# 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 plant facilitation system

# Research article

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

There are x number of words in the main body of the text. 5733

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## Abstract

In arid ecosystems, shrub facilitation is a critical process driving plant community structure and assembly including 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 had indirect negative effects on pollinator visitation to a flowering annual plant. This apparent competition intensified with *L. tridentata* blooming. Phenology and life-stage can thus shift the net outcome of association with foundation plant species in facilitation complexes. Ecological trade-offs advance both interaction theory and assessment of selection processes that drive co-evolutionary relationships between shrubs, annual plants, and pollinators.

GOOD – do you need to also introduce pollinator mediated facilitation and competition as an important and overlooked dimension of facilitation between plants? It is shorter now so there is room if you want. Unless does not with rest of ms.

**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 annuals with shrubs in arid ecosystems (Holzapfel et al 2005, Pugnaire 2011, [Facelli and Temby 2002](#_ENREF_27)). Foundation shrubs act as keystone facilitators directly benefiting understory annual plants via multiple mechanistic pathways across all life stages of the protégé species ([Filazzola and Lortie 2014](#_ENREF_28)). These benefits can 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, i.e. apparent competition (citation). 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 can 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 can facilitate their annual understory if they provide refuge to pollinators like they do for other species (citations to arthropod facilitation) from harsh conditions. Consequently, direct and indirect shrub effects on other species function simultaneously to shift net outcomes even within predominantly net positive facilitation complexes. Redundant?

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) – ok – check my PhD work on facilitation because I tested this and at that time had citations and you could cite one of those papers – ie I found facilitation early because of high mortality. 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 also critical because a showy floral canopy can potentially change net outcomes for annuals through changes in the pollinator community. Intra-seasonal phenology is thus a component of interactions in tightly coupled plant systems sharing pollinators that must be examined to better examine sensitivity of positive interactions and selection processes that stabilize diversity.

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 or indirect interactions in general that can influence biodiversity 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" \o "Roll, 1997 #232)); however, interspecific studies have primarily focused on competition within cacti systems in the Sonoran Desert ([Fleming et al. 2001](#_ENREF_30" \o "Fleming, 2001 #233)) cut and save for discussion – breaks flow here and not needed. 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. – still clunky – how about these? **We examined the hypothesis that net outcomes in a typical shrub-annual facilitation complex can shift with phenology within a season.** Or say **common** shrub-annual facilitation complex or maybe say **representative**. One more idea – We examined the hypothesis that pollinator-mediated interactions between a foundation shrub species and a common annual species shift with phenology and life-stage. The following three predictions were tested: 1) visitation rates to an annual phytometer species differ under a shrub canopy relative to paired open microsites in general? Or maybe put 1 and 2 together and just say depending on phenology of the shrub species then cut 2; 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 – again I think this is just confirming that the annuals are in general facilitated and you are confirming this before moving to the flowering test right?. 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 will buffer the effects of pollinator declines on the plant community, but if shrubs typically interfere with pollination for annuals, the sensitivity to change for the community increases.

## Methods

Study site

The pollinator interaction 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. 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 plant facilitation? 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)). Is it the shrub species with the most documented diversity of associated pollinators – if so – state – cool fact and important to this study.

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 evenly distributed across the first study site (mean shrub 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*. Visitations were recorded from 11:30 am to 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) were recorded 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 with the phytometer in the center of each plot, 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 an insect visitor flew on and touched the open side of a flower rework. 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 same Flower visits were defined as flying insect contact with the open size of flower, and foraging instance as a total net visits to a single plant before departure from field of view. Foraging duration thus included flower-to-flower travel time on the same plant. Total flowers was coded as the sum of all flowers visited per forgaing instance (or did you mean per replicate – ie sum of all flowers within the phytometer pot – but you added only one plant right?). 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). All stills of visits are archived at figshare (then cite Braun and Lortie, 2019 for this dataset – they give you a doi and citation etc).

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. THIS seems really good to me and does not really pop in the Intro or abtract – so propose you mention in AB: Pollen dep was also assayed in an adjacent population and we found that… Then in INTRO – maybe never end – highlight very briefly with one prediction? Or at least mention in that final paragraph as a means to double check visitation rate measures observation data with actual pollen dep. THIS will be a big thing that we do not want readers to wait for too long. Mention soon and mention ofen. Haha.

