Desert shrub facilitation shapes pollination network topology

Running title: < 45 characters

Letter

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All data and R code are available on Github in reproducible documents https://jennabraun.github.io/foundation-pollination/

The title page must also contain:

 - the number of words in the abstract, the number of words in the main text (excluding abstract, acknowledgements, references, table and figure legends), and the number of words in each text box **Up to 5000, at ~4600**  
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Abstract (150 words) too long still

Plant-plant interactions for pollinators underlie the structure and function of plant communities. Downscaling interaction networks from species to individual 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 had higher access to the conspecific mating pool suggesting widespread and diffuse pollination facilitation within this community. Further, shrub density 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 mediate 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.

**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. A plant’s attractiveness to pollinators is influenced by phenotypic variation in traits that improve pollinator foraging efficiency including floral display size ([Thomson 1981](#_ENREF_52); [Ohashi & Yahara 1998](#_ENREF_35)) and plant height ([Donnelly *et al.* 1998](#_ENREF_10); [Toräng *et al.* 2006](#_ENREF_53)). Plant attractiveness to pollinators is also a consequence of the floral composition of the surrounding area due to density-dependent interactions between the local co-blooming floral neighbourhood and the focal plant ([Rathcke 1983](#_ENREF_42); [Seifan *et al.* 2014](#_ENREF_49)). Within season phenological variation in the density and composition of co-flowerings plants can lead to temporal shifts in interactions among plants ([Aizen & Rovere 2010](#_ENREF_1); [Runquist 2013](#_ENREF_45)). Plant-pollinator mutualisms physically take place within natural communities and are embedded within complex webs of interactions ([Montoya *et al.* 2006](#_ENREF_32)). Plant-pollinator interactions are not only the outcome of co-evolution between the direct participants; they also reflect interactions within the entire surrounding community. However, relatively few papers examine how plants interact for pollinators at a whole community level and even these generally examine pairwise interactions ([Hegland *et al.* 2008](#_ENREF_24); [Tur *et al.* 2016](#_ENREF_55)). Consequently…

Network analysis has emerged as a valuable tool for studying plant-pollinator interactions ([Bascompte & 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 them. The recognition that patterns between interacting individuals drive the patterns between interacting species has driven recent interest in downscaling from populations to individuals ([Dupont *et al.* 2011](#_ENREF_14); [Gómez & Perfectti 2011](#_ENREF_21); [Dupont *et al.* 2014](#_ENREF_15); [Tur *et al.* 2014](#_ENREF_56); [Valverde *et al.* 2016](#_ENREF_59); [Rumeu *et al.* 2018](#_ENREF_44)). These have been used to explore specialization of pollen use ([Tur *et al.* 2014](#_ENREF_56)) and interaction rewiring with phenology ([Valverde *et al.* 2016](#_ENREF_59)). Species and individual approaches are complementary, for example they have been used to study changes in specialization across a gradient of elevation in hummingbird-plant networks ([Maglianesi *et al.* 2015](#_ENREF_28)). An advantage of individual-based networks is the ability to explore the contribution of individual variation to the structure and pattern of relations at the whole network level. Modules are network structures consisting of densely connected nodes that interact more strongly with each other than the rest of the network. In species 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_33)) and their membership is constrained by phenology ([Tur *et al.* 2015](#_ENREF_54); [Valverde *et al.* 2016](#_ENREF_59)) 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_54)). Downscaling to individuals is a fundamental step to shed light on the underlying drivers of network topology and community functioning.

The functional role of a node within a community can be described by its centrality i.e. the node’s topological position within the network (Dupont and Olesen 2009). Centrality quantifies how a node is connected to the rest of the community through pollinator sharing and its importance to maintaining network structure (Jordan 2007). In food webs, centrality measures have received attention for their ability to identify keystone species (Jordan 2006, Estrada 2007). Recently these measures have been applied to pollination networks to study changes in species roles after ecological invasions ([Santos *et al.* 2012](#_ENREF_48); [Emer *et al.* 2016](#_ENREF_17)). 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 & Perfectti 2011](#_ENREF_21)). Within multi-species interaction networks, individuals are linked with both conspecifics and heterospecifics therefore increasing centrality will not improve access to the conspecific mating pool if individuals are primarily connected with heterospecifics. 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 ([Rathcke 1983](#_ENREF_42); [Mitchell *et al.* 2009](#_ENREF_31); [Braun & Lortie 2018](#_ENREF_7)). Therefore, association with other species can contribute to an individual’s centrality through changes in its attractiveness but if this increases access to conspecifics is unknown. Here, downscaling provides information about how individual traits and local context contribute to an individual’s importance relative to other members of the co-flowering community.

