

EXTENDING PLANT-PLANT FACILITATION THEORY TO POLLINATORS: DO
DESERT SHRUBS ACT AS MAGNETS?

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Abstract

The magnet hypothesis proposes that flowering plants that attract pollinators can increase the relative pollination rates of neighbouring plants. The principal objective of this thesis was to 1) systematically review the theoretical and methodological trends in pollinator facilitation and magnet hypothesis literature, 2) to determine whether desert shrubs act as ‘magnets’ for pollinators, and 3) extend the study of shrubs as magnets by exploring reciprocity—testing whether the floral island they facilitate in their understory can also act as a ‘double magnet’ for pollinators. Video and *in-situ* observation techniques were used to monitor pollinator visitation for both insect and wind-pollinated shrubs and their understories. Shrubs were found to increase bee pollination frequency (but not duration) for understory plants, supporting the magnet hypothesis for shrubs. Evidence for the double magnet hypothesis was not found, as shrub flowers did not show increased pollination rates with the presence of understory annuals.

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General Introduction

Facilitation is an ecological theory in which organisms of different species interact positively so that at least one contributor benefits and neither are harmed (Bruno et al. 2003). When both contributors benefit from an interaction, this is considered a type of mutualism (Bruno et al. 2003). Mutualisms often involve obligate relationships that have co-evolved over a long evolutionary time-period, such as the relationship between Yucca moths (*Tegeticula spp.* and *Parategeticula spp.*) and *Yucca brevifolia*, or fig wasps and figs. These organisms have evolved together so that each provides necessary food or reproductive services for the other, and thus they rely on each other for survival. Another striking example of this is the bee orchid (*Orphrys*) and orchid bee (tribe: Euglossini). This relationship has become so highly evolved that these orchids can attract male pollinators by emitting pheromones and mimicking the look and feel of the female bee of that species (Schiestl 2005; Stokl et al. 2009). These signals stimulate mating behavior in the male bees visiting the plant who transfer pollen to their bodies and bring it to other orchids in the area. Facilitative and mutualistic relationships between plants are also common in nature. In some cases, they are the only way certain plants can sustain their populations when conditions might otherwise be unfavourable for survival or reproduction (He et al. 1997; Filazzola and Lortie 2014). Facilitation between plants can take on many forms; in cold, rocky, alpine conditions, cushion plants can facilitate the species that live on them by acting as temperature moderators, increasing the quantity and quality of soil nutrients, protecting from high winds, and absorbing and storing water which can then supply their subordinate species (Nunez et al. 1999; Cavieres et al. 2006; Nyakatya and McGeoch 2008; Reid et al. 2010). In the hot, arid conditions of deserts, shrubs act in similar ways to cushion plants

and can facilitate plants that grow within their understories both biotically and abiotically (Filazzola and Lortie 2014). This may be done by camouflaging them to reduce consumer pressure and damage by trampling, modifying the substrate and increasing understory nutrients, retaining and storing water, and/or by providing shade and protection from the wind and sun (Bruno et al. 2003; Filazzola and Lortie 2014). These interactions are most common in stressful environments, where there is competition for the limited resources that are necessities for sustaining plant life. The stress-gradient hypothesis proposes that facilitative interactions are most common in areas of high abiotic stress, while competition between species is more common in areas where abiotic stress is low, living conditions are moderate, and there is sufficient access to resources such as water and soil nutrients (Bertness and Callaway 1994). Though there has been some debate over the soundness and rigidity of this hypothesis (see: Maestre et al. 2005; Holmgren and Scheffer 2010), there has generally been support for this idea and thus much of the research on facilitation has taken place in ecosystems subject to abiotic stress such as the alpine and the desert (Lortie and Callaway 2006). Though the strength of facilitation and the mechanisms through which it occurs can differ between species and environments, mutualisms and plant-plant facilitation are nonetheless frequent mechanisms of survival for plants in high-stress ecosystems.

Facilitation between plants has been shown to span multiple trophic levels, scaling to some insect groups including arthropods and important pollinators such as bees. This scaling of facilitation pathways can be classified as a type of indirect interaction. An indirect interaction is one where the effect of one species on another is moderated by a separate,

third species (Sotomayor and Lortie 2015). In this case, that would mean that the facilitation of insects and pollinators (A) to the primary plant species (B), is mediated by a secondary plant species (C). The alpine cushion plant, *Silene acaulis*, and its subordinate species are a good example of this type of indirect interaction. Cushions have been shown to provide increased diversity and visitation by pollinators and other arthropods for their subordinate species compared to plants growing without cushions (Molenda et al. 2012; Reid and Lortie 2012). Here, the cushion is acting as the mediating species (C) between the plants growing on the cushions (B), and the insects and pollinators that are attracted to them (A). There are very few other known examples of this scaling of plant-plant facilitation to the insect community, but there is some evidence that shrubs in arid environments can facilitate insects in similar ways to cushions in the alpine. One study utilized pan-trapping to contrast insect abundance and diversity between shrub and open microsites and found that certain insect families (Sphecidae, Formicidae, Bradynobaenidae and Lauxaniidae) were positively associated with shrubs (Ruttan et al. 2016). However, the pan-trapping method of data collection made it unclear whether the increased insect populations in the understory of shrubs had any direct effect on understory annual plants (e.g. through pollination), or whether they were just attracted to the shrub itself. Shrubs could be acting as ‘magnets’ for the pollination of understory plant species. The magnet hypothesis (or magnet species effect) states that the presence of an attractive floral species can increase pollination for neighbouring plants (Lavery 1992). In the context of shrubs, this could mean that attractive, flowering shrubs draw in pollinators that are then shared with their understory species. This would increase understory plant pollination to levels that they would not experience without shrubs (Molina-Montenegro et al. 2008). The addition of

insects to the study of plant-plant facilitation and the direct examination of understory pollination is therefore a novel research gap in this body of literature. This plant-pollinator-plant interaction needs to be addressed to more completely understand the complexity of facilitation networks for the functioning of desert ecosystems.

The major objective of this program of study was to explore the facilitative relationship between plants and pollinators using a systematic review of the literature to date on pollinator facilitation and the magnet hypothesis (Chapter 1), as well as a manipulative study testing importance of desert shrubs for the pollination of their understory species (Chapter 2). The reciprocal facilitation of understory plants on shrub pollination was also tested to determine whether there was bi-directionality in this facilitation pathway, a cost of facilitation for shrubs, or if shrub pollination was unaffected by its understory. This thesis extends a previous study on the role of desert shrubs for insect communities by directly examining the pollination of annual plants growing under shrubs. Video and *in-situ* observation techniques were used in tandem to determine if there were differences in pollinator visitation rates to the understories of both insect and wind-pollinated desert shrubs relative to nearby open areas. To explore reciprocal effects, pollinator visitation to flowering shrubs was compared with and without annual plants in their understories. The hypotheses and major objectives/predictions from each chapter of this thesis are summarized in Table I.1. This thesis extends the knowledge of plant-plant facilitation in deserts by examining whether these interactions are mediated by pollinators. Shrubs could be very important contributors in deserts, and the results of this study have implications for the management and conservation of interactions in degraded desert systems.

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Tables

Table I.1. A Summary of the main purpose, hypotheses and associated objectives/predictions for each chapter of this thesis

Chapter	Purpose	Main hypothesis	Objectives/Predictions
1	Summarize research on the magnet hypothesis and pollinator facilitation to infer common practices and detect novel opportunities for future research and management	n/a	<ol style="list-style-type: none"> 1. What is the geographic extent of this research? 2. What observation techniques are used to study pollination in this field 3. What ecosystems are used to study these ideas? 4. What additional ecological theories are studied alongside the magnet hypothesis/pollinator facilitation? 5. What types of pollinators are used to study the magnet hypothesis/pollinator facilitation? 6. How many plant and pollinator species are used to study these ideas, and are these numbers related?
2	To contrast the direct and indirect pathways of facilitation via shrubs (and their associated annual community) on desert pollinators	The floral resource island created by shrubs and the beneficiary annual plants will have positive non-additive effects on pollinator visitation rates.	<ol style="list-style-type: none"> 1. Annual plants under shrubs will have a higher frequency of pollinator visitations than annual plants in the open 2. Annual plants under flowering insect-pollinated shrubs will have a higher frequency of pollinator visitations than annual plants under wind-pollinated shrubs 3. Shrubs with annuals in their understory will have a higher frequency of pollinator visitations than shrubs without annuals 4. Sites with both shrubs and annuals will have the highest frequency of pollinator visitations to both the shrubs and the annuals

Chapter 1: All for one, one for all: a systematic review of the magnet species effect for pollination

Summary

The magnet species effect proposes that an attractive, flowering plant can draw in pollinators and increase the pollination rate of neighbouring plant species, thereby facilitating reproduction. This formal systematic review summarizes the literature to date on the magnet species effect and pollinator facilitation in general to summarize research practices and detect novel opportunities for future research and management. Within each individual primary study, data were collected on the geographic location/ecosystem type, the underlying theories that were being studied alongside pollinator facilitation, pollinator richness and type, floral richness, and observational approach. The magnet species effect was tested most frequently in (often invasive) grassland ecosystems and few studies took place in stressful ecosystems such as desert and alpine environments. Most papers observed either all insect pollinators that visited experimental plots or a single social bee species (namely *Apis mellifera*). Relatively few studies focused on solitary bees, and this is unfortunate because these species are important pollinators of wild plants and excellent indicator species in many ecosystems. Pollinator and floral species richness were positively correlated, suggesting that diversity at some levels may be linked to diversity at other levels. Finally, few studies utilized alternative observation techniques to *in-situ* monitoring, including video, collection of specimens, or proxy measurements (e.g. seed counts and fruit set), providing opportunities for novel approaches to studying these ideas. Pollinator facilitation is thus an important research topic because it provides insights into community

theory, highlights the importance of interactions in the study of biodiversity, and provides alternative approaches to studying plant-animal interactions.

Keywords: bees, diversity, magnet species effect, magnet hypothesis, pollinator, plant-pollinator interaction, facilitation, synthesis, Web of Science, PRISMA, positive interactions.

Introduction

Pollinators and plants share a long evolutionary history and depend on one another for important functions. For many plants that reproduce sexually, visitation by pollinators is essential for fertilization (Kearns et al. 1998; Kreman et al. 2007), with 78-94% of angiosperms requiring animals for pollination, and thus reproduction (Ollerton et al. 2011). Pollinators benefit from this relationship through access to nutrient sources including pollen and nectar, and some take advantage of flowers for protection from abiotic conditions and for shelter while sleeping (Dafni et al. 1981; Sapir et al. 2006). While many insects can act as pollinators for plants, bees are the most dominant and efficient pollinators and are obliged to visit flowers for survival (Kearns et al. 1998). Thus, plants and pollinators have co-evolved to meet the needs of both taxa (Pyke 2016). Mutualisms, whereby species interact directly to provide mutual benefits for one another (Bronstein 2001), are well studied between plants and pollinators (Kearns et al. 1998; Bascompte et al. 2003). These obligate mutualistic interactions, along with facultative interactions between plants and pollinators represent a direct pathway of facilitation. However, there are also indirect pathways of facilitation (Michalet et al. 2014), and it has been proposed that these indirect positive interactions are crucial in maintaining plant-animal complexes in many ecosystems (Sargent and Ackerly 2008; Lortie et al. 2016). Indirect interactions necessarily involve a third species, and studies of plant-pollinator interactions at this level of complexity are thus important to advance ecological and evolutionary theory.

Plants and pollinators frequently interact indirectly. In most flowering plant communities, there is an overlap in bloom period for some length of time that predisposes communities to

these indirect plant-pollinator interactions (Ghazoul 2006). Competition for pollinators is frequently reported in co-flowering communities (Anderson et al. 1980; Pleasants 1980; Bell et al. 2005), but pollinator facilitation has also been reported and become widely recognized as a mechanism for both conspecific and heterospecific plants to share access to generalist pollinators (Rathcke 1983; Feldman et al. 2004; Ghazoul 2006). Many instances of diverse floral displays encouraging a net increase in pollination frequency and pollinator diversity have been reported (Ghazoul 2006, Duffy and Stout 2011, Liao et al. 2011, Wirth et al. 2011). This indirect pathway of neighbour-mediated pollinator facilitation is often termed the magnet hypothesis or the magnet species effect (Lavery 1992). The magnet species effect proposes that the presence of an attractive, flowering plant species draws in pollinators and generates a net increase in pollination for neighbouring, often less attractive plant species. The magnet species effect is important in many ecological situations including the spread of invasive species (Carvallo et al. 2013; Castillo et al. 2014). Native plants that co-flower in the same area as invasive plants have been shown to facilitate the diversity and abundance of pollinators, assisting in the reproduction and spread of the invader (Parker and Haubensak 2002; Carvallo et al. 2013). The opposite has also been reported wherein the presence of invaders increases pollinator abundance and diversity for native plants (Dietzsch et al. 2011; Waters et al. 2014). This facilitative interaction is critical for the persistence of many endangered plant species that rely on their neighbours to provide increased access to pollination to compensate for the negative consequences of rarity (Geer et al. 1995; Duffy and Stout 2011). The experimental approaches used to investigate pollinator facilitation and the magnet species effect vary widely and include observational counts, abundance data, pollen limitation, seed and fruit set, visitation rates,

and diversity measures (e.g. Ollerton et al. 2007; Carmona-Díaz and García-Franco 2009; Reid and Lortie 2012). A synthesis is now needed to examine the relative frequency of the key concepts and methods used to study this subset of plant-pollinator interactions.

Systematic reviews are an important formalized synthesis tool for ecology because they are transparent, reproducible, and can capture many of the quantitative dimensions of the primary studies (Lortie 2014). A systematic review was done here on the magnet-species effect for pollination to assess the scope of scientific inquiry into this hypothesis.

Specifically, the ecosystems in which these studies were carried out, the associated ecological theories, the reported levels of floral and insect diversity, and the methodological approaches, were extracted and categorized from the current primary research. Plant-pollinator interactions are strongly linked in many ecosystems, and it is therefore critical to identify research gaps because there are important implications for management and restoration of degraded ecosystems and the conservation of important species—both plant and pollinator alike. Understanding this body of literature will enhance how we study plant-pollinator interactions, and it will provide a focus for researchers in this field.

Methods

Literature search

Thomson Reuters Web of Science was used to conduct a systematic search of the literature in January, 2017. Through this search, we captured studies that directly tested and mentioned the ‘magnet hypothesis’ or ‘magnet species effect’, including those that tested very similar concepts such as pollinator facilitation and differences in pollination levels

with co-flowering plants in the same area. The following search terms were used: (magnet hypothesis OR magnet species OR pollinator facilitation OR co-flower) AND (pollinat*). The results were refined to English studies only, and the following discipline categories were selected: ecology, plant sciences, entomology, evolutionary biology, behavioural sciences, biodiversity conservation, environmental sciences, and forestry. This returned a total of 240 results (Appendix Fig. A.1) An initial title and abstract screen was conducted to ensure studies were relevant to the topic of pollinator facilitation and/or magnet theory and that this topic was the primary focus of the study. Additionally, included studies were refined to include only empirical research studies and to ensure that the ‘magnet’ species was different from the ‘target’ species—i.e. there needed to be a minimum of two plant species. Of the 66 studies that were retained at this stage (174 removed; Appendix Fig. A.1), a total of 48 remained after the full-text article was processed (18 removed; Appendix Fig. A.1). The final 48 publications spanned 22 years, from 1994 to 2016, and were published in a variety of journals including *Oecologia* (n=7), *Journal of Ecology* (n=5), *Ecology* (n=5), *Biological Invasions* (n=4), and *Plant Ecology* (n=4).

