# **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 (Kjellberg et al, 2001; Cook et al, 2003). However, these strong examples of co-speciation are relatively rare. Plants frequently share pollinators (Waser 1996, Mitchell 2009) and pollination syndromes are dynamic (Waser, 1996). Plants can also impact the pollination of other plant species without sharing pollinators by providing habitat to another species’ pollinator (Hansen 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). 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 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 by Macior (1971) that suggested morphologically similar plants can maintain pollinator interest by increasing the ‘functional’ size of the floral display. This was followed up by Bobisud and Neuhaus (1975) who provided theoretical models showing facilitation can occur if pollinators do not distinguish between the plants. 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) explained the facilitation of non-rewarding orchids by rewarding species with the magnet species effect, where a particularly attractive species facilitates its less attractive neighbours by increasing local pollinator abundances. Increases in floral diversity can 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 interaction may even dominate (Hegland, 2009).

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 (Potts 2010, NRC 2007). 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, 2009). The increasingly early onset of seasonal shifts may cause phenological mismatches between plants and their pollinators (Kudo 2013). Experimental evidence suggests that early flowering species have an increased risk of decreased visitation but that many species experienced no mismatch (Rafferty 2015). Mismatches are not an issue if another pollinator or interactor can fill its place (CaraDonna et al, 2017) Thus, understanding of 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 are 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 found that negative impacts of invasive species on the pollination of natives are more common (Morales and Traveset, 2009). However, another recent meta-analysis found that there are no negative overarching effects of invasives (Charlesbois 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.

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), such as stress amelioration, improved water and nutrient availability (Whitford et al, 1994) and seed trapping (Flores and Jurado, 2003). 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, 2005). 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, 2012; Ruttan, 2016). For plants, the shift from vegetative growth to reproductive growth is a major life-history step and the shift in life stage by a foundational plant can potentially cascade through beneficiary communities.

The overarching objective of this thesis is to examine the mechanisms of pollination facilitation and test the importance of foundation plants interactions on their respective communities. 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.* By disentangling blooming and non-blooming pathways as *L. tridentata* shifts through natural phenology, I quantified their contributions to the net observed interactions. I also assessed if *L. tridentata* acts as a foundation species in this system by sampling plant and arthropod communities, and testing the shrubs ability to create milder 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.

# **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 theoretically and empirically address 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 which included: 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 are mediated by a third species, and fall into two categories: trait-mediated and density-mediated (Werner and Peacor, 2003). The conceptual framework was developed directly from the empirical literature; the individual concepts synthesized are exclusively from the perspective of the plant. It broadly separates the pollinator responses into behavioural and population, reflecting these categories. Overall, specific pollinator responses have been neglected within this field. Ghazoul (2005) proposed that facilitation can result from the behavioural responses of pollinators to other pollinators, namely the competitive displacement of pollinators to the less desirable plant. 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 (Jackobsson and Padron, 2014). By tracking bumblebee abundances while testing for differences in visitation rates, Jackobsson and Padron (2014) separated facilitation via the magnet species effect from effects on population sizes, finding that the invasive *Lupinus* facilitated 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.

Stress-gradient hypothesis predicts that positive interactions are more common in harsh environments (Bertness and Callaway, 1994). Stress is…. and 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 and Cortina, 2004, Maestre et al, 2009). Pollen limitation is an external factor that negatively influences the reproductive capacity of plants (Rhodes, 2001) 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. Meta-analyses show that most sexually producing plants are pollen-limited (Larson and Barrett, 1999, Knight et al, 2005) and that the alpine is no more or less pollen-limited than more temperate lowlands (Raul Garcia-Comacho, 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 buffering them as the weather got harsher, 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, 2015). Our 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 our 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 pollen deposition showed no difference between microsites. Without incorporating the temporal dimensions, the conclusions would be 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.