

# Genotypic variation in a foundation tree directs ecological network structure

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1 **Biological evolution occurs in the context of complex networks of**  
2 **interacting species in which natural selection defines the structure**  
3 **of ecological networks. Fundamental to this evolutionary process**  
4 **is the discovery of a genetic basis to ecological network structure.**  
5 **Although previous work has demonstrated that tree genotype con-**  
6 **tributes to interaction network structure at the scale of forest stands,**  
7 **the contribution of tree genetics to localized interaction networks at**  
8 **the scale of individual trees has not yet been explored. To test the de-**  
9 **gree to which tree genetics can contribute to network structure, we**  
10 **conducted quantitative modeling of interaction network for a commu-**  
11 **nity of epiphytic lichens in a long-term experimental common garden**  
12 **of genotyped trees of a foundation species (*Populus angustifolia*).**  
13 **We found three main results: 1) bark roughness and lichen commu-**  
14 **nities displayed significant responses to tree genotype, 2) tree geno-**  
15 **type strongly contributed to network structure, explaining a third of**  
16 **the variation in lichen interaction networks, and 3) several metrics of**  
17 **interaction network structure varied in response to genotype, includ-**  
18 **ing the number of interactions and centralization. These results sup-**  
19 **port the hypothesis that variation in ecological interaction networks**  
20 **can result from genetically based variation in foundation species.**  
21 **This study opens the possibility for a genetic basis to both direct**  
22 **and indirect interactions among species in complex communities.**

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

1 **E**volution occurs in the context of complex networks of  
2 interacting species. In ecological communities, community  
3 dynamics depend on key interactions (1) that occur in  
4 species interaction networks, such as: trophic (2) and  
5 mutualistic (3) interaction networks. Phylogenetic patterns in  
6 ecological networks support the importance of evolutionary  
7 processes in shaping species interactions, community structure  
8 and ecosystem processes (13? ?). Community genetics  
9 studies (?) have shown that genetic variation in foundation  
10 species (4) plays a significant role in defining distinct communi-  
11 ties of interacting organisms: such as, endophytes, pathogens,  
12 lichens, arthropods, and soil microbes. Multiple studies have  
13 now demonstrated that genetic variation influences numerous  
14 functional traits (e.g., phytochemical, phenological, morpho-  
15 logical) produces a multivariate phenotype (5) that contributes  
16 to variation in associated communities (6).

17 Additional work has provided support for the hypothesis  
18 that not only does composition vary among genetically distinct  
19 genotypes of foundation species but it also impacts the struc-  
20 ture of the network of species interactions in these communities  
21 (? ?). Also, work by (? ? ?) observed consistent patterns  
22 of centralized interactions of species modules focused around  
23 hubs of plant-fungal interactions. In other words, a small  
24 number of plant and fungal symbionts tended to have have  
25 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 (7, 8). 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 (9? ? ? ?). 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.

## Materials and Methods

- 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.

## 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.

M.L. and L.L. conceived the study, M.L. and L.L. conducted the field work, R.N. assisted in lichen identifications, M.L. wrote the first draft of the manuscript, S.B. and T.W. contributed substantially to the conceptual development, T.W. established the common garden. All authors contributed to revisions of the manuscript.

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57 Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize,  
 58 only pure or advanced generation backcrosses of *P. angustifolia* were  
 59 sampled in order to avoid the effect of the hybridization between  
 60 these two species.

