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), such as stress amelioration, 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, Hozalpfel) and it is posited that their relative importance varies with abiotic stress (Bertness and Callaway, Schafer et al, 2012). These pairwise interactions are often inadequate to predict observed outcomes in ecosystems (Callaway and Pennings, 2000). Indirect interactions arise when a third species alters the interaction between two other species (Wootton, 1994, Callaway and Pennings 2000, Callaway and Walker, 2007). These interactions may be mediated by another plant, or by organisms belonging to other trophic levels such as mycorrhizae (File et al, 2012) and pollinators (Rathcke, 1983). A plant’s life stage can alter the balance of facilitative and competitive interactions (Callaway, 1997), for example the nurse plant syndrome young plant establish themselves under large plants, but later compete with them for resources. Biomass of annuals often greater under shrubs than in open areas (many citations).

Interactions for pollinators between plants forms a continuum from competition to facilitation (Ratchke, 1983). However, how these indirect interactions shift with changes in a plant’s life cycle are underexplored. This is particularly true in arid ecosystems where facilitation of shared pollinators can be particularly important in deserts because harsh environmental conditions can lead to large spatial variation in floral abundances and pollinator populations (Rathcke, 1983). Bruno et al. (2003) predicts temporal flips in relative interactions from competition to facilitation, however few studies have documented the effect.

Harsh environments are a good place to study these interactions because plants tend to benefit more from amelioration. The question of mechanisms in this case is an insight into the potential intense environmental and interspecific pressures. Deserts are typified by harsh climate, high species specialization, short blooming periods, all of which may intensify positive and negative interactions. There have been no studies testing for interspecific facilitation in deserts, however intraspecific density has be shown to be positive (Roll et al, 1997). Interspecific studies have primarily focused on cacti systems (Fleming 2001 Sonoran). Competition for pollination is a driving factor for diverging phenologies, and the evolution of specialized mutualisms. Harsh environmental conditions strongly constrain when flowers can bloom in the desert. And they are apparently really specialized. But there isn’t really empirical evidence for the interactions between pollinators. 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. Chung et al removed the flowers from Rosa multiflora (2014), but found no effect on bee visitation rates to co-blooming annuals. Shading by the shrub Lonicera decreased visitation and pollen deposition to annuals beneath it (McKinney, 2011). The majority of facilitation studies involving shrubs involve invasive species, however this is about foundation species. Reid found cushions facilitated. However, the same attributes that make a plant act as a magnet are the same that may cause it to compete. Mechanisms? Understanding mechanisms is important because… Facilitation pathways that don’t involve co-blooming are critically understudied. There are several pathways to facilitation: Change in behaviour (attracting more to area), change in population (concentrate pop). By sampling arthropod community, can try to see the pathways better. Community level interaction pathways very complicated. During the flowering period of the focal plant it may not be possible to separate interactions for pollinators from those that do not require co-blooming. If the shrub is providing wind-blocking or habitat, may see facilitation without flowers. On the competition side, it may not be possible to separate competition due to parasitizing pollinator visits versus interference. While one study has tested for mechanistic differences (Jacobsen), this is a test for sequential mutualism.

Creosote bush, *Larrea tridentata* (Zygophyllaceae) has been a dominant flowering shrub of the southwest USA for 25 000 years (Batancourt 1990). Individuals that are several thousand years old have been documented (Vasek, 1980). L. tridentata is a generalist shrub. The 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 only interact with 20% of the full guild, but there is a stable core guild (Cane and Minkley). L. tridentata acts as a nurse shrub for some species (which, cite). It also competes with some species through allelopathy (Mahill and Callaway). L. tridentata is one of the most reliable flowerer’s in the Mojave, and therefore may provide critical resources to pollinators in drought years. Whether it competes for pollinators is not known. 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. Understanding interactions for pollination at a community level is critical for understanding potential impacts of any decline.

