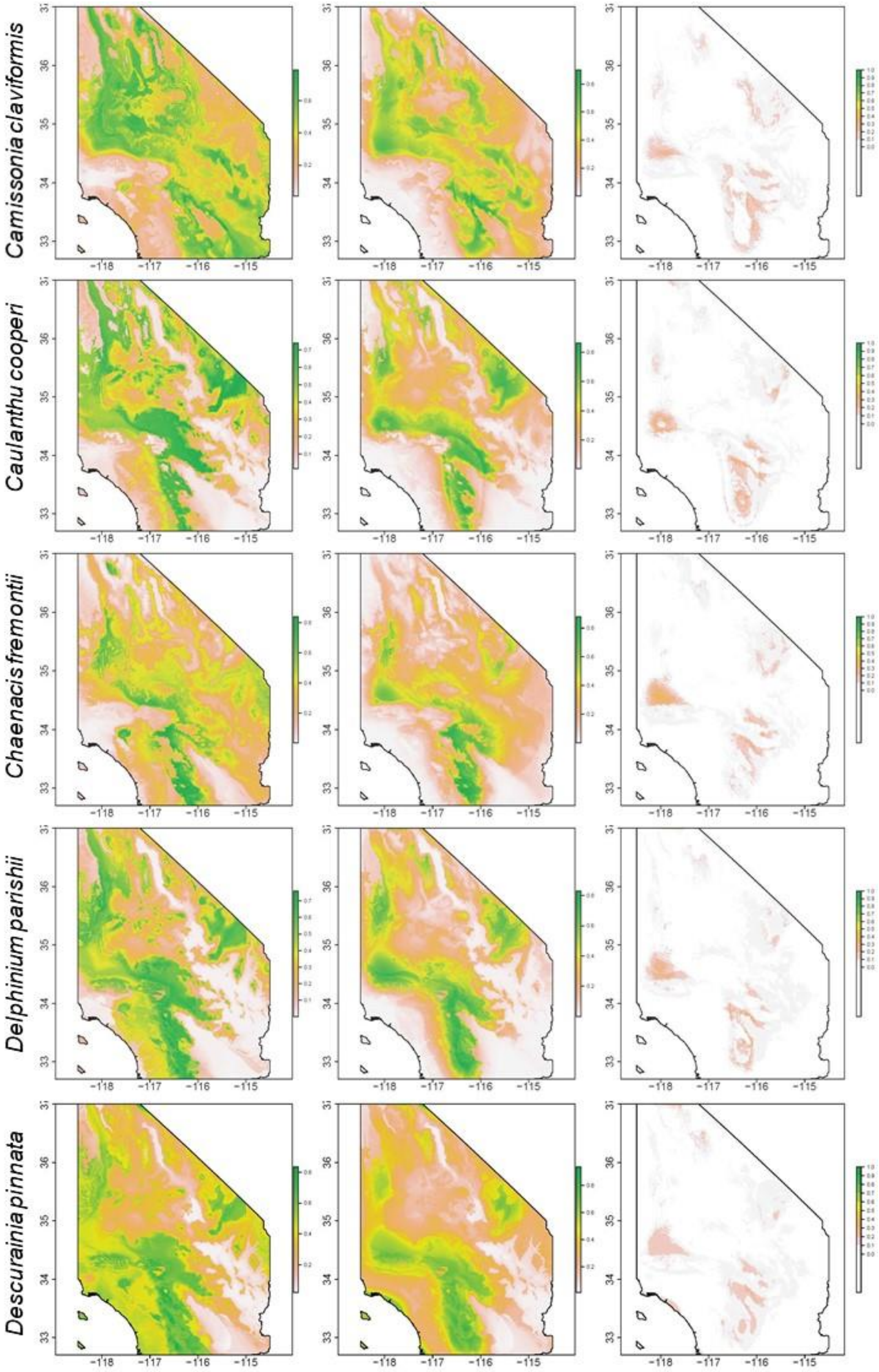
