POLLINATOR-MEDIATED INTERACTIONS OF FOUNDATION PLANTS IN THE MOJAVE DESERT

JENNA BRAUN

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL

FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

GRADUATE PROGRAM IN BIOLOGY, YORK UNIVERSITY, TORONTO, CANADA

OCTOBER 2018

© Jenna Braun 2018

# **Abstract**

Pollination facilitation is an indirect interaction whereby one plant species positively influences the reproductive success of another plant species through pollinators. This thesis contributes to the field of pollination facilitation using two approaches. First, we conducted a systematic review of the experimental pollination facilitation literature. We found that the field of pollination facilitation advanced seven mechanistic hypotheses which we synthesized into a conceptual framework to summarize the extent of mechanisms tested to date. Co-flowering interactions including the magnet species effect are the most frequently studied; however, the capacity for plants to facilitate the pollination of other plants through pathways that do not require co-blooming is an important research gap identified in this literature. We addressed several research gaps identified by the literature review. We tested the capacity for the dominant, foundation shrub *Larrea tridentata* to facilitate its annual understory. We separated blooming and non-floral interactions while incorporating the temporal dimension by tracking pollinator visitation to the understory as *L. tridentata* went through spring flowering phenology. *L. tridentata* interfered with the pollination of *Malacothrix glabrata* before it bloomed, and visitation was significantly reduced with blooming. *L. tridentata* supported plant and arthropod communities while creating locally stable microclimates demonstrating that positive and negative effects by foundation plants occur simultaneously. This project contributes to a better understanding of the underlying mechanisms driving interactions whole in a critically understudied arid environment.

# **Acknowledgements**

Thank you to my advisor Dr. Christopher Lortie for providing guidance and advice, fielding countless changes to my experimental designs and always being so supportive and encouraging of my many ideas. Thanks also to Dr. Amro Zayed for providing solid, constructive feedback and advice for this project.

I would like to thank my partner Brian Tammi for his extensive support over the last two years: for listening to me talk about bees for endless hours, always making sure I eat dinner and bringing snacks all the way to the Mojave National Preserve. Without his help I don’t think I would have got through this all.

Thank you to everyone in the ecoblender lab and especially Alex Filazzola for providing input, willingness to brainstorm ideas and jump out of a car into a sandstorm. Thanks to Daisy Goulart for providing field assistance in 2017 and enduring seemingly endless windstorms. Thanks also to everyone that helped me process data: Stephanie Haas, Diana Pik, Charlie West, Shobika Baskaran and Shima Sadat Rafizadeh Amirsalami. Thanks to Ally Ruttan for giving me advice based on her experiences.

Finally thank you to Tasha LaDoux and Jim Andre of the Sweeney Granites Desert Research Centre (University of California, Riverside) for hosting me over both field seasons, providing expert advice, introducing me to flora of the area and inviting me over to watch Star Wars. It is such a fantastic place.

**Table of Contents**

[**Abstract** i](#_Toc526773169)

[**Acknowledgements** ii](#_Toc526773170)

[**List of Tables** iii](#_Toc526773171)

[**List of Figures** iv](#_Toc526773172)

[**General Introduction** 1](#_Toc526773173)

[**Chapter One** 6](#_Toc526773174)

[Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. 6](#_Toc526773175)

[Abstract 7](#_Toc526773176)

[Introduction 8](#_Toc526773177)

[Conceptual framework 10](#_Toc526773178)

[Methods 12](#_Toc526773179)

[Systematic Review 12](#_Toc526773180)

[Data Analysis 13](#_Toc526773181)

[Results 14](#_Toc526773182)

[Discussion 15](#_Toc526773183)

[Research gaps in pollination facilitation studies 16](#_Toc526773184)

[Scale dependent effects are highly variable 19](#_Toc526773185)

[Conclusions 20](#_Toc526773186)

[Literature Cited 21](#_Toc526773187)

[Figures and Tables 28](#_Toc526773188)

[Supplemental Information 34](#_Toc526773189)

[**Appendix** 38](#_Toc526773190)

[List of studied included in systematic review 38](#_Toc526773191)

[**Chapter 2:** Disentangling the drivers and trade-offs of pollinator-mediated interactions between creosote bush (Larrea tridentata) and desert dandelion (Malacothrix glabrata). 44](#_Toc526773192)

[**Synthesis and General Conclusions** 45](#_Toc526773193)

# 

# **List of Tables**

**Table 1:** A summary of the mechanistic hypotheses generated by a systematic review of the pollination facilitation literature, a concise definition for each, the proposed umbrella mechanism under which it falls and examples of reference articles.

# **List of Figures**

**Figure 1:** A conceptual framework to model the mechanisms and hypotheses associated with pollinator-mediated facilitation. The concepts were extracted from a systematic review of 100 studies on this topic. The seven mechanistic hypotheses tested within the literature can be categorized into four umbrella hypotheses. Refer to Table 1 for a description of the seven mechanistic hypotheses. Each mechanism (A) can lead to a behavioral or demographic responses (B) that increases pollinator visitation or conspecific pollen deposition (C) that leads to an increase in fitness for another plant species (D).

**Figure 2:** A map showing geographic distribution of studies testing for pollination facilitation. The islands Seychelles and Mauritius each have one publication but are not visible on this map.

**Figure 3:** The frequency of pollination facilitation studies tested in each ecosystem type and their corresponding scale of study.

**Figure 4:** The number of studies testing each mechanism and their corresponding scale of study.

**Figure 5:** The number of associated studies based on spatial grain size and each testable mechanism.

# **General Introduction**

Interactions for pollination between plants directly involves reproductive success forming an interface between ecology and evolutionary biology that has captured the attention of biologists for more than 100 years. From an evolutionary perspective, mutualisms between plants and pollinators are adaptations evolved to meet the pollen dispersal needs of plants and the energy requirements of pollinators. These co-adaptations are at their most extreme within obligate mutualisms, e.g. between figs (*Ficus*) and wasps in the family *Agaonidae*, who are both pollinators and obligate seed parasites (Cook and Rasplus, 2003; Kjellberg et al., 2001). However, these strong examples of co-speciation are relatively rare. Plants frequently share pollinators (Mitchell et al., 2009; Waser et al., 1996) and pollination syndromes are dynamic (Waser et al., 1996). Plants can also impact the pollination of other plant species without sharing pollinators by providing habitat to another species’ pollinator (Hansen et al., 2007) or by shading a neighbour (McKinney and Goodell, 2010). Plant-pollinator mutualisms physically take place within natural communities and are embedded within complex webs of interactions (Montoya et al., 2006). Therefore, plant-pollinator interactions are not only the outcome of co-evolution between the direct participants; they also reflect interactions within the surrounding community.

Competition has conceptually dominated the field of ecology for most of the last century. More recently this dominance has been challenged and facilitation is now recognized as a fundamental process that contributes to function of plant communities (Bruno et al., 2003; Callaway, 1995). Pollinator-mediated facilitation is any interaction where one plant species positively influences the reproductive success of another plant species via pollinators. It is now recognized that these interactions form a continuum from competition to facilitation (Rathcke, 1983). This shift began with early theoretical work that suggested morphologically similar plants can maintain pollinator interest by increasing the functional size of the floral display (Macior, 1971). This was followed up by theoretical models showing facilitation can occur if pollinators do not distinguish between the plants (Bobisud and Neuhaus, 1975). The first empirical support for pollinator-mediated facilitation was provided when hawkweeds (*Hieracium*) were shown to receive more visits in mixed stands than alone (Thomson, 1978). Laverty (1992) documented the facilitation of non-rewarding orchids by rewarding species via the magnet species effect, where a particularly attractive species facilitates its less attractive neighbours by increasing local pollinator abundances. More recently, increases in floral diversity were shown to result in facilitation, demonstrating that morphological similarity is not a requirement for facilitation (Ghazoul, 2006). The majority of empirical evidence comes from pairwise interactions, however positive interactions can be diffuse and in some communities, positive pollinator-mediated interactions may even dominate (Hegland et al., 2008).

Understanding the ecological and individual contexts that mediate the outcome of pollinator-mediated interactions is necessary research to address currently rising challenges in conservation and applied ecology. Pollination services are foundational to the self-sufficiency of ecosystems, but pollinators are undergoing a decline globally (NRC, 2007; Potts et al., 2010). Recent estimates report that 87.5% of global angiosperms are animal pollinated (Ollerton et al., 2011). Under declining pollinator availability competition between plants may intensify, potentially leading to competitive displacement or loss of species. Therefore, understanding how plants interact via pollinators is necessary to understand the potential impacts of these declines. Climate change is driving geographic shifts in species distributions leading to novel interactions between species (Hegland et al., 2009). The increasingly early onset of seasonal shifts may cause phenological mismatches between plants and their pollinators (Kudo and Ida, 2013). Experimental evidence suggests that early flowering species have an increased risk of decreased visitation but that many species experienced no mismatch (Rafferty and Ives, 2011). Mismatches are not an issue if another pollinator or interactor can fill its place (CaraDonna et al., 2017). Thus, studying the outcomes of pollinator sharing and how interactions shift with phenology will better help us understand the implications of shifting climates on pollination services. Another important source of novel interactions is introduced and invasive species. Interactions for pollination provide a framework to explain the impact of invasive plant species on the fitness of native species. One meta-analysis concluded that negative impacts of invasive species on the pollination of natives are more frequent (Morales and Traveset, 2009). However, another recent meta-analysis found concluded that there are no negative overarching effects of invasives (Charlebois and Sargent, 2017). This ‘evening out’ of interaction signs again highlights that interactions are a continuum from negative to positive, indicating the need to better understand underlying mechanisms.

The overarching objective of this thesis is to examine the mechanisms of pollinator-mediated interactions and contrast their relative importance to the plant and arthropod communities associated with foundation plants. The first chapter of this thesis is a systematic review of the experimental pollination facilitation literature. I extracted and catalogued the extent of mechanisms tested by previous researchers to synthesize a literature-driven conceptual framework. I also summarized the scales of study, ecosystem and ecological themes to determine major research gaps and biases within the literature. The second chapter is an experimental approach to measuring interactions between the ecologically dominant shrub species *L. tridentata* and the commonly co-blooming annual *Malacothrix glabrata.* I hypothesized that foundational, desert shrubs that act as benefactors impact the net outcome of pollination for associated annual plants depending on the phenological stage of the shrub. By disentangling blooming and non-blooming pathways as *L. tridentata* shifts through natural phenology, I was able to quantify their contributions to the net observed interactions. I also confirmed the role of *L. tridentata* as a foundation species in this system by sampling its associated plant and arthropod communities, and testing the shrubs ability to stabilize local microclimates. These projects contribute to a better understanding of the underlying mechanisms controlling these interactions, from across a wide spread of literature but also in a critically understudied desert ecosystem. The maintenance of pollination mutualisms is an important aspect of conservation and therefore of management, and these findings can be used to inform best management practices within arid regions.

**Literature Cited**

Bobisud, L.E., Neuhaus, R.J., 1975. Pollinator constancy and survival of rare species. Oecologia 21, 263-272.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18, 119-125.

Callaway, R.M., 1995. Positive interactions among plants. Botanical Review 61, 306-349.

CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., Sanders, N.J., 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. Ecology letters 20, 385-394.

Charlebois, J.A., Sargent, R.D., 2017. No consistent pollinator-mediated impacts of alien plants on natives. Ecology letters 20, 1479-1490.

Cook, J.M., Rasplus, J.-Y., 2003. Mutualists with attitude: coevolving fig wasps and figs. Trends in Ecology & Evolution 18, 241-248.

Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94, 295-304.

Hansen, D.M., Kiesbüy, H.C., Jones, C.G., Müller, C.B., 2007. Positive indirect interactions between neighboring plant species via a lizard pollinator. The American Naturalist 169, 534-542.

Hegland, S.J., Grytnes, J.-A., Totland, Ø., 2008. The relative importance of positive and negative interactions for pollinator attraction in a plant community. Ecological Research 24, 929-936.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12, 184-195.

Kjellberg, F., Jousselin, E., Bronstein, J.L., Patel, A., Yokoyama, J., Rasplus, J.-Y., 2001. Pollination mode in fig wasps: the predictive power of correlated traits. Proceedings of the Royal Society of London B: Biological Sciences 268, 1113-1121.

Kudo, G., Ida, T.Y., 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. Ecology 94, 2311-2320.

Laverty, T.M., 1992. Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia 89, 502-508.

Macior, L.W., 1971. Co-evolution of plants and animals. Systematic insights from plant-insect interactions. Taxon, 17-28.

McKinney, A.M., Goodell, K., 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biological Invasions 12, 2751-2763.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M., Karron, J.D., 2009. New frontiers in competition for pollination. Annals of Botany 103, 1403-1413.

Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. Nature 442, 259.

Morales, C.L., Traveset, A., 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecology letters 12, 716-728.

NRC, 2007. Status of pollinators in North America. National Academies Press.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321-326.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends in ecology & evolution 25, 345-353.

Rafferty, N.E., Ives, A.R., 2011. Effects of experimental shifts in flowering phenology on plant–pollinator interactions. Ecology Letters 14, 69-74.

Thomson, J.D., 1978. Effects of Stand Composition on Insect Visitation in Two-Species Mixtures of *Hieracium*. American Midland Naturalist 100, 431-440.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems, and why it matters. Ecology 77, 1043-1060

# **Chapter One**

# Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation.

**Under review at Perspectives in Plant Ecology, Evolution and Systematics. Submitted March 2018, revisions submitted August 2018.**

## Abstract

Pollination facilitation is an indirect interaction whereby one plant species positively influences the reproductive success of another plant species through pollinators. A formal systematic review including 100 directly relevant papers was used to categorize the literature into a conceptual framework summarizing all mechanisms underlying pollination facilitation tested to date. We also summarized the spatial scale and grain size of each study, classified the theme, and recorded the ecosystem. Pollination facilitation research advanced seven major mechanistic hypotheses that can be synthesized into the following four umbrella mechanisms: trait-based effects, floral display size, floral diversity, and apparent pollination support. Co-flowering interactions including the magnet species effect are the most frequently studied; however, the capacity for plants to facilitate the pollination of other plants through pathways that do not require co-blooming is an important research gap identified in this literature. We propose that the term ‘apparent pollination support’ be used to describe pollination facilitation between plants through non co-blooming mechanisms. Most studies have been conducted using a relatively small spatial grain (< 1 m2) but there was evidence from all scales in most ecosystems of facilitation suggesting it may be more prevalent than previously assumed globally. Most studies (87.5%) that tested for facilitation at multiple scales reported scale dependence highlighting the need to explicitly consider spatial dimensions in future experiments on these topics. Invasion biology, agricultural science, mimicry systems, and conservation of rare plant species all examined pollination facilitation. Research gaps included the need to decouple mechanisms, explore the temporal dimensions and examine the relative importance of scale on the underlying processes that influence plant and pollinator community dynamics.

**Keywords**

Pollinator, facilitation, plant-plant, systematic review, scale dependence

## Introduction

Positive interactions between plant species, i.e. facilitation, are increasingly incorporated into ecological theory (Bertness and Callaway, 1994; Bruno et al., 2003; Callaway, 1995). Facilitation has been documented in most ecosystems as a fundamental process driving plant community structure and dynamics (Callaway, 1995). Pollinators provide critical ecosystem services, and there is increasing concern over their potentially global decline (Kearns et al., 1998; NRC, 2007). Recent estimates report that 87.5% of global angiosperms are animal pollinated (Ollerton et al., 2011). Therefore, understanding how plants interact via pollinators is necessary to understand the potential impacts of these declines. Co-flowering species of plants are common, and while there are a few salient examples of obligate plant-pollinator specialization, many species of plants share pollinators (Mitchell et al., 2009). Pollinator sharing leads to interactions between plants that can influence the reproductive success of one or both species forming a continuum of competitive to facilitative interactions (Rathcke, 1983). Competition between species for pollination profoundly influences the reproductive success of plants driving the evolution of floral morphology, phenology and reproductive strategies thereby integrating ecological and evolutionary perspectives (Mitchell et al., 2009). Mounting evidence shows that selection on reproductive plant traits and the development of ecological relationships are not driven exclusively by competition and that facilitation plays an important role.

Pollination facilitation influences many ecological and evolutionary processes. Facilitation has been demonstrated in plant mimicry systems (Benitez-Vieyra et al., 2007; Jersáková et al., 2009; Johnson et al., 2003; Peter and Johnson, 2008) and can promote the convergence of floral morphologies (Schemske, 1981). Facilitative interactions can also contribute to the evolution of complex mutualisms such as pollinator pollen placement mechanisms (Sun et al., 2011; Yang et al., 2013) and mitigate selection on mating traits that promote selfing (Moeller and Geber, 2005). Integrating pollinator mediated facilitation with current ecological theory will help to explain the coexistence of species with apparent niche overlaps (Moeller, 2004; Moeller and Geber, 2005) i.e. the joint use of resources by different species (Colwell and Futuyma, 1971) as well as the persistence of rare plants (Ghazoul, 2006; Moeller, 2004). Additionally, pollinator-mediated plant-plant interactions provide a framework for predicting the impact of invasive plant introduction on native plant communities (Bartomeus et al., 2008; Charlebois and Sargent, 2017; Molina-Montenegro et al., 2008; Morales and Traveset, 2009). Therefore, pollination facilitation has a wide-reaching and general capacity to serve as a model integrating ecological and evolutionary perspectives.

Pollinator mediated interactions are scale-dependent (Hegland and Kudo, 2014) meaning that the sign or strength of the interaction differs depending on the scale of observation. The recognition of spatial scale as a central concept to ecology has become well established (Levin, 1992; Sandel, 2015; Wiens, 1989), and increasingly, ecologists are explicitly incorporating spatial dimensions into their experimental design (Hegland and Kudo, 2014; Schmid et al., 2016; Spellman et al., 2016). Nonetheless, the current inconsistency in reporting in part stems from the terminology used by researchers (Sandel, 2015). Spatial scale as a descriptive measurement is distinct from the hierarchal, organizational levels frequently used by ecologists. Spatial scale is comprised of two components: grain, the size of the smallest unit of observation, and extent, the total sampling area (Scheiner et al., 2000; Turner, 1989). In field studies, grain and extent are often defined relative to the organism. Grain is often an individual or cluster of plants, and extent as a forest. Alternatively, they can be defined in absolute terms i.e. experimental plots. In both cases, these two scale components are finite measures that limit experimental resolution and therefore define the degree of generalization possible. It is not possible to infer patterns below measured grain size or above extent size (Wien, 1989). Scale of study has critical implications for applied ecology of plant-pollinator interactions and to experimental design because the mobility of animal pollinators increases the scale over which plants interact (Moeller, 2004). For example, some attractive plants facilitate their immediate neighbors while competing with others over a larger spatial scale (Hegland and Kudo, 2014; Schmid et al., 2016). Thus, a given scale can lead to erroneous conclusions when generalizing.

Although previously predicted to be a rare phenomenon (Feldman et al., 2004), there has been an increase in the publication of papers reporting facilitative interactions over the last three decades. Given this apparent prevalence a better understanding of the underlying mechanisms and potential outcomes of this interaction is needed. To this end, we conducted a formalized systematic review of the pollination facilitation literature published. Using the literature, we developed a typology for the research and classified all studies into this conceptual framework. The synthetic framework visualizes all the pathways tested in the literature where plants induce a response in pollinators leading to an increase in fitness for another plant species (Figure 1) describing a total of seven mechanistic hypotheses (Table 1). We focused on facilitation only because competition is comparatively well researched and mechanisms of facilitation are likely to be distinct from those underlying competition.

The primary goal of this review and conceptual framework was to link current research with ecological theory. Previous reviews of plant-plant facilitation have identified the need to understand indirect pathways (Filazzola and Lortie, 2014) and the individual mechanisms leading to facilitation (Brooker et al., 2008). The following specific objectives were addressed using this systematic review: to determine the frequency that each mechanism has been tested, to describe research gaps, to highlight the most common applications of pollination facilitation, and to assess the geographic and ecological scope of pollination facilitation studies. Pollination is an important ecosystem service therefore we examine the frequencies of publications within each to determine publication biases and ecosystem-specific gaps. In this systematic review, grain size and scale dependence in the primary literature were also synthesized to provide an estimate of the relative context and importance of pollinator facilitation at different scales and in effect to describe the potential scope that this set of mechanisms could be important to be pollinator communities*.*

## Conceptual framework

The seven hypotheses tested in the literature were classified into four umbrella mechanisms (Table 1). Pollination facilitation is an indirect interaction between plants mediated by the pollinator and the concepts were organized to reflect this plant-pollinator-plant interaction. The conceptual framework is comprised of trait-based effects, increasing floral display size, increasing floral diversity, and pollinator support as ‘umbrella’ mechanisms (Figure 1, A)*.* We use the umbrella term “trait-based effects” to include both the magnet species effect and mimicry and to reflect that these interactions are trait-mediated. In the magnet species effect, a particularly attractive plant species increases local pollinator abundances, thereby facilitating their co-blooming but often less attractive neighbors (Laverty, 1992; Thomson, 1978). The traits that magnet species exhibit are those that make a plant attractive to pollinators such as showy displays (Molina-Montenegro et al., 2008) or offering substantial resources (Johnson et al., 2003). The magnet species effect is not exclusively related to resources. For example, the sexually deceptive orchid *Ophrys fusca* acts as a magnet for a rewarding iris (Pellegrino et al., 2016) and tall-scaped *Primula farinosa* facilitate their short-scaped morphs (Toräng et al., 2006).In mimicry systems, less attractive plant species improve their fitness by mimicking a more preferred species (reviewed by Jersáková et al., 2009). In these cases, the trait is the resemblance to the model species. It can include mimicry of overall floral morphology (Carmona-Díaz and García-Franco, 2008), UV reflectance (Peter and Johnson, 2008), UV spectra and nectar content (Benitez-Vieyra et al., 2007). Facilitation due to the magnet species effect and mimicry is not commonly separated, and the degree of resemblance between the species is the major difference between these mechanisms (Carmona-Díaz and García-Franco, 2008). In both cases, the addition of another plant increases pollinator attraction disproportionate to the size of a display increase.

Facilitation can occur when plants growing together increase their combined floral display size by co-blooming (Feldman, 2006; Thomson, 1981). Many pollinators forage optimally (Pyke et al., 1977), and the nectar and pollen content of flowers influences their foraging decisions (Heinrich and Raven, 1972; Real, 1981). This leads to pollinators preferentially visiting larger displays (Chittka and Thomson, 2001; Thomson, 1981). There are two major ways to describe the size of a floral display: density i.e. the interplant distance and abundance, the total number of individuals (Kunin, 1997). Patch area and floral density interact to determine attractiveness for pollinators (Thomson, 1981). However, in many studies abundance and density are unavoidably confounded. Pollinator responses to floral display size are density-dependent (reviewed by Feldman, 2006). Per flower visitation rates are expected to increase with floral density until pollinators become ‘saturated’ by the overabundance of floral resources leading to a shift from facilitation to competition between plants (Rathcke, 1983). Pollinator densities mediate the shifting point (Ye et al., 2013).

When plants co-bloom, the increase in floral diversity can lead to improved pollination services by offering complementary resources to foragers (i.e. both pollen and nectar) or via sampling effort: more diverse displays may attract more diverse pollinators (Ghazoul, 2006), leading to the attraction of more effective pollinators. The umbrella term apparent pollination support includes all mechanisms for which co-blooming is not required. Sequential mutualisms arise when earlier blooming plants facilitate later blooming plants by increasing local pollinator abundance, or improving population longevity or stability (Waser and Real, 1979). We expand on this by including the mechanism of providing habitat for another plant’s pollinator (Hansen, 2007). This final mechanism is a novel extension to the literature because it does not require shared pollinators.

Each mechanism leads to either of two functional responses by pollinators (Figure 1, B): the change in behavior of individual pollinators or demography of pollinator populations. The conceptual framework by Moeller (2004) recognized two major responses by pollinators including aggregative (joint attraction) and numerical (joint maintenance) responses. We expand upon this; the most frequently documented behavioral response leading to facilitation is the joint attraction of pollinators (sensu Schemske 1981; Thomson 1978). There are other foraging-related behaviors that arise from context-dependent species preferences beyond attracting additional pollinators (Hersch and Roy, 2007). Pollinators can exert positive frequency dependent selection by preferentially visiting the most abundant plant. Thus plants can increase their fitness by co-blooming (Ghazoul, 2006; Toräng et al., 2008). Similarly, pollinators that show floral constancy, i.e. the tendency to facultatively specialize, can lead to facilitation between multiple species (Bobisud and Neuhaus, 1975) or among mimicry partners (Schiestl and Johnson, 2013). Some pollinators exhibit site-fidelity greater than floral constancy that leads to sequential facilitation of plants growing in that site (Ogilvie and Thomson, 2016). Demographic pollinator responses, sensitive to the local habitat or landscape (Grab et al., 2017; Jakobsson and Padron, 2014), can change the pollinator abundance, composition, or longevity thereby benefiting spatially or temporally associated plants. Both behavioral and demographic responses can improve the quality and quantity components of pollination (Figure 1, C). Visitation rates form the quantity component and conspecific pollen deposition is the quality component (Herrera, 1989). Increased visitation will not lead to increased fitness if excessive heterospecific pollen is deposited (Morales and Traveset, 2008). Furthermore, increased visitation is not necessary to increase conspecific deposition if more effective pollinators visit. This increase in conspecific deposition leads to increased seed set or viability (Figure 1, D).

