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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)

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Short Title:	Trade-offs of shrub-annual facilitation
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Abstract:	In arid ecosystems, shrub facilitation is a critical process driving plant community structure and assembly, often resulting in 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 which intensified into exploitation competition upon blooming. Phenology and life-stage can thus shift the net outcome of association with foundation plant species in facilitation complexes. 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.

1 Facilitation with a grain of salt: disentangling the drivers and trade-offs of

2 pollinator-mediated interactions between the foundation shrub Creosote bush

3 (*Larrea tridentata*) and the annual desert dandelion (*Malacothrix glabrata*).

4 Running title: Trade-offs of shrub-annual facilitation

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

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14 List of all the elements of the manuscript:

15 Article

16 Figures and Tables

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18 Appendix

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22

23 **Abstract**

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25 assembly, often resulting in increased densities of annual plants beneath shrub canopies.

26 Pollinator-mediated interactions have fitness consequences for participants but are largely

27 unexplored as an indirect consequence of shrub-annual facilitation. We tested the capacity of the

28 geographically widespread Creosote bush, *Larrea tridentata,* to influence the pollination of its

29 annual understory during its phenological shift into spring flowering. In this system, we

30 confirmed that *L. tridentata* had a positive ecological effect on annual plant cover. This shrub

31 species also facilitated abundance and richness of the arthropod community but had indirect

32 negative effects on pollinator visitation to a flowering annual plant which intensified into

33 exploitation competition upon blooming. Phenology and life-stage can thus shift the net outcome

34 of association with foundation plant species in facilitation complexes. There is the capacity for

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36 offs will advance both ecological interaction theory and assessment of selection processes that

37 drive co-evolutionary relationships between shrubs, annual plants, and pollinators.

38

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). These positive interactions lead to patterns in species coexistence within plant communities (Valiente- Banuet and Verdú 2007; Brooker et al. 2008) including the frequent association of annuals with shrubs in arid ecosystems (Facelli and Temby 2002; Holzapfel et al. 2006; Pugnaire et al. 2011). 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). These benefits can include stress amelioration (McIntire and Fajardo 2014), improved water and nutrient availability (Franco et al. 1994), and seed trapping (Flores and Jurado 2003). Direct interactions between shrubs and annuals can be simultaneously facilitative and competitive (Bertness and Callaway 1994; Callaway and Walker 1997; Holzapfel and Mahall 1999). 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; Callaway and Walker 1997; Callaway and Pennings 2000). This is important because indirect interactions can significantly influence net ecological outcomes (Wootton 1994)

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

62   increase local pollinator abundances which benefits their less attractive neighbours (Thomson

63   1978; Laverty 1992). Many pollinators forage optimally (Pyke et al. 1977; Pyke 2016), thus co-

64   blooming, associated plants can jointly improve their pollination success by combining their

65   floral displays to increase the size or diversity of the resource pool (Ghazoul 2006). If shrubs

66   concentrate pollinators that do not in turn visit their neighbours, competition or interference

67   rather than facilitation will arise. Similarly, an increase in floral density that is greater than

68   pollinator availability can have a dilution effect decreasing visitation rates (Rathcke 1983; Ye et

69   al. 2013). Simultaneous flowering is not however a necessary condition for plants to interact via

70   pollinators (Hansen et al. 2007; Braun and Lortie 2018). Shrubs are salient features of desert

71   scrub ecosystems due their large size and structural complexity relative to ephemeral plants.

72   Annuals growing under shrubs can be physically obscured from foraging pollinators or shaded

73   thereby reducing pollinator visitation (i.e. through interference). For example, shading by the

74   shrub *Lonicera* decreases pollinator visitation and pollen deposition to its understory annuals

75   (McKinney and Goodell 2010). Alternatively, shrubs can facilitate their annual understory if they

76   provide refuge from harsh conditions to pollinators as they do for other species (Ruttan et al.

77   2016). Consequently, direct and indirect shrub effects on other species function simultaneously

78   to shift net outcomes even within predominantly net positive facilitation complexes.

79   Shifts in net interactions are driven by both biotic and abiotic drivers within a system. The

80   relative importance of net outcomes versus net interactions is a critical concept in the ecological

81   literature for communities (Brooker et al. 2005; Lortie et al. 2016). The context-dependence of

82   species interactions leads to shifts in their strength or sign across gradients, space and time

83   (Chamberlain et al. 2014), as well as across the life stage of the protégé species (Valiente-Banuet

84   et al. 1991; Pugnaire et al. 1996; Callaway and Walker 1997; Rousset and Lepart 2000; Bruno et

4

85   al. 2003). There is evidence that earlier life stages experience higher relative mortality rates

86   (Fenner 1987) and that annuals benefit most from shrub facilitation (Holzapfel and Mahall

87   1999). However, the life stage shift from vegetative growth to reproductive growth is a major

88   event in resource allocation (Bazzaz et al. 1987), and thus reproductive output and fitness

89   consequences are ultimately also important life stages. The life stage of the foundation plant, i.e.

90   flowering, is also critical because a showy floral canopy can potentially change net outcomes for

91   annuals through changes in the pollinator community. Intra-seasonal phenology is thus a

92   component of interactions in tightly coupled plant systems sharing pollinators that must be

93   examined to better examine sensitivity of positive interactions and selection processes that

94   stabilize diversity.

95   The Mojave Desert is a biodiversity hotspot supporting at least 659 species of bees (Saul-

96   Gershenz et al. 2012) and 1680 species of vascular plants (Rundel and Gibson 2005). Despite the

97   celebrated biodiversity of Southwestern Deserts, pollinator-mediated interactions or indirect

98   interactions in general that can influence biodiversity in this region are infrequently studied.

99   Plant-pollinator systems in southwest deserts are home to rare obligate mutualisms such as the

100   Joshua tree *Yucca brevifolia* and Yucca moths (Pellmyr 2003), and the senita cactus *Pachycereus*

101   *schottii* and senita moths (Fleming and Holland 1998) and are often considered highly

102   specialized. The degree of specialization of species in desert ecosystems is a subject of ongoing

103   debate (Chesson et al. 2004). Desert organisms are hypothesized to adapt to high environmental

104   variability by generalizing resource use (Chesson et al. 2004), and this hypothesis has been

105   supported to an extent through pollination network studies (Chacoff et al. 2012). Overall, few

106   one-to-one relationships (i.e. matching between a single species of pollinator with a single

107   species of plant) have been found with solitary bees (Simpson and Neff 1987), and bees still visit

108	even the senita cactus (Holland and Fleming 2002). Despite the high number of specialist

109	pollinators present in the Mojave, most plant species nonetheless interact through pollinators and

110	therefore there is the potential for competition and facilitation between neighbouring plants to

111	occur.

