

# 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, commu-  
3 nity dynamics depend on key interactions (1) that occur in  
4 species interaction networks, such as: trophic (2) and mu-  
5 tualistic (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 (4–6).

More on ecological networks

10 Community genetics studies (?) have shown that genetic  
11 variation in foundation species (7) plays a significant role in  
12 defining distinct communities of interacting organisms: such as,  
13 endophytes, pathogens, lichens, arthropods, and soil microbes.  
14 Multiple studies have now demonstrated that genetic variation  
15 influences numerous functional traits (e.g., phytochemical, phe-  
16 nological, morphological) produces a multivariate phenotype  
17 (8) that contributes to variation in associated communities (9).

18 Additional work has provided support for the hypothesis  
19 that not only does composition vary among genetically distinct  
20 genotypes of foundation species but it also impacts the struc-  
21 ture of the network of species interactions in these communities  
22 (? ?). Also, work by (10 ? ?) observed consistent patterns  
23 of centralized interactions of species modules focused around  
24 hubs of plant-fungal interactions. In other words, a small  
25 number of plant and fungal symbionts tended to have have

disproportionate numbers of interactions with other species  
26 and likely are the drivers in determining community assembly,  
27 structure and dynamics.

28 Here, we investigate how genetic variation in a foundation  
29 tree species determines the structure of a network of inter-  
30 actions among a community of tree associated lichen species.  
31 Using a long-term (20+ years), common garden experiment  
32 with replicated individuals of known genetic identity and a  
33 naturally established stand of *Populus angustifolia*. We fo-  
34 cused on a model community of 9 epiphytic lichens species,  
35 as previous research has demonstrated significant compo-  
36 sitional responses of epiphytes to genotypic variation (11, 12).  
37 In addition, the life-history characteristics of lichen, having  
38 highly localized, direct contact interactions and slow popula-  
39 tion turnover rates, allowed us to assess interactions among  
40 lichen species on individual trees. We hypothesize that in natu-  
41 ral systems evolution occurs in a community context involving  
42 interactions of complex networks of interacting species (13)?  
43 ? ? ? . If correct, we should expect to find that network  
44 structure is genetically based in which different plant geno-  
45 types support different interaction networks and that these  
46 interactions networks can function as indicators of ecological  
47 dynamics important for conserving biodiversity. Applying  
48 a probability-theory based network modeling approach, we  
49 constructed a set of interaction network models for the lichen  
50 associated with individual trees. Using these models, we then  
51 examined the genetic basis a foundation tree species on the  
52 structure of ecological networks.

## Materials and Methods

54 The study was conducted along the Weber River, UT (USA),  
55 which is a cottonwood (*Populus* spp.) dominated riparian ecosystem.  
56

## Significance Statement

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

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

68 The authors have no conflicts of interest.

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58 Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize,  
 59 only pure or advanced generation backcrosses of *P. angustifolia* were  
 60 sampled in order to avoid the effect of the hybridization between  
 61 these two species (?). Bark lichen have been extensively study  
 62 in this system previously, and provide an ideal system in which  
 63 to observe and model lichen interaction networks, as their sessile  
 64 nature permits accurate identification of individuals (? ? ?).

65 A long-term, common garden experiment was used to isolate the  
 66 effect of tree genotype from the effect of the localized microenvironment  
 67 associated with each individual and spatial autocorrelation.  
 68 Established in 1992, asexually propagated clones of genotyped *P.*  
 69 *angustifolia* individuals were obtained from wild collections and  
 70 planted randomly in a single field ( $0.025 \text{ km}^2$ ) at the Ogden Nature  
 71 Center, Ogden, UT. From the population of established individuals  
 72 in the common garden, we chose a total of thirteen genotypes,  
 73 replicated between 3 and 8 times each, for sampling. In this study,  
 74 we use the genotype notations previously published in (?).

