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

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 the capacity of creosote bush to influence the pollination of the annual understory during its phenological shift into flowering. Pollinator visitation rates to the phytometer desert dandelion, *Malacothrix glabrata,* 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. Decreases in visitation were driven by syrphid flies and the responses of solitary bees. In this system, we found that *L. tridentata* had a positive ecological effect on annual plant cover, as well as the abundance and diversity of the arthropod community but that it also had indirect negative effects on pollinator visitation to a representative flowering annual plant. These finding suggesting that the net outcome of association with foundation plant species can be positive or negative depending on both the life-history stage of the protégé species tested and on the phenology of the foundation species. There is the capacity for these trade-offs to be widespread and an increasing focus on further documenting these trade-offs will advance both facilitation theory and assessment of selection processes that can drive co-evolutionary relationships between shrubs, annual plants, and pollinators.

Keywords: Facilitation, *Larrea tridentata*, plant-pollinator, trade-off, nurse plant

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_26)). 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_28)). These include stress amelioration ([McIntire and Fajardo, 2014](#_ENREF_50)), improved water and nutrient availability ([Franco et al., 1994](#_ENREF_32)), and seed trapping ([Flores and Jurado, 2003](#_ENREF_31)). Direct interactions between shrubs and annuals can be simultaneously facilitative and competitive ([Bertness and Callaway, 1994](#_ENREF_7); [Callaway and Walker, 1997b](#_ENREF_18); [Holzapfel and Mahall, 1999](#_ENREF_40)), and it has been proposed that the relative importance of negative versus positive effects covaries with abiotic stress ([Bertness and Callaway, 1994](#_ENREF_7); [Schafer et al., 2012](#_ENREF_73); [Tielbörger and Kadmon, 2000](#_ENREF_85)). These complex sets of interactions lead to patterns in species coexistence and structure plant communities ([Brooker et al., 2008](#_ENREF_12); [Valiente‐Banuet and Verdú, 2007](#_ENREF_88)). The facilitative effects of desert shrubs can lead to concentrations of annual plants beneath the shrub canopy ([Facelli and Temby, 2002](#_ENREF_27)). This close spatial proximity of shrubs and annuals undoubtedly gives rise to indirect interactions ([Sotomayor and Lortie, 2015](#_ENREF_80)). Indirect interactions occur whenever a third species alters the interaction between two other species ([Callaway and Pennings, 2000](#_ENREF_16); [Callaway and Walker, 1997b](#_ENREF_18); [Wootton, 1994](#_ENREF_94)). If the associated annual is a flowering plant, then there is the capacity for the plants to interact indirectly via pollinators.

Mechanisms that require co-blooming dominate the study of pollinator-mediated interactions. These hypotheses are primarily extensions to optimal foraging theory ([Pyke, 1984](#_ENREF_65); [Pyke et al., 1977](#_ENREF_66)) 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_74)) or to make the patch offering more diverse ([Ghazoul, 2006](#_ENREF_34)). 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_46); [Thomson, 1978](#_ENREF_84)). If shrubs concentrate pollinators that do not in turn visit their neighbours, competition or interference 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 can 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_51)). 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 life stage ([Bruno et al., 2003](#_ENREF_14); [Callaway and Walker, 1997a](#_ENREF_17); [Pugnaire et al., 1996](#_ENREF_64); [Rousset and Lepart, 2000](#_ENREF_69); [Valiente-Banuet et al., 1991](#_ENREF_87)). For example within some nurse-plant systems, young plants are facilitated during establishment but later compete with their nurses for resources ([Yeaton, 1978](#_ENREF_95)). For plants, the life stage shift from vegetative growth to reproductive growth is a major event in resource allocation ([Bazzaz et al., 1987](#_ENREF_6)). Phenological shifts are likely a critical mediator of the sign of net outcomes of interactions with flowering, foundation plant species such as shrubs.

