Shrubs as magnets for pollination: A test of facilitation and reciprocity in a shrub-annual facilitation system

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ABSTRACT

The magnet species hypothesis proposes that flowering plants that are attractive to pollinators can increase the relative pollination rates of neighbouring plants by acting as 'magnets.' Here, we test the hypothesis that insect-pollinated shrub species *Larrea tridentata* and wind-pollinated shrub species *Ambrosia dumosa* act as magnets for the pollinator visitation of understory annual plant species in an arid ecosystem. As an extension to the magnet species hypothesis, we propose the double magnet species 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 used an annual plant placed near each shrub and the open to measure the effect of shrubs on annuals. The double magnet species hypothesis was tested using L. *tridentata* with and without surrounding annuals. 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 insect-pollinated shrubs act as better pollinator magnets than wind-pollinated shrubs (to determine the effects of the floral resource itself), and whether shrubs with annuals in their understory have higher pollinator visitation rates relative to shrubs without annuals. We found that insect-pollinated shrubs increased the visitation rate and duration of visits by pollinators to their understory plants and that wind-pollinated shrubs decreased the duration of visits of some insect visitors, but these relationships varied between years. While the presence of annuals did not change the visitation rate of all possible pollinators to L. *tridentata* flowers, they did decrease the visitation duration of specifically bees, indicating a negative reciprocal effect of the understory on pollination. Thus, the concentrated floral resources of flowers on insect-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 species hypothesis as an additional mechanism of facilitation by insect-pollinated shrubs to other plant species within arid ecosystems.

1. Introduction

Positive interactions between plants are a common way to increase survivability for many species. Facilitation is a type of positive interaction where a benefactor species provides benefit to a protégé without necessarily receiving any benefit or cost in return (Schöb et al., 2014; Stachowicz, 2001; Brooker and Callaway, 2009). Plant-plant facilitation is especially frequent and well documented in arid environments (Brooker et al., 2008; Filazzola and Lortie, 2014; He et al., 2013; García-cervigón et al., 2016; Fagundes et al., 2018; Badano et al., 2016; Lucero et al., 2019), where many plants rely on these interactions to better cope with the high levels of environmental stress (He et al., 2013; García-cervigón et al., 2016; Filazzola et al., 2017; Maestre et al., 2009). Shrubs are common benefactor species that represent a dominant component to many desert landscapes where they provide important re-

sources for other plants (García-cervigón et al., 2016; Badano et al., 2016; Filazzola et al., 2017, 2019; van Zonneveld et al., 2012); they give shelter from extreme heat and desiccation, wind, trampling, and herbivory (Brooker et al., 2008; Filazzola and Lortie, 2014; Fagundes et al., 2018; Perea and Gil, 2014; Ploughe et al., 2019; Armas and Pugnaire Francisco, 2009). Shrubs can also provide access to retained water sources and increased soil nutrient levels (Filazzola and Lortie, 2014; Ploughe et al., 2019; Reynolds et al., 1999). In communities where facilitation by shrubs is common, there is a distinct spatial aggregation of annual plants (Badano et al., 2016); annuals form concentrated patches under shrubs (Tirado and Pugnaire, 2003; Foronda et al., 2019) and fewer plants live out in the open. While shrubs can facilitate plants in a variety of ways, the strength and mechanism of this facilitation may depend on shrub species (Fagundes et al., 2018; Gómez-Aparicio et al., 2004; Rolo et al., 2013).

One mechanism of shrub facilitation that is rarely studied is by increasing pollinator visitation. Shrubs can increase the density and diversity of annuals (and therefore flowers) surrounding them (Lucero et al., 2019; Filazzola et al., 2019; McIntire and Fajardo, 2014) and increases in floral density and diversity can increase pollinator visitation (Hegland and Boeke, 2006; Fowler et al., 2016; Ghazoul, 2006). Therefore, facilitation of flowering plants through the standard mechanisms (as outlined above) can further result in increased pollinator visitation (Ghazoul, 2006; Ponisio et al., 2019; Papanikolaou et al., 2017). 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-pollinated shrubs may be able to further facilitate their understories through their own flowering in addition to the ameliorative effects and abiotic resources they provide (Ruttan et al., 2016). Shrubs also provide habitat and shelter for a variety of animals, including insects (Filazzola et al., 2017; Ruttan et al., 2016), potentially increasing pollination through apparent pollination support (increasing pollination through mechanisms other than co-blooming) (Braun and Lortie, 2019). Pollinator interactions have generally not been included in the shrub facilitation literature despite being an important aspect of many angiosperms' reproduction and representing an important part of desert facilitation networks that need to be investigated.

