TITLE:. Genetics of a foundation species structures community interaction networks.

AUTHORS:. Matthew K. Lau, L. James Lamit and Thomas G. Whitham Take-Home: Foundation species genetics influences the structure of interactions among bark lichen species most likely by altering the trajectory of community assembly.

### 1. Abstract

* The ecology and evolution of communities requires greater understanding of interaction networks as the interactions among species are as important as other metrics such a species richness and abundance in structuring the community.
* We present a study of bark lichen communities associated with Populus angustifolia (narrowleaf cottonwood), where we applied quantitative network modeling to investigate the genetic effects of a foundation tree species on bark-lichen community interaction networks.
* There were three main findings:
  1. Genotype significantly predicted the similarity of lichen interactions networks. Species richness explained additional variation in network similarity.
  2. Both genotype and richness significantly predicted the variation in three network structural metrics (size, degree and centralization).
  3. All network metrics were highly correlated with each other and lichen species richness. Thus, after controlling for the variation explained by lichen species richness, all three network metrics significantly predicted variation in the similarity of networks but only network size explained a biologically relevant amount of variation in network similarity.
* These results strongly support the hypothesis that there is a genetic component to the structure of species interactions. Our quantitative network modeling and network analyses show that this genetic effect is not due to variation in lichen species richness arising from genotype, but by some other causal pathway. These results indicate that the variation in network structure among genotypes arises from the communities being at different levels of community assembly, as both species richness and the size of the network independently explained the most variation in network similarity.
* These findings are particularly important as they suggest that quantitative modeling of community-wide interaction networks can aid our understanding of community dynamics and that we need to place interactions among species within an evolutionary framework.
* Important to note that while many studies have now been published on interaction networks, this is the first to show that the networks of individual genotypes are significantly different. Such findings suggest that natural selection can act on networks and that different networks have the potential to differentially feed back to affect the fitness of the individual genotypes they occupy. Although such feedbacks may not occur in this system, several studies have now emerged in which strong positive and negative feedbacks have been demonstrated (e.g., negative – Packer and Clay 2000, Michalet et al. 2011; positive – Pregitzer et al. 2010, Smith et al. 2011)

### 2. Introduction

* Understanding complex species interactions is important for ecology (reviewed in Bascompte 2009, and others...).
* A substantial body of evidence provides support for the value in putting communities and ecosystems into an evolutionary framework (Whitham et al. 2003, 2006, Johnson and Stinchcombe 2007, Wade et al. 2007, Haolin and Strauss 2008, Hughes et al. 2008, Bailey et al. 2009, Wymore et al. 2011, Rountree et al. 2011). However, there is still little known about how genetic variation in a foundation species affects the interactions among multiple species in complex communities (but see Bailey et al 2005).
* Defining species interactions and obtaining quantitative data for interactions in complex communities presents a challenge to ecologists.
* Newly developed quantitative network modeling methods provide one means to not only obtain estimates of species interactions but also circumvent the need to limit interactions to one or few categories (e.g. trophic, mutualistic or host-parasite interactions).
* Here, we present the results of a study of how foundation species genetics influences variation in interactions among multiple species in a group of organisms (lichens) that might be imagined to have weak interactions with a foundation tree species. Might say something about the lichen itself being an impressive interaction of organisms.
* Here and/or in the discussion I think you need to explicitly develop the biology of lichens (growth, importance of substrate, size as a surrogate for fitness).
* Important to emphasize how lichens compete or interact with one another and the long-term nature of these interactions as they can grow so slowly. Some readers might be skeptical that such interactions exist and that the bark substrate is important. Need to diffuse that up front.
* Do you have some cool photos of lichens on cottonwood trunks that might be included in the paper?

### 3. Methods

* Garden description.
* Samling description. The presence of bark lichen species were assessed within 50 replicate 1 cm2 grid cells of 10 cm2 quadrats on replicate clones of known genotype in a common garden at the Ogden Nature Center (Utah, USA). 50 out of the 100 cells in each quadrat were sampled in a checker-board pattern in order to minimize the probability of individuals overlapping between cells. 122 trees sampled, 13 genotypes, 5800 grid cells.
* Network modeling. Network models were generated using a correlation based algorithm to detect species interactions on each individual tree. Thus, we produced a quantitative, undirected model of species interactions on each individual tree.
* Statistical methods for network similarity. We then applied network analyses and mutlivariate statistical methods to test for the effect of genotype on lichen community interaction network structure. In order to compare networks, we measured the similarity between networks as the sum of the Euclidean distance for all edges between each network pair for all networks. This formed a distance matrix that we then used in PerMANOVA analyses of the factors influencing network similarity. We used ANOVA to analyze the effect of genotype and richness on the network structural metrics. To visualize the similarity of network genotypes, we applied prinicipal components analysis to the network distances and used ordination vector fitting methods to explore the possible sources of similarity among netowrks.

### 4. Results

1. We found significant variation in network structure among tree genotypes (Fig. 1). Genotype and lichen species richness were both significant predictors of the structural similarity of the lichen community networks with tree genotype and richness explaining 32% and 22% of the variation in lichen network similarity, respectively (Table 1).
2. We investigated several network statistics to explore the structural variation responsible for the variation in network similarity and found that genotype and richness significantly predicted the variation in all three network metrics (Fig. 2 and Tables 2-4). Note that bark roughness was not a significant predictor of network similarity (p = 0.983).
3. All network metrics were highly correlated with each other and lichen species richness (Fig. 3). Thus, after controlling for the variation explained by lichen species richness, all three network metrics significantly predicted variation in the similarity of networks but only network size explained a biologically relevant amount of variation in network similarity. (r2 = 0.48) after controlling for the variation explained by lichen species richness (Table 5).