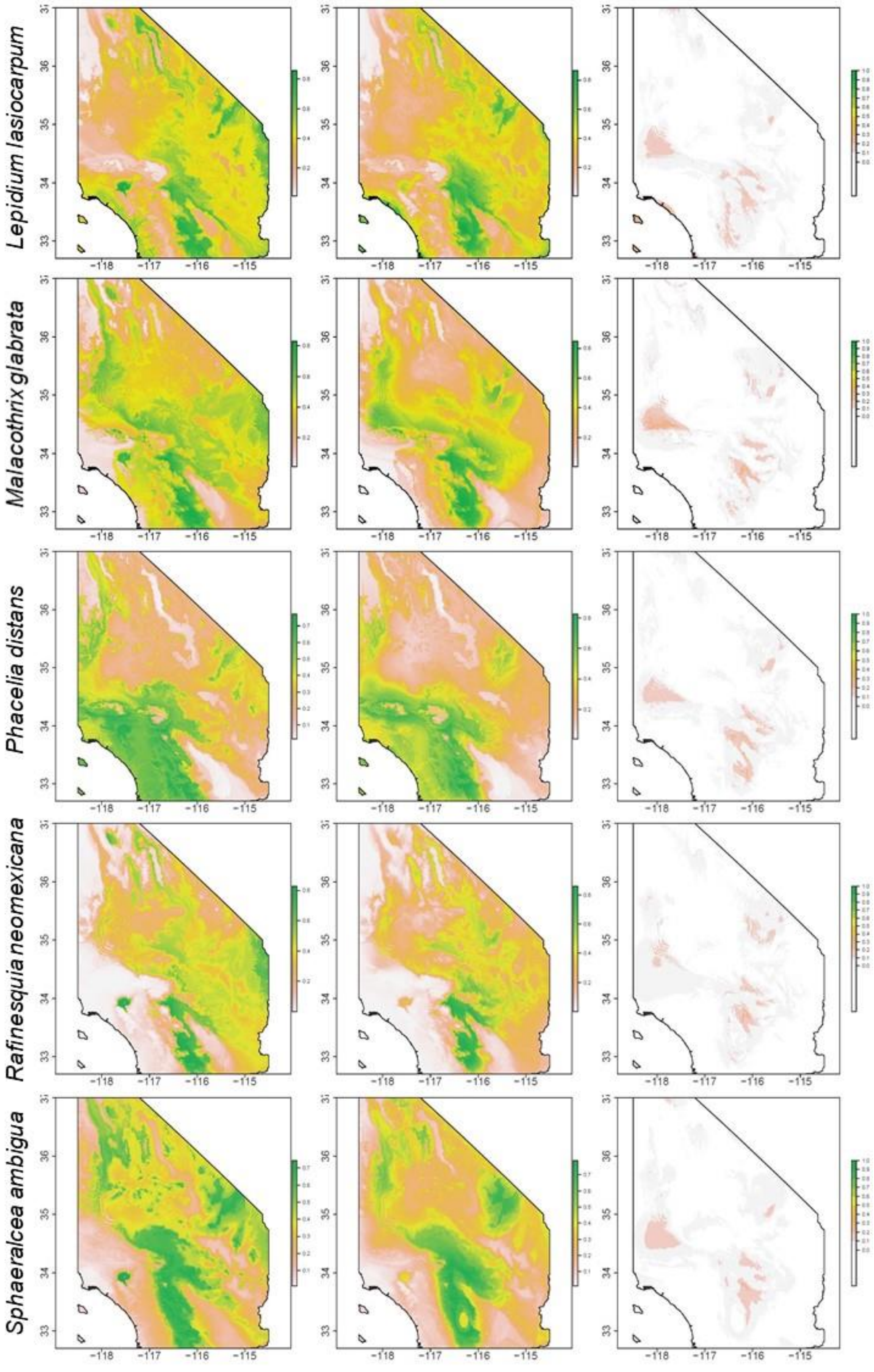