Analysis

Data were extracted from each study for multiple factors. (1) Geographic location/ecosystem: the GPS coordinates and ecosystem type that the study was performed in according to author (when not listed, this was determined via 3rd party descriptions of study location). (2) Underlying theories/topics studied concurrently with (and excluding) pollinator facilitation (3) Pollinator richness: the total number of pollinator species observed (if all available pollinators were sampled for a certain taxon, this was indicated). (4) Pollinator species (if given) and type (classified into: all visitors present, all insects

present (and not well distinguished), all bees present, solitary bees only, social bees only, single focal bee species only, and birds). (5) Floral richness: the total number of all floral species used including the magnet species (an average between sites was taken when appropriate). (6) Observational approach: (*In-situ*: observed pollination first hand in the field, video: video recording device used to observe pollination, proxy: visitation determined via a proxy for pollination e.g. seed set or fruit set, collection: insects collected via traps to determine pollinator abundance). Studies that encompassed more than one category for any of the above factors were classified into the dominant or primary category described for most cases so that each study was treated as one independent test of methodologies/theories. In cases where one category could not accurately describe the contents of the study, characters were double-coded into the two most applicable categories. Sensitivity analyses were done to ensure this coding did not conflate trends.

An evidence map (McKinnon et al. 2015) indicating the GPS locations of all studies on pollinator facilitation and magnet hypothesis used in this review (n=48) was created using the ggplot2 package in R (R version 3.3.2). A non-parametric Spearman rank-order correlation was used to compare pollinator richness and floral richness for the 19 studies used in this review that directly reported both pollinator and floral richness values (R version 3.3.2). A GLM (Poisson distribution) was conducted on the hypotheses tested as well as ecosystems used when studying the magnet species effect, to determine if there were any significant differences in the number of studies utilizing each of these categories (R version 3.3.2)

Results

The magnet hypothesis has been studied worldwide but most frequently in Europe and North America (Fig. 1). Grassland ecosystems were most commonly used to study pollinator facilitation and the magnet hypothesis (GLM, $\chi^2=17.956$, $df=6$, $p=0.006$; Fig. 2). More extreme environments such as the desert and alpine were studied infrequently (GLM, $\chi^2=12.237$, $df=3$, $p=0.007$; Fig. 2). Invasion biology ($n=18$) and competition ($n=7$) were the underlying theories that were most frequently studied following the magnet hypothesis/pollinator facilitation, particularly in grasslands (Fig. 2). Niche theory ($n=1$), conservation ($n=4$), mimicry ($n=4$), and indirect interactions ($n=1$) were least-frequently studied with the magnet hypothesis/pollinator facilitation (Fig. 2). Most papers observed all insect pollinators (Fig. 3) or a single, target bee species, predominantly the social bee species, *Apis mellifera* (Fig. 3). Studies that observed all visitors to flowers, birds only, all bees, and all social bees (not just one target social bee species) were infrequent in this review (Fig. 3). We found a strong positive correlation between pollinator and floral species richness in the 19 studies that reported both variables (Spearman rank correlation, $p=0.002$, $df=17$; Fig. 4). *In-situ* observation techniques were the most commonly utilized in all systems ($n=43$, Fig. 5). In general, collection, proxy measurements (such as seed and fruit set), and video observation were not well represented, together representing only five instances throughout the 48 studies (Fig. 5).

Discussion

Pollinator facilitation including the magnet species effect is an important ecological concept for evolutionary research and for restoration and management, especially because

of the rapid and significant decline in global pollinator communities. This synthesis effectively summarized the literature to date on this subject and suggests that it is a viable research hypothesis because of extent of study and the positive biodiversity relationships identified. If positive plant-pollinator interactions scale to higher level biodiversity patterns, this ecological effect is likely to be an extremely important subset of positive interactions within communities that needs to be examined more extensively. This review identified several theoretical and methodological trends. Grasslands are well studied but more extreme ecosystems such as the alpine and the desert are not. Pollinators are declining in these ecosystems too and we need to understand how interactions influence the function of these specific ecosystems (Scaven and Rafferty 2013). As such, the ecological theories associated with these stressful ecosystems (e.g. the stress gradient hypothesis; Bertness and Callaway 1994) need to be incorporated into the magnet-species literature. There was also a considerable research gap in the use of video observation techniques, pollinator collection, and proxy measurements when testing the magnet species effect on pollination. Video and camera observation is increasingly common in animal ecology in general with camera traps (Noble et al. 2016) and pollinators can also be more effectively examined using similar technologies that more comprehensively monitor a system (Lortie et al. 2012). We need to monitor threatened and declining pollinator species using technologies that can collect relevant data as rapidly as possible, and ensure that these pollinators are studied in the context of ecological interactions to most effectively protect remaining ecosystem functions.

Integration into ecological theory

The integration of the magnet species effect with more traditional ecological theories was most frequently done in grassland ecosystems. Concurrent testing with other ecological theories was rarely seen in more stressful environments such as desert and alpine ecosystems. While many theories such as competition, invasion, mimicry, and to a lesser extent, indirect interactions and niche theory, have been tested in grassland ecosystems, there are many other ecosystem types that lend themselves to the testing of both these and additional ecological theories. Arid and alpine environments, for example, have been hotspots for testing the stress gradient hypothesis (Lortie and Callaway 2006; Maestre et al. 2009). The stress gradient hypothesis predicts that facilitative and competitive interactions are inversely related and vary in intensity according to the amount of abiotic stress in an area, with instances of facilitation being greater when abiotic stress is high, and instances of competition being greater when abiotic stress is low (Bertness and Callaway 1994; Armas et al. 2011). While this hypothesis is predominantly used to test plant-plant facilitation and competition theory, insects in arid and alpine environments can be facilitated in similar ways to plants (Ruttan et al. 2016; Molenda et al. 2012). The stress gradient hypothesis is also likely pertinent for pollinators and the magnet species effect. In seasons with more stress and fewer flowers for instance, the strength of positive interactions between benefactor plants and other plants changes (Soliveres and Maestre 2014; Butterfield et al. 2015), and it is also reasonable to predict that this changes subsequent interactions with pollinators. Thus, these ideas should be tested in ecosystems that allow for similar gradients of stress (e.g. elevation, rain/snowfall, temperature, humidity, wind, etc.). These extreme ecosystems are highly sensitive to global change and interactions between species are likely being lost even more rapidly than the species themselves (Valiente-Banuet et al.

2015). As a result, pollinator facilitation and the magnet species effect need to be studied more extensively in these systems now, before these interactions become threatened or lost completely. The relationships between the plant community, the insect community, and the stress within an ecosystem is an important and novel research gap in light of global change and declines in pollinator populations worldwide.

Increased diversity in the floral display used to observe pollinators was positively correlated with the number of flower species observed when studying the magnet species effect. In general, the more diverse the floral display used to observe pollinators, the more diverse range of pollinators observed. This is likely the case because generalist flowers attract a wide range of pollinators whilst specialists attract fewer, more specific pollinator species (Motten et al. 1981). It is important to study both generalist and specialist pollinators in the context of the magnet species effect in order to understand whether this theory applies in all situations. Generalist social bee species such as *Apis mellifera* were studied frequently in the studies covered by this review, while many specialist bees and solitary bees in general were neglected—even though very few studies in this review were conducted in agricultural ecosystems. Arguably, plants that are pollinated by a wide range of generalist bee species are probably more likely to act as magnets, draw in pollinators, and increase the pollination of neighbouring plants than plants pollinated by specialists. However, this has not been tested and represents an interesting research gap in this literature because specialist bees have been found to have higher pollination effectiveness relative to generalists (Larsson 2005). Solitary bees also represent a huge gap in this research. They are the primary pollinators in many natural systems and it is important to

determine whether they respond in ways similar to honey bees and other insects to the presence of magnet flower species. Determining whether generalists or specialists are more tightly coupled via positive plant-pollinator interactions is critical for systems with solitary bees as the dominant pollinators. Although this was a cross-study synthesis and not an experimental study, the positive diversity relationships between plants and pollinators also suggests that the frequency of positive interactions between different taxa can sometimes relate to the underlying diversity within the community. It is also reasonable to propose that higher diversity levels correlate with the frequency of positive interactions across systems. This is a novel hypothesis for pollinators and plants because it suggests that plant-pollinator interactions can be a foundational interaction set for communities that scales to larger patterns of diversity.

Observation techniques

Methodologies associated with the magnet species effect have seen little advancement over the course of nearly three decades. *In-situ* observation was the most frequent method for pollinator observation when testing the magnet species effect. This is likely due at least in part to this being a convenient, cost-effective way of measuring pollination rates.

Furthermore, it does not require extensive post-processing of data or samples outside of the time spent in the field. *In-situ* observation nonetheless has many limitations that need to be considered when designing experiments to test pollinator visitation. *In-situ* observation can be very time consuming in the field, and even with plot randomization, it can lead to temporal biases in the data that are collected. There are limited hours of active pollination per day (Herrera 1990; Stone et al. 1999), and the number of replicates and individual plots that can be monitored are thus inherently restricted. The addition of multiple observers can

be used to increase the number of plots that can be monitored at the same time, but this adds in observer biases that are difficult to control and standardize between replicates (Ruttan and Lortie 2014). The physical act of being within or nearby plots during observation periods can also be disruptive to the natural behaviour of pollinators. The sight and scent of humans, as well as additional odors including those from sunscreen, insect repellent, etc., can significantly alter the results that would have occurred in a non-disturbed environment. Additionally, while ‘on-the-wing’ pollinator identification is practical and can provide instant results/data, it has not been shown to be particularly accurate (Becker et al. 1991) and should be used in conjunction with one, or a combination of other techniques. One of the most recent technological advances in pollinator research is the incorporation of video into experimental designs. Video observation is passive and drastically reduces the disruption of natural pollination (Lortie et al. 2012). The use of video recording devices such as the iPod Nano (5th generation) and Polaroid Cube allows for simultaneous observation of many plots at the same time. This reduces temporal and observation biases and increases the number of replicates that can be executed during limited hours of peak pollination (Lortie et al. 2012). While recording pollinators does produce much more post-processing work once fieldwork terminates, it can be easily disseminated using citizen science (Newman et al. 2012). Videos can be uploaded to open science databases, or even simple video platforms such as YouTube and processed by multiple people. Unlike *in-situ* data, video data can become part of bigger data networks, and can be re-watched and reused multiple times for different purposes and to answer many different ecological/behavioural questions (Gura 2013). *In-situ* observation is also not reproducible whilst recorded observations can be validate by additional researchers, shared, and

published online similar to camera trap imagery data (Noble et al. 2016). Hence, open data, open science, and alternative, affordable, and more reproducible contemporary monitoring solutions such as video, can be better advanced for plant-pollinator studies to explore visitations to target plant species in the field.

The collection of physical specimens—both of pollinators visiting flowers and the pollen/seed/fruit set of plants within experimental plots—is another useful addition to pollinator observation studies. The collection of visiting pollinators allows for accurate taxonomic identification and can even allow for the extraction of pollen from the body of the organism that can often be used to assess the species of plant that the pollinator has frequented (MacIvor et al. 2015). Through this technique we can determine the instances of effective pollen transfer, i.e. how much pollen on a bee collected from one plant species belonged to a conspecific versus a heterospecific species (MacIvor et al. 2015), as opposed to just the overall rate of flower visitation. Pollen, seed, and fruit samples directly from flowers provide another estimate of effective pollination rates as well as fertilization frequencies and reproductive success. While *in-situ* observation can be a good overall strategy for measuring pollinator visitation rates and has its place in pollination research, it should be incorporated with some of the other many underused technological and methodological advances in this field, such as the collection of pollinators and plant material, as well as video observation, to ensure that studies are producing both accurate and comprehensive results.

Conclusion

The magnet species effect has been studied globally for over two decades, but has not been extensively explored. Future studies should focus on the less-studied ecosystems such as the desert and alpine which are highly threatened by global change, and we need to test additional ecological theories that are likely linked to the magnet species effect, such as the stress gradient hypothesis. The loss of interactions and the sensitivity of generalist versus specialist pollinators are also critical sets of issues for ecosystems at large. This body of literature has lacked enough specific attention to social bees other than honey bees, and to solitary bees. More focus on these groups is needed as they are important pollination contributors in natural systems and these data would be very informative in developing management and restoration plans in sensitive systems. Furthermore, the *in-situ* methodology that has been used to study the magnet species effect is outdated and falls short of the technological and methodological advances that are readily and affordably available. Additional approaches such as the use of video recording devices, the collection of pollen and seed samples as proxy measurements for pollination success, and the collection of pollinator samples would vastly improve both the efficiency of data collection in the field, increase the accuracy of results, and provide opportunities for re-analysis for novel questions using the archived primary observational video.

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Figures

Figure 1.1. An evidence map showing the GPS locations of studies on pollinator facilitation and the magnet species effect for ecology. A systematic review was done using the Web of Science with specific terms and exclusions (n=48 independent studies, full criteria described in Methods).

Figure 1.2. The frequency of studies in this systematic review (n=48) discussing different ecological theories (e.g. none, niche theory, mimicry, invasion biology, indirect interactions, conservation, and competition) in addition to pollinator facilitation, and the various ecosystems these studies were conducted in worldwide (GLM_{theories}, $\chi^2=17.9567$, df=6, p=0.006341; GLM_{ecosystem}, $\chi^2=12.237$, df=3, p=0.006614)

Figure 1.3. The frequency of studies (n=48) on pollinator facilitation that observed different types of pollinators (all visitors, birds only, all insects, all bees, social bees, and one target bee species (social or solitary)). The size of the circle represents the relative number of papers utilizing each species category (actual number in parentheses within circle). Note that some circles encompass others, i.e. “all visitors” also includes studies that looked at birds in addition to other pollinators, whereas “birds” includes studies on birds only. Similarly, “target bee species” also includes social bees when only one species was used, as opposed to studies including all social bees.

Figure 1.4. Spearman rank correlation ($t = 3.6668$, $p = 0.001911$, $df=17$) between pollinator richness and floral richness in a subset of studies on pollinator facilitation used in this systematic review ($n=19$). Studies that reported that all floral species or all pollinators in a given area were observed, but did not list a specific number of species, were excluded from this evaluation.

Figure 1.5. The frequency of studies ($n=48$) utilizing different pollinator observation techniques (e.g. video, proxy, collection and *in-situ*) in various ecosystems worldwide from a systematic review of the literature on pollinator facilitation and the magnet species effect

Figure A1.1. PRISMA flow diagram depicting the workflow for the search and exclusion process of this systematic review on pollinator facilitation and the magnet species effect on pollination.