112	The purpose here was to examine both the direct and indirect effects of *Larrea tridentata* on the

113	general success of its annual understory. Single species of plants that are sensitive to

114	environmental variation are called phytometers in the plant sciences (Clements and Goldsmith

115	1924) and have been recommended as a tool to study the relative importance versus intensity of

116	plant-plant interactions as well (Brooker et al. 2005). We used the commonly co-occurring

117	annual *Malacothrix glabrata* as a phytometer to measure variation in pollination services with

118	local environmental context. These species co-flower at beginning and ends of their bloom

119	period (Jennings 2001), and are thus a relevant system to model changes in net interactions

120	within a growing season. We examined the hypothesis that pollinator-mediated interactions

121	between a foundation shrub species and a common annual species shift with phenology and life-

122	stage. The following three predictions were tested: 1) Pollinator visitation rates to a common

123	annual changes with shrub phenology. 2) Conspecific pollen deposition to a common annual

124	varies with distance from the shrub canopy. 3) Shrubs facilitate annuals and arthropods through

125	amelioration benefiting abundance and richness. Understanding interactions for pollination a

126	community level is critical for understanding potential impacts of any decline in pollinator

127	populations. If shrubs tend to facilitate their understory annuals, they will buffer the effects of

128	pollinator declines on the plant community, but if shrubs typically interfere with pollination for

129	annuals, the sensitivity to change for the community increases

Methods

Study site

The primary 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 km^2. 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* (author pers. obs). The secondary study site is located

approximately 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). It is able to maintain

photosynthesis even under high temperatures and low water potentials (Barbour et al. 2007).

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). The full pollinator guild contains 22 specialist pollinators and more than 80 generalists

(Minckley et al. 1999), making it one of the most diverse guilds documented (Wcislo and Cane

1996). The associated guilds are highly variable over space, and most shrubs will only interact

with 20% of their full guild (Cane et al. 2005). *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

153 (Bowers and Dimmitt 1994). It produces copious nectar and pollen rich flowers (Simpson et al.

154 1977) and provides critical resources to pollinators in drought years. *L. tridentata* functions as a

155 benefactor species for other desert perennials such as *Opuntia leptocaulis* (Yeaton 1978),

156 *Peniocereus striatus* (Suzán et al. 1994), and facilitates native annuals (Schafer et al. 2012).

157 <u>Phytometer species</u>

158 We used the desert dandelion *Malacothrix glabrata* (Asteraceae) as a phytometer to measure

159 pollination services. *M. glabrata* is an abundant, native annual wildflower that commonly co-

160 occurs with *L. tridentata*. The flowerheads are dense with yellow corollas and grow up to 40 cm

161 tall (Morhardt and Morhardt, 2004). *M. glabrata* is insect-pollinated including bees in the genera

162 *Nomadopsis* (Rutowski and Alcock 1980) and *Anthidium* (Wainwright 1978) as well as short-

163 winged flower beetles of the family *Kateretidae* (Cline and Audisio 2010). Several of the 24

164 species of *Malacothrix* are self-compatible (Davis and Philbrick 1986), however the reproductive

165 biology of *M. glabrata* has not been studied in detail

166 <u>Study design</u>

167 A total of 60 *L. tridentata* shrubs with developed floral buds and minimal perennial understory

168 were chosen evenly distributed across the primary study site (mean shrub width: 336 cm, mean

169 height: 209 cm). Paired shrub-open microsites were selected inside the dripline of the focal shrub

170 and a minimum of 1.5 m away in an open area respectively. Both microsites were sampled on the

171 south side of the shrub to minimize shading and were paired to minimize variation due to

172 environmental heterogeneity. To separate floral and non-floral interaction pathways, interactions

173 were tested prior to focal shrubs blooming and repeated using the same shrubs after they had

174 entered into full bloom. Shrubs with fewer than five open blooms were considered non-blooming

175 ("pre-blooming"). The mean number of blooms per shrub of the 'blooming' treatment was 300.2

176   (min: 102, max: 1080). The repeated-measures study design was chosen to measure relative

177   changes in interactions with natural shrub phenology and to reduce between shrub variability. In

178   two cases, a focal shrub did not bloom within the study period and was replaced by a different

179   blooming shrub.

180   <u>Visitation and Pollen Deposition</u>

181   *M. glabrata* were gathered freshly each morning from nearby (< 3 km) populations where they

182   seasonally coexist with *L. tridentata.* These plants were transplanted into 15 cm diameter black

183   pots and one pot was placed at each microsite for a total of six shrub/open pairs per day

184   Conspecific floral density influences pollinator visitation (Bosch and Waser 200). Therefore,

185   transplants of similar size, floral number and habit were paired between paired microsites, but

186   left to vary between replicates. The mean number of flowers per pot was 10 (min 6, max 20)

187   Polaroid Cube+ HD video cameras (1080p) were used to record pollinator activity to each potted

188   *M. glabrata*. Visitations were recorded from 11:30 am to 4:00 pm (mean length: 1:19 hr:min)

189   The use of video technology allows for higher temporal resolution and replication beyond what

190   is possible using traditional *in situ* observations (Lortie et al. 2012). Ten days of pre-blooming

191   trials (60 shrub/open pairs) were conducted between April 10 and April 20, and ten days of

192   blooming trials (60 shrub/open pairs) were recorded between April 21 and May 2. To test for any

193   influence of naturally co-occurring annuals and blooming shrubs, heterospecific annual floral

194   density was measured within a 0.25 m^2 quadrat in each microsite with the phytometer in the

195   center of each plot, and the number of heterospecific shrubs in bloom were counted within a 2 m

196   radius of each microsite. The number of open flowers for each *L. tridentata* shrub were counted

197   at the same time.