In this study, we addressed the influence of pollinator sharing on the topological shape of the pollinator-visitation network of a spring blooming desert shrub and cactus community. We explored the interplay between individual floral display size, the local floral neighbourhood, and within-season phenology on pollinator visitation, centrality measures and network modularity. 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 are thus a model system for studying how multi-level variation in floral density influences community interactions. We hypothesized that focal plants growing in denser areas would be more attractive to pollinators because of optimal foraging. We used an individual based pollinator-visitation network to explore how variation in the individual context in terms of floral display size and neighbourhood density contribute to individual plants roles and positions within the network and to overall network structure. We assessed if centrality improves access to other conspecifics. 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. In sensitive ecosystems such as deserts phenological shifts in interactions are happening already and we need a better understanding of the higher-level patterns of interactions that function at the community level to determine biodiversity to better understand the impact of these changes.

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 collection was carried out between April 20th and May 9th, 2018 which included the flowering period of most spring blooming shrubs and cacti at the site. The experiment ended when it was not possible to located blooming shrubs that had not yet been observed. 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. All focal plants were georeferenced using a Garmin 64st handheld GPS.

Flower-visitor interactions for each focal plant were recorded 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 comparison to the frequently used method of transect walks in which the most abundant interactions are most frequently observed ([Westphal *et al.* 2008](#_ENREF_61)).

Only visitors that made contact with the reproductive organs of the flowers were recorded. Visitors from taxonomic groups known not be pollinators were excluded (i.e. Coccinellidae ladybird beetles, *Carpophilus* sp. pollen beetles and spiders). Soft-winged flower beetles (Melyridae) in the subfamily Dasytinae were excluded because they were observed but were stationary deep within flowers and without disturbing the flower could not be effectively counted. Very small pollinators, i.e. < 2 mm e.g. micro-beeflys (Mythicomyiidae) were also excluded from analyses because it was not realistic to accurately track visitation to large shrubs such as *L. 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 identifications which 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 & Beattie 1993](#_ENREF_39)). This method provides information about the linkages between different genera and functional groups.

Floral display size and height are known to influence attractiveness of plants to pollinators, and consequently, the number of open flowers and the height of each focal plant directly before the observation period were recorded. As a measure of the immediate floral neighbourhood, we recorded the abundance and identity of all blooming shrubs and cactus 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.

To track pollinator population changes throughout the study period, yellow, white, and blue coloured six-inch diameter plastic bowls filled with water with a few drops of dish detergent were placed in arrays of three at six locations in open areas, every other day. The number of pollinators were extracted from these data to estimate the abundances of the observed floral visitors during the experiments (hereafter termed ‘pollinators’).

**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 imputeTS, ([Moritz & Bartz-Beielstein 2017](#_ENREF_34)). The species-specific values were summed to fill in the missing dates.

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 predictor variables. 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. Height and floral display size were positively correlated (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 vif (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 spdep ([Bivand *et al.* 2011](#_ENREF_5)).

Network analyses

To facilitate the discovery of general trends, pollinators were classified into 17 distinct functional groups (Table S1). 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)). 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. 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 & Stouffer 2013](#_ENREF_47)). All bipartite network indices were calculated using functions within the bipartite package ([Dormann *et al.* 2008](#_ENREF_12)).

