Chapter 2: A title goes here

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Abstract

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_14)). 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_16)). These include stress amelioration ([McIntire and Fajardo, 2014](#_ENREF_30)), improved water and nutrient availability ([Franco et al., 1994](#_ENREF_20)), and seed trapping ([Flores and Jurado, 2003](#_ENREF_19)). Direct interactions between shrubs and annuals may be simultaneously facilitative and competitive ([Bertness and Callaway, 1994](#_ENREF_3); [Callaway and Walker, 1997b](#_ENREF_10); [Holzapfel and Mahall, 1999](#_ENREF_25)) and it is posited that their relative importance varies with abiotic stress ([Bertness and Callaway, 1994](#_ENREF_3); [Schafer et al., 2012](#_ENREF_45); [Tielbörger and Kadmon, 2000](#_ENREF_51)). These complex sets of interactions lead to patterns in species coexistence and structure plant communities (([Valiente‐Banuet and Verdú, 2007](#_ENREF_53))Brooker et al, 2008). The facilitative effects of desert shrubs can lead to concentrations of annual plants beneath the shrub canopy ([Facelli and Temby, 2002](#_ENREF_15)). 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_8); [Callaway and Walker, 1997b](#_ENREF_10); [Wootton, 1994](#_ENREF_56)). 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 extensions to optimal foraging theory ([Pyke, 1984](#_ENREF_37); [Pyke et al., 1977](#_ENREF_38)) with flowers as the central resources for which pollinators forage. Thus plants can benefit from combining floral displays to be larger ([Schemske, 1981](#_ENREF_46)), or more diverse ([Ghazoul, 2006](#_ENREF_21)). 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_27); [Thomson, 1978](#_ENREF_50)). The comparatively large size of shrubs to annuals makes them salient features of desert scrub ecosystems. This, combined with their structural complexity suggests that non-co-blooming pathways of interactions are likely prominent in desert systems. For example, a non-blooming shrub could facilitate its understory if it offers shelter or habitat for pollinators ([Hansen et al., 2007](#_ENREF_23)). Conversely, shrubs may interfere with the pollination of their understory. Shading by the shrub *Lonicera* decreased pollinator visitation and pollen deposition to annuals growing beneath ([McKinney and Goodell, 2010](#_ENREF_31)). In forests, pollination rates tend to be higher under canopy gaps ([Proctor et al., 2012](#_ENREF_35); [Walters and Stiles, 1996](#_ENREF_55)). 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_44)) and 1680 species of vascular plants ([Rundel and Gibson, 2005](#_ENREF_42)). 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_40)), however interspecific studies have primarily focused on competition within cacti systems in the Sonoran Desert ([Fleming et al., 2001](#_ENREF_18)). Plant-pollinator systems in southwest deserts are home to rare obligate mutualisms such as *Yucca brevifolia*, Joshua tree ([Pellmyr, 2003](#_ENREF_34)), and *Pachycereus schottii*, Senita cactus ([Fleming and Holland, 1998](#_ENREF_17)) 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_13)), and has recent empirical support in pollination networks ([Chacoff et al., 2012](#_ENREF_12)). Few one-to-one relationships have been found with solitary bees ([Simpson and Neff, 1987](#_ENREF_48)), and bees still visit even Senita cactus ([Holland and Fleming, 2002](#_ENREF_24)). 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_4)). Highly tolerant to temperature extremes, it is able to maintain photosynthesis even under high temperatures and low water potentials ([Barbour et al., 2007](#_ENREF_1)). *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_54)). The full pollinator guild contains 22 specialist pollinators and more than 80 generalists ([Minckley et al., 1999](#_ENREF_33)). 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_11)). *L. tridentata* is one of the most reliable flowerer’s in the Mojave as it has one of the lowest rainfall thresholds to blooming (12 mm in one event) ([Bowers and Dimmitt, 1994](#_ENREF_5)) and it produces copious nectar and pollen rich flowers ([Simpson et al., 1977](#_ENREF_47)) - can’t access, 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_57)), *Peniocereus striatus* ([Suzán et al., 1994](#_ENREF_49)), as well as facilitating native annuals ([Schafer et al., 2012](#_ENREF_45)). Conversely, it also competes with some species through allelopathy ([Mahall and Callaway, 1991](#_ENREF_28), [1992](#_ENREF_29)).