75 **Bark Lichen Observations.** On each tree, presence or absence of  
 76 each lichen species was assessed in 50 total  $1 \text{ cm}^2$  cells arrayed in  
 77 a checkerboard pattern. Given the small size and sessile nature of  
 78 lichen, we were able to rapidly assess lichen interactions by  
 79 quantifying thalli in close contact. Sampling was restricted to  
 80 the northern aspect of the trunk to maximize the abundance of  
 81 lichen and control for the effect of trunk aspect. Two adjacent  
 82  $10 \text{ cm}^2$  quadrats centered at 50 cm and 85 cm from ground level  
 83 were sampled (Fig 1 A and B). The bark lichen community in this  
 84 system is comprised of fourteen species; however, only 9 species  
 85 were observed within our study quadrats (Fig 1 C-K). The observed  
 86 lichen community included (abbreviations are given for species  
 87 present in study): Xg = *Xanthomendoza galericulata*, Xm = *X.*  
 88 *montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*,  
 89 Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Ls = *Lecanora*  
 90 sp., Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu =  
 91 *Physcia undulata*. Several other species were not observed in the  
 92 present study but are known to occur in this region: *Phaeophyscia*  
 93 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia sublivacea*, *Meanelia*  
 94 *elegantula*. Species accumulation curves indicated that communities  
 95 in the the common garden were thoroughly sampled and similar in  
 96 composition and richness to nearby naturally established cottonwood  
 97 stands (Supplementary Materials).

98 The cell size and checkerboard sampling pattern was chosen to  
 99 isolate the individuals in each cell. In a previous survey of lichen  
 100 thallus size in this common garden, we had observed a median thallus  
 101 size of  $0.12 \pm 0.001 \text{ cm}^2$  (S.E.) (?). Based on this, we expected  
 102 thalli observed in each cell to generally be spatially independent  
 103 of the other cells in the quadrat but exposed to similar micro-  
 104 environmental conditions created by the bark and the location of the  
 105 sampling area on an individual tree. Therefore, we were confident  
 106 in treating the cell-wise observations in quadrats as independent  
 107 with respect to lichen-lichen interactions.

108 As bark roughness had previously been shown to be an important,  
 109 genetically based tree trait impacting bark lichen, we measured the  
 110 percentage of rough bark on each tree following the methods of (?).  
 111 Briefly, the number of cells containing disrupted, fissured bark  
 112 were counted within each quadrat on each tree. The number of  
 113 rough bark containing cells were then summed and divided by the  
 114 total number of cells surveyed. This was done for all quadrats on  
 115 all trees in which lichen communities were also observed.

116 **Lichen Network Modeling and Analysis.** We used the observations of  
 117 lichen in the  $1\text{cm}^2$  cells on individual trees of *P. angustifolia*. Uni-  
 118 partite networks were generated using the conditional probabilities  
 119 of each species pair, i.e. the probability of observing one species  
 120 given an observation of another species  $P(S_i|S_j)$ , based on the  
 121 method developed by (14). To calculate conditional probabilities,  
 122 we quantified the individual probabilities of species occurrences  
 123  $P(S_i)$  and the joint probability of co-occurrences  $P(S_i, S_j)$  using  
 124 the frequencies of each species and their co-occurrences. We were  
 125 then able to calculate the conditional probabilities of each species  
 126 pair as  $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$ , based on the axioms of probability.  
 127 This yielded an asymmetric matrix, that is  $P(S_i|S_j)$  does not have  
 128 to be equal to  $P(S_j|S_i)$ , that also had a diagonal  $S_{ii}$  equal to one

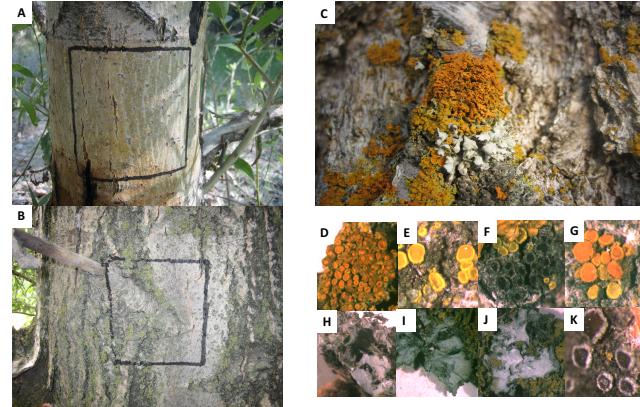
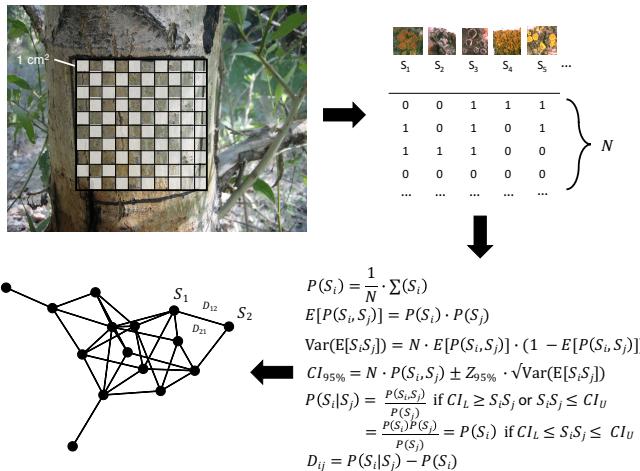


