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

Abstract

In arid ecosystems, the facilitative effects of shrubs can lead to concentrations of annual plants beneath the canopy. When the beneficiary blooms, there is the potential for them to interact with shrubs indirectly via pollinators. Creosote bush, *Larrea tridentata* is a common, dominant shrub of the Mojave Desert. Its structural complexity, evergreen canopy and copious nectar-rich flowers suggest it has the capacity to influence the pollination of associated plants both florally and non-florally. We hypothesized that prior to blooming, *L. tridentata* would interfere with pollination of its annuals, and that this would be alleviated by the magnet species effect when *L. tridentata* entered a full bloom. Using the abundant desert dandelion, *Malacothrix glabrata,* as a phytometer we tested for changes in pollinator visitation rates when placed under the shrub. *L. tridentata* interfered with the pollination of *M. glabrata*, and this competition intensified when *L. tridentata* entered a full bloom. The decrease in visitation was driven by behavioural responses of solitary bees and syrphid flies. In this system, we found that *L. tridentata* supports annual and arthropod communities and provided stable microclimates. This study highlights the positive role of *L. tridentata* as a foundation plant and shows that it engages in dynamic positive and negative interactions with the surrounding communities simultaneously.

Introduction

Foundation plants positively influence the structure of the surrounding plant communities by creating locally stable conditions for other species ([Ellison et al., 2005](#_ENREF_24)). In arid environments, shrubs can act as keystone facilitators, directly benefiting associated understory annual plants via multiple mechanistic pathways across all life stages ([Filazzola and Lortie, 2014](#_ENREF_26)). These include stress amelioration ([McIntire and Fajardo, 2014](#_ENREF_48)), improved water and nutrient availability ([Franco et al., 1994](#_ENREF_30)), and seed trapping ([Flores and Jurado, 2003](#_ENREF_29)). Direct interactions between shrubs and annuals may be simultaneously facilitative and competitive ([Bertness and Callaway, 1994](#_ENREF_5); [Callaway and Walker, 1997b](#_ENREF_13); [Holzapfel and Mahall, 1999](#_ENREF_36)) and it is posited that their relative importance varies with abiotic stress ([Bertness and Callaway, 1994](#_ENREF_5); [Schafer et al., 2012](#_ENREF_74); [Tielbörger and Kadmon, 2000](#_ENREF_83)). These complex sets of interactions lead to patterns in species coexistence and structure plant communities ([Brooker et al., 2008](#_ENREF_9); [Valiente‐Banuet and Verdú, 2007](#_ENREF_86)). The facilitative effects of desert shrubs can lead to concentrations of annual plants beneath the shrub canopy ([Facelli and Temby, 2002](#_ENREF_25)). This close spatial proximity of shrubs and annuals undoubtedly gives rise to indirect interactions. Indirect interactions arise whenever a third species alters the interaction between two other species ([Callaway and Pennings, 2000](#_ENREF_11); [Callaway and Walker, 1997b](#_ENREF_13); [Wootton, 1994](#_ENREF_92)). If the associated annual is a flowering plant, then there is the possibility for the plants to interact indirectly via pollinators.

The study of the underlying mechanisms of pollinator mediated interactions is dominated by pathways requiring co-blooming. These are primarily extensions to optimal foraging theory ([Pyke, 1984](#_ENREF_64); [Pyke et al., 1977](#_ENREF_65)) with flowers as the central resources for which pollinators forage. Thus plants can become more attractive by combining their floral displays to be larger ([Schemske, 1981](#_ENREF_75)), or more diverse ([Ghazoul, 2006](#_ENREF_31)). Flowering desert shrubs offer concentrations of floral resources for foraging pollinators, and may facilitate their co-blooming annuals via the magnet species effect. Magnet species are particularly attractive to pollinators, increasing local pollinator abundances which benefit their less attractive neighbours ([Laverty, 1992](#_ENREF_44); [Thomson, 1978](#_ENREF_82)). The relatively large size of shrubs makes them salient features of desert scrub ecosystems. This, combined with their structural complexity suggests that non-co-blooming pathways of interactions may be prominent in desert systems. Shrubs may facilitate their annual understory by offering shelter or habitat for pollinators. Conversely, shrubs may interfere with the pollination of their understory. For example, shading by the shrub *Lonicera* decreased pollinator visitation and pollen deposition to its understory annuals ([McKinney and Goodell, 2010](#_ENREF_49)). In forests, pollination rates tend to be higher under canopy gaps ([Proctor et al., 2012](#_ENREF_62); [Walters and Stiles, 1996](#_ENREF_90)). Alternatively, annuals growing under shrubs could be obscured from foraging pollinators. Therefore, there is the potential for these indirect interactions to be simultaneously positive and negative.

