Article

IMPORTANT POLLINATOR SPECIES FOR CONSERVING RARE PLANT SPECIES ENDEMIC TO SAN CLEMENTE ISLAND, CALIFORNIA

J. A. Hazlehurst[1]*, S. Calloway[2], D. Knapp[3]

[1]*California State University East Bay, 25800 Carlos Bee Blvd, Hayward, CA.*
[2]*Eldorado National Forest, Pacific Ranger District, 7887 Highway 50, Pollock Pines, CA.*
[3]*Santa Barbara Botanic Garden, 1212 Mission Canyon Rd, Santa Barbara, CA.*

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*Corresponding author:
jenny.hazlehurst@csueastbay.edu

Abstract—Much effort has been spent on the conservation of rare, threatened, and endangered plants in the biodiversity hotspot of the California Floristic Province, however little is known about the identity of their pollinators. In this study we provide the first formal study on the identity of the invertebrate pollinators of five rare endemic island plant species from San Clemente Island, the southernmost of the California Channel Islands: *Delphinium variegatum* ssp *kinkiense*, *Lithophragma maximum*, *Malacothamnus clementinus*, *Malva assurgentiflora* ssp *glabra*, and *Sibara filifolia*. We surveyed plant-pollinator interactions at populations of each focal plant species using timed sweep-netting. We used pollinator capture data to compile bipartite interaction networks for each plant population, and calculated centrality indices (degree, betweenness centrality, and closeness centrality) of pollinators to identify species important to network stability. We found a significant effect of pollinator taxonomic group (fly, bee, wasp, or Lepidopteran) on some indices of pollinator centrality in interaction networks, and variation in pollinator centrality between different locations. Hoverflies, moths, and butterflies were important generalists with higher network centrality across all plant populations, while bees tended to be more specialists within their networks, except for the *Malva assurgentiflora* ssp *glabra* network, where bees were on average of higher centrality than flies. We recommend targeted restoration practices for future study that could support pollination both directly and indirectly to focal rare plant species of conservation interest across plant populations. These practices could augment general pollinator conservation best practices such as reducing pesticide use and planting native plant species to provide increased pollination to endangered plants.

Keywords—California Channel Islands, endangered plants, pollination, conservation

INTRODUCTION

A great deal of effort has been invested in the protection of endangered and threatened plant species in the California Floristic Province, a biodiversity hotspot (Mittermeier et al. 2011), yet relatively little is known about the identity and natural history of their pollinators. For many zoophilic plants, outcrossing can lead to improved seed set, seed mass, and higher germination rates (Sihag 1986; Waser & Price 1989; Waser & Price 1991). As endangered plant conservation requires achieving genetically diverse populations, increased number of populations, and larger population sizes (e.g. Schemske et al. 1994), it is thus of critical importance to plant conservation to conduct detailed studies of the pollinators of endangered plant species. Network analysis tools can be used to identify pollinator species that support plants of conservation concern and that contribute to the overall stability of the plant-pollinator interaction network to which that plant belongs.

A plant-pollinator interaction network is constructed by setting plants and pollinators as different categories of nodes, with a link between them indicating that the plant node in question is visited by the pollinator node in question. The position of an individual plant or pollinator node within the network can vary from central (connected, directly or indirectly, to many other species in the network) to non-central (connected to only one or a few other species). High-centrality species are important to the stability of networks, and when they are removed from ecosystems network structure decays more rapidly (Memmott et al. 2004). These species can thus serve as potential priorities for conservation of plant-pollinator interactions (e.g. Crespo et al. 2022) because they may indirectly support the focal endangered or threatened plant species, in addition to those pollinators that directly interact with the focal plant species. These priority species can be supported in addition to the application of general best practices for pollinator conservation such as reduction in pesticide use (e.g. Goulson et al. 2015) and augmenting pollinator habitat broadly with native plants (e.g. Wratten et al. 2012).

The California Channel Islands are home to an incredible diversity of endemic species, including many rare, threatened, and endangered plants. Many endemic plants on the islands have been decimated by browsing, grazing, and disturbance from introduced livestock and game (McEachern et al. 2016). San Clemente Island was transferred to the U.S. Navy in 1934. The island was used as ranchland for sheep, cattle, and goats since the early 1800's, following the residence of Tongva peoples since the middle Holocene (Byrd & Raab 2007). Pigs and mule deer were also introduced to the island for sport hunting in the 1950's and 1960's. While all feral ungulates have been removed from San Clemente Island (McEachern et al. 2016), plant populations are still recovering and face threats from invasive plants, climate change, low genetic diversity, and human disturbance, including military training exercises (U.S. Fish & Wildlife Service 2021). For this study, we conducted pollinator surveys on the southernmost Channel Island, San Clemente Island (Fig. 1), for five different focal endangered or threatened plant species, some of which have been recently de-listed but are still of concern: *Delphinium variegatum* Torr. & A. Gray ssp. *kinkiense* (Munz) (Family: Ranunculaceae), *Lithophragma maximum* Bacig. (Family: Saxifragaceae), *Malacothamnus clementinus* Munz & I. M. Johnst. (Family: Malvaceae), *Malva assurgentiflora* ssp *glabra* (Kellogg) M.F. Ray (Family: Malvaceae), and *Sibara filifolia* (Greene) Greene (Family: Brassicaceae) (Fig. 2).

In this study, we identify species that have the potential to directly or indirectly affect plant reproduction at these five focal plant species on San Clemente Island across their entire blooming period. We identify the direct invertebrate floral visitors to our focal plants, and also use bipartite plant-pollinator interaction networks to calculate the centrality indices of normalized degree (number of links with other species divided by total number of possible links), closeness (the average number of steps between the pollinator

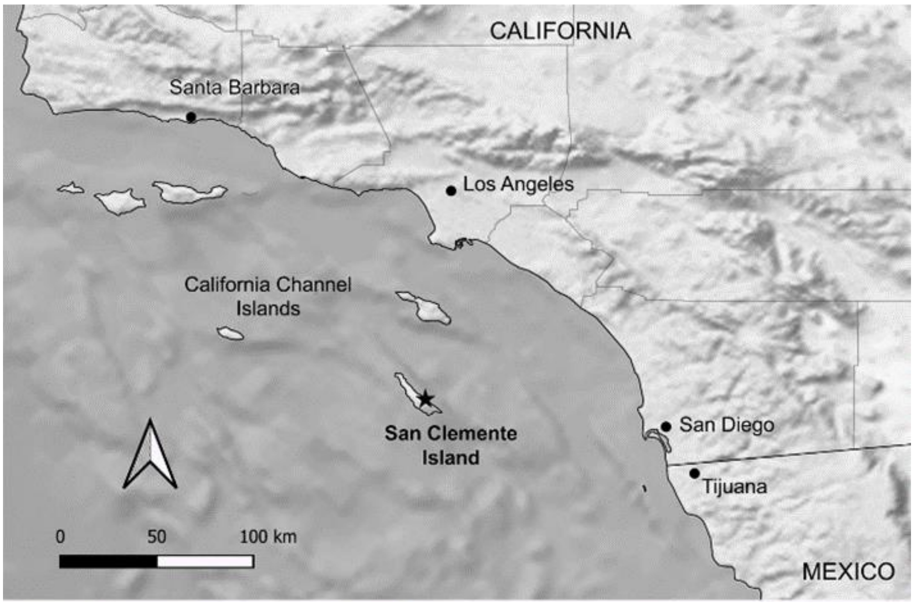

Figure 1. Map of California Channel Islands and location of San Clemente Island. Plant population sampling sites are obscured to protect the plants and island security.

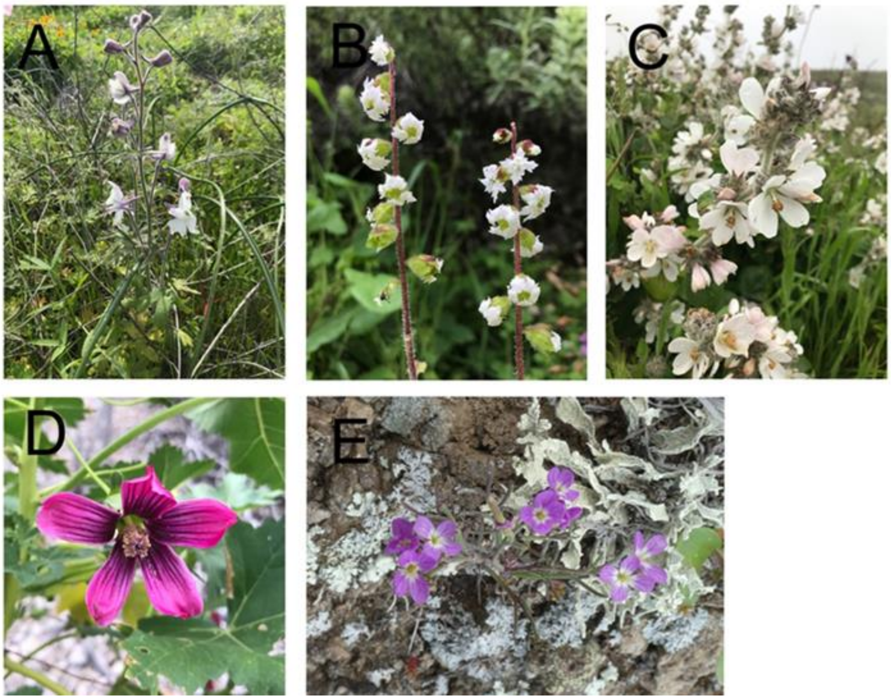

Figure 2. Focal rare island endemic plant species (A) *D. variegatum kinkiense* (B) *L. maximum* (C) *M. clementinus* (D) *M. assurgentiflora* ssp *glabra* (E) *S. filifolia*

node and every other pollinator node in the network), and betweenness (the number of shortest paths between every pollinator node in the network that pass through a given pollinator node) for the broader interaction network that each focal plant species belongs to (Elle et al. 2012, Crespo et al. 2022).

