# Facilitation with a grain of salt: 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).*

Running title: 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. These effects can lead to increased densities of annual plants beneath shrub canopies. Pollinator-mediated interactions have fitness consequences for participants but are largely unexplored as an 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 confirmed that *L. tridentata* had a positive ecological effect on annual plant cover. This shrub species also facilitated abundance and richness of the arthropod community but that it also had indirect negative effects on pollinator visitation to the 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 ecological interaction theory and assessment of selection processes that drive co-evolutionary relationships between shrubs, annual plants, and pollinators.

**Introduction**

Interactions between species are fundamental drivers of ecological community assembly and the evolutionary processes that influence long-term dynamics in biodiversity. Foundation species physically structure plant communities by creating locally stable conditions for other species ([Ellison et al. 2005](#_ENREF_26)). These positive interactions lead to patterns in species coexistence within plant communities ([Valiente‐Banuet and Verdú 2007](#_ENREF_88); [Brooker et al. 2008](#_ENREF_12)) including the frequent association of shrub and annuals in arid ecosystems (Holzapfel et al 2005, Pugnaire 2011, [Facelli and Temby 2002](#_ENREF_27)). Foundation shrubs act as keystone facilitators, directly benefiting associated understory annual plants via multiple mechanistic pathways across all life stages of the protégé species ([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)). However, these pairwise interactions are often inadequate to predict actual observed net outcomes in natural ecosystems (Callaway and Pennings, 2000). If the associated annual species are animal-pollinated, there is the capacity for the plants to also interact indirectly via pollinators. 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), Sotomayor and Lortie 2015). This is important because indirect interactions can significantly influence net ecological outcomes (citation).

Plants can interact through pollinators in many capacities mechanistically (Braun and Lortie, 2018). Shrubs and annuals with overlapping phenologies likely interact through mechanisms mediated by pollinator responses to floral resources. Highly attractive plants i.e. magnet species increase local pollinator abundances which benefits their less attractive neighbours ([Laverty 1992](#_ENREF_46), McKinney). 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). Simultaneous flowering is not however a necessary condition for plants to interact via pollinators (Hansen 2007, Braun and Lortie 2018). Shrubs are salient features of desert scrub ecosystems due their large size and structural complexity relative to ephemeral plants. Annuals growing under shrubs could be physically obscured from foraging pollinators or shaded thereby reducing pollinator visitation (i.e. through interference). 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 could facilitate their annual understory if they improve conditions for pollinators by offering shelter or habitat, however, the frequency with which these occur is unexplored. Consequently, direct and indirect shrub effects on other species function simultaneously to determine net outcomes.

Shifts in net interactions are driven by both biotic and abiotic drivers within a system. The relative importance of net outcomes versus net interactions is a critical concept in the ecological literature for communities (Brooker et al 2005, Lortie et al 2016). The context-dependence of species interactions leads to shifts in their strength or sign across gradients, space and time (Chamberlain 2014), as well as across the life stage of the protégé species ([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)). There is evidence that earlier life stages experience higher relative mortality rates (Fenner 1987). However, the life stage shift from vegetative growth to reproductive growth is a major event in resource allocation ([Bazzaz et al. 1987](#_ENREF_5)) and thus reproductive output and fitness consequences are ultimately also important life stages. The life stage of the foundation plant i.e. flowering is important too because of fitness effects mediated through pollination competition and facilitation. Thus, within season phenology is 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 the plant sciences ([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 local 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 foundation shrubs both positively and negatively influence pollination success of beneficiary annual plants dependent on phenological overlap due to pollinator responses to the large floral display size provided by the foundation shrub. 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 tend to facilitate their understory annuals they may have a buffering effect for the community under pollinator population declines, but if shrubs typically interfere with pollination for annuals, the sensitivity to change for the community increases.

## Methods

Study site

The main study site is located in Sunset Cove at 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 area has an extent of 0.07 km2, and it 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* (Braun pers. obs). The secondary study site is located approximate 2.7 km away and is a flat typical *Larrea tridentata* and *Ambrosia dumosa* shrubland (34°44'42.9"N 115°39'37.8"W).

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)).

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 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”). The mean number of blooms per shrub 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.

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 flowers for each *L. tridentata* shrub were 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 (n = 235 videos).

