

# Current Research in Insect Science

## Shrubs as magnets for pollination: a test of facilitation and reciprocity in an established shrub-annual system --Manuscript Draft--

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<b>Abstract:</b>	<p>The magnet hypothesis proposes that flowering plants that are attractive to pollinators can increase the relative pollination rates of neighbouring plants by acting as a 'magnet'. Here, we test the hypothesis that an animal-pollinated shrub species, <i>Larrea tridentata</i>, and a wind-pollinated shrub species, <i>Ambrosia dumosa</i>, act as magnets for the pollination of understory annual plant species. As a novel extension to the magnet hypothesis, we propose the double magnet hypothesis in which we further test for reciprocity by the floral island created in the understory of the benefactor shrubs as an additional pollinator magnet for the shrub itself. We measured pollinator visitation and visit duration using video and in-situ observation techniques to test whether shrubs increase pollinator visitation to understory annual plants, if animal-pollinated shrubs act as better pollinator magnets than wind-pollinated shrubs, and whether shrubs with annuals in their understory have higher pollinator visitation rates relative to shrubs without annuals. We found evidence that animal-pollinated shrubs increase the visitation rate and duration of visits by pollinators to their understory plants and that wind-pollinated shrubs decrease the duration of visits of some insect visitors, but these relationships vary between years. While the presence of annuals did not change the visitation rate of pollinators to <i>L. tridentata</i> flowers, they did decrease the visitation duration of bees, indicating a negative reciprocal effect of the understory on pollination. Thus, the concentrated floral resources of flowers on animal-pollinated shrubs can act as a magnet that attract pollinators but that in turn provide a cost to pollination of the shrub. However, while wind-pollinated shrubs may provide other benefits, they may provide a cost to the pollination of their understory. These findings support the magnet hypothesis as an additional mechanism of facilitation by animal-pollinated shrubs to other plant species within arid ecosystems.</p>
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Current Research in Insect Sciences is an open access journal which charges an Article Publishing Charge (APC) to cover the cost associated with the publication process. All articles published Open Access will be immediately and permanently free on ScienceDirect for users to read, download, and use in accordance with the author's selected Creative Commons user license. The APC can be found on the open access page of the Journal Homepage. As an introductory offer, you will not have to pay the APC when your article has been submitted before 31st December 2020. This is a compulsory checkbox, so you can complete your submission. We will waive the APC after acceptance of your article.	As an Author, I acknowledge I need to pay the Article Publishing Charge if my manuscript is accepted for publication
Briefly describe the key finding or conclusion of your work (If a Methods Reports article: what does it allow you to measure?; If a Graphical Review article: what is the topic?)	Shrubs can act as pollinator magnets for their annual plant understory; however, this effect varies between years. Additionally, we found limited evidence that wind-pollinated shrubs may reduce pollination. Facilitation of annuals also comes at a cost to animal-pollinated shrubs via reduced pollination.
Why is this novel/ exciting/ of value to your sub-discipline?	This work increases the body of literature that tests the magnet hypothesis while uniquely adding both the concept of a non-flowering plant as a possible pollinator magnet and a first test of the double-magnet hypothesis. This work also significantly advances facilitation theory in deserts by adding pollination facilitation as an additional mechanism.

<p>Why is it of interest to a broad community of insect scientists?</p>	<p>We are confident that this is a novel synthesis ideal for Current Research in Insect Science because it examines the function of plants as insect attractants both in terms of floral resources and possible refuge or habitat. We further show how foundation species such as shrubs not only impact other plants, but also influence insect choice and foraging.</p>
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Editorial Board  
Current Research in Insect Science

Dear Editors,

We are submitting an original research paper entitled “Shrubs as magnets for pollination: a test of facilitation and reciprocity in an established shrub-annual system” by Ally Ruttan, Christopher Lortie, and Stephanie Haas. We examine shrubs as magnet species for pollination and the propose the double magnet hypothesis in which the floral understory of shrubs in turn act as magnets for pollinators.

Shrubs commonly facilitate desert annuals and animals in a variety of ways; however, the question of whether shrubs can increase the pollination of their understory has not yet been answered. In this study we examine the effects of both an insect-pollinated shrub and wind-pollinated shrub on the pollinator visitation and visit duration to an annual insect-pollinated phytometer species. Additionally, we examined the bidirectional effect of flowering annuals on the pollination of an animal-pollinated shrub. This work increases the body of literature that tests the magnet hypothesis while uniquely adding both the concept of a non-flowering plant as a possible pollinator magnet and a first test of the double-magnet hypothesis. This work also significantly advances facilitation theory in deserts by adding pollination facilitation as an additional mechanism. We are confident that this is a novel synthesis ideal for Current Research in Insect Science because it examines the function of plants as insect attractants both in terms of floral resources and possible refuge or habitat. We further show how foundation species such as shrubs not only impact other plants, but also influence insect choice and foraging.

This study has not been published or submitted elsewhere. We confirm that all authors have read and approved the manuscript and have no conflicts of interest to disclose.

Thank you for your consideration,

Steph Haas, Christopher Lortie, and Ally Ruttan

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# **Shrubs as magnets for pollination: a test of facilitation and reciprocity in an established shrub-annual system**

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## Abstract

The magnet hypothesis proposes that flowering plants that are attractive to pollinators can increase the relative pollination rates of neighbouring plants by acting as a ‘magnet’. Here, we test the hypothesis that an animal-pollinated shrub species, *Larrea tridentata*, and a wind-pollinated shrub species, *Ambrosia dumosa*, act as magnets for the pollination of understory annual plant species. As a novel extension to the magnet hypothesis, we propose the double magnet hypothesis in which we further test for reciprocity by the floral island created in the understory of the benefactor shrubs as an additional pollinator magnet for the shrub itself. We measured pollinator visitation and visit duration using video and *in-situ* observation techniques to test whether shrubs increase pollinator visitation to understory annual plants, if animal-pollinated shrubs act as better pollinator magnets than wind-pollinated shrubs, and whether shrubs with annuals in their understory have higher pollinator visitation rates relative to shrubs without annuals. We found evidence that animal-pollinated shrubs increase the visitation rate and duration of visits by pollinators to their understory plants and that wind-pollinated shrubs decrease the duration of visits of some insect visitors, but these relationships vary between years. While the presence of annuals did not change the visitation rate of pollinators to *L. tridentata* flowers, they did decrease the visitation duration of bees, indicating a negative reciprocal effect of the understory on pollination. Thus, the concentrated floral resources of flowers on animal-pollinated shrubs can act as a magnet that attract pollinators but that in turn provide a cost to pollination of the shrub. However, while wind-pollinated shrubs may provide other benefits, they may provide a cost to the pollination of their understory. These findings support the magnet hypothesis as an additional mechanism of facilitation by animal-pollinated shrubs to other plant species within arid ecosystems.

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49           **Keywords:** bees, deserts, indirect interactions, magnet hypothesis, pollinator facilitation,

50   positive interactions

## 1. Introduction

Positive interactions between plants are a common method of survival for many species. Plant-plant facilitation is especially frequent and well documented in arid environments [1–7], where many plants rely on these interactions to better cope with the high levels of environmental stress [3,4,8,9]. Shrubs are common benefactor species that represent a dominant component to many desert landscapes where they provide important resources for other plants [4,6,10–12]. Shrubs are important benefactor species likely because of their relative size, canopy, and capacity to generate an ameliorated microhabitat [1,5,13]. In communities where facilitation by shrubs is common, there is a distinct spatial aggregation of annual plants [6,14–16]. Annuals form concentrated patches under shrubs [14,16], and fewer plants live out in the open where they are not afforded shelter from extreme heat and desiccation, trampling, and herbivory [2,17,18]. Proximity to shrubs can also result in access to retained water sources and increased soil nutrient levels [2,18,19]. While shrubs can facilitate plants in a variety of ways, the strength and mechanism of this facilitation varies depending on shrub species [5,20,21].

One mechanism of shrub facilitation that is rarely studied is through increases in pollination. Shrubs can increase the density and diversity of annuals (and therefore flowers) surrounding them [7,11,22], thereby attracting more pollinators [23–25]. Shrubs also provide habitat and shelter for a variety of animals, including insects [10,26], potentially increasing pollination through apparent pollination support (increasing pollination through mechanisms other than co-blooming) [27]. However, flowering insect-pollinated shrubs can provide additional attraction to pollinators since their own flowering increases the total abundance and diversity of flowers available. Given that many annual plants are insect-pollinated, insect-



74 pollinated shrubs may be able to facilitate their understories through pollination in addition to the  
75 ameliorative effects and abiotic resources they provide [26]. Pollinator interactions have  
76 generally not been included in the literature and they represent an important part of desert  
77 facilitation networks that need to be investigated.

78         Plants and animals constantly interact, and plant-plant facilitation may be mediated by  
79 animals, including herbivores and pollinators. The scaling of plant-plant facilitation to insects is  
80 rarely examined, particularly in deserts [but see - 26,28,29]. Insects have a strong relationship  
81 with plants of all types, and many insects function as pollinators that are essential for plant  
82 reproduction and species survival [30,31]. The study of pollinator facilitation was proposed more  
83 than 35 years ago [32], and predicts that the presence of co-flowering plants increases pollination  
84 levels for the surrounding neighbourhood. Most studies examining pollinator facilitation build on  
85 an adaptation of the resource concentration hypothesis which suggests that the more resources  
86 that are available in an area, the more likely that herbivores are to visit [33–35]. These patterns  
87 have also been seen in pollinators; increased concentrations of floral resources attract higher  
88 numbers of pollinators and positively affect pollinator visitation for individual plants within a  
89 stand [23,34,36,37].

90         The magnet hypothesis (or the magnet species effect) is a more recent development of  
91 pollinator facilitation that proposes that a flowering plant that is attractive to pollinators (but not  
92 necessarily abundant) can act as a ‘magnet’ and increase the relative rate of pollination for  
93 neighbouring plant species [34,38,39]. This idea is generally tested using co-flowering plant  
94 species [40–42], but it has not been tested in documented plant-plant facilitation assemblages.  
95 Shrub-annual facilitation complexes in deserts are a good place to test the magnet hypothesis  
96 because deserts have a rich diversity of solitary bee species compared to other ecosystems [43].