198   Plant-pollinator interactions were estimated using the timestamps of the video. Only insect

199   visitors that flew on and touched the open side of the flower were considered in these analyses. A

200   foraging instance was measured between initial floral contact and when the visitor departed from

201   physical contact of the final flower and left the field of view. Foraging duration thus included

202   flower-to-flower travel time on the same plant and multiple flowers could be visited during one

203   foraging instance. Total floral visitation was coded as the sum of flower visits made by insects

204   per video replicate. Proportion of flowers visited is the number of unique flowers visited per

205   foraging instance divided by the number of flowers in the field of vision. Floral visitors were

206   identified to recognizable taxonomic units (RTU) including the following categories: honeybees,

207   solitary bees, Lepidoptera, syrphid flies, bombyliid flies and other, which was comprised

208   primarily of small beetles and muscoid flies. A total of five videos were omitted due to

209   disturbance or battery failure (n = 235 videos).

210   To quantify the influence of proximity to *L. tridentata* on pollen deposition, stigma were excised

211   from *M. glabrata* at the nearby secondary site using a naturally occurring, co-blooming

212   population of *M. glabrata* and *L. tridentata* between April 31st and May 2nd, 2017. Three stigma

213   from each of three flowers per *M. glabrata* (nine stigma per plant) growing under the dripline

214   and in nearby open areas were collected generating a total of 298 stigma from 13 shrub/open

215   pairs. Distance to the nearest *L. tridentata* and three nearest *M. glabrata* neighbours were also

216   recorded, and the number of *M. glabrata* flowers per plant was counted. The stigmas were stored

217   individually in micro-centrifuge tubes filled with denatured alcohol. The tubes were spun down

218   in a centrifuge at 4200 rpm for 4.5 minutes and the pellet pipetted onto the slide. This along with

219   the stigma were mounted in fuchsin jelly (Kearns and Inouye 1993). At 100 x magnification, 10

220   longitudinal transects (18 mm long) of pollen in addition to the stigma were counted per slide.

221 Heterospecific pollen grains were imaged using a Canon 60D SLR with 60mm macro lens into

222 microscope afocally.

223 <u>Community-level effects of *L. tridentata*</u>

224 The arthropod communities were sampled to provide an estimate of pollinator availability for

225 each microsite and to assess if *L. tridentata* acts as a foundation species for other taxa at the

226 primary site. Yellow, white, and blue coloured six-inch diameter plastic bowls filled with water

227 with a few drops of dish detergent added to sample via pan trapping. Each study day, pan traps

228 were set out by 10 am and collected by 5:30 pm. Arrays of three pan traps were deployed in a

229 triangular shape at each microsite, marginally embedded in the ground to prevent disturbance.

230 Total percent vegetation cover (a proxy for annual biomass) and annual species richness were

231 recorded within a 0.25 m^2 quadrat when the traps were laid out. Arthropod sampling was

232 conducted within two days of the video test but never on the same day to avoid influencing

233 visitation. Nine days (54 shrub/open pairs) of sampling were completed before blooming, and 10

234 days (60 shrub/open pairs) during full bloom.

235 Bees and syrphid flies were identified to species or genus (Michener et al. 1994; Michener 2000;

236 Miranda et al. 2013; Ascher and Pickering 2015). The majority of remaining individuals was

237 identified to at least the taxonomic resolution of family (Teskey et al. 1981; Grissell and Schauff

238 1990; Triplehorn and Johnson 2005; Marshall 2012), except Thysanoptera, Orthoptera and

239 Arachnida which were resolved to order. Recognizable taxonomic unit (RTU) is a suitable

240 approximation of traditional species richness (Oliver and Beattie 1993). Using RTU limits

241 resolution compared with species-level identification, however many desert insect species have

242 not been described and furthermore useful keys are often lacking. This method of categorizing

243 diversity was a trade-off between maximizing resolution and speed given the high diversity of

244 desert species. Related groups may be identified to different levels. E.g. wasps in the genus

245 *Miscophus* and subfamily *Pemphredoninae* are both within the family *Crabronidae*. No

246 individuals were double counted, and these groups were considered distinct, exclusive RTUs for

247 diversity analyses. Nymphs were included in abundance analyses provided they could be

248 identified at least to taxonomic order. Hemipteran nymphs that could not be identified to family

249 were aggregated for diversity analyses. Mites (Acari) and springtails (Collembola) were

250 excluded from all analyses due to biases in collection methods. The full dataset of 119 RTU

251 archived online (links are available from the journal office). All physical specimens are archived

252 at *redacted*.

253 To determine which pollinator species visited *L. tridentata* flowers during the study period, 15-

254 minute *in-situ* observation periods were completed at up to 6 shrubs per day for 10 days when

255 blooming (14.5 hours) at the primary study site. The same focal shrubs were observed but on

256 different days than pan trap sampling and video trials. Due to the large size of the shrubs, it was

257 not possible to accurately track flower visits per foraging instance, therefore only the frequency

258 of foraging instances was recorded. The identity and behaviour of the visitors were recorded and

259 voucher insects were collected to facilitate identification.

260 To assess the influence of *L. tridentata* on microclimate, a total of 16 HOBO pendant data

261 loggers were used to record micro-environmental conditions. Ground level temperature and light

262 availability were recorded every 30 minutes between March 19th and May 14th, 2017 at eight

263 microsite pairs. Daytime (9am to 9pm) and nighttime (9pm to 9am) averages and daily

264 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 (links are available from the 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 et al. 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). 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 et al. 2009).

Interactive, additive, and intercept only models were compared by AIC and likelihood ratio tests

with $\chi 2$ 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

287 variables. Least-squares *post hoc* tests (lsmeans, Russel 2016) were used on any significant

288 interactions and the individual microsite was included as a random effect.

289 To test for the influence of proximity to *L. tridentata* on pollen deposition to *M. glabrata*,

290 quasipoisson models (glmmPQL, MASS) were fit with conspecific and heterospecific pollen

291 deposition as response variables. Distance to *L. tridentata*, distance to the nearest conspecific

292 neighbour and the number of *M. glabrata* flowers were modeled as predictors. The sample ID

293 nested in the flower ID nested in the plant was included as a random effect to account for the

294 within plant correlation structure.

295 <u>Shrub effects on the local community</u>

296 GLMMs (glmmTMB) were used to test for shrub effects on the local community (negative

297 binomial: arthropod abundance, percent annual cover, annual species richness, annual bloom

298 density, bee richness, poisson: arthropod species richness and bee abundance). Beetles from the

299 family *Melyridae* comprised 1248 of the 3384 total arthropods captured, therefore abundance

300 models were fit with *Melyridae* excluded, included and individually to explore model

301 sensitivities. Least-squares *post hoc* tests (lsmeans) were used on significant interactions, and the

302 individual microsite was included as a random effect to control for repeated measures.

