Desert shrub facilitation shapes pollination network topology

Foundation species facilitation influences network topology of pollinators.

Running title: < 45 characters - but regular title presumably longer?

Letter

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Keywords: arid, desert, Pollination, foundation plants, deserts, facilitation, foundation species, positive interactions, non-trophic?, etc. network up to 10 keywords

Authorship statement: JB and CJL designed the survey, JB collected data, performed modelling and analysis and wrote the first draft. JB and CJL contributed substantially to revisions.

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**  
 - the number of references **61 so far**  
 - the number of figures, tables, and text boxes **Max six – have 8**

Abstract (150 words) too long still

Plant-plant interactions with pollinators? can support? the structure and function of natural communities. - topic sentence a bit obtuse here - do you mean plant-plant interactions that include pollinator mediated effects better predict community structure and function? Downscaling interaction networks from species to individuals? 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 good - what is that - can you state in a few words only I know space is limiting here . We studied the influence of inter-individual variation in plants?? what is that? 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 greater access to the conspecific mating pool suggesting widespread and diffuse pollination facilitation within this community - clunky. Shrub density also influenced the role of the network metric betweenness centrality more than species identity?? meaning?. Individual traits and contexts?? predicted network roles for individual nodes? and the formation of modules??. Ecological and individual context mediate the outcome of pollinator-mediated interactions and are fundamental drivers of whole community structure so confusing. Exploring these individual-community interactions will improve our understanding of drivers that promote species coexistence and plant fitness. ok - this needs to be less jargony and much more direct.

Pollinator-mediated facilitation is

To test pmf interactions between plants including association? with pollinators is measured and network analytics used

here we used a desert shrub system to examine this by measuring plant density, associations, and visitation rates by pollinators including pollen etc.

then state results as you did and mention network metrics but just had 2-3 words with each explaining what they mean/imply

then your final implication is ok - coexistence and key drivers but can you be more specific - ie if you do not consider pmf then only direct interactions suggest that? or by considering pmf you can assess both key factors that influence plant fitness and community structure drivers that reciprocally impact pollinator community too such as density?

**Introduction**

Interactions between species structure plant communities and contribute to biodiversity maintenance globally. Interacting populations are aggregations of interacting individuals, thus the outcome of interactions between species (i.e. plant fitness) can be influenced by both intraspecific and interspecific variation in attractiveness to pollinators. Attractiveness to pollinators is influenced by phenotypic variation in plant traits that can improve pollinator foraging efficiency including floral display size ([Thomson 1981](#_ENREF_52); [Ohashi & Yahara 1998](#_ENREF_35)) and plant height ([Donnelly *et al.* 1998](#_ENREF_10); [Toräng *et al.* 2006](#_ENREF_53)). The floral composition of the surrounding area can also influence attractiveness due to density-dependent interactions between the local co-blooming floral neighbourhood and the focal plant ([Rathcke 1983](#_ENREF_42); [Seifan *et al.* 2014](#_ENREF_49)). Consequently, both individual traits and community-level attributes can function in a network capacity to impact interactions with pollinator that in turn influence fitness? Within season phenological variation in the density and composition of co-flowerings plants can also lead to temporal shifts in interactions among plants ([Aizen & Rovere 2010](#_ENREF_1); [Runquist 2013](#_ENREF_45)). Plant-pollinator mutualisms occur within the spatial context? of natural communities and are embedded within complex webs of interactions meaning? including competition, facilitation, and other processes including herbivory ([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 through pollinators at the community level. Pairwise interactions between plants and pollinators have been documented ([Hegland *et al.* 2008](#_ENREF_24); [Tur *et al.* 2016](#_ENREF_55)) but a larger scope of interactions from a network perspective are more likely to better estimate key drivers of community structure or provide the capacity to contrast direct plant interactions with indirect interactions through pollinators (cite the new review?). Consequently, facilitation or positive interactions between plants that includes pollinators in desert ecosystems is an ideal system to examine this approach.