The Mojave Desert is a biodiversity hotspot supporting 659 species of bees ([Saul-Gershenz et al., 2012](#_ENREF_73)) and 1680 species of vascular plants ([Rundel and Gibson, 2005](#_ENREF_70)). Despite the celebrated biodiversity of South Western deserts, pollinator-mediated interactions in this region are largely unstudied. Intraspecific density has been shown to be positive for desert mustard ([Roll et al., 1997](#_ENREF_68)), however interspecific studies have primarily focused on competition within cacti systems in the Sonoran Desert ([Fleming et al., 2001](#_ENREF_28)). Plant-pollinator systems in southwest deserts are home to rare obligate mutualisms such as the Joshua tree *Yucca brevifolia* and Yucca moths ([Pellmyr, 2003](#_ENREF_61)), and the Senita cactus *Pachycereus schottii* and senita moths ([Fleming and Holland, 1998](#_ENREF_27)), and are often considered highly specialized. The degree of specialization of desert ecosystems is a subject of ongoing debate. Desert organisms are hypothesized to adapt to high environmental variability by generalizing resource use ([Chesson et al., 2004](#_ENREF_18)), and this has garnered recent empirical support in pollination networks ([Chacoff et al., 2012](#_ENREF_17)). However, few one-to-one relationships have been found with solitary bees ([Simpson and Neff, 1987](#_ENREF_78)), and bees still visit even Senita cactus ([Holland and Fleming, 2002](#_ENREF_35)). Therefore, despite the high number of specialists present there is the potential for interactions between most plant species.

*Larrea tridentata* (Zygophyllaceae) or creosote bush, has been a dominant flowering shrub of the southwestern United States for 25 000 years ([Betancourt et al., 1990](#_ENREF_6)). Highly tolerant to temperature extremes, it is able to maintain photosynthesis even under high temperatures and low water potentials ([Barbour et al., 2007](#_ENREF_4)). *L. tridentata* primarily reproduces clonally leading to individuals that are exceptionally long lived. Clones that are over 1000 years old have been documented ([Vasek, 1980](#_ENREF_87)). The full pollinator guild contains 22 specialist pollinators and more than 80 generalists ([Minckley et al., 1999](#_ENREF_53)). The associated pollinator guilds are highly variable over space and most shrubs will only interact with 20% of their full guild, but there is a stable core guild ([Cane et al., 2005](#_ENREF_15)). *L. tridentata* is one of the most reliable flowerer’s in the Mojave as it has one of the lowest rainfall thresholds (12 mm) to blooming ([Bowers and Dimmitt, 1994](#_ENREF_8)) It produces copious nectar and pollen rich flowers ([Simpson et al., 1977](#_ENREF_77)) and therefore provides critical resources to pollinators in drought years. *L. tridentata* acts as a nurse shrub for other desert perennials such as *Opuntia leptocaulis*, ([Yeaton, 1978](#_ENREF_93)), *Peniocereus striatus* ([Suzán et al., 1994](#_ENREF_79)), as well as facilitating native annuals ([Schafer et al., 2012](#_ENREF_74)), but competes with some species through allelopathy ([Mahall and Callaway, 1991](#_ENREF_45), [1992](#_ENREF_46)).

A plant’s life stage can alter the balance of facilitative and competitive interactions ([Bruno et al., 2003](#_ENREF_10); [Callaway and Walker, 1997a](#_ENREF_12); [Pugnaire et al., 1996](#_ENREF_63); [Rousset and Lepart, 2000](#_ENREF_69); [Valiente-Banuet et al., 1991](#_ENREF_85)). The majority of research on plant-plant interactions focusses at one life stage ([Goldberg et al., 2001](#_ENREF_32); [Tielbörger and Kadmon, 2000](#_ENREF_83)) which is inadequate for making conclusions about fitness levels within populations ([McPeek and Peckarsky, 1998](#_ENREF_50)). For example, within some nurse plant systems young plants are facilitated during establishment, but later compete with their nurses for resources ([Yeaton, 1978](#_ENREF_93)). For plants, the shift from vegetative growth to reproductive growth is a major event. Foundation plants have benefits that can scale to trophic levels beyond their surrounding plant community ([Reid and Lortie, 2012](#_ENREF_66); [Ruttan et al., 2016](#_ENREF_72)), however if these benefits change with reproductive shifts is not known.