303 To explore if *L. tridentata* individuals with more flowers were more attractive to pollinators, a

304 quasipoisson GLM (glm) with visitation rates as the response and flower number and height as

305 predictors. To test for the capacity of *L. tridentata* to create stable microclimates beneath the

306 canopy, Gamma GLMMs (glmmTMB) were fit using microsite as a predictor and mean daytime

307 temperature, mean nighttime temperatures, and daily temperature variance as response variables.

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

Ecological effect sizes

310 To compare the ecological effect of shrubs and blooming on five community response metrics

311 (hourly floral visitation of *M. glabrata*, arthropod abundance, arthropod species richness, percent

312 annual cover and annual species richness), and to estimate the biological importance of

313 statistically significant differences the effect size estimate Relative Interaction Index (RII) was

314 calculated (Armas et al., 2004). The equation: $RII = \frac{treatment - control}{treatment + control}$ was used. Treatments

315 were shrub microsite or blooming, while the controls were open microsite or pre-blooming. Only

316 paired microsites in the data were used to calculate effect sizes. This measure ranges from −1 to

317 +1, is symmetric around 0, and negative values indicate relative competition whilst positives

318 indicate facilitation (Armas et al., 2004). To determine if the effect was significantly different

319 from 0, 95% confidence intervals around mean values were bootstrapped (package boot, Canty

320 and Riply 2017) and stratified by the focal shrub ID to account for the repeated measures study

321 design. Only matched microsites were used for these calculations.

322 **Results**

323 Shrub effects on pollinator visitation to phytometer species

324 A total of 697 flying insects visited 925 flowers (hereafter "pollinators") to *M. glabrata* in 303

325 hours of video recording. No pollinators were observed in 61 of the 235 video observation

326 periods. Foraging instance frequency and total floral visitation by pollinators to *M. glabrata* were

327 significantly lower at the shrub microsite relative to open areas pre-blooming and were further

328 reduced at both microsites when *L. tridentata* entered full bloom (Table 1, A2). There was a

329 positive effect of *M. glabrata* floral display size on both the frequency of foraging instances and

330 floral visitation (Table 1). There was a significant, positive effect of heterospecific annual floral

331 density on the frequency of foraging instances (Table 1, A2) but not to total flowers visited. The

332　influence of heterospecific blooming shrub density on foraging instance frequency was not

333　statistically significant (Table A3) and was not included from the final models. Pollinator

334　foraging duration was shorter when *L. tridentata* was blooming and did not differ between the

335　microsites (Table 1). The proportion of flowers visited per foraging instance was positively

336　influenced by the size of *M. glabrata* floral display but otherwise did not differ between

337　microsites or shrub blooming stage (Table 1).

338　The frequency of foraging instances and flower visits by Syrphids and solitary bees declined

339　significantly with shrub blooming (Table 2). There was no significant difference between RTU

340　visiting the microsites nor were there significant interactions between RTU, microsite, and

341　blooming on the total flowers visited or frequency of foraging instances (Table A4). Floral

342　visitation rates (flowers/hr) were significantly correlated between paired shrub/open microsites

343　(Pearson's = 0.262, t = 2.8708, df = 112, p-value = 0.004898).

344　<u>Shrub effects on pollen deposition to natural population of *M. glabrata*</u>

345　A total of 16209 grains of conspecific pollen and 1719 of heterospecific grains were recorded on

346　*M. glabrata* stigma. At the nearer site, there was no significant influence of proximity to *L.*

347　*tridentata* (GLMM, $\chi2$= 0.3099, p = 0.5777), nearest conspecific plant (GLMM, $\chi2$= 2.3299, p =

348　0.1269) or the number of conspecific flowers on conspecific pollen deposition (GLMM, $\chi2$=

349　0.6290, p = 0.4277). Heterospecific pollen deposition increased significantly with distance from

350　*L. tridentata* (GLMM, $\chi2$= 5.8389, p = 0.0157), but there was no influence of nearest conspecific

351　(GLMM, $\chi2$= 0.1082, p = 0.7422) or floral number (GLMM, $\chi2$= 1.8422, p = 0.1747).

352　Conspecific and heterospecific pollen deposition were significantly correlated (Pearson's = 0.15,

353　t = 2.397, df = 229, p = 0.01).

354 <u>Shrub effects on plant community</u>

355 A total of 3384 arthropods spanning 118 taxonomic groups were caught in 19 days of pan

356 trapping. Arthropod abundance (Melyridae excluded) and richness were higher in the shrub

357 microsite and both decreased with shrub blooming (Table 3). Arthropod abundance (Melyridae

358 excluded) was significantly correlated between paired shrub/open microsites (Pearson's = 0.46, p

359 < 0.001). Melyridae beetle abundance was significantly lower at the shrub microsites, and

360 decreased with blooming at the open microsite only (Table A7). A total of 144 bees were

361 captured in pan traps comprising 22 taxonomic groups. Bee abundance and richness were

362 consistent between all treatments (Table 3).

363 Percent cover of ground vegetation was significantly higher in shrub microsites, and declined

364 with shrub blooming in open areas only (Table 3). Heterospecific annual floral density did not

365 differ between shrub and open microsites, also declined with shrub blooming (Table 3). There

366 was no significant difference in annual species richness between any of the treatments (Table 3).

367 Shrubs exerted a competitive effect (RII < 0) on hourly floral visitation rates to *M. glabrata* and

368 a facilitative effect (RII > 0) on arthropod abundance, arthropod species richness, and annual

369 percent cover (Figure 3A, Appendix 1000). Negative effects (RII < 0) were observed for most

370 community metrics within individual microsites however percent cover at the shrub microsite's

371 interaction index was 0 (Figure 3B).

372 Pollinator visitation to *L. tridentata* increased with floral abundance of the shrub canopy (Figure

373 2, GLM: Est: 0.0013408, $\chi2$: 4.6383, p = 0.02283). Floral abundance and shrub height (Pearson's

374 = 0.335, t = 2.6659, df = 56, p = 0.01002) were correlated, however height was not a significant

375 predictor of pollinator visitation (GLM: Est: 0.0054, $\chi2$: 3.6066, p = 0.061). *L. tridentata*

376 received 197 floral visit over 14.5 hours of observations. Of 169 visits made by bees, *Apis*

377   *mellifera* was the most frequent visitor (32%), followed by *Centris* sp. (21%), *Hesperapis sp.*

378   (18%) and *Megandrena enceliae* (7%) and other solitary bees (23%) including *Hoplitis* and

379   *Megachile*.