The shift from vegetative growth to reproductive is a major event. A plant’s life stage can alter the balance of facilitative and competitive interactions ([Bruno et al., 2003](#_ENREF_7); [Callaway and Walker, 1997a](#_ENREF_9); [Pugnaire et al., 1996](#_ENREF_36); [Rousset and Lepart, 2000](#_ENREF_41); [Valiente-Banuet et al., 1991](#_ENREF_52)). The majority of research on plant-plant interactions focusses at one life stage ([Goldberg et al., 2001](#_ENREF_22); [Tielbörger and Kadmon, 2000](#_ENREF_51)) which is inadequate for making conclusions about fitness levels within populations ([McPeek and Peckarsky, 1998](#_ENREF_32)). For example, within some nurse plant systems young plants are facilitated during establishment, but later compete with their nurses for resources ([Yeaton, 1978](#_ENREF_57)). Foundation plants have benefits that can scale to trophic levels beyond their surrounding plant community ([Reid and Lortie, 2012](#_ENREF_39); [Ruttan et al., 2016](#_ENREF_43)), however if these benefits change with reproductive shifts is not known. Spring time flowering is often triggered by rainfall in the winter ([Beatley, 1974](#_ENREF_2)). Despite the importance of water availability, interactions are still really important for structuring desert communities ([Chesson et al., 2004](#_ENREF_13)). Here the differences in pathways both looks at shifts in life stages but also offer insight into adaptations to environment and neighbours?

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*. The bloom periods of *L. tridentata* and *M. glabrata* overlap at beginning and ends of their phenology ([Jennings, 2001](#_ENREF_26)), making it an interesting system to test for changes in interactions for pollinators over a season. I hypothesize that *L. tridentata* interferes with the pollination of *M. glabrata* before blooming because it obscures them from pollinators, but after blooming acts as a magnet species because it acts as a concentration of floral resources. Visitation rates are commonly used as a proxy for pollination success, and measure the behavioural response of pollinators. The prediction is that M. glabrata will receive more visits in open areas, prior to L. tridentata entering a full bloom. After L. tridentata enters full bloom, M. glabrata will receive more visits in the shrub microsite benefitting from facilitation. The secondary goal is to determine if *L. tridentata* is acting as a foundation plant within this ecosystem. I assessed this this by looking for positive effects that extend to plants and arthropod communities, and if L. tridentata is capable of stabilizing climate using its canopy. If they facilitate their understory, then they may be able to buffer their associates from a pollinator decline. But if they outcompete them, then their associates may be extra vulnerable, and the longterm success of these communities may be at risk. Understanding interactions for pollination at a community level is critical for understanding potential impacts of any decline.

**Methods**

Study site

The study area has an extent of 0.07 km2, and is located in the mouth of Sunset Cove part of the UCNRS reserve 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 an environmental indicator (Clements and Goldsmith, 1924). We used the *Malacothrix glabrata* (Asteracae), desert dandelion 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 (Morhardt, book, California desert flowers), and grow up to 40 cm tall. M. glabrata is insect-pollinated, including bees in the genus Nomadopsis (Rutowski) and Anthidium (Wainwright), as well as short-winged flower beetles (Cline, 2010). Some of the 24 species of *Malacothrix* are self-compatible (Davis 1986), however these studies have not been done for *M. glabrata*.

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 interaction 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). 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 and annual species richness were measured within a 0.25 m2 quadrat in each microsite and the number of heterospecific shrubs and cacti in bloom were counted within a 2 m radius of each microsite. The number of blooms of each L. tridentata were counted, and the dimensions were measured along the widest axis, the perpendicular axis and the height.