The aim of this study was to test for the influence of *Larrea tridentata* on the pollination of the commonly co-occurring annual *Malacothrix glabrata*. *L. tridentata* and *M. glabrata* co-flower at beginning and ends of their bloom period ([Jennings, 2001](#_ENREF_40)), making it an interesting and relevant system to model changes in interactions over a season. The main hypothesis is that *L. tridentata* interferes with the pollination of *M. glabrata* it large size obscures them from pollinators, but the interaction shifts to facilitation when co-blooming because it acts as a magnet species due to its high abundance of floral resources. Understanding interactions for pollination at a community level is critical for understanding potential impacts of any decline in pollinator populations. If shrubs facilitate their understory annuals, they may be able to buffer their associates from a pollinator decline. How if they outcompete them, their associates may be particularly vulnerable. Species interactions are important for structuring desert communities despite intense environmental pressure ([Chesson et al., 2004](#_ENREF_18)). By separating mechanistic interaction pathways (i.e. co-blooming, not co-blooming), we may gain insight into adaptations to both environmental and species interactions.

**Methods**

Study site

The study area has an extent of 0.07 km2, and is located in the mouth of Sunset Cove on the property of the Granites Mountains Desert Research Station, within the Mojave National Preserve in California (34°46'26.5"N 115°39'31.3"W). The cove is created by tall rock formations on three sides, gently sloping and widening to the south. The diverse shrub and cactus community includes *Larrea tridentata*, *Acamptopappus sphaerocephalus*, *Ambrosia salsola, Eriogonum fasciculatum, Cylindropuntia acanthacarpa, Cylindropuntia echinocarpa* and *Thamnosa montana*. The most common flowering annuals present during the study period were *Cryptantha sp, Phacelia fremontii, Eriophyllum wallacei, Gilia sp., Phacelia tanacetifolia, Malacothrix glabrata* and *Chaenactis fremontii*.

Phytometer species

Phytometers are individual plants used in a controlled way as environmental indicators ([Clements and Goldsmith, 1924](#_ENREF_19)). We used the desert dandelion *Malacothrix glabrata* (Asteracae) as a phytometer to measure pollination services. *M. glabrata* is an abundant, native annual wildflower that commonly co-occurs with *L. tridentata*. The flowerheads are dense with yellow corollas and grow up to 40 cm tall ([Morhardt and Morhardt, 2004](#_ENREF_56)). *M. glabrata* is insect-pollinated, including bees in the genus *Nomadopsis* ([Rutowski and Alcock, 1980](#_ENREF_71)) and *Anthidium* ([Wainwright, 1978](#_ENREF_89)) as well as short-winged flower beetles ([Cline and Audisio, 2010](#_ENREF_20)). Several of the 24 species of *Malacothrix* are self-compatible ([Davis and Philbrick, 1986](#_ENREF_22)), however the reproductive biology of *M. glabrata* has not been studied in detail.

Study design

60 medium-sized (mean width: 336 cm, mean height: 209 cm) *L. tridentata* shrubs possessing developed floral buds and minimal perennial understory were chosen across the study site. Microsites were located in a paired fashion; one inside the dripline of the focal plant (“shrub”) and one a minimum of 1.5 m away in an open area (“open”), both on the south side of the shrub to minimize shading. Microsites were paired to minimize variation due to environmental heterogeneity. To separate co-blooming and non co-blooming interaction pathways, shrubs were tested prior to blooming, and the same shrubs re-tested after entering into full bloom. Shrubs with fewer than five open blooms were considered non-blooming (“pre-blooming”). The average number of blooms for ‘blooming’ treatment was 300.2 ± 176.72SD (min: 102, max: 1080). In two cases, a focal shrub did not bloom within the study period and was replaced by a different blooming shrub. These two cases were excluded from later RII calculations. The repeated measures study design was chosen to measure relative changes in interactions with natural shrub phenology and to reduce between shrub variability.

