MULTIPLE INTERACTIONS AND PLANT REPRODUCTION: THE INTERSECTION OF HERBIVORE, POLLINATOR, AND PLANT-PLANT INTERACTIONS

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Abstract

Plants interact with a variety of organisms. Both positive and negative interactions exist between plants and other plant species as well as animals. Because these plants and animals exist in communities simultaneously, these interactions will in turn interact. In this dissertation, I examine both the costs and benefits of interactions between plants, herbivores, pollinators, and other plants and how these interactions impact plant reproduction. To start I synthesize the literature on herbivore-pollinator interactions, followed by updating a meta-analysis on the same topic. I then examine both direct and indirect interactions between shrubs and the surrounding desert annual plant community before testing how the same shrub benefactor can change the impact of pollination and herbivory on the reproductive output of one of its proteges. I found that plant reproductive output was dependent on all three types of interactions (pollination, herbivory, and plant-plant interactions) to varying degrees. I compared damage to different types of plant tissues in the literature as well as in the field using artificial damage. I found that damage to flowers and leaves generally decreased plant reproductive output in the literature, but that the relationship was more complex in the field, depending on the presence of other factors. While the interaction between both types of damage were not commonly studied in the literature, I found that applying both types of damage was required to consistently observe decreases in reproduction in response to damage. When testing the effects of shrubs on annuals, shrubs had a mixed effect on plant species density and floral density that depended on annual species identity. Indirect effects of shrubs through the plant community were more consistent between protege species. However, when examining individual plants (as opposed to populations or communities) of one species that was associated with the shrub species in an experimental setting, facilitation was only observed in the presence of damage. I show that herbivory is integral in driving the coevolution between plants and pollinators as well as facilitators and their proteges.

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Stephanie is first author on all chapters of this dissertation. She collected, processed, and analysed the data, as well as wrote and edited the manuscripts.

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Chapter 1: Introduction

Interactions between species are fundamental determinants of the growth, development, and reproduction of plants (Garcia and Eubanks 2019; Moreira et al. 2019). Plants experience a variety of types of interactions with the surrounding community of species (Sotomayor and Lortie 2015; Underwood et al. 2020). These interactions include both positive and negative interactions with other plants as well as animals (García-Cervigón et al. 2016; Pilosof et al. 2017; Underwood et al. 2020). Because these direct interactions occur simultaneously indirect interactions occur between species (Proulx et al. 2005; Kral-O'Brien et al. 2023). Therefore, the net effect of the community on plant reproduction is the sum of these direct and indirect interactions (Michalet and Pugnaire 2016).

Plant-Plant Interactions

Competition

Interactions between plants are often negative. One of the more ubiquitous negative plant interactions is competition. Competition is present throughout plant communities and is an important driver in community assembly processes (Callaway and Walker 1997). When resources are limiting, plants will interact negatively to compete for these scarce resources with the stronger competitors often limiting other species' growth and reproduction (Moreira et al. 2019; Sandner 2020; Postma et al. 2021). For instance, plant neighbours can compete directly for resources such as nutrients (Jia et al. 2020), water (Trautz et al. 2017), and light (de Vries et al. 2019). However, negative interactions between plants are not always mediated through resource availability; plants can have other direct negative effects on each other such as allelopathy (the release of chemicals into the environment that can have an inhibitory effect on other plants) (Zhang et al. 2021). They can also compete indirectly through mechanisms such as apparent competition (competition through a common consumer) (Barbosa et al. 2009;

Sotomayor and Lortie 2015; Revilla et al. 2021). Despite the ubiquity of negative interactions, species coexist within communities without resulting in the most competitive species excluding all others. One reason for this continued diversity is that competitive interactions among species are intransitive (interactions are not hierarchical) (Gallien 2017). In a community with strictly transitive competition, some species are more competitive than all other species, eventually leading to competitive exclusion (Gallien 2017). Instead, in a diverse community of species in which competition is intransitive, competitive interactions between two species can leave room for an independent species to coexist (i.e. "the enemy of my enemy is my friend") (McIntire and Fajardo 2014; Kinlock 2019). Similarly, interspecific competition (competition between two species) can relieve intraspecific competition (competition between individuals within a species) (Adler et al. 2018). Intraspecific competition is often more negative than interspecific competition since individuals of the same species have complete niche overlap while other species at best only have partial niche overlap (Adler et al. 2018). Therefore, even negative interactions can promote coexistence and net positive interactions.

Facilitation

Positive interactions are also abundant in plant communities (Filazzola and Lortie 2014). In contrast to apparent competition, plants can experience associational resistance where the ability of plants to physically block access by herbivores (Chaneton et al. 2010; Guignabert et al. 2020; Bustamante et al. 2021) or deter herbivores reduces herbivory of neighbouring plants (Barbosa et al. 2009; Underwood et al. 2012; Field et al. 2020). In a similar but opposite manner, plants can attract pollinators to the area, increasing the pollination of neighbouring plants (Fowler et al. 2016; Underwood et al. 2020). Neighbouring plants can attract pollinators by simply providing or contributing to a larger floral display, but they can also attract pollinators by acting as magnets (resource-rich plants that are particularly attractive to pollinators) that increase pollination of surrounding plants through spillover (Laverty 1992; Braun and Lortie 2019; Gilpin et al. 2019). Plants can also modify the soil in such a way that benefits other plants. For instance, some plants provide hydraulic lift, bringing water to the surface that is otherwise inaccessible (Dawson 1993; Ploughe et al. 2019), and some plants are nitrogen-fixers, increasing the nitrogen content of the soil (Abdallah et al. 2016; Yu et al. 2021). Other plants support a network of mychorrizal fungi that can transfer water and nutrients between plants and modify the microbial content of the soil to benefit plants (Rodríguez-Echeverría et al. 2016). Beyond blocking herbivores, the physical structure of (particularly larger) plants can positively impact other plants. Large plants such as shrubs and trees can block excessive light and wind (Michalet et al. 2015; Ploughe et al. 2019), but also block anemochorous (wind-dispersed) seeds, causing seeds to congregate around these large plants (Bullock and Moy 2004; Filazzola and Lortie 2014; Erfanzadeh et al. 2020). Similarly, large plants can also "trap" seeds by providing habitat and perches for animals that disperse seeds (such as birds and rodents) (Filazzola and Lortie 2014). If coupled with other forms of facilitation (positive interactions of one plant onto another without necessarily reciprocating), trapping seeds can be greatly beneficial to the germination and growth of seedlings (Filazzola and Lortie 2014). Despite the prevailing nature of negative interactions in the literature, these positive interactions are common (He et al. 2013) and shed light on how the relationship between neighbouring plants is more complicated than strictly competitive or facilitative.

Plant-Animal Interactions

Plant-Herbivore Interactions

Plant-animal interactions can also vary between positive and negative. Even a classically negative interaction such as herbivory does not necessarily have a strictly negative net outcome on plants or plant reproduction (Garcia and Eubanks 2019). For one, damage is not always sufficient to prompt a response from plants, resulting in a neutral result (Ramula et al. 2019; Wise and Mudrak 2021). For instance, one strategy to deal with florivory (damage to flowers) is to overproduce flowers so that more flowers than would ever set seed are produced and so fewer flowers are aborted to avoid decreases in seed production (Wise et al. 2008; Wise and Mudrak 2023). This type of plant defense is known as constitutive defense, where the physical or chemical defense is present before herbivory occurs (Wittstock and Gershenzon 2002; Chen et al. 2020). Other constitutive defenses include trichomes, thorns, and secondary metabolites already present in plant tissues and nectar (Wittstock and Gershenzon 2002). However, constitutive defenses are costly; resources are used to produce these structures and metabolites when damage may not occur (Wittstock and Gershenzon 2002; Liu et al. 2020). Instead, inducible responses and defenses occur in response to damage (Liu et al. 2020; Chen et al. 2020). Inducible defenses can include secretion of secondary metabolites in response to damage that deters either current or future herbivores (Kessler and Chautá 2020). These defenses save the cost of production if no damage is experienced but are risky if the initial damage received is great (Wittstock and Gershenzon 2002). Regardless of whether the defense is induced, in most cases the net effect of damage is mediated by an induced response. Plants can compensate for damage by reallocating resources and producing new tissue (both vegetative and floral) (Garcia and Eubanks 2019). In some cases, plants will overcompensate for damage and produce more seeds than without the damage, resulting in a net positive interaction (Garcia and Eubanks 2019; Ramula et al. 2019). For some species, compensation in response to herbivory is the only way the species maximizes reproductive success. For instance, scarlet gilia (*Ipomopsis aggregata*) produces a single inflorescence in the absence of damage, but with the removal of the apical meristem, it branches into several inflorescences (Paige and Whitham 1987). Therefore, an interaction that seems strictly negative like herbivory can still have net positive effects.

Plant-Pollinator Interactions

Positive and negative interactions with other plants and animals can determine the outcome of interactions with other species (Michalet et al. 2015). Pollination is a generally positive interaction between plants and animals, with most angiosperms either requiring animal pollination for reproduction or animal pollination increasing reproductive output (Ollerton et al. 2011). Because pollinators in turn rely on plants for resources, relationships between plants and their pollinators are frequently tightly coevolved and can lean towards specialization (Brosi 2016). The symmetry, size, shape, colour, volatile compounds, and even abundance of flowers (both the number of flowers per plant and the number of same-species plants that cluster) are all tailored towards attracting pollinators and influencing pollinator choice in order to promote plant reproduction (Møller and Eriksson 1995; Fowler et al. 2016; Moyroud and Glover 2017; Guo et al. 2020; Brunet et al. 2021). Sometimes floral traits are specific so as to target specific pollinator species (or more general taxa) (Brosi 2016). For instance, colour pigments (like anthocyanins or carotenoids) allow flowers to contrast against mostly green foliage, making them more visible (Moyroud and Glover 2017; Rudall 2020); however, these pigments also align with colours that are most visible to preferred pollinators (Rudall 2020). By specializing, plants reduce interspecific pollen deposition while pollinators increase efficiency by decreasing learning time at each new plant species (Brosi 2016). The plant neighbourhood can also be highly influential on pollinator attraction (Underwood et al. 2020). A large floral display (even of differing species) can attract pollinators to the area, increasing pollination for multiple species in the area (Ruttan and Lortie 2013; Brunet et al. 2021). However, plants can also compete for pollinators as they do for other resources when pollinators are limiting (Wenninger et al. 2016; Richardson et al. 2021) or display attributes like floral constancy (a preference to forage on only the same species) (Schmid et al. 2016; Bruninga-Socolar et al. 2022). Therefore, the plant neighbourhood has the potential to either increase or decrease pollinator attraction and therefore plant reproduction.

Plant-Plant and Plant-Animal Interactions

As stated, the plant neighbourhood has the potential to impact both herbivore and pollinator attraction, either as deterrents or magnets; however, herbivory and other direct stressors (like competition) can also impact pollinator attraction (Underwood et al. 2020; Cutter et al. 2021; da Silva et al. 2022). Damage to flowers is the most direct way in which herbivores can influence pollination (Lucas-Barbosa et al. 2016). Removal of flowers reduces the resources available to pollinators (Guy et al. 2021; Kral-O’Brien et al. 2023) and partial damage to flowers can decrease the attractiveness of flowers (Mothershead and Marquis 2000; Tsuji and Ohgushi 2018). Damage to other tissues and competition from other plants can also reduce the resources available to the plant, causing it to produce fewer or smaller flowers that are less attractive (Barber et al. 2011; Muola and Stenberg 2018; Rusman et al. 2019). However, compensation for herbivory can increase flower production resulting in a net positive for potential reproductive output (Garcia and Eubanks 2019), but also for pollinator attraction (Garrido et al. 2019). Similarly, positive interactions between plants can also increase pollinator attraction by increasing the quality of the floral display (Losapio and Schöb 2020). Because these interactions don't occur in isolation, interactions between species act as a network, where indirect interactions abound (Borrett et al. 2010). In this dissertation, we investigate how plant-plant, plant-herbivore, and plant-pollinator interactions intersect. In each chapter we focus on one or two interaction types before bringing them together in one study that incorporates all three sets of interactions.

Aims and Scope

Chapter 2 is a systematic review covering direct and indirect damage to plants and how this damage impacts pollination. Direct damage to flowers can have obvious negative effects on plant reproduction (Moreira et al. 2019). The removal of reproductive structures without compensation will decrease plant reproductive output (Garcia and Eubanks 2019). However, direct damage to flowers can also have indirect effects on plant reproduction through pollination (Lucas-Barbosa 2016). By changing the floral display directly, whether changing aspects such as display size or floral symmetry, damage to flowers can decrease pollinator attraction which in turn can decrease plant reproduction (Moreira et al. 2019). Similarly, damage to other vegetative plant tissues (i.e. leaves, roots, and stems) can indirectly change the floral display (Hladun and Adler 2009; Moreira et al. 2019; Dube et al. 2019). Damage to vegetative tissues can result in reallocation of resources to vegetative compensation, potentially reducing the quantity or quality of flowers produced (Garcia and Eubanks 2019). The aim of this chapter is to explore these different types of mechanisms, comparing and contrasting the effect of damage to floral and vegetative tissues on pollination and the state of the scientific literature on these mechanistic pathways.

Chapter 3 builds on Chapter 2, taking the studies from the published systematic review (Haas and Lortie 2020) and from a meta-analysis published around the same time as Chapter 2 (Moreira et al. 2019), integrating the two studies and updating the older meta-analysis (Moreira et al. 2019). The aim in this chapter is similar to that of Chapter 2: to compare the effect of damage to different plant tissues on pollination. However, we take a qualitative approach in Chapter 2, describing mechanisms and specific studies. Here, we instead take a quantitative approach. In Chapter 3 we aim to quantify the differences in effect size of florivory (damage to flowers), folivory (damage to leaves), root herbivory, stem herbivory, and mixed (or undifferentiated) damage on pollination using meta-analytic tools. We greatly expand the number of studies previously included in the meta-analysis and so we also explore sensitivity to sample size within this meta-analysis.

Chapter 4, the first of two chapters based on field data, examines strictly plant-plant interactions. In Chapter 4 we perform an observational experiment where we catalog the species and number of plants and flowers both under shrubs and in the open. In this observational experiment we test the hypothesis that shrubs facilitate their understory plant community composition and reproduction through both direct and indirect mechanisms. Shrubs can facilitate plant growth and reproduction through numerous mechanisms (Filazzola and Lortie 2014; Ploughe et al. 2019). They can directly modify the abiotic conditions surrounding them through mechanisms such as resource sequestration (Rodríguez-Echeverría et al. 2016) and shading (Smit et al. 2008), but they can also impact how species interact (Schöb et al. 2013). While shrubs can change plant -animal interactions (as examined in Chapter 5) in this chapter, we focus only on how shrubs change the interaction between other plants found within their understory. The interaction between annuals within a community are complex and themselves can range from facilitative to competitive (Tielbörger and Kadmon 2000; Droz and Pękalski 2013; Trautz et al. 2017). The presence of other species can relieve intra-specific competition (competition between individuals within a species) and often as the number of species increases inter-specific competition between any two individual species can also be relieved (e.g. through indirect facilitation) (Adler et al. 2018). However, an increase in the density of plants (regardless of species) increases total competition for resources, with the most obvious being competition for space (Postma et al. 2021). Given that shrubs are predicted to increase both species richness and density (Gómez-Aparicio et al. 2004; Filazzola and Lortie 2014; Rolhauser and Pucheta 2016; Wang et al. 2020), a mix of positive and negative indirect interactions are likely to be present (Molina-Montenegro et al. 2020; Lortie et al. 2021), making the effect of shrubs to be less straightforward than strictly facilitative. This mix of positive and negative interactions is also likely to vary based on plant protege species (Filazzola et al. 2020). For instance, shade tolerant species are likely to be more competitive under shrubs while plants with adaptations to minimize loss to evapotranspiration are likely to be more competitive in the open (McIntire and Fajardo 2014; Rolhauser and Pucheta 2016). Here, we aim to distinguish between the direct impact of shrubs on plant proteges and the indirect effect of shrubs through changes to the understory plant community.

Chapter 5 is the final field chapter that ties the previous three chapters together in one four-way interaction. In Chapter 5, we examine the effect of shrub facilitation on plant reproductive compensation in response to herbivory and pollen limitation. Shrubs such as the focal species (*Larrea tridentata*) are known facilitators of annual plant proteges in desert systems (Whitford et al. 1997; Schafer et al. 2012; Filazzola and Lortie 2014; Flores-Torres and Montana 2015). Shrubs can deter herbivores, thereby decreasing the amount of damage received by proteges (Lortie et al. 2016; Bustamante et al. 2021). Additionally, shrubs can facilitate plants by increasing the amount of resources available that promote growth in proteges (Pugnaire et al. 2004; Abdallah et al. 2016). However, little is known about how shrubs may interact with species in the presence of herbivore damage. The increased soil resources may allow proteges to better compensate for damage (Garcia and Eubanks 2019). If shrubs increase pollinator visitation to the understory (Ruttan et al. 2021) then this increase may offset any decrease in visitation associated with herbivore damage (as explored in Chapters 2 and 3). We investigate these mechanisms in Chapter 5 by testing the hypothesis that shrubs facilitate the reproduction of desert plants by increasing compensation for herbivory and pollinator visitation. However, we also investigate the possibility that the relationship between *L. tridentata* and its protege *Malacothrix glabrata* is not strictly facilitative. As we find in Chapter 4, interactions between shrubs and their proteges are often a mix of positive and negative. Therefore, it is plausible that shrub association represents a trade-off between the associated costs (such as decreased pollination services) and the benefits (such as increased capacity to compensate for damage). We present both of these mechanisms with the aim to summarize the intricacies of the observed relationship between shrub and protege using a manipulative experiment that examines the effects of shrubs on compensation to different types of damage as well as pollen limitation in an insect-pollinated annual.

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Chapter 2: A systematic review of the direct and indirect effects of herbivory on plant reproduction mediated by pollination

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Abstract

Plant reproduction is influenced by the net outcome of plant-herbivore and plant-pollinator interactions. While both herbivore impacts and pollinator impacts on plant reproduction have been widely studied, few studies examine them in concert. In this chapter, we review the contemporary literature that examines the net outcomes of herbivory and pollination on plant reproduction and the impacts of herbivores on pollination through damage to shared host plants using systematic review tools. The direct or indirect effects of herbivores on floral tissue and reported mechanisms were compiled including the taxonomic breadth of herbivores, plants, and pollinators. A total of 4304 studies were examined producing 59 relevant studies for synthesis that reported both pollinator and herbivore measures. A total of 53% of studies examined the impact of direct damage to floral tissue through partial florivory while 35% of studies also examined the impact of vegetative damage on pollination through folivory, root herbivory, and stem damage. Only 4 studies examined the effects of both direct and indirect damage to pollination outcomes within the same study. It is not unreasonable to assume that plants often sustain simultaneous forms of damage to different tissues and that the net effects can be assessed through differences in reproductive output. Further research that controls for other relative drivers of reproductive output but examines more than one pathway of damage simultaneously will inform our understanding of the mechanistic relevance of herbivore impacts on pollination and also highlight interactions between herbivores and pollinators through plants. It is clear that herbivory can impact plant fitness through pollination; however, the relative importance of direct and indirect damage to floral tissue on plant reproduction is still largely unknown.

Introduction

Plant fitness is determined in part by the net outcome of interactions with other species. All species within a community experience multiple direct interactions ranging from negative to positive (García-Cervigón et al. 2016; Pilosof et al. 2017). However, the sum of the direct interactions between two species do not represent the net outcome of the relationship since they are non-additive; these direct interactions can in turn interact (Proulx et al. 2005). When each species interacts with at least one third party species, indirect interactions quickly occur (Borrett et al. 2010). It is the sum of these direct and indirect interactions that represent the net outcome of the interaction between any two species (Michalet et al. 2015).

For most angiosperms, interactions with herbivores and pollinators impact fitness. Herbivory can be generally classified as having a direct negative effect on plants, while pollinators can be similarly classified as having a direct positive effect. Typically, herbivory and pollination are examined one at a time; however, these effect pathways frequently co-occur and therefore interact and so the net outcome is not necessarily as straightforward as these simple classifications (Strauss et al. 1996; Vulliamy et al. 2006; Tsuji et al. 2016; Chalcoff et al. 2019; Rusman et al. 2019; Scopece et al. 2019). In this chapter, we have outlined a conceptual framework (Fig. 2.1) to illustrate the direct and indirect ways in which the negative effects of herbivory can both directly and indirectly affect plant fitness via animal pollinators and pollination. Here, we outline the general ways in which different types of herbivory can impact plant fitness and how this interacts with pollination as outlined in Fig. 2.1, followed by a synthesis of the contemporary literature on herbivore-pollinator interactions.

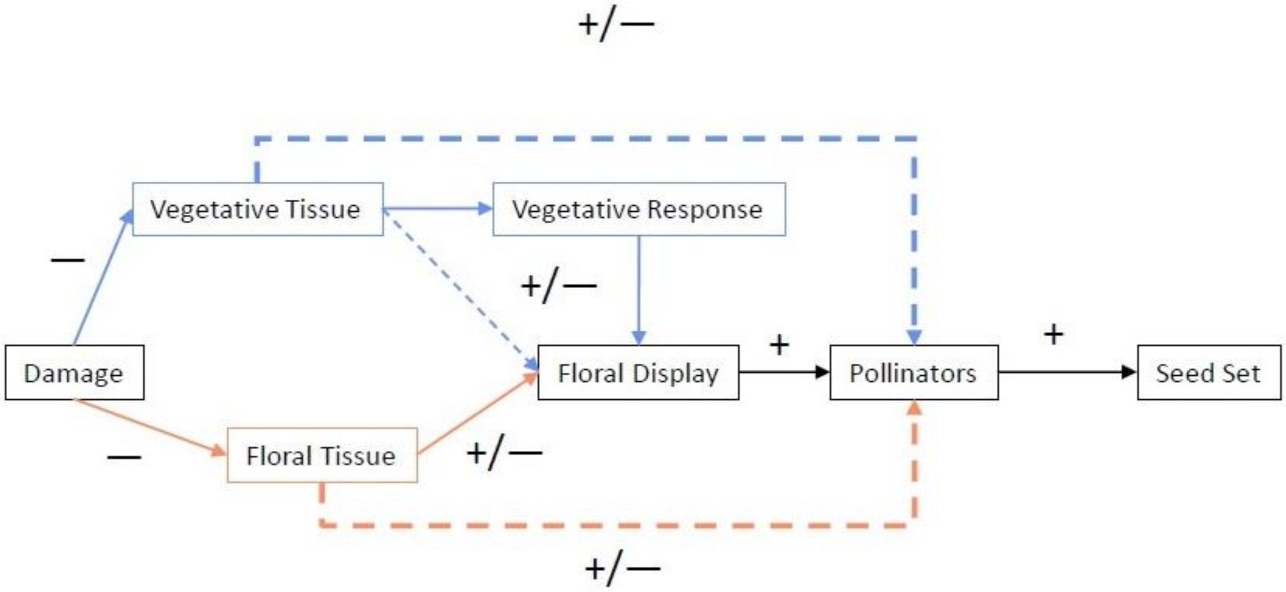

Figure 2.1: Mechanisms of damage by herbivores that can impact pollination and therefore seed set. Solid lines represent direct interactions and dotted lines indirect interactions. The two main pathways are direct (direct damage to floral tissue influences pollinators; shown lighter in orange) and indirect (damage to vegetative tissue indirectly effects floral traits; shown darker in blue). Lines and boxes in black represent interactions and steps shared by both pathways. The dotted lines represent the net indirect interaction of plant damage on pollinators (and pollination) that was the focus of this review.

Herbivory alone can impact plant reproduction both directly and indirectly, regardless of pollination. Partial florivory (damage to floral tissue) or complete florivory (complete removal of flowers; see Table 2.1 for a list of definitions) can reduce plant fitness by directly reducing the capacity of a flower to produce seeds. However, herbivores can also remove or damage non-floral (vegetative) structures such as leaves (folivory), stems (stem damage), and roots (root herbivory). Damage to these structures can cause a plant to either not produce flowers, fruits or seeds, or produce structures of poor quality (i.e., non-viable seeds Brody 1997; Mothershead and Marquis 2000; Lucas-Barbosa et al. 2016; Rusman et al. 2019). Regardless

Table 2.1: Definitions and study counts of all types of herbivory as well as floral, pollinator, and plant responses included in Chapter 2. Study counts include artificial herbivory versions for each herbivory category (e.g., both floral herbivory done by animals and human removal of petals would be included under florivory).

Term	Definition	Category	Number of Studies
Florivory	Flower consumption, including removal of flowers and inflorescences (complete florivory) and partial removal of flowers and petals (partial or incomplete florivory)	Floral Herbivory	29
Folivory	Leaf consumption	Vegetative Herbivory	16
Stem damage	Damage to the stem, including puncture damage and meristem removal.	Vegetative Herbivory	5
Root herbivory	Damage to or consumption of roots	Vegetative Herbivory	3
Open (herbivory)	Open to all herbivores that could consume any or all plant tissues.	Both vegetative and floral herbivory with unknown proportions	3
Grazing	Indiscriminate consumption of plants by mammalian herbivores	Both vegetative and floral herbivory with unknown proportions	12
Flower morphology/architecture and size	Refers to flower symmetry (both due to faulty growth and partial floral damage), inflorescence shape, and architecture, as well as aspects of floral morphology relating to size including diameter, surface area, and corolla length	Floral Response	16
Flowering phenology	The timing of flowers, including when flowers are produced and when they open	Floral Response	5
Flower abundance	The number of flowers in total. Also	Floral	24

Term	Definition	Category	Number of Studies
	includes the presence/absence of flowers when flowers are considered individually	Response	
Sex ratio	The relative proportion of male and female flowers	Floral Response	1
Floral diversity	Number of species or other diversity metric of flowering species	Floral Response	2
Pollen production	The amount of pollen produced by a flower or stigma	Floral Response	5
Pollen deposition	The amount of pollen deposited by a pollinator	Pollinator Effect	6
Pollinator visitation	The frequency with which a flower or plant is visited by pollinators	Pollinator Effect	35
Pollinator abundance	The abundance of pollinators found in the local environment	Pollinator Effect	4
Pollinator diversity	The number of pollinator species (or other diversity metric) that either visit a flower/plant or are found in the local environment	Pollinator Effect	3
Fruit set	A number of measures that represent the amount of fruit produced including number of fruits, fruit size, and fruit mass	Plant Response	26
Seed set	A number of measures that represent the amount of seed produced including number of seeds, seed size, and seed mass. In some cases, only viable seeds are considered.	Plant Response	29

of any indirect interactions via pollinators herbivores can result in a negative net outcome on plant fitness.

The results of these types of damage influence floral display and therefore pollinator visitation. Removal of flowers not only eliminates a potential source of resources for pollinators, but also decreases the overall size of the floral display. Rather than removing flowers, partial florivory can make flowers directly less attractive to pollinators by reducing symmetry (Botto-Mahan et al. 2011). Partial florivory can also have indirect effects on floral traits and pollinator attraction similar to consumption of vegetative (non-floral) tissues (discussed below) such as reduction in flower size and nectar production (Krupnick et al. 1999; Mothershead and Marquis 2000).

Vegetative herbivory such as folivory, root herbivory, and stem damage (Table 2.1) can indirectly influence floral display (similar to partial florivory). They can cause plants to produce fewer and smaller flowers (Strauss et al. 1996; Hambäck 2001; Hladun and Adler 2009) as well as change the morphology of flowers (including symmetry or architectural structure) (Strauss et al. 1996; Mothershead and Marquis 2000; Suárez et al. 2009). Phenology, sex ratio, and pollen production can further shift with vegetative herbivory (Strauss et al. 1996; Mothershead and Marquis 2000; Avila-Sakar et al. 2003; Arceo-Gómez et al. 2009). In these ways, both vegetative and floral damage can interact with pollination.

While herbivory is inherently negative and can have negative impacts on pollination, the net outcome of herbivory both on pollination and plant reproduction is not necessarily negative. The net outcome is mediated by plant responses (Santangelo et al. 2019) in terms of resistances, allocation strategies, and defenses (see Hawkes and Sullivan 2001). Plants can overproduce in preparation for herbivory or compensate for herbivory received by producing more structures or switching to self-pollination, reducing the overall impact (Garcia and Eubanks 2019). Plants can also deter herbivores through defenses including constitutive (e.g., thorns) or inducible (e.g., volatile release) defenses that can be both mechanical or chemical (Chen 2008). Plants may also reduce herbivory by interacting with other non-herbivore species such as other plants (Ruttan and Lortie 2013) and predators (Heil 2008). By reducing herbivory or mitigating the damage caused by herbivores, plants are able to reduce their impact on pollination and plant reproduction. However, a cost to some defenses includes deterring pollinators (Lucas-Barbosa et al. 2011).