The magnet species hypothesis (or the magnet species effect) is a more recent development of pollinator facilitation that proposes that a flowering plant that is attractive to pollinators (but not necessarily abundant) can act as a 'magnet' and increase the relative rate of pollination for neighbouring plant species (Laverty, 1992; Molina-Montenegro et al., 2006; Underwood and Hambäck, 2020). This hypothesis is generally tested using co-flowering plant species (Gilpin et al., 2019; Thomson et al., 2019; Mesgaran et al., 2017), but it has not been tested in plant-plant facilitation assemblages. Both insect-pollinated flowering shrubs and non-flowering (or wind-pollinated) shrubs have the potential to be attractive to insect pollinators (as outlined above) both because of and regardless of flowering. Therefore, shrubs can potentially act as magnet species. Shrub-annual facilitation complexes in deserts are good study systems to test the magnet species hypothesis with shrubs both because shrubs are already known to benefit other plants and animals through other mechanisms in desert systems (Brooker et al., 2008; He et al., 2013; Filazzola et al., 2017; Ploughe et al., 2019) and because deserts have a rich diversity of solitary bee species giving ample opportunity for shrubs to act as magnets for different bee species (Minckley, 2008). The magnet species effect could represent another essential ecological function that shrubs play in deserts.

Facilitation pathways are often multi-directional and non-binary (Rathcke, 2012; Lortie et al., 2016; Schöb et al., 2014; Montesinos-Navarro et al., 2019; Holzapfel and Mahall, 1999; Bronstein, 2009); however, bidirectional interactions that include facilitation are less commonly tested (but see – Schöb et al., 2014a, 2014b; Montesinos-Navarro et al., 2019; Sortibrán et al., 2014; Opedal and Hegland, 2020). Most of the literature that does report on bidirectional interactions indicates that feedback for the benefactor species is negative (Michalet et al., 2011; Cranston et al., 2012; Schöb et al., 2013; Rodríguez-Buriticá and Miriti, 2009) and that there are costs associated with facilitation for the benefactor species (Schöb et al., 2014b; Michalet et al., 2011). These costs may include below ground competition for water and nutrient resources that can lead to slowed growth and reduced flower and seed production (Schöb et al., 2014b; Michalet et al., 2011; Ludwig et al., 2004). However, 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 (Montesinos-Navarro et al., 2019; Sortibrán et al., 2014; Pugnaire et al., 1996; Armas and Pugnaire, 2005). The indirect effect of pollinators on the benefactor is typically not examined in studies of bidirectional facilitation between plants and represents a novel research gap in this literature. We propose the double magnet species hypothesis in which the floral island created under shrubs due to plant-plant facilitation pathways not only benefit from increased pollination levels but can in turn facilitate the benefactor through increased pollinator service; thus making facilitation bidirectional between shrubs and surrounding annuals. Examining whether bidirectional interactions are positive, neutral, or negative is important when considering the ecological and evolutionary impacts of these interactions on ecosystem functioning (Schöb et al., 2014b).

Here, we investigated whether desert shrubs and annual plants facilitate each other by increasing pollinator attraction. We hypothesized that the floral resource island created by shrubs and their understory annual plants will have positive effects on pollinator visitation to both the annuals and the shrub. 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 because of the higher concentrations of floral resources surrounding shrubs, (2) annuals under flowering insect-pollinated shrubs (*Larrea tridentata* (D. C.) Coville) will have a higher frequency and duration of pollinator visitations than annuals under wind-pollinated shrubs (*Ambrosia dumosa* (A. Gray) W. W. Payne) 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, we explore how pollinators respond to different desert plant communities including both insect and wind-pollinated shrubs and their associated annual plants.

2. Material and methods

2.1. Study species

We used two shrub species as study species that overlap in range and are common throughout the Mojave Desert and the Southwestern United States (Calflora, 2014). *Larrea tridentata* (Zygophyllaceae) is a large (average 1.6-m height in the study area; $n = 114$), flowering, entomophilous (insect-pollinated) shrub, commonly referred to as creosote bush (Schafer et al., 2012). It is one of the most widely distributed plants found in arid areas of the southwestern United States (Lajtha and Whitford, 1989). *Ambrosia dumosa* (Asteraceae) is a smaller (average 0.56-m height in the study area; $n = 27$) anemophilous (wind-pollinated) shrub, that is also widely distributed in this area (Lajtha and Whitford, 1989). Both L. *tridentata* and A. *dumosa* can facilitate annual plants through physical protection from herbivores and increased water and nutrient access (Filazzola et al., 2019; Rodríguez-Buriticá and Miriti, 2009; Whitford et al., 1997; Miriti, 2006; Schafer et al., 2012). In addition, L. *tridentata* can increase the abundance and diversity of insect species relative to open sites (Ruttan et al., 2016); however, the ability of either shrub to facilitate plants through pollination has not yet been tested.