Visitation to *Malacothrix glabrata*

Each morning of each study day, *M. glabrata* were gathered from nearby (< 3 km) populations where they seasonally coexist with *L. tridentata.* These were transplanted into 15 cm diameter black pots and one pot was placed per microsite for a total of six shrub/open pairs per day. Conspecific floral density influences pollinator visitation ([Bosch and Waser, 2001](#_ENREF_7)). Transplants of similar size and habit were paired, and the flowerheads of *Malacothrix* were trimmed to equal numbers between paired microsite, but left to vary between replicates. The mean number of flowers per pot was 10 (min 6, max 20). Polaroid Cube+ HD video cameras (1080p) were used to record pollinator activity to each potted *M. glabrata*. Recording periods were timed to coincide with peak pollinator activity (between 11:30 am and 3:30 pm, average length: 1:19 h:min). The use of video technology allows for higher temporal resolution, and replication beyond what is possible using traditional insitu observations. Ten days of pre-blooming trials (60 shrub/open pairs) were conducted between April 10 and April 20 and ten days of blooming trials (60 shrub/open pairs) between April 21 and May 5.

To test for the potential influence of naturally co-occurring annuals and blooming shrubs, heterospecific annual floral density was measured within a 0.25 m2 quadrat in each microsite and the number of heterospecific shrubs in bloom were counted within a 2 m radius of each microsite. The number of open blooms of each *L. tridentata* were counted at the same time.

Video footage was reviewed in lab. All arthropod visitation to *M. glabrata* was recorded, however a “pollinator visit” was defined as when an insect visitor flew on and touched the open side of the flower. A foraging bout was defined as a single plant visit and multiple flowers could be visited during one foraging bout. “Total flowers” are the total number of flowers visited per replicate. Visit duration refers to the length of the foraging bout, which began when a flying visitor touched a flower and ended when the visitor left the final flower, therefore including inter-flower travel time. Proportion of flowers visited is the number of unique flowers visited per foraging bout divided by the number of flowers in the field of vision. Floral visitors were identified to recognizable taxonomic units (RTU): honeybees, solitary bees, Lepidoptera, syrphid flies, bombylid flies and other, which was comprised primarily of small beetles and muscoid flies. Five videos were omitted due to disturbance or battery failure.

Arthropod and plant community sampling

Foundation species have positive effects that scale to trophic levels beyond plants ([Reid and Lortie, 2012](#_ENREF_66); [Ruttan et al., 2016](#_ENREF_72)). The arthropod communities were sampled to address two major goals: 1) To test for differences in pollinator populations between microsites and changes blooming 2) To assess if *L. tridentata* is a foundation species within this system. Yellow, white and blue coloured, six-inch diameter plastic bowls were used as pan traps. At each microsite, arrays of three pan traps were deployed in a triangular shape, slightly embedded in the ground to prevent blowing away. The pan traps were filled with water with a few drops of Dawn original dish detergent added, and set out for the time between 10 am and 5:30pm, on sunny days only. As a proxy for annual biomass, total percent vegetation cover was recorded within a 0.25 m2 quadrat when the traps were laid out. Annual species richness was also recorded. Focal shrubs were pan trapped within two days of the video test, but never on the same day to avoid influencing visitation. Nine days (54 shrub/open pairs) of sampling were completed before blooming, and 10 days (60 shrub/open pairs) during full bloom.

Bees and syrphid flies were identified to species or genus ([Ascher and Pickering, 2015](#_ENREF_3); [Michener, 2000](#_ENREF_51); [Michener et al., 1994](#_ENREF_52); [Miranda et al., 2013](#_ENREF_54)). The majority of remaining individuals were identified to a minimum of family ([Grissell and Schauff, 1990](#_ENREF_33); [Marshall, 2012](#_ENREF_47); [Teskey et al., 1981](#_ENREF_81); [Triplehorn and Johnson, 2005](#_ENREF_84)) Thysanoptera, Orthoptera and Arachnida which were left to order. RTU is a suitable approximation of traditional species richness ([Oliver and Beattie, 1993](#_ENREF_60)). Using RTU limits resolution compared with species-level identification, however many desert insect species have not been described and furthermore useful keys are often lacking. This method of categorizing diversity was a trade-off between maximizing resolution and speed given the high diversity of desert species. Related groups may be identified to different levels. E.g. wasps in the genus Miscophus and subfamily Pemphredoninae are both within the family Crabronidae. No individuals were double counted, and these groups were considered distinct, exclusive RTUs for diversity analyses. Nymphs were included in abundance analyses provided they could be identified at least order. Hemipteran nymphs that could not be identified to family were lumped together for diversity analyses, otherwise all nymphs were assigned to family. Mites (Acari) and springtails (Collembola) were excluded from all analyses due to biases in collection methods. A full list of the 122 RTU are provided in Appendix B and the associated dataset has been published openly to KNB (Braun, 2018). All specimens are located within the collection in Lortie Lab at York University.