To quantify the influence of proximity to *L. tridentata* on pollen deposition, stigma were excised from *M. glabrata* at the nearby secondary site 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 was 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 resolved 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 119 RTU archived online (see journal office). All physical specimens are archived at *redacted*.

To determine which pollinator species 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 to facilitate identification.

To assess the influence of *L. tridentata* on 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 Version 3.4.2 (R Core Team, 2017), and all code is available on GitHub (url available from journal office).

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 (glmmTMB, Brooks 2017). 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 (Zuur 2009). 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)). Instead, the number of *M. glabrata* flowers within the pot was included as a covariate to account for the influence of conspecific floral density. 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 (Zuur 2009). Interactive, additive, and intercept only models were compared by AIC and likelihood ratio tests with χ2 approximations (Table A1, A2). The influence of heterospecific blooming annuals and shrubs on visitation to *M. glabrata* was tested by adding the covariates to the additive model.

A quasipoisson GLMM (glmmPQL, MASS, Venables 2002) was used to explore which pollinator groups were driving observed visitation patterns by including them as a factor in the GLMM.

In order to test for differences in foraging behaviours, Gamma GLMM (glmmTMB) were fit with foraging duration and proportion of flowers visited per foraging instance as response variables. Least-squares *post hoc* tests (lsmeans, Russel 2016) were used on any significant interactions and the individual microsite was included as a random effect.

To test for the influence of proximity to *L. tridentata* on pollen deposition to *M. glabrata*, 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 to account for the within plant correlation structure.

Community-level shrub effects

GLMMs (glmmTMB) were used to test for shrub effects on the local community (negative binomial: arthropod abundance, percent annual cover, annual species richness, annual bloom density, bee richness, poisson: arthropod species richness and bee abundance). Beetles from the family *Melyridae* comprised 1248 of the 3384 total arthropods captured, therefore abundance models were fit with *Melyridae* excluded, included and individually to explore model sensitivities. 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. To test for the capacity of *L. tridentata* to create stable microclimates beneath the canopy, Gamma GLMMs (glmmTMB) were fit using microsite as a predictor and mean daytime temperature, mean nighttime temperatures, and daily temperature variance as response variables. 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 (hourly 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. 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 (package boot, Canty and Riply 2017), stratified by the focal shrub ID to account for the repeated measures study design. Only matched microsites were used for these calculations.

## 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, A2). There was a positive effect of *M. glabrata* floral display size on both the frequency of foraging instances and floral visitation (Table 1). There was a significant, positive effect of heterospecific annual floral density on the frequency of foraging instances (Table 1, A2) but not flowers visited. The influence of heterospecific blooming shrub density on foraging instance frequency was insignificant (p > 0.09) and excluded from the final models. Pollinator foraging duration was shorter when *L. tridentata* was blooming and did not differ between the microsites (Table 1). The proportion of flowers visited per foraging instance was positively influenced by the size of *M. glabrata* floral display but otherwise did not differ between microsites or shrub blooming stage (Table 1).

The frequency of foraging instances and flower visits by Syrphids and solitary bees declined significantly with shrub 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). 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).

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* (GLMM, *χ*2= 0.3099, p = 0.5777), nearest conspecific plant (GLMM, χ2= 2.3299, p = 0.1269) or the number of conspecific flowers on conspecific pollen deposition (GLMM, χ2= 0.6290, p = 0.4277). Heterospecific pollen deposition increased significantly with distance from *L. tridentata* (GLMM, χ2= 5.8389, p = 0.0157),but there was no influence of nearest conspecific (GLMM, χ2= 0.1082, p = 0.7422) or floral number (GLMM, χ2= 1.8422, p = 0.1747)*.* 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. Arthropod abundance (Melyridae excluded) and richness were higher in the shrub microsite and both decreased with shrub blooming (Table 3). Arthropod abundance (Melyridae excluded) was significantly correlated between paired shrub/open microsites (Pearson’s = 0.46, p < 0.001). Melyridae beetle abundance was significantly lower at the shrub microsites, and decreased with blooming at the open microsite only (Table A7). A total of 144 bees were captured in pan traps comprising 22 taxonomic groups. Bee abundance and richness were consistent between all treatments (Table 3).

