Genotypic variation in a foundation tree drives ecological network structure

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Biological evolution occurs in the context of complex networks of interacting species in which natural selection defines the structure of ecological networks. Fundamental to this evolutionary process is the discovery of a genetic basis to ecological network structure. Although previous work has demonstrated that tree genotype contributes to interaction network structure at the scale of forest stands, the contribution of tree genetics to localized interaction networks at the scale of individual trees has not yet been explored. To test the degree to which tree genetics can contribute to network structure across scales from trees to stands, we conducted quantitative modeling of interaction network for a community of epiphytic lichens in a long-term experimental common garden of genotyped trees of a foundation species (*Populus angustifolia*). We found three main results: 1) Tree genotype strongly contributed to network structure explaining over a third of the variation in lichen interaction networks, 2) Multiple aspects of interaction network structure varied in response to genotype, including network size, the number of interactions, linkage density and connectance, 3) At the stand scale, we also found signficant modular structure of plant-lichen networks resulting in part from the combination of trees of the same genotype tending to have similar community compositions and supporting similar lichen interaction networks dominated by positive interactions. These results support the hypothesis that variation in ecological interaction networks can result from genetically based variation in foundation species. Although these results are for a community of sessile organisms in close proximity to the tree, this study opens the possibility for a genetic basis to both direct and indirect interactions among species in complex communities.

Keyword 1 | Keyword 2 | Keyword 3 | ...

Evolution occurs in the context of complex networks of interacting species. In ecological communities, community dynamics depend on key interactions (**?**) that occur in species interaction networks, such as: trophic (**?**) and mutualistic (**?**) interaction networks. Phylogenetic patterns in ecological networks support the importance of evolutionary processes in shaping species interactions, community structure and ecosystem processes (**? ? ?**). Community genetics studies (**?**) have shown that genetic variation in foundation species (**?**) plays a significant role in defining distinct communities of interacting organisms: such as, endophytes, pathogens, lichens, arthropods, and soil microbes. Multiple studies have now demonstrated that genetic variation influences numerous functional traits (e.g., phytochemical, phenological, morphological) produces a multivariate phenotype (**?**) tha contributes to variation in associated communities (**?**).

Additional work has provided support for the hypothesis that not only does composition vary among genetically distinct genotypes of foundation species but it also impacts the structure of the network of species interactions in these communities (**? ?**). Also, work by (**? ? ?**) observed consistent patterns of centralized interactions of species modules focused around hubs of plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have have disproportionate numbers of interactions with other species and likely are the drivers in determining community assembly, structure and dynamics.

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of lichen species. Using a long-term (20 years+), common garden experiment with replicated individuals of known genetic identity and a naturally established stand of *P. angustifolia*. We focused on a model community of 9 epiphytic lichens species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (**? ?**). In addition, the life-history characteristics of lichen, having highly localized, direct contact interactions and slow population turnover rates, allowed us to assess interactions among lichen species on individual trees. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (**? ? ? ? ?**). If correct, we should expect to find that network structure is genetically based in which different plant genotypes support different interaction networks and that these interactions networks can function as indicators of ecological dynamics important for conserving biodiversity. Applying a dual-scale (lichen-lichen and genotype-lichen interactions) network modeling and analyses, we then examined the genetically based impacts of *P. angustifolia* on network structure.

Significance Statement

Authors must submit a 120-word maximum statement about the significance of their research paper written at a level understandable to an undergraduate educated scientist outside their field of speciality. The primary goal of the Significance Statement is to explain the relevance of the work in broad context to a broad readership. The Significance Statement appears in the paper itself and is required for all research papers.
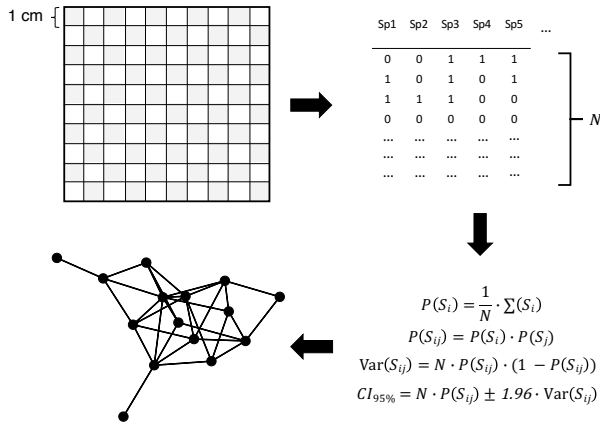

Materials and Methods

- Common garden
  - Cottonwoods in the west
  - Restoration site
  - Wild stand
- Lichen observations
  - Grid system
  - Two grids (upper and lower)
  - Lichen size distribution (dominant Xgal)
- Network modeling
  -
- Network metrics
- Statistical analyses and software

Field observations in common garden and natural riparian forest stands. The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled in order to avoid the effect of the hybridization between these two species.