The Mojave Desert is a biodiversity hotspot supporting 659 species of bees ([Saul-Gershenz et al., 2012](#_ENREF_72)) and 1680 species of vascular plants ([Rundel and Gibson, 2005](#_ENREF_70)). Despite the celebrated biodiversity of Southwestern Deserts, pollinator-mediated interactions in this region are infrequently studied. Increases in intraspecific density can benefit the pollination of desert mustard *Lesquerella fendleri* ([Roll et al., 1997](#_ENREF_68)); however, interspecific studies have primarily focused on competition within cacti systems in the Sonoran Desert ([Fleming et al., 2001](#_ENREF_30)). 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_61)), and the senita cactus *Pachycereus schottii* and senita moths ([Fleming and Holland, 1998](#_ENREF_29)) and are often considered highly specialized. The degree of specialization of species in desert ecosystems is a subject of ongoing debate (Chesson et al, 2004). Desert organisms are hypothesized to adapt to high environmental variability by generalizing resource use ([Chesson et al., 2004](#_ENREF_22)) and this hypothesis has been supported to an extent through pollination network studies ([Chacoff et al., 2012](#_ENREF_21)). Overall, few one-to-one relationships (i.e. matching between a single species of pollinator with a single species of plant) have been found with solitary bees ([Simpson and Neff, 1987](#_ENREF_79)), and bees still visit even the senita cactus ([Holland and Fleming, 2002](#_ENREF_39)). Despite the high number of specialist pollinators present in the Mojave, most plant species nonetheless interact through pollinators and therefore there is the potential for competition and facilitation between neighbouring plants to occur.

The purpose here was to examine both the direct and indirect effects of *Larrea tridentata* on the general success of its annual understory. Single species of plants that are sensitive to environmental variation are called phytometers in plant science ([Clements and Goldsmith, 1924](#_ENREF_23)) and have been recommended as a tool to study the relative importance versus intensity of plant-plant interactions as well ([Brooker et al., 2005](#_ENREF_11)). We used the commonly co-occurring annual *Malacothrix glabrata* as a phytometer to measure variation in pollination services by environmental context*.* These species co-flower at beginning and ends of their bloom period ([Jennings, 2001](#_ENREF_44)), and are thus a relevant system to model changes in net interactions within a growing season. We hypothesize that desert shrubs can positively and negatively influence the net outcome of pollination for associated annual plants through effects of large floral offering and extent of co-blooming with the community in addition to directly facilitating vegetative performance measures at earlier life stages. The following three predictions were tested: 1) visitation rates to an annual phytometer species differ under a shrub canopy relative to paired open microsites; 2) phenological stage of the shrub influences the pollination rates to the phytometer species; 3) annual community performance metrics including cover and richness will be higher under the shrub canopy. 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 shrubs 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_57)). *M. glabrata* is insect-pollinated, including bees in the genera *Nomadopsis* ([Rutowski and Alcock, 1980](#_ENREF_71)) and *Anthidium* ([Wainwright, 1978](#_ENREF_92)) as well as short-winged flower beetles of the family *Kateretidae* ([Cline and Audisio, 2010](#_ENREF_24)). Several of the 24 species of *Malacothrix* are self-compatible ([Davis and Philbrick, 1986](#_ENREF_25)), 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_8)). It is able to maintain photosynthesis even under high temperatures and low water potentials ([Barbour et al., 2007](#_ENREF_5)). 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_90)). The full pollinator guild contains 22 specialist pollinators and more than 80 generalists ([Minckley et al., 1999](#_ENREF_55)). 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_19)). *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_10)). It produces copious nectar and pollen rich flowers ([Simpson et al., 1977](#_ENREF_78)) 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_95)), *Peniocereus striatus* ([Suzán et al., 1994](#_ENREF_82)), and facilitates native annuals ([Schafer et al., 2012](#_ENREF_73)).

Study design

A total of 60 *L. tridentata* shrubs with developed floral buds and minimal perennial understory were chosen across the study site haphazardly (mean width: 336 cm, mean height: 209 cm). 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

*M. glabrata* were gathered freshly each morning from nearby (< 3 km) populations where they seasonally coexist with *L. tridentata.* These plants were transplanted into 15 cm diameter black pots and one pot was placed at each microsite for a total of six shrub/open pairs per day. Conspecific floral density influences pollinator visitation ([Bosch and Waser, 2001](#_ENREF_9)). 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 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 *in situ* observations ([Lortie et al., 2012](#_ENREF_48)). 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.

Plant-pollinator 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 floral contact and when the visitor departed from physical contact of the final flower and left the field of view. Foraging duration included flower-to-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. A total of 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_45)). At 100 x magnification, 10 longitudinal transects (18 mm long) of pollen in addition to the stigma were counted per slide. Heterospecific pollen grains were imaged using a Canon 60D SLR with 60mm macro lens into microscope afocally.