Numerous mechanistic pathways can integrate the direct and indirect impacts of herbivores on plant reproduction through plant tissue, allocation strategies, and timing that impact plant pollination (Strauss et al. 1996; Mothershead and Marquis 2000; Kelly et al. 2008; Botto-Mahan et al. 2011). In turn, negative impacts to pollinators can amplify the negative effects of herbivores on plant fitness by reducing both potential seed set (e.g. number of flowers available to set seed) (Strauss et al. 1996; Hambäck 2001; Rusman et al. 2019) and actual seed set (i.e. flowers are not all pollinated due to decreased pollinator visitation) (Adler et al. 2001; Benning and Moeller 2019). The nature of how not only each type of herbivory, but also the joint impact of multiple types of herbivory impact pollination and plant reproduction are the basis of Fig. 2.1.

In this systematic review, we synthesize the contemporary literature on herbivore-plant-pollinator interactions with a specific focus on studies that examined the joint impact of herbivores and pollinators on plant reproduction or the impact of herbivores on pollination using the mechanistic pathways proposed in our conceptual framework (Fig. 2.1). The frequency of mechanisms tested and the frequency that direct vs indirect floral damage pathways are contrasted is important to both ecology and evolution. This includes examining the diversity of types of damage—both the tissue targeted and the taxa causing the damage. Finally, we examine how each mechanism is tested.

Materials and Methods

A search for papers that examine the impact of herbivores on pollinators or the pollination of plants in October 2019 using Web of Science and the search terms “herbivor* AND pollinat*”, “floriv*”, “foliv* AND pollinat*”, “herbivor* AND flower*”, and “foliv* AND flower” was conducted by S. Haas-Desmarais (no review protocol was registered). This resulted in 3681 papers (Fig. 2.2). Papers had to meet the criteria that they directly tested the impact of herbivory on animal-mediated pollination. The indirect effect of herbivores on pollinators or the indirect effect of herbivores on plants via pollinators must have been reported to be included in this synthesis (e.g. through measuring pollen deposition or comparing open pollination to supplementary hand pollination). After review, 59 papers were included in the final analysis (Fig. 2.2). Papers that were excluded were reviews and descriptions of the natural history of plants or animals (including diet). Studies were also excluded if they examined the impact of herbivores on plants but not pollination. Studies had to specifically test some effect pathway from herbivores to pollinators; studies that included both herbivores and pollinators but examined their effects on plants independently or examined the effect of some other factor on each group were not included. Studies on other types of consumption, such as nectar robbing, gall-forming insects, seed predation, and frugivory (consumption of fruits) were excluded. Plants also had to be animal-pollinated (at least in part). Data extracted included the physical location of all study sites and the taxa examined, as well as the analyses performed (including type of herbivory, response variable, and general direction of effect each variable had on each response) and the general structure of

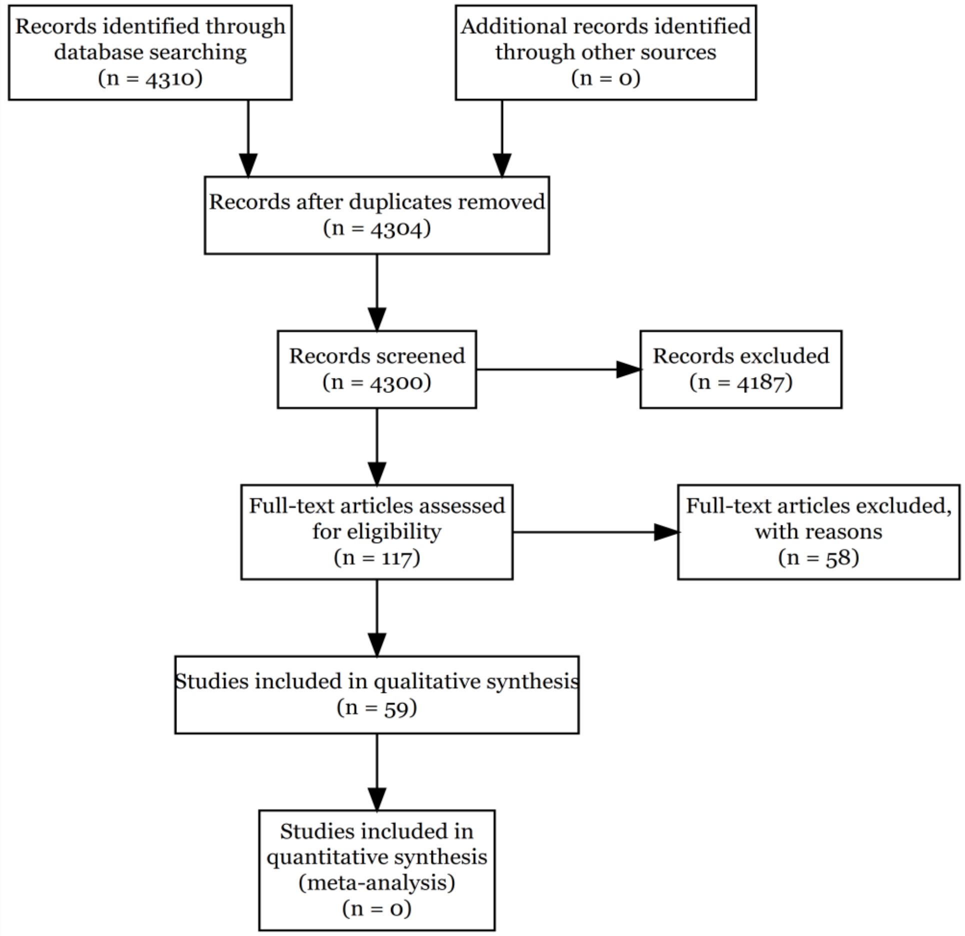

Figure 2.2: PRISMA diagram for the progression of papers included in Chapter 2.

the experimental design. Site biomes were calculated using biomes from Terrestrial Ecoregions of the World, originating from the World Wildlife Fund (Olson et al. 2001, CC BY-NC 3.0) using the software QGIS (QGIS Development Team 2019).

Results

In total, 59 papers met all criteria to be included in the final analysis. These papers ranged from 1995 to 2019 spanning 18 different countries and 11 (of 14) different biomes (Fig. 2.3). The majority were done in the United States and the temperate broadleaf & mixed forests biome. The only biomes not represented were tropical & subtropical coniferous forests,

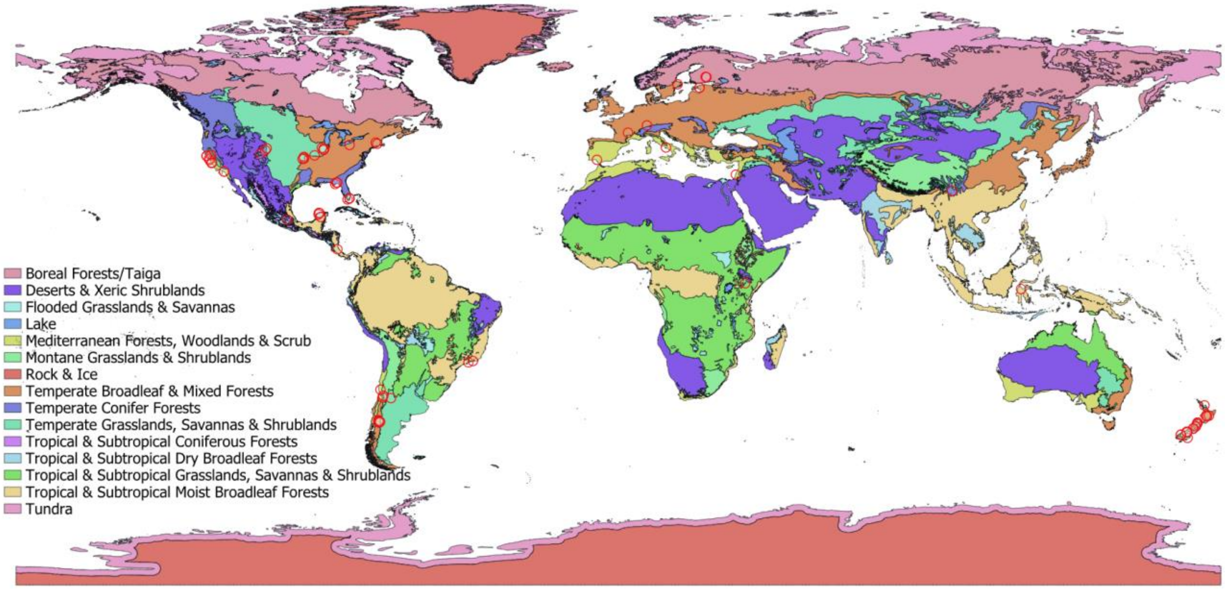

Figure 2.3: Geographical distribution of studies (N = 56; 3 studies had no geographic information) across biomes that examined the impact of both herbivores and pollinators. Studies spanned over 20 countries and 11 biomes. Biomes were generated from Terrestrial Ecoregions of the World, originating from the World Wildlife Fund (Olson et al., 2001). This figure incorporates data from the Terrestrial Ecoregions of the World database which is © World Wildlife Fund, Inc. (2006–2024) and has been used herein under license. WWF has not evaluated the data as altered and incorporated within the figure, and therefore gives no warranty regarding its accuracy, completeness, currency or suitability for any particular purpose.

tropical & subtropical grasslands, savannas & shrublands, and tundra. Of the 51 papers in which site information could be taken (that were not greenhouse experiments) all but three studies were located within a single biome. A total of 47 plant taxa, 27 herbivore taxa, and 18 pollinator taxa were studied in these papers (Table A.1; Fig. 2.4). Almost all herbivores (81%) and pollinators (78%) were insects. A total of 90% of studies (N=55) examined a single plant species while only 43% of studies (N=26) examined a single herbivore and 10% a single pollinator (N=6; Table A.2 and A.3). It was most common to examine the entire community of pollinators (72% of studies; N=44). Pollination was most frequently measured through direct

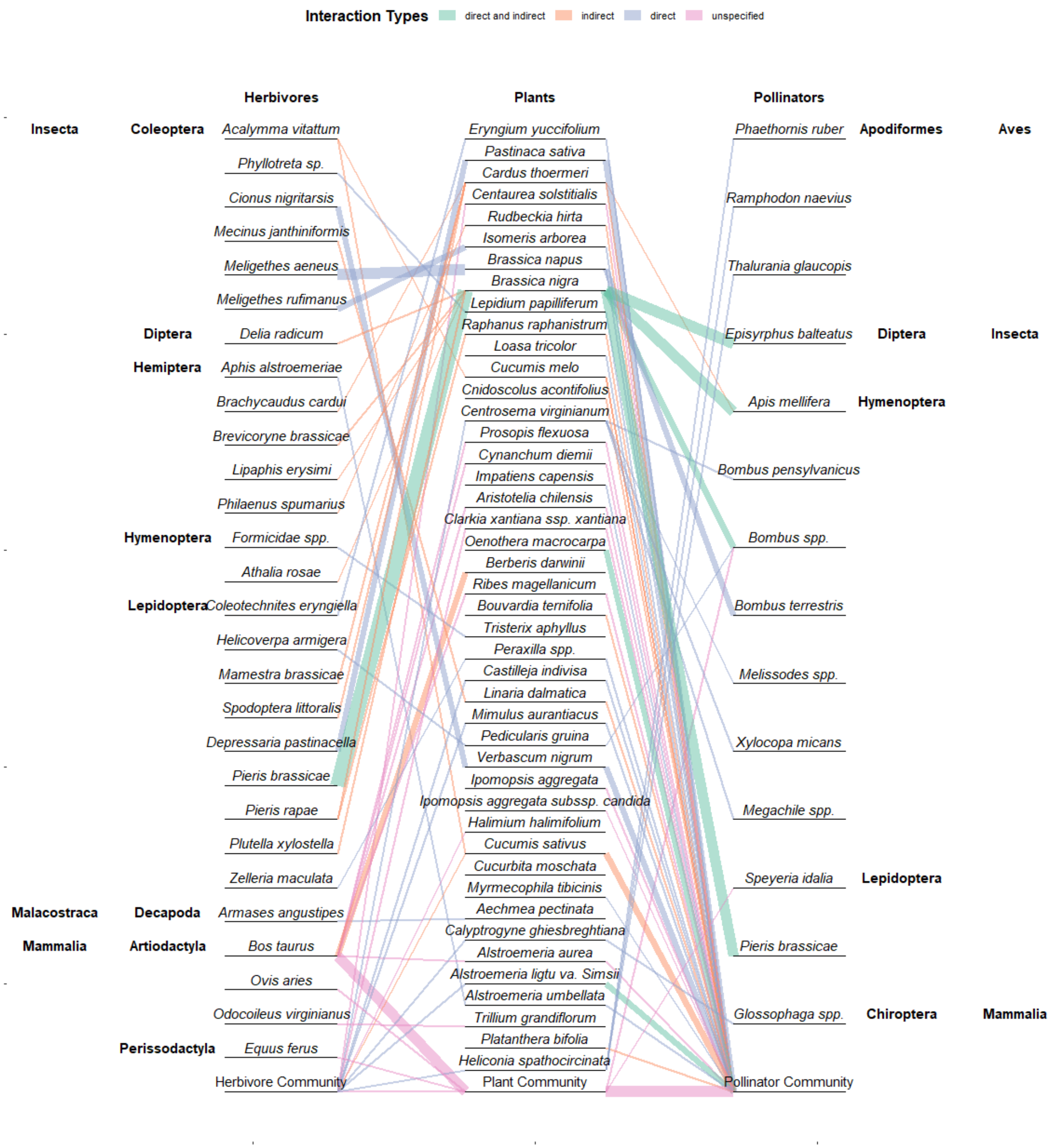

Figure 2.4: Network showing the interactions between herbivores, plants, and pollinators found within the 59 studies included in Chapter 2. Links are colored by whether herbivores had a direct, indirect, or unspecified effect (or both direct and indirect) on floral tissue within the study. Line thickness represents multiple interactions between those two species. Community refers to studies where the herbivores, plants, or pollinators consisted of whatever species were found within the natural community and not restricted. Plant species in which no herbivores or pollinators were used within the study (e.g., herbivory was artificially mimicked and pollination was measured passively through hand pollination) are not included.

pollinator visitation (57% of studies); however, 25% used supplemental pollination (Table 2.1). Herbivory was also most frequently (67%) observed directly by animals although 33% of studies (N=20) applied some form of artificial herbivory, and 22% artificially reduced herbivory by excluding herbivores or applying pesticides.

The most common type of herbivory examined was florivory (49%; Fig. 2.5, Table 2.1), with every one of these studies examining partial florivory and only one also examining complete florivory. This was followed by folivory (27%) and grazing (20%). However, stem

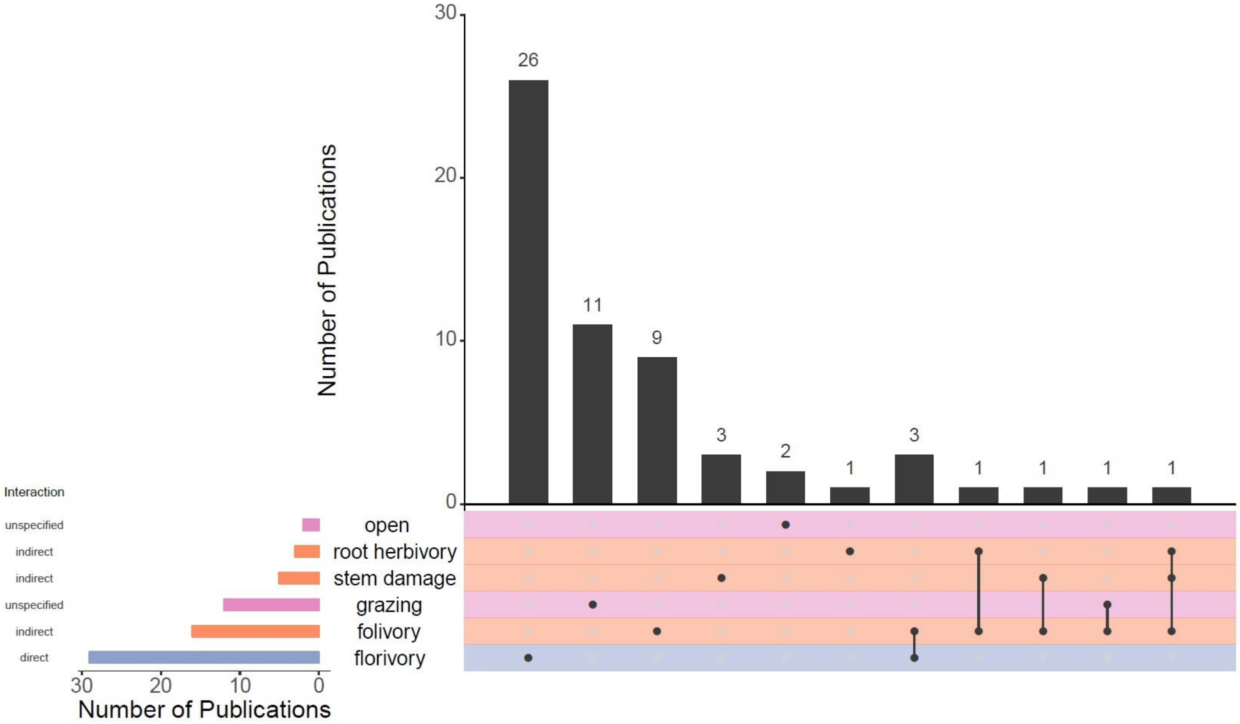

Figure 2.5: UpSet plot showing the number of publications (N = 59) that examined each type of herbivory both individually and simultaneously. The black vertical bars represent the number of publications that looked at exactly one, two or three types of herbivory. The dots directly below black bars correspond to which type(s) of herbivory are represented within that category. The colored horizontal bars to the left of the list of herbivory types show the number of publications that included each herbivory type (regardless of whether another type of herbivory was also examined). Horizontal bars and rows are colored according to the interaction type of each form of herbivory (i.e., direct, indirect, or unspecified). Unspecified interaction pathways are those in which one or both of direct and indirect pathways are possible, but not specified.

damage (8%) and root herbivory (5%) were also utilized. For 5% of studies, herbivory was non-specific (i.e. “open” to all herbivores). Almost all studies (88%) looked at only one form of herbivory. Of the other 12% of studies, two or three types of herbivory were examined. Hladun and Adler (2009) examined the interaction between two types of vegetative herbivory—root herbivory and folivory. Buchanan (2015) also compared two types of vegetative herbivory: leaf damage and meristem damage, while Rusman et al. (2019) looked at all three types of vegetative herbivory (folivory, stem damage, and root herbivory). Similarly, Sasal et al. (2017) looked at both general grazing (in the form of ungulates) and specifically folivory (in the form of insect herbivory). Lucas-Barbosa et al. (2013), Lucas-Barbosa et al. (2016), and Mothershead and Marquis (2000) compared the effects of florivory and folivory representing the only papers that compared vegetative and floral herbivory.

Florivory was found to have some negative impact on floral expression, pollination, or seed production in 86% of papers. Some positive effect of florivory was found in 24% of papers and a neutral effect in 48% of papers. For folivory, 81% of papers each found some negative effect or neutral effect, while only 31% found any positive effect. Grazing had 67% of papers each find some negative or neutral effect, and 33% found some positive effect. Similar proportions were found in each of the other types of herbivory.

Only 19% of papers took a full mechanistic approach to the effects of herbivores on pollinators (Table 2.2). These studies examined each point of the mechanism in Fig. 2.1: the effects of herbivory on floral display, pollinators, and plant reproduction. Most frequently (24%), papers examined the effect on pollinators and plant reproduction while skipping the mechanistic step of the impact on the flower. Otherwise, there was an approximately equal split between only examining effects on pollinators (15%), only examining the effect of

Table 2.2: Distribution of studies based on herbivore-pollinator mechanism examined. Unspecified refers to damage that may include either of vegetative or floral tissue or both.

Indirect	n	Direct	n	Unspecified	n
Vegetative damage-floral response-pollinator	5	Floral damage-floral response-pollinator	1	Unspecified damage-Unspecified response-pollinator	6
Vegetative damage-floral response-pollinator-seed set	9	Floral damage-floral response-pollinator-seed set	6	Unspecified damage-Unspecified response-pollinator-seed set	2
Vegetative damage-pollinator	3	Floral damage-pollinator	7	Unspecified damage-pollinator	0
Vegetative damage-pollinator-seed set	4	Floral damage-pollinator-seed set	13	Unspecified damage-pollinator-seed set	6

supplemental pollination on reproduction (12%), examining the floral attributes and reproduction without the pollinator (15%), or the floral attributes and pollinator without reproduction (15%).

Discussion

Herbivory and reproduction in plants are intimately linked through interactions with animals. In this systematic review, we examined the relative frequencies and the extent that these important processes are studied in concert. While the effect of herbivores on plants have long been studied, and it has been well shown that herbivores can directly and indirectly impact plant reproduction, growth, and population dynamics (Hawkes and Sullivan 2001; Ohgushi 2005; Boivin et al. 2019; Garcia and Eubanks 2019), the small number of studies that were located within this review indicate how infrequently the effects of herbivores on pollination are studied. These studies were also heavily biased towards damage done by insects, temperate biomes, and the effects of a single herbivore species on a single plant species. Furthermore, only a handful of studies compared direct and indirect effects of herbivory on floral traits and pollination. Given that most animal-pollinated plants are likely to experience damage to multiple tissues as well as pollination (Lucas-Barbosa, 2016), this is an unfortunate gap in the literature. In addition, those few studies that do examine both herbivory and pollination frequently examine only the net outcome and not the underlying mechanism (i.e., how herbivory impacts floral traits and how floral traits impact pollination). That is, most studies do not fully examine the interaction network outlined in our framework (Fig. 2.1). Examining the impacts of multiple herbivores as well as multiple types of herbivory is important in determining how plants and pollinators are impacted by real communities of herbivores.

Effects of Florivory on Pollination

Direct damage to floral tissue is an important factor in determining plant reproductive output. Complete florivory has been shown to have direct impacts on floral abundance. The net outcome of this form of direct damage is dependent on the strategy of the plant (Juenger and Bergelson 1997; Wise et al. 2008; Garcia and Eubanks 2019). In some cases, plants will over-produce flowers as a defense against florivory creating more flowers than the plant is able to bring to seed (e.g., Huth and Pellmyr 1997). Therefore, florivory frequently results in no net loss in reproductive output for the plant. In other cases, plants can compensate or overcompensate for herbivory, replacing the flowers lost (sometimes producing more flowers than initially), delaying phenology (Wise et al. 2008; Garcia and Eubanks 2019), or changing mating system (i.e., shifting to self-pollination) (Penet et al. 2009). If the plant is able to completely compensate (reproduce flowers of equal or greater quality and quantity) then the net effect of complete florivory is neutral or even positive. How plants interact with florivores can influence communities and population resilience through these differences in reproductive output. While the impact of removal of flowers on overall plant reproduction has been studied numerous times (see McCall and Irwin 2006), the impact of this removal specifically on pollination or pollinator visitation is rarely studied. Out of the 29 papers that examined the impact of florivory on pollination found in this review, only one examined complete florivory (Sutter and Albrecht 2016). Changes in plant population and community dynamics due to changes in reproduction have the potential to impact pollinators; for instance, patches with more flowers tend to attract more pollinators (Lázaro and Totland 2010). Pollinators in turn interact with plants to determine reproductive output. Therefore, the indirect interactions between herbivores and pollinators fosters even further co-evolutionary processes such that plants not only sufficiently compensate for lost reproductive structures due to herbivores, but also to produce flowers of quality and quantity sufficient to attract pollinators. This interaction requires further research into the implications of complete florivory on plant compensation, pollination, and reproduction.

Incomplete florivory can also impact both pollination and plant reproduction. Incomplete florivory can result in flowers that are less attractive to pollinators despite offering the same reward (Mothershead and Marquis 2000). Pollinators can use visual cues such as floral symmetry to choose between flowers (Rodríguez et al. 2004). A loss of symmetry can result in decreased visitation (McCall 2010). When other cues are more important, there may be no effect of incomplete florivory (Malo et al. 2001) and plants can mitigate or eliminate the negative effects of herbivory on floral display by reproducing via self-pollination (with or without pollinators) in some cases including several species in this systematic review (e.g. Cardel and Koptur 2010). While this review focused on animal-pollinated plants, many plants are not wholly reliant on animals for reproduction (Culley et al. 2002). However, since animal pollination frequently increases plant fitness (Klein et al. 2007; Cardel and Koptur 2010; Jorge et al. 2015) this strategy may only limit the effects of incomplete florivory as opposed to eliminating them. In addition, the actual presence of florivores in flowers can deter pollinators. For example, Canela and Sazima (2003) found that florivorous crabs not only decreased the attraction of flowers to pollinators through damage but that pollinators were less likely to visit flowers while the crabs were present. All of the 29 studies we found that examined the impact of florivory on pollination examined partial florivory. In most studies, partial florivory was found to decrease pollinator visitation or pollen deposition as well as plant reproduction (fruit set or seed set). By decreasing pollinator visitation, incomplete florivory can indirectly decrease plant reproduction (via pollen limitation). As with complete florivory decreases in reproduction can impact population dynamics, while indirect effects on pollinators can drive the coevolutionary arms race between herbivores and plants that might not otherwise occur under the limited damage of incomplete florivory (that is, florivory that keeps ovules and stigmas intact).

Effects of Vegetative Herbivory on Pollination

While direct damage to floral tissue is the most common way to examine the effects of herbivores on pollinators (Fig. 2.4), damage to vegetative tissue also had indirect effects on floral attributes. The main mechanism that folivory, root damage and stem damage impact pollinators is through decreasing both resources and the ability for plants to produce resources (Mothershead and Marquis 2000). By decreasing the amount of photosynthetic and absorptive area available to a plant or siphoning off xylem or phloem, fewer or smaller flowers may be produced (Mothershead and Marquis 2000; Hambäck 2001; Hladun and Adler 2009). These flowers may be less attractive to pollinators (Mothershead and Marquis 2000) or theoretically be less fertile, producing fewer seeds. While plants are also able to compensate for vegetative damage, resources are often allocated to regrowth instead of reproduction and so vegetative damage can still decrease fitness (Pratt et al. 2005; Garcia and Eubanks 2019). Root herbivory can also change how the plant interacts with aboveground herbivores and mutualists (Barber et al. 2015). For instance, root herbivory can decrease aboveground herbivory and increase the nectar in extrafloral nectaries (Hladun and Adler 2009; Soler et al. 2012).

While folivory, root herbivory, and stem damage can decrease reproductive output (Mutikainen and Delph 1996; Lehtilä and Strauss 1999; Pratt et al. 2005; Lopez-Toledo et al. 2018), it is less clear whether they impact pollinators or pollination. Folivory, root damage, and stem damage were found to negatively impact several floral traits, as well as pollinator visitation and reproduction (Mutikainen and Delph 1996; Strauss et al. 1996; Mothershead and Marquis 2000; Hambäck 2001; Arceo-Gómez et al. 2009; Hladun and Adler 2009; Barber and Gorden 2013; Sasal et al. 2017). Folivory was found to have negative effects on most floral traits including floral morphology, abundance, and phenology. Stem damage was found to have a negative effect on floral morphology, size, and abundance while root herbivory affected floral abundance and pollen production. However, the number of studies that found each of these effects is low and each type of vegetative damage was also frequently observed to have no effect on each of these respective traits and occasionally a positive effect. It is also possible that plants are better able to compensate for or resist vegetative damage such that there will be no change in floral display or reproduction. For instance, (as with incomplete florivory) plants may switch to self-pollination if floral display is compromised or pollination is limited.

While it is clear that vegetative damage can impact pollination and plant reproduction, vegetative damage was also frequently observed to have no effect. This lack of effect may be only representative of small sample size and more studies would find the proportions more similar to what is found with florivory. However, finding fewer studies may be because few studies examined different types of herbivory (Fig. 2.5) or different taxa simultaneously (Fig. 2.4; Supplemental Table A.3). The same herbivore can feed on multiple tissues (at the same time or switching ontogenetically, e.g. Lucas-Barbosa et al. 2016) or multiple herbivores can feed on different tissues (or even the same tissue) simultaneously (e.g. Barber et al. 2011). Therefore, it is difficult to determine whether different types of herbivory may act synergistically or if they interfere with each other (as seen between root herbivory and aboveground herbivory in Barber et al. (2015)). The larger proportion of neutral effects of vegetative herbivory on pollination may only be an indication of not considering damage to all types of vegetative tissues.