Percent cover of ground vegetation was significantly higher in shrub microsites, and declined with shrub blooming in open areas only (Table 3). Heterospecific annual floral density did not differ between shrub and open microsites, also declined with shrub blooming (Table 3). There was no significant difference in annual species richness between any of the treatments (Table 3).

Shrubs exerted a competitive effect (RII < 0) on hourly floral visitation rates to *M. glabrata* and a facilitative effect (RII > 0) on arthropod abundance, arthropod species richness, and annual percent cover (Figure 3A, Appendix 1000). Negative effects (RII < 0) were observed for most community metrics within individual microsites however percent cover at the shrub microsite’s interaction index was 0 (Figure 3B).

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, χ2:84.959, p <0.0001), and mean nighttime temperatures were significantly higher under the shrub canopy (χ2: 49.635, p <0.0001). Overall temperature variation was significantly lower in the shrub microsites (χ2: 519.9, p <0.0001).

## Discussion

Foundation species are critical in structuring desert plant communities; however, we cannot assume that all effects of foundation species are positive. 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), Holzapel and Mahall 1999, Maestre 2003, Graff et al 2007). We hypothesized that facilitated annuals would experience a shift in their pollination mediated through the flowering of their beneficiary shrub. *L. tridentata* interfered with the pollination of the representative phytometer species *M. glabrata*. 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 relative outcomes into facilitation via the magnet species effect. 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. We also found evidence of positive indirect interactions between *M. glabrata* and other flowering heterospecific annuals. Pollinator-mediated facilitation has not previously been documented in any desert ecosystem globally (Braun and Lortie, 2018). Positive direct and indirect effects were simultaneous with negative indirect effects therefore reproductive outcomes and indirect interactions in general cannot be ignored in ecological studies of facilitation.

Plants that employ a cornucopian flowering strategy produce abundant floral resources over an extended period of time and can attract a wide range of pollinators to the localized area ([Mosquin 1971](#_ENREF_57); [Gentry 1974](#_ENREF_33)). Pollinators showed a behavioural response to the increased floral resources of *L. tridentata*, decreasing overall visitation and visit duration to *M. glabrata*. 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. 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)) and this foraging behaviour likely contributed to the outcomes observed. 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. In the alpine, similar exploitation competition of spring annuals by later-blooming resource-rich cornucopia plants has contributed to phenological divergence (Mosquin 1971). Over the study period additional foundation species including *Acamptopappus sphaerocephalus*, *Opuntia sp*. and *Ericameria cooperi* entered into bloom alongside *L. tridentata* while annual floral density decreased, a consistent occurrence throughout Southwestern Deserts ([Cable 1969](#_ENREF_15); [Halvorson and Patten 1975](#_ENREF_37); [Jennings 2001](#_ENREF_44)). The cornucopia flowering strategy by benefactors likely introduces directional selection in the protégé species to flower sooner and to avoid competition in desert shrub-annual facilitation systems.

Phenology is a critical mediator of net outcomes between multiple trophic levels. Interactions even in relatively short growing season systems can shift depending on life-stage and timing. 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*. 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)). Substantial within season changes to the intensity of facilitation and competition between shrubs and annuals has been documented in both the Mojave Desert (Holzapfel and Mahall 1999) and the Negev (Schiffers and Tielbörger 2006). Foundation species provide a complex suite of mechanisms to facilitate but also interact with plant and arthropod communities and we need to better describe the richness of these interactions.

Mechanisms extending through insect communities can come into play treating shrubs as a key interactor in deserts – for instance pollinators can also interact with one another at these floral islands. *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)). 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.

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 or parasitism later in life ([Yeaton 1978](#_ENREF_95); [Valiente-Banuet et al. 1991](#_ENREF_87), Llambi et al 2018, Flores-Torres and Montana 2015). 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)) because of the potential for this to influence long-term coexistence and stability. Here, we show the mechanisms by which a shrub can facilitate for density while decreasing fitness indirectly through effects on pollination. The extent of these tradeoffs is likely underestimated in arid environments and important for structuring desert communities.