Community-level effects of shrub species

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 for other taxa. 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_4); [Michener, 2000](#_ENREF_53); [Michener et al., 1994](#_ENREF_54); [Miranda et al., 2013](#_ENREF_56)). The majority of remaining individuals was identified to at least the taxonomic resolution of family ([Grissell and Schauff, 1990](#_ENREF_36); [Marshall, 2012](#_ENREF_49); [Teskey et al., 1981](#_ENREF_83); [Triplehorn and Johnson, 2005](#_ENREF_86)) 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_60)). 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 to taxonomic order. Hemipteran nymphs that could not be identified to family were aggregated for diversity analyses. Mites (Acari) and springtails (Collembola) were excluded from all analyses due to biases in collection methods. The full dataset of 118 RTU is available online (KNB, Braun and Lortie, 2018). 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 the frequency of foraging instances was recorded. The identity and behaviour of the visitors were recorded and voucher insects were collected when possible 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

All statistical analyses were performed using R (R development core team 2018) and all code is available in this project’s repository (https://github.com/jennabraun/larrea.facilitation).

Visitation and Pollen Deposition

To test for evidence that *L. tridentata* mediates pollinator visitation to *M. glabrata*, generalized linear mixed-models using negative binomial error distributions with a loglink function to account for overdispersion were fit (GLMM, lme4). 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 (Table B1, B2). To test for the influence of heterospecific blooming annuals and shrubs, negative binomial GLMMs (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 foraging 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 foraging duration as the response variable; 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.

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

Community-level shrub effects

Negative binomial GLMMs 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 (glmer.nb, lme4). Beetles from the family *Melyridae* comprised 1217 of the 3384 total arthropods captured, therefore abundance models were fit with *Melyridae* excluded, included and individually to explore model sensitivities. Poisson GLMMs (lme4) were used to determine differences in arthropod species richness and bee abundance between the treatments, and negative binomial GLMMs (glmer.nb, lme4) were used to test for differences in bee richness. 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 and height 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.

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

Redundancy analysis was used to test for the influence of microsite and associated annual communities on insect community composition (RDA, vegan). . Arthropod abundances were Hellinger transformed to lower the weight of rare RTU ([Legendre and Gallagher, 2001](#_ENREF_47)). Microsite, percent annual cover, annual richness and heterospecific annual bloom density were used as constraining variables in the ordination.

In order to examine the change in interaction between the vegetation factors and arthropod communities with the phenological shift, rather than the effect of blooming itself, the dataset was split into pre-blooming and blooming, and analyses were run separately on each subset. In order to test for the significance of the constraining variables in explaining the variation, a permutation-like ANOVA was used on each RDA (anova.cca, vegan).

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_3)). The equation: was used. Treatments were shrub microsite or blooming, while the controls were open microsite or pre-blooming. Only paired microsites in the data were used to calculate effect sizes. This measure ranges from −1 to +1, is symmetric around 0, and negative values indicated relative competition whilst positives indicate facilitation (Armas et al., 2004). To determine if the effect was significantly different from 0, 95% confidence intervals around mean values were bootstrapped (boot), 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 visited 925 flowers (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 and were reduced at both microsites when *L. tridentata* entered full bloom (Table 1). There was a positive effect of *M. glabrata* conspecific density on both the frequency of foraging instances and floral visitation (Table 1). The frequency of flower visits by syrphids and solitary bees declined significantly with blooming (Table 1). There was no significant difference between RTU visiting the microsites (Figure 1) nor were there significant interactions between RTU, microsite, and blooming on the total flowers visited or frequency of foraging instances (Appendix B).

There was no significant influence of heterospecific shrub blooming density on foraging instance frequency or total flowers visited (Table 2). There was a significant, positive effect of heterospecific annual floral density on foraging instances 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 was a negative effect of *L. tridentata* blooming on *M. glabrata* foraging 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 foraging 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 RTU specific response to blooming or microsite (Appendix B).

A total of 16209 grains of conspecific pollen and 1719 of heterospecific grains were recorded on *M. glabrata* stigma. At the nearby site, there was no significant influence of proximity to *L. tridentata* or the number of conspecific flowers on conspecific pollen deposition, however there was a marginally significant effect of distance to nearest conspecific neighbour (Figure 3a, Table 5). Heterospecific pollen deposition increased significantly with distance from *L. tridentata* (Figure 3b)*.* 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 A) 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 5). 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 C). There was no significant difference in bee abundance or richness caught in pan traps between any of the treatments (Table 5).