This lack of directly comparing individual species of herbivores is one weakness of some of the papers included in this study. While comparing the effects of a broader taxonomic scope or community of herbivores or pollinators is good for comparing the net outcomes of interactions, the exact effects and net outcomes of individual species is lost. More research that examines specific species, especially multiple specific species could help illuminate these differences. This is particularly prevalent with how few studies examined individual pollinator species compared to those that studied the entire community (Fig. 2.4). In contrast, the indirect pathway from vegetative damage to changes in pollination may simply be more heavily regulated by plant physiological responses with plants preferentially allocating resources to reproduction over regrowth (Fig. 2.1). Considering multiple species in this case may not change this result. Regardless, the small sample size makes any conclusions about the relative proportion of studies to find significant or neutral effects of vegetative damage dubious.

Integrating the Effects of Floral and Vegetative Herbivory

Vegetative herbivory can impact plant populations and communities through plant reproduction, but the role of the indirect effect of vegetative herbivory on pollinators and the role of pollinators in driving co-evolution between plants and non-floral herbivores is less distinct than when examining florivores. In order to determine the relative effect of direct and indirect damage to floral tissue on pollination, these two mechanisms need to be compared more frequently. In this chapter, only three studies examined the direct and indirect effects of herbivory on floral display and pollination (Fig. 2.5). Specifically, these three studies compared florivory to folivory. Lucas-Barbosa et al. (2013) examined the behaviour of pollinators of *Brassica nigra* in response to the specialist caterpillar *Pieris brassicae*. *Pieris brassicae* feeds on the leaves of *B. nigra* at a younger stage, and progress later to consuming flowers. Therefore, while examining damage to two types of tissues, the damage was done by the same individuals. They found there was no effect of *P. brassicae* on pollinators during the folivory stage, while there was an effect at the florivory stage. In a study with the same system by many of the same authors (Lucas-Barbosa et al. 2016) where the effect of damage to vegetative and floral tissues on floral volatiles detected by pollinators was studied, neither folivory nor florivory influenced pollinators.

Finally, Mothershead and Marquis (2000) examined the effect of artificial damage to both leaves and buds to the floral traits and seed set of *Oenothera macrocarpa* in the presence and absence of supplemental hand pollination. Both folivory and florivory affected floral traits (both morphology and size), that in turn impacted pollination and seed set. Folivory was not found to directly reduce seed set through reduced floral resources, but rather only indirectly through floral morphology. However, floral damage decreased fruit set (68% reduction) more than foliar damage (18% reduction). While two of these studies point towards florivory having a greater impact on pollination than folivory, two of three studies are not sufficient sample size to determine the relative importance of direct (florivory) over indirect (vegetative herbivory) damage. Only multiple studies that directly compare florivory and other types of herbivory within the same system will be sufficient to determine their relative importance.

Similarly, the larger proportion of papers that examined florivory over other forms of herbivory (Fig. 2.5) or the greater proportion of studies with a negative impact on pollination or reproduction due to florivory is not sufficient to make the claim that florivory has a greater impact on pollination than damage to vegetative tissue. Florivory is the more obvious choice when studying the effects of herbivory on pollination and so a bias in papers towards florivory is expected. Similarly, the sample size of studies that examine any other form of herbivory is particularly low, and so proportions are not necessarily representative. While it is intuitive and may be true that direct damage to floral tissue has a greater impact than indirect damage on pollination, there is not sufficient evidence to make this claim.

Some herbivores act as both herbivores and pollinators at different ontogenetic stages (Lucas-Barbosa et al. 2016). This type of switch is commonly seen in pollinating insects with a herbivorous larval form (Nakazawa 2015). However, only a single species, the *B. nigra* specialist *P. brassicae*, was examined as both a herbivore and a pollinator. Furthermore, *P. brassicae* was only examined as both herbivore and pollinator of *B. nigra* in a single study (Lucas-Barbosa et al. 2016), although it was also used as a herbivore in Lucas-Barbosa et al. (2013) and as a pollinator in Rusman et al. (2019). The intricate relationship and co-evolution between species that change between negative and positive interactions is not one that is unstudied (see Nakazawa 2015). Strategies that reduce the impact of herbivores at an early stage that might negatively impact the later production of floral resources would be beneficial to both plant and herbivore in this case, even more so than with species that do not share this relationship. However, clearly the net outcome of early-stage herbivory on plant reproduction and late-stage pollination is lacking within the literature.

Effects of Damage to Unspecified Tissue on Pollination

The joint impact of damage to multiple tissues can be extended to the effects of herbivores that do not have a plant tissue preference. Most studies examined damage to specific tissues; however, a number of studies examined damage to unspecified tissues, representing both direct and indirect mechanisms that are not differentiated. Grazing encompasses possible damage to flowers, leaves, and stems. Grazing is of particular import because of its potential severity and anthropogenic causes. The agricultural industry plays a large role in the impact humans have in creating disturbed ecosystems (Kitzes et al. 2008). Most studies that examined direct or indirect damage to floral tissue used insects as focal herbivores; those that looked at unspecified damage exclusively used mammals (Fig. 2.4). While studies frequently look at grazing by large mammals such as deer and cattle at a community level—examining the plant, or even floral diversity of a system (Olff and Ritchie 1998; Kohyani et al. 2008; Herrero-Jáuregui and Oesterheld 2018), it is rare for these studies to further examine the pollination consequences of grazing. Studies that examined grazing reported some negative effects of grazing on plant reproduction or pollinator visitation. Grazing also impacted floral morphology, number, phenology, and pollen production, but the mechanisms were not clearly reported in primary studies. By studying the synergistic effects of multiple effect pathways, we can better understand how grazing can impact vegetation.

Other Interactions

While the indirect effects of herbivory on pollination are the focus of this review; there are other ways in which pollinators and herbivores interact. For instance, there are direct interactions between herbivores and pollinators where the presence of herbivores actively deters pollinators from approaching flowers (Canela and Sazima 2003). Additionally, pollination may impact herbivory by facilitating the successful reproduction of herbivore plant hosts. However, these types of interactions are neither included in this review nor the conceptual framework.

Conclusions

Both direct and indirect damage to floral tissue can impact pollination and plant reproduction. However, direct and indirect damage to floral tissue is rarely examined in concert, nor is damage by different herbivores. The relative importance of the direct and indirect mechanisms and synergistic effects of multiple herbivores have important implications for ecological resilience and stability in evolutionary processes. However, this relative importance is almost never examined with the focus lying on each type and each herbivore individually. The indirect effect of herbivores on pollinators can mediate co-evolutionary processes between plants and herbivores and plants and pollinators. The collection of herbivores that interact with plants can include species that feed on all types of tissue either simultaneously or temporally separated that the plant then integrates into growth, allocation, defense, or phenology. This in turn can impact pollinators and pollination, making these two plant-animal interactions intimately linked.

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Chapter 3: The effect of herbivory on pollinators: a revisited meta-analysis

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Abstract

Plant-herbivore and plant-pollinator interactions are intimately linked through their concurrent influences on plant reproduction. By changing the floral expression of plants, herbivores can impact the attraction of pollinators to plants that in turn can mediate plant reproduction. The relationship between these plant-animal interactions has been examined for nearly thirty years and previously summarized in a meta-analysis. The field is growing fast and needs a new quantitative analysis. Here, we update this most recent synthesis and quantitatively summarize the effects of natural and simulated herbivory on floral traits, pollinator attraction, and reproductive success with additional primary studies from 2018-2023. We reexamined the effect of damage to roots, leaves, and flowers, and also examined two new tissues: damage to stems and mixed damage (indiscriminate damage to multiple tissues, e.g., grazing). We increase the number of studies from 88 to 171, and the number of independent observations from 568 to 1361. Our results showed a net negative effect of herbivory on floral traits, pollinator attraction, and reproductive success. However, these effects were dependent on the tissue damaged and whether herbivore damage was natural or simulated. Natural damage to flowers and leaves (but not roots, stems, or mixed damage) had a net negative effect on the response variables, decreasing plant floral traits, fitness, and pollinator attraction. Simulated damage to flowers, leaves, and stems negatively influenced floral traits and plant reproductive success while simulated damage to leaves also decreased pollinator attraction. In the previous meta-analysis simulated damage had no effect on any response and natural damage to flowers did not have an effect on plant reproductive response. The revised meta-analysis validated the results regarding natural damage in all instances, except for the effect on flower reproduction, which transitioned from slightly positive to significantly negative. Moreover, the initially non-significant but slightly negative impacts of

simulated damage on leaves and flowers became significantly negative. Our results provide an updated insight into the mechanism and directionality of the effects of herbivores on pollinators.

Introduction

A large body of research has demonstrated that herbivores negatively impact plant fitness (e.g., Marquis 1984; Maron 1998). Early on, it became well established that herbivory can directly cause strong reductions in plant growth, survival, and reproductive output (reviewed by Karban and Agrawal 2002). However, it was later realized that herbivory could also affect plant fitness indirectly by influencing other plant-associated mutualistic or antagonistic interactions, as summarized qualitatively in Chapter 2. A notable example of this comes from research demonstrating that herbivores can affect floral traits, hence pollinator visits to flowers and in turn (indirectly) affect plant reproductive success (reviewed by Bronstein et al. 2007; Kessler and Halitschke 2009; Jones and Agrawal 2017). For instance, by removing or damaging flowers, herbivores can reduce the size and symmetry of the floral display which can decrease floral attractiveness to pollinators (Mothershead and Marquis 2000; Botto-Mahan et al. 2011; Tsuji and Ohgushi 2018). Herbivores can also impact the floral display by damaging vegetative tissues (Lucas-Barbosa 2016). Herbivores feeding on leaves, roots, and stems can reduce the resources available for floral and nectar production (Bruinsma et al. 2014; Burkle and Runyon 2016; Zhang et al. 2019; Haas and Lortie 2020). Smaller displays with fewer rewards are also less attractive to pollinators (Mitchell et al. 2004; Parachnowitsch et al. 2019; Hernández-Villa et al. 2020; Brunet et al. 2021). By contrast, herbivory can indirectly positively affect pollinators if plants exhibit reproductive overcompensation. For example, plants may increase flower production in response to damage (e.g., Strauss et al. 2001; Irwin et al. 2004; Schiestl et al. 2014), with this leading to a concomitant increase in pollinator attraction.

The impact of herbivores on pollinators has been studied extensively. Several recent syntheses (including Chapter 2 of this dissertation; Haas and Lortie 2020) have examined the relationship between herbivores and pollinators (Lucas-Barbosa 2016; Moreira et al. 2019; Underwood et al. 2020; Jacobsen and Raguso 2021), summarizing some of the relatively extensive volume of studies published on this topic. The number of studies yearly published on plant-herbivore-pollinator interactions has been raising rapidly so that continuous updates and extension of older meta-analyses such as Moreira et al. (2019) are already warranted (van Wely 2014; Bashir et al. 2018). Replication science is considered the cornerstone of science (Fraser et al. 2020), but in practice is often neglected (Baker 2016). Synthesis science is no exception and can benefit from updated examinations of novel research (Garner et al. 2016). Meta-analyses indeed strive to be reproducible and updatable (Gurevitch et al. 2018), and therefore replication and extension should be expected after sufficient new studies have been published, new methods emerge, or the credibility of findings merit examination with new research or methods (Garner et al. 2016). By updating the literature of published meta-analyses, the certainty of results can be validated (Jennions et al. 2013; Gurevitch et al. 2018). Given the increased body of work (more than doubling the number of cases) examining the intersection of plant-herbivore-pollinator interactions and necessity to understand complex ecological interactions in the face of changing climate (Schleuning et al. 2020; Fricke et al. 2022), we believe that a synthesis update of this topic is now much needed.

By building on the dataset compiled by Moreira et al. (2019) and adding more than twice the number of study cases, here, we quantitatively examine how natural and simulated herbivory of various plant tissues (roots, flowers, leaves, stems, and mixed damage) affects floral traits, pollinator attraction, and plant reproductive success (Moreira et al. 2019). In particular, we compare how increasing the sample size (i.e., including new studies) changes (or not) the outcome from the previous meta-analysis by Moreira et al. (2019). This is a current and relevant research topic that examines dominant ecological processes in plant-animal theory and supports a deeper understanding of fitness in plants.

Materials and Methods

Studies listed in Moreira et al. (2019) (n = 88) and Chapter 2 (n = 59) were compiled. Duplicates between the two papers were removed (n = 12), and the studies included in Chapter 2 were checked to make sure they met the criterion established in Moreira et al. (2019). Specifically, studies needed to (1) include data on pollinators and/or floral traits (of animal-pollinated plant species) in response to damage, and (2) include either raw data in a table, supplementary material, or published in a third party website (e.g. Dryad) or reported treatment level means with some measurement of variability (i.e. standard deviation, standard error, or variance) as well as sample sizes (Moreira et al. 2019). Reported means were extracted from the text, tables, figures, and supplemental material. A total of 15 studies were eliminated because they did not meet these criterion, resulting in 120 studies and 888 study cases from these two reviews, with 568 study cases originating from Moreira et al. (2019).

We then updated the Web of Science literature search using the terms in both publications. From Moreira et al. (2019), we searched “(Plant OR tree OR shrub) AND (herbivore OR herbivores OR herbivorous) AND (flower OR floral OR nectar OR inflorescence OR pollinator OR pollination),” not including records published prior to June 2018 (the date of first search). From Chapter 2, we used “(herbivor* AND pollinat*) OR floriv* OR (foliv* AND pollinat*) OR (herbivor* AND flower*") OR (foliv* AND flower)," not including records published prior to October 2019 (the date of first search). These two searches were consolidated and searched simultaneously on Web of Science to limit duplicates between the search terms. A total of 894 papers were returned in this search. After removing studies that did not fit the criteria mentioned previously, 51 new studies and 473 new study cases were added to the previously included set for a total of 171 studies (see Appendix C for complete list) and 1361 study cases.

In addition to collecting data on pollinator attraction and floral traits, we also collected data on the effects of plant fitness because this can correlate with pollinator attraction (Underwood et al. 2020). We compiled all data included in Moreira et al. (2019) studies, including plant species and type (i.e. annual or perennial), damage type (natural or simulated), plant tissue damaged (flowers, leaves, roots), floral traits (flower number, flower size/morphology, nectar concentration or volume, and/or flowering phenology), pollinator attraction (pollinator abundance and diversity, number of visits/flowers visited, and/or duration of visits), and plant reproductive success (seed or fruit abundance/weight, seed viability). We also included two novel plant tissue categories: damage to stems and mixed damage (damage potentially occurred on multiple tissues; this category includes both grazing and open damage from Chapter 2). We collected data on these two types of damage in both the new studies and the previous studies from Moreira et al. (2019).

Statistical Analyses

Our statistical analyses followed those of Moreira et al. (2019). For each study case, we estimated effect size by calculating Hedges' g (Hedges 1981) using the metafor package (Viechtbauer 2010) in R version 4.3.1 (R Core Team 2023). Negative values represent a negative effect of herbivory and positive values the opposite. We conducted an omnibus test (including all study cases) of the effect of any type of damage on all response variables. We first tested whether the overall effect size across study cases (not differentiating between response variables) differed from zero. We then tested whether total heterogeneity could be accounted for by the following moderators: response variable (floral traits, pollinator attraction, and plant reproduction), plant tissue damaged (roots, flowers, leaves, stems, or mixed), and type of damage (natural or simulated). We tested each of these moderators individually at first to get their overall effects, and then again in a crossed design to examine their interaction. All tests were performed using multilevel error meta-analysis (i.e. random mixed effects) with random effects of replicate analysis nested within study ID to account for increased homogeneity between analyses within the same study. We also accounted for dependence between study cases with shared controls within studies by using a variance-covariance matrix of the sampling errors that gives the correlation between effect sizes within our analysis (Gleser and Olkin 2009). We further performed a sensitivity and a bias analysis (see Appendix B).

Results

The sample size of study cases of sets of moderators (i.e. a given type and tissue damaged for each response variable) increased for all cases except one (the effect of simulated damage to roots on floral traits), ranging from an increase of 20% (the effect of natural damage to roots on plant reproductive success) to 920% (the effect of simulated damage to leaves on plant reproductive response; Table 3.1). The net effect size of all responses was negative (mean ± SE: -0.421 ± 0.058) and significant ($z = -7.32$, $p < 0.0001$). There was a significant

Table 3.1: The estimated effect size (and standard deviation) and number of study cases (k) of damage to each tissue in the original data set (from Moreira et al. 2019) and the complete data set (including the original set and papers since 2018). The effects of natural and simulated damage to floral traits, attraction to pollinators, and plant reproductive success are included. The percentage in parentheses gives the percent increase in study cases from the previous study to the update. *p < 0.05

	Original Dataset		**Updated Dataset**		
Tissue induced	**Estimate (SD)**	**k**	**Estimate (SD)**	**k**	**Test**
Floral traits					
Natural					
roots	-2.05 (1.04)	9	-0.106 (0.257)	12	increased sample size (33.3%) and certainty
leaves	-0.682 (0.34)*	129	-0.478 (0.092)*	176	increased sample size (36.4%) and certainty
flowers	-2.43 (1.16)*	33	-0.402 (0.142)*	59	increased sample size (78.8%) and certainty
stem		0	-0.397 (0.243)	56	novel response
mixed		0	-0.154 (0.224)	149	novel response
Floral traits					
Simulated					
roots	-7.42 (0.242)	2	-0.908 (0.606)	2	no change
leaves	-1.12 (0.403)	49	-0.342 (0.139)*	79	sensitivity to sample size (61.2%)
flowers	1.74 (1.33)	38	-0.535 (0.17)*	46	sensitivity to sample size (21.1%)
stem		0	-1 (0.262)*	20	novel response
mixed		0	0.148 (0.484)	11	novel response
Pollinators					
Natural					

	Original Dataset		Updated Dataset		
Tissue induced	Estimate (SD)	k	Estimate (SD)	k	Test
roots	-0.282 (1.87)	6	0.0242 (0.241)	12	increased sample size (100%) and certainty
leaves	-0.837 (0.261)*	126	-0.453 (0.0971)*	189	increased sample size (50%) and certainty
flowers	-11.4 (5.02)*	23	-0.269 (0.128)*	81	increased sample size (252%) and certainty
stem		0	-0.337 (0.245)	12	novel response
mixed		0	-0.164 (0.266)	24	novel response
Pollinators					
Simulated					
leaves	4.98 (1.74)	3	-2.14 (0.391)*	9	sensitivity to sample size (200%)
flowers	1.18 (1.05)	30	-0.204 (0.21)	44	increased sample size (46.7%) and certainty
mixed		0	-0.603 (0.48)	12	novel response
Plant reproductive success					
Natural					
roots	-2.63 (0.797)	10	-0.237 (0.271)	12	increased sample size (20%) and certainty
leaves	-0.763 (0.381)*	69	-0.38 (0.109)*	112	increased sample size (62.3%) and certainty
flowers	-0.543 (2.56)	17	-0.748 (0.153)*	57	sensitivity to sample size (235%)
stem		0	-0.363 (0.27)	14	novel response
mixed		0	-0.325 (0.241)	44	novel response

	Original Dataset		Updated Dataset		
Tissue induced	Estimate (SD)	k	Estimate (SD)	k	Test
Plant reproductive success					
Simulated					
leaves	-0.385 (0.488)	5	-0.348 (0.156)*	51	sensitivity to sample size (920%)
flowers	1.26 (2.79)	17	-0.364 (0.176)*	46	sensitivity to sample size (171%)
stem		0	-0.838 (0.257)*	29	novel response
mixed		0	-0.353 (0.624)	3	novel response

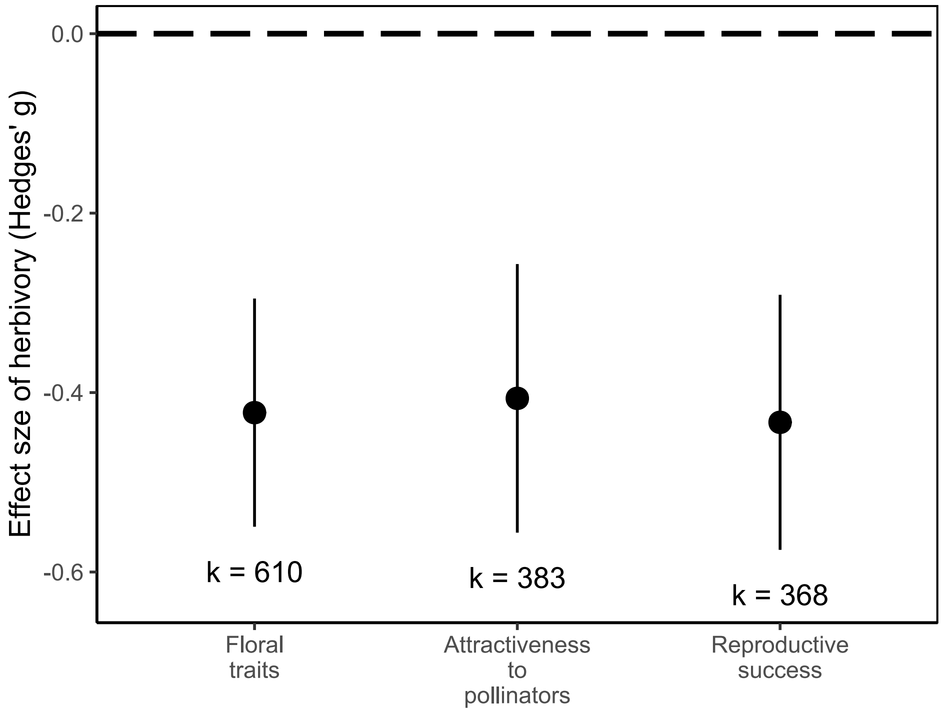

Figure 3.1: The mean effect size (Hedges' g) of damage on floral traits, attractiveness to pollinators, and reproductive success. The dashed line represents no net effect of damage on pollination processes synthesized. Error bars show the 95% confidence intervals, and k = number of study cases. All means differed significantly from 0 in post-hoc t-tests ($p < 0.05$).

heterogeneity across studies ($\tau^2 = 0.828$, $Q_T = 10153.6$, $p < 0.0001$), mostly occurring between and not within studies ($I^2 = 86.3\%$).

Plant damage significantly decreased floral traits, pollinator attraction, and plant reproduction ($Q_M = 53.7$, $p < 0.0001$; Fig. 3.1). Both natural and simulated damage also decreased plant response variables ($Q_M = 54.2$, $p < 0.0001$), as did the plant tissue damaged ($Q_M = 59.1$, $p < 0.0001$, Fig. 3.2). However, the effect of damage on each response variable was highly dependent on the plant tissue and type of damage ($\chi^2 = 16.8$, $p = 0.0048$). Floral traits and plant reproduction were reduced by both natural and simulated damage to flowers and leaves, but only by simulated damage to stems (i.e. the effect size was significantly less than 0; Fig. 3.2). Pollinator attraction was decreased by natural damage to leaves and flowers, as well as simulated damage to leaves (Fig. 3.2). Damage to roots and mixed damage (natural or simulated) did not significantly affect floral traits, pollinator attraction, nor plant reproduction (i.e. the effect size did not significantly differ from 0; Fig. 3.2).

Discussion

Herbivory and pollination are key ecological processes relevant to better understanding plant reproduction (Underwood et al. 2020). The finding by Moreira et al. (2019) that herbivore damage decreased net pollinator visitation, reduced floral attraction, and decreased plant fitness was confirmed here by including more than double the number of study cases. These herbivore effects were dependent on the tissue damaged and the type of damage, similar to previous findings. We found many (but not all) of the same patterns as Moreira et al. (2019) in response to natural damage to flowers, leaves, and roots, that damage to leaves and flowers decrease floral traits, and pollination, natural damage to leaves decreases plant fitness, and that damage to roots has no overall impact. However, we also observed some differences between the

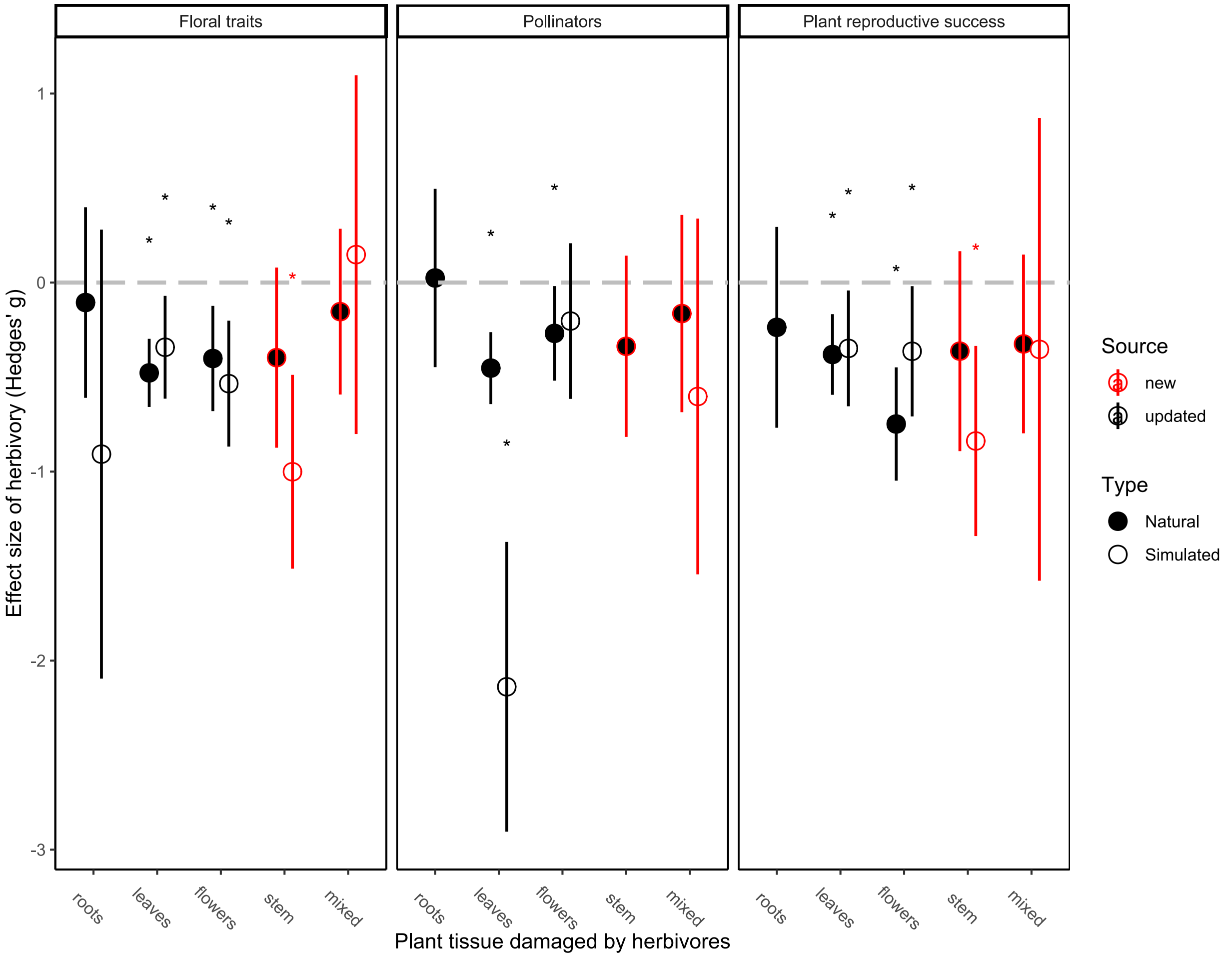

Figure 3.2: The mean effect size (Hedges' g) of natural and simulated damage to different plant tissues on each of floral traits, attractiveness to pollinators, and plant reproductive success from one model including all three moderators. The dashed line represents no effect of damage. Error bars represent 95% confidence intervals. Novel response variables are outlined in red for the sake of illustration (not as part of the model). An asterisk is placed over values significantly different from 0 in a post-hoc t-test ($p < 0.05$).

previous and the current meta-analysis. Specifically, we found that natural damage to flowers decreased plant reproductive success when previously no effect was found (see Table 3.1). We also found that simulated damage to flowers and leaves decreased floral attraction and plant reproductive success and simulated damage to leaves also decreased pollinator attraction whereas in Moreira et al. (2019), simulated damage did not impact the response variables in any way (Table 3.1). Regarding the damage to stems and mixed damage (effects not assessed in the previous meta-analysis), we found no overall effect of mixed damage on any response variable, whereas simulated damage (but not natural damage) to stems decreased floral attributes and plant reproductive success but not pollination.