Larrea tridentata 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 (Calflora, 2020). Over 120 species of bees (Hymenoptera: Apoidea) are known to visit the flowers of L. *tridentata* (Hurd and Linsley, 1975; Minckley et al., 1999, 2000). It is therefore a useful species for the study of the magnet species 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 because it will not provide any of its own floral resources but may still provide benefit to pollinators through other mechanisms. Bees and other pollinators typically prefer colourful flowers with easy access to pollen and nectar (Lunau and Wester, 2017; McCall and Primack, 1992; Miller et al., 2011). 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 (Filazzola and Lortie, 2014; Holzapfel and Mahall, 1999; Rodríguez-Buriticá and Miriti, 2009). By facilitating other annuals *A. dumosa* may increase the floral display in its understory even if it does not provide its own floral resources.

We used the annual *Malacothrix glabrata* (A. Gray ex D. C. Eaton) A. Gray as a phytometer to test for differential effects of microsite on pollinators in this study. A phytometer is a plant 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 (Clements and Goldsmith, 1924; Mwangi et al., 2007). Using a phytometer allowed us to ensure the presence of annuals (background levels were low) as well as allow for consistency between experimental plots that could not have been attained using the existing annual populations. We chose our phytometer, *M. glabrata,* because it is already a wide-spread insect-pollinated native annual plant in the area (Calflora, 2014; André, 2006; Wainwright, 1978) and it has bright, symmetrical yellow flowers that are comparable to L. *tridentata* (the shrub treatment that was insect-pollinated).

2.2. Study site

We conducted this study 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. S1) 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 (Bowers, 1984; Lei, 1998). Annual plants are common in the area and include the following native species: *M. glabrata, Chaenactis fremontii* A. Gray, *Eriophyllum wallacei* (A. Gray) A. Gray, *Cryptantha micrantha* (Torr.) I. M. Johnst., *Camissonia claviformis* (Torr. & Frém.) A. Heller, *Phacelia distans* Benth., *Pectocarya spp.*, *Eriophyllum lanosum* (A. Gray) A. Gray, and *Rafinesquia neomexicana* A. Gray (André, 2006). Insects and pollinators are also abundant (Ruttan et al. 2016). Precipitation is sporadic and low with a 10-year mean accumulated annual precipitation (2004–2014) of 138 mm in the Mojave Desert (Bowers, 1984; Smith et al., 2014). The average daily maximum temperatures in the summer is 40 °C, and the minimum is 1 °C in January (1937–2007 records) (WRCC 2020).

2.3. Study design

To determine whether desert shrubs act as pollinator magnets, we compared pollinator visitation rates between three microsites: 1) under L. *tridentata* shrubs, 2) under *A. dumosa* shrubs (2016 only), and 3) an open area at least 1 m from the drip line of any adjacent shrubs. To determine whether annual communities act as pollinator magnets for shrubs, we compared pollinator visitations between two treatments: 1) L. *tridentata* with surrounding annuals (the same as 1 in the previous experiment) and 2) L. *tridentata* without surrounding annuals. We harvested a total of 20 *Malacothrix glabrata* plants per treatment (80 total) 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 m 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 (still parallel to the ground), and the height (Filazzola et al., 2017). We randomly selected 4 of these 32 sites (new sites every day) for video recording each morning using a random number generator to avoid repeated measures. We did not use selected sites that did not have flowering L. *tridentata*, the nearest flowering L. *tridentata* was chosen instead. We randomly allocated the two L. *tridentata* shrubs within each site to a treatment (annuals present or annuals not present).

We recorded visitation by pollinators over 8 days during peak flowering: between April 1st and April 10th, 2015, and April 6th and April 17th, 2016. 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 h each day. Videos were recorded between 10:30AM and 12:00PM, when pollinator activity was at its peak. Four replicates were filmed per treatment per day (one replicate per site). Two microsites (L. *tridentata* and open) were filmed in 2015 and three microsites (L. *tridentata, A. dumosa,* and open) were filmed in 2016. *Larrea tridentata* are too large (approximately 200 flowers per shrub) to capture visitations accurately with video whilst retaining enough detail for pollinator identification; therefore, following video recording of *M. glabrata* pollinator visits, two researchers recorded pollinator visits to L. *tridentata* pollinator with 15 min *in-situ* observations. Visitations and the duration of the visit (only in 2016) that lasted at least 1 s were recorded.

In order to determine differences in temperature between microsites, we randomly placed 20 HOBO pendent loggers at five areas within the study site, so that there were five replicates per unique treatment type. In each of the five areas, we placed a logger under a L. *tridentata* shrub with annuals present, under a L. *tridentata* shrub with annuals removed, under an *A. dumosa* shrub, and in an adjacent open area. Loggers were placed on the north side of the shrub in all cases and recorded temperature hourly for the duration of the study period each year. Environmental data (including daily mean temperature, precipitation, and mean radiation) for the rainy season before each year (November – April) was downloaded from the Western Regional Climate Center for the nearest weather station (WRCC 2020).