380   Mean daytime temperatures were significantly lower (Figure 3, χ^2:84.959, p <0.0001), and mean

381   nighttime temperatures were significantly higher under the shrub canopy (χ^2: 49.635, p

382   <0.0001). Overall temperature variation was significantly lower in the shrub microsites (χ^2:

383   519.9, p <0.0001).

384   **Discussion**

385   Foundation species are critical in structuring desert plant communities; however, we cannot

386   assume that all effects of foundation species are universally positive. Net interaction theory

387   proposes that both positive and negative interactions are common in most interactions between

388   different species in a system (Callaway and Walker 1997; Holzapfel and Mahall 1999; Maestre

389   et al. 2003; Graff et al. 2007). We hypothesized that facilitated annuals would experience a shift

390   in their pollination mediated through the flowering of their beneficiary shrub. *L. tridentata*

391   interfered with the pollination of the representative phytometer species *M. glabrata*. The

392   phenological shift into blooming by *L. tridentata* intensified the negative interaction with the

393   development of exploitation competition with *M. glabrata* at both microsites rather than shifting

394   net relative outcomes into facilitation via the magnet species effect. This study nonetheless

395   confirmed the general role of the desert shrub *L. tridentata* as a foundation species in this system

396   through its positive effects on annual plants and arthropod communities, and through its ability

397   to stabilize microclimates. We also found evidence of positive indirect interactions between *M.*

398   *glabrata* and other flowering heterospecific annuals. Pollinator-mediated facilitation has not

399   previously been documented in any desert ecosystem globally (Braun and Lortie, 2018). Positive

400   effects were concurrent with negative effects; therefore, reproductive outcomes and indirect

401   interactions can be pivotal to shrub-facilitation complexes in deserts.

402   Plants that employ a cornucopian flowering strategy produce abundant floral resources over an

403   extended period of time and can attract a wide range of pollinators to the localized area (Mosquin

404   1971; Gentry 1974). Pollinators showed a behavioural response to the increased floral resources

405   of the foundation species *L. tridentata* thereby decreasing overall visitation and visit duration to

406   the phytometer *M. glabrata*. When choosing between resources, bees commonly stay for a few

407   visits before leaving to the superior resource (Sowig 1989) with larger floral displays (Bosch and

408   Waser 2001) or richer rewards (Robertson et al. 1999) because it improves their foraging

409   efficiency. Feral honeybees, *Apis mellifera,* were the most frequent floral visitors to *L. tridentata*

410   but only visited *M. glabrata* prior to *L. tridentata* blooming. Honeybees prefer larger floral

411   patches (Sih and Baltus 1987) and exhibit floral constancy; the facultative specialization on

412   different flower species at different times by individuals (Waser 1986) and this foraging

413   behaviour likely contributed to the outcomes observed. Facilitation via honeybees and solitary

414   bees has been documented in previous studies (Albrecht et al. 2016; Bruckman and Campbell

415   2016), however in most cases, the magnet plant does not offer such disproportionately abundant

416   resources. In the alpine, similar exploitation competition of spring annuals by later-blooming

417   resource-rich cornucopia plants has contributed to phenological divergence (Mosquin

418   1971)Mosquin 1971). Over the study period, additional foundation species including

419   *Acamptopappus sphaerocephalus*, *Opuntia sp*. and *Ericameria cooperi* entered into bloom

420   alongside *L. tridentata* while annual floral density decreased. This is a consistent shift

421   throughout Southwestern Deserts (Cable 1969; Halvorson and Patten 1975; Jennings 2001). The

422 cornucopia flowering strategy by benefactors can introduce directional selection in the protégé

423 species to flower sooner to avoid competition in desert shrub-annual facilitation systems.

424 Phenology is a critical mediator of net outcomes between multiple trophic levels. Interactions

425 even in relatively short growing season systems can shift depending on life-stage and timing.

426 Despite the interference by the canopy for pollinator visitation, we found no influence of

427 proximity to *L. tridentata* on conspecific pollen deposition but did not test how deposition

428 changes with phenology. Generally, the relative effect of blooming i.e. the temporal shift was

429 greater in annual and arthropod communities than the effect of spatial association with *L.*

430 *tridentata*. The majority of research on plant-plant interactions focuses on a single life stage or a

431 single measurement (Tielbörger and Kadmon 2000; Goldberg et al. 2001). These singular foci

432 are inadequate for estimating fitness levels within plant populations (McPeek and Peckarsky

433 1998). Substantial within-season changes to the intensity of facilitation and competition between

434 shrubs and annuals have been documented in both the Mojave Desert (Holzapfel and Mahall

435 1999) and the Negev (Schiffers and Tielbörger 2006). Foundation species provide a complex

436 suite of mechanisms to facilitate but also interact with plant and arthropod communities more

437 richly and we need to better describe the diversity of these concurrent interactions.

438 Mechanisms extending through insect communities can come into play treating shrubs as a key

439 interactor in deserts – for instance pollinators can also interact with one another at these floral

440 islands. *Eupeodes volucris* (Diptera: Syrphidae) was the most frequent floral visitor to *M.*

441 *glabrata*. However, *E. volucris* did not switch despite being known to visit *L. tridentata* (Hurd Jr

442 and Linsley 1975). The additional bees attracted by *L. tridentata* may have competitively

443 excluded Syrphids from the immediate area. Competition between syrphids and other pollinators

444 is understudied (Inouye et al. 2015), but competition between bee species is better known.

445   *Centris* sp. bees were frequent visitors to *L. tridentata* flowers during this study. They are

446   territorial and are known to chase away other bees from shrubs (Alcock et al. 1977). Similarly,

447   honeybees can reduce visitation by solitary bees (Shavit et al. 2009) through competitive

448   displacement (Cane and Tepedino 2017). Alternatively, syrphid visitation may have declined due

449   to changes in local abundances particularly if their phenology is linked with annuals. *E. volucris*

450   is multivoltine (Vockeroth 1992), but the phenology of *E. volucris* in desert systems has not been

451   studied. Larval *E. volucris* are aphid predators and their phenology appears to be tied to prey

452   availability rather than floral resource availability (Noma and Brewer 2008; Iler et al. 2013). This

453   suggests the influence of indirect shrub effects can be mediated through pollinator-pollinator

454   interactions. This is a novel mechanism of pollinator-mediated competition in arid ecosystems

455   that has the potential to be widespread and should be examined directly through observational

456   studies of co-occurrence between pollinator guilds to focal plant species.