The type of tissue damaged is a key component of herbivore-pollinator research because it speaks to the direct and indirect effects of herbivores on the pollination syndrome. We found that the conclusions in Moreira et al. (2019) regarding the effects of damage to roots were not sensitive to increased sample size. Damage to roots continues to have no effect on any response variables. Root damage is well-documented to have mixed effects on plants (Poveda et al. 2005; Knochel et al. 2010; Barber et al. 2015; Ghyselen et al. 2016; Rusman et al. 2018). Therefore, continuing to see no net effect of roots is unsurprising and suggests that this indirect herbivore-pollinator pathway is not necessarily an important process to understanding pollination or reproduction when generalizing. Given that damage to roots can impact these response variables (Poveda et al. 2005; Knochel et al. 2010; Ghyselen et al. 2016), it is likely a species-specific trait. However, we only increased the number of study cases that examined root herbivory from 25 to 38 and, thus, further research is still required to determine how robust our conclusions are. Within this meta-analysis, natural damage to both leaves and flowers exhibited consistent findings across multiple studies, confirming its negative impact on floral attractiveness, pollinator attraction, and plant reproduction, in line with the findings reported in our study and Moreira et al. (2019). The increased sample size in our study enhanced the certainty of these results. Moreover, our comprehensive study revealed a significant decrease in plant reproduction due to natural damage to flowers, whereas in the previous study (Moreira et al. 2019; See Table 3.1), the effect had been slightly positive but non-significant. This outcome underscores the sensitivity of this particular effect to variations in sample size. This sensitivity makes sense because this category (natural damage to leaves and plant reproduction) had a particularly small sample size in Moreira et al. (2019) when compared to other response variables examining the effects of natural damage to flowers and leaves (i.e., 17 study cases).

A novel finding herein is that simulated damage can elicit the same fitness, floral, and pollinator response of natural damage to leaves and flowers. The previous meta-analysis by Moreira et al. (2019) found a range of negative to positive effects (but all non-significant) of damage to leaves and flowers (the only two tissues tested for simulated damage) (Table 3.1). Our updated analysis found that simulated damage to leaves and flowers decreased floral traits and plant reproductive success while simulated damage to only leaves decreased pollination (Table 3.1). In several cases of simulated damage, we included more than double the number of study cases (see Table 3.1 for exact numbers); for instance, the number of studies that examined simulated damage to leaves on fitness went from only 5 study cases to 51. These particular examples were a mix of positive and negative (but non-significant) effects in the original meta-analysis but, by increasing the power of our analysis, we showed that these effects are sensitive to increased sample size. While there was also evidence that newer studies had increases in sample size within studies ($N_{new} = 449 \pm 3435$, $N_{previous} = 65 \pm 59$) which could also increase certainty (Ledolter and Kardon 2020), this difference was not significant ($t = -1.61$, $p = 0.11$).

Damage in natural systems is diverse and can impact all plant organs. Many important agricultural pests are stem-boring (Vitorio et al. 2019; e.g., Szczepaniec and Alnajjar 2023; Perish et al. 2023), and the response to removal of the apical meristem is one of the more well-documented examples of overcompensation in response to herbivory (Garcia and Eubanks 2019). Based on this synthesis, simulated (but not natural) damage to stems decreased floral traits and plant fitness (no studies on pollinator attraction were found), suggesting that indirect effects to reproduction mediated through stems is an important herbivore-pollinator mechanism. Stem damage can hamper flowering and plant fitness by reducing resources for growth and reproduction (Dube et al. 2019; Conrad et al. 2021), but the frequently documented overcompensation in response to stem damage can conversely result in increased flowering (Lennartsson et al. 2018; Garcia and Eubanks 2019; Ramula et al. 2019) that can in turn increase pollinator attraction which would suggest a positive effect size (Lay et al. 2011; Hernández-Villa et al. 2020). Given that natural damage did not significantly impact any response variable, the reality of the effect of stem damage is likely mixed and may not be important when generalizing (similar to damage to roots). Mixed damage encompasses all forms of damage that could occur simultaneously (e.g. grazing), such as damage to leaves and flowers (that showed significantly negative impacts on pollinator attraction). While it can be difficult to discern the specific mechanism in which mixed damage impacts plant fitness and pollinator attraction, many herbivores feed indiscriminately on multiple plant tissues; hence, understanding the impact of damage to multiple tissues is also relevant to natural and agricultural systems (Freeman et al. 2003; Benning and Moeller 2019; Mikulka et al. 2020; Cutter et al. 2022). Mixed damage did not affect any response variable, suggesting that the generalist effects may not be important mediators of pollinator interactions nor reproductive outcomes and that focusing on damage to more specific tissues is still warranted. Indiscriminate herbivores that cause mixed damage, such as grazers, are well known to modify both the plant and pollinator community (Almaududi Pulungan et al. 2019; Allan 2022; Kral-

O’Brien et al. 2023), and grazing is a key process in many ecosystems that can influence individual species and communities as a whole. However, the overall effects of broad-scale damage like grazing is insufficient to detect a difference here. For both damage to stems and mixed damage, further studies are required to determine the sensitivity to sample size and how robust our results are.

Conclusions

We assessed the sensitivity to sample size and credibility of the findings in the previous meta-analysis by Moreira et al. (2019). We found that the effects of natural damage to roots and leaves were certain and robust with additional studies, but that natural damage to flowers and simulated damage to flowers and leaves were sensitive to increases in sample size. The sign of the effect did not change, but rather the strength of the effect. However, stem damage and mixed tissue damage studies suggest that methods and studies included in syntheses and done in primary research are needed to best understand herbivore-mediated pollinator interactions. Despite greatly increasing the sample size, further studies examining the effects of simulated damage to plants and damage to tissues other than leaves and flowers are required to better confirm the certainty of these results before additional re-analysis. The ecological implication of our synthesis is that meta-analytical summary statistics may not always tell the whole story. Alternative interpretations of differences in effect sizes (or lack thereof) are possible because studies will vary in their ability to test specific predictions of a hypothesis, and furthermore, a certain level of judgement is required to infer the relative importance of certain ideas to synthetic progress within a discipline. In short, this synthesis both confirmed previous work on how herbivory interacts with pollination processes, advances novel theory (i.e. the type of tissue damaged matters), and increased the credibility and robustness of the key findings.

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Chapter 4: Direct and indirect interactions between shrubs and the flowering annual community in an arid ecosystem

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Abstract

Shrubs commonly shape the plant community in arid ecosystems such as deserts. Plant interactions between shrubs and the associated species can be both negative and positive, and direct and indirect. The importance of shrub effects on reproduction is also a key component of facilitation studies in deserts. Here, we tested the hypothesis that shrubs facilitate understory plant community composition and reproduction through both direct and indirect interactions mediated by the associated plant neighbourhood. Using the shrub species *Larrea tridentata*, we tested the effects of facilitation on understory plant density, floral density, and species richness in the Mojave Desert, California. We found that shrubs decreased the net community-wide plant assembly measures relative to open microsites including total density and species richness at the site tested. There was also evidence that shrubs directly decreased plant fitness by reducing floral density, but this effect depended on the species. The net density and diversity of the annual plant community also influenced plant and floral density under shrubs suggesting significant indirect effects between shrubs and all abundant annual plant species. While both direct and indirect interactions between shrubs and the annual plant community were species-specific, the effects of these interactions had a greater impact on plant density than floral density measures. Annual plant density and to a lesser extent floral density are thus driven by both direct and indirect interactions with shrubs.

Introduction

Shrubs are important in shaping the structure of the plant community in desert ecosystems. In deserts, shrubs modify the environment directly around them (Miriti 2006; Lara-Romero et al. 2017; Lortie et al. 2018). They provide shelter from the sun and wind (Michalet and Pugnaire 2016; Ploughe et al. 2019), enhance the soil nutrient content (Pugnaire et al. 2004; Filazzola and Lortie 2014; Ploughe et al. 2019) and, depending on the species, either attract or deter animals such as herbivores (Chaneton et al. 2010; Guignabert et al. 2020; Bustamante et al. 2021), seed predators (Smit et al. 2008; Ziffer-Berger et al. 2017), and pollinators (Braun and Lortie 2020; Ruttan et al. 2021). By changing the microsite within and directly surrounding their canopy, shrubs can influence the relative density, diversity, and fitness of plants relative to the open (Smit et al. 2008; Landero and Valiente-Banuet 2010; He et al. 2013; García-Cervigón et al. 2016; Filazzola et al. 2020). These interactions are frequently positive with shrubs enhancing the density and diversity of species compared to open microsites (Smit et al. 2008; Landero and Valiente-Banuet 2010; He et al. 2013; García-Cervigón et al. 2016; Filazzola et al. 2020). Shrubs can however also compete with the surrounding flora thereby deterring some species from associating with their canopy (Holzapfel and Mahall 1999; Chaneton et al. 2010; Schöb et al. 2014; Bulleri et al. 2016; Lucero et al. 2019; Soliveres and Eldridge 2020). Together, these positive and negative effects influence the net plant community assembly processes near shrubs (Shmida and Whittaker 1981; Callaway and Walker 1997; Schafer et al. 2012; Foronda et al. 2019; Filazzola et al. 2020). So, to best consider and evaluate the influence of foundation species such as shrubs in arid and semi-arid systems, we need to test for net effects including both positive and negative drivers of community assembly.

One important metric of community stability beyond community composition and relative species abundance is mean fitness of populations within the community. Plant community composition gives insight to the current population, but by exploring the fitness consequences of shrubs, we can infer the stability and trajectory of the plant population and seed bank through time (Nakabayashi and Leubner-Metzger 2021). Reproductive and vegetative responses to stimuli such as stress, competition, and facilitation often differ (e.g. Tielbörger and Kadmon 2000; He et al. 2013; Molina-Montenegro et al. 2020; Wedel et al. 2021). Thus, it is best not to necessarily assume that the effects of shrubs on plant reproduction will be the same as on plant community composition (Tielbörger and Kadmon 2000; He et al. 2013; Molina-Montenegro et al. 2020; Wedel et al. 2021) and therefore the long-term stability of the community. Evidence of the effects of shrubs on the relative abundance and density of protege species is common (Pugnaire et al. 2004; He et al. 2013; Michalet et al. 2015; Lucero et al. 2019), but evidence for changes in estimated fitness responses is much less common (Holzapfel and Mahall 1999; Tielbörger and Kadmon 2000; He et al. 2013; but see - García-Cervigón et al. 2016). Therefore, while it is known that many plant species associate or disassociate with shrubs in desert systems, the relative benefits to populations including reproduction are typically assumed based on association and not directly tested. One estimate of plant reproduction is flowering. Flowering is relatively easy to document, can correlate with plant fitness (Campbell 1991), and has strong connections to other taxa such as pollinators, providing an estimate of the fitness consequences of interaction with shrubs. By examining the effects of shrubs on population and community flowering, we can gain an estimate of community stability in desert ecosystems.

Interactions in ecology such as those between shrubs and other species can be complex and include both different taxa and direct and indirect interactions. This network of interactions is particularly relevant to community assembly processes such as community density and diversity (Ohgushi 2005; Schöb et al. 2013; Lamy et al. 2020; Wang et al. 2021). While direct interactions are often the focus of interaction networks and community dynamics, indirect interactions (interactions between two species that are mediated by a third species

(Levine 1976; Holt 1977; Abrams 1987; Strauss 1991)) can also be as important as direct interactions when net interactions are considered (Fath 2007; He et al. 2013; Filazzola and Lortie 2014). For instance, by changing the environment around them, shrubs can affect the interspecific interactions between protege species (Michalet et al. 2015). By increasing species density, shrubs can indirectly increase interspecific competition (Adler et al. 2018), but by increasing species diversity they can decrease intraspecific competition (Mahaut et al. 2020). These positive indirect interactions (e.g. associational resistance (Field et al. 2020)) as well as any negative indirect interactions (e.g. apparent competition (Chaneton et al. 2010)) can either compound (act with the same direction of effect) or offset (act with the opposite direction of effect) the direct effect of shrubs, making the net effect of shrubs more positive or switching it to a neutral or negative interaction. However, indirect effects can also act as the primary mechanism driving the net effect of interactions with other plants (Poulos et al. 2014; Michalet et al. 2015; Sotomayor and Lortie 2015; García-Cervigón et al. 2016; Ruttan et al. 2021; Wang et al. 2021). Therefore, the commonly tested direct effects of shrubs do not necessarily encompass the net effect of shrubs on their surrounding microsites. These fine-scale patterns are important in plant communities, particularly in systems such as deserts and semi-arid grasslands.

Species specificity is a key concept in the plant-plant interaction literature. Species identity is important in predicting the outcome of all forms of pairwise (Callaway 1998; Filazzola et al. 2020; Mahaut et al. 2020) and community (Lortie and Turkington 2008; Zhang and Zhao 2015; Hupp et al. 2017) plant-plant interactions (including competition, facilitation, and direct and indirect interactions). The response of potential protege species will vary as a function of the mechanisms provided by shrubs such as amelioration of stress and resource sequestration (Filazzola and Lortie 2014; Filazzola et al. 2020). For instance, heat-tolerant species may suffer from close proximity to shrubs whereas shade-tolerant species may not survive in a desert system without association with shrubs (Hubbell et al. 2001; Reyes-Olivas et al. 2002; Ploughe et al. 2019; Ghazian et al. 2020). Shrubs do not always modify the microclimate in ways that benefit all species equally (based on their thermal tolerances) and the effect of these modifications of temperature can vary by season (Lortie et al. 2022). Thus, there are likely species within a community that have an obligate positive relationship with shrubs while other species more strongly associate with open sites without a canopy (likely due to light availability) (Forseth et al. 2001; Weedon and Facelli 2008; Helluy et al. 2021; Ahmadian et al. 2022). These shrub association patterns within a community are critical to document because shrubs have the potential to shape and stabilize ecosystems even at fine scales (Zhang et al. 2016). We can better understand the role of shrubs as foundation species in deserts by observing how they influence species to varying degrees.

In this study, we tested the hypothesis that shrubs facilitate understory plant community composition and reproduction through both direct and indirect interactions mediated by the associated plant neighbourhood. The following predictions were tested: (1) shrubs directly interact with annuals by increasing plant community density, species richness, and floral density relative to open microsites, (2) shrubs positively influence annual species indirectly through neighbourhood-level plant density and species richness, (3) floral density and plant density differ in their response to plant association with shrubs, and (4) species differ in their propensity to associate with shrub canopies.

Materials and Methods

Study Area

Fieldwork was conducted in the Mojave Desert (34.72, -115.68) at peak flowering in April 2019. The Mojave region study site is an arid shrubland composed mostly of *Larrea tridentata* and surrounding annuals (Fig. D.1). *Larrea tridentata* is a common desert shrub species that forms a sparse canopy 1-2m high (Calflora 2014). *Larrea tridentata* is a well-known benefactor of desert annual species that creates “islands of fertility” in desert systems (Whitford et al. 1997; Schafer et al. 2012; Flores-Torres and Montana 2015). The site has a long-term mean of 175-mm of precipitation per year and a long-term mean daily temperature of 17.5°C (WRCC 2020).

Experimental Design

A total of 20 *L. tridentata* shrubs that were each at least 5-m apart were selected along each of five parallel 100-m transects for a cumulative total of 100 shrubs. Transects ran east to west and were separated by an average of 80-m (distance varied based on the landscape and to ensure high shrub density). Shrubs were chosen no more than 20-m from each transect. One square 0.25-m^2 quadrat was placed on the north side of each shrub to sample vegetation, and one again in the nearest open-gap microsite without a vegetation canopy that was at least 1.5-m and no more than 3-m away from the dripline of the shrub canopy. These open microsites were directly to the north of the shrub plots if possible because the north side of shrubs tend to be more favourable for facilitation given the increased amount of shade in the Northern Hemisphere (Schafer et al. 2012). All annuals were identified to species within the plots. While some few perennials also exist in the study site (but not the plots), most perennials are other shrubs that form their own canopies (e.g. *Ambrosia* spp.) and were therefore avoided or are uncommon and rarely associated with *L. tridentata* (e.g. *Linum* spp.) and not found within the plots. The population density for each species was estimated by recording the number of individual plants for each species in a plot. The total number of flower heads per species was recorded by recording total flower heads for every individual of every species in every plot. Each plot was repeatedly sampled three times (2 weeks apart) at peak flowering beginning in April 2019 in order to ensure that we sampled flowering for all species at the site and within each plot. Plant density per species was calculated from the maximum plant density defined as the maximum number of plants of a given species observed within any one census while plant species richness and floral abundance were summed across censuses. Net community plant density for each community (defined as shrub or open) and total species richness were then used as response variables to determine the direct effect of shrubs on the local assembly processes. The plant neighbourhood interactions surrounding each species were also estimated using these community variables as covariates and defined as the indirect effect of the community present at each microsite.

Statistical Analyses

We examined the direct effects of shrubs on plant community (predictions 1 & 3) by comparing three net community responses in shrub and open microsites. These responses were net community plant density (the total number of plants of all species in each plot), net community floral density (the total number of flowers of all species in each plot, summed across censuses), and species richness (the total number of species found in each plot across all censuses). We modeled each of these three community responses against microsite (shrub or open) independently using generalized linear mixed models (GLMMs) (Wolfinger and O’Connell 1993). The model for species richness was fit to a Poisson distribution (Consul and

Jain 1973). Due to overdispersion, the net floral density and net plant density were fit to a negative binomial distribution (Bliss and Fisher 1953).

We examined the indirect effects (predictions 2 & 3) of shrubs on annuals through plant community and the species-specificity of direct (predictions 3 & 4) and indirect effects by modeling species plant and floral density of annuals as a function of species, microsite, species richness, neighbourhood plant density, and their interaction terms using GLMMs. Both models were fit to a negative binomial distribution (Bliss and Fisher 1953). Significant interaction effects between microsite and community plant density or species richness would represent indirect effects and interactions of these effects with species would show species specificity of these indirect effects. A significant interaction between microsite and species would support the species-specificity test for direct effects of shrubs on annuals. This global model (defined as the model including both the direct variables of microsite and species and the indirect variables of community plant density and species richness as well as their interaction terms) provides the means to directly contrast the direct and indirect interactions of shrubs on each species.

In all GLMM models, shrub id was included as a random effect (Hedeker 2005). An offset term accounting for net plant density was also included in all cases where floral density was a response variable. The community response models included all species (including rare species) summed together, but each species-specific model included only species that were found in at least 30 unique plots (six species were found in at least 30 plots: *Cryptantha circumscissa*, *Chaenactis fremonti*, *Eriophyllum wallacei*, *Malcothrix glabrata*, *C. angustifolia*, and *Chylismia claviformis* subsp. *auranticus*). If these rare species were included, the species-specific models failed to converge.

To examine and compare the effect size of the direct effect of shrubs on protege species, the relative interaction index (RII) measure for both plant and floral density responses were calculated for each plot and each species present (with more than 5 total observations). By using RII and comparing each species individually we are able to analyze more species than with the GLMMs and calculate standardized effect sizes of the relative associational patterns between protege species and shrubs that are directly comparable. The effect size metric RII was calculated using the differences in density between associated (shrub) and unassociated (open) microsites to create a standardized association in which values between -1 and 1 are produced ($RII = (S - O)/(S + O)$ where S is density associated with shrubs and O is density found in the open) (Armas et al. 2004). Positive values indicate positive association and negative values negative association and neutral values no association. The associational effect of shrubs on each species was tested using two-sided t-tests compared to 0 (Walsh 1947). This metric estimates the relative strength and sign of association patterns for all species to shrubs versus open microsites. We only tested species that occurred in at least 5 shrub-open pairings and each species was tested separately (see Fig. 4.1 for a complete list) (DePatta Pillar 1998).

All statistical analyses were performed using R Statistical Software version 4.3.1 (R Core Team 2023) with the packages glmmTMB for GLMMs (Brooks et al. 2022), performance for tests of overdispersion and underfitting of zeros (Lüdecke et al. 2021), emmeans for post hoc contrasts (Lenth 2021), and vegan for the t-tests (Oksanen et al. 2020). Data and code are published in the Knowledge Network for Biodiversity (Haas-Desmarais and Lortie 2022).

Results

A total of 15 plant species across 6 families (Asteraceae, Boraginaceae, Fabaceae, Onagraceae, Plantaginaceae, and Polemoniaceae) and 14 genera were observed throughout the

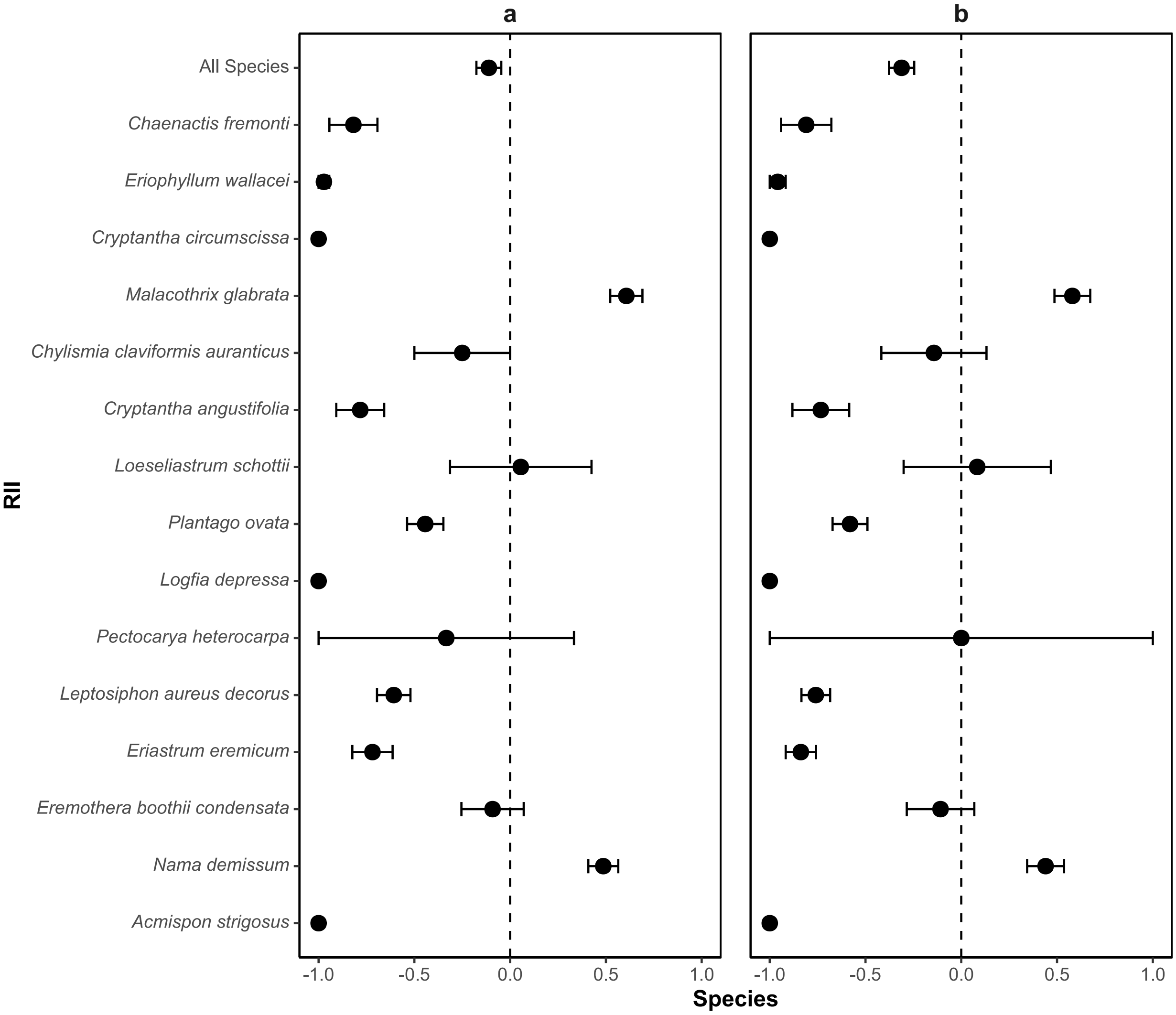

Figure 4.1: The mean direct effects of shrubs on annuals in the Mojave Desert. The relative interaction index (RII) and standard error of both a) plant and b) floral density of each species as well as all species together is presented. Species are listed from most to least abundant. Indices to the left of the dashed line represent disassociation and competition while indices to the right of the line represent association and facilitation.

study. All species were native herbaceous annuals (Calflora 2014). Of these species, 6 were found in at least 30 plots and were included in the subsequent species analyses. The most abundant and frequent species (in descending order of abundance) were *Cryptantha circumscissa, Chaenactis fremonti*, *Eriophyllum wallacei*, *Malcothrix glabrata*, *Chylismia claviformis* subsp. *auranticus,* and *C. angustifolia* (see Fig. 4.1 for a complete list).

Direct Effects of Shrubs on Community Responses

At this desert site, total plant density, (Fig. 4.1, Table A.1) and species richness (χ^2 = 13.7, df = 1, $p < 0.0001$) were greater in open microsites (10 ± 1 plants, 3 ± 0.2 species) than near shrubs (6 ± 0.6 plants, 2 ± 0.1 species). However, there was no statistically significant difference between floral density under shrubs (24 ± 3 flowers) than in open (69 ± 8 flowers) microsites after accounting for plant density (Fig. 4.1, Table A.2).

Species-Specificity

The effect of microsite on population plant and floral density was dependent on species (Table A.1). Plant density differed significantly between microsites for five of the six species tested in the GLMMs (Table A.2) and floral density differed significantly between microsites for three of the six species tested (Table A.2). *Cryptantha circumscissa*, *C. angustifolia*, and *E. wallacei* were more abundant and had higher floral densities in the open than under shrubs (Fig. 4.1, Table 4.1). However, *M. glabrata* and *C. fremonti* were significantly more abundant under shrubs than in the open (although floral density did not differ; Fig. 4.1, Table 4.1). *Chylismia claviformis* subsp. *auranticus* was similarly abundant and had similar floral densities in the open as under shrubs (Fig. 4.1, Table 4.1). The same results were observed for plant density of these six species when RII was calculated (Fig. 4.1). The same results were also observed for most species for the RII of flowering as the GLMMs, except *C. fremonti* and

M. glabrata had positive RII values instead of neutral RII values (the GLMMs would predict neutral RII values). However, given that the RII analysis did not account for plant density nor indirect interactions, these RII values are likely a product of the correlation between plant density and floral density. All rare species ($5 < n < 30$) included in the RII analysis were either disassociated with shrubs (mean RII < 0) or had no association with shrubs (mean RII ≈ 0; Fig. 4.1).

Table 4.1: A comparison of plant and floral density under shrubs and in the open. Direct effects represent differences in overall plant or floral abundance between microsites for each species, while indirect effects represent whether the effect of community plant density or species richness are more or less positive under shrubs than in the open. Negative effects of shrubs are represented by '-' and positive interactions '+'. If abundances or the effects of the community are similar between microsites, they are represented with '0'.

	Direct		**Indirect**			
			Density		**Richness**	
Species	**Plant**	**Flower**	**Plant**	**Flower**	**Plant**	**Flower**
Chaenactis fremonti	+	0	-	-	0	0
Chylismia claviformis auranticus	0	0	-	0	+	0
Cryptantha angustifolia	-	-	-	-	+	+
Cryptantha circumscissa	-	-	-	0	+	0
Eriophyllum wallacei	-	-	0	0	+	0
Malacothrix glabrata	+	0	-	0	0	+

Indirect Effects of Shrubs Through Plant Community

Shrubs indirectly influenced all species through relative differences in plant community density and species richness, as indicated by the significant interactions found between plant community density, species richness, and microsite (Table A.1). Increasing neighbourhood plant densities significantly reduced individual species' plant density under shrubs (for all species except *E. wallacei* which had no relation) while in the open plant density had no effect on four of six species (including *E. wallacei*) and increased species' plant density in one case (*C. claviformis* subsp. *auranctiucus*) (Table A.2). The abundance of *C. fremonti* decreased with increasing community plant density both under shrubs and in the open (Table 4.2), but this effect was stronger (i.e. more negative) under shrubs (Table 4.1). Increasing neighbourhood plant density significantly reduced floral density under shrubs of two species (*C. angustifola* and *M. glabrata*) but did not influence floral density of any species in the open (Table 4.2).

Table 4.2: Direction of the effect of community plant density and species richness on plant and floral density. Negative effects of plant community are represented by '-' and positive interactions '+'. If interactions are neither overly negative nor overly positive they are represented with '0'.