Fig. 1. The communities of bark lichen were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). Lichen were sampled within a fixed area (10cm by 10cm) on individual trees (A and B). (C) a photo of a typical community 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*.

130 for all species present and zero for species that were not observed  
 131 on the tree.

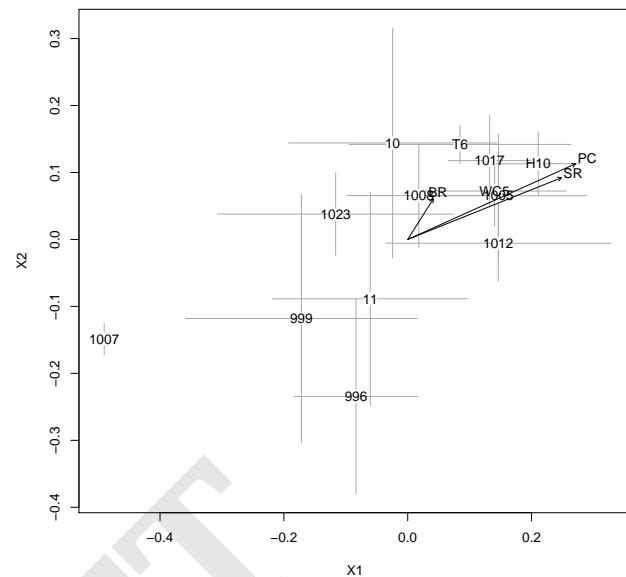
132 We then applied an analytical procedure to remove non-  
 133 significant links between species. This procedure determines if  
 134 the joint probability of a species pair (i.e.  $P(S_i, S_j)$ ) is different  
 135 from zero (Fig. 2). Here, a confidence interval  $CI_{95\%}$  is calculated  
 136 as  $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$ , where the expected  
 137 frequency of co-occurrences  $E(S_i S_j)$  is the total number of cells  
 138 surveyed ( $N$ ) times the independent probabilities of each species  
 139  $P(S_i) * P(S_j)$ ,  $Z_{95\%}$  is the Z-score for 95% from a Z-distribution  
 140 and the expected variance of  $E(S_i S_j)$  is the total number of cells  
 141 times the expected probability of  $S_i S_j$  and its compliment (i.e.  
 142  $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$ ). If the observed  
 143 number of co-occurrence falls outside of the confidence interval,  
 144 the joint probability  $P(S_i, S_j)$  is determined to be equal to the  
 145 product of the individual probabilities (i.e.  $P(S_i)P(S_j)$ ), and the  
 146 conditional probability reduces to the individual probability of that  
 147 species  $P(S_i)$ . Therefore, unless the co-occurrence of a species  
 148 pair falls outside the confidence interval, the probability that the  
 149 observation of one species given the other is no different than  
 150 simply observing that species alone. This enables us to remove  
 151 links from a given network by re-scaling the resulting conditional  
 152 probabilities by subtracting the individual probabilities from the  
 153 conditional probabilities (i.e. how different the conditional probabili-  
 154 ty is from the independent probability), which makes any species  
 155 with a non-significant conditional probability zero. The resulting  
 156 matrix ( $\mathbf{D} = D_{ij}$ ) can be interpreted as how one species impacts  
 157 another with zero being no effect and values less than or greater  
 158 than zero interpreted as negative and positive effects, respectively.  
 159 Here, we will refer to this matrix ( $\mathbf{D}$ ) as an interaction matrix with  
 160 the properties that it can be assymetric (i.e.  $P_{ij}$  does not necessarily  
 161 equal  $P_{ji}$ ), and the diagonal ( $P_{ii}$ ) is zero (i.e. a species does not  
 162 influence it's own probability of being observed).