## Methods

### Systematic Review

To review the field of pollination facilitation, we used the search terms “pollinat\* facilitat\*” in ISI Web of Science (WoS) and SCOPUS in November 2017. Results from these searches were exported as bibtex files and are available within the associated repository. We also consulted book chapter bibliographies and did supplemental searches using Google Scholar to ensure that the literature was well represented within the WoS. Only primary, English language experimental research papers published since 1970 in peer-reviewed journals were included. The following inclusion criteria were used: 1) explicitly tested for pollination facilitation; 2) tested interspecific plant-plant interactions including a plant-mimic or object (e.g. hummingbird feeder, (Brockmeyer and Schaefer, 2012); 3) net facilitation was tested using at least one indicator of reproductive success (see Supporting Information, S1). We screened a total of 1501 papers by abstract and 268 full-text articles leading to the inclusion of a total of 100 papers in this review (Appendix A).

We classified the literature using our synthetic framework by the mechanistic hypotheses testable given the variables and experimental design utilized by the authors (Table S2). Articles were further reviewed for spatial scale, country and ecosystem of study, main methods, theme of study and spatial grain size was categorized. Small grain was defined as one individual plant or a plot 1m2 or less, medium between 1 m2 and 20 m2, large between 20 m2 and 500 m2, and very large greater than 500 m2. Scale dependence was defined as a significant change in the value of a variable or the importance of a model predictor variable when either the grain or extent was changed within the experiment. Studies were classified as broad if they were very large grained, had extents greater than 10000 m2, or self-reported as landscape scale; otherwise they were classified as narrow. Ecosystems were simplified to agricultural, alpine, wetland, beaches, experimental, forest, grassland, semi-arid, tropical forest and urban/disturbed.

### Data Analysis

When multiple ecosystems were tested within the same publication, they were treated as independent observations. Publications testing for interactions using multiple grain sizes were considered independent for grain size graphs and subsequent frequency testing. Multiple mechanisms could also be tested with the same publication, and they were classified independently for graphs and frequency testing. However, the mechanism by grain size analysis was restricted to single scale studies because it was necessary for them to be paired within a study. We tested the relative frequencies of each tested mechanism, grain size, and ecosystem using Pearson’s chi-squared tests (chisq.test function) in R version 3.4.2 (R Development Core Team, 2016). As a post hoc test we used the standardized residuals to compare the proportion of each grouping. We fit a linear model using the log-transformed publication count as the response and year as the predictor (lm function) in R version 3.4.2 (R Development Core Team, 2016) to test for a publication frequency increase over time.

## Results

A total of 100 papers reported testing for pollination facilitation (Figure S3). The number of papers published per year has increased exponentially since 1978 (Adjusted R2 = 0.6426, p < 0.0001). Studies from 27 countries have been published with the majority in the USA (Figure 2).

There were significant differences in the frequency of tested mechanisms (Figure 3, χ2 = 119.21, df = 6, n = 162, p < 0.0001). The majority of papers addressed the magnet species effect (64%). Pollinator support is an unstudied mechanistic pathway. Habitat provisioning and sequential mutualisms were examined in only five papers each. A single mechanism was tested within 47% of papers, two mechanisms in 42% of papers, and only one paper examined four potential mechanisms. The framework did not apply to one paper that tested for facilitation at a community level using a novel network approach (Tur et al, 2016).

The largest proportion (28.3%) of studies was conducted in grasslands or meadows (χ2 = 66.057, n = 106, df = 10, p < 0.0001). In most ecosystems, narrow scales were more frequently used, but in agricultural lands broader scales were more frequently tested (Figure 3). Alpine ecosystems, wetlands and tropical forests lacked studies that consider both scales within the same paper.

All but three studies reported spatial grain size, and these ranged from 0.009 m2 to 35900 m2. However, most reported grain qualitatively (55%) as either an individual plant, clump, or a number of stems. Pollination facilitation is tested most frequently (61% of studies) with a small spatial grain (< 1 m2). Very large grain sizes greater than 500 m2 were tested the least comprising only 3.8% of studies (χ2 = 151.74, n = 105, df = 5, p < 0.0001). Extent was not consistently reported preventing full quantitative scale reporting. Instead, we classified studies into the categories of narrow and broad. These two scales of study were well distributed between tested mechanisms (Figure 4). Sequential mutualisms were the exception and have not been studied at both broad and narrow scales within a given study. The mechanisms of pollination facilitation have been studied using a range of spatial grain sizes (Figure 5). A total of 25 studies tested for interactions at multiple scales or explicitly included spatial dimensions into the experimental design with 21 of them reporting scale-dependence.

Invasion biology was the most frequently theme addressed (29% of studies) followed by agriculture (12%), deceptive pollination (9%), conservation (6%), and rare species (5%). Most papers studied unidirectional or bidirectional interactions; only nine used a network approach to either directly study interactions or supplement more traditional testing.

The most frequent method of assessing reproductive success was tracking pollinator visitation rates (86% of studies). Of the 63 papers that used seed/fruit set as a response variable, 54 controlled for potential confounding effects of plant-plant interactions (Table S5). The methods include using potted plants (19), testing for pollen limitation by hand-pollination (18), and pollinator exclusion (6). Of the nine that did not, two were very large-scale agricultural experiments that tracked pollinator visitation. Of the remaining six, two measured both pollen deposition and visitation, one measured pollen deposition, one study measured visitation, and one tracked pollen dispersal with dyes. There was only one study with no supplemental measurements or controls.

## Discussion

This systematic review is the first formal synthesis of pollination facilitation providing an overview of the underlying mechanisms that have been tested to date. The conceptual framework proposed effectively classified the state of research of pollination facilitation based on the mechanistic pathways examined in the individual studies reviewed. This framework is nonetheless sufficiently flexible to included future novel hypotheses because of the use of umbrella terms that provide for the inclusion of additional mechanisms as they arise from future studies. Co-flowering interactions are the most frequently studied. The capacity for plants to facilitate the pollination of other plants through pathways that do not require co-blooming is an important research gap. Many studies do not explicitly differentiate between the mechanistic hypotheses. Another significant research gap is the study of joint multiple mechanisms. To better test the underlying drivers of pollinator mediated interactions and to integrate these findings into applied ecology, we need to study more than one mechanism in a given system preferably in the same experiment. Facilitative interactions between plants can increase under declining pollinator availability (Lazaro et al., 2014) highlighting the increasing importance to study these interactions as a means to better model resilience of pollinator and plant communities.

### Research gaps in pollination facilitation studies

In natural systems, multiple mechanisms of facilitation operate concurrently. There is always the potential for interactions between display size and other mechanisms of facilitation. These mechanisms can collectively inform applied ecology. For example, when the magnet species effect interacts with floral density, both the presence and density of the attractive species contribute to its effect on other species. In a simulated invasion, facilitation by *Taraxacum officinale* shifted to competition with high densities of the invader (Muñoz and Cavieres, 2008). This is applicable to applied invasion biology because it suggests for some species there is a density threshold at which an attractive plant can become a competitor. Seifan (2014) manipulated both the density and aggregation of attractive plants finding again a shift from facilitation to competition with increasing density, but also that at low densities, they were better facilitators when regularly spaced then aggregated. Magnet plants have the capacity to improve the self-sufficiency of restored ecosystems (Dixon, 2009). Thus better understanding interactions between attractiveness, density, and aggregation will improve restoration.

Biodiversity continues to decline with human expansion (Butchart et al., 2010). Therefore, understanding the influence of floral diversity and display size jointly is important to for predicting the impacts of this decline. Experiments along gradients of fragmentation could provide a convenient and applicable system, particularly if pollinator populations are sampled. For example, along an urban diversity gradient, flower rich urban areas supported richer bee communities, leading to improved seed set for focal plant species (Theodorou et al., 2017). Incorporating pollinator identity is important to a better understanding of the mechanisms, as well as for predicting the impact of pollinator declines. For example, network analysis of island plant-pollinator visitation networks has shown that invasion intensity influenced the behavior of *Apis mellifera*, leading to community wide simplification of interactions despite having no negative influence on native seed set (Kaiser-Bunbury et al., 2011). Network approaches are labor and resource intensive but when combined with manipulative experiments will provide community-level and highly explanatory results.

Apparent pollination support is the least studied mechanism of pollination facilitation. It is the most likely to generate novel hypotheses because co-flowering is not a requirement. The study of pollination support in the literature takes two distinct streams including sequential mutualism (temporal facilitation) and habitat provisioning. Competition can shift to facilitation as floral phenologies diverge if shared pollinator populations are supported leading to a ‘sequential mutualism’, i.e. facilitation follows competitive interactions (Moeller, 2004; Waser and Real, 1979). Sequential mutualisms are likely an outcome rather than a cause of phenological divergence (Waser and Real, 1979) particularly because sequential flowering is not exclusively maintained by competition. This form of mutualism can also be maintained by herbivory (Brody, 1997). Alternatively, earlier blooming plants such as mass flowering crops can create resource pulses for pollinators that support later blooming plants (Grab et al., 2017). This effect had been termed ‘temporal spillover’ in agricultural studies (Riedinger et al., 2014). Evidence for temporal facilitation has also been found in invasive/native pairs (Ferrero et al., 2013), agricultural systems (Grab et al., 2017), and experimental arrays (Ogilvie and Thomson, 2016). Temporally separated mutualisms are generally predicted to be widespread (Waser and Real, 1979). Inclusion of the temporal dimension increases the complexity of interactions and presents considerable difficulty to experimental design. However, integrating the temporal dimension is likely critical in applied contexts because of the capacity for support. For example, the rare plant *Symphyotrichum* *sericeum* shares pollinators with earlier blooming plants (Robson, 2012) suggesting that conservation efforts to support the pollination of some rare plants need to consider both the immediate neighbors but also earlier blooming interacting plants. There is widespread potential for pollination facilitation to inform applied conservation practices.

Habitat loss is one of the most important drivers of wild bee abundance and diversity declines (Brown and Paxton, 2009; Potts et al., 2010). The mechanisms of habitat provisioning are thus critical to the conservation of both pollinator and plant populations. Cavity-nesting bees including *Megachile* leafcutter bees, *Hylaeus*, *Ceratina* (Michener, 2000) and agriculturally important *Osmia* bees (Cane et al., 2007) use pithy stems and dead wood as nesting sites, but this pathway for facilitation is likely trait-mediated (i.e. pithiness) rather than species-specific. Accordingly, habitat provisioning is addressed at a community level by agricultural studies showing that proximity to hedgerows (Dainese et al., 2017) and semi-natural lands (Norfolk et al., 2016) benefits crop pollination. In natural ecosystems, the only published example of facilitation by habitat provisioning is species-specific. The *Pandanus* shrub provides habitat for the gecko *Phelsuma cepediana* which is the main pollinator of *Trochetia blackburniana* (Hansen et al., 2007), and this shrub is a species of conservation concern in Mauritius. Shrubs of *T. blackburnia* experienced better pollination growing near *Pandanus*. The frequency that this mechanism functions is needed to better inform targets for conservation. Potential relationships can include facilitation by plants that act as hosts to pollinating Lepidoptera or within any system where the larva of a generalist pollinator requires a specific host plant. Plants growing in harsh environments benefit from close association to nurse plants due to abiotic stress amelioration (Filazzola and Lortie, 2014). Pollination facilitation has not been tested in arctic or desert ecosystems. Overall, pollination facilitation in harsh environments is a research gap. Pollination facilitation is very understudied in these harsh environments and can be a very important pathway to both conservation and agriculture.

Mensurative experiments that use seed-set or fruit-set as a response variable may be confounded by pollinator independent plant-plant interactions (Lachmuth et al., 2018). This review found the majority of experimental designs controlled for these sources of micro-environmental variation. Several authors have used methods to measure the presence of these interactions in tandem with tracking pollinator visits or pollen transfer. For example, Kaiser-Bunbury (2011) used the ratio of native to invasive flowers as a proxy for plant-plant competition. Molina-Montenegro (2008) corrected for potential bottom-up facilitation by measuring nitrogen and water availability, as well as visitation rates and seed output. The majority of papers overall use pollinator visitation as a response variable, which directly addresses pollinator behavioral or demographic responses. However, increased visitation does not always lead to increased seed set. For example, pollen deposition can be facilitated but not visitation rates (Muir and Vamosi, 2015) if more effective pollinators visit. Plants can simultaneously compete and facilitate different portions of the pollination process. In orchids, different interaction signs for pollinator attraction, pollen removal and pollen deposition have been reported concurrently (Duffy and Stout, 2011). It is not known how the mechanisms underlying the interaction influences the quality and quantity aspects of pollination. However, it is unlikely there is a consistent, overarching mechanistic influence because pollinator behavioral and demographic response to each mechanism depend on the identity of the interactors, as well as the context. The continued publications of papers that measure multiple metrics of reproduction will allow for future quantitative analyses as to the strength of interaction operating on each part of the pollination framework and enable this to be tested rigorously.

