Desert shrub facilitation shapes pollination network topology

Research Article

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Abstract

Interactions for pollination are dependent on ecological context. Network analysis lets us explore all interactions simultaneously. We built individual pollinator visitation networks of foundation shrubs and cactus in a desert ecosystem. We found positive effects of shrub density on the pollination of neighbouring foundation plants. Shrub density influenced centrality and generality of focal plants. Denser patches had higher access to the conspecific population.

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 et al 1982, Ohasi and Yahara, 1998, Miyake and Sakai 2005) and plant height (Donnely and Lortie 1998, Torang 2006). Plant attractiveness to pollinators is also a consequence of the density and composition of the local floral neighbourhood due to density-dependent intra and interspecific interactions between the local co-blooming floral neighbourhood and the focal plant (Rathcke 1984, Thomson 1981, Siefan). Within season phenological variation in the density and composition of co-flowerings plants can lead to temporal shifts in interactions among plants (Runquist 2013, Aizen and Roveres 2010). Few papers still examine how plants interact for pollinators at a whole community level (but see Moeller, Hegland, a couple newers ones). Community level studies are lacking from sensitive desert ecosystems (Braun).

Network analysis has emerged as a valuable tool for studying plant-pollinator interactions (Jordano et al, 2003 etc). 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 (Olesan 2010, Dupont 2011, Rumeu 2018, ([Gómez and Perfectti 2011](#_ENREF_2); [Dupont et al. 2014](#_ENREF_1); [Tur et al. 2014](#_ENREF_6); [Valverde et al. 2016](#_ENREF_7)). These have been used to explore specialization of pollen use ([Tur et al. 2014](#_ENREF_6)) and interaction rewiring with phenology ([Valverde et al. 2016](#_ENREF_7)). 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_3)). Network approaches to studying plant-plant interactions can let us better describe the influence of neighbours beyond just visitation rates.

Centrality measures describe the topological position of a node and describe how a node is connected to the rest of the community through pollinator sharing. Degree centrality is the number of links per node i.e. other interacting individuals. In plant-plant interaction networks, links between individuals act as mating probabilities within populations (Gomez and Perfectti, revise). Centrality improve plant fitness (Gomez Perfectii). However, in a multi-species individual interaction network, individuals are connected with both conspecifics and heterospecifics. Thus increasing centrality will not improve access to conspecifics if individuals are primarily connected with individuals of other species. The increased linkage to heterospecifics may be facilitative or competitive. In some communities, facilitative interactions for pollination are dominant (Hegland, Tur) and they can be quite diffuse. Alternatively, association with other species can lead to a dilution in pollinators leading to decreased visitation. So there may be 2 different consequences of pollinator sharing here: Changes in visitation rates and changes in access to the mating pool.

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. Differences in the number of links per plant can lead to a core-periphery structure due to differences in pollinator sharing (Valverde). Thus, variation in floral display size, height and the local floral neighbourhood may contribute to network structure if variation leads to variation in links. Modules are network structures consisting of nodes that interact more strongly with each other than the rest of the network. These arise due to patterns in pollinator sharing. For example, within module degree is influence by both individual floral display size and local conspecific density (Dupont 2011). Previous work has found that module can arise even in very short flowering seasons (Morente-Lopez et al, 2018). Within modules, individual play different roles. There’s connectivity and participation. There is evidence that plant-plant facilitation shapes pollination networks (Losapio et al 2018). Thus, neighbours can shift and be an indirect part of interaction networks even if those neighbours are not observed.

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 modularity. In desert ecosystems, the majority of flowering times are restricted to a relatively short blooming period in the spring time which is strongly constrained by climatic conditions. Spring blooming shrubs represent individual concentrations of resources and are thus a model system for studying how multi-level variation in floral density influences community interactions. We hypothesize that desert foundation plants act as concentrations of floral resources for foraging pollinators, and that pollination facilitation by co-blooming plants improves access to both pollinators and conspecifics. We predict that 1) Pollinator visitation to individual plants will depend on floral display size and local floral neighbour density. 2) Floral display size and neighbour density contribute to an individual plants’ centrality 3) Access to conspecifics will increase with an individual plants centrality. 4) The plant-plant network will be modular, and this is influences by floral display size, visitation and the floral neighbourhood. 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 (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.

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. ladybird beetles, Carpophilus sp. pollen beetles and spiders). Soft-winged flower beetles 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. 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. We collected x number of voucher specimens to verify the identification. We wanted to minimize any artefacts of destructive sampling. Morphotyping and RTU are useful methods for characterizing and quantifying pollinator communities (Memmott & Godfray 1993; Oliver et al). 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 three x by x band transects on x number of 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.

Time periods, density and miscellany

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 (imputeTS, Appendix). 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, 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 multicolinearity using vif (car).

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 (vignette citation).

