An individual-based approach to studying pollinator-mediated interactions between desert, foundation plants

Abstract (<300 words)

Downscaling interaction networks from species to individuals has emerged as a valuable tool to study community-wide patterns of pollinator sharing but has not been applied to the study of pollinator-mediated facilitation and competition. We studied the influence of inter-individual variation on pollinator sharing between foundation shrubs and cactus in a desert ecosystem using quantitative, individual-based pollinator visitation networks. Foundation plants growing in denser shrub patches had higher pollinator visitation rates, higher pollinator diversity (effective partners), and greater access to the conspecific mating pool suggesting widespread and diffuse pollination facilitation within this community. Shrub density also influenced the role of betweenness centrality more than species identity. Individual traits and contexts predicted individuals’ network roles and the formation of modules. Ecological and individual context influence the outcome of pollinator-mediated interactions and are fundamental drivers of whole community structure. Exploring these individual-community interactions will improve our understanding of drivers that promote species coexistence and plant fitness.

**Keywords: arid, desert, pollination, foundation plants, deserts, facilitation, foundation species, positive interactions, non-trophic, network**

**Introduction**

Interactions between species structure plant communities and contribute to biodiversity maintenance globally. Interacting populations are aggregations of interacting individuals, thus the outcome of interactions between species (i.e. plant fitness) can be influenced by both intraspecific and interspecific variation in attractiveness to pollinators. Attractiveness to pollinators is influenced by phenotypic variation in plant traits that can improve pollinator foraging efficiency including floral display size ([Ohashi and Yahara 1998](#_ENREF_34), [Thomson 1981](#_ENREF_51)) and plant height ([Donnelly*, et al.* 1998](#_ENREF_10), [Toräng*, et al.* 2006](#_ENREF_52)). The floral composition of the surrounding area can also influence attractiveness due to density-dependent interactions between the local co-blooming floral neighbourhood and the focal plant ([Rathcke 1983](#_ENREF_41), [Seifan*, et al.* 2014](#_ENREF_48)). Spatial association with co-blooming heterospecifics can alter the attractiveness of an individual plant leading to increases (facilitation) or decreases (competition) in pollinator visitation rates ([Braun and Lortie 2018](#_ENREF_7), [Mitchell*, et al.* 2009](#_ENREF_31), [Rathcke 1983](#_ENREF_41)). Consequently, both individual phenotypic traits and community-level attributes impact interactions with pollinators that in turn influence plant fitness.

Network analysis has emerged as a valuable tool for studying plant-pollinator interactions ([Bascompte and Jordano 2013](#_ENREF_3)). Most pollinator visitation networks are species-based; each node represents a population of plants or pollinators and links are the sum of interactions between the populations. The recognition that patterns between interacting individuals drive the patterns between interacting species has driven recent interest in downscaling interaction networks from populations to individuals ([Dupont*, et al.* 2011](#_ENREF_14), [Dupont*, et al.* 2014](#_ENREF_15), [Gómez and Perfectti 2011](#_ENREF_21), [Rumeu*, et al.* 2018](#_ENREF_43), [Tur*, et al.* 2014](#_ENREF_55), [Valverde*, et al.* 2016](#_ENREF_58)). An advantage of individual-based networks is the ability to integrate individual variation to the study of structure and pattern of relations within ecological networks (Olesen 2010, Losapio 2019). Individual-based networks have been used to explore specialization of pollen use ([Tur*, et al.* 2014](#_ENREF_55)) and interaction rewiring with phenology ([Valverde*, et al.* 2016](#_ENREF_58)). Species and individual-based approaches are complementary, and for instance, these coupled approaches have been used to study changes in specialization across a gradient of elevation in hummingbird-plant networks ([Maglianesi*, et al.* 2015](#_ENREF_28)). Downscaling to individuals is a fundamental step to shed light on the underlying drivers of community functioning.

Because of pollinator foraging preferences, relative differences in attractiveness could contribute to an individual plant’s role in the network because it introduces differences in the number of links which determine where in the network an individual is located. Centrality describes the node’s topological position within the network i.e. its functional role within a community (Dupont and Olesen 2009). Centrality measures are estimates of relative influence, for example in food webs, centrality measures have received attention for their ability to identify keystone species (Jordan 2006, Estrada 2007). Within populations, links between nodes act as mating probabilities and centrality has been shown to increase plant fitness due to relative differences in attractiveness between conspecifics ([Gómez and Perfectti 2011](#_ENREF_21)) i.e. more attractive plants were more central and had higher fitness. Centrality has never been investigated within an individual based pollinator visitation network containing more than one or two species making it difficult to generalize. Within a multi-species assemblage, being more attractive is only a benefit if the visitors also visit other members of the same species. By considering the network of interactions within a system, a greater scope of interactions can be detected that can help us understand more of the mechanisms within a system and they can be used to calculate how individual attractiveness leads to potential mate availability. An individual-based network approach can provide insight into the quality component of pollination.

Using a trait-based individual approach can provide a more mechanistic understanding of network structures that arise from pollinator sharing (Woodward). Modules are network structures consisting of densely connected nodes that interact more strongly with each other than the rest of the network. Within species-based interaction networks, modules can be considered biologically significant co-evolutionary units (Olesen 2007, Donatti 2011). These structures can arise even in very short flowering seasons ([Morente-López*, et al.* 2018](#_ENREF_32)), and their membership is constrained by phenology ([Tur*, et al.* 2015](#_ENREF_53), [Valverde*, et al.* 2016](#_ENREF_58)) and spatial location ([Dupont*, et al.* 2014](#_ENREF_15)). Previous individual-based approaches have revealed the importance of inter-individual variation as conspecifics can belong to different modules ([Tur*, et al.* 2015](#_ENREF_53)). Individual based modularity will shed light on how pollinator preferences structure plants into groups that interact more strongly with each other. Nestedness is a quantitative measure describing the hierarchy of the interactions of the network. In nested networks, specialized nodes i.e. those with fewer interactions are linked with generalized nodes i.e. well connected nodes. Individuals may differ in their contributions. Differences in attractiveness may also contribute to the structure of the network as a whole. By better understanding the attributes that give rise to network structures, we begin to give them more explanatory power.