163 **Statistical Analyses, Software and Data.** We used a combination of  
 164 parametric and non-parametric, permutation based frequentist stat-  
 165 tistical analyses to test for the effects of genetic variation on lichen  
 166 communities and their interaction networks. To assess the effect of  
 167 genotype on univariate responses, we used additive, random effects  
 168 models with Restricted Maximum Likelihood (REML). We used  
 169 a combination of Least Squares Regression, Analysis of Variance  
 170 (ANOVA) and correlation tests to quantify and test for the rela-  
 171 tionship among other variables. Bark roughness, lichen cover and  
 172 species richness were square-root transformed to meet the assump-  
 173 tions of heterogeneity of variance and heteroskedasticity for these



**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 (14), 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,  $S_iS_j$ , to that expected due to chance alone,  $E[P(S_i,S_j)] = P(S_i)P(S_j)$ , and  $P(S_i|S_j)$  reduces to  $P(S_i)$ , the observed individual probability of species  $S_i$ .

## Results



**Fig. 3.** Lichen community composition varied among genotypes. Plot of the ordinated centroids ( $\pm 1\text{ S.E.}$ ) from the NMDS ordinated community composition of each genotype (indicated by centroid labels). Centroids that are closer together have more similar lichen communities. Arrows show the direction and magnitude of correlation between bark roughness (BR), percent lichen colonization (PC) and lichen species richness (SR) and the ordinated community scores.x

tests. For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PerMANOVA) and Mantel tests. For all analyses, community composition was relativized by species maxima to reduce the effect of the highly abundant *X. galericulata*. For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (?) to produce dimensionally reduced ordinations of these multi-variate responses and fitted vectors for continuous predictor variables to the ordinated values (?). For community composition we used Bray-Curtis dissimilarity, which has optimal performance with count data (?). To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the  $\mathbf{D}$  interaction matrices among all pairs of trees.

For each network, we also calculated two network metrics that measure different structural aspects. We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (?). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (?). In a network with a low level of centralization species have similar amount of interaction in the network, while a network with a high level of centralization tends to one or small subset of species that interact with other species. We used a related function to calculate the centrality of each species in each network as well. Although there are many other metrics, see (?), we focus on a subset for the sake of simplicity and because some metrics are not appropriate for our relatively small communities. In particular, we do not present analysis of the modularity (i.e. the degree of sub-grouping) because our community has relatively few species to form modules. As with the other response variables, the number of links was log-transformed and centralization scores were square-root transformed to meet variance and normality assumptions.

We have made all code and data available online. Code is available at [github.com/communitygenetics/lcn](https://github.com/communitygenetics/lcn). Data is available via the Harvard Dataverse (needs project ID). The project is also archived via Zenodo at [zenodo.com/doi/XXXXXX](https://zenodo.com/doi/XXXXXX). All analyses were conducted using the programming language R version 3.4.2 (R Development Core Team 2018).

Bark roughness and lichen communities responded to tree genotype. Percent rough bark varied significantly among genotypes (REML  $R^2 = 0.378$ , RLRT = 10.69, p-value = 0.0001), as did total lichen cover (REML  $R^2 = 0.172$ , RLRT = 2.9627, p-value = 0.0375). However, lichen species richness did not show a significant response to genotype (REML  $R^2 = 0.0981$ , RLRT = 1.0001, p-value = 0.1366). Community composition was also affected by tree genotype (PerMANOVA  $R^2 = 0.243$ , F 12 = 1.8221, p-value = 0.0029). In addition, community composition was correlated with bark roughness (PerMANOVA  $R^2 = 0.039$ ,  $F_1 = 3.7408$ , p-value = 0.0064), lichen cover (PerMANOVA  $R^2 = 0.342$ ,  $F_1 = 32.8482$ , p-value = 0.0001) and lichen species richness (PerMANOVA  $R^2 = 0.069$ ,  $F_1 = 6.5958$ , p-value = 0.0002) (Fig. 3). However, after controlling for the effect of tree genotype on community composition, bark roughness did not significantly predict community composition (PerMANOVA  $R^2 = 0.011$ ,  $F_1 = 0.9938$ , p-value = 0.3841) but lichen cover (PerMANOVA  $R^2 = 0.236$ ,  $F_1 = 21.2661$ , p-value = 0.0001) and lichen species richness (PerMANOVA  $R^2 = 0.054$ ,  $F_1 = 4.9036$ , p-value = 0.0011) were still significantly correlated with lichen composition.