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 at this secondary site?? If so – many name the sites above when you describe – ie the phytometer interaction study site and the population and community-level interaction site?. 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 ah so you did at first site? Ok so make clear sooner. 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*.? What happened? Not with Packer anymore? If not, perhaps offer up to McMaster or in our lab?

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). You can publish on Zenodo, get a DOI and make it a citable object here if you want?

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 or offset 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. Like.

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. Good!

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) and 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 pre-blooming? and were further? 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 to annuals? (Table 1) – so does this mean it counteracts the net negative effect to some extent?. There was a significant, positive effect of heterospecific annual floral density on the frequency of foraging instances (Table 1, A2) but not to total flowers visited. The influence of heterospecific blooming shrub density on foraging instance frequency was not statistically significant (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). OK great – complex though.

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).

*M. glabrata* population-study – maybe c9nsider grouping up somehow like this with another heading to match it clearer and match how you explained above? Hmm see below – work on subheadings so that really clear refer to the key process measured

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 – could flip this subheading a bit – Shrub effects on plant community

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 of shrub canopy? (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). solid.

## Discussion

Foundation species are critical in structuring desert plant communities; however, we cannot assume that all effects of foundation species are universally 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 or just call it apparent competition with *M. glabrata* at both microsites rather than shifting net relative outcomes into facilitation via the magnet species effect. This study nonetheless confirmed the general 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) OK sweet – make this pop in the Abstract then please and perhaps consider setting up as the hypothesis of paper too? Or at least mention – see track changes in that para in the Intro. Positive effects were concurrent with negative effects. Reproductive outcomes and indirect interactions can be pivotal in shrub-facilitation complexes in deserts.

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 the foundation species *L. tridentata* thereby decreasing overall visitation and visit duration to the phytometer *M. glabrata*. When choosing between resources, bees commonly stay for a few visits before leaving to the superior resource ([Sowig 1989](#_ENREF_81)) with larger floral displays ([Bosch and Waser 2001](#_ENREF_8)) or richer rewards ([Robertson et al. 1999](#_ENREF_67)) because it improves 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 getting clunky. 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. This is a consistent shift throughout Southwestern Deserts ([Cable 1969](#_ENREF_15); [Halvorson and Patten 1975](#_ENREF_37); [Jennings 2001](#_ENREF_44)). The cornucopia flowering strategy by benefactors can introduce directional selection in the protégé species to flower sooner to avoid competition in desert shrub-annual facilitation systems. Facilitation with a grain of salt. Oh wait, facilitation with a grain of pollen. Harhar.

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 have 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 more richly, and we need to better describe the diversity of these concurrent interactions. POP – love it

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 can be mediated through pollinator-pollinator interactions. This is a novel mechanism of pollinator-mediated competition in arid ecosystems that has the potential to be widespread and should be examined directly through observational studies of co-occurrence between pollinator guilds to focal plant species. OK?

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 be life-stage specific. For example, thorny plants can facilitate other species in at germination but negatively impact at later life stages through decoy effects that deflect herbivores towards the protégé species it facilitated ([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 then reduces pollination services through non-floral interference? ([Petit and Dickson 2005](#_ENREF_61)). To our knowledge, our study is the first demonstration of a benefactor flowering plant engaging in exploitation competition with its protégés (check and use same term throughout – sorry if changing incorrectly) 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 costs with plant density effects ([Tielbörger and Kadmon 2000](#_ENREF_85)) because of the potential for this to influence long-term coexistence and stability. Here, we show two mechanistic pathways for a foundation species to facilitate density but decrease net fitness. The extent of these tradeoffs is likely underestimated in arid environments and important for structuring desert communities.

Whilst biodiversity can generally be maintained in high-stress systems through species interactions (cite McIntire and Fajardo Tansley review in J Ecol here), pollinator-mediated interactions in addition to gradients and other factors influence the net outcome. 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. This para a bit repetitive – cut I think.

**Acknowledgements**

Redacted - See journal office.