They are also highly stressed and thus pre-disposed to many types of facilitation pathways [1,3,18]. The magnet effect could represent another essential ecological function that shrubs play in deserts.

Facilitation pathways are often multi-directional and non-binary [32,44–48]; however, bidirectional interactions that include facilitation are less commonly tested [but see - 45,46,49,50]. Most of the literature that does report on bidirectional interactions indicates that feedback for the benefactor species is negative [51–54]. There can be costs associated with facilitation that negatively affect the benefactor species [45,51]. These costs may include below ground competition for water and nutrient resources that can lead to fitness costs including slowed growth and reduced flower and seed production for the benefactor species [45,51,55]. Neutral and positive reciprocal effects also exist and are important because they increase the potential for co-evolutionary processes to occur within plant-plant interactions [46,49,56,57]. Examining whether bidirectional interactions are positive, neutral, or negative is important when considering the ecological and evolutionary impacts of these interactions on ecosystem functioning [45].

The indirect effect of pollinators is typically not examined in studies of bidirectional facilitation between plants and represents a novel research gap in this literature. If shrubs can facilitate the pollination of their understory plants, there may also be reciprocal effects on the shrub that should be examined as well. The double-magnet hypothesis that we propose here suggests that the floral island created under shrubs due to plant-plant facilitation pathways not only benefits from increased pollination levels but can also bidirectionally facilitate the shrub through increased pollinator service. Thus, the directionality and reciprocity of facilitation

pathways is incredibly important and can both strengthen or weaken evolutionary relationship between organisms.

Here, we investigated whether desert shrubs and annual plants facilitate each other through pollination. We hypothesized that the floral resource island created by shrubs and their understory annual plants will have positive effects on pollinator visitation. Specifically, we examine the following predictions: (1) the frequency and duration of pollinator visitations to annuals will be greater under shrubs than in the paired, open microsites, (2) annuals under flowering animal-pollinated shrubs (*Larrea tridentata*) will have a higher frequency and duration of pollinator visitations than annuals under wind-pollinated shrubs (*Ambrosia dumosa*) because of the higher concentrations of appropriate floral resources on shrubs, and (3) shrubs with annuals in their understory will have a higher frequency and duration of pollinator visitations than shrubs without annuals in their understory due to increased concentrations of floral resources for pollinators. Collectively, these predictions explore how pollinators respond to differential desert plant communities including both insect and wind-pollinated shrubs and their associated annual plants. The relationship between pollinators and plant-plant facilitation networks is important because of their inherent dependence on one another, and for the conservation of ecosystem functioning considering anthropogenic threats to desert ecosystems worldwide.

## **2. Material and Methods**

### ***2.1. Study species***

This study utilized two shrub species that overlap in range and are common throughout the Mojave Desert and the Southwestern United States [58]. *Larrea tridentata* (Zygophyllaceae)

is a large, flowering, entomophilous (insect-pollinated) shrub, commonly referred to as creosote bush [59]. It is one of the most widely distributed plants found in arid areas of the southwestern United States, including the Mojave Desert [59]. *Ambrosia dumosa* (Asteraceae) is a smaller anemophilous (wind-pollinated) shrub, that is also widely distributed in this area [59]. Both *L. tridentata* and *A. dumosa* have been shown to facilitate annual plants through physical protection from herbivores and increased water and nutrient access but not through pollination [11,54,60–62]; although *L. tridentata* has been shown to increase the abundance and diversity of all insect species relative to open sites [26].

Over 120 species of bees have been reported visiting the flowers of *L. tridentata* [63–65]. It has densely-packed, medium yellow flowers (<2.5 cm diameter) that frequently bloom for several weeks at a time during peak flowering for many desert annual plants: between April and May each year [66]. It is therefore a model species for the study of the magnet effect with shrubs, as the shrub itself provides both significant and attractive floral resources. *Ambrosia dumosa* blooms between January and February each year but is wind-pollinated and is thus a good comparison to *L. tridentata* in this study. Bees and other pollinators typically prefer colourful flowers with easy access to pollen and nectar [67–69]. While *A. dumosa* does not have big, attractive, showy flowers to act as a magnet for the pollination of understory annuals, the shrub can still provide abiotic mechanisms of facilitation including shade, a windbreak, and protection from predators [2,47,54].

The annual *Malacothrix glabrata* was used as a phytometer species to test for differential effects of microsite on pollinators in this study. A phytometer is a species that is representative of the community that can be easily cultivated and controlled, and can be used to test the influence of environmental factors biotically [70,71]. Background annuals were present in this

system but at very low levels, so using a phytometer species allowed us to ensure the presence of annuals as well as allow for consistency between experimental plots that could not have been attained using the existing annual populations. *Malacothrix glabrata* was chosen as the phytometer species for this experiment because it is already a wide-spread insect-pollinated native annual plant in the area [58,72,73], and it has bright, symmetrical yellow flowers that are comparable to *L. tridentata* (the shrub treatment that was animal-pollinated).

## 2.2. Study Site

This study was conducted in a 1.5 km by 0.5 km area along Kelbaker Road in the Mojave Desert, just north of Kelso, California, USA (35°3'41" N, 115° 39'52" W; elevation: 779 m; Fig. A.1) in April of 2015 and 2016. This area is highly dominated by the shrubs *L. tridentata* and *A. dumosa*, with shrubs frequently spaced less than two metres apart [74,75]. Annual plants are common in the area and include the following native species: *M. glabrata*, *Chaenactis fremontii*, *Eriophyllum wallacei*, *Cryptantha micrantha*, *Camissonia claviformis*, *Phacelia distans*, *Pectocarya* spp., *Eriophyllum lanosum*, and *Rafinesquia neomexicana* [72]. Insects and pollinators are also abundant, with a relatively high richness of solitary bee species compared to mesic systems (Minckley 2008). Precipitation is sporadic and low with a 10-year mean accumulated annual precipitation (2004-2014) of 138 mm in the Mojave Desert [74,76]. The average daily maximum temperatures in the summer is 40°C, and the minimum is 1°C in January (1937–2007 records; WRCC 2008).

## 2.3. Experimental design

To determine whether desert shrubs act as pollinator magnets, pollinator visitation rates were compared between three microsites: 1) under *L. tridentata* shrubs, 2) under *A. dumosa* shrubs (2016 only), and 3) an open area at least 1 metre from the drip line of any adjacent shrubs.

To determine whether annual communities act as pollinator magnets for shrubs, pollinator visitations were compared between two treatments: 1) *L. tridentata* with surrounding annuals (the same as 1 in the previous experiment) and 2) *L. tridentata* without surrounding annuals. A total of 20 *Malacothrix glabrata* plants per treatment (80 total) were harvested from nearby areas and transplanted into 60-cm by 15-cm planters. Thirty-two sites (each consisting of two *L. tridentata* shrubs, one *A. dumosa* shrub, and an adjacent southern open area) were chosen at random and marked. Open microsites were located 1-m to the south of the chosen shrubs and at a minimum of 1 metre away from the drip line of any other shrub. Shrub dimensions were measured for each shrub by first measuring the shrub at the widest point parallel to the ground, the perpendicular axis, and the height [10]. Four of these 32 sites (a new site every day) were randomly selected for video recording each morning using a random number generator to avoid repeated measures. Selected sites that did not have flowering *L. tridentata* were not used, the nearest flowering *L. tridentata* was chosen instead. The two *L. tridentata* shrubs within each site were randomly allocated to a treatment (annuals present or annuals not present).

Visitation by pollinators was recorded over 8 days during peak flowering: between April 1<sup>st</sup> and April 10<sup>th</sup>, 2015, and April 6<sup>th</sup> and April 17<sup>th</sup>, 2016. Days were non-consecutive in some cases due to inclement weather. Days with temperatures below 15°C by 10AM, any sort of precipitation, heavy cloud cover, or excessive wind were excluded from this study. Pollinator visitations to *M. glabrata* were recorded using Polaroid CUBE Lifestyle HD Action Cameras focussed on a single transplanted *M. glabrata* plant for 1.5 hours each day. Videos were recorded between 10:30AM and 12:00PM, when pollinator activity was at its peak. Each day four sites were recorded so as to film four replicates per treatment per day. Two microsites (*L. tridentata* and open) were filmed in 2015 and three microsites (*L. tridentata*, *A. dumosa*, and open) were

211 filmed in 2016. *Larrea tridentata* are too large (approximately 200 flowers per shrub) to capture  
212 visitations accurately with video whilst retaining enough detail for pollinator identification;  
213 therefore, following video recording of *M. glabrata* pollinator visits, *L. tridentata* pollinator  
214 visitation were recorded with 15-minute *in-situ* observations by two researchers. Visitations and  
215 the duration of the visit (only in 2016) that lasted at least 1 second were recorded.

216 In order to determine differences in temperature between microsites, 20 HOBO pendent  
217 loggers were randomly placed at five areas within the study site, so that there were five replicates  
218 per unique treatment type. In each of the five areas, a logger was placed under a *L. tridentata*  
219 shrub with annuals present, under a *L. tridentata* shrub with annuals removed, under an *A.*  
220 *dumosa* shrub, and in an adjacent open area. Loggers were placed on the north side of the shrub  
221 in all cases and recorded temperature hourly for the duration of the study period each year.  
222 Environmental data (including daily mean temperature, precipitation, and mean radiation) for the  
223 rainy season previous to each year (November – April) was downloaded from the Western  
224 Regional Climate Center from the nearest weather station [77].

#### 225 **2.4. Analysis**

226 Videos were processed and visitation data were collected each time an insect visited an  
227 open flower for a minimum of one second. The type of pollinator, number of flowers visited,  
228 duration of pollination (difference between pollination start and stop times) were recorded.  
229 Insects were identified to their lowest recognizable taxonomic unit (RTU). From these data, the  
230 total number of visitations and total visitation duration by pollinators were calculated. While  
231 cameras were each set out for 90 minutes, inconsistency in battery lifetime and other  
232 malfunctions meant that actual film time varied greatly. Instances in which videos were less than  
233 15 minutes were excluded since these time periods were not long enough to garner a significant

sample (two videos were less than 15 minutes). Mean video time (not including times of less than 15 minutes) was 81 minutes (standard deviation = 9.8 minutes). Both floral density (number of flowers in frame) and total film time were recorded.