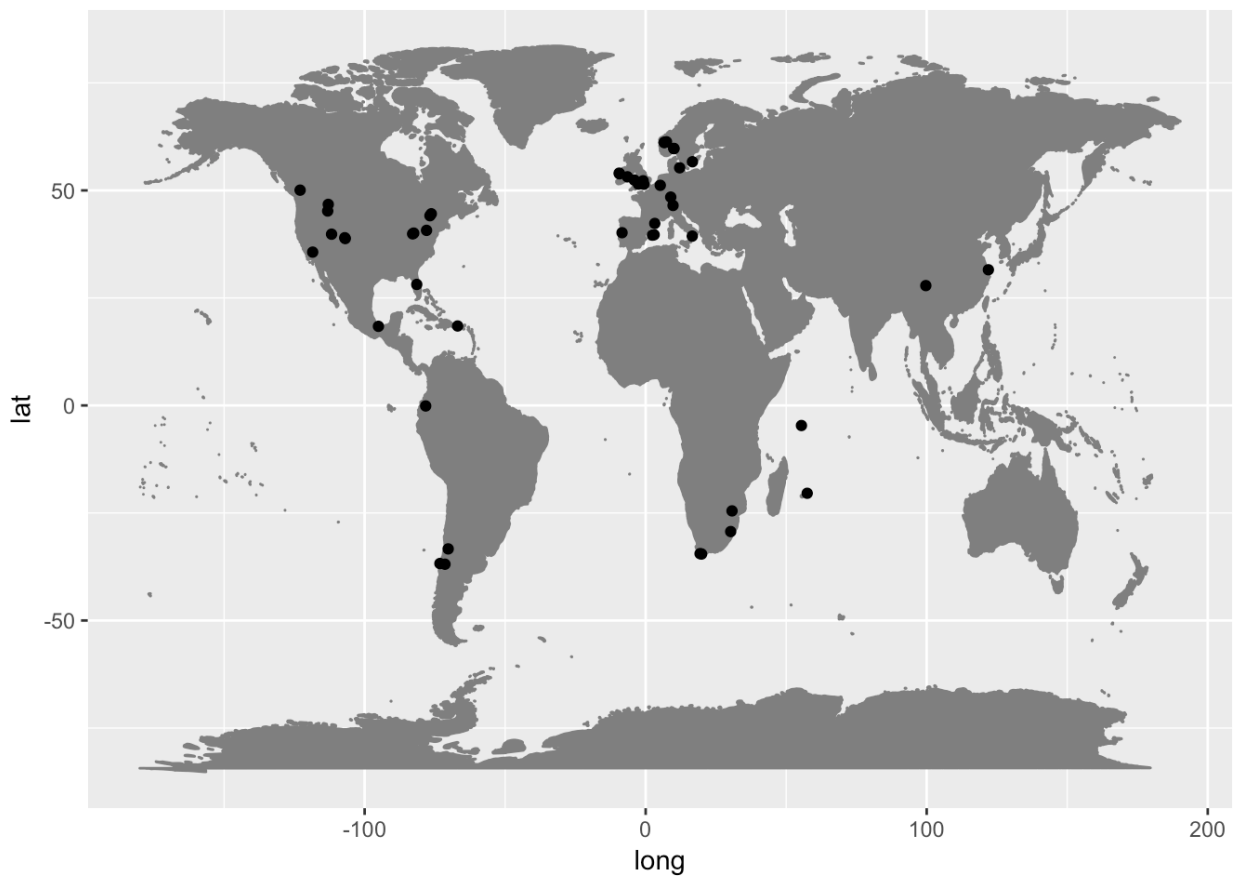


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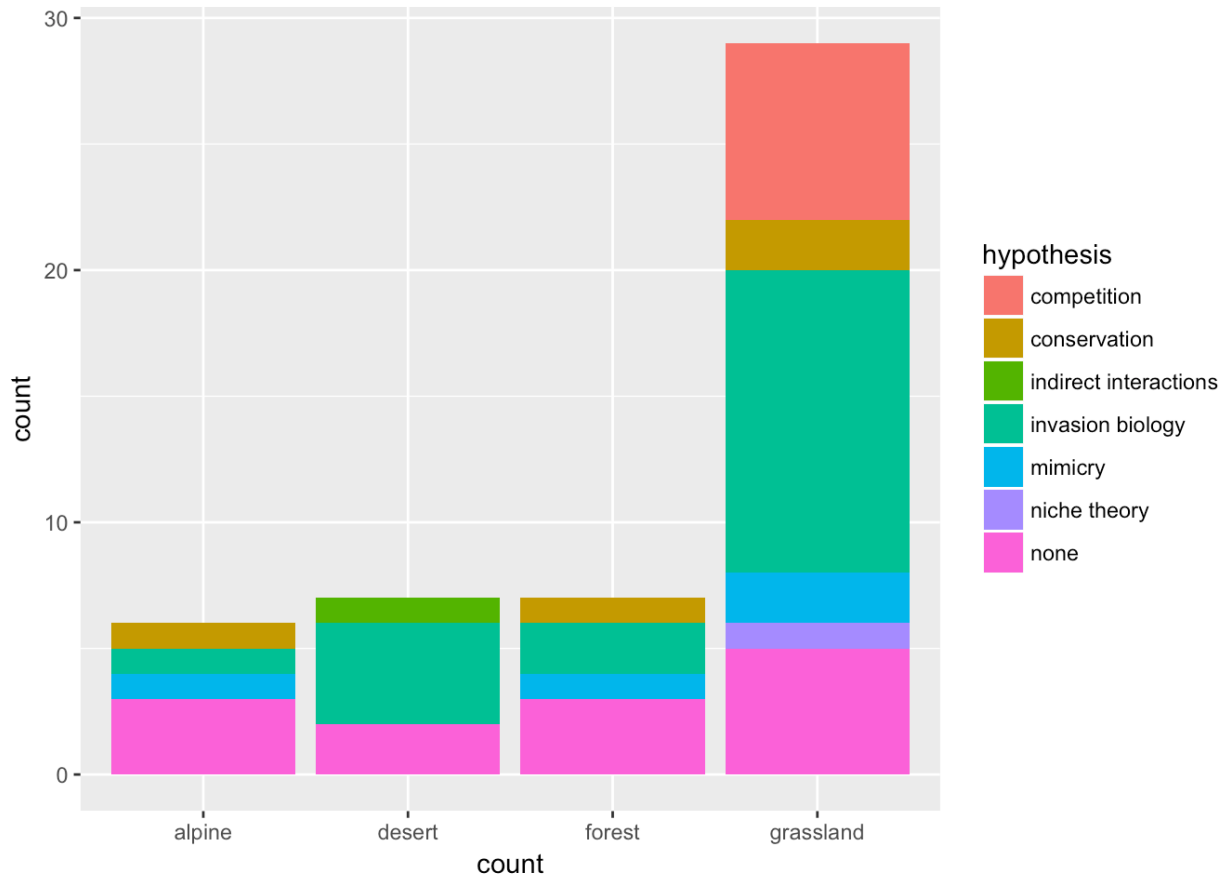


Figure 1.2. The frequency of studies in this systematic review (n=48) discussing different ecological theories (e.g. none, niche theory, mimicry, invasion biology, indirect interactions, conservation, and competition) in addition to pollinator facilitation, and the in various ecosystems these studies were conducted in worldwide.

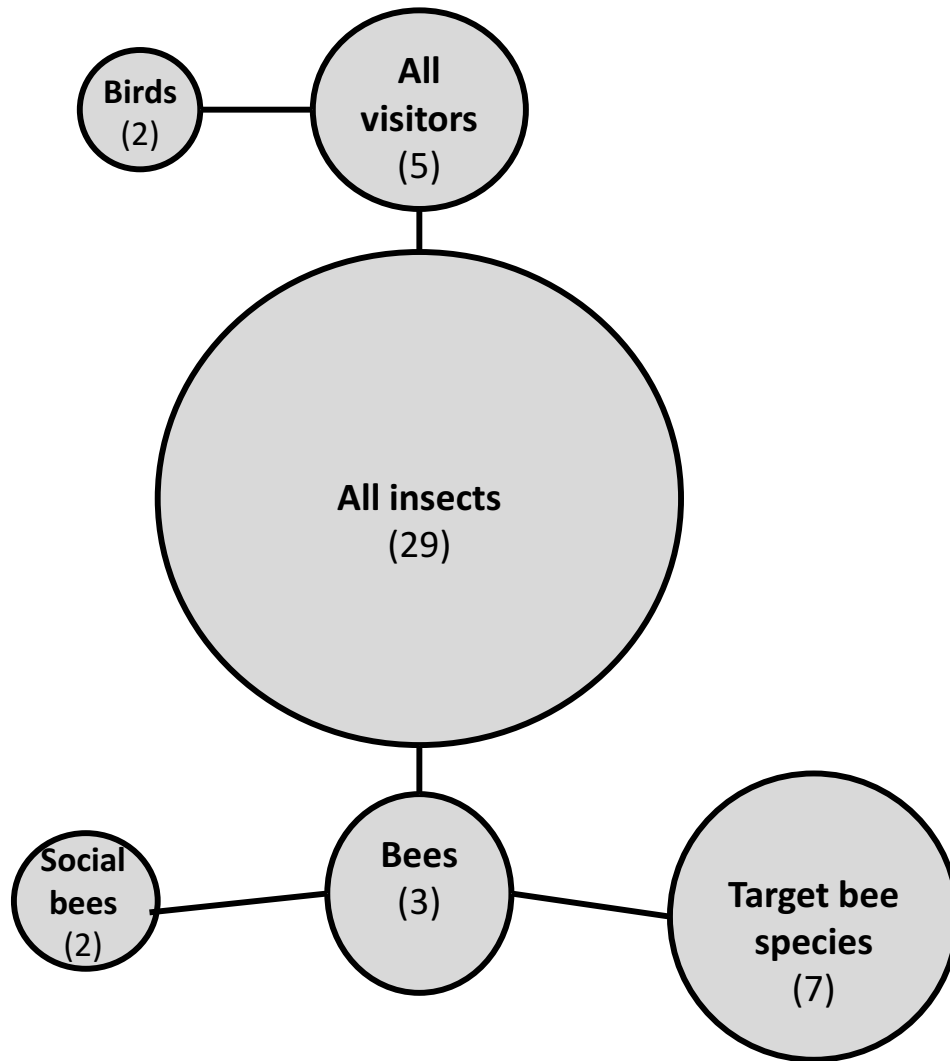


Figure 1.3. The frequency of studies ($n=48$) on pollinator facilitation that observed different types of pollinators (all visitors, birds only, all insects, all bees, social bees, and one target bee species (social or solitary)). The size of the circle represents the relative amount of papers utilizing each species category (actual number in parentheses within circle). Note that some circles encompass others, i.e. “all visitors” also includes studies that looked at birds in addition to other pollinators, whereas “birds” includes studies on birds only. Similarly, “target bee species” also includes social bees when only one species was used, as opposed to studies including all social bees.

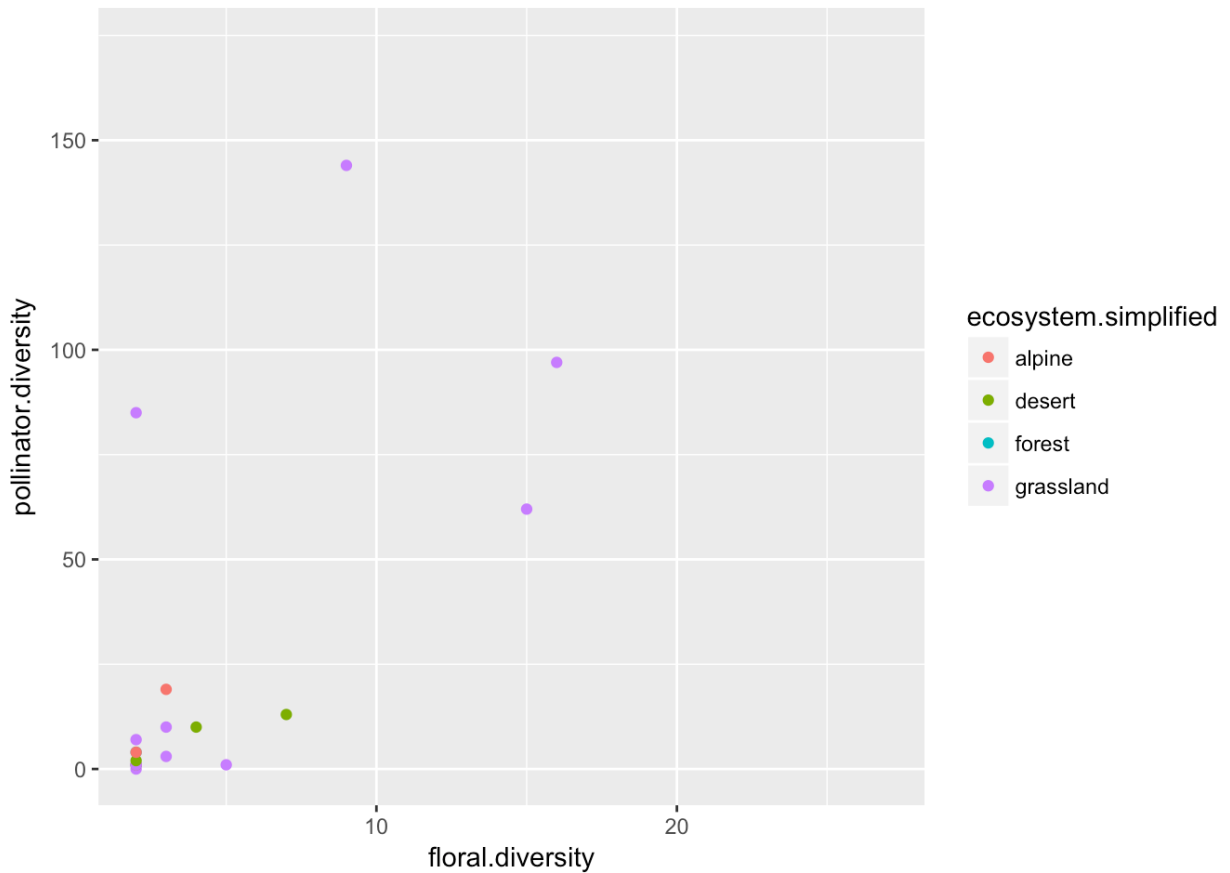


Figure 1.4. Spearman rank correlation ($t = 3.667$, $p = 0.002$, $df = 17$) between pollinator richness and floral richness in a subset of studies on pollinator facilitation used in this systematic review ($n = 19$). Studies that reported that all floral species or all pollinators in a given area were observed, but did not list a specific number of species, were excluded from this evaluation.

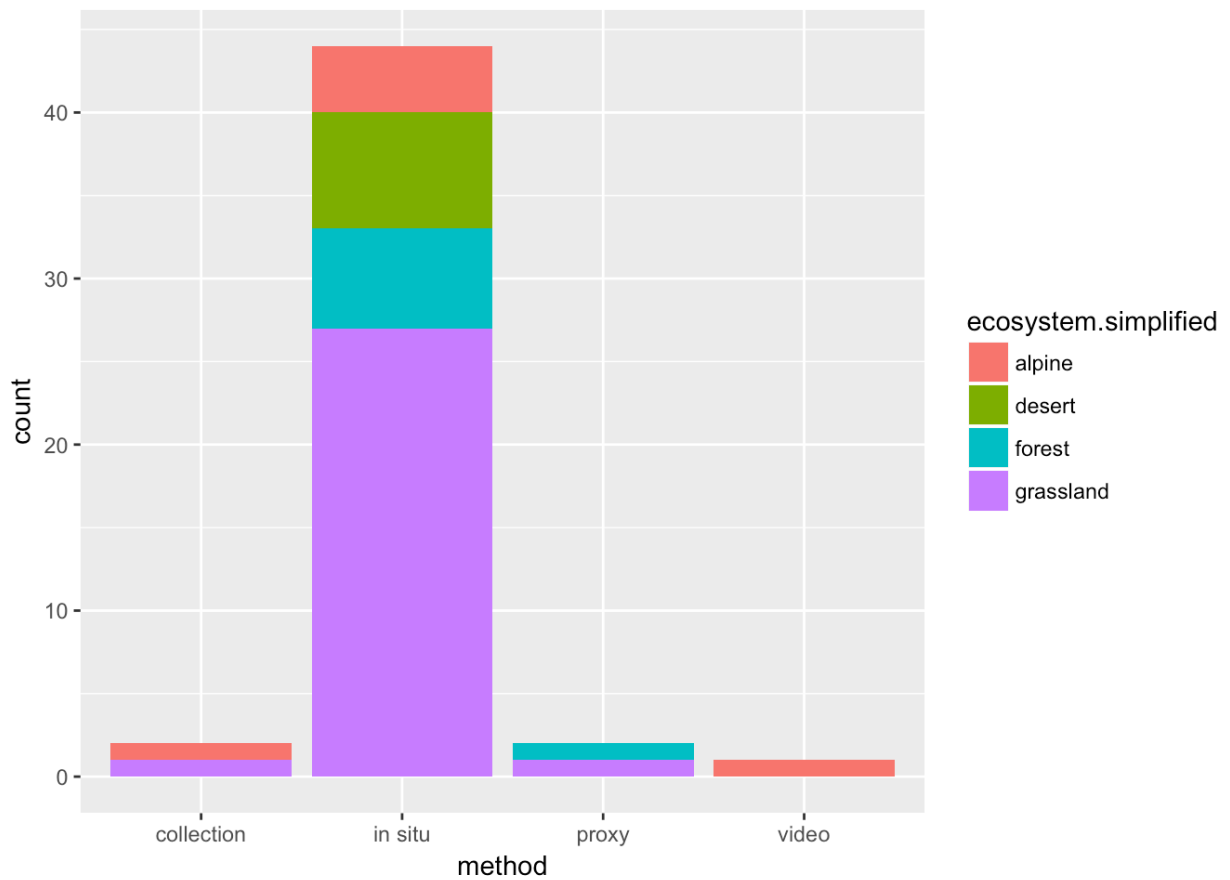


Figure 1.5. The frequency of studies (n=48) utilizing different pollinator observation techniques (e.g. video, proxy, collection and *in-situ*) in various ecosystems worldwide from a systematic review of the literature on pollinator facilitation and the magnet species effect.