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 visitors touched a flower and ends 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, comprised primarily of small beetles and muscoid flies. Five videos were omitted due to disturbance or battery failure.

Arthropod community sampling

Foundation species have positive effects that scale to trophic levels beyond plants (Reid 2012, Ruttan, 2016). 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. 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 was done 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, 2018, Michener et al, 1994, Michener 2000, Miranda et al, 2013, Packer). The majority of the remaining individuals were identified to a minimum of family (Borror and Delong, Marshall, 2017, Grissell and Chauf 1990, McAlpine et al, 1993) except Thysanoptera, Orthoptera and Arachnida which were left to order. RTU is a suitable proxy for diversity analyses (cite, cite). 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. For example, wasps in the genus Miscophus and subfamily Pemephrinae are both within the family Crabronidae. These three groups were considered distinct, exclusive RTUs for diversity analyses and no individuals were double counted. 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. Mites (Acari) and springtails (Collembola) were excluded from all analyses due to biases in collection methods. 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.

Arthropod visitation to Larrea tridentata

Pan traps are insufficient to quantify the pollinator guild of L. tridentata (Cane et al, 2000). To determine what pollinators visited L. tridentata during the study period, and how arthropod use changed with blooming, 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 blooming (15 hours). Observations were done on same focal shrubs, but on different days than pan traps or video trials. Due to the large size of the shrubs, it was not possible to accurate track flower visits per foraging bout, therefore only the frequency of visits was recorded. The identity of the visitors was recorded and visitors were collected when possible to aid identification. The part of the plant that was visited was recorded (branch, flower, understory – which includes the ground itself and plants growing under the shrub), and the general behaviour of the visitor – landing, touchdown (land then fly away), hovering/inspecting, crawling (understory only).

Microclimates

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

Weather data

A Campbell weather station ([www.wrcc.dri.edu/ucnrs](http://www.wrcc.dri.edu/ucnrs)) in the adjacent Granite Cove provided hourly site-level environmental data. Data logged between 10 am and 5:00 pm were used to correspond with study timings. The mean of hourly wind speed (m/s), mean temperature (ºC) and mean solar radiation were calculated for that time period daily.

Pollen deposition

To quantify how pollen deposition changes with proximity of L. tridentata, I collected stigma from M. glabrata at a nearby site (3 km) with a naturally occurring population of Malacothrix and L. tridentata. It was not possible to do this at my main study site because I could not ensure that the Malacothrix had not been pollinated prior to moving them to my site. I collected three stigma from each of three flowers from one Malacothrix (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 killed the Malacothrix. The distances and to the nearest L. tridentata. The number of Malacothrix flowers per plant were counted and the distance to the three closest Malacothrix neighbours were measured as a measures on conspecific density. 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 book). At 100 x magnification, 10 longitudinal transects (18 mm by x mm) 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. 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 null models were compared used max-likelihood (Wald test) and AIC (Appendix C). To test for influence of potentially interacting blooming annuals or shrubs, I added each covariate to each base model (microsite + blooming + flowers.pot), one at a time, and tested if adding the variable significantly improved model fit by likelihood anova.

To explore which visitors were driving the observed visitation patterns, I fit quasipoisson GLMM (MASS, glmmPQL) to account for dispersion in the data using the number of flowers visited as a response, and the repID as a random effect. Least-squares post hoc tests (lsmeans) were used on any significant interactions.

To determine if L. tridentata influences pollinator behaviour, I fit gamma GLMM models (lme4) with visit duration and proportion of flowers visited per visit as response variables. As a post-hoc exploration, fit linear mixed models using log-transformed visit duration as the response with subsets of solitary bees and other. Least-squares post hoc tests (lsmeans) were used on any significant interactions. To explore any RTU-specific proportion response, I add RTU\*microsite, and RTU\*blooming to the models as processing a three-way interaction was not tractable.

Positive influences on other communities

To quantify if shrubs influence arthropod communities, I fit negative binomial GLMM (lme4, glmer.nb) with rep ID as a random effect with abundance and species richness as response. 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.

