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

Abstract (<300 words)

A central focus of ecology is understanding the mechanisms underlying interaction patterns in natural communities. Network analysis has emerged as a valuable tool for understanding plant pollinator interactions, but these networks are primarily built by aggregating interactions within species. Interactions are actually made between individuals and an advantage of individual-based networks is the ability to integrate individual traits and therefore promote mechanistic understanding of the drivers of network structure. In all plant communities, focusing only on the drivers of pairwise interactions limits our capacity to describe and predict community resilience, structure, and composition. We used a desert shrub and cactus community as a model system to study the underlying drivers of network topology. We hypothesized that the traits that alter attractiveness of plants to pollinators can predict an individual plant’s role within the visitation network and contribute to the structure of network. We found that floral display size increased pollinator visitation early in the study but contrary to our expectations did not directly influence individual plant’s centrality or the formation of any network structures. Neighbourhood shrub density positively influenced pollinator visitation rates indicating diffuse facilitation was prevalent in this system. In addition, plants growing in denser shrub patches had roles important to connecting the network. Overall, the individual-based network resembled the aggregated species network indicating that this was a reasonable approach to explaining interaction patterns. The results show that neighbours, as well as individual phenotypic traits and taxonomic identity are important in structuring plant-pollinator interactions at the community level.

**Keywords: arid, desert, pollination, facilitation, centrality, 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_37), [Thomson 1981](#_ENREF_54)) and plant height ([Donnelly*, et al.* 1998](#_ENREF_11), [Toräng*, et al.* 2006](#_ENREF_55)). 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_46), [Seifan*, et al.* 2014](#_ENREF_50)). 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_6), [Mitchell*, et al.* 2009](#_ENREF_34), [Rathcke 1983](#_ENREF_46)). Consequently, both individual phenotypic traits and neighbourhood context 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_2)). 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_15), [Dupont*, et al.* 2014](#_ENREF_16), [Gómez and Perfectti 2011](#_ENREF_22), [Rumeu*, et al.* 2018](#_ENREF_48), [Tur*, et al.* 2014](#_ENREF_57), [Valverde*, et al.* 2016](#_ENREF_60)). 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 ([Losapio*, et al.* 2019](#_ENREF_31), [Olesen*, et al.* 2010](#_ENREF_40)). Individual-based networks have been used to explore specialization of pollen use ([Tur*, et al.* 2014](#_ENREF_57)) and interaction rewiring with phenology ([Valverde*, et al.* 2016](#_ENREF_60)). 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_32)). Downscaling to individuals is a fundamental step to shed light on the underlying drivers of community functioning.

Relative differences in attractiveness can contribute to an individual plant’s role in the network if pollinator foraging preferences introduce differences in the number or distribution of links connecting nodes. Centrality describes the node’s topological position within the network i.e. its functional role within a community ([González*, et al.* 2010](#_ENREF_23)). Centrality measures are estimates of relative influence, for example in food webs, centrality measures have received attention for their ability to identify keystone species ([Estrada 2007](#_ENREF_18), [Jordán*, et al.* 2006](#_ENREF_28)). 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_22)) i.e. more attractive plants were more central and had higher fitness. Within a community, being more attractive is only a benefit if the pollinators also visit other members of the same plant species. For example, if pollinator-mediated facilitation through increases in joint attractiveness than a plant will be more central, but primarily connected to heterospecifics. Thus using an individual-network approach can provide novel approach to the mechanisms that underlie how plants influence the interactions of other plants.