Figure K.1: A workflow of species selection, model inputs, and adjustments for survey bias in MaxEnt models. Solid lines represent consistent inputs for every MaxEnt model and dashed lines represents the changing input of species. Every species was modelled 40 times and a mean was used for the output statistics, such as AUC.

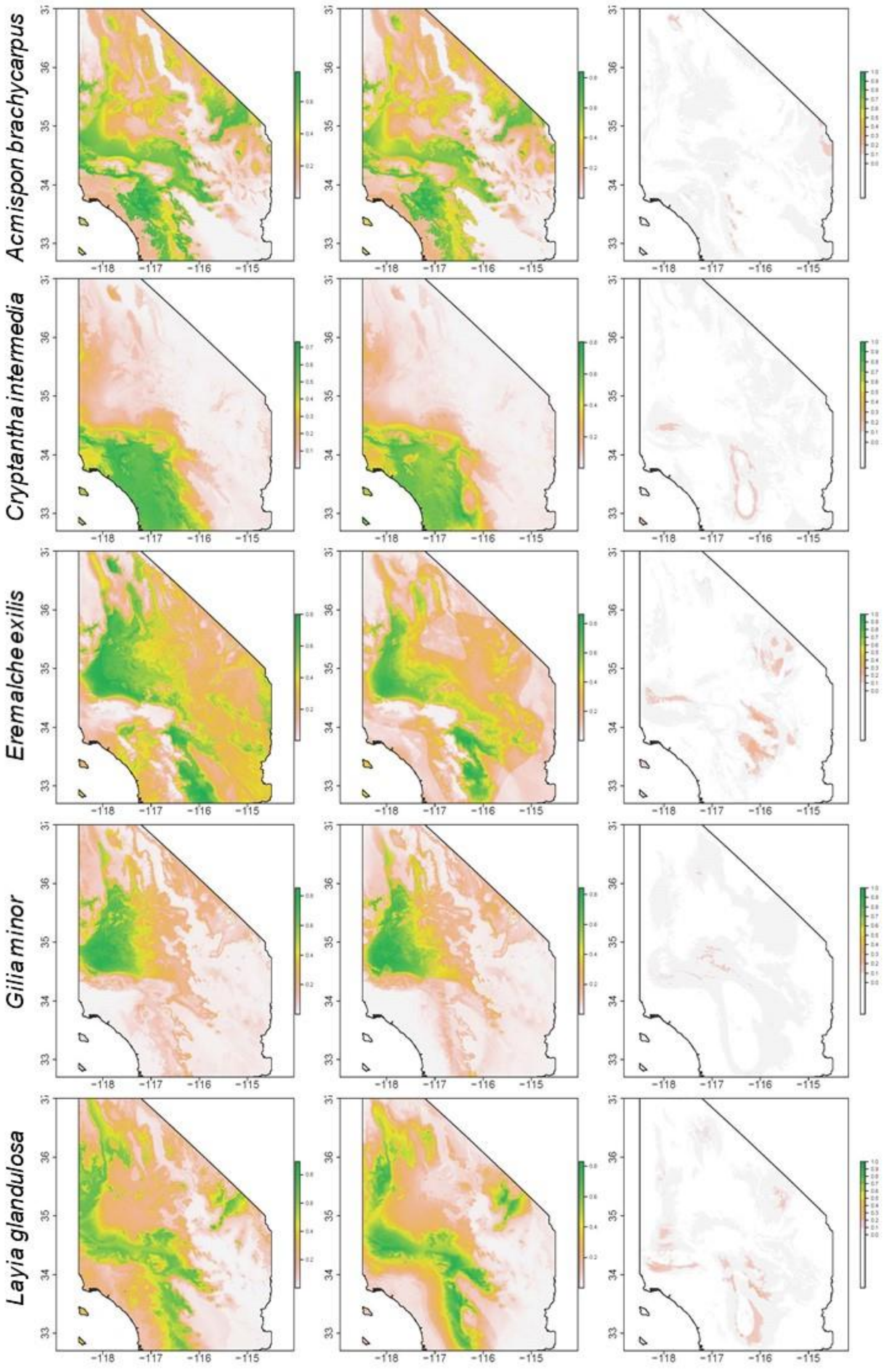
Appendix L – MaxEnt models of each annual species

Beneficiary




Lepidium lasiocarpum
Malacothrix glabrata
Phacelia distans
Rafinesquia neomexicana
Sphaeralcea ambigua
33
34
35
36
−118
−117
−116
−115

Unreported


Acmispon brachycarpus
Cryptantha intermedia
Eremalche exilis
Gilia minor
Layia glandulosa
33
34
35
36
−118
−117
−116
−115