Generalized linear mixed models (GLMM; using the R package glmmTMB) [78] were used to compare both the number of pollinators (visitation frequency per flower) and duration of pollination (visitation time per flower) of three main insect types (bees, flies, other) for each experiment. Microsite, insect type, and mean temperature during the hours of recording were treated as fixed factors within models measuring visits to *M. glabrata* while treatment type (annual community presence or absence), insect type, mean temperature, shrub volume, and year were fixed factors for visits to *L. tridentata*. Site id and day were included as random factors in both cases, while video length was used as an offset variable to account for differences in total recording time between videos (for visits to *M. glabrata*). Pollinator visitation data errors were modelled with a Poisson distribution [79] and visitation duration data errors were modelled with a Tweedie distribution [80]. Post hoc comparisons were done using the emmeans package in R [81]. Data for 2015 and 2016 were analyzed separately for visits to *M. glabrata* because the level of factors tested were non-orthogonal due to the addition of the *A. dumosa* treatment in 2016. However, to examine only the effects of year, models were fit to all visitation and visit duration data excluding *A. dumosa* with year as an extra factor. Linear models were used to compare mean temperature and visitation rates, and number of visits and net floral density (by insect type). Temperature data during the study period was compared between years for all microsites except annuals under *A. dumosa* using a GLMM fit against treatment with site id as a random factor and a heterogeneous unstructured covariate included to account for the time series [78]. Error was modeled to a normal distribution. Additional GLMM's fitting just the data from 2016



(including the *A. dumosa* microsite) were also fit. Temperature was tested for both during the study period (10:00AM to 12:00PM) and for all days throughout the study period (April 1, 2015 – April 10, 2015 and April 6, 2016 – April 17, 2016). Mean daily temperature, mean daily precipitation, and mean daily radiation of the previous rainy seasons were compared between the 2015 rainy season (November 2014 – April 2015) and 2016 rainy season (November 2015 – April 2016) using t-tests [82]. All data were analyzed using R version 4.0.2 [83].

### 3. Results

*Malacothrix glabrata* had increased rates (Fig. 1) and duration (Fig. 2) of pollination when associated with *L. tridentata* (the animal-pollinated shrub) relative to the open in 2015, but not 2016 (Table 1). Fly visitation duration was lower for plants associated with *A. dumosa* than for plants in the open but otherwise there was no difference in visitation rate or duration to *M. glabrata* between microsites in 2016 (Fig. 2, Table A.1). In both years, bees were the most common visitors and visited for the longest periods of time (Fig. 1 & Fig. 2, Table A.1). While there was no difference in the effects of microsite or the total number or duration of visits between 2015 and 2016 (all  $p > 0.05$ ), there were significantly more bee visits in 2016 than 2015 (post-hoc test:  $p < 0.05$ ) and significantly longer visits by flies and other pollinators in 2016 than 2015 (post-hoc tests:  $p < 0.05$ ).

The presence of annuals had no effect on the number of visitors to *L. tridentata* (Fig. 3, Table 1) but the duration of visits was depressed in the presence of annuals (Fig. 4, Table 1). This effect was driven by bees (the most abundant visitor; Fig. 3, Table A.1), which had a longer duration per visit on *L. tridentata* flowers without annuals than with annuals (Fig. 4, Table A.1).

Mean temperature (during observation hours) positively predicted visitation of insects to *M. glabrata* in 2015, but not 2016 (Table 1). Similarly, visitation duration marginally predicted visitation duration in 2015, but not 2016 (Table 1). Bees and flies both had increased visits with increasing temperature in 2015 (Fig. A.2, Bees:  $r^2_{\text{adjusted}} = 0.0958$ ,  $p = 0.0092$ ; Flies:  $r^2_{\text{adjusted}} = 0.181$ ,  $p = 0.00037$ ). In 2016, insects other than bees and flies had decreased visitation with increased temperatures (Fig. A.2,  $r^2_{\text{adjusted}} = 0.121$ ,  $p = 0.00069$ ). Temperature did not predict insect visitation to *L. tridentata* (all  $p > 0.05$ , Fig. A.3). Floral density of *M. glabrata* positively predicted bee visitation, but only in 2016 (Fig. A.4,  $r^2_{\text{adjusted}} = 0.125$ ,  $p = 0.00057$ ).

The mean daily temperature in the previous rainy season was higher in 2015 than 2016 (Fig. A.5; t-test:  $t = 3.03$ ,  $p = 0.0026$ ); however, the daily precipitation and mean daily radiation in the 2015 and 2016 rainy seasons were similar (radiation: mean 2015 = 378.0 Ly, mean 2016 = 374.4 Ly, t-test:  $t = 0.224$ ,  $p = 0.82$ ; precipitation: total 2015 = 91.9mm, total 2016 = 100.6 mm, t-test:  $t = -0.171$ ,  $p = 0.86$ ). The average temperature during collection (10:00AM – 12:00 PM) was similar in 2015 and 2016 (Fig. A.6, Table A.2 & Table A.3); however, the average temperature during the entire study period was significantly lower in 2016 than 2015 (Fig. A.6; Table A.2 & Table A.3). Similarly, temperatures were higher in 2016 than 2015 in the open and under *L. tridentata* (with annuals) throughout the study period, but not within recording times (Fig. A.6; Table A.3). As expected, temperatures were always higher in the open than under shrubs, both during collection and throughout the study period for both years (Fig. A.6, Table A.3). There was no difference between temperatures near *L. tridentata* and *A. dumosa*; however, *L. tridentata* with annuals had significantly higher temperatures than *L. tridentata* without surrounding annuals, but only in 2016 (Fig. A.6, Table A.3).

#### 4. Discussion

Shrubs are a foundation species within desert ecosystems, and some can positively influence pollination in their understories. The insect-pollinated shrub *L. tridentata* facilitated understory plants by increasing visitation rates and duration of pollinator visits in one year, although not the other. However, the wind-pollinated shrub *A. dumosa* did not facilitate plant pollination, rather it decreased the duration of visits by flies. These findings support the magnet hypothesis for pollinators in desert shrub-annual systems, with the caveat that the effects are conditional. While the supplementary floral resources provided by the insect-pollinated shrub *L. tridentata* did not increase pollination for understory plants relative to the wind pollinated shrub *A. dumosa*, the year in which both shrubs were studied *L. tridentata* did not increase pollination relative to the open either. Distinguishing the relative overall effects of wind-pollinated and insect-pollinated shrubs on the pollination of their understory is not possible due to this lack of difference; highlighting the importance of examining interactions over multiple years. The only evidence of a difference in the impact on pollination is that the duration of visits by flies to the understory of *A. dumosa* was lower than visits by flies in the open, suggesting a potential cost to association with the wind-pollinated shrub. The third prediction associated with the double magnet hypothesis was not supported, but rather the opposite was observed; visitation duration of pollinators was higher in the absence of annuals than in the presence of annuals. This difference suggests a cost to facilitation for insect-pollinated shrubs. These findings support the overarching hypothesis that the floral resource island created by insect-pollinated shrubs has positive effects on pollinator visitation rates for understory plants, but that this facilitation comes at a cost to pollination for the shrub. As such, it is clear the shrubs form important linkages between plant and pollinator taxa and are important components of desert interaction networks.

#### 4.1 Magnet hypothesis

Shrubs are important players in desert communities that mediate pollinator interactions with understory plant species. Shrubs like *L. tridentata* can act as magnets for pollinators and increase the pollination frequency and duration for understory annual plants; however, there is evidence that wind-pollinated shrubs may decrease pollination of their understory. While visitation rate did not differ between the open and under the canopy of *A. dumosa*, the duration of visits by flies was lower under the canopy of *A. dumosa* than the open. *Ambrosia dumosa* in itself does not hold attraction for pollinators in terms of floral resources since it is neither pollinated by insects nor flowering during the study period, so this is not likely a consequence of floral dilution (where increased floral resources leads to a reduction of pollination for each flower [84]). Rather, it is possible that the shrub increases the risk of predation to flies. Shrubs have been shown to facilitate animals in similar ways to plants: by providing shelter and habitat [10] and to increase the abundance of animals surrounding them relative to the open [26,85]. Therefore, it is not unlikely that there are increased levels of predators for flies in these areas. While the same increase in predation risk could occur under *L. tridentata*, it is possible that the two shrub species do not harbour the same predators or that the increased floral resources provided by *L. tridentata* offsets any increased risk of predation. Regardless of the reason for a reduction in floral visit duration by flies under *A. dumosa*, there is no evidence that this reduction impacts the pollination of *M. glabrata*. Not all visitors of flowers are effective pollinators [86–88]. While *M. glabrata* is known to be insect pollinated [73], the relevant pollinators are still unknown. While it is possible that flies are relevant pollinators of *M. glabrata*, it is more likely that bees are the most important pollinators given that they were by far the most frequent visitors in our study. Further investigation into the pollinators of *M. glabrata* and the specific mechanism

of the effects of wind-pollinated shrubs like *A. dumosa* on pollinators is needed to understand how shrubs impact pollinators.