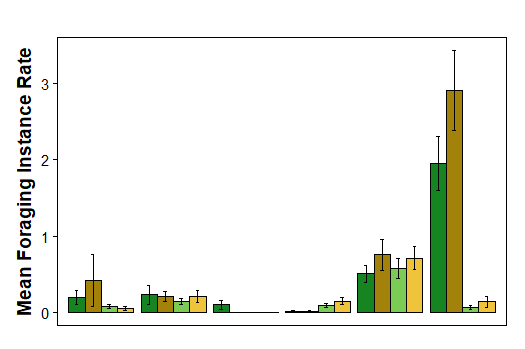
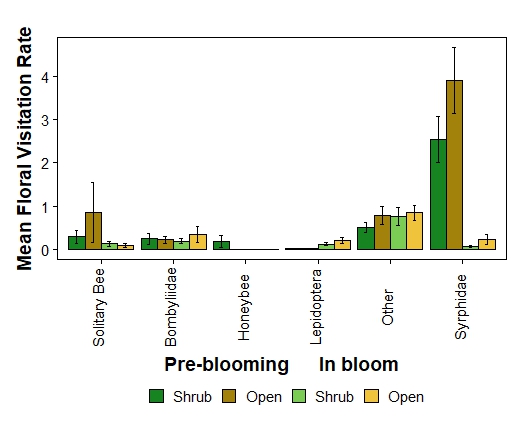


Figure 1: Visitation and flower visitation hourly rates to M. glabrata for each RTU (recognizable taxonomic unit) considered in this study.

FOR ALL three figures – I would facet wirth color same palette too.

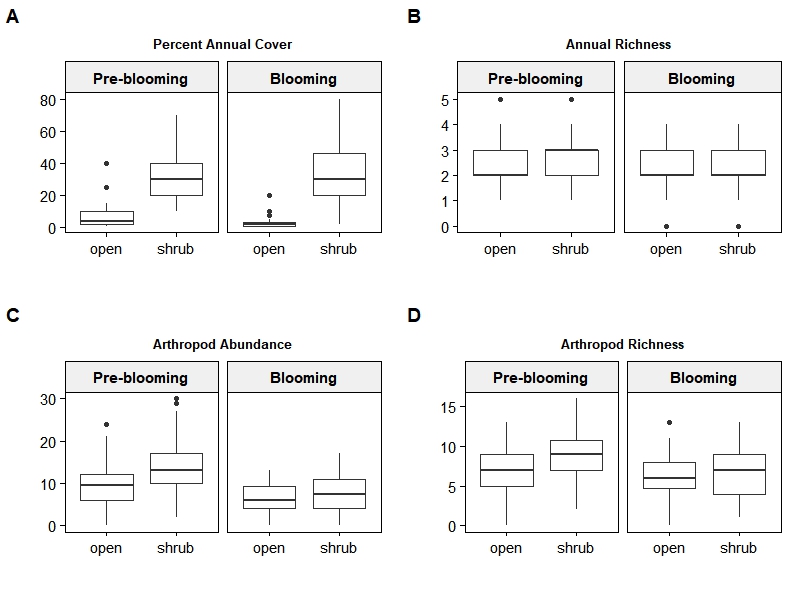


Figure 2: Is still open. Can discuss next week – I don’t really like the veg bloxplots because they seem a bit repetitive of the RII and the third results tables. Could do a conceptual diagram of floral/non-floral pollinator interaction pathways. I like really – so easy to see

Good – like – could also consider using colour to show pre and bloom?

## 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.

Make dots a bit bigger – hard to see and the dots vs solid are really hard to see – try color?

Can you use color on all three?

SO – do you have a figure for each major category of finding

1. Visitation to phyto

2. Pollen dep

3. Community effects

4. net effects that pull it all together into RII?

## Tables

Table 1: Generalized linear mixed model results testing for influences of *L. tridentata* on plant-pollinator interactions of *M. glabrata*.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | | Coeff | χ2 | p |  |  | Coeff | χ2 | p |
| Total flower visits : | |  |  |  | Foraging instances : | |  |  |  |
|  | Microsite (shrub) | -0.3375 | 4.1903 | 0.0407 |  | Microsite | -0.3145 | 4.6621 | 0.0308 |
|  | Blooming (bloom) | -1.7294 | 15.4730 | <0.0001 |  | Blooming | -1.6201 | 10.9910 | 0.0009 |
|  | RTU | NA | 197.0575 | < 0.0001 |  | RTU | NA | 211.6795 | <0.0001 |
|  | *M. glabrata* floral density | 0.0643 | 7.8743 | 0.0050 |  | *M. glabrata* floral density | 0.0521 | 5.7558 | 0.0164 |
|  | RTU\*blooming | NA | 70.0222 | <0.0001 |  | Heterospecific Annual Display Size | 0.0356 | 5.0319 | 0.02488 |
|  | Heterospecific Annual display size | NA | NA | NA |  | RTU\*blooming | NA | 66.1569 | <0.0001 |
| 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 | 1.6201873 | 0.491 | 3.27 | 0.0010 |
| Bombyliidae | 0.04603 | .3886 | 0.118 | 0.9057 | 0.3655708 | 0.366 | 1.003 | 0.3163 |
| Honeybee | 24.9969 | 77838 | 0.000 | 0.9997 | 24.3087556 | 67451 | 0.000 | 0.9997 |
| Lepidoptera | -2.4017 | 1.28900 | -1.862 | 0.0629 | -2.0398717 | 1.08 | -1.884 | 0.0598 |
| Other | -0.0197 | .2403 | -0.082 | 0.9347 | 0.1092906 | 0.212 | 0.514 | 0.6072 |
| Syrphidae | 3.0563 | .3347 | 8.813 | <0.0001 | 3.0599947 | 0.346 | 8.842 | <0.0001 |