MATERIALS AND METHODS

STUDY PLANT SPECIES

The San Clemente Island larkspur (*D. variegatum* ssp *kinkiense*) (Fig. 2A) is a perennial herb limited to the island. At the time of writing, it is listed by the federal government and state of California as endangered, though it has been proposed for federal delisting (U.S. Fish & Wildlife Service 2021) and may be delisted soon. It has flowers of a light blue to white color with bilateral symmetry and nectar spurs. Other members of the genus are visited by flies, hawkmoths, bumble bees, and hummingbirds (Williams et al. 2001; Ramírez-Rodríguez & Amich 2017). The San Clemente Island Larkspur is thought to be self-incompatible (Junak & Wilken 1998), however no detailed study has been done. Historically, threats to larkspur on the island included grazing by feral animals, however those animals were removed in 1992 (Kellogg & Kellogg 1994). Remaining threats to this species include competition with non-native plant species, erosion, and potentially ongoing military training activities (U. S. Fish & Wildlife Service 2008). The San Clemente Island woodland-star (*L. maximum*) (Fig. 2B) is a perennial herb limited to the island, and is listed by the federal government and state of California as endangered. There are 33 point localities, with population sizes ranging from between 2 and 363 plants distributed patchily along the sides of 8 extremely steep canyons on the island (U.S. Fish & Wildlife Service 2020a). The San Clemente Island woodland-star has white flowers with an open shape and 5 petals, with a bell-shaped hypanthium. While no prior studies exist about the pollination of the San Clemente Island woodland-star, members of the same genus on the mainland are often both pollinated and parasitized by *Greya* moths (Thompson 1997; Friberg et al. 2013) or by moths and solitary bees (Taylor 1965). All other plants in the genus that have been investigated were found to be self-incompatible, and while no peer-reviewed study exists for San Clemente Island woodland-star, pollination experiments have been done that showed some evidence of selfing (B. Munson, *personal communication*). Since removal of feral grazers from the island in 1992, remaining and emerging threats to Island woodland-star include erosion and fire ignition on steep canyon slopes, in addition to a general lack of information about its demographics due to the difficulty of accessing populations (U.S. Fish & Wildlife Service

2020a). A study by Wallace et al. (2006) found a high degree of genetic divergence between populations, likely due to the steep terrain placing limits on pollen and seed dispersal between populations. The San Clemente Island bush-mallow (*M. clementinus*) (Fig. 2C) is a perennial shrub. At the time of writing, it is listed by the federal government and state of California as endangered, though it has been proposed for federal delisting (U.S. Fish & Wildlife Service, 2021) and may be delisted soon. The San Clemente Island bush-mallow has pink, lavender, or whitish flowers that have an open shape with 5 petals. Other species in the family Malvaceae are pollinated by bees in the genus *Diadasia*, and incidental observations of San Clemente Island bush-mallow have recorded floral visitation by wasps and butterflies (U. S. Fish & Wildlife Service 2007). Flowers are self-compatible, however selfing does not seem to occur in nature (U. S. Fish & Wildlife Service 2007). In greenhouse experiments, outcrossing had a positive effect on the seed set (U. S. Fish & Wildlife Service 2007). Bush-mallow was historically threatened on the island by feral animal grazing, but has recovered. Threats to bush-mallow from non-native plant species have been mitigated by control and treatment of target invasive plant species, and the latest assessment suggests that they are under control, however some threats remain from increased fire ignition and low genetic diversity (U. S. Fish & Wildlife Service 2021). The Southern Island mallow (*M. assurgentiflora* ssp *glabra*) (Fig. 2D) is a perennial shrub limited to two of the Channel Islands (San Clemente and Santa Catalina), and is not federally listed, however it is listed as rare (CRPR Rank 1B) and critically imperiled (State Rank S1) within the state of California by the California Native Plant Society (CNPS) (California Native Plant Society 2022). The Southern Island mallow produces large pink blooms with an open shape and five petals. It is also cultivated as an ornamental plant in mainland California outside of its native range. It is thought to be self-pollinating (Fernandez de Castro et al. 2017), however no specific studies have been conducted. While no detailed studies of pollination have been conducted in this species, there have been casual observations of hummingbird visitation within its native range on San Clemente Island, which is consistent with other island species in the Malvaceae family (Fernandez de Castro et al. 2017). The Island rock cress (*S. filifolia*) (Fig. 2E) is an annual herb that currently occurs on two of the Channel Islands (Santa Catalina and San Clemente) and has only 3 known extant occurrences. It has been federally listed since 1975. The Island rockcress produces light purple or lavender flowers with 4 petals and a cup-shaped hypanthium. There is no known documentation of pollinators of this species, and the population on San Clemente Island has a very high selfing rate of 0.92 (McGlaughlin et al. 2015). Very little is known about pollination in the genus *Sibara*, however other genera in the Brassicaceae family are visited by bees, hoverflies, and butterflies (Badenes-Pérez 2022). It is threatened by habitat degradation, fire, herbivory, and invasive plants (U. S. Fish & Wildlife Service 2020b).

POLLINATOR SURVEYS

We conducted a total of 7 bi-weekly surveys for pollinators at each site on San Clemente Island between March and June of 2019. We conducted repeated sampling at each site in order to get a more complete picture of potentially important pollinators for our focal plants, as pollinator community and plant-pollinator networks can shift over time (e.g. Valverde et al. 2016). Our sites included one location each for *D. variegatum*, *L. maximum*, and *M. assurgentiflora* ssp *glabra*, and two locations each for *M. clementinus* and *S. filifolia, for a total of 7 sites*. Duplicate sites for *M. clementinus* and *S. filifolia* were at least 0.5 km apart from one another; more detail is not provided to protect the locations of the plants and the security of the island. At each study site, we designated ten 2 x 4 m plots over focal plants. In some cases, population sizes of focal plant species were very small and it was not possible to designate 10 plots that contained the focal plant species (*D. variegatum* = 10, *L. maximum* = 2, *M. assurgentiflora* ssp *glabra* = 10, *M. clementinus* = 10 and 10, *S. filifolia* = 5 and 7). Plots were oriented to include the maximum number of flowering individuals across all plant species present in the survey site. During each sampling survey, every plot was sampled for 30 min, and surveys were not conducted if the temperature was below 18°C or if wind speed was sufficient to cause large movement in vegetation. Due to the variable blooming period of each focal plant species, the number of pollinator surveys conducted every 2 weeks during the blooming period of the focal plant varied between species (*D. variegatum* = 3 surveys, *M. assurgentiflora* ssp *glabra* = 5 surveys, *M. clementinus* = 5 surveys, *L. maximum* = 2 surveys, *S. filifolia* = 1 survey), and thus not all sampling occurred during the blooming period of each focal plant species. Before each sampling survey, the number of open blooms of all plant species in the plot were counted, wind speed was measured using a handheld wind meter, and cloud cover (percent cover based on a visual assessment of the atmosphere to the nearest 10%) was estimated. Any flying insect observed making contact with the anthers or stigma of flowers of any plant species was collected by one observer with a sweep net. Specimens were then prepared and pinned as museum specimens with associated data regarding date of collection, study site, plot number, and the species of flowering plant upon which it was collected. Taxonomic experts were contracted for each order of invertebrates collected to determine the highest level of identification for each specimen possible.

DATA ANALYSIS

All analyses were conducted in the statistical software R (R Core Team 2023). For each focal endangered plant species, potential pollinator taxa were ranked by the average number of specimens captured per plot on each focal plant species. Averages were calculated using a dataset including only plots in which the focal threatened plant species was blooming at the time of invertebrate sampling. To analyze patterns in pollinator species positions within their plant-pollinator interaction networks, we constructed weighted networks for each sampling survey at each sampling site using the package 'tnet' in R (Opsahl 2009). Weights were derived from the mean number of individual invertebrates captured at each plant species per site per sampling survey. A unimodal projection of the bimodal plant-pollinator network was generated using the sum method with the function 'projecting_tm' in the tnet package (Opsahl 2009) a necessary transformation to calculate centrality metrics from bipartite networks. The relative role of each species in each sampling site network was calculated using three measures of species centrality: degree (number of links with other species), closeness (the average number of steps between the pollinator node and every other pollinator node in the network), and betweenness (the number of shortest paths between every pollinator node in the network that pass through a given pollinator node) using the functions 'degree_w', 'closeness_w' and 'betweenness_w' (where 'links' refers to a known visit of that pollinator to that plant). For each site, we determine which species have higher centrality by ranking them by average values of each centrality index per site. To visualize each pollinator's overall role in their network, we also calculated a 'centrality index' by conducting a principal component analysis (PCA) on degree, closeness, and betweenness derived from the combined network for each study site (Sazima et al. 2010; Crespo et al. 2022). The principal component which accounted for most of the variance in the data was used as the centrality index for each pollinator species. The centrality index could not be calculated in this way at the level of each site and sampling survey due to some of the networks containing too few plants or pollinators for indices to be calculated. Thus, interpretation of the centrality index should be cautious, as these cumulative networks may include forbidden links (links between species that do not actually co-occur in time; Olesen et al. 2011). Nonetheless, it is interesting to visualize this index. A centrality index score of > 0 indicates that a species is very central and is important to the stability of the network and that its removal would have widespread cascading effects, whereas an index score of < 0 indicates that a species is peripheral (Sazima et al. 2010; Crespo et al. 2022).