Facilitation is well known to vary with environmental variables. The stress gradient hypothesis (SGH) states that as stress increases, so do positive interactions [9]. Both 2015 and 2016 were the last two years of a 5-year long drought in California where there was both decreased precipitation levels and increased temperatures [89]. While temperatures were similar during collection for both years and there were similar levels of precipitation and radiation, the study period and previous rainy season of 2015 was significantly hotter than in 2016. The increased temperatures of 2015 could lead to decreased floral resources available to pollinators. If there are fewer flowers overall, larger patches such as those created by *L. tridentata* could have a greater draw. However, it is also possible that there are not only more flowers associated with shrubs, but flowers under shrubs could be more rewarding. Nectar levels in flowers have been shown to decrease with high temperatures [90], therefore there may be higher levels of nectar in flowers in the cooling shade of a shrub and this pattern would likely be more pronounced the higher the temperatures in the open. Lower temperatures under shrubs in extreme heat could also decrease the heat stress of pollinators, leading to increased pollinator activity [91]. While pollinator activity has previously been found to be negatively correlated with temperature [91–93], this explanation, though plausible, is less likely given that a positive correlation between pollinator visitation and temperature was observed in this study. Based on the results from this study, it is likely temperature and possibly other environmental factors are key in regulating the facilitation of pollination by shrubs.

Pollinators are responsive to increased floral density, and it can influence visitation rates to flowers. Concentrated floral resources provided within the canopies of facilitative shrubs

allow for optimal pollinator foraging. Increased floral resources can positively affect pollination for individual and neighbouring plants because pollinators are more likely to forage where they can obtain the most resources with the least amount of effort [32,94] —i.e. dense stands with more individual flowers and less distance between them [94–96]. This supports the increased pollinator visitation rates seen for annual plants under *L. tridentata* in 2015 and the positive correlation between bee visitation and floral density in this experiment. However, the increased floral concentration of *L. tridentata* in 2016 did not result in increased pollinator visitations. This difference may be because of a difference in pollinator availability between years; there were, on average, more bee visitations across microsites in 2016 relative to 2015 which may be reflective of a higher population of bees in 2016. Lázaro et al. [97] previously found that when pollinators were less available, positive effects of floral density on pollination increased. This effect could be the case here, where limited availability of pollinators in 2015 resulted in positive effects of shrubs (and the resultant increased floral density) on pollinators while in 2016 pollinator availability was saturated. This would be a further extension of the SGH where in this case pollinators are the resources that, when limited, increase stress and therefore positive plant-plant interactions. It is therefore likely that resource concentration, floral density, and pollinator availability are drivers of the facilitative relationship between shrubs and annuals for pollination in deserts.

Finally, shrubs likely act as a refuge for some pollinators. Shrubs have been found to provide refuge and to have non-trophic interactions with several other animal species, including insects, small mammals, and lizards [10,26,44]. Similar relationships have been found between cushion plants and insects in the alpine where the abundance of both arthropods and pollinators were higher on cushions in contrast to open areas due to the amelioration of abiotic stress

[28,29,98]. Cushion plants act similarly to desert shrubs by facilitating the species that grow on them through biotic and abiotic mechanisms [98]. The shrub species (*L. tridentata* and *A. dumosa*) could therefore provide a refuge for pollinators through access to resources, shelter, and protection from predators. However, given that association was only seen in one year, quality of and preference for these resources may be dependent on environmental variables if they are, indeed relevant. In addition, increased resources for nesting and protection from predators could also increase the number of intermediate predators that prey on pollinators, offsetting other benefits provided by shrubs. Thus, the net positive effect of shrubs on the pollination of understory annuals likely involves a complex network of drivers including resource concentration, increased floral density, pollinator abundance, access to abiotic resources and protection from predators, as well as other environmental variables. We need to better understand how this facilitative relationship works, the factors that contribute to it, and why it varies to be able to conserve the ecosystem functions that these interactions provide.

#### ***4.2 Double magnet hypothesis***

Annuals in this system negatively influence the pollination of the shrubs that facilitated them. While we proposed the prospect of the double magnet effect where shrubs increase pollination of annuals and annuals increased the pollination of shrubs due to increased floral density, floral density is not always positively associated with pollination. Large floral patches can increase the likelihood of pollinator attraction, but floral oversaturation can also max out the density-visitation curve and eventually result in a dilution effect. Resource dilution is where high concentrations of a resource (flowers in this case) result in a lower density of resource-users (pollinators in this case) per plant rather than drawing in more resource-users [99]. While annuals did not increase visitation rate, indicating a simple saturation of the resource

concentration effect on density, annuals decreased pollination visitation duration. This trend of decreased visitation duration at higher floral densities and complexities has been seen previously [100,101]. Visitors of *L. tridentata* may choose to leave flowers earlier if they have a higher preference for other flowers present that they have been foraging on. Additionally, temperatures of *L. tridentata* shrubs without annuals were significantly lower than shrubs with annuals in 2016 (the only year in which visitation duration was measure for *L. tridentata*) which may discourage bee visitation since bee visitation was positively correlated with temperature. This decrease in the quality of pollination in the presence of annuals adds further evidence that there is a cost to facilitation for benefactor species.

#### ***4.3 Shrubs as foundation species***

The ability of shrubs to facilitate pollination for their understory species indicates that they are a foundation species within desert ecosystems. Foundation species are often abundant species that encompass certain structural or functional characteristics that have a strong, defining influence on ecological communities [102,103]. The foundation effect of shrubs on desert plant and pollinator communities should be considered alongside current and emerging ecological threats to these areas. Climate change, the resulting desertification processes, and significant recent declines in pollinator populations are issues that pose an immense threat to deserts [104–106]. Climate change can result in a phenological mismatch due to flowers using temperature as a cue for emergence and senescence, and bees primarily using rainfall [107–109]. However, these increased temperatures would be detrimental to both taxa because they disrupt the network structure of plant-pollinator interactions, even if species aren't initially lost [110]. Declines in pollinators would have a strong, negative impact on seed recruitment and survival in animal-pollinated species, which would have cascading effects to other trophic levels [97,111]. Shrubs



can thus act as a buffer to mediate the effects of warming in desert systems by increasing the pollination of plants around them. This effect is of particular importance if facilitation of pollination by shrubs is stronger when there are fewer pollinators. The protection and management of desert shrub species could be an important first step in conserving desert biodiversity and plant-pollinator interactions.

## **5. Conclusion**

The desert shrub species *L. tridentata* is an important foundation species within the desert community that can facilitate other plants both directly and indirectly. Shrubs like *L. tridentata* have been shown to facilitate their understories directly by providing physical protection, shade, and access to extra water and nutrient resources, but we provide evidence that they also provide indirect benefit by providing increased access to pollinators. We propose that pollinator visitation is increased through increased floral density and by providing abiotic refuge for pollinators but that these effects are conditional on other factors such as environmental variables and pollinator abundance. Furthermore, facilitation of plants comes at a cost to the quality of pollination received by insect-pollinated shrubs. These findings represent a profound ecological effect that is likely to be an extremely important subset of positive interactions within desert communities. These interactions will be especially important to consider in light of climate change and pollinator declines that threaten these areas, solidifying the position of shrubs as foundation species within deserts.

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## Tables

**Table 1.** A summary of the general linear mixed models used to test for differences in pollinator visitation rates (per flower) and duration to the annual plant *Malacothrix glabrata* and *Larrea tridentata*. Visits to *M. glabrata* were compared between *L. tridentata* and adjacent open microsites in 2015 and between *L. tridentata*, *Ambrosia dumosa*, and adjacent open microsites in 2016. Visits to *L. tridentata* were compared between shrubs with annuals present and with annuals removed in both 2015 and 2016. This study was conducted in the Mojave Desert, California (35.0612°, -115.6643°), using video (for *M. glabrata*) and *in-situ* (for *L. tridentata*) observation techniques. Pollinator visitation rate was standardized by flower density within plots, and total video length was used as an offset variable within models.

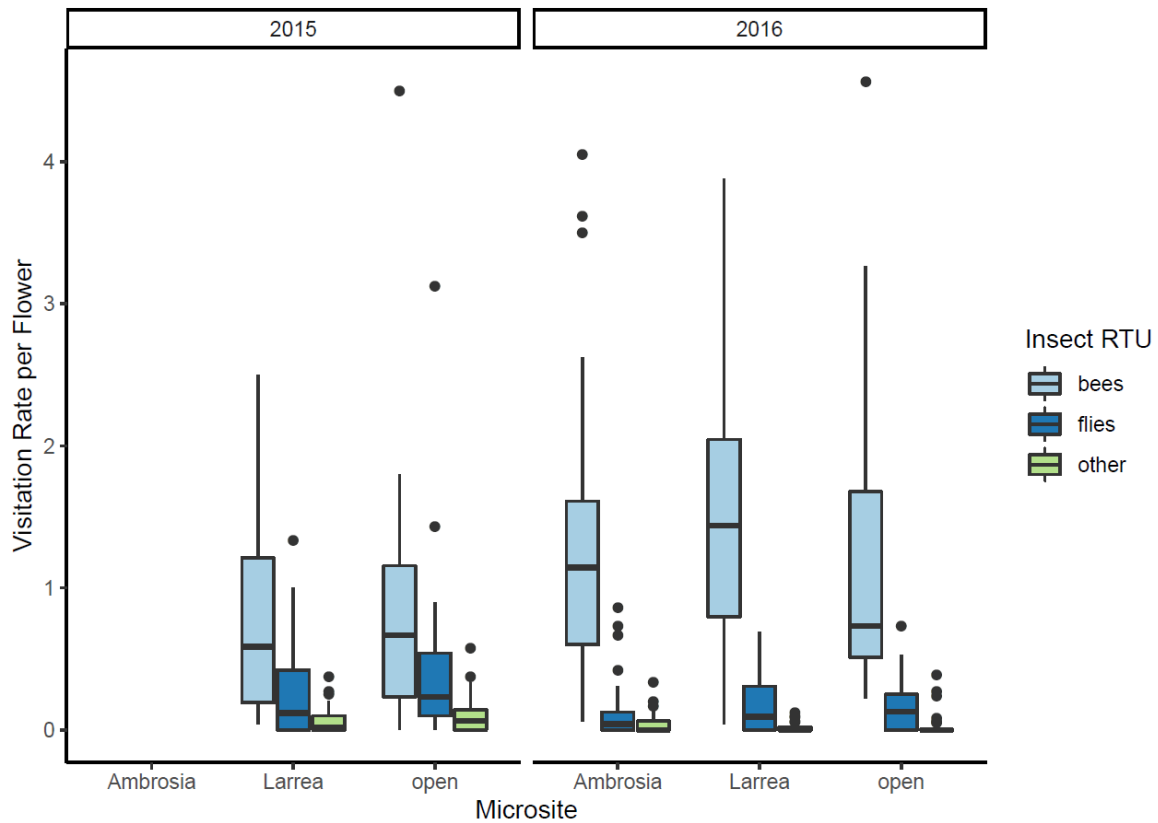
	Visitation Rate			Visitation Duration		
	$\chi^2$	df	p	$\chi^2$	df	p
Visits to <i>M. glabrata</i> (2015)						
Microsite	8.63	1	0.0033*	4.23	1	0.040*
Insect RTU	30.1	2	<0.0001*	84.2	2	<0.0001*
Temperature	15.2	1	<0.0001*	3.71	1	0.054
Microsite: Insect RTU	0.610	2	0.74	3.53	2	0.17
Visits to <i>M. glabrata</i> (2016)						
Microsite	2.4	2	0.3	4.23	2	0.12
Insect RTU	84.2	2	<0.0001*	316	2	<0.0001*
Temperature	1.96	1	0.16	0.244	1	0.62
Microsite: Insect RTU	0.693	4	0.95	7.85	4	0.097
Visits to <i>L. tridentata</i>						
<i>Larrea</i> treatment	0.0202	1	0.89	8.26	1	0.0041*
Insect RTU	0.389	2	0.53	32.3	2	<0.0001*
Year	0.0136	1	0.91			
Temperature	0.0047	1	0.95	2.63	1	0.10