Appendix

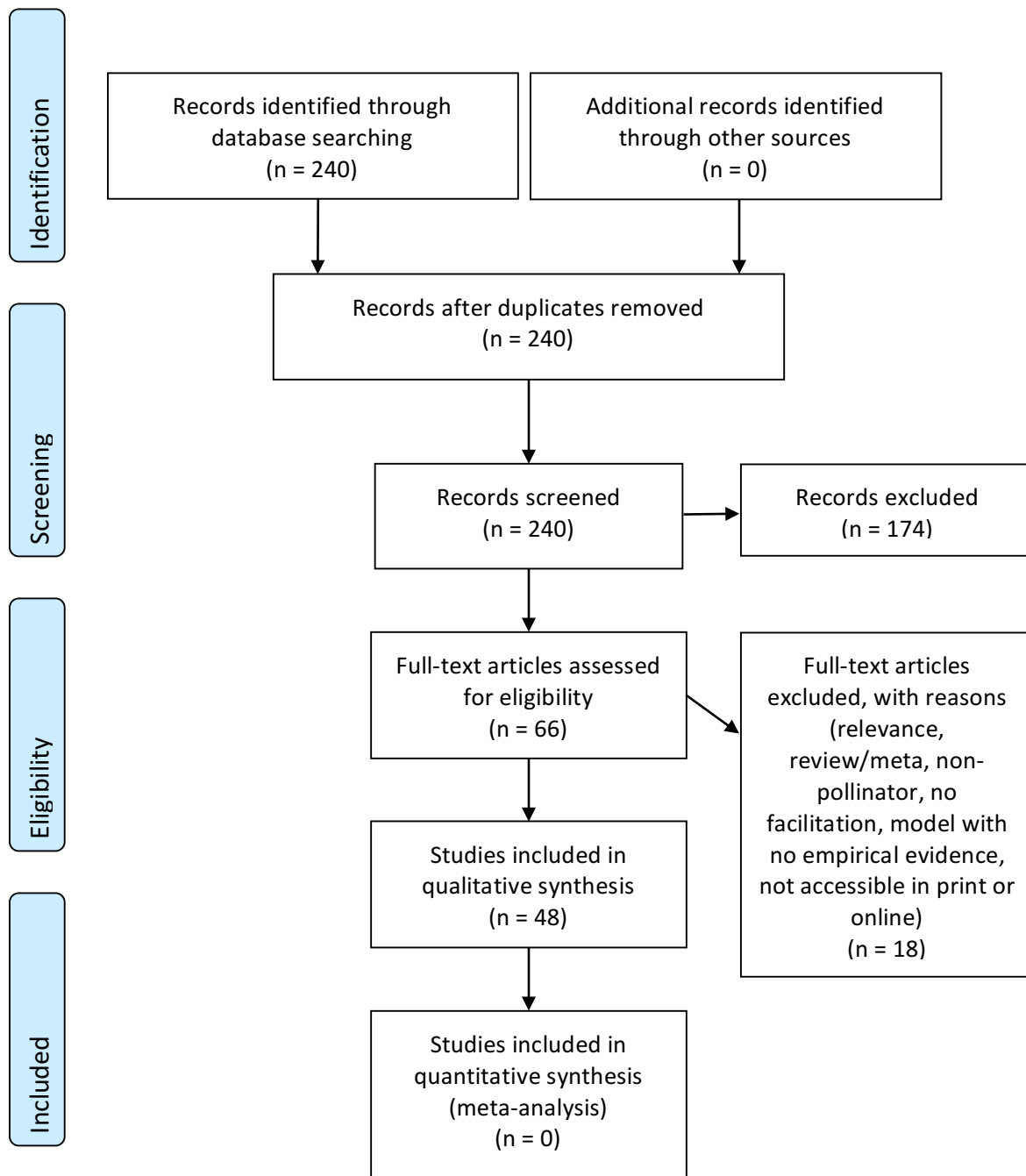


Figure A1.1. PRISMA flow diagram depicting the workflow for the search and exclusion process of this systematic review on pollinator facilitation and the magnet species effect on pollination.

Chapter 2: Shrubs as magnets for pollination: a test of facilitation and reciprocity in an established shrub-annual system

Summary

The magnet hypothesis proposes that flowering plants that are attractive to pollinators can increase the relative pollination rates of neighbouring plants by acting as a ‘magnet’. Here, we test the hypothesis that an animal-pollinated shrub species, *Larrea tridentata*, and a wind-pollinated shrub species, *Ambrosia dumosa*, act as magnets for the pollination of understory annual plant species. As a novel extension to the magnet hypothesis, we further test for reciprocity by the floral island created in the understory of the benefactor shrubs as an additional pollinator magnet for the shrub itself. We monitored pollinators using a combination of video and *in-situ* observation techniques to test the following predictions: 1) shrubs increase pollinator visitation to understory annual plants relative to paired open microsites, 2) annuals under animal-pollinated shrubs benefit through increased pollinator visitation relative to annuals under wind-pollinated shrubs due to the shrub flowers acting as a magnet for the understory, and 3) shrubs with annuals in their understory have higher visitation rates relative to shrubs without annuals due to a concentration of floral resources. Bees were the primary group of pollinators that responded to the treatments in this experiment. We found that both animal and wind-pollinated shrubs increased the visitation rate (but not the duration of visits) by bees to their understory plants. There was no significant difference in pollinator visitation rates between the understories of *Larrea tridentata* and *Ambrosia dumosa*, indicating that shrubs with animal-pollinated flowers do not act as an additional magnet to pollinators. No reciprocal annual-shrub effect was detected, suggesting that the presence of flowering annuals does not influence benefactor shrub species, but also that there is no pollination cost to shrubs. Thus, the concentrated floral resources under

desert shrubs likely provide both resources and refuge for bees and act as a search image, but it is likely a commensalistic relationship. These findings support the magnet hypothesis as an additional mechanism of facilitation by shrubs to other plant species within arid ecosystems.

Keywords: bees, deserts, indirect interactions, *Larrea tridentata*, magnet hypothesis, magnet species effect, Mojave Desert, pollinator facilitation, positive interaction

Introduction

Positive interactions between plants are a common method of survival for many species. Plant-plant facilitation is especially frequent and well documented in arid environments (Brooker et al. 2008; Filazzola and Lortie 2014, He et al. 2013), where many plants rely on these interactions to survive the high levels of environmental stress (Holmgren et al. 1997; He et al. 2013). While a wide variety of different plant species can facilitate others, the strength of this facilitation varies significantly (Gómez-Aparicio et al. 2004). Shrubs represent a dominant component of many desert landscapes and provide important biotic and abiotic resources for other plants (Castro et al. 2004; Brooker et al. 2008; Filazzola and Lortie 2014). Shrubs are a common benefactor species in desert ecosystems likely because of their relative size, canopy, and capacity to generate an ameliorated microhabitat (Brooker et al. 2008; Armas and Pugnaire 2009). Plants growing in the understory of shrubs are more abundant and have higher growth and survival rates compared to plants growing in the open (He et al. 2013; Filazzola and Lortie 2014). In communities where facilitation by shrubs is common, this leads to a distinct spatial aggregation of annual plants (Pugnaire et al. 1996b; Reynolds et al. 1999; Tirado and Pugnaire 2003; Castellanos et al. 2014). Annuals form concentrated patches under shrubs (Tirado and Pugnaire 2003), and fewer plants live out in the open where they are not afforded shelter from extreme heat and desiccation, trampling, and herbivory (Filazzola and Lortie 2014; Perea 2014). Facilitation by resources can also include access to retained water sources and increased soil nutrient levels (Reynolds et al. 1999; Filazzola and Lortie 2014). Flowering shrubs provide significant resources for pollinators both on the shrub, and within their facilitated understories. Given that many annual plants are insect-pollinated, shrubs may be able to

facilitate their understories through pollination in addition to the ameliorative effects and abiotic resources they provide (Ruttan et al. 2016). Pollinator interactions have generally not been included in this literature and they represent an important part of desert facilitation networks that needs to be investigated.

Plants and animals constantly interact and plant-plant facilitation may be mediated by animals, including herbivores and pollinators. The scaling of plant-plant facilitation to insects is rarely examined, particularly in deserts (but see: Molina-Montenegro et al. 2006; Molenda et al. 2012; Ruttan et al. 2016). Insects have a strong relationship with plants of all types, and many insects function as pollinators that are essential for plant reproduction and species survival (Allsopp et al 2008). The study of pollinator facilitation was proposed nearly 35 years ago (Rathcke 1983), and predicts that the presence of co-flowering plants increases pollination levels for the surrounding neighbourhood (Feldman et al. 2004). Most of these studies build on an adaptation of the resource concentration hypothesis which suggests that the more resources that are available in an area, the more likely that herbivores are to visit (Root 1973; Kunin 1997). These patterns have also been seen in pollinators. Increased concentrations of floral resources attract higher numbers of pollinators and positively affect pollinator visitation for individual plants within a stand (Ghazoul 2006). The magnet hypothesis (or the magnet species effect) is a more recent development of pollinator facilitation that proposes that a flowering plant that is attractive to pollinators (but not necessarily abundant) can act as a ‘magnet’ and increase the relative rate of pollination for neighbouring plant species (Lavery 1992; Molina-Montenegro et al. 2008). This idea is generally tested using co-flowering plant species, but it has not been

tested in documented plant-plant facilitation assemblages. Shrub-annual facilitation complexes in deserts are a good place to test the magnet hypothesis because deserts have a rich diversity of solitary bee species compared to other ecosystems (Minckley 2008) and are highly stressed and thus pre-disposed to many types of facilitation pathways (Brooker et al. 2008). The magnet effect could represent another essential ecological function that shrubs play in deserts.

Facilitation pathways are often multi-directional and non-binary (Rathcke 1983; Pugnaire et al. 1996a; Lortie et al. 2016), but bidirectional interactions that include facilitation are not commonly tested (Bronstein 2009; Schöb et al. 2014). Most of the literature that does report on bidirectional interactions indicates that feedback for the benefactor species is negative (Michalet et al. 2011; Cranston et al. 2012; Schöb et al. 2013). There can be costs associated with facilitation that negatively affect the benefactor species (Michalet et al. 2011). These may include below ground competition for water and nutrient resources that can lead to fitness costs including slowed growth and reduced flower and seed production for the benefactor species (Ludwig et al. 2004; Michalet et al. 2011). Neutral and positive interactions also exist and are important because they increase the potential for co-evolutionary processes to occur within plant-plant interactions (Pugnaire et al. 1996; Armas and Pugnaire 2005). Examining whether bidirectional interactions are positive, neutral, or negative is important when considering the ecological and evolutionary impacts of these interactions on ecosystem functioning (Schöb et al. 2014). The indirect effect of pollinators is typically not examined in studies of bidirectional facilitation between plants, and represents a novel research gap in this literature. If shrubs can facilitate the pollination of

their understory plants, there may also be reciprocal effects on the shrub that should be examined as well. The double-magnet hypothesis that we propose here suggests that the floral island created under shrubs due to plant-plant facilitation pathways not only benefits from increased pollination levels but can also bidirectionally facilitate the shrub through increased pollinator service. Thus, the directionality and reciprocity of facilitation pathways is incredibly important, and can both strengthen or weaken evolutionary relationship between organisms.

This study investigated whether desert shrubs and annual plants facilitate each other through pollination. We hypothesized that the floral resource island created by shrubs and their understory annual plants will have positive non-additive effects on pollinator visitation rates —i.e. would lead to a non-linear increase (Gomez 2005) in pollinator visitations to annual plants under shrubs compared to those in the open. Specifically, we examine the following predictions: (1) the frequency and duration of pollinator visitations to annuals will be greater under shrubs than in the paired, open microsites (magnet hypothesis due to a concentration of understory resources), (2) annuals under flowering animal-pollinated shrubs (*Larrea tridentata*) will have a higher frequency and duration of pollinator visitations than annuals under wind-pollinated shrubs (*Ambrosia dumosa*) because of the higher concentrations of appropriate floral resources on shrubs (specificity of pollinator facilitation), and (3) shrubs with annuals in their understory will have a higher frequency and duration of pollinator visitations than shrubs without annuals in their understory due to increased concentrations of floral resources for pollinators (reciprocal or bidirectional pollinator facilitation, i.e. the double magnet effect). Collectively, these

predictions explore how pollinators respond to differential desert plant communities including both insect and wind-pollinated shrubs and their associated annual plants. The relationship between pollinators and plant-plant facilitation networks is important because of their inherent dependence on one another, and for the conservation of ecosystem functioning considering anthropogenic threats to desert ecosystems worldwide.

Methods

Study species

This study utilized two shrub species that overlap in range, and are common throughout the Mojave Desert and the Southwestern United States. *Larrea tridentata* (Zygophyllaceae) is a large, flowering, entomophilous (insect-pollinated) shrub, commonly referred to as creosote bush (Lajtha and Whitford 1989). It is one of the most widely distributed plants found in arid areas of the southwestern United States, including the Mojave Desert (Lajtha and Whitford 1989). *Ambrosia dumosa* (Asteraceae) is a smaller anemophilous (wind-pollinated) shrub, that is also widely distributed in this area (Lajtha and Whitford 1989). Both *L. tridentata* and *A. dumosa* have been shown to facilitate annual plants through physical protection from herbivores and increased water and nutrient access but not through pollination (Whitford et al. 1997; Miriti 2006).

L. tridentata is insect pollinated, and over 120 species of bees have been reported visiting its flowers (Hurd and Linsley 1975; Minckley et al. 1999; Minckley et al. 2000). It has densely-packed, medium yellow flowers (<2.5 cm diameter) that frequently bloom for several weeks at a time, between April and May each year (Porter 2014). It is therefore a

model species for the study of the magnet effect with shrubs, as the shrub itself provides both significant and attractive floral resources. *A. dumosa* blooms between January and February each year, but is wind-pollinated and is thus a good comparison to *L. tridentata* in this study. Bees and other pollinators typically prefer colourful flowers with easy access to pollen and nectar (McCaul and Primack 1992). Plants with green flowers, such as *A. dumosa*, are visited much less frequently by pollinators and are often pollinated primarily in other ways (McCaul and Primack 1992). While *A. dumosa* does not have big, attractive, showy flowers to act as a magnet for the pollination of understory annuals, the shrub can still provide abiotic mechanisms of facilitation including shade, a windbreak, and protection from predators (Holzapfel and Mahall 1999).

Study Site

This study was conducted in a 1 mile by 0.25 mile area along Kelbaker Road in the Mojave Desert, just north of Kelso, California, USA (35.061279° -115.664356°; elevation: 779 m; Appendix, Fig. A.1). This area is highly dominated by the shrubs *L. tridentata* and *Ambrosia dumosa*, with shrubs frequently spaced less than two metres apart (Bowers 1984; Lei 1998). Annual plants are common in the area and include the following native species: *Malacothrix glabrata*, *Chaenactis fremontii*, *Eriophyllum wallacei*, *Cryptantha micrantha*, *Camissonia claviformis*, *Phacelia distans*, *Pectocarya spp.*, *Eriophyllum lanosum*, and *Rafinesquia neomexicana* (André 2006). Insects and pollinators are also abundant, with a relatively richness of high solitary bee species compared to mesic systems (Minckley 2008). Precipitation is sporadic and low with the 10-year mean accumulated annual precipitation (2004-2014) in for the Mojave Desert at 138 mm (Bowers 1987; Smith et al.