Using a trait-based, individual approach can provide a more mechanistic understanding of network structures that arise from pollinator sharing ([Woodward*, et al.* 2010](#_ENREF_63)). 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 ([Donatti*, et al.* 2011](#_ENREF_10), [Olesen*, et al.* 2007](#_ENREF_39)). These structures can arise even in very short flowering seasons ([Morente-López*, et al.* 2018](#_ENREF_35)), and their membership is constrained by phenology ([Tur*, et al.* 2015](#_ENREF_56), [Valverde*, et al.* 2016](#_ENREF_60)) and spatial location ([Dupont*, et al.* 2014](#_ENREF_16)). Previous individual-based approaches have revealed the importance of inter-individual variation as conspecifics can belong to different modules ([Tur*, et al.* 2015](#_ENREF_56)). 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 functional redundancy of a network i.e., resilience ([Bascompte and Jordano 2013](#_ENREF_2)). In nested networks, specialized nodes i.e. those with fewer interactions are linked with generalized nodes i.e. well connected nodes. Differences in attractiveness can alter quantity and breadth of floral visitors, thus these trait-mediated influences of generalization can contribute to overall network hierarchy and provide information on traits that contribute to network stability.

In all plant communities, focusing only on the drivers of pairwise interactions limits our capacity to describe and predict community resilience, structure, and composition. We used a spring blooming, desert shrub and cactus community as a model system to study the underlying drivers of interaction network topology to improve our understanding of how pollinator preferences change interactions between plants. We hypothesized that traits associated with attractiveness to pollinators such as floral display size, plant height and neighbourhood floral density predict an individual plant’s role within the pollinator visitation network 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 explore if network-level attributes are emergent properties of individual interactions. Understanding the traits and contexts that give rise to network structures gives them more explanatory power.

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_62)).

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 (Figure A1). 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_42)). 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_36)). 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_64)). Height and floral display size were positively correlated (Figure A2), 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_19)).

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_4)).

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_12)). 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_13)).

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 i.e. 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_20), [Martín-González*, et al.* 2010](#_ENREF_33)). We tested for difference in centrality between species using Kruskal-Wallis tests.

We fit GLMM (glmmTMB) ([Brooks*, et al.* 2017](#_ENREF_7)) 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_15), [Guimera and Amaral 2005](#_ENREF_25)). 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).

We created unweighted, unipartite networks for each plant species and used these networks to count the number of linked conspecifics and heterospecific plants. 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_61)) 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_14)). 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_38)). 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_61)) 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_5)). 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_1)). Weighted connectance is the linkage density divided by the total number of interactors (species or individuals) ([Tylianakis*, et al.* 2007](#_ENREF_59)). It is a central network property that drives other network properties such as nestedness ([Poisot and Gravel 2014](#_ENREF_44)). It measures of the complexity of the network. The modularity of each network was assessed using DirtLPA algorithm implemented in bipartite ([Beckett 2016](#_ENREF_3)). 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. We used the Z-scores as effect size measures of the deviation from random as a method to compare the networks.

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), 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). Neighbourhood shrub density increased linkage to 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 individual-based, unipartite 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 neighbourhood shrub density were also important (9.397, df = 4, 0.0518980). The modules had unequal numbers of individuals, with module 0 with only three members, and the last module with only nine individuals.

The individual-based and species-based bipartite networks were both significantly different than random in connectance, specialization, nestedness and modularity (Table 4). Both bipartite networks were less cohesive and less nested than random networks, and more specialized and modular than random networks. When downscaled from species to individual, 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 them 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**

This study highlights the complexities that arise when moving beyond pairwise interactions to describe and predict community structure. We hypothesized that individual traits that are associated with attractiveness to pollinators can predict an individual plant’s role with whole interaction network. 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 rates. The competitive advantage of a large floral display size was lost in the later time period suggesting that the relative importance of individual traits to attractiveness has a temporal component within this system. Flowering shrub density influenced network topology in addition to increasing visitation rates. The effects included betweenness centrality and modularity showing that the floral attributes of a plant’s neighbourhood contributes to the role of that plant within the whole network and subsequently the structure of the network as a whole.

