CH3 Write up

Introduction

Community-level plant-pollinator interactions are complex, but are increasingly being describe using network theory. Within a community, interactions for pollination form a continuum from competitive to facilitative with the output being reproduction, it is important to understand how these interactions come about. Pairwise interactions are inadequate to describe a community level. Therefore, network approaches increasingly being used to characterize community interactions. However, plant-pollinator visitation networks are generally summarized by species which gives an overview but less information about the interactions between individuals. These networks can be downscaled (Tur 2014) into species-individual networks. Information can be lost at the species level, particularly when trying to understand the context that leads to an interaction being competitive or facilitative. Individual level variation…..Dupont and Olesan (2011) talk about hierarchy theory in terms of networks. Most networks are built on populations.

We explored patterns in pollinator sharing and visitation by constructing species-species and species-individual visitation networks. Pollinator responses are density-dependent. Flowering shrubs are an interesting system because they can represent multiple scales of floral density. Each plan forms a resource concentration, however the density of these concentrations vary through space. Finally, the relative density at a large scale can matter as well. Here, a network approach lets us better understand how the network rewires over the study seasons, and how intra and interspecific variation is visitation and sharing is influences by individual traits and neighbourhood composition. Competition and facilitation between plants shapes visitation networks.

Several author’s have called for the scaling-down of interaction networks (Olensen, Dupont, Tur) because individual level forces drive dynamics at the species level. Whole network downscaling has been done by Tur, which looked at the pollen load of pollinators and left plants as species. Peerj paper did an i-I network. Because it is very labour intensive to characterize very species rich ecosystems, we used a natural system, an arid shrubland where the shrubs and cactus were blooming, but too late in the year for annuals to grow. Thus, the majority of blooms available for foraging species came from a elatively small set of species.

Pollinator visitation networks are a quantitative method to visualize and analyze the many interactions within a community. Species that have a disproportionate effect on a community can be identified by looking at degrees of the many nodes (Dale and Fortin). Down-scaling to plant individuals can help resolve questions about intra vs interspecific pollinator sharing i.e. niche breadth. Most network indices are sensitive to size (Dormann 2009, Tur), we used a null model approach. Tur said the differences in network structure may be due to differences in pollen use due to foraging patterns and behavioural differences, as well as conspecific variability. On the plant side, differences in network structure may arise from differences in individual traits and floral offerings, pollinator availability and behaviour. Plant pollinator use can be defined with linkage density i.e. abundance of visits and diversity of visits. These hubs/dis inviduals – why are they like that? Is this repeatable or random? Are they clustered through space?

Motifs are repeatable shapes of network interactions. Motifs (see Fig 1) can represent shared resources, in either direction. First we asked, as Tur did, how does network structure change when downscaling to an individual network. We calculated regular quantitative and qualitative network indices. Second we asked, how does this individual network structure compare to facilitation/competitive interactions between neighbours? Third, how do individual level traits, neighbour density etc interaction to determine network topology?

Here we ask two complementary questions:

1) How do neighbours influence pollination rates to foundation plants? Three scales of density-dependence.

2) Using a network approach. I will analyze the plant-pollinator network at a community level. Secondly, I will create an individual-based network (as in Dupont et al, 2014), and calculate network indices for each individual. This makes it possible to use individual attributes to predict network topology using GLM.

Networks are comprised of nodes and links. Nodes are defined by the analyst. In this case nodes are species or individuals. Links, are the connections between nodes, in this case floral visits. Attributes are intrinsic characteristics of the nodes (size, floral number). Network topology are the patterns of relations.

Methods

Study site

The study area has an extent of x km2, and is located in the mouth of 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). The cove is created by tall rock formations on three sides, gently sloping and widening to the south. The diverse shrub and cactus community. Figure 1 lists the plant species.

Visitation network

To create a pollinator visitation network, I quantified visitation to blooming foundation plants in 10-minute observation sessions. Over a period of 19 days I observed 395 individuals, comprising seven species of shrub and three species of cactus for a total of 66 hours of observation. This approach to creating a pollinator visitation network allows visitation rates to be standardized between individuals, compared with the frequently used method of transect walks.

In a quantitative visitation network, each link is weighted or assigned a strength. In a pollinator visitation, this is weighted by the number of visited. In our case, it is the number of foraging bouts and not floral visits per se. This is because insects were sampled mid foraging. Additionally, the number of flowers alters the number of possible visits made. However, anytime a visitor left and came back it was counted as a new visitor. In a qualitative network all observed links are the same strength.

Visitors were identified on the wing when possible, and as many as possible were caught for later identification. Only individuals that touched the reproductive organs of the plants were included. Melyrid beetles in the subfamily Dasytinae and pollen beetles Carpophilus sp. were excluded because while abundant, they were generally stationary deep within the flowers. It would not be possible to extract all of them from large shrubs. All visitors, with the exception of Costa’s hummingbird Calpte costa were insects. Very small pollinators, such as the micro-beeflys (Mythicomyiidae) were observed where possible but excluded in analyses as it was not possible to consistently track their visits to, very large shrubs such as L. tridentata.

Visitors were identified to RTU. Insects were identified to species, genus, or family. Species were morphotyped within these categories. Morphotyping and RTU are still useful methods for characterizing and quantifying pollinator communities (Memmott & Godfray 1993; Oliver

et al). The method, despite not being species level all the way through, still provides information about the linkages between different genera and functional groups. Also, because the pollinator diversity is really high at our study site, can’t do species ID on the wing. Wanted it to be a quantitative network. We collect x number of vouchers to verify the ids.