We looked for patterns in which broad higher taxonomic groups played important roles in interaction networks across sites by analyzing the effect of pollinator broad taxonomic group (bees, beetles, flies, lepidoptera, and wasps) on the centrality indices normalized degree and normalized closeness centrality using generalized linear mixed models (GLMMs) in the packages 'lme4' (Bates et al. 2015) statistical software program R (R Core Team 2023). The centrality index derived from PCA for cumulative site networks was not used for modeling because it was not possible to calculate it at the level of each sampling survey x site, as mentioned previously, and cumulative networks combined across sampling surveys can create forbidden links

(Olesen et al. 2011). We were also not able to model the effect of broad taxonomic group on betweenness centrality, as only 11 species had a betweenness of > 0, likely due to the small size of each network at the sampling survey x site level (which avoids forbidden links). Each index (normalized degree and normalized closeness centrality) was used as the dependent variable in its own model, with pollinator taxa, floral abundance, cloud cover, and wind as fixed effects, and site and sampling survey as random effects. Two sets of models were run for each index, one with the complete dataset, and one including only bees and flies, as Lepidoptera, beetles, and wasps accounted for very few specimens (*N* = 8, 6, and 7 out of 140 specimens) and were not present at all sites, whereas bees (*N* = 36) and flies (*N* = 83) were found at all sites and sampling surveys. For the normalized degree model, we used a GLMM with a Poisson distribution, where normalized degree was the dependent variable, broad higher taxonomic group was the fixed effect, and the site and sampling survey were random effects. For the normalized closeness model, we used a GLMM with a Poisson distribution, where normalized closeness was the dependent variable, broad higher taxonomic group, floral abundance, cloud cover, and wind speed were fixed effects, and the site and sampling survey were random effects. For both sets of models, we tested every possible combination of broad higher taxonomic group, cloud cover, wind, and floral abundance as fixed effects in separate models. We also included an offset for network size (total number of plants and pollinators) in all models. Models exhibited overdispersion initially, so an observation-level random effect was added to all of the models. Model selection for each index model (normalized degree, normalized closeness centrality) was based on AICc using the function 'model.sel' in the package 'MuMIn' (Barton 2022). Models were checked for assumptions of residual distribution, homogeneity of variance, autocorrelation (using function 'acf'), and overdispersion (using function 'gof').

RESULTS

The average number of individual flowers of *D. variegatum* ssp *kinkiense* was 2.82 ± 1.83 (SD) per plot in which it was blooming. A total of 22 plots were sampled (11 hours of sampling) containing blooming individuals across sampling periods. Floral visitors from 3 orders (Hymenoptera, Lepidoptera, and Diptera) and 5 species were captured on *D. variegatum* during both surveys during its blooming period (March and May) (Table 1). No visitors were collected on *D. variegatum* during the 3rd survey of the plot as no individuals were blooming at that time.

The average number of individual flowers of *M. clementinus* was 2.26 ± 1.36 (SD) per plot in which it was blooming. A total of 81 plots (40.5 hours of sampling) were sampled with blooming *M. clementinus* from March through June of 2019. Floral visitors from 4 orders and 12 species were captured on *M. clementinus* across all 5 surveys during its blooming period (March to June) (Table 1).

The number of individual flowers of *M. assurgentiflora* ssp *glabra* was on average 2.07 ± 1.03 (SD) per plot in which it was blooming. A total of 57 plots (28.5 hours of sampling) were sampled with blooming *M. clementinus* from March through June of 2019. Floral visitors from 3 orders (Hymenoptera, Coleoptera, and Diptera) and 18 species were captured on *M. assurgentiflora* ssp *glabra* during 5 out of 5 surveys during its blooming period (Table 1). In addition, observers noted low levels of visitation by Anna's hummingbirds (*Calypte anna*).

There were no floral visitors captured from surveys of *L. maximum* or *S. filifolia*. A total of 2 plots containing *L. maximum* (this plant had very low abundance) were sampled a total of 4 times (a total of 2 hours of sampling). Visits to the *L. maximum* site were cut short due to concerns about soil erosion. However, supplemental photography by field crew did reveal visitation of *L. maximum* by suspected alfalfa looper moths (*Autographa californica*) and urbane digger bees (*Anthophora urbana* ssp. *clementina*) (Fig. 3). A total of 12 plots containing *S. filifolia* were sampled a total of 13 times (during 2 surveys) while the plant was blooming (a total of 6.5 hours of sampling); blooming occurred earlier than expected and thus it was only blooming during our first two visits to the sites.

Centrality of pollinator species in visitation networks – We constructed 6 weighted plant-pollinator interaction networks at the site level

Table 1. Ranked order of floral visitors to 3/5 focal rare island endemic plant species: *D. variegatum* ssp *kinkiense*, *M. clementinus*, and *M. assurgentiflora* ssp *glabra*. The other 2 species monitored, *L. maximum* and *S. filifolia*, had no observed floral visitors during standardized sampling.

Focal plant species	Pollinator species	Broad taxon	Mean num cap/plot	SD	*N*
D. variegatum ssp *kinkiense*	*Anthophora edwardsii*	bee	0.23	0.8	22
	Copestylum avidum	fly	0.09	0.3	23
	Anthidium collectum	bee	0.05	0.2	22
	Autographa californica	moth	0.05	0.2	22
	Bombylius facialis	fly	0.05	0.2	22
M. clementinus	*Copestylum marginatum*	fly	0.65	2.1	81
	Copestylum avidum	fly	0.07	0.3	81
	Eupeodes volucris	fly	0.06	0.3	81
	Vanessa cardui	butterfly	0.06	0.3	81
	Anthophora urbana clementina	bee	0.05	0.2	38
	Lasioglossum (Dialictus)	bee	0.05	0.3	38
	Autographa californica	fly	0.04	0.3	81
	Agapostemon texanus	bee	0.03	0.2	38
	Copestylum sp 5	fly	0.03	0.2	38
	ammophila 1	wasp	0.02	0.2	81
	Bombylius facialis	fly	0.01	0.1	81
	Osmia 1	bee	0.01	0.1	81
M. assurgentiflora ssp *glabra*	*Diadasia bituberculata*	bee	0.21	0.7	57
	Agapostemon texanus	bee	0.18	0.9	57
	Habropoda depressa	bee	0.11	0.4	57
	Listrus sp	fly	0.05	0.2	57
	Sphecid 1	wasp	0.05	0.2	57
	Anthophora urbana clementina	bee	0.04	0.2	57
	Camponotus bakeri	ant	0.04	0.2	57
	Copestylum avidum	fly	0.04	0.2	57
	Trichochrous sp	beetle	0.04	0.2	57
	Allograpta obliqua	fly	0.02	0.1	57
	Anthophora edwardsii	bee	0.02	0.1	57
	Copestylum mexicanum	fly	0.02	0.1	57
	Diadasia rinconis	bee	0.02	0.1	57
	Eupeodes volucris	fly	0.02	0.1	57
	Lauxannidae 1	fly	0.02	0.1	57
	Osmia 1	bee	0.02	0.1	57
	Pompillid 1	wasp	0.02	0.1	57
	Tachinidae 1	fly	0.02	0.1	57

averaged across sampling surveys (Supplementary Materials, Fig S1A-G). The only species to occur at least once during a sampling survey at each site was a fly species, *Copestylum avidum*. A related species, *Copestylum marginatum*, was found at every site except for the *M. assurgentiflora* ssp *glabra* site. Flies, especially in the genus *Copestylum*, consistently had the highest centrality index, and were almost always at > 0, while bees, wasps, and beetles consistently had centrality index values < 0 (Fig. 4 – 10, Table 2). The only site that reversed this trend was the *M. assurgentiflora* ssp *glabra* site, where bees, specifically *Diadasia* and *Agapostemon*, had high centrality index values (Fig. 8, Table 2), though a fly, *Eupeodes volucris*, still had the highest index. The *L. maximum* site was only sampled 4 times to avoid impacting delicate soils that were easily

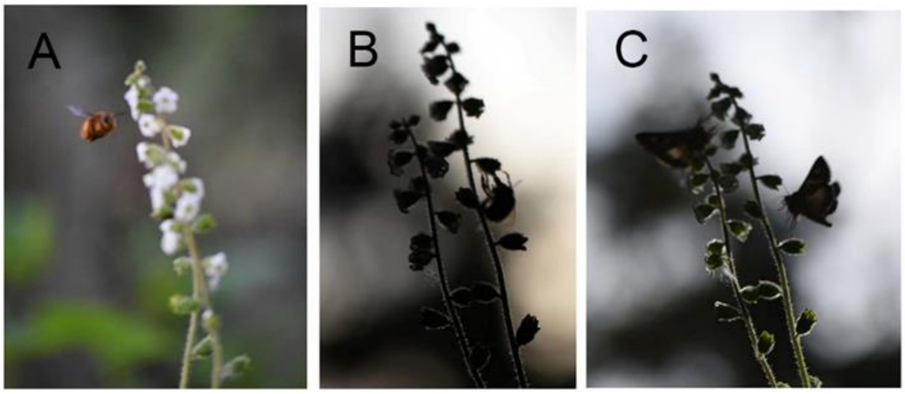

Figure 3. Opportunistic photographic observations of invertebrate floral visitors to *Lithophragma maximum*. The visitors include (A) A suspected *Anthophora urbana* ssp *clementina* bee, (B) A large bee observed at dawn, and (C) Two moths suspected to be *Autographa californica*, at dawn.

eroded. The *M. clementinus* site A was only sampled 5 times, and site B only 4 times due to weather and logistical constraints. The *S. filifolia* site B was sampled 3 times due to weather and logistical constraints. These networks combined data across sampling surveys, and thus may contain forbidden links and should be interpreted with some caution (Olesen et al. 2011; Table 2).