2.4. Analysis

We processed videos and collected visitation data each time an insect visited an open flower for a minimum of one second. The type of pollinator, number of flowers visited, duration of pollination (difference between pollination start and stop times) were recorded. Insects were identified to their lowest recognizable taxonomic unit (RTU). The RTU is highly variable between taxa when based only on video imagery. Some few insects can be reliably identified to species (e.g. *Apis mellifera*) and several to genus (e.g. *Bombus*) and family (e.g. Bombyliidae, the bee flies); however, the finest RTU that all pollinators could be identified to based on their profile, colouring, and movement was either order (e.g. Diptera, the flies) or superorder (e.g. Apoidea, the bees). Enough detail was available to distinguish between bees and their mimics. From these data, we calculated the total number of visitations and total visitation duration by pollinators. While cameras were each set out for 90 min, inconsistency in battery lifetime and other malfunctions meant that actual film time varied greatly. We excluded instances in which videos were less than 15 min since these time periods were not long enough to garner a significant sample (two videos were less than 15 min). Mean video time (not including times of less than 15 min) was 81 min (standard deviation = 9.8 min). Both floral density (number of flowers in frame) and total film time were noted.

We modelled both the number of pollinators (visitation frequency per flower) and the visitation time per flower of visitors to *M. glabrata* using generalized linear mixed models (GLMM; using the R package glmmTMB) (Brooks et al., 2017) with microsite (open, under L. *tridentata*, or under *A. dumosa*), insect RTU (bees, flies or other), and mean temperature during the hours of recording as fixed factors. Site id and day were included as random factors while video length was used as an offset variable to account for differences in total recording time between videos. We analysed data for 2015 and 2016 separately 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 effect of year, we fit models to all visitation and visit duration data excluding *A. dumosa* with year as an additional fixed factor. In order to examine
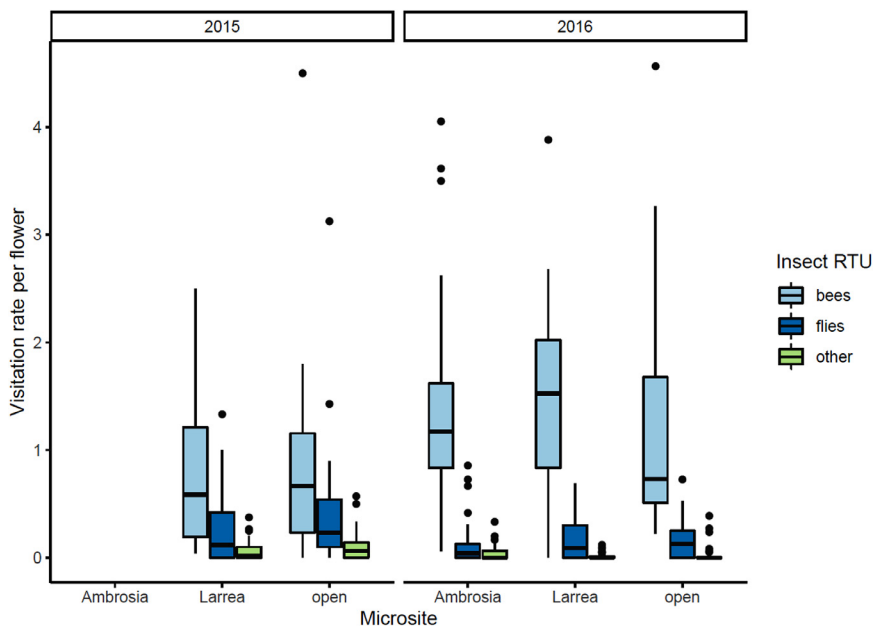
Fig. 1. Visitation rate of pollinators to the annual plant *Malacothrix glabrata* obtained through video. Visitation was compared between the three treatment groups (annuals under wind-pollinated *Ambrosia dumosa*, annuals under insect-pollinated *Larrea tridentata,* annuals in the open), for bees, flies, and other insect pollinators in 2016 and two treatment groups in 2015. The *Ambrosia dumosa* treatment was only tested 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.

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*. 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. This study was conducted in the Mojave Desert, California (35.0612°, −115.6643°), using video observation. Models include microsite (presence, species, and absence (open) of a shrub), insect RTU (recognizable taxonomic unit), and temperature (during study observations). 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		
	χ^2	df	p	χ^2	df	p
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
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

* $p < 0.05$.

how different insect types responded to temperature and floral density we used linear models to model visitation rate of each insect type to *M. glabrata* as a function each of temperature (during the study time) and floral density (number of *M. glabrata* flowers).