To contrast the contribution of individual traits and floral neighbourhood density on pollinator visitation, I counted the number of flowers and measured the height of each focal plant. I recorded the abundance and identity of blooming shrubs and cactus in a 3 m radius around the focal plant. 2018 was a drought year and annual bloom density was negligible. It was not feasible to count the blooms of all neighbouring shrubs, so the surrounding shrub density is a proxy for neighbourhood floral bloom density. I also measured the distance to and identity of the focal shrub’s nearest blooming neighbour, as well of the distance to the nearest blooming L. tridentata.

I recorded shrub phenology and estimated blooming shrub density of each species using band transects on most study days. Therefore, there are three scales of floral density measures: individual, neighbourhood and site. I also used pan traps placed in open areas to track pollinator population changes throughout the study period. I quantified the number of ‘large bodied’ pollinators to reflect the sizes of those observed during the experiments (hereafter just ‘pollinators’).

Data analysis

Pollinator-mediated interactions, density-dependence

To explain floral visitation in response to individual floral traits, number, patch density and site-level density, generalized linear mixed models were fit with species included as a random effect. To explain differences in foraging preferences by function pollinator groups, separate models were created for all pollinators, honeybees, solitary bees, all bees and flies. These analyses were repeated for all plants, just shrubs and just cacti, because the visitation network showed that cacti interact with other cacti via pollinators more often than they do shrubs.

We plotted density-visitation curves for each species that had >10 observations?

I used imputeTS to fill in densities for the days they weren’t sampled using the linear interpolation.

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 to test for autocorrelation of visitation rates.

Network topology

I constructed species level interaction networks for: all plants, just shrubs and just cacti. I used bipartite to calculate: linkage density, connectance, betweenness and a few other things.

Modularity was assess using netcarto r package. These were done for individual networks: again at all plants, just shrubs and just cacti.

I counted the number of times each species (s-s) and individual (s-i) was a part of each motif.

Individual plant traits

To determine how individual plant traits influence network topology, the network trait was used as a response variable, and the individual traits and neighbourhood densities as predictor variables in GLMM with the shrub species as a random effect.

Trait-based cluster

Like in that other paper, we used cluster analysis to create a neighbourhood or maybe trait based network like in peerj paper.

Results

Major findings: Current analyses are focused on interactions between shrubs only, because the visitation network (Figure 3) shows that cacti interact primarily with other cacti. Local shrub density had a positive influence on pollinator visitation (Table 2). There is a significant interaction between individual flower number and site level shrub density. When site level shrub density is high, the slope of this relationship is steeper, suggesting individuals with lower flower number are at a disadvantage when site level shrub density is higher (Figure 5).

Visitation responses to individual shrub floral density

We tested several models for different types of density: total density, shrub density, cactus density, conspecific and heterospecific.

Additive model:

Fixed effects:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 0.38125 0.41853 0.911 0.3623

shrub.density 0.08558 0.04204 2.036 0.0418 \*

N.flowers.scaled 0.40650 0.09743 4.172 3.01e-05 \*\*\*

site.density -4.53886 10.25546 -0.443 0.6581

Site density was not measured each day. There is a significant interaction, however the positive effect of individual flower number was unchanged – it just became more positive. Therefore, we feel comfortable still including it in models.

**Summary results:**

394 observation periods, a total of 634 potentially pollination visits were recorded. Nectar robbing and visits by non-pollinating insects excluded.

10 functional groups, 62 RTU of visitors

Interactions between shrubs

All observations – positive density dependence, interaction between site level density and individual flower numbers. This is true for shrubs but not cacti – is it sample size? Shrubs interact with shrubs, cacti not so much.

Discussion

There are interactions of different scales of density.

This has been found before in these papers:

Individual traits influence network topology.

What do these mean.

Implications for community interactions.

Suggestions for future work based on these results.

Appendix

Imputation: Missing values (4) of site level density for imputed using the package imputeTS (cite) to be able to use the most response data in the analysis. All species were imputed individually because different plants have different flowering strategies. We used time series because the number of flowers opened each days has temporal dependencies. “his process is a commonly used statistical method for

substituting missing values in a time series with values following the same temporal or spatial pattern

created by existing data (Schneider, 2001; Moritz, 2015)

“

Used linear interpolation – I expect there to be a trend but no seasonality.

Table 1: Imputation of site density measurements.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Parameter | Mean | | Standard deviation | | % DAta |
|  | Before | After | Before | After | Before |
| LT | 0.011858974 |  | 0.00312757 |  | 76.5% |
| SD | 7.69E-05 |  | 0.00027735 |  | 76.5% |
| SM | 0.000521368 |  | 0.000874754 |  | 76.5% |
| SC | 0.002653846 |  | 0.002230327 |  | 76.5% |
| AS | 0.015478632 |  | 0.009804953 |  | 76.5% |
| EL | 0 |  | 0 |  | 76.5% |
| EC | 0.002405983 |  | 0.003057944 |  | 76.5% |
| PP | 0.000115385 |  | 0.000416025 |  | 76.5% |
| HH | 3.85E-05 |  | 0.000138675 |  | 76.5% |
| BW | 0.001 |  | 0.001607275 |  | 76.5% |

Table 2: List of shrub species, number of observation periods and blooming period

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Foundation plant species | Observation periods and length | Mean height +/- SD | Mean floral number | Blooming period |
| Acamptappapus | 96 |  |  |  |
| Buckwheat | 31 |  |  |  |
| Ericameria cooperi | 55 |  |  |  |
| Ericameria lineafolia | 4 |  |  |  |
| Larrea tridentata | 80 |  |  |  |
| S Mexicana | 12 |  |  |  |
| Salvia dorri | 13 |  |  |  |
| Hedgehog | 5 |  |  |  |
| Prickly pear | 29 |  |  |  |
| Silver cholla | 69 |  |  |  |