Neighbours and networks: An individual-based, community level pollinator-visitation network.

P1: Neighbours and individual traits. Density-dependence.

P2: Network analysis for visitation networks. Links ideas of traits and networks. Topology is just pattern of relations etc.

Some interactions are better analyzed by projecting to a unipartite network. Each link is a shared pollinator group leading to potentially interactions individuals. We used several metrics from social network analysis to describe the traits or contexts that lead to an individual plant being more influential. Degree centrality is an importance score based on the number of links held by a node. Species that have a disproportionate effect on a community can be identified by looking at degrees of the many nodes (Dale and Fortin). Here, individuals with the highest degree have the highest number of potential mates, and the highest number of potential competitors/facilitators, and therefore the largest capacity to influence the surrounding community. Eigancentrality takes this one step further, taking into account how well-connected their associated nodes are. Similarly, to bipartite networks, plants sharing similar pollinators can be structured into modules. Modules tend to mate within themselves more often.

P4: In this study we address. In this study we aim to: 1) 2) 3) 4). We expect that these traits will influence an invididual’s role within the network. We hypothesize that traits and neighbours that are known to influence pollinator foraging preferences will help structure the visitation network. We expect that traits such as height, floral number and density will be more influential within the network. We hypothesize that as site level density increases and then decreases, interactions will shift. We expect plant-plant competition to decrease but pollinator-pollinator competition.

We expect a change in the influence of neighbours or of individual plant traits over the study period ie scale dependence.

1. Resource partitioning hypothesis:

-increased specialization, modularity

-decreased nestedness, connectance

1. Specialization breakdown (free-for-all)

-decreased specialization, modularity

-Increased nestedness, connectance

Finally, the influence of a plant should shift over the study period.

Methods

Study site

Plant-pollinator interactions were studied at Sunset Cove on the property of the Sweeney Granite Mountains Desert Research Station within the Mojave National Preserve in California (34°46'26.5"N 115°39'31.3"W). Interactions were surveyed over 19 days, between April 20st and May 9th for a total of 16 days of sampling.

Field data collection

The experiment was carried out between April 20th and May 9th, 2018 for a total of 16 sampling days. This range of dates comprised the bloom periods of most shrubs at the site. All observations were carried out between 9:00 AM and 5:30 PM in the absence of strong winds. comprising seven species of shrub and three species of cactus for a total of 66 hours of observation.

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 was 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. This approach to creating a pollinator visitation network allows visitation rates to be standardized between individual plants, compared with the frequently used method of transect walks. We recorded the number of foraging bouts per plant, but not the number of flowers visited. Only visitors that made contact with the reproductive organs of the flowers were counted. Visitors from taxonomic groups known not be pollinators were excluded (i.e. ladybird beetles, pollen beetles and spiders). Soft-winged flower beetles in the subfamily Dasytinae were excluded because while abundant, were generally stationary deep within flowers and it would not be realistic count them without disturbing the flower. Very small pollinators, i.e. micro-beeflys (Mythicomyiidae) were excluded from analyses as it was not realistic to accurately track visitation to large shrubs such as *L. tridentata*.

Most floral visitors were identified to genus or species, however some groups (Tachinidae, Sarcophagidae) were left as family due to the difficulty of identifying them on the wing. Some specimens 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.

To quantify the influence of plant traits, we counted the number of open flowers and measured the height of each focal plant directly before the observation period. To determine the floral neighbourhood, we recorded the abundance and identity of all blooming shrubs and cactus in a 3 m radius around the focal plant. This late in the season annual bloom density was negligible. We also measured the distance to and identity of the focal shrub’s nearest blooming neighbour.

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. It is not realistic to count the number flowers on each shrub so this measurement forms a proxy for floral abundance.

To track pollinator population changes throughout the study period, I placed yellow, white, and blue coloured six-inch diameter plastic bowls filled with water with a few drops of dish detergent added. These were placed in arrays of three at six locations in open areas, every other day. I quantified the number of ‘large bodied’ pollinators to reflect the sizes of those observed during the experiments (hereafter just ‘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.