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

70 **Bark Lichen Observations.** On each tree, presence or absence of each  
 71 lichen species was assessed in 50 total  $1 \text{ cm}^2$  cells arrayed in a  
 72 checkerboard pattern. Sampling was restricted to the northern  
 73 aspect of the trunk to maximize the abundance of lichen and  
 74 control for the effect of trunk aspect. Two adjacent  $10 \text{ cm}^2$  quadrats  
 75 centered at 50 cm and 85 cm from ground level were sampled (Fig 1  
 76 A and B). The checkerboard sampling pattern was chosen to isolate  
 77 each cell based on an average thallus size of  $1 \text{ cm}^2$  (Supplementary  
 78 Materials). The thalli in each cell are expected to be spatially  
 79 independent of the other cells in the quadrat, but exposed to similar  
 80 micro-environmental conditions created by the bark and the location  
 81 of the sampling area on an individual tree. The bark lichen commu-  
 82 nity in this system is comprised of fourteen species; however, only 9  
 83 species were observed within our study quadrats (Fig 1 C-K). The  
 84 observed lichen community included (abbreviations are given for  
 85 species present in study): Xg = *Xanthomendoza galericulata*, Xm =  
 86 *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subde-  
 87 flexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Ls = *Lecanora*  
 88 sp., Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu =  
 89 *Physcia undulata*. Several other species were not obesrvd in the  
 90 present study but are known to occur in this region: *Phaeophyscia*  
 91 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia sublivacea*, *Meanelia*  
 92 *elegantula*. We were able to rapidly assess lichen interactions by  
 93 quantifying thallus in closed contact as assessed using  $1\text{cm}^2$  cells.  
 94 Species accumulation curves showed that communities in the wild  
 95 and the common garden were thoroughly sampled and with very  
 96 similar species richness (Supplementary Materials). As bark rough-  
 97 ness had previously been shown to be an important, genetically  
 98 based, tree trait impacting this lichen community, we measured the  
 99 percentage of rough bark on each tree following the methods of (? ).  
 100 Briefly, the number of cells containing disrupted, fissured bark were  
 101 counted within each quadrat on each tree. The number of rough  
 102 bark containing cells were then summed and divided by the total  
 103 number of cells surveyed.

104 **Lichen Network Modeling and Analysis.** We used the observations of  
 105 lichen in the  $1\text{cm}^2$  cells on individual trees of *P. angustifolia*. Uni-  
 106 partite networks were generated using the conditional probabilities  
 107 of each species pair, i.e. the probability of observing one species  
 108 given an observation of another species ( $P(A|B)$ ), based on the  
 109 method developed by (10). To calculate conditional probabilities,  
 110 we quantified the individual probabilities of species occurrences  
 111 ( $P(A)$ ) and the joint probability of co-occurrences ( $P(A, B)$ ) using  
 112 the frequencies of each species and their co-occurrences. We were  
 113 then able to calculate the conditional probabilities of each species  
 114 pair as  $P(A|B) = \frac{P(A,B)}{P(B)}$ , based on the axioms of probability. This  
 115 yielded an asymmetric matrix, that is  $P(A|B)$  does not have to be  
 116 equal to  $P(B|A)$  with a trace equal to the identity matrix (i.e.  
 $P(A|A) = 1$ ).

117 Once these network matrices were constructed using the condi-  
 118 tional probabilities of species pairs, we then applied an analytical  
 119 procedure to remove non-significant links between species (Fig. 2).  
 120 This procedure determines if the joint probability of a species  
 121 pair (i.e.  $P(S_i S_j)$ ) is different from zero. If the frequency of co-  
 122 occurrences ( $S_i S_j$ ) falls outside of the interval ( $CI_{95\%}$ ), the joint  
 123 probability is inferred to be non-zero. Here,  $CI_{95\%}$  is calculated  
 124 as as  $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$ , where the expected  
 125 frequency of co-occurrences ( $E(S_i S_j)$ ) is the total number of cells  
 126 surveyed ( $N$ ) times the independent probabilities of each species  
 127 ( $P(S_i) * P(S_j)$ ),  $Z_{95\%}$  is the Z-score for 95% from a Z-distribution

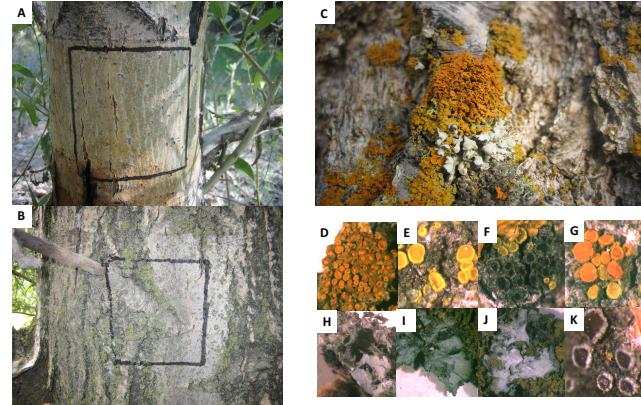


Fig. 1. The communities of bark lichen were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). Lichen were sampled within a fixed area ( $10\text{cm} \times 10\text{cm}$ ) on individual trees (A and B). (C) a photo of a typical community of bark lichen species interacting on the trunk of a cottonwood tree, including one of the more abundant species, *Xanthomendoza galericulata*, in the center. (D-K) shows the other main lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanachra*, *Physcia undulata* and *Lecanora hagenii*

and the expected variance of  $E(S_i S_j)$  is the total number of cells times the expected probability of  $S_i S_j$  and its compliment (i.e.  $V(S_i S_j) = N * E[P(S_i S_j)] * (1 - E[P(S_i S_j)])$ ). Since the conditional probability is calculated using the joint probability as the numerator, whenever the joint probability is determined to be zero the conditional probability is determined to also be zero, since  $P(S_i | S_j) = \frac{P(S_i S_j)}{P(S_j)} = \frac{0}{P(S_j)} = 0$ .