Network analysis has emerged as a valuable tool for studying plant-pollinator interactions ([Bascompte & Jordano 2013](#_ENREF_3" \o "Bascompte, 2013 #368)) plus maybe 2 more cites. Most pollinator visitation networks are species based, and each node represents a population of plants or pollinators. The links are the sum of interactions between the plants and the pollinators, i.e a bipartite network (citation). The recognition that patterns between interacting individuals drive the patterns between interacting species has driven recent interest in downscaling from populations to individuals or the inclusion of interactions within at least one set of nodes, ie the plants, to the connections with the pollinators? ([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, and for instance, these coupled approaches have been used in concert? 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 (cite that review?). 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 or the shape of interactions? and community functioning. good - could be a bit more direct for readers but depends on journal. if say for instance Bioscience - then need to be a bit simpler - if Oikos of New Phyto of J Ecology - likely ok with the more technical terms assuming that readers are familiar with network terms a bit more.

Topic sentence? Network metrics provide a deeper insight into interactions within populations? and between species. 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), and it has been proposed that foundation plant species function similarly in non-trophic networks (cite review). Recently these specific 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 lost.. sorry. 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)) good but flow... hard to see connections here. Therefore, association with other species can contribute to centrality of an individual? bit confusing what an individual is? an individual entity, an individual-based network, a species? sorry maybe either define what you mean somehow or try to keep reader on track> through changes in its attractiveness but if this increases access to conspecifics is unknown??. Here, downscaling from ? larger mixed species? community networks? or from networks that include pollinators? provides information about how individual traits and local context contribute to an individual’s importance relative to other members of the co-flowering community. meh - be more explicit what the benefit is - ie you are doing X to be able to contrast individual trait-driven factors such as floral display versus network-level? measures such as density? to better predict interactions with pollinators such as visitation or pollen dep?

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 meaning? what does this do ecologically? state idea first? or purpos In thius study, we directly contrast plant-plant interactions with a foundation shrub species typically functioning as a benefactor with individual plant traits to examine pollinator interactions with the protege species? then get to network - same as what we said before - YOu can GO either way - ie the idea and network is the TOOL or if you want, NETWORK is the tool and we are using this system as a case study. The paragraphs above flip-flop really - I recommend picking one and setting entire focus that way then re-edit abstract and edit to set main idea first then back with secondary. It will be just cutting and pasting..

Network theory and analyses great enhance studies of population and community structure because a. most interactions are not just pairwise, b. pollinators and plant interact, and c.similar to keystone species in foodweb studies, foundation plant species in plant communities can have dramatic network-level and hence community-level impacts on dynamics. Individual trait level factors are relevant in this context such as floral display etc however neighbourhood-level measures from network analyses cannot be ignored. Pollinator-mediated facilitation is... and it is a perfect set of interactions to advance ecological network theory models for community assembly and contrasts of traits versus community importance. Using a desert shrub system typically described by facilitation, we examined pmf to test network dynamics etc...

something like that flow.

OR go the other way

Ecological interactions can be simplified to direct and indirect or positive and negative. However, interactions do not occur in isolation, only in populations, and without interactions with other taxa such as pollinators. etc. then spin up value of looking at the bigger picture, through network analyses, on the relative importance of traits, interactions with neighbours mediated through pollinators, and the relative importance of overarching foundation plant species?

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?? why?. 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" \o "Jennings, 2001 #5)). 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 does not fit well. We tested the hypothesis that focal plants growing in denser areas would be more attractive to pollinators because of optimal foraging?? hmmm but you do not track foraging of pollinators - I would not use this a H. We tested the hypothesis that neighbourhood level measures of plant-plant interactions with a foundation plant species can be mediated by interactions with pollinators. 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 - meaning?. We assessed if centrality improves access to other conspecifics same? ok you are stroingly gravitated towards the network focus - so maybe that is the way to do this paper. 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?? no idea what this means. In sensitive ecosystems such as deserts, phenological shifts in interactions in plants and pollinators are a critical conservation challenge. Higher-level patterns of interactions that function at the community level to determine biodiversity to better understand the impact of these changes. - revise

OK - BIG ideas in there - I think flow needs to be worked out and decide on focus.

I think you need a better hypothesis too.

I tried one above - I think there are least two options.

Keeping it first principles - and honest

a. I wanted to see this done because I want to know if there are network-level, ie neighbourhood and community-level interactions are at least associations that influence outcomes at the individual level.

b. I want to know if foundation plant species CHANGE how plants connect to one another through pollinators. (\*and network analysis is the tool).

c. I wanted to see how network analysis tools can be applied to a foundation plant facilitation complex to test if network approaches better describe how plants interactions in deserts at least in the context of shrub systems.