457   In this study, facilitation in germination and early growth came at a potential net fitness cost via

458   competition for pollination during reproductive life stages. Life-stage dependent tradeoffs within

459   nurse-protégé associations between perennials are well documented with facilitation in early life

460   shifting to resource competition or parasitism later in life (Yeaton 1978; Valiente-Banuet et al.

461   1991). Trade-offs between animal-mediated indirect interactions can be life-stage specific. For

462   example, thorny plants can facilitate other species in germination but negatively impact at later

463   life stages through decoy effects that deflect herbivores towards the protégé species it facilitated

464   (Van Der Putten 2009). Grass-tree (*Xanthorrhoea semiplana*) facilitates the pink-lipped spider

465   orchid (*Caladenia syn. Arachnorchis behrii*) by protecting it from herbivores but then reduces

466   pollination services through non-floral interference (Petit and Dickson 2005). To our knowledge,

467   our study is the first demonstration of a benefactor flowering plant engaging in exploitation

468   competition with its protégés for pollinators. In arid environments, annuals invest more into

469   reproduction than growth (Petrů et al. 2006) and are often found concentrated under shrubs

470   (Facelli and Temby 2002). Therefore, germination-pollination tradeoffs should be common

471   within plant communities in desert ecosystems. To quantify the net effects of facilitation, it is

472   necessary to consider fitness alongside density effects (Tielbörger and Kadmon 2000) because of

473   the potential for this to influence long-term coexistence and stability. Here, we show two

474   mechanistic pathways for a foundation species to facilitate density while decreasing fitness

475   indirectly through effects on pollination. The extent of these tradeoffs is likely underestimated in

476   arid environments and important for structuring desert communities.

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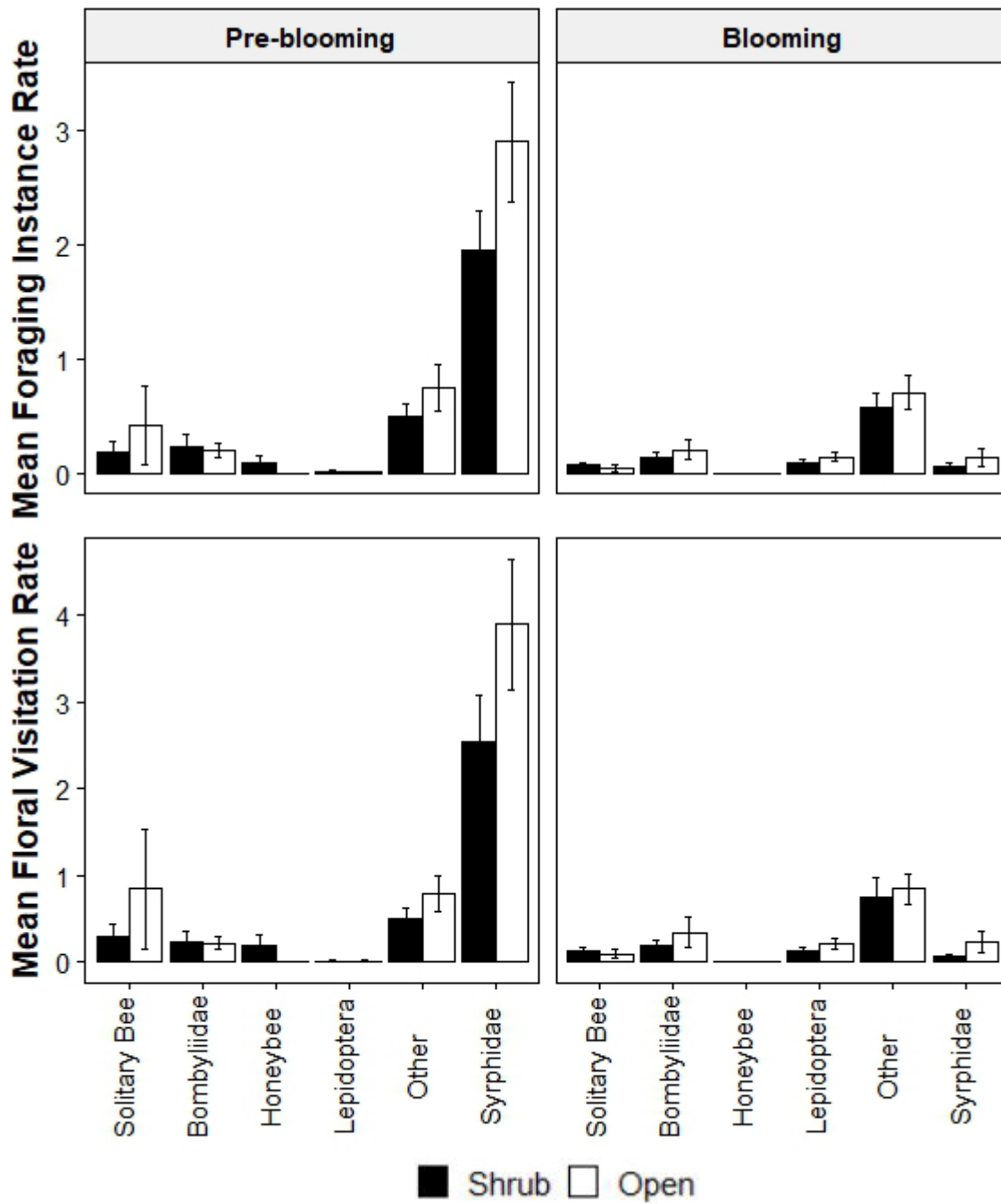
495 Figure 1: Mean foraging instance and flower visitation hourly rates (±SE) to desert dandelion *M.*
496 *glabrata* by each RTU (recognizable taxonomic unit) considered in this study.