In this study, we observed flower visitors to a spring blooming desert shrub and cactus community to investigate drivers that lead to differences in pollinator visitation rates. In desert ecosystems, peak flowering periods are restricted to a relatively short period in the spring time which is strongly constrained by climatic conditions ([Jennings 2001](#_ENREF_26)). Spring blooming shrubs and cacti represent individual concentrations of floral resources and we used them as a model system for studying how variation in floral density influences community interactions. We used these data to build an individual based pollinator-visitation network to complement the visitation rates survey and to identify potential ways that these contexts can influence an individual’s role.. We hypothesized that individual variation in traits associated with pollinator attractiveness predict an individual’s role within pollinator visitation networks and give rise to network structures. Finally, we compared the species level and individual level networks in terms of nestedness, modularity and specialization to contribute to a better understanding of how individual interactions scale up into species-level patterns – to see which network properties are emergent properties of individual interactions.

Methods

Field data collection

Plant-pollinator interactions were studied at Sunset Cove at the Sweeney Granite Mountains Desert Research Station within the Mojave National Preserve in California (1280 MASL, 34°46'26.5"N 115°39'31.3"W). Data were collected between April 20th and May 9th, 2018 encompassing the flowering period of most spring blooming shrubs and cacti at the site. The experiment ended when it was not possible to locate additional individuals of blooming shrubs. Focal plants were chosen by walking in a line starting in a different quadrant of the study site each day to avoid confounding area by time of day. To avoid oversampling the most abundant species, up to six individuals of a single species were sampled per observer per day. We georeferenced all focal plants using a Garmin 64st handheld GPS.

We recorded flower-visitor interactions for each focal plant within 10-minute in-situ observation periods between 9:00 AM and 5:30 PM in the absence of strong winds. Observations were focused on seven species of shrub and three species of cactus for a total of 66 hours of observation (Table 1). This approach to creating a pollinator visitation network allows visitation rates to be compared between individual plants in contrast to the frequently used method of transect walks in which the most abundant interactors are observed for longer ([Westphal*, et al.* 2008](#_ENREF_60)).

Only potential pollinators that made direct contact with plant reproductive organs were considered in this study. Taxonomic groups previously documented as non-pollinating visitors were excluded such as Coccinellidae ladybird beetles, *Carpophilus* sp. pollen beetles and spiders. Soft-winged flower beetles (Melyridae) in the subfamily Dasytinae were also excluded because they were observed but were stationary deep within flowers and could not be effectively counted. Finally, pollinators < 2 mm in size such as micro-beeflys (Mythicomyiidae) were excluded from analyses because it was not viable to accurately track visitation to large shrubs such as *Larrea tridentata*. Most floral visitors were identified to genus or species on the wing to minimize any artefacts of destructive sampling. We collected voucher specimens to verify the on-the-wing identifications, and samples are archived at York University. Some groups e.g. Tachinidae and Sarcophagidae were resolved to family due to the difficulty of identifying them on the wing (Appendix A). Some visitors were morphotyped within these categories. Morphotyping and RTU (recognizable taxonomic unit) are useful methods for characterizing and quantifying pollinator communities ([Oliver and Beattie 1993](#_ENREF_38)). This method provides information about the linkages between different genera and functional groups.

We recorded the number of open flowers and the height of each focal plant directly before the observation period as individual-level traits. As a measure of the immediate floral neighbourhood, we recorded the abundance and identity of all blooming shrubs and cacti within a 3 m radius around the focal plant. We tracked shrub phenology and estimated site-level floral density by counting the number of blooming shrubs of each species in four 10 m by 50 m band transects on 13 days over the study period. This was a proxy for net floral abundance at the site level.

**Data analysis**

All statistical analyses were performed using R Version 3.4.2 (R Core Team, 2017), and all code is available on GitHub at https://github.com/jennabraun/foundation-pollination. Site-level density values for non-density-sampling days (~3) were imputed for each species separately using linear interpolation because there was no expectation for seasonality using the R package imputeTS, ([Moritz and Bartz-Beielstein 2017](#_ENREF_33)). The species-specific values were summed to complete missing date observations.

Influence of individual traits and floral neighbourhood on pollinator visitation

To test for between-plant variation in pollinator visitation rates, we fit generalized linear mixed models (GLMM) with the number of visits as the response variable and individual floral display size, floral neighbourhood density, site density, and study day as predictors. The shrub species was included in the models as a random effect. To account for over dispersion in the model, we used a negative binomial error distribution ([Zuur*, et al.* 2009](#_ENREF_61)). Height and floral display size were positively correlated (Figure A1), Pearson’s = 0.537, p < 0.0001, df = 392), and thus, only floral display size was included in finals models. We assessed model fit by comparing candidate models to each other and to the intercept only model using AIC and likelihood ratio tests. In cases when AIC < 2 and there were no differences in likelihood ratio test, we chose the simpler of the models. We tested the final chosen predictors for multicollinearity using the vif function from the R package car ([Fox*, et al.* 2012](#_ENREF_18)).