2014). The average daily maximum temperatures in the summer reaches 40°C, and the minimum reaches 1°C in January (1937–2007 records; WRCC 2008).

Experimental design

To determine whether desert shrubs and their associated understory annual communities act as pollinator magnets, pollinator visitation rates were compared between four treatment groups: 1) *L. tridentata* shrub with understory annuals, 2) *L. tridentata* shrub without understory annuals, 3) *A. dumosa shrub* with understory annuals (in 2016 only), and 4) annuals in an open area at least 1 metre from the drip line of any adjacent shrubs.

Background annuals were present in this system but at very low levels. Thus, the annual plant, *Malacothrix glabrata*, was used as a single, controlled phytometer species to test for differential pollinator effects. A phytometer is a species that is representative of the community that can be easily cultivated and controlled, and can be used to test the influence of environmental factors biotically (Clements and Goldsmith 1924; Mwangi et al. 2007). *M. glabrata* was chosen as the phytometer species for this experiment because it is already a wide-spread native annual plant in the area, and it has bright, symmetrical yellow flowers that are comparable to *L. tridentata*. The use of a single, controlled phytometer species allowed for consistency between experimental plots that could not have been attained using *in-situ* annual populations. *M. glabrata* were harvested from nearby areas and transplanted at approximately 20 plants per treatment into 24"x6" planters. Thirty-two sites (each consisting of two *L. tridentata* shrubs, one *A. dumosa* shrub, and an adjacent southern open area) were chosen at random and marked. Open microsites were located 1m to the south of the chosen shrubs and at a minimum of 1 metre away from the drip line of any other shrub. Shrub dimensions were measured for each shrub by first measuring the

shrub at the widest point, the perpendicular axis, and the height (Filazzola et al. 2017). Four of these 32 sites (a new site every day) were randomly selected for video recording each morning using a random number generator to avoid repeated measures. Selected sites that did not have flowering *L. tridentata* were not used, the nearest flowering *L. tridentata* was chosen instead. The two *L. tridentata* shrubs within each site were randomly allocated to a treatment (annuals present or annuals not present).

Visitation by pollinators was recorded over an 8-day period during peak flowering, between March 31st and April 12th, 2015, and March 24th and April 17th, 2016. Days were non-consecutive in some cases due to inclement weather. Days with temperatures below 15°C by 10AM, any sort of precipitation, heavy cloud cover, or excessive wind, were excluded from this study. Four replicates of each treatment group were recorded using Polaroid CUBE Lifestyle HD Action Cameras and three 24"x6" planters of transplanted *M. glabrata* flowers, and two similar-sized branches of flowering *L. tridentata* were recorded for each 'replicate', for 1.5 hours daily. Videos were recorded between 10:30AM and 12:00PM, when pollinator activity was at its peak. Fifteen minute *in-situ* observations of plots were performed following video recording by two researchers in a randomly generated order to avoid temporal and observer biases. These data were used to supplement video data and observe pollinator visitation for a greater surface area of the shrubs (approximately 200-flower area). This area was too big to be documented by video whilst retaining enough detail for pollinator identification. Shrub flower density (within a randomly positioned 15cm diameter ring) and *M. glabrata* floral density was also recorded following all daily

observations, so as not to disrupt pollinators during data collection. New sites were randomly chosen without replacement each day so that there were no repeated measures.

Twenty HOBO pendent loggers were randomly placed at four areas within the study site, so that there were five replicates per treatment. In each of the four areas, a logger was placed under a *L. tridentata* shrub with annuals present, under a *L. tridentata* shrub with annuals removed, under an *A. dumosa* shrub, and in an adjacent open area to record differences in temperature in each of our treatment groups on an hourly basis. Loggers were placed on the north side of the shrub in all cases.

Analysis

Videos were processed and visitation data were collected each time an insect visited an open flower for a minimum of one second. The type of pollinator, number of flowers visited, duration of pollination (difference between pollination start and stop times), and any notable behaviours or occurrences (e.g. mating or interactions between pollinators) were recorded. From these data, the total number of visitations and total visitation duration by pollinators were calculated. Due to differences in flower densities between plots, values were standardized by dividing by the number of flowers in the field of view. *In-situ* observations were combined with these data and incorporated into the final values.

An additive term generalized linear model (function: glm) was used to compare both the number (visitation frequency per flower) and duration (visitation time per flower) of pollination of three main insect types (bees, flies, other) (both fit to quasi-Poisson) for each treatment. The treatment group (microsite), insect type, and mean temperature during the

hours of recording were treated as fixed factors within each model. Day was modeled as the replicate. Mean video length per treatment per day was used as an offset variable (Thomas et al. 2013), to account for differences in total recording time between videos. An offset variable acts similarly to a covariate in the model, and it takes mean video length into account when modelling interactions. Post hoc comparisons were done using the `lsmeans` package in R (`adjust=tukey`) (Lenth 2016). Data for 2015 and 2016 were analyzed separately because the level of factors tested were non-orthogonal due to the addition of the *Ambrosia* treatment in 2016. Linear models were used to compare mean temperature and visitation rates, and number of visits and net floral density (by insect type). All data were analyzed using R version 3.3.2.

Results

Both shrub species tested, *A. dumosa* (wind-pollinated shrub) and *L. tridentata* (animal-pollinated shrub), had increased visitations to understory plants by pollinators in both years of this study (Fig. 1; Table 1). In 2015, All insect types (bees, flies, and other) had increased visitation rates to *M. glabrata* in the understory of *L. tridentata*, relative to open areas (Fig. 1; Table 1; post hoc, least squared means, bees: $p < 0.0001$, flies: $p < 0.0001$, other: $p = 0.004$). In 2016, bee visitation to *M. glabrata* under *A. dumosa* and *L. tridentata* was also greater relative to *M. glabrata* in the open (Fig. 1; Table 1; post hoc, least squared means, *Larrea*: $p = 0.016$, *Ambrosia*: $p = 0.043$). The visitation duration of pollinators of *M. glabrata* was consistent between treatments, and was unaffected by the presence or absence of *A. dumosa* or *L. tridentata* shrubs for both 2015 and 2016 (Fig. 2). The presence of understory annuals had no reciprocal effects on shrub pollination for either year. Shrubs

with *M. glabrata* in their understory did not differ in the frequency or duration of visitation by pollinators of any taxa (bees, flies, or other) compared to shrubs without understory annuals (Fig. 3; Fig. 4; Table 2).

Mean temperature (during video recording hours) positively predicted visitation of bees to annual plants for both 2015 (linear regression, $r^2_{\text{adjusted}}=0.112$, $df=60$, $p=0.004$) and 2016 (linear regression, $r^2_{\text{adjusted}}=0.038$, $df=82$, $p=0.040$; Fig. A.2). Floral density positively predicted counts of visitations by bees to annual flowers in 2015 ($r^2_{\text{adjusted}}=0.274$, $df=60$, $p<0.0001$) and 2016 ($r^2_{\text{adjusted}}=0.880$, $df=82$, $p<0.0001$; Fig. A.4). Bee visitation to shrub flowers was also positively predicted by shrub flower density for both years (2015: $r^2_{\text{adjusted}}=0.445$, $df=58$, $p<0.0001$; 2016: $r^2_{\text{adjusted}}=1.0$, $df=48$, $p<0.0001$; Fig. A.5)

Discussion

Shrubs are a foundation species within the desert ecosystem and positively influence pollination in their understories. Both the insect-pollinated shrub *L. tridentata* and the wind-pollinated shrub *A. dumosa* facilitated understory plants by increasing visitation rates by bees. These findings support the magnet hypothesis for pollinators in a desert shrub-annual systems. The supplementary floral resources provided by the insect-pollinated shrub *L. tridentata* did not increase pollination for understory plants relative to the wind-pollinated shrub *A. dumosa*. This suggests that the identity and direct food resources provided by the shrub matter less to pollinators than the resources that the shrubs provided beneath them. The third prediction associated with the double magnet hypothesis was not supported because shrubs did not receive reciprocal benefits from pollinators when annuals

were present. There was also no evidence of competition between shrubs and their understories for pollination, suggesting that there is no pollination cost to shrubs in functioning as floral benefactors to others. These findings support the overarching hypothesis that the floral resource island created by shrubs has positive effects on pollinator visitation rates for understory plants. As such, it is clear the shrubs form important linkages between plant and pollinator taxa and are important components of desert interaction networks.

Magnet hypothesis

Shrubs are important players in desert communities that mediate pollinator interactions with understory plant species. Shrubs acted as magnets for pollinators and increased the pollination frequency for understory annual plants. Interestingly, these results were not limited to or amplified by the flowering shrub *L. tridentata*. The same patterns of pollinator facilitation were seen in the understory of the wind-pollinated shrub, *A. dumosa*. This suggests that shrubs may act as magnets in a different way than we originally predicted. The floral resources provided by shrubs do not appear to compete with annuals for pollination, but they are also likely not the primary source of the magnet effect demonstrated by shrubs. Thus, shrubs act as magnets and facilitate understory plant pollination through three probable pathways. Firstly, shrubs facilitate an abundance of plants in their understory that provide an area of concentrated floral resources for pollinators. This small area of easily accessible resources allows for increased pollinator productivity in a shorter timeframe (Pyke 1979; Knight 2003). Secondly, shrubs can act as search images for pollinators. The shape and size of shrubs may signal to insects that there are abundant resources nearby, and thus draw them in (Goulson 2000). Thirdly, shrubs can provide abiotic refuge for pollinators to shelter them from intense sun, wind, and even

predators (Chaneton et al. 2010). Each of these three pathways of pollinator facilitation represents a novel research gap within the shrub-annual facilitation complex.

Pollinators are responsive to increased floral density, and it can influence visitation rates to flowers. Concentrated floral resources provided within the canopies of facilitative shrubs allow for optimal pollinator foraging. Increased floral resources (to a certain extent) can positively affect pollination for individual and neighbouring plants because pollinators are more likely to forage where they can obtain the most resources with the least amount of effort (Rathcke 1983) —i.e. dense stands with more individual flowers and less distance between them (Pyke 1979; Knight 2003). This supports the increased pollination rates seen for annual plants under *L. tridentata* and *A. dumosa* in this experiment. The facilitation by shrubs caused these plants to form concentrated islands of resources within their understories that provided ample resources for pollinators, and thus increased visitation. It is therefore likely that resource concentration and floral density are drivers of the facilitative relationship between shrubs and annuals for pollination in deserts.

The shape and size of shrubs may also play a role in the attraction of pollinators to their understory. Shrubs can act as search images for pollinators—pollinators could use the shape of shrubs as a general indicator of dense understory floral resources that are often scarce in deserts (Rausher 1978; Msnzsr 1985; Goulson 2000). The use of search images in insects is not a novel concept, and it has been shown to increase the rate of discovery of host plants in butterflies and influence foraging in honey bees (Rausher 1978; Msnzsr 1985). Solitary bees were the most frequent pollinators seen in this experiment, with the

most common genera visiting both shrubs and annual plants consisting of: *Ashmeadiella*, *Hoplitis*, *Megachile*, *Lasioglossum* (particularly the subgenus *Dialictus*), *Dieunomia*, *Andrena*, *Agapostemon*, *Anthidium*, *Dianthidium*, *Habropoda*, and *Perdita*. It is not unreasonable to predict that the solitary bees in this system respond to the presence of shrubs in similar ways that some butterflies and social bees respond to certain images in their environments. The large, regular appearance of shrubs could act as a search image that attracts pollinators and subsequently increases visitation to beneficiary plants in their understories. The use of shrubs as a search image represents another pathway of indirect interactions between pollinators, shrubs and annual plants that needs further research.

Finally, shrubs likely act as a refuge for pollinators. Shrubs have been found to provide refuge and interact non-trophically with several other animal species, including small mammals and lizards (Lortie et al. 2016, Filazzola et al. 2017). Similar relationships have been found between cushion plants and insects in the alpine where the abundance of both arthropods and pollinators were higher on cushions in contrast to open areas due to the amelioration of abiotic stress (Molina-Montenegro et al. 2006; Molenda et al. 2012; Reid and Lortie 2012). Cushion plants act similarly to desert shrubs by facilitating the species that grow on them through biotic and abiotic mechanisms (Reid and Lortie 2012). The shrub species, *L. tridentata* and *A. dumosa*, could therefore provide a refuge for pollinators through access to resources, shelter, and protection from predators. Thus, the net positive effect of shrubs on the pollination of understory annuals likely involves a complex network of drivers including resource concentration and increased floral density, the ability of shrubs to act as search images for pollinators, and access to abiotic resources and protection

from predators. We need to better understand how this facilitative relationship works and the factors that contribute to it to be able to conserve the ecosystem functions that these interactions provide.

Double magnet hypothesis

Annuals in this system did not influence the pollination of the shrubs that facilitated them. This may be due to an oversaturation in flower density that is above the maximum point in the density-visitation curve, meaning that the addition of shrub flowers and further floral resources no longer had a positive effect on net pollination frequency (Rathcke 1983; Bruninga-Socular et al. 2016). Though there was no support for the proposed double magnet hypothesis, there was also no pollination cost to shrubs and they may be reciprocally facilitated in other ways. By increasing the frequency of pollination in their understories, shrubs decrease the likelihood that these plants are left un-pollinated. This effectively increases understory plant reproduction, survival and abundance over time. Healthy understory plant populations provide the shrub and its microhabitat with increased water retention and cooling of the soil, seed trapping, increased plant litter, and therefore increased nutrient content (Holmgren et al. 2015; Tirado et al. 2015). The maintenance of a healthy understory can alleviate stress on the shrubs and can positively affect their growth, reproduction, and survival (Sortibrán et al. 2014; Tirado et al. 2015). Shrubs showed no net cost of facilitating understory plant pollination and can even indirectly benefit from this facilitation. This indicates that this is at the very least a commensalistic—but likely mutualistic—relationship.

Shrubs as foundation species

The ability of shrubs to facilitate pollination for their understory species indicates that they are a foundation species within desert ecosystems. Foundation species are often abundant species that encompass certain structural or functional characteristics that have a strong, defining influence on ecological communities (Ellison et al. 2005). The foundation effect of shrubs on desert plant and pollinator communities should be considered alongside current and emerging ecological threats to these areas. Climate change, the resulting desertification processes, and significant recent declines in pollinator populations are issues that pose an immense threat to deserts (Potts et al. 2010; Scaven and Rafferty 2013). The effects of climate change have caused overall warmer annual temperatures and extreme droughts throughout desert systems, including in California where this study was conducted (Kelly and Goulden 2008; Mann and Gleick 2015). Increasing temperatures pose threats to desert biodiversity and are predicted to decrease species abundance and richness and increase species turnover, with sensitive species being extirpated, and monocultures of more stress-tolerant species taking over (Zeng et al. 2016). Global climate change is also expected increase the occurrence of sustained drought periods, which will deplete ground water stores and may exceed the dormancy allowance for many plant species (Taylor et al. 2013; Carta et al. 2016). This will have negative effects on other levels of biodiversity such as small mammals, reptiles, insects, and pollinators that rely on the rich diversity of plants that are available currently. Climate change has also resulted in significant pollinator declines which present additional challenges in desert ecosystems (Kerr et al. 2015). Climate change can result in a phenological mismatch due to flowers using temperature as a cue for emergence and senescence, and bees primarily using rainfall (Danforth 1986; Forrest 2015). This modifies the temporal overlaps that are required for plant-pollinator

interactions (Scaven and Rafferty 2013; Forrest 2015). These increased temperatures would be detrimental to both taxa because they disrupt the network structure of plant-pollinator interactions, even if species aren't initially lost (Scaven and Rafferty 2013). Declines in pollinators would have a strong, negative impact on seed recruitment and survival in animal-pollinated species, which would have cascading effects to other trophic levels (Lundgren et al. 2015). Shrubs can thus act as a buffer to mediate the effects of warming in desert systems. Their ability to ameliorate abiotic stress in their understories could allow plants to flower for longer periods, avoid early senescence (Talukder et al. 2014), and therefore reduce phenological mismatch and re-introduce temporal overlaps between plants and pollinators. The protection and management of desert shrub species could be an important first step in conserving desert biodiversity and plant-pollinator interactions.

