

# 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 ecosystems of  
2 interacting species in which natural selection defines the structure  
3 of ecological networks. Fundamental to understanding evolutionary  
4 processes is illuminating the genetic basis to ecological network  
5 structure. Although previous work has demonstrated that genotypic  
6 variation in foundation species contributes to interaction network  
7 structure, we are not aware of a study that has quantified the genetic  
8 contribution to network structure. To examine this we observed  
9 epiphytic lichens associated with genotypes of (*Populus angustifolia*), a foundation species of riparian ecosystems. We constructed  
10 signed, weighted, directed interaction networks for the lichens and  
11 conducted genetic analyses of whole network similarity and network  
12 degree and centralization. We found three primary results. First,  
13 tree genotype significantly predicted lichen network similarity, i.e.  
14 clonal replicates of the same genotype tended to support more similar  
15 lichen networks, using multiple network metrics. Third, one of  
16 the examined tree traits, bark roughness, was both predicted by tree  
17 genotype and correlated with lichen network similarity, supporting a  
18 mechanistic pathway from variation in a heritable tree trait and the  
19 genetically based variation in lichen network structure. We conclude  
20 that tree genotype can influence not only the relative abundances of  
21 organisms but also the interaction network structure of associated  
22 organisms. Given that variation in network structure can have consequences  
23 for the dynamics of communities through altering the stability of the system and modulating or amplifying perturbations, these  
24 results have important implications for the evolutionary dynamics of  
25 ecosystems.

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

1 Evolution occurs in the context of complex ecological networks. Community genetics studies  
2 have shown that genetic variation in foundation species, which have large effects on communities  
3 and ecosystems by modulating and stabilizing local conditions (1), plays a significant role in defining distinct  
4 communities of interacting organisms: such as, endophytes, pathogens, lichens, arthropods, and soil  
5 microbes (2–4). Multiple studies have now demonstrated that genetic variation influences numerous  
6 functional traits (e.g., phytochemical, phenological, morphological) produces a multivariate phenotype

(5) that contributes to variation in associated communities (6). The importance of genetic variation in structuring ecological systems was recently reviewed (7), 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. There is now evidence to

## Significance Statement

Evolution occurs in the context of ecosystems comprised 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 analyses. Here, we use a long-term common garden experiment to reveal the effect that genotypic variation 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 roughness. 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 assessing 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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support that selection, acting on this heritable variation, tends to occur among groups of species (8) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly (9) and species interactions (6, 10, 11), shaping the structure of ecological interaction networks (12–14).

The genetic similarity rule provides a useful framework for approaching the nexus of evolutionary and community dynamics in the context of complex interaction networks. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, (15) observed that individuals of a foundation species, such as cottonwoods, that are more genetically similar will tend to have similar traits and thus tend to have similar interactions with other species than individuals that are less similar. However, studies in the network ecology literature generally do not include a genetic component (16); and, community genetics studies have primarily focused on community composition in terms of the abundance of species (7). There are studies that have examined the effects of genetic variation on trophic chains, such as several in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (17–21) and generally found that increasing genotypic diversity leads to increased trophic complexity. Only two other studies, that we are aware of, have explicitly examined the effect of genotypic variation on the structure of interaction networks between tree individuals and associated herbivores (22, 23) and both found that genotypic diversity generates increased network modularity (i.e. compartmentalization). However, both of these studies were at the scale of forest stands, rather than individual trees; therefore, neither was able to observe replicated networks in order to statistically test for genetic effects on network structure and quantify the genetic component (i.e. heritable variation) in network structure.

What are the potential issues/concerns of not considering network structure? Network theory and evidence from empirical studies in ecology have demonstrated that indirect effects can lead to self-organization, producing sign-changing, amplifying and/or dampening effects (24, 25). The development of indirect genetic effects (IGE) and its community-level extension, inter-specific indirect genetic effects (IIGE) (26) NEED TO ADD WHITHAM2020 in evolutionary biology point to the importance of

studying the genetic basis of interaction network structure. IGE and IIGE theory develop a quantitative framework that demonstrates the importance of the indirect effect of genetic variation of one individual on other individuals of the same (IGE) or different species (IIGE). Evolutionary applications of network theory have demonstrated that, at least at the population scale, indirect effects of interactions can lead to network structures that can amplify or dampen the effects of selection (27). For example, networks that form a star-like structure in which there is a central species or core group of species that interact with other, peripheral species, can greatly amplify selection events. Empirically, network analysis of the structure of bipartite (i.e. two-mode) mutualistic networks has shown in multiple cases that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability and resilience to disturbances (28) NEED TO ADD BASCOMPTE2014. Therefore, observing not only *if* but *how* networks of genetically similar individuals are more similar, is essential to fully understanding evolutionary dynamics in real ecosystems.

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 (29). Here we examine the genetic basis of network structure on a community of sessile lignicolous (i.e. bark) lichens 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 (30, 31). In addition, the life-history characteristics of lichens, having highly localized, direct contact interactions and slow population turnover rates, facilitated the assessment of 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 (22, 23, 28, 32). 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 net-

118 works can function as indicators of ecological dynamics  
119 important for conserving biodiversity. Applying a  
120 probability-theory based network modeling approach,  
121 we constructed a set of interaction network models  
122 for the lichens associated with individual trees. Using  
123 these models, we then examined the genetic basis of  
124 the structure of these ecological networks via several  
125 network metrics that measures different aspects of  
126 network structure at the scale of individual species  
127 (i.e. nodes) or the entire network observed on each  
128 tree. In particular, we focus the metric of centrality  
129 for individual species and centralization for whole  
130 networks, which measures how much a species is con-  
131 nected in the network relative to other species. Based  
132 on previous community genetics studies, particularly  
133 the community similarity rule (15), we hypothesize  
134 that trees will vary in some phenotypic traits and  
135 those trees of the same genotype will tend to have  
136 similar traits leading to similarities in lichen network  
137 structure.