We modelled both the number of pollinators (visitation frequency per flower) and the visitation time per flower of visitors to L. *tridentata* using generalized linear mixed models (GLMM; using the R package glmmTMB) (Brooks et al., 2017) with treatment type (annual community presence or absence), insect RTU, mean temperature, shrub volume, and year as fixed factors. Site id and day were included as random factors. Pollinator visitation data errors (in both cases) were modelled with a Poisson distribution (Consul and Jain, 1973) and visitation duration data errors (in both cases) were modelled with a Tweedie distribution (Candy, 2004). Post hoc comparisons were done using the emmeans package in R (Lenth, 2019). In order to examine how different insect types responded to temperature we used linear models to model visita-

tion rate of each insect type to L. *tridentata* as a function of temperature (during the study time).

We compared temperature data during the study period between years for all microsites and treatments (except annuals under *A. dumosa*) using a GLMM fit against treatment and year with site id as a random factor and a heterogeneous unstructured covariate included to account for the time series (Brooks et al., 2017). Error was modeled to a normal distribution. We fit additional GLMM's using just the data from 2016 (including the *A. dumosa* microsite) to compare temperatures between all microsites. We tested temperature 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 (Walsh, 1947). All data were analyzed using R version 4.0.2 (R Core Team 2018). All code is available at https://cjlortie.github.io/magnet.hypothesis.Mojave/ and all data is deposited at the Knowledge Network for Biocomplexity (KNB; https://knb.ecoinformatics.org/view/doi:10.5063/H41PTW) (Ruttan et al., 2020).

3. Results

In 2015, a total of 838 insects were video recorded visiting *M. glabrata* while 2578 were recorded in 2016 after an extra microsite was added. In contrast, we directly observed 210 insects visiting L. *tridentata* in 2015 and 150 insects in 2016. In all cases bees were the most common visitors making up more than 60% of sightings followed by flies and then all other insects.

Pollinators visited *Malacothrix glabrata* more frequently (Fig. 1) and for longer (Fig. 2) when associated with L. *tridentata* (the insect-pollinated shrub) relative to the open in 2015, but not 2016 (Table 1; prediction 1). Flies visited *M. glabrata* plants associated with *A. dumosa* for a shorter time period 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 S1, predictions 1 & 2). In both years, bees were the most common visitors and visited for the longest periods of time (Fig. 1& Fig. 2, Table S1). While there was no difference in the effects of microsite or in the total number or duration of visits between 2015 and 2016 (all $p > 0.05$), bees visited *M. glabrata* more frequently in
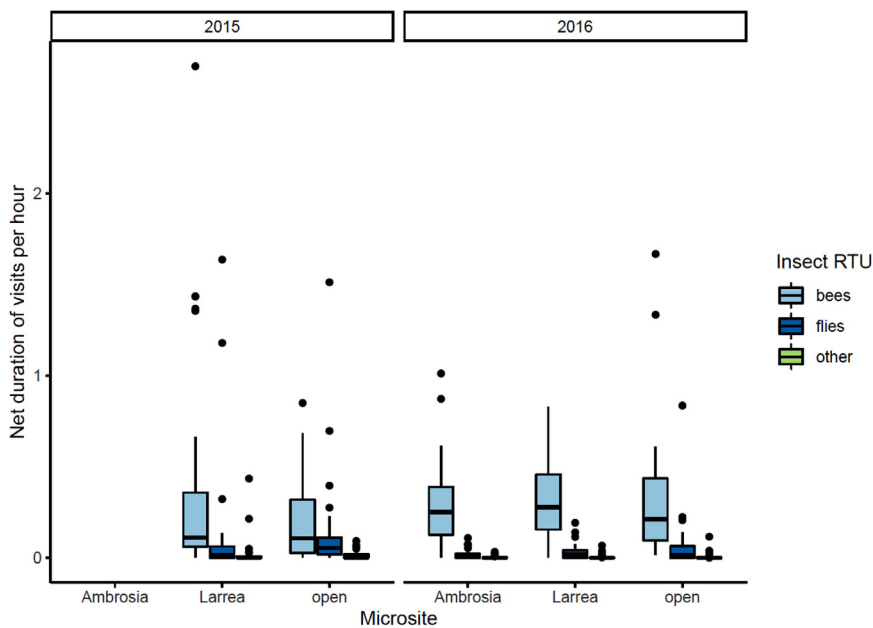
Fig. 2. The duration of visits (in hours) by pollinators to the annual plant *Malacothrix glabrata,* obtained through video. Visitation was compared between the three treatment groups (annuals under wind-pollinated *Ambrosia dumosa*, annuals under insect-pollinated *Larrea tridentata,* annuals in the open), for bees, flies, and other insect pollinators. The *Ambrosia dumosa* treatment was only tested in 2016. 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.
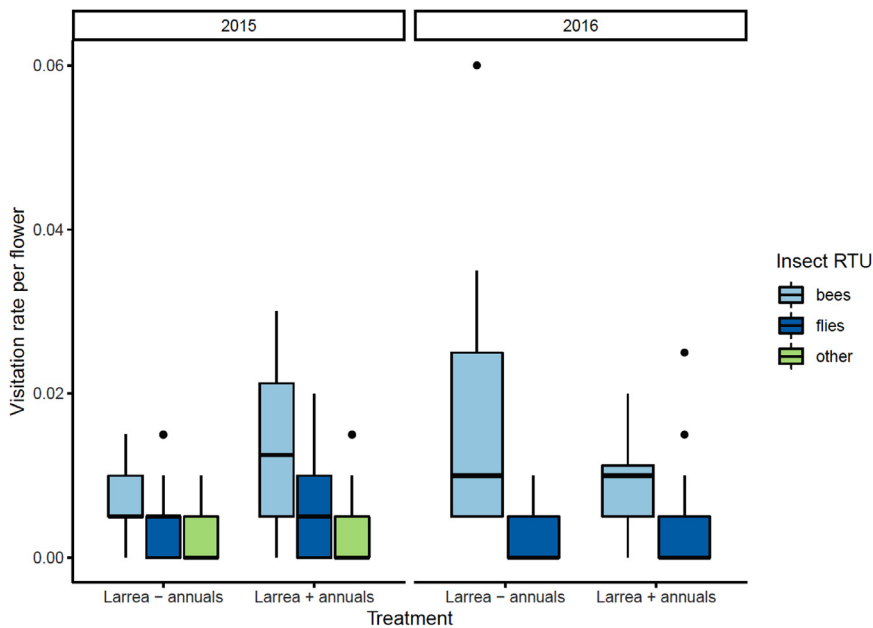
Fig. 3. Visitation rate by pollinators to *Larrea tridentata,* obtained through *in-situ* observation. Visitation was compared between the two treatment groups (L. *tridentata* with understory annuals present and L. *tridentata* with understory annuals absent) for bees, flies, and other insect pollinators. Insects other than bees and flies were not observed visiting L. *tridentata* 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.