Conclusions

The desert shrub species *L. tridentata* and *A. dumosa* are important foundation species within the desert community that can facilitate other plants both directly and indirectly. These shrubs facilitate their understories not only by providing physical protection, shade, and access to extra water and nutrient resources, but also by indirectly providing increased access to pollinators. It is proposed that this pollinator facilitation occurs due to concentrated floral resources within their canopies, by providing a search image for pollinators to be able to locate these abundant floral resources, and by providing abiotic refuge for pollinators in similar ways to how they provide them for plants and other animals. This appears to be a commensalistic relationship because shrubs do not receive reciprocal pollinator facilitation from annual plants, although they may be reciprocally

facilitating shrubs indirectly in other ways. These findings represent a profound ecological effect that is likely to be an extremely important subset of positive interactions within desert communities. These interactions will be especially important to consider in light of climate change and pollinator declines that threaten these areas, solidifying the position of shrubs as foundation species within deserts.

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Tables

Table 1. A summary of the general linear models used to test for differences in pollinator visitation rates (per flower) to the annual plant *Malacothrix glabrata* between two shrub microsites (*Larrea tridentata* and *Ambrosia dumosa*), and adjacent open microsites. This study was conducted in the Mojave Desert, California (35.061279°, -115.664356°), using video and *in-situ* observation techniques. Pollinator visitation rate (response variable) was standardized by flower density within plots, and total video length was used as an offset variable within models. Boldface denotes significance at $p < 0.05$ for post hoc contrasts using least squared means.

Table 2. A summary of the general linear models used to test for differences in pollinator visitation rates (per flower) to shrub species, *Larrea tridentata*, with the presence of understory annuals (*Malacothrix glabrata*), and without. This study was conducted in the Mojave Desert, California (35.061279°, -115.664356°), using video and *in-situ* observation techniques. Pollinator visitation rate (response variable) was standardized by shrub flower density, and total video length was used as an offset variable within models. Boldface denotes significance at $p < 0.05$ for post hoc contrasts using least squared means.

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Year	Generalized linear model					
2015	Factor	Df	Deviance	P-value		
	microsite	1	0.236	0.254		
	insect.RTU	2	10.943	<0.0001		
	mean.temp	1	15.232	<0.0001		
	mictosite:insect.RTU	2	0.310	0.003		
	Post Hoc, least squared means					
	Contrasts	Estimate	SE	Df	Z-ratio	P-value
	Larrea,bees - Open,bees	1.701	0.323	NA	5.263	<.0001
	Larrea,flies - Open,flies	2.052	0.362	NA	5.676	<.0001
Larrea,other - Open,other	2.017	0.570	NA	3.541	0.004	
Year	Generalized linear model					
2016	Factor	Df	Deviance	P-value		
	microsite	2	1.373	0.214		
	insect.RTU	2	73.156	<0.0001		
	mean.temp	1	7.848	<0.0001		
	mictosite:insect.RTU	4	1.007	0.687		
	Post Hoc, least squared means					
	Contrasts	Estimate	SE	Df	Z-ratio	P-value
	Ambrosia,bees - Larrea bees	-0.059	0.150	NA	-0.391	1.0000
	Ambrosia,bees - Open bees	0.554	0.176	NA	3.149	0.043
	Larrea,bees - Open,bees	0.613	0.177	NA	3.464	0.016
	Ambrosia,flies - Larrea,flies	-0.023	0.453	NA	-0.051	1.000
	Ambrosia,flies - Open,flies	0.422	0.461	NA	0.916	0.992
	Larrea,flies - Open,flies	0.445	0.438	NA	1.017	0.984
	Ambrosia,other - Open,other	0.014	0.866	NA	0.016	1.000
	Larrea,other - Open,other	-0.959	1.133	NA	-0.847	0.995

Table 2. A summary of the general linear models used to test for differences in pollinator visitation rates (per flower) to shrub species, *Larrea tridentata*, with the presence of understory annuals (*Malacothrix glabrata*), and without. This study was conducted in the Mojave Desert, California (35.061279°, -115.664356°), using video and *in-situ* observation techniques. Pollinator visitation rate (response variable) was standardized by shrub flower density, and total video length was used as an offset variable within models. Boldface denotes significance at $p < 0.05$ for post hoc contrasts using least squared means.

Year	Generalized linear model					
2015	Factor	Df	Deviance	P-value		
	net.treatment	1	2.557	0.187		
	insect.RTU	2	2.334	0.009		
	mean.temp	1	2.334	0.931		
	net.treatment:insect.RTU	2	2.285	0.361		
	Post Hoc, least squared means					
	Contrasts	Estimate	SE	Df	Z-ratio	P-value
	Larrea w/annuals,bees - Larrea w/o annuals, bees	0.075	0.206	NA	-0.364	0.999
	Larrea w/annuals,flies - Larrea w/o annuals, flies	0.357	0.320	NA	1.115	0.876
	Larrea w/annuals,other - Larrea w/o annuals, other	0.780	0.533	NA	-1.465	0.687
Year	Generalized linear model					
2016	Factor	Df	Deviance	P-value		
	net.treatment	1	0.023	0.045		
	insect.RTU	1	0.022	0.049		
	mean.temp	1	0.001	0.614		
	net.treatment:insect.RTU	1	0.028	0.024		
	Post Hoc, least squared means					
	Contrasts	Estimate	SE	Df	Z-ratio	P-value
	Larrea w/annuals,bees - Larrea w/o annuals, bees	0.643	0.286	NA	-2.252	0.110
	Larrea w/annuals,flies - Larrea w/o annuals, flies	0.447	0.497	NA	0.899	0.805
	Larrea w/annuals,other - Larrea w/o annuals, other	NA	NA	NA	NA	NA

Figures

Figure 1. Visitation rate by pollinators to the annual plant *Malacothrix glabrata*, obtained through video and *in-situ* observation. Visitation was compared between the three treatment groups (annuals under *Ambrosia dumosa*, annuals under *Larrea tridentata*, annuals in the open), for bees, flies, and other insect pollinators. Visitation rate was standardized by number of flowers in the field of view of the video. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Shrub treatments that were significantly higher than their open counterpart are denoted with asterisk(s).

Significance at $\alpha < 0.05$: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

Figure 2. The duration of visits by pollinators to the annual plant *Malacothrix glabrata*, obtained through video and *in-situ* observation. Visitation was compared between the three treatment groups (annuals under *Ambrosia dumosa*, annuals under *Larrea tridentata*, annuals in the open), for bees, flies, and other insect pollinators. Raw visitation times were standardized by total video length. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Shrub treatments that were significantly higher than their open counterpart are denoted with asterisk(s). Significance at $\alpha < 0.05$: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

Figure 3. Visitation rate by pollinators to *L. tridentata*, obtained through video and *in-situ* observation. Visitation was compared between the two treatment groups (*L. tridentata* with understory annuals present and *L. tridentata* with understory annuals absent), for bees, flies, and other insect pollinators. Visitation rate was standardized by number of flowers in the field of view of the video. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Significance at $\alpha < 0.05$ is denoted as: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

Figure 4. The duration of visits by pollinators to *L. tridentata*, obtained through video and *in-situ* observation. Visitation was compared between the two treatment groups (*L. tridentata* with understory annuals present and *L. tridentata* with understory annuals absent), for bees, flies, and other insect pollinators. Visitation rate was standardized by total video length. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Significance at $\alpha < 0.05$ is denoted as: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

Figure A.1. A map of the location of the study site located 3.5 miles North of Kelso, San Bernardino, California, USA, on Kelbaker Road. (central coordinates: 35.061279° - 115.664356°; elevation: 779 m). The blue circle represents the approximate area used for data collection. Map generated in R version 3.3.2.

Figure A.2. The correlation between mean temperature during hours of video recording, and pollination rate per flower for *Malacothrix glabrata* (frequency of pollination events standardized by the number of flowers in the field of view). Pollination rates were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between temperature and visitation rate to flowers (2015: $r^2_{\text{adjusted}}=0.11$, $df=60$, $p=0.004$; 2016: $r^2_{\text{adjusted}}=0.04$, $df=82$, $p=0.04$).

Figure A.3. The correlation between mean temperature during hours of video recording, and pollination rate per flower for *L. tridentata* (frequency of pollination events standardized by the number of flowers in the field of view). Pollination rates were separated by three distinct recognizable taxonomic units of insects (RTUs). No significant correlations were present.

Figure A.4. The correlation between floral density, and raw pollinator count for *Malacothrix glabrata* during the length of video recording. Pollinator counts were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between floral density and pollinator counts (2015: $r^2_{\text{adjusted}}=0.27$, $df=60$, $p<0.0001$; 2016: $r^2_{\text{adjusted}}=0.88$, $df=82$, $p<0.0001$).

Figure A.5. The correlation between floral density, and raw pollinator count for *Larrea tridentata* during the length of video recording. Pollinator counts were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between floral density and pollinator counts (2015: $r^2_{\text{adjusted}}=0.45$, $df=58$, $p<0.0001$; 2016: $r^2_{\text{adjusted}}=1$, $df=48$, $p<0.0001$).

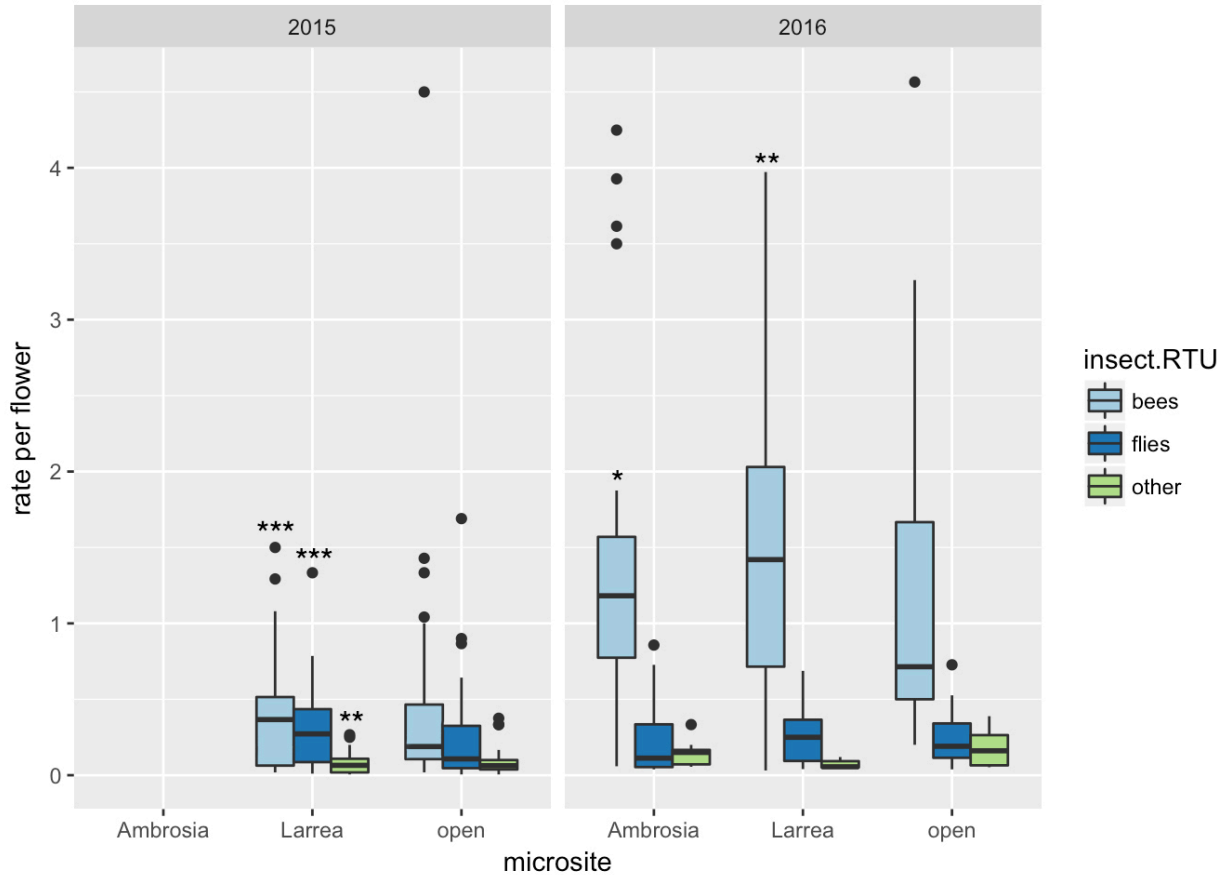


Figure 1. Visitation rate by pollinators to the annual plant *Malacothrix glabrata*, obtained through video and *in-situ* observation. Visitation was compared between the three treatment groups (annuals under *Ambrosia dumosa*, annuals under *Larrea tridentata*, annuals in the open), for bees, flies, and other insect pollinators. Visitation rate was standardized by number of flowers in the field of view of the video. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Shrub treatments that were significantly higher than their open counterpart are denoted with asterisk(s). Significance at $\alpha < 0.05$: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

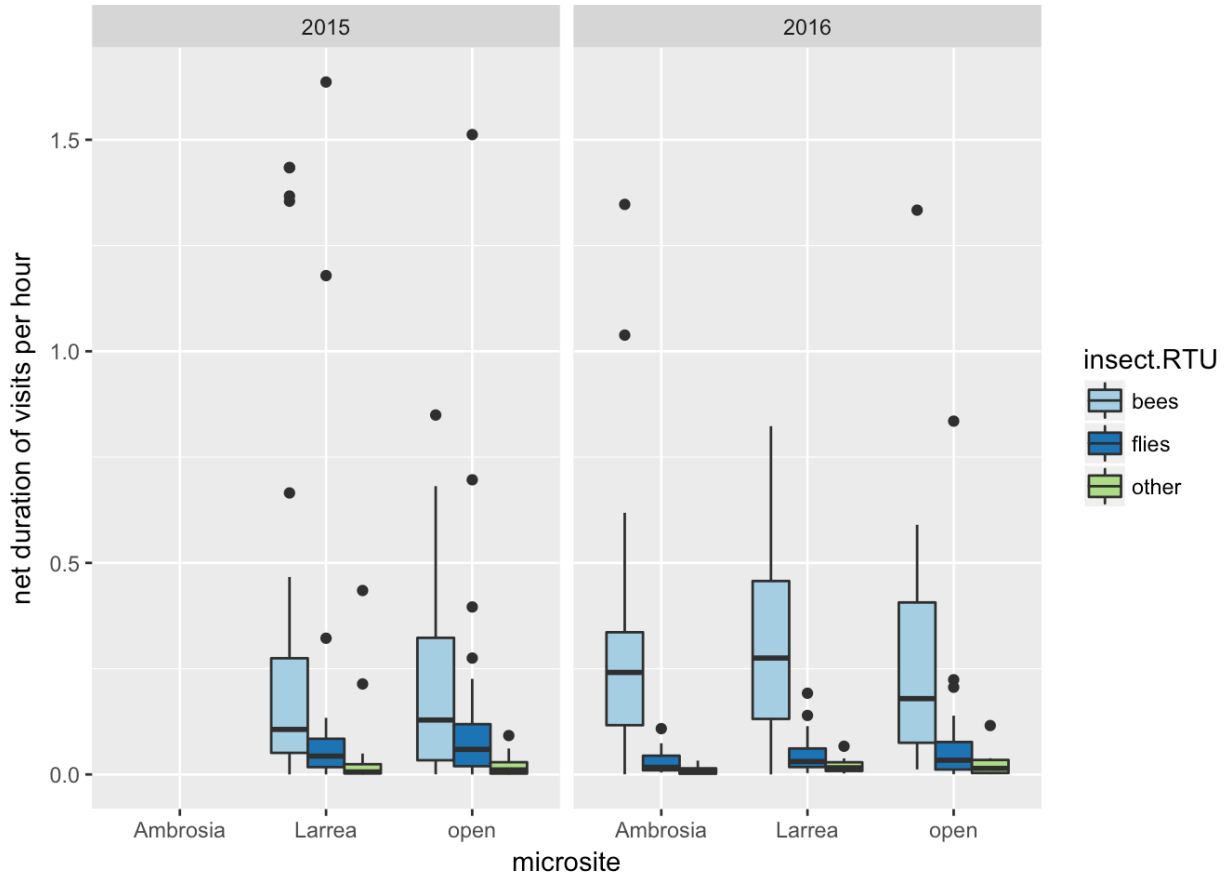


Figure 2. The duration of visits by pollinators to the annual plant *Malacothrix glabrata*, obtained through video and *in-situ* observation. Visitation was compared between the three treatment groups (annuals under *Ambrosia dumosa*, annuals under *Larrea tridentata*, annuals in the open), for bees, flies, and other insect pollinators. Raw visitation times were standardized by total video length. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Shrub treatments that were significantly higher than their open counterpart are denoted with asterisk(s). Significance at $\alpha < 0.05$: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