A common garden was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated with each individual and spatial autocorrelation. Asexually propagated clones of genotyped *P. angustifolia* individuals were obtained from wild collections and planted randomly in a single field (0.025 km^2) at the Ogden Nature Center, Ogden, UT in 1992. A total of thirteen genotypes replicated between 3 and 8 times each, were chosen for sampling. Genotype names were previously published (**?**).

Observations were made in the common garden in October 2010 and May 2011.

$$P(S_i) = \frac{1}{N} \cdot \sum (S_i)$$
$$P(S_{ij}) = P(S_i) \cdot P(S_j)$$
$$\mathrm{Var}(S_{ij}) = N \cdot P(S_{ij}) \cdot (1 - P(S_{ij}))$$
$$CI_{95\%} = N \cdot P(S_{ij}) \pm 1.96 \cdot \mathrm{Var}(S_{ij})$$

Fig. 1. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 10 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying a null-model based procedure (**?**), we calculated and removed non-significant ($\alpha = 0.05$) co-occurrences to produce the network associated with an individual tree.

Make a figure of the field site and lichen on trees

Results

Primary Findings:

Interactions between lichens and trees depended on tree genotype

- abundance
- roughness predicted by genotype
- richness not predicted by genotype
- composition

Genotype-Lichen Interactions contributed to stand-level bipartite interaction network structure

- bipartite network structure different from random modularity
- for wild stand and garden

Lichen interaction network structure was genotype dependent

- unipartite network structure predicted by genotype

Interaction network structure was related to composition but not roughness

- unipartite correlation with community composition
- unipartite not predicted by roughness

Structural characteristics of networks were not predicted by genotype

- network statistics global level
- network statistics node level

Trees acted as environmental filters contributing to interaction
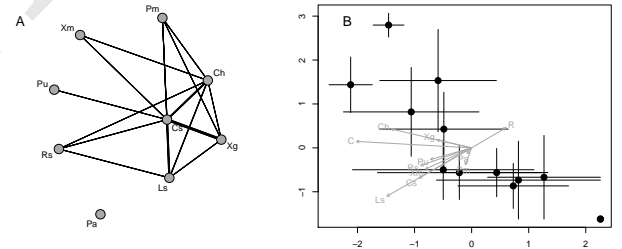Interaction network structure depending on tree genotype

Fig. 2. Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. A) A network diagram showing significant interactions averaged over all trees shown as edges connecting lichen species shown as vertices. B) Genotype centroids (points) of NMDS ordinated lichen networks ($\pm$ 1 S.E.). Arrows show the magnitude and direction of correlation of the ordinated networks with tree bark roughness (R), network connectance and lichen species abundances (Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rs = *Rinodina* (unknown species), Ls = *Lecanora* (unknown species), Pm = *Phyciella melanchra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*).

Response	Predictor	p-value	H2
Percent Lichen Cover	Tree Genotype	0.0396	0.17
Lichen Species Richness	Tree Genotype	0.1351	0.1
Percent Rough Bark	Tree Genotype	2e-04	0.38
Lichen Network	Genotype	0.0411	0.17
Number of Network Links	Genotype	0.0812	0.15
Network Centrality	Genotype	0.1299	0.12

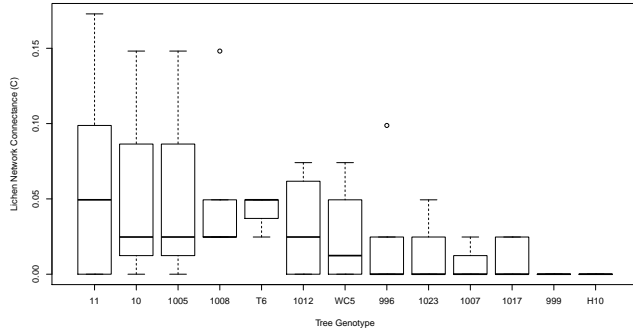**Table 1. Genotypic effects of cottonwood trees on the associated lichen community.**

Fig. 3. Connectance significantly varied among genotypes.

Discussion

Trait variation + assembly + ecosystem function

These findings support the hypothesis that genotypic variation in a foundation species contributes to the structure of a network of interacting species that might be least expected to exhibit such structure.

