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

Like title – could also have a snap/joke/metaphor or link to the bigger idea? PMI is the idea or theory – but could use a more general eco-term that ie broader – facilitation, indirect interactions, collective attraction – attractant/decoy etc. think over.

Abstract

In arid ecosystems, the facilitative effects of shrubs can lead to concentrations of annual plants beneath the canopy. The indirect interactions that arise from the close spatial proximity of nurse-protégé relationships can have important implications for community structure and assembly. Creosote bush, *Larrea tridentata* is a dominant shrub of the Mojave Desert. Here, we test for the capacity of creosote bush to influence the pollination of its annual understory during its phenological shift into flowering. Pollinator visitation rates to the phytometer desert dandelion were significantly lower as the understory of creosote bush, and when creosote bush entered into a full bloom, visitation rates declined significantly at both understory and nearby open microsites. The decrease in visitation was driven by syrphid flies and the behavioural responses of solitary bees. In this system, we found that *L. tridentata* has a positive ecological effect on associated annual plants and the arthropod community, but this shrub further had negative indirect effects on pollination of a representative flowering annual plant. This study confirms the positive role of *L. tridentata* as a foundation plant but more importantly suggests that the net outcome of interactions can be negative or positive depending on the specific shrub function tested or the recipient taxa.

Introduction

Foundation species positively influence the structure of the surrounding plant communities by creating locally stable conditions for other species ([Ellison et al., 2005](#_ENREF_24)). In arid environments, foundation shrubs can act as keystone facilitators, directly benefiting associated understory annual plants via multiple mechanistic pathways across all life stages ([Filazzola and Lortie, 2014](#_ENREF_26)). These include stress amelioration ([McIntire and Fajardo, 2014](#_ENREF_47)), improved water and nutrient availability ([Franco et al., 1994](#_ENREF_30)), and seed trapping ([Flores and Jurado, 2003](#_ENREF_29)). Direct interactions between shrubs and annuals can be simultaneously facilitative and competitive ([Bertness and Callaway, 1994](#_ENREF_5); [Callaway and Walker, 1997b](#_ENREF_13); [Holzapfel and Mahall, 1999](#_ENREF_36)), and it has been proposed that the relative importance of negative versus positive effects covaries with abiotic stress ([Bertness and Callaway, 1994](#_ENREF_5); [Schafer et al., 2012](#_ENREF_72); [Tielbörger and Kadmon, 2000](#_ENREF_82)). These complex sets of interactions lead to patterns in species coexistence and structure plant communities ([Brooker et al., 2008](#_ENREF_9); [Valiente‐Banuet and Verdú, 2007](#_ENREF_85)). The facilitative effects of desert shrubs can lead to concentrations of annual plants beneath the shrub canopy ([Facelli and Temby, 2002](#_ENREF_25)). This close spatial proximity of shrubs and annuals undoubtedly gives rise to indirect interactions ([Sotomayor and Lortie, 2015](#_ENREF_77)). Indirect interactions arise whenever a third species alters the interaction between two other species ([Callaway and Pennings, 2000](#_ENREF_11); [Callaway and Walker, 1997b](#_ENREF_13); [Wootton, 1994](#_ENREF_90)). If the associated annual is a flowering plant, then there is the capacity for the plants to interact indirectly via pollinators.

Interaction pathways requiring co-blooming dominate the study of the underlying mechanisms of pollinator-mediated interactions. These are primarily extensions to optimal foraging theory ([Pyke, 1984](#_ENREF_62); [Pyke et al., 1977](#_ENREF_63)) with flowers as the central resources for which pollinators forage. Thus plants can become more attractive by combining their floral displays to increase net floral patch size ([Schemske, 1981](#_ENREF_73)) or to make the patch offering more diverse ([Ghazoul, 2006](#_ENREF_31)). Flowering desert shrubs offer concentrations of floral resources for foraging pollinators, and this can facilitate co-blooming annuals. Magnet species are particularly attractive to pollinators increasing local pollinator abundances that benefit their less attractive neighbours ([Laverty, 1992](#_ENREF_44); [Thomson, 1978](#_ENREF_81)). If shrubs concentrate pollinators which do not in turn visit their neighbours, competition rather than facilitation will arise. Shrubs are salient features of desert scrub ecosystems due their large size and structural complexity relative to ephemeral plants and can also influence the pollination of associated plants via non-floral mechanistic pathways. Shrubs may facilitate their annual understory by improving conditions for pollinators by offering shelter or habitat. Alternatively, annuals growing under shrubs can be physically obscured from foraging pollinators or shaded thereby reducing visitation. For example, shading by the shrub *Lonicera* decreases pollinator visitation and pollen deposition to its understory annuals ([McKinney and Goodell, 2010](#_ENREF_48)). Consequently, direct and indirect shrub effects on other species function simultaneously to determine net outcomes. The balance of facilitative and competitive interactions can be further altered by a plant’s life stage ([Bruno et al., 2003](#_ENREF_10); [Callaway and Walker, 1997a](#_ENREF_12); [Pugnaire et al., 1996](#_ENREF_61); [Rousset and Lepart, 2000](#_ENREF_67); [Valiente-Banuet et al., 1991](#_ENREF_84)). For example, within some nurse plant systems young plants are facilitated during establishment, but later compete with their nurses for resources ([Yeaton, 1978](#_ENREF_91)). For plants, the life stage shift from vegetative growth to reproductive growth is a major event. Thus incorporating phenological shifts adds another dimension to estimating net interactions.

## The Mojave Desert is a biodiversity hotspot supporting 659 species of bees ([Saul-Gershenz et al., 2012](#_ENREF_71)) and 1680 species of vascular plants ([Rundel and Gibson, 2005](#_ENREF_68)). Despite the celebrated biodiversity of Southwestern Deserts, pollinator-mediated interactions in this region are infrequently tested. Intraspecific density has been shown to benefit the pollination of desert mustard *Lesquerella fendleri* ([Roll et al., 1997](#_ENREF_66)); however, interspecific studies have primarily focused on competition within cacti systems in the Sonoran Desert ([Fleming et al., 2001](#_ENREF_28)). Plant-pollinator systems in southwest deserts are home to rare obligate mutualisms such as the Joshua tree *Yucca brevifolia* and Yucca moths ([Pellmyr, 2003](#_ENREF_60)), and the senita cactus *Pachycereus schottii* and senita moths ([Fleming and Holland, 1998](#_ENREF_27)) and are often considered highly specialized. The degree of specialization of desert ecosystems is a subject of ongoing debate. Desert organisms are hypothesized to adapt to high environmental variability by generalizing resource use ([Chesson et al., 2004](#_ENREF_18)), and this has garnered recent empirical support in pollination networks ([Chacoff et al., 2012](#_ENREF_17)). Overall, few one-to-one relationships have been found with solitary bees ([Simpson and Neff, 1987](#_ENREF_76)), and bees still visit even senita cactus ([Holland and Fleming, 2002](#_ENREF_35)). Despite the high number of specialist pollinators present in the Mojave, most plant species nonetheless interact through pollinators.

The purpose here was to examine both the direct and indirect effects of *Larrea tridentata* on the pollination of its annual understory. Phytometers are individual plants used in a controlled way as environmental indicators ([Clements and Goldsmith, 1924](#_ENREF_19)). We used the commonly co-occurring annual *Malacothrix glabrata* as phytometer to measure pollination services*.* These species co-flower at beginning and ends of their bloom period ([Jennings, 2001](#_ENREF_40)), therefore it is a relevant system to model changes in interactions within a season. We hypothesize that desert shrubs that function through some mechanistic pathways as benefactors can also positively and negatively impact the net outcome of pollination for associated annual plants through effects of large floral offering and extent of co-blooming with the community. We have four predictions: 1) Visitation rates to an associated annual phytometer species tested differ under a shrub canopy relative to open microsites. 2) Phenological stage of the shrub determines whether the net pollination rates to the annual species are negative (non-co-blooming) or positive (co-blooming). 3) The shrub species tested can simultaneously have positive effects on an annual plant community through increases in relative abundances whilst having different pollination effects. 4) Net effects of the shrub on surround annual and arthropod communities are positive. Understanding interactions for pollination at a community level is critical for understanding potential impacts of any decline in pollinator populations. If shrubs facilitate their understory annuals, they can buffer pollinator declines but if shrub typically interfere with pollination for annuals, the sensitivity to change for the community increases.

**Methods**

Study site

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

Phytometer species

We used the desert dandelion *Malacothrix glabrata* (*Asteraceae*) as a phytometer to measure pollination services. *M. glabrata* is an abundant, native annual wildflower that commonly co-occurs with *L. tridentata*. The flowerheads are dense with yellow corollas and grow up to 40 cm tall ([Morhardt and Morhardt, 2004](#_ENREF_55)). *M. glabrata* is insect-pollinated, including bees in the genus *Nomadopsis* ([Rutowski and Alcock, 1980](#_ENREF_69)) and *Anthidium* ([Wainwright, 1978](#_ENREF_88)) as well as short-winged flower beetles ([Cline and Audisio, 2010](#_ENREF_20)). Several of the 24 species of *Malacothrix* are self-compatible ([Davis and Philbrick, 1986](#_ENREF_22)), however the reproductive biology of *M. glabrata* has not been studied in detail.

Study species

Creosote bush, *Larrea tridentata* (Zygophyllaceae), has been a dominant flowering shrub of the southwestern United States for 25 000 years ([Betancourt et al., 1990](#_ENREF_6)). It is able to maintain photosynthesis even under high temperatures and low water potentials ([Barbour et al., 2007](#_ENREF_4)). This shrub species also primarily reproduces clonally leading to individuals that are exceptionally long lived. Clones that are over 1000 years old have been documented ([Vasek, 1980](#_ENREF_86)). The full pollinator guild contains 22 specialist pollinators and more than 80 generalists ([Minckley et al., 1999](#_ENREF_52)). The associated pollinator guilds are highly variable over space, and most shrubs will only interact with 20% of their full guild ([Cane et al., 2005](#_ENREF_15)). *L. tridentata* is one of the most reliable flowering plants in the Mojave because it has one of the lowest rainfall thresholds (12 mm) for blooming ([Bowers and Dimmitt, 1994](#_ENREF_8)). It produces copious nectar and pollen rich flowers ([Simpson et al., 1977](#_ENREF_75)) and provides critical resources to pollinators in drought years. *L. tridentata* functions as a benefactor species for other desert perennials such as *Opuntia leptocaulis*, ([Yeaton, 1978](#_ENREF_91)), *Peniocereus striatus* ([Suzán et al., 1994](#_ENREF_78)), and facilitates native annuals ([Schafer et al., 2012](#_ENREF_72)).