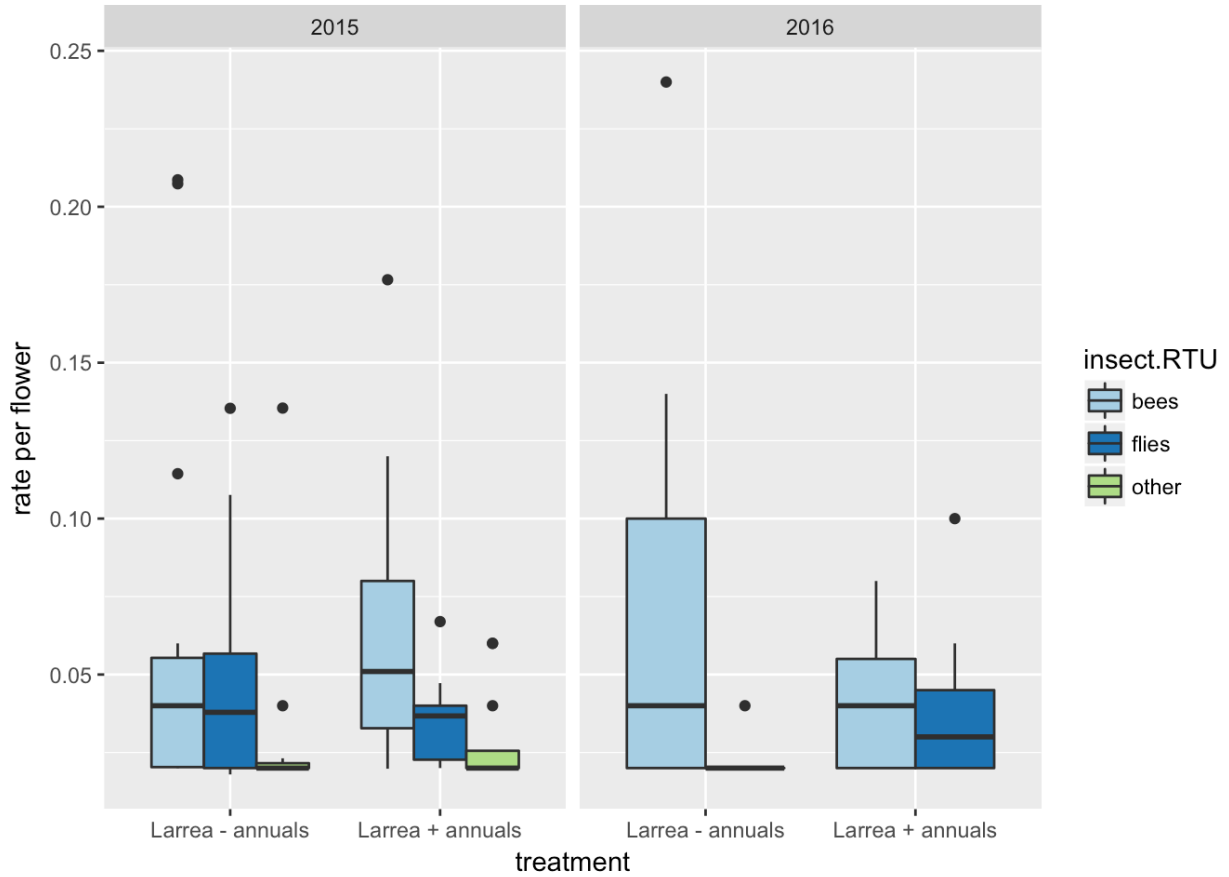


Figure 3. Visitation rate by pollinators to *L. tridentata*, obtained through video and *in-situ* observation. Visitation was compared between the two treatment groups (*L. tridentata* with understory annuals present and *L. tridentata* with understory annuals absent), for bees, flies, and other insect pollinators. Visitation rate was standardized by number of flowers in the field of view of the video. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range.

Significance at $\alpha < 0.05$ is denoted as: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

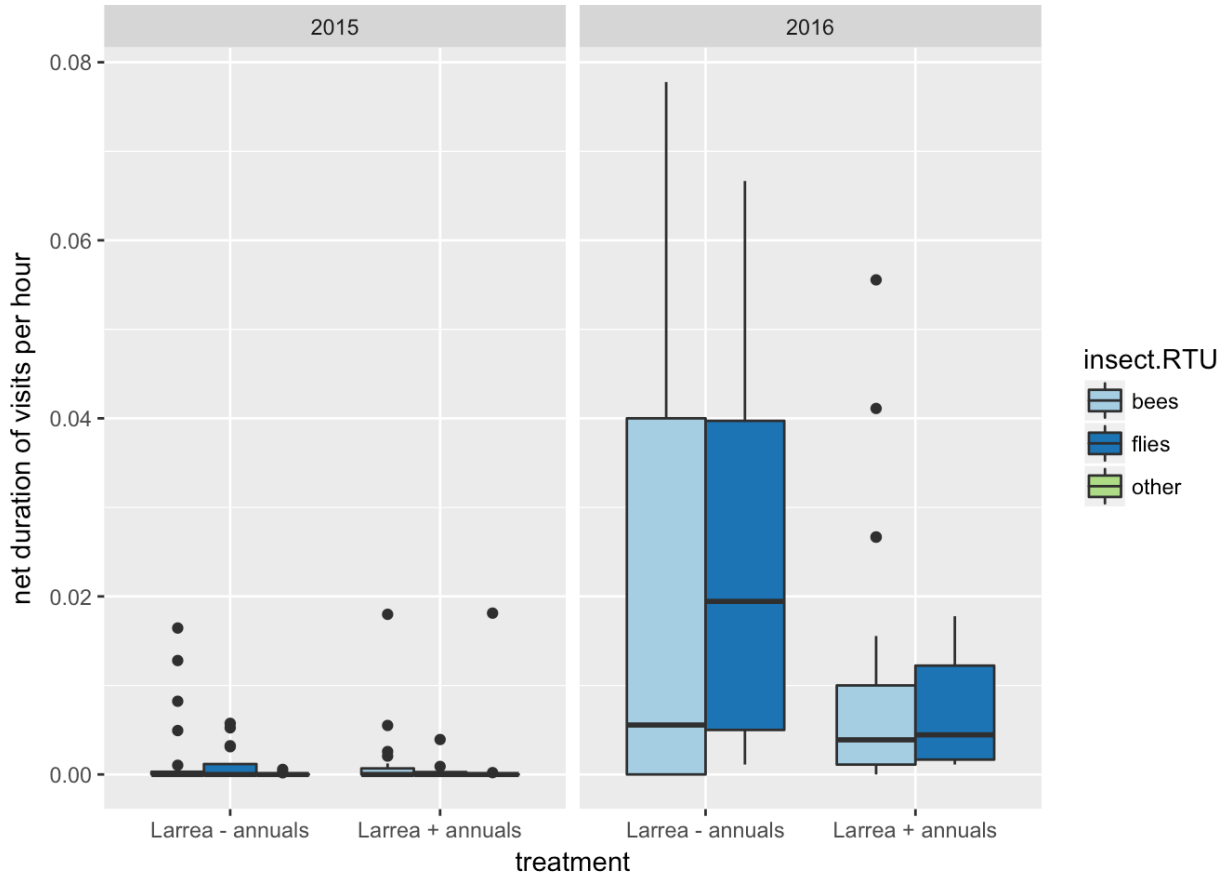


Figure 4. The duration of visits by pollinators to *L. tridentata*, obtained through video and *in-situ* observation. Visitation was compared between the two treatment groups (*L. tridentata* with understory annuals present and *L. tridentata* with understory annuals absent), for bees, flies, and other insect pollinators. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Visitation rate was standardized by total video length. Significance at $\alpha < 0.05$ is denoted as: *** = ≤ 0.001 , ** = ≤ 0.01 , * = ≤ 0.05 .

Appendix

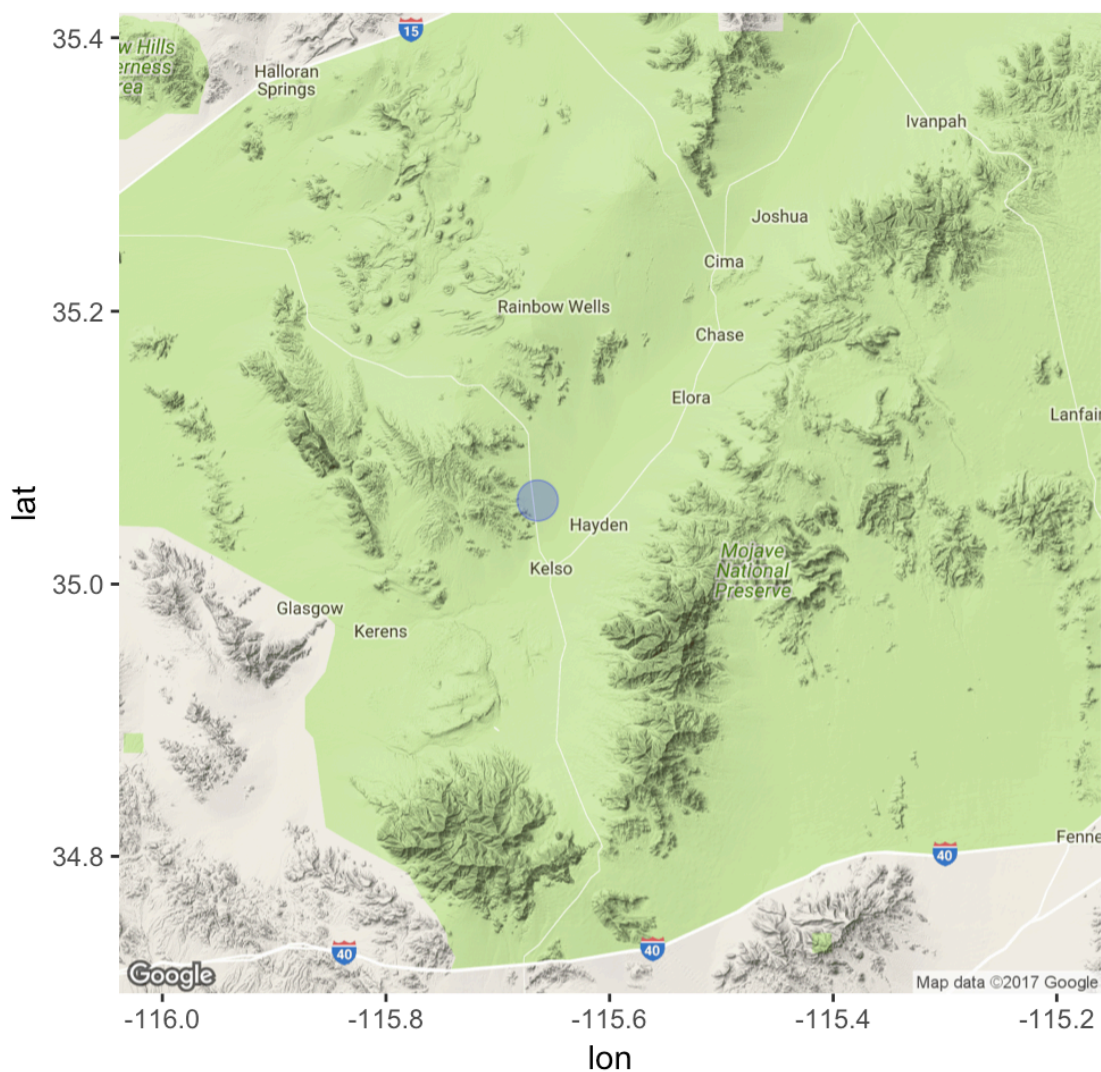


Figure A.1. A map of the location of the study site located 3.5 miles North of Kelso, San Bernardino, California, USA, on Kelbaker Road. (central coordinates: 35.061279° - 115.664356° ; elevation: 779 m). The blue circle represents the approximate area used for data collection. Map generated in R version 3.3.2.

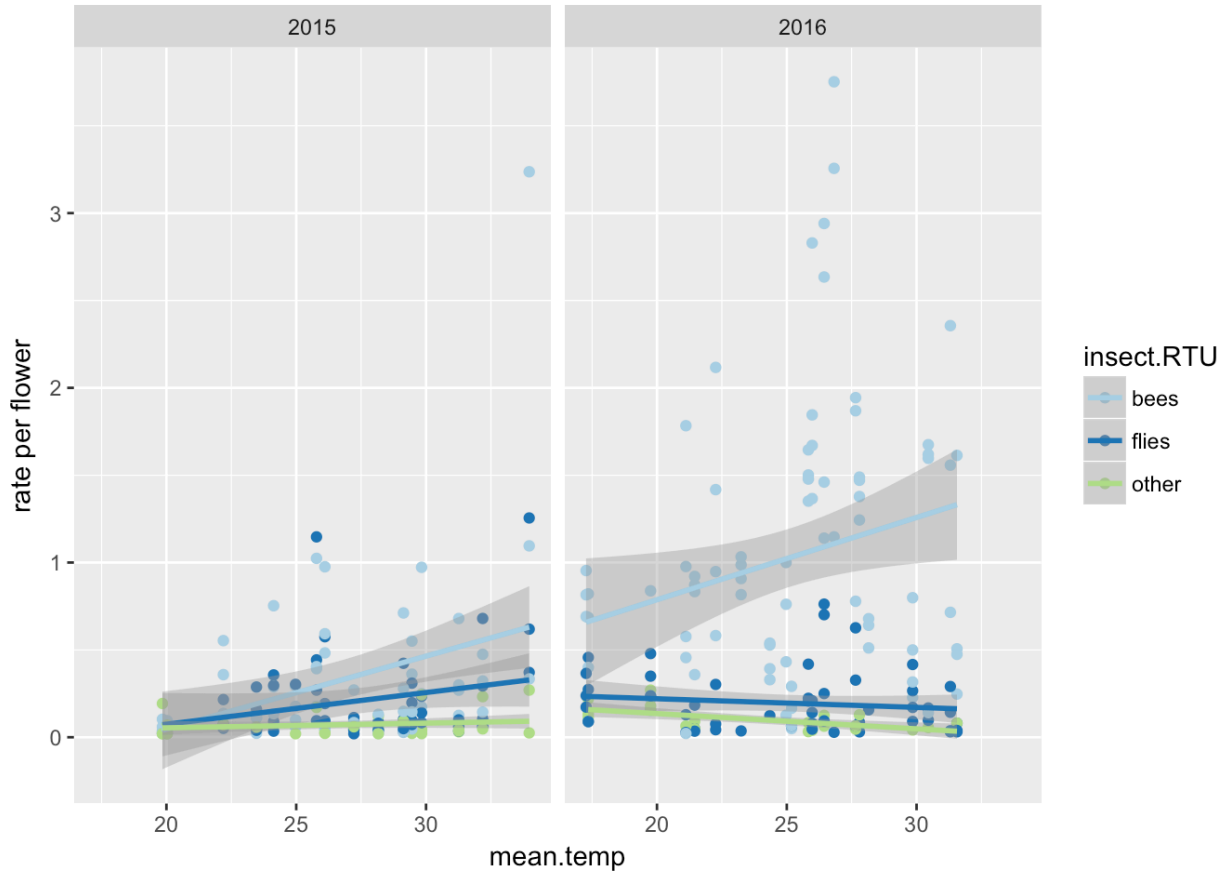


Figure A.2. The correlation between mean temperature during hours of video recording, and pollination rate per flower for *Malacothrix glabrata* (frequency of pollination events standardized by the number of flowers in the field of view). Pollination rates were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between temperature and visitation rate to flowers (2015:

$r^2_{\text{adjusted}}=0.11$, $df=60$, $p=0.004$; 2016: $r^2_{\text{adjusted}}=0.04$, $df=82$, $p=0.04$).

