Introduction

Foundation plants positively influence the structure of the surrounding plant communities by creating locally stable conditions for other species (Ellison, 2005). 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). These include stress amelioration (McIntire and Fajardo, 2013), improved water and nutrient availability (Whitford et al, 1994) and seed trapping (Flores and Jurado, 2003). Direct interactions between shrubs and annuals may be simultaneously facilitative and competitive (Callway 1994, Callaway 1997, Hozlapfel, 1999) and it is posited that their relative importance varies with abiotic stress (Bertness and Callaway, Schafer et al, 2012, Tielborger, 2000). These complex sets of interactions lead to patterns in species coexistence and structure plant communities (Brooker et al, 2007, Valiente-Banuet, 2007). The facilitative effects of desert shrubs can lead to concentrations of annual plants beneath the shrub canopy (Emmerson & Facelli 1996, Facelli 2002). 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 (Wootton, 1994, Callaway and Pennings 2000, Callaway and Walker, 2007). If the associated annual is a flowering plant, then there is the possibility for the plants to interact indirectly via pollinators.

The majority of research on pollinator mediated interactions is focused on co-blooming, centred around adaptations to optimal foraging theory with flowers as central resources for which pollinators forage. Flowering desert shrubs offer concentrations of floral resources for foraging pollinators. Shrubs can facilitate co-blooming if they act as a magnet, increasing local pollinator abundances which would spill-over to benefit the annuals, alternatively they may facilitate by combining floral displays to be larger, or more diverse. These changes to pollinator behaviour or demography improve the reproductive success of the annuals. Their height makes them salient features, and their structural complexity may mean that non-co-blooming pathways of interactions are likely prominent in this system. If the shrub is providing wind-blocking or habitat, may see facilitation without flowers. Shrubs may negatively influence the pollination of associated annuals by interfering, by obscuring them from foraging pollinators. Shading by the shrub Lonicera decreased visitation and pollen deposition to annuals beneath it (McKinney, 2011). Therefore, there is the potential for these indirect interactions to be simultaneously positive and negative.

A plant’s life stage can alter the balance of facilitative and competitive interactions (Callaway, 1997, Bruno 2003). The nurse plant syndrome young plant establish themselves under large plants, but later compete with them for resources. However, how these indirect interactions shift with changes in a plant’s life cycle are underexplored. The majority of facilitation studies involving shrubs try to determine if shrubs will facilitate invasive species species. However better understanding how foundation species interact is important to ecology too. Reid found cushions facilitate for pollinators as well (Reid, 2012). Because foundation plants have benefits that scale to other trophic levels, there could be changes in interactions between them. 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.

The pollination networks of deserts is.. Deserts are home to a really high diversity of pollinators. Competition for pollination is a driving factor for diverging phenologies, and the evolution of specialized mutualisms. There have been no studies testing for interspecific facilitation in deserts, however intraspecific density has been shown to be positive (Roll et al, 1997). Interspecific studies have primarily focused on cacti systems (Fleming 2001 Sonoran). Deserts are typified by harsh climate, high species specialization, short blooming periods, all of which may intensify positive and negative interactions. Harsh environmental conditions strongly constrain when flowers can bloom in the desert. The question of mechanisms in this case is an insight into outcomes from the potential intense environmental and interspecific pressures. Researchers have found that within season flowering phenologies within the desert are predictable (Jennings, 2001). *Ambrosia dumosa* increased seed set in annuals, however it is not possible to know if this was due to pollinator visits or a more direct sort of facilitation.