In unipartite networks, each link is a shared pollinator functional group connecting potentially interacting individual plants. From the individual based unipartite network, we calculated several centrality measuresthat are frequently used to describe influence in social network analysis using igraph ([Csardi & Nepusz 2006](#_ENREF_9)). In species networks, these measures describe the importance of species (Gonzalez 2010, Jordano 2006). Degree centrality is the number of links per individual. In plant-plant networks it describes the number of interactions with conspecifics i.e. the mating pool and the number of heterospecifics i.e. potential competitors/facilitators. 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 poised to influence the full network. They interact with dense substructures within the network. Betweenness is 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 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), so we first modelled 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 ([Guimera & Amaral 2005](#_ENREF_23); [Dupont *et al.* 2011](#_ENREF_14)). We then log-transformed the continuous part to meet the assumptions of normality and modelled it using a Gaussian error distribution (residuals: W = 0.98854, p-value = 0.5491). These indices provide information about how individual context contributes to node positioning, importance and overall network structure.

Access to conspecifics

To relate an individual plant’s access to conspecifics and exposure to heterospecifics to centrality and individual context, we used an unweighted, unipartite network i.e. interaction strength is not considered to count the number of linked conspecifics and heterospecifics for each individual. The number of connected and unconnected conspecific or heterospecific plants were used as binomial response variable in quasibinomial GLMM (MASS) ([Venables & Ripley 2013](#_ENREF_60)) 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). Thus, only degree centrality was included in these models because it is the most commonly reported measure. Betweenness centrality, study day, visitation rates, shrub density and floral display size were also used as predictors. Models were compared to random intercept using AIC and likelihood ratio tests.

Unipartite modularity

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 rnetcarto, ([Doulcier & 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 & Blanchet](#_ENREF_36)). 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 phenology, individual traits and neighbourhood on modularity, and therefore ecological dynamics, we built multinomial models (nnet)([Venables & Ripley 2013](#_ENREF_60)) using 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. H2` is the degree of complementary specialization of the whole network of interacting species. It 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` is for the network. H2` does not vary significantly with network size ([Blüthgen *et al.* 2006](#_ENREF_6)). Weighted nestedness (WNODF) is a quantitative measure which 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 & 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_58)). It is a central network property that drives other network properties such as nestedness ([Poisot & Gravel 2014](#_ENREF_41)). 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 ([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

A total of 635 foraging instances 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 RTU 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). 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, floral display size became unimportant late in the study period. Site level density decreased over the study period (Pearson’s = -0.4978227, df = 18, p-value = 0.02551). Site level density interacted with floral display size in the same way as study day, but the models had a poorer fit (Table Ax), thus only study day was used for subsequent models.

Floral display size and neighbourhood effects on centrality and network topology

Only visitation rate was a significant predictor of degree centrality (GLMM: Est: 0.20863, χ2:80.891, P < 0.0001) and eigancentrality (Est: 0.055032, χ2: 97.755, p < 0.0001), there was no day effect (Table A3). Foundation plants differed in their degree (Kruskal-Wallis: 44.913, df = 9, p < 0.0001, Figure 1) and eigancentrality (Kruskal-Wallis: 84.285, df = 9, p < 0.0001, Figure 1)

The probability of an individual having a betweenness > 0 increased with local shrub density (GLMM, Est: 0.20559, chi, p = 0.018) and visitation rate (Est: 0.83234, chi, p <0.001). Of those individuals with betweenness greater than zero, betweenness increased with visitation rates only (GLMM: Est: 0.18868, χ2: 26.336, p < 0.0001). Betweenness did not differ between species (Kruskal-Wallis: 6.7085, df = 9, p-value = 0.6674).

The number of effective partners 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). Species did not differ in their number of effective partners (Kruskal-Wallis: 15.056, df = 9, p-value = 0.08941).

Only visitation rates predicted an individual’s contribution to nestedness (GLMM: Est: 0.10362, χ2: 31.931, p < 0.001).

Access to conspecifics

Access to both conspecific and heterospecific plant individuals increased with degree centrality (Figure 2, Table 4). The interaction between degree and visitation rates is most likely an artefact of the difference between qualitative and quantitative networks. Degree is quantitative, thus it is weighted by the number of visits. However, the proportion is not weighted by visitation, so at high degree those extra pollinator visits are to individuals that a plant is already connected with. Shrub density increased access to conspecifics, but not heterospecifics (Table 4) and there was no influence of floral display nor a day effect (Appendix for full models).