### Scale dependent effects are highly variable

The outcome of scale-dependency was highly variable across the pollination facilitation literature reviewed here. Facilitation typically decreased with distance likely because the influence of a plant cannot extend beyond the foraging range of its pollinators. For example, facilitation occurs at only very short distances from the invasives *Lupinus* (Jakobsson et al., 2015) and *Brassica nigra* (Bruckman and Campbell, 2016) suggesting that these invasives have little overall effect on pollinations in these systems. In almond orchards, floral abundance under trees is positively associated with their seed set while floral abundance within the landscape is not (Norfolk et al., 2016). Conversely, the invasive *Ranunculus ficaria* has a stronger magnet effect when present at the landscape scale suggesting presence in landscape is more important than local floral abundances some systems (Masters and Emery, 2015). Facilitation shifting to competition with increasing scale was reported in several systems including insect-pollinated red clover (Hegland and Kudo, 2014) and nectar-feeding birds within a fynbos ecosystem (Schmid et al., 2016). Scale dependence can arise at least in part from underlying mechanisms. Spatial scale dependence can manifest as magnet plants first influence the probability of a pollinator entering a patch, and then within the patch influence the pollinator’s choices between individual flowers (Seifan et al., 2014). These effects can lead to relatively small-scale facilitation between neighbors but competition between patches. Floral abundance is likely important at larger scales because it relates to the total pollen and nectar resource content of a community, and therefore to the carrying capacity of pollinator populations, and density may be more important at smaller scales because it is related to individuals’ foraging habits and preferences; these hypotheses are yet to be tested. The perception of floral display size by pollinators differs at multiple scales because at small scales increases in density are attractive to pollinators but at larger scales, as density increases, the displays become more diluted relative to pollinator abundances (Rathcke, 1983), and increases in display size become less visible. These perceptual biases by pollinators can lead to changes in interaction sign with increasing scale. Understanding the underlying mechanisms of scale-dependency is important to the effective experimental design of studies looking at pollination interactions. For instance, a recent meta-analysis found that the distance between control and neighboring plants influences the sign of an interaction more than the identity of the interactors (Charlebois and Sargent, 2017). A quantitative estimate of grain and extent is needed for pollinator mediated interaction studies because changes in strength and sign of interactions have been reported to change with scale and without measures in spatial dimensions we cannot effectively model its importance. Pollinator mediated facilitation has been nonetheless reported across a wide range of spatial grain sizes and in a variety of ecosystems. This suggests that these interactions are prevalent and are not restricted to small scales.

## Conclusions

Positive interspecific and intraspecific interactions between plants for pollinators can dominate in some plants communities (Hegland et al., 2008; Tur et al., 2016) and were relatively ubiquitous here. The scope of pollinator mediated facilitation is thus relatively broad encompassing most major ecosystems. Most pollinator mediated facilitation experiments to date use only a small spatial grain. This suggests that scale dependence can be a serious issue in these studies. It has been suggested that pollination as an ecosystem service operates on a local scale and at the ecological levels of the individual and population (Andersson et al., 2015). This review further suggests that pollination also operates on a community level for plants and their animal pollinators. The mechanisms categorized here likely do not function in isolation, and experiments that examine more than one pathway concurrently are needed. Furthermore, distributional asynchrony can result from shifts in the spatial distribution of species under climate change scenarios (Hegland et al., 2009) and this can lead to novel interactions between plants and pollinators highlighting the increasing need to understand the underlying drivers. Studies of pollinator-mediated facilitation must now begin to explore the relative importance of scale, temporal interactions, and the relative changes in one mechanism over another with these changes.

## Literature Cited

Andersson, E., McPhearson, T., Kremer, P., Gomez-Baggethun, E., Haase, D., Tuvendal, M., Wurster, D., 2015. Scale and context dependence of ecosystem service providing units. Ecosystem Services 12, 157-164.

Bartomeus, I., Vila, M., Santamaria, L., 2008. Contrasting effects of invasive plants in plant-pollinator networks. Oecologia 155, 761-770.

Benitez-Vieyra, S., Hempel de Ibarra, N., Wertlen, A.M., Cocucci, A.A., 2007. How to look like a mallow: evidence of floral mimicry between *Turneraceae* and *Malvaceae*. Proc Biol Sci 274, 2239-2248.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends in Ecology & Evolution 9, 191-193.

Bobisud, L.E., Neuhaus, R.J., 1975. Pollinator constancy and survival of rare species. Oecologia 21, 263-272.

Brockmeyer, T., Schaefer, H.M., 2012. Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds? Basic and Applied Ecology 13, 294-300.

Brody, A.K., 1997. Effects of pollinators, herbivores, and seed predators on flowering phenology. Ecology 78, 1624-1631.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M., Anthelme, F., 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96, 18-34.

Brown, M.J., Paxton, R.J., 2009. The conservation of bees: a global perspective. Apidologie 40, 410-416.

Bruckman, D., Campbell, D.R., 2016. Pollination of a native plant changes with distance and density of invasive plants in a simulated biological invasion. Am J Bot 103, 1458-1465.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18, 119-125.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global Biodiversity: Indicators of Recent Declines. Science.

Callaway, R.M., 1995. Positive interactions among plants. Botanical Review 61, 306-349.

Cane, J.H., Griswold, T., Parker, F.D., 2007. Substrates and materials used for nesting by North American *Osmia* bees (Hymenoptera: Apiformes: *Megachilidae*). Annals of the Entomological Society of America 100, 350-358.

Carmona-Díaz, G., García-Franco, J.G., 2008. Reproductive success in the Mexican rewardless *Oncidium cosymbephorum* (*Orchidaceae*) facilitated by the oil-rewarding *Malpighia glabra* (*Malpighiaceae*). Plant Ecology 203, 253-261.

Charlebois, J.A., Sargent, R.D., 2017. No consistent pollinator‐mediated impacts of alien plants on natives. Ecology letters 20, 1479-1490.

Chittka, L., Thomson, J., 2001. Behavioral responses of pollinators to variation in floral display size an. d their influences on the evolution of floral traits. Cognitive ecology of pollination, 274-296.

Colwell, R.K., Futuyma, D.J., 1971. On the measurement of niche breadth and overlap. Ecology 52, 567-576.

Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., Marini, L., 2017. High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. Journal of Applied Ecology 54, 380-388.

Dixon, K.W., 2009. Pollination and restoration. Science 325, 571-573.

Duffy, K.J., Stout, J.C., 2011. Effects of conspecific and heterospecific floral density on the pollination of two related rewarding orchids. Plant Ecology 212, 1397-1406.

Feldman, T., 2006. Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low‐densities? Oikos 115, 128-140.

Feldman, T., Morris, W., Wilson, W., 2004. When can two plant species facilitate each other's pollination? Oikos 105, 197-207.

Ferrero, V., Castro, S., Costa, J., Acuña, P., Navarro, L., Loureiro, J., 2013. Effect of invader removal: pollinators stay but some native plants miss their new friend. Biological Invasions 15, 2347-2358.

Filazzola, A., Lortie, C.J., 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Global Ecology and Biogeography 23, 1335-1345.

Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94, 295-304.

Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Scientific Reports 7, 45296.

Hansen, D.M., Kiesbüy, H.C., Jones, C.G., Müller, C.B., 2007. Positive indirect interactions between neighboring plant species via a lizard pollinator. The American Naturalist 169, 534-542.

Hegland, S.J., Grytnes, J.-A., Totland, Ø., 2008. The relative importance of positive and negative interactions for pollinator attraction in a plant community. Ecological Research 24, 929-936.

Hegland, S.J., Kudo, G., 2014. Floral neighbourhood effects on pollination success in red clover are scale-dependent. Functional Ecology 28, 561-568.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12, 184-195.

Heinrich, B., Raven, P.H., 1972. Energetics and pollination ecology. Science 176, 597-602.

Herrera, C.M., 1989. Pollinator abundance, morphology, and flower visitation rate: analysis of the “quantity” component in a plant-pollinator system. Oecologia 80, 241-248.

Hersch, E.I., Roy, B.A., 2007. Context‐dependent pollinator behavior: An explanation for patterns of hybridization among three species of Indian paintbrush. Evolution 61, 111-124.

Jakobsson, A., Padron, B., 2014. Does the invasive *Lupinus polyphyllus* increase pollinator visitation to a native herb through effects on pollinator population sizes? Oecologia 174, 217-226.

Jakobsson, A., Padrón, B., Ågren, J., 2015. Distance-dependent effects of invasive *Lupinus polyphyllus* on pollination and reproductive success of two native herbs. Basic and Applied Ecology 16, 120-127.

Jersáková, J., Johnson, S.D., Jürgens, A., 2009. Deceptive behavior in plants. II. Food deception by plants: from generalized systems to specialized floral mimicry, Plant-Environment Interactions. Springer, pp. 223-246.

Johnson, S.D., Peter, C.I., Nilsson, L.A., Agren, J., 2003. Pollination success in a deceptive orchid is enhance by co-occuring magnet plants. Ecology 84, 2919-2927.

Kaiser-Bunbury, C.N., Valentin, T., Mougal, J., Matatiken, D., Ghazoul, J., 2011. The tolerance of island plant-pollinator networks to alien plants. Journal of Ecology 99, 202-213.

Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. Endangered mutualisms the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29, 83-112.

Kunin, W.E., 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology, 225-234.

Lachmuth, S., Henrichmann, C., Horn, J., Pagel, J., Schurr, F.M., 2018. Neighbourhood effects on plant reproduction: An experimental–analytical framework and its application to the invasive *Senecio inaequidens*. Journal of Ecology 106, 761-773.

Laverty, T.M., 1992. Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia 89, 502-508.

Lazaro, A., Lundgren, R., Totland, O., 2014. Experimental reduction of pollinator visitation modifi es plant–plant interactions for pollination. Oikos, 1037-1048.

Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology 73, 1943-1967.

Masters, J.A., Emery, S.M., 2015. The showy invasive plant *Ranunculus ficaria* facilitates pollinator activity, pollen deposition, but not always seed production for two native spring ephemeral plants. Biological Invasions 17, 2329-2337.

Michener, C.D., 2000. The bees of the world. JHU press.

Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M., Karron, J.D., 2009. New frontiers in competition for pollination. Annals of Botany 103, 1403-1413.

Moeller, D.A., 2004. Facilitative interactions among plants via shared pollinators. 85 12.

Moeller, D.A., Geber, M.A., 2005. Ecological context of the evolution of self-pollination in *Clarkia xantiana*: Population size, plant communities and reproductive assurance. Evolution 59, 786-799.

Molina-Montenegro, M.A., Badano, E.I., Cavieres, L.A., 2008. Positive interactions among plant species for pollinator service: assessing the ‘magnet species’ concept with invasive species. Oikos 117, 1833-1839.

Morales, C.L., Traveset, A., 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. Critical Reviews in Plant Sciences 27, 221-238.

Morales, C.L., Traveset, A., 2009. A meta‐analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co‐flowering native plants. Ecology letters 12, 716-728.

Muir, J.L., Vamosi, J.C., 2015. Invasive Scotch broom (*Cytisus scoparius, Fabaceae*) and the pollination success of three Garry oak-associated plant species. Biological Invasions 17, 2429-2446.

Muñoz, A.A., Cavieres, L.A., 2008. The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. Journal of Ecology 96, 459-467.

Norfolk, O., Eichhorn, M.P., Gilbert, F., Stewart, A., Brady, S., 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. Insect Conservation and Diversity 9, 236-243.

NRC, 2007. Status of pollinators in North America. National Academies Press.

Ogilvie, J., Thomson, J.D., 2016. Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. Ecology 97, 1442–1451.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321-326.

Pellegrino, G., Bellusci, F., Palermo, A.M., 2016. Who helps whom? Pollination strategy of *Iris tuberosa* and its relationship with a sexually deceptive orchid. J Plant Res 129, 1051-1059.

Peter, C.I., Johnson, S.D., 2008. Mimics and magnets: The importance of color and ecological facilitation in floral deception. Ecology 89, 1583–1595.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends in ecology & evolution 25, 345-353.

Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal foraging: a selective review of theory and tests. The quarterly review of biology 52, 137-154.

Rathcke, B., 1983. Competition and facilitation among plants for pollination. Pollination biology, 305-329.