Whilst biodiversity can be maintained in high-stress systems through species interactions, there can be sensitivity that arises as well. In this system, annuals growing under shrubs may more likely to establish and survive longer in the season due to climate amelioration by the canopy. Despite the interference by the canopy for pollinator visitation, we found no difference in conspecific pollen deposition suggesting shrubs had a net positive effect on annuals but interactions mediated through shrub phenology were critical mediators of the sign of the net outcome of association. Therefore, plant fitness is sensitive to global change effects including droughts, temperature shifts, and variation in timing of rainfall these potentially sensitive overlaps and relationships are fundamental to document. The loss of interactions can proceed the loss of species through these phenological relationships in facilitation systems.

**Acknowledgements**

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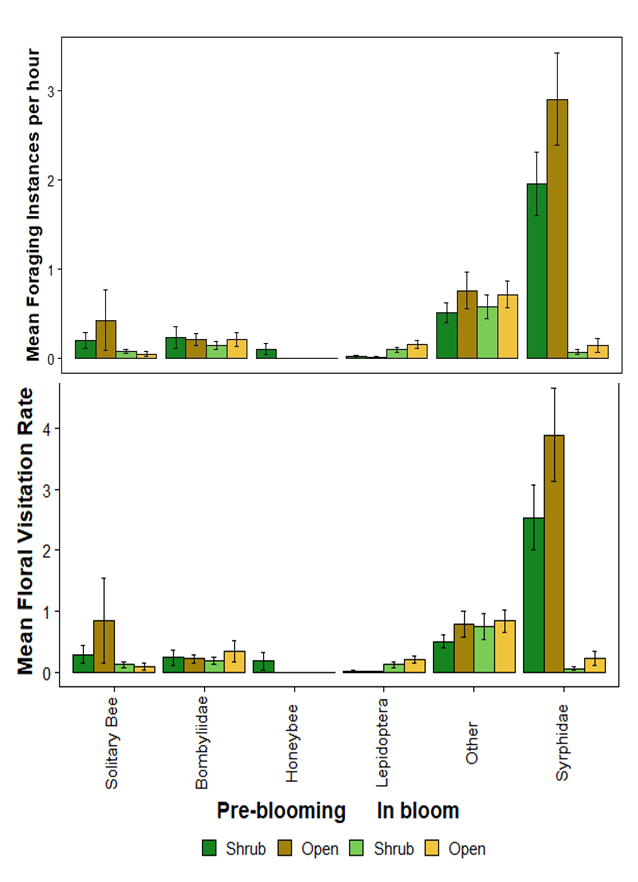


Figure 1: Visitation and flower visitation hourly rates…

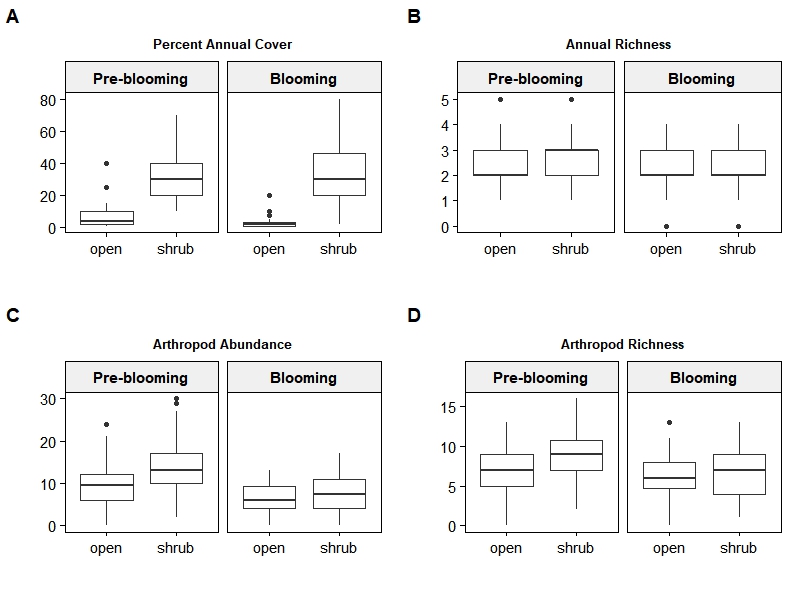


Figure 2: Is still open. Can discuss next week – I don’t really like the veg bloxplots because they seem a bit repetitive of the RII and the third results tables. Could do a conceptual diagram of floral/non-floral pollinator interaction pathways.