ALL are true and viable - I think maybe picking one and making it the focus best. However, there could be another reason you did this too - you can easily convince of me that too.

d. In all plant communities, focusing only on direct plant-plant interactions and/or pairwise interactions limits our capacity to describe and predict community resilience, structure, and composition. Including interactions with pollinators is a critical advance to theory because this interaction set can mediate many interactions between plants including facilitation and can be as important or even more so than direct interactions??? Something like that - ie make the pollinators the focus and you use the shrub contrast model simply as a means to nest and simplify plant community structure.

Methods

Field data collection

Plant-pollinator interactions were studied at Sunset Cove at the Sweeney Granite Mountains Desert Research Station within the Mojave National Preserve in California (1280 MASL, 34°46'26.5"N 115°39'31.3"W). Data were collected between April 20th and May 9th, 2018 encompassing the flowering period of most spring blooming shrubs and cacti at the site. The experiment ended when it was not possible to locate additional individuals of blooming shrubs. Focal plants were chosen by walking in a line starting in a different quadrant of the study site each day to avoid confounding area by time of day. To avoid oversampling the most abundant species, up to six individuals of a single species were sampled per observer per day. 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 instead of the more frequently used method of transect walks that captures only the most frequent interactions ([Westphal *et al.* 2008](#_ENREF_61)).

Visitation was coded only when potential pollinators made direct contact with plant reproductive organs. Taxonomic groups previously documented as non-pollinating species were excluded such as Coccinellidae ladybird beetles, *Carpophilus* sp. pollen beetles and spiders. Soft-winged flower beetles (Melyridae) in the subfamily Dasytinae were also excluded because they were observed but were stationary deep within flowers and could not be effectively counted. Finally, pollinators < 2 mm in size such as micro-beeflys (Mythicomyiidae) were excluded from analyses because it was viable 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 on-the-wing identifications, and samples are archived at York University. Some groups e.g. Tachinidae and Sarcophagidae were resolved to family due to the difficulty of identifying them on the wing (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.

The number of open flowers and the height of each focal plant directly before the observation period were recorded as trait-level measures. To estimate the immediate floral neighbourhood measures, we recorded the abundance and identity of all blooming shrubs and cacti within a 3 m radius around the focal plant. We tracked shrub phenology and estimated site-level floral density by counting the number of blooming shrubs of each species in four 10 m by 50 m band transects on 13 days over the study period. This was a proxy for net floral abundance at the site level?.

To track pollinator population changes throughout the study period, three colours of six-inch diameter pan traps (yellow, blue and white) with water with a few drops of dish detergent were placed in arrays of three at six locations in open areas on every other day. The number of pollinators were extracted from these data to estimate the net population-level abundance 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 the R package imputeTS, ([Moritz & Bartz-Beielstein 2017](#_ENREF_34)). The species-specific values were summed to complete missing date obervations.

Influence of individual traits and floral neighbourhood on pollinator visitation

To test for between-plant variation in pollinator visitation rates, we fit generalized linear mixed models (GLMM) with the number of visits as the response variable and individual floral display size, floral neighbourhood density, site density, and study day as predictors. The shrub species was also included in the models as a random effect. To account for over dispersion in the model, we used a negative binomial error distribution (citation). Height and floral display size were positively correlated (Appendix B (have a plot), Pearson’s = 0.537, p < 0.0001, df = 392), and thus, only floral display size was included in finals models. We assessed model fit by comparing candidate models to each other and to the intercept only model using AIC and likelihood ratio tests. In cases when AIC < 2 and there were no differences in likelihood ratio test, we chose the simpler of the models. We tested the final chosen predictors for multicollinearity using the vif function from the R package car ([Fox *et al.* 2012](#_ENREF_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 the R package spdep ([Bivand *et al.* 2011](#_ENREF_5)). Great stats btw. nice nice, I need to get way better. help me. :)