Pollinator visitation to *Larrea tridentata*

Pan traps are insufficient to quantify the pollinator guild of L. tridentata (Cane et al, 2000). To determine which pollinators visited *L. tridentata* during the study period, visitation to *L. tridentata* was observed in 15-minute time periods. Four individuals were observed per day, 10 days pre-blooming (10 hours) and 6 individuals per day for 10 days when blooming (15 hours). Observations were done on same focal shrubs, but on different days than pan trap sampling or video trials. Due to the large size of the shrubs, it was not possible to accurately track flower visits per foraging bout, therefore only the frequency of foraging bouts was recorded. The identity and behaviour of the visitors was recorded and visitors were collected when possible to aid identification.

Microclimates

To determine if L. tridentata creates locally stable microclimates, 16 HOBO pendant data loggers were used to record micro-environmental conditions. Ground level temperature and light availability were recorded every 30 minutes between March 19th and May 14th, 2017 at eight microsite pairs. Daytime (9am to 9pm) and nighttime (9pm to 9am) averages and daily temperature variance were calculated.

Pollen deposition

To quantify how pollen deposition changes with proximity of *L. tridentata*, over a period of three days I collected stigma from *M. glabrata* at a nearby site (3 km) with a naturally occurring, co-blooming populations of *M. glabrata* and *L. tridentata*. It was not possible to do this at the main study site because I could not ensure that *M. glabrata* had not been previously pollinated. I collected three stigma from each of three flowers from one *M. glabrata* (nine stigmas per plant) growing each of under the dripline and in a nearby open area, 298 in total. Only 13 pairs were tested because a heatwave followed by a wind storm triggered all *M. glabrata* to go to seed. Distance to the nearest *L. tridentata*, distance to the three nearest *M. glabrata* neighbours were measured and the number of *M. glabrata* flowers per plant were counted. The stigmas were stored individually in micro centrifuge tubes filled with denatured alcohol. The tubes were spun down in a centrifuge at 4200 rpm for 4.5 minutes and the pellet pipetted onto the slide. This along with the stigma were mounted in fuchsin jelly ([Kearns and Inouye, 1993](#_ENREF_42)). At 100 x magnification, 10 longitudinal transects (18 mm long) of pollen were counted per slide. Heterospecific pollen grains were imaged using a Canon 60D SLR with 60mm macro lens into microscope afocally.

Statistical Analysis

To test for evidence that *L. tridentata* mediates pollinator visitation to *M. glabrata*, I fit generalized linear mixed-models (GLMM, lme4) using negative binomial error distributions with a loglink function to account for overdispersion within the data with rep ID as a random effect. I used the number of foraging bouts (visits to plant) and the total number of flowers visited as response variables. To test for the influence of conspecific floral density, the number of *M. glabrata* blooms were included in as a predictor (flowers.pot). Video length was log-transformed to match the loglink function and used as an offset to maintain the count structure of the data. In the past, some have chosen to standardize visitation to visits/hour/flower, this makes the assumption that pollinators respond linearly to the floral density and that the slope of the relationship does not change with any treatment. The method used allows for the original data distribution to be maintained (Reitan and Nielson, 2006), and for pollinator response to conspecific density to be tested rigorously. The rep ID (focal shrub number + microsite) was used as a random effect to account for the repeated measures study design. Interactive, additive and intercept only models were compared by AIC and likelihood ratio tests with χ2 approximations. To test for the influence of heterospecific blooming annuals and shrubs, I used quasipoisson GLMM (MASS, glmmPQL) and added each covariate to each base model (microsite + blooming + flowers.pot).

To explore which visitors were driving observed visitation patterns, I fit quasipoisson GLMM (MASS, glmmPQL) and used least-squares post hoc tests (lsmeans) on any significant interactions. To determine if *L. tridentata* influences foraging behaviour, I fit gamma GLMM models (lme4) with visit duration and proportion of flowers visited per foraging bout as response variables. As a post-hoc exploration, I subsetted responses of solitary bees and ‘other’ RTUs to fit linear mixed models using log-transformed visit duration as the response variable. Least-squares post hoc tests (lsmeans) were used on any significant interactions.

Positive influences on other communities

To quantify how shrubs influence arthropod and plant communities, I fit negative binomial GLMM (lme4, glmer.nb) with rep ID as a random effect, and abundances, arthropod species richness, percent annual cover, annual species richness and annual bloom density as responses. Beetles from the family Melyridae made up 1217 of the 3384 total arthropods captured, therefore abundance models were fit with Melyridae excluded, included and individually to avoid bias. A poisson GLMM (lme4) was used to determine differences in bee abundance between the treatments.