To test if L. tridentata has a positive influence on associated annual communities, I fit negative binomial GLMM for percent annual cover, annual species richness and annual bloom density.

Pollen

I fit quasipoisson models (MASS, glmmPQL) with conspecific and heterospecific pollen counts as response variables, and the sample nested in the flower nest 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.

Visits to Larrea

I used a quasipoisson GLM (glm) with visitation rates as response, and height and flower number as predictors.

RII

The relative intensity of interaction (Rii) effect size was calculated to enable contrasts between blooming and not blooming, and compare the relative responses of indirect and direct interactions, and to estimate the biological importance of the statistically significant differences. It allows for the comparing the relative magnitude of the effects on the different communities.

Equation for metric:

This metric is symmetric around 0, ranges from −1 to +1, and negative values denote relativecompetition whilst positives denote facilitation (cite). This metric was calculated where shrub microsites are the treatment and open areas are the control. These were then compared to bootstrapped confidence intervals to determine if each one is different than zero. The shrub/open microsites were paired and had the same number of flowers. Visitation was standardized by video length. I calculated RII for total flower visits, bee visits, syrphid visits, percent cover, annual richness, arthropod abundance (3 measures), species richness.

**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 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. The frequency of flower visits by Syrphids and solitary bees declined significantly with blooming (Figure 1, Table 3).

There was also a negative effect of L. tridentata blooming on M. glabrata visit duration, but no microsite effect (Table 1, Figure 3). This was driven by visitors in the ‘other’ category, no difference in solitary bee visit duration.

The proportion of flowers visited per visit decreased significantly with blooming at the shrub microsite only (Table x, Figure 4), but there was no significant interaction between RTU and blooming or RTU and microsite.

Effects on arthropod communities

3400 arthropods spanning 122 taxonomic groups were caught in 19 days of pan trapping. 1217 of the arthropods were Melyridae beetles in the subfamily Dastyinae. There was a positive effect of shrub microsite on arthropod abundance (Melyridae excluded), and a negative effect of blooming (Table 4). There was a negative effect of shrub microsite on Melyridae abundance, which didn’t change with blooming. Arthropod species richness were higher in the shrub microsites, and decreased at both microsite with blooming (Table ).

Eupuodes volucris was an indicator species for the pre treatment (p < 0.001). There was no significant difference in bee abundance caught in pan traps between any of the treatments (all p > 0.68, Table x).

There is a significant correlation of insect abundance (Melyridae excluded) between the paired shrub/open microsites (p = 4.41e-07, 0.4576805).

Plant-plant facilitation

Percent cover of ground vegetation was significantly greater in shrub microsites before and after blooming, decrease in cover in open areas but not under shrubs (Table 2). Prior to blooming, no significant different in annual floral density or plant species richness. Significant decrease in annual floral density with blooming.

Visitation to larrea

Prior to blooming, 138 insect uses on and under larrea occurred over 10 hours. During blooming, 401 uses in 15 hours, 13.8/hr vs. 26.7/hr. 197 of these were flower visits. 94% of these floral visits were by bees (169 / 179). The most frequent floral visitors to L.tridentata were bees (115): Apis mellifera (54 visits), Centris rhodapus (35), Hesperapis larrea (30), Megandrena enceliae. (11) and other solitary bees (39) including Hoplitis and Megachile. The remaining visitors were primarily flies, hemipterans and lepidopterans. Floral number had a significant, positive effect on visitation frequency. The number of flowers and the height of the shrub (Pearson’s, 0.3185, p = 0.03511) were correlated.

Pollen Deposition

At the nearby site, there was no difference in conspecific pollen deposition to M. glabrata with proximity to L. tridentata, but there was a marginally significant effect of distance to nearest conspecific neighbour, and flower number didn’t matter. However, heterospecific pollen deposition increased with distance away from L. tridentata. Conspecific and heterospecific pollen deposition were significantly correlated (0.15, p = 0.01). Mean distance to shrub was 1.83 m, mean distance to nearest conspecific neighbour was 0.79 m and mean number of flowers of M. glabrata was 7.