Modularity

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). Visitation rates, study day and species were significant predictors of module, and shrub density was marginally significant (p = 0.051, Table 3).

Effects of downscaling the whole community

The individual and species level bipartite networks were significantly modular, but the species was more modular (Table 5). When downscaled, the network become more nested, more generalized and more cohesive relative to the species network. All indices were significant (Table 5).

**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. Downscaling the community interaction network revealed that individuals are more variable than their aggregations of conspecifics in the key network role of betweenness centrality. Flowering shrub density shaped topology beyond increases in visitation rates including betweenness, access to conspecifics and modularity, and this effect was time invariant. In general floral display size influenced network measures indirectly through its strong influence on visitation rates. However, 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 aspect. This may be due to the overall decrease in plant density over the study period, and the results of pollinators becoming less choosy as availability decreases. For species networks, traits are increasingly being recognized as driving forces of network structure ([Olesen *et al.* 2010](#_ENREF_37); [Eklöf *et al.* 2013](#_ENREF_16); [Dupont *et al.* 2014](#_ENREF_15); [Olito & Fox 2015](#_ENREF_38)). 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.

Positive, diffuse pollinator-mediated interactions between co-blooming foundation plants dominated in this system. 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 & Lortie 2018](#_ENREF_7)). Intraspecific density has been reported to benefit the pollination of desert mustard *Lesquerella fendleri* ([Roll *et al.* 1997](#_ENREF_43)). Interestingly, shrubs, but not cacti density exhibited this positive effect. Shrubs were taller than cacti with larger floral displays, and this attractiveness may have drawn in pollinators via the magnet species effect leading to improved visitation to focal plants (sensu Laverty 1992). This suggests some level of species specificity in benefactors. Foundation plants growing in denser patches 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_50); [Steffan‐Dewenter 2003](#_ENREF_51)). Increases in pollinator diversity can increase plant fitness ([Klein *et al.* 2003](#_ENREF_27); [Gómez *et al.* 2007](#_ENREF_20); [Perfectti *et al.* 2009](#_ENREF_40)) through several mechanisms. Pollinator-pollinator interactions can lead to increases in pollen deposition by displacing pollinators to other plants and decreasing geitonogamy ([Heinrich 1979](#_ENREF_25); [Greenleaf & Kremen 2006](#_ENREF_22)). Alternatively, the likelihood of attracting more effective pollinators increases with pollinator diversity through sampling effort (Ives 2005?). Diversity-pollination relationship are strongest when floral resources are heterogeneously distributed ([Tylianakis *et al.* 2008](#_ENREF_57)) suggesting this relationship is likely important for plant fitness in desert ecosystems which are characterized by heterogeneity. Shrub density improved access to conspecifics which may be a novel pathway of pollination facilitation. 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. Our results show the potential of interactions however, pollen flow analysis as well as genetic testing will be necessary to confirm these predictions.

Node attributes influence network topology (Bianconi et al, 2009). 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 no effect on closeness ([Gómez & Perfectti 2011](#_ENREF_21)). Interestingly, plants growing denser patches had a betweenness roles which indicates 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_46)). Species with high BC are hypothesized to mediate co-evolutionary cascades moving through mutualistic networks ([Martín-González *et al.* 2010](#_ENREF_29)) and keep community from being fragmented (Newman 2004, Jeong 2000). 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.

Unipartite modularity in 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 may have been influenced by site level density decreases. Changes in the availability of resources can alter pollinator foraging preferences (cite). As Tur (2015) found, conspecifics could be members of different modules and previous individual, community work has found divergences between taxonomic similarities and trait similarities (Rumeu 2018). Modules can be considered co-evolutionary subunits, therefore studies of individual-based modularity can be used to identify specific changes during plant invasions and describe how interactions are shifting with phenological changes? 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). 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.

Final paragraph contrasting species and individual networks & conclusions:

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.