Pollen

I fit quasipoisson models (MASS, glmmPQL) with conspecific and heterospecific pollen counts as response variables, and the sample nested in the flower nested in the plant as a random effect. I used the distance to *L. tridentata*, distance to the nearest conspecific neighbour and the number of *M. glabrata* flowers as predictors.

Pollinator visitation to *L. tridentata*

To test if *L. tridentata* individuals with more flowers are more attractive to pollinators, I used a quasipoisson GLM (glm) with visitation rates as the response and flower number as predictors.

Ecological effects

To compare the ecological effect of shrubs and blooming on five community response metrics (floral vistiation to M. glabrata, arthropod abundance, arthropod species richness, percent annual cover and annual species richness), and to estimate the biological importance of statistically significant differences the effect size estimate RII was calculated ([Armas et al., 2004](#_ENREF_2)). The equation: was used. Treatments was shrub or blooming, while control was open or pre-blooming. Microsites were matched when calculated the metric and non-matching sites were excluded from calculation. This metric is symmetric around 0, ranges from −1 to +1, and negative values denote relativecompetition whilst positives denote facilitation. To determine if the effect was significantly different from 0, 95% confidence intervals around mean values were bootstrapped (boot, R), stratified by the microsite ID to account for the repeated measures.

**Results**

Pollinator visitation

A total of 697 flying insects made 925 potentially pollinating flower visits (hereafter “pollinators”) to *M. glabrata* in 303 hours of video recording. No pollinators were observed in 61 of the 235 video observation periods. Foraging bout frequency and total floral visitation by pollinators to *M. glabrata* were significantly lower at the shrub microsite relative to open areas (Table 1), and were reduced at both microsites when *L. tridentata* entered full bloom. There was a positive effect of *M. glabrata* conspecific density on both the frequency of foraging bouts and floral visitation.

There was no significant influence of heterospecific shrub blooming density on foraging bout frequency or total flowers visited. The was a significant effect of heterospecific annual floral density on foraging bouts, but not flowers visited (Table 2).

There was a significant correlation between flowers visited per hour between paired shrub/open microsites (0.262, t = 2.8708, df = 112, p-value = 0.004898).

There was no significant difference between RTU visiting the microsites (Figure 1, Table B1), nor were there significant interactions between RTU, microsite and blooming (Table B1) on the total flowers visited.

There were RTU specific changes in the number of foraging bouts and flowers visited with blooming (Table 3). The frequency of flower visits by syrphids and solitary bees declined significantly with blooming (Table 4).

There was also a negative effect of L. tridentata blooming on M. glabrata visit duration, but no microsite effect (Table 5). This was driven by visitors in the ‘other’ category (Figure 2, Est: -1.0703, χ2: 12.274, t: -3.503, p = 0.000605). There was no difference in solitary bee visit duration (Est: -0.9341, χ2: 1.9017, t: -1.379, p = 0.208).

The proportion of flowers visited per visit decreased significantly with blooming at the shrub microsite only (Table 5), but there was no significant interaction between RTU and blooming or RTU and microsite (Appendix).

Pollen Deposition

At the nearby site, there was no significant influence of proximity to *L. tridentata* or the number of conspecific flowers (Figure 3) on conspecific pollen deposition, however there was a marginally significant effect of distance to nearest conspecific neighbour (Table 6). Heterospecific pollen deposition increased significantly with distance from *L. tridentata*. Conspecific and heterospecific pollen deposition were significantly correlated (0.15, p = 0.01).

Visitation to larrea

Pollinator visitation to *L. tridentata* increased with floral abundance (GLM: Est: 0.0013408, χ2: 4.6383, p = 0.02283). Floral abundance and shrub height (Pearson’s, 0.3185, p = 0.03511) were correlated. *L. tridentata* received 197 floral visit over 15 hours of observations. Of 169 visits made by bees, *Apis mellifera* was the most frequent visitor (32%), *Centris* sp. (21%), *Hesperapis larrae* (18%) and *Megandrena enceliae* (7%) and other solitary bees (23%) including *Hoplitis* and *Megachile*.

Positive influences on other communities

3400 arthropods spanning 121 taxonomic groups (Appendix B) were caught in 19 days of pan trapping. There was a positive effect of shrub microsite on both arthropod abundance (Melyridae excluded) and arthropod species richness, and a negative effect of blooming (Table 7, 8). There is a significant correlation of insect abundance (Melyridae excluded) between the paired shrub/open microsites (p = 4.41e-07, 0.4576805).