Climate amelioration

Mean daytime temperatures were significantly lower, and mean nighttime temperatures were significantly higher under the shrub canopy. Overall temperature variation was significantly lower in the shrub microsites (Figure 6, Table infinity).

Relative effects

RII (Figure 5)

**Discussion**

*Larrea tridentata* engages in simultaneous positive and negative interactions with the surrounding plant and arthropod communities. While facilitating annual biomass beneath its canopy, and buffering them against increasingly harsh weather, it indirectly competed for pollinators. There was partial support for the main hypothesis. *L. tridentata* appears to interfere 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. Magnet species refers to highly attractive species (Laverty, Molina-Montenegro), however the traits that lead a plant being attractive, such as flower number (Bosch and Waser, 2001), height (Lortie and Aarssen, 1999), abundant rewards or “showiness”, are the same traits that make a plant capable of being a good competitor. Therefore, in many cases, “context” is what leads to differences in responses, rather than something intrinsic to the plant. I propose that the context leading to competition in this system is the identity, phenology and behaviour of the associated pollinator communities.

The decrease in visitation during co-blooming was driven by syrphid flies and solitary bees. The most frequent floral visitor to M. glabrata was *Eupeodes volucris* (Diptera: Syrphidae), the bird hoverfly. This species is known to visit L. tridentata (Hurd and Linsely, 1975), however only a single syrphid floral visit to L. tridentata was recorded. Pre-blooming, it would “inspect” larrea buds, but this may be more related to mate finding than pollination. This change in visitation could be due seasonal changes in Syrphid abundance.Within season, spring flowering phenologies in the Mojave Desert are predictable (Jennings, 2001), and solitary bees are also fairly predictable. However, phenology of E. volucris is not studied. Syrphid flies are multivoltine… Syrphid flies are generalists. The larvae of E. volucris eat aphids, if it is eating aphids from larrea than pollination understory really interesting mutualism. Despite being important… In Utah, Eupeodes populations peaked in late spring (Terry and Nelson, 2018). The only study looking at hoverfly abundances in USA, the authors think that syrphid flies coincide with cooler periods in spring and September. The genus Eupeuodes requires specific larval resources (Henderson). They found some individuals throughout the season. In a Rocky Mountain alpine community, early snowmelt triggered flowering, but not syrphid fly emergence suggesting their phenology not closely ties to weather (Iler et al 2013). In an ag study, they were rarely found but the flies correspond to aphid densities (Noma and Brewer, 2008).

Floral constancy may be high in Syrphids as well (Ssymank, 2003). Competition between syrphids and other pollinators in fairly unstudied (Inouye, 2015), but there’s a bit of work with bees.

Alternatively, bees may be competitively excluding Syrphids altogether. If Larrea is influencing nearby… could be

However, if there is a partitioning of pollinators between shrubs and annuals we might see patterns we saw. There was also a significant decrease in the number of annual blooms after blooming and shrubs more after blooming, suggesting a general phenology change consistent with that observed by Jennings (2001). There was an effect of facilitation of annual heterospecific blooms on number of foraging bouts made, but not flower visits.