A total of 29 weighted plant-pollinator interaction networks at the sampling survey x site level were used to calculate centrality indices (degree, closeness, betweenness). A few of the networks were excluded from modeling as they were too small or modular to calculate centrality indices (*D. variegatum* trip 1 and 6, *L. maximum* trip 1, *M. clementinus* site A trip 5, *S. filifolia* site B trip 1 and 3), and as a result it was not possible to use PCA to calculate the centrality index at the site x sampling survey level. Instead, we analyze its component indices (degree, closeness, betweenness) for the networks where their values could be calculated. The centrality of different pollinator taxonomic groups varied across sites (Table 3). The best model for the effect of broad taxonomic group (bee, beetle, fly, Lepidoptera, wasp) on normalized degree included broad taxonomic group, cloud cover, and floral abundance as fixed effects. There was a significant positive effect of the fly factor level on normalized degree (Estimate = 0.54, z-value = 2.11, $P < 0.05$),

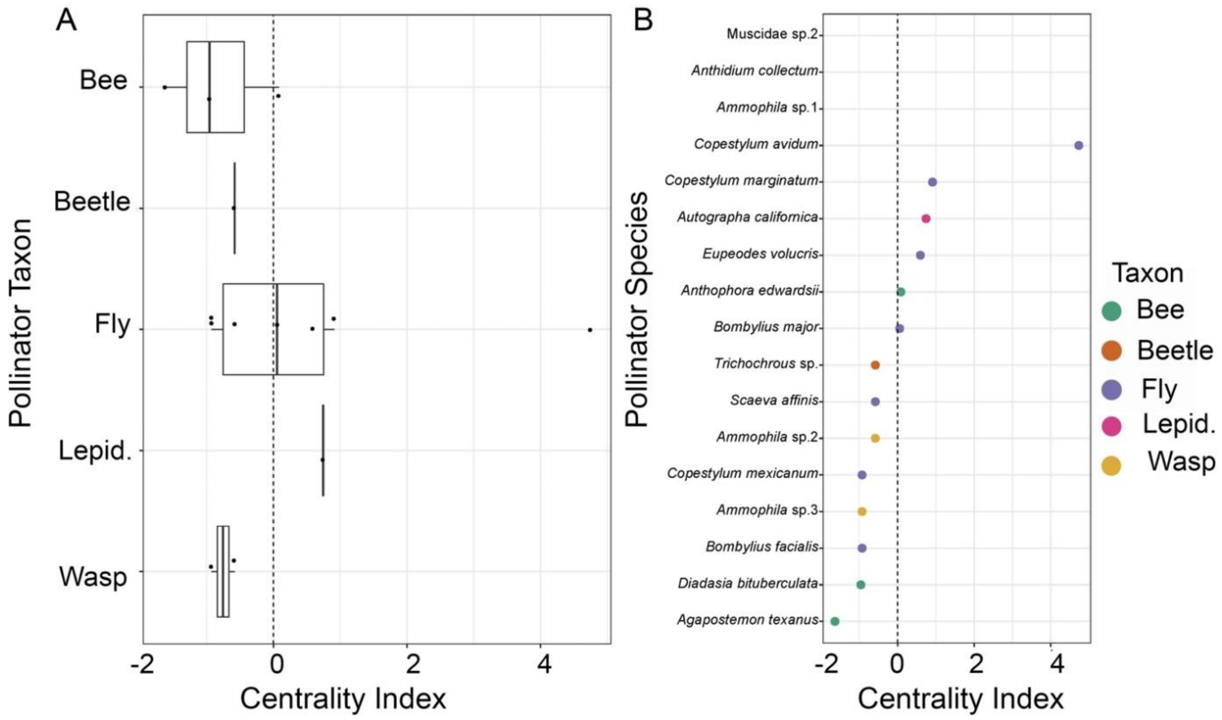

Figure 4. *Delphinium variegatum* ssp. *kinkiense* centrality indices by (A) broad pollinator taxon and (B) pollinator species.

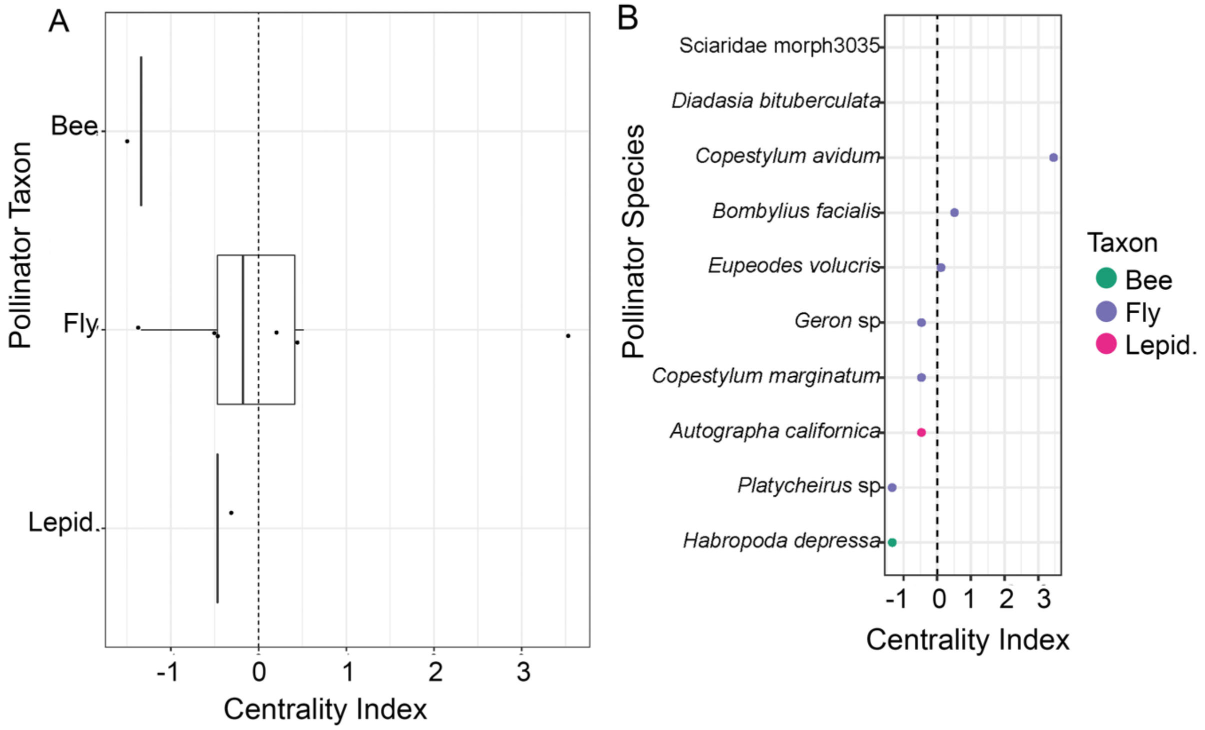

Figure 5. ***Lithophragma maximum*** **centrality indices by (A) broad pollinator taxon and (B) pollinator species.**

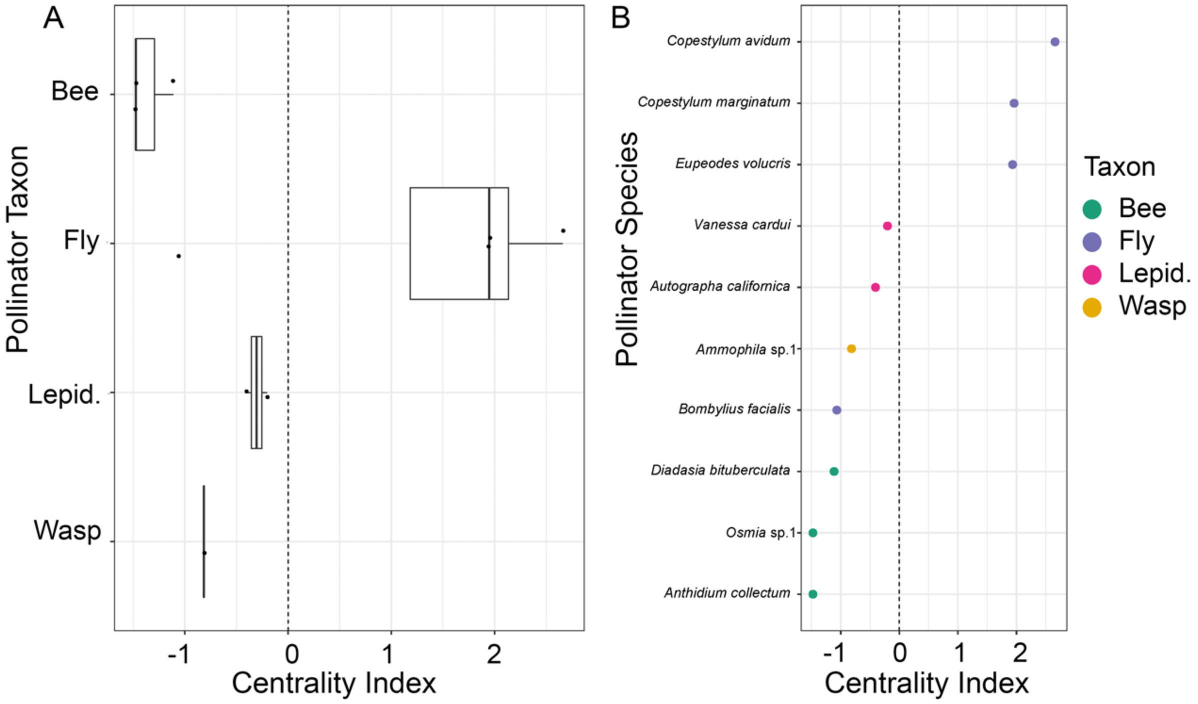

Figure 6. ***Malacothamnus clementinus*** **site centrality indices by (A) broad pollinator taxon and (B) pollinator species.**