Network Analyses

To facilitate the discovery of general trends, pollinators were classified into 17 distinct functional groups (Appendix A). We built a quantitative, bipartite network using visitation frequencies to each individual plant as the measure of interaction strength. All bipartite network indices were calculated using functions within the bipartite package (vignette citation). 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). We also calculated the degree to which each plant’s interaction contributes to network nestedness in comparison to a random null model that controls for degree differences (Saavedra et al. 2011).

To complement these individual measures, we also calculated H2 and WNODF for the entire 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 (Bluthgen and Menzel, 2006). Weighted nestedness (WNODF) 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 (Almeida-Neto & Ulrich, 2011). This measure ranges from 0 to 100. We calculated both H2 and WNODF for the species level and individual networks. Because NODF is sensitive to network size… null models. We calculated them for the aggregrated species network to facilitate a better understanding the patterns of downscaling whole networks.

In one-mode 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 (vignette citation). Degree centrality is the number of links per individual. In a plant-plant network it describes the number of interacting conspecifics i.e. mating pool and the number of heterospecifics such as the number of 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 influential individuals are more poised to influence the full 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.

We fit GLMM (glmmTMB) using the network indices as response variables the individual plant traits, local floral neighbourhood and study day as predictors. Plant species was included in all models as a random effect. We compared results to a null random intercept model. 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. 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).

Access to conspecifics

To determine each individual’s access to conspecifics, we used an unweighted network i.e. plants have the same number of links with one shared pollinator versus several. We counted the number of linked conspecifics and heterospecifics for each individual. These were modelled using quasibinomial GLMM (MASS) to account for overdispersion. The binomial response was the number of connected, number of unconnected. Species was included as a random effect. Closeness centrality, eigancentrality and degree centrality were all strongly correlated with each other (Appendix). Thus, only one centrality measure was included in the proportion models. I chose degree centrality because it is likely the most commonly computed centrality measure. We used study day, visitation rates, shrub density and the number of flowers as potential predictors, and omitted insignificant predictors and compared models to random intercept and simpler models using anova.

Modularity

Modularity was calculated for each network using simulated annealing (netcarto, vignette) and compared to 1000 random networks created using Patefield’s to assess significance (permatful, vegan). Modularity describes how plant communities are structured into groups by pollinator sharing and how this structure changes with phenology. To explore the role of phenology, individual traits and neighbourhood on modularity, and therefore ecological dynamics, we built multinomial models (nnet) using the module as the response, and individual floral display size and local floral neighbourhood as the predictors. Plant species was included as a covariate in all models to account for species-specific responses. We also looked at how sampling day was distributed throughout the modules. Modularity here provides insight into how functional groups structure the plant community into interacting groups.

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. 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 showed the same interaction with floral display size, but the models had a poorer fit (see Appendix). Thus day was used instead.

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: , P < 0.0001) and eigancentrality (Est: 0.055032, χ2: 97.755, p < 0.0001), there was no day effect. Foundation plants differed in their degree and eigancentrality.

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, chi, p < 0.001) and shrub density (Est: 0.05054, p = 0.0445).

Only visitation rates and species predicted an individual’s contribution to nestedness.

Access to conspecifics

Plants interacted with a higher proportion of conspecifics than heterospecifics (Figure). Shrub density improved access to conspecifics but not heterospecifics. Access to both increases with degree centrality, however, in very high degree individuals, those with slighter lower visitation rates had more access to both cons and hets. There was no influence of floral display nor a day effect (Appendix for full models). The interaction is due to the difference between qualititave and quantitative methods. 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.

Modularity

The plant-plant interaction network was significantly modular (mod score, Z, p). It formed 4 modules. Modules x and ay…

**Discussion:**

Our study found evidence of the contribution of individual variation in terms of floral display size and the local floral neighbourhood on both visitation and network topology. In general, floral display primarily influences visitation which in turn influences most centrality measures. In constrast, neighbourhood density showed influences beyond increases in visitation. Some measures varied throughout the season, however some were time invariant. Thus fine scale network topology is contextual within this desert system and depends on both the local floral neighbourhood and time. We found evidence for diffuse, positive pollinator-mediated interactions between co-blooming foundation plants due to density. Density is a frequently studied mechanism of pollination facilitation (Braun, cite, cite) but has not been reported previously for desert ecosystems. The competitive advantage of a large floral display size was lost in the later time period suggesting that 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.

Centrality measures increased access to both conspecifics and heterospecifics. Shrub density improved aspects to cons, not hets which may be another facet of facilitation. In plant-plant interaction networks, individuals with the highest degree have the highest number of potential mates, and/or the highest number of potential competitors/facilitators, and therefore the largest capacity to influence the surrounding community. While it seems obvious that visitation rates should increase centrality measures, they don’t always. In a population individual network, closeness centrality did not depend on visitation rates (Gomez and Perfectii 2011). They found it had a positive effect on degree but negative effect on betweeness.