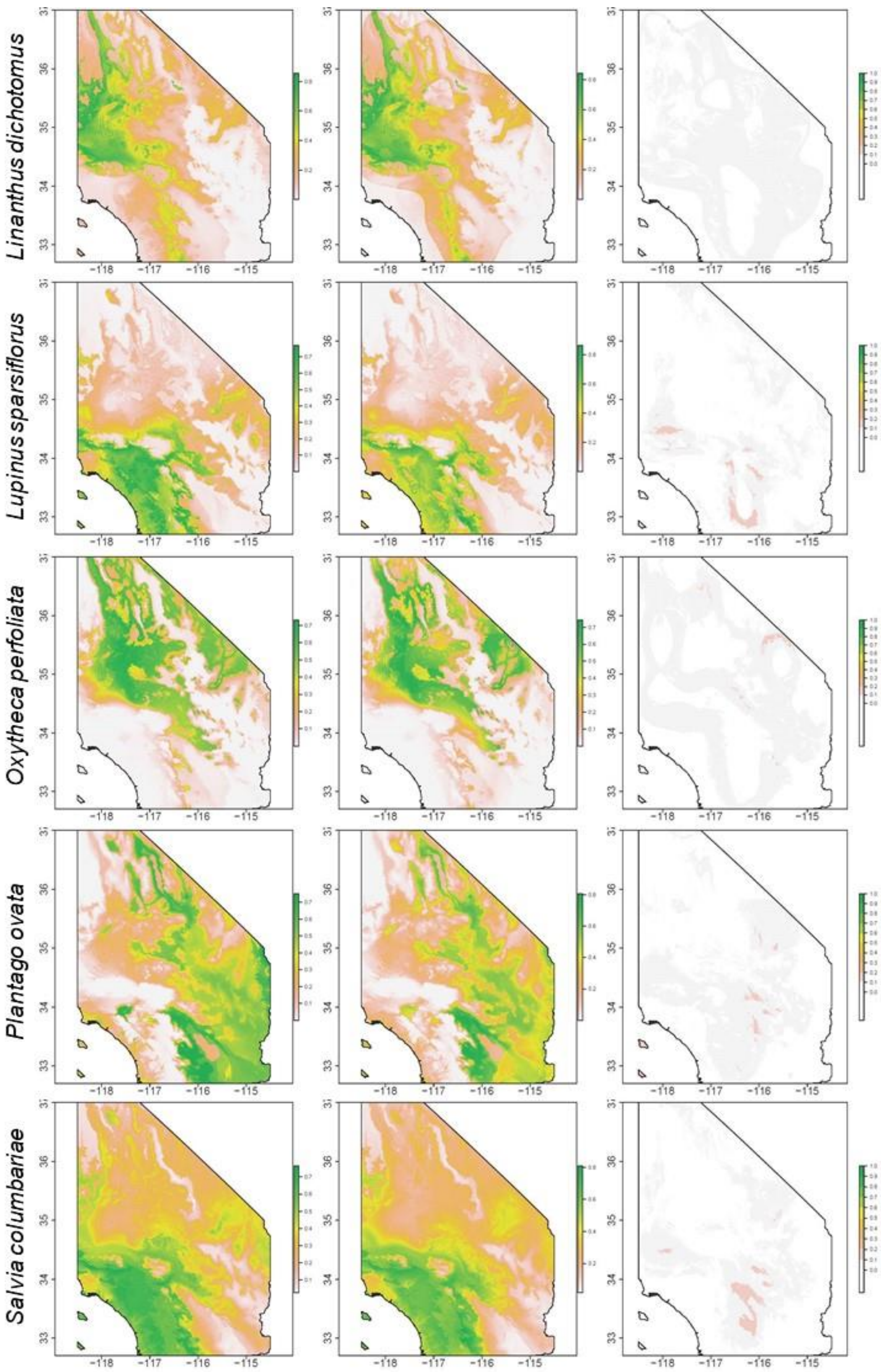

Linanthus dichotomus
Lupinus sparsiflorus
Oxytheca perfoliata
Plantago ovata
Salvia columbariae
37
36
35
34
33
−118
−117
−116
−115

Figure L.1. An example iteration of the species distribution models for each species. Each map represents probability of occurrence for each species between 0 (low) and 1 (high probability). The panels from left to right correspond to the climate only model (m_{env}), climate and shrub model ($m_{shrub.env}$), and the difference between both models (HS_{diff}).