2016 than 2015 (post-hoc test: $p < 0.05$) and flies and other pollinators visited significantly longer in 2016 than 2015 (post-hoc tests: $p < 0.05$).

The presence of annuals did not affect the number of visitors to L. *tridentata* (Fig. 3, Table 2, prediction 3); however, the presence of annuals decreased the duration of visits to L. *tridentata* (Fig. 4, Table 2). Bees (the most abundant visitors) drove this effect (Fig. 3, Table S1) by visiting for longer periods of time on L. *tridentata* flowers without annuals than with annuals (Fig. 4, Table S1).

Mean temperature (during observation hours) positively predicted visitation rate and duration of insects to *M. glabrata* in 2015, but not 2016 (Table 1). Bees and flies both visited *M. glabrata* more frequently with increasing temperature in 2015 (Fig. S2, Bees: $r^2_{adjusted} = 0.0708$, $df = 59$, $p = 0.022$; Flies: $r^2_{adjusted} = 0.181$, $df = 59$, $p = 0.00037$). In 2016, insects other than bees and flies visited *M. glabrata* less frequently with increased temperatures (Fig. S2, $r^2_{adjusted} = 0.120$, $df = 82$, $p = 0.00073$). Temperature did not predict insect visitation to L. *tridentata* (all $p > 0.05$,

Fig. S3). Bees visited *M. glabrata* with more flowers more frequently, but only in 2016 (Fig. S4, $r^2_{adjusted} = 0.125$, $df = 82$, $p = 0.00057$).

The mean daily temperature in the previous rainy season was higher in 2015 than 2016 (Fig. S5; $t_{357} = 3.03$, $p = 0.0026$); 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, $t_{356} = 0.224$, $p = 0.82$; precipitation: $total_{2015} = 91.9$ mm, $total_{2016} = 100.6$ mm, $t_{356} = -0.171$, $p = 0.86$). The average temperature during collection (10:00AM – 12:00 PM) was similar in 2015 and 2016 (Fig. S6, Table S2 & Table S3); however, the average temperature during the entire study period (24 hour cycle) was significantly lower in 2016 than 2015 (Fig. S6; Table S2 & Table S3). Similarly, temperatures were higher in the open and under L. *tridentata* (with annuals) in 2016 than 2015 throughout the study period, but not within recording times (Fig. S6, Table S3). As expected, temperatures were always higher in the open than under any shrub, both during collection and throughout the study period for both years (Fig. S6,
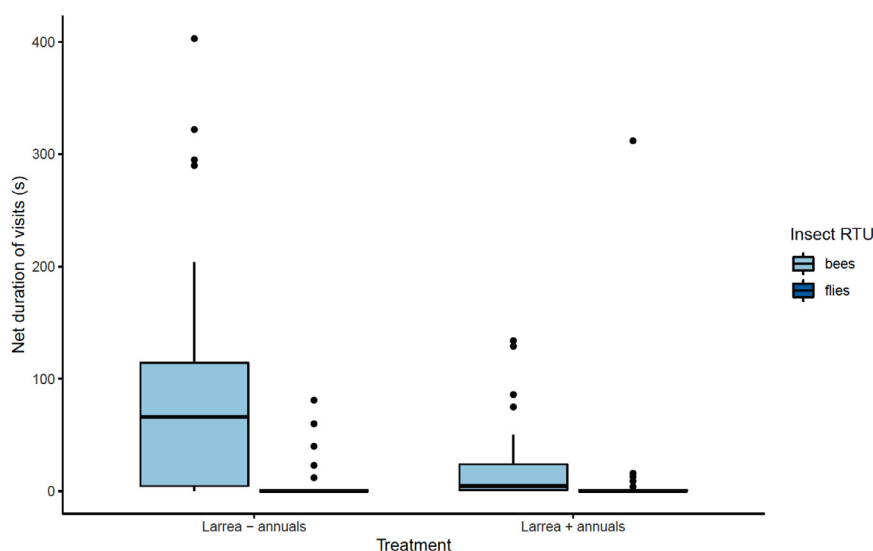
Fig. 4. The duration of visits (in seconds) by pollinators to L. *tridentata,* obtained in 2016 through *in-situ* observation. Visitation was compared between the two treatment groups (L. *tridentata* with understory annuals present and L. *tridentata* with understory annuals absent) for bees and flies. Insects other than bees and flies were not observed visiting L. *tridentata* 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.