To test for pollination hotspots that can arise from habitat preferences or spatial heterogeneity locally rather than floral preferences, we used Moran’s I and Geary’s C (k = 4) to test for spatial autocorrelation of visitation rates using the R package spdep ([Bivand*, et al.* 2011](#_ENREF_5)).

Network analyses

Pollinators were classified into 17 distinct functional groups (Table S1) to facilitate the detection of general trends. We built a quantitative, bipartite network using visitation frequencies to each individual plant as the measure of interaction strength. As a measure of individual generalization, we calculated the effective number of interaction partners, eH, where H is the Shannon Diversity of functional groups visiting the individual plant ([Dormann 2011](#_ENREF_11)). We also calculated the extent to which each plant’s interaction contributes to network nestedness in comparison to a random null model that controls for degree differences (Saavedra and Stouffer 2013). All bipartite network indices were calculated using functions within the bipartite R package ([Dormann*, et al.* 2008](#_ENREF_12)).

In unipartite networks, each link is a shared pollinator functional group connecting potentially interacting individual plants. We projected the quantitative bipartite network into an individual based unipartite network and calculated several centrality measuresthat are frequently used to describe influence in social network analysis using igraph ([Csardi and Nepusz 2006](#_ENREF_9)). In species networks, these measures describe the importance of species (Gonzalez 2010, Jordano 2006). Degree is the number of links per individual. In plant-plant networks, degree centrality quantifies the number of potential interactions between plants mediated through pollinators. Eigancentrality extends the concept of degree centrality but takes into the account of the importance degree of the interactors. Individuals that interact frequently with other highly connected individuals are more likely to influence the full network because they can interact with dense substructures within the network. Betweenness is the number of times a node lies on the shortest path between other nodes and describes the importance of a node on connecting the parts of the network ([Freeman 1978](#_ENREF_19), [Martín-González*, et al.* 2010](#_ENREF_29)). We used Kruskal-Wallis tests to test for the difference in centrality between species.

We fit GLMM (glmmTMB) ([Brooks*, et al.* 2017](#_ENREF_8)) using the bipartite and unipartite network indices as response variables and the individual plant traits, local floral neighbourhood and study day as predictors. Plant species was included in all models as a random effect and the link function depended on the distribution of the indice variable (Table A2). Models were compared to intercept only models using AIC and likelihood ratio tests with χ2 approximations.

Betweenness values were continuous and zero-inflated (n = 141, Figure A2). Consequently, we first modeled the likelihood of an individual having a betweenness value > 0 using a binomial mixed effect model. A high number of ultra-peripheral nodes is typical in pollination networks ([Dupont*, et al.* 2011](#_ENREF_14), [Guimera and Amaral 2005](#_ENREF_23)). We then log-transformed the continuous part to meet the assumptions of normality and modeled it using a Gaussian error distribution (residuals: W = 0.98854, p-value = 0.5491).

To calculate the proportion of linked conspecifics and heterospecific plants, we created a series of unweighted, unipartite networks. We calculated these for each individual plant.

The number of linked and unlinked conspecific or heterospecific plants were used as a binomial response variable. Quasibinomial family GLMM (MASS) ([Venables and Ripley 2013](#_ENREF_59)) was used to account for overdispersion and plant species was included as a random effect. Degree, eiganvector, and closeness centrality measures were strongly and positively correlated with each other (Table A3). Hence, only degree centrality was included in these models because it is the most commonly reported measure in the network literature. Betweenness centrality, study day, visitation rates, shrub density and floral display size were used as predictors. Models were compared to random intercept only models using AIC and likelihood ratio tests to identify the most parsimonious models.

Overall network structure

Modularity describes how plant communities are structured into clusters or modules of densely interacting individuals by pollinator sharing. Modularity was calculated for the plant-plant interaction network using simulated annealing in the R package rnetcarto, ([Doulcier and Stouffer 2015](#_ENREF_13)). This value was compared to the modularity of 1000 random networks generated holding the totals of rows and columns fixed based on Patefields’ (1981) algorithm ([Oksanen and Blanchet](#_ENREF_35)). Z-scores were calculated to assess significance of results and facilitate comparison between the different networks. Z-scores were calculated using: Z:Score = (Observed value - mean (null)/sd\*null). Positive value denote the observed value is higher than the mean of the null distribution. To explore the role of individual traits and neighbourhood on modularity, and therefore ecological dynamics, we built multinomial models using the nnet package ([Venables and Ripley 2013](#_ENREF_59)) with the module as the response, and plant species, individual floral display size, visitation rate, study day and local floral neighbourhood as the predictors.

Down-scaling effects on whole network measures

To complement these individual measures and facilitate comparison of this network to other visitation networks, we calculated several common indices for the individual and species bipartite network. The metric H2` is the degree of complementary specialization of the whole network of interacting species and measures the deviation of observed interactions from those expected given the marginal totals of the species. This quantitative measure ranges from 0 and 1; the higher the selectivity of the species, the higher H2` for the network. H2` does not vary significantly with network size ([Blüthgen*, et al.* 2006](#_ENREF_6)). Weighted nestedness (WNODF) is a quantitative measure that ranges between 0 and 100 and describes the hierarchy of the interactions of the network. In nested networks, specialized nodes i.e. those with fewer interactions are linked with well-connected nodes ([Almeida-Neto and Ulrich 2011](#_ENREF_2)). Weighted connectance is the linkage density divided by the total number of interactors (species or individuals) ([Tylianakis*, et al.* 2007](#_ENREF_57)). It is a central network property that drives other network properties such as nestedness ([Poisot and Gravel 2014](#_ENREF_40)). It measures of the complexity of the network. The modularity of each network was assessed using DirtLPA algorithm implemented in bipartite ([Beckett 2016](#_ENREF_4)). Modularity can differ for the same network between unipartite and bipartite forms ([Martin Gonzalez*, et al.* 2012](#_ENREF_30)). Indices were compared to the indices from 1000 random networks generated holding the totals of rows and columns fixed based on Patefields’ (1981) algorithm using Z-scores.