### 5. Conclusion

* Tree genotype influences the size, degree and centralization of lichen community interaction networks. It is important to note that none of these network metrics were significantly predicted by the number of trees sampled for a given genotype (i.e. variation in the number of observations did not produce these patterns).
* This pattern does not seem to be related to the bark roughness, as richness and community composition seem to be. This is intriguing since roughness seems to be an important factor in lichen establishment and a good predictor of the genotype effect on the distribution of the dominant lichen species (Lamit et al. 2010).
* These results are particularly striking given that lichen species are very slow growing and that our communities are all likely to be in the early stages of establishment.
* These findings are important as they present a step toward putting complex, community-wide interactions in an evolutionary framework.
* The importance of interaction networks in conserving biodiversity – Because the interactions of species are widely thought to play a major role in structuring whole communities and ecosystems, the conservation of interaction networks may be as important as the conservation of the species themselves. When we lose a species, we also lose its interactions with other species. If this species is a strong interactor, foundation species (i.e., a node with many connections), the whole community may be threatened.

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|  |  |  |  |  |  |  |
|  | Df | SumsOfSqs | MeanSqs | F.Model | R2 | Pr(>F) |
|  |  |  |  |  |  |  |
| Genotype | 12 | 1.14 | 0.10 | 2.16 | 0.32 | 0.0266 |
| Richness | 1 | 0.79 | 0.79 | 17.93 | 0.22 | 0.0002 |
| Genotype:Richness | 11 | 0.22 | 0.02 | 0.45 | 0.06 | 0.9509 |
| Residuals | 33 | 1.46 | 0.04 |  | 0.40 |  |
| Total | 57 | 3.61 |  |  | 1.00 |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |

Table 1: ANOVA table for the PerMANOVA test of the effect of genotype and lichen species richness on the similarity of the lichen interaction networks.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |
|  | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|  |  |  |  |  |  |
| Genotype | 12 | 42.85 | 3.57 | 3.52 | 0.0020 |
| Richness | 1 | 36.66 | 36.66 | 36.17 | 0.0000 |
| Genotype:Richness | 11 | 7.94 | 0.72 | 0.71 | 0.7183 |
| Residuals | 33 | 33.45 | 1.01 |  |  |
|  |  |  |  |  |  |
|  |  |  |  |  |  |

Table 2: ANOVA table for the tests of the effects of genotype and richness on network size (i.e. the number of species in the network).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |
|  | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|  |  |  |  |  |  |
| Genotype | 12 | 10.84 | 0.90 | 3.25 | 0.0036 |
| Richness | 1 | 8.72 | 8.72 | 31.34 | 0.0000 |
| Genotype:Richness | 11 | 1.80 | 0.16 | 0.59 | 0.8245 |
| Residuals | 33 | 9.18 | 0.28 |  |  |
|  |  |  |  |  |  |
|  |  |  |  |  |  |

Table 3: ANOVA table for the tests of the effects of genotype and richness on network degree (i.e. the number of connections).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |
|  | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|  |  |  |  |  |  |
| Genotype | 12 | 0.48 | 0.04 | 2.80 | 0.0096 |
| Richness | 1 | 0.34 | 0.34 | 23.87 | 0.0000 |
| Genotype:Richness | 11 | 0.05 | 0.00 | 0.32 | 0.9759 |
| Residuals | 33 | 0.48 | 0.01 |  |  |
|  |  |  |  |  |  |
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Table 4: ANOVA table for the tests of the effects of genotype and richness on network centralization (i.e. the degree to which the network is dominated by one species).

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| --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |
|  | Df | SumsOfSqs | MeanSqs | F.Model | R2 | Pr(>F) |
|  |  |  |  |  |  |  |
| Richness | 1 | 1.13 | 1.13 | 232.43 | 0.31 | 0.0001 |
| Size | 1 | 1.74 | 1.74 | 356.67 | 0.48 | 0.0001 |
| Degree | 1 | 0.24 | 0.24 | 49.15 | 0.07 | 0.0001 |
| Centralization | 1 | 0.24 | 0.24 | 49.84 | 0.07 | 0.0001 |
| Residuals | 53 | 0.26 | 0.00 |  | 0.07 |  |
| Total | 57 | 3.61 |  |  | 1.00 |  |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |

Table 5: ANOVA table for the PerMANOVA test of the effects of the network metrics (size, degree and centralization) on network similarity after removing the variance explained by richness.

Figure 1: Network graphs for each genotype. Points represent species scaled by the log of there total frequency of occurrence and lines show the means of significant connections between species across genotype replicates scaled by their magnitudes. Species points that had zero frequencies are colored white.

Figure 2: Principle components ordination plot of the similarity between networks. Points represent the genotype means for the ordinated scores and bars show the spread (1 S.E.). Vectors show the strength (vector length) and the direction of spread networks (vector direction) of the correlation between roughness, the network metrics (size, degree and centralization) and richness and the ordinated networks.

Figure 3: Matrix of bivariate plots for the network structure statistics (size = number of species in the network, degree = number of connections and centralization = dominance of the network by one species) and species richness (measured as the number of species present in the quadrat). Note that although a species may have been present in a quadrat, it may not have a significant connection to any other species in the community.