Real, L.A., 1981. Uncertainty and pollinator‐plant interactions: The foraging behavior of bees and wasps on artificial flowers. Ecology 62, 20-26.

Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., Holzschuh, A., 2014. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. Landscape Ecology 29, 425-435.

Robson, D.B., 2012. An assessment of the potential for pollination facilitation of a rare plant by common plants: *Symphyotrichum sericeum* (*Asteracae*) as a case study. Botany 91, 34-42.

Sandel, B., 2015. Towards a taxonomy of spatial scale-dependence. Ecography 38, 358-369.

Scheiner, S., Cox, S.B., Mittelbach, G.G., Osenberg, C., Kaspari, M., 2000. Species richness, species–area curves and Simpson’s paradox. Evolutionary Ecology Research 2, 791-802.

Schemske, D.W., 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. Ecology 62, 946-954.

Schiestl, F.P., Johnson, S.D., 2013. Pollinator-mediated evolution of floral signals. Trends in Ecology & Evolution 28, 307-315.

Schmid, B., Nottebrock, H., Esler, K.J., Pagel, J., Pauw, A., Böhning-Gaese, K., Schurr, F.M., Schleuning, M., 2016. Responses of nectar-feeding birds to floral resources at multiple spatial scales. Ecography 39, 619-629.

Seifan, M., Hoch, E.-M., Hanoteaux, S., Tielbörger, K., Bartomeus, I., 2014. The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. Journal of Ecology 102, 953-962.

Spellman, K.V., Mulder, C.P.H., Carlson, M.L., 2016. Effects of invasive plant patch size and distance on the pollination and reproduction of native boreal plants. Botany 94, 1151-1160.

Sun, H.Q., Huang, B.Q., Yu, X.H., Kou, Y., An, D.J., Luo, Y.B., Ge, S., 2011. Reproductive isolation and pollination success of rewarding *Galearis diantha* and non-rewarding *Ponerorchis chusua* (*Orchidaceae*). Ann Bot 107, 39-47.

Theodorou, P., Albig, K., Radzeviute, R., Settele, J., Schweiger, O., Murray, T., Paxton, R., 2017. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. Functional ecology 31.

Thomson, J.D., 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. American Midland Naturalist 100, 431-440.

Thomson, J.D., 1981. Spatial and temporal components of resource assessment by flower-feeding insects. The Journal of Animal Ecology 50, 49-59.

Toräng, P., Ehrlén, J., Ågren, J., 2006. Facilitation in an insect-pollinated herb with a floral display dimorphism. Ecology 87, 2113-2117.

Toräng, P., Ehrlén, J., Ågren, J., 2008. Mutualists and antagonists mediate frequency-dependent selection on floral display. Ecology 89, 1564-1572.

Tur, C., Saez, A., Traveset, A., Aizen, M.A., 2016. Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities. Ecol Lett 19, 576-586.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annual review of ecology and systematics 20, 171-197.

Waser, N.M., Real, L.A., 1979. Effective mutualism between sequentially flowering plant species. Nature 281, 670.

Wiens, J.A., 1989. Spatial Scaling in Ecology. Functional Ecology 3, 385-397.

Yang, C.F., Wang, Q.F., Guo, Y.H., 2013. Pollination in a patchily distributed lousewort is facilitated by presence of a co-flowering plant due to enhancement of quantity and quality of pollinator visits. Ann Bot 112, 1751-1758.

Ye, Z.-M., Dai, W.-K., Jin, X.-F., Gituru, R.W., Wang, Q.-F., Yang, C.-F., 2013. Competition and facilitation among plants for pollination: can pollinator abundance shift the plant–plant interactions? Plant Ecology 215, 3-13.

## Figures and Tables

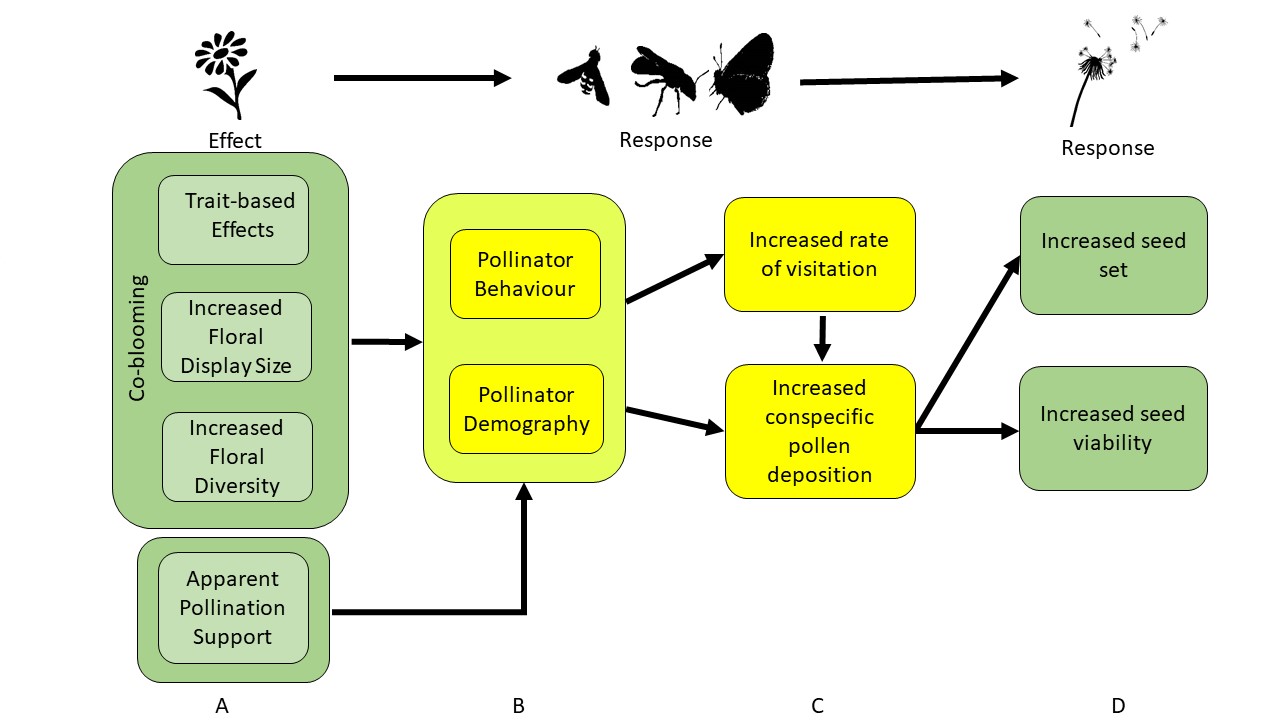


Figure 1: A conceptual framework to model the mechanisms and hypotheses associated with pollinator-mediated facilitation. The concepts were extracted from a systematic review of 100 studies on this topic. The seven mechanistic hypotheses tested within the literature can be categorized into four umbrella hypotheses. Refer to Table 1 for a description of the seven mechanistic hypotheses. Each mechanism (A) can lead to a behavioral or demographic responses (B) that increases pollinator visitation or conspecific pollen deposition (C) that leads to an increase in fitness for another plant species (D).

Table 1: A summary of the mechanistic hypotheses generated by a systematic review of the pollination facilitation literature, a concise definition for each, the proposed umbrella mechanism under which it falls and examples of reference articles.

|  |  |  |  |
| --- | --- | --- | --- |
| Mechanism | Description | Umbrella mechanism applicable | Key Paper(s) |
| Magnet Species Effect | Attractive plant increases pollination success of less attractive neighbors disproportionate to the size of the shared floral display | Trait Based Effect | Thomson 1978, Laverty 1992 |
| Mimicry | Mutualistic (Mullerian) or  unilateral (Batesian) facilitation between two or more species that share similar display patterns or colors | Trait Based Effect | Peter and Johnson, 2008  Jeraskova, 2009 |
| Floral Neighborhood Abundance | Increased pollination services due combining floral display and therefore increasing number of flowers | Floral Display Size | Thomson 1981 |
| Floral Neighborhood Density | Increased pollination success by combining floral display and therefore decreasing overall interplant distance | Floral Display Size | Rathcke, 1983  Feldman 2006 |
| Diversity | Improved pollination services due to growing in more diverse floral stands or area | Diversity | Ghazoul 2006 |
| Sequential Mutualism | Earlier blooming plants attract, maintain or increase pollinator population that then pollinates later blooming plant | Pollinator Support | Waser and Real 1979  Ogilvie and Thomson 2016 |
| Habitat Provisioning | One or more plants provide habitat for the pollinators of another plant | Pollinator Support | Hansen, 2007 |

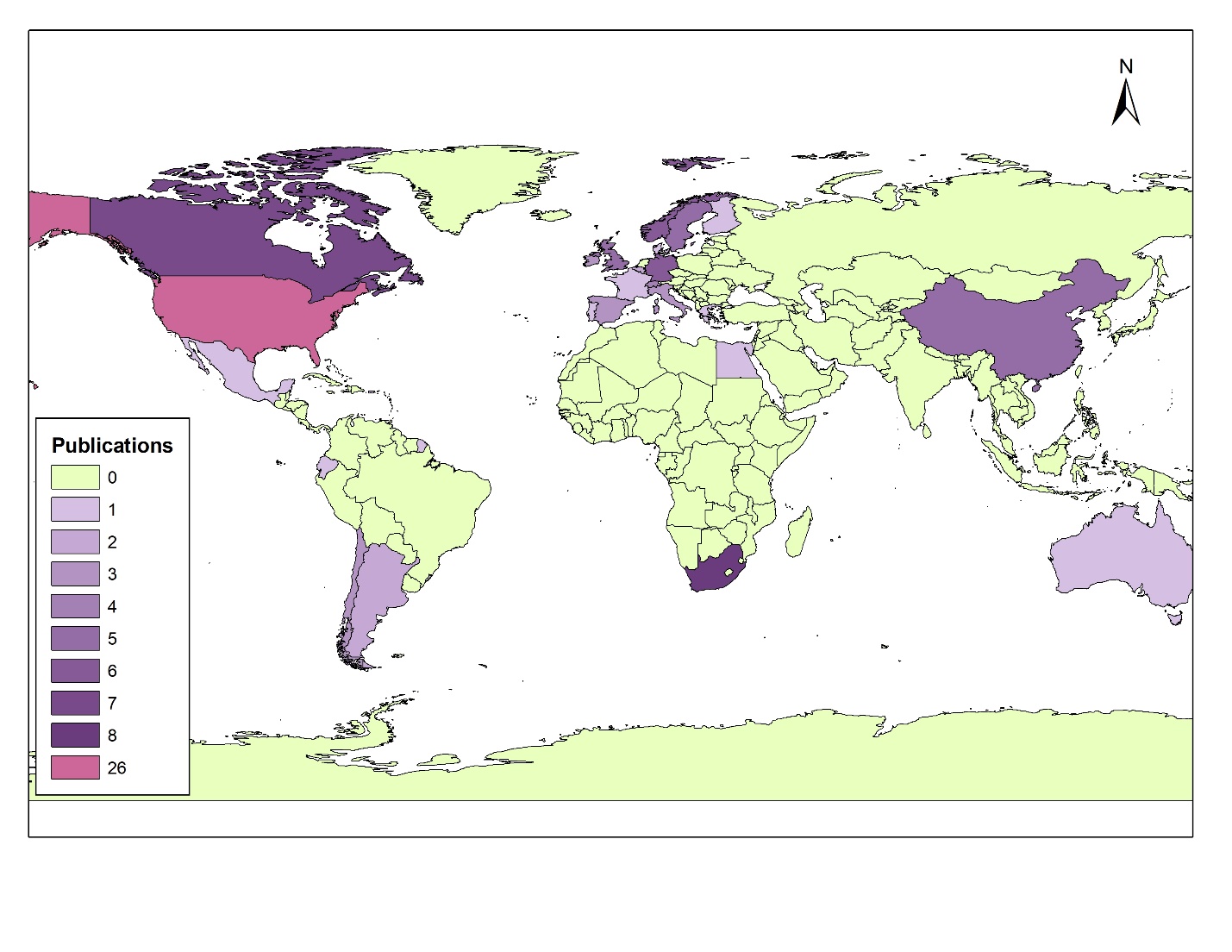


Figure 2: A map showing geographic distribution of studies testing for pollination facilitation. The islands Seychelles and Mauritius each have one publication but are not visible on this map.