Influence of neighbours etc 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 the plant traits, floral neighbourhood, site density and time period 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 the number of flowers was positively correlated and so floral number only was included in models. We assessed model fit by comparing candidate models to each other and to the intercept using AIC and likelihood ratio tests. In cases when AIC < 2 and no difference in likelihood ratio test, we chose the simpler of the models.

To test for spatial autocorrelation, to look for pollination hotspots that may arise from habitat preferences rather than floral preferences, we used Moran’s I and Geary’s C (k = 4) to test for autocorrelation of visitation rates using spdep (vignette citation).

Network differences in topology

To measure changes in the whole community pollinator visitation network with time/density, I created several quantitative networks. For each time period, I built a species level network, individual network and a floral number network. The floral trait network was built by clustering the floral traits together using vegdist and hclust. The tree was cut at five clusters to maximize the differences between the clusters while maintaining an easy to interpret number (see Appendix for dendrogram). A total of 9 networks. For each network, several commonly used indices were calculated. H2 specialization is… Weighted nestedness… Connectance… Interaction eveness… The modularity of each network was assessed using QuBiMao algrorithm. All were done in bipartitie. Indices can vary depending on interactions, so for each of the 9 networks, 1000 random networks (permatfull, vegan) holding totals of rows and columns steady Patefields’ algorithm. Each of the 4 indices and modularity were calculated for each random network. 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.

Influence of traits and neighbours on the individual network topology

To explore the influence of floral number on the influence of an individual on the network, we projected our bipartite network into a one-mode network. For each time period, We calculated local centrality, which is the number of links per individual. In a bipartite network **degree centrality** is the abundance of visits, in a plant-plant network it describes the number of conspecifics ie mating pool and the number of heterospecifics ie the number of potential competitors. We also calculated **eigancentrality**, which extend the previous idea but includes the importance of the interactors. Individuals that interact with other highly influential individuals are more poised to influence the full network. We calculated **betweenness**, number of times a node lies on the shortest path between other nodes. Important to the cohesiveness of a network.

We then fit GLMM using the network indices as response variables, and the individual plant traits and the time period as predictors.

Plant-plant network modularity.

To test for how functional groups of pollinators structure the plant community. I used the individual based network, one-mode projection using simulated annealing. To test if the system is significantly **modular**, we compared our network to a null model. I built multinomial model using nnet to test for the influence of individual traits etc on modularity.

Misc.

I used imputeTS to fill in densities for the days they weren’t sampled using the linear interpolation because I expect to see a trend but no seasonality.

See Appendix for full list of visitors and the functional group they were assigned to.

Results

A total of 635 foraging bouts were recorded over 394 observation periods. 430 visits were to shrubs and 205 were to cactus. The pollinators make up 17 functional groups spanning 62 RTU of visitors. With the exception of hummingbird Calpte sp., all floral visitors were insects. There was no difference in pollinator visitation rates between time periods (GLMM: Chisq, p=). There was a difference in site level shrub density between the time periods (GLM: ).

There was positive influence of neighbourhood shrub density on pollinator visitation rates (Table 1). There was a significant interaction between the number of flowers and time period. During the early time period, visitation increases sharply with individual flower number. However, floral number becomes unimportant in the later time period. There was no spatial autocorrelation detected for visitation rates (Moran’s: -0.055108, p = 0.953, Geary: 1.0442, p = 0.8145).

At the level of the community, specialization of species interactions increases over the study period. The network is significantly specialized. The network is significantly less nested than expected. The network is less connected than expected, and decreases over the study period. Interaction evenness is much less than expected and this decreases over the study period. The network is modular and the modularity increases over the study period.

At the individual network, specialization is less than the species network but this still increases over the study period. Less nested than species, but decreases over period. Connectance about the same as species, decreases over time. Less evenness than species, decreases. Less modular, icreases.

For the floral cluster network, less specialized tha species and ind, but increases and is similar to ind at the end. Changes to floral cluster network less pronounce except evenness decrease a lot.