Results

General patterns

A total of 635 foraging bouts were recorded over 394 observation periods, 163 periods had zero visits. A total of 430 visits were to shrubs and 205 were to cactus. The pollinators made up 17 functional groups spanning 62 RTUs of visitors (Table 1). With the exception of hummingbirds (*Calypte* sp.), all floral visitors were insects. There was no spatial autocorrelation detected for visitation rates (Moran’s: -0.055108, p = 0.953, Geary: 1.0442, p = 0.8145), and there was no significant correlation between site-level floral density and local neighbourhood floral density (Pearson’s = 0.11, p = 0.1187, df = 178).

There was a consistent, positive influence of neighbourhood shrub density on pollinator visitation rates throughout the study period (n = 395, Table 2). There was a significant interaction between floral display size and study day, but floral display size became unimportant later in the study period (Table 2). Site-level density of blooming plants decreased over the duration of study (Pearson’s = -0.4978227, df = 18, p-value = 0.02551). Site-level density interacted with floral display size similarly to day effects, but these models had higher AIC scores (Table Ax), and only study day was used for all subsequent models.

Floral display size and neighbourhood effects on centrality, effective partners and module membership

Individual plants that received more pollinator visits were more central within the network. Pollinator visitation rate was a significant predictor of degree centrality (GLMM: Est: 0.20863, χ2:80.891, P < 0.0001), eigancentrality (Est: 0.055032, χ2: 97.755, p < 0.0001) and betweenness centrality (GLMM: Est: 0.18868, χ2: 26.336, p < 0.0001, logistic part: Est: 0.83234, chi, p <0.001). The probability of an individual plant having a betweenness > 0 increased with local shrub density (GLMM, Est: 0.20559, chi, p = 0.018). The number of effective partners (eH) increased with pollinator visitation rate (GLMM, Est: 0.08167, χ2: 20.2173, p < 0.001) and shrub density (Est: 0.05054, χ2: 4.0376, p = 0.0445). The size of an individual plant’s floral display and study day were unimportant to a plant’s centrality (Table A3).

Foundation plant species differed in their degree centrality (Kruskal-Wallis: 44.913, df = 9, p < 0.0001, Figure 1) and eigancentrality (Kruskal-Wallis: 84.285, df = 9, p < 0.0001, Figure 1). However, betweenness did not differ between plant species (Kruskal-Wallis: 6.7085, df = 9, p-value = 0.6674) nor did the number of effective partners (Kruskal-Wallis: 15.056, df = 9, p-value = 0.08941).

Individual plants that were more central to the network had a greater probability of interacting with both conspecific and heterospecific plant individuals (Figure 2, Table 3). Blooming shrub density increased the probability of interaction with a greater proportion of conspecifics, but not heterospecifics (Table 4). We believe that the interaction between degree and visitation rate is an artefact rather than an ecological trend (cause?). At a high degree, increased visitation results in links to individuals that a plant is already linked to rather than increasing the proportion of potential interactors. Again, there was no influence of floral display size nor a day effect (Table A4).

The plant-plant interaction network was significantly modular (0.335, Z = 17.57, p < 0.001). It was made up of five modules (Figure 3). Species identity was the strongest predictor of module membership (266.689, df = 36, < 0.0001), however conspecifics belonged to different modules. Visitation rate (20.085, df = 4, p = 0.0004805), study day (20.085, df = 4, 0.0025540) and shrub density were also important (9.397, df = 4, 0.0518980). The modules had unequal numbers of individuals, with module 0 with only 3 members, and the last module with only 9 individuals.

The individual-based and species-based bipartite networks were both significantly different than random in connectance, specialization, nestedness and modularity (Table 4). The networks were less cohesive and less nested than random networks, and more specialized and modular than random networks. When downscaled, the pollinator visitation network become more nested, more generalized, more cohesive and less modular relative to the species network (Table 4).

NOTE Chris could you please check if I am interpreting the Z-scores correctly? I am trying to use the as effect sizes i.e. distance from random network it’s a bit complicated because the +/- aspect of them and maybe I am confused

**Discussion**

Our study found evidence that the ecological features of individual plants can determine the role of a plant within the network and subsequently the structure of the network as a whole. We hypothesized that individual traits that are associated with attractiveness to pollinators would give rise to an individual’s role with whole interaction network. If visitation networks are created by the foraging preferences of pollinators… The results were variable. Contrary to our predictions, we found no direct influence of floral display size on network roles or structures despite its strong influence on pollinator visitation. Interestingly this influence on visitation decreased at the end of the study period. The competitive advantage of a large floral display size was lost in the later time period suggesting that the relative importance of individual traits have a temporal component. Because visitation rates influence most network roles, display size etc had an indirect effect. Flowering shrub density influenced the patterns of interactions beyond increasing visitation rates including effects on betweenness centrality and modularity. The study of pollination networks is dominated by those that aggregate individuals to species. For species networks, traits are increasingly being recognized as driving forces of network structure ([Dupont*, et al.* 2014](#_ENREF_15), [Eklöf*, et al.* 2013](#_ENREF_16), [Olesen*, et al.* 2010](#_ENREF_36), [Olito and Fox 2015](#_ENREF_37)). These are evident as driving forces at the individual level as well, and traits can be considered intrinsic phenotypic traits but also the floral neighbourhood an individual is embedded in.

