FOUNDATION SPECIES GENETICS STRUCTURES LICHEN COMMUNITY INTERACTION NETWORKS

M.K. LAU, L.J. LAMIT, T.G. WHITHAM

Contents

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

- Understanding the complexities of community dynamics requires a greater understanding of the interactions among species and the forces that influence the structure of these interactions.
- 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 interactions 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 quantative 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.

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 (reviewed in PRS-B 2011, Johnson and Agrawal 200?, Whitham et al. 2008 and Whitham et al. 2007). 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.

3. Methods

- Garden description.
- Samling description. The presence of bark lichen species were assessed within 50 replicate 1 cm^2 grid cells of 10 cm^2 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 genotype and richness explaining 25% and 33% of the variation in lichen network similarity (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 ($p = 0.763$).
(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. ($r^2 = 0.06$) after controlling for the variation explained by lichen species richness (Table 5).

5. Conclusion

- 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.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Genotype	13	0.56	0.04	2.49	0.25	0.0009
Richness	1	0.75	0.75	43.14	0.33	0.0001
Genotype:Richness	12	0.34	0.03	1.62	0.15	0.0353
Residuals	34	0.59	0.02		0.26	
Total	60	2.23			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	13	43.48	3.34	3.21	0.0032
Richness	1	37.32	37.32	35.80	0.0000
Genotype:Richness	12	7.94	0.66	0.63	0.7976
Residuals	34	35.45	1.04		

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	13	10.99	0.85	2.97	0.0054
Richness	1	8.89	8.89	31.21	0.0000
Genotype:Richness	12	1.80	0.15	0.53	0.8819
Residuals	34	9.68	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	13	0.48	0.04	2.35	0.0229
Richness	1	0.36	0.36	22.74	0.0000
Genotype:Richness	12	0.06	0.00	0.29	0.9865
Residuals	34	0.54	0.02		

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).