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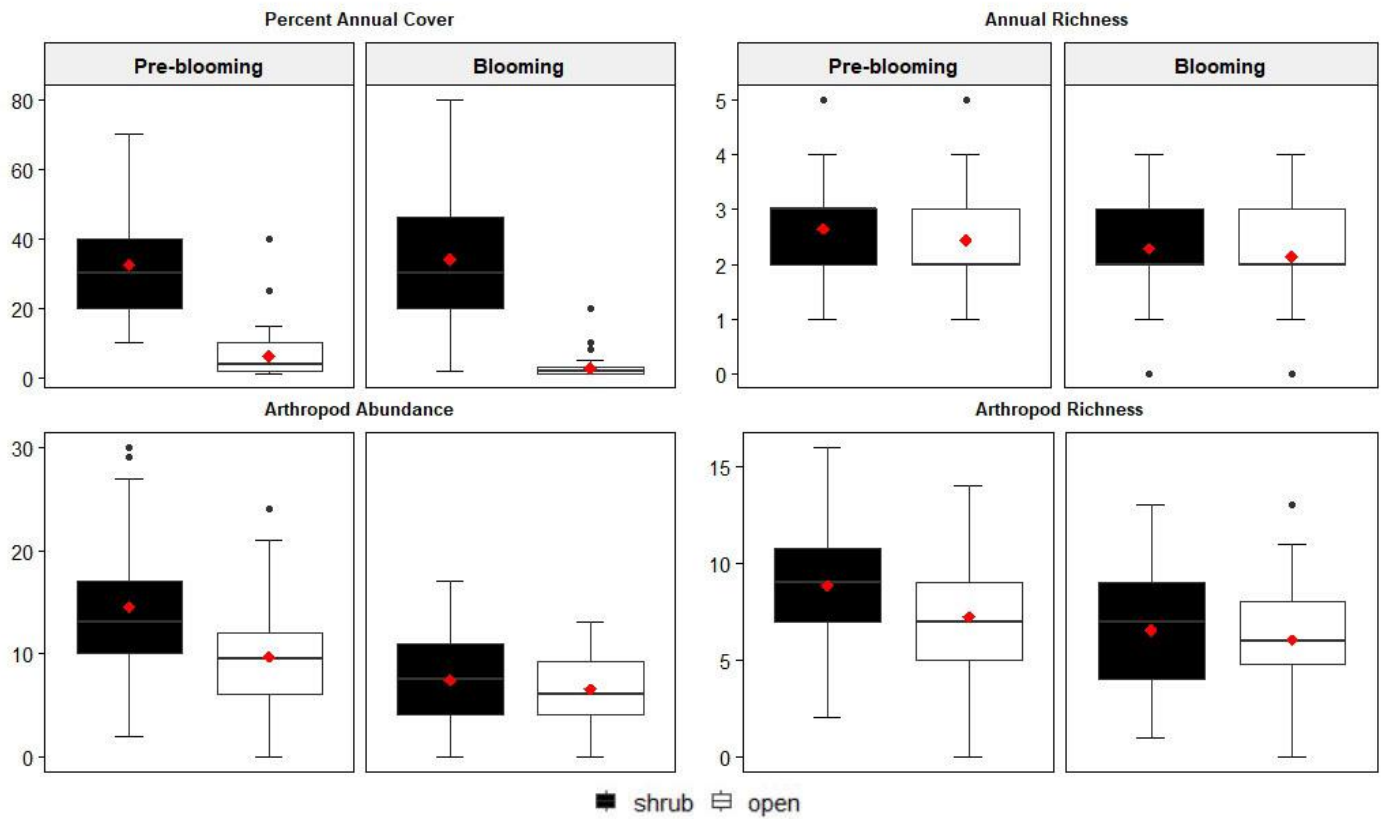
Figure 2: Shrub effects on arthropod and annual communities for each microsite and shrub blooming stage. Mean is indicated with a red diamond.

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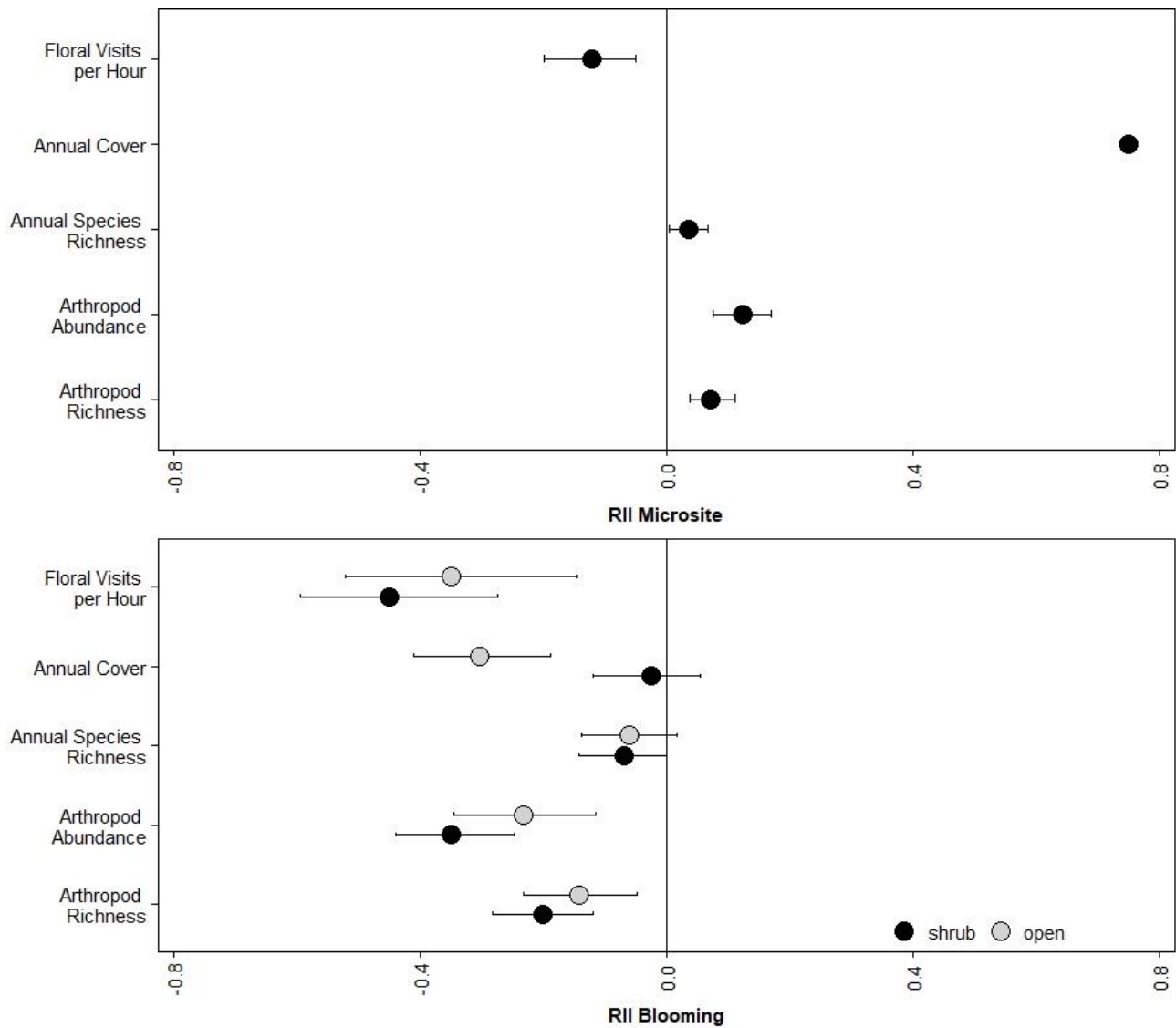
505   Figure 3: Relative Interaction Index (RII) values for five community interaction metrics among