*Larrea tridentata* (Zygophyllaceae) or creosote bush, has been a dominant flowering shrub of the southwestern United States for 25 000 years (Batancourt 1990). It is highly tolerant to temperature extremes (Barbour, 2007), it’s evergreen habit allows for photosynthesis year round, it can maintain photosynthesis even under high temperatures and low water potentials. (Barbour, 2007). These adaptations mean it provides a canopy year round. It primarily reproduces clonally, therefore individuals can be exceptionally long lived, clones can reach over one thousand years old have been documented (Vasek, 1980). L. tridentata is a generalist shrub whole full pollinator guild contains 22 specialist pollinators and more than 80 generalists (Minkley et al, 1999). 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 and Minkley). L. tridentata is one of the most reliable flowerer’s in the Mojave (need citation), and therefore may provide critical resources to pollinators in drought years. L. tridentata acts as a nurse shrub for other desert perennials such as Opuntia leptocaulis, (Yeaton, 1978), Peniocereus striatus (Suzan et al, 1994), as well as facilitating annuals (Schafer, 2012 – inconsistent). Conversely, it also competes with some species through allelopathy (Mahill and Callaway).

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. Larrea and Malacothrix overlap at beginning and ends of their phenology (cite), making it an interesting system to test for changes in interactions for pollinators. 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 because it acts as a concentration of floral resources. To disentangle potential mechanisms and changes with reproductive shifts, the experiments took place before and during a full bloom. Furthermore, I assessed if L. tridentata is acting as a foundation plant within this ecosystem. This has been assessed in an area where L. tridentata is much more dominant – at my site it is not the most common shrub. This is assessed by looking for positive effects that extend to plants and arthropod communities, and if L. tridentata is capable of stabilizing climate using its canopy.

**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*. The Mojave Desert is a biodiversity hotspot supporting 659 species of bees (Saul-Gershenz et al, 2012) and 1680 species of vascular plants (Rundel and Gibson, 2005).

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*. Paper on chemical cues has analyzed both pollen.

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. Open area at least 1 m away from dripline of any larrea. Only 13 pairs were tested because a heatwave followed by a wind storm killed the Malacothrix. The distances to the three closest Malacothrix neighbours were measured and to the nearest L. tridentata. The number of Malacothrix flowers per plant were counted, and each Larrea was rated on a Likert scale (1 to 5) to quantify how in bloom it is. The x, y and z were quantified – this with the Likert scale forms a proxy for the number of flowers. 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. All stigma were also imaged.

Statistical Analysis

Hypothesis testing

To test for evidence of shrubs mediating pollinator visitation to *M. glabrata*, I fit generalized linear mixed-models (GLMM, lme4, R, glmer.nb) using a 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 in two separate models. To test for the influence of conspecific density, the number of *M. glabrata* blooms were included in all visitation models as a predictor (flowers.pot). Video length was log-transformed to match the log link and used as an offset in the model to maintain the count structure of the data. In the past it has been common 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 more information to be maintained by not standardizing (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 determine which visitors were driving the observed patterns, I fit a similar models as above, but the full model has a three way interactions. These were fit using glmmPQL and a quasipoisson distribution that corrects for dispersion. Least-squares post hoc tests were used to see which constrasts were significant. It was not possible to make a lme4 neg binomial model converge.

To test for influence of potentially interacting annuals or shrubs, I added each covariate to the base model (microsite + blooming + flowers.pot), one at a time, and tested if adding the variable significantly improved model fit by likelihood anova, and by AIC.

To look at the differences in visit duration and proportion of flowers visited per visit as measures of pollinator efficiency. I fitted gamma GLMM visit duration and proportion of flowers visited per visit. Following the data visualization in Figure x, I subsetted out bees and other?, and fit separate linear mixed models, using log-transformed visit duration as the response, and compared these to a null model of just the random intercept. I used another gamma GLMM to test for the proportion of flowers visited, and followed up with a least squares mean estimate to determine significantly different contrasts. There was a change just at shrub site. To determine if the interaction was due to species-specific responses, I tested models with RTU\*microsite, and RTU\*blooming. Three-way interaction model was not tractable.