	Density				**Richness**			
	Plant		**Flower**		**Plant**		**Flower**	
Species	**Open**	**Shrub**	**Open**	**Shrub**	**Open**	**Shrub**	**Open**	**Shrub**
Chaenactis fremonti	-	-	0	0	+	+	+	+
Chylismia claviformis auranticus	+	-	0	0	+	+	+	+
Cryptantha angustifolia	0	-	0	-	+	+	+	+
Cryptantha circumscissa	0	-	0	0	+	+	0	+
Eriophyllum wallacei	0	0	0	0	+	+	0	0
Malacothrix glabrata	0	-	0	-	+	+	0	+

Increasing species richness significantly increased all individual species' plant density both under shrubs and in the open (Table 4.2). However, the effect of species richness was stronger (i.e more positive) under shrubs than in the open in all cases except *C. fremonti* and

M. glabrata (the effect of species richness was the same in both microsites for these two species) (Table A.2). Increasing species richness also increased floral density for three species in the open (*C. fremonti*, *C. claviformis* subsp. *auranticus*, and *C. angustifolia*) and five species under shrubs (all species except *E. wallacei*) (Table 4.2). The effect of species richness on flowering density was significantly greater (more positive) under shrubs than in the open for two species (*C. angustifolia* and *M. glabrata*) (Table 4.1).

Discussion

Positive and negative interactions in plant communities are typically species-specific and vary by interaction type, particularly in most high-stress ecosystems (Callaway 1998; Zhang and Zhao 2015; Hupp et al. 2017; Filazzola et al. 2020; Mahaut et al. 2020). Here, we explored these ecological processes by examining the hypothesis that shrubs facilitate understory plant community composition and reproduction through both direct and indirect interactions mediated by the associated plant neighbourhood. This hypothesis was not supported because the effect of shrubs was overall negative, although these responses were highly species-specific. In contrast to our prediction, shrubs directly decreased total community plant density and species richness and total floral density was similar between both shrub and open microsites (prediction 1). Only two species experienced the positive associations with shrubs we predicted while the flowering of species was only ever decreased by shrubs or was not affected (prediction 1). The prediction that indirect interaction effects through the annual plant neighbourhood positively influence community assembly for differences between microsites was supported through plant species richness but not density (prediction 2). The prediction that direct and indirect effects of shrubs on annual plant density differed from floral density was also supported because the effects on annual plant density were stronger than the effects of shrubs on floral density (prediction 3). Species-specificity was also the norm for all interaction types (prediction 4); the sign or the magnitude of the effect of shrubs was never consistent between all species. Therefore, shrubs shape the shrub-understory plant community through both direct and indirect interactions that vary depending on interaction type and understory species.

Direct Effects of Shrubs

In this chapter, we found that shrubs decreased the density and species richness of the plant community surrounding shrubs through direct interactions. Shrubs can have positive and negative direct effects depending on the mechanism and species. Positive direct effects can include increased soil nutrients and providing thermal refuge (Walker et al. 2001; Filazzola and Lortie 2014; Ploughe et al. 2019). These positive effects exist in this environment despite the overall negative effect of shrubs on the plant community, explaining the association of some species with shrubs. We predicted that annuals will positively associate with shrubs because of the relative importance and frequency of shrubs as foundation species reported in desert ecosystems (Filazzola and Lortie 2014; Perea and Gil 2014; Molina-Montenegro et al. 2020; Han et al. 2021), including with *L. tridentata* specifically (Walker et al. 2001; Drezner 2006; Schafer et al. 2012; Poulos et al. 2014; Badano et al. 2016). However, it is not uncommon for negative interactions to concurrently function within the larger framework of net facilitation and benefit of foundation species (Zhang and Zhao 2015; e.g. Badano et al. 2016; Lortie et al. 2021). Consequently, we found several common and uncommon species within the site that were disassociated with shrubs. This supports existing literature that showed negative direct effects of shrubs can include competition for nutrients (between shrubs and proteges) and allelopathy (Mahall and Callaway 1992; Schafer et al. 2012) that could lead to the results observed here (e.g. Soliveres and Eldridge 2020). Whilst we did not measure mechanisms directly, the trend that some species associate while others disassociate from shrubs suggests that divergent mechanisms within the Mojave Desert shrub communities influence potential protege species differently. Some species are competitively excluded from under a canopy in deserts because of these negative effects (Pescador et al. 2014; Foronda et al. 2019; Lucero et al. 2019), particularly if the competing species are dominant competitors. For instance, *L. tridentata* can have allelopathic effects on the roots of other plant species (Mahall and Callaway 1992). The relative strength of these positive and negative effects of shrubs can also vary with abiotic factors such as resource scarcity and thermal stress (Maestre et al. 2009; Malanson and Resler 2015; Filazzola et al. 2020). Shrubs can directly benefit other species by reducing heat stress and sequestering resources such as water and nitrogen when these resources are scarce (Michalet and Pugnaire 2016; Ploughe et al. 2019) and so facilitation is often more likely when conditions are harsh, such as during droughts (He et al. 2013; Ploughe et al. 2019). Given that 2019 was neither a drought year (National Drought Mitigation Center 2019) nor an uncommonly hot year in the Mojave Desert (WRCC 2020), it is not unsurprising that the negative interactions between shrubs and the plant community would prevail. Examining the same system over multiple years (both drought and non-drought years) would strengthen our conclusions and further elucidate the mechanisms behind facilitation by *L. tridentata*.

Species-Specificity of Direct Interactions

The sign of shrub effects on other plants was species-specific. Species-specificity of shrub association is commonly observed in shrub-annual systems (Callaway 1998; Michalet et al. 2015; Badano et al. 2016; Fagundes et al. 2018). Species specificity of association with shrubs is likely best explained in this system by annual physiology. There were three main size elements that varied among the observed species that likely correlate with shrub association: plant size, leaf size, and seed size. Our two shrub-associated species, *C. fremonti* and *M. glabrata*, are larger plants that have both longer leaves and larger seeds than the three open-associated plants (Jepson Flora Project 2021). Larger species are likely more able to capitalize on the reduced temperatures, wind shelter and increased nutrients provided by shrubs (Franco and Nobel 1989; Berntson and Wayne 2000; Schwinning and Weiner 2012; Wang et al. 2012; Fernández-Marín et al. 2020). Small leaves are a well-known adaptation among desert plants for dissipating heat and reducing water loss (Fernández-Marín et al. 2020; Peguero-Pina et al. 2020; Nardini 2022) and smaller seeds are more likely to require light for germination (Koutsovoulou et al. 2014; Zhang et al. 2014; El-Keblawy et al. 2018), making these plants better adapted to open microsites. The unassociated plant *C. claviformis* subsp. *auranticum* is both intermediate in size and seed size between the larger shrub-associated and smaller open-associated plants (Jepson Flora Project 2021), which may explain why it was found equally in both microsites. Therefore, the direction (negative or positive) and extent (inclusion of multiple response variables or not) of the effect of shrubs varies between species and is likely reliant on various aspects of size. However, annual traits (including size) were not the focus of this study and further research that examines shrub facilitation while accounting for variations in size both within and between annual species would better solidify this trend.

Indirect Effects of Shrubs Through Plant Community

The indirect effects of shrubs through community plant density on other plant species were largely the same between species in this study despite some species-specificity. There are two likely explanations for the negative effects of community plant density: resource competition and apparent competition. High densities of annuals can result in limited resources and therefore increased interspecific competition for resources (Adler et al. 2018). Apparent competition occurs in cases of high plant density when the negative effects between species occur through a common herbivore (Long et al. 2012; Sotomayor and Lortie 2015; Downey et al. 2018). Both forms of competition can lead to decreased population and floral densities even with increased community density. In our results, the negative correlation with plant density was present only under shrubs where densities were lower than in the open microsites. This disparity means that competition due to increased density alone is unlikely. Rather, the shrub may create conditions (such as shrub-protege competition and allelopathy) such that resource limitation and apparent competition between annuals are greater even at lower densities than what is found in the open. This is particularly evident for floral density where the only negative effects of increasing community plant density were observed under shrubs.

The density of all species consistently increased with increasing species richness both under shrubs and in the open and the floral density of most species also increased with increasing species richness. Increased species richness can decrease intraspecific competition leading to both increased floral and plant population densities (Michalet et al. 2006; Mahaut et al. 2020). The open sites had greater species richness than the shrub sites in this study. This increased species richness may explain why some species preferred the open and had increased flowering in the open if intraspecific competition is more relevant for these species than interspecific competition (Mahaut et al. 2020). However, the effect of species richness was more positive under shrubs than in the open (for only two species in the case of floral density). This increased benefit suggests that if some species occur under shrubs more frequently in some years (such as drought years), the increased species richness has a higher potential to draw other species as well, creating a positive feedback loop that also increases annual reproductive output for some species.

Shrubs influence the understory community in this system through different mechanisms. This supports previous similar work that reported direct and indirect pathways can have contrasting effects (Schöb et al. 2013; Michalet et al. 2015; Wang et al. 2019; Soliveres and Eldridge 2020). One mechanism was positive (by decreasing neighbourhood plant density) and one was negative (by decreasing species richness). However, these effects were more important for predicting plant population density and therefore community composition rather than floral density. By depressing plant community density and species richness, shrubs likely manipulate the inter- and intra-specific competition experienced between understory plants. Further manipulative studies are needed in which both neighbouring understory species and the shrub are systematically removed to determine how specifically the inter and intra-specific interactions vary with community neighbourhood and shrub presence.

Conclusion

Shrubs can change the complexity and stability of communities through a combination of direct and indirect effects by increasing the relative plant and floral density of some species but not others. In particular, shrubs had either direct positive or negative effects on most species plant density, but only negative effects (if any) on floral density. Shrubs however, also influenced local species indirectly through differences in plant community density and richness at the neighbourhood scale and these interactions were variable between species and dependent on the response traits. Shrubs affected floral density in some cases, but more consistently influenced plant density through direct and indirect interactions. Therefore, changes in diversity at larger scales or even small-scale community levels are thus critical considerations for the maintenance of community composition and to a lesser extent population stability through differences in relative reproductive outputs. Managing and measuring species diversity and density at fine scales will likely suggest viable conservation strategies, particularly for relatively less common plant species in desert ecosystems.

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Chapter 5: Consumer pressure and supplemental pollination mediate shrub facilitation of a native annual desert plant

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Abstract

Shrubs are important factors in the assembly of desert plant and animal communities. By providing shelter and resources to other plants and animals, shrubs can change plant-animal interactions including those with consumers and pollinators. Here, we test the hypothesis that shrubs facilitate the reproduction of other desert plants by influencing pollination and compensation for consumer pressure. We used the known benefactor *Larrea tridentata* as our focal shrub species and the flowering annual *Malacothrix glabrata* as a potential protege in the Mojave Desert. We tested the effects of facilitation (shrub microsite), consumer pressure (both artificial folivory and florivory), and pollination (ambient or supplemented) on flower and seed production of the annual *M. glabrata*. We found that floral production and seed mass were similar between microsites but that pollen was limited under shrubs in the absence of any other manipulation. Plants under shrubs produced more flowers and seeds than in the open when folivory and florivory treatments were applied. *Malacothrix glabrata* experienced a cost to association with *L. tridentata* in terms of pollen limitation but plants were better able to compensate for consumer pressure under shrubs through increased flower and seed production when damaged. Therefore, association with shrubs involves a reproductive trade-off between costs to pollination and benefits to compensation for consumer pressure.

Introduction

Plants interact with their immediate neighbours. As explored in Chapter 4, these interactions can vary from competitive or net negative to facilitative where at least one of the associated species benefits. For instance, individual plants can compete directly for resources such as water (Trautz et al. 2017), light (de Vries et al. 2019), nitrogen (Jia et al. 2020), and pollinators (Braun et al. 2021) or indirectly through apparent competition, i.e., competition through a common consumer (Barbosa et al. 2009). However, positive interactions between plants are common and abundant (He et al. 2013; Michalet and Pugnaire 2016). Plants can increase available resources for their neighbours through mechanisms such as nitrogen fixation (Yu et al. 2021), hydraulic redistribution (Ploughe et al. 2019), pollinator attraction (Fowler et al. 2016; Underwood et al. 2020), and associational resistance (reduction in consumer pressure due to the defenses of neighbouring plants) (Barbosa et al. 2009). This set of positive and negative interactions are integral for discerning plant community dynamics because they can shape local distribution and potential fitness of resident, associated species.

Shrubs are important benefactor species in desert ecosystems. Benefactors are species that facilitate another species or protege (Maestre et al. 2009). Positive interactions between plants are particularly important in stressful ecosystems such as deserts (Maestre et al. 2009; Dangles 2019). Shrubs directly benefit their plant proteges by increasing nutrients and reducing heat stress (Michalet and Pugnaire 2016; Ploughe et al. 2019). These benefits can influence consumer pressure because plants are often better able to compensate for damage when resources are not limiting (Zhang et al. 2018) or when environmental stress is relatively low within a system (Lama et al. 2019). Flowering shrubs can also increase pollinator abundance that in turn benefits protege species (Iler and Goodell 2014; Fowler et al. 2016; Underwood et al. 2020). Together, these benefits show that shrubs can increase the reproductive output, seedling survival, and growth of other plants (He et al. 2013; García-Cervigón et al. 2016; Dangles 2019). Shrubs that function in this capacity are foundation species in desert ecosystems. Foundation species often significantly influence local and neighbouring species through enhanced stability and increased relative diversity of desert communities at fine scales.

The facilitative effects of shrubs on their protege species are likely not independent of other mechanisms when plants associate with one another. Consumer-pollinator interactions are well-documented within the literature (Moreira et al. 2019; Haas and Lortie 2020) and shrubs interact with both plant-consumer and plant-pollinator interactions. Therefore, it is reasonable that they would impact consumer-pollinator interactions. We present a conceptual framework outlining how shrubs can mediate the reproductive response of proteges to consumption and pollen limitation (Fig. 5.1). Here, we present the scenario when there is a trade-off between consumer pressure and pollen limitation and when both mechanisms are facilitative. In Fig. 5.1 we predict that facilitation by shrubs leads to compensation (similar or increased reproductive output) in proteges when either damage to reproductive or vegetative tissues occurs. Damage to reproductive organs (i.e. florivory) can directly reduce reproduction by removing reproductive structures (Muñoz-Gallego et al. 2022) while damage to vegetative tissues (e.g. folivory) can reduce reproduction by causing plants to reallocate resources such that fewer seeds or pollen are produced (Pratt et al. 2005; Muola and Stenberg 2018). Consumption can also indirectly impact reproduction by influencing pollinator attraction and thereby increase pollen limitation (Muñoz-Gallego et al. 2022). Therefore, if flowering shrubs attract pollinators and reduce pollen limitation (Iler and Goodell 2014; Fowler et al. 2016; Underwood et al. 2020), they may further offset the effects of consumption. As outlined, these two effects of shrubs (increased compensation and reduced pollen limitation) would represent strict facilitation. However, flowering shrubs can also compete with proteges for pollinators (Braun et al. 2021; Richardson et al. 2021). In this case, association with shrubs functions as a trade-off between a benefit (increased compensation) and a cost (increased pollen limitation). Manipulation of consumers and addition of pollen will begin to decouple these effects of shrubs reported in the literature, leading to either two synergistic or antagonistic mechanisms that impact pollen limitation.

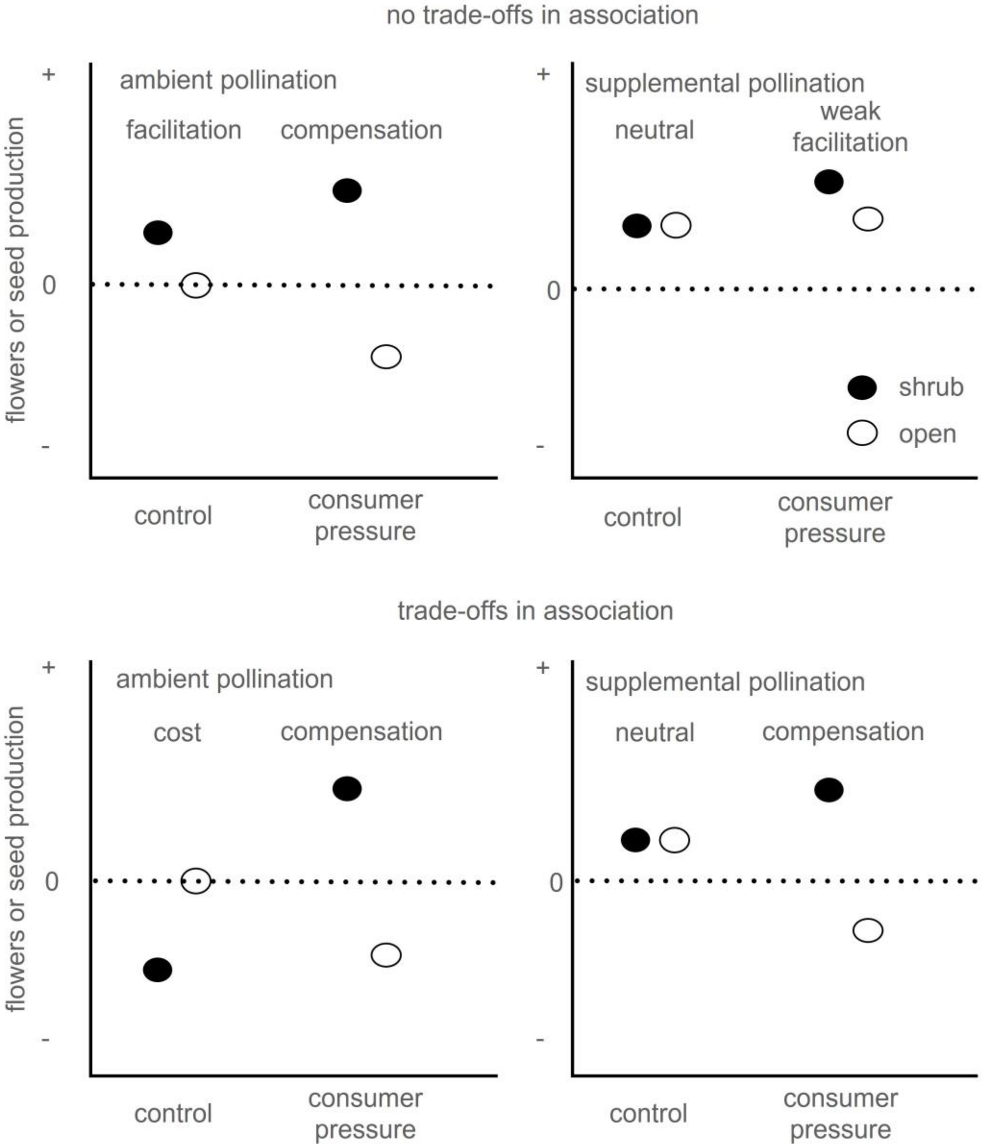

Figure 5.1: Conceptual framework showing the expected reproductive output of annuals when associated with shrubs and open microsites under consumer pressure and supplemental pollination with and without trade-offs in association. The dashed line represents a theoretical neutral effect represented by the plants without damage or supplemental pollination in the open. Control treatments have no damage applied and consumer pressure treatments have damage (of any type) applied. Ambient pollination is natural levels of pollination with no supplement, and supplemental pollination is where pollen limitation has been removed manually.

Here, we test the hypothesis that shrubs facilitate the reproduction of other desert plants by influencing pollination and compensation. We explore the two mechanisms outlined in the conceptual framework: (i) increasing the compensatory response of plants in response to consumer pressure and (ii) increased attraction of pollinators (Fig. 5.1). We explored these mechanisms using two types of consumer pressure (damage to flowers and damage to leaves). We also tested for pollen limitation by using supplemental hand pollination in the absence and presence of shrubs. We tested the following predictions. (1) Damaged plants have greater reproductive output under shrubs than in the open. (2) Compensation for folivory will be greater under shrubs than compensation for florivory (aligned with Chapter 2). (3) Pollen limitation will be greater in the open than under shrubs. (4) Damage will have a greater impact on pollen limitation in the open than under shrubs. By decoupling the effects of compensation and pollen limitation within the context of shrub facilitation, the mechanistic pathways of facilitation by shrubs are examined in concert to explore trade-offs in desert plant communities.

Materials and Methods

Study System

As in Chapter 4, we used the shrub *Larrea tridentata* (creosote bush) as the benefactor plant species in this study. *Larrea tridentata* is a common shrub and known benefactor in the Mojave Desert (Fig. D.1) (Schafer et al. 2012; Ruttan et al. 2021) that is insect-pollinated (Hurd Jr. and Linsley 1975). *Larrea tridentata* is known to host a variety of insects (Hurd Jr. and Linsley 1975; Braun and Lortie 2020) including more than 120 bee species documented as associated with this shrub species (Hurd Jr. and Linsley 1975; Minckley et al. 2000). As a potential protege species, we used the common annual *Malacothrix glabrata* (the desert dandelion). *Malacothrix glabrata* is a relatively large annual in the Mojave Desert (growing up to 40 cm tall) (Davis 2012) with dense yellow flowers (Fig. D.1). *Malacothrix glabrata* is primarily pollinated by bees (Ruttan et al. 2021), but it is also visited by other pollinators such as flies, beetles, and butterflies (Braun and Lortie 2020; Ruttan et al. 2021). This annual is frequently associated with *L. tridentata* (Chapter 4; Shmida and Whittaker 1981; Liczner et al. 2017; Braun and Lortie 2020). However, *M. glabrata* is not confined to association with shrubs, and it is also frequently found in the open (Shmida and Whittaker 1981; Liczner et al. 2017; Braun and Lortie 2020). It is thus an ideal test species because facilitation is facultative (Shmida and Whittaker 1981; Liczner et al. 2017; Braun and Lortie 2020), and it is a generalist species (Davis 2012). *Malacothrix glabrata* also relies on seed banks to persist in deserts (Davis 2012; Liczner et al. 2017).

Study Area

The study site was in the Mojave Desert (34.72N, 115.68W) and research was done in March-April 2019. The site studied was a shrubland dominated largely by *L. tridentata* and *Ambrosia dumosa* (burroweed). The site typically receives 175-mm of annual rainfall and it has an average daily temperature of 17.5°C (WRCC 2020). The annual community is dominated by *Cryptantha circumscissa*, *C. angustifolia*, *Chaenactis fremonti*, *M. glabrata*, and *Eriophyllum wallacei* (Chapter 4; Calflora 2014). The year of study was not a drought year (National Drought Mitigation Center 2019) with a cumulative rainfall of 305-mm in 2019 compared to the long-term average of 175-mm (WRCC 2020).

Experimental Design

A total of 320 pre-blooming *M. glabrata* plants were selected for study in March 2019 under shrubs and in the open. Treatments included microsite (shrub or open), pollination (supplemental hand pollination or natural ambient pollination), folivory (removal of 50% of leaves or no leaf removal), and florivory treatments (removal of 50% of flowers or no flower removal) in a fully crossed design with 20 replicates per treatment level.

A single individual of *M. glabrata* was randomly selected under each shrub and open microsite. Shrub plots were at least 5-m from another selected shrub and open plots were at least 1.5-m away from the dripline of any *L. tridentata*. We measured the height (h), width (w) and length (l) of each shrub in order to calculate the volume (v) of shrubs based on an estimate of the volume of a dome ($v = 2/3 * \pi * w/2 * l/2 * h$) (Filazzola et al. 2017). After initial setup, each plant was monitored approximately every third day for both flowering and signs of floral senescence. Pollination was supplemented by rubbing the anthers and stamen of each flower with that of another *M. glabrata* flower not used in the experiment collected nearby (Kearns and Innouye 1993). Pollen was supplemented each time new flowers were observed.

Artificial folivory was applied by removing approximately half of the many grass-like leaves on each *M. glabrata* by hand (this ranged from as few as ten leaves to upwards of one hundred). Folivory treatments were applied upon experimental setup before plants were flowering so that the effect of leaf removal could be tested on both flower and seed production. The artificial florivory treatment was applied when at least 3 flowers were present (timing ranged from 3 to 10 days after setup depending on flowering phenology). Florivory treatments were applied when at least half of all buds were flowering when there were fewer than 5 flowers and buds. This treatment consisted of removal of half of all flowers and half of all buds (rounded up in the case of an odd number).

The total number of flowers to set seed for each plant was recorded as flowers started to senesce and seeds were collected. A mesh bag was fixed around each flower in order to avoid losing the anemochorous seeds to the wind (Baskin and Baskin 2014). Seeds were stored in seed envelopes for 40-90 days then separated from the chaff and weighed to the nearest tenth of a milligram.

Statistical Analyses

We used the total number of flowers to set seed and total seed mass produced by each plant as response variables. We used microsite, pollination, artificial florivory, and artificial folivory as predictor variables. All predictor variables and their interaction terms were included in each generalized linear mixed model (Wolfinger and O'Connell 1993) along with shrub-open pairing as a random effect, and the initial number of buds at experimental setup as an offset term (as a control for the variation in *M. glabrata* floral production) (Zuur et al. 2009). The number of flowers to set seed was subsequently included as an offset term for total seed mass models. Error for the number of flowers was modeled to a quasi-Poisson distribution (Ver Hoef and Boveng 2007) because of its distribution tested with the performance package (Lüdecke et al. 2021), and error for seed mass was modeled to a Tweedie distribution (a type of general exponential dispersion model) (Jorgensen 1987; Niku et al. 2017). All statistics were performed using R Statistical Software version 4.3.1 (R Core Team 2023), and the package glmmTMB was used for the generalized linear mixed models (Brooks et al. 2022) with emmeans for post hoc comparisons (Lenth 2021). Data are openly published at KNB (Haas-Desmarais and Lortie 2021).

Results

Individuals of *M. glabrata* began the study with a mean of 6 ± 5 buds at setup and had 4 ± 4 flowers that set seed. A mean of 4 ± 0.4 flowers set seed in the open and 3 ± 0.3 flowers set seed under shrubs. The grand mean seed mass per plant was 66.5 ± 8.9mg. The mean seed mass of plants in the open was 81.5 ± 8.1mg and under shrubs was 51.5 ± 5.6mg. Out of the total 320 plants, 40 failed to set seed after applying treatments. Of these 40 plants, 33 had received the 50% florivory treatment and 3 had received the 50% folivory treatment.

Floral production

The total number of flowers to set seed in the full control (i.e. no damage or pollination treatments) individuals of *M. glabrata* did not differ between microsites (Fig. 5.2 & Table F.1). When both folivory and florivory treatments were together applied to this species however, number of flowers to set seed was 4-fold higher under shrubs with ambient pollination and 18-fold when pollination was supplemented (Fig. 5.2 & Table F.1). Plants that experienced 50% florivory at setup had the same number of flowers set seed per plant relative to those that did not experience florivory in all treatment sets except two sets of conditions: plants experienced the folivory treatment, were in the open and had supplemental pollination, or they did not receive the folivory treatment, were under shrubs and received supplemental pollination (Table F.1). The number of flowers to set seed was 70-fold and 41-fold higher (respectively) in plants that did not receive floral damage than those that were damaged for these two cases. The number of flowers to set seed of *M. glabrata* did not differ between plants that experienced 50% folivory and no folivory nor between plants with supplemental and ambient pollination (Table 5.1 & F.1). Floral density was slightly positively correlated with shrub size (slope = 0.582±0.004 flowers/m^2, χ^2 = 15770, p < 0.0001).

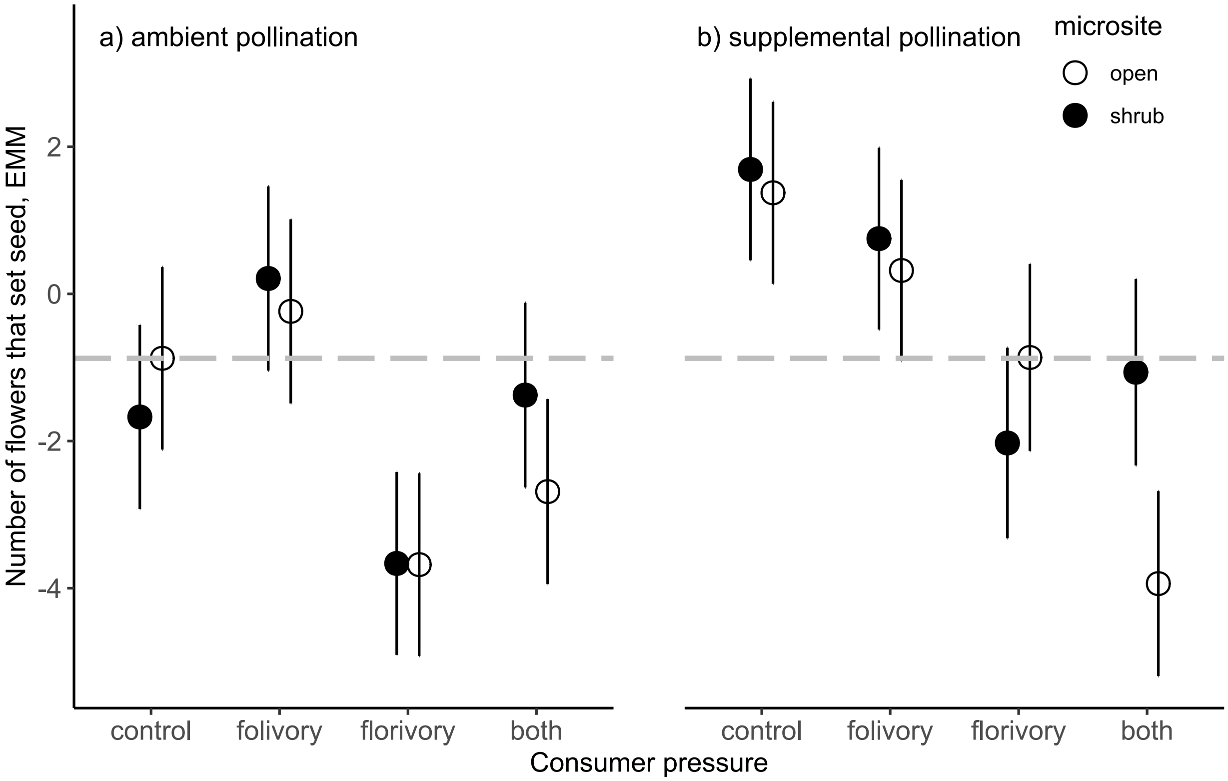

Figure 5.2: Estimated marginal means (logarithm-transformed; EMM) of the number of flowers that set seed (±SE) of *Malacothrix glabrata* plants in the open and under *Larrea tridentata* shrubs as a function of folivory and florivory treatments. The dashed line shows the neutral effect of plants in the open without damage or pollen supplement.