Study design

A total of 60 medium-sized (mean width: 336 cm, mean height: 209 cm) *L. tridentata* shrubs with developed floral buds and minimal perennial understory were chosen across the study site haphazardly. Paired shrub-open microsites were selected inside the dripline of the focal shrub and a minimum of 1.5 m away in an open area respectively. Both microsites were sampled on the south side of the shrub to minimize shading and were paired to minimize variation due to environmental heterogeneity. To separate floral and non-floral interaction pathways, interactions were tested prior to focal shrubs blooming and repeated using the same shrubs after they had entered into full bloom. Shrubs with fewer than five open blooms were considered non-blooming (“pre-blooming”) because 5 is less than 1% of mean blooming observed throughout the season. The mean number of blooms of the ‘blooming’ treatment was 300.2 (min: 102, max: 1080). The repeated measures study design was chosen to measure relative changes in interactions with natural shrub phenology and to reduce between shrub variability. 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

Visitation and Pollen Deposition

Each morning of each study day, *M. glabrata* were gathered from nearby (< 3 km) populations where they seasonally coexist with *L. tridentata.* These were transplanted into 15 cm diameter black pots and one pot was placed per microsite for a total of six shrub/open pairs per day. Conspecific floral density influences pollinator visitation ([Bosch and Waser, 2001](#_ENREF_7)). Therefore, transplants of similar size and habit were paired, and the flowerheads of *M. glabrata* were trimmed to equal numbers between paired microsites, 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 took place between 11:30 am and 3:30 pm (mean length: 1:19 hr:min). The use of video technology allows for higher temporal resolution, and replication beyond what is possible using traditional insitu observations ([Lortie et al., 2012](#_ENREF_45)). 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 2. To test for any influence of naturally co-occurring annuals and blooming shrubs, heterospecific annual floral density was measured within a 0.25 m2 quadrat in each microsite and the number of heterospecific shrubs in bloom were counted within a 2 m radius of each microsite. The number of open blooms of each *L. tridentata* was counted at the same time.

In the manual video processing post-season insect-phytometer plant pollination interactions were estimated using the timestamps of the videos. A flower visit was defined as when an insect visitor flew on and touched the open side of a flower. A foraging instance was defined as one plant visit, measured between initial contact and when visitor departed from physical contact of the final flower and left the field of view. Visit duration included inter-flower travel time and multiple flowers could be visited during one foraging instance. Total flowers is the sum of all flowers visited per replicate. Proportion of flowers visited is the number of unique flowers visited per foraging instance divided by the number of flowers in the field of vision. Floral visitors were identified to recognizable taxonomic units (RTU) including the following categories: honeybees, solitary bees, Lepidoptera, syrphid flies, bombyliid flies and other, which was comprised primarily of small beetles and muscoid flies. Five videos were omitted due to disturbance or battery failure.

To quantify how pollen deposition is influenced by proximity to *L. tridentata*, stigma were excised from *M. glabrata* at a nearby site (3 km) with a naturally occurring, co-blooming population of *M. glabrata* and *L. tridentata* between April 31st and May 2nd, 2017. Three stigma from each of three flowers per *M. glabrata* (nine stigma per plant) growing under the dripline and in nearby open areas were collected generating a total of 298 stigma from 13 shrub/open pairs. Distance to the nearest *L. tridentata* and three nearest *M. glabrata* neighbours were also recorded, and the number of *M. glabrata* flowers per plant were counted. The stigmas were stored individually in micro-centrifuge tubes filled with denatured alcohol. The tubes were spun down in a centrifuge at 4200 rpm for 4.5 minutes and the pellet pipetted onto the slide. This along with the stigma were mounted in fuchsin jelly ([Kearns and Inouye, 1993](#_ENREF_42)). At 100 x magnification, 10 longitudinal transects (18 mm long) of pollen were counted per slide. Heterospecific pollen grains were imaged using a Canon 60D SLR with 60mm macro lens into microscope afocally.

Extended and community-level effects of shrub species

Foundation plant species often have positive effects that scale to trophic levels beyond plants ([Reid and Lortie, 2012](#_ENREF_64); [Ruttan et al., 2016](#_ENREF_70)). The arthropod communities were sampled to provide an estimate of pollinator availability for each microsite and to assess if *L. tridentata* acts as a foundation species within this system. Yellow, white, and blue coloured six-inch diameter plastic bowls filled with water with a few drops of dish detergent added to sample via pan trapping. Each study day, pan traps were set out by 10 am and collected by 5:30 pm. Arrays of three pan traps were deployed in a triangular shape at each microsite, marginally embedded in the ground to prevent disturbance. Total percent vegetation cover (a proxy for annual biomass) and annual species richness were recorded within a 0.25 m2 quadrat when the traps were laid out. Arthropod sampling was conducted within two days of the video test but never on the same day to avoid influencing visitation. Nine days (54 shrub/open pairs) of sampling were completed before blooming, and 10 days (60 shrub/open pairs) during full bloom.

Bees and syrphid flies were identified to species or genus ([Ascher and Pickering, 2015](#_ENREF_3); [Michener, 2000](#_ENREF_50); [Michener et al., 1994](#_ENREF_51); [Miranda et al., 2013](#_ENREF_53)). The majority of remaining individuals was identified to at least the taxonomic resolution of family ([Grissell and Schauff, 1990](#_ENREF_33); [Marshall, 2012](#_ENREF_46); [Teskey et al., 1981](#_ENREF_80); [Triplehorn and Johnson, 2005](#_ENREF_83)) Thysanoptera, Orthoptera and Arachnida which were left to order. Recognizable taxonomic unit (RTU) is a suitable approximation of traditional species richness ([Oliver and Beattie, 1993](#_ENREF_59)). Using RTU limits resolution compared with species-level identification, however many desert insect species have not been described and furthermore useful keys are often lacking. This method of categorizing diversity was a trade-off between maximizing resolution and speed given the high diversity of desert species. Related groups may be identified to different levels. E.g. wasps in the genus *Miscophus* and subfamily *Pemphredoninae* are both within the family *Crabronidae*. No individuals were double counted, and these groups were considered distinct, exclusive RTUs for diversity analyses. Nymphs were included in abundance analyses provided they could be identified at least order. Hemipteran nymphs that could not be identified to family were lumped together for diversity analyses, otherwise all nymphs were assigned to family. Mites (Acari) and springtails (Collembola) were excluded from all analyses due to biases in collection methods. The full list of the 118 RTU is available online (Citation to knb). All physical specimens are archived at York University.

To determine which pollinators visited *L. tridentata* flowers during the study period, 15-minute observation periods were completed at 4 shrubs for 10 days pre-blooming (10 hours) and up to 6 shrubs per day for 10 days when blooming (14.5 hours). The same focal shrubs were observed but on different days than pan trap sampling and video trials. Due to the large size of the shrubs, it was not possible to accurately track flower visits per foraging instance, therefore only foraging instance frequency was recorded. The identity and behaviour of the visitors were recorded and insects were collected to facilitate identification.

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

Statistical Analysis

Visitation and Pollen Deposition

To test for evidence that *L. tridentata* mediates pollinator visitation to *M. glabrata*, generalized linear mixed-models (GLMM, lme4) using negative binomial error distributions with a loglink function to account for overdispersion were fit. The number of foraging instances and total number of flowers visited were treated as response variables. Video length was log-transformed for the loglink function and used as an offset to maintain the count structure of the data. To test for the influence of conspecific floral density, the number of *M. glabrata* blooms was included as a factor in models. We did not standardize visitation to visits/hour/flower because this assumes that pollinators respond linearly to conspecific floral density and that the slope of the relationship does not change with treatment (Reitan and Nielson, 2006). The focal ‘replicate shrub + microsite’ (Rep ID) was used as a random effect to account for the repeated measures study design in all models. Interactive, additive and intercept only models were compared by AIC and likelihood ratio tests with χ2 approximations (Appendix B?). To test for the influence of heterospecific blooming annuals and shrubs, negative binomial GLMM (glmmTMB) with each covariate included to the additive model were used. A quasipoisson GLMM (glmmPQL, MASS) was used to explore which visitors were driving observed visitation patterns.

Gamma GLMM models (glmer, lme4) with visit duration and proportion of flowers visited per foraging instance as response variables tested for behavioural differences. Solitary bees and ‘other’ RTUs were subsetted to fit linear mixed models for both RTU using log-transformed visit duration as the response variable, and in all cases least-squares post hoc tests (lsmeans) were used on any significant interactions and the Rep ID was included as a random effect.

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

Extended and community level shrub effects

Negative binomial GLMM (lme4, glmer.nb) with arthropod abundance, percent annual cover, annual species richness and annual bloom density as response variables were used to test for relative shrub effects on the local community. Beetles from the family *Melyridae* made up 1217 of the 3384 total arthropods captured, therefore abundance models were fit with *Melyridae* excluded, included and individually to explore model sensitivities. Poisson GLMM (lme4) were used to determine differences in arthropod species richness and bee abundance between the treatments. To test if *L. tridentata* individuals with more flowers were more attractive to pollinators, a quasipoisson GLM (glm) with visitation rates as the response and flower number as predictors. In all cases least-squares post hoc tests (lsmeans) were used on any significant interactions and the Rep ID was included as a random effect to control for repeated measures.