The most frequent floral visitors to L. tridentata were feral honeybees, *Apis mellifera*. They visited M. glabrata pre-blooming, suggesting they switched to the superior resource. Floral constancy is a common feature of social bees, where even individuals from the same colony will specialize on different flower species at difference times (Waser, lots). Floral constancy differs from oligolecty in that preferences are facultative. Honeybees have been shown to preferentially forage on particularly abundant flowers. Furthermore, because honeybees communicate the location of good food sources, arriving bees from the same colony may be looking for Larrea, not openly foraging. Among honeybees, color is not always the key factor in flower constancy (Greggers and Menzel 1993). Pollinator visitation to other shrubs was not measured, however there was no influence of non Larrea shrub density on M. glabrata visitation. Oil specialist Centris bees were the second most frequent visitor to Larrea, but never visited Malacothrix. There was a significant decline in solitary bee visitation when larrea bloomed. About 30% of visitors to Larrea were solitary bees, some of which visited Malacothrix. Megandrena encelia and hesperapis larrae are both locally oligolectic, generally only visiting Larrea as long it is present (Hurd and Linsely, 1975). Pollinators (mostly bees) responded positively to the floral density of Larrea i.e. concentrations of floral resources, however this did not benefit M. glabrata. There was no difference in bee abundances in the pan traps suggesting that their response was behavioral. Differences in visitation due to microsite were much less than due to blooming. There was no significant differences in microsite with rtu, so the observed is probably obscuring, which would be ammensalism rather than competition.

Centris sp. bees are territorial, and will hover near shrubs chasing off other bees (Alcock et al, 1977).

The switching to a cornucopia species during a spring bloom has been observed in the alpine (Mosquin, 1971). Several author’s have Campbell and Motton (1985), Waser (1978) have manipulated bloom times and found competition between sequential bloomers.

Bumblebees outcompete Toxomerus (Morse 1983).

After blooming, pollinators spent less time on M. glabrata, and the proportion of the flowers visited decreased at the shrub microsite. This is consistent with pollinator parasitism by Larrea.

The biologically relevant differences were much greater between blooming/not blooming rather than microsites. The coinciding decrease in pollinator visitation to open microsites suggests that *L. tridentata*’s influence extends beyond its canopy. The scale at which to study interactions is critical. Pollinators change the scale at which plants interact, upon flowering this may change. While M. glabrata were manipulated, it was not feasible to manipulate the locations of large shrubs. The microsites were chosen to minimize variation due to environmental heterogeneity, however the strong correlations indicate that they were not independent. The pollen deposition at nearby sites suggests this as well, however the sample size was too low to conclude this for sure. The increase in heterospecific deposition with distance to larrea suggests that M. glabrata interacts with more plants indirectly the farther it is from larrea. The ability of plants to do this is a very interesting and underexplored area.

My findings suggest that even though facilitation or neutral interactions may be measured during co-blooming, competition may be more biologically relevant overall. Therefore, experimental design is key to separating out net interactions. This may also explain why despite facilitation in some systems there is still diverging phenologies. Flowering time, within a species, can have strong effects on fitness (Lacey, 2003). In this case, the flowering time of dominant plants drive these fitness effects through pollination competition. Diverging phenologies are hypothesize to result from competition avoidance. These plants overlap at the beginning/end of their phenologies, maybe to avoid the apparent competition.

*L. tridentata* is a foundation plant with positive effects that scale to annual and arthropod communities, and it is capable of creating stable microclimates. There were measureable shifts in the abundance and diversity of associated plant and arthropod communities. There was a significant decrease in abundance with blooming, though that may be due to associated arthropods responding to larrea flowers instead of pan traps. Abundance decreased with blooming at the shrub microsite only. Further research should look into how larrea supports arthropods after blooming. Larrea buffered the annuals through the study period, likely through ameliorating the harsh climate. This is consistent with previous research that found L. tridentata facilitated annuals by providing shade (Mahill and Callaway). The highly abundant Melyridae beetles were associated with open sites, so there is species specificity here. Larrea opens new flowers throughout the day (Hurd and Linsely, 1975)

Larrea supports species richness and ecosystems processes. Trophic interactions vary with environmental conditions. Larrea mediates the environmental conditions. Cornucopia species are super-generalist plants that have a wide range of visitors due to rewards. Larrea has the second largest pollinator guild, mass-flowers and flowers for a long time, even in droughts. The loss of Larrea tridentata would likely cascade throughout the ecosystem. In restoration studies, it did not come back easily. The shrubs are really long lived. Old growth forests are defined as having trees over 250 years old. There are multiple shrublands like this. Given the longstanding relationship larrea has it is not surprising how influential it is.

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