## 138 Materials and Methods

139

140 **Study System.** The study was conducted along the We-  
141 ber River, UT (USA), which is a cottonwood (*Populus*  
142 spp.) dominated riparian ecosystem. Although two native  
143 species, *Populus angustifolia* (James) and *Populus fremontii*  
144 (S. Watson), occur here and are known to hybridize,  
145 only pure or advanced generation backcrosses of *P. angusti-  
146 folia* were sampled. Bark lichens have been extensively  
147 studied in this system and provide an ideal system in  
148 which to observe and model lichen interaction networks,  
149 as their sessile nature permits accurate identification of  
150 individuals (33).

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

162 **Bark Lichen and Trait Observations.** On each tree, pres-  
163 ence or absence of each lichen species was assessed in 50  
164 total 1 cm<sup>2</sup> cells arrayed in a checkerboard pattern. Given  
165 the small size and sessile nature of lichens, we were able to  
166 rapidly assess lichen interactions by quantifying thalli in

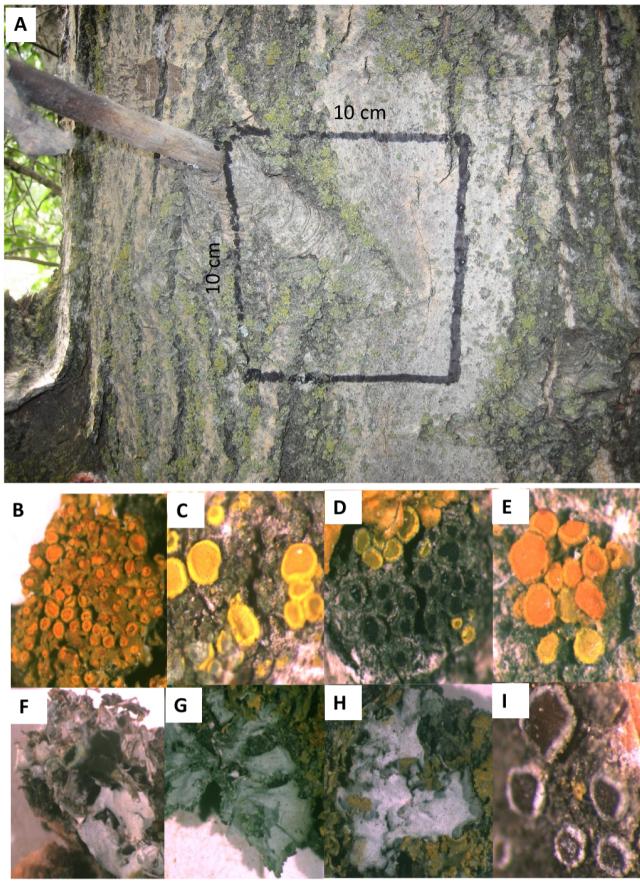
167 close contact. Sampling was restricted to the northern as-  
168 pect of the trunk to maximize the abundance of lichen and  
169 control for the effect of trunk aspect. Two adjacent 100  
170 cm<sup>2</sup> quadrats centered at 50 cm and 95 cm from ground  
171 level were sampled (Fig 1 A and B). The observed lichen  
172 community included (abbreviations are given for species  
173 present in study): Xg = *Xanthomendoza galericulata*, Xm  
174 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Cande-*  
175 *lariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora*  
176 *hagenii*, Pm = *Phyciella melanochra*, Pa = *Physcia adscen-*  
177 *dens*, Pu = *Physcia undulata*. Several other species were  
178 not obesrvd in the present study but are known to occur  
179 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia*  
180 *ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

181 The cell size and checkerboard sampling pattern was  
182 chosen to isolate the individuals in each cell. In a previous  
183 survey of lichen thallus size in this common garden, we  
184 had observed a median thallus size of 0.12 ± 0.001 cm<sup>2</sup> (1  
185 S.E.) (see Supporting Information). Based on the median  
186 thallus size, we expected thalli observed in each cell to  
187 generally be spatially independent of thalli present in  
188 other cells but exposed to similar micro-environmental  
189 conditions created by the bark and the location of the  
190 sampling area on an individual tree. Therefore, we were  
191 confident in treating the cell-wise observations in quadrats  
192 as independent with respect to lichen-lichen interactions.

193 We also measured several bark traits for each tree:  
194 including, bark roughness, condensed tannin, carbon and  
195 nitrogen concentrations and pH. **ADD METHODS  
196 FROM JAMIE.**

197 **Lichen Network Modeling and Analysis.** For each tree,  
198 repeated observations of lichen were made in order to con-  
199 struct replicated interaction networks for each genotype.  
200 We conducted a modified sampling procedure originally  
201 developed by (34) with the addition that we quantified  
202 the presence of lichen in the 1 cm<sup>2</sup> cells on individual  
203 trees of *P. angustifolia*. Unipartite networks were gener-  
204 ated using the conditional probabilities of each species  
205 pair, i.e. the probability of observing one species given  
206 an observation of another species  $P(S_i|S_j)$ , based on  
207 the method developed by (35). To calculate conditional  
208 probabilities, we quantified the individual probabilities  
209 of species occurrences  $P(S_i)$  and the joint probability  
210 of co-occurrences  $P(S_i, S_j)$  using the frequencies of each  
211 species and their co-occurrences. We were then able to  
212 calculate the conditional probabilities of each species pair  
213 as  $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$ , based on the axioms of probability.  
214 This yielded a matrix that could possibly be asymmetric, i.e.  
215  $P(S_i|S_j)$  does not have to be equal to  $P(S_j|S_i)$ . Another  
216 important property of this matrix is that the diagonal  
217 ( $S_{ii}$ ) was equal to one for all species present and zero for  
218 species that were not observed in any cell.