To test for the capacity of *L. tridentata* to create stable microclimates, I used GLMM (glmer, lme4) with Gamma error distributions with mean daytime temperature, mean nighttime temperatures and daily temperature variance as response variables. I used the shrub ID + microsite as a random effect to control for the repeated measures.

To test for compositional shifts in bee and arthropod communities, reduncancy analysis was used (RDA, vegan) on the Hellinger transformed abundances to lower the weight of rare RTU (Legendre). Then I used ANOVA to test for significance of the predictor variables in explaining differences in composition.

Then I used indicator analysis looking for RTU as ‘good’ indicators of each treatment.

Ecological effect sizes

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

**Results**

Shrub effects on visitation rates and pollen deposition to phytometer species

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

There was no significant influence of heterospecific shrub blooming density on foraging bout frequency or total flowers visited. There was a significant, positive effect of heterospecific annual floral density on foraging bouts, but not flowers visited (Table 2). Floral visitation rates (flowers/hr) were significantly correlated between paired shrub/open microsites (Pearson’s = 0.262, t = 2.8708, df = 112, p-value = 0.004898).

There were RTU specific changes in the number of foraging bouts and flowers visited with blooming (Figure 1, Table 3). The frequency of flower visits by syrphids and solitary bees declined significantly with blooming (Table 3). There was no significant difference between RTU visiting the microsites (Figure 1, Table C1), nor were there significant interactions between RTU, microsite and blooming (Table C1) on the total flowers visited.

There was also a negative effect of *L. tridentata* blooming on *M. glabrata* visit duration, but no microsite effect (Table 5). This was driven by visitors in the ‘other’ category (Figure 2, Est: -1.0703, χ2: 12.274, t: -3.503, p = 0.000605). There was no difference in solitary bee visit duration between blooming treatments (Est: -0.9341, χ2: 1.9017, t: -1.379, p = 0.208). The proportion of flowers visited per visit decreased significantly with blooming at the shrub microsite only (Table 5), but there were no significant interactions between RTU and blooming or RTU and microsite (Appendix).

A total of 16209 grains of conspecific pollen and 1719 of heterospecific grains were counted. At the nearby site, there was no significant influence of proximity to *L. tridentata* or the number of conspecific flowers (Figure 3a) on conspecific pollen deposition, however there was a marginally significant effect of distance to nearest conspecific neighbour (Figure 3b, Table 5). Heterospecific pollen deposition increased significantly with distance from *L. tridentata.* Conspecific and heterospecific pollen deposition were significantly correlated (Pearson’s = 0.15, t = 2.397, df = 229, p = 0.01).

Extended and community-level effects of shrub species.

A total of 3987 arthropods spanning 118 taxonomic groups (Appendix B?) were caught in 19 days of pan trapping. There was a positive effect of shrub microsite on both arthropod abundance (Melyridae excluded) and arthropod species richness, and a negative effect of blooming (Table 6, 8). Insect abundance (Melyridae excluded) was significantly correlated between paired shrub/open microsites (Pearson’s = 0.46, p < 0.001). Melyridae abundance was significantly lower at the shrub microsites, and decreased with blooming at the open microsite only (Appendix Cx). There was no significant difference in bee abundance or species richness caught in pan traps between any of the treatments (Table 6). Percent cover of ground vegetation was significantly greater in shrub microsites (Table 6) and it decreased with blooming in the open microsite only. There was a significant decrease in annual floral density with blooming, but no difference between the microsites. There was no significant difference in annual species richness between any of the treatments. Effect size calculations indicated that shrubs had a competitive effect on floral visitation of *M. glabrata,* a facilitative effect on arthropod abundance, arthropod species richness, annual percent cover and a neutral effect on annual richness. Blooming had a negative effect on all metrics (Figure 4).

Pollinator visitation to *L. tridentata* increased with floral abundance (Figure 5, GLM: Est: 0.0013408, χ2: 4.6383, p = 0.02283). Floral abundance and shrub height (Pearson’s = 0.335, t = 2.6659, df = 56, p = 0.01002) were correlated. *L. tridentata* received 197 floral visit over 15 hours of observations. Of 169 visits made by bees, *Apis mellifera* was the most frequent visitor (32%), *Centris* sp. (21%), *Hesperapis larrae* (18%) and *Megandrena enceliae* (7%) and other solitary bees (23%) including *Hoplitis* and *Megachile*.

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

Arthropod community composition was significantly influenced by blooming (F = 15.1586, p < 0.001) and microsite (F = 8.7573, p < 0.001). The RDA was significant at (F = 5.3289, p = 0.001) the environmental variables explained 11.5 % of the total variation. Of this, the first axis explains 68% and the 2nd explains 22%.

**Discussion**

Net interaction theory proposes that both positive and negative interactions are common in most sets of interactions between different species in a system. This study confirmed the role of the desert shrub *L. tridentata* as a foundation species in this system through its positive effects on annual and arthropod communities. However, the net outcome of these interactions was both positive and negative depending on the specific mechanistic pathway and phenological stage of the shrub. *L. tridentata* interfered with the pollination of the representative phytometer species *M. glabrata* and this relative negative outcome of association was not alleviated when *L. tridentata* entered full bloom. The phenological shift into blooming by *L. tridentata* intensified competition with *M. glabrata* at both microsites rather than triggering facilitation via the magnet species effect. Multi-trophic biotic interactions structure desert communities and this study demonstrates that shrubs function as hubs of interaction networks.

Shrub effects on visitation rates and pollen deposition to phytometer species

Plants that engage in cornucopian flowering strategy produce many flowers over an extended period of time, attracting a wide range of pollinators to the area (Mosquin, Gentry, 1974). Producing 300 flowers per shrub on average, *L. tridentata* exemplified this pattern in this system. Pollinators responded positively to the floral density of *L. tridentata* i.e. concentrations of floral resources at a cost to *M. glabrata*. Exploitation competition of early spring annuals by later blooming plants offering copious resources has also been observed in the alpine (Mosquin, 1971). After *L. tridentata* flowered, not only did visitation to the phytometer decrease, but pollinators spent less time per foraging instance on *M. glabrata* and visited few flowers per visit (at shrub only) indicating a behavioural change in pollinators. Pollinator foraging for many groups is driven by energetic considerations (Heinrich, 1975). When choosing between resources, bees will stay for a few visits and then leave to a superior one (Sowig, 1989). It is not possible to know which sign an interaction will have, because the traits that make a plant attractive to pollinators such as a large floral display ([Bosch and Waser, 2001](#_ENREF_7)), height ([Donnelly et al., 1998](#_ENREF_23)) or rich rewards ([Robertson et al., 1999](#_ENREF_65)) and thus likely act as a magnet, also increase its competitive ability. The sign of this interaction is context dependent. In this system the context was the identity and behaviour of visiting pollinators.

There were species-specific changes when larrea bloomed because pollinators have differential foraging strategies. Feral honeybees, *Apis mellifera,* the most frequent floral visitors to *L. tridentata*, only visited *M. glabrata* prior to *L. tridentata* blooming. Honeybees prefer larger floral patches (Sih and Baltus, 1987) and exhibit floral constancy, where individuals facultatively specialize on different flower species at different times ([Waser, 1986](#_ENREF_89)). Furthermore, honeybees communicate the locations of food sources to the colony, thus arriving bees may be searching for *L. tridentata* rather than openly foraging. The decline in solitary bee visitation to *M. glabrata* when co-blooming was not driven by local changes in bee abundances. The bee community became more diverse when L. tridentata bloomed, suggesting it was a behavioural response.

*Eupeodes volucris* (Diptera: Syrphidae), the bird hoverfly, was the most frequent floral visitor to *M. glabrata.* It is known to visit *L. tridentata* ([Hurd Jr and Linsley, 1975](#_ENREF_37)) but made one floral visit to *L. tridentata*. We cannot attribute the decrease to a behavioural response for certain, as syrphid abundance also declined in pan traps. *E. volucris* is multivoltine ([Vockeroth, 1992](#_ENREF_87)) and *Eupeodes* abundances peaked in late spring but individuals were found throughout the season ([Terry and Nelson, 2017](#_ENREF_79)). Larval *E. volucris* are aphid predators and members of the genus *Eupeodes* requires specific larval resources ([Henderson, 1982](#_ENREF_34)). Overall their phenology appears to be tied to prey availability rather than floral resource availability ([Noma and Brewer, 2008](#_ENREF_58), [Iler et al., 2013](#_ENREF_38)), though the phenology of *E. volucris* in desert systems has not been studied. Thus, the additional bees attracted by *L. tridentata* may have competitively excluded Syrphids from the immediate area. Competition between Syrphids and other pollinators is fairly unstudied ([Inouye et al., 2015](#_ENREF_39)). Bumblebees outcompete *Toxomerus* ([Morse, 1981](#_ENREF_56)) leading to the temporal partitioning of pollinators. *Centris* sp. bees, which were frequent visitors to Larrea flowers are territorial, and will hover near shrubs chasing off other bees ([Alcock et al., 1977](#_ENREF_1)). Honeybees can reduce visitation by solitary bees ([Shavit et al., 2009](#_ENREF_74)), through competitive displacement ([Cane and Tepedino, 2017](#_ENREF_16)).

There was evidence of facilitation by both conspecific and heterospecific annual bloom density for visitation concurrent with the interference by shrubs highlighting the importance of the timing of blooming in this system. Non-larrea shrub species also entered into a bloom alongside L. tridentata, while annual density decreased with blooming signifying a shift from annual bloom dominance to shrub dominance. Phenological separation has been documented between annuals and shrubs in South Western desert ecosystems (Cable 1969, Halvorsen and Patten, 1975, Jennings 2001), thus this pattern is likely widespread. Shrub facilitation has been show to facilitate floral development for the beneficiary (Garcia-Cervigon, 2016) but this was not the case in this system. We did not detect indirect effects of L. tridentata on the understory via the annuals. At the nearby site, there was no change in stigma conspecific pollen loads with distance to *L. tridentata* or conspecific density, however the sample size was too low to conclude there was no effect. There was a marginally significant effect of distance to nearest conspecific suggesting that there was an increase in intraspecific competition when L. tridentata is blooming, likely because it’s stealing of pollinators decreases availability to M. glabrata, leading to a switch of interaction sign. Thus M. glabrata that flower before larrea but alongside heterospecific can get higher visitation.