Table 2

A summary of the general linear mixed models used to test for differences in pollinator visitation rates (per flower) and duration to the insect-pollinated shrub *Larrea tridentata*. 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 *in-situ* observation. Models include treatment (presence or absence of annuals), insect RTU (recognizable taxonomic unit; bees, flies, or other), temperature (during study observations), year (for visitation rate only) and shrub volume.

	Visitation Rate			Visitation Duration		
	χ^2	df	p	χ^2	df	p
Larrea treatment	0.0163	1	0.9	9.93	1	0.0016*
Insect RTU	0.396	2	0.53	31.4	2	<0.0001*
Year	0.0024	1	0.96			
Temperature	0.0063	1	0.94	3.67	1	0.055
Shrub Volume	0.0043	1	0.95	0.732	1	0.39
Larrea treatment: Insect RTU	0.0023	2	0.96	4.61	2	0.032*

* $p < 0.05$.

Table S3). There was no difference between temperatures near L. *tridentata* and *A. dumosa*; however, temperatures near L. *tridentata* with annuals were significantly higher than temperatures near L. *tridentata* without surrounding annuals, but only in 2016 (Fig. S6, Table S3).

4. Discussion

Shrubs are a foundation species within desert ecosystems, and some can positively influence pollination of flowering plants or plants within their understory. The insect-pollinated shrub L. *tridentata* facilitated understory plants by increasing visitation rates and duration of pollinator visits in one year (supporting the first prediction), 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 species hypothesis for increased pollinator visitation to less attractive plant species 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 pollinator visitation or visit duration for understory plants relative to the wind pollinated shrub *A. dumosa* (contrary to the second prediction), the year in which both shrubs were studied L. *tridentata* did not increase pollinator visitation or visit duration relative to the open treatment 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 third prediction associated with the double magnet species hypothesis was not supported, but rather the opposite was observed; pollinators visited for longer periods of time 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 that shrubs form important linkages between plant and pollinator taxa and are important components of desert interaction networks.

4.1. Magnet species hypothesis

Shrubs are important species in desert communities that mediate pollinator interactions with understory plant species. Shrubs like L. *tridentata* can act as magnets for pollinators and increase the pollinator visitation frequency and duration for understory annual plants; however, 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*, flies visited the flowers of *M. glabrata* for less time under the canopy of *A. dumosa* than in 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 effect is not likely a consequence of floral dilution (where increased floral resources leads to a reduction of pollination for each flower (Wenninger et al., 2016)). Rather, it is possible that the shrub increases the risk of predation to flies. Shrubs facilitate animals in similar ways to plants: by providing shelter and habitat (Filazzola et al., 2017) thereby increasing the abundance of animals surrounding them relative to the open (Ruttan et al., 2016; Lortie et al., 2020). Therefore, it is not unlikely that there are more 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 the amount of time flies spend on flowers under *A. dumosa*, there is no evidence that this reduction impacts the pollination of *M. glabrata*. Not all visitors of flowers are effective pollinators (Sahli and Conner, 2007; de Santiago-Hernández et al., 2019; Gallagher and Campbell, 2020). While *M. glabrata* is known

to be insect pollinated (Wainwright, 1978), 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 (Ploughe et al., 2019). The stress gradient hypothesis (SGH) states that as stress increases, so do positive interactions (Maestre et al., 2009). Both 2015 and 2016 were the last two years of a 5-year long drought in California where precipitation levels were decreased and temperatures increased (Lund et al., 2018). While temperatures were similar during collection for both years (aside from within the L. *tridentata* without annuals treatment) and precipitation and radiation levels were similar, 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 floral patches such as those created by L. *tridentata* could have a greater draw.