219 We then applied an analytical procedure to remove  
220 non-significant links between species. This procedure  
221 determines if the joint probability of a species pair



**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). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Physciella melanachra*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (B-D) and R.R. Naesbourn (E-I).

(i.e.  $P(S_i, S_j)$ ) is different from zero (Fig. 2). Here, a confidence interval  $CI_{95\%}$  is calculated as  $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$ , where the expected frequency of co-occurrences  $E(S_i S_j)$  is the total number of cells surveyed ( $N$ ) times the independent probabilities of each species  $P(S_i) * P(S_j)$ ,  $Z_{95\%}$  is the Z-score for 95% from a Z-distribution 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.  $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$ ). If the observed number of co-occurrence falls outside of the confidence interval, the joint probability  $P(S_i, S_j)$  is determined to be equal to the product of the individual probabilities (i.e.  $P(S_i)P(S_j)$ ), and the conditional probability reduces to the individual probability of that species  $P(S_i)$ . Therefore, unless the co-occurrence of a species pair falls outside the confidence interval, the probability that the observation of one species given the other is no different than simply observing that species alone.

This enables us to remove links from a given network by re-scaling the resulting conditional probabilities by subtracting the individual probabilities from the conditional probabilities (i.e. how different the conditional probability is from the independent probability), which makes any species with a non-significant conditional probability zero. The resulting matrix ( $\mathbf{D} = D_{ij}$ ) can be interpreted as how one species impacts another with zero being no effect and values less than or greater than zero interpreted as negative and positive effects, respectively. Here, we will refer to this matrix ( $\mathbf{D}$ ) as an interaction matrix with the properties that it can be asymmetric (i.e.  $P_{ij}$  does not necessarily equal  $P_{ji}$ ), and the diagonal ( $P_{ii}$ ) is zero (i.e. a species does not influence its own probability of being observed).

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

#### ADD EQUATIONS FOR METRICS

$$\sum x_i \quad [1]$$

- Node degree
- Node centrality
- Network degree
- Centralization
- In vs out
- Pos vs neg

To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (36). We used the `signnet` package version ????, which is available at ???.

**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. To assess the effect of genotype on univariate responses, we used additive, random effects models



**Fig. 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  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 (35), 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.

with Restricted Maximum Likelihood (REML). We used a combination of Least Squares Regression, Analysis of Variance (ANOVA) and correlation tests to quantify and test for the relationship among other variables. Bark roughness, lichen cover and species richness were square-root transformed to meet the assumptions of homogeneity of variance and normality for these 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. 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 visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (37) to

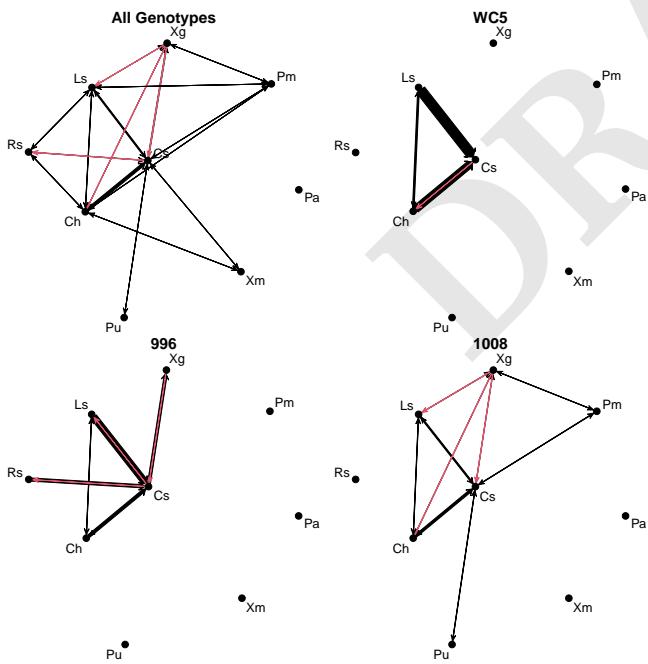
produce dimensionally reduced ordinations of these multi-variate responses and fitted vectors for continuous predictor variables to the ordinated values (38). Using random initial configurations with a maximum of 500 iterations and a change in stress threshold of less than  $10^{-12}$ . Final configurations has the lowest stress with at most a stress level of 0.10.

For each network, we also calculated metrics that measure different structural aspects. Although there are many other metrics, for the sake of simplicity we focus on a subset that represent several interesting features of network structure (see (16)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (22, 39). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (40). In a network with a

324 low level of centralization species have similar amount of  
 325 interaction in the network, while a network with a high  
 326 level of centralization tends to have one or small number  
 327 of species that interact with other species. We used a  
 328 related function to calculate the centrality of each species  
 329 (i.e. node level centrality) in each network as well.

330 For all tests where genotype was used as a predictor,  
 331 we quantified the heritability of the response variable. Be-  
 332 cause the trees in the garden were clonal replicates of each  
 333 genotype, we calculated broad-sense heritability, which  
 334 is the genotypic variance divided by the total phenotypic  
 335 variance (41). This can be interpreted as a measure of  
 336 the phenotypic variance due to genotypic variation. We  
 337 also apply this to the community genetics context as the  
 338 variance in *extended* phenotypic variance due to genotypic  
 339 variation (42). For the multivariate analyses, where we  
 340 employ PERMANOVA, we followed the methods of (26)  
 341 to adjust the degrees of freedom for unbalanced genotype  
 342 replicates.

343 All code and data for the project are openly avail-  
 344 able online. Code and data are available at [github.com/  
 345 ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo  
 346 at [zenodo.com/doi/XXXXXX](https://zenodo.com/doi/XXXXXX). All analyses were conducted  
 347 using the programming language R version 3.6.1 (R De-  
 348 velopment Core Team 2019).