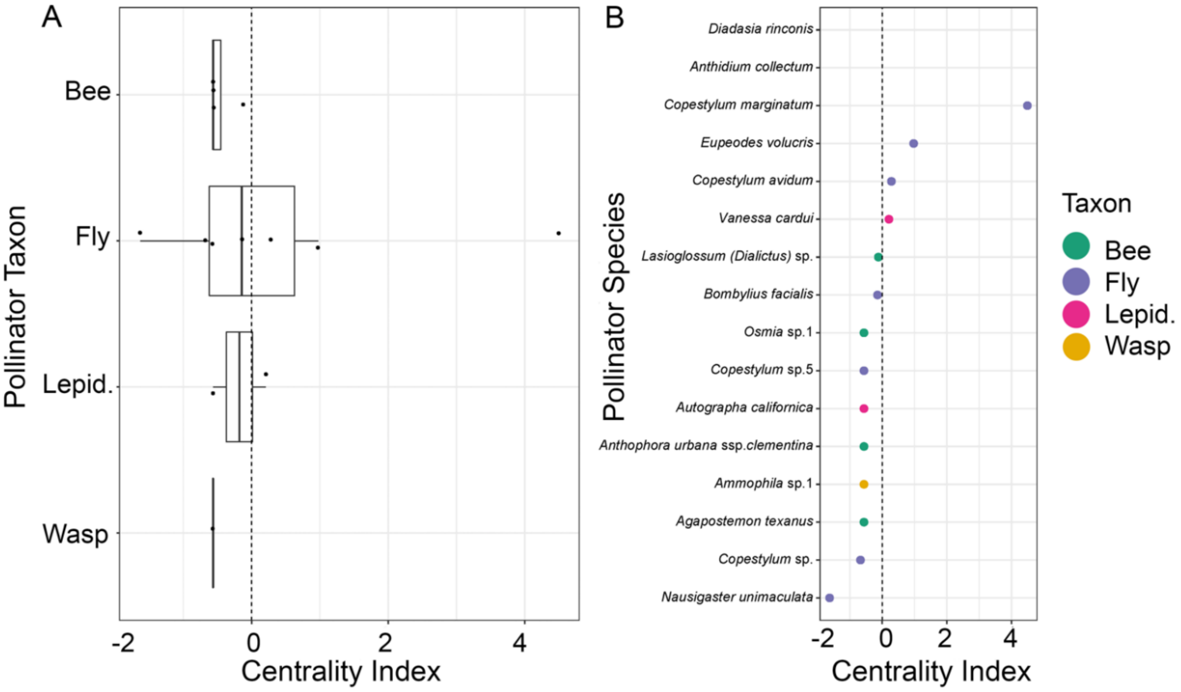

Figure 7. ***Malacothamnus clementinus*** **site B centrality indices by (A) broad pollinator taxon and (B) pollinator species.**

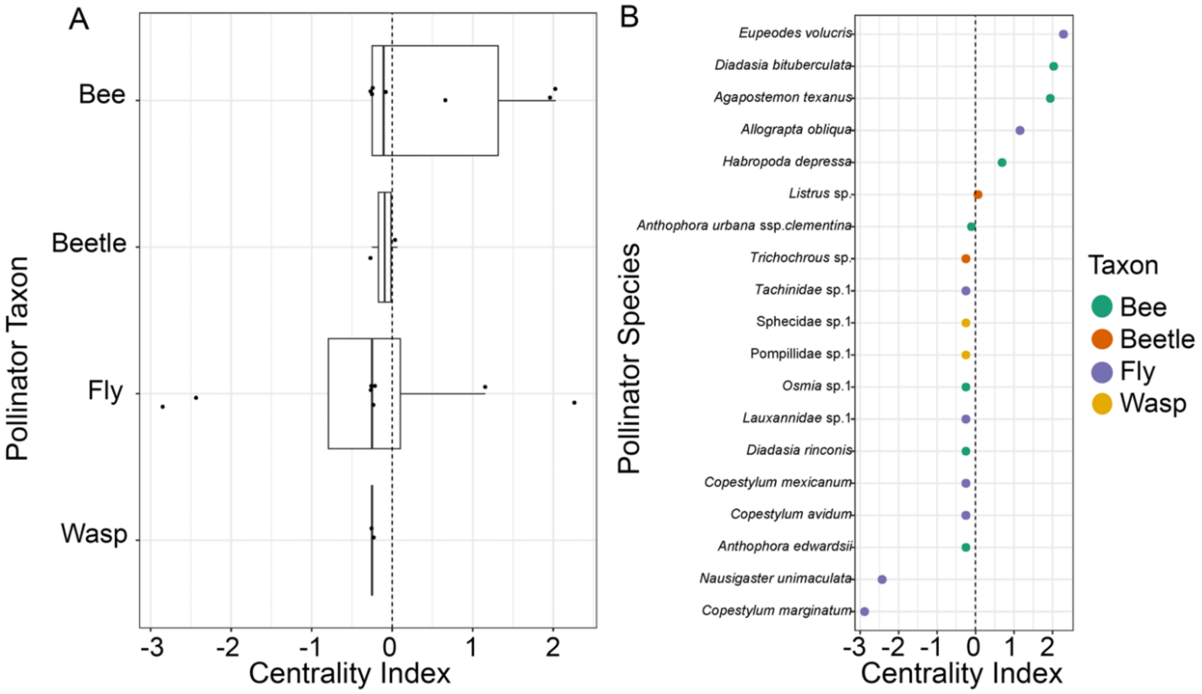

Figure 8. ***Malva assurgentiflora*** **ssp.** ***glabra*** **centrality indices by (A) broad pollinator taxon and (B) pollinator species.**

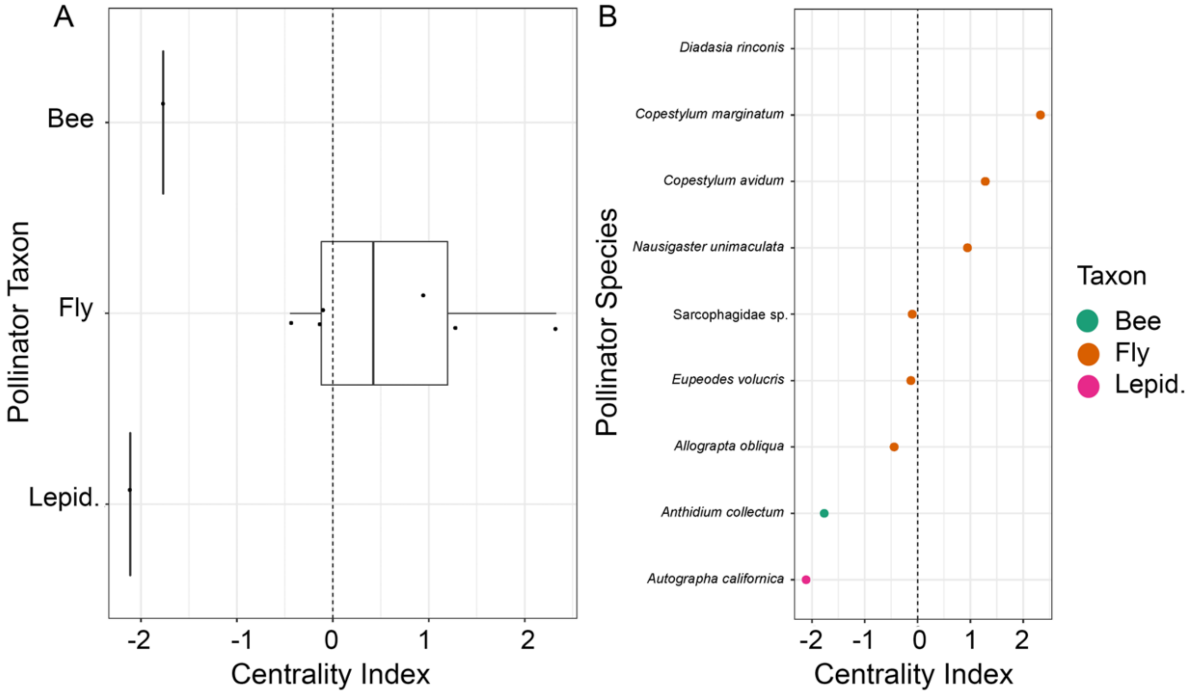

Figure 9. ***Sibara filifolia*** **site A centrality indices by (A) broad pollinator taxon and (B) pollinator species.**