Association with a dominant, benefactor plant species can be positive in some respects but we found that facilitation in germination and early growth may come at a fitness cost via competition for pollination during reproductive life stages. In arid environments, annuals invest more into reproduction than growth (Petrů *et al*. 2006) and are often concentrating under shrubs (cite, cite), therefore this tradeoff is likely widespread and has the capacity to substantially impact fitness. To our knowledge this is the first demonstration of a generally beneficial flowering nurse plant engaging in exploitation competition with its beneficiaries for pollinators. There are also few examples of beneficial plants interfering with pollination. Grass-tree facilitates the pink-lipped spider orchid by protecting it from herbivores, however it also reduced its pollinator services through a non-floral interaction with pollinators (Petit, 2005). There are examples of other animal-mediated indirect interactions involve trade-offs between life stages. For example, thorny plants can facilitate for germination, but later competing by herbivory decoy effects (cite, cite). Life history trade-offs are an important part of every aspect of every organism’s life, and all mutualisms likely involve some trade-offs. The indirect tradeoffs between multispecies interactions understudied and super interesting. Previous authors have called for the need to consider fitness effect, rather than density (Tielborger and Kadmon, 2000) – here we show the mechanisms by which a shrub can facilitate for density, and but decrease fitness indirectly through effects on pollination.

The intensity of facilitation or competition depended on both the mechanism tested and the phenological stage of *L. tridentata*. No previous publication on shrub-annual facilitation complexes has contrasted interaction strengths (Lortie et al). In general, the relative effect of blooming/temporal shifts was greater than the effects of spatial association. Substantial within season changes between the intensity of facilitation and competition between shrubs and annuals has been documented in the Mojave Desert (Holzapfel and Mahall, 1999). Similarly, Schiffers and Tielborger, 2006 found that direction/intensity of interaction between annuals via multiple metrics varied with both life stages and temporal changes throughout a season. The majority of research on plant-plant interactions focusses on a single life stage or a single measurement ([Goldberg et al., 2001](#_ENREF_32); [Tielbörger and Kadmon, 2000](#_ENREF_82), Schiffers and Tielborger, 2006) which is inadequate for making conclusions about fitness levels within populations ([McPeek and Peckarsky, 1998](#_ENREF_49)). This research shows how big the differences are in this system across multiple metrics. Our results show that the positive influence of *L. tridentata* on annual abundance via climate amelioration was maintained throughout the study period. This is consistent with many results in desert ecosystems (Filazzola and Lortie, 2014; etc; etc). Effects on annual cover were considerably stronger than those arthropod communities. Understory annual metrics were not significant predictors of arthropod community composition suggesting direct shrub effects rather than those of facilitation complexes (sensu Lortie). Positive shrub effects here appear to be independent of its positive effects on annuals. Our results show that distinct communities are there. Microsite was a less reliable predictor of arthropod community composition after blooming. This may be in part by increased mobility of pollinators. Bee diversity increased.

The net positive effects were greater than the net negative effects, even including the large decrease with blooming. Shrubs have the capacity to buffer annuals under climate warming scenarios, may continue to buffer. Under pollinator declines, community may be more sensitive. Biotic interactions are important to desert ecosystem functioning. Any desert diversity sampling schemes in deserts need to be sensitive to both distance and blooming stages of shrubs.

Literature Cited

Alcock, J., Jones, C.E., Buchmann, S.L., 1977. Male mating strategies in the bee Centris pallida Fox (Anthophoridae: Hymenoptera). The American Naturalist 111, 145-155.

Armas, C., Ordiales, R., Pugnaire, F.I., 2004. Measuring plant interactions: a new comparative index. Ecology 85, 2682-2686.

Ascher, J., Pickering, J., 2015. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila).

Barbour, M., Keeler-Wolf, T., Schoenherr, A.A., 2007. Terrestrial vegetation of California. Univ of California Press.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends in Ecology & Evolution 9, 191-193.

Betancourt, J.L., Van Devender, T.R., Martin, P.S., 1990. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press.

Bosch, M., Waser, N.M., 2001. Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. Oecologia 126, 76-83.

Bowers, J.E., Dimmitt, M.A., 1994. Flowering phenology of six woody plants in the northern Sonoran Desert. Bulletin of the Torrey Botanical Club, 215-229.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M., Anthelme, F., 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96, 18-34.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18, 119-125.

Callaway, R.M., Pennings, S.C., 2000. Facilitation may buffer competitive effects indirect and diffuse interactions among salt marsh plants. American Naturalist 156, 416-424.

Callaway, R.M., Walker, L.R., 1997a. Competition and Facilitation A Synthetic Approach to Interactions in Plant Communities. Ecology 78, 1958-1965.

Callaway, R.M., Walker, L.R., 1997b. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958-1965.

Campbell, D.R., Motten, A.F., 1985. The mechanism of competition for pollination between two forest herbs. Ecology 66, 554-563.

Cane, J.H., Minckley, R., Kervin, L., Roulston, T.A., 2005. Temporally persistent patterns of incidence and abundance in a pollinator guild at annual and decadal scales: the bees of Larrea tridentata. Biological Journal of the Linnean Society 85, 319-329.

Cane, J.H., Tepedino, V.J., 2017. Gauging the effect of honey bee pollen collection on native bee communities. Conservation Letters 10, 205-210.

Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J., Padrón, B., 2012. Evaluating sampling completeness in a desert plant–pollinator network. Journal of Animal Ecology 81, 190-200.

Chesson, P., Gebauer, R.L., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S., Sher, A., Novoplansky, A., Weltzin, J.F., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141, 236-253.

Clements, F.E., Goldsmith, G.W., 1924. phytometer method in ecology.

Cline, A.R., Audisio, P., 2010. Revision of the new world short-winged flower beetles (Coleoptera: Kateretidae). Part I. Generic review and revision of Anthonaeus Horn, 1879. The Coleopterists Bulletin, 173-186.

Conner, J.K., Rush, S., 1996. Effects of flower size and number on pollinator visitation to wild radish, Raphanus raphanistrum. Oecologia 105, 509-516.

Davis, W., Philbrick, R., 1986. Natural hybridization between Malacothrix incana and M. saxatilis var. implicata (Asteraceae: Lactuceae) on San Miguel Island, California. Madroño, 253-263.

Donnelly, S.E., Lortie, C.J., Aarssen, L.W., 1998. Pollination in Verbascum thapsus (Scrophulariaceae): the advantage of being tall. American Journal of Botany 85, 1618-1625.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479-486.

Facelli, J.M., Temby, A.M., 2002. Multiple effects of shrubs on annual plant communities in arid lands of South Australia. Austral ecology 27, 422-432.

Filazzola, A., Lortie, C.J., 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. Global Ecology and Biogeography 23, 1335-1345.

Fleming, T.H., Holland, J.N., 1998. The evolution of obligate pollination mutualisms: senita cactus and senita moth. Oecologia 114, 368-375.

Fleming, T.H., Sahley, C.T., Holland, J.N., Nason, J.D., Hamrick, J., 2001. Sonoran Desert columnar cacti and the evolution of generalized pollination systems. Ecological Monographs 71, 511-530.

Flores, J., Jurado, E., 2003. Are nurse‐protégé interactions more common among plants from arid environments? Journal of Vegetation Science 14, 911-916.

Franco, A., De Soyza, A., Virginia, R., Reynolds, J., Whitford, W., 1994. Effects of plant size and water relations on gas exchange and growth of the desert shrub Larrea tridentata. Oecologia 97, 171-178.

Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94, 295-304.

Goldberg, D.E., Turkington, R., Olsvig-Whittaker, L., Dyer, A.R., 2001. Density dependence in an annual plant community: variation among life history stages. Ecological Monographs 71, 423-446.

Grissell, E.E., Schauff, M.E., 1990. A handbook of the families of Nearctic Chalcidoidea (Hymenoptera). A handbook of the families of Nearctic Chalcidoidea (Hymenoptera).

Henderson, D.H., 1982. Fine structure and neurophysiology of a gustatory sensillum on the ovipositors of Metasyrphus venablesi and Eupeodes volucris (Diptera: Syrphidae). Canadian Journal of Zoology 60, 3187-3195.

Holland, N.J., Fleming, T.H., 2002. Co-pollinators and specialization in the pollinating seed-consumer mutualism between senita cacti and senita moths. Oecologia 133, 534-540.

Holzapfel, C., Mahall, B.E., 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology 80, 1747-1761.

Hurd Jr, P.D., Linsley, E.G., 1975. Some insects other than bees associated with Larrea tridentata in the southwestern United States. Proceedings of the Entomological Society of Washington.

Iler, A.M., Inouye, D.W., Høye, T.T., Miller‐Rushing, A.J., Burkle, L.A., Johnston, E.B., 2013. Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. Global Change Biology 19, 2348-2359.

Inouye, D.W., Larson, B.M., Ssymank, A., Kevan, P.G., 2015. Flies and flowers III: ecology of foraging and pollination. Journal of Pollination Ecology 16, 115-133.

Jennings, W.B., 2001. Comparative flowering phenology of plants in the western Mojave Desert. Madroño, 162-171.

Jones, C.R., 1922. A contribution to our knowledge of the Syrphidae of Colorado. Agricultural Experiment Station of the Agricultural College of Colorado.

Kearns, C.A., Inouye, D.W., 1993. Techniques for pollination biologists. University press of Colorado.

King, C., Ballantyne, G., Willmer, P.G., 2013. Why flower visitation is a poor proxy for pollination: measuring single‐visit pollen deposition, with implications for pollination networks and conservation. Methods in Ecology and Evolution 4, 811-818.