Here we test for the influence of larrea onto its commonly co-occurring annual Malacothrix glabrata. Larrea and Malacothrix overlap at beginning and ends of their phenology. This makes it an interesting system to test for changes in interactions for pollinators. Malacothrix was chosen as a phytometer because it commonly co-occurs with L. tridentata, and was the only annual growing sufficiently nearby in high enough abundances to use for experiments. I predict that they will compete prior to Larrea blooming due to interference, and that Malacothrix will show increased visitation when larrea is blooming. More visits underneath than in open areas. I also want to look deeper to see which pollinators are driving the changes. To disentangle potential mechanisms and changes with reproductive shifts, the experiments took place before and during a full bloom.

**Methods**

Study site

The main study site is located in the opening Sunset Cove on 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 gently sloping, and with tall rock formations on three sides, with the opening side widening to the south. It is a diverse shrub and cactus dominated community. The most abundant shrub is *Acamptopappus sphaerocephalus*, but larrea likely has the greatest biomass. Also common *is Ambrosia salsola, Eriogonum fasciculatum, Cylindropuntia acanthacarpa, Cylindropuntia echinocarpa* and *Thamnosa montana*. The most common flowering annuals present during the study period were small Boraginaceous, 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). The study took place between April 10th, 2017 and May 5th, 2017.

Phytometer species

Phytometers are individual plants used in controlled way as an environmental indicator (Clements and Goldsmith, 1924) and we used the dandelion to measure pollination services. *Malacothrix glabrata*, desert dandelion, was used as a phytometer. Malacothrix glabrata (Asteracae), desert dandelion, is a native annual wildflower. Germination of Mojave annuals is thought to be spurred by a certain amount of rainfall (Jennings, 2001) but are predictable within years. Bees in the genus Nomadopsis visit M. glabrata for pollen (Rutowski). There are 24 species of Mathacothrix, some are self-compatible (M. incarnata which is Agapostemon pollinated, Davis 1986). It is visited by short-winged flower beetles (Cline, 2010). Anthidium bees (Wainwright). The flowerheads are dense with yellow corollas (Morhardt, book, California desert flowers), and grow up to 40 cm tall. They grow in clumps. 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. The paired sites were used to minimize potential differences due to environmental heterogeneity.

To disentangle co-blooming and non co-blooming interaction pathways, as well as to minimize variation due to individual shrub differences and to focus on relative shifts in supported communities and interactions, a repeated measure study design was used. A repeated measures study design was chosen to minimize differences due to individual variation in the shrubs and better approximate the change in pollination to the understory with shrub phenology. Individuals 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. The minimum tested was 102, the maximum was 1080. In two cases, a focal shrub did not bloom and were replaced by a new blooming shrub. These cases were excluded from later RII calculations.

Visitation to Malacothrix glabrata

Each morning of each study day, fresh *M. glabrata* were gathered from nearby (< 3 km) populations where they seasonally coexist with *L. tridentata* and transplanted into 15 cm diameter black pots. Transplants of similar size and habit were paired, 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). The flowerheads of *Malacothrix* were trimmed to equal numbers between paired microsite, but left to vary between replicates. The mean number of flowers of *M. glabrata* per pot was 10, and there was no significant difference in flower number between any treatments (stats here). Polaroid Cube+ HD (1080 p, recording time ~ 1.5 hrs) cameras were used to record pollinator activity to each M. glabrata. Recording periods were timed to coincide with peak pollinator activity (between 11:30 am and 3:30 pm). The use of video technology allows for higher temporal resolution…. 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.

Floral density can influence pollinator visitation (Bosch and Waser, 2001), we ensured that there were no blooming M. glabrata in the direct vicinity of the experiment. Heterospecific annual floral density and annual species richness were measured within a 0.25 m2 quadrat in each microsite. 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 Larrea were counted, and the shrub dimensions were measured by….