Table 3: GLMM results showing community-level effects of *L. tridentata*.

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

Literature Cited

Albrecht, M., M. R. Ramis, and A. Traveset. 2016. Pollinator-mediated impacts of alien invasive plants on the pollination of native plants: the role of spatial scale and distinct behaviour among pollinator guilds. Biological Invasions 18:1801-1812.

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

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

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

Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. BioScience 37:58-67.

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

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

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

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

Braun, J., and C. Lortie. 2018. Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. Perspectives in Plant Ecology, Evolution and Systematics.

Brooker, R., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. Oikos 109:63-70.

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

Bruckman, D., and D. R. Campbell. 2016. Pollination of a native plant changes with distance and density of invasive plants in a simulated biological invasion. Am J Bot 103:1458-1465.

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

Cable, D. R. 1969. Competition in the semidesert grass‐shrub type as influneced by root systems, growth habits, and soil moisture extraction. Ecology 50:27-38.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Gentry, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica:64-68.

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

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

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

Halvorson, W. L., and D. T. Patten. 1975. Productivity and flowering of winter ephemerals in relation to Sonoran Desert shrubs. American Midland Naturalist:311-319.

Heinrich, B., and P. H. Raven. 1972. Energetics and pollination ecology. Science 176:597-602.

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

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

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

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

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

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

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

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

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271-280.

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

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

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

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

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

Michener, C. D. 2000, The bees of the world, v. 1, JHU press.

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

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

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

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

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

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

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

Petit, S., and C. R. Dickson. 2005. Grass-tree (Xanthorrhoea semiplana, Liliaceae) facilitation of the endangered pink-lipped spider orchid (Caladenia syn. Arachnorchis behrii, Orchidaceae) varies in South Australia. Australian Journal of Botany 53:455-464.

Petrů, M., K. Tielbörger, R. Belkin, M. Sternberg, and F. Jeltsch. 2006. Life history variation in an annual plant under two opposing environmental constraints along an aridity gradient. Ecography 29:66-74.

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

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

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

Reitan, T., and A. Nielsen. 2016. Do not divide count data with count data; a story from pollination ecology with implications beyond. PloS one 11:e0149129.

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

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

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

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

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

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

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

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

Schiffers, K., and K. Tielbörger. 2006. Ontogenetic shifts in interactions among annual plants. Journal of Ecology 94:336-341.

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

Sih, A., and M.-S. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. Ecology 68:1679-1690.

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

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

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

Sowig, P. 1989. Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia 78:550-558.

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

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

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

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

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

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

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

Van Der Putten, W. H. 2009. A multitrophic perspective on functioning and evolution of facilitation in plant communities. Journal of Ecology 97:1131-1138.

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

Vockeroth, J. 1992, The flower flies of the subfamily Syrphinae of Canada, Alaska, and Greenland: Diptera, Syrphidae, v. 1867, Agriculture Canada.

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

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

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

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

Brooks, Mollie, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400.

Oksansen, J, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs and Helene Wagner (2018). vegan: Community Ecology Package. R package version 2.5-1. https://CRAN.R-project.org/package=vegan

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Venables, W. N. & Ripley, B. D. (2002) MASS. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Russell V. Lenth (2016). Least-Squares Means: The R Package lsmeans. Journal of Statistical Software, 69(1), 1-33.

Angelo Canty and Brian Ripley (2017). boot: Bootstrap R (S-Plus) Functions. R package version 1.3-20.