Network analyses

Pollinators were classified into 17 distinct functional groups (Table S1), and 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.good but clunky 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)) - love. All bipartite network indices were calculated using functions within the bipartite R 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)) - also LOVE. 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, centrality describes the number of interactions with conspecifics such as the mating pool and the number of heterospecifics and?or? the potential competitors/facilitators. Eigancentrality extends the concept of degree centrality but takes into the account of the importance of degree of the interactors?? degree means number of? or extent of?. Individuals that interact frequently with other highly connected individuals are more likely to influence the full network because they can interact with dense substructures within the network. Betweenness is the number of times a node lies on the shortest path between other nodes and describes the importance of a node on connecting the parts of the network ([Freeman 1978](#_ENREF_19); [Martín-González *et al.* 2010](#_ENREF_29)) and estimates what process?.

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). Consequently, we first modeled the likelihood of an individual having a betweenness value > 0 using a binomial mixed effect model. A high number of ultra-peripheral nodes is typical in pollination networks ([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 modeled it using a Gaussian error distribution (residuals: W = 0.98854, p-value = 0.5491). These indices describe individual context contributions to node positioning, importance, and the 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). Hence, only degree centrality was included in these models because it is the most commonly reported measure in the network literature. Betweenness centrality, study day, visitation rates, shrub density and floral display size were used as predictors. Models were compared to random intercept only models using AIC and likelihood ratio tests to identify best models or maybe say the most parsimonious models.

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 the R package 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 using the nnet package ([Venables & Ripley 2013](#_ENREF_60)) with the module as the response, and plant species, individual floral display size, visitation rate, study day and local floral neighbourhood as the predictors.

Down-scaling effects on whole network measures

To complement these individual measures and facilitate comparison of this network to other visitation networks, we calculated several common indices for the individual and species bipartite network. The metric H2` is the degree of complementary specialization of the whole network of interacting species and measures the deviation of observed interactions from those expected given the marginal totals of the species. This quantitative measure ranges from 0 and 1; the higher the selectivity of the species, the higher H2` for the network. H2` does not vary significantly with network size ([Blüthgen *et al.* 2006](#_ENREF_6)). Weighted nestedness (WNODF) is a quantitative measure that ranges between 0 and 100 and describes the hierarchy of the interactions of the network. In nested networks, specialized nodes i.e. those with fewer interactions are linked with well-connected nodes ([Almeida-Neto & 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 meaning that? ([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.

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 and Stouffer 2013).

Results

General patterns

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 RTUs of visitors (Table 1). With the exception of hummingbirds (*Calypte* sp.), all floral visitors were insects. There was no spatial autocorrelation detected for visitation rates (Moran’s: -0.055108, p = 0.953, Geary: 1.0442, p = 0.8145), and there was no significant correlation between site-level floral density and local neighbourhood floral density (Pearson’s = 0.11, p = 0.1187, df = 178).

There was a consistent, positive influence of neighbourhood shrub density on pollinator visitation rates throughout the study period (n = 395, Table 2). There was a significant interaction between floral display size and study day, but floral display size became unimportant later in the study period. Site-level density of blooming plants decreased over the duration of study (Pearson’s = -0.4978227, df = 18, p-value = 0.02551). Site-level density interacted with floral display size similar to day effects, but these models had higher AIC scores? (Table Ax), and only study day was used for all subsequent models.

Floral display size and neighbourhood effects on centrality and network topology

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 effect od day on any network metrics? (Table A3). Foundation plants differed in their degree?? of (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 plant? 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). Betweenness measures for individuals with scores > 0 increased with visitation rates (GLMM: Est: 0.18868, χ2: 26.336, p < 0.0001), and the betweenness measure did not differ between plant? 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) GREAT. 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). OK so it seems like a general thing that visitation rate was an important predictor for many network measures.

I propose you take all of above stats, put in a table, and cite that - measure, estimate, p-value, and sign? or importance as columns and then the predictors as rows.

Then start with section with Visitation rate was the most consistent significant predictor of network indices (or measures/metrics whatever term best) (Table 1). Then compile all and just state VR significantly predicted xyz in next sentence. then mention other predictors and also a statement on which ones were less important.

Access to conspecifics all this little subsections can be combined?