**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 (996, WC5 and 1008) 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.

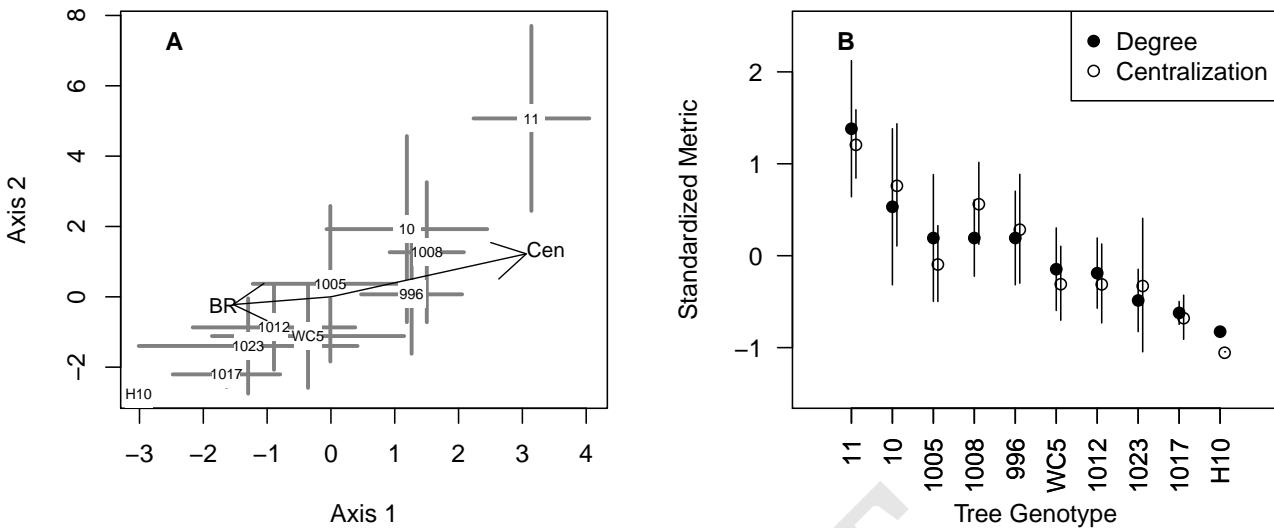
## Results

Tree genotype influenced lichen network structure and multiple lichen network metrics were heritable. Tree genotype significantly predicted the structural 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) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ ,  $p\text{-value} = 0.3446$ ).

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



**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 network similarity ( $\pm 1 \text{ S.E.}$ ). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated network similarity. B. Plot showing the standardized ( $\frac{x-\bar{x}}{\sigma}$ ) means ( $\pm 1 \text{ S.E.}$ ) 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.

( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 1$ ) 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 3) 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).

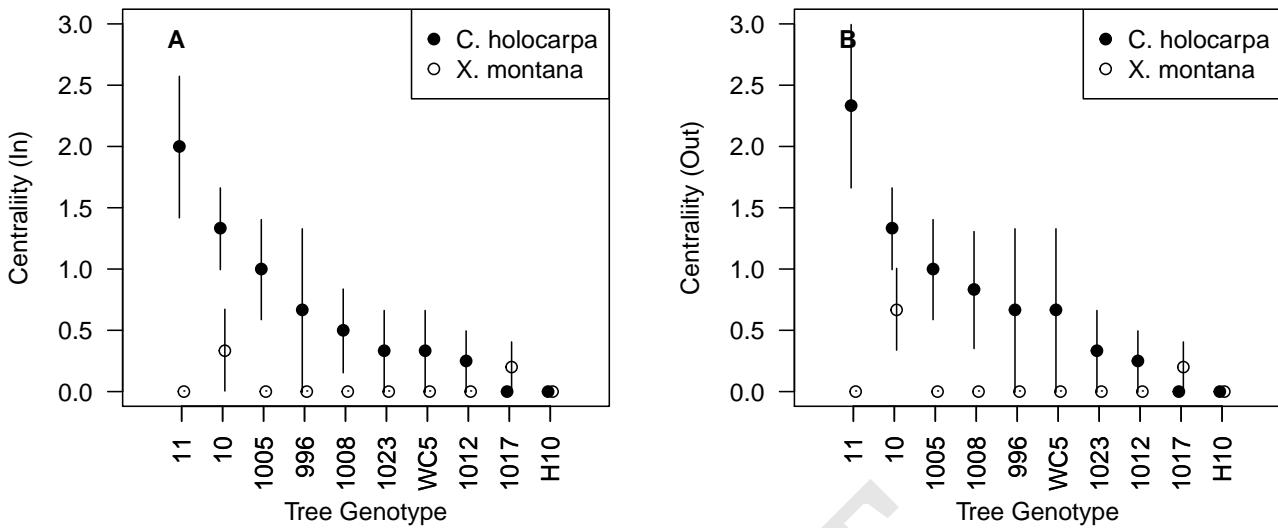
#### 394 Add transformations of variables to methods.