There was a negative effect of shrub microsite on Melyridae abundance, and a negative effect of blooming at the open microsite only (Table 7)

There was no significant difference in bee abundance caught in pan traps between any of the treatments (Table 8).

Percent cover of ground vegetation was significantly greater in shrub microsites (Table 9). There was a significant decrease with blooming in the open microsite only. There was a significant decrease in annual floral density with blooming. There was no significant difference in annual species richness between any of the treatments.

Ecological effects

Shrubs had a competitive effect on floral visitation of *M. glabrata,* a facilitative effect on arthropod abundance, arthropod species richness, percent cover and a neutral effect on annual richness. Blooming had a negative effect on all metrics (Figure 5).

Climate amelioration

Mean daytime temperatures were significantly lower (Figure 6, GLMM: Est: -0.064678, χ2:85.51, p <0.0001), and mean nighttime temperatures were significantly higher under the shrub canopy (GLMM: Est: 0.059203, χ2: 50.121, p <0.0001). Overall temperature variation was significantly lower in the shrub microsites (GLMM: Est: -0.27977, χ2: 523.38, p <0.0001).

**Discussion**

*Larrea tridentata* engaged in simultaneous positive and negative interactions with the surrounding plant and arthropod communities. There was partial support for the main hypothesis. *L. tridentata* interfered with the pollination of *M. glabrata* but this was not alleviated when *L. tridentata* entered full bloom. *L. tridentata* competed with, rather than facilitated *M. glabrata* by co-blooming. There was an effect of facilitation of annual heterospecific blooms on number of foraging bouts made, but not flower visits. The observed negative effect of the shrub microsite was likely due to obscuring or shading because there was no species specific response. The term magnet species refers to a highly attractive plant species ([Laverty, 1992](#_ENREF_44); [Molina-Montenegro et al., 2008](#_ENREF_55)). However, the traits that make a plant attractive to pollinators, such as a large floral display ([Bosch and Waser, 2001](#_ENREF_7)), height ([Donnelly et al., 1998](#_ENREF_23)), flower size ([Conner and Rush, 1996](#_ENREF_21)) or rich rewards ([Robertson et al., 1999](#_ENREF_67)) also make it likely to be a good competitor. Thus, the sign of this interaction is likely context-dependent. In this study, the context leading to competition was the identity, phenology and behaviour of the associated pollinator communities.

Pollinator-mediated interactions

The decrease in visitation during co-blooming was driven by syrphid flies and solitary bees. *Eupeodes volucris* (Diptera: Syrphidae), the bird hoverfly, was the most frequent floral visitor to *M. glabrata* and is known to visit *L. tridentata* ([Hurd Jr and Linsley, 1975](#_ENREF_37)). Only one syrphid floral visit to *L. tridentata* was recorded. This change in visitation could be due seasonal changes in Syrphid abundance particularly if it is tied to the phenology of annuals. *E. volucris* is multivoltine ([Vockeroth, 1992](#_ENREF_88)) and the average maturation time is 21 days in lab ([Jones, 1922](#_ENREF_41)) however the phenology of *E. volucris* in desert systems has not been studied. In the only study measuring seasonal hoverfly abundances in USA, *Eupeodes* abundances peaked in late spring but individuals were found throughout the season ([Terry and Nelson, 2017](#_ENREF_80)). Larval *E. volucris* are aphid predators and members of the genus *Eupeodes* requires specific larval resources ([Henderson, 1982](#_ENREF_34)). In an agricultural study aphid-eating hoverflies, including *E. volucris* abundances corresponded to aphid densities ([Noma and Brewer, 2008](#_ENREF_59)). In a Rocky Mountain alpine community, early snowmelt triggered flowering, but not syrphid fly emergence suggesting their phenology not closely tied to weather ([Iler et al., 2013](#_ENREF_38)). Rather, their phenology appears to be tied to prey availability rather than floral resource availability. More research is required to understand the likely complex relationships between pollinators that have predatory larva and the plants that host their prey.

Alternatively, bees may have competitively excluded Syrphids from the immediate area. Competition between Syrphids and other pollinators is fairly unstudied ([Inouye et al., 2015](#_ENREF_39)). Bumblebees outcompete *Toxomerus* ([Morse, 1981](#_ENREF_57)), leading to the temporal partitioning of pollinators. That is unlikely to be the case in this study as there were few Syrphids caught in pan traps relative to pre-blooming. *Centris* sp. bees, which were frequent visitors to Larrea flowers are territorial, and will hover near shrubs chasing off other bees ([Alcock et al., 1977](#_ENREF_1)). Honeybees have been shown to reduce visitation by native, solitary bees but the effect is not consistent ([Shavit et al., 2009](#_ENREF_76)), and they can compete via multiple mechanisms including resources depletion and competitive displacement ([Cane and Tepedino, 2017](#_ENREF_16)). If the pollinators of one plant displace the pollinators of another plant, this would be a novel mechanism pollinator competition in arid environments.