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Richness	1	0.89	0.89	49.55	0.40	0.0001
Size	1	0.14	0.14	7.88	0.06	0.0007
Degree	1	0.07	0.07	3.67	0.03	0.0171
Centralization	1	0.14	0.14	7.58	0.06	0.0003
Residuals	56	1.00	0.02		0.45	
Total	60	2.23			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.
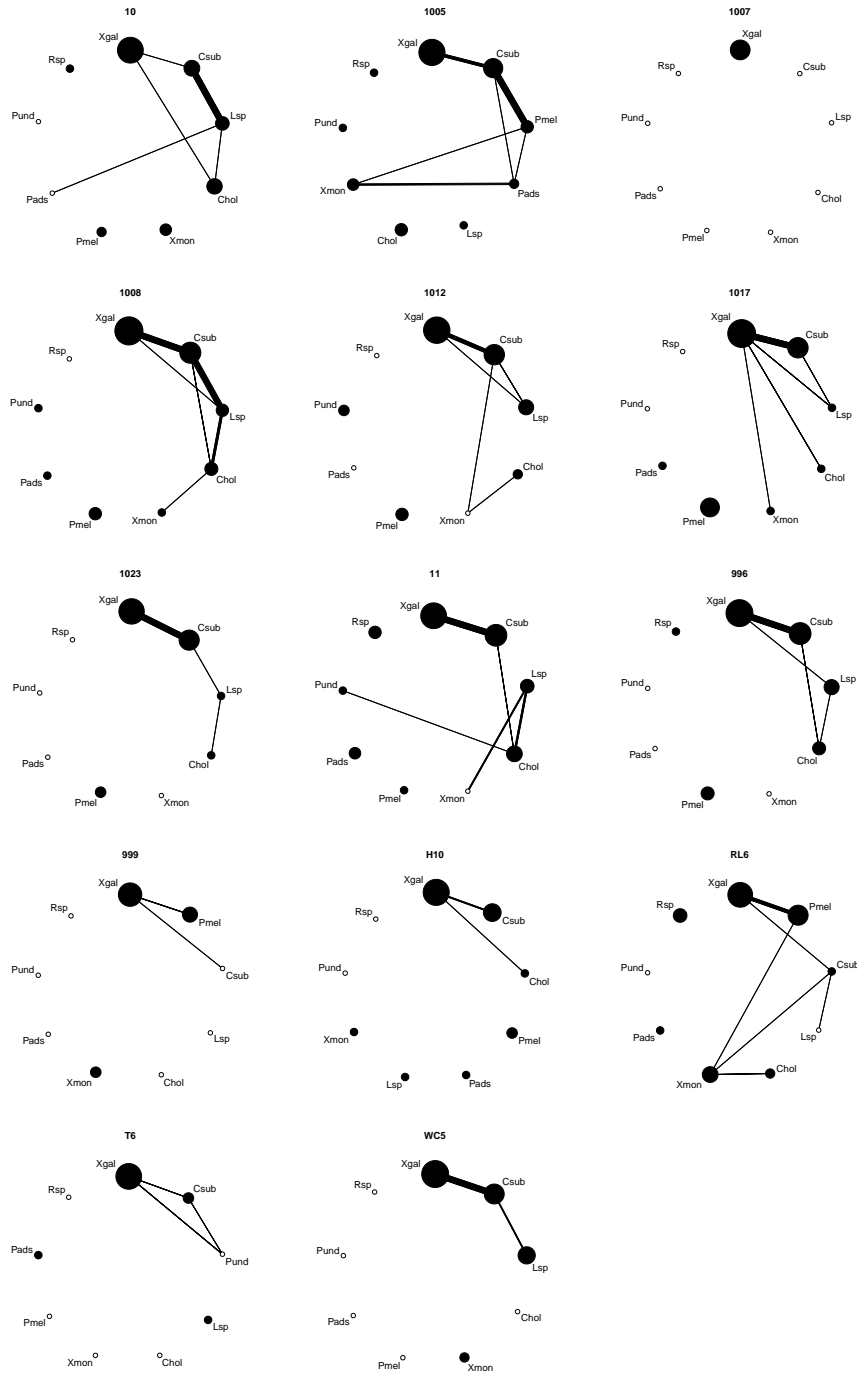
FIGURE 1. Network graphs for each genotype. Points represent species scaled by the log of there total frequency of occurrence and lines show the means of significant connections between species across genotype replicates scaled by their magnitudes. Species points that had zero frequencies are colored white.
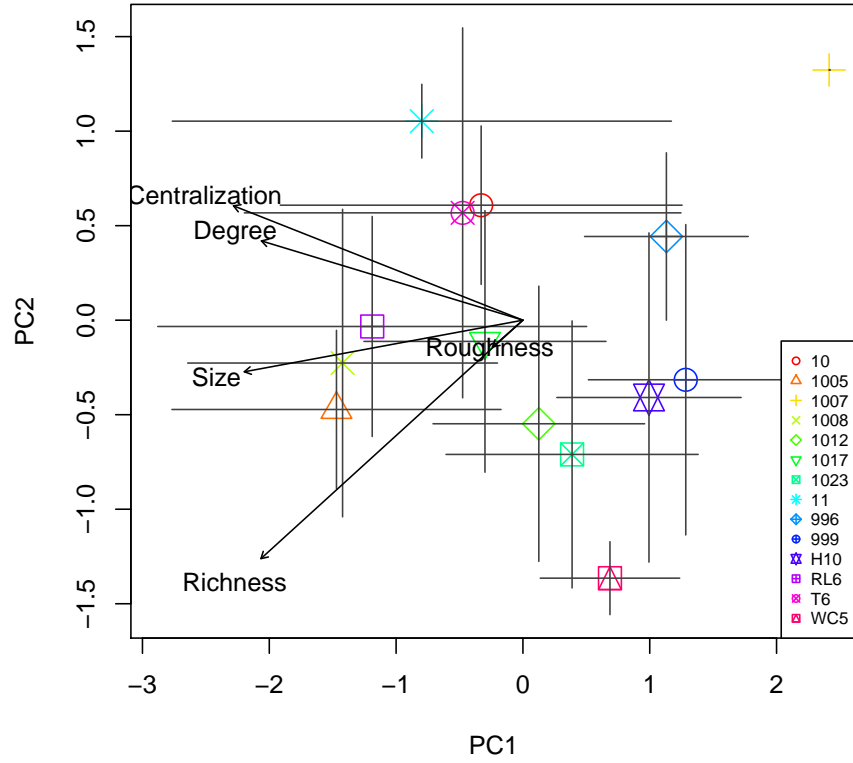
FIGURE 2. Principle components ordination plot of the similarity between networks. Points represent the genotype means for the ordinated scores and bars show the spread (1 S.E.). Vectors show the strength (vector length) and the direction of spread networks (vector direction) of the correlation between roughness, the network metrics (size, degree and centralization) and richness and the ordinated networks.
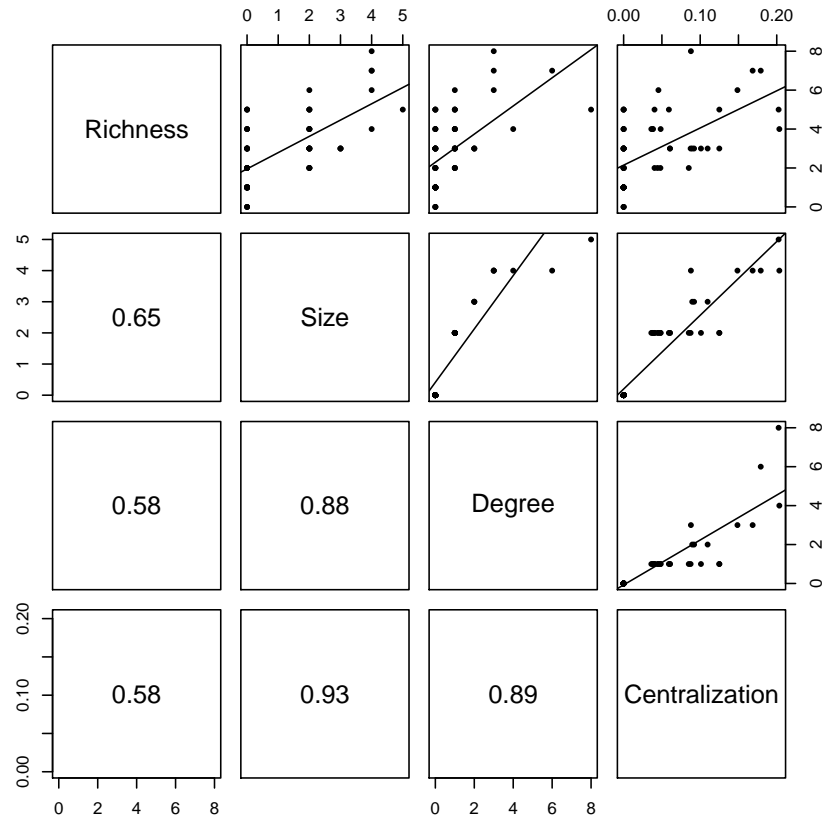
FIGURE 3. Matrix of bivariate plots for the network structure statistics (size = number of species in the network, degree = number of connections and centralization = dominance of the network by one species) and species richness (measured as the number of species present in the quadrat). Note that although a species may have been present in a quadrat, it may not have a significant connection to any other species in the community.