Appendix M – Species list

Table M.1: A list of all the identified desert annuals species within this project

Genus	Species	Common name	Origin
Aristida	adscensionis	sixweeks treeawn	native
Camissonia	brevipes	yellow cups	native
Camissonia	claviformis	brown-eyed primrose	native
Camissoniopsis	cheiranthifolia	beach suncup	native
Camissoniopsis	pallida	pale primrose	native
Chaenactis	fremontii	Fremont's pincushion	native
Chorizanthe	rigida	Devil's spineflower	native
Cryptantha	intermedia	common cryptantha	native
Eremalche	exilis	white mallow	native
Eriastrum	eremicum	desert woolystar	native
Eriophyllum	wallacei	woolly daisy	native
Eschscholzia	californica	poppy	native
Eschscholzia	minutiflora	coville poppy	native
Gilia	achilleifolia	gilia	native
Langloisia	setosissima	bristly langlosia	native
Lupinus	arizonicus	Arizona's lupin	native
Lupinus	sparsiflorus	Coulter's lupin	native
Malacothrix	glabrata	desert dandelion	native
Monoptilon	bellioides	desert star	native
Nama	demissum	purple mat	native
Oenothera	deltoides	desert lantern	native
Phacelia	distans	Lace leaf phacelia	native
Plagiobothrys	nothofulvus	popcorn flower	native
Rafinesquia	neomexicana	desert chicory	native
Deinandra	kelloggii	tarweed	native
Acmispon	wrangelianus	Chilean bird's-foot trefoilë_	native
Amsinckia	grandiflora	common fiddleneck	native
Amsinckia	tesselata	bristly fiddleneck	native
Brassica	nigra	black mustard	non-native
Bromus	diandrus	ripgut brome	non-native
Bromus	hordeaceus	soft brome	non-native
Bromus	madritensis	red brome	non-native
Calyptridium	monandrum	sand cress	native
Castilleja	exserta	owls clover	native
Caulanthus	coulteri	lemmon jewel-flower	native
Caulanthus	lasiophyllus	California mustard	native
Cryptantha	barbigera	bearded cryptantha	native

Erodium	cicutarium	filaree	non-native
Eschscholzia	glyptosperma	desert poppy	native
Hordeum	vulgare	barley	non-native
Lasthenia	gracilis	gold fields	native
Layia	heterotricha	pale-yellow layia	native
Lepidium	nitidum	shining pepperweed	native
Leptosiphon	aureus	golden lianthus	native
Mentzelia	affinis	yellow comet	native
Monolopia	lanceolata	common monolopia	native
Pectocarya	setosa	comb-burr	native
Phacelia	crenulata	notch-leaf phacelia	native
Phacelia	tanacetifolia	blue tansy	native
Plantago	ovata	desert plantain	native
Salvia	columbariae	desert chia	native
Schismus	barbatus	kelch grass	non-native
Astragalus	lentiginosus	spotted locoweed	non-native
Dichelostemma	capitatum	blue dicks	native
Ephedra	californica	mormon tea	native
Erinoginum	fasciculatum	buckwheat	native
Poa	secunda	bluegrass	native
Amsinckia	tessellata	Bristly fiddleneck	native
Eriogonum	spp	Buckwheat	native
Poa	secunda	Bunch grass	native

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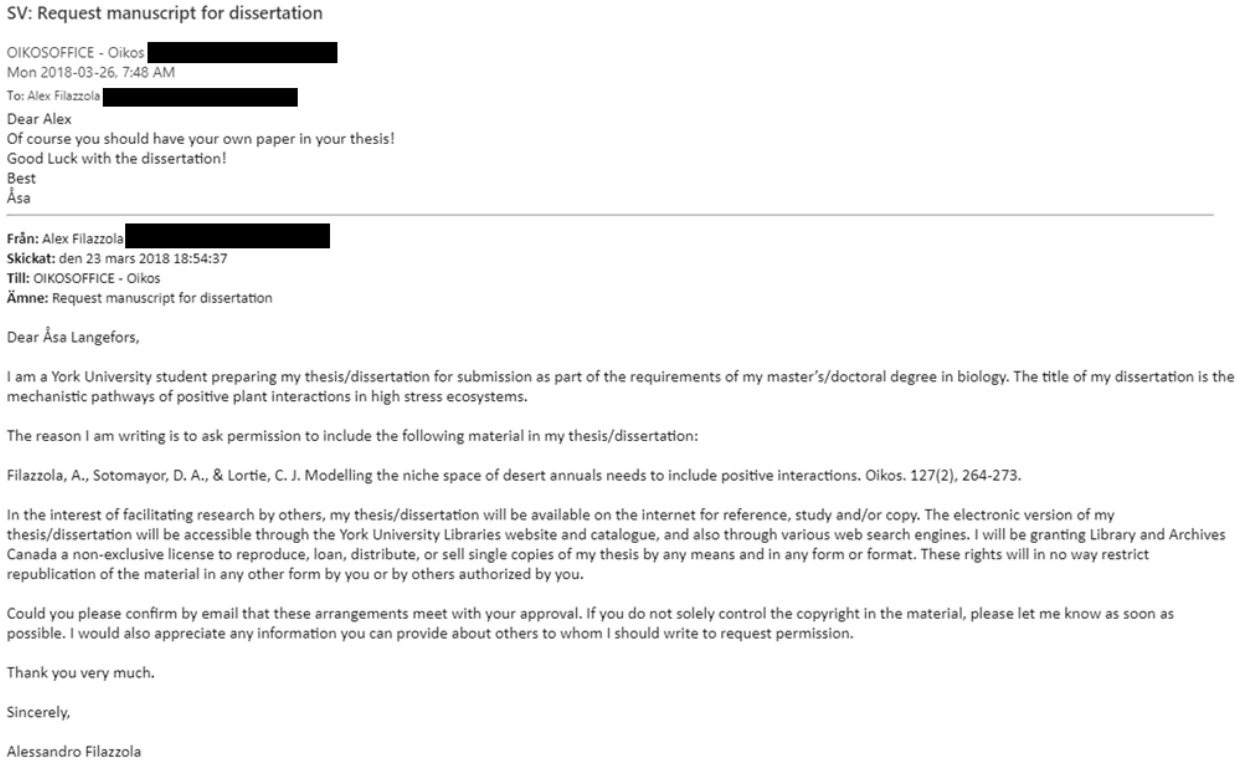