Laverty, T.M., 1992. Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia 89, 502-508.

Lortie, C.J., Budden, A.E., Reid, A.M., 2012. From birds to bees: applying video observation techniques to invertebrate pollinators. Journal of Pollination Ecology 6, 125-128.

Marshall, S., 2012. Flies. The natural history and diversity of Diptera.

McIntire, E.J., Fajardo, A., 2014. Facilitation as a ubiquitous driver of biodiversity. New Phytologist 201, 403-416.

McKinney, A.M., Goodell, K., 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biological Invasions 12, 2751-2763.

McPeek, M.A., Peckarsky, B.L., 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. Ecology 79, 867-879.

Michener, C.D., 2000. The bees of the world. JHU press.

Michener, C.D., McGinley, R.J., Danforth, B.N., 1994. The bee genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press.

Minckley, R.L., Cane, J.H., Kervin, L., Roulston, T., 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. Biological Journal of the Linnean Society 67, 119-147.

Miranda, G., Young, A., Locke, M., Marshall, S., Skevington, J., Thompson, F., 2013. Key to the genera of Nearctic Syrphidae. Canadian Journal of Arthropod Identification 23, 351.

Molina-Montenegro, M.A., Badano, E.I., Cavieres, L.A., 2008. Positive interactions among plant species for pollinator service: assessing the ‘magnet species’ concept with invasive species. Oikos 117, 1833-1839.

Morhardt, S., Morhardt, E., 2004. California desert flowers: an introduction to families, genera, and species. Univ of California Press.

Morse, D.H., 1981. Interactions among syrphid flies and bumblebees on flowers. Ecology 62, 81-88.

Mosquin, T., 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos, 398-402.

Noma, T., Brewer, M.J., 2008. Seasonal abundance of resident parasitoids and predatory flies and corresponding soybean aphid densities, with comments on classical biological control of soybean aphid in the Midwest. Journal of Economic Entomology 101, 278-287.

Oliver, I., Beattie, A.J., 1993. A possible method for the rapid assessment of biodiversity. Conservation biology 7, 562-568.

Pellmyr, O., 2003. Yuccas, yucca moths, and coevolution: a review. Annals of the Missouri Botanical Garden, 35-55.

Pugnaire, F.I., Haase, P., Puigdefabregas, J., 1996. Facilitation between higher plant species in a semiarid environment. Ecology 77, 1420-1426.

Pyke, G.H., 1984. Optimal foraging theory: a critical review. Annual review of ecology and systematics 15, 523-575.

Pyke, G.H., Pulliam, H.R., Charnov, E.L., 1977. Optimal foraging: a selective review of theory and tests. The quarterly review of biology 52, 137-154.

Reid, A.M., Lortie, C.J., 2012. Cushion plants are foundation species with positive effects extending to higher trophic levels. Ecosphere 3.

Robertson, A.W., Mountjoy, C., Faulkner, B.E., Roberts, M.V., Macnair, M.R., 1999. Bumble bee selection of Mimulus guttatus flowers: the effects of pollen quality and reward depletion. Ecology 80, 2594-2606.

Roll, J., Mitchell, R.J., Cabin, R.J., Marshall, D.L., 1997. Reproductive Success Increases with Local Density of Conspecif ics in a Desert Mustard (Lesquerella fendleri) El Exito Reproductivo Incrementa con la Densidad Local de Coespecificos en la Mostaza del Desierto (Lesquerella fendleri). Conservation biology 11, 738-746.

Rousset, O., Lepart, J., 2000. Positive and negative interactions at different life stages of a colonizing species (Quercus humilis). Journal of Ecology 88, 401-412.

Rundel, P.W., Gibson, A.C., 2005. Ecological communities and processes in a Mojave Desert ecosystem. Cambridge University Press.

Rutowski, R.L., Alcock, J., 1980. Temporal variation in male copulatory behaviour in the solitary bee Nomadopsis puellae (Hymenoptera: Andrenidae). Behaviour 73, 175-187.

Ruttan, A., Filazzola, A., Lortie, C.J., 2016. Shrub-annual facilitation complexes mediate insect community structure in arid environments. Journal of Arid Environments 134, 1-9.

Saul-Gershenz, L., Millar, J., McElfresh, J., 2012. Mojave National Preserve. National Park Service U.S. Department of the Interior. , https://[www.nps.gov/moja/learn/nature/upload/201204MOJAscience.pdf](http://www.nps.gov/moja/learn/nature/upload/201204MOJAscience.pdf).

Schafer, J., Mudrak, E., Haines, C., Parag, H., Moloney, K., Holzapfel, C., 2012. The association of native and non-native annual plants with Larrea tridentata (creosote bush) in the Mojave and Sonoran Deserts. Journal of arid environments 87, 129-135.

Schemske, D.W., 1981. Floral convergence and pollinator sharing in two bee‐pollinated tropical herbs. Ecology 62, 946-954.

Shavit, O., Dafni, A., Ne'eman, G., 2009. Competition between honeybees (Apis mellifera) and native solitary bees in the Mediterranean region of Israel—Implications for conservation. Israel Journal of Plant Sciences 57, 171-183.

Simpson, B., Neff, J., Moldenke, A., 1977. Reproductive systems of Larrea. Mabry, T, J,, Hunziker, J, H,, DiFeo, D, R,, jr ed (s). Creosote bush: biology and chemistry of Larrea in the New World deserts. Stroudsburg, Dowden, Hutchinson & Ross Inc, 92-114.

Simpson, B.B., Neff, J.L., 1987. Pollination Ecology in the Southwest. Aliso: A Journal of Systematic and Evolutionary Botany 11, 417-440.

Sotomayor, D.A., Lortie, C.J., 2015. Indirect interactions in terrestrial plant communities: emerging patterns and research gaps. Ecosphere 6, art103.

Suzán, H., Nabhan, G.P., Patten, D.T., 1994. Nurse plant and floral biology of a rare night‐blooming cereus, Peniocereus striatus (Brandegee) F. Buxbaum. Conservation Biology 8, 461-470.

Terry, T.J., Nelson, C.R., 2017. Composition and seasonal abundance of hover flies (Diptera: Syrphidae) at a midelevation site in central Utah. Western North American Naturalist 77, 487-499.

Teskey, H., Vockeroth, J., Wood, D., 1981. Manual of Nearctic Diptera. Ottawa, Research Branch, Agriculture Canada, Monograph 27.

Thomson, J.D., 1978. Effects of Stand Composition on Insect Visitation in Two-Species Mixtures of Hieracium. American Midland Naturalist 100, 431-440.

Tielbörger, K., Kadmon, R., 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology 81, 1544-1553.

Triplehorn, C., Johnson, N.F., 2005. Borror and delong’s introduction to the study of insects. Brooks. Cole, Belmont, California, USA.

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Nuñez, H., Barnard, G., Vazquez, E., 1991. Spatial relationships between cacti and nurse shrubs in a semi‐arid environment in central Mexico. Journal of Vegetation Science 2, 15-20.

Valiente‐Banuet, A., Verdú, M., 2007. Facilitation can increase the phylogenetic diversity of plant communities. Ecology letters 10, 1029-1036.

Vasek, F.C., 1980. Creosote bush: long‐lived clones in the Mojave Desert. American Journal of Botany 67, 246-255.

Vockeroth, J., 1992. The flower flies of the subfamily Syrphinae of Canada, Alaska, and Greenland: Diptera, Syrphidae. Agriculture Canada.

Wainwright, C.M., 1978. Hymenopteran territoriality and its influences on the pollination ecology of Lupinus arizonicus. The Southwestern Naturalist, 605-615.

Waser, N.M., 1986. Flower constancy: definition, cause, and measurement. The American Naturalist 127, 593-603.

Wootton, J.T., 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25, 443-466.

Yeaton, R.I., 1978. A cyclical relationship between Larrea tridentata and Opuntia leptocaulis in the northern Chihuahuan Desert. The Journal of Ecology, 651-656.

Figures



Figure 1: The contribution of each recognizable taxonomic group (RTU) to the total number of flowers visited (weighted by video length) for each treatment.



Figure 2: RTU specific responses in visit duration before and during blooming at each microsite.



Figure 3: Heterospecific pollen deposition on the stigmas of Malacothrix glabrata increased with distance (in cm). There was a marginally significant effect of distance to nearest M. glabrata on conspecific pollen deposition. Mean distance to shrub was 1.83 m, mean distance to nearest conspecific neighbour was 0.79 m and mean number of flowers of M. glabrata was 7.



Figure 4: Pollinator visitation rates increased with the number of *Larrea tridentata* flowers.



Figure 5: Relative Interaction Index (RII) values for five community interaction metrics among two treatments: Microsite and Blooming. Values shown are means ± 95% bootstrapped confidence intervals. Values greater than zero indicate positive effects, while values that are significantly lower than zero indicate negative effects. Values that are not significantly different from zero are neutral.



Figure 6: Hobo Pendant Data Loggers recorded microenvironmental conditions for the extent of the study period. Values shown are mean hourly temperatures for all microsites (eight open and eight shrub) between March 17th and May 14th.