Pollinators responded positively to the floral density of *L. tridentata* i.e. concentrations of floral resources, however this did not benefit *M. glabrata*. This can be explained in part by the identity and behaviour of the visitors to *L. tridentata*. *Megandrena encelia* and *Hesperapis larrae* are both locally oligolectic, generally visiting *L. tridentata* only as long it is present ([Hurd Jr and Linsley, 1975](#_ENREF_37)). The most frequent floral visitors to *L. tridentata* were feral honeybees, *Apis mellifera*. Honeybees preferentially forage on particularly abundant flowers, exhibiting floral constancy. This is a common feature of social bees, where individuals facultatively specialize on different flower species at difference times ([Waser, 1986](#_ENREF_91)). Furthermore, because honeybees communicate the locations of food sources to the colony, arriving bees may be looking for *L. tridentata*, rather than openly foraging. The significant decline in solitary bee visitation to *M. glabrata* when co-blooming was not driven by local changes in bee abundances suggests that it was a behavioural response. Switching to a plant species offering superior resources during a spring bloom has been observed in the alpine ([Mosquin, 1971](#_ENREF_58)). Manipulation experiments have found competition between sequential bloomers ([Campbell and Motten, 1985](#_ENREF_14)). During co-blooming, pollinators spent less time foraging on *M. glabrata*, and visited fewer flowers per visit, which is consistent with pollinator parasitism by *L. tridentata* (cite?).

Overall, the negative, ecological effect of blooming was greater than the microsite effect. Differences in visitation do not necessarily lead to differences in fitness ([King et al., 2013](#_ENREF_43)). Syrphid flies and solitary bees are well known as effective pollinators, so the reduction in their visits likely led to a reduction in pollen deposition, and subsequently fitness. When co-blooming, the difference in visitation between microsites was small. At the nearby site, there was no change in stigma conspecific pollen loads with distance to *L. tridentata*, however the sample size was too low to conclude there was no effect. Heterospecific pollen deposition increased with distance to *L. tridentata,* suggesting that *L. tridentata* influences interactions between *M. glabrata* and other plants. The ability of plants to do this is a very interesting and underexplored area. After blooming, microsite differences were very small. The coinciding decrease in pollinator visitation to open microsites suggests that *L. tridentata*’s influence extends beyond its canopy. Further experiments examining the zone of influence and how it changes size with pollinator identity would help make better predictions as well as aid future experimental design.

Interactions with surrounding communities

*L. tridentata* is a foundation plant with positive effects that scaled to annual and arthropod communities. It buffered annuals through the study period by ameliorating and stabilizing understory microclimate, a frequent mechanism within nurse plant systems ([Filazzola and Lortie, 2014](#_ENREF_26)). *L. tridentata* supports arthropod community diversity, which show family specific associations with *L. tridentata* (Hurd and Linsely, 1975, Ruttan, 2016). There were measureable shifts in the abundance and diversity of associated plant and arthropod communities when L. tridentata entered into bloom. Research to disentangle what is happening is necessary before it is possible to conclude that the blooming had a negative effect. For example, if the beneficiaries are spring ephemerals, then the overall effect of *L. tridentata* is still positive. Scaling up of interactions through multiple trophic levels highlights the importance of positive interactions in deserts but the potential shifts when *L. tridentata* entered into a reproductive state suggest that they may change throughout the year and are complex.

Need a short paragraph here tying in literature on reproductive shifts & arthropod communities? Tie into conservation or evolutionary theory? Trophic interactions vary with environmental conditions. Larrea mediates the environmental conditions, etc.

Conclusions

My findings suggest that even though facilitation or neutral interactions between plants for pollinators may be measured during co-blooming, competition may be more biologically relevant overall. Therefore, experimental design is key to separating out net interactions. Diverging phenologies are hypothesized to result from competition avoidance (Waser and Real). These plants species overlap at the beginning and ends of their phenologies, potentially to avoid the observed competition. The positive effect on annual abundance was greater than the negative effect on pollinator visitation. L. tridentata is an important species that supports plant, pollinator and arthropod communities.

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