Seed mass

Net seed mass for control *M. glabrata* plants did not differ between microsites (Fig. 5.3 & Table F.2). Seed mass was however greater under shrubs when either folivory or florivory treatments were applied (Table 5.1 & F.2). Seed mass was 10-fold higher under shrubs in the presence of folivory and 19-fold higher under shrubs in the presence of florivory, but more than 1000-fold higher under shrubs in the presence of both types of damage. Seed mass per *M. glabrata* was also 43-fold higher under shrubs than in the open when pollen was supplemented. Supplemental pollination increased total seed mass per plant by 216-fold relative to plants with only ambient pollination, but only under shrubs and in the absence of

Table 5.1: The effect of microsite, 50% flower removal (florivory), 50% leaf removal (folivory), and supplemental pollination on number of flowers to set seed and mass of seeds. *p <0.05

	Flower Number		**Seed Mass**	
Factor	χ^2	**p-value**	χ^2	**p-value**
microsite	8.24	0.0041*	250	0.0001*
folivory	0.0339	0.85	1.01	0.32
florivory	9.19	0.0024*	0.73	0.39
pollination	2.22	0.14	2.05	0.15
microsite:folivory	11.7	0.00063*	28.9	0.0001*
microsite:florivory	6.09	0.014*	56.2	0.0001*
folivory:florivory	0.00225	0.96	0.00589	0.94
microsite:pollination	2.1	0.15	6.15	0.013*
folivory:pollination	2.1	0.15	2.56	0.11
florivory:pollination	0.197	0.66	0.00909	0.92
microsite:folivory:florivory	6.72	0.0095*	7.18	0.0074*
microsite:folivory:pollination	0.318	0.57	1.74	0.19
microsite:florivory:pollination	0.0328	0.86	8.28	0.004*
folivory:florivory:pollination	0.0244	0.88	0.0871	0.77
microsite:folivory:florivory:pollination	6.59	0.01*	7.65	0.0057*

any damage treatments (Table 5.1 & F.2). Folivory decreased seed mass relative to plants by 225-fold with undamaged leaves in the presence of florivory when plants were under shrubs and pollen was not supplemented (Table 5.1 & F.2). Florivory alone did not affect seed mass (Table 5.1 & F.2). Seed mass was not correlated with shrub size (χ^2 = 0.163, p = 0.68).

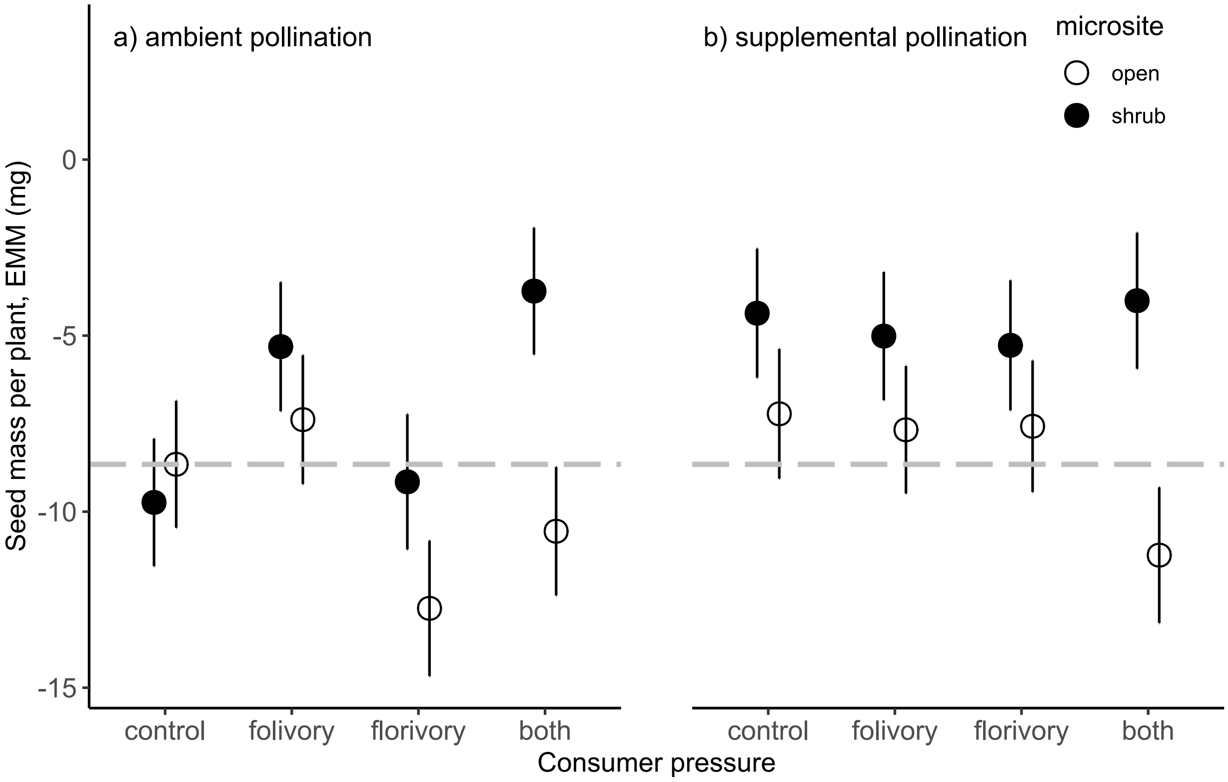

Figure 5.3: Estimated marginal means (logarithm-transformed; EMM) of the mass of seeds per plant (±SE) of *M. glabrata* plants in the open and under *L. tridentata* shrubs as a function of pollination, folivory, and florivory treatments. The dashed line shows the neutral effect of plants in the open without damage or pollen supplement.

Discussion

Shrubs can mediate the extent of pollen limitation and compensation to consumer pressure of the annual protege species. Using the shrub *L. tridentata* and the desert annual *M. glabrata,* we tested whether shrubs could facilitate proteges through direct and indirect mechanisms related to consumer pressure and pollination. The findings here support this hypothesis because shrubs indirectly increased protege reproduction through compensation for damage although this facilitation was not observed through pollination. The first prediction that compensation for damage would be greater under shrubs was supported for both number of flowers to set seed and seed production. The second prediction that compensation for folivory would be greater than compensation for florivory under shrubs was supported because compensation in terms of both number of flowers to set seed and seed production occurred in every case for folivory but not florivory. The third and fourth predictions regarding the relative effects of shrubs and consumers on pollen limitation were not supported because pollen limitation was only observed under shrubs, suggesting an overall negative effect of shrubs on pollination. Our results imply that the mechanism behind facilitation by *L. tridentata* is associated with consumer pressure and not pollination, but that the negative effects of shrubs on pollination are offset by facilitation in the presence of consumer pressure.

Consumer Pressure and Facilitation

Shrubs can increase the reproduction of their protege species when these individuals are damaged. While the facilitation literature is often focused on the positive effects of shrubs on vegetative responses such as plant density, diversity, and growth (Pugnaire et al. 2004; He et al. 2013; Michalet et al. 2015), we provide further evidence that the effect of compensation for damage on reproduction is also an important form of facilitation. These results support other research showing that shrubs had positive effects on the production of reproductive structures through mechanisms not including consumer pressure (Holzapfel and Mahall 1999; García-Cervigón et al. 2016). *Ambrosia dumosa* increased seed production of *Chaenactis fremontii* A. Gray, *Schismus barbatus* (L.) Thell., and *Bromus matridensis* (L.) ssp. *rubens* (L.) without consumer pressure in a similar *Larrea-Ambrosia* scrub community within the Mojave Desert (Holzapfel and Mahall 1999). However, *Juniperus sabina* had a mix of positive and negative effects on the production of reproductive structures of *Helleborus foetidus* that depended on the level of abiotic stress (García-Cervigón et al. 2016). Thus, higher stress led to increased facilitation of carpel production and fruit set despite decreases in flower production.

Similarly, here we found that shrub facilitation of reproduction was dependent on consumer pressure.

Shrubs caused plants to increase their compensation for damage, but the specific mechanism behind increased tolerance can still be further elucidated. Previous mechanisms have been tested for how shrubs deter consumers (Guignabert et al. 2020; Ruttan et al. 2021), but not for coping with damage. The increased resources often sequestered by shrubs (Ploughe et al. 2019) is a likely mechanism to compensate for damage (Brody and Irwin 2012; Zhong et al. 2021). However, it is unclear whether the resources provided by shrubs are sufficient to increase the compensatory response of their proteges. In addition, increased resources are not always correlated with compensation (Brody and Irwin 2012; Hernán et al. 2019). Another possible mechanism is that shrubs increase the compensation of plants directly surrounding them by decreasing abiotic stress. Shrubs can increase growth and reproduction of surrounding plants through reductions in stress (García-Cervigón et al. 2016; Ploughe et al. 2019). However, the study year was not a drought year (WRCC 2020) and so the environmental stress was likely already low compared to the previous drought years (Lund et al. 2018). Further data that manipulated stress and soil nutrients could distinguish between these two mechanisms. Changes in the facilitation of reproduction with consumer pressure, environmental stress, and soil nutrients have important implications for the stability of desert communities and seedbanks in the face of a changing climate.

Folivory vs. Florivory

Florivory is a form of consumer pressure that influences plant reproduction directly by removing reproductive structures. Most plants in our study were able to compensate for this removal of reproductive tissues by producing more flowers such that the initial removal of flowers was not detectable. Compensation by producing more flowers did not occur in two specific cases (in the open, in the presence of folivory, with supplemental pollination; and under shrubs, without any folivory, with supplemental pollination). In these two cases, there were fewer flowers than in the control, but no difference in the total seed mass. Therefore, compensation occurred through increasing seed set in the fewer remaining flowers (rather than by producing more flowers). Compensation by producing more flowers and more seeds in response to florivory has been consistently documented in the literature using both artificial and natural forms of florivory (e.g., Aguirrebengoa et al. 2021; Wise and Mudrak 2021). A similar study found that *Helianthus annuus* (a plant in the same family as *M. glabrata*: Asteraceae) compensated fully in response to artificial removal of buds (Pilson and Decker 2002). Plants produced more flowers and increased overall seed mass when buds were removed (Pilson and Decker 2002). In a Chapter 3, a meta-analysis of the effects of different types of damage on plant floral and reproductive attributes florivory also negatively impacted floral traits (e.g. floral production) but not reproductive success of plants (e.g. seed mass). Regardless of microsite or the mechanism for compensation, removal of flowers by florivores was not impactful for this species. However, it is possible that this type of damage will be of greater concern under higher levels of environmental stress and the increased compensatory response observed under shrubs will be of greater import.

In contrast to florivory, folivory removes non-reproductive structures (i.e. leaves), but the removal of leaves can still impact reproduction. Most plants were able to tolerate damage to vegetative tissues, receiving no impact to floral production or seed mass. However, plants produced a higher seed mass when subjected to folivory than those that received no folivory damage (i.e. plants over-compensated for folivory) specifically when *M. glabrata* were associated with shrubs and also received the florivory treatment (but not supplemental pollination). This over-compensation for folivory represents a reallocation of resources towards seed production (Garcia and Eubanks 2019) similar to what was observed in response to florivory. However, in contrast to florivory, in most cases folivory did not trigger any reproductive compensatory response (increasing seed mass in only a single case). These results differ from a meta-analysis by Moreira et al. (2019) where folivory negatively influenced both floral traits and the reproductive success of plants even to a greater degree than florivory (e.g. Schiestl et al. 2014). However, primary research studies have found both no effect of folivory on floral traits or reproduction (e.g. Litto et al. 2015; Wise and Mudrak 2021) and over-compensation in response to folivory (e.g. Schiestl et al. 2014; Livingstone et al. 2020). This difference suggests that context (such as availability of resources or species identity) is important. Supporting this, Livingstone et al. (2020) found that *Vincetoxicum rossicum* increases its seed production in response to folivory only in shaded conditions and not sun. This body of work (including this experiment) suggests that identifying key factors, both direct and indirect, associated with consumer pressure can help us better understand patterns in compensation and plant responses to consumer pressure.

Facilitation and Pollen Limitation

There are at least two explanations for trade-offs associated with protege species pollination and shrubs in deserts: interference and pollinator competition. Each of these mechanisms could act to decrease the pollinator visitation of protege species and therefore could explain the pollen limitation under shrubs observed in this study. To start, shrubs can interfere with pollinator visitation by physically blocking pollinator access (Cádiz-Véliz et al. 2021). For instance, the shrub *Flourensia thurifera* excludes pollinators from sheltered cacti species in a similar way to an exclosure (Cádiz-Véliz et al. 2021). This interference effect could be a valid conceptual explanation for *L. tridentata* effects, but the majority of the visitors of *M. glabrata* are insects (Braun and Lortie 2020) as opposed to the larger hummingbirds observed in Cádiz-Véliz et al. (2021), making this explanation less likely. In a previous study with *L. tridenta* and *M. glabrata*, *L. tridentata* increased the pollinator visitation to *M. glabrata* (Ruttan et al. 2021), also suggesting interference is not the most viable explanation. Since the effect of *L. tridentata* on *M. glabrata* has varied between studies (Braun and Lortie 2020; Ruttan et al. 2021), it is more likely that the mechanism behind pollen limitation is dependent on some variable that fluctuates year to year (unlike interference).

Another mechanism to explain the pollen limitation caused by shrubs is competition for pollinators. *Larrea tridentata* blooms concurrently with *M. glabrata* (Calflora 2014) and so increases total floral density (Ghazoul 2006). Increased floral density generally increases total pollinator abundance and therefore pollination of other nearby plants (Ghazoul 2006; Losapio and Schöb 2020). However, resource dilution can also occur. Resource dilution is defined as an over-saturation of resources (i.e. flowers) such that not all resources are visited by consumers (i.e. pollinators) (Wenninger et al. 2016). This phenomenon results in pollen limitation due to insufficient pollinators for the number of flowers (Wenninger et al. 2016). While resource dilution is not common in pollination systems outside of mass flowering crops (Holzschuh et al. 2016), it has been previously documented in natural systems (Wenninger et al. 2016). Pollinators can also exhibit floral constancy (Bruninga-Socolar et al. 2022). Pollinators prefer to forage on the same species without switching so long as there are sufficient floral resources (Bruninga-Socolar et al. 2022). Therefore, while large patches of flowers such as those found in *L. tridentata* shrub populations can increase the total number of pollinators in the area, they may also reduce the number of pollinators visiting non-*L. tridentata* flowers through both resource dilution and floral constancy (Bergamo et al. 2021). This decrease in pollination has been observed in other systems (Cohen et al. 2021) as well as this system (Braun and Lortie 2020). Competition for pollinators may therefore mean that mass-flowering animal-pollinated shrubs make worse benefactors than wind-pollinated shrubs such as *Ambrosia dumosa* (Ruttan et al. 2021) and *Ephedra californica* (Vanderplank and Ezcurra 2016). Therefore, while shrubs can facilitate plants in terms of growth (Montesinos-Navarro et al. 2019), population density (Han et al. 2021), and compensation following damage in deserts (as seen here), there can be a trade-off for those species in terms of pollination.

Conclusion

The net effect of shrubs on their proteges in terms of reproduction and pollen limitation is usually dependent on the presence, but not the type of consumer damage. However, the mechanistic pathway of shrub-annual plant pollination facilitation did vary based on damage type in this study. There is a cost to association with shrubs in terms of pollen limitation, and consumer pressure reduces this cost of association in deserts. Therefore, the potential fitness benefits associated with facultative facilitation by shrubs for flowering species is best modeled as an ecological trade-off in a reduction of pollination but increased compensation for consumer damage. Further research that examines multiple years, including both drought and non-drought years as well as varying levels of natural consumer damage are warranted. Greater depth to this research will allow us to better understand the importance of shrubs for compensation to damage and pollination and how facilitation of compensation has the potential to offset the costs of association with shrubs.

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Chapter 6: Conclusion

Over-arching Aims and Hypotheses

Plant communities are complex networks of interactions that include interactions between plants as well as between plants and animals. While interactions are often examined in isolation, focusing on two individuals or species, understanding plant community interactions takes broader approaches that include multiple species and multiple types of interactions (Bascompte et al. 2003; Desurmont et al. 2014). The purpose of this research was to better understand how interactions with other species impact plant reproduction. To do this we examined the overall complex of interactions that include the intersection of plant-plant and herbivore-pollinator interactions, each chapter focusing on a specific aspect of this overall network of interactions (Table 6.1). We started by summarizing (Chapter 2) and then quantifying (Chapter 3) the oft-studied herbivore-pollinator interactions. Herbivores and

Table 6.1: Main implications and related papers for chapters 2-5.

Chapter	Implications	Related Paper(s)
Chapter 2	The effects of direct and indirect damage to plant floral tissue on reproduction and pollination are important for ecological resilience and stability	Garcia and Eubanks 2019; Moreira et al. 2019; Lucas-Barbosa 2016
Chapter 3	In general, natural damage to flowers and leaves are the most likely to influence plant-pollinator processes since they are the most robust to changes in sample size.	Moreira et al. 2019
Chapter 4	The effect of shrubs on plant community diversity and density are critical considerations for population stability through relative changes in reproductive output.	Filazzola et al. 2020; Flores-Torres and Montana 2015; Michalet et al. 2015
Chapter 5	There is a cost to association with shrubs in terms of pollen limitation and consumer pressure reduces this cost of association in deserts.	Mothershead 2000; Braun and Lortie 2020

pollinators can have both direct and indirect effects on plant reproduction (Ollerton et al. 2011; Moreira et al. 2019). Herbivores can directly remove reproductive tissues and indirectly remove plant resources needed to reproduce (Moreira et al. 2019), while pollinators directly increase reproductive output for a large proportion of angiosperms (Ollerton et al. 2011). Next, we specifically examined the direct and indirect interactions between desert shrubs and their protege species (Chapter 4), testing how shrubs change plant community interactions. Desert shrubs are well known to facilitate the surrounding plant species through a variety of mechanisms (see Filazzola and Lortie 2014) that can in turn change how plant species interact with each other (Michalet et al. 2015). Finally, we tie these interactions together in one large manipulative study in which we test how herbivory, pollination, and plant interactions together affect plant reproduction (Chapter 5). Altogether we tested the following aims and hypotheses:

Chapter 2: We aimed to synthesize the literature on herbivore-plant-pollinator interactions, focusing on describing and contrasting direct and indirect damage to reproductive tissues and their impact on plant reproduction and pollination.

Chapter 3: We aimed to quantify the effects of both natural and simulated damage to roots, flowers, leaves, stems, and mixed damage on plant floral traits, pollination, and reproductive success with a focus on how these effects changed with increasing sample size.

Chapter 4: We tested the hypothesis that shrubs facilitate understory plant community composition and reproduction through both direct and indirect interactions mediated by the associated plant neighbourhood.

Chapter 5: We tested the hypothesis that shrubs facilitate the reproduction of other desert plants by influencing pollination and compensation. We examined two specific mechanisms (outlined in Fig. 5.1): (i) shrubs increase the compensatory response of plants in response to consumer pressure and (ii) shrubs increase the attraction of pollinators.

Summary of General Findings

Herbivory decreases plant reproduction and pollination, but the effect is dependent on the tissue damaged (Chapter 2, 3, and 5). Through synthesis (Chapter 2), we found that most studies find a decrease in plant reproduction, floral attributes, and pollination when floral tissues are damaged both directly (i.e. florivory; e.g. Mothershead and Marquis 2000; McCall 2010; Missagia and Alves 2017) and indirectly through damage to vegetative tissues (e.g. folivory, root damage; e.g. Rusman et al. 2019; Motzke et al. 2015; Barber et al. 2015). While not every study found this decrease (e.g., Mothershead and Marquis 2000; Hladun and Adler 2009), it was more common in direct damage than indirect damage; however, few studies examined both in concert, so comparison was difficult. When examined quantitatively through meta-analysis (Chapter 3), this difference was pronounced for damage to some vegetative tissues. Our quantitative analysis further separated types of damage. Natural damage to roots and stems (classified as vegetative damage in Chapter 2) and mixed damage did not impact plant reproduction, floral attributes nor pollinator attraction. Natural damage to floral tissues and leaves (vegetative) both decreased each of these response variables and were found to be robust to increases in sample size given that they remained significantly negative between Moreira et al. (2019) and our revisit in Chapter 3. Furthermore, simulated damage to flowers, leaves, and stems also decreased plant reproductive attributes. We further tested the effects of florivory and folivory experimentally (Chapter 5), finding that folivory and florivory alone were not often sufficient to decrease flowering or seed production, but when applied together they depressed both floral and seed production. We therefore provide both experimental and meta-analytic evidence of the negative effect of florivory and folivory on plant reproductive traits that is supported by our Chapter 2 synthesis.

The effect of shrubs on understory plants is species-specific (Chapter 4). Shrub facilitation of plant abundance and density is well-documented in desert ecosystems (Filazzola and Lortie 2014; Perea and Gil 2014; Molina-Montenegro et al. 2020; Han et al. 2021), including the system we use in Chapter 3 (Drezner 2006; Schafer et al. 2012; Badano et al. 2016; Braun and Lortie 2020). We add to this body of work by providing evidence of two species (*Malacothrix glabrata* and *Chaenactis fremontii*) that are indeed more abundant under *Larrea tridentata* shrubs than in the open. However, we also found three species that were more abundant in the open (*Cryptantha angustifolia*, *C. circumscissa*, and *Eriophylum wallacei*), and one that was equally abundant in both microsites (*Chylismia claviformis* subsp. *auranticus*). Thus, we also find that this facilitative effect is highly dependent on species, further adding to the body of literature finding that even the common effect of shrub facilitation is species-specific (Callaway 1998; Michalet et al. 2015; Filazzola et al. 2020). Furthermore, the effect of shrubs on plant reproduction (in the form of flowering) was not facilitative, despite facilitation in two species. All species experienced less flowering or no difference in flowering under shrubs or in the open. When focusing on a single species (*M. glabrata*), both flowering and seed set were similar in shrub and open microsites (Chapter 5), providing similar findings for the species in both Chapter 4 and 5.

Shrubs shape the plant community by decreasing plant density but increasing species richness (Chapter 4). Shrubs are well-documented as foundation species because of their ability to shape the community around them (Smit and Ruifrok 2011; Filazzola and Lortie 2014). We found that by changing the density and species richness of the plant community, shrubs had secondary indirect effects on the plant community. Community plant density decreased most individual species population density under shrubs but not in the open while the positive effect of increased species richness was greater under shrubs than in the open. This effect on the plant community as a whole instead of only individual species means that shrubs have secondary, indirect effects on individual species by shaping other plant interactions.

Shrubs were found to decrease pollination relative to open microsites (Chapter 5). *Malacothrix glabrata* was pollen-limited under shrubs, but not in the open. That is, seed set of plants under shrubs increased with supplemental pollination but there was no significant increase in seed set with supplemental pollination in the open. This pollen limitation represents a cost to association with shrubs that matches literature that has found this shrub (*Larrea tridentata*) to decrease pollinator visitation to *M. glabrata* in the past (Braun and Lortie 2020). From Chapter 4, we observed that *M. glabrata* is more abundant under shrubs than in the open, so clearly the shrubs provide some benefit, whether to germination or growth, but not to this aspect of reproduction. However, we also see other species disassociated with shrubs in Chapter 4. This pollen limitation discovered for *M. glabrata* in Chapter 5 may also be a negative interaction between shrubs and other annual species that promotes association with open-gap microsites.

Association with shrubs is an ecological trade-off between reduced pollination and increased compensation for herbivory (Chapter 5). Shrub facilitation was only apparent in the presence of artificial herbivory, with both increased flowering and seed set in the presence of both types of damage particularly accentuating the difference between plants in the open and under shrubs. The cost of association in terms of pollen limitation was entirely absent in the presence of folivory. This ecological trade-off between decreased pollination and increased reproductive compensation for herbivory adds novel insight into the many interactions between shrubs and their proteges that frequently result in a net positive effect.

Implications of General Findings

The co-evolution between plants and their pollinators is an important part of ecological stability (Bascompte and Scheffer 2023). For many angiosperms, pollinators are vital for plant reproduction, with some plants unable to reproduce without pollinators and others having greatly depressed reproduction (Ollerton et al. 2011). Maintaining these relationships is an important focus of preserving and restoring ecosystems in the face of threats such as climate change and habitat degradation (Hall and Martins 2020; Vasiliev and Greenwood 2020). These threats have resulted in widespread declines in a variety of pollinator species (van der Sluijs 2020; LeBuhn and Vargas Luna 2021) which have in turn threatened the stability of plant-pollinator networks (Bennett et al. 2018; Bascompte and Scheffer 2023). Much research has gone into assessing the robustness and stability of plant-pollinator networks by exploring various metrics that examine the effects of plant and pollinator specialization, niche overlap, and redundancy (Bascompte et al. 2003; Bennett et al. 2018; Bergamo et al. 2021; Guy et al. 2021; Bascompte and Scheffer 2023). However, these networks exist beyond the context of their plants and pollinators (e.g. Guy et al. 2021). We provide an important addition to this work by extending these co-evolutionary processes to include herbivores. While plants coevolve with pollinators, they are also simultaneously involved in a coevolutionary arms race with their herbivores (Santangelo et al. 2019; Underwood et al. 2020). We show that herbivory is not only a secondary determinant of plant reproduction that happens in addition to and concurrent with pollination, but also can impact both pollinators and therefore pollination by impacting floral display (Chapter 2, 3, and 5).

Both the damage herbivores inflict and the defenses against herbivores have the potential to impact plant-pollinator interactions (Lucas-Barbosa et al. 2016; Kessler and Chautá 2020), making herbivores a crucial part of this picture that drives co-evolution between plants and pollinators. Damage that reduces pollination may weaken the relationship between plants and pollinators by deterring pollinators (Jacobsen and Raguso 2018) and encourage plants to allocate resources towards defense and compensatory responses (Lucas-Barbosa 2016). These defenses can in turn further decrease pollinator visitation (Lucas-Barbosa et al. 2011). Volatiles produced to deter herbivores have been shown to also sometimes deter pollinators (Desurmont et al. 2014; Jacobsen and Raguso 2018; Sasidharan et al. 2023). This link between herbivores and pollinators is of particular import when considering invasive herbivores. Native plants often have defenses or strategies (e.g., associating with well-defended species) to sufficiently tolerate native herbivores within this coevolutionary arms race (Mithöfer and Boland 2012; Ida et al. 2018; Underwood et al. 2020). Novel damage outside of co-evolutionary history can circumvent defense and compensatory responses, disrupting this balance and potentially devastating a plant population (Radville et al. 2011; Gormley et al. 2012; Desurmont et al. 2014; Latham et al. 2020; Muñoz-Gallego et al. 2022). By changing ecosystem and plant community dynamics, invasive herbivores can further impact pollinator communities and plant-pollinator interactions (e.g. Guy et al. 2021).