Tables

Table 1: Results from negative binomial generalized linear mixed models (lme4, glmer.nb) testing for differences in the frequency of pollinator floral visits and foraging bouts in response to microsite (shrub and open) and blooming stage (pre-blooming and full bloom). Conspecific floral density was included as a predictor and the log-transformed length of video was used as an offset as a measure of exposure. The repID (shrub ID + microsite) was used a random effect in both models to account for the repeated measures study design. Significance was denoted at α = 0.05 and shown in bold. Non-significant interactions were excluded from all models.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Total flower visits | | | Foraging bouts | | |
|  | **Coeff** | **χ2** | **p** | **Coeff** | **χ2** | **p** |
| Microsite (shrub) | -0.3493 | 4.4979 | **0.03396** | -0.3258 | 5.1183 | **0.0237** |
| Blooming (bloom) | -1.2473 | 61.52 | **<0.0001** | -1.2513 | 76.883 | **<0.0001** |
| Flowers.pot | 0.0694 | 6.9013 | **0.0086** | 0.0474 | 4.1109 | **0.0426** |
| Microsite \* Blooming | NA | NA | NA | NA | NA | NA |

Table 2: Results from GLMM (glmmTMB) testing for the influence of heterospecific annual floral density and shrub blooming density on the frequency of pollinator floral visits and foraging bouts. The log-transformed length of video was used as an offset as a measure of exposure. The repID (shrub ID + microsite) was used a random effect in both models to account for the repeated measures study design. Significance was denoted at α = 0.05 and shown in bold.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Total flower visits | | | |  | Foraging bouts | | | |
|  | **Coeff** | **SE** | **z** | **p** |  | **Coeff** | **SE** | **z** | **p** |
| Microsite (shrub) | -0.3660 | 0.16944 | -2.160 | **0.03077** |  | -0.33019 | 0.14706 | -2.25 | **0.02475** |
| Blooming (bloom) | -1.2396 | 0.16353 | -7.581 | **<0.0001** |  | -1.24571 | 0.14513 | -8.58 | **<0.0001** |
| Flowers.pot | 0.08084 | 0.02711 | 2.981 | **0.00287** |  | 0.05943 | 0.02374 | 2.503 | **0.01230** |
| Heterospecific  annual bloom density | 0.04013 | 0.02342 | 1.713 | 0.08664 |  | 0.04086 | 0.01984 | 2.059 | **0.03950** |
| Microsite (shrub) | -0.3289 | 0.16998 | -1.935 | **0.05301** |  | -0.31539 | 0.14829 | -2.13 | **0.033435** |
| Blooming (bloom) | -1.1662 | 0.18601 | -6.269 | **<0.0001** |  | -1.20875 | 0.16707 | -7.24 | **<0.0001** |
| Flowers.pot | 0.07598 | 0.02703 | 2.811 | **0.00494** |  | 0.05296 | 0.02376 | 2.229 | **0.025799** |
| Heterospecific  blooming shrub density | -0.0494 | 0.04093 | -1.207 | 0.22744 |  | 0.03124 | 0.03744 | -0.84 | 0.403997 |

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Total flower visits | | |  | Foraging bouts | | |
|  | **Coeff** | **χ2** | **p** |  | **Coeff** | **χ2** | **p** |
| Microsite (shrub) | -0.337480 | 4.1903 | **0.040655** |  | -0.311383 | 4.6322 | **0.03137** |
| Blooming (bloom) | -1.729417 | 15.4730 | **< 0.0001** |  | -1.683054 | 12.2157 | **0.0004739** |
| RTU | NA | 197.0575 | **<0.0001** |  | NA | 217.5031 | **<0.00001** |
| Flowers.pot | 0.064325 | 7.8743 | **0.005014** |  | 0.042763 | 4.0741 | 0.4354 |
| RTU\*blooming | NA | 70.0222 | **<0.0001** |  | NA | 70.35 | **<0.0001** |

Table 3: Results from quasi-Poisson GLMM (MASS, glmmPQL) testing for RTU specific responses to blooming stage. The log-transformed length of video was used as an offset as a measure of exposure. The repID (shrub ID + microsite) was used a random effect to account for the repeated measures study design. Posthoc comparisons (lsmeans) contrasting RTU specific responses between pre-blooming and blooming were done on significant interactions. Significance was denoted at α = 0.05 and shown in bold.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Contrast: Pre blooming vs blooming | | | | |  | | | |
| RTU | **Estimate** | **SE** | **t.ratio** | **p** | **estimate** | **SE** | **t.ratio** | **p** |
| Solitary bee | 1.7294 | .4419 | 3.914 | **0.0001** | 1.6831 | .4840 | 3.478 | **0.0005** |
| Bombyliidae | 0.04603 | .3886 | 0.118 | 0.9057 | 0.3956 | .3.5568 | 1.112 | 0.2662 |
| Honeybee | 24.9969 | 77838 | 0.000 | 0.9997 | 24.3349 | 65302.3 | 0.000 | 0.9997 |
| Lepidoptera | -2.4017 | 1.28900 | -1.862 | 0.0629 | -2.0771 | 1.0625 | -1.955 | 0.0508 |
| Other | -0.0197 | .2403 | -0.082 | 0.9347 | 0.1341 | .2065 | 0.64 | 0.5163 |
| Syrphid | 3.0563 | .3347 | 8.813 | **<0.0001** | 3.1228 | .3404 | 9.173 | **<0.0001** |

Table 4: Results from Gamma GLMM (lme4, glmer.nb) testing for differences visit duration and the proportion of flowers visited per visit in response to microsite (shrub and open) and blooming stage (pre-blooming and full bloom). The repID (shrub ID + microsite) was used a random effect in both models to account for the repeated measures study design. Significance was denoted at α = 0.05 and shown in bold. Non-significant interactions were excluded from all models.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Visit duration | | | | Proportion of flowers visited | | |
|  | **Coef** | | **χ2 value** | **p – value** | **Coef** | **χ2 value** | **p – value** |
| Microsite | -0.047260 | 0.0464 | | 0.8295 | -0.03538 | 1.0051 | 0.46515 |
| Blooming | -0.777931 | | 23.1788 | **<0.0001** | 0.0805 | 0.5335 | 0.31609 |
| Microsite \* Blooming | NA | | NA | NA | -0.20443 | 7.0691 | **0.00784** |

Table 5: Results from quasi-Poisson GLMM (MASS, glmmPQL) testing for the influence of *L. tridentata*, and two metrics of conspecific density on conspecific and heterospecific pollen deposition. Sample ID nested in flower ID nested in plant was used as a random effect to account for multiples samples coming from individual plants. Significance was denoted at α = 0.05 and shown in bold.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Conspecific Pollen Deposition | | | Heterospecific Pollen Deposition | | |
|  | **Coef** | **χ2 value** | **p – value** | **Coef** | **χ2 value** | **p – value** |
| Distance to *L. tridentata* | 0.0002 | 0.8803 | 0.3533 | 0.00130 | 23.7883 | **<0.0001** |
| Distance to *M. glabrata* | 0.0015 | 3.8146 | 0.0541 | -0.0014 | 2.1656 | 0.1411 |
| *M. glabrata* floral number | 0.0089 | 2.0027 | 0.1620 | -0.0122 | 2.3713 | 0.1236 |

Table 6: Results from negative binomial generalized linear mixed models (lme4, glmer.nb) testing for differences in arthropod abundance in response to microsite (shrub and open) and blooming stage (pre-blooming and full bloom). Melyridae beetles comprised 1217/3384 individuals, models were fit with them excluded, included and individually. The repID (shrub ID + microsite) was used a random effect in both models to account for the repeated measures study design. Significance was denoted at α = 0.05 and shown in bold. And Poisson models (species richness and bee abundance)

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Insect abundance (Melyridae: excluded) | | | Arthropod Species Richness | | | Bee abundance | | |
|  | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p |
| Microsite  (shrub) | 0.40610 | 15.4926 | **<0.0001** | 0.14541 | 6.6289 | **0.01** | 0.05766 | 0.0792 | 0.778323 |
| Blooming  (in bloom) | -0.39624 | 13.5868 | **0.000228** | -0.25442 | 25.6295 | **<0.0001** | -0.0787 | 0.2104 | 0.646419 |
| Microsite \* Blooming | -0.27673 | 3.4553 | 0.063049 | NA | NA | NA | NA | NA | NA |

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Percent cover | | | Annual Richness | | | Annual Bloom Density | | |
|  | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p |
| Microsite | 1.7599 | 165. | **<0.0001** | 0.0719 | 0.7071 | 0.40 | -0.28 | 0.601 | 0.438 |
| Blooming | -0.793 | 34.180 | **<0.0001** | 0.1407 | 2.7010 | 0.10 | -1.36 | 13.3646 | **0.0003** |
| Microsite \* blooming | 0.794 | 22.806 | **<0.0001** | NA | NA | NA | NA | NA | NA |

RDA output

Df Variance F Pr(>F)

blooming 1 0.03778 15.2304 0.001 \*\*\*

treatment 1 0.02011 8.1045 0.001 \*\*\*

percent.cover 1 0.00269 1.0850 0.310

understory.richness 1 0.00238 0.9585 0.496

het.annual.floral.density 1 0.00314 1.2659 0.187

Residual 205 0.50857

---

Appendix:

