# **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](#_ENREF_6); [Kjellberg et al., 2001](#_ENREF_15)). However, these strong examples of co-speciation are relatively rare. Plants frequently share pollinators ([Mitchell et al., 2009](#_ENREF_20); [Waser et al., 1996](#_ENREF_30)) 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](#_ENREF_12)) or by shading a neighbour ([McKinney and Goodell, 2010](#_ENREF_19)). Plant-pollinator mutualisms physically take place within natural communities and are embedded within complex webs of interactions ([Montoya et al., 2006](#_ENREF_21)). 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](#_ENREF_2); [Callaway, 1995](#_ENREF_3)). 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](#_ENREF_18)). This was followed up by theoretical models showing facilitation can occur if pollinators do not distinguish between the plants ([Bobisud and Neuhaus, 1975](#_ENREF_1)). 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](#_ENREF_29)). 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 ([Laverty, 1992](#_ENREF_17)). More recently, increases in floral diversity were shown to result in facilitation demonstrating that morphological similarity is not a requirement for facilitation ([Ghazoul, 2006](#_ENREF_11)). The majority of empirical evidence comes from pairwise interactions, however positive interactions can be diffuse and in some communities, positive pollinator mediated interaction may even dominate ([Hegland et al., 2008](#_ENREF_13)).

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](#_ENREF_23); [Potts et al., 2010](#_ENREF_25)). Recent estimates report that 87.5% of global angiosperms are animal pollinated ([Ollerton et al., 2011](#_ENREF_24)). 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](#_ENREF_14)). The increasingly early onset of seasonal shifts may cause phenological mismatches between plants and their pollinators ([Kudo and Ida, 2013](#_ENREF_16)). 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](#_ENREF_26)). Mismatches are not an issue if another pollinator or interactor can fill its place ([CaraDonna et al., 2017](#_ENREF_4)). 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 conceptual 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 common ([Morales and Traveset, 2009](#_ENREF_22)). However, another recent meta-analysis found concluded that there are no negative overarching effects of invasives ([Charlebois and Sargent, 2017](#_ENREF_5)). 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.

In arid environments, shrubs can act as keystone facilitators, directly benefiting associated plants via multiple mechanistic pathways across all life stages ([Filazzola and Lortie, 2014](#_ENREF_8)) such as stress amelioration, improved water and nutrient availability ([Franco et al., 1994](#_ENREF_10)) and seed trapping ([Flores and Jurado, 2003](#_ENREF_9)). Shrubs can also act as foundation species, which positively influence the structure of the surrounding plant communities by creating locally stable conditions for other species ([Ellison et al., 2005](#_ENREF_7)). Arthropod and plant communities are tightly linked, and interact with each other throughout their lifecycles. The benefits of foundation plants can scale up to other trophic levels including arthropods ([Reid and Lortie, 2012](#_ENREF_27); [Ruttan et al., 2016](#_ENREF_28)). For plants the shift from vegetative growth to reproductive growth is a major life-history step and this shift in life stage by a foundational plant can potentially cascade through its beneficiary communities.

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 create 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.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479-486.

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.

Flores, J., Jurado, E., 2003. Are nurse‐protégé interactions more common among plants from arid environments? Journal of Vegetation Science 14, 911-916.

Franco, A., De Soyza, A., Virginia, R., Reynolds, J., Whitford, W., 1994. Effects of plant size and water relations on gas exchange and growth of the desert shrub Larrea tridentata. Oecologia 97, 171-178.

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.

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

Ruttan, A., Filazzola, A., Lortie, C.J., 2016. Shrub-annual facilitation complexes mediate insect community structure in arid environments. Journal of Arid Environments 134, 1-9.

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.