Percent cover of ground vegetation was significantly greater in shrub microsites, and it decreased with blooming in the open microsite only (Table 5). There was a significant decrease in heterospecific annual floral density with blooming, but there were no significant differences between the microsites (Table 5). There was also no significant difference in annual species richness between any of the treatments (Table 5).

Shrubs had a competitive effect on floral visitation of *M. glabrata,* a facilitative effect on arthropod abundance, arthropod species richness, and on annual percent cover but no significant effect on annual plant richness (Figure 5A). Blooming had a negative effect on floral visitation, arthropod abundance, and arthropod species richness and a neutral effect on annual richness at both microsites. Blooming had no significant effect on annual cover at the shrub microsite, however there was a significant, negative effect at the open microsite (Figure 5B).

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, however height was not a significant predictor of pollinator visitation (GLM: Est: 0.0054, χ2: 3.6066, p = 0.061). *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%), followed by *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 microsite for both blooming treatments (Table 6). There was no significant effect of the annual understory. The constraining variables of the pre-blooming RDA explained more variation (12.5%) than blooming (4%). Only the pre-blooming RDA was significant (pre: F = 3.3448, df = 4, p = 0.001, blooming: F = 1.1862, df = 4, p = 0.118).

**Discussion**

Net interaction theory proposes that both positive and negative interactions are common in most interactions between different species in a system ([Callaway and Walker, 1997b](#_ENREF_18)). This study confirmed the role of the desert shrub *L. tridentata* as a foundation species in this system through its positive effects on annual plants and arthropod communities and through its ability to stabilize microclimates. 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 with the addition of exploitation competition with *M. glabrata* at both microsites rather than triggering facilitation via the magnet species effect.

Plants that employ a cornucopian flowering strategy produce abundant floral resources over an extended period of time, and this strategy can attract a wide range of pollinators to the localized area ([Gentry, 1974](#_ENREF_33); [Mosquin, 1971](#_ENREF_58)). This positive response by pollinators to the floral density of *L. tridentata* i.e. concentrations of floral resources was at a cost to the phytometer species tested *M. glabrata*. Pollinator visitation frequency and the foraging behaviour of pollinators changed in response to the large increase of floral resources by *L. tridentata*. The foraging strategies of many pollinator groups are centered around energetic considerations ([Heinrich and Raven, 1972](#_ENREF_38); [Pyke, 1984](#_ENREF_65)). When choosing between resources, bees commonly stay for a few visits before leaving to the superior resource ([Sowig, 1989](#_ENREF_81)), where the larger floral display ([Bosch and Waser, 2001](#_ENREF_9)) or richer rewards ([Robertson et al., 1999](#_ENREF_67)) will improve their foraging efficiency. We found that pollinator preferences of L. *tridentata* over *M. glabrata* were species-specific.Feral honeybees, *Apis mellifera,* were the most frequent floral visitors to *L. tridentata* but only visited *M. glabrata* prior to *L. tridentata* blooming. Honeybees prefer larger floral patches ([Sih and Baltus, 1987](#_ENREF_77)) and exhibit floral constancy; the facultative specialization on different flower species at different times by individuals ([Waser, 1986](#_ENREF_93)). Solitary bees also showed a behavioural response by shifting their preference to *L. tridentata*. Facilitation via honeybees and solitary bees has been documented in previous studies ([Albrecht et al., 2016](#_ENREF_1); [Bruckman and Campbell, 2016](#_ENREF_13)), however in most cases the magnet plant does not offer such disproportionately abundant resources as *L. tridentata* relative to the potted annuals. The cornucopia flowering strategy by benefactors is likely to introduce significant decoy effects in shrub-annual facilitation systems.