Shrub Volume	0.009	1	0.92	0.705	1	0.40
<i>Larrea</i> treatment: Insect RTU	0.0027	2	0.96	4.57	2	0.033*

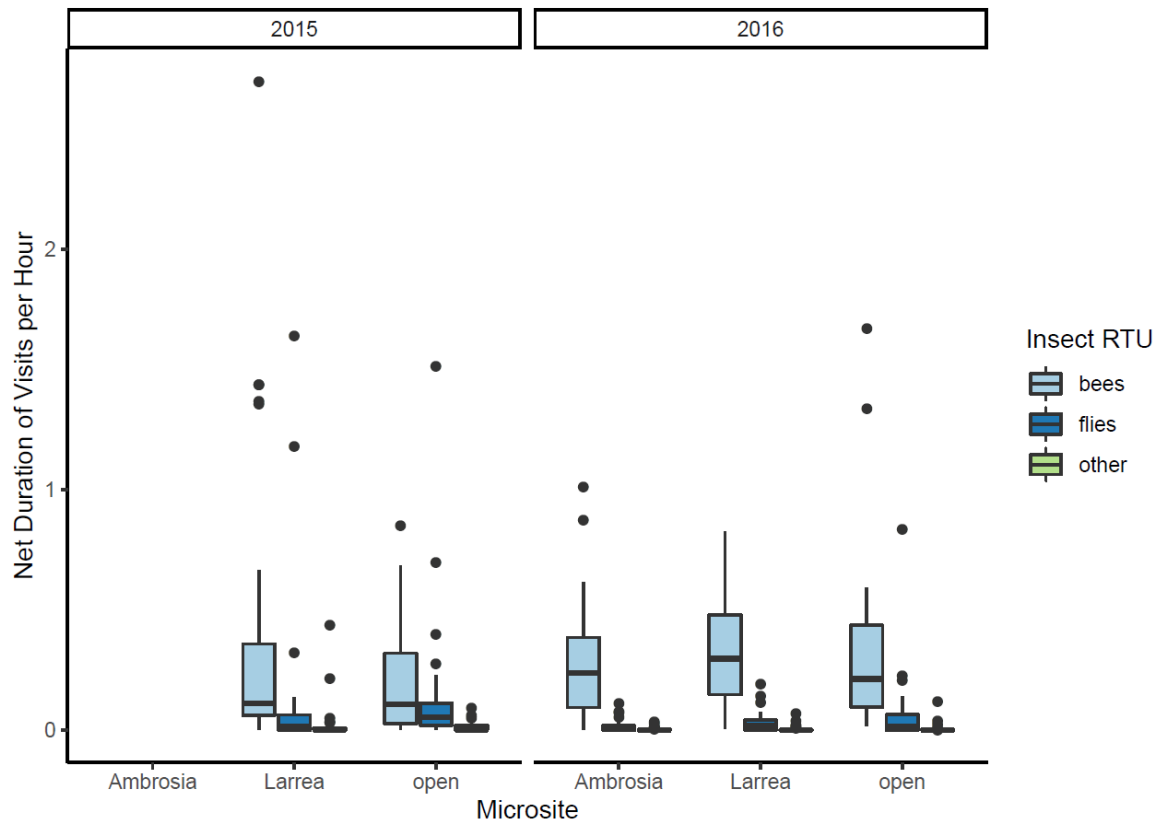
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\*p < 0.05

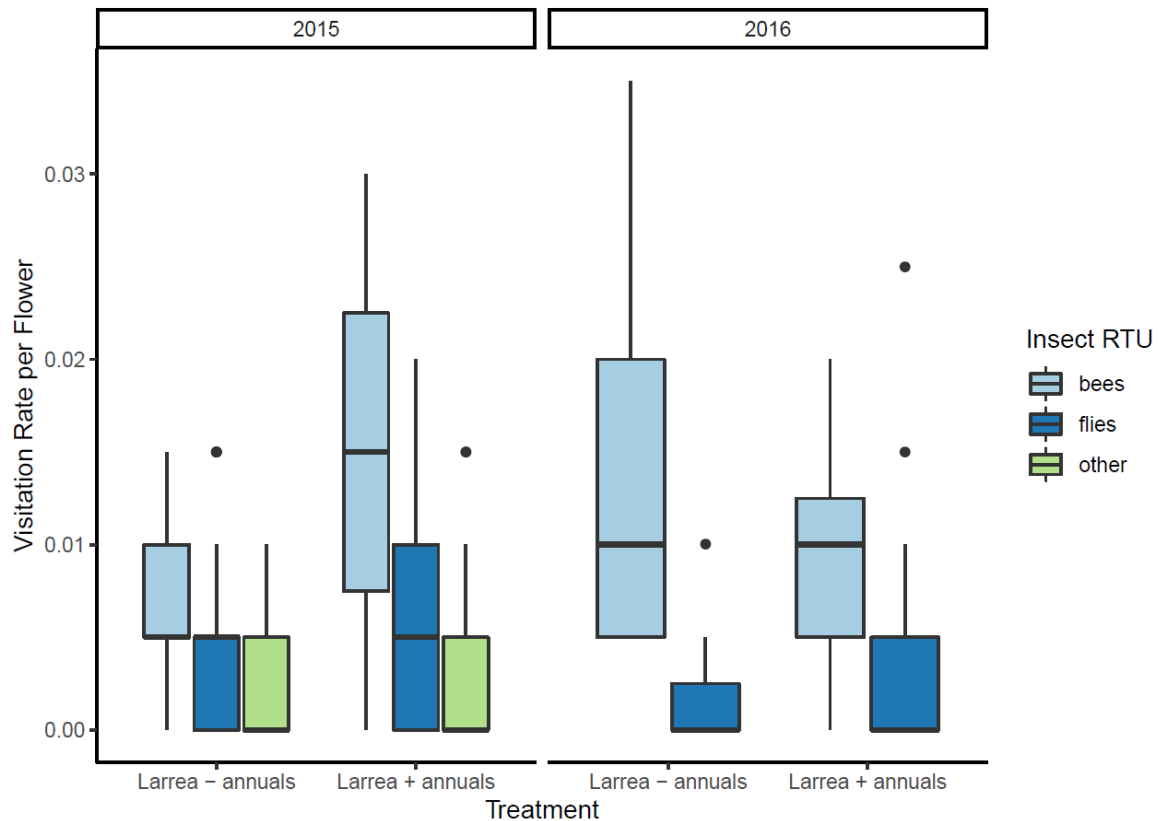
## Figures



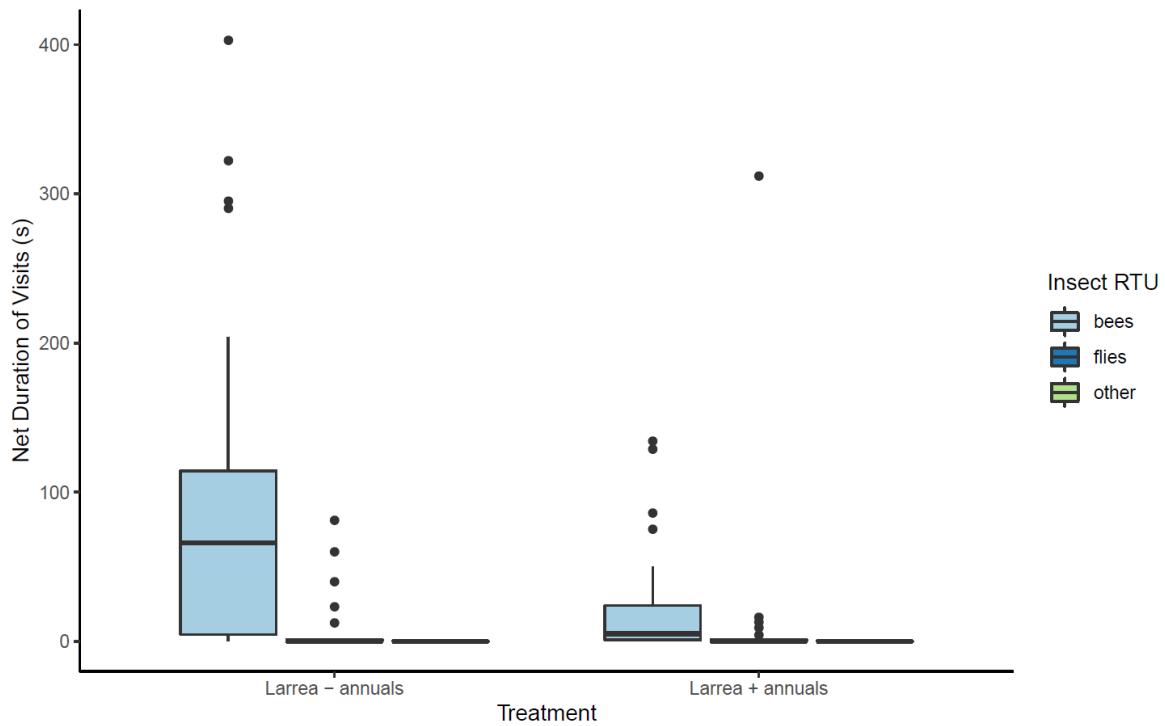
**Figure 1.** Visitation rate of pollinators to the annual plant *Malacothrix glabrata*, obtained through video. Visitation was compared between the three treatment groups (annuals under *Ambrosia dumosa*, annuals under *Larrea tridentata*, annuals in the open), for bees, flies, and other insect pollinators in 2016 and two treatment groups in 2015. Visitation rate was standardized by number of flowers in the field of view of the video. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range.