Shrubs are frequently considered foundation species in desert systems (Prevéy et al. 2010; Peters and Yao 2012; Ruttan et al. 2021; Lortie et al. 2022). They shape the surrounding environment, providing shelter and resources for other plants (Filazzola and Lortie 2014;

Molina-Montenegro et al. 2020; Han et al. 2021) and animals alike (Ruttan et al. 2016; Filazzola et al. 2017; Zhang et al. 2022). This role as facilitators of other plants makes them potential tools for restoration of degraded habitats (Gómez-Aparicio et al. 2004; Jensen et al. 2012; Westphal et al. 2018). By planting shrubs, other plants can get a foothold into harsh environments (Gómez-Aparicio et al. 2004). With the increasing desertification of ecosystems (Huang et al. 2020) and efforts to restore habitats suffering from anthropogenic degradation (Gómez-Aparicio et al. 2004; Jensen et al. 2012; Westphal et al. 2018), shrubs as tools to aid in establishment and succession is an important field of study. However, we provide evidence that not all species benefit from the presence of shrubs. Some species avoid shrubs and shrubs have the potential to decrease plant density (Chapter 4) and pollination (Chapter 5). This makes the use of shrubs as tools of restoration less clear. While many species of shrub (including *Larrea tridentata*) can facilitate other plant species (Schafer et al. 2012; Lortie et al. 2014), the negative impact of *L. tridentata* and only conditional positive impact (i.e. only some species and some response variables responded positively to the shrub; Chapters 4 & 5) means that for a specific restoration goal, care should be taken as to the specific shrub species chosen. For instance, if *L. tridentata* reduced pollination of *M. glabrata* because it drew pollinators away from the understory (as has been suggested in another study (Braun and Lortie 2020)), zoochorous shrubs with similar flowering phenology to potentially supported plants (like *L. tridentata* and *M. glabrata*) may be less facilitative than anemochorous shrubs. In contrast, flowering shrubs that have a mismatched phenology with the annual plant community could increase pollination by supporting the pollinator community when annual flowering resources are scarce but not drawing pollinators away when annuals bloom (Oleques et al. 2017;

Duchenne et al. 2021). These forms of potentially conditional (rather than strict) facilitation make the selection of dedicated facilitators for restoration a complex one.

Shrubs do not universally facilitate all annual plant species within their desert habitats, but they still act as foundation species by shaping the community around them and providing net benefit effects. While restoration may require targeted benefits to specific native plants, the more complex mix of negative and positive interactions of shrubs can still result in net positive effects for plant communites (Chapters 4 & 5). For instance, by increasing the density of some species but not others, shrubs increase the species richness and heterogeneity of ecosystems (Lortie et al. 2022). Increased species richness can further benefit plants by decreasing intraspecific competition (Michalet et al. 2006; Mahaut et al. 2020). Furthermore, despite costs to association with shrubs such as decreases in pollination, shrubs can still have a net benefit through increases in compensation resulting in ecological trade-offs of shrub association (Chapter 5). These trade-offs are likely more evident under higher levels of stress (Maestre et al. 2009). The stress-gradient hypothesis (SGH) states that positive interactions (such as facilitation) increase with stress levels (Maestre et al. 2009). While the SGH is often tested using abiotic stress (e.g. decreased water availability and increased temperatures) (Lortie and Callaway 2006; Casalini and Bisigato 2018), we found a similar result using biotic stress. That is, costs to pollination were offset when consumer pressure was artificially increased by applying damage to plant vegetative and floral tissues. This support of the SGH indicates that the negative interactions we observed in our studies may be less prevalent in years where biotic or possibly abiotic stress is higher (for instance drought years) (Ploughe et al. 2019). We therefore provide greater insight into how and when shrubs are useful facilitators that shape the plant communities around them despite apparent negative interactions between shrubs and their proteges.

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Appendix A: Chapter 2 Included Species and Papers

Table A.1: List of all pollinator, herbivore, and plant species included in the review. For specific association with a given study, see table A.2.

Type	Class	Order	Family	Genus	Species
plant	Dicotyledons	Apiales	Apiaceae	*Eryngium*	*yuccifolium*
plant	Dicotyledons	Apiales	Apiaceae	*Pastinaca*	*sativa*
plant	Dicotyledons	Asterales	Asteraceae	*Cardus*	*thoermeri*
plant	Dicotyledons	Asterales	Asteraceae	*Centaurea*	*solstitialis*
plant	Dicotyledons	Asterales	Asteraceae	*Rudbeckia*	*hirta*
plant	Dicotyledons	Brassicales	Cleomaceae	*Isomeris*	*arborea*
plant	Dicotyledons	Capparales	Brassicaceae	*Brassica*	*napus*
plant	Dicotyledons	Capparales	Brassicaceae	*Brassica*	*nigra*
plant	Dicotyledons	Capparales	Brassicaceae	*Brassica*	*rapa*
plant	Dicotyledons	Capparales	Brassicaceae	*Lepidium*	*papilliferum*
plant	Dicotyledons	Capparales	Brassicaceae	*Raphanus*	*raphanistrum*
plant	Dicotyledons	Cornales	Loasaceae	*Loasa*	*tricolor*
plant	Dicotyledons	Cucurbitales	Cucurbitaceae	*Cucumis*	*sativus*
plant	Dicotyledons	Euphorbiales	Euphorbiaceae	*Cnidoscolus*	*acontifolius*
plant	Dicotyledons	Fabales	Fabaceae	*Centrosema*	*virginianum*
plant	Dicotyledons	Fabales	Fabaceae	*Prosopis*	*flexuosa*
plant	Dicotyledons	Fabales	Fabaceae	*Vicia*	*faba*
plant	Dicotyledons	Gentianales	Asclepiadaceae	*Cynanchum*	*diemii*
plant	Dicotyledons	Geraniales	Balsaminaceae	*Impatiens*	*capensis*
plant	Dicotyledons	Malvales	Elaeocarpaceae	*Aristotelia*	*chilensis*
plant	Dicotyledons	Myrtales	Onagraceae	*Oenothera*	*macrocarpa*
plant	Dicotyledons	Ranunculales	Berberidaceae	*Berberis*	*darwinii*
plant	Dicotyledons	Rosales	Grossulariaceae	*Ribes*	*magellanicum*
plant	Dicotyledons	Rubiales	Rubiaceae	*Bouvardia*	*ternifolia*
plant	Dicotyledons	Santalales	Loranthaceae	*Tristerix*	*aphyllus*
plant	Dicotyledons	Santales	Loranthaceae	Peraxilla	spp.

Type	**Class**	**Order**	**Family**	**Genus**	**Species**
plant	Dicotyledons	Scrophulariaceae	Scrophulariaceae	*Castilleja*	*indivisa*
plant	Dicotyledons	Scrophulariales	Acanthaceae	*Ruellia*	*nudiflora*
plant	Dicotyledons	Scrophulariales	Scrophulariaceae	*Linaria*	*dalmatica*
plant	Dicotyledons	Scrophulariales	Scrophulariaceae	*Mimulus*	*aurantiacus*
plant	Dicotyledons	Scrophulariales	Scrophulariaceae	*Pedicularis*	*gruina*
plant	Dicotyledons	Scrophulariales	Scrophularicaeae	*Verbascum*	*nigrum*
plant	Dicotyledons	Solanales	Hydrophyllaceae	*Nemophila*	*menziesii*
plant	Dicotyledons	Solanales	Polemoniaceae	*Ipomopsis*	*aggregata*
plant	Dicotyledons	Solanales	Polemoniaceae	*Ipomopsis*	*aggregata* subssp. *Candida*
plant	Dicotyledons	Violales	Cistaceae	*Halimium*	*halimifolium*
plant	Dicotyledons	Violales	Cucurbitaceae	*Cucumis*	*melo*
plant	Dicotyledons	Violales	Cucurbitaceae	*Cucurbita*	*moschata*
plant	Monocotyledons	Asparagales	Orchidaceae	*Myrmecophila*	*tibicinis*
plant	Monocotyledons	Bromeliales	Bromeliaceae	*Aechmea*	*pectinata*
plant	Monocotyledons	Geonomeae	Arecaceae	*Calyptrogyne*	*ghiesbreghtiana*
plant	Monocotyledons	Liliales	Liliaceae	*Alstroemeria*	*aurea*
plant	Monocotyledons	Liliales	Liliaceae	*Alstroemeria*	*ligtu* va. *Simsii*
plant	Monocotyledons	Liliales	Liliaceae	*Alstroemeria*	*umbellata*
plant	Monocotyledons	Liliales	Liliaceae	*Trillium*	*grandiflorum*
plant	Monocotyledons	Liliales	Pontederiaceae	*Eichhornia*	*crassipes*
plant	Monocotyledons	Orchidales	Orchidaceae	*Platanthera*	*bifolia*
plant	Monocotyledons	Zingiberales	Heliconiaceae	*Heliconia*	*spathocircinata*
herbivore	Insecta	Coleoptera	Chrysomelidae	*Acalymma*	*vitattum*
herbivore	Insecta	Coleoptera	Chrysomelidae	Phyllotreta	sp.
herbivore	Insecta	Coleoptera	Curculionidae	*Cionus*	*nigritarsis*

Type	**Class**	**Order**	**Family**	**Genus**	**Species**
herbivore	Insecta	Coleoptera	Curculionidae	*Mecinus*	*janthiniformis*
herbivore	Insecta	Coleoptera	Meligethes	*Meligethes*	*aeneus*
herbivore	Insecta	Coleoptera	Nitidulidae	*Meligethes*	*rufimanus*
herbivore	Insecta	Diptera	Anthomyiidae	*Delia*	*radicum*
herbivore	Insecta	Hemiptera	Aphididae	*Aphis*	*alstroemeriae*
herbivore	Insecta	Hemiptera	Aphididae	*Brachycaudus*	*cardui*
herbivore	Insecta	Hemiptera	Aphididae	*Brevicoryne*	*brassicae*
herbivore	Insecta	Hemiptera	Aphididae	*Lipaphis*	*erysimi*
herbivore	Insecta	Homoptera	Aphrophoridae	*Philaenus*	*spumarius*
herbivore	Insecta	Hymenoptera	Tenthredinidae	*Athalia*	*rosae*
herbivore	Insecta	Lepidoptera	Gelechiidae	*Coleotechnites*	*eryngiella*
herbivore	Insecta	Lepidoptera	Noctuidae	*Helicoverpa*	*armigera*
herbivore	Insecta	Lepidoptera	Noctuidae	*Mamestra*	*brassicae*
herbivore	Insecta	Lepidoptera	Noctuidae	*Spodoptera*	*littoralis*
herbivore	Insecta	Lepidoptera	Oecophoridae	*Depressaria*	*pastinacella*
herbivore	Insecta	Lepidoptera	Pieridae	*Pieris*	*brassicae*
herbivore	Insecta	Lepidoptera	Pieridae	*Pieris*	*rapae*
herbivore	Insecta	Lepidoptera	Plutellidae	*Plutella*	*xylostella*
herbivore	Insecta	Orthoptera	Tettgoniidae	Tettgoniidae	spp.
herbivore	Malacostraca	Decapoda	Grapsidae	*Armases*	*angustipes*
herbivore	Mammalia	Artiodactyla	Bovidae	*Bos*	*taurus*
herbivore	Mammalia	Artiodactyla	Bovidae	*Ovis*	*aries*
herbivore	Mammalia	Artiodactyla	Cervidae	*Odocoileus*	*virginianus*
herbivore	Mammalia	Perissodactyla	Equidae	*Equus*	*ferus*
pollinator	Aves	Apodiformes	Trochilidae	*Phaethornis*	*ruber*
pollinator	Aves	Apodiformes	Trochilidae	*Ramphodon*	*naevius*
pollinator	Aves	Apodiformes	Trochilidae	*Thalurania*	*glaucopis*
pollinator	Insecta	Coleoptera			spp.

Type	**Class**	**Order**	**Family**	**Genus**	**Species**
pollinator	Insecta	Diptera	Syrphidae	*Episyrphus*	*balteatus*
pollinator	Insecta	Diptera	Syrphidae		spp.
pollinator	Insecta	Hymenoptera			spp.
pollinator	Insecta	Hymenoptera	Apidae	*Apis*	*mellifera*
pollinator	Insecta	Hymenoptera	Apidae	*Bombus*	*pensylvanicus*
pollinator	Insecta	Hymenoptera	Apidae	Bombus	spp.
pollinator	Insecta	Hymenoptera	Apidae	*Bombus*	*terrestris*
pollinator	Insecta	Hymenoptera	Apidae	Melissodes	spp.
pollinator	Insecta	Hymenoptera	Apidae	*Xylocopa*	*micans*
pollinator	Insecta	Hymenoptera	Megachilidae	Megachile	spp.
pollinator	Insecta	Lepidoptera			spp.
pollinator	Insecta	Lepidoptera	Nymphalidae	*Speyeria*	*idalia*
pollinator	Insecta	Lepidoptera	Pieridae	*Pieris*	*brassicae*
pollinator	Mammalia	Chiroptera	Glossophaginae	Glossophaga	spp.

Table A.2: List of authors with their identification as well as a list of all plant, herbivore, and pollinator species examined. The type(s) of herbivory utilized is also provided.

Author	Plant Species	Herbivore Species	Pollinator Species	Herbivory Types
Adler, 2000	*Castilleja indivisa*			florivory
Adler, Karban & Strauss, 2001	*Castilleja indivisa*			florivory
Agrawal et al., 2000	*Centaurea solstitialis*			open
Åhman, Lehrman & Ekbom, 2009	*Brassica napus*	*Meligethes aeneus*	*Bombus terrestris*	none, florivory
Arceo-Gómez, Parra-Tabla & Navarro, 2009	*Cnidoscolus acontifolius*			folivory
Aschero & Vázquez, 2009	*Prosopis flexuosa*	*Bos taurus*		grazing
Barber et al., 2015	*Cucumis sativus*	*Acalymma vitattum*		root herbivory
Benning & Moeller, 2019	*Clarkia xantiana ssp. xantiana*			open
Botto-Mahan et al., 2011	*Alstroemeria ligtu va. Simsii*			florivory
Brody & Irwin, 2012	*Ipomopsis aggregata*			grazing
Bruinsma et al., 2008	*Brassica nigra*		*Apis mellifera*	none
Buchanan, 2015	*Eichhornia crassipes*			folivory, stem damage
Caballero et al., 2013	*Tristerix aphyllus*	*Formicidae spp.*	*Sephanoides sephanoides*	florivory
Canela & Sazima, 2003	*Aechmea pectinata*	*Armases angustipes*	*Trochilidae spp.*	florivory
Cardel & Koptur, 2010	*Centrosema virginianum*		*Melissodes spp,* *Megachile spp,*	florivory

Author	**Plant Species**	**Herbivore Species**	**Pollinator Species**	**Herbivory Types**
			Bombus pensylvanicus, Xylocopa micans	
Cares-Suárez et al., 2011	*Loasa tricolor*			florivory
Cariveau & Norton, 2014	*Linaria dalmatica*	*Mecinus janthiniformis*		stem damage
Chalcoff, Lescano & Devegili, 2019	*Cardus thoermeri*	*Brachycaudus cardui*		stem damage
Cunningham, 1995	*Calyptrogyne ghiesbreghtiana*		*Glossophaga spp*	florivory
Danderson & Molano-Flores, 2010	*Eryngium yuccifolium*	*Coleotechnites eryngiella*		florivory
Ravetto Enri et al., 2017		*Bos taurus, Ovis aries*		grazing
Garrido et al., 2019		*Equus ferus*	*Lepidoptera spp., Bombus spp.*	grazing
Soper Gorden & Adler, 2016	*Impatiens capensis*			florivory
Hambäck, 2001	*Rudbeckia hirta*	*Philaenus spumarius*		stem damage
Hladun & Adler, 2009	*Cucurbita moschata*	*Acalymma vittatum*		root herbivory, folivory
Hoffmeister & Junker, 2017	*Vicia faba*		*Bombus terrestris*	none
Juenger & Bergelson, 1997	*Ipomopsis aggregata subssp. Candida*			grazing
Kelly et al., 2008	*Peraxilla spp.*	*Zelleria maculata*		florivory
Knight, 2004	*Trillium grandiflorum*	*Odocoileus virginianus*		grazing

Author	Plant Species	Herbivore Species	Pollinator Species	Herbivory Types
Krupnick & Weis, 1999	*Isomeris arborea*	*Meligethes rufimanus*		florivory
Krupnick, Weis & Campbell, 1999	*Isomeris arborea*	*Meligethes rufimanus*		florivory
Leavitt & Robertson, 2006	*Lepidium papilliferum*	*Phyllotreta sp.*		florivory
Liao et al., 2013	*Pedicularis gruina*	*Helicoverpa armigera*	*Bombus spp.*	florivory
Lohman, Zangerl & Berenbaum, 1996	*Pastinaca sativa*	*Depressaria pastinacella*		florivory
Louthan et al., 2019		*Mammalia spp.*		grazing
Lucas-Barbosa et al., 2016	*Brassica nigra*	*Pieris brassicae*	*Episyrphus balteatus, Pieris brassicae*	florivory, folivory
Lucas-Barbosa et al., 2013	*Brassica nigra*	*Pieris brassicae*	*Bombus spp, Apis mellifera*	florivory, folivory
McCall, 2010	*Nemophila menziesii*			florivory
Missagia & Alves, 2017	*Heliconia spathocircinata*	*Diptera spp.*	*Phaethornis ruber, Ramphodon naevius, Thalurania glaucopis*	florivory
Moranz, Fuhlendorf & Engle, 2014		*Bos taurus*	*Speyeria idalia*	grazing
Mothershead & Marquis, 2000	*Oenothera macrocarpa*			florivory, folivory
Motzke et al., 2015	*Cucumis sativus*			folivory
Munguía-	*Ruellia nudiflora*			folivory

Author	Plant Species	Herbivore Species	Pollinator Species	Herbivory Types
Rosas et al., 2015				
Sasal, Farji-Brener & Raffaele, 2017	*Berberis darwinii*	*Bos taurus*		grazing, folivory
Rusman et al., 2019	*Brassica nigra*	*Athalia rosae, Plutella xylostella, Brevicoryne brassicae, Lipaphis erysimi, Delia radicum*	*Episyrphus balteatus, Pieris brassicae*	stem damage, root herbivory, folivory
Scopece, Frachon & Cozzolino, 2019	*Cardus thoermeri*	*Pieris rapae, Mamestra brassicae, Spodoptera littoralis*	*Apis mellifera*	folivory
Sõber, Moora & Teder, 2010	*Verbascum nigrum*	*Cionus nigritarsis*		florivory
Sõber, Teder & Moora, 2009	*Verbascum nigrum*	*Cionus nigritarsis*		florivory
Strauss & Murch, 2004	*Cucumis melo*			folivory
Suárez, Gonzáles & Gianoli, 2009	*Alstroemeria ligtu va. Simsii*			folivory
Suárez-Esteban, Delibes & Fedriani, 2014	*Halimium halimifolium*			grazing
Sutter & Albrecht, 2016	*Brassica napus*	*Meligethes aeneus*		florivory
Torres et al., 2008	*Bouvardia ternifolia*			folivory
Tsuji et al., 2016	*Mimulus aurantiacus*			florivory
Valdivia & Niemeyer, 2005	*Alstroemeria umbellata*	*Aphis alstroemeriae*		florivory

Author	**Plant Species**	**Herbivore Species**	**Pollinator Species**	**Herbivory Types**
Vallius & Salonen, 2006	*Platanthera bifolia*			folivory
Vazquez & Simberloff, 2004	*Alstroemeria aurea, Aristotelia chilensis, Cynanchum diemii, Ribes magellanicum*	*Bos taurus*		grazing
Vulliamy, Potts & Willmer, 2006		*Bos taurus*		grazing
Zangerl & Berenbaum, 2009	*Pastinaca sativa*	*Depressaria pastinacella*		florivory
Malo, Leirana-Alcocer & Parra-Tabla, 2001	*Myrmecophila tibicinis*			florivory
Strauss, Conner & Rush, 1996	*Raphanus raphanistrum*	*Pieris rapae*		folivory

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Zangerl AR, Berenbaum MR (2009) Effects of florivory on floral volatile emissions and pollination success in the wild parsnip. Arthropod-Plant Interactions 3:181–191. https://doi.org/10.1007/s11829-009-9071-x

Table A.3: Counts of the number of studies that examined a given diversity of species for each of plants, herbivores, and pollinators. When no herbivores were examined, herbivory was mimicked through either artificial herbivory or application of chemicals. When no pollinators were examined, pollination was studied through supplemental hand pollination. Community refers to herbivory or pollination that was not restricted, that is the entire community or order (or family) of herbivores and pollinators had access to the plant.

	Plants	**Herbivores**	**Pollinators**
One Species	55	26	6
Two Species	0	2	3
Three Species	0	1	1
Four Species	1	1	0
Six Species	0	1	0
Community	5	11	44
None	0	19	7

Appendix B: Chapter 3 Sensitivity and Bias Analysis

We tested whether our results were robust to the inclusion of any one study by rerunning the full model and systematically removing each of our 171 studies one at a time to observe changes in the final outcome. This type of bias is particularly important given the range of study cases sourced from each primary study (from 1 to 68). Given this disparity in study cases per study, we also addressed the bias associated with multiple study cases coming from the same study. We re-ran the model 1000 times, each time selecting only a single study case at random from each study. For both sensitivity analyses we compared how the effect size and 95% confidence intervals varied. Finally, we tested for bias by performing a cumulative meta-analysis in which we examined how the effect sizes varied as years progressed. We also examined the visual effect of precision (the inverse of standard deviation) on effect size with a funnel plot.

Removing most studies had no effect on our results (i.e. significant negative effects stayed negative and non-significant effects stayed non-significant). However, removing 19 specific studies changed the significantly negative effects of simulated damage to non-significant (Fig. B.1). The effect of floral production was sensitive to studies of simulated damage to leaves (but not flowers or stems), and the effect of pollinators was sensitive to studies of simulated damage to flowers. The effect of plant reproduction was sensitive to studies on simulated damage to leaves, flowers and stems. In addition, the effect of pollinators was also sensitive to studies on natural damage to flowers. The results of our sensitivity analysis lend support to our conclusions regarding natural damage; however, the negative effects of simulated damage are likely still sensitive to sample size. Further research is required on simulated damage to increase the certainty of these results.

The funnel plot (Fig. B.3) is symmetrical, indicating that studies with high precision were not likely to have large effect sizes. In contrast, studies with high precision had effect sizes close to zero and the studies with the largest effect sizes and the lowest symmetry had very low precision (precision close to zero). Based on the cumulative meta-analysis (Fig. B.4), the effect size was highly variable in early years (particularly the 1990s), becoming less variable in the 2000s, before stabilizing with less variation in the 2010s and 2020s. Aside from a tendency to become more precise as the years progressed, there is little temporal correlation with effect size.

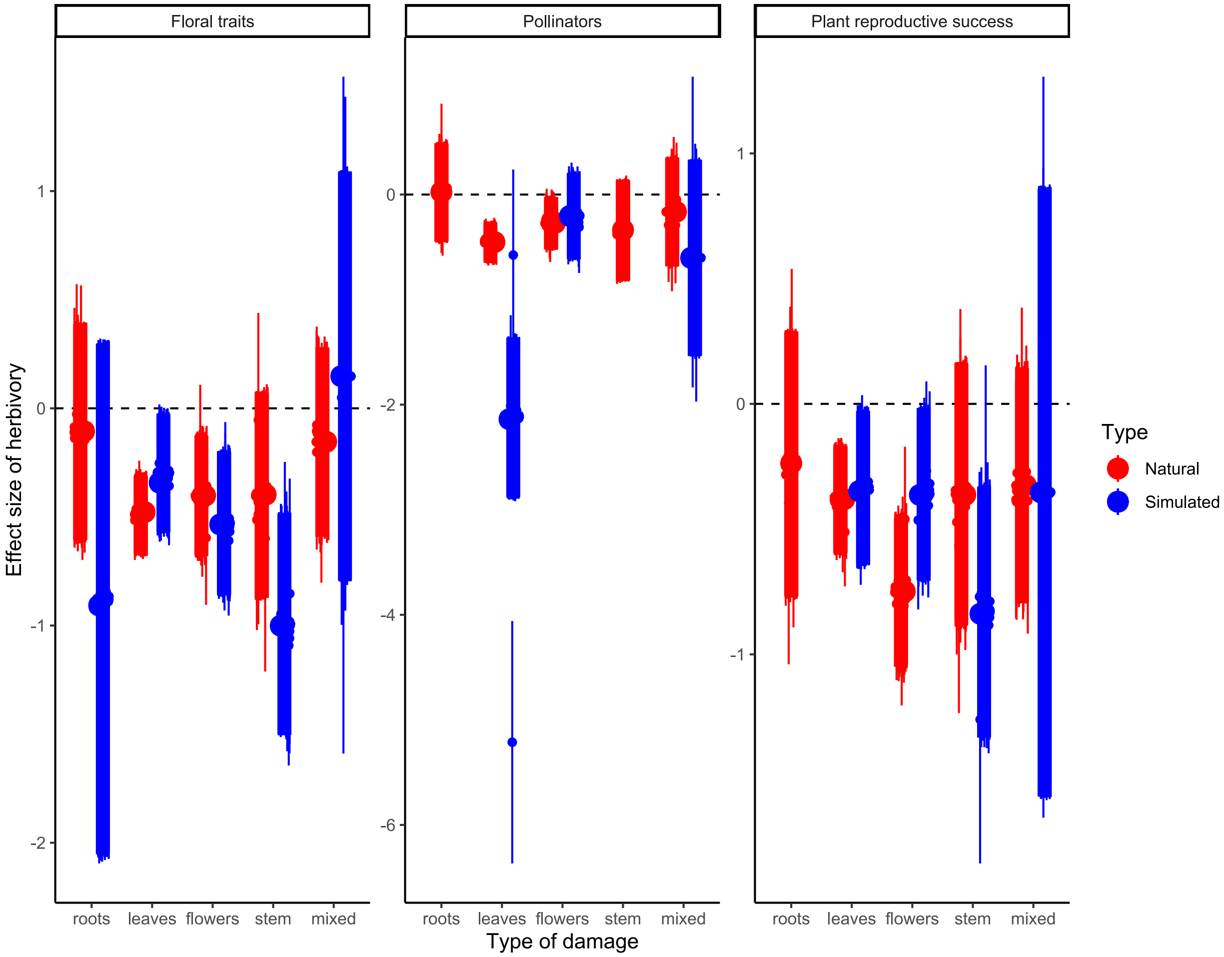

Figure B.1: Sensitivity analysis in which each study is removed one by one and the analysis rerun. Small dots and lines indicate effect sizes and 95% confidence intervals for each analysis. Large dots represent the mean from the main analysis.

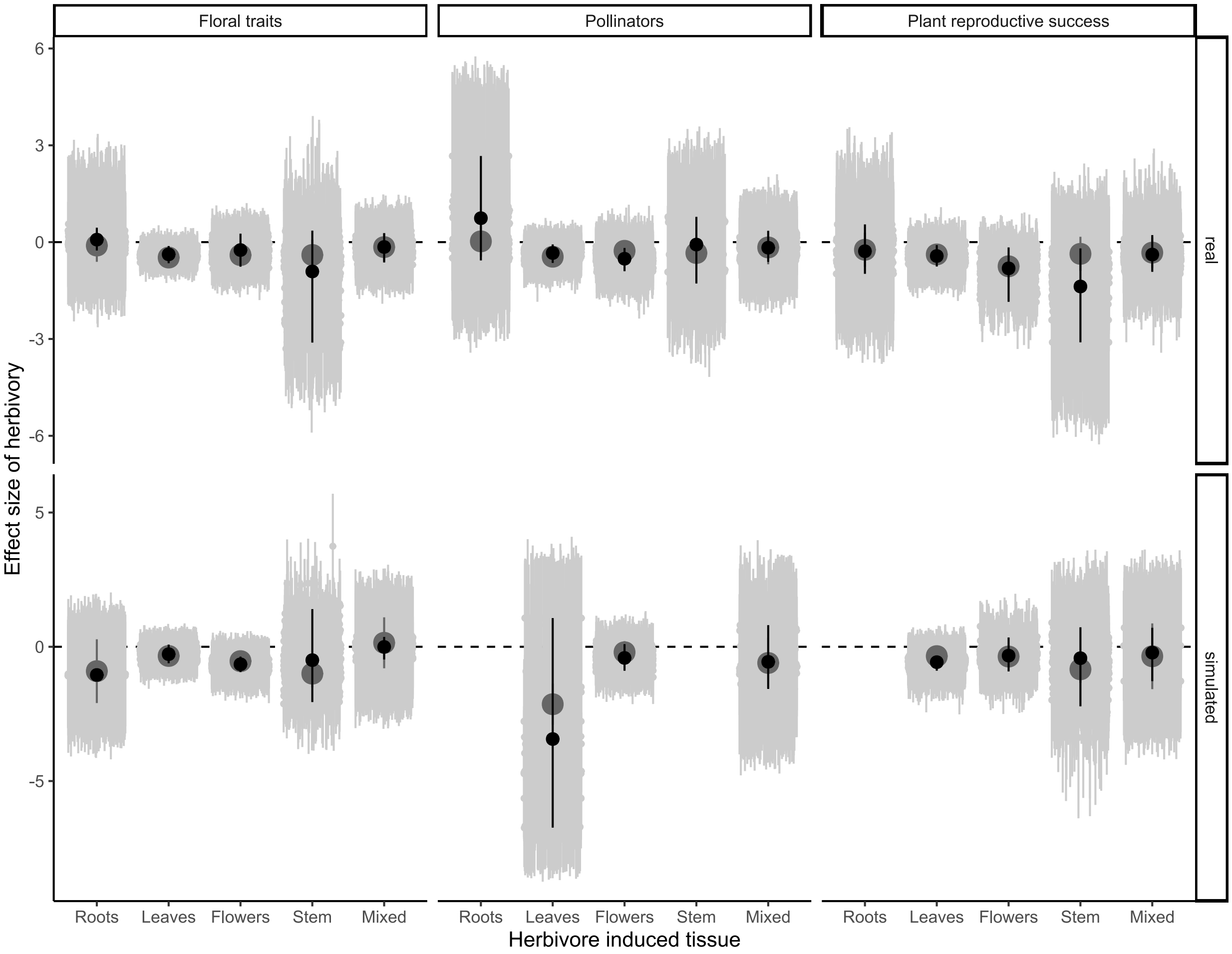

Figure B.2: Sensitivity analysis in which a single study case per study was randomly selected to run the random-effect meta-analysis. This random sampling process was repeated 1000 times. The gray lines plotted are the 95% confidence intervals from these 1000 trials and the black dot and error bars are the grand mean of all 1000 trials and 95% confidence interval. The large dark gray dot is the mean from the main analysis.