**Statistical Analyses, Software and Data.** We used a combination of parametric and non-parametric, permutation based frequentist statistical analyses to test for the effects of genetic variation on lichen communities and their interaction networks.

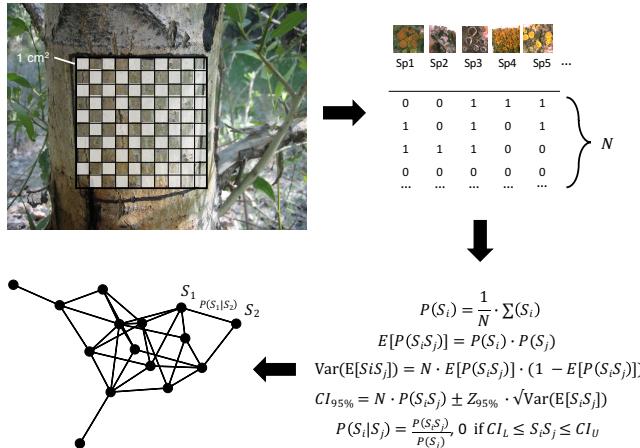
- REML
- Least squares models
- PerMANOVA
- Mantel tests
- Code and data available via github and zenodo

All analyses were conducted using the programming language R version 3.4.2 (R Development Core Team 2018).

## Results

Figure: Community composition NMDS with vectors

Bark roughness and some lichen community characteristics responded to tree genotype. Percent rough bark varied significantly among genotypes (REML RLRT = 10.69, p-value = 3e-04), as did total lichen cover (REML RLRT = 2.9627, p-value = 0.0375) and community composition (PerMANOVA R2 = 0.243, F 12 = 1.8221, p-value = 0.0029). However, lichen species richness did not show a significant response to genotype (REML RLRT = 0.13047, p-value = 0.3134). Community composition was correlated with lichen cover (PerMANOVA R2 = 0.236, F 1 = 21.2661, p-value = 9.99e-05) and richness (PerMANOVA spr.onc R2 = 0.054, F 1 = 4.9036, p-value = 0.0011) after controlling for tree genotype effects. Roughness did not predict community composition (PerMANOVA R2 = 0.011, F 1 = 0.9938, p-value = 0.3841) even though it was correlated with total lichen cover (ANOVA  $F_{1,55} = 6.797$ ,  $p - value = 0.01173$ ). Roughness was not correlated with lichen species richness (ANOVA  $F_{1,55} = 1.509$ ,  $p - value = 0.2246$ ).



**Fig. 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $10 \text{ cm}^2$  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 the probability-based network modeling method adapted from (10), we calculated the conditional probabilities,  $P(S_i | S_j)$ , for all species pairs and removed (i.e. set equal to zero) species pairs whose joint probabilities,  $P(S_i, S_j)$ , were not significant using a confidence interval based comparison of their observed co-occurrence frequency,  $S_i, S_j$ , to that expected due to chance alone,  $E[P(S_i, S_j)] = NP(S_i)P(S_j)$ .

165 **Tree genotype influenced lichen network similarity.** Figure: Genotype networks + Genotype network similarity by genotype  
166

We observed significant lichen network structure. Lichen species varied in their centralization in the networks with *C. subdeflexa* having the highest average centrality (0.93), followed by *Ca. holocarpa* (0.62). The centralization of the remaining species were *L. hagenii* (0.48), *X. galericulata* (0.23), *R. sp.* (0.21), *P. melanura* (0.09), *X. montana* (0.07) and *Ph. undulata* (0.02). *Physcia adscendens* was generally not connected to other species in the networks and had a centralization score of zero.

Lichen networks observed on trees of the same genotype tended to be similar in structure. Tree genotype significantly predicted the similarity of lichen interaction networks (PerMANOVA R<sup>2</sup> = 0.33795, F 12 = 2.5379, p-value = 0.0050). Lichen species richness was also a significant predictor of network similarity after controlling for genotype (PerMANOVA R<sup>2</sup> = 0.3413, F 1 = 2.5417, p-value = 0.007399); however, neither total cover (PerMANOVA R<sup>2</sup> = 0.023, F 1 = 2.0628, p-value = 0.1487) nor roughness (PerMANOVA R<sup>2</sup> = 0.011, F 1 = 0.0497, p-value = 0.3394) predicted network similarity and community similarity was not correlated with network similarity (Mantel Rho spearman = 0.012, p-value = 0.337).