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent cover of rough bark ( $RLRT = 4.8526$ ,  $H^2 = 0.3221$ ,  $p\text{-value} = 0.0113$ ) and condensed tannins ( $RLRT = 3.0522$ ,  $H^2 = 0.3205$ ,  $p\text{-value} = 0.0343$ ) both displayed significant responses to tree genotype. None of the other bark traits, 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 (Table 2); therefore, we focused our analysis on bark roughness. We found that bark roughness was significantly correlated with network similarity (PER<sub>428</sub>

MANOVA: Pseudo- $F_{1,32} = 13.029$ ,  $R^2 = 0.26$ ,  $p\text{-value} = 0.0096$ ) and other lichen network metrics, including negative correlations with overall network degree ( $df = 35$ ,  $t = -2.13$ ,  $r = -0.34$ ,  $p\text{-value} = 0.04$ ) and centralization ( $df = 35$ ,  $t = -2.52$ ,  $r = -0.39$ ,  $p\text{-value} = 0.02$ ). In other words, trees with more similar levels of bark roughness tended to have lichen interaction networks with similar structure. To quantify the genetic bases of this effect of bark roughness on network structure, 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



**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.

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1.0000	20850.0933	0.2574	12.9234	0.0101
CT	1.0000	5993.6629	0.0740	3.7150	0.0813
pH	1.0000	1273.1905	0.0157	0.7892	0.3712
CN	1.0000	3896.1754	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

**Table 2. PERMANOVA Pseudo-F Table of lichen network similarity response to bark traits.**

positive interactions and largely driven by *C. holocarpa*. The genetically based trait, bark roughness, was the only trait observed to effect network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control (43), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (34); however this is the first demonstration of a link from genes to lichen network structure. As such these results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species.

**Heritability of Interaction Network Structure.** Revisit the community similarity rule.

Add more text here on positive and negative interactions of lichen from the literature.

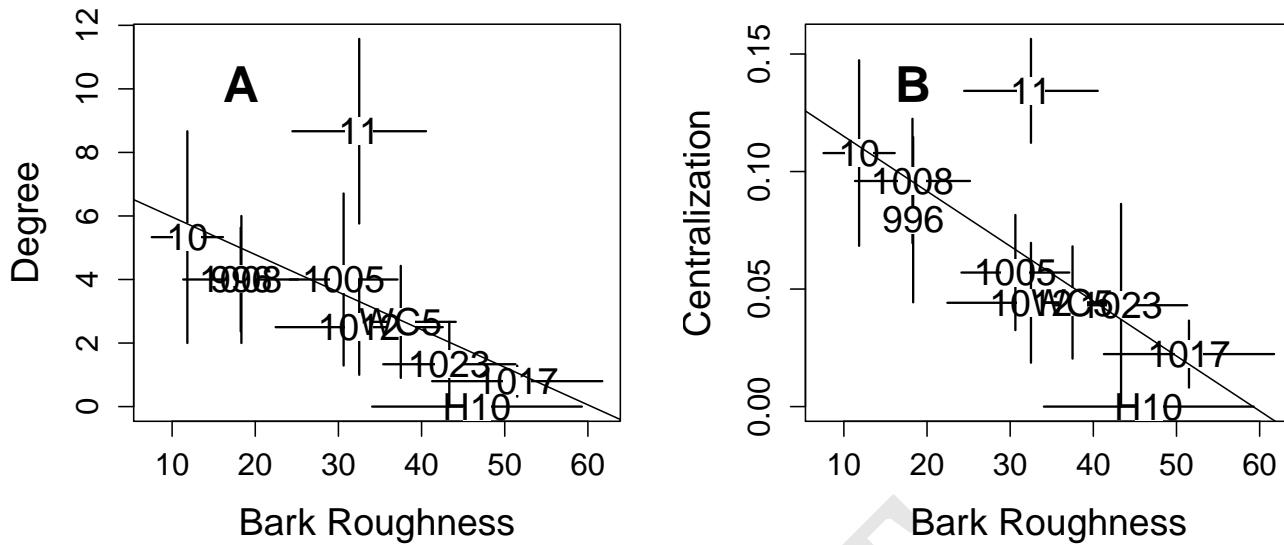
Elaborate on how many species might be supported by each lichen thallus including the symbionts and other species.

Elaborate on the importance of identifying the species/node level patterns in network structure response to genotype.

What is the relationship between tree growth, bark roughness and disruption of the lichen community? Tree grow and the bark expands over time, causing furrows.

Does bark roughness increase habitat and decrease interactions?

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



**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.

quadrats per tree. Regardless, this could result in 481  
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situation in which abundance based investigation 488  
of community-level genetic effects may miss important variation in the interactions among individuals 489  
in these communities, leading to an underestimate of 490  
genetic effects in ecosystems. It is possible that these 491  
underlying differences in interactions among lichen 492  
could lead to differences in community composition 493  
at a future point in time, however, this is not needed 494  
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 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.

There are several important points to consider with regard to the generalization of the observed genetically based response of the lichen networks. Body size and sessile nature of lichen important to observing genotype responses. As bark lichen individuals do not move, but grow in a largely two dimensional plane, these communities and their interactions occur in the highly localized context of the tree's bark surface. Lichen individuals are many orders of magnitude smaller than the tree individual and the life-span of a tree is many times that of a lichen. For these reasons, any genetic effects on these communities is not dampened by the movement of individuals and the mixing of the effect of different tree genotypes on the lichen community, as might occur for more mobile species (e.g. insects and birds).

We only looked at lichen, other species whose distribution, abundance or interactions respond to tree genotype, such as epiphytic plants (e.g. moss and liverworts), algae or insects, could be playing a role. Other traits could also be playing a role, such as traits that are correlated with bark roughness, such as micro-aspect, albedo, moisture, etc.

Bark roughness could possibly be 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* centrality. We did not observe specific microscopic dynamics, such as photobionts, mycobionts, endolichenic fungi and bacteria, but variation in these underlying interactions could also be playing a role. Although we can not rule out the possibility that other unmeasured tree traits or organisms correlated with bark roughness are underlying the observed patterns in bark lichen network structure, substantial research supports the importance of genetically based tree traits for communities and ecosystems (7), and in particular bark roughness for bark lichen communities (33, 34, 43).

In the present study, lichen cover, lichen species richness and composition were not responsive to tree genotype, unlike what was found in (34). This is likely, at least in part, the result of differences in sampling method and the choice of genotypes sampled leading to overall higher abundances of observed lichens. In the current study mean % total lichen cover among genotypes ranges from 60-93% cover; whereas the range reported in (34) is 0.86-18.73%. The previous study used a visual estimation method, unlike the current study, which observed lichen at the scale of 1 cm<sup>2</sup> cells, which could over-estimate cover depending on the frequency at which actual thallus size was less than 1 cm<sup>2</sup>. The previous study used samples from both the northern and southern aspects of each tree; whereas, the current study only observed lichen on the northern aspect. Also, our current results are likely different from the previous study because the current study selected genotypes that tended to have bark lichen, with the interest of focusing on generating networks for comparison. These differences do not negate the findings of either study but is important to explain the differences in the findings, particularly in the community-level effects of tree genotype.

**Implications for Interspecific Indirect Genetic Effects (IIGEs).** Initially, evolution in a community context was focused on examples of highly co-evolved pairs of species (e.g. Darwin's famous prediction of the Sphinx Moth and Christmas Orchid) (8). However, studies of diffuse co-evolution (*sensu* (44)) (45, 46), geographic mosaics of co-evolution (32) and community genetics (10) have provided an in-road for ecological network approaches (20, 23, 47) to illuminate a more complex perspective of the interface between ecological and evolutionary dynamics.

Interspecific indirect genetic effects (IIGE) theory as provided a quantitative framework within which to approach evolutionary theory at higher levels of biological organization: from populations to communities and ecosystems. To date, this theory has focused on modeling the strong effects of foundation species (26, 48), but it has not yet integrated developments in the ecological or evolutionary network theory literature. This is to say that it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated this network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be dampened or magnified within the system of interacting species. For example, (23) 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 (49). Furthermore, in a predator-prey-plant study, Smith (19), showed that the interactions among species across trophic levels depended on plant genotype. Also, work by (50-52) observed consistent patterns of centralized interactions of species modules focused around hubs of plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have disproportionate numbers of interactions with other species and likely are the drivers in determining community assembly, structure and dynamics.

The results of the current study provides clear empirical evidence that networks points to the need to expand IIGEs encompass the structure of interaction networks. Although such a synthesis necessitates a much greater effort than can be afforded in this paper, it is possible to point to several productive

pathways forward. In terms of interaction networks, foundation species are relatively central within the system of interactions, that is their direct and/or indirect effects are greater than other species. So, when the more centralized (foundation) species have genetically based interactions, genetic effects will tend to be magnified in the community. Here, we found that even though more abundant or more centralized (i.e. “important”) species were present in the community, their effects were not the main component responding to genetic effects. Considering the impact of network structure would be a productive path forward for the theoretical development and application of the IIGE concept.

With regard to the evolutionary implications of network structure, ecological network studies have focused on asymmetry and the quantification of its structure in communities, with qualitative discussion of the impacts on evolutionary dynamics (28, 32, 53, 54). More specific predictions, with a quantitative framework, can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities. One seemingly useful direction from evolutionary network developments from game theory is the classification of networks into two general categories, rooted and cyclic, in which rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but these effects do not have connections back to the origins, whereas cyclic networks contain feedbacks to one or more origins. Although it did not explicitly define it in this context, the previous work (16), developed that the structure of the network in the context of a foundation species, such as cottonwoods in which there are demonstrable community level genetic effects, is that of a multiple origin network. This builds on many previous studies demonstrating that the community level effects vary among multiple genotypes. It is not clear what potential there is for feedbacks there are to the origins (e.g. the cottonwood genotypes) from the community, and as such it cannot be determined whether these networks are cyclic or rooted. In other systems, lignicolous lichens can have demonstrable positive effects on the availability of nutrients for the trees that they are associated with, but this has not been measured in the current system. Illucidating the absence and/or presence and quantifying such feedbacks would allow for the determination of the

cyclic nature and potential evolutionary dynamics of this system. The presence of feedbacks would provide the potential for non-linear dynamics in which evolutionary effects are damped or amplified by the structure of the network. For example, a star structure in which there is a primary or core set of central species with feedbacks from the radiating species has been demonstrated to be a structure that amplifies evolutionary dynamics (27). If such feedbacks do not exist, and these sub-networks of the lichen and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to generally promote diversification as variation arising from the shifting distribution of the “roots”, i.e. genotypes; however, loss of genotype/root diversity could lead to fixation of a single genotype in the population and a decrease in community-wide diversity.

**Conclusion.** 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 (48, 55). In the face of the high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed to some in previous studies (15, 56, 57). In the present study, we 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 (58). 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 influ-

ence 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 result in differences in rates of 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 (3, 32).

*Add evolutionary unit to the larger narrative. That is mainly that identifying how evolution might be acting on multiple species is useful for conservation and management.*

*Discuss the impacts of P. betae removal on network structure per Lau 2016 and Keith 2017. Also, what about Barbour 2016.*

## Other studies that should be discussed:

- 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). Also discuss Lamit 2015 and Holeski's multivarite phenotype paper.
- 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).

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## Supplementary Materials

### Tables.

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	df	SS	R2	F	p-value
geno	9.0000	44078.1324	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	
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	0.4543	
Percent Rough Bark	4.8526	0.3221	0.0113	
pH	0.0000	0.0000	1.0000	
Carbon-Nitrogen Ratio	0.0000	0.0000	1.0000	
Condensed Tannins	3.0522	0.3205	0.0343	
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.**

lichen species	mean	statistic	H2	p-value
Positive				
In-Degree				
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
Out-Degree				
X. galericulata	0.027	0	0	0.4543
C. subdeflexa	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4247
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
Negative				
In-Degree				
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
Out-Degree				
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 3. 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 4. 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 5. Pseudo-F Table of lichen community similarity  
PERMANOVA.**

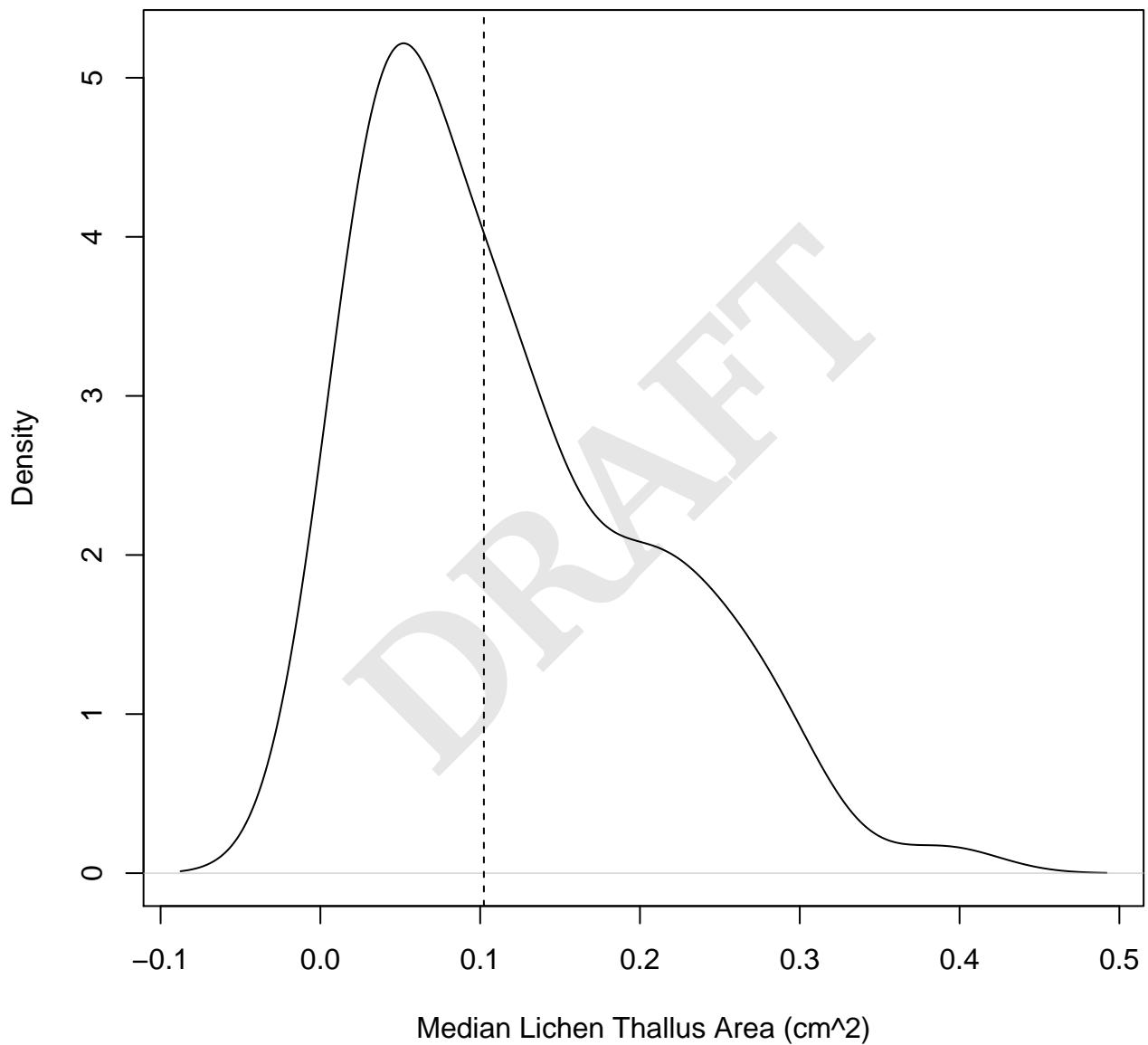
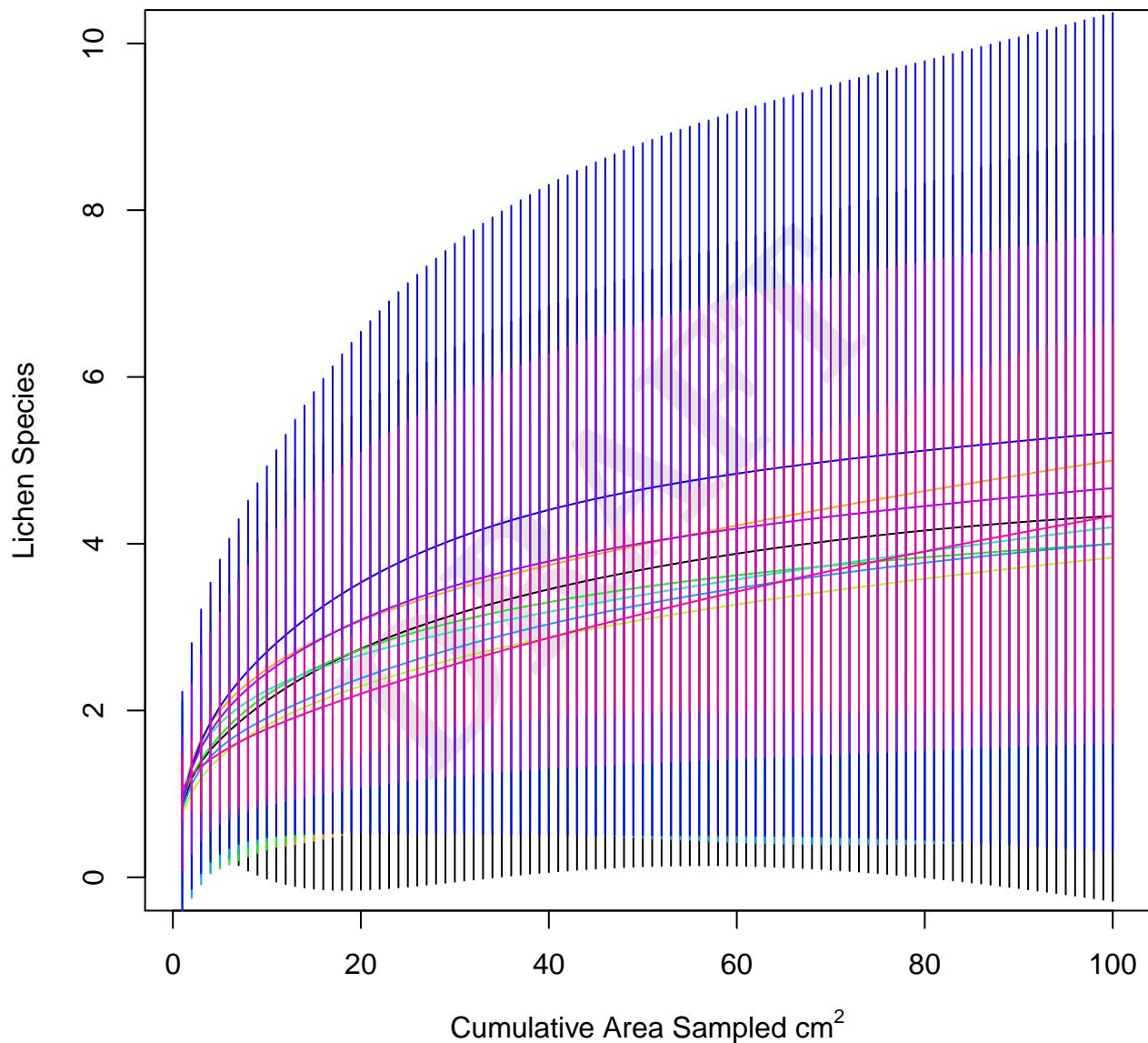