TGW: MIGHT BE GOOD TO CITE PAPERS ON COMPETTITION IN LICHENS OR OTHER ORGANIZING FACTORS TO BACK UP THE LEAST EXPECTED STATEMENT. AS EPIPHYTES WE MIGHT NOT EXPECT THEM TO CARE.

MKL: This is a job for Lamit and Rikke.

Several lines of evidence support this conclusion. First, the wild stand showed significant interaction network structure (Fig. 1a and b); and both tree genotype and the genetically based tree trait, bark roughness, was a strong predictor of co-occurrence patterns (Fig. 2a).

TGW: I THINK WE NEED TO EMPHASIZE THE LONG-TERM NATURE OF OUR COMMON GARDEN STUDY AS VERY FEW COMMON GARDEN STUDIES OF LICHENS LIKELY EXIST. ANY REFS ON THIS? IF TRUE MIGHT WANT TO MENTION THIS UP FRONT IN INTRO.

MKL: Same here. This is a job for Lamit and Rikke.

Second, in a long-term common garden study, network (Fig. 1b) structure showed a high degree of similarity to the wild stand network structure (Fig. 1c and d). Third, tree genotype was a significant predictor of SES values (Fig. 2a), displaying significant correlation with a genetically linked trait, bark roughness, both in the common garden (Fig. 2a) and in a naturally established stand of trees (Fig. 2b). Last, both of the bipartite genotype-species networks in the common garden and natural stand displayed significant modularity, suggesting that genotypic variation is leading to the formation of evolutionarily dynamic compartments within the community. Thus, just as numerous studies have shown that plant genotype can affect species richness, abundance, diversity, and composition and previous work has demonstrated that evolutionary processes shape ecological networks (**? ?**), our study includes genetics in an empirical investigation that combines both experimental common garden findings along with studies in the wild that are in close agreement.

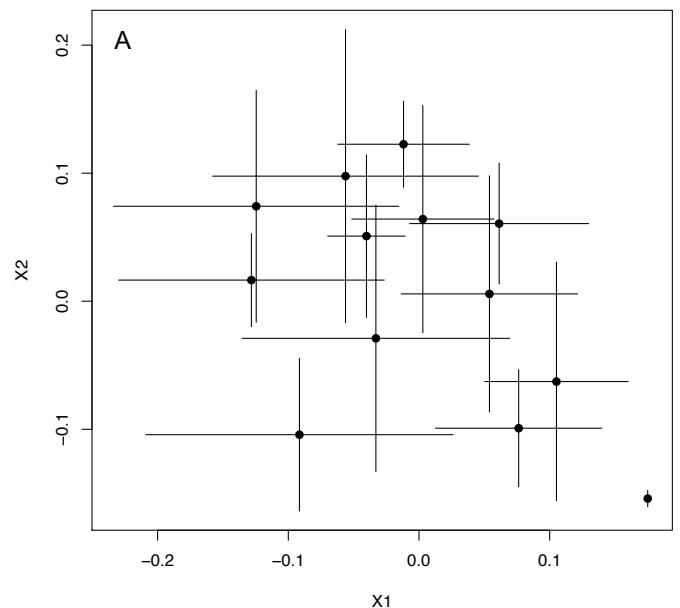Our results point to the importance of understanding the

Fig. 4. Tree genotype varition in lichen community composition also contributed to genotype-species bipartite intrreaction network structure at the scale of the common garden stand. A) Plot of the ordinated community composition scores shown as centroids ($\pm$ 1 S.E.). B) Bipartite interaction network based on the occurrences of lichen on individual cottonwood trees in the common garden. Edges connecting trees to lichen are scaled by the relative abundance of lichen. Nodes of lichen and trees are colored by their module membership.

community level effects of genetic variation and corroborate previous findings of the importance of plant genetics in shaping community structure and ecosystem processes (**?**). This study highlights the potential for indirect effects of genetic variation to propagate through networks of interacting species and trophic levels. Altering the structure of interaction networks presents a means for genetic effects to be magnified within the system of interacting species. For example, Keith et al. (2017) showed that the genetics based interations of aphid resistant and aphid susceptible trees resulted in different interaction networks of their associated arthropod communities composed of 139 species. At the scale of ecosystems, trophic networks or food webs direct and control the rates of energy and nutrient flux (**?**). Furthermore, in a predator-prey-plant study, Smith (**?**), showed that the interactions among species across trophic levels depended on plant genotype.

A. Units of evolutionary potential: Moving beyond species pairs. Although our study was conducted with a community of lichens, these results should be generalized to other groups of diverse organisms around the world that also exhibit significant genetic signals at the community level (**? ?**), although spatial scale of interactions should be considered (**?**) Bangert et al. 2006. As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (**?**). With such findings, it appears that we are closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.