These patterns of structural similarity among networks on similar genotypes could be partially explained by several networks. Tree genotype marginally predicted the number of links (REML RLRT = 2.0221, p-value = 0.0657) and centrality (REML RLRT = 2.0915, p-value = 0.0627) of lichen networks. Total cover was correlated with the number of links (ANOVA F 1 = 6.867, p-value = 0.0114) and centrality (ANOVA F 1 = 8.093, p-value = 0.0063). Lichen species richness was also correlated with the number of links (ANOVA F 1 = 29.436, p-value = 1.46e-06) and centrality (ANOVA F 1 = 39.488, p-value = 6.38e-08). Bark roughness, however, did not significantly predict the number of links (ANOVA F 1 = 2.897, p-value = 0.0946) nor the centrality (ANOVA F 1 = 2.591, p-value = 0.1134) of lichen networks. The number of network links (PerMANOVA R<sup>2</sup> = 0.392, F 1 = 72.4348, p-value = 0.001) and network centrality (PerMANOVA R<sup>2</sup> = 0.309, F 1 = 57.0440, p-value = 0.001) were highly correlated with network similarity.

**Figure: (A) Linkage and centrality by genotype and (B) Total cover and species richness predict L and Cen**

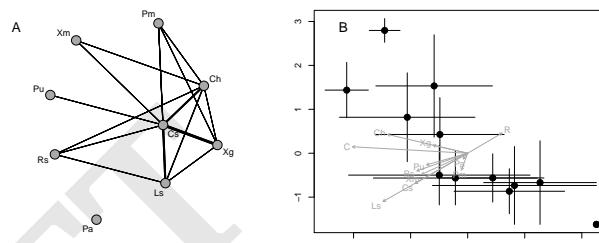
204 **Heritability estimates for lichen networks.** Table: heritability

- 205 • Compare all trait heritabilities

Response	H2	R2	p-value
Percent Rough Bark	0.37835	0.37835	4e-04
Lichen Network	0.2784	0.3413	0.0074
Percent Lichen Cover	0.17279	0.17279	0.0362
Number of Network Links	0.16892	0.16892	0.0689
Network Centrality	0.17248	0.17248	0.0627
Lichen Community Composition	0.08526	0.27703	0.09529
Network Modularity	0.04511	0.04511	0.2941
Lichen Species Richness	0.03578	0.03578	0.3137

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

Supplementary: Stats tables



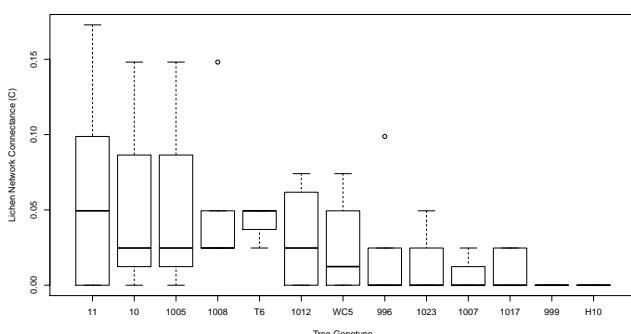
**Fig. 3.** Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. A) A network diagram showing significant interactions averaged over all trees shown as edges connecting lichen species shown as vertices. B) Genotype centroids (points) of NMDS ordinated lichen networks ( $\pm 1 \text{ S.E.}$ ). 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 melanura*, 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 2. Genotypic effects of cottonwood trees on the associated lichen community.**

208 **Discussion**

- Rehash of results support hypothesis of genetic basis to network structure
- Genotypic environmental filtering leads to altered interaction network structure and potentially dynamics
- Indirect effects of genotypes (G → rough → cover → richness → links → networks)
- Importance of indirect effects and complexity and relevance to IIGEs
- Conclusion



**Fig. 4.** Connectance significantly varied among genotypes.

#### 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 COMPEITION 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 (11, 12), 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 community level effects of genetic variation and corroborate previous findings of the importance of plant genetics in shaping

community structure and ecosystem processes (13). 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 interactions 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 (14). Furthermore, in a predator-prey-plant study, Smith (15), 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 (16, 17), although spatial scale of interactions should be considered (18) 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 (19). 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.

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