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, traits and visitation rate.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Foundation plant species | Observation periods | Mean height (cm) +/- SD | | Mean floral number | Mean visitation rate (per 10 min) |
| *Acamptopappus sphaerocephalus* | 96 | | 51.08333 | 45.156250 | 0.8750000 |
| *Eriogonum fasciculatum* | 31 | | 44.03226 | 16.709677 | 2.3870968 |
| *Ericameria cooperi* | 55 | | 49.34545 | 124.363636 | 1.6909091 |
| *Ericameria linearifolia* | 4 | | 69.25000 | 46.500000 | 0.2500000 |
| *Larrea tridentata* | 80 | | 189.87500 | 127.137500 | 1.9125000 |
| *Scutellaria mexicana* | 12 | | 72.92857 | 24.142857 | 0.857142 |
| *Salvia dorri* | 13 | | 55.83333 | 27.000000 | 1.0833333 |
| *Echinocereus engelmannii* | 5 | | 27.80000 | 2.400000 | 1.6000000 |
| *Opuntia basilaris* | 28 | | 25.14286 | 4.714286 | 1.6428571 |
| *Cylindropuntia echinocarpa* | 69 | | 56.01449 | 8.028986 | 2.1884058 |

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 | -0.6084442 | 4.1535 | 1 | 0.0415481 |
| Shrub Density | 0.0746825 | 4.1168 | 1 | 0.0424593 |
| Day | 0.0463114 | 5.1650 | 1 | 0.0230469 |
| Floral Display Size | 0.0116170 | 14.8479 | 1 | 0.0001165 |
| Floral Display:Day | -0.0005315 | 4.1515 | 1 | 0.0415967 |

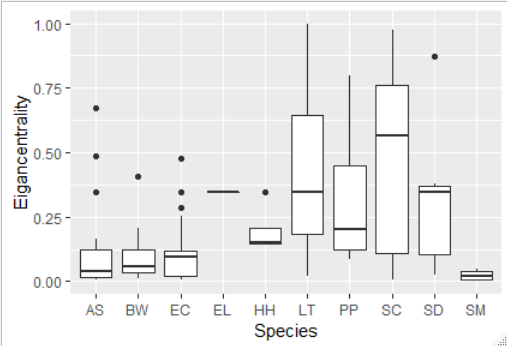
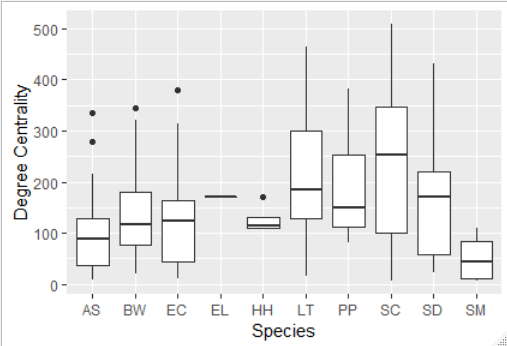
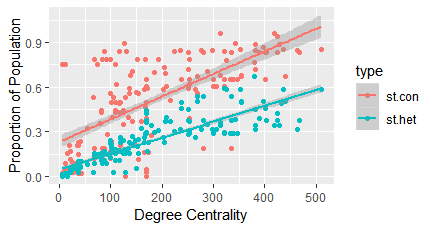


Figure 1: Species differed in their degree centrality and eiganvector centrality.



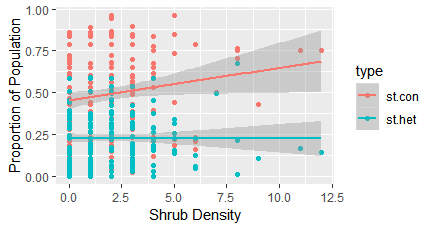


Figure 2: Foundation plants interact with a greater proportion of conspecifics than heterospecifics. Proportions inreased with degree, and proportion conspecifics only increased with shrub density. Values are the number of interactors standardized by the number of potentially interacting plants within the network.