Access to both conspecific and heterospecific plant individuals increased with degree centrality (Figure 2, Table 4). 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. revise Shrub density increased access to conspecifics, but not heterospecifics (Table 4 ? and then table 3 in next section? maybe re-order?) 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 same - combine with above

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). hmmm

**Discussion**

topic sentence first - for whatever focus you decide - the ecological one or the network one - ie remind reader the purpose 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 determined? topology beyond increases?/ in addition to or more important than or in contrast to? in visitation rates including betweenness, access to conspecifics and modularity, and this effect was time invariant meaning? even if you do not take the ecological approach you can still say what it means to network reasoning and to later to network theory? So this would be something like - Blooming shrub density neighbourhood influenced network metrics for visitation rates including .... or say network topology - assuming that means these measures so can use that term instead of metrics? . In general, floral display size influenced network measures indirectly through its strong influence on visitation rates?? - supporting the prediction that individual-level traits are more important than neighbourhood level metrics?. OK stopping for a second here - If you revise intro and have a clear hypothesis, either focus, then maybe we need a few predictions? these sentences are good and seem like they are supporting implicit assumptions you had or predictions? 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 component. 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. ? focus again - this will tidy up once you set the state in Intro.

Put network ones first if focus..

then

Ecological implications

Diffuse pollinator-mediated facilitation between co-blooming foundation plants was prevalent in this system. Facilitation between co-blooming plants through increased? 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 however? been reported to benefit the pollination of desert mustard *Lesquerella fendleri* ([Roll *et al.* 1997](#_ENREF_43)). Interestingly, shrubs, but not cacti densities elicited this positive effect. Shrubs were taller than cacti with larger floral displays, and this attractiveness can bring in pollinators via the magnet species effect leading to improved visitation to associated 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?) why ?. 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 need to work on flow - fading here sorry. Shrub density improved access to conspecifics, and this is 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 great idea just state as implication.

Network theory implications - with use subheadings or cut but if cut maybe use the heading idea a the topic sentence in some form to guide the reader on what to expect from that paragraph.

topic sentence needed Node attributes influence network topology??? and?? (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 were not correlated with closeness ([Gómez & Perfectti 2011](#_ENREF_21)). Interestingly, plants growing denser patches had a betweenness roles that showed that shrub facilitation contributes to the cohesiveness of the network - flow - so floral traits important but also facilitation by shrubs? - directly by increasing density. 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 structure? 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. revise

topic sentence - what are unipartite stats testing - start with that idea - are they testing the individual-level traits? 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) etc. 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 can be influenced by decreases in net site-level density. Changes in the availability of resources can alter pollinator foraging preferences (cite). Conspecifics can be members of different modules (Tur 2015), and previous individual, community work has found divergences between taxonomic similarities and trait similarities ??(Rumeu 2018). 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 yah good keep). 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 good - further to that review - I think finding diffuse facilitation networks is actually really cool - ie many species share neighbourhoods and I think this suggests resilience provided the foundation species are intact and protected in these systems right?.

Conclusions

Nestedness, modularity, and the correlation between degree and other centrality measures are considered universal features of networks (Martin) - like nice topic if networks are the main focus of paper.. 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. sure

Better understanding the contexts that lead to individual roles within networks could be really helpful to applied ecology and understanding co-evolutionary cascades YES and resiliene -ie weak diffuse faciltation ONLY really tested with network analyses and you did that there - I think that is really novel and important - beyond pairwise, still used traits, but also examined the larger community context through neighbourhoods and through foundation species. LIKE . 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. OK

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| 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 |

