# **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.

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