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 inner part of the flowering. A foraging bout/plant visited is defined as a single plant visits, whereas “total flowers” are the total number of flowers visited by all pollinators per replicates. Visit duration refers to the length of the foraging bout, to all of flowers per plant visit and included inter-flower travel time. Proportion of flowers visits are the number of flowers visited per foraging bout divided by the number of flowers in the field of vision.

Floral visitors were identified to RTU – recognizable taxonomic unit. These were honeybees, solitary bees, lepidoptera, syrphid flies, bombylid flies and other, which was primarily muscoid flies and small beetles. Five videos were omitted due to disturbance or battery failure (n = 235).

Arthropod community sampling

Foundation plants can have effects that scale to trophic level beyond plants (Reid, Ruttan). To quantify pollinator populations associated with each microsite, as well as to assess if L. tridentata is acting as a foundation species within this system, the arthropod communities were sampled using pan traps in the same study design as above. There were 9 days of sampling pre-blooming and 10 days post blooming. The same focal shrubs were used, but on different days as to not influence pollinator visitation to *Malacothrix*. Yellow, white and blue six-inch diameter plastic bowls (Solo) were filled with water with a few drops of Dawn original dish detergent added. One of each colour were placed in a triangular shape at each microsite, slightly embedded in the ground to prevent blowing away. To capture peak pollinator activity, they were deployed by 10 am and 5:30 pm on sunny days only. As a proxy for annual biomass, total percent vegetation cover was also recorded in a 0.25 m2 quadrat.

Bees (Discoverlife, Bees of North America, Bees of the world) and syrphid flies (Miranda et al, 2013) were identified to species or genus. The rest were identified to a minimum of family (Borror and Delong, Marshall, 2017, Grissell and Chauf 1990, McAlpine et al, 1993, Packer andreninae key)) except Thysanoptera, Orthopteran and Arachnida which were left to order.

RTU (recognizable taxonomic unit) 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. Therefore, related groups were 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 RTU for diversity analyses. Individuals of Miscophus or Pemephrinae were not counted within Crabronidae: no individuals were double counted. This way of categorizing diversity was a trade-off between maximizing resolution and speed given the high diversity of desert species. A full list of the 130 RTU are provided in the appendix and the associated dataset has been published openly to KNB (Braun, 2018). All specimens are located within our 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 often insufficient to quantify pollinator guild of Larrea (Cane et al, 2000). Therefore, arthropod activity on and under *L. tridentata* was observed in 15-minute time periods. Four individuals were observed per day, 10 days pre-blooming and 6 individuals per day for 10 days blooming. These were the same focal shrubs, but on different days than pan traps or video trials. The number of visits and identity of the visitors were 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

Foundation plants create locally stable microclimates (Ellison). To measure the microclimates of the microsites, 16 HOBO pendant data loggers were used to record temperature and light availability. Eight loggers were placed on the south side under *L. tridentata* and eight in open areas for between March x and May 14th. They take readings every ½ hour. I calculated the average daily maximum and minimum temps and light availability.

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 the effect of microsite and blooming on pollinator visitation to *M. glabrata*, as well as any possible interactions, I fitted generalized linear mixed-models (GLMM, lme4, R, glmer.nb). I used negative binomial error distributions to account for overdispersion within the data with a loglink function. 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 density, the number of *M. glabrata* blooms were included in all models. To maintain the count structure of the data, the length of the video as an offset, this was log-transformed to match the log link. Some previous work standardized visitation to visits/hour/flower, however 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 was used as a random effect (focal shrub number + microsite) to accounted for the repeated measures study design.

Syrphid fly and bee responses were subsetted and analyzed individually using additional GLMM negative binomial models. These three RTU were modelled individually, rather than including them as a factor within the main hypothesis model. They are the most frequent visitors to Malacothrix and Larrea respectively, and are well known pollinator guilds. Pollinator species identity is both a predictor and response – here I am more interested in species-specific responses rather than controlling for the influence of species identity within the main model. Modelling species response individually is commonly done in plant facilitation studies (cite, cite, cite, city), as well as pollination facilitation studies (cite, cite, cite, cite). Multiple testing is an issue, however if we assume visitor identity are independent of each it may not be necessary (cite, cite).Models were compared used max-likelihood (Wald test) and AIC. Models were compared to null models of M. glabrata + random intercept models using likelihood (Appendix X).