Table 3: Result from multinomial regression showing influencers on plant-plant interaction network modularity.

|  |  |  |  |
| --- | --- | --- | --- |
|  | χ2 | df | p-value |
| Species | 266.689 | 36 | < 0.0001 |
| Shrub density | 9.397 | 4 | 0.0518980 |
| Visitation rate | 20.085 | 4 | 0.0004805 |
| Study day | 20.085 | 4 | 0.0025540 |

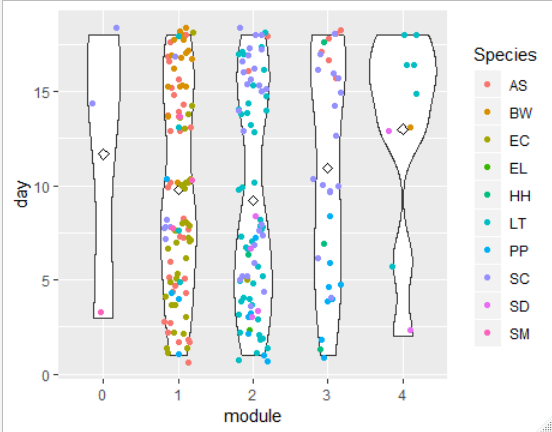


Figure 3: Modules are structured by day. Conspecifics can be found in multiple modules.

Table 4: 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 | 0.0664044 | 5.9352 | 0.01484 | NA | NA | NA |
| Degree | 0.0086369 | 181.586 | <0.0001 | 0.0098692 | 424.347 | <0.0001 |
| Visitation Rate | 0.0716480 | 3.0502 | 0.08073 | 0.0441913 | 1.4427 | 0.2297 |
| Degree: Visitation rate | -0.0004229 | 6.0923 | 0.01358 | -0.0005467 | 24.9489 | <0.0001 |

Table 5: Species network to individual network comparisons

|  |  |  |
| --- | --- | --- |
| Indice | Species Level | Individual |
| Weighted Connectance | 0.15038761  -40.94254  Mean: 0.2756232 | 0.08094487  Z: -16.11034  Mean 0.1311256  0.1196121 |
| H2 | 0.42532319  Z-score 57.16165  0.0475812  Max: 0.06940527 | 0.56665181  Z: 26.14875  Mean: 0.2004796  0.2428269 |
| WNODF | 32.82754538  Z: -8.393687  Mean: 63.15026  72.83434 | 4.65012620  Z: -6.40035  Mean: 8.128909  9.844356  6.190922 |
| Modularity | Obs :0.4358832  Random value: 0.09052169  Z: 36.35723  Random comp i:sp | 0.5893211  Random value: 0.3842228  24.35 |

**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 |  |

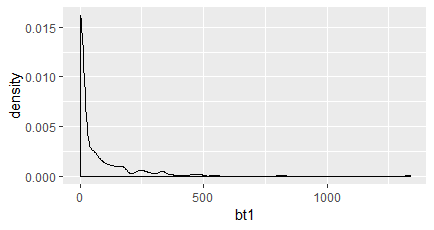


Figure A1: Betweenness values were very zero-inflated. Most models for zero-inflation are for count data, not continuous data.

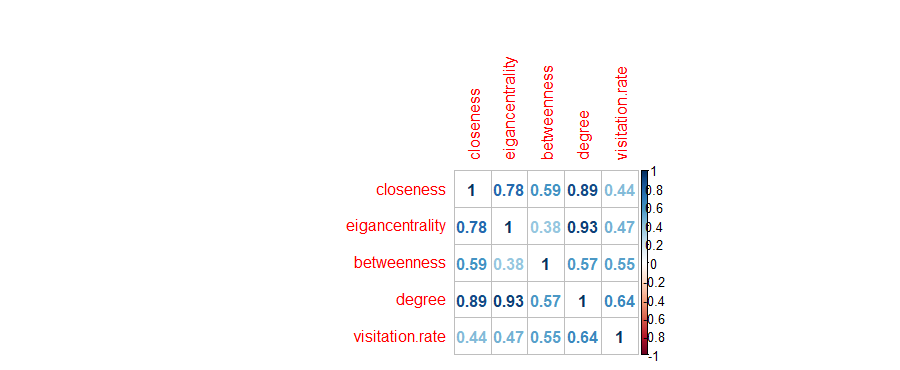


Figure A2: Correlation coefficients between centrality measures and visitation rates.

Comparing best model to null (Visitation rates) using car::Anova = Chi square: 40.687, df=4,p <0.001

**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 |

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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