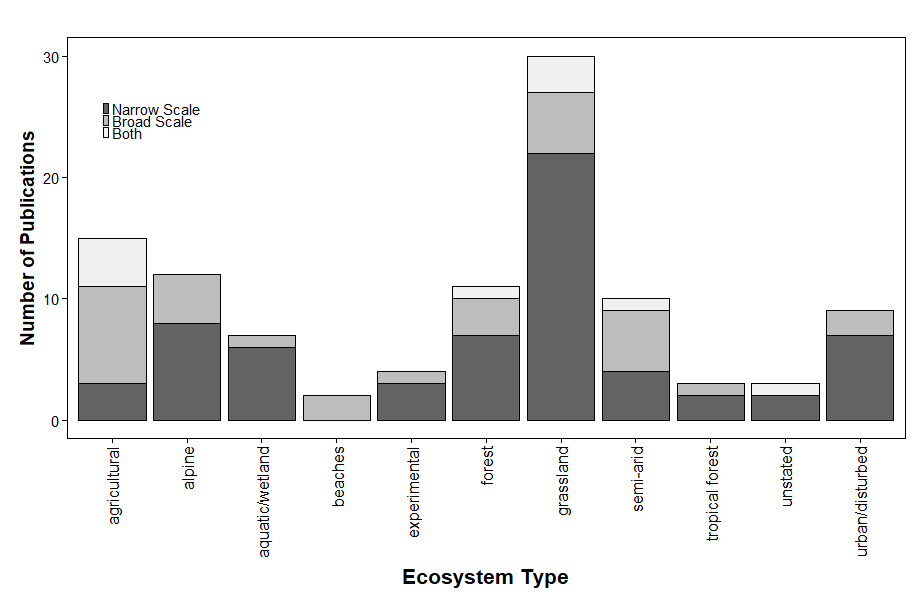


Figure 3: The frequency of pollination facilitation studies tested in each ecosystem type and their corresponding scale of study.

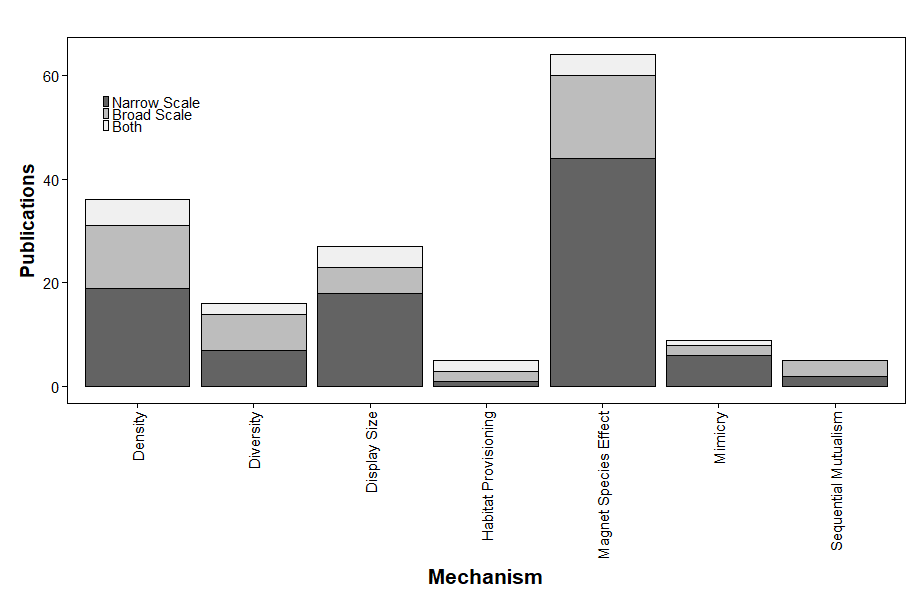


Figure 4: The number of studies testing each mechanism and their corresponding scale of study.

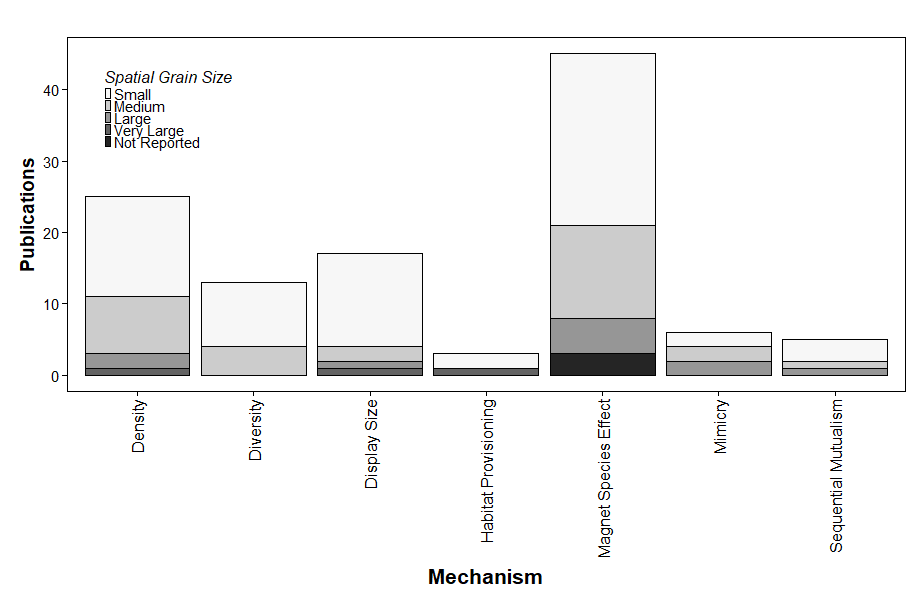


Figure 5: The number of associated studies based on spatial grain size and each testable mechanism.

## Supplemental Information

S1: Criteria for measuring reproductive success

1. Measured rates of pollinator visitation to flowers
   1. Observed in-situ
   2. Observed by technology
   3. Collected from flowers
2. Quantified pollen deposition to stigmas of beneficiary
   1. Conspecific pollen deposition
   2. Release from pollen limitation
      1. Hand pollination experiments
3. Measured seed production
   1. Per fruit
   2. Per plant
4. Measured fruit production

S2: Criteria for defining mechanistic hypotheses based upon predictor variables.

Magnet species effect – Presence/absence of a certain species, species specific effect controlled for beyond abundance/diversity.

Abundance – used heterospecific or combined floral abundance as predictor

Density – used heterospecific or combined floral density as predictor. Includes aggregation.

Mimicry – tested for facilitation between similar appearing species by author’s definition or in some cases authors tested for degree of similarity using floral traits

Sequential Mutualism – earlier blooming plants facilitate later blooming plants or other temporal effect

Habitat Provisioning – Provided habitat to known pollinator (Hansen 2007), alternatively author’s referred to semi-natural areas as wild bee habitats, such as hedgerows, grasslands and meadows as these areas provide nesting sites to pollinator populations.

Diversity: Use floral diversity as a predictor variable

Full-text articles assessed for eligibility (n = 268)

(n = )

Papers obtained through database searching (Web of Science) and Scopus November, 2017 Keywords:

Pollinat\* facilitat\*

(n = 1490)

Identification

Papers obtained from other sources, such as book chapter bibliographies, google scholar and WOS alerts (n = 11)

Records excluded for:

Relevance

(n = 1232)

Eligibility

Records screened by abstract or summary (n = 1501)

Full-text articles excluded:

Not explicitly testing facilitation (n = 96)

Not testing interspecific interactions (n = 27)

Not plant-plant (n = 20)

Unable to obtain (n = 5) Conference abstract (n =2) Review (n = 7)

Not english (n = 11)

n = 168

Screening

Include in synthesis (n = 100)

Extracted data:

Ecosystem

Grain size, extent size

Response variables measured

Scale (fine/broad)

Theme

Multi-scale, Scale dependence

Methods

Included

S3: PRISMA diagram (Moher et al, 2009) of workflow for pollination facilitation systematic review describes the identification of relevant studies.

S4: Tables showing frequency of ecosystems tested, theme of study and mechanism of study. Standardized residuals signify how much a value contributes to the overall chi-squared value. Significance at the 95% level is assessed at values > 1.96 and < 1.96. Some authors report experiments with multiple ecosystems or address multiple mechanism within a single paper so papers may be counted more than once.

* 1. Ecosystems tested.

|  |  |  |
| --- | --- | --- |
| Ecosystem | Frequency | Standardized Residuals |
| Agricultural | 15 | 1.81 |
| Alpine | 12 | 0.79 |
| Aquatic/wetland | 7 | -0.89 |
| Beaches | 2 | -2.5 |
| Experimental | 4 | -1.90 |
| Forest | 11 | 0.46 |
| Grassland | 30 | **6.88** |
| Semi-arid | 10 | 0.12 |
| Tropical forest | 3 | **-2.24** |
| Unstated | 3 | **-2.24** |
| Urban/disturbed | 9 | -0.21 |

* 1. Ecological themes of studies.

|  |  |  |
| --- | --- | --- |
| Theme | Frequency | Standardized residuals |
| Agriculture | 12 | **3.02** |
| Community ecology theory | 4 | -0.56 |
| Conservation | 6 | 0.33 |
| Deceptive pollination | 9 | 1.67 |
| Diversity | 1 | -1.91 |
| Floral traits selection | 1 | -1.91 |
| Foundation plants | 2 | -1.46 |
| Invasive species | 29 | **10.63** |
| Mating systems | 1 | -1.91 |
| Mechanical pollen isolation | 1 | -1.91 |
| Mimicry | 4 | -0.56 |
| Niche theory | 1 | -1.91 |
| Pollination theory | 1 | -1.91 |
| Rare plants | 5 | -0.12 |
| Relatedness | 2 | -1.46 |
| Stress gradient | 1 | -1.91 |
| Species coexistence | 5 | -1.12 |
| Urban ecology | 2 | -1.46 |
| No theme | 13 | **3.46** |

|  |  |  |
| --- | --- | --- |
| Mechanism | Frequency | Standardized residuals |
| Floral density | 36 | **2.89** |
| Diversity | 16 | -1.60 |
| Floral abundance | 27 | 0.86 |
| Habitat Provisioning | 5 | **-4.07** |
| Magnet species effect | 64 | **9.17** |
| Mimicry | 9 | **-3.18** |
| Sequential Mutualism | 5 | **-4.07** |

* 1. Mechanism tested

Table S5: Methods that authors used to control for confounding effects of plant-plant interactions and environmental variation. Methods are exclusive here but in a few cases multiple methods were used, papers were assigned to the most frequent method.

|  |  |
| --- | --- |
| Method Used | N |
| Potted plants | 19 |
| Pollen supplementation to measure pollen limitation | 18 |
| Pollinator exclusion to determine degree of self and subsequent seed set | 6 |
| Focal plant removal | 2 |
| Floral removal to maintain equal densities | 1 |
| Measured micro-environmental variables (e.g. nitrogen availability) | 3 |
| Measured genetic quality of offspring to determine distance of outcrossing | 1 |
| Focal plant translocations | 1 |
| Spatial separation of plants & measured distance | 2 |
| Individuals within a consistent monoculture (agricultural study distance to hedgerows measured) | 1 |
| **Total** | **54** |

# **Appendix**

## List of studied included in systematic review

A list of all studies included in this systematic review from the Web of Science and SCOPUS using the term pollinat\* facilitat\* and supplemental searches using Google Scholar.

Albrecht, M., Ramis, M.R., Traveset, A., 2016. Pollinator-mediated impacts of alien invasive plants on the pollination of native plants: the role of spatial scale and distinct behaviour among pollinator guilds. Biological Invasions 18, 1801-1812.

Alexandersson, R., Agren, J., 1996. Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa* Oecologia 107, :533-540.

Bartomeus, I., Vila, M., Santamaria, L., 2008. Contrasting effects of invasive plants in plant-pollinator networks. Oecologia 155, 761-770.

Benitez-Vieyra, S., Hempel de Ibarra, N., Wertlen, A.M., Cocucci, A.A., 2007. How to look like a mallow: evidence of floral mimicry between *Turneraceae* and *Malvaceae*. Proc Biol Sci 274, 2239-2248.

Brockmeyer, T., Schaefer, H.M., 2012. Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds? Basic and Applied Ecology 13, 294-300.

Brookes, B., Small, E., Lefkovitch, L.P., Damman, H., Fairey, D.T., 1994. Attractiveness of alfalfa (*Medicago satiua L*.) to wild pollinators in relation to wildflower. Canadian Journal of Plant Science, 779-783.

Brown, J., York, A., 2017. Fire, food and sexual deception in the neighbourhood of some Australian orchids. Austral Ecology 42, 468-478.

Bruckman, D., Campbell, D.R., 2016. Pollination of a native plant changes with distance and density of invasive plants in a simulated biological invasion. Am J Bot 103, 1458-1465.

Bruninga-Socolar, Crone, E.E., Winfree, R., 2016. The role of floral density in determining bee foraging behavior a natural experiment. Natural Areas Journal 36.

Caraballo-Ortiz, M.A., Santiago-Valentín, E., Carlo, T.A., 2011. Flower number and distance to neighbours affect the fecundity of *Goetzea elegans* (*Solanaceae*). Journal of Tropical Ecology 27, 521-528.

