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

*Malacothrix glabrata*, desert dandelion, was used as a phytometer. Phytometer, definition here, are commonly employed in agricultural studies to measure pollination services.

Microsites

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 ensure the plants were not shaded. The paired sites were used to minimize potential differences due to environmental heterogeneity.

Visitation to Malacothrix glabrata

In the 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. Transplants of similar size and habit were paired and one pot was placed per microsite. Conspecific density influences pollinator visitation (Bosch and Waser), so *Malacothrix* to equalize floral number between shrub and open sites, but left to vary between replicates. The mean number of flowers of *M. glabrata* per pot was 10.

Polaroid Cube+ HD cameras were used to record pollinator activity on M. glabrata. They capture video in 1080p, and have an approximate run time of 1.5 hours.

Six shrub/open pairs were tested each day between the hours of 11:30 am and 3:30 pm to capture peak pollinator activity. Ten days of trials (60 shrub/open pairs) were conducted prior to *L. tridentata* blooming between April 10 and April 20. Individuals with fewer than five open blooms were considered non-blooming. Ten days of trials (60 shrub/open pairs) were conducted using the same shrub/open pairs between April 21 and May 5, after the shrub had entered a full bloom. 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. 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. The average number of blooms for ‘blooming’ treatment was 300.2 ± 176.72SD. The minimum tested was 102, the maximum was 1080.

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.

Five videos were omitted due to disturbance or battery failure. Video footage was reviewed in lab. Pollinator visitation, the number of flowers visited, duration of visit, and identity of visitor were recorded. A pollinator visit was defined as when an insect flew onto the flower, touching the reproductive organs. Visitation rates are a commonly used proxy of pollination (cite).

Arthropod community sampling

To determine if there are certain arthropod communities associated, and if shrubs can influence different trophic levels and if this influence changes with blooming.

The arthropod communities associated with each microsite were sampled using pan traps.

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 were placed in a triangular shape at each microsite, slightly embedded in the ground to prevent blowing away. The same focal shrubs were used, but on difference days as to not influence pollinator visitation to *Malacothrix*. To capture peak pollinator activity, they were deployed by 10 am and 5:30 pm on sunny days only. Percent vegetation cover was 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) 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 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 were considered distinct RTU in the Miscophus or Pemephrinae were not counted in 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 used provided in the appendix.

Mites (Acari) and springtails (Collembola) were excluded from analyses. Nymphs were included in analyses provided they could be identified to order. All specimens are located within our collection in Lortie Lab at York University. Each pinned specimen has unique ID. These data have been made publicly available: KNB, doi: Hemipteran nymph were lumped together. Other nymphs were added to family as long as they could be IDed (example, coccinelidae, ladybug larvae).

Arthropod visitation to Larrea tridentata

Pan traps are often insufficient to quantify pollinator guild of Larrea. 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).

To measure the microclimates of the microsites, 16 HOBO pendant data loggers were used to record temperature and light availability. Eight loggers were placed 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 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.

Heterospecific pollen were identified using a reference collection created of 38 species from surrounding sites in 2017 and 2018. This reference collection was photographed using Lumenera microscope camera at 100 x and 400x and the size of grains were measured using Infinity Analyze to aid identification. The digitized reference collection was uploaded to global pollen project (DOI) and the slides are in Lortie Lab at York University.

Statistical Analysis

To quantify differences in pollinator visitation to M. glabrata, I fitted a generalized linear mixed-model (GLMM, lme4, R, glmer.nb) using a negative binomial error distribution to account for overdispersion of the data. I used both the number of foraging bouts (visits to plant) and the total number of flowers visited as response variables. To maintain the count structure of the data I included the number of *M. glabrata* blooms as a predictor variable, and the length of the video as an offset. It is not uncommon to convert 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. This method allows for more information to be maintained by not standardizing (cite), 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. I also looked at bee responses specifically by subsetting visits by bees. Models were compared used max-liklihood and 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.

RTU (recognizable taxonomic unit): these were honeybees, solitary bees, lepiodeptera, syrphid, bombyliid and other. These were integrated into models and using post-hoc tests I determined if there were RTU specific responses. Models were compared to null models of random intercept models using likelihood.

Diversity indices of pan traps were calculated using the r package vegan.

GLMM, again shrub identifier as a random effect. Species richness was modelled using a linear mixed model. Beetles from the family Melyridae made up ~1000 of the total arthropods captured, so we ran analyses with them excluded, included and on their own because their high numbers really swamped out the responses from other insects. I fitted GLMM (glmer.nb) for abundance, and linear mixed models (LMM, lme4, lmer) to look at species richness.

To see if communities were different under shrubs, used rda ordination methods. Alpha diversity: Beta diversity, arthropod community turnover was also calculated for shrub open and pre-post.

Pollen

Vegetation surveys

To look at plant-plant facilitation, and assess differences in bloom density. Linear models for percent cover and neg binomial GLMM annual richness and annual bloom density (glmer.nb, lme4)

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.

**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 difference in number *M. glabrata* flowers visited or foraging bouts made by solitary bees between the microsites, but when L. tridentata entered into full bloom there was a significant decrease in both foraging bouts made and visitation to M. glabrata in open areas (Table 2). There was a positive effect of M. glabrata conspecific density.

When honeybees are pooled with solitary bees in the model, there was a significant decrease in foraging bouts and floral visitation to M. glabrata in both microsites when L. tridentata entered into full bloom.

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 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).

Rtu differences

RDA of visitor identity?

Effects on arthropod communities

3400 arthropods spanning 130 taxonomic groups were caught in 19 days of pan trapping.

~1000 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).

Predatory and parasitoid wasps were more abundant in shrub microsites. Velvet ants were only associated with open sites.

No significant correlation between visitation and abundance, or diversity from pan traps.

Guild specific changes.

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 richness and 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

Changes to visitor community

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.

Blooming changes to bees, specialists and generalists.

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