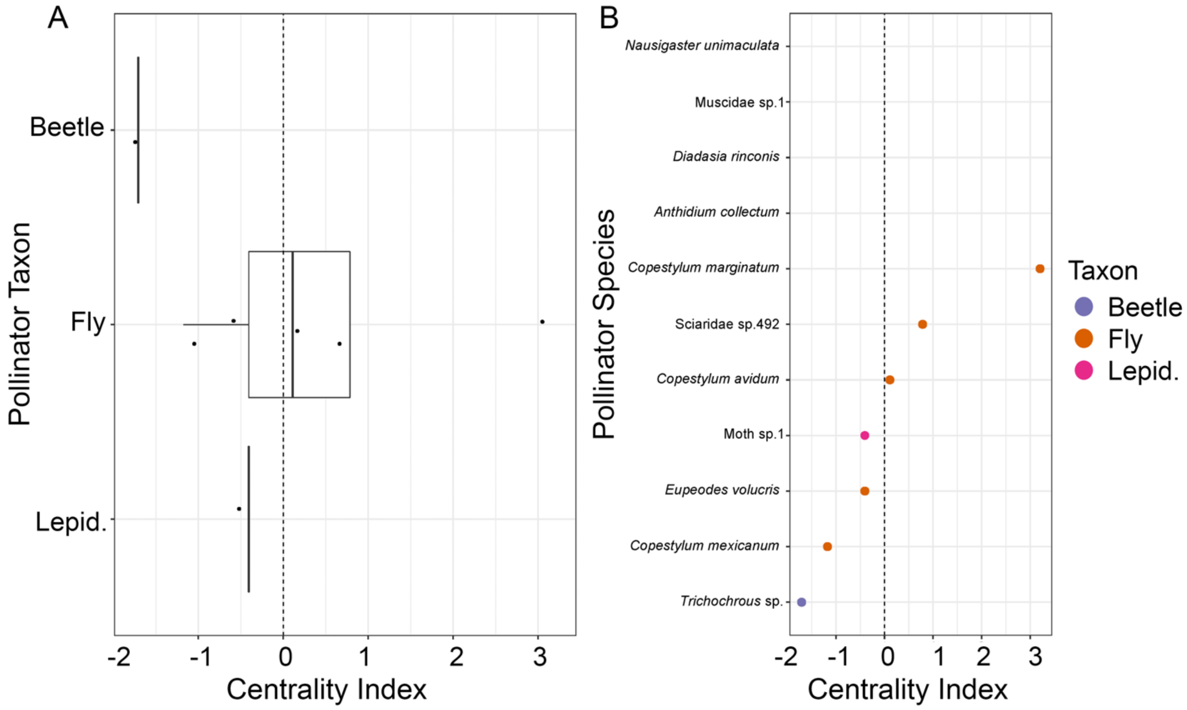

Figure 10. ***Sibara filifolia*** **site B centrality indices by (A) broad pollinator taxon and (B) pollinator species.**

but this relationship disappeared in pairwise comparisons (Table 4), and no other fixed effects were significant. When the same models were run with a dataset including only bees and flies (due to unbalanced occurrences and low sample size of beetles, Lepidoptera, and wasps), the best model included the broad pollinator taxa (bee or fly) and floral abundance as fixed effects. Flies had a slightly significantly higher normalized degree than bees (Estimate = 0.56, z-value = 2.0 2, $P < 0.05$) and there was no significant effect of floral abundance (Table 5).

Table 2. Results of network analysis of cumulative bipartite plant-pollinator networks across sampling surveys at each site. The plant column indicates which focal plant species population site was sampled and pollinator indicates the lowest taxonomic level identification of each specimen in that site network. Values shown for each pollinator species are degree (number of links), closeness (proximity to all other nodes), and betweenness (how many paths between other nodes do they lie upon), and the centrality index (CI) score calculated based on a PCA of degree, closeness, and betweenness. This table should be interpreted with caution, as it includes forbidden links between species that may not co-occur in time, as it was calculated by combining networks across survey sampling periods in order to enable calculation of the CI.

Plant	Pollinator	Taxon	Degree	Closeness	Betweenness	CI
D. variegatum ssp *kinkiense*	Muscidae sp. 1	fly	0	NA	0	NA
	Bombylius major	fly	3	0.05	0	0.05
	Copestylum avidum	fly	11	0.05	98	4.73
	Anthophora edwardsii	bee	3	0.05	0	0.08
	Bombylius facialis	fly	3	0.03	0	-0.93
	Autographa californica	lep	6	0.04	6	0.74
	Copestylum marginatum	fly	5	0.04	44	0.91
	Eupeodes volucris	fly	5	0.04	8	0.59
	Copestylum mexicanum	fly	3	0.03	0	-0.93
	Scaeva affinis	fly	4	0.03	0	-0.58
	Ammophila sp. 2	wasp	4	0.03	0	-0.58
	Anthidium collectum	bee	1	NA	0	NA
	Ammophila sp. 1	wasp	1	NA	0	NA
	Diadasia bituberculata	bee	2	0.03	0	-0.96
	Ammophila sp. 3	wasp	3	0.03	0	-0.93
	Agapostemon texanus	bee	2	0.02	0	-1.64
	Trichochrous sp.	beetle	4	0.03	0	-0.58
L. maximum	Sciaridae sp. 3035	fly	0	NA	0	NA
	Copestylum avidum	fly	7	0.17	20	-3.46
	Bombylius facialis	fly	5	0.13	0	-0.51
	Geron sp.	fly	5	0.06	0	0.47
	Habropoda depressa	bee	2	0.07	0	1.34
	Platycheirus sp.	fly	2	0.07	0	1.34
	Autographa californica	lep	5	0.06	0	0.47
	Diadasia bituberculata	bee	0	NA	0	NA
	Eupeodes volucris	fly	5	0.10	0	-0.11
	Copestylum marginatum	fly	5	0.06	0	0.47
M. clementinus site A	*Eupeodes volucris*	fly	9	0.08	16	1.93
	Copestylum avidum	fly	8	0.10	24.5	2.66
	Copestylum marginatum	fly	6	0.11	17.5	1.96
	Vanessa cardui	lep	5	0.07	0	-0.20
	Autographa californica	lep	5	0.06	0	-0.41
	Ammophila sp. 1	wasp	5	0.04	0	-0.82
	Bombylius facialis	fly	3	0.05	0	-1.07
	Anthidium collectum	bee	3	0.03	0	-1.47
	Osmia sp. 1	bee	3	0.03	0	-1.47
	Diadasia bituberculata	bee	1	0.07	0	-1.11
M. clementinus site B	*Copestylum marginatum*	fly	13	0.21	66.8333333	4.50
	Copestylum avidum	fly	12	0.09	0	0.28
	Agapostemon texanus	bee	11	0.04	0	-0.57
	Eupeodes volucris	fly	13	0.12	4.83333333	0.97
	Bombylius facialis	fly	12	0.06	0	-0.15
	Osmia sp. 1	bee	11	0.04	0	-0.57
	Nausigaster unimaculata	fly	3	0.03	0	-1.63

Table 2 continued

Plant	Pollinator	Taxon	Degree	Closeness	Betweenness	CI
M. clementinus site B	*Anthidium collectum*	bee	0	NA	0	NA
	Ammophila sp. 1	wasp	11	0.04	0	-0.57
	Anthophora urbana ssp *clementina*	bee	11	0.04	0	-0.57
	Copestylum sp. 5	fly	11	0.04	0	-0.57
	Lasioglossum (Dialictus)	bee	11	0.07	0	-0.12
	Vanessa cardui	lep	13	0.07	0	0.21
	Autographa californica	lep	11	0.04	0	-0.57
	Diadasia rinconis	bee	0	NA	0	NA
	Copestylum sp.	fly	5	0.08	0	-0.67
M. assurgentiflora ssp glabra	*Eupeodes volucris*	fly	19	0.05	48	2.28
	Allograpta obliqua	fly	19	0.05	20	1.16
	Anthophora urbana ssp. *clementina*	bee	18	0.04	0	-0.11
	Agapostemon texanus	bee	17	0.11	0	1.94
	Diadasia bituberculata	bee	17	0.08	25.5	2.03
	Habropoda depressa	bee	17	0.07	0	0.69
	Listrus sp.	beetle	17	0.05	0	0.06
	Trichochrous sp.	beetle	17	0.04	0	-0.25
	Sphecidae sp. 1	wasp	17	0.04	0	-0.25
	Camponotus bakeri	NA	17	0.04	0	-0.25
	Lauxannidae sp. 1	fly	17	0.04	0	-0.25
	Anthophora edwardsii	bee	17	0.04	0	-0.25
	Pompillidae sp. 1	wasp	17	0.04	0	-0.25
	Copestylum avidum	fly	17	0.04	0	-0.25
	Osmia sp. 1	bee	17	0.04	0	-0.25
	Tachinidae sp. 1	fly	17	0.04	0	-0.25
	Diadasia rinconis	bee	17	0.04	0	-0.25
	Copestylum mexicanum	fly	17	0.04	0	-0.25
	Nausigaster unimaculata	fly	4	0.03	0	-2.43
	Copestylum marginatum	fly	3	0.02	0	-2.88
S. filifolia site A	*Copestylum marginatum*	fly	5	0.07	16.5	2.33
	Nausigaster unimaculata	fly	4	0.08	4.5	0.94
	Copestylum avidum	fly	4	0.07	12	1.28
	Sarcophagidae sp.	fly	3	0.08	0	-0.10
	Eupeodes volucris	fly	3	0.07	3.5	-0.13
	Allograpta obliqua	fly	3	0.07	0	-0.44
	Anthidium collectum	bee	2	0.05	0	-1.77
	Autographa californica	lep	2	0.04	0	-2.11
	Diadasia rinconis	bee	0	NA	0	NA
S. filifolia site B	*Copestylum marginatum*	fly	6	0.16	24	3.20
	Sciaridae sp. 492	fly	4	0.15	0	0.78
	Moth sp. 1	lep	4	0.07	0	-0.41
	Eupeodes volucris	fly	4	0.07	0	-0.41
	Camponotus bakeri	NA	4	0.07	0	-0.41
	Copestylum avidum	fly	3	0.08	12	0.11
	Copestylum mexicanum	fly	2	0.07	0	-1.17
	Nausigaster unimaculata	fly	1	NA	0	NA
	Anthidium collectum	bee	1	NA	0	NA
	Trichochrous sp.	beetle	1	0.06	0	-1.71
	Muscidae sp. 1	fly	0	NA	0	NA
	Diadasia rinconis	bee	0	NA	0	NA

Table 3. Cumulative network metrics at each site from networks compiled using specimen data across all survey visits to sites. Pollinator taxon refers to the broad taxonomic group (Bee = bees, Fly = flies, Lep = moths or butterflies, Wasp = wasps). Degree refers to the number of links that pollinator node has, closeness centrality measures how close the node is to all other nodes in the network, and betweenness centrality quantifies how many shortest paths between all other nodes in the network the node in question lies upon.