Carmona-Díaz, G., García-Franco, J.G., 2008. Reproductive success in the Mexican rewardless *Oncidium cosymbephorum* (*Orchidaceae*) facilitated by the oil-rewarding *Malpighia glabra* (*Malpighiaceae*). Plant Ecology 203, 253-261.

Caruso, C., 2001. Differential selection on floral traits of *Ipomopsis aggregata* growing in contrasting environments. Oikos, 295-302.

Carvalheiro, L.G., Seymour, C.L., Nicolson, S.W., Veldtman, R., Clough, Y., 2012. Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. Journal of Applied Ecology 49, 1373-1383.

Carvallo, G.O., Medel, R., Navarro, L., 2013. Assessing the effects of native plants on the pollination of an exotic herb, the blueweed *Echium vulgare* (*Boraginaceae*). Arthropod-Plant Interactions 7, 475-484.

Chung, Y.A., Burkle, L.A., Knight, T.M., 2014. Minimal effects of an invasive flowering shrub on the pollinator community of native forbs. PLoS One 9, e109088.

Cussans, J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B., Osborne, J.L., 2010. Two bee-pollinated plant species show higher seed production when grown in gardens compared to arable farmland. PLoS One 5, e11753.

Da Silva, E.M., King, V.M., Russell-Mercier, J.L., Sargent, R.D., 2013. Evidence for pollen limitation of a native plant in invaded communities. Oecologia 172, 469-476.

Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., Marini, L., 2017. High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. Journal of Applied Ecology 54, 380-388.

de Waal, C., Anderson, B., Ellis, A.G., Bartomeus, I., 2015. Relative density and dispersion pattern of two southern African *Asteraceae* affect fecundity through heterospecific interference and mate availability, not pollinator visitation rate. Journal of Ecology 103, 513-525.

Dietzsch, A.C., Stanley, D.A., Stout, J.C., 2011. Relative abundance of an invasive alien plant affects native pollination processes. Oecologia 167, 469-479.

Duffy, K.J., Johnson, S.D., 2017. Effects of distance from models on the fitness of floral mimics. Plant Biology, 438-443.

Duffy, K.J., Stout, J.C., 2008. The effects of plant density and nectar reward on bee visitation to the endangered orchid *Spiranthes romanzoffiana*. Acta Oecologica 34, 131-138.

Duffy, K.J., Stout, J.C., 2011. Effects of conspecific and heterospecific floral density on the pollination of two related rewarding orchids. Plant Ecology 212, 1397-1406.

Feldman, T.S., 2008. The plot thickens: does low density affect visitation and reproductive success in a perennial herb, and are these effects altered in the presence of a co-flowering species? Oecologia 156, 807-817.

Ferrero, V., Castro, S., Costa, J., Acuña, P., Navarro, L., Loureiro, J., 2013. Effect of invader removal: pollinators stay but some native plants miss their new friend. Biological Invasions 15, 2347-2358.

Fitch, G.M., 2017. Urbanization-mediated context dependence in the effect of floral neighborhood on pollinator visitation. Oecologia 185, 713-723.

Flanagan, R.J., Mitchell, R.J., Karron, J.D., 2010. Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. Oecologia 164, 445-454.

Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94, 295-304.

Goodell, K., Parker, I.M., 2017. Invasion of a dominant floral resource: effects on the floral community and pollination of native plants. Ecology 98, 57-69.

Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. Scientific Reports 7, 45296.

Ha, M.K., Ivey, C.T., 2017. Pollinator-mediated interactions in experimental arrays vary with neighbor identity. Am J Bot 104, 252-260.

Hansen, D.M., Kiesbüy, H.C., Jones, C.G., Müller, C.B., 2007. Positive indirect interactions between neighboring plant species via a lizard pollinator. The American Naturalist 169, 534-542.

Hegland, S.J., Grytnes, J.-A., Totland, Ø., 2008. The relative importance of positive and negative interactions for pollinator attraction in a plant community. Ecological Research 24, 929-936.

Hegland, S.J., Kudo, G., 2014. Floral neighbourhood effects on pollination success in red clover are scale-dependent. Functional Ecology 28, 561-568.

Hegland, S.J., Totland, O., 2012. Interactions for pollinator visitation and their consequences for reproduction in a plant community. Acta Oecologica, 95-103.

Herron-Sweet, C., Lehnhoff, E.A., Burkle, L.A., Littlefield, J., Mangold, J.M., 2016. Temporal- and density-dependent impacts of an invasive plant on pollinators and pollination services to a native plant. Ecosphere 7.

Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. Proc Biol Sci 278, 3444-3451.

Holzschuh, A., Dudenhöffer, J.-H., Tscharntke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biological Conservation 153, 101-107.

Internicola, A., Juillet, N., Smithson, A., Gigord, L.D.B., 2006. Experimental investigation of the effect of spatial aggregation on reproductive success in a rewardless orchid. Oecologia.

Jakobsson, A., Lazaro, A., Totland, O., 2009. Relationships between the floral neighborhood and individual pollen limitation in two self-incompatible herbs. Oecologia 160, 707-719.

Jakobsson, A., Padron, B., 2014. Does the invasive *Lupinus polyphyllus* increase pollinator visitation to a native herb through effects on pollinator population sizes? Oecologia 174, 217-226.

Jakobsson, A., Padrón, B., Ågren, J., 2015. Distance-dependent effects of invasive *Lupinus polyphyllus* on pollination and reproductive success of two native herbs. Basic and Applied Ecology 16, 120-127.

Johnson, S.D., Peter, C.I., Nilsson, L.A., Agren, J., 2003. Pollination success in a deceptive orchid is enhance by co-occuring magnet plants. Ecology 84, 2919-2927.

Juillet, N., Gonzalez, M.A., Page, P.A., Gigord, L.D.B., 2007. Pollination of the European food-deceptive *Traunsteinera globosa* (*Orchidaceae*): the importance of nectar-producing neighbouring plants. Plant Systematics and Evolution 265, 123-129.

Kaiser-Bunbury, C.N., Valentin, T., Mougal, J., Matatiken, D., Ghazoul, J., 2011. The tolerance of island plant-pollinator networks to alien plants. Journal of Ecology 99, 202-213.

Kipling, R.P., Warren, J., 2013. How generalists coexist: the role of floral phenotype and spatial factors in the pollination systems of two *Ranunculus* species. Journal of Plant Ecology 7, 480-489.

Kovács-Hostyánszki, A., Haenke, S., Batary, P., Jauker, B., Baldi, A., Tscharntke, T., Holzschuh, A., 2013. Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial Ecological Applications 23, 1938–1946.

Lammi, A., Kuitunen, M., 1995. Deceptive pollination of *Dactylorhiza incarnata*: an experimental test of the magnet species hypothesis. Oecologia 101, 500-503.

Landry, C.L., 2013. Pollinator-mediated competition between two co-flowering Neotropical mangrove species, *Avicennia germinans* (*Avicenniaceae*) and *Laguncularia racemosa* (*Combretaceae*). Ann Bot 111, 207-214.

Laverty, T.M., 1992. Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia 89, 502-508.

Laverty, T.M., Plowright, R., 1988. Fruit and seed set in mayapple (*Podophyllum peltatum*): influence of intraspecific factors and local enhancement near *Pedicularis canadensis*. Canadian Journal of Botany 66, 173-178.

Lazaro, A., Lundgren, R., Totland, O., 2014. Experimental reduction of pollinator visitation modifies plant–plant interactions for pollination. Oikos, 1037-1048.

Lázaro, A., Lundgren, R., Totland, Ø., 2009. Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species. Oikos 118, 691-702.

Lazaro, A., Totland, O., 2010. Population dependence in the interactions with neighbors for pollination: A field experiment with *Taraxacum officinale*. Am J Bot 97, 760-769.

Liao, K., Gituru, R.W., Guo, Y.H., Wang, Q.F., 2011. The presence of co-flowering species facilitates reproductive success of *Pedicularis monbeigiana* (*Orobanchaceae*) through variation in bumble-bee foraging behaviour. Ann Bot 108, 877-884.

Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R., Memmott, J., 2007. The impact of an alien plant on a native plant-pollinator network: an experimental approach. Ecol Lett 10, 539-550.

Masters, J.A., Emery, S.M., 2015. The showy invasive plant *Ranunculus ficaria* facilitates pollinator activity, pollen deposition, but not always seed production for two native spring ephemeral plants. Biological Invasions 17, 2329-2337.

McKinney, A.M., Goodell, K., 2010. Plant–pollinator interactions between an invasive and native plant vary between sites with different flowering phenology. Plant Ecology 212, 1025-1035.

Moeller, D.A., 2004. Facilitative interactions among plants via shared pollinators. 85 12.

Moeller, D.A., Geber, M.A., 2005. Ecological Context of the Evolution of Self-Pollination in Clarkia Xantiana: Population Size, Plant Communities and Reproductive Assurance. Evolution 59, 786-799.

Molina-Montenegro, M.A., Badano, E.I., Cavieres, L.A., 2008. Positive interactions among plant species for pollinator service: assessing the ‘magnet species’ concept with invasive species. Oikos 117, 1833-1839.

Moragues, E., Traveset, A., 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation 122, 611-619.

Muir, J.L., Vamosi, J.C., 2015. Invasive Scotch broom (*Cytisus scoparius*, *Fabaceae*) and the pollination success of three Garry oak-associated plant species. Biological Invasions 17, 2429-2446.

Muñoz, A.A., Cavieres, L.A., 2008. The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. Journal of Ecology 96, 459-467.

Nel, L., Pryke, J.S., Carvalheiro, L.G., Thebault, E., Frank van Ween, F., Seymour, C.L., 2017. Exotic plants growing in crop field margins provide little support to mango crop flower visitors. Agriculture, Ecosystems and Environment, 72-80.

Nielsen, C., Heimes, C., Kollmann, J., 2008. Little evidence for negative effects of an invasive alien plant on pollinator services. Biological Invasions 10, 1353-1363.

Norfolk, O., Eichhorn, M.P., Gilbert, F., Stewart, A., Brady, S., 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. Insect Conservation and Diversity 9, 236-243.

Ogilvie, J., Thomson, J.D., 2016. Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. Ecology 97, 1442–1451.

Ollerton, J., Stott, A., Allnutt, E., Shove, S., Taylor, C., Lamborn, E., 2007. Pollination niche overlap between a parasitic plant and its host. Oecologia 151, 473-485.

Pauw, A., Johnson, C.M., 2017. Mutualism between co‐occurring plant species in South Africa's Mediterranean climate heathland is mediated by birds. Plant Biology 20, 224-230.

Pellegrino, G., Bellusci, F., Musacchio, A., 2008. Double floral mimicry and the magnet species effect in dimorphic co-flowering species, the deceptive orchid *Dactylorhiza sambucina* and rewarding *Viola aethnensis*. Preslia, 411-422.

Pellegrino, G., Bellusci, F., Palermo, A.M., 2016. Who helps whom? Pollination strategy of Iris tuberosa and its relationship with a sexually deceptive orchid. J Plant Res 129, 1051-1059.

Peter, C.I., Johnson, S.D., 2008. Mimics and magnets: The importance of color and ecological facilitation in floral deception. Ecology 89, 1583–1595.

Reid, A.M., Lortie, C.J., 2012. Cushion plants are foundation species with positive effects extending to higher trophic levels. Ecosphere 3.

Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., Holzschuh, A., 2014. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. Landscape Ecology 29, 425-435.

Robson, D.B., 2012. An assessment of the potential for pollination facilitation of a rare plant by common plants: *Symphyotrichum sericeum* (*Asteracae*) as a case study. Botany 91, 34-42.

Roy, B., 1996. A plant pathogen influences pollinator behavior and may influence reproduction of nonhosts. Ecology 77.8, 2445.

Sargent, R.D., Kembel, S.W., Emery, N.C., Forrestel, E.J., Ackerly, D.D., 2011. Effect of local community phylogenetic structure on pollen limitation in an obligately insect-pollinated plant. Am J Bot 98, 283-289.

Schmid, B., Nottebrock, H., Esler, K.J., Pagel, J., Pauw, A., Böhning-Gaese, K., Schurr, F.M., Schleuning, M., 2016. Responses of nectar-feeding birds to floral resources at multiple spatial scales. Ecography 39, 619-629.

Schuepp, C., Herzog, F., Entling, M.H., 2014. Disentangling multiple drivers of pollination in a landscape-scale experiment. Proc Biol Sci 281, 20132667.

Seifan, M., Hoch, E.-M., Hanoteaux, S., Tielbörger, K., Bartomeus, I., 2014. The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. Journal of Ecology 102, 953-962.