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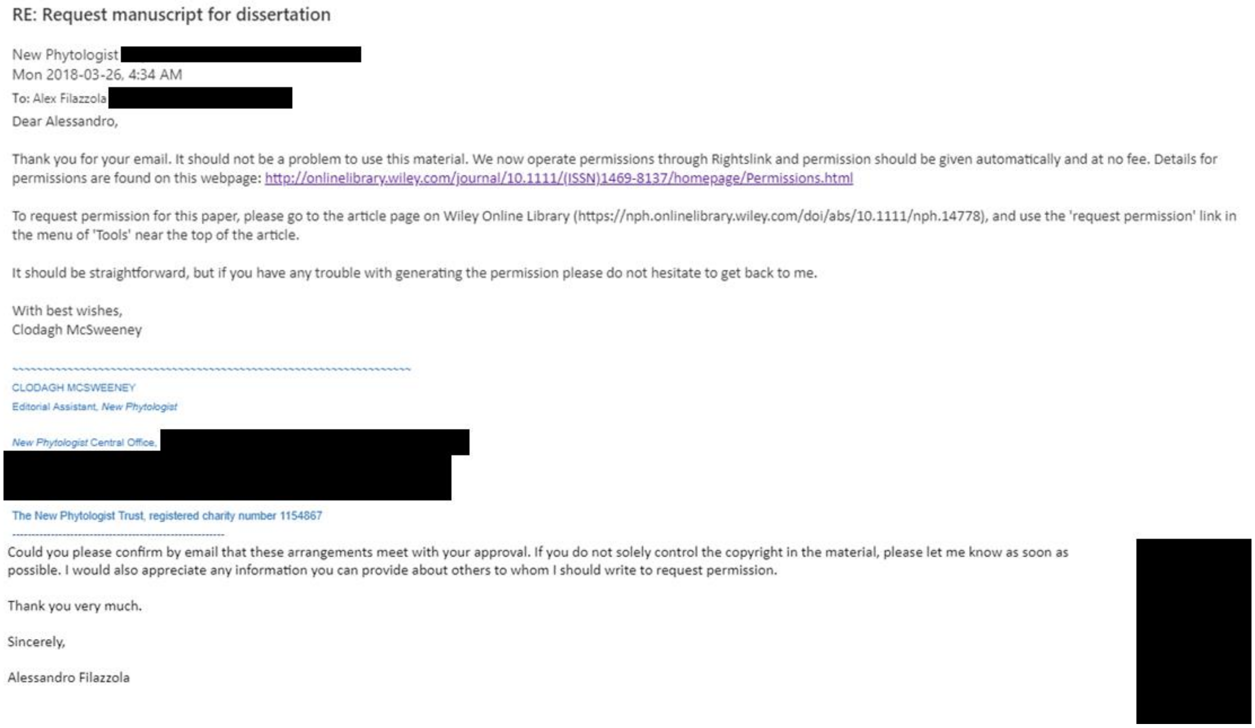

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