Site	Pollinator taxon	Degree	Closeness centrality	Betweenness centrality
D. variegatum ssp *kinkiense*	Bee	1.33 ± 1.21	NA	0 ± 0
	Fly	1.91 ± 1.14	NA	0.36 ± 1.21
	Lep	4 ± 0	0.14 ± 0	1.00 ± 0
	Wasp	1 ± 0	NA	0 ± 0
L. maximum	Bee	NA	NA	NA
	Fly	NA	NA	NA
	Lep	1 ± 0	0.4 ± 0	0 ± 0
M. clementinus site A	Bee	2 ± 1.73	NA	NA
	Fly	2.5 ± 1.43	0.54 ± 0.54	1.03 ± 2.34
	Lep	2 ± 2.83	NA	0.42 ± 0.59
	Wasp	3 ± 0	0.10 ± 0	NA
M. clementinus site B	Bee	NA	NA	NA
	Fly	3.93 ± 1.87	0.23 ± 0.29	3.33 ± 6.79
	Lep	7 ± 1.41	0.09 ± 0.04	0 ± 0
	Wasp	4 ± 0	0.04 ± 0	0 ± 0
M. assurgentiflora ssp *glabra*	Ant	4 ± 0	0.18 ± 0	0 ± 0
	Bee	3.17 ± 1.27	NA	0.5 ± 1.73
	Beetle	2.8 ± 1.64	NA	0 ± 0
	Fly	2.79 ± 1.51	NA	0 ± 0
	Wasp	3.75 ± 1.89	0.18 ± 0.12	0 ± 0
S. filifolia site A	Bee	NA	NA	NA
	Fly	NA	NA	NA
	Lep	2 ± 0	0.5 ± 0	0 ± 0
S. filifolia site B	Beetle	1 ± 0	NA	0 ± 0
	Fly	NA	NA	NA
	Lep	1 ± 0	0.57 ± 0	0 ± 0

Normalized closeness centrality was highest on average for beetles (0.35 ± 0.55, *N* = 5), followed by flies (0.29 ± 0.42, *N* = 64), lepidoptera (0.21 ± 0.25, *N* = 7), bees (0.15 ± 29, *N* = 22), and wasps (0.03 ± 0.02, *N* = 6) (Table 3). At the *D. variegatum kinkiense* site, the highest normalized closeness centrality (ncc) value was a bee species (*Diadasia bituberculata*). At the *L. maximum* site, the highest ncc value was a fly (*Eupeodes volucris*). At the *M. clementinus* site A, it was a fly (*Copestylum marginatum*) and at site B it was an unidentified fly in the same genus (*Copestylum* sp.). At the *M. assurgentiflora* ssp *glabra* site, the highest ncc value was a bee (*Habropoda depressa*). At the *S. filifolia* site A, it was a bee (*Anthidium collectum*), and at site B it was a beetle (*Trichochrous* sp.) (Fig. 5b). The best model for the effect of broad taxonomic group (bee, beetle, fly, Lepidoptera, wasp) on normalized closeness included broad taxonomic group, cloud cover, and floral abundance as fixed effects. There was a significant positive effect of floral abundance on closesness (Est = 0.12, z-value = 2.69, *P* < 0.01; Table 6). When the same models were run with a dataset including only bees and flies (due to unbalanced occurrences and low sample size of beetles, Lepidoptera, and wasps), the best model included broad pollinator taxa (bee or fly), cloud cover, and floral abundance as fixed effects. There was a significant positive effect of floral abundance on closeness (Est = 0.12, z-value = 2.35, *P* < 0.05; Table 7).

Flies had on average the highest betweenness centrality across sites and sampling trips (0.97 ± 3.91, *N* = 64), followed by Lepidopterans (0.62 ± 1.06, *N* = 7), bees (0.27 ± 0.1.28, *N* = 22), and beetles (*N* = 5) and wasps (*N* = 6) had 0 betweenness

Table 4. Results of best model for the effect of broad taxonomic group (bee, beetle, fly, Lepidopteran, wasp) on normalized degree at the sampling survey x site network level. Model was fitted using a GLMM with a Poisson distribution. An offset term was included for network size. Random effects are indicated with the syntax (1|effect). Significant effects are shown with the following symbols: * P < 0.05, ** P < 0.01, *** P < 0.001.

Model formula	Normalized degree ~ taxon + cloud cover + floral abundance + offset(log(network size)) + (1|site) + (1|sampling survey) + (1|observation level effect)			
Effect	Estimate	SE	z-value	P-value
Intercept	0.79	0.46	1.7	0.08
Beetle	0.32	0.53	0.6	0.55
Fly	0.54	0.26	2.11	0.04*
Lepidoptera	0.8	0.48	1.65	0.1
Wasp	0.42	0.50	0.84	0.40
Cloud cover	0.01	0.00	1.87	0.06
Floral abundance	0.04	0.03	1.16	0.25

Table 5. Results of best model for the effect of broad taxonomic group with a reduced dataset including only bees and flies on normalized degree at the sampling survey x site network level. Model was fitted using a GLMM with a Poisson distribution. An offset term was included for network size. Random effects are indicated with the syntax (1|effect). Significant effects are shown with the following symbols: * P < 0.05, ** P < 0.01, *** P < 0.001.

Model formula	Normalized degree ~ taxon + floral abundance + offset(log(network size)) + (1|site) + (1|sampling survey) + (1|observation level effect)			
Effect	Estimate	SE	z-value	P-value
Intercept	1.26	0.45	2.78	0.005**
Fly	0.56	0.28	2.02	0.04*
Floral abundance	0.02	0.04	0.50	0.62

centrality in every network they occurred in. There were only 11 instances of species in networks with a betweenness centrality of greater than 0, likely due to the small size of many of the individual networks from each site x sampling trip, with 8/11 instances being a *Copestylum* fly. The *D. variegatum kinkiense* site had a fly and a Lepidopteran with the highest betweenness centrality values (*Copestylum avidum* and *Autographa californica*). The *L. maximum* site had 0 values for all pollinator taxa for betweenness centrality. The *M. clementinus* site A had a Lepidopteran (*Vanessa cardui*) with highest betweenness centrality, while site B had a fly (*Eupeodes volucris*). The *M. assurgentiflora* ssp *glabra* site had only one species with non-zero betweenness centrality, a bee (*Diadasia bituberculata*). The *S. filifolia* site A had only one species with non-zero betweenness centrality, the fly *Copestylum marginatum*, while site B had all 0 values (Table 3). Due to the low number of species with a betweenness centrality score > 0 (N = 11) at the sampling survey x site level, we did not model the effects of broad taxonomic group on betweenness centrality due to unmanageable zero-inflation.

DISCUSSION

Not all floral visitors are pollinators, and not all pollinators are equal in terms of the pollination services they provide (Jauker et al. 2016; Willcox et al. 2017). Nonetheless, recording floral visitors can provide critical preliminary data about potential pollinators and is a widely accepted method for identifying important pollinators (e.g. Cayenne Engel and Irwin 2003). Due to the widespread, global declines in many insect populations, it is important to assess the vulnerability of endangered plant species to loss of invertebrate pollinators. Of our focal plant species, *L. maximum* and *S. filifolia* are cause for concern if no nocturnal pollination is documented, as we did not capture any daytime visitors to these flowers (though we

Table 6. Results of best model for the effect of broad taxonomic group (bee, beetle, fly, Lepidopteran, wasp) on normalized closeness centrality at the sampling survey x site network level. Model was fitted using a GLMM with a Poisson distribution. An offset term was included for network size. Random effects are indicated with the syntax (1|effect). Significant effects are shown with the following symbols: * P < 0.05, ** P < 0.01, *** P < 0.001.

Model formula	Normalized closeness ~ taxon + cloud cover + floral abundance + offset(log(network size)) + (1|site) + (1|sampling survey) + (1|observation level effect)			
Effect	Estimate	SE	z-value	P-value
Intercept	-0.15	0.72	-0.21	0.83
Beetle	0.39	0.62	0.63	0.53
Fly	-0.19	0.31	-0.63	0.53
Lepidoptera	-0.29	0.53	-0.55	0.59
Wasp	-0.88	0.54	-1.61	0.11
Cloud cover	0.01	0.00	1.75	0.08
Floral abundance	0.12	0.04	2.69	0.007**

Table 7. Results of best model for the effect of broad taxonomic group with a reduced dataset including only bees and flies on normalized closeness centrality at the sampling survey x site network level. Model was fitted using a GLMM with a Poisson distribution. An offset term was included for network size. Random effects are indicated with the syntax (1|effect). Significant effects are shown with the following symbols: * P < 0.05, ** P < 0.01, *** P < 0.001.