Foundation plants growing in denser patches were visited by a higher diversity of pollinator functional groups i.e. were more generalized. Through sampling effort, these plants have a higher likelihood of attracting effective pollinators. We found shrub facilitation improved access to conspecifics not heterospecifics which could improve the quality of the visitation. Improved pollen diversity can also increase fitness beyond just seed set by improving genetic diversity. In shrubs, which have lots of flowers per plant, this means a capacity to improve fitness massively by increased paternal diversity and genetic diversity within a single year.

Interestingly, plants growing denser patches had a betweenness roles which indicates that shrub facilitation contributes to the cohesiveness of the network. There was no difference between species suggests that betweenness may be contextual. Russo et al (2013) also reported low separation between species for betweenness (and closeness) because a subset of species had a high number of connections. Species with high BC may modulate “modulate coextinction and coevolutionary cascades that propagate through the network (Barthélemy 2004, Martín González et al. 2009) by connecting subgroups of interacting species (e.g. modules or compartments, Olesen et al. 2007).”

It is interesting that it was shrub density and not foundation plant density. This suggests that blooming cactus density did not facilitate. However, visually from the species network they interact primarily with each other. Another possibility is that the shrubs tended to have way more flowers, and were taller, so it could have been the magnet species effect in addition to density causing the improved visitation to the focal plants. We didn’t track reproductive output, and manipulations are not feasible with long-lived perennials. Thus they might have been exposed to more het pollen. However, the effects of this on fitness for these species is also unknown. Some community level studies have found that visitation rates are more important than variation in pollination effectiveness per visit (Rader et al., 2016; Sahli & Conner, 2006; Vazquez et al., 2005).

There was significantly modularity and the modules were formed during different time intervals. Traits mattered for x. density for x. The roles in modules are x. Other work has found x.The individual network was very similar to the species network. It differed in a couple ways. Individual contribution to nestedness… Overall both networks were fairly generalized. They are at a similar level to other papers.

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).

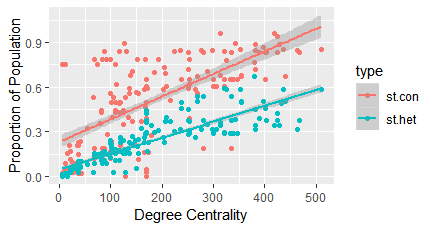
Tables & Figures

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

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Foundation plant species | Observation periods and length | Mean height +/- SD | | Mean floral number | Mean visitation rate |
| *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 |



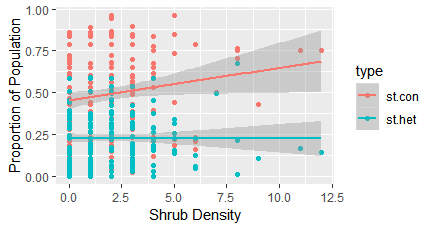


Figure 1: Foundation plants interact with a greater proportion of conspecifics than heterospecifics. Proportions inreased with degree, and proportion conspecifics only increased with shrub density.

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, Hylaues |
| Short-tongued very small | StVSbee | Perdita, Lasioglossum |
| Honeybees | Honeybee |  |
| Small flies | SmDi | Agromyzidae, Richaardiae, Tephritidae |
| Large flies | LgDi | Muscidae, Sarcophagidae, Tachinidae |
| Nectar-seeking wasps | Nwasp | Ammophila, Bembecini, black/blue apoidea, Eumeninae, Pompilidae |
| Long proboscis bee-fly | LpBeefly | Bombylinae |
| Short proboscis bee-fly | SpBeefly | Anthracinae etc |
| Syrphid fly |  | Allograpta exotica, E. volucris, Eristalis sp., pseudodoros clavatus |
| Humming bird | hummingbird | Calypte sp. |
| Beetles |  | click beetle, chrysomelidae |
| Small Day flying moths | MicroLep | Coleophora, |
| Butterfly | butterfly | Desert swallowtail, Mojave blue |

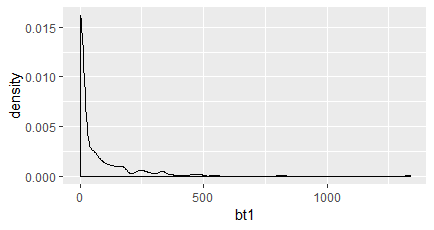


Figure A1: Betweenness values were very zero-inflated. Most models for zero-inflation are for count data, not continuous data.

Comparing best model to null (Quantity)

mnull 3 1362.2 1374.1 -678.10 1356.2

m4 7 1329.5 1357.3 -657.76 1315.5 40.687 4 3.12e-08 \*\*\*

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