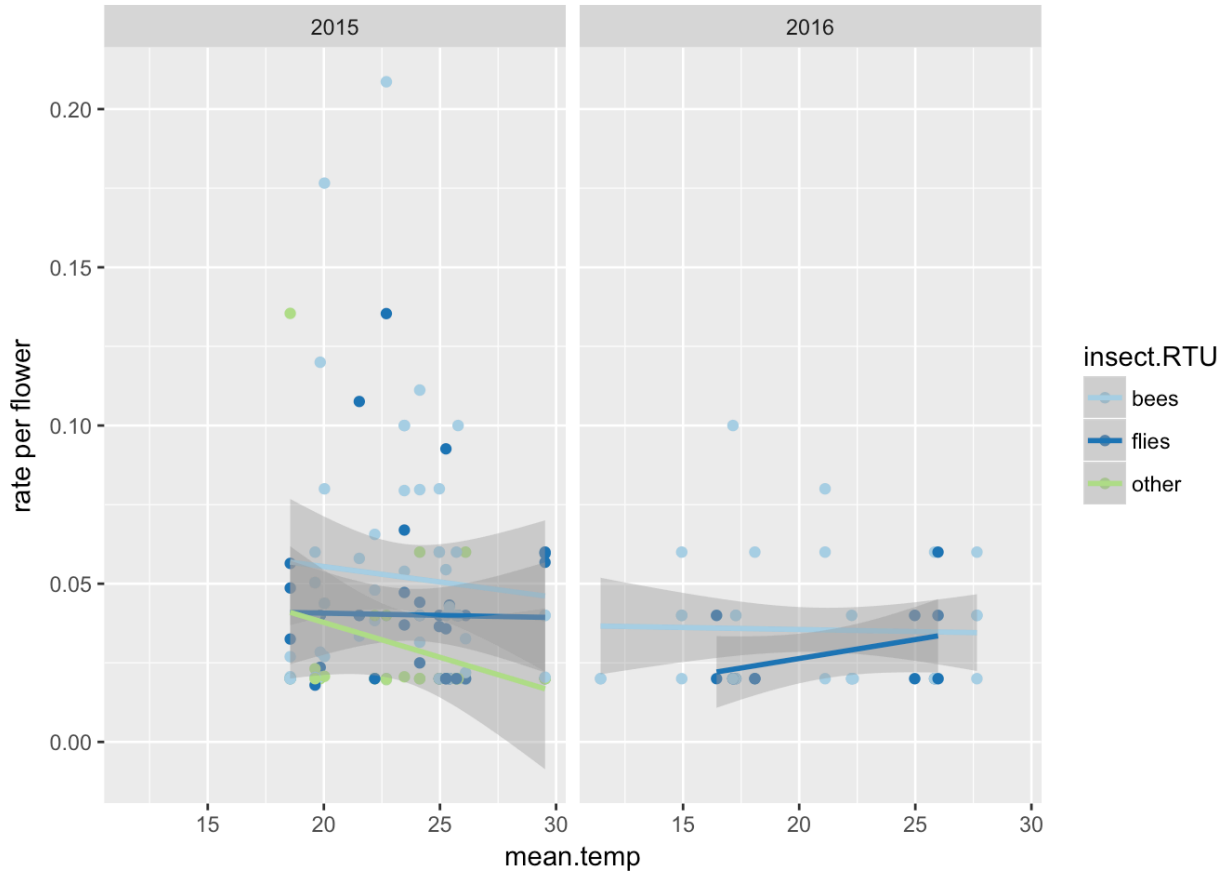


Figure A.3. The correlation between mean temperature during hours of video recording, and pollination rate per flower for *L. tridentata* (frequency of pollination events standardized by the number of flowers in the field of view). Pollination rates were separated by three distinct recognizable taxonomic units of insects (RTUs). No significant correlations were present.

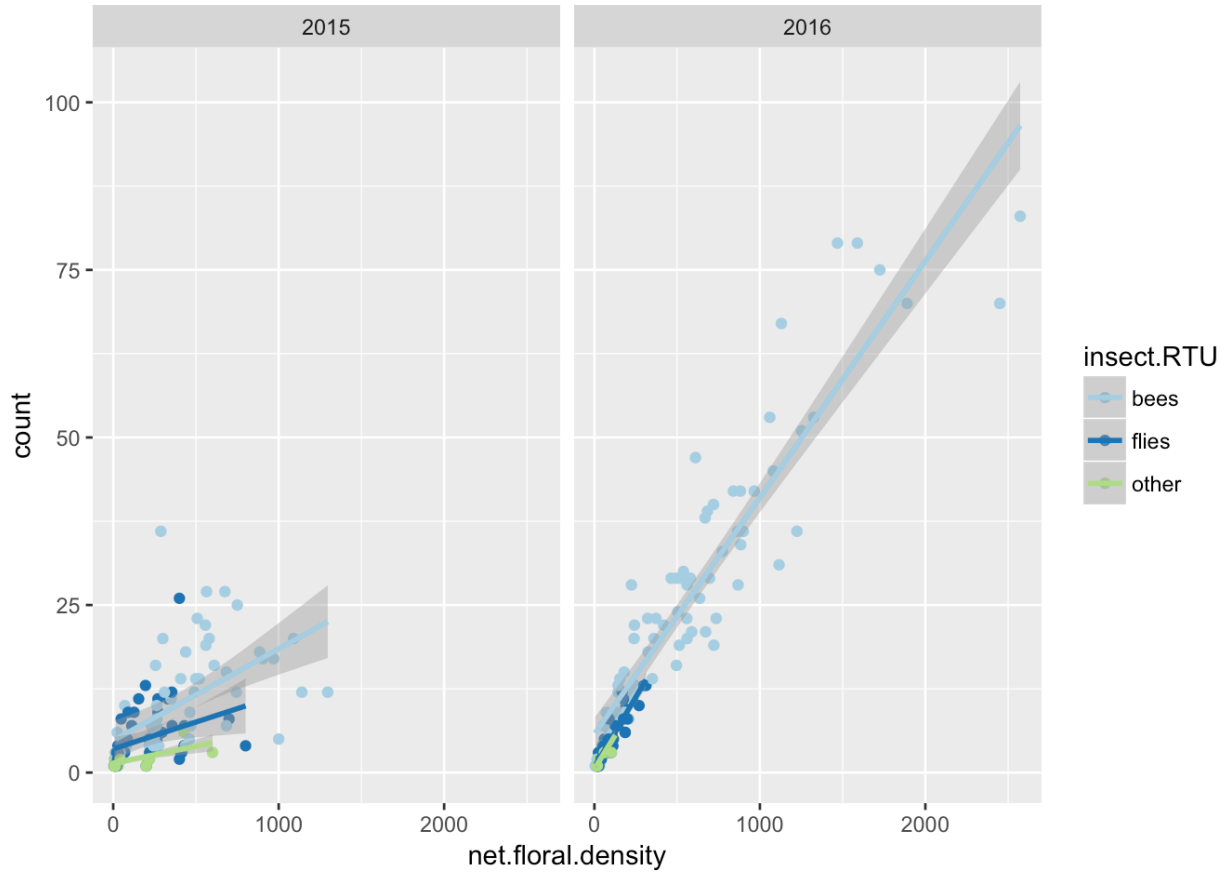


Figure A.4. The correlation between floral density, and raw pollinator count for *Malacothrix glabrata* during the length of video recording. Pollinator counts were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between floral density and pollinator counts (2015: $r^2_{\text{adjusted}}=0.27$, $df=60$, $p<0.0001$; 2016: $r^2_{\text{adjusted}}=0.88$, $df=82$, $p<0.0001$).

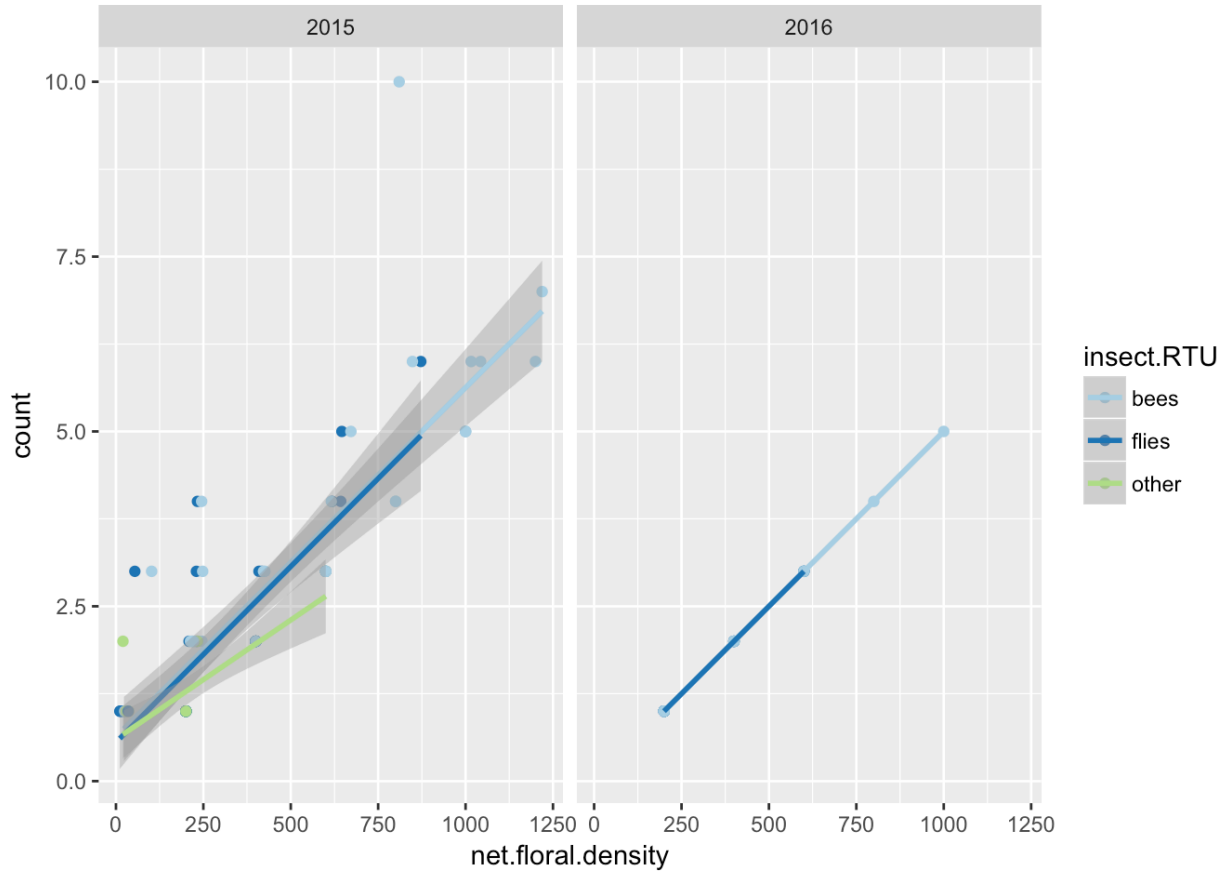


Figure A.5. The correlation between floral density, and raw pollinator count for *L. tridentata* during the length of video recording. Pollinator counts were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between floral density and pollinator counts (2015: $r^2_{\text{adjusted}}=0.45$, $df=58$, $p<0.0001$; 2016: $r^2_{\text{adjusted}}=1$, $df=48$, $p<0.0001$).

Summary and General Conclusions

Facilitation between plants for pollination has been studied in many contexts. It has been researched most primitively using an adaptation of the resource concentration hypothesis, predicting that individual plants in areas with higher flower densities receive increased access to pollinators (Rathcke 1983; Bruninga-Socular et al. 2016). More recently, the concept that attractive plants can act as magnets for the pollination of other, less-attractive plants (the magnet hypothesis) has been considered (Lavery 1992). A systematic review of the literature on plant-plant facilitation through pollination was conducted in Chapter one of this thesis. It revealed that these studies have generally neglected high-stress ecosystems such as the desert and alpine, where facilitative interactions are typically most common (Bertness and Callaway 1994; Lortie and Callaway 2006; Maestre et al. 2009). It was also clear that there has been a lack of research on whether pollinator facilitation and the magnet hypothesis apply to solitary bee pollinators, as much of the current research has been on social bees. Additionally, the observation of pollinators has been dominated by *in-situ* methodology, but this comes with many short-falls including observer and temporal biases. Thus, the findings of this systematic review provided many novel methodological and theoretical opportunities to advance future research on pollinator facilitation.

Chapter two of this thesis used the research gaps that were established through the systematic review to advance the study of the magnet hypothesis by combining it with the idea of plant-plant facilitation in a manipulative experiment. An established facilitation assemblage including two dominant desert shrubs (*Larrea tridentata* and *Ambrosia dumosa*) and their facilitated annual plants were used to determine if shrubs could act as

magnets for the pollination of their understories, and if there were any reciprocal effects of flowering understories on shrub pollination. Both flowering insect-pollinated shrubs and wind pollinated shrubs were found to increase pollination rates in their understories, but no reciprocal effects were found for the shrubs. Since both flowering and non-flowering shrubs facilitated understory pollination in the same way, we predict that shrubs are acting as magnets by facilitating the growth of concentrated floral resources within their canopies, providing a search image for pollinators to be able to find these resources, and providing a refuge for pollinators from stressors such as heat, wind, and predation, much like they do for the plants they facilitate. Regardless of the pathway that shrubs facilitate understory plant pollination, this positive relationship likely perpetuates the co-evolution of this facilitation assemblage (Punaire et al. 1996; Armas and Pugnaire 2005).

Shrubs are thus a foundation species within desert ecosystems. Their facilitation of annual plants and indirect interactions with other taxa such as pollinators allows them to contribute strongly to the structure and function of their communities (Ellison et al. 2005). It will be important to consider the widespread and positive effects that shrubs have on desert ecosystems for the remediation of declining pollinator populations due to climate change. Warming in deserts has already started to cause significant phenological mismatches between plants and pollinators, decreasing their overlap times and reducing pollination (and therefore reproduction) rates for plants, and food sources for pollinators (Scaven and Rafferty 2013; Forrest 2015). The cooling effect of shrubs may allow annual plants to flower for longer periods underneath them than they would regularly in the hotter, open areas (Talukder et al. 2014). This, combined with the knowledge that shrubs increase pollination in their understories, indicates that they may be a critical species for increasing

the overlap period between peak plant and pollinator phenology in warm years. Thus, shrubs are important contributors in desert systems that have facilitative properties that extend beyond plants to pollinators, indicating their importance for ecosystem function and the maintenance of healthy arid environments.

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