# Disentangling the drivers and trade-offs of pollinator-mediated interactions between the foundation shrub Creosote bush (*Larrea tridentata*) and the annual desert dandelion (*Malacothrix glabrata)*

Pollinator competition is a trade-off of foundation plant facilitation

Blooming intensifies pollinator-mediated competition in a nurse facilitation system

# Research article

**Keywords:** Pollination, competition, facilitation, *Larrea tridentata*, arid environments, community assembly

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## Abstract

In arid ecosystems shrub facilitation is a critical process driving plant community structure and assembly, which leads to concentrations of annuals beneath the shrub canopies. Pollinator-mediated interactions have fitness consequences for their participants but are a largely unexplored indirect consequence of shrub-annual facilitation. We tested the capacity of the geographically widespread Creosote bush *Larrea tridentata* to influence the pollination of its annual understory during its phenological shift into spring flowering. In this system, we found that *L. tridentata* had a positive ecological effect on annual plant cover, as well as the abundance and richness of the arthropod community but that it also had indirect negative effects on pollinator visitation to a representative flowering annual plant which intensified when *L. tridentata* bloomed. These finding suggest 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.

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 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_6); [Callaway and Walker 1997a](#_ENREF_17); [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_6); [Tielbörger and Kadmon 2000](#_ENREF_85)). These complex sets of interactions lead to patterns in species coexistence and structure plant communities ([Valiente‐Banuet and Verdú 2007](#_ENREF_88); [Brooker et al. 2008](#_ENREF_12)). An emergent pattern of these interactions is the frequent close association of shrub and annuals in arid ecosystems (Holzapfel et al 2005, Pugnaire 2011, ([Facelli and Temby 2002](#_ENREF_27)). Indirect interaction occurs whenever a third species alters the interaction between two other species ([Wootton 1994](#_ENREF_94); [Callaway and Walker 1997b](#_ENREF_18); [Callaway and Pennings 2000](#_ENREF_16)) and undoubtedly arise from the close spatial proximity of shrubs and annuals ([Sotomayor and Lortie 2015](#_ENREF_80)). If the associated annual is animal-pollinated there is the capacity for the plants to interact indirectly via pollinators.

Simultaneous flowering is not a necessary condition for plants to interact via pollinators ([Braun and Lortie 2018](#_ENREF_10)). Shrubs are salient features of desert scrub ecosystems due their large size and structural complexity relative to ephemeral plants. Annuals growing under shrubs may be physically obscured from foraging pollinators or shaded thereby reducing pollinator visitation. For example, shading by the shrub *Lonicera* decreases pollinator visitation and pollen deposition to its understory annuals ([McKinney and Goodell 2010](#_ENREF_51)). Alternatively, shrubs may facilitate their annual understory by improving conditions for pollinators by offering shelter or habitat. Shrubs and annuals with overlapping phenologies likely interact through floral pathways as well. Highly attractive plants i.e. magnet species increase local pollinator abundances which benefits their less attractive neighbours ([Laverty 1992](#_ENREF_46), McKinney). Additionally, shrubs with large floral displays may increase pollinator availability for the understory through demographic responses in pollinator populations. Many pollinators forage optimally (Pyke 1977, Pyke 2016), thus co-blooming, associated plants can jointly improve their pollination success by combining their floral displays to increase the size or diversity of the resource pool (Ghazoul, 2006). If shrubs concentrate pollinators that do not in turn visit their neighbours, competition or interference rather than facilitation will arise. Similarly, an increase in floral density that is greater than pollinator availability can have a dilution effect decreasing visitation rates (Rathcke 1983, Ye 2013).

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 ([Valiente-Banuet et al. 1991](#_ENREF_87); [Pugnaire et al. 1996](#_ENREF_63); [Callaway and Walker 1997b](#_ENREF_18); [Rousset and Lepart 2000](#_ENREF_69); [Bruno et al. 2003](#_ENREF_14)). 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_5)). 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 at least 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_60)), 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](#_ENREF_22)). 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 with 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). *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_7)). 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_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_9)). 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_8)). Therefore, transplants of similar size, floral number and habit were paired 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 4:00 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 *L. tridentata*

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 ([Michener et al. 1994](#_ENREF_54); [Michener 2000](#_ENREF_53); [Miranda et al. 2013](#_ENREF_56); [Ascher and Pickering 2015](#_ENREF_3)). The majority of remaining individuals was identified to at least the taxonomic resolution of family ([Teskey et al. 1981](#_ENREF_83); [Grissell and Schauff 1990](#_ENREF_36); [Triplehorn and Johnson 2005](#_ENREF_86); [Marshall 2012](#_ENREF_49)), except 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 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 *in-situ* observation periods were completed at 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 Core Team, 2017) 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 [GLMM] were fit using negative binomial error distributions with a loglink function to account for overdispersion (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 covariate. 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 Nielsen 2016](#_ENREF_66)). The individual microsite i.e. shrub ID + microsite 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 A1, A2). To test for the influence of heterospecific blooming annuals and shrubs, negative binomial GLMMs (glmmTMB) with each covariate included in the additive model were used. A quasipoisson GLMM (glmmPQL, MASS) was used to explore which visitors were driving observed visitation patterns.