Positive influences on other communities

To quantify if shrubs influence arthropod communities, I calculated arthropod abundance and species (RTU) richness were calculated using the r package vegan. I fitted GLMM (glmer.nb) for abundance, with rep ID as a random effect. Beetles from the family Melyridae made up 1217 of the 3384? total arthropods captured, therefore abundance models were fit with them excluded, included and individually because their high numbers really swamped out the responses from other insects. Posthoc tests (lsmeans) were carried out on any significant interactions. To test if L. tridentata has a positive influence on associated annual communities, I fit GLMM for percent cover, and annual species richness.

Pollen

GLMM were used….

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 (hereafter “pollinators”) made 925 flower visits to *M. glabrata* in 303 hours of video recording. No pollinators were observed in 61 of the 235 video observation periods. Frequency of foraging bouts 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. There was no significant influence of heterospecific annual bloom density, percent annual cover, or shrub blooming density on frequency of foraging bouts or total floral visitation. There was a significant correlation between flowers visited per hour between paired shrub/open microsites.

There was no significant difference between RTU visiting the microsites (Figure 1, Table x), nor were there significant interactions between RTU, microsite and blooming(Table x). The frequency of flower visits by Syrphids and solitary bees declined significantly with blooming (Figure 1,Table 3).

Duration of foraging bout was significantly shorter when larrea was in bloom. There was no difference in RTU. There was also a negative effect of L. tridentata blooming on M. glabrata visit duration, but no microsite effect (Table 1, Figure 3). Proportion of flowers visited results.

Hoverflies (Syrphidae: Eupeodes and Toxomerus) (%) were the most frequent visitor. Others (primarily small beetles and flies). After them were solitary bees. After that flies in the Bombyliidae family (mainly Anthrancinae, Usiinae and Bombyliinae).

There was no significant interaction between shrub flower number 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. When Melyridae are excluded from analyses, (report lsmeans numbers here). Abundance of all arthropods including Melyridae decreased with blooming, but was the same under shrubs and open areas. Melyridae were significantly less abundant under shrubs (lsmeans numbers). No difference in bee abundance in pan trap with blooming or microsite. 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).

Arthropod species richness and Shannon’s Diversity index were higher in the shrub microsites, and both microsites decreased with blooming (Table ). The species accumulation curve suggests an adequate amount of sampling (Figure x)

There is a significant correlation of insect abundance 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.

Co-blooming foundation plants

Prior to blooming, there was no difference in the number of blooming shrubs in a radius around the shrub and open microsites. There is a significant increase in the number of surrounding shrubs with larrea blooming, and after larrea blooms there is a significant difference between shrub and open sites. Logical given the open sites were chosen to be away from shrubs.

Visitation to larrea

The number of flowers and the height of the shrub (Pearson’s, 0.3185, p = 0.03511), number of flowers and width (Pearson’s, 0.462, p = 0.001595) and width and height (Pearson’s, 0.6915, p = 2.02e-07), all tested using cor.test function in r. Visitors and insect uses of L. tridentata was significantly different after blooming. L. tridentata received 197 floral visits/10 hours when blooming, 85 % of which were bees. It increased from x to 400ish, 179 of which were flower visits. 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. Visitation by all visitors was positively associated with flower number, height and width. Visitation to larrea much greater. 17.13 floral visits to the plants per hour.

Pollen Deposition

At the nearby site, there was no difference in conspecific pollen deposition to M. glabrata with proximity to L. tridentata. Conspecific pollen deposition increased with distance to nearest conspecific neighbour. M. glabrata 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). The average distance for M in non shrub sites was x. The average number of M flowers was x

Climate amelioration

Average daytime temperatures were lower, and nighttime temperatures higher under the shrub canopy. Daily max were lower under shrub, and daily min was higher.

Relative effects

RII

**Discussion**

*Larrea tridentata* interacts with multiple trophic levels both directly and indirectly. There is partial support for the hypothesis – L. tridentata appears to interfere with M. glabrata but this was not alleviated by blooming. Instead, L. tridentata competes with, rather than facilitates Malacothrix. The decrease in visitation to open microsites suggests that L. tridentata’s influence may extend beyond its canopy. L. tridentata has positive effects of both the annual plant and arthropod communities. L. tridentata stabilized microclimates.