Table A1: A list of all RTU for Chapter 2. All RTU all exclusive and no individuals were double counted. 121 taxonomic groups were counted.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Order | Superfamily | Family | Subfamily | Genus | Species | Total Collected |
| Aranae |  |  |  |  |  | 14 |
| Coleoptera |  | Buprestidae |  |  |  | 67 |
|  |  | Chrysomelidae |  |  |  | 7 |
|  |  | Coccinellidae |  |  |  | 6 |
|  |  | Curculionidae |  |  |  | 15 |
|  |  | Meloidae | Meloinae | Cysteodemus |  | 2 |
|  |  | Meloidae | Meloinae | Eupompha | Eupompha elegans | 3 |
|  |  | Meloidae | Meloinae | Lytta | Lytta auriculata | 3 |
|  |  | Meloidae | Meloinae | Lytta |  | 1 |
|  |  | Melyridae |  |  |  | 1243 |
| Diptera |  |  |  |  | Acalyptrate - Tiny | 1 |
|  |  | Anthomyiidae |  |  |  | 4 |
|  |  | Asilidae |  |  |  | 76 |
|  |  | Bombyliidae | Ussinae |  |  | 8 |
|  |  | Bombyliidae | Anthracinae | Aphoebantus |  | 2 |
|  |  | Bombyliidae |  |  |  | 23 |
|  |  | Calliphoridae |  |  |  | 1 |
|  |  | Canacidae |  |  |  | 1 |
|  |  | Cecidomyiidae |  |  |  | 55 |
|  |  | Chamaemyiidae |  |  |  | 1 |
|  |  | Chloropidae |  |  |  | 21 |
|  |  | Chyromyidae |  |  |  | 1 |
|  |  | Drosophilidae |  |  |  | 1 |
|  |  | Ephydridae |  |  |  | 12 |
|  |  | Heleomyzidae |  |  |  | 73 |
|  |  | Milichiidae |  |  |  | 10 |
|  |  | Muscidae |  |  |  | 3 |
|  |  | Mythicomyiidae |  |  |  | 258 |
|  |  | Phoridae |  |  |  | 17 |
|  |  | Pipunculidae |  |  |  | 8 |
|  |  | Richardiidae |  | Omomyia |  | 3 |
|  |  | Sarcophagidae |  |  |  | 22 |
|  |  | Sciaridae |  |  |  | 6 |
|  |  | Syrphidae | Syrphinae | Eupeodes | Eupeodes volucris | 19 |
|  |  | Syrphidae | Syrphinae | Toxomerus | Toxomerus marginatus | 1 |
|  |  | Tachinidae |  |  |  | 17 |
|  |  | Tephritidae |  |  |  | 7 |
|  |  | Therevidae |  |  |  | 4 |
| Hemiptera |  | Anthocoridae |  |  |  | 3 |
|  |  | Aphididae |  |  |  | 10 |
|  |  | Berytidae | Gampsocorinae |  | Pronotacantha annulata | 17 |
|  |  | Berytidae |  |  |  | 4 |
|  |  | Cercopidae |  |  |  | 6 |
|  |  | Cicadellidae |  |  |  | 351 |
|  |  | Delphacidae |  |  |  | 2 |
|  |  | Geocoridae |  |  |  | 14 |
|  |  | Membracidae |  |  |  | 1 |
|  |  | Miridae |  |  |  | 96 |
|  |  | Nymph |  |  |  | 176 |
|  |  | Pentamoidae |  |  |  | 6 |
|  |  | Reduviidae | Harpactorinae |  |  | 10 |
|  |  | Rhopadilae |  |  |  | 7 |
|  |  | Tingidae |  |  |  | 2 |
|  | Lygaeoidea |  |  |  |  | 21 |
|  | Psylloidea |  |  |  |  | 2 |
| Hymenoptera | Apoidea (Anthophila) | Andrenidae | Andreninae |  | Ancylandrena larreae | 1 |
|  |  |  | Andreninae | Andrena |  | 2 |
|  |  |  | Panurginae | Calliopsis |  | 1 |
|  |  |  | Andreninae |  | Megandrena encelia | 14 |
|  |  | Apidae | Apinae |  | Apis mellifera | 4 |
|  |  |  | Apinae | Diadasia |  | 12 |
|  |  |  | Apinae | Eucera |  | 2 |
|  |  |  | Apinae | Mellisodes |  | 4 |
|  |  | Andrenidae | Panurginae | Perdita |  | 1 |
|  |  | Colletidae | Colletinae | Colletes |  | 2 |
|  |  | Halictidae | Halictinae | Halictus |  | 7 |
|  |  |  | Halictinae | Lasioglossum |  | 72 |
|  |  | Megachilidae | Megachilinae | Anthidium |  | 4 |
|  |  |  | Megachilinae | Ashmeadiella |  | 4 |
|  |  |  | Megachilinae | Atoposmia |  | 1 |
|  |  |  | Megachilinae | Hoplitis |  | 1 |
|  |  |  | Megachilinae | Megachile |  | 1 |
|  |  |  | Megachilinae | Osmia |  | 9 |
|  |  | Melittidae | Dasypodainae | Hesperapis |  | 2 |
|  | Apoidea (wasps) | Crabronidae |  |  |  | 39 |
|  |  | Crabronidae | Pemphredoninae |  |  | 27 |
|  |  | Crabronidae | Astatinae | Dryudella |  | 1 |
|  |  | Crabronidae | Crabroninae | Miscophus |  | 25 |
|  |  | Sphecidae | Ammophilinae | Ammophila |  | 4 |
|  |  | Sphecidae |  |  |  | 1 |
|  | Chrysidoidea | Chrysididae |  |  |  | 12 |
|  |  | Dryinidae |  |  |  | 1 |
|  | Formicidoidea | Formicidae |  |  |  | 71 |
|  | [Pompiloidea](https://bugguide.net/node/view/787796) | Mutillidae |  |  |  | 11 |
|  |  | Myrmosidae |  |  |  | 1 |
|  |  | Pompilidae |  |  |  | 13 |
|  | [Vespoidea](https://bugguide.net/node/view/117329) | Vespidae | Eumeninae |  |  | 1 |
| Parasitica |  | Ceraphronidae |  |  |  | 6 |
|  |  | Megaspilidae |  |  |  | 1 |
|  | Ceraphronoidea |  |  |  | wingless | 1 |
|  |  | Platygastridae |  |  |  | 7 |
|  | Chalcidoidea | Chalcididae |  |  |  | 3 |
|  |  | Encrytidae |  |  |  | 23 |
|  |  | Eucharitidae |  |  |  | 2 |
|  |  | Eulophidae |  |  |  | 16 |
|  |  | Eupelmidae |  |  |  | 13 |
|  |  | Eurytomidae |  |  |  | 4 |
|  |  | Mymaridae |  |  |  | 1 |
|  |  | Perilampidae |  |  |  | 1 |
|  |  | Pteromalidae |  |  |  | 25 |
|  |  | Torymidae |  |  |  | 10 |
|  |  | Trichogrammatidae |  |  |  | 4 |
|  |  | Signiphoridae |  |  |  | 3 |
|  | [Cynipoidea](https://bugguide.net/node/view/14738) | Figitidae |  |  |  | 1 |
|  | Ichnuemoidea | Braconidae |  |  |  | 1 |
|  |  | Ichneumonidae | Tersilochinae |  |  | 1 |
|  |  | Ichneumonidae |  |  |  | 1 |
| Lepidoptera | Adeloidea |  |  |  |  | 1 |
| Lepidoptera |  | Nymphalidae |  |  |  | 2 |
| Lepidoptera |  | Papilionidae |  |  |  | 1 |
| Lepidoptera |  |  |  |  |  | 1 |
| Microcorphyia |  |  |  |  |  | 1 |
| Neuroptera |  | Chrysopidae |  |  |  | 1 |
| Orthoptera |  |  |  |  |  | 19 |
| Solifugae |  |  |  |  |  | 3 |
| Thysanoptera |  |  |  |  |  | 137 |
| Trichoptera |  |  |  |  |  | 1 |

Appendix B

Model selection from results of Table 1 and full model of Table 3.

Table B1: Likelihood ratio test comparison of random intercept model, additive and interaction GLMM negative binomial models for where total flower visits are the response variable. Null model is flowers.pot with the random intercept, additive is flower.pot + blooming + microsite and interaction in flowers.pot + blooming \* microsite.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | DF | AIC | BIC | Chisq | P > Chisq |
| Null | 4 | 1164.8 | 1178.6 |  |  |
| Additive | 6 | 1111.6 | 1132.3 | 57.1788 | <0.00001 |
| Interaction term | 7 | 1113.6 | 1137.8 | 0.0322 | 0.8576 |

Table B2: Likelihood ratio test comparison of random intercept model, additive and interaction GLMM negative binomial models for where total plant visits are the response variable. Null model is flowers.pot with the random intercept, additive is flower.pot + blooming + microsite and interaction in flowers.pot + blooming \* microsite.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | DF | AIC | BIC | Chisq | P > Chisq |
| Null | 4 | 1066.0 | 1079.8 |  |  |
| Additive | 6 | 1000.7 | 1021.5 | 69.2940 | <0.00001 |
| Interaction term | 7 | 1002.7 | 1026.9 | 0.0072 | 0.9326 |

Table B3: Full models. Quasipoisson GLMM (glmmPQL, MASS) with three-way interaction term for RTU\*blooming\*microsite. This output from Wald’s Type 3 test. Total flower visits and foraging bouts as response. Rep ID as random effect.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Flower visits | | | Foraging bouts | | |
|  | Chisq | Df | P |  |  |  |
| Flowering | 16.3114 | 1 | **<0.0001** | 11.2812 | 1 | **0.0007829** |
| Rtu | 121.6832 | 5 | **<0.0001** | 131.340 | 5 | **<0.0001** |
| Treatment | 6.7008 | 1 | **0.009637** | 3.6569 | 1 | 0.0558390 |
| Flowers.pot | 9.4194 | 1 | **0.002147** | 4.5640 | 1 | **0.0326507** |
| Flowering:rtu | 56.9111 | 5 | **<0.0001** | 53.0033 | 5 | **<0.0001** |
| Flowering:treatment | 3.6394 | 1 | 0.056426 | 2.3436 | 1 | 0.1258002 |
| Rtu:treatment | 5.4996 | 5 | 0.357984 | 3.8289 | 5 | 0.5743031 |
| Flowering:rtu:treatment | 7.5190 | 5 | 0.184812 | 4.1995 | 5 | 0.5210663 |

Full models for proportions of flowers visited – because blooming was significant but microsite was not