Diffuse pollinator-mediated facilitation between co-blooming plants was prevalent in this system and network analyses revealed additional, potential mechanisms by which 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 but has not been reported previously for desert ecosystems ([Braun and Lortie 2018](#_ENREF_6)). Intraspecific density has however been reported to benefit the pollination of desert mustard *Lesquerella fendleri* ([Roll*, et al.* 1997](#_ENREF_47)). Interestingly, shrub, but not cactus density 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_52), [Steffan‐Dewenter 2003](#_ENREF_53)). Increases in pollinator diversity can increase plant fitness ([Gómez*, et al.* 2007](#_ENREF_21), [Klein*, et al.* 2003](#_ENREF_29), [Perfectti*, et al.* 2009](#_ENREF_43)) 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_24), [Heinrich 1979](#_ENREF_26)). Alternatively, the likelihood of attracting more effective pollinators increases with pollinator diversity through sampling effort (Ives 2005). The positive relationship between pollinator 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_58)). Plants growing in denser areas were linked to a higher proportion of the conspecific population. This is a novel pathway of pollination facilitation as improved pollen diversity can also increase fitness through increases in genetic diversity (Desrocher and Rieseberg 1998). 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.

Plant species did not differ in betweenness centrality suggesting this network role is contextual in this system. Low differences between plant species have also been reported among hedgerow perennials in agricultural systems ([Russo*, et al.* 2013](#_ENREF_49)). Species with high betweenness centrality are hypothesized to mediate co-evolutionary cascades moving through mutualistic networks ([Martín-González*, et al.* 2010](#_ENREF_33)) and keep communities from being fragmented (Newman 2004, Jeong 2000). A meta-analysis confirmed the importance of central, generalized species and demonstrated their similarity of roles across geographical regions and ecosystems ([Martín-González*, et al.* 2010](#_ENREF_33)). In this system, shrub facilitation contributes to the cohesiveness of the network because plants with betweenness > 0 connect areas of the network that would otherwise be fragmented (Newman 2004). An intriguing possibility raised by these results is that density promotes betweenness because pollinators attracted by mixed patches of flowers are more gregarious. The next step here is to determine how the co-blooming neighbourhood influences centrality measures in the absence of facilitation.

Our study supports the findings of previous work that modules are not temporally stable structures ([Stanoev*, et al.* 2011](#_ENREF_51))and can change over short time periods due to phenology ([Morente-López*, et al.* 2018](#_ENREF_35), [Valverde*, et al.* 2016](#_ENREF_60)). 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 ([Bascompte and Jordano 2013](#_ENREF_2), [CaraDonna*, et al.* 2017](#_ENREF_8), [Poisot*, et al.* 2015](#_ENREF_45)). In addition to potential short-term phenological variation, the decreases in net site-level floral density may have contributed to day dependent modularity because changes in resource availability can alter pollinator foraging behaviour ([Jha and Vandermeer 2009](#_ENREF_27)). The species-based network was more modular than the individual-based network suggesting that aggregating to species overestimates compartmentalization of individual interactions.

Overall, the structure of the bipartite individual-based network resembled the species-based network indicating that this was a reasonable approach to explaining the aggregated patterns of species networks. However, in this system the species network was more specialized than the individual-based network. A similar increase in specialization has also been reported within a population of *Sinapis arvenis (*[Kuppler, *et al*. 2016](#_ENREF_30))*.* Rumeu (2018) found that a multi-species network built with traits to be less specialized than species and suggests that species networks may overestimate specialization. The degree of specialization of species in desert ecosystems is a subject of ongoing debate (Chesson et al, 2004). Desert organisms are hypothesized to adapt to high environmental variability by generalizing resource use (Chesson et al., 2004) and our study suggests this adaptation may occur at the individual level. Connectance i.e. the density of interactions, and nestedness were lower than an equivalent random network indicating this system may be particularly sensitive to perturbation. Only visitation rates contributed to the individual network’s nestedness highlighting the importance of generalist plants in this system for stability.