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.

Diversity indices including species richness and Shannon’s Diversity index of pan traps were calculated using the r package vegan. I fitted GLMM (glmer.nb) for abundance, and linear mixed models (LMM, lme4, lmer) to look at species richness, with rep ID as a random effect. Beetles from the family Melyridae made up 1217 of the 3400 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.

I also built models just for bees.

Vegetation covariates

To determine the importance of covariates, used a correlation matrix? Weather and vegetation covariates were added one at a time with microsite and treatment as fixed variables. Annual bloom density, shrub surround density, cactus density, annual richness and percent cover are potential confounding variables so were included in a full-model? A backwards selection method using likelihood to compare models was used. This method is more rigorous than using p-values. See appendix B.

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.

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, Shannon’s.

**Results**

Camera test

A total of 697 flying visitors made 925 flower visits to *M. glabrata* in 303 hours of video recording. 61 of the 235 observation periods had no flying visitors. Frequency of foraging bouts and total floral visitation by pollinators to *M. glabrata* were significantly lower at the shrub microsite relative to open areas. Frequency of foraging bouts and total floral visitation by pollinators were reduced to M. glabrata in both microsites when *L. tridentata* was in bloom relative to pre-blooming (Table 1). There was no significant influence of heterospecific annual bloom density, percent annual cover, or shrub blooming density on visitation to M. glabrata by any of the groupings of pollinators. There was a positive effect of M. glabrata conspecific density.

There was no significant difference between RTU visiting the microsites (Figure X). The frequency of flower visits by Syrphids and solitary bees declined significantly with blooming (Table 3).

Visit during. Prop flowers. RTU level effects?

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.

There was a significant correlation between flowers visited per hour between paired shrub/open microsites.

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).

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.

The most frequent floral visitors to L.tridentata were bees (115): Apis mellifera (54 visits), Centris rhodapus (35), Hesperapis larrea (30), Eucera sp. (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. However, heterospecific pollen deposition increased with distance away from L. tridentata.

Climate amelioration

Data logger data analysis goes here

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.

Interference and Competition

Syrphid flies

Some of this competition can be explained by the identity of Larrea’s pollinators. Honeybees were the most frequent visitor to L. tridentata, however despite being generalists they tend not to switch foraging sources (cite, cite). 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. Centris was also a visitors. 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. Visitation to Larrea increased with both flower number and height, however this attractiveness to mainly bees did not spill over to M. glabrata.

Species composition of pollinators to M. glabrata was significantly different blooming to pre-blooming. Syrphid flies made the majority of floral visits to M. glabrata pre-blooming, but were mainly absent after larrea bloomed. This decrease is evident from both visits to M. glabrata (Figure 1), visits to L. tridentata (38 pre, 7 post: only one of which was a flower visit) and pan traps (18 pre, 2 post). Indicator analysis (indicspecies, R) using pan trap data of 3400 specimens spanning 130 taxonomic groups showed that Scaeva pyrastri (the primary syrphid visitor to Malacothrix, pre-blooming) is an indicator species for the pre-open+pre-shrub group (p = 0.001). It is possible that syrphid flies were competitively excluded from the shrubs and surrounding area once L. tridentata was blooming, or that their lifecycle is closely linked to the phenology of annuals.

Bees

L. tridentata received 197 floral visits/10 hours when blooming, 85 % of which were bees. There was no significant difference in bee abundance caught in pan traps between any of the treatments (all p > 0.68). There was no difference in number M. glabrata flowers visited by solitary bees between the microsites, but there was a significant decrease in visitation with L. tridentata blooming at the open microsite only (Table 1). When honeybees are included in the model, there is a significant decrease in visits with L. tridentata at the shrub microsite as well. Talk about temporal partitioning. Syrphid fly phenology. 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.