Proportions: RTU \* blooming

floweringbloom -0.116064 0.140156 -0.828 0.40761

rtu.agbombylid -0.247470 0.112323 -2.203 0.02758 \*

rtu.aghoneybee 0.186243 0.240711 0.774 0.43910

rtu.aglep -0.329590 0.262264 -1.257 0.20886

rtu.agother -0.300436 0.095633 -3.142 0.00168 \*\*

rtu.agsyrphid -0.173276 0.085192 -2.034 0.04196 \*

floweringbloom:rtu.agbombylid 0.202234 0.174650 1.158 0.24689

floweringbloom:rtu.aglep 0.069411 0.297303 0.233 0.81540

floweringbloom:rtu.agother 0.033465 0.153065 0.219 0.82693

floweringbloom:rtu.agsyrphid 0.006737 0.171338 0.039 0.96863

(Intercept) -1.6545 0.1142 -14.490 < 2e-16 \*\*\*

## micrositeshrub -0.2956 0.1499 -1.973 0.04852 \*

## rtu.agbombylid -0.3373 0.1226 -2.752 0.00592 \*\*

## rtu.aghoneybee 0.3531 0.2415 1.462 0.14375

## rtu.aglep -0.4734 0.1472 -3.215 0.00131 \*\*

## rtu.agother -0.4738 0.1117 -4.243 2.2e-05 \*\*\*

## rtu.agsyrphid -0.3421 0.1079 -3.172 0.00152 \*\*

## micrositeshrub:rtu.agbombylid 0.2888 0.1717 1.682 0.09253 .

## micrositeshrub:rtu.aglep 0.2057 0.2111 0.974 0.32988

## micrositeshrub:rtu.agother 0.2655 0.1486 1.787 0.07399 .

## micrositeshrub:rtu.agsyrphid 0.3527 0.1410 2.502 0.01235 \*

Proportions: RTU\*microsite

$contrasts

contrast estimate SE df z.ratio p.value

open,bee - shrub,bee 0.2956276573 0.14985202 NA 1.973 0.7122

open,bee - open,bombylid 0.3373346514 0.12256770 NA 2.752 0.2009

open,bee - shrub,bombylid 0.3441132058 0.14651352 NA 2.349 0.4416

open,bee - open,honeybee nonEst NA NA NA NA

open,bee - shrub,honeybee -0.0574869201 0.25355693 NA -0.227 1.0000

open,bee - open,lep 0.4733697023 0.14724349 NA 3.215 0.0588

open,bee - shrub,lep 0.5633106534 0.17433386 NA 3.231 0.0559

open,bee - open,other 0.4737968665 0.11166278 NA 4.243 0.0013

open,bee - shrub,other 0.5039043466 0.13091459 NA 3.849 0.0066

open,bee - open,syrphid 0.3420691106 0.10785656 NA 3.172 0.0669

open,bee - shrub,syrphid 0.2850254482 0.12878960 NA 2.213 0.5399

shrub,bee - open,bombylid 0.0417069941 0.12615312 NA 0.331 1.0000

shrub,bee - shrub,bombylid 0.0484855485 0.12020937 NA 0.403 1.0000

shrub,bee - open,honeybee nonEst NA NA NA NA

shrub,bee - shrub,honeybee -0.3531145774 0.24153215 NA -1.462 0.9507

shrub,bee - open,lep 0.1777420450 0.14698298 NA 1.209 0.9884

shrub,bee - shrub,lep 0.2676829961 0.15108510 NA 1.772 0.8336

shrub,bee - open,other 0.1781692092 0.11358834 NA 1.569 0.9205

shrub,bee - shrub,other 0.2082766893 0.09790312 NA 2.127 0.6029

shrub,bee - open,syrphid 0.0464414533 0.11193343 NA 0.415 1.0000

shrub,bee - shrub,syrphid -0.0106022091 0.09076039 NA -0.117 1.0000

open,bombylid - shrub,bombylid 0.0067785545 0.12221348 NA 0.055 1.0000

open,bombylid - open,honeybee nonEst NA NA NA NA

open,bombylid - shrub,honeybee -0.3948215715 0.24089088 NA -1.639 0.8948

open,bombylid - open,lep 0.1360350509 0.12259911 NA 1.110 0.9943

open,bombylid - shrub,lep 0.2259760021 0.15473968 NA 1.460 0.9510

open,bombylid - open,other 0.1364622151 0.07698542 NA 1.773 0.8332

open,bombylid - shrub,other 0.1665696953 0.10315326 NA 1.615 0.9041

open,bombylid - open,syrphid 0.0047344593 0.07415790 NA 0.064 1.0000

open,bombylid - shrub,syrphid -0.0523092032 0.10021837 NA -0.522 1.0000

shrub,bombylid - open,honeybee nonEst NA NA NA NA

shrub,bombylid - shrub,honeybee -0.4016001260 0.24177578 NA -1.661 0.8858

shrub,bombylid - open,lep 0.1292564964 0.14359931 NA 0.900 0.9991

shrub,bombylid - shrub,lep 0.2191974476 0.15004047 NA 1.461 0.9509

shrub,bombylid - open,other 0.1296836607 0.10918274 NA 1.188 0.9900

shrub,bombylid - shrub,other 0.1597911408 0.09347639 NA 1.709 0.8644

shrub,bombylid - open,syrphid -0.0020440952 0.10744288 NA -0.019 1.0000

shrub,bombylid - shrub,syrphid -0.0590877576 0.09455611 NA -0.625 1.0000

open,honeybee - shrub,honeybee nonEst NA NA NA NA

open,honeybee - open,lep nonEst NA NA NA NA

open,honeybee - shrub,lep nonEst NA NA NA NA

open,honeybee - open,other nonEst NA NA NA NA

open,honeybee - shrub,other nonEst NA NA NA NA

open,honeybee - open,syrphid nonEst NA NA NA NA

open,honeybee - shrub,syrphid nonEst NA NA NA NA

shrub,honeybee - open,lep 0.5308566224 0.25220463 NA 2.105 0.6193

shrub,honeybee - shrub,lep 0.6207975736 0.25742634 NA 2.412 0.3979

shrub,honeybee - open,other 0.5312837866 0.23440374 NA 2.267 0.5008

shrub,honeybee - shrub,other 0.5613912668 0.23199483 NA 2.420 0.3923

shrub,honeybee - open,syrphid 0.3995560308 0.23341944 NA 1.712 0.8633

shrub,honeybee - shrub,syrphid 0.3425123683 0.22770807 NA 1.504 0.9399

open,lep - shrub,lep 0.0899409512 0.17203545 NA 0.523 1.0000

open,lep - open,other 0.0004271642 0.10980099 NA 0.004 1.0000

open,lep - shrub,other 0.0305346444 0.12772068 NA 0.239 1.0000

open,lep - open,syrphid -0.1313005916 0.10732476 NA -1.223 0.9872

open,lep - shrub,syrphid -0.1883442541 0.12543347 NA -1.502 0.9406

shrub,lep - open,other -0.0895137870 0.14459661 NA -0.619 1.0000

shrub,lep - shrub,other -0.0594063068 0.13290699 NA -0.447 1.0000

shrub,lep - open,syrphid -0.2212415428 0.14319762 NA -1.545 0.9280

shrub,lep - shrub,syrphid -0.2782852052 0.13056337 NA -2.131 0.5999

open,other - shrub,other 0.0301074801 0.08727658 NA 0.345 1.0000

open,other - open,syrphid -0.1317277558 0.05018389 NA -2.625 0.2655

open,other - shrub,syrphid -0.1887714183 0.08385587 NA -2.251 0.5120

shrub,other - open,syrphid -0.1618352360 0.08503134 NA -1.903 0.7575

shrub,other - shrub,syrphid -0.2188788984 0.06367091 NA -3.438 0.0290

open,syrphid - shrub,syrphid -0.0570436624 0.08160285 NA -0.699 0.9999

Full models for visit duration

Appendix C

Table C1: GLMM for arthropod abundance – Melyridae included and Melyridae only.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Insect abundance (Melyridae: included) | | | Melyridae: abundance only | | |
|  | **Coef** | **χ2** | **p** | **Coef** | **χ2** | **p** |
| Microsite (shrub) | -0.09872 | 1.808 | 0.1787 | -1.1920 | 38.0394 | **0<0.0001** |
| Blooming (in bloom) | -0.39280 | 33.553 | **<0.00001** | -0.2989 | 3.3485 | 0.067267 |
| Microsite \* Blooming | NA | NA | NA | 0.6521 | 7.1290 | **0.007585** |

Table C2: Post-hoc contrasts interaction for abundance (Melyridae only) for microsite by

blooming. Significant is at alpha < 0.05 and indicated in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Contrast | Estimate | SE | Z | p |
| pre,open - post,open | 0.2989089 | 0.1633482 | 1.830 | 0.2592 |
| pre,open - post,open | 1.1920062 | 0.1932688 | 6.168 | **<.0001** |
| pre,open - post,shrub | 0.8388073 | 0.1826136 | 4.593 | **<.0001** |
| post,open - pre,shrub | 0.8930973 | 0.1906721 | 4.684 | **<.0001** |
| post,open - post,shrub | 0.5398984 | 0.1799142 | 3.001 | **0.0143** |
| pre,shrub - post,shrub | -0.3531989 | 0.1815186 | -1.946 | 0.2090 |

Appendix D: Post-hoc contrasts

Table D1: Results from post-hoc test (lsmeans, Tukey’s) for the Gamma generalized linear mixed model on significant interaction for proportion of flowers visited. Significance was denoted at α = 0.05 and shown in bold. Proportion of flowers visited

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Proportion of flowers visited | | | |
| Contrast | **Estimate** | **SE** | **t.ratio** | **p** |
| pre,open - post,open | 0.03537548 | 0.04843350 | 0.730 | 0.8849 |
| pre,open - pre,shrub | -0.08050042 | 0.08029773 | -1.003 | 0.7479 |
| pre,open - post,shrub | 0.15930471 | 0.08775466 | 1.815 | 0.2660 |
| post,open - pre,shrub | -0.11587589 | 0.08384195 | -1.382 | 0.5106 |
| post,open - post,shrub | 0.12392924 | 0.09113159 | 1.360 | 0.5247 |
| pre,shrub - post,shrub | 0.23980513 | 0.05952906 | 4.028 | **0.0003** |

Bee species diversity GLM, negative binomial

Fixed effects:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.55101 0.15266 -3.610 0.000307 \*\*\*

treatmentshrub -0.06457 0.18278 -0.353 0.723865

bloomingpre -0.05632 0.18327 -0.307 0.758612

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Overdispersion parameter for nbinom2 family (): 15.7

Conditional model:

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.55102 0.15266 -3.610 0.000307 \*\*\*

treatmentshrub -0.06457 0.18278 -0.353 0.723866

bloomingpre -0.05632 0.18327 -0.307 0.758617

---