Sieber, Y., Holderegger, R., Waser, N.M., Thomas, V.F.D., Braun, S., Erhardt, A., Reyer, H.-U., Wirth, L.R., 2011. Do alpine plants facilitate each other’s pollination? Experiments at a small spatial scale. Acta Oecologica 37, 369-374.

Spellman, K.V., Mulder, C.P.H., Carlson, M.L., 2016. Effects of invasive plant patch size and distance on the pollination and reproduction of native boreal plants. Botany 94, 1151-1160.

Spellman, K.V., Schneller, L.C., Mulder, C.P., Carlson, M.L., 2015. Effects of non-native *Melilotus albus* on pollination and reproduction in two boreal shrubs. Oecologia 179, 495-507.

Stiers, I., Coussement, K., Triest, L., 2014. The invasive aquatic plant *Ludwigia grandiflora* affects pollinator visitants to a native plant at high abundances. Aquatic Invasions 9, 357-367.

Sun, H.Q., Huang, B.Q., Yu, X.H., Kou, Y., An, D.J., Luo, Y.B., Ge, S., 2011. Reproductive isolation and pollination success of rewarding *Galearis diantha* and non-rewarding *Ponerorchis chusua* (*Orchidaceae)*. Ann Bot 107, 39-47.

Sun, S.-G., Montgomery, B.R., Li, B., 2013. Contrasting effects of plant invasion on pollination of two native species with similar morphologies. Biological Invasions 15, 2165-2177.

Theodorou, P., Albig, K., Radzeviute, R., Settele, J., Schweiger, O., Murray, T., Paxton, R., 2017. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. 31.

Thomson, J.D., 1978. Effects of Stand Composition on Insect Visitation in Two-Species Mixtures of *Hieracium.* American Midland Naturalist 100, 431-440.

Thomson, J.D., 1981. Spatial and temporal components of resource assessment by flower-feeding insects. The Journal of Animal Ecology 50, 49-59.

Tscheulin, T., Petanidou, T., Potts, S.G., Settele, J., 2009. The impact of *Solanum elaeagnifolium*, an invasive plant in the Mediterranean, on the flower visitation and seed set of the native co-flowering species *Glaucium flavum*. Plant Ecology, 77-85.

Tubbesing, C., Strohm, C., DeBano, S.J., Gonzalez, N., Kimoto, C., Taylor, R.V., 2014. Insect visitors and pollination ecology of spalding's catchfly (*Silene spaldingii*) in the Zumwalt prairie of Northeastern Oregon. Natural Areas Journal 34, 200-211.

Tur, C., Saez, A., Traveset, A., Aizen, M.A., 2016. Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities. Ecol Lett 19, 576-586.

Van Rossum, F., Vereecken, N.J., Bredat, E., Michez, D., 2013. Pollen dispersal and fruit production in *Vaccinium oxycoccos* and comparison with its sympatric congener *V. uliginosum*. Plant Biol (Stuttg) 15, 344-352.

Vrdoljak, S.M., Samways, M.J., Simaika, J.P., 2016. Pollinator conservation at the local scale: flower density, diversity and community structure increase flower visiting insect activity to mixed floral stands. Journal of Insect Conservation 20, 711-721.

Waters, S., Fisher, S., Hille Ris Lambers, J., 2014. Neighborhood-contingent indirect interactions between native and exotic plants: multiple shared pollinators mediate reproductive success during invasions. Oikos 123, 443-440.

Wirth, L.R., Waser, N.M., Graf, R., Gugerli, F., Landergott, U., Erhardt, A., Linder, H.P., Holderegger, R., 2011. Effects of floral neighborhood on seed set and degree of outbreeding in a high-alpine cushion plant. Oecologia 167, 427-434.

Woods, T.M., Jonas, J.L., Ferguson, C.J., 2011. The invasive *Lespedeza cuneata* attracts more insect pollinators than native congeners in tallgrass prairie with variable impacts. Biological Invasions 14, 1045-1059.

Yang, C.F., Wang, Q.F., Guo, Y.H., 2013. Pollination in a patchily distributed lousewort is facilitated by presence of a co-flowering plant due to enhancement of quantity and quality of pollinator visits. Ann Bot 112, 1751-1758.

Ye, Z.-M., Dai, W.-K., Jin, X.-F., Gituru, R.W., Wang, Q.-F., Yang, C.-F., 2013. Competition and facilitation among plants for pollination: can pollinator abundance shift the plant–plant interactions? Plant Ecology 215, 3-13.

# **Chapter 2:** Disentangling the drivers and trade-offs of pollinator-mediated interactions between creosote bush (Larrea tridentata) and desert dandelion (Malacothrix glabrata).

**Synthesis and General Conclusions**

The direct and indirect interactions between *Larrea tridentata* and its associated plant, arthropod and pollinator communities were examined within a diverse shrub and succulent desert scrub ecosystem located in the Mojave National Preserve. This thesis used a mechanistic approach to conceptually and empirically examine pollinator-mediated interactions of this foundational plant. Mechanistic approaches in community ecology are defined as the integration of individual-ecological concepts into the creation of theoretical frameworks (Schoener, 1986). A formal systematic review including 100 directly relevant papers was used to categorize the literature into a conceptual framework summarizing all mechanisms underlying pollination facilitation tested to date. Pollination facilitation research advanced a total of seven major mechanistic hypotheses that can be synthesized into the following four umbrella mechanisms: trait-based effects, floral display size, floral diversity, and apparent pollination support. This review revealed several research gaps that were then experimentally addressed: the need to include the temporal dimension, to test multiple mechanisms jointly, to incorporate interactions that do not require co-blooming and to study these interactions in harsh environments.

Foundational, desert shrubs that act as benefactors were hypothesized to impact the net outcome of pollination for associated annual plants depending on the phenological stage of the shrub. As predicted, *L. tridentata* interfered with the pollination of the representative phytometer species *Malacothrix glabrata* and facilitated associated annuals through its effects on climate amelioration. However, the interaction via pollinators shifted to exploitation competition upon blooming instead of the magnet species effect as predicted. This study confirmed the positive role of *L. tridentata* as a foundation plant but importantly suggests that facilitation for germination and growth early in life may involve a trade-off for reproduction later in life. The work from this thesis can be further framed into three important themes in ecology: Indirect interactions, stress gradients and functional ecology.

Indirect interactions between species require the presence of a mediating, third species (Wootton, 1994). This diverse range of interactions falls into two general categories: trait-mediated and density-mediated (Werner and Peacor, 2003). Consequently, the conceptual framework broadly separates pollinator responses into behavioural and population responses. The framework was developed directly from the empirical literature and the individual concepts synthesized are exclusively from the perspective of the plant. Overall the specific mechanisms underlying pollinator responses have been neglected within this field. Ghazoul proposed that facilitation can result from the competitive displacement of pollinators to the less desirable plant (2006). In this study, competitive displacement of syrphid flies by bees may have contributed to the observed decrease in visitation rates to *M. glabrata*. At this time, empirical evidence connecting pollinator-pollinator interactions to competition or facilitation between plants is still lacking. Facilitation through population responses has rarely been studied and has been excluded from meta-analyses, despite the potential prevalence in natural systems (Jakobsson and Padron, 2014). In one of the few studies explicitly tested for population responses, Jackobsson and Padron (2014) separated facilitation via the magnet species effect from effects on population sizes. By tracking bumblebee abundances while testing for differences in visitation rates, they found that the invasive *Lupinus* facilitated native plants via pollinator population growth. Experimental work has found that pollinator densities mediate the density-dependence of pollinator mediated interactions (Ye et al., 2013). Integrating pollinator identity, interactions and behavioural ecology is the next step towards a fully mechanistic understanding of the framework and more complete understanding of plant-pollinator interactions at the community level.

Stress-gradient hypothesis predicts that positive interactions are more common in harsh environments (Bertness and Callaway, 1994). Stress can result from environmental factors such as heat and salinity, or resource scarcity ie. droughts. When two organisms share the fundamental resource whose scarceness is the stressor, it is predicted that facilitation can only occur when neighbours increases the availability of this resource (Callaway, 2007; Maestre et al., 2009; Maestre and Cortina, 2004). Pollen limitation is an external factor that negatively influences the reproductive capacity of plants (Knight et al., 2005) and can be considered a stress that leads to inhibited seed production. Therefore, when a plant attracts additional pollinators or contributes to the maintenance of local pollinator populations, it increases local pollinator resource availability for neighbours. However, this systematic review revealed that neither desert nor arctic ecosystems have been studied in these contexts. Several meta-analyses have concluded that most sexually producing plants are pollen-limited (Knight et al., 2005; Larson and Barrett, 2000) and that the alpine is no more or less pollen-limited than more temperate lowlands (García-Camacho and Totland, 2009). This suggests the potential ubiquity of pollinator-mediated facilitation. As expected under the stress gradient hypothesis, *L. tridentata* facilitated understory annuals while stabilizing microclimates throughout the season. This is a frequently examined mechanism underlying nurse-protégé studies (Filazzola and Lortie, 2014). Facilitation was not measured between *L. tridentata* and *M. glabrata*, so this project still provides no evidence of pollination facilitation in desert ecosystems. Indirect interactions are mediated by organisms rather than the abiotic environment, therefore unless the harshness of an ecosystem directly leads to pollen limitation i.e. inhibits pollinators, it is unlikely that the frequency of pollination facilitation would increase with stress.

Understanding the function of communities through both time and space is a fundamental goal of community ecology. Any interaction is observed within a snapshot of time and space, and interaction networks are treated as stable, static entities (Poisot et al., 2015). This review revealed that incorporating interaction pathways that do not require co-blooming into experimental design is important because they operate concurrently with those that require co-blooming. This prediction was confirmed by the empirical experiment which demonstrated an intensification of competitive interactions when blooming. The difference in pollination rates between microsites was very small when *L. tridentata* was blooming and there was no difference in conspecific pollen deposition between microsites. Without incorporating the temporal dimensions, the conclusions of this experiment would have been very different and the ‘snapshot’ would not reflect these important interactions. Interactions are dynamic and networks frequently ‘rewire’ (CaraDonna et al., 2017). Competition between plants can influence linkage of plant-pollinator interactions (Carstensen et al., 2014). When a dominant plant blooms, it may induce a large scale rewiring within the community. Cornucopia plants sensu (Mosquin, 1971) continuously bloom for long periods, produce an abundance of nectar or pollen resources and are thus important to pollinators. Both the ecological function of *L. tridentata* and pollinator responses suggest that *L. tridentata* is a cornucopia species in this system, and our results suggest that pollinators switched to it when it entered a full bloom. Thus, a future model system for investigating how plants can rewire pollination networks and influence interaction turnover is cornucopia species.

Literature Cited

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends in Ecology & Evolution 9, 191-193.

Callaway, R.M., 2007. Positive interactions and interdependence in plant communities. Springer.

CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., Sanders, N.J., 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. Ecology letters 20, 385-394.

Carstensen, D.W., Sabatino, M., Trøjelsgaard, K., Morellato, L.P.C., 2014. Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. PLoS One 9, e112903.

Filazzola, A., Lortie, C.J., 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Global Ecology and Biogeography 23, 1335-1345.

García-Camacho, R., Totland, Ø., 2009. Pollen limitation in the alpine: a meta-analysis. Arctic, Antarctic, and Alpine Research 41, 103-111.

Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94, 295-304.

Jakobsson, A., Padron, B., 2014. Does the invasive *Lupinus polyphyllus* increase pollinator visitation to a native herb through effects on pollinator population sizes? Oecologia 174, 217-226.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J., Ashman, T.-L., 2005. Pollen limitation of plant reproduction: pattern and process. Annu. Rev. Ecol. Evol. Syst. 36, 467-497.

Larson, B.M., Barrett, S.C., 2000. A comparative analysis of pollen limitation in flowering plants. Biological journal of the Linnean Society 69, 503-520.

Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress‐gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 97, 199-205.

Maestre, F.T., Cortina, J., 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. Proceedings of the Royal Society of London B: Biological Sciences 271, S331-S333.

Mosquin, T., 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos, 398-402.

Poisot, T., Stouffer, D.B., Gravel, D., 2015. Beyond species: why ecological interaction networks vary through space and time. Oikos 124, 243-251.

Schoener, T.W., 1986. Mechanistic approaches to community ecology: a new reductionism. American Zoologist 26, 81-106.

Werner, E.E., Peacor, S.D., 2003. A review of trait‐mediated indirect interactions in ecological communities. Ecology 84, 1083-1100.

Wootton, J.T., 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25, 443-466.

Ye, Z.-M., Dai, W.-K., Jin, X.-F., Gituru, R.W., Wang, Q.-F., Yang, C.-F., 2013. Competition and facilitation among plants for pollination: can pollinator abundance shift the plant–plant interactions? Plant Ecology 215, 3-13.