## 

Figure 3: 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.

## Tables

Table 1: Generalized linear mixed model results testing for influences on visitation to M. glabrata.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | | Coeff | χ2 | p |  | |  | | Coeff | χ2 | p |
| Total flower visits | |  |  |  | Foraging instances | | |  | |  |  |
|  | Microsite (shrub) | -0.3375 | 4.1903 | 0.0407 |  | -0.311383 | | 4.6322 | | 0.0314 | 0.0101 |
|  | Blooming (bloom) | -1.7294 | 15.4730 | <0.0001 |  | Blooming | | -1.6830 | | 12.216 | 0.0005 |
|  | RTU | NA | 197.0575 | < 0.0001 | RTU | |  | | NA | 217.503 | <0.0001 |
|  | M. glabrata floral display size | 0.0643 | 7.8743 | 0.0050 | M. glabrata floral display size | |  | | 0.0428 | 4.074 | 0.0435 |
|  | RTU\*blooming | NA | 70.0222 | <0.0001 | RTU\*blooming | |  | | NA | 70.35 | <0.0001 |
|  | Heterospecific Annual display size | NA | NA | NA | Heterospecific Annual Display Size | |  | |  |  |  |
| Visit Duration | |  |  |  | Proportion of flowers visited | | |  | |  |  |
|  | Microsite | -0.0235 | 0.0131 | 0.9201 |  | Microsite | | 0.0003 | | 0.320 | 0.9952 |
|  | Blooming | -0.7623 | 18.8636 | <0.0001 |  | Blooming | | -0.0213 | | 0.000 | 0.5718 |
| M. glabrata floral display size | | -0.0016 | 0.0912 | 0.9575 | M. glabrata floral display size | | | -0.0566 | | 75.226 | <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 | 0.2884 | 14.940 | 0.0001 |  | Microsite | | 0.1454 | 6.6195 | 0.0101 |
|  | Blooming | -0.5496 | 56.082 | <0.0001 |  | Blooming | | -0.2544 | 25.5826 | <0.0001 |
|  | Microsite \* Blooming | na | na | na |  | |  |  |  |  |
| Bee Abundanceb | |  |  |  | Bee Richnessb | | |  |  |  |
|  | Microsite | -0.0556 | 0.1111 | 0.7389 |  | Microsite | | -0.0645 | 0.1290 | 0.7195 |
|  | Blooming | 0.09348 | 0.3073 | 0.5793 |  | Blooming | | -0.0552 | 0.0936 | 0.7597 |
| Annual Percent Cover c | |  |  |  | Annual Richnessb | | |  |  |  |
|  | Microsite | 1.7641 | 163.649 | <0.0001 |  | Microsite | | 0.0719 | 0.707 | 0.40 |
|  | Blooming | -0.8027 | 33.998 | <0.0001 |  | Blooming | | 0.1407 | 2.701 | 0.10 |
|  | Microsite \* Blooming | 0.8048 | 22.837 | <0.0001 |  | |  |  |  |  |
| Heterospecific Annual Floral Density | |  |  |  | Heterospecific Blooming Shrub Density | | |  |  |  |
|  | Microsite | -0.28 | 0.601 | 0.438 |  | Microsite | | 0.366 | 4.0892 | 0.04316 |
|  | Blooming | -1.36 | 13.36 | 0.0003 |  | Blooming | | 1.67 | 150.748 | <0.0001 |

Note: a Melyridae excluded

b model showed improvement over intercept only model

c results from posthoc in table A4

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## Appendix: Additional and supporting analyses

## 

Table A1: Model comparison

|  |  |  |  |
| --- | --- | --- | --- |
| Model | AIC | Delta AIC from null model | Chisq |
| Foraging Instances |  |  |  |
| Intercept Only |  |  |  |
| Additive  Microsite + blooming |  |  |  |
| Interactive  Microsite \* blooming |  |  |  |
| Flowers visited |  |  |  |
| Intercept Only |  |  |  |
| Additive  Microsite + blooming |  |  |  |
| Interactive  Microsite \* blooming |  |  |  |

Table A2: Results from negative binomial generalized linear mixed models (glmmTMB) 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). Non-species specific