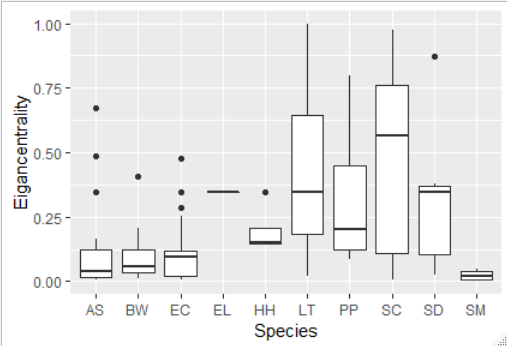
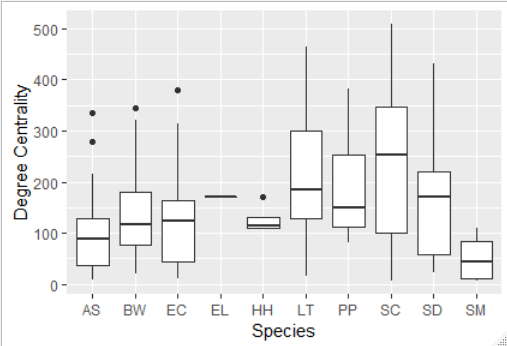
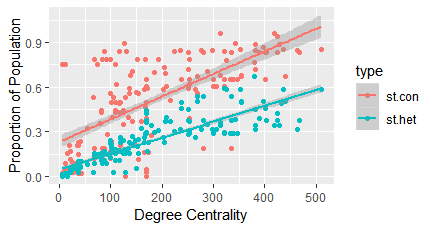


Figure 1: Species differed in their degree centrality and eiganvector centrality.

Might cut this figure unless it is showing something important.



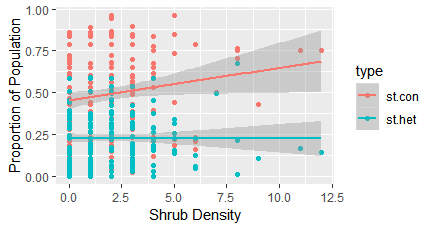


Figure 2: Foundation plants interact with a greater proportion of conspecifics than heterospecifics. Proportions inreased with degree, and proportion conspecifics only increased with shrub density. Values are the number of interactors standardized by the number of potentially interacting plants within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

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 |

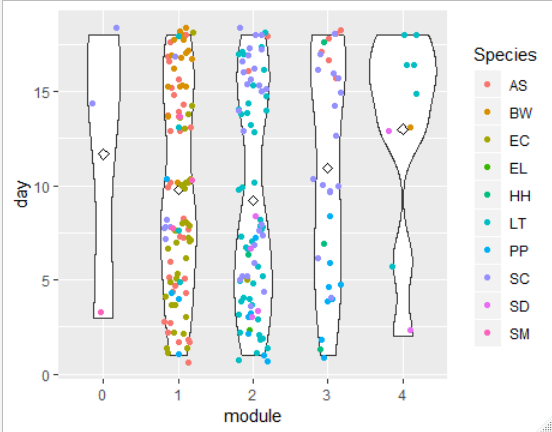


Figure 3: Modules are structured by day. Conspecifics can be found in multiple modules.

hmm i like violin plots but ther are not popping

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 |  |

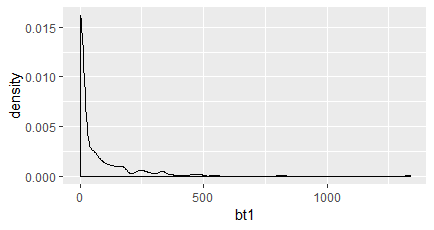


Figure A1: Betweenness values were very zero-inflated. Most models for zero-inflation are for count data, not continuous data.

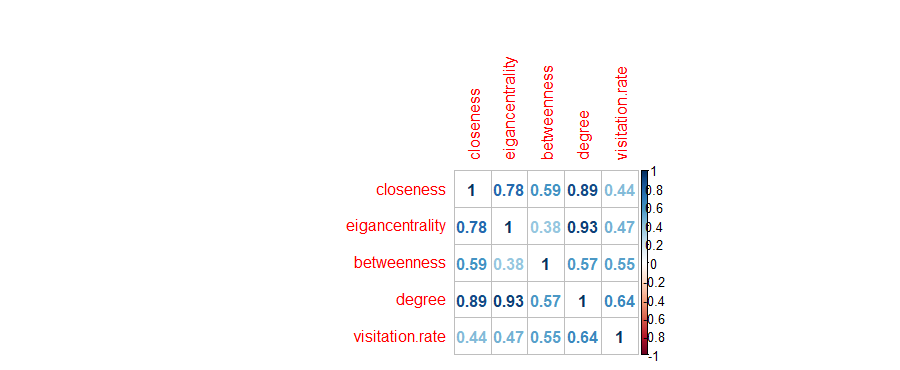


Figure A2: Correlation coefficients between centrality measures and visitation rates.

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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