**Figure 2.** The duration of visits (in hours) by pollinators to the annual plant *Malacothrix glabrata*, obtained through video. Visitation was compared between the three treatment groups (annuals under *Ambrosia dumosa*, annuals under *Larrea tridentata*, annuals in the open), for bees, flies, and other insect pollinators. Raw visitation times were standardized by total video length. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range.



**Figure 3.** Visitation rate by pollinators to *L. tridentata*, obtained through *in-situ* observation. Visitation was compared between the two treatment groups (*L. tridentata* with understory annuals present and *L. tridentata* with understory annuals absent) for bees, flies, and other insect pollinators. Insects other than bees and flies were not observed in 2016. Visitation rate was standardized by number of flowers in the field of view of the video. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range.



**Figure 4.** The duration of visits (in seconds) by pollinators to *L. tridentata*, obtained in 2016 through *in-situ* observation. Visitation was compared between the two treatment groups (*L. tridentata* with understory annuals present and *L. tridentata* with understory annuals absent) for bees and flies. Insects other than bees and flies were not observed in 2016. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range. Visitation rate was standardized by total video length.

## Appendix A

**Table A.1.** A summary of the post-hoc comparisons of the general linear mixed models used to test for differences in pollinator visitation rates (per flower) and duration to the annual plant *Malacothrix glabrata* and *Larrea tridentata*. Visits to *M. glabrata* were compared between *L. tridentata* and adjacent open microsites in 2015 and between *L. tridentata*, *Ambrosia dumosa*, and adjacent open microsites in 2016. Visits to *L. tridentata* were compared between shrubs with annuals present and with annuals removed in both 2015 and 2016. This study was conducted in the Mojave Desert, California (35.0612°, -115.6643°), using video (for *M. glabrata*) and *in-situ* (for *L. tridentata*) observation techniques. Pollinator visitation rate was standardized by flower density within plots, and total video length was used as an offset variable within models.

Contrast		log estimate (SE)	t.ratio	p
Visits to <i>M. glabrata</i> (2015)				
2015				
	bees - flies	0.892 (0.264)	2.38	0.0023*
	bees - other	2.28 (0.468)	4.87	<0.0001*
	flies - other	1.39 (0.499)	2.78	0.016*
	<i>Larrea</i> - open	1.36 (0.589)	2.31	0.022*
2016				
	bees - flies	2.10 (0.289)	7.28	<0.0001*
	bees - other	3.71 (0.644)	5.77	<0.0001*
	flies - other	1.61 (0.693)	2.33	0.054
Visitation duration to <i>M. glabrata</i>				
2015				
	bees - flies	1.02 (0.255)	4	0.0003*
	bees - other	2.78 (0.305)	9.13	<0.0001*
	flies - other	1.76 (0.327)	5.4	<0.0001*
	<i>Larrea</i> - open	1.18 (0.557)	2.12	0.035*
2016				
	bees - flies	2.18 (0.184)	11.9	<0.0001*



	bees - other	4.16 (0.270)	15.4	<0.0001*
	flies - other	1.98 (0.296)	6.66	<0.0001*
bees	Ambrosia - Larrea	-0.106 (0.229)	-0.464	0.89
	Ambrosia - open	-0.206 (0.302)	-0.682	0.77
	<i>Larrea</i> - open	-0.100 (0.323)	-0.310	0.95
flies	Ambrosia - Larrea	-0.475 (0.417)	-1.14	0.49
	Ambrosia - open	-1.38 (0.437)	-3.16	0.005*
	<i>Larrea</i> - open	-0.906 (0.432)	-2.10	0.092
other	Ambrosia - Larrea	-0.442 (0.629)	-0.702	0.76
	Ambrosia - open	-0.703 (0.639)	-1.10	0.52
	<i>Larrea</i> - open	-0.262 (0.622)	-0.420	0.91
Ambrosia	bees - flies	2.70 (0.349)	7.74	<0.0001*
	bees - other	4.44 (0.493)	9.01	<0.0001*
	flies - other	1.74 (0.557)	3.13	0.0056*
Larrea	bees - flies	2.33 (0.321)	7.26	<0.0001*
	bees - other	4.10 (0.454)	9.04	<0.0001*
	flies - other	1.77 (0.509)	3.48	0.0017*
open	bees - flies	1.52 (0.282)	5.40	<0.0001*
	bees - other	3.94 (0.447)	8.82	<0.0001*
	flies - other	2.42 (0.475)	5.09	<0.0001*
Visitation duration to <i>L. tridentata</i>				
	bees - flies	1.93 (0.36)	5.33	<0.0001*
	with annuals - without annuals	-2.05 (0.911)	-2.55	0.026*
with annuals	bees - flies	1.17 (0.54)	2.17	0.033*
without annuals	bees - flies	2.69 (0.47)	5.71	<0.0001*
	with annuals - without annuals	-2.81 (0.892)	-3.15	0.0022*
bees	with annuals - without annuals	-1.30 (1.06)	-1.23	0.22
flies				

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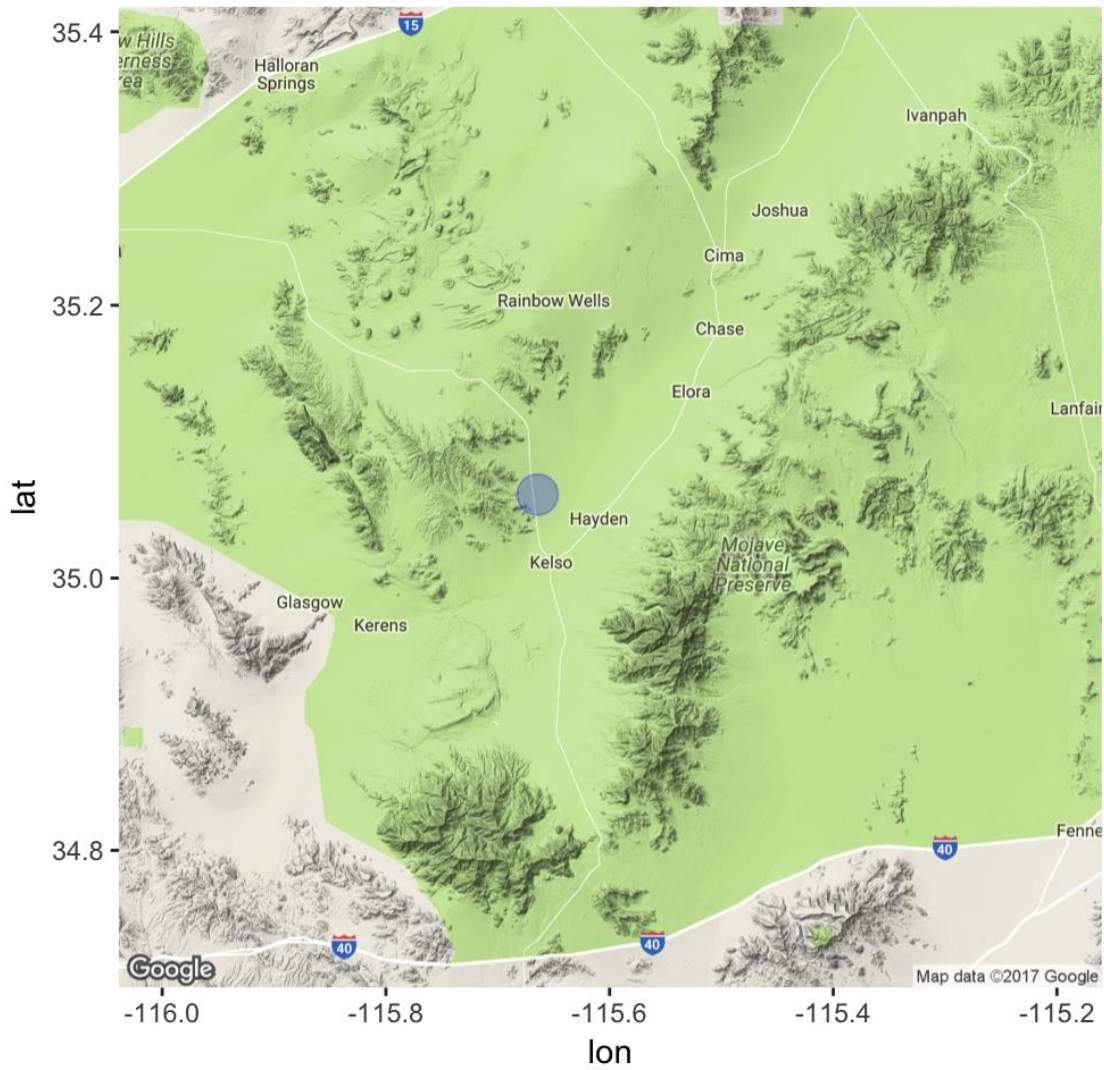
**Table A.2.** A summary of the general linear mixed models used to test for differences in temperature between microsites in 2015 and 2016. Tests of the average temperature during hours (10:00AM – 12:00PM) and specific days of collection and tests of average daily temperature throughout the study period are presented. Tests with year in the model examine microsites under *Larrea tridentata* with annuals, *L. tridentata* without annuals and adjacent open areas. Additional tests of only 2016 (in which an additional microsite of under *A. dumosa* was examined) are also included.