In addition to decreased abundance of floral resources, it is also possible that flowers under shrubs could be more rewarding in hotter years. Nectar levels often decrease with high temperatures (Takkis et al., 2018), therefore flowers may have more nectar in the cooling shade of a shrub. This pattern of increased nectar under shrubs would likely be more pronounced the higher the temperatures in the open. The heat stress of pollinators in extreme heat may also decrease in the lower temperatures under shrubs, potentially leading to increased pollinator activity (Nikolova et al., 2016). While pollinator activity is often negatively correlated with temperature (Nikolova et al., 2016; Omoloye and Akinsola, 2006; Hamblin et al., 2018), 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 floral density can influence visitation rates to flowers. Concentrated floral resources provided both by and 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 (Rathcke, 2012; Klumpers et al., 2019) —i.e. dense stands with more individual flowers and less distance between them (Klumpers et al., 2019; Pyke, 1979; Knight, 2003). This relationship supports the increase in pollinator visitation rates observed for annual plants under L. *tridentata* in 2015 and the positive correlation between bee visitation and floral density in this experiment.

In contrast to 2015, the increased floral concentration of L. *tridentata* did not result in increased pollinator visitation in 2016. A difference in pollinator availability between years may explain this difference; there was, on average, higher bee visitation across microsites in 2016 relative to 2015 (even accounting for the extra microsite surveyed) which may be reflective of a higher population of bees in 2016. Lundgren et al. (2015) 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 (due to their increased floral density) on pollinators while in 2016 pollinator availability was saturated. This explanation 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 in terms of both 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 provide refuge and have other non-trophic interactions with several an-

imal species including insects in general, small mammals, and lizards (Filazzola et al., 2017; Ruttan et al., 2016; Lortie et al., 2016). Similar relationships also occur between cushion plants and insects in alpine environments where the abundance of both arthropods in general and specifically pollinators were higher on cushions in contrast to open areas (Molina-Montenegro et al., 2006; Molenda et al., 2012; Reid and Lortie, 2012). Cushion plants act similarly to desert shrubs by facilitating the species that grow on them through biotic and abiotic mechanisms (Reid and Lortie, 2012). The shrub species (L. *tridenta* and *A. dumosa*) could therefore similarly 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 pollinator visitation 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 species hypothesis

Annuals in this system decreased the duration of pollinator visits to the shrubs that facilitated them. We proposed the double magnet species effect where shrubs increase pollination of annuals and annuals increased the pollination of shrubs due to increased floral density. However, floral density is not always positively associated with pollinator visitation. 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 (Otway et al., 2005). While annuals did not increase visitation rate, indicating a simple saturation of the resource concentration effect on density, annuals decreased the duration of pollinator visits. Previous studies (Iler and Goodell, 2014; Muñoz and Cavieres, 2008) also reported this trend of decreased visitation duration at higher floral densities and complexities. 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.

In addition to the possible effect of resource dilution, differences in temperature could also explain the decrease in visit duration in the presence of annuals. Temperatures of L. *tridentata* shrubs without annuals were significantly lower than shrubs with annuals in 2016 (the only year in which visitation duration was measured for L. *tridentata*). Because bee visitation was positively correlated with temperature, this disparity in temperature could explain differences in bee visit duration between L. *tridentata* with and without annuals. This potential 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 further adds to the function of shrubs as 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 (Ellison et al., 2005; Lamy et al., 2020). The effect of shrubs on desert plant-pollinator

networks 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 (Potts et al., 2010; Weiner et al., 2014; Goulson et al., 2015). These stressors drive species towards positive interactions. Both increased temperatures (a symptom of climate change) and lower pollinator populations are possible explanations for the facilitation observed in 2015 but not 2016.

Furthermore, 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 (Piao et al., 2019; Forrest, 2015, 2016). The reduced temperature found under shrubs has the potential to offset this phenological mismatch, making shrubs increasingly important as both refuges and magnets in maintaining the network structure of plant-pollinator interactions, even if species aren't initially lost (Scaven and Rafferty, 2013). 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 (Lundgren et al., 2015; Ramos-Jiliberto et al., 2020). However, if the magnet effect of shrubs increases with decreased pollinator abundance then shrubs can act as a buffer to mediate the effects of warming in desert systems by increasing the pollination of plants around them. 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. We provide evidence that shrubs like L. *tridentata* give indirect benefit by increasing access to pollinators. We propose that increased floral density and by providing abiotic refuge for pollinators shrubs increase pollinator visitation 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 important subset of positive interactions within desert communities. These interactions will be especially important to consider considering climate change and pollinator declines that threaten these areas, solidifying the position of shrubs as foundation species within deserts.

Declaration of Competing Interest

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.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cris.2021.100008.

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