*Eupeodes volucris* (Diptera: Syrphidae) was the most frequent floral visitor to *M. glabrata.* However *E. volucris* did not switch despite being known to visit *L. tridentata* ([Hurd Jr and Linsley, 1975](#_ENREF_41)). Therefore, this change cannot be attributed to exploitation competition however it may be due to interactions between the pollinators. The additional bees attracted by *L. tridentata* may have competitively excluded Syrphids from the immediate area. Competition between Syrphids and other pollinators is understudied ([Inouye et al., 2015](#_ENREF_43)), but competition between bee species is better known. *Centris* sp. bees were frequent visitors to *L. tridentata* flowers during this study. They are territorial and are known to chase away other bees from shrubs ([Alcock et al., 1977](#_ENREF_2)). Similarly, honeybees can reduce visitation by solitary bees ([Shavit et al., 2009](#_ENREF_76)) through competitive displacement ([Cane and Tepedino, 2017](#_ENREF_20)). Alternatively, syrphid visitation may have declined due to changes in local abundances, particularly if their phenology is linked with annuals. *E. volucris* is multivoltine ([Vockeroth, 1992](#_ENREF_91)) but the phenology of *E. volucris* in desert systems has not been studied. Larval *E. volucris* are aphid predators and their phenology appears to be tied to prey availability rather than floral resource availability ([Iler et al., 2013](#_ENREF_42); [Noma and Brewer, 2008](#_ENREF_59)). Integrating the temporal dimension into experimental design is challenging because it is necessary to consider the phenology of the pollinator as well.

There was evidence of facilitation by conspecific and heterospecific annual floral density for visitation concurrent with interference by shrubs suggesting that phenological matching with other flowering species within the community mediates pollination success in this system. Additional foundation species including *Acamptopappus sphaerocephalus*, *Opuntia sp*. and *Ericameria cooperi* entered into bloom alongside *L. tridentata* while annual floral density decreased, signifying a seasonal shift from annual floral dominance to shrub floral dominance. Phenological separation between annuals and shrubs is frequently observed in South Western desert ecosystems ([Cable, 1969](#_ENREF_15); [Halvorson and Patten, 1975](#_ENREF_37); [Jennings, 2001](#_ENREF_44)). Exploitation competition of early-blooming spring annuals by later-blooming cornucopia plants offering copious resources contributes to phenological divergence in the alpine (Mosquin, 1971). Thus the timing of blooming is critically important for competition avoidance, but also to benefit from co-blooming with conspecifics and facilitating heterospecifics. Generally, the relative effect of blooming i.e. the temporal shift was greater on annual and arthropod communities than the effect of spatial association with *L. tridentata* but the intensity of the interaction depended on the specific metric measured. In the Mojave Desert, substantial within season changes to the intensity of facilitation and competition between shrubs and annuals can occur ([Holzapfel and Mahall, 1999](#_ENREF_40)). Similarly, near the Negev desert the intensity of interactions between annuals varies with both life stage and temporal changes ([Schiffers and Tielbörger, 2006](#_ENREF_75)). Overall, *L. tridentata* had stronger effect on annual communities than arthropod communities and its effects on arthropod community composition were independent of its effects on annuals. Surprisingly, microsite became a less reliable predictor of arthropod community composition after blooming. Phenology is a critical mediator of net outcomes between multiple trophic levels.

In this study, facilitation in germination and early growth came at a potential net fitness cost via competition for pollination during reproductive life stages. Life-stage dependent tradeoffs within nurse-protégé associations between perennials are well documented with facilitation in early life shifting to resource competition later in life ([Valiente-Banuet et al., 1991](#_ENREF_87); [Yeaton, 1978](#_ENREF_95)). Trade-offs between animal-mediated indirect interactions can also occur between different life stages. For example, thorny plants can facilitate for germination, but later these benefactors compete through decoy effects by deflecting herbivores towards the beneficiary ([Van Der Putten, 2009](#_ENREF_89)). Grass-tree (*Xanthorrhoea semiplana*) facilitates the pink-lipped spider orchid (*Caladenia syn. Arachnorchis behrii*) by protecting it from herbivores but reduces its pollination services through non-floral interference ([Petit and Dickson, 2005](#_ENREF_62)). To our knowledge, our study is the first demonstration of a beneficial flowering nurse plant engaging in exploitation competition with its beneficiaries for pollinators. In arid environments, annuals invest more into reproduction than growth ([Petrů et al., 2006](#_ENREF_63)) and are often found concentrated under shrubs (Facelli and Temby, 2002). Therefore, germination-pollination tradeoffs should be common within plant communities in desert ecosystems. To quantify the net effects of facilitation, it is necessary to consider fitness alongside density effects ([Tielbörger and Kadmon, 2000](#_ENREF_85)). Here we show the mechanisms by which a shrub can facilitate for density while decreasing fitness indirectly through effects on pollination.