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Total flower visits** | | | **Foraging bouts** | | |
|  | Coeff | χ2 | p | Coeff | χ2 | p |
| **Microsite (shrub)** | -0.35032 | 4.4102 | 0.035726 | -0.32818 | 5.1248 | 0.02359 |
| **Blooming (bloom)** | -1.25514 | 61.1040 | <0.0001 | -1.25629 | 76.4608 | <0.0001 |
| **Flowers.pot** | 0.06992 | 6.8749 | 0.008742 | 0.04757 | 4.0952 | 0.04301 |
| **Annual Blooms** |  |  |  |  |  |  |
| **Shrub blooms** |  |  |  |  |  |  |

Table A3: Full models with RTU-specificity. 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 |
| Annual Bloom |  |  |  |  |  |  |
| Shrub Blooming |  |  |  |  |  |  |
| 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 |

## Sensitivity of arthropod community models

Table A4: Negative binomial GLMM (glmmTMB) for arthropod abundance – Melyridae included and Melyridae only. Type 3 Wald’s.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Insect abundance (Melyridae: included) | | | Melyridae: abundance only | | |
|  | Coef | χ2 | p | Coef | χ2 | p |
| Microsite (shrub) | -0.07724 | 1.1031 | 0.2936 | -1.2018 | 37.6021 | 0<0.0001 |
| Blooming (in bloom) | -0.39826 | 38.7043 | <0.0001 | -0.3004 | 3.3081 | 0.068938 |
| Microsite \* Blooming | NA | NA | NA | 0.6585 | 7.0759 | 0.007813 |

Table A5: Post-hoc contrasts interaction for abundance (Melyridae only) for microsite by

Blooming (lsmeans).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Contrast | Estimate | SE | Z | p |
| pre,open - post,open | 0.3004437 | 0.1651855 | 1.819 | 0.2644 |
| pre,open – pre, shrub | 1.2017858 | 0.1959841 | 6.132 | <0.0001 |
| pre,open - post,shrub | 0.8437044 | 0.1849410 | 4.562 | <0.0001 |
| post,open - pre,shrub | 0.9013421 | 0.1933146 | 4.663 | <0.0001 |
| post,open - post,shrub | 0.5432607 | 0.1822078 | 2.982 | 0.0152 |
| pre,shrub - post,shrub | -0.3580813 | 0.1842929 | -1.943 | 0.2101 |

Table A6: Summary of calculated RII (relative interaction index) indices

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Metric** | Mean RII |  | Lower CI | Upper CI | N |
| **Flowers visited per hour** | -0.12170398 |  | -0.20091973 | -0.05018725 | 114 |
| **Annual Species Richness** | 0.03644528 |  | 0.00674589 | 0.06810371 | 114 |
| **Arthropod abundance (Melyridae excluded)** | 0.12424698 |  | 0.07468910 | 0.17056080 | 102 |
| **Percent Annual Cover** | 0.74984026 |  | 0.72892343 | 0.77203101 | 102 |
| **Arthropod Richness** | 0.07254366 |  | -0.20091973 | 0.10632974 | 102 |

Table A7: RII values for microsite comparisons

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Metric | Microsite |  | Mean RII | Lower CI | Upper CI | N |
| visits | shrub |  | -0.44977898 | -0.5960356 | -0.2779737016 | 57 |
| visits | open |  | -0.34892797 | -0.5276026 | -0.1422394549 | 55 |
| percent.cover | shrub |  | -0.02534138 | -0.1142842 | 0.0569258459 | 51 |
| percent.cover | open |  | -0.30349291 | -0.4098193 | -0.1935318376 | 51 |
| annual.richness | shrub |  | -0.06817043 | -0.1434419 | 0.0005847953 | 51 |
| annual.richness | open |  | -0.05930736 | -0.1411254 | 0.0140259740 | 55 |
| arth.abundance | shrub |  | -0.34849316 | -0.4377806 | -0.2451645921 | 51 |
| arth.abundance | open |  | -0.23281150 | -0.3448487 | -0.1104013715 | 51 |
| arth.richness | shrub |  | -0.20151195 | -0.2849635 | -0.1198198052 | 51 |
| arth.richness | open |  | -0.14259236 | -0.2349986 | -0.0470499509 | 51 |



Figure A1: Variation in temperature under the canopy.