	$\chi^2$	df	p
Temperature during collection			
Microsite	327	2	<0.0001*
Year	4.24	1	0.04
Microsite:Year	67.2	2	<0.0001*
2016			
Microsite	165	3	<0.0001*
Temperature throughout study			
Microsite	102	2	<0.0001*
Year	7.97	1	0.0047*
Microsite:Year	15.9	2	0.00035*
2016			
Microsite	39.5	3	<0.0001*

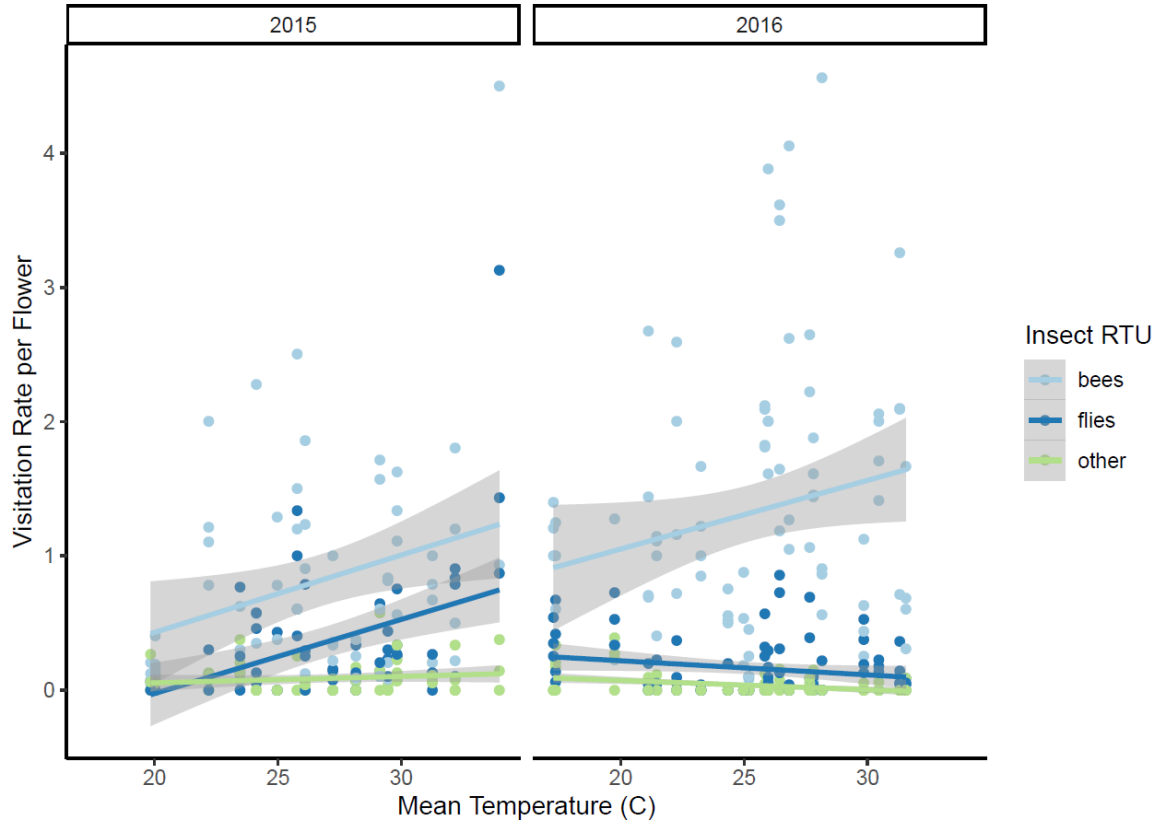
**Table A.3.** A summary of the post-hoc tests associated with general linear mixed models used to test for differences in temperature between microsites in 2015 and 2016. Tests of the average temperature during hours (10:00AM – 12:00PM) and specific days of collection and tests of average daily temperature throughout the study period are presented. Tests with year in the model examine microsites under *Larrea tridentata* with annuals, *L. tridentata* without annuals and adjacent open areas. Additional tests of only 2016 (in which an additional microsite of under *A. dumosa* was examined) are also included.

	Contrast	log estimate (SE)	t.ratio	p	
2015	Temperature during collection				
	2015 - 2016	2.87 (1.62)	1.78	0.077	
	<i>Larrea</i> with annuals - open	-5.09 (0.558)	-9.12	<0.0001*	
	<i>Larrea</i> with annuals - <i>Larrea</i> without annuals	-8.94 (0.483)	-18.5	<0.0001*	
	<i>Larrea</i> with annuals - open	-5.68 (0.891)	-6.38	<0.0001*	
	<i>Larrea</i> with annuals - <i>Larrea</i> without annuals	0.354 (0.693)	0.511	0.87	
2016	<i>Larrea</i> with annuals - open	-4.49 (0.942)	-4.76	<0.0001*	
open	Ambrosia - <i>Larrea</i> with annuals	0.502 (0.942)	0.532	0.95	
	Ambrosia - open	-3.99 (0.942)	-4.23	0.0003*	
	<i>Larrea</i> with annuals - <i>Larrea</i> without annuals	7.35 (0.942)	7.8	<0.0001*	
	2015 - 2016	1.34 (1.75)	0.766	0.44	
	<i>Larrea</i> with annuals	2015 - 2016	0.143 (1.73)	0.082	0.93
	<i>Larrea</i> without annuals	2015 - 2016	7.14 (1.68)	4.25	<0.0001*
2015	Temperature throughout study				
	2015 - 2016	-1.17 (0.353)	-3.31	0.0010*	
	<i>Larrea</i> with annuals - open	-1.70 (0.332)	-5.12	<0.0001*	
	<i>Larrea</i> with annuals - <i>Larrea</i> without annuals	0.974 (0.296)	3.29	0.0032*	
	<i>Larrea</i> with annuals - open	-1.23 (0.551)	-2.23	0.068	

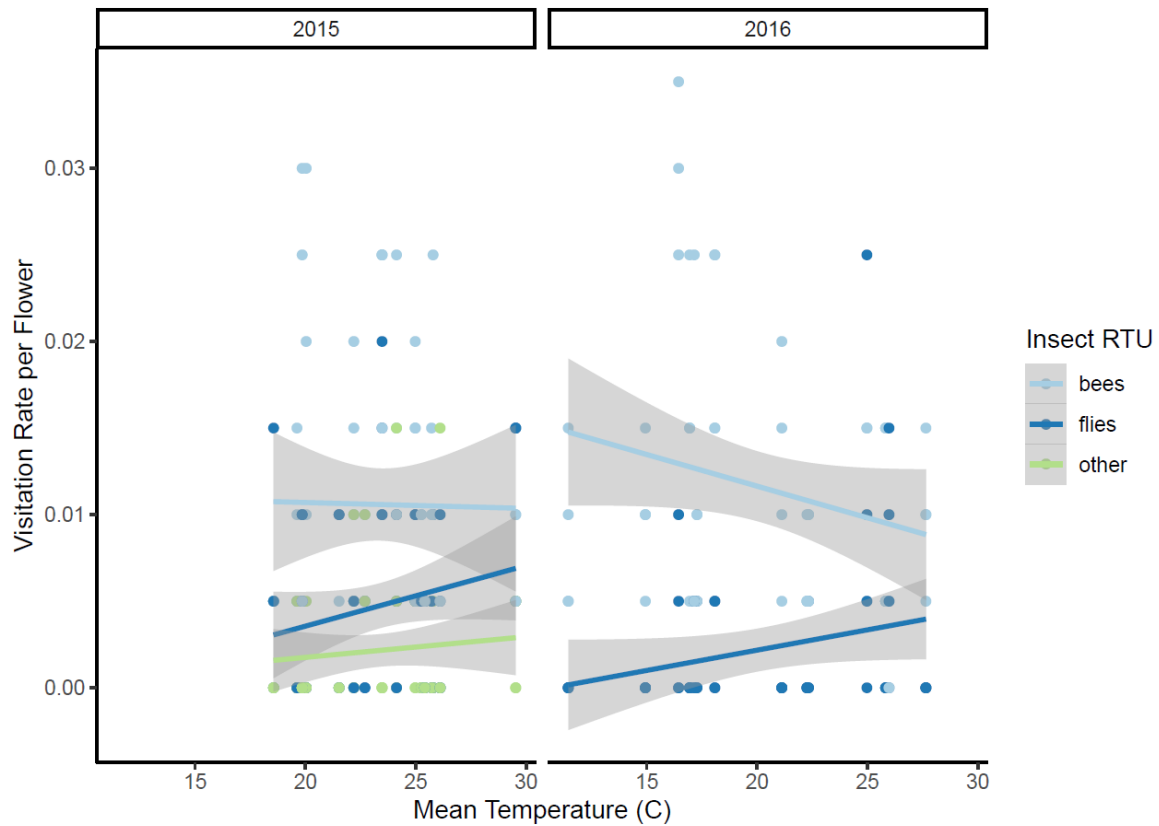
	<i>Larrea</i> with annuals - <i>Larrea</i> without annuals	0.298 (0.461)	0.646	0.79
2016	<i>Larrea</i> with annuals - open	-2.17 (0.61)	-3.56	0.0025*
	Ambrosia - <i>Larrea</i> with annuals	0.158 (0.61)	0.259	0.99
	Ambrosia - open	-2.01 (0.61)	-3.3	0.0061*
	<i>Larrea</i> with annuals - <i>Larrea</i> without annuals	1.65 (0.61)	2.7	0.037*
open	2015 - 2016	-2.25 (0.530)	-4.25	<0.0001*
<i>Larrea</i> with annuals	2015 - 2016	-1.30 (0.523)	-2.5	0.013*
<i>Larrea</i> without annuals	2015 - 2016	0.0467 (0.448)	0.104	0.92