Fig. 1



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

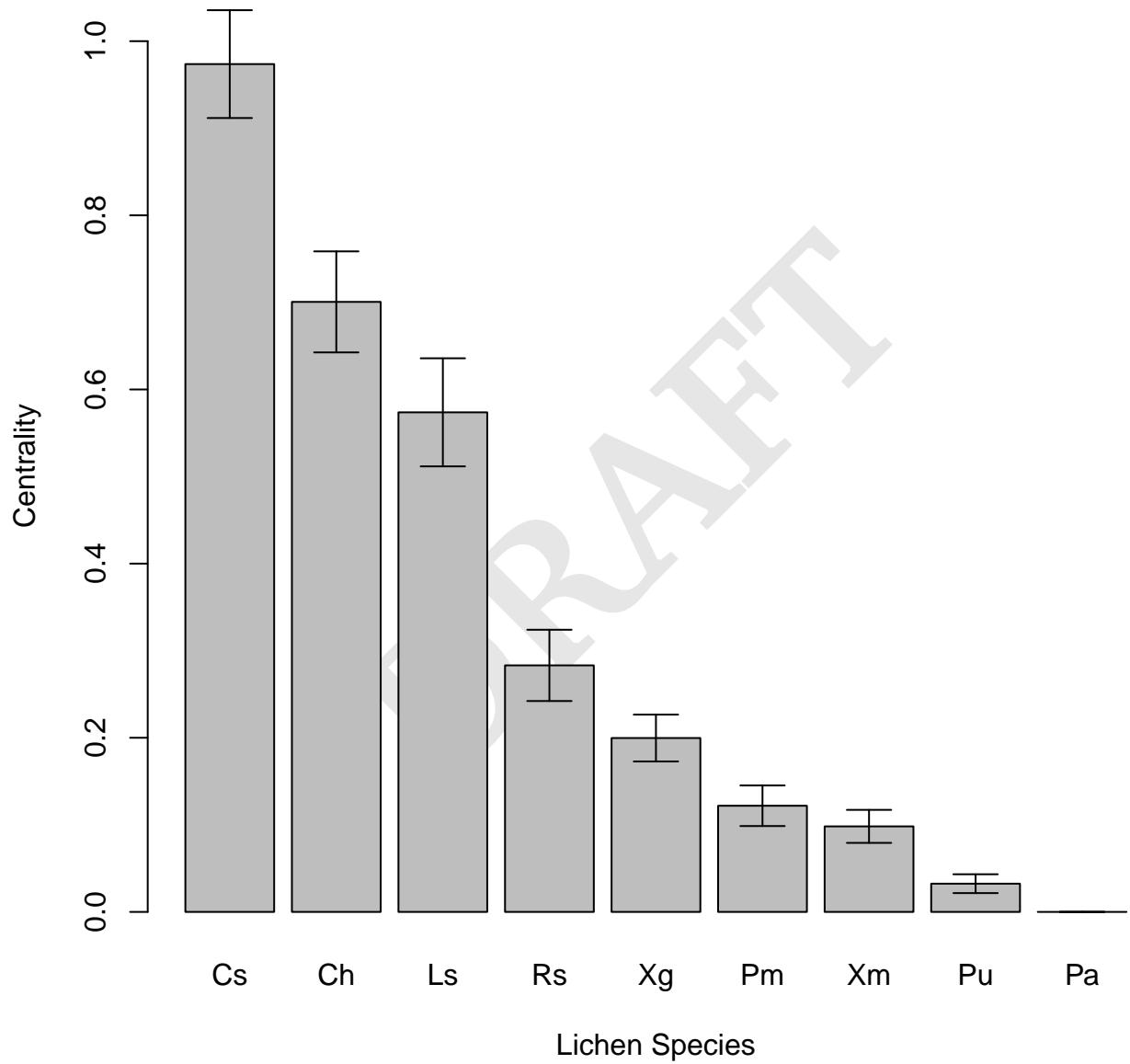


Fig. 3