Floral neighbourhood contributions to network positions and structure

Centrality implications In this system, we found the influence of individual floral display size mediated through visitation rates influenced almost all aspects of network topology. Intuitively, visitation rates should increase centrality measures, however, it doesn’t always happen. In a population network of *Erysimum mediohispanicum*, visitation rates were correlated with degree, negatively correlated with betweenness, and were not correlated with closeness ([Gómez and Perfectti 2011](#_ENREF_21)). Interestingly, plants growing denser patches had a betweenness roles that showed that shrub facilitation contributes to the cohesiveness of the network.

Plant species did not differ in betweenness centrality suggesting this role is contextual in this system. Low differences between species have also been reported in agricultural systems ([Russo*, et al.* 2013](#_ENREF_45)). Species with high betweenness centrality are hypothesized to mediate co-evolutionary cascades moving through mutualistic networks ([Martín-González*, et al.* 2010](#_ENREF_29)) and keep communities from being fragmented (Newman 2004, Jeong 2000). Node attributes influence network topology (Bianconi et al, 2009). A meta-analysis confirmed the importance of generalized species and demonstrated their similarity of roles across geographical regions and ecosystems ([Martín-González*, et al.* 2010](#_ENREF_29)). Further research is necessary to distinguish between contextual, individual roles and species roles in structuring ecological interaction networks. The next step here is to determine how the co-blooming neighbourhood influences centrality measures in the absence of facilitation. Downscaling the community interaction network revealed that individuals are more variable than their aggregations of conspecifics in the key network role of betweenness centrality.

Modules. This system was influenced by species identity, study day, visitation rates and also weak effects of the local shrub density. Previous work has found that modules are not stable structures (Valverde) and change over short time periods (Stanoev). Temporal variations in plant-pollinator interactions are not well documented at the community level and the causes of short-term visitation network dynamics are critically understudied (CarraDonna, Poisot 2014, Bascompte and Jordano 2013). In addition to potential short-term phenological variation, modularity can be influenced by decreases in net site-level density. Changes in the availability of resources can alter pollinator foraging preferences (cite). Conspecifics can be members of different modules (Tur 2015), and previous individual, community work has found divergences between taxonomic similarities and trait similarities – networks built on traits are different than those built with species (Rumeu 2018). Conversely, only visitation rates contributed to the individual networks nestedness which suggests it is the generalists contributing to nestedness, not the specialists (this is maybe too obvious. Not sure yah good keep). Nestedness is a function of redundancy and it hypothesized to increase a network’s stability (Bascompte and Jordano 2007) so these findings highlight the importance of generalist plants in this system.

Downscaling from species to individual network

Nestedness, modularity, and the correlation between degree and other centrality measures are considered universal features of networks (Martin). Our individual network structures resembled the species network indicating that this was a reasonable approach to explaining the aggregated patterns of species networks. When downscaling, the network was still modular, less nested than expected, less generalized and more cohesive…. Here, we showed that variation in individual context due to variation in display size and the number of neighbours that is present in any ecosystems may give rise to some of the universally detected network structures.

Pollinator-mediated interactions between foundation plants

Diffuse pollinator-mediated facilitation between co-blooming foundation plants was prevalent in this system. There were several ways that plants may have benefited from their neighbours. Facilitation between co-blooming plants through increases in local, interspecific density is a frequently studied mechanism within many ecosystems globally but has not been reported previously for desert ecosystems ([Braun and Lortie 2018](#_ENREF_7)). Intraspecific density has however been reported to benefit the pollination of desert mustard *Lesquerella fendleri* ([Roll*, et al.* 1997](#_ENREF_42)). Interestingly, shrubs, but not cacti densities elicited this positive effect. Shrubs were taller than cacti with larger floral displays, and this attractiveness can bring in pollinators via the magnet species effect leading to improved visitation to neighbouring plants (sensu Laverty 1992). This suggests some level of species specificity in benefactors. Foundation plants growing in denser areas of flowering shrubs were visited by a higher diversity of pollinator functional groups i.e. were more generalized. Pollinator abundance-richness relationships are commonly reported for plant-pollinator interactions ([Steffan-Dewenter*, et al.* 2002](#_ENREF_49), [Steffan‐Dewenter 2003](#_ENREF_50)). Increases in pollinator diversity can increase plant fitness ([Gómez*, et al.* 2007](#_ENREF_20), [Klein*, et al.* 2003](#_ENREF_27), [Perfectti*, et al.* 2009](#_ENREF_39)) through several mechanisms. Pollinator-pollinator interactions can lead to increases in pollen deposition by displacing pollinators to other plants and decreasing geitonogamy ([Greenleaf and Kremen 2006](#_ENREF_22), [Heinrich 1979](#_ENREF_25)). Alternatively, the likelihood of attracting more effective pollinators increases with pollinator diversity through sampling effort (Ives 2005). The positive relationship between diversity and pollination success is likely important in desert ecosystems because that relationship is strongest when floral resources are heterogeneously distributed ([Tylianakis*, et al.* 2008](#_ENREF_56)). Shrub density improved access to conspecifics, and this is a novel pathway of pollination facilitation. This means that the additional visitors are shared with other members.

Visitation rates are a commonly used proxy of pollination success within community-level studies of plant-pollinator interactions.

Improved pollen diversity can also increase fitness improving genetic diversity (cite). Desert foundation plants have multiple flowers, and there is strong potential to increase genetic diversity of seed set from a single foundation plant within a single flowering season.