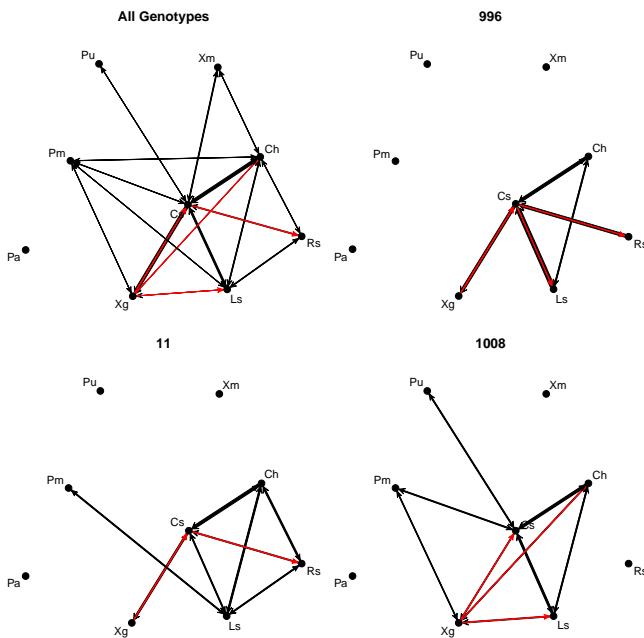
**Tree genotype influenced lichen network similarity.** We observed significant lichen network structure. This structure varied among genotypes (Fig. 4) and lichen species varied in their importance in the network. *Candaleriella subdeflexa* was generally the most central species (i.e. being the most highly connected) having the highest average centrality (0.73), followed by *Ca. holocarpa* (0.54) and *L. hagenii* (0.40). The centralization of the remaining species were *R. sp.* (0.18), *X. galericulata* (0.14), *P. melanura* (0.08), *X. montana* (0.06) 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  $R^2 = 0.33795$ , F 12 = 2.5379, p-value = 0.0050). Bark roughness

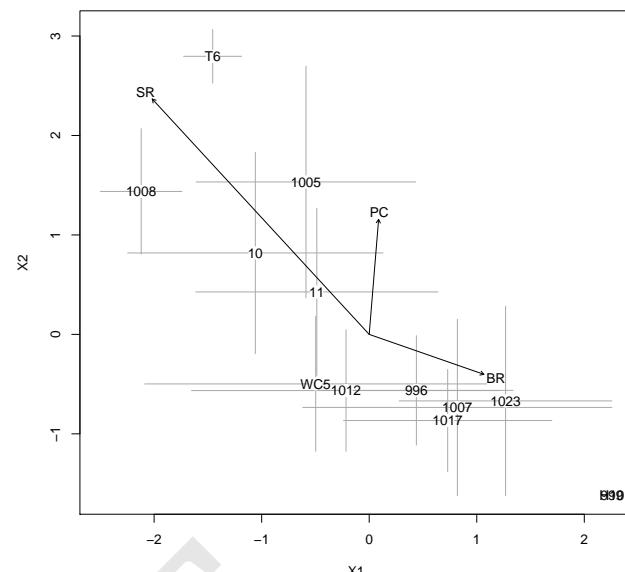
tests. For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PerMANOVA) and Mantel tests. For all analyses, community composition was relativized by species maxima to reduce the effect of the highly abundant *X. galericulata*. For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (?) to produce dimensionally reduced ordinations of these multi-variate responses and fitted vectors for continuous predictor variables to the ordinated values (?). For community composition we used Bray-Curtis dissimilarity, which has optimal performance with count data (?). To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the  $\mathbf{D}$  interaction matrices among all pairs of trees.

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**Fig. 4.** Lichen networks varied in structure among genotypes. Network diagrams of the mean lichen interaction matrices (i.e.  $\mathbf{D}$ ) averaged for all trees and for several individual genotypes showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species (abbreviated by the first letter of the genus and specific epithet), which are scaled by their magnitude.



**Fig. 5.** Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. The plot shows genotype centroids of NMDS ordinated lichen networks ( $\pm 1$  S.E.). Centroids that are closer are more similar in the structure of their lichen networks. Arrows show the magnitude and direction of correlation of the ordinated networks with tree bark roughness (BR), percent cover of lichens (PC) and lichen species richness (SR).