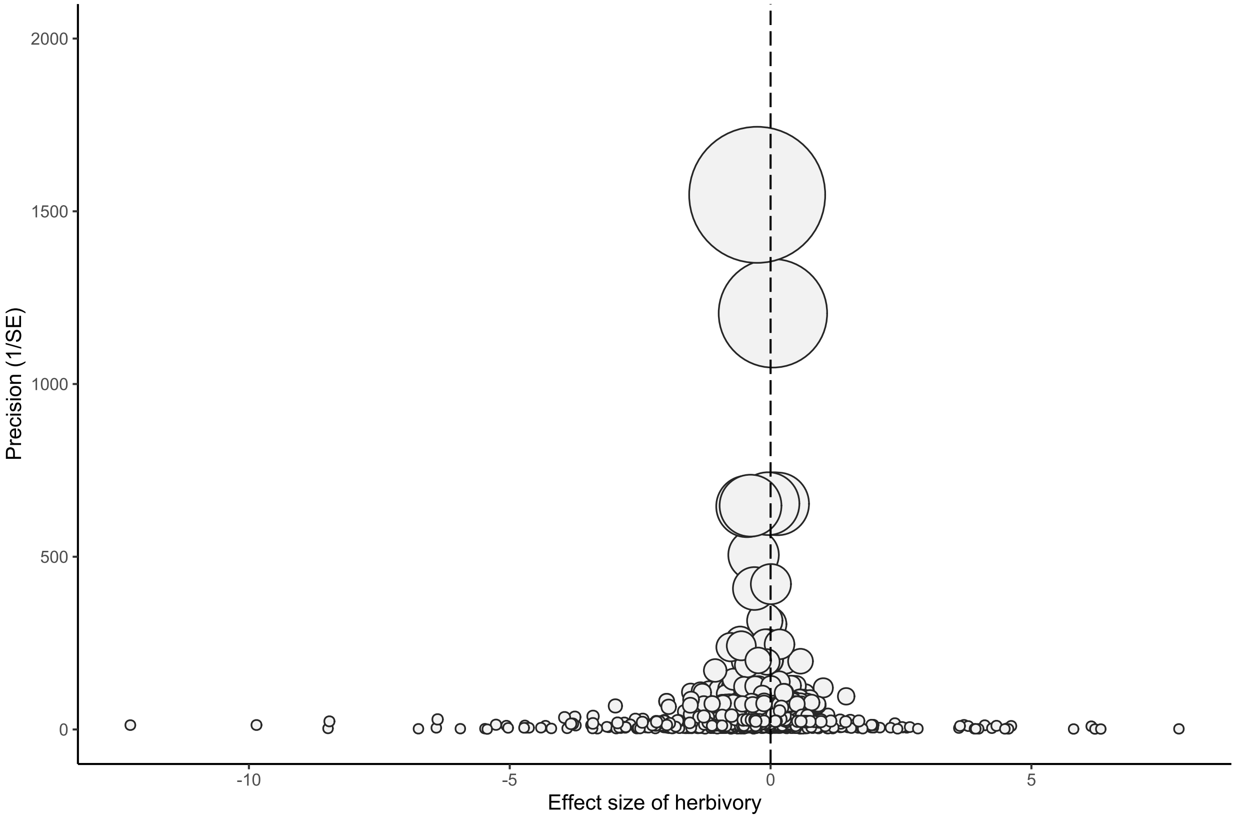

Figure B.3: Funnel plot of the relationship between effect size and precision. Dot size is relative to the inverse of standard error.

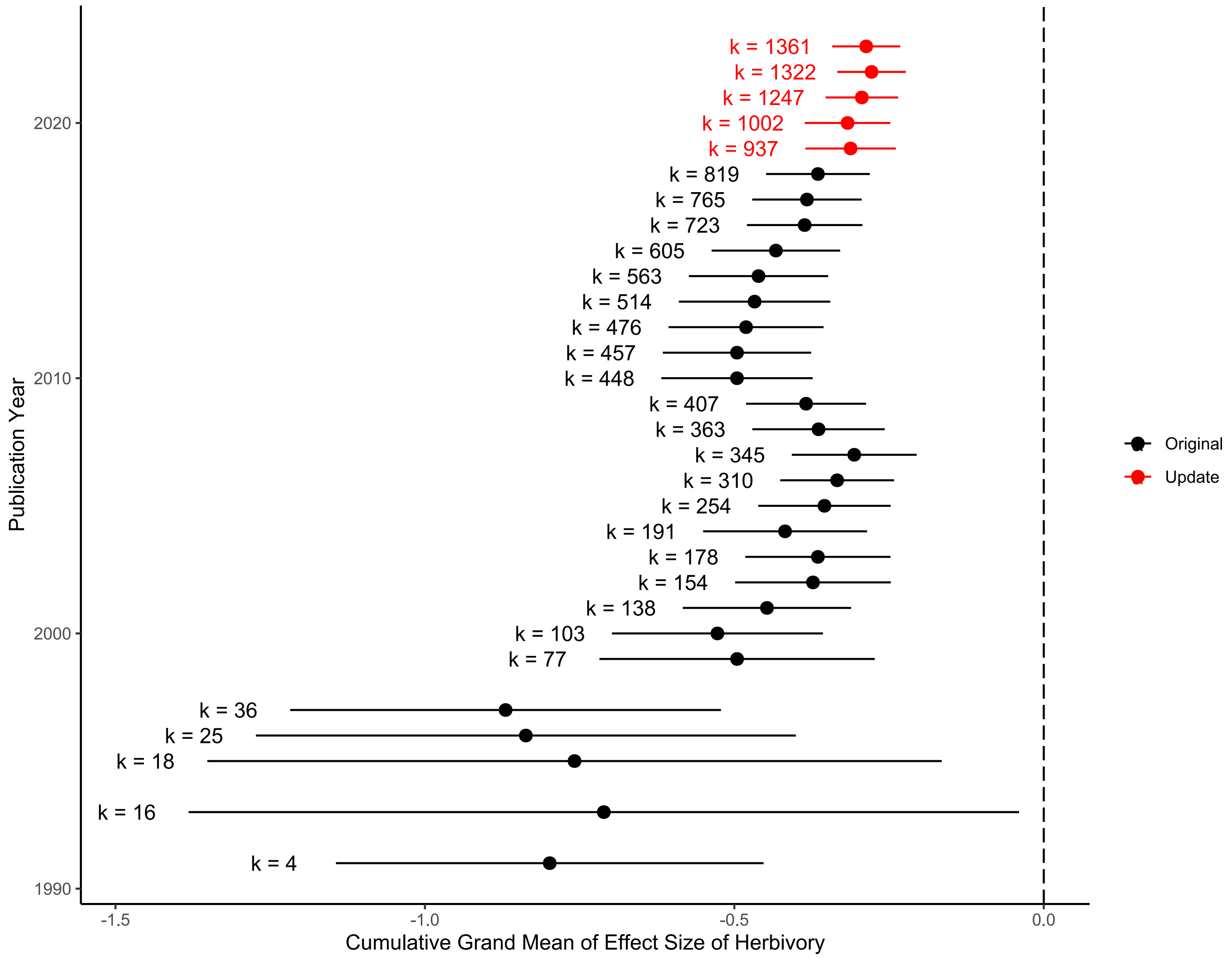

Figure B.4: The cumulative mean effect size of herbivory on reproduction calculated with increasing year. The dashed vertical line represents no effect of herbivory. Bars represent 95% confidence intervals and k = cumulated number of study cases. Publications before 2019 (sourced from Moreira et al. 2019 and Haas et al. 2020) are indicated in black and publications from the updated search are in red.

Appendix C: Chapter 3 List of Included Papers

Adler LS (2000) Alkaloid uptake increases fitness in a hemiparasitic plant via reduced herbivory and increased pollination. The American Naturalist 156:92–99. https://doi.org/10.1086/303374

Agrawal AA, Strauss SY, Stout MJ (1999) Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. Evolution 53:1093–1104. https://doi.org/10.1111/j.1558-5646.1999.tb04524.x

Aguirre LA, Adler LS (2022) Interacting antagonisms: parasite infection alters *Bombus impatiens* (Hymenoptera: Apidae) responses to herbivory on tomato plants. Journal of Economic Entomology 115:688–692. https://doi.org/10.1093/jee/toac023

Åhman I, Lehrman A, Ekbom B (2009) Impact of herbivory and pollination on performance and competitive ability of oilseed rape transformed for pollen beetle resistance. Arthropod-Plant Interactions 3:105–113. https://doi.org/10.1007/s11829-009-9061-z

April V, Simelane DO, Robertson MP (2021) Co-existence between two leaf-feeding biological control agents of *Lantana camara* alters their herbivory under semi-field conditions. Neotropical Entomology 50:959–965. https://doi.org/10.1007/s13744-021-00909-8

Arceo-Gómez G, Parra-Tabla V, Navarro J (2009) Changes in sexual expression as result of defoliation and environment in a monoecious shrub in Mexico: Implications for pollination. Biotropica 41:435–441. https://doi.org/10.1111/j.1744-7429.2009.00502.x

Aschero V, Vázquez DP (2009) Habitat protection, cattle grazing and density-dependent reproduction in a desert tree. Austral Ecology 34:901–907. https://doi.org/10.1111/j.1442-9993.2009.01997.x

Ashman T-L, Cole DH, Bradburn M (2004) Sex-differential resistance and tolerance to herbivory in a gynodioecious wild strawberry. Ecology 85:2550–2559. https://doi.org/10.1890/03-0495

Avila-Sakar G, Stephenson AG (2006) Effects of the spatial pattern of leaf damage on growth and reproduction: Whole plants. International Journal of Plant Sciences 167:1021–1028. https://doi.org/10.1086/505609

Balbuena MS, Broadhead GT, Dahake A, et al (2022) Mutualism has its limits: Consequences of asymmetric interactions between a well-defended plant and its herbivorous pollinator. Philosophical Transactions of the Royal Society B: Biological Sciences 377:20210166. https://doi.org/10.1098/rstb.2021.0166

Barber NA, Milano NJ, Kiers ET, et al (2015) Root herbivory indirectly affects above- and below-ground community members and directly reduces plant performance. Journal of Ecology 103:1509–1518. https://doi.org/10.1111/1365-2745.12464

Barragán-Fonseca KY, Greenberg LO, Gort G, et al (2023) Amending soil with insect exuviae improves herbivore tolerance, pollinator attraction and seed yield of *Brassica nigra* plants. Agriculture, Ecosystems & Environment 342:108219. https://doi.org/10.1016/j.agee.2022.108219

Beckett K, Elle E, Kremen C, et al (2022) Hyperabundant black-tailed deer impact endangered Garry oak ecosystem floral and bumblebee communities. Global Ecology and Conservation 38:e02237. https://doi.org/10.1016/j.gecco.2022.e02237

Benning JW, Moeller DA (2019) Maladaptation beyond a geographic range limit driven by antagonistic and mutualistic biotic interactions across an abiotic gradient. Evolution 73:1–16. https://doi.org/10.1111/evo.13836

Blatt SE, Smallegange RC, Hess L, et al (2008) Tolerance of *Brassica nigra* to *Pieris brassicae* herbivory. Botany 86:641–648. https://doi.org/10.1139/B08-040

Boalt E, Lehtilä K (2007) Tolerance to apical and foliar damage: Costs and mechanisms in *Raphanus raphanistrum*. Oikos 116:2071–2081. https://doi.org/10.1111/j.2007.0030-1299.16056.x

Botto-Mahan C, Ramírez PA, Ossa CG, et al (2011) Floral herbivory affects female reproductive success and pollinator visitation in the perennial herb *Alstroemeria ligtu* (Alstroemeriaceae). International Journal of Plant Sciences 172:1130–1136. https://doi.org/10.1086/662029

Brody AK, Irwin RE (2012) When resources don’t rescue: Flowering phenology and species interactions affect compensation to herbivory in *Ipomopsis aggregata*. Oikos 121:1424–1434. https://doi.org/10.1111/j.1600-0706.2012.20458.x

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Bruinsma M, Lucas-Barbosa D, ten Broeke CJM, et al (2014) Folivory affects composition of nectar, floral odor and modifies pollinator behavior. Journal of Chemical Ecology 40:39–49. https://doi.org/10.1007/s10886-013-0369-x

Brys R, Shefferson RP, Jacquemyn H (2011) Impact of herbivory on flowering behaviour and life history trade-offs in a polycarpic herb: A 10-year experiment. Oecologia 166:293–303. https://doi.org/10.1007/s00442-010-1842-7

Buchanan AL (2015) Effects of damage and pollination on sexual and asexual reproduction in a flowering clonal plant. Plant Ecology 216:273–282. https://doi.org/10.1007/s11258-014-0434-8

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Bustos-Segura C, Hernandez-Cumplido J, Traine J, Benrey B (2021) Herbivory and jasmonate treatment affect reproductive traits in wild Lima bean, but without transgenerational effects. American Journal of Botany 108:2096–2104. https://doi.org/10.1002/ajb2.1786

Caballero P, Ossa CG, Gonzáles WL, et al (2013) Testing non-additive effects of nectar-robbing ants and hummingbird pollination on the reproductive success of a parasitic plant. Plant Ecology 214:633–640. https://doi.org/10.1007/s11258-013-0195-9

Camara T, Arnan X, Barbosa VS, et al (2020) Disentangling the effects of foliar vs. floral herbivory of leaf-cutting ants on the plant reproductive success of *Miconia nervosa* (Smith) Triana (Family Melastomataceae). Bulletin of Entomological Research 110:77–83. https://doi.org/10.1017/S0007485319000294

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Cardoso JCF, Johnson SD, Maciel AA, Oliveira PE (2021) Florivory can facilitate rain-assisted autogamy in a deceptive tropical orchid. Science of Nature 108:39 https://doi.org/10.1007/s00114-021-01752-y

Cares-Suárez R, Poch T, Acevedo RF, et al (2011) Do pollinators respond in a dose-dependent manner to flower herbivory?: An experimental assessment in *Loasa tricolor* (Loasaceae). Gayana Botánica 68:176–181. https://doi.org/10.4067/S0717-66432011000200007

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Appendix D: ***Malacothrix glabrata***

Figure D.1: *Larrea tridentata* shrub and *Malacothrix glabrata* in the Mojave Desert.

Appendix E: Chapter 4 Post-Hoc Analyses

Table E.1: Effect of microsite on net plant density and net floral density, as well as the effect of microsite, species, species richness, and net plant density (density) on species-level plant density and flowers per plant (floral density).

	Plant Density		Flower Density	
Factor	χ^2	**p-value**	χ^2	**p-value**
Direct Community Effects				
microsite	11.3	0.00077*	3.53	0.06
Species-Specific Effects				
microsite	2.6	0.11	7.32	0.0068*
species	70.9	< 0.0001*	19.2	0.0018*
plant diversity	185	< 0.0001*	34.9	< 0.0001*
plant density	14.8	0.00012*	11.8	0.00059*
microsite:species	79.5	< 0.0001*	48.5	< 0.0001*
microsite:plant diversity	14.1	0.00017*	7.1	0.0077*
species:plant diversity	5.56	0.35	12.3	0.03*
microsite:plant density	4.27	0.039*	5.48	0.019*
species:plant density	28.2	< 0.0001*	4.67	0.46
plant diversity:plant density	1.54	0.21	1.53	0.22
microsite:species:plant diversity	7.39	0.19	6.75	0.24
microsite:species:plant density	24.2	2e-04*	10.9	0.053
microsite:plant diversity:plant density	14.8	0.00012*	0.469	0.49
species:plant diversity:plant density	3.34	0.65	10.3	0.067
microsite:species:plant diversity:plant density	7.83	0.17	2.58	0.76

Table E.2: The post-hoc difference between shrub and open microsites for each of the 6 most common species and all species pooled for both direct and indirect interactions. Direct interactions contrast the number of plants, the number of flowers per plant, and species richness between microsites while indirect interactions contrast the slope of the effect of either community plant density or species richness on species' plant or floral density. The log estimate of the difference between open and shrub microsites (negative values are greater under shrubs and positive values are greater in the open), the t-ratio and associated p-value are presented. If no species is provided, the contrast is model-wide.

Species	Log Estimate (SE)	z ratio	p-value
Plant Density			
Direct Interaction			
	0.499 (0.149)	3.3600	0.00077*
Chaenactis fremonti	-0.76 (0.364)	-2.0900	0.037*
Chylismia claviformis auranticus	0.191 (0.567)	0.3360	0.74
Cryptantha angustifolia	5.79 (2.24)	2.5900	0.0096*
Cryptantha circumscissa	2.26 (0.392)	5.7700	< 0.0001*
Eriophyllum wallacei	1.01 (0.285)	3.5500	0.00038*
Malacothrix glabrata	-0.891 (0.343)	-2.6000	0.0094*
Plant Density			
Indirect Interaction: Plant Density			
Chaenactis fremonti	0.222 (0.069)	3.2100	0.0013*
Chylismia claviformis auranticus	0.373 (0.11)	3.3900	0.00069*
Cryptantha angustifolia	1.23 (0.494)	2.5000	0.012*
Cryptantha circumscissa	0.269 (0.0896)	3.0000	0.0027*
Eriophyllum wallacei	0.0046 (0.058)	0.0793	0.94
Malacothrix glabrata	0.157 (0.0607)	2.5900	0.0097*
Plant Density			
Indirect Interaction: Species Richness			
Chaenactis fremonti	-0.46 (0.244)	-1.8800	0.06
Chylismia claviformis auranticus	-1.02 (0.348)	-2.9300	0.0034*
Cryptantha angustifolia	-2.73 (0.949)	-2.8800	0.004*

Species	Log Estimate (SE)	z ratio	p-value
Cryptantha circumscissa	-0.798 (0.268)	-2.9700	0.0029*
Eriophyllum wallacei	-0.543 (0.192)	-2.8200	0.0048*
Malacothrix glabrata	-0.424 (0.249)	-1.7000	0.089
Floral Density Per Plant			
Direct Interaction			
	0.72 (0.383)	1.8800	0.06
Chaenactis fremonti	0.403 (0.607)	0.6630	0.51
Chylismia claviformis auranticus	-0.275 (0.653)	-0.4220	0.67
Cryptantha angustifolia	5.13 (1.34)	3.8300	0.00013*
Cryptantha circumscissa	2.7 (0.955)	2.8300	0.0046*
Eriophyllum wallacei	1.19 (0.489)	2.4200	0.015*
Malacothrix glabrata	-0.802 (0.449)	-1.7900	0.074
Floral Density Per Plant			
Indirect Interaction: Plant Density			
Chaenactis fremonti	0.266 (0.127)	2.1000	0.036*
Chylismia claviformis auranticus	0.144 (0.138)	1.0400	0.3
Cryptantha angustifolia	0.904 (0.354)	2.5500	0.011*
Cryptantha circumscissa	0.157 (0.222)	0.7090	0.48
Eriophyllum wallacei	-0.0856 (0.0825)	-1.0400	0.3
Malacothrix glabrata	0.126 (0.0692)	1.8300	0.067
Floral Density Per Plant			
Indirect Interaction: Species Richness			
Chaenactis fremonti	-0.424 (0.421)	-1.0100	0.31
Chylismia claviformis auranticus	-0.19 (0.545)	-0.3500	0.73
Cryptantha angustifolia	-2.41 (0.967)	-2.4900	0.013*
Cryptantha circumscissa	-1.01 (0.606)	-1.6600	0.096
Eriophyllum wallacei	0.0115 (0.342)	0.0336	0.97

Species	**Log Estimate (SE)**	**z ratio**	**p-value**
Malacothrix glabrata	-0.678 (0.303)	-2.2400	0.025*
Species Richness			
Direct Interaction			
	0.331 (0.0896)	3.7000	0.00022*

*p < 0.05

Appendix F: Chapter 5 Post-Hoc Analyses

Table F.1: The post-hoc multiple comparisons of flowering between treatment levels of each of microsite (open - shrub), supplemental pollination (normal - supplemental), 50% florivory (florivory - no florivory), and 50% folivory (folivory - no folivory). Each contrast is presented under all iterations of each other fixed grouping factor. The logarithm of the estimated marginal mean (and standard error) of the difference in flowering between each treatment level, the t-ratio, and associated p-value are presented. Degrees of freedom are 301 in all cases.

Fixed Trait 1	Fixed Trait 2	Fixed Trait 3	Contrast	Log Estimate (SE)	t ratio	p-value
control	control	ambient pollination	open - shrub	0.797 (0.523)	1.52	0.13
folivory	control	ambient pollination	open - shrub	-0.447 (0.574)	-0.779	0.44
control	florivory	ambient pollination	open - shrub	-0.0159 (0.516)	-0.0308	0.98
folivory	florivory	ambient pollination	open - shrub	-1.31 (0.497)	-2.64	0.0083*
control	control	supplemental	open - shrub	-0.318 (0.41)	-0.775	0.44
folivory	control	supplemental	open - shrub	-0.432 (0.37)	-1.17	0.24
control	florivory	supplemental	open - shrub	1.16 (0.749)	1.55	0.12
folivory	florivory	supplemental	open - shrub	-2.87 (0.541)	-5.31	0.0001*
control	control	open	ambient pollination - supplemental	-2.25 (1.75)	-1.28	0.2
folivory	control	open	ambient pollination - supplemental	-0.556 (1.76)	-0.317	0.75
control	florivory	open	ambient pollination - supplemental	-2.81 (1.78)	-1.59	0.11
folivory	florivory	open	ambient pollination - supplemental	1.25 (1.78)	0.703	0.48
control	control	shrub	ambient pollination - supplemental	-3.36 (1.76)	-1.91	0.056
folivory	control	shrub	ambient pollination -	-0.541	-0.308	0.76

Fixed Trait 1	Fixed Trait 2	Fixed Trait 3	Contrast	Log Estimate (SE)	t ratio	p-value
			supplemental	(1.76)		
control	florivory	shrub	ambient pollination - supplemental	-1.64 (1.79)	-0.913	0.36
folivory	florivory	shrub	ambient pollination - supplemental	-0.31 (1.78)	-0.174	0.86
control	open	ambient pollination	control - folivory	-0.638 (1.76)	-0.362	0.72
florivory	open	ambient pollination	control - folivory	-0.992 (1.77)	-0.561	0.57
control	shrub	ambient pollination	control - folivory	-1.88 (1.77)	-1.06	0.29
florivory	shrub	ambient pollination	control - folivory	-2.29 (1.77)	-1.3	0.19
control	open	supplemental	control - folivory	1.06 (1.74)	0.605	0.55
florivory	open	supplemental	control - folivory	3.07 (1.79)	1.72	0.085
control	shrub	supplemental	control - folivory	0.94 (1.75)	0.538	0.59
florivory	shrub	supplemental	control - folivory	-0.961 (1.81)	-0.531	0.6
control	open	ambient pollination	control - florivory	2.8 (1.75)	1.6	0.11
folivory	open	ambient pollination	control - florivory	2.45 (1.77)	1.38	0.17
control	shrub	ambient pollination	control - florivory	1.99 (1.76)	1.13	0.26
folivory	shrub	ambient pollination	control - florivory	1.58 (1.77)	0.895	0.37
control	open	supplemental	control - florivory	2.24 (1.77)	1.26	0.21
folivory	open	supplemental	control - florivory	4.26 (1.76)	2.42	0.016*
control	shrub	supplemental	control - florivory	3.72 (1.79)	2.08	0.038*
folivory	shrub	supplemental	control - florivory	1.82 (1.77)	1.03	0.3

Table F.2: The post-hoc multiple comparisons of seed mass between treatment levels of each of microsite (open - shrub), supplemental pollination (normal - supplemental), 50% florivory (florivory - no florivory), and 50% folivory (folivory - no folivory). Each contrast is presented under all iterations of each other fixed grouping factor. The logarithm of the estimated marginal mean (and standard error) of the difference in seed mass between each treatment level, the t-ratio, and associated p-value are presented. Degrees of freedom are 300 in all cases.

Fixed Trait 1	**Fixed Trait 2**	**Fixed Trait 3**	**Contrast**	**Log Estimate (SE)**	**t ratio**	**p-value**
control	control	ambient pollination	open - shrub	1.08 (0.563)	1.92	0.055
folivory	control	ambient pollination	open - shrub	-2.07 (0.71)	-2.92	0.0035*
control	florivory	ambient pollination	open - shrub	-3.59 (0.738)	-4.87	0.0001*
folivory	florivory	ambient pollination	open - shrub	-6.82 (0.466)	-14.6	0.0001*
control	control	supplemental	open - shrub	-2.86 (0.626)	-4.57	0.0001*
folivory	control	supplemental	open - shrub	-2.66 (0.468)	-5.69	0.0001*
control	florivory	supplemental	open - shrub	-2.3 (0.695)	-3.31	0.00094*
folivory	florivory	supplemental	open - shrub	-7.23 (0.825)	-8.76	0.0001*
control	control	open	ambient pollination - supplemental	-1.43 (2.58)	-0.556	0.58
folivory	control	open	ambient pollination - supplemental	0.29 (2.57)	0.112	0.91
control	florivory	open	ambient pollination - supplemental	-5.17 (2.68)	-1.93	0.054
folivory	florivory	open	ambient pollination - supplemental	0.679 (2.65)	0.256	0.8
control	control	shrub	ambient pollination - supplemental	-5.37 (2.58)	-2.08	0.037*
folivory	control	shrub	ambient pollination - supplemental	-0.3 (2.58)	-0.116	0.91
control	florivory	shrub	ambient pollination	-3.88 (2.66)	-1.46	0.15

Fixed Trait 1	Fixed Trait 2	Fixed Trait 3	Contrast	Log Estimate (SE)	t ratio	p-value
			- supplemental			
folivory	florivory	shrub	ambient pollination - supplemental	0.273 (2.64)	0.103	0.92
control	open	ambient pollination	control - folivory	-1.27 (2.57)	-0.494	0.62
florivory	open	ambient pollination	control - folivory	-2.19 (2.65)	-0.826	0.41
control	shrub	ambient pollination	control - folivory	-4.42 (2.58)	-1.72	0.086
florivory	shrub	ambient pollination	control - folivory	-5.42 (2.63)	-2.06	0.04*
control	open	supplemental	control - folivory	0.454 (2.58)	0.176	0.86
florivory	open	supplemental	control - folivory	3.66 (2.68)	1.36	0.17
control	shrub	supplemental	control - folivory	0.65 (2.58)	0.252	0.8
florivory	shrub	supplemental	control - folivory	-1.27 (2.67)	-0.474	0.64
control	open	ambient pollination	control - florivory	4.09 (2.64)	1.55	0.12
folivory	open	ambient pollination	control - florivory	3.17 (2.59)	1.23	0.22
control	shrub	ambient pollination	control - florivory	-0.585 (2.64)	-0.221	0.82
folivory	shrub	ambient pollination	control - florivory	-1.58 (2.57)	-0.614	0.54
control	open	supplemental	control - florivory	0.354 (2.62)	0.135	0.89
folivory	open	supplemental	control - florivory	3.56 (2.64)	1.35	0.18
control	shrub	supplemental	control - florivory	0.912 (2.6)	0.351	0.73
folivory	shrub	supplemental	control - florivory	-1 (2.65)	-0.378	0.71