In order to test for differences in foraging behaviours, Gamma GLMM models (glmer, lme4) were fit with foraging duration and proportion of flowers visited per foraging instance as response variables. Least-squares *post hoc* tests (lsmeans) were used on any significant interactions and the individual microsite 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 included 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 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. Least-squares *post hoc* tests (lsmeans) were used on significant interactions, and the individual microsite was included as a random effect to control for repeated measures. To explore 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.

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 logger IDs were included as a random effect to control for the repeated measures.

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 Relative Interaction Index (RII) was calculated (Armas et al., 2004). The equation: was used and modified from (Filazzola). 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 indicate 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, A3). 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 2). There was no significant difference between RTU visiting the microsites nor were there significant interactions between RTU, microsite, and blooming on the total flowers visited or frequency of foraging instances (Table A4).

There was no significant influence of heterospecific shrub blooming density on foraging instance frequency (stats: ) or total flowers visited (stats: ). There was a significant, positive effect of heterospecific annual floral density on foraging instances (stats: ) but not flowers visited (stats: Table A5 full models). 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 (blooming, χ2 value: 23.1788, p <0.0001; microsite, χ2: 0.0464, p =0.8295). The proportion of flowers visited per visit decreased significantly with blooming at the shrub microsite only (microsite \* blooming: χ2 = 7.0691, p =0.00784, microsite: χ2 = 1.0051, p =0.46515; blooming: χ2 = 0.5335, p =0.31609).

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* (*χ*2= 0.4686, p = 0.4936), nearest conspecific plant (χ2= 2.4188, p = 0.1199) or the number of conspecific flowers on conspecific pollen deposition (χ2= 0.6184, p = 0.4316). Heterospecific pollen deposition increased significantly with distance from *L. tridentata* (χ2= 6.7835, p = 0.0092),but there was no influence of nearest conspecific (χ2= 0.2256, p = 0.6348) or floral number (χ2= 1.6668, p = 0.1967)*.* Conspecific and heterospecific pollen deposition were significantly correlated (Pearson’s = 0.15, t = 2.397, df = 229, p = 0.01).

### Community-level shrub effects

A total of 3384 arthropods spanning 118 taxonomic groups 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 3). 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 (Table A7). There was no significant difference in bee abundance or richness caught in pan traps between any of the treatments (Table 3).

Percent cover of ground vegetation was significantly greater in shrub microsites, and it decreased with blooming in the open microsite only (Table 3). There was a significant decrease in heterospecific annual floral density with blooming, but there were no significant differences between the microsites (Table 3). There was also no significant difference in annual species richness between any of the treatments (Table 3).

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 1A). 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 1B).

Pollinator visitation to *L. tridentata* increased with floral abundance (Figure 2, 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 14.5 hours of observations. Of 169 visits made by bees, *Apis mellifera* was the most frequent visitor (32%), followed by *Centris* sp. (21%), *Hesperapis sp.* (18%) and *Megandrena enceliae* (7%) and other solitary bees (23%) including *Hoplitis* and *Megachile*.

Mean daytime temperatures were significantly lower (Figure 3, χ2:85.51, p <0.0001), and mean nighttime temperatures were significantly higher under the shrub canopy (χ2: 50.121, p <0.0001). Overall temperature variation was significantly lower in the shrub microsites (χ2: 523.38, p <0.0001).

## 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 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 the negative interaction with the development of exploitation competition with *M. glabrata* at both microsites rather than shifting net outcomes into 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 ([Mosquin 1971](#_ENREF_57); [Gentry 1974](#_ENREF_33)). 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_64)). 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_8)) 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, the decrease in visitation cannot be attributed to direct shrub effects. 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 ([Noma and Brewer 2008](#_ENREF_58); [Iler et al. 2013](#_ENREF_42)). This suggests the influence of indirect shrub effects i.e. mediated through pollinator-pollinator interactions. This is a novel mechanism of pollinator-mediated competition in arid ecosystems that has the potential to be widespread.