Table 3: Results of GLMM of density-dependence. P-values from type 3 wald’s chisq test

|  |  |  |  |
| --- | --- | --- | --- |
| Variable | Coeff | Chisq | p |
|  |  |  |  |
| Shrub.density |  |  |  |
| N.flowers.scaled |  |  |  |
| Time |  |  |  |
| Nflowers:Time |  |  |  |

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | early |  |  | mid |  |  | later |  |
|  | species | indiv | Floral cluster | Species | indiv | Floral cluster | Species | indiv | Floral cluster |
| H2 | 0.440530212 | 0.489959742 | 0.25225958 | 0.482783785 | 0.621956202 | 0.216002591 | 0.586625276 | 0.555407695 | 0.362405639 |
| Null | 0.1173248  ± 0.01780742 | 0.2101766 ± 0.02660272 | 0.08999786  ±  0.01814376 | 0.08509987  ±  0.01335935 | 0.20885 ±  0.02849614 | 0.06172699  ±  0.01354978 | 0.07248752  ±  0.01668926 | 0.2172549 ±  0.02153668 | 0.07646419  ±  0.01737156 |
| Z-score | 18.15004 | 10.51709 | 8.943113 | 29.76822 | 14.49692 | 11.38584 | 30.80651 | 15.70125 | 16.46032 |
| NODF | 19.99861573 | 5.857134551 | 37.72015656 | 22.23290598 | 3.970084582 | 50.17032967 | 24.20576132 | 4.67516622 | 30.92948718 |
| Null | 44.60665  ± 4.117881 | 7.79292 ± 1.077128 | 47.3017  ±  4.425313 | 54.71193  ± 4.960883 | 7.542507  ± 0.7520636 | 50.46597  ±  4.259654 | 55.7986  ± 5.506919 | 11.43236  ± 1.307187 | 57.48506  ±  6.000158 |
| Z-score | -5.975897 | -1.797172 | -2.165169 | -6.547025 | -4.750161 | -0.06940389 | -5.736936 | -5.169264 | -4.425812 |
| Modularity | 0.4227771 | 0.5756044 | 0.3189985 | 0.4668279 | 0.6330944 | 0.2849728 | 0.4937964 | 0.5760421 | 0.3297472 |
| Null (mean, sd) | 0.1714602  ± 0.01816764 | 0.4230303  ± 0.016119 | 0.1456206  ± 0.01947618 | 0.1402465  ± 0.01653756 | 0.4167989  ± 0.01372572 | 0.1233561  ± 0.0162736 | 0.1237126  ± 0.01733665 | 0.3608365  ± 0.01472917 | 0.1154369  ± 0.0167716 |
| Z-score | 13.83321 | 9.465481 | 8.902053 | 19.74786 | 15.75841 | 9.93122 | 21.34691 | 14.61085 | 12.77817 |
| Connectance | 0.294117647 | 0.099480969 | 0.541176471 | 0.319444444 | 0.093085106 | 0.575 | 0.333333333 | 0.112318841 | 0.5 |
| Null | 0.3934773 ±  0.01701243 | 0.1233791  ± 0.002883881 | 0.5736185  ±  0.02389222 | 0.4553171  ± 0.01775105 | 0.1297416  ±  0.003058225 | 0.6734848  ±  0.02196303 | 0.5164141  ± 0.01697283 | 0.1530431  ±  0.003286136 | 0.5949495  ±  0.03045777 |
|  | -5.840412 | -8.286803 | -8.286803 | -7.654341 | -11.98619 | -11.98619 | -10.7867 | -12.39275 | -12.39275 |
| Evenness | 0.636026052 | 0.648008704 | 0.72624926 | 0.617493838 | 0.646101087 | 0.765089666 | 0.597698765 | 0.649358119 | 0.672582658 |
| Null | 0.735953  ± 0.005505604 | 0.6922153  ± 0.004203311 | 0.776471  ±  0.005615691 | 0.7505133  ± 0.004468506 | 0.7106089 ±  0.004449763 | 0.8185303  ±  0.004683652 | 0.7462023 ±  0.004820523 | 0.7153161  ±  0.00420081 | 0.7487632  ±  0.004628134 |
|  | -18.15004 | -10.51709 | -8.943113 | -29.76822 | -14.49692 | -11.41004 | -30.80651 | -15.70125 | -16.46032 |
|  |  |  |  |  |  |  |  |  |  |

Discussion:

Results suggest a decrease in plant plant competition, but an increase in pollinator competition. This is consistent with density.