Response	H2	R2	p-value
Percent Rough Bark	0.37835	0.37835	1e-04
Network Centrality	0.20166	0.20166	0.04076
Percent Lichen Cover	0.17279	0.17279	0.033
Number of Network Links	0.17016	0.17016	0.06602
Lichen Community Composition	0.16093	0.24287	0.0029
Lichen Species Richness	0.09815	0.09815	0.14
Lichen Network	0.06252	0.29111	0.0094
Network Modularity	0.05731	0.05731	0.2809

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

- 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

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 COMEPTITION IN LICHENS OR OTHER ORGANIZING FACTORS TO BACK UP THE LEAST EXPECTED STATEMENT. AS EPIPHYTES WE MIGHT NOT EXPECT THEM TO CARE.**

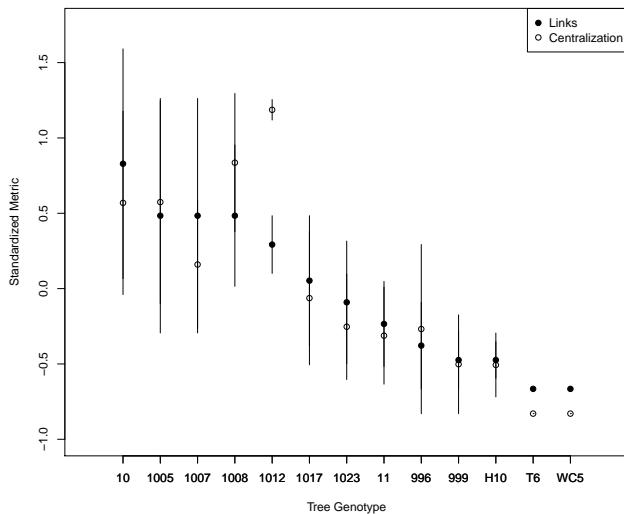
(PerMANOVA  $R^2 = 0.040$ ,  $F_1 = 4.1680$ , p-value = 0.03770) and lichen species richness (PerMANOVA  $R^2 = 0.424$ ,  $F_1 = 44.5034$ , p-value = 9.999e-05) were significant predictors of lichen network similarity, while total lichen cover was a weak, marginally significant predictor (PerMANOVA  $R^2 = 0.032$ ,  $F_1 = 3.3573$ , p-value = 0.06779). However, after controlling for the effect of tree genotype on lichen network similarity, only species richness was a significant predictor of lichen network similarity (PerMANOVA  $R^2 = 0.300$ ,  $F_1 = 33.3755$ , p-value = 0.00001), and neither bark roughness (PerMANOVA  $R^2 = 0.019$ ,  $F_1 = 2.0858$ , p-value = 0.14699) nor lichen cover (PerMANOVA  $R^2 = 0.019$ ,  $F_1 = 2.1504$ , p-value = 0.14409) were significant predictors. Community similiarty was not correlated with network similiarity (Mantel Rho spearman = 0.092, p-value = 0.09500).

(Fig. 5).

The observed genotypic patterns of network similarity could be summarize by several network metrics. The number of links (PerMANOVA  $R^2 = 0.392$ , F 1 = 72.4348, p-value = 0.001) and network centrality (PerMANOVA  $R^2 = 0.309$ , F 1 = 57.0440, p-value = 0.001) were highly correlated with network similarity. Tree genotype singificantly predicted network centrality (REML  $R^2 = 0.202$ , RLRT = 2.7801, p-value = 0.04012) but marginally predicted the number of links (REML  $R^2 = 0.170$ , RLRT = 2.0484, p-value = 0.065) (Fig. 6). 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.

## Discussion

- Rehash of results support hypothesis of genetic basis to network structure



**Fig. 6.** The impact of tree genotype on lichen network structure was indicative of variation in both the number variation in lichen interactions among species. This Cleveland plot shows the means ( $\pm 1$  S.E.) for lichen network metrics (number of links and centralization) for each genotype. Both metrics are presented as standardized scores ( $\frac{x-\bar{x}}{\sigma}$ ).

#### 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 (15, 16), 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 (6). 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 (17). Furthermore, in a predator-prey-plant study, Smith (18), 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 (19, 20), although spatial scale of interactions should be considered (21) 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 (22). 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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