Conclusions

The majority of research on plant-plant interactions focuses on a single life stage or a single measurement ([Goldberg et al., 2001](#_ENREF_35); [Tielbörger and Kadmon, 2000](#_ENREF_85)). These singular foci are inadequate for estimating fitness levels within plant populations ([McPeek and Peckarsky, 1998](#_ENREF_52)). The extent of these tradeoffs is likely underestimated in arid environments and important for structuring desert communities. Shrubs had a net positive effect on annuals but interactions mediated through flowering at different life-stages and also shrub phenology were critical mediators of the sign of the net outcome of association by annual plants with a foundation plant species.

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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 foraging duration before and during blooming at each microsite. The foraging duration did not vary with microsite but showed a significant decrease with blooming. This was driven by pollinators in the ‘other’ category, which was comprised of primarily beetles and muscoid flies.



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: A) Microsite (Shrub – Open) B) Blooming (Pre-Blooming – 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 quasi-Poisson GLMM (glmmPQL, MASS) 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. *Post hoc* 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.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | 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** |

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| 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 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 |

Table 3: Results from Gamma GLMM (lme4, glmer.nb) testing for differences foraging 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.

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

Table 4: 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** | **p** | **Coef** | **χ2** | **p** |
| 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 |

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Insect abundance (Melyridae: excluded) | | | Arthropod Species Richness | | | Bee abundance | | | Bee richness | | |
|  | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p | Coef | **χ**2 | p |
| Microsite | 0.406 | 15.49 | **<0.0001** | 0.1454 | 6.62 | **0.01** | 0.058 | 0.079 | 0.778 | -0.065 | 0.125 | 0.724 |
| Blooming | -0.396 | 13.59 | **0.00023** | -0.254 | 25.63 | **<0.0001** | -0.08 | 0.21 | 0.646 | -0.056 | 0.094 | 0.759 |
| Microsite \* Blooming | -0.277 | 3.455 | 0.063 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
|  | **Percent cover** | | | **Annual Richness** | | | **Annual Bloom Density** | | | **Blooming shrub density within 2 m** | | |
|  | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p | **Coef** | **χ**2 | p |
| Microsite | 1.7599 | 165.4 | **<0.0001** | 0.0719 | 0.707 | 0.40 | -0.28 | 0.601 | 0.438 | 0.366 | 4.083 | **0.04331** |
| Blooming | -0.793 | 34.18 | **<0.0001** | 0.1407 | 2.701 | 0.10 | -1.36 | 13.36 | **0.0003** | 1.67 | 149.7 | **<0.0001** |
| Microsite \* blooming | 0.794 | 22.81 | **<0.0001** | NA | NA | NA | NA | NA | NA | NA | NA | NA |

Table 5: Results from GLMM testing for differences in arthopod, bee and plant communities in response to response to microsite (shrub and open) and blooming stage (full bloom and pre-blooming). 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 all models to account for the repeated measures study design. Significance was denoted at α = 0.05 and shown in bold.

Table 6: Permutation test ANOVA on RDA testing for changes in influence of shrub microsite and understory annual vegetation on arthropod community composition with phenological shift into flowering of *Larrea tridentata*. The constraining variables of the pre-blooming RDA explained 12.5% of the total variation and the blooming RDA explained 4%.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Pre-blooming | | | | Blooming | | | |
|  | **Df** | **Variance** | **F** | **p** | **Df** | **Variance** | **F** | **p** |
| Microsite | 1 | 0.04396 | 9.5687 | **0.001** | 1 | 0.01074 | 2.0561 | **0.005** |
| Percent cover | 1 | 0.00688 | 1.4983 | 0.087 | 1 | 0.00507 | 0.9700 | 0.471 |
| Annual richness | 1 | 0.00443 | 0.9653 | 0.449 | 1 | 0.00701 | 1.3421 | 0.119 |
| Annual bloom density | 1 | 0.00619 | 1.3470 | 0.131 | 1 | 0.00197 | 0.3765 | 0.995 |

Appendix A

Model selection from results of Table 1, full model of Table 1 and RTU interaction models for Table 3