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 net 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](#_ENREF_57)). Thus the timing of blooming is 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 in annual and arthropod communities than the effect of spatial association with *L. tridentata.* However, 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)). The shifts in both arthropod composition and annual performance measures show that 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 ([Yeaton 1978](#_ENREF_95); [Valiente-Banuet et al. 1991](#_ENREF_87)). 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_61)). 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_62)) and are often found concentrated under shrubs ([Facelli and Temby 2002](#_ENREF_27)). 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 ([Tielbörger and Kadmon 2000](#_ENREF_85); [Goldberg et al. 2001](#_ENREF_35)). 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: 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 2: Pollinator visitation rates increased with the number of *Larrea tridentata* flowers.



Figure 3: 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: Output from generalized linear mixed model of visitation results

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Total flower visits | | |  | Foraging instances | | |
|  | 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 | 0.04354 |
| RTU\*blooming | NA | 70.0222 | <0.0001 |  | NA | 70.35 | <0.0001 |

Table 2: Post-hoc least squares contrasts of significant RTU \* blooming interactions from GLMM visitation model.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Total flower visits | | | | Foraging instances | | | |
| 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 3: GLMM results showing community-level effects.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | |  | | Coeff | χ2 | p |  | |  | Coeff | χ2 | p |
| Arthropod Abundance a | |  | |  |  |  | Arthropod Species Richness | | |  |  |  |
|  | Microsite |  | | 0.406 | 15.49 | <0.0001 |  | Microsite | | 0.1454 | 6.62 | 0.01 |
|  | Blooming | | -0.396 | | 13.59 | 0.00023 |  | Blooming | | -0.254 | 25.6 | <0.0001 |
|  | Microsite \* Blooming | | -0.277 | | 3.455 | 0.063 |  | |  |  |  |  |
| Bee abundance | |  | |  |  |  | Bee richness | |  |  |  |  |
|  | Microsite | | 0.058 | | 0.079 | 0.778 |  | Microsite | | -0.065 | 0.125 | 0.724 |
|  | Blooming | | -0.08 | | 0.21 | 0.646 |  | Blooming | | -0.056 | 0.094 | 0.759 |
| Annual percent cover b | |  | |  |  |  | Annual Richness | |  |  |  |  |
|  | Microsite | | 1.7599 | | 165.4 | <0.0001 |  | Microsite | | 0.0719 | 0.707 | 0.40 |
|  | Blooming | | -0.793 | | 34.18 | <0.0001 |  | Blooming | | 0.1407 | 2.701 | 0.10 |
|  | Microsite \* Blooming | | 0.794 | | 22.81 | <0.0001 |  | |  |  |  |  |
| Annual Bloom Density | |  | |  |  |  | Blooming Shrub Density | | |  |  |  |
|  | Microsite | | -0.28 | | 0.601 | 0.438 |  | Microsite | | 0.366 | 4.083 | 0.04331 |
|  | Blooming | | -1.36 | | 13.36 | 0.0003 |  | Blooming | | 1.67 | 149.7 | <0.0001 |

Note: a Melyridae excluded

b results from posthoc in table A4

## Appendix: Additional and supporting analyses

Table A1: Statistical comparison of additive, interactive and null models with no species specificity.

Null model is flowers.pot with the random intercept, additive is flower.pot + blooming + microsite and interaction is 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 is 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).

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

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: 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.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Total flower visits | | | Foraging bouts | | |
|  | Coeff | χ2 | p | Coeff | χ2 | p |
| Microsite (shrub) | -0.3660 | 4.6655 | 0.030774 | -0.33019 | 5.0412 | 0.02475 |
| Blooming (bloom) | -1.2396 | 57.4645 | 3.441e-14 | -1.24571 | 73.6776 | < 2e-16 |
| Flowers.pot | 0.08084 | 8.8892 | 0.002869 | 0.05943 | 6.2673 | 0.01230 |
| Heterospecific  annual bloom density | 0.04013 | 2.9358 | 0.086636 | 0.04086 | 4.2393 | 0.03950 |
| Microsite (shrub) | -0.3289 | 3.7437 | 0.053008 | -0.31539 | 4.5234 | 0.03343 |
| Blooming (bloom) | -1.1662 | 39.3038 | 3.627e-10 | -1.20875 | 52.3453 | 4.655e-13 |
| Flowers.pot | 0.07598 | 7.9027 | 0.004936 | 0.05296 | 4.9695 | 0.02580 |
| Heterospecific  blooming shrub density | -0.0494 | 1.4568 | 0.227438 | 0.03124 | 0.6964 | 0.40400 |

## 

Table A6: 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 | | | |
| 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 |

## Sensitivity of arthropod community models

Table A7: 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 A8: 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 |

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