506   two treatments: microsite (Shrub – Open) and blooming (Pre-Blooming – Blooming). Values

507   shown are means ± 95% bootstrapped confidence intervals. Values greater than zero indicate

508   positive effects, while values that are significantly lower than zero indicate negative effects.

509   Values that are not significantly different from zero are neutral.

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

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	Coeff	χ^2	p		Coeff	χ^2	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

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520　Table 2: Post-hoc least squares contrasts of significant RTU * blooming interactions from
521　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

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533 Table 3: GLMM results showing community-level effects of *L. tridentata*.
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	Coeff	χ^2	p		Coeff	χ^2	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 Abundance[b]				Bee Richness[b]			
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 Richness[b]			
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

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537   Note: a Melyridae excluded

538   b model showed no improvement over intercept only model

539   c results from posthoc in table A4

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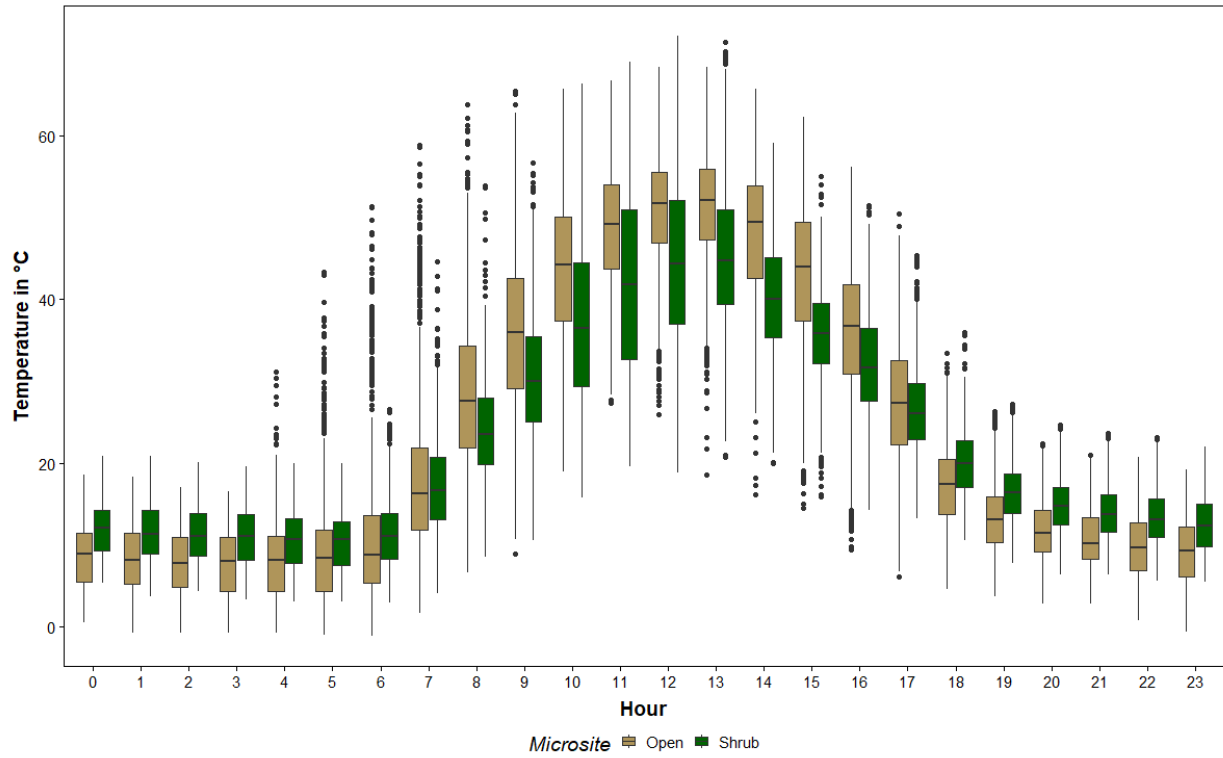**Appendix: Additional and supporting analyses**

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811   Figure A1: Variation in temperature under the canopy.

812   Table A1: Model comparison using likelihood ratio test (car::Anova) comparing models to null
813   model
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Model	AIC	ΔAIC	χ^2	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

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816 Table A2: Results from negative binomial generalized linear mixed models (glmmTMB) testing
817 for differences in the frequency of pollinator floral visits and foraging bouts in response to
818 microsite (shrub and open) and blooming stage (pre-blooming and full bloom). Non-species
819 specific

	Total flower visits			Foraging bouts		
	Coeff	χ^2	p	Coeff	χ^2	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

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821 Table A3: Full models with RTU-specificity. Quasipoisson GLMM (glmmPQL, MASS) with
822 three-way interaction term for RTU*blooming*microsite. This output from Wald's Type 3 test.
823 Total flower visits and foraging bouts as response. Rep ID as random effect.
824

	Foraging bouts			Flower Visits		
	χ^2	Df	p	χ^2	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

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Sensitivity of arthropod community models

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

	Insect abundance (Melyridae: included)			Melyridae: abundance only		
	Coef	χ^2	p	Coef	χ^2	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

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831 Table A5: Post-hoc contrasts interaction for abundance (Melyridae only) for microsite by
832 Blooming (lsmeans).
833

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

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RII Summary Calculations

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

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

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

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