## Appendix: Additional and supporting analyses

## 

Table A1: Model comparison using likelihood ratio test (car::Anova) comparing models to null model

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | AIC | ΔAIC | χ2 | p |
| Foraging Instances |  |  |  |  |
| Intercept Only | 1066.0 |  |  |  |
| Additive:  Microsite + blooming | 1000.7 | 65.3 | 69.251 | <0.0001 |
| Interactive:  Microsite \* blooming | 1002.7 | 63.3 | 0.017 | 0.8961 |
| Flowers visited |  |  |  |  |
| Intercept Only | 1164.4 |  |  |  |
| Additive:  Microsite + blooming | 1111.4 | 53 | 56.9782 | <0.0001 |
| Interactive:  Microsite \* blooming | 1113.4 | 51 | 0.0271 | 0.8691 |

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) | -0.3773 | 5.0352 | 0.02483 | -0.3447 | 5.5618 | 0.0184 |
| Blooming (bloom) | -1.2271 | 56.8850 | <0.0001 | -1.22921 | 72.2217 | <0.0001 |
| Flowers.pot | 0.0803 | 8.8120 | 0.00299 | 0.05874 | 6.1351 | 0.0133 |
| Heterospecific Annual Bloom Density | 0.03984 | 2.9200 | 0.0875 | 0.0405 | 4.1772 | 0.0410 |

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.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Foraging bouts | | | Flower Visits | | |
|  | χ2 | Df | p | χ2 | Df | p |
| Blooming (bloom) | 9.7626 | 1 | 0.0018 | 13.4297 | 1 | 0.00025 |
| RTU | 130.6380 | 5 | <0.0001 | 122.2774 | 5 | <0.0001 |
| Microsite (shrub) | 3.5703 | 1 | 0.0588 | 6.5276 | 1 | 0.0106 |
| *M. glabrata* Floral Display Size | 6.9279 | 1 | 0.0085 | 12.0057 | 1 | 0.0005 |
| Heterospecific Annual Bloom Density | 5.9225 | 1 | 0.0150 | 3.0404 | 1 | 0.0812 |
| Heterospecific Blooming Shrub Density | 1.4648 | 1 | 0.2262 | 3.1998 | 1 | 0.0737 |
| Blooming \* RTU | 51.4774 | 5 | <0.0001 | 56.2173 | 5 | <0.0001 |
| Blooming \* Microsite | 2.5109 | 1 | 0.1131 | 3.8934 | 1 | 0.0485 |
| RTU \* Microsite | 3.8084 | 5 | 0.57731 | 5.5265 | 5 | 0.3550 |
| Blooming \* RTU \* Microsite | 4.4364 | 5 | 0.4884 | 8.0131 | 5 | 0.1556 |

## 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 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Metric | Mean RII | Lower CI | Upper CI | N |
| Flowers visited per hour | -0.12170398 | -0.20091973 | -0.05018725 | 114 |
| Arthropod 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 |
| Annual Species Richness | 0.07254366 | -0.20091973 | 0.10632974 | 102 |

Table A6: Summary of calculated RII (relative interaction index) indices for shrub-open comparisons.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Metric | Microsite |  | Mean RII | Lower CI | Upper CI | N |
| Flowers visited per hour | shrub |  | -0.44977898 | -0.5960356 | -0.2779737016 | 57 |
| Flowers visited per hour | open |  | -0.34892797 | -0.5276026 | -0.1422394549 | 55 |
| Percent Annual Cover | shrub |  | -0.02534138 | -0.1142842 | 0.0569258459 | 51 |
| Percent Annual Cover | open |  | -0.30349291 | -0.4098193 | -0.1935318376 | 51 |
| Annual Species Richness | shrub |  | -0.06817043 | -0.1434419 | 0.0005847953 | 51 |
| Annual Species Richness | open |  | -0.05930736 | -0.1411254 | 0.0140259740 | 55 |
| Arthropod abundance (Melyridae excluded) | shrub |  | -0.34849316 | -0.4377806 | -0.2451645921 | 51 |
| Arthropod abundance (Melyridae excluded) | open |  | -0.23281150 | -0.3448487 | -0.1104013715 | 51 |
| Arthropod Richness | shrub |  | -0.20151195 | -0.2849635 | -0.1198198052 | 51 |
| Arthropod Richness | open |  | -0.14259236 | -0.2349986 | -0.0470499509 | 51 |

Table A7: Summary of calculated RII indices for pre-blooming – blooming, split by microsite.



Figure A1: Variation in temperature under the canopy.