Model formula	Normalized closeness ~ taxon + floral abundance + cloud cover + offset(log(network size)) + (1|site) + (1|sampling survey) + (1|observation level effect)			
Effect	Estimate	SE	z-value	P-value
Intercept	-0.211	0.76	-0.28	0.78
Fly	-0.18	0.33	-0.56	0.58
Cloud cover	0.01	0.01	1.59	0.11
Floral abundance	0.12	0.05	2.35	0.02*

were able to observe 2 visitors to *L. maximum*) despite hours of observation during their peak bloom. There is some photographic evidence to suggest that flowers may be visited at dusk by moths, potentially the Alfalfa looper (*Autographa californica*) (Fig. 3). On the other end of the spectrum, *M. assurgentiflora* ssp *glabra* and *M. clementinus* both had relatively high species richness of floral visitors (18 and 12 respectively), while *D. variegatum kinkiense* had only 4 collected taxa as visitors.

We found that at *D. variegatum kinkiense, L. maximum, M. clementinus, and M. assurgentiflora* ssp *glabra,* the urbane digger bee (*Anthophora urbana* ssp *clementina*) was a visitor. This species is a good candidate for future pollinator population assessment as it is easily identified in the field due to its distinct reddish coloration, striping on the abdomen, and large size. Larger bees can be more effective pollinators, even within the same species (Willmer & Finlayson 2014). The importance of this species, as well as other ground nesting bees (Michener 2007) specific to each plant species, such as, *Habropoda depressa* and *Agapostemon texanus, Anthophora edwardsii, Diadasia bituberculata,* and *Lasioglossum (Dialictus)* suggests that habitat restoration which leaves patches of suitable bare soil for these bees to nest in could potentially have positive effects on their population and the reproductive success of *D. variegatum kinkiense, L. maximum, M. clementinus, and M. assurgentiflora* ssp *glabra* (Antoine & Forrest 2021), and future studies should experimentally assess if this approach will have the desired effect. While each species may have distinct preferences in terms of the slope, soil type, and orientation of bare nesting patches (Antoine & Forrest 2021), their exact preferences can't be known without further study and bare ground patches in the vicinity of endangered plant populations could prove beneficial. If no suitable bare soil patches are left for bees, they may choose to nest in roads or walkways, which could limit their reproductive success due to trampling and compression under heavy vehicles. Some of these species nest in aggregations in large bare soil patches (Michener 2007), so alternatively if aggregations are discovered in heavily trafficked roads or walkways they could be roped off to protect the nests. All of these recommendations should be tested with future research efforts.

Syrphid flies in the genus *Copestylum* were found visiting *D. variegatum kinkiense, M. clementinus*, and *M. assurgentiflora* ssp *glabra*, and Bombyliid flies in the genus *Bombylius* (bee-flies) were found visiting *D. variegatum* and *M. clementinus*. Flies exhibit high morphological variation that could affect interspecific pollen loads. For example, Wiesenborn (2015) found that *Copestylum* flies in the Mojave Desert carried similar pollen loads to bees in the genus *Andrena*, while *Bombylius* flies carried relatively little pollen. Sahli & Conner (2007) found that certain syrphid flies are just as effective pollinators as bees, while Bischoff et al. (2013) found that another genus of Syrphid flies carried 1/10th the pollen load of bees in the genus *Hylaeus*. Yoshida et al. (2021) found that *Bombylius* flies can be effective pollinators in some systems. Given the abundance and high visitation rates of *Copestylum* flies at endangered plant species on the island, and how frequently they were observed with pollen on their bodies (S. Calloway, *personal communication*) this is another group of interest for preserving pollination services. Larvae of this genus in the Mojave Desert feed on decaying plant material, especially cacti. As cacti are abundant on the island, there is likely not an issue with locating habitat for their life cycle. A greater threat to *Copestylum* pollinators may be posed by the fungal pathogen *Entomophtora muscae*, which has been observed in syrphid flies on San Clemente Island based on iNaturalist records. Future research should attempt to compare the pollen loads of these potentially important visitors to focal plant species.

Several beetle species were observed visiting flowers of *M. assurgentiflora* ssp *glabra*, all in the family Melyridae. However, it is possible that our sampling methods, which utilized sweep-netting, were not adequate for truly sampling the abundance and diversity of flower beetles. Given the known importance of Melyrid beetles to pollination services in other systems (Mawdsley 2003), future studies should conduct surveys on San Clemente Island focused on these diminutive pollinators.

Butterflies and moths (Order Lepidoptera) of two species, *Vanessa cardui* and *Autographa californica*, were found to visit *M. clementinus*, though at relatively low rates compared to bees and flies. A trap camera caught what is thought to be *A. californica* visiting *L. maximum* (Fig. 3). Lepidoptera can carry substantial pollen loads, primarily on their face (Courtney et al. 1982). The painted lady butterfly (*Vanessa cardui*) is a globally widespread (except for South America) super generalist in terms of both its nectar sources and host plants for eggs and larvae that is known for its migratory behaviour and year-round mating (Celorio-Mancera et al. 2016). The caterpillars of *V. cardui* have also been recorded skeletonizing foliage of *M. assurgentiflora* on another Channel Island, Anacapa (*S. Calloway, personal communication*), and is known to prefer seasonal rain, which seems to contribute to higher offspring productivity. *Autographa californica* is widespread and abundant in North America, and its larvae is a common agricultural pest. Like the painted lady, it is a generalist and tends to lay eggs on a wide variety of host plants. While it is unknown whether either of these species' larvae feed on *M. clementinus* leaves, it is a possibility given their generalist habits. To support Lepidoptera pollinators, it is important to ensure that there is sufficient host plant population size to support them, however given that both of these species are generalists this is a lower priority for conservation of pollination services to *M. clementinus*. More research is needed to determine if additional moth species are providing pollination services to *L. maximum,* especially since so little pollination was observed during the daytime and circumstantial photographic evidence suggests that crepuscular moths may visit *L. maximum* in the dawn hours (Fig. 3).

Our data paints a complex picture of the position of individual species within their pollination networks. Flies emerge as an important central taxonomic group in terms of centrality index, degree, closeness centrality, and betweenness centrality. Flies in the genus *Copestylum* tended to have the highest centrality values across sites. Lepidopterans (moths and butterflies) varied in their role depending on the centrality index used, with higher centrality in terms of degree but lower values for closeness and betweenness centrality. Beetles, bees, and wasps tended to have lower centrality values, however certain bees and sites reversed this trend, with bees having higher centrality in terms of degree than flies at the *M. assurgentiflora* ssp *glabra* site, and higher closeness centrality than flies at the *S. filifolia* site A (though closeness was not statistically significant in the model). Since flies, especially genus *Copestylum*, are abundant and central across all sites, they are a potentially important species for conservation of pollination services to focal threatened plant species on the island. This is because their centrality indicates that they have the potential to directly or indirectly support pollination at threatened plant species. Flies are considered more generalist species in terms of the floral species they visit (Kearns 2001), and this is supported by our findings on San Clemente Island. Bees consistently had the lowest centrality (with the exception of the *M. assurgentiflora* ssp. *glabra* site). This does not indicate that they are not important; rather, it suggests that they are more specialist pollinators than flies, which is a well-known aspect of bee natural history. Given the direct interactions of bees with most of our focal plant species, including the highly endangered *L. maximum*, they should also be a priority for conservation. This is especially true at the *M. assurgentiflora* ssp *glabra* site, where bees are both direct pollinators of *M. assurgentiflora* ssp *glabra* and also had high centrality index values. Across all sites, and especially at the *M. assurgentiflora* ssp *glabra* site, the habitat needs of ground-nesting bees should be prioritized to conserve pollination services.

Future research should prioritize better understanding the habitat needs of flies (especially in the genus *Copestylum*) and bee species on San Clemente Island. Threats to Syrphid fly populations from infection by the fungal pathogen *Entomophthora muscae* and the effects of climate change on the dynamics of this pathogen should be investigated to protect both direct and indirect pollination services to focal threatened plant species. Habitat restoration and monitoring of bee populations, which are known to be susceptible to the effects of climate change, should also be considered given their importance at multiple scales within plant-pollinator interaction networks of threatened focal plant species. All of the bee species identified are known to be ground-nesting, with the exception of *Osmia* species that were observed using alternative cavities in small hollows of rocky outcroppings at the *L. maximum* site (J. Hazlehurst, *personal observation*). Established means for supporting ground-nesting bees include protecting nesting aggregation sites and providing suitable bare ground patches with the correct soil types (Severns 2004), and future research on the island should test the effectiveness of augmenting habitat for ground-nesting bees, especially in the vicinity of *M. assurgentiflora* ssp. *glabra* populations. Future studies should also consider how additional environmental factors, such as the presence of non-native plant species, might alter the structure of pollination networks on the island.

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AUTHOR CONTRIBUTION

The research concept was developed by D. Knapp and J. Hazlehurst. Fieldwork was conducted by S. Calloway, J. Hazlehurst, and D. Knapp. Data entry and initial identification and visualization of pollinator specimens was conducted by S. Calloway. D. Knapp provided taxonomic expertise on Diptera specimen identification. Data analysis and visualization was conducted by J. Hazlehurst.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

The data used to write this article are available at Dryad repository 10.5061/dryad.6djh9w17b.

APPENDICES

Additional supporting information may be found in the online version of this article:

Figure S1. Bipartite plant-pollinator interaction networks weighted by mean number of individuals captured per plant species per plot across all sampling time intervals

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