Modularity and the correlation between degree and other centrality measures are considered universal features of ecological networks ([Martín-González*, et al.* 2010](#_ENREF_33)) and were present at the individual level as well showing the importance of intraspecific interactions to overall community structure. 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_16), [Eklöf*, et al.* 2013](#_ENREF_17), [Olesen*, et al.* 2010](#_ENREF_40), [Olito and Fox 2015](#_ENREF_41)). Our results indicate that the floral neighbourhood an individual is embedded in also contributes to network structure. Further research is necessary to distinguish between contextual, individual roles and species roles in structuring ecological interaction networks but is fundamental to predict interaction network structure, and therefore its functioning and response to disturbances.

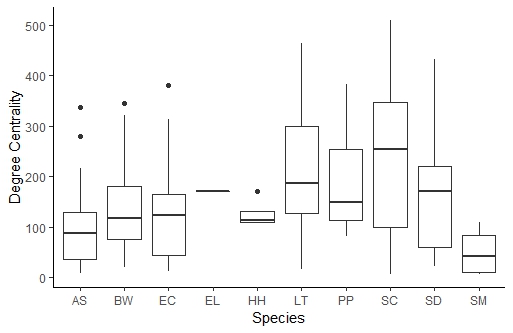
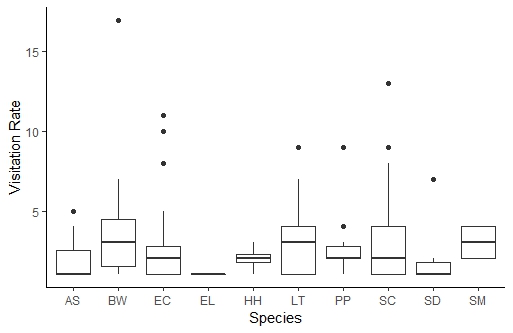
Tables & Figures

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 |



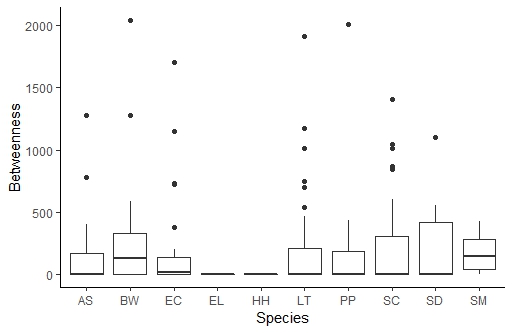
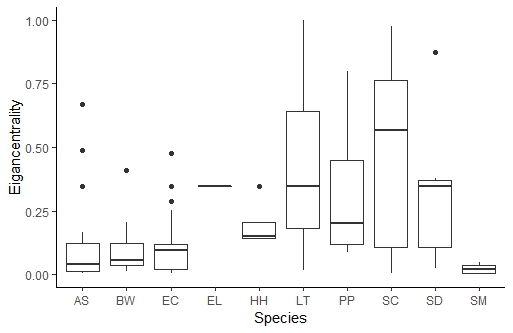
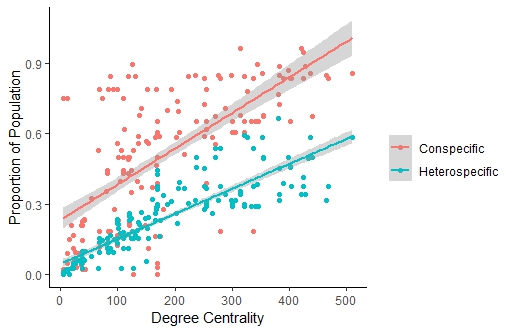


Figure 1: Species differed in their degree centrality and eiganvector centrality, but not betweenness.