Table A1: 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 A2: 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 A3: 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 A4: 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 | | |
|  | **χ2** | Df | p | **χ2** | Df | p |
| Blooming | 16.3114 | 1 | **<0.0001** | 11.2812 | 1 | **0.0007829** |
| RTU | 121.683 | 5 | **<0.0001** | 131.340 | 5 | **<0.0001** |
| Microsite | 6.7008 | 1 | **0.009637** | 3.6569 | 1 | 0.0558390 |
| Flowers.pot | 9.4194 | 1 | **0.002147** | 4.5640 | 1 | **0.0326507** |
| Blooming:RTU | 56.9111 | 5 | **<0.0001** | 53.0033 | 5 | **<0.0001** |
| Blooming:microsite | 3.6394 | 1 | 0.056426 | 2.3436 | 1 | 0.1258002 |
| Rtu:microsite | 5.4996 | 5 | 0.357984 | 3.8289 | 5 | 0.5743031 |
| Blooming:RTU:  microsite | 7.5190 | 5 | 0.184812 | 4.1995 | 5 | 0.5210663 |

Table A5: Gamma GLMM (glmer lme4) models for proportions of flowers visited including Blooming \* RTU interaction to test for differences in RTU response to blooming stage.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Std Error | Z | P |
| Blooming | -0.116064 | 0.140156 | -0.828 | 0.40761 |
| RTU.Bombylid | -0.247470 | 0.112323 | -2.203 | 0.02758 |
| RTU.Honeybee | 0.186243 | 0.240711 | 0.774 | 0.43910 |
| RTU.Lep | -0.329590 | 0.262264 | -1.257 | 0.20886 |
| RTU.Other | -0.300436 | 0.095633 | -3.142 | 0.00168 |
| RTU.Syrphid | -0.173276 | 0.085192 | -2.034 | 0.04196 |
| Blooming \* RTU.Bombylid | 0.202234 | 0.174650 | 1.158 | 0.24689 |
| Blooming\* RTU.Lep | 0.069411 | 0.297303 | 0.233 | 0.81540 |
| Blooming \* RTU.Other | 0.033465 | 0.153065 | 0.219 | 0.82693 |
| Blooming \* Syrphid | 0.006737 | 0.171338 | 0.039 | 0.96863 |

Table A6: Gamma GLMM (glmer lme4) for proportions of flowers visited including Microsite \* RTU interaction to test for differences in RTU response to microsite.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Std Error | Z | P |
| Microsite | -0.2956 | 0.1499 | -1.973 | 0.04852 |
| RTU.Bombylid | -0.3373 | 0.1226 | -2.752 | 0.00592 |
| RTU.Honeybee | 0.3531 | 0.2415 | 1.462 | 0.14375 |
| RTU.Lep | -0.4734 | 0.1472 | -3.215 | 0.00131 |
| RTU.Other | -0.4738 | 0.1117 | -4.243 | 2.2e-05 |
| RTU.Syrphid | -0.3421 | 0.1079 | -3.172 | 0.00152 |
| Microsite \* RTU.Bombylid | 0.2888 | 0.1717 | 1.682 | 0.09253 |
| Microsite \* RTU.Lep | 0.2057 | 0.2111 | 0.974 | 0.32988 |
| Microsite \* RTU.Other | 0.2655 | 0.1486 | 1.787 | 0.07399 |
| Microsite \* Syrphid | 0.3527 | 0.1410 | 2.502 | 0.01235 |

Table B7: Post-hoc constrast (lsmeans) on significant interaction from Table A6.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Proportion of flowers visited | | | |
| Contrast | **Estimate** | **SE** | **t.ratio** | **p** |
| Open, bee – shrub, bee | 0.2956276573 | 0.14985202 | 1.973 | 0.7122 |
| Open, bombylid – shrub, bombylid | 0.0067785545 | 0.12221348 | 0.055 | 1.0000 |
| Open, honeybee – shrub, honeybee | nonEst | NA | NA | **NA** |
| Open, lep – Shrub, lep | 0.0899409512 | 0.17203545 | 0.523 | 1.0000 |
| Open, other – Shrub, other | 0.0301074801 | 0.08727658 | 0.345 | 1.0000 |
| Open, syrphid – shrub, syrphid | -0.0570436624 | 0.08160285 | -0.699 | 0.9999 |

Appendix B

Table B1: A list of all RTU for Chapter 2. All RTU all exclusive and no individuals were double counted. 118 taxonomic groups were counted. The full dataset has been published openly (Braun and Lortie, 2018).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| 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 C

Table C1: Negative binomial GLMM (glmer.nb, lme4) 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 (lsmeans).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 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** |