Conclusions

Better understanding the contexts that lead to individual roles within networks could be really helpful to applied ecology and understanding co-evolutionary cascades. We identified three likely ways that shrub density facilitates by combining classic pollinator observations with an individual-based network approach.

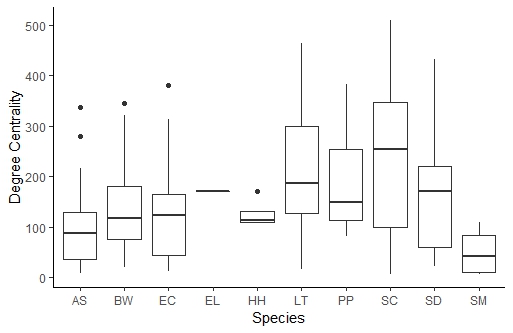
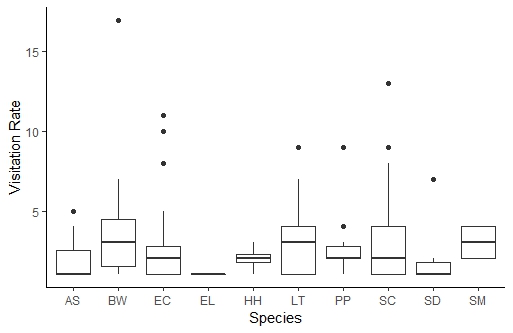
Tables & Figures

Table 1: List of foundation species, number of observation periods, phenotypic traits and visitation rate.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Foundation plant species | Observation periods | Mean height (cm) | | Mean floral number | Mean visitation rate (per 10 min) |
| *Acamptopappus sphaerocephalus* | 96 | | 51.08 | 45.16 | 0.88 |
| *Eriogonum fasciculatum* | 31 | | 44.03 | 16.71 | 2.39 |
| *Ericameria cooperi* | 55 | | 49.35 | 124.36 | 1.69 |
| *Ericameria linearifolia* | 4 | | 69.25 | 46.50 | 0.25 |
| *Larrea tridentata* | 80 | | 189.88 | 127.14 | 1.91 |
| *Scutellaria mexicana* | 12 | | 72.93 | 24.14 | 0.86 |
| *Salvia dorri* | 13 | | 55.83 | 27.00 | 1.08 |
| *Echinocereus engelmannii* | 5 | | 27.80 | 2.40 | 1.60 |
| *Opuntia basilaris* | 28 | | 25.14 | 4.71 | 1.64 |
| *Cylindropuntia echinocarpa* | 69 | | 56.01 | 8.03 | 2.19 |

Table 2: Summary of the GLMM showing the influence of floral display size, floral neighbourhood and time on pollinator visitation rates to desert foundation plants (n = 395 plants). Species was included as a random effect in the models.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | χ2 | Df | p |
| Intercept | -0.61 | 4.15 | 1 | 0.042 |
| Shrub Density | 0.074 | 4.12 | 1 | 0.042 |
| Day | 0.046 | 5.17 | 1 | 0.023 |
| Floral Display Size | 0.012 | 14.85 | 1 | 0.00012 |
| Floral Display:Day | -0.00053 | 4.15 | 1 | 0.042 |



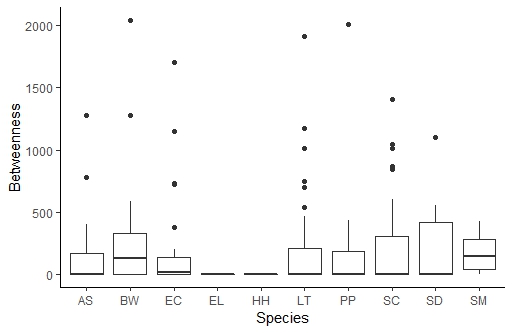
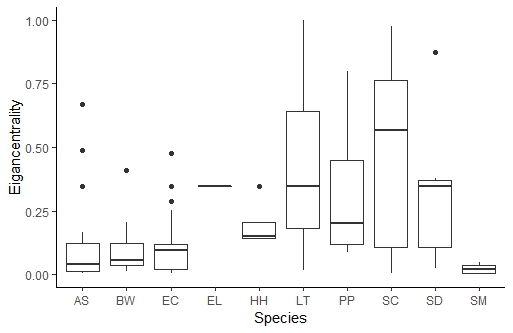
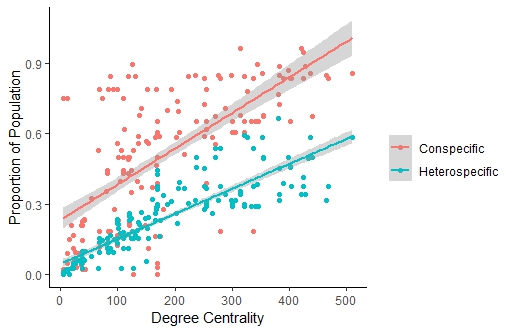


Figure 1: Species differed in their degree centrality and eiganvector centrality, but not betweenness.



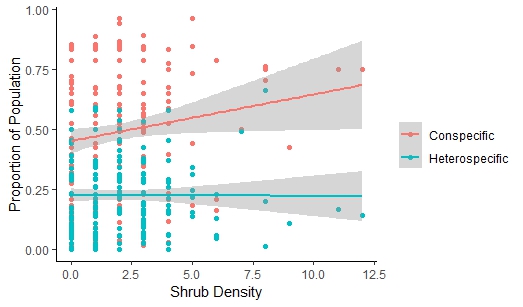


Figure 2: Foundation plants interact with a greater proportion of conspecifics than heterospecifics. Values are the number of interactors standardized by the number of potentially interacting plants within the network. Degree centrality increased both the proportion of conspecifics and heterospecifics. Shrub density increased the proportion of conspecifics only.

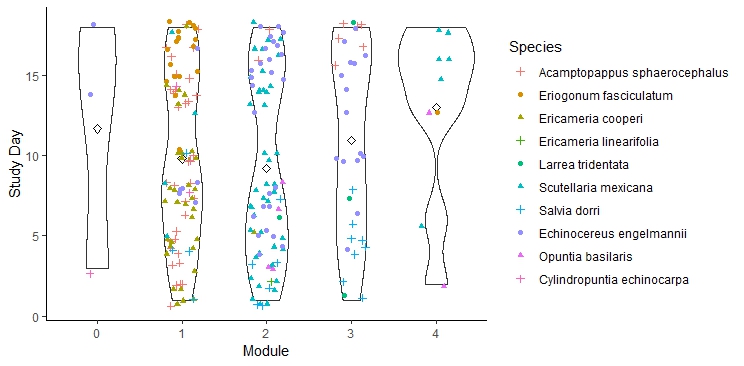


Figure 3: Plant-plant modules were structured by species identity and day. Conspecifics can be found in multiple modules.

Table 3: Results from GLMM showing predictors of proportion of conspecific and heterospecific interactors

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Proportion of Conspecifics | | | Proportion of heterospecifics | | |
|  | Estimate | χ2 | p | Estimate | χ2 | p |
| Shrub density | 0.066 | 5.93 | 0.015 | NA | NA | NA |
| Degree | 0.0086 | 181.59 | <0.0001 | 0.01 | 424.35 | <0.0001 |
| Visitation Rate | 0.072 | 3.05 | 0.08 | 0.044 | 1.44 | 0.23 |
| Degree: Visitation rate | -0.000423 | 6.09 | 0.016 | -0.00055 | 24.95 | <0.0001 |

Table 4: Comparison of common quantitive network indices between the species network and the downscaled individual-based network. Indices were calculated for random networks of the same size and compared to the observed networks using Z-scores.

|  |  |  |
| --- | --- | --- |
| Indice | Species-based network | Individual-based network |
| Weighted Connectance | Observed: 0.15 (Z: -40.9\*\*\*)  Random: 0.27 | 0.08 (Z: -16.1)  Random 0.13 |
| H2 | 0.43 (Z: 57.16)  Random 0.05 | 0.57 (Z: 26.1)  Random: 0.2004796 |
| WNODF | 32.83 (Z: -8.39)  Random: 63.15 | 4.65 (Z: -6.40)  Random: 8.13 |
| Modularity | Obs :0.44 (Z: 36.4)  Random: 0.09 | 0.59 (Z: 24.35)  Random: 0.38 |

**Appendix**

Table A.1: Functional groups

|  |  |  |
| --- | --- | --- |
| Functional group | Key | Taxons |
| Long-tongued very large bees | LtLbee | Anthophora |
| Short-tongued very large bees | StVLbee | Centris |
| Short-tongued large | StLBee | Diadasia, Mellisodes |
| Short-tongued medium | StMbee | Megachile, Colletes, Ashmeadiella, Hoplitis, Osmia, Lasioglossum |
| Short-tongued small | StSmbee | Lasioglossum (Lasioglossum), Hesperapis, Hylaeus |
| Short-tongued very small | StVSbee | Perdita, Lasioglossum |
| Honeybees | Honeybee | Apis mellifera |
| Small flies | SmDi | Agromyzidae, Richaardiae, Tephritidae |
| Large flies | LgDi | Muscidae, Sarcophagidae, Tachinidae |
| Nectar-seeking wasps | Nwasp | Ammophila, Bembecini, Eumeninae, Pompilidae |
| Long proboscis bee-fly | LpBeefly | Bombylinae |
| Short proboscis bee-fly | SpBeefly | Anthracinae etc |
| Syrphid fly | Syrphid | Allograpta exotica, Eupeodes volucris, Eristalis sp., Pseudodoros clavatus |
| Humming bird | hummingbird | Calypte sp. |
| Beetles | beetle | Elaterinae, Chrysomelidae |
| Small Day flying moths | MicroLep | Coleophora, Lithariapteryx |
| Butterfly | butterfly | Desert swallowtail (Papilio polyxenes coloro), Mojave blue (Euphilotes mojave Mojave) |

Table A2

List of model types used throughout paper. Will maybe integrate into text.

|  |  |  |
| --- | --- | --- |
| Response | Error distribution | Log link |
| Visitation | Negative binomial | default |
| Degree | Negative binomial |  |
| Eigancentrality | Gaussian |  |
| Betweenness | Logistic binomial, log transformed Gaussian |  |
| Proportion conspecifics | Quasibinomial |  |
| Proportion heterospecifics | Quasibinomial |  |
| EH | Poisson |  |
| Contribution to nestedness | Gaussian |  |

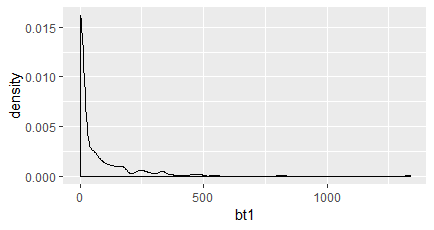


Figure A1: Betweenness values were very zero-inflated. Most models for zero-inflation are for count data, not continuous data.

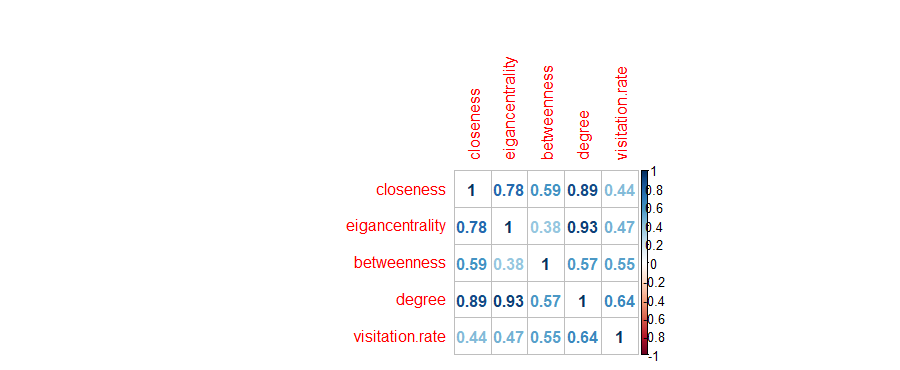


Figure A2: Correlation coefficients between centrality measures and visitation rates.

Comparing best model to null (Visitation rates) using car::Anova = Chi square: 40.687, df=4,p <0.00

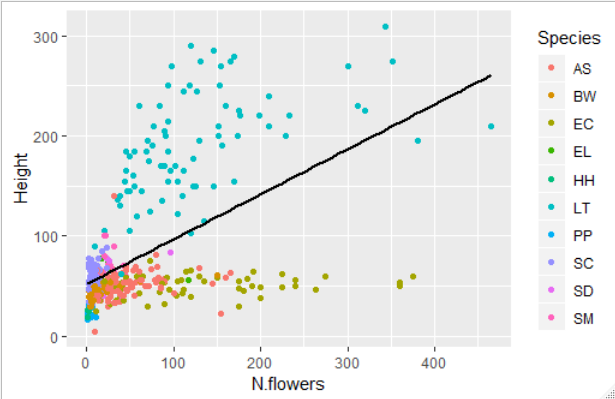


Figure A3: Correlation between the number of flowers and height, split by foundation plant species.

**Full Models for centrality**

Table A4

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Degree | | | Eiganvector | | |
|  | Estimate | χ2 | p | Estimate | χ2 | p |
| Visitation rate | 0.2042996 | 75.5616 | < 0.0001 | 0.0543331 | 91.4049 | < 0.001 |
| Shrub density | 0.0034335 | 0.0184 | 0.8921 | -0.0028750 | 0.1577 | 0.6913 |
| Study day | -0.0076894 | 0.8207 | 0.3650 | 0.0001981 | 0.8769 | 0.3490 |
| Floral display size | 0.0007984 | 1.2705 | 0.2597 | -0.0026972 | 1.1406 | 0.2855 |

(Intercept) 4.326e+00 2.522e-01 17.154 <2e-16 \*\*\*

Quantity 2.025e-01 2.356e-02 8.598 <2e-16 \*\*\*

shrub.density 3.445e-03 2.724e-02 0.126 0.899

day -6.199e-04 1.753e-02 -0.035 0.972

N.flowers 1.739e-03 2.221e-03 0.783 0.434

day:N.flowers -9.339e-05 2.020e-04 -0.462 0.644

Table A5

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | | Betweenness (binomial) | | | Betweenness > 0, gaussian | | |
|  | Estimate | χ2 | p | Estimate | χ2 | p |
| Visitation rate | 0.835882 | 41.864 | < 0.0001 | 0.1906119 | 26.5317 | < 0.0001 |
| Shrub density | 0.256831 | 7.6533 | 0.00567 | 0.0033480 | 0.0065 | 0.9357 |
| Study day | -0.008943 | 0.0926 | 0.76089 | 0.0066236 | 0.1842 | 0.6678 |
| Floral display size | 0.003956 | 3.5005 | 0.06135 | -0.0012015 | 1.5460 | 0.2137 |

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | | Effective partners | | | Nestedness contribution | | |
|  | Estimate | χ2 | p | Estimate | χ2 | p |
| Visitation rate | 0.0795522 | 18.2781 | <0.0001 | 0.1015193 | 29.5833 | <0.0001 |
| Shrub density | 0.0484860 | 3.6568 | 0.0558 | -0.0106382 | 0.1963 | 0.658 |
| Study day | 0.0013102 | 0.0188 | 0.8908 | -0.0126016 | 2.3509 | 0.125 |
| Floral display size | 0.0006251 | 1.1940 | 0.2745 | 0.0007321 | 1.1543 | 0.283 |

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | | Proportion of Conspecifics | | | Proportion of Heterospecifics | | |
|  | Estimate | χ2 | p | Estimate | χ2 | p |
| Visitation rate |  |  |  | -0.1233885 |  | 0.0000 |
| Shrub density |  |  |  | 0.0162254 |  | 0.3509 |
| Degree |  |  |  | 0.0084822 |  | 0.0000 |
| Study day |  |  |  | -0.0009280 |  | 0.8828 |
| Floral display size |  |  |  | -0.0004064 |  | 0.4406 |

AIC table for nnet models

|  |  |  |
| --- | --- | --- |
| Candidate model | Df | AIC |
| Intercept only |  | 555.3168 |
| Species + shrub.density + Quantity + N.flowers\*day | 60 | 364.1505 |
| Species + shrub.density + Quantity +day + N.flowers | 56 | 365.7156 |
| Species + shrub.density + Quantity + day | 52 | 360.2055 |
| Species + shrub.density + Quantity + site level density |  | 368.5406 |

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