Floral constancy

Some of this competition can be explained by the identity of Larrea’s pollinators. Honeybees were the most frequent visitor to L. tridentata. Despite being generalists, and having visited M. glabrata previously, they did not make any visits after Larrea bloomed. Floral constancy is a common feature of social bees, where even individuals from the same colony will specialize on different flower species, and this specialization can ‘switch’ from time to time (Waser, lots). Floral constancy differs from oligolecty in that preferences are facultative. Does the communication of honeybees lead to this as well? If the honeybees are communicating the location of strongly blooming larrea to the hive – it is less likely that they will bother with annuals lower to the ground. Among honeybees, color is not always the key factor in flower constancy (Greggers and Menzel 1993). It was a good rain year, and lots of shrubs were blooming. Maybe if there were lots of honeybees they would spill over to Malacothrix. Changes to bee behaviour. Optimal foraging. Generalists and specialists. Floral constancy.

The second most common visitor to Larrea was Centris. They did not make any visits to Malacothrix, nor were they caught in pan traps. Centris are oil specialists, however they visit different plants to collect nectar. There was a significant decline in solitary bee visitation when larrea bloomed. About 30% of visitors to Larrea were solitary bees – including Halictus and Megachile. These bees did visit Malacothrix prior to blooming, however for the most part it was not possible to ID them from the videos. The rest of the visitors were dominated by specialists: Megandrena encelia and hesperapis larrae are both locally oligolectic, generally only visiting Larrea as long it is present (Hurd and Linsely, 1975). Found them both in pan trap and they visited larrea. Part of the hypothesis again was supported, pollinators (mostly bees) responded positively to floral number and height, i.e. concentrations of floral resources – this just didn’t spill over to M. glabrata.

Competitive exclusion? Is there evidence of competitive exclusion between different plant species – can they just be excluded from the area?

The major driver was the decrease in visitation by syrphid flies. The main syrphid visitor to M. glabrata was Eupeuodes volucris, which does visit L. glabrata (Hurd and Linsely, 1975). It did not make any visits after blooming to larrea, still visited M. glabrata a bit. I observed it “inspecting” larrea buds pre-blooming x number of times. Talk about temporal partitioning. The correlation between the microsites suggests that shrub influence the open areas as well. It may be possible to test this at a site where L. tridentata are less dense.

RII suggests no difference between microsites after blooming. 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.

Alternatively, because visitation was so low to both microsites after blooming, it is unlikely that there would be any biologically relevant difference between them. My findings suggest that even though facilitation or neutral interactions may be measured during co-blooming, competition may be more biologically relevant. 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.

Stealing pollinators is parasitism.

Flowering time, within a species, can have strong effects on fitness (Lacey, 2003).

Larrea is a foundation species.

RII indicates that larrea has different influences on different trophic levels. Foundation plants often modulate temperature. The data loggers suggests that L. tridentata is creating microclimates. Facilitates vegetation growth but competes for pollinators. Ruttan 2016 found that velvet ants were indicators, this study also found that. She also found no difference in the number of bees in pan traps. Foundation species influences are not completely positive. These findings provide evidence of a single shrub species have simultaneously positive and negative itneractions.Just because it concentrates insects doesn’t mean that benefits plants.

Interactions change with life cycle.

My findings support the predictions of many author’s – that interactions change, or as I found, intensify with shifts in reproductive cycles. Shrub-annual phenology. Phenological divergence. Unavailability of rainfall likely prevents annuals from adjusting their phenology. The warmth and moisture required would put a hard limit on when they can flower. Germination of Mojave annuals is thought to be spurred by a certain amount of rainfall (Jennings, 2001) but are predictable within years.

Conclusions: