

# Genotypic variation in a foundation tree alters ecological network structure of an associated community

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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**  
8 **at the scale of individual trees has not yet been explored. To test**  
9 **the degree to which tree genetics can contribute to network struc-**  
10 **ture we conducted quantitative modeling of interaction networks. We**  
11 **constructed networks of epiphytic lichen associated with individual**  
12 **trees that were a part of a long-term experimental common garden**  
13 **of genotypes of (*Populus angustifolia*), a foundation species. We**  
14 **found three main results. First, tree genotype significantly predicted**  
15 **lichen network similarity, i.e. trees of the same genotype had more**  
16 **similar lichen networks. Second, positive interactions of one lichen**  
17 **species, *Caloplaca holocarpa* drove the genetically based variation**  
18 **in network structure. Third, bark roughness was both predicted by**  
19 **tree genotype and correlated with lichen network similarity. We con-**  
20 **clude that tree genotype can influence not only the relative abun-**  
21 **dances of organisms but also the interaction network structure of**  
22 **associated organisms. Given that variation in network structure can**  
23 **have consequences for the dynamics of communities through alter-**  
24 **ing the stability of the system and modulating or amplifying perturba-**  
25 **tions, these results have important implications for the evolutionary**  
26 **dynamics of ecosystems.**

networks | heritability | community | genetics | lichen | cottonwood |  
*Populus* | common garden

1 **E**volution occurs in the context of complex eco-  
2 logical networks. Initially, evolution in a com-  
3 munity context was focused on examples of highly  
4 co-evolved pairs of species (e.g. Darwin's famous  
5 prediction of the Sphinx Moth and Christmas Or-  
6 chid) (1). However, studies of diffuse co-evolution  
7 (*sensu* (2)) (3, 4), geographic mosaics of co-evolution  
8 (5) and community genetics (6) have provided an  
9 in-road for ecological network approaches (7–9) to  
10 illuminate a more complex perspective of the inter-  
11 face between ecological and evolutionary dynamics.  
12 There is now evidence to support that selection tends  
13 to occur among groups of species (1) favoring the  
14 development of small webs (10, 11) and that genetic

15 variation and phylogenetic relatedness contributes  
16 to variation in community assembly (12) and species  
17 interactions (6, 13, 14), which shapes the ecological  
18 interaction networks (15).

19 Community genetics studies (16) have shown that  
20 genetic variation in foundation species (17) plays a  
21 significant role in defining distinct communities of in-

## Significance Statement

Evolution occurs in the context of ecosystems com-  
prised of complex ecological networks. Research at  
the interface of ecology and evolution has primarily  
focused on pairwise interactions among species and  
have rarely included a genetic component to anal-  
yses. Here, we use a long-term common garden  
experiment to reveal the effect that genotypic varia-  
tion can have on networks of lichens that occur on  
the bark of a foundation tree species. We found that  
lichen interaction network structure is genetically  
based and primarily driven by a tree trait, bark rough-  
ness. These findings demonstrate the importance  
of genetic variation and evolutionary dynamics in  
shaping ecological networks as evolved traits. In  
particular, this study points to the importance of as-  
sessing the effect of foundation species genetics on  
the structure of interactions, given that interaction  
network structure has systems-level properties that  
could affect the response of these communities to  
selection.

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 substantively to the conceptual development, T.W. established the common garden. All authors contributed to revisions of the manuscript.

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teracting 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 (18) that contributes to variation in associated communities (13). The importance of genetic variation in structuring ecological systems was recently reviewed (19), and not only were many instances of strong genetic effects found in many ecosystems but the effect of intraspecific variation was at times greater than *inter-specific* variation.

Additional work has provided support for the hypothesis that not only does composition vary among genetically distinct genotypes of foundation species but that it also impacts the structure of species interactions. However, studies in the network ecology literature generally do not include a genetic component (20); and, community genetics studies have primarily focused on community composition in terms of the abundance of species (19). Multiple studies from different plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) have examined the effect of genetic variation on trophic interactions (7, 21–24) and generally found that increasing genotypic diversity leads to increased trophic complexity. Similarly, two other studies have examined the effect of genotypic variation on the structure of interactions between tree individuals and the associated community (8, 25) and both found that genotypic diversity generates increased network modularity (i.e. compartmentalization).

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of tree associated lichen species. Previous studies have examined aspects of networks (26). Here we examine the genetic basis of network structure on a community of sessile lignicolous (i.e. bark) lichen on cottonwood trees. Using a long-term (20+ years), common garden experiment with replicated individuals of known genetic identity and a naturally established stand of *Populus angustifolia*. We focused on a model community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (27, 28). In addition, the life-history characteristics of lichens, 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 (5, 8, 25, 29). If correct, we 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 probability-theory based network modeling approach, we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks. Based on previous community genetics studies, particularly (30) which proposed the community similarity rule, we hypothesize that trees will vary in some phenotypic traits and those trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure.

## Materials and Methods

**Study System.** 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. Bark lichens have been extensively studied in this system and provide an ideal system in which to observe and model lichen interaction networks, as their sessile nature permits accurate identification of individuals (31).

A long-term, common garden experiment was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated with each individual and spatial autocorrelation. Established in 1992, asexually propagated clones of genotyped *P. angustifolia* individuals were obtained from wild collections and planted in fully randomized design at the Ogden Nature Center, Ogden, UT. From the population of established individuals in the common garden, we chose a total of thirteen genotypes, replicated between 3 and 8 times each, for sampling.

**Bark Lichen and Trait Observations.** On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm<sup>2</sup> cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens, we were able

121 to rapidly assess lichen interactions by quantifying thalli  
 122 in close contact. Sampling was restricted to the northern  
 123 aspect of the trunk to maximize the abundance of lichen  
 124 and control for the effect of trunk aspect. Two adjacent 10  
 125 cm<sup>2</sup> quadrats centered at 50 cm and 85 cm from ground  
 126 level were sampled (Fig 1 A and B). The observed lichen  
 127 community included (abbreviations are given for species  
 128 present in study): Xg = *Xanthomendoza galericulata*, Xm  
 129 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were  
 133 not observed in the present study but are known to occur  
 134 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegantula*.

136 The cell size and checkerboard sampling pattern was  
 137 chosen to isolate the individuals in each cell. In a previous  
 138 survey of lichen thallus size in this common garden, we  
 139 had observed a median thallus size of  $0.12 \pm 0.001$  cm<sup>2</sup> (1  
 140 S.E.) (see Supporting Information). Based on the median  
 141 thallus size, we expected thalli observed in each cell to  
 142 generally be spatially independent of thalli present in  
 143 other cells but exposed to similar micro-environmental  
 144 conditions created by the bark and the location of the  
 145 sampling area on an individual tree. Therefore, we were  
 146 confident in treating the cell-wise observations in quadrats  
 147 as independent with respect to lichen-lichen interactions.

148 We also measured several bark traits for each tree:  
 149 including, bark roughness, condensed tannin, carbon and  
 150 nitrogen concentrations and pH. **ADD METHODS  
 151 FROM JAMIE.**

152 **Lichen Network Modeling and Analysis.** For each tree,  
 153 repeated observations of lichen were made in order to con-  
 154 struct replicated interaction networks for each genotype.  
 155 We quantified the presence of lichen in the 1 cm<sup>2</sup> cells on  
 156 individual trees of *P. angustifolia*. Unipartite networks  
 157 were generated using the conditional probabilities of each  
 158 species pair, i.e. the probability of observing one species  
 159 given an observation of another species  $P(S_i|S_j)$ , based on  
 160 the method developed by (32). To calculate conditional  
 161 probabilities, we quantified the individual probabilities  
 162 of species occurrences  $P(S_i)$  and the joint probability  
 163 of co-occurrences  $P(S_i, S_j)$  using the frequencies of each  
 164 species and their co-occurrences. We were then able to  
 165 calculate the conditional probabilities of each species pair  
 166 as  $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$ , based on the axioms of probability.  
 167 This yielded a matrix that could possibly be asymmetric, i.e.  
 168  $P(S_i|S_j)$  does not have to be equal to  $P(S_j|S_i)$ . Another  
 169 important property of this matrix is that the diagonal  
 170 ( $S_{ii}$ ) was equal to one for all species present and zero for  
 171 species that were not observed in any cell.

172 We then applied an analytical procedure to remove  
 173 non-significant links between species. This procedure  
 174 determines if the joint probability of a species pair  
 175 (i.e.  $P(S_i, S_j)$ ) is different from zero (Fig. 2). Here, a

176 confidence interval  $CI_{95\%}$  is calculated as  $CI_{95\%} =$   
 177  $E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$ , where the expected fre-  
 178 quency of co-occurrences  $E(S_i S_j)$  is the total number  
 179 of cells surveyed ( $N$ ) times the independent probabili-  
 180 ties of each species  $P(S_i) * P(S_j)$ ,  $Z_{95\%}$  is the Z-score  
 181 for 95% from a Z-distribution and the expected vari-  
 182 ance of  $E(S_i S_j)$  is the total number of cells times the  
 183 expected probability of  $S_i S_j$  and its compliment (i.e.  
 184  $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$ ). If the  
 185 observed number of co-occurrence falls outside of the  
 186 confidence interval, the joint probability  $P(S_i, S_j)$  is de-  
 187 termined to be equal to the product of the individual  
 188 probabilities (i.e.  $P(S_i) \bar{P}(S_j)$ ), and the conditional prob-  
 189 ability reduces to the individual probability of that species  
 190  $P(S_i)$ . Therefore, unless the co-occurrence of a species  
 191 pair falls outside the confidence interval, the probabili-  
 192 ty that the observation of one species given the other  
 193 is no different than simply observing that species alone.  
 194 This enables us to remove links from a given network by  
 195 re-scaling the resulting conditional probabilities by sub-  
 196 tracting the individual probabilities from the conditional  
 197 probabilities (i.e. how different the conditional probability  
 198 is from the independent probability), which makes any  
 199 species with a non-significant conditional probability zero.  
 200 The resulting matrix ( $\mathbf{D} = D_{ij}$ ) can be interpreted as  
 201 how one species impacts another with zero being no effect  
 202 and values less than or greater than zero interpreted as  
 203 negative and positive effects, respectively. Here, we will  
 204 refer to this matrix ( $\mathbf{D}$ ) as an interaction matrix with  
 205 the properties that it can be asymmetric (i.e.  $P_{ij}$  does not  
 206 necessarily equal  $P_{ji}$ ), and the diagonal ( $P_{ii}$ ) is zero (i.e.  
 207 a species does not influence its own probability of being  
 208 observed).

209 **Network Metrics.** To quantify the structural variation of  
 210 lichen networks we calculated several metrics at both  
 211 the node and whole-network level. For individual nodes  
 212 (i.e. species) in each network, we calculated both the  
 213 degree Eq. (1) and the centrality. We also calculated two  
 214 similar global network metrics: degree and centralization.  
 215 The first was network degree, which is a count of the  
 216 total number of links in a network. As the networks  
 217 contained not only positive and negative connections,  
 218 as well as directional connections (both in-coming and  
 219 out-going), we calculated the same network metrics for  
 220 all combinations of these types of connections in each  
 221 network. Although there are many more possible network  
 222 metrics that could have been examined, we chose to focus  
 223 on a restricted set for the sake of clarity. Also, degree and  
 224 centrality form the basis of many other network metrics.

#### 225 ADD EQUATIONS FOR METRICS

$$226 \sum x_i [1]$$

- 227 • Node degree
- 228 • Node centrality



**Fig. 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). Lichens were sampled within a fixed area ( $10 \text{ cm}^2$ ) on individual trees at two heights, 40cm and 80cm from the ground (A and B, respectively). (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 lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanchra*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (A-C) and R.R. Naesbourg (D-K).

- 229 • Network degree
- 230 • Centralization
- 231 • In vs out
- 232 • Pos vs neg

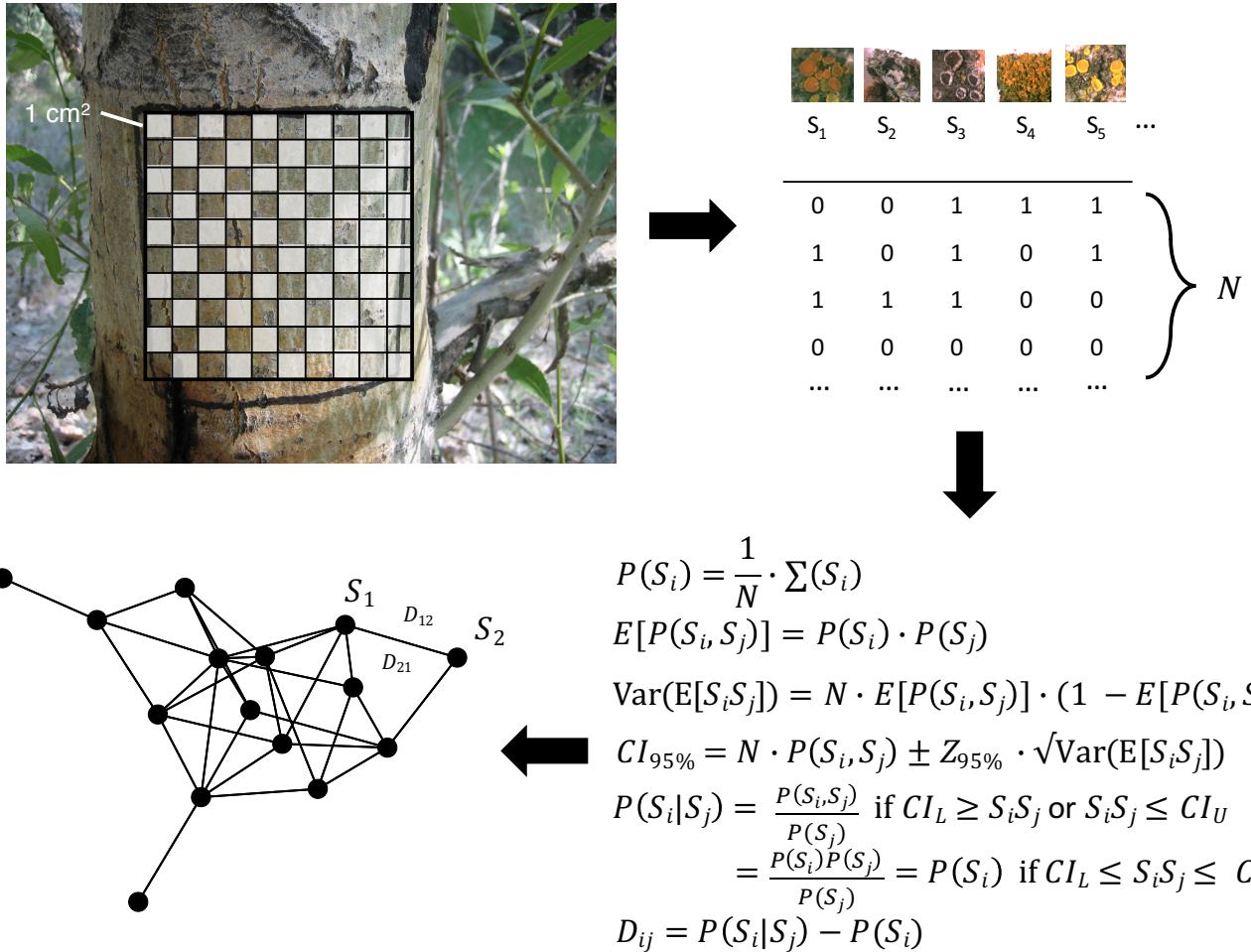
233 To calculate separate metrics for positive and negative  
 234 links, we applied methods for calculating the centrality  
 235 accounting for the sign differences (33). We used the  
 236 `signnet` package version ????, which is available at ???.

237 **Statistical Analyses, Software and Data.** We used a com-  
 238 bination of parametric and non-parametric, permutation  
 239 based frequentist statistical analyses to test for the effects  
 240 of genetic variation on lichen communities and their inter-  
 241 action networks. To assess the effect of genotype on uni-  
 242 variate responses, we used additive, random effects models  
 243 with Restricted Maximum Likelihood (REML). We used  
 244 a combination of Least Squares Regression, Analysis of  
 245 Variance (ANOVA) and correlation tests to quantify and  
 246 test for the relationship among other variables. Bark  
 247 roughness, lichen cover and species richness were square-  
 248 root transformed to meet the assumptions of homogeneity  
 249 of variance and normality for these tests.

For multivariate response variables, such as lichen com-  
 250 munity composition and network structure, we used dis-  
 251 tance based multivariate statistical approaches, including  
 252 Permutational Analysis of Variance (PERMANOVA) and  
 253 Mantel tests. To quantify the similarity of lichen net-  
 254 works among individual trees, we calculated the pairwise  
 255 Euclidean distance of the **D** interaction matrices among  
 256 all pairs of trees.  
 257

For visualization of multivariate patterns, we used  
 258 Non-metric Multi-Dimensional Scaling (NMDS) (?) to  
 259 produce dimensionally reduced ordinations of these multi-  
 260 variate responses and fitted vectors for continuous predic-  
 261 tor variables to the ordinated values (?). Using random  
 262 initial configurations with a maximum of 500 iterations  
 263 and a change in stress threshold of less than  $10^{-12}$ . Final  
 264 configurations has the lowest stress with at most a stress  
 265 level of 0.10.  
 266

For each network, we also calculated metrics that mea-  
 267 sure different structural aspects. Although there are many  
 268 other metrics, for the sake of simplicity we focus on a  
 269 subset that represent several interesting features of net-  
 270 work structure (see (34)). We calculated the number of  
 271 interactions or “links” in each network, which provides a  
 272



**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 (32), 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,  $E[P(S_i S_j)] = P(S_i) P(S_j)$ , and  $P(S_i | S_j)$  reduces to  $P(S_i)$ , the observed individual probability of species  $S_i$ . In the context of these networks, asymmetry and positive/negative valued connections are distinct quantities. In-coming and out-going connections can be interpreted as “influenced by” and “influenced”, respectively; while positive and negative should be seen as one species increasing or decreasing, respectively, the probability of another species’ occurrence.

measure of the size of the network (20, 25). 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 have one or small number of species that interact with other species. We used a related function to calculate the centrality of each species (i.e. node level centrality) in each network as well.

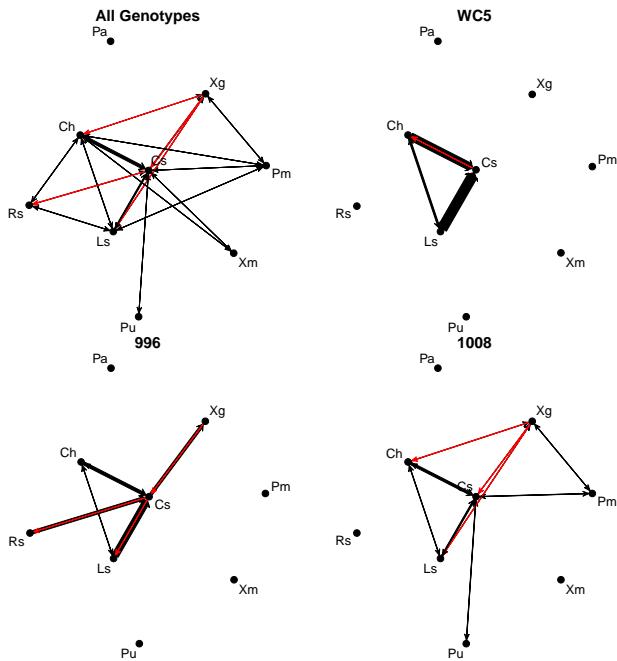
For all tests where genotype was used as a predictor, we quantified the heritability of the response variable. Because the trees in the garden were clonal replicates of each genotype, we calculated broad-sense heritability, which is the genotypic variance divided by the total phenotypic variance (35). This can be interpreted as a measure of the phenotypic variance due to genotypic variation. We

also apply this to the community genetics context as the variance in *extended* phenotypic variance due to genotypic variation (36). For the multivariate analyses, where we employ PERMANOVA, we followed the methods of (37) to adjust the degrees of freedom for unbalanced genotype replicates.

All code and data for the project are openly available online. Code and data are available at [github.com/ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo at [zenodo.com/doiXXXXXX](https://zenodo.com/doiXXXXXX). All analyses were conducted using the programming language R version 3.6.1 (R Development Core Team 2019).

## Results

Tree genotype influenced lichen network structure. Tree genotype significantly predicted the struc-



**Fig. 3.** Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices 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. The sign of the interaction is indicative of greater (positive) or lesser (negative) paired occurrences than expected relative to the overall frequency of occurrence of each species. Ecologically, the links in the network are likely the product of multiple types of interactions (e.g. mutualism, parasitism, competition, facilitation) that could vary over both space and time.

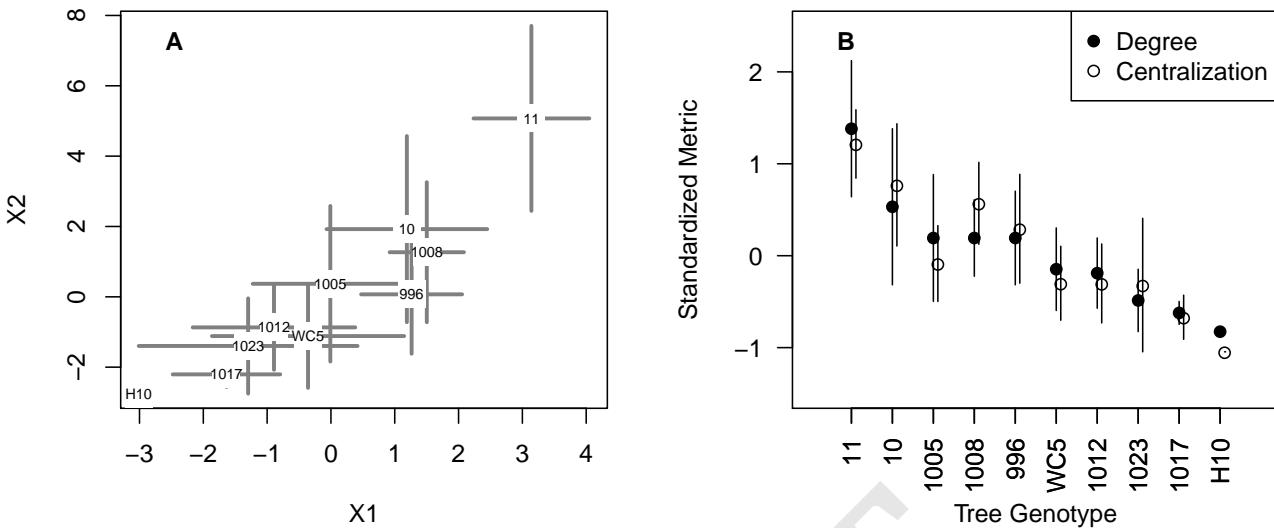
	response	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537	
Degree	3.5175	0.3156	0.0255	
Degree (positive)	3.6925	0.3242	0.0229	
Degree (negative)	0.0327	0.0318	0.3859	
Centralization	4.0444	0.3305	0.0184	
Centralization In-Degree	4.4812	0.3487	0.0142	
Centralization In-Degree (positive)	3.9852	0.3309	0.0190	
Centralization In-Degree (negative)	0.3304	0.1057	0.2508	
Centralization Out-Degree	3.8615	0.3193	0.0205	
Centralization Out-Degree (positive)	3.5585	0.3119	0.0248	
Centralization Out-Degree (negative)	0.0862	0.0513	0.3446	

**Table 1. Genotypic effects on the associated lichen network structure.**

The genetic response of network centralization was driven by variation in *Caloplaca holocarpa*. Centrality varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ ,  $p\text{-value} << 0.0001$ ). *Caloplaca holocarpa* centrality was the main species to exhibit a significant response to tree genotype in terms of positive centrality for both the in-coming ( $RLRT = 3.61$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0240$ ) and out-going ( $RLRT = 3.13$ ,  $H^2 = 0.30$ ,  $p\text{-value} = 0.0327$ ) perspectives, but not for either negative centrality metrics in-coming ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 1$ ) or out-going ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 0.4543$ ). None of the other species' centralities showed a genotypic response (Supplementary Table 6) with the exception of *X. montana* ( $RLRT = 2.92$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0375$ ); however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent of rough bark was the only tree trait that displayed a significant response to genotype ( $RLRT = 4.8526$ ,  $H^2 = 0.3221$ ,  $p\text{-value} = 0.0113$ ). None of the other bark traits, condensed tannins ( $RLRT = 0.0007$ ,  $H^2 = 0.0041$ ,  $p\text{-value} = 0.4439$ ), pH ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ) or carbon-nitrogen Ratio ( $RLRT = 0.0000$ ,  $H^2 = 0.0000$ ,  $p\text{-value} = 1.0000$ ), showed a significant response to tree genotype and none other than bark roughness were correlated with network similarity (Supplementary Table 5); therefore, we focused our analysis on bark roughness. We found that bark roughness was significantly correlated with network similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$ ,  $R^2 = 0.26$ ,  $p\text{-value} = 0.0096$ ) and other lichen net-

tural similarity of lichen networks (PERMANOVA: Pseudo- $F_{9,27} = 3.58$ ,  $H^2 = 0.41$ ,  $p\text{-value} = 0.0537$ ) (Fig. 4). Overall network level metrics responded significantly to tree genotype (Table 1), including network degree ( $RLRT = 3.52$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0255$ ) and centralization including both in-coming and out-going links ( $RLRT = 4.04$ ,  $H^2 = 0.33$ ,  $p\text{-value} = 0.0184$ ) or when separated into in-coming only ( $RLRT = 3.9852$ ,  $H^2 = 0.3309$ ,  $p\text{-value} = 0.0190$ ) or out-going only ( $RLRT = 3.8615$ ,  $H^2 = 0.3193$ ,  $p\text{-value} = 0.0205$ ). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree ( $RLRT = 3.6925$ ,  $H^2 = 0.3242$ ,  $p\text{-value} = 0.0229$ ), positive in-going centralization ( $RLRT = 4.4812$ ,  $H^2 = 0.3487$ ,  $p\text{-value} = 0.0142$ ). Metrics calculated with negative links were not significant, including degree (negative) ( $RLRT = 0.0327$ ,  $H^2 = 0.0318$ ,  $p\text{-value} = 0.3859$ ) and both in-coming (negative) ( $RLRT = 0.3304$ ,  $H^2 = 0.1057$ ,  $p\text{-value} = 0.2508$ ) and out-going centralization (negative) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ ,  $p\text{-value} = 0.3446$ ).



**Fig. 4.** The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ( $R^2 = 0.999$ , stress = 0.008) lichen networks ( $\pm 1$  S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. B. Plot showing the standardized ( $\frac{x - \bar{x}}{\sigma}$ ) means ( $\pm 1$  S.E.) for the two of the genetically based lichen network metrics: overall degree (i.e. total number of links) and centralization, which is a measure of the dominance of one species in the network.

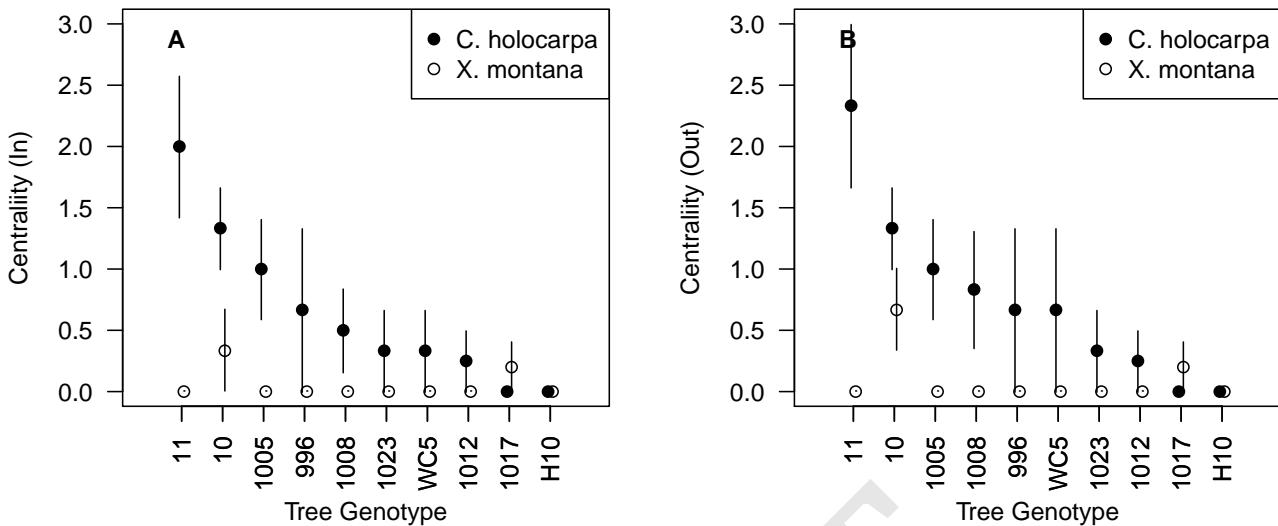
work metrics, including negative correlations with overall network degree ( $df = 35$ ,  $t = -2.13$ ,  $r = -0.34$ ,  $p\text{-value} = 0.04$ ) and centralization ( $df = 35$ ,  $t = -2.52$ ,  $r = -0.39$ ,  $p\text{-value} = 0.02$ ). To determine how much of the effect of bark roughness was genetically based, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ) or centralization ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

## Discussion

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *C. holocarpa*. Bark roughness was the primary genetically based trait driving network structure. The genetically based trait, bark roughness, was the main driver of network variation. Not only was bark roughness

the only trait observed to be genetically based, it was correlated with network structure and residual variation from this correlation was not explained by tree genotype. These results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species.

Differences in distributions below the quadrat scale are leading to shifting patterns of interactions among lichen species, largely increased positive incoming and out-going interactions. It could also be that some other variable correlated with bark roughness is altering the quality (i.e. how) the lichen species are interacting, that is as opposed to simply the "quantity" of interactions. Bark roughness effect was negative, possibly serving the role that other lichen play in facilitating the success of new propagule attachment and the growth of establishing thalli. This is supported by the patterns overall being positive, including *C. holocarpa*'s centrality being positive both in and out. We don't know specific micro-scopic dynamics, such as photobionts, mycobionts, endolichenic fungi and bacteria, but variation in these underlying interactions could also be playing a role. Also, bark roughness had previously been shown to be an important tree trait influencing bark

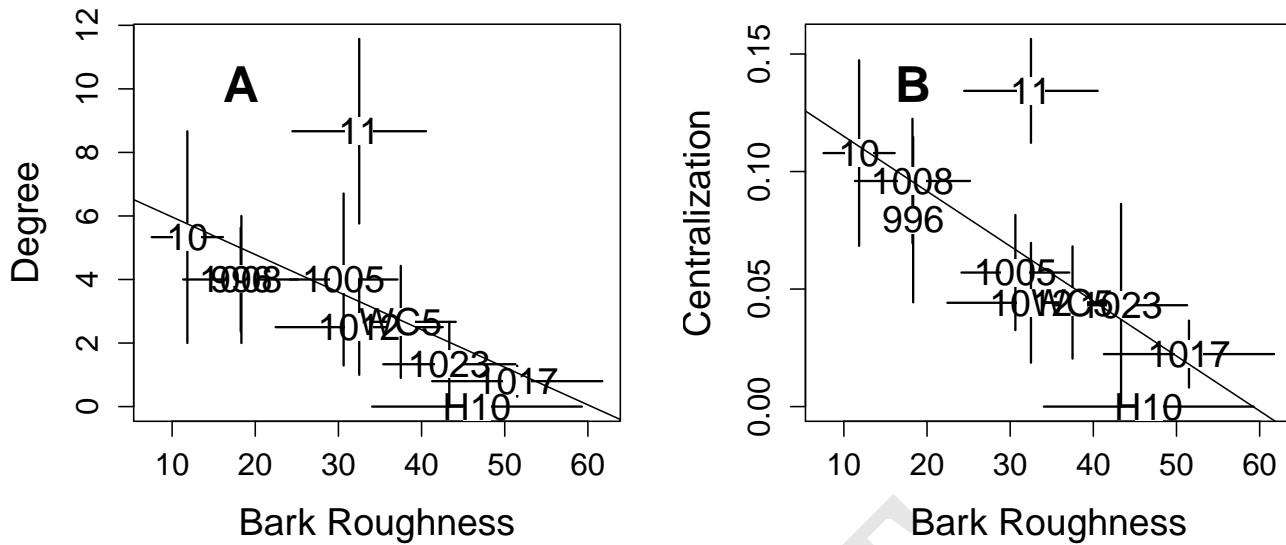


**Fig. 5.** Dot-plots showing the mean (dot) and  $\pm 1$  SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for two genotypes, and only out-degree centrality displayed a significant response to genotype.

lichen (31) that is under strong genetic control (38). There are important functional ramifications of genetically based variation in network structure. First, even if the composition of the communities is the same among individuals and genotypes, interactions may not be. We didn't observe compositional differences using the same data from which the lichen networks were derived. If we only had our composition dataset from this study, we would have concluded no response of the lichen community to tree genotype, even though the underlying interactions among lichen species does vary among genotypes. Community composition of lichen has previously been observed to be different among tree genotype in the same experimental garden, though this was observed with a larger sampling of total area and quadrats per tree. Regardless, this could result in a situation in which abundance based investigations of community-level genetic effects may miss important variation in the interactions among individuals in these communities, leading to an underestimate of genetic effects in ecosystems. It is possible that these underlying differences in interactions among lichen could lead to differences in community composition at a future point in time, however, this is not needed for evolutionary dynamics to play out.

Second, following on the previous point, genetic

diversity could be influencing the stability of communities through the effects on the structure of interactions. Some network structures are likely to be more stable, either in response to disturbance or via self-organized dynamics. For example, centralized networks, although more efficient, are theorized to be more susceptible to targeted attacks on the center of the network. For example, consider a forest with two genotypes that support lichen communities that are similar in total abundances of each species but differ in terms of the structure. Extensions of game theory to evolutionary biology have demonstrated that network structure can lead to variation in evolutionary dynamics. Some structures tend toward dominance and dampening of selection, while others lead to amplification of selection (Newman). One class of networks that are theorized to have amplifying effects on networks have "star" shapes with one or a few species at the center and radiating interactions out from the central core (Leiberman). This is structurally what we have observed with the networks that tend to occur on some of the genotypes in our study, i.e. the more centralized networks. It is possible that these more centralized networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the network structure fostered on that tree genotype.



**Fig. 6.** Bivariate plots of the relationship between bark roughness and three network metrics: A) degree and B) centralization. Each plot displays the genotype mean  $\pm$  1 S.E. for both variables and a least-squares regression calculated using the genotype means.

468 Altering the structure of interaction networks  
 469 presents a means for genetic effects to be magnified  
 470 within the system of interacting species. For  
 471 example, (8) showed that the genetics based interac-  
 472 tions of aphid resistant and aphid susceptible trees  
 473 resulted in different interaction networks of their  
 474 associated arthropod communities composed of 139  
 475 species. At the scale of ecosystems, trophic net-  
 476 works or food webs direct and control the rates of  
 477 energy and nutrient flux (39). Furthermore, in a  
 478 predator-prey-plant study, Smith (23), showed that  
 479 the interactions among species across trophic levels  
 480 depended on plant genotype. Also, work by (40–42)  
 481 observed consistent patterns of centralized interac-  
 482 tions of species modules focused around hubs of  
 483 plant-fungal interactions. In other words, a small  
 484 number of plant and fungal symbionts tended to  
 485 have disproportionate numbers of interactions with  
 486 other species and likely are the drivers in determining  
 487 community assembly, structure and dynamics.

488 There are several important points to consider  
 489 with regard to the generalization of the observed  
 490 genetically based response of the lichen networks.  
 491 Body size and sessile nature of lichen important to  
 492 observing genotype responses. As bark lichen  
 493 individuals do not move, but grow in a largely two  
 494 dimensional plane, these communities and their in-

teractions occur in the highly localized context of  
 495 the tree's bark surface. Lichen individuals are many  
 496 orders of magnitude smaller than the tree individual  
 497 and the life-span of a tree is many times that of a  
 498 lichen. For these reasons, any genetic effects on these  
 499 communities is not dampened by the movement of  
 500 individuals and the mixing of the effect of different  
 501 tree genotypes on the lichen community, as might  
 502 occur for more mobile species (e.g. insects and birds).  
 503 We only looked at lichen, other species whose distri-  
 504 bution, abundance or interactions respond to tree  
 505 genotype, such as epiphytic plants (e.g. moss and  
 506 liverworts), algae or insects, could be playing a role.  
 507 Other traits could also be playing a role, such as  
 508 traits that are correlated with bark roughness, such  
 509 as micro-aspect, albedo, moisture, etc.

510  
 511 Although our study was conducted with a commu-  
 512 nity of lichens, these results should be generalized to  
 513 other groups of diverse organisms around the world  
 514 that also exhibit significant genetic signals at the  
 515 community level (43, 44). In the face of the high de-  
 516 gree of complexity and potential context dependency  
 517 of ecological processes, the current study points to  
 518 the utility of considering the spatial and temporal  
 519 scales of interactions, as discussed to some in pre-  
 520 vious studies (30, 45, 46). In the present study, we  
 521 found that community assembly processes, such as

environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. We suggest that future work would be aided by determining these modules within the biotic community that include species with similar differences in body-size and time-scales. 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 (47). 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.

Future work should consider the potential influence on evolutionary dynamics of the associated communities. The network of interactions of species that are strongly influenced by a foundation species, could amplify the effects of genotype, this serves as a means for genetic effects to increase rather than diffuse through an ecosystem either through space or over time, as has been proposed in the construction of the genetic diffusion hypothesis. Altered abundances can lead to differences in interactions Genotype effects on abundances of individual abundances may cancel out. Specifically for asexually reproducing species, such as many lichen are, shifting interaction frequencies could lead to evolutionary outcomes, given the potential to take-up symbionts and genetic material from thalli that they come into contact with. Altering interaction frequencies could differences in the frequencies the exchange of genetic materials among lichen that could then be passed on to vegetative and possibly sexually produced reproductive propagules. The larger scale (stand or region) effects of these "evolutionary units" on each tree would depend on the connectivity and rate of movement of propagules among trees per the geographic mosaic of co-evolution hypothesis (5, 48).

**Other studies that should be discussed:** Trait plasticity is more important than genetic variation in determining species richness of associated communities. Synthesis: These results indicate that trait

plasticity can be a dominant driver of above- and below-ground biodiversity (Barbour 2018).

Multiple plant traits shape the genetic basis of herbivore community assembly. Synthesis: Taken together, our results support that the genetic basis of herbivore community assembly occurs through a suite of plant traits for different herbivore species and feeding guilds (Barbour 2015).

Contingency rules for pathogen competition and antagonism in a genetically based, plant defense hierarchy. Synthesis: Our results point to a *Populus* defense hierarchy with resistance genes on top, followed by pathogen competition, and finally pathogen antagonism by endophytes. We expect these rules will help to explain the variation in pathogen antagonism that is currently attributed to context dependency (Busby 2019).

Linking plant genes to insect communities: Identifying the genetic bases of plant traits and community composition. Synthesis: These findings support the concept that particular plant traits are the mechanistic link between plant genes and the composition of associated insect communities (Barker 2019).

Genotypic variation in phenological plasticity: Reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. Synthesis: Trees transferred to warmer climates generally showed small to moderate shifts in an adaptive direction, a hopeful result for climate change. Trees experiencing cooler climates exhibited large, non-adaptive changes, suggesting smaller transfer distances for assisted migration (Cooper 2018).

Epigenetic inheritance across the landscape. Synthesis: Transgenerational epigenetic variation may alter the interpretation of landscape genomic studies that rely upon phenotypic analyses, but should have less influence on landscape genomic approaches that rely upon outlier analyses or genome-environment associations (Whipple 2018).

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721 **Supplementary Materials**

722 **Tables.**

	df	SS	R2	F	p-value
geno	9.0000	44078.1327	0.5442	3.5821	0.0537
Residual	27.0000	36915.4605	0.4558		
Total	36.0000	80993.5932	1.0000		

**Table 1. PERMANOVA Pseudo-F Table of lichen network similarity to genotype.**

response	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Average Mutual Information	3.5235	0.3101	0.0254
Centralization	4.0444	0.3305	0.0184
Centralization In-Degree	4.4812	0.3487	0.0142
Centralization Out-Degree	3.8615	0.3193	0.0205
Centralization In-Degree (positive)	3.9852	0.3309	0.0190
Centralization In-Degree (negative)	0.3304	0.1057	0.2508
Centralization Out-Degree (positive)	3.5585	0.3119	0.0248
Centralization Out-Degree (negative)	0.0862	0.0513	0.3446
Number of Network Links (Degree)	3.5175	0.3156	0.0255
Degree (positive)	3.6925	0.3242	0.0229
Degree (negative)	0.0327	0.0318	0.3859
Percent Lichen Cover	0.0000	0.0000	1.0000
Lichen Species Diversity	0.0000	0.0000	0.4543
Lichen Species Richness	0.0000	0.0000	0.4543
Lichen Species Evenness	0.0000	0.0000	1.0000
Percent Rough Bark	4.8526	0.3221	0.0113
pH	0.0000	0.0000	1.0000
Carbon-Nitrogen (CN) Ratio	0.0000	0.0000	1.0000
Condensed Tannins (CT)	0.0007	0.0041	0.4439
BR-L Residuals	0.0000	0.0000	1.0000
BR-Cen Residuals	0.0000	0.0000	1.0000

**Table 2. Genotypic effects on tree traits and bark lichen.**

	r	R2	estimate	SE	t	p-value
br_L	-0.34	0.11	-0.07	0.03	-2.13	0.04
br_Cen	-0.39	0.15	-0.00	0.00	-2.52	0.02
ct_L	0.34	0.11	0.57	0.27	2.13	0.04
ct_Cen	0.08	0.01	0.00	0.00	0.46	0.65
ph_L	0.08	0.01	0.67	1.41	0.48	0.64
ph_Cen	0.13	0.02	0.02	0.02	0.78	0.44
cn_L	0.06	0.00	50.19	145.84	0.34	0.73
cn_Cen	0.16	0.03	2.14	2.18	0.98	0.33

**Table 3. Tests of the correlation between tree bark traits and lichen network structure**

	df	SS	R2	F	p-value
geno	9.0000	44078.1327	0.5442	3.5821	0.0537
Residual	27.0000	36915.4605	0.4558		
Total	36.0000	80993.5932	1.0000		

**Table 4. PERMANOVA Pseudo-F Table of lichen network similarity to genotype.**

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1.0000	21021.8765	0.2595	13.0299	0.0096
CT	1.0000	2349.3142	0.0290	1.4562	0.2016
pH	1.0000	2098.8999	0.0259	1.3010	0.2899
CN	1.0000	3896.1757	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

**Table 5. PERMANOVA Pseudo-F Table of lichen network similarity response to bark traits.**

lichen species	mean	statistic	H2	p-value
<b>Positive</b>				
<i>In-Degree</i>				
X. galericulata	0.2703	0	0	1
C. subdeflexa	0.8919	2.1926	0.2158	0.0595
L. spp.	0.4324	0	0	1
C. holocarpa	0.5946	3.6146	0.3241	0.024
X. montana	0.0541	0	0	0.4543
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.1351	2.049	0.2613	0.0656
<i>Out-Degree</i>				
X. galericulata	0.027	0	0	0.4543
C. subdeflexa	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4246
C. holocarpa	0.7027	3.1318	0.2981	0.0327
X. montana	0.0811	2.9228	0.3163	0.0375
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.2973	0.1505	0.0612	0.3119
<b>Negative</b>				
<i>In-Degree</i>				
X. galericulata	0			
C. subdeflexa	0.1892	0	0	0.4543
L. spp.	0.1892	0.0015	0.0057	0.4398
C. holocarpa	0.1351	0	0	1
X. montana	0.027	0.0377	0.0394	0.3807
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0.1622	0	0	1
<i>Out-Degree</i>				
X. galericulata	0.2432	0	0	1
C. subdeflexa	0.4054	0	0	0.4543
L. spp.	0.027	0	0	0.4543
C. holocarpa	0.027	0	0	0.4543
X. montana	0			
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0			

**Table 6. REML tests of the effect of tree genotype on lichen species centrality.**

	BR	CT	pH	CN	PC	SR	SE	SD	L	Cen
BR									-0.34	-0.39
CT								-0.34		0.34
pH										
CN										
PC								0.49		-0.46
SR									0.76	0.47
SE									0.85	0.45
SD									0.59	0.33
L										0.88
Cen										

**Table 7. Matrix of correlations among tree traits, lichen community metrics and network metrics**

	Df	SumOfSqs	R2	F	Pr(>F)
geno	9.0000	1.5049	0.2001	0.7507	0.8878
Residual	27.0000	6.0143	0.7999		
Total	36.0000	7.5193	1.0000		

**Figures.**

**Table 8. Pseudo-F Table of lichen community similarity  
PERMANOVA.**

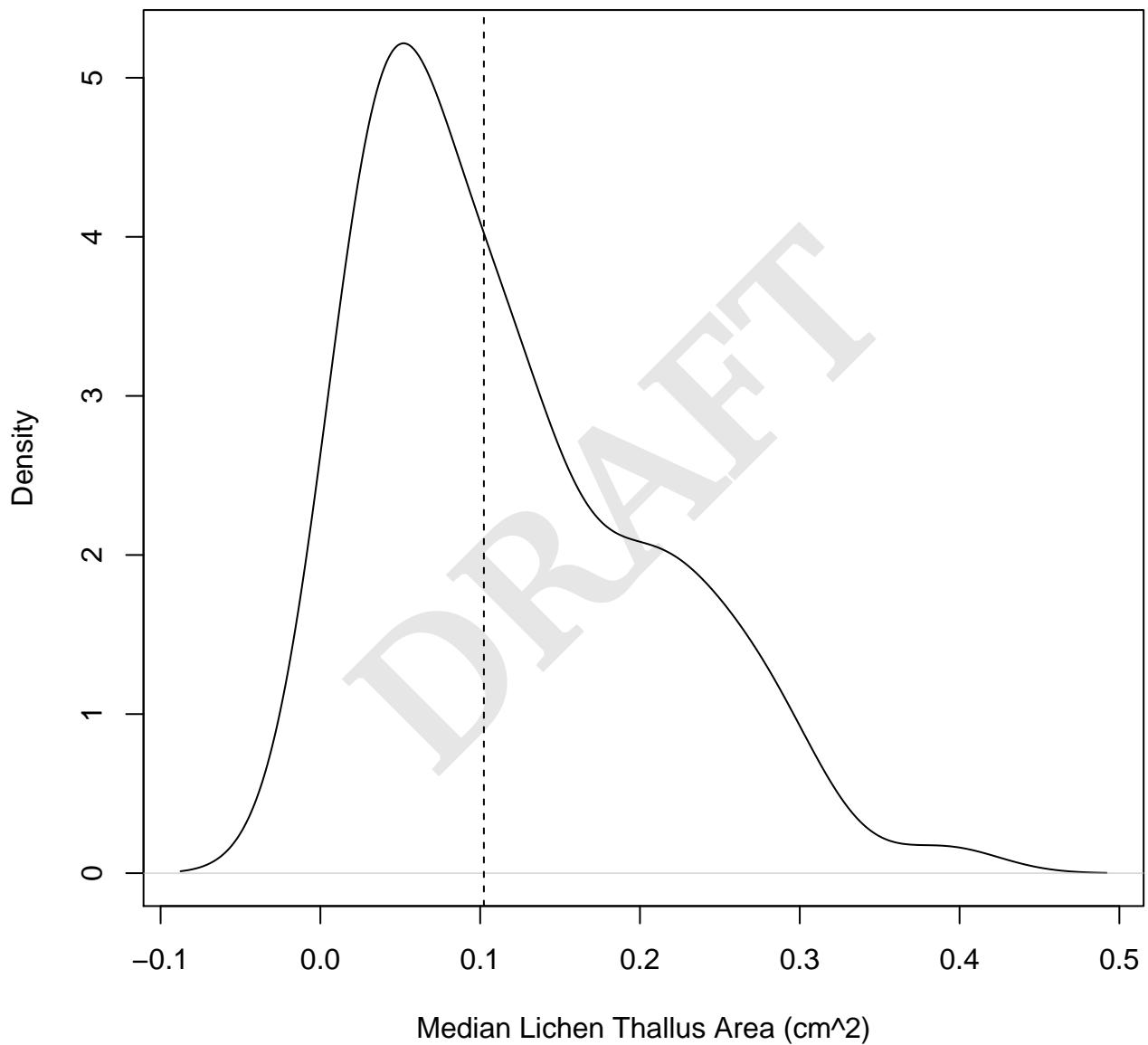
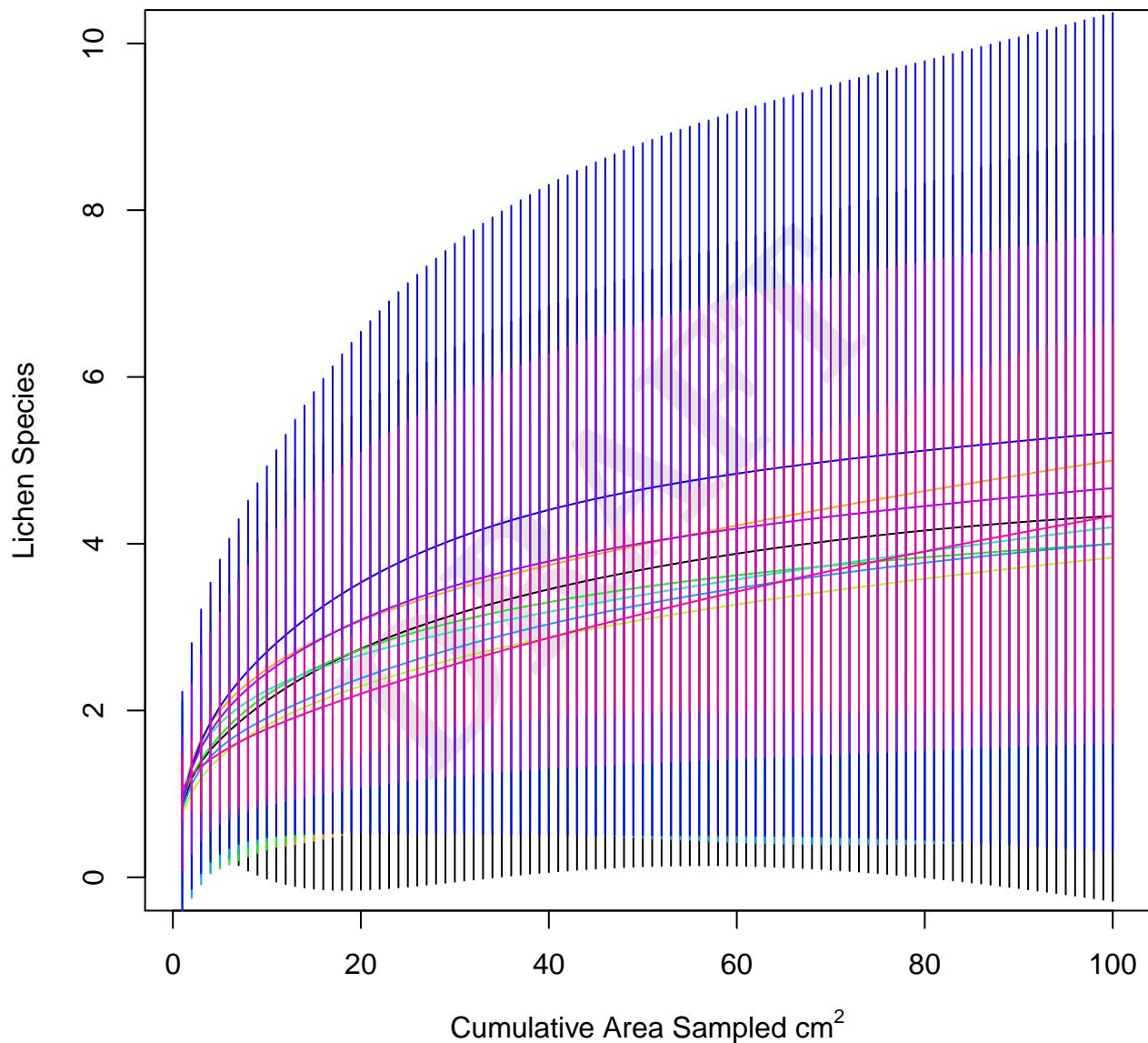


Fig. 1



**Fig. 2.** Species area curve by genotype.

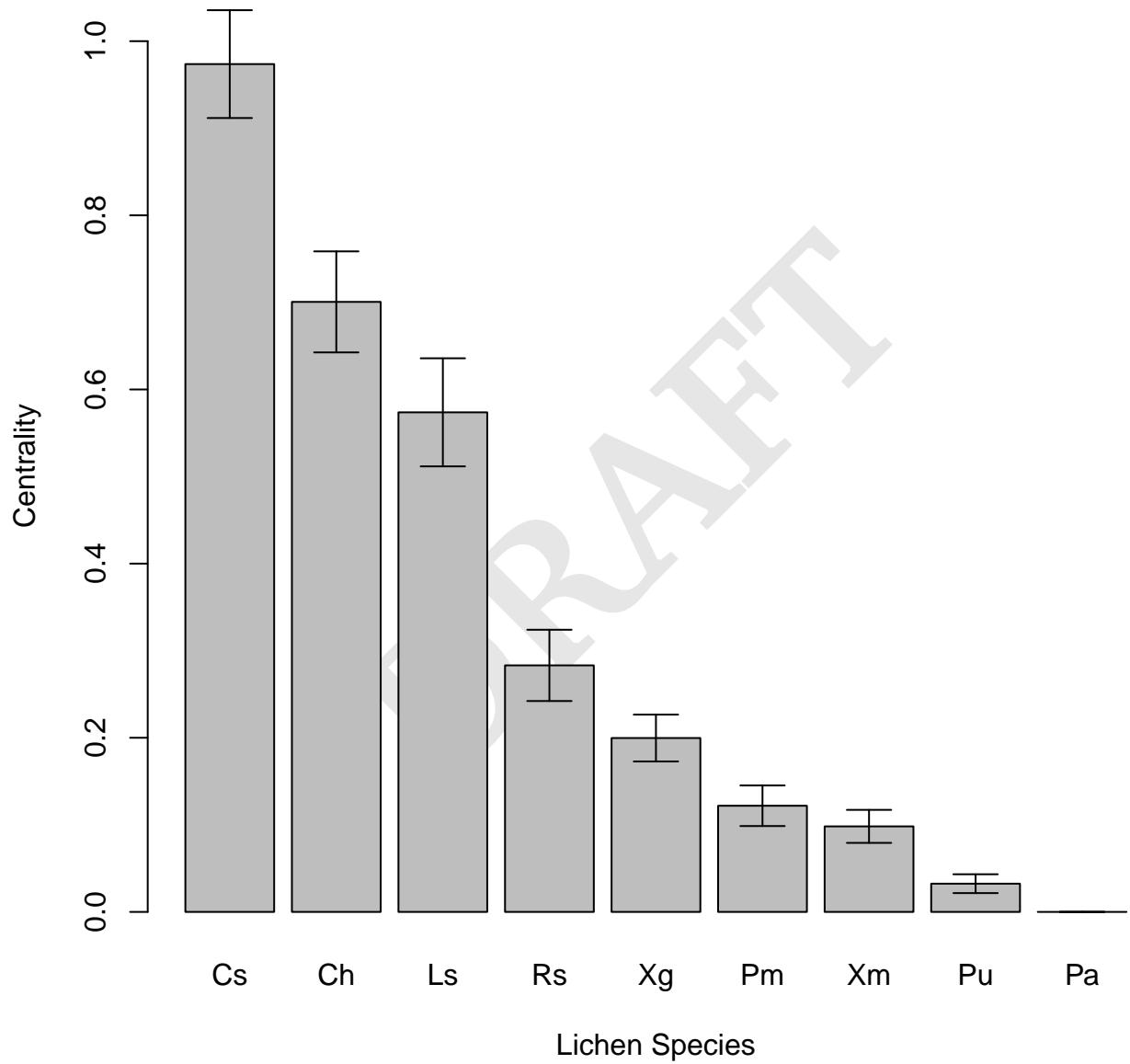


Fig. 3