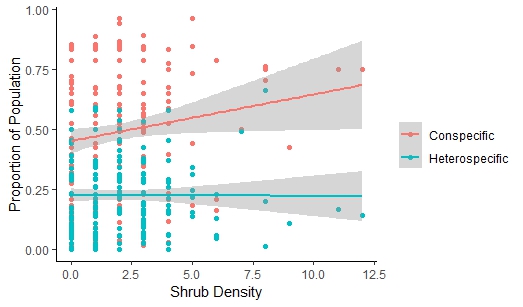


Figure 2: Foundation plants interact with a greater proportion of conspecifics than heterospecifics. Values are the number of interactors standardized by the number of potentially interacting plants within the network. Degree centrality increased both the proportion of conspecifics and heterospecifics.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

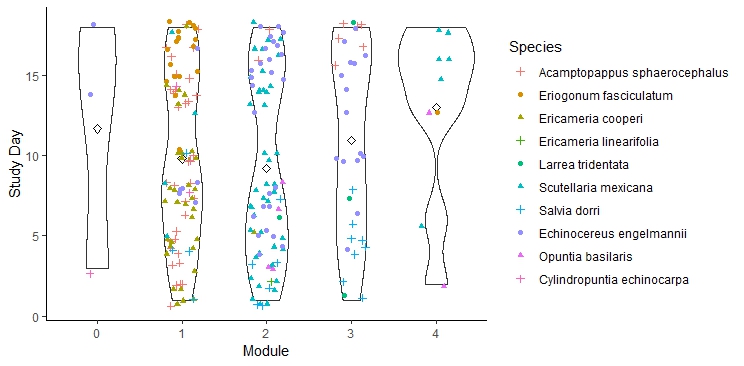


Figure 3: Plant-plant modules were structured by species identity and day. Conspecifics can be found in multiple modules.

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 |  |

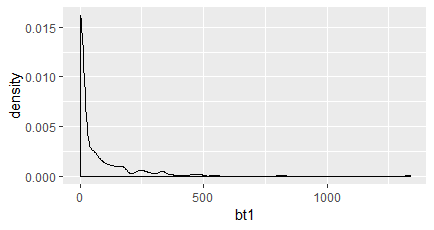


Figure A1: Betweenness values were very zero-inflated. Most models for zero-inflation are for count data, not continuous data.

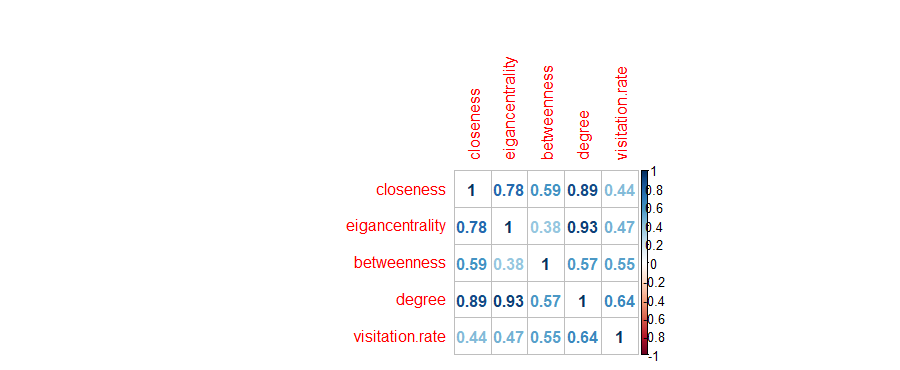


Figure A2: Correlation coefficients between centrality measures and visitation rates.

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

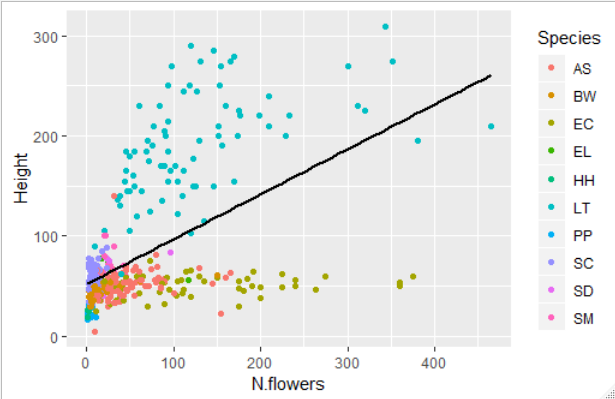


Figure A3: Correlation between the number of flowers and height, split by foundation plant species.

**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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