Larrea is a foundation species

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.

No effect on pollinator abundances – thus likely behavioural? Just because it concentrates insects doesn’t mean that benefits plants. No difference in bees in pan traps. Lack of visitation to Malacothrix not due to lack of bees – Larrea was visited. If the bees that visited were oligolectic but main visitor to Larrea was the honeybee. A generalist. Honeybees often forage only on one resource type. They were feral honeybees. The other bees, Centris sp. are oil specialists and the others are specialists. Larrea with more flowers received more visits. Dilution effect – not only was larrea flowering – surround shrubs and cactus were as well. dominant, foundational plants all flowering, and potentially life cycle shifting of certain pollinators. 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.

Interactions change with life cycle.

Table: Total arthropod abundance for each treatment

|  |  |  |  |
| --- | --- | --- | --- |
|  | Shrub | Open | Total |
| Pre-blooming | 935 | 973 | 1908 |
| Blooming | 692 | 777 | 1469 |
| Total | 1627 | 1750 | 3377 |

Table 2: Mean ± SD, arthropod abundance per shrub for each treatment, 3 pan traps. Including flower beetles.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Shrub | Open | Total |
| Pre-blooming | 17.31481 ± 7.947526 | 18.01852 ± 10.074235 | 17.66667 ± 9.037823 |
| Blooming | 11.53333 ± 6.217708 | 12.95000 ± 7.601126 | 12.24167 ± 6.951205 |
| Total | 14.27193 ± 7.630035 | 15.35088 ± 9.177678 |  |

Table 3: Total arthropod abundance without Melyrid beetles

|  |  |  |  |
| --- | --- | --- | --- |
|  | Shrub | Open | Total |
| Pre-blooming | 783 | 510 | 1293 |
| Blooming | 435 | 359 | 794 |
| Total | 1218 | 869 | 2087 |

Mean plant visits per hour. This is just the mean number of potential foraging bouts. ± the standard deviation.

|  |  |  |
| --- | --- | --- |
|  | Open | Shrub |
| Pre-blooming | 4.2955249 ± 4.621614 | 2.9976793 ± 3.134733 |
| Blooming | 1.2526164 ± 1.376179 | 0.9458532 ± 1.271302 |

Mean number of flowers visited per hour. ± standard deviation.

|  |  |  |
| --- | --- | --- |
|  | Open | Shrub |
| Pre-blooming | 5.758404 ± 7.547992 | 3.776575 ± 4.742340 |
| Blooming | 1.722185 ± 2.218946 | 1.268643 ± 2.047149 |

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Percent cover | | Annual Richness | | Annual bloom density | |
|  | **χ**2 value | |  | |  | |
|  |  | p – value | **χ**2 value | p – value | **χ**2 value | p – value |
| Microsite | **165.399** | **<0.0001** | 0.7071 | 0.40 | 0.6009 | 0.438 |
| Blooming | **34.180** | **<0.0001** | 2.7010 | 0.10 | **13.3646** | **0.0003** |
| Microsite \* blooming | **22.806** | **<0.0001** | NA | NA | NA | NA |

Table 2: GLMM results for pan trap abundances. Non-significant interactions were removed models.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Insect abundance (Melyridae: Dastyine excluded) | | Insect abundance (Melyridae: Dastyine included) | | Insect species richness | |
|  |  | |  | |  | |
|  | **χ**2 value | p – value | **χ**2 value | p – value | **χ**2 value | p – value |
| Microsite | 13.4645 | **0.0008** | 1.7201 | 0.1897 |  |  |
| Blooming | 11.3074 | **0.0002** | 33.6643 | **<0.0001** |  |  |
| Microsite \* Blooming | 3.8427 | **0.04996** | NA | NA |  |  |

Supplemental Data

* All camera stuff with all visitors included, along with model outputs