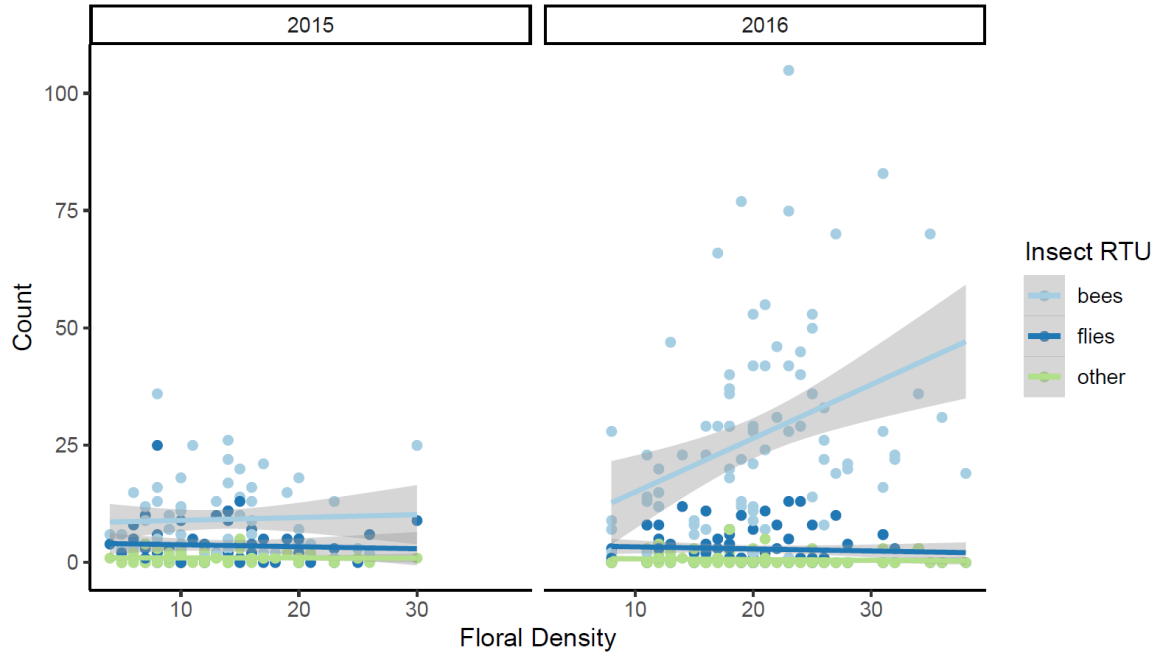
**Figure A.1.** A map of the location of the study site located 3.5 miles North of Kelso, San Bernardino, California, USA, on Kelbaker Road. (central coordinates:  $35.061279^{\circ}$  -  $115.664356^{\circ}$ ; elevation: 779 m). The blue circle represents the approximate area used for data collection. Map generated in R version 3.3.2.



**Figure A.2.** The correlation between mean temperature (°C) during hours of video recording, and pollination rate per flower for *Malacothrix glabrata* (frequency of pollination events standardized by the number of flowers in the field of view). Pollination rates were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees and flies showed a significant correlation between temperature and visitation rate to flowers in 2015 (bees:  $r^2_{\text{adjusted}}=0.0958$ ,  $p=0.0092$ , flies:  $r^2_{\text{adjusted}}=0.181$ ,  $p=0.0004$ ) and other species a negative correlation in 2016 (other:  $r^2_{\text{adjusted}}=0.121$ ,  $p=0.0006$ ).

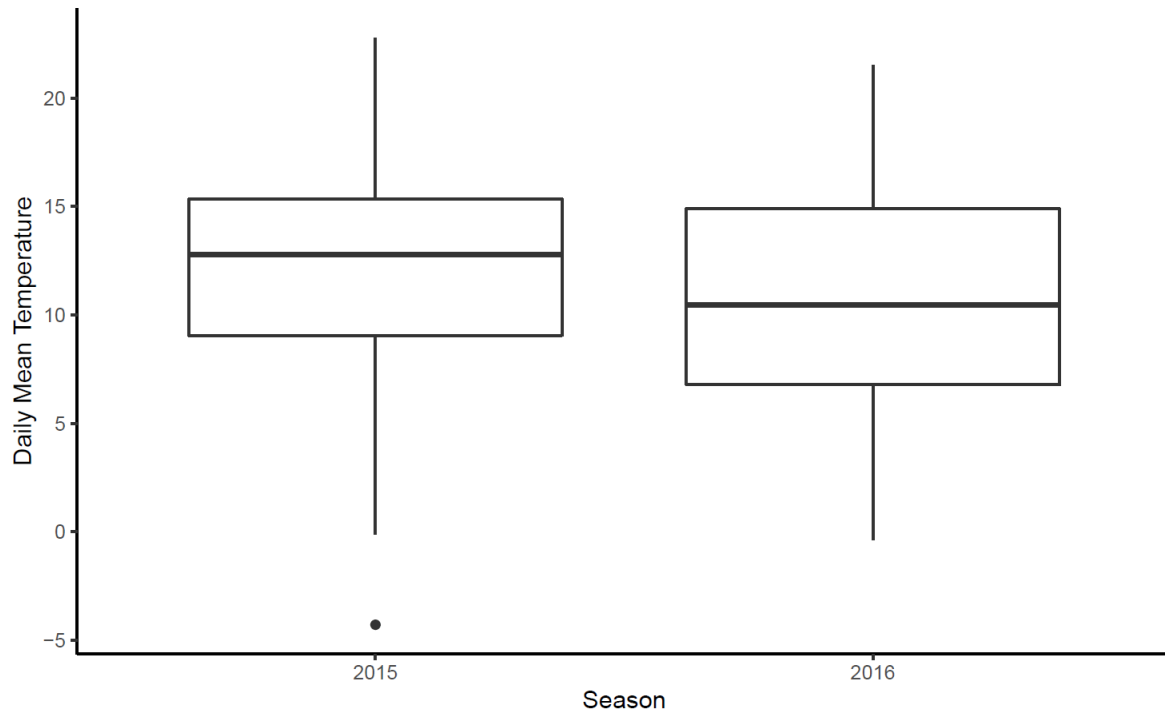


**Figure A.3.** The correlation between mean temperature during hours of video recording, and pollination rate per flower for *L. tridentata* (frequency of pollination events standardized by the number of flowers in the field of view). Pollination rates were separated by three distinct recognizable taxonomic units of insects (RTUs). No significant correlations were present.

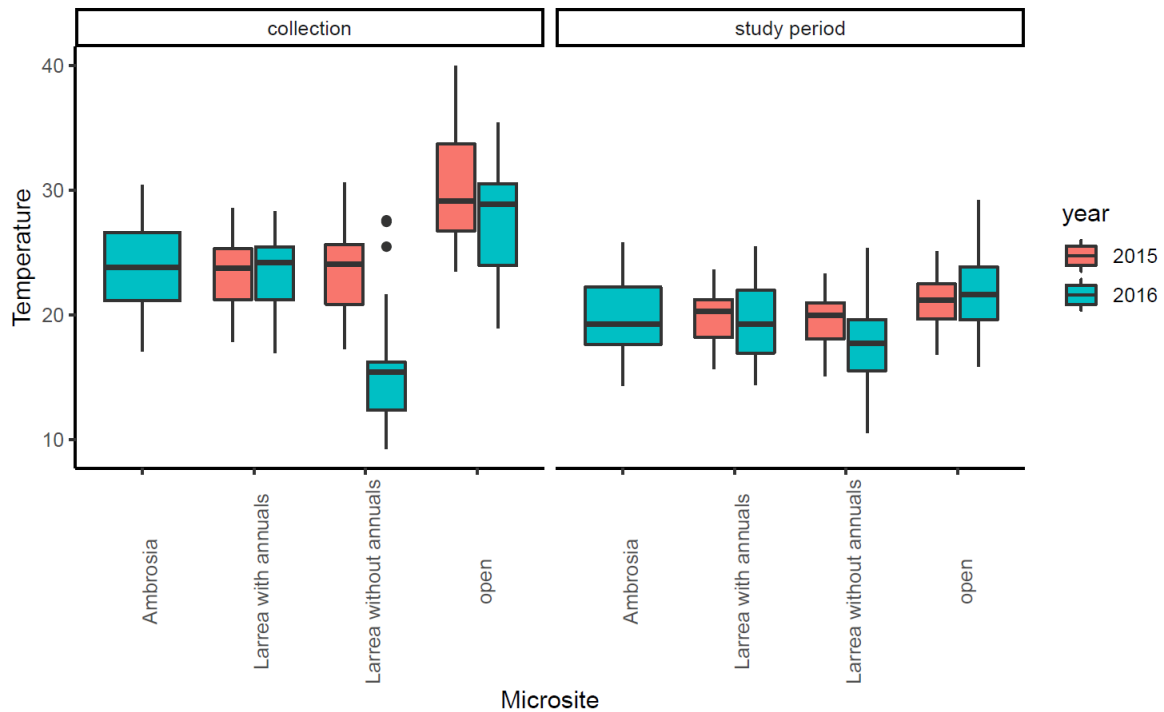


**Figure A.4.** The correlation between floral density, and raw pollinator count for *Malacothrix glabrata* during the length of video recording. Pollinator counts were separated by three distinct recognizable taxonomic units of insects (RTUs). Bees showed a significant correlation between floral density and pollinator counts in 2016 ( $r^2_{\text{adjusted}} = 0.125$ ,  $p = 0.00057$ ).





**Figure A.5.** Distribution of the daily average temperature (°C) during the previous rainy season of each year (2015: November 2014 – April 2015; 2016, November 2015 – April 2016). Data is based off of records from the closest weather station at the Sweeney Granite Mountains Desert Research Center [77]. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range.



**Figure A.6.** Distribution of the average temperature (°C) during collection of data (10:00AM – 12:00AM) and throughout the study period (April 1, 2015 – April 10, 2015 and April 6, 2016 – April 17, 2016) in 2015 and 2016 for each microsite. The horizontal lines show the median whereas the boxes represent the interquartile range, whiskers extend to maximum and minimum values unless there are outliers (circles), i.e. data points that are 1.5 times the interquartile range.

**Declaration of interests**

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: