

# Genotypic variation in a foundation tree results in heritable ecological network structure of lignicolous lichen

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1 Biological evolution occurs in the context of complex ecosystems of  
2 interacting species whereby natural selection defines the structure  
3 of ecological networks. Fundamental to understanding evolutionary  
4 processes is elucidating the genetic basis to ecological network  
5 structure, which is defined by interactions among species. Although  
6 previous work has demonstrated that genotypic variation in foundation  
7 species contributes to interaction network structure, we are not  
8 aware of a study that has quantified the genetic contribution to network  
9 structure or shown network structure to be a heritable trait. To  
10 examine this, in a 20+ year common garden we observed interactions  
11 among nine epiphytic lichen species associated with genotypes of  
12 (*Populus angustifolia*), a foundation species of riparian ecosystems.  
13 We constructed signed, weighted, directed interaction networks for  
14 the lichens and conducted genetic analyses of whole network similarity,  
15 degree and centralization. We found three primary results.  
16 First, using multiple metrics, tree genotype significantly predicted  
17 lichen network structure; i.e., clonal replicates of the same genotype  
18 tended to support more similar lichen networks than different genotypes.  
19 Second, broad sense heritability estimates show that plant  
20 genotype explains network similarity ( $H^2 = 0.41$ ), network degree  
21 ( $H^2 = 0.32$ ) and network centralization ( $H^2 = 0.33$ ). Third, one of  
22 the examined tree traits, bark roughness, was also heritable ( $H^2 = 0.32$ )  
23 and significantly correlated with lichen network similarity ( $R^2 = 0.26$ ), supporting a mechanistic pathway from variation in a heritable  
24 tree trait and the genetically based variation in lichen network  
25 structure that selection can act upon. We conclude that tree genotype  
26 can influence not only the relative abundances of organisms but also the interaction network structure of associated organisms.  
27 Given that variation in network structure can have consequences for  
28 the dynamics of communities through altering system-wide stability  
29 and resilience and modulating perturbations, these results have im-  
30 portant implications for the evolutionary dynamics of ecosystems.

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

1 Evolution occurs in the context of complex ecolog-  
2 ical networks. Community genetics studies have  
3 shown that genetic variation in foundation species,  
4 which have large effects on communities and ecosystems by modulating and stabilizing local conditions  
5 (1), plays a significant role in defining distinct communities of interacting organisms: such as, endophytes,  
6 pathogens, lichens, arthropods, and soil microbes (2–

4). Multiple studies have now demonstrated that genetic variation influences numerous functional traits (e.g., phytochemical, phenological, morphological) that in combination results in a multivariate functional trait phenotype (5) in which individual plant genotypes support different communities and ecosystem processes (6, 7). The importance of genetic variation in structuring ecological systems was reviewed

## 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 network structure. Here, we used a 20+ year common garden experiment to reveal the effect that genotypic variation can have on networks of lichens that colonize the bark of a foundation tree species. We found that lichen interaction network structure is genetically based and primarily driven by 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 species interactions that can generate heritable network variation that selection can act upon.

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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(8), 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 support that selection, acting on this heritable variation, tends to occur among groups of species (9) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly (10) and species interactions (6, 11, 12), which shape the structure of ecological interaction networks (13–15).

In this community-level context, the “genetic similarity rule” provides a useful framework we can apply to interaction networks at the nexus of ecological and evolutionary dynamics. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, (16) observed that individuals genotypes that are more genetically similar will tend to have similar phytochemical 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 (17) and community genetics studies have primarily focused on community composition in terms of the abundance of species (8). Some studies have examined the effects of genetic variation on trophic chains in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (18–22) 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 (23, 24) and both found that genotypic diversity generates increased network modularity (i.e., compartmentalization). However, both of these studies were examining networks at the scale of forest stands, rather than networks associated with 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. 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 (25, 26).

The development of interspecific indirect genetic

effects (IIGE) theory (27) in evolutionary biology points to the importance of studying the genetic basis of interaction network structure because genetic based differences in network structure among individuals can be acted upon by natural selection when there are fitness consequences of different networks of IIGEs that can result in community evolution (28). For example, although the analysis was of abundances rather than interaction networks, (29, 30) found that the mycorrhizal communities on the roots of drought tolerant and intolerant trees are dominated by different orders of ectomycorrhizal fungal mutualists that also differ in the benefits they provide that enhance tree performance. Because drought tolerant genotypes are three times more likely to survive record droughts, selection acts both on the tree and its fungal community and with increased drought the community phenotype has changed over time. Also, in an antagonistic interaction context, (2) found that with the addition of a damaging leaf pathogen to cottonwoods in a common garden, the impacts of these strong interactors results in a different and diminished community of arthropods relative to control trees. Thus, selection acting on the tree may alter the network structure of associated communities in which different networks of communities are most likely to survive pathogen outbreaks. Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative fitness of the tree), selection on tree, community or both can change network structure (28) and thereby alter community dynamics. Evolutionary applications of network theory have demonstrated that indirect effects of interactions among species can lead to network structures that amplify or dampen the effects of selection (31). 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 amplify selection events.

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. 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 clonally replicated *Populus angustifolia* individuals of known genetic identity . We

115 focused on a community of 9 epiphytic lichen species,  
116 as previous research has demonstrated significant  
117 compositional responses of epiphytes to genotypic  
118 variation (32, 33). Applying a probability-theory  
119 based network modeling approach, we constructed a  
120 set of interaction network models for the lichens asso-  
121 ciated with individual trees. Using these models, we  
122 then examined the genetic basis of the structure of  
123 these ecological networks via several network metrics  
124 that measures different aspects of network structure  
125 at the scale of individual species (i.e., nodes) or the  
126 entire network observed on each tree genotype. In  
127 particular, we focus the metric of centrality for indi-  
128 vidual species and centralization for whole networks,  
129 which measures how much a species is connected in  
130 the network relative to other species. We hypothe-  
131 size that in natural systems evolution occurs in a  
132 community context involving interactions of complex  
133 networks of interacting species (23, 24, 34, 35). If  
134 correct, we expect to find that network structure  
135 is genetically based, or, in other words, plant geno-  
136 types will support different and heritable interac-  
137 tion networks. Based on community genetics theory,  
138 particularly the community similarity rule (16), we  
139 hypothesize that trees will co-vary in functional phe-  
140 notypic traits such as bark roughness and chemical  
141 composition and trees of the same genotype will tend  
142 to have similar traits leading to similarities in lichen  
143 network structure. This work is important because it  
144 provides a mechanistic basis for understanding how  
145 community network theory is intimately associated  
146 with the evolutionary process and how human alter-  
147 ations of the environment (e.g., climate change, inva-  
148 sive species, pollution) may have cascading, indirect  
149 effects that alter network structure and evolution.

## 150 Materials and Methods

151

152 **Study System.** The study was conducted along the We-  
153 ber River, UT (USA), which is a cottonwood (*Populus*  
154 spp.) dominated riparian ecosystem. Although two native  
155 species, *Populus angustifolia* (James) and *Populus fremontii*  
156 (S. Watson), occur here and are known to hybridize,  
157 only pure or advanced generation backcrosses of *P. angus-*  
158 *tifolia* were sampled. Bark lichens have been intensively  
159 sampled in this system and provide an ideal community in  
160 which to observe and model interaction networks, as their  
161 sessile nature permits accurate identification of individu-  
162 als and their highly localized, direct contact interactions  
163 and slow population turnover rates facilitate the assess-

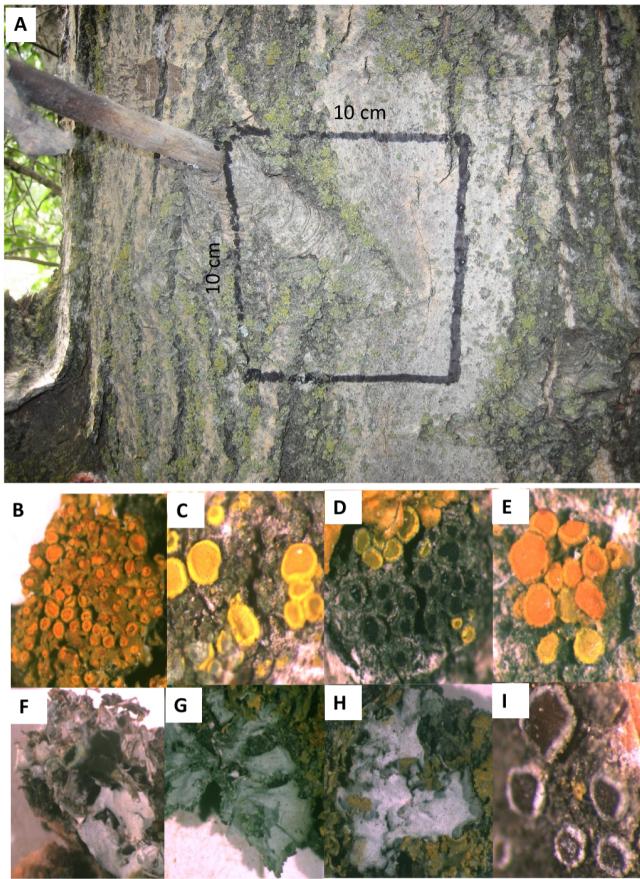
164 ment of interactions among lichen species on individual  
165 trees (36).

166 A long-term, common garden experiment was used  
167 to isolate the effect of tree genotype from the effect of  
168 the localized microenvironment associated with each indi-  
169 vidual and spatial autocorrelation. Established in 1992,  
170 asexually propagated clones of genotyped *P. angustifo-*  
171 *lia* individuals were obtained from wild collections and  
172 planted in fully randomized design at the Ogden Nature  
173 Center, Ogden, UT. From the population of established  
174 individuals in the common garden, we chose a total of  
175 ten genotypes, replicated between 3 and 8 times each, for  
176 sampling.

177 **Bark Lichen and Trait Observations.** On each tree, pres-  
178 ence or absence of each lichen species was assessed in 50  
179 total 1 cm<sup>2</sup> cells arrayed in a checkerboard pattern. Given  
180 the small size and sessile nature of lichens, we were able to  
181 rapidly assess lichen interactions by quantifying thalli in  
182 close contact. Sampling was restricted to the northern as-  
183 pect of the trunk to maximize the abundance of lichen and  
184 control for the effect of trunk aspect. Two adjacent 100  
185 cm<sup>2</sup> quadrats centered at 50 cm and 95 cm from ground  
186 level were sampled (Fig 1 A and B). The observed lichen  
187 community included (abbreviations are given for species  
188 present in study): Xg = *Xanthomendoza galericulata*, Xm  
189 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Cande-*  
190 *lariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora*  
191 *hagenii*, Pm = *Phyciella melanchra*, Pa = *Physcia adscen-*  
192 *dens*, Pu = *Physcia undulata*. Several other species were  
193 not obesrvd in the present study but are known to occur  
194 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia*  
195 *ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

196 The cell size and checkerboard sampling pattern was  
197 chosen to isolate the individuals in each cell. In a previous  
198 survey of lichen thallus size in this common garden, we  
199 had observed a median thallus size of  $0.12 \pm 0.001 \text{ cm}^2$  (1  
200 S.E.) (see Supporting Information). Based on the median  
201 thallus size, we expected thalli observed in each cell to  
202 generally be spatially independent of thalli present in  
203 other cells but exposed to similar micro-environmental  
204 conditions created by the bark and the location of the  
205 sampling area on an individual tree. Therefore, we were  
206 confident in treating the cell-wise observations in quadrats  
207 as independent with respect to lichen-lichen interactions.  
208 We quantified the texture of the bark in the quadrat is  
209 the percent of 1 cm<sup>2</sup> cells with rough bark. In addition to  
210 bark roughness, we also measured several bark chemistry  
211 traits by taking bark samples immediately adjacent to  
212 each quadrat using the methods of (36): including, the  
213 concentration of condensed tannins, pH and carbon and  
214 nitrogen concentrations and pH.

215 **Lichen Network Modeling and Analysis.** For each tree,  
216 repeated observations of lichen were made in order to con-  
217 struct replicated interaction networks for each genotype.  
218



**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*, *Phyciella melanura*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (B-D) and R.R. Naesbourg (E-I).

We conducted a modified sampling procedure originally developed by (37) with the addition that we quantified the presence of lichen in the  $1 \text{ cm}^2$  cells on individual trees of *P. angustifolia*. Unipartite networks were generated using the conditional probabilities of each species pair, i.e. the probability of observing one species given an observation of another species  $P(S_i|S_j)$ , based on the method developed by (38). To calculate conditional probabilities, we quantified the individual probabilities of species occurrences  $P(S_i)$  and the joint probability of co-occurrences  $P(S_i, S_j)$  using the frequencies of each species and their co-occurrences. We were then able to calculate the conditional probabilities of each species pair as  $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$ , based on the axioms of probability. This yielded a matrix that could possibly be asymmetric, i.e.  $P(S_i|S_j)$  does not have to be equal to  $P(S_j|S_i)$ . Another important property of this matrix is that the diagonal,  $P(S_i|S_i)$ , was equal to one for all species present and zero for species that were not observed in any cell.

We then applied an analytical procedure to remove non-significant links between species. This procedure determines if the joint probability of a species pair (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 one species' impact on another with zero being no effect and values less than or greater than zero being negative and positive effects, respectively. Here, we will refer to  $\mathbf{D}$  as a signed, weighted interaction matrix. As such,  $\mathbf{D}$  has the properties that it can be asymmetric (i.e.  $D_{ij}$  does not necessarily equal  $D_{ji}$ ) and it scales between -1 and 1, and, therefore, does not have the mathematical properties of a probabilistic network (39). Also, as the method does not track individuals within species and interactions such as competitive exclusion or facilitation within species would result in the same species being observed. Therefore, the results of intra-specific interactions always results in the same species being observed and a resulting  $D_{ii} = 0$ .

**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 and the Freeman's centrality (40). 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



**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 (38), 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.

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. To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (41) using the `signnet` package (42).

**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 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) (43) to produce dimensionally reduced ordinations of these multivariate responses and fitted vectors for continuous predictor variables to the ordinated values (44). Using random

325 initial configurations with a maximum of 500 iterations  
 326 and a change in stress threshold of less than  $10^{-12}$ . Final  
 327 configurations has the lowest stress with at most a stress  
 328 level of 0.10.

329 For each network, we also calculated metrics that measure  
 330 different structural aspects. Although there are many  
 331 other metrics, for the sake of simplicity we focus on a  
 332 subset that represent several interesting features of net-  
 333 work structure (see (17)). We calculated the number of  
 334 interactions or “links” in each network, which provides a  
 335 measure of the size of the network (23, 45). We also calcu-  
 336 lated the centralization of each network, which measures  
 337 the evenness of the distribution of interactions among  
 338 the species in the network (40). In a network with a low  
 339 level of centralization species have similar amount of  
 340 interaction in the network, while a network with a high  
 341 level of centralization tends to have one or small number  
 342 of species that interact with other species. We used a  
 343 related function to calculate the centrality of each species  
 344 (i.e. node level centrality) in each network as well.

345 For all tests where genotype was used as a predictor,  
 346 we quantified the heritability of the response variable. Be-  
 347 cause the trees in the garden were clonal replicates of each  
 348 genotype, we calculated broad-sense heritability, which  
 349 is the genotypic variance divided by the total phenotypic  
 350 variance (46). This can be interpreted as a measure of  
 351 the phenotypic variance due to genotypic variation. We  
 352 also apply this to the community genetics context as the  
 353 variance in *extended* phenotypic variance due to genotypic  
 354 variation (47). For the multivariate analyses, where we  
 355 employ PERMANOVA, we followed the methods of (27)  
 356 to adjust the degrees of freedom for unbalanced genotype  
 357 replicates.

358 All code and data for the project are openly avail-  
 359 able online. Code and data are available at [github.com/](https://github.com/)  
 360 [ecgen/comgen](https://ecgen/comgen). The project is also archived via Zenodo  
 361 at [zenodo.com/doiXXXXXX](https://zenodo.com/doiXXXXXX). All analyses were conducted  
 362 using the programming language R version 3.6.1 (R De-  
 363 velopment Core Team 2019).

## 364 Results

365 Tree genotype influenced lichen network structure  
 366 and multiple lichen network metrics were herita-  
 367 ble. Tree genotype significantly predicted the struc-  
 368 tural similarity of lichen networks (PERMANOVA:  
 369 Pseudo- $F_{9,27} = 3.58$ ,  $H^2 = 0.41$ ,  $p\text{-value} = 0.0537$ )  
 370 (Fig. 4). Overall network level metrics responded  
 371 significantly to tree genotype (Table 1), including  
 372 network degree ( $RLRT = 3.52$ ,  $H^2 = 0.32$ ,  $p\text{-value} =$   
 373 0.0255) and centralization including both in-coming  
 374 and out-going links ( $RLRT = 4.04$ ,  $H^2 = 0.33$ ,  $p\text{-value} =$   
 375 0.0184) or when separated into in-coming only  
 376 ( $RLRT = 3.9852$ ,  $H^2 = 0.3309$ ,  $p\text{-value} =$   
 377 0.0190) or out-going only ( $RLRT = 3.8615$ ,  $H^2 =$

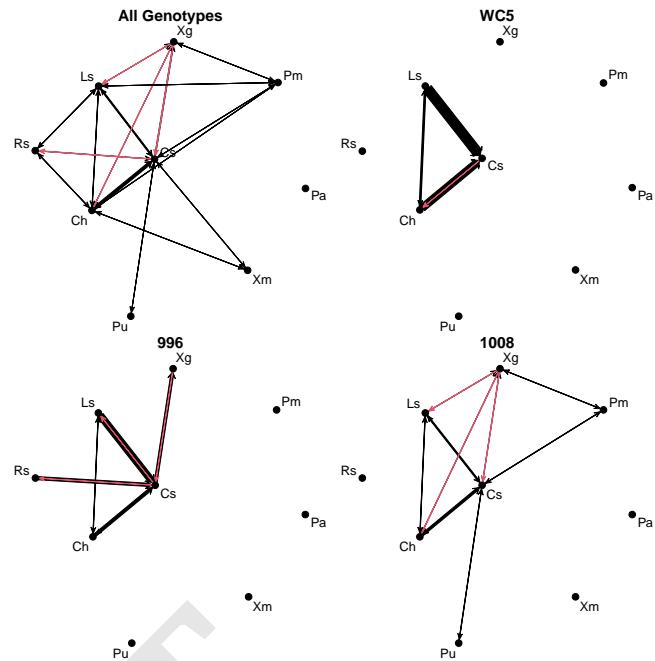
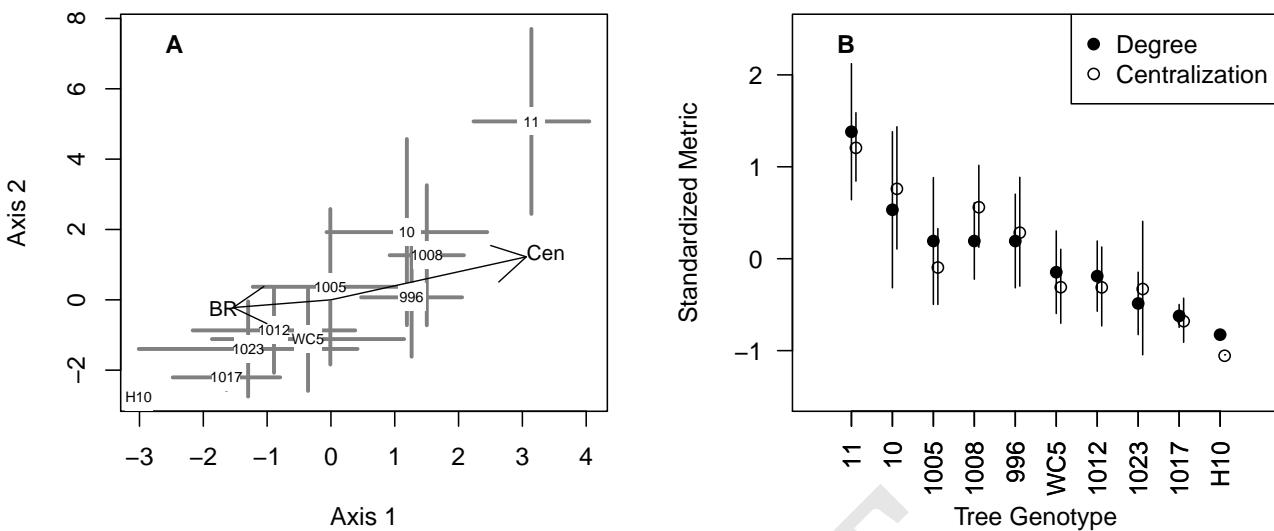


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, 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.

378 0.3193,  $p\text{-value} = 0.0205$ ). Metrics including only  
 379 positive links also showed a significant effect of tree  
 380 genotype, including positive degree ( $RLRT = 3.6925$ ,  
 381  $H^2 = 0.3242$ ,  $p\text{-value} = 0.0229$ ), positive in-going  
 382 centralization ( $RLRT = 4.4812$ ,  $H^2 = 0.3487$ ,  $p\text{-value} =$   
 383 0.0142). Metrics calculated with negative  
 384 links were not significant, including degree (negative)  
 385 ( $RLRT = 0.0327$ ,  $H^2 = 0.0318$ ,  $p\text{-value} = 0.3859$ )  
 386 and both in-coming (negative) ( $RLRT = 0.3304$ ,  $H^2 =$   
 387 0.1057,  $p\text{-value} = 0.2508$ ) and out-going centraliza-  
 388 tion (negative) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ ,  
 389  $p\text{-value} = 0.3446$ ).

390 The genetic response of network centralization was  
 391 driven by variation in *Caloplaca holocarpa*. Central-  
 392 ity varied significantly among species ( $F_{8,324} = 7.99$ ,  
 393  $R^2 = 0.16$ ,  $p\text{-value} < 0.0001$ ). *Caloplaca holocarpa*  
 394 centrality was the main species to exhibit a signifi-  
 395 cant response to tree genotype in terms of positive  
 396 centralization for both the in-coming ( $RLRT = 3.61$ ,  $H^2 =$   
 397 0.32,  $p\text{-value} = 0.0240$ ) and out-going ( $RLRT =$   
 398 3.13,  $H^2 = 0.30$ ,  $p\text{-value} = 0.0327$ ) perspectives, but  
 399 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 ( $\pm 1$  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 ( $\pm 1$  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.

response	df	statistic	H2	p-value
Lichen Network Similarity	9	3.5821	0.41	0.0537
Degree		3.5175	0.32	0.0255
Degree (positive)		3.6925	0.32	0.0229
Degree (negative)		0.0327	0.03	0.3859
Centralization		4.0444	0.33	0.0184
Centralization In-Degree		4.4812	0.35	0.0142
Centralization In-Degree (positive)		3.9852	0.33	0.0190
Centralization In-Degree (negative)		0.3304	0.11	0.2508
Centralization Out-Degree		3.8615	0.32	0.0205
Centralization Out-Degree (positive)		3.5585	0.31	0.0248
Centralization Out-Degree (negative)		0.0862	0.05	0.3446

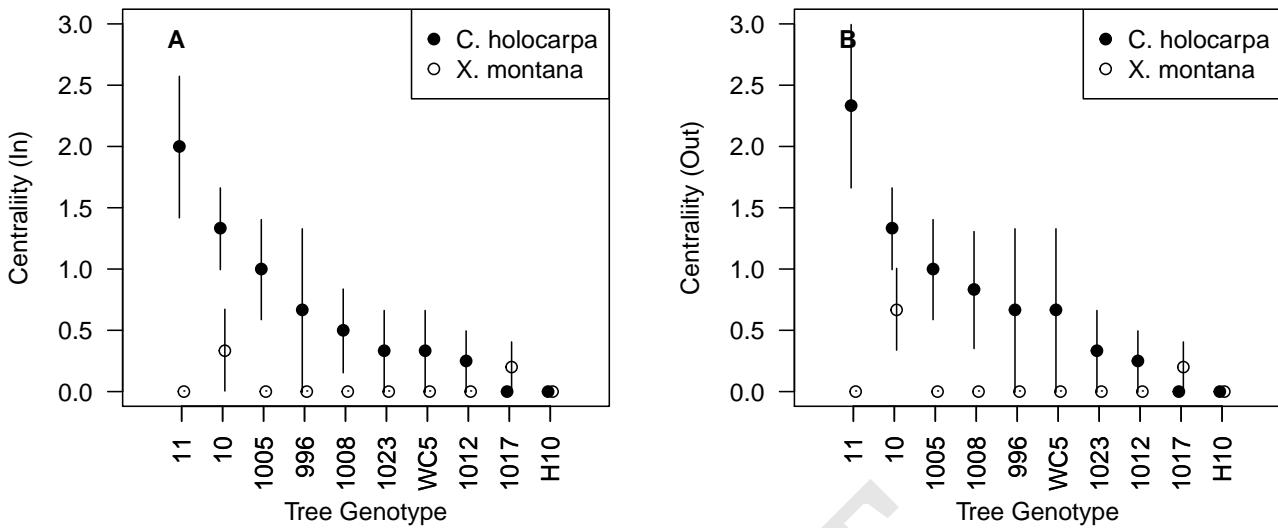
**Table 1. Genotypic effects on the associated lichen network structure.**

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

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 was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen network structure via 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 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 cen-



**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.

tralization 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).

	df	SumOfSqs	R2	F	Pr(>F)
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

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

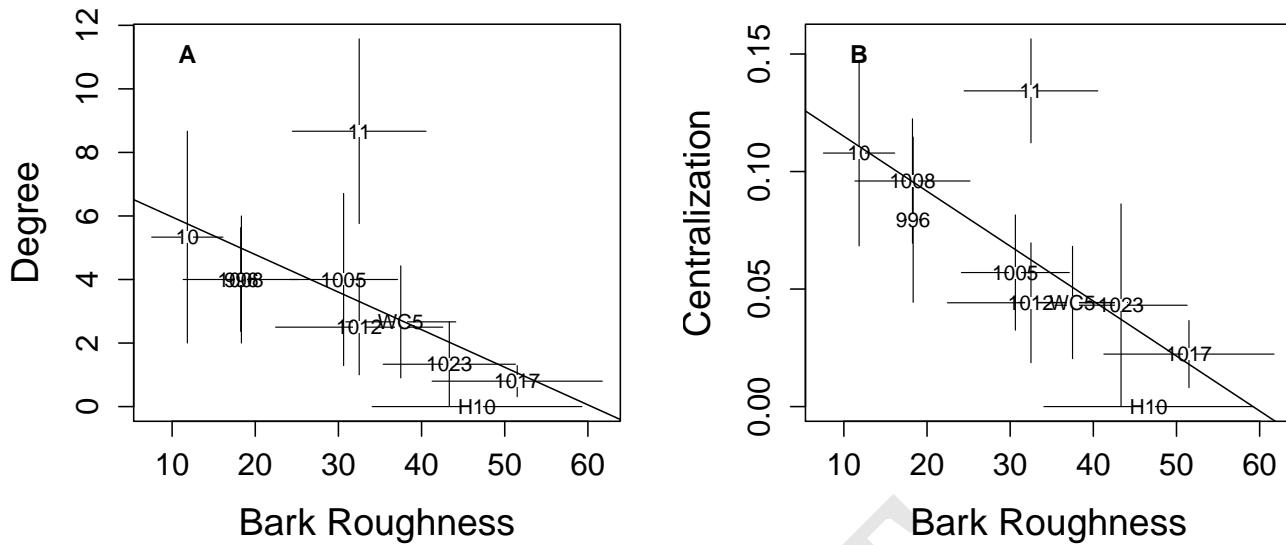
## Discussion

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*. The genetically based trait, bark roughness, was the only trait observed to effect network vari-

ation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control (48), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (37); 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.

## Implications of the Heritability of Interaction Network Structure.

We found significant heritability of lichen interaction network structure, and, in line with the genetic similarity rule, networks observed on trees of the same genotype tended to be structurally similar. Although previous studies have examined aspects of networks, such as trophic (49) and forest stand-level interaction network structure (24, 50), this is the first study that we are aware of to examine the heritability of network structure with replicated networks at the genotype scale. Previous work in the evolution of ecological networks have primarily focused on macro-evolutionary dynamics (13, 51–53) or have been simulation based individual-level models that integrate intraspecific variation to the species level (54), even though recent syntheses ave pointed



**Fig. 6.** Bivariate plots of the negative relationship between bark roughness and two 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 line calculated using the genotype means. Generally, as roughness increased the number of interactions (degree) and dominance of those interactions decreased.

to the importance of processes operating across scales of organization (55). There are several important functional ramifications of genetically based variation in network structure. First, intra-specific diversity could be creating lichen interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily determined by another organism, these communities inherently form modules within the larger ecosystem, as they tend to interact more with each other than with other individuals (17). Our study demonstrates that the environmental differences determined by the genetic variation within a single species can create differences that not only impacts community composition, as repeatedly demonstrated in other community genetics studies (8, 11), but also the structure of interactions among individuals within these modules. 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 demon-

strated 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. 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 (56). 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 that is found on that tree genotype.

Second, 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. As such differences in network structure could occur without observable differences in species richness or community composition, which have been the pri-

533 mary focus of almost all previous community genetics  
534 studies (8). Community composition of lichen has  
535 previously been observed to be different among tree  
536 genotype in the same experimental garden (36, 37),  
537 the difference between the present study is likely a re-  
538 sult of differences in sampling method and the choice  
539 of genotypes leading to overall higher abundances of  
540 observed lichens to assure the possibility of observing  
541 xlichen interactions. The previous study also used a  
542 visual estimation method, unlike the current study,  
543 which observed lichen at the scale of 1 cm<sup>2</sup> cells,  
544 which could over-estimate cover depending on the  
545 frequency at which actual thallus size was less than  
546 1 cm<sup>2</sup>, as well as both the northern and southern  
547 aspects of each tree. These differences do not negate  
548 the findings of either study. The present study's  
549 finding of differences in network structure without  
550 significant compositional differences points to the  
551 importance of quantifying how network structure  
552 changes in response to genetic variation in order to  
553 fully understand evolutionary dynamics in complex  
554 communities. Having not observed a compositional  
555 effect of tree genotype without measuring the net-  
556 work structure could lead to the conclusion of no  
557 genetic effect on the community, even though im-  
558 portant variation in network structure are leading  
559 to evolutionary dynamics. It is possible that these  
560 underlying differences in interactions among lichen  
561 could lead to differences in community composition  
562 at a future point in time via there effects on species  
563 abundances (27); however, this is not needed for  
564 evolutionary dynamics to play out via selection that  
565 leads to shifts in trait distributions without shifting  
566 species abundance distributions, which is possible  
567 under stabilizing, disruptive and directional selection  
568 (46). Thus, it is imperative that further community  
569 genetics research assess or at least be aware of the  
570 potential effects of variation in interactions and not  
571 just observe species abundances.

572 **Evolutionary Implications of a Genetic Basis to**  
573 **Network Structure.** A genetic basis to network struc-  
574 ture suggests that some amount of interaction net-  
575 work complexity is determined and therefore could  
576 be predicted. Variation in space and time create  
577 variation in ecological networks that influences evo-  
578 lutionary dynamics via shifts in ecological dynamics,  
579 such as population demographics (55). Given that  
580 ecosystems are comprised of hundreds and thousands  
581 of species, each having a multitude of interactions,

582 the potential to find traction for making predictions  
583 in the context of ecological, let alone evolutionary, dy-  
584 namics seems daunting. The promise of predictability  
585 lies in the presence of assymetries in ecosystems that  
586 contribute to the occurrence of foundation species,  
587 such as hierarchy and nestedness created by body  
588 size differences or life-history strategies, has been  
589 widely observed (1). The second part is that heri-  
590 tability (i.e., genetic determination) means that there  
591 is structure in the spatial or temporal variation that  
592 is created by individuals of foundation species whose  
593 traits are in part determined by underlying trait  
594 differences. Although this variation is inherently  
595 a function of both genetics and environmental ef-  
596 fects (46), the community and network level effects  
597 are also a function of the scale of the interaction  
598 (27). Self-organization of the dynamics within these  
599 communities also points to a mechanism for strong  
600 community and ecosystem effects of genetic variation,  
601 contributing to what may seem unlikely magnitudes  
602 of genetic effects as has been observed in some sys-  
603 tems, such as forest in riparian ecosystems (16).  
604

605 Ecological network studies have focused on asym-  
606 metry and the quantification of its structure in com-  
607 munities, with qualitative discussion of the impacts  
608 on evolutionary dynamics (34, 35, 57, 58). More spe-  
609 cific predication, within a quantitative framework,  
610 can be found in applications of evolutionary game  
611 theory, and although developed at the population  
612 scale, such theory can apply to communities. One  
613 seemingly useful direction from evolutionary network  
614 developments from game theory is the classification  
615 of networks into two general categories, rooted and  
616 cyclic, in which rooted networks have interactions  
617 in which evolutionary effects emanate from one or  
618 multiple origins but these effects do not have con-  
619 nections back to the origins, whereas cyclic networks  
620 contain feedbacks to one or more origins. Although  
621 it did not explicitly define it in this context, the  
622 previous work of (17) developed the perspective that  
623 the structure of the network in the context of a foun-  
624 dation species, such as cottonwoods in which there  
625 are demonstrable community level genetic effects, is  
626 inherently created when trait variation among geno-  
627 types of a foundation species has ecological effects  
628 on associated species.  
629

630 This builds on many previous studies demon-  
631 strating that the community level effects vary among  
632 multiple genotypes. It is not clear what potential  
633

631 there is for feedbacks there are to the origins (e.g. the  
632 cottonwood genotypes) from the community, and as  
633 such it cannot be determined whether these networks  
634 are cyclic or rooted. In terrestrial ecosystems, lichen  
635 play important ecological roles, such as substrate  
636 stabilization (59) and nutrient fixation (60). In some  
637 systems lignicolous lichens can have demonstrable ef-  
638 fects on the availability of nutrients for the trees that  
639 they are associated with (61), although this has not  
640 been measured for the lichen in the current study's  
641 systemq. Elucidating the absence and/or presence of  
642 and quantifying such feedbacks would allow for the  
643 determination of the cyclic nature and potential evo-  
644 lutionary dynamics of this system. The presence of  
645 feedbacks would provide the potential for non-linear  
646 dynamics in which evolutionary effects are damped  
647 or amplified by the structure of the network. For  
648 example, a star structure in which there is a primary  
649 or core set of central species with feedbacks from  
650 the radiating species has been demonstrated to be a  
651 structure that amplifies evolutionary dynamics (31).  
652 If such feedbacks do not exist, these sub-networks of  
653 the lichen and tree genotypes are likely to be multi-  
654 rooted networks. Such a structure is theorized to  
655 generally promote diversification as variation aris-  
656 ing from the shifting distribution of the “roots”, i.e.  
657 genotypes; however, loss of genotype/root diversity  
658 could lead to fixation of a single genotype in the pop-  
659 ulation and a decrease in community-wide diversity.  
660 However, such feedbacks to tree fitness are not nec-  
661 essary for evolutionary dynamics to play out within  
662 the lichen networks through the effects of altered  
663 network structure on lichen interaction outcomes,  
664 such as competitive exclusion leading to selection.

665 Since lichen are multi-species complexes, there is  
666 also the potential for evolutionary dynamics to shift  
667 within the context of the lichen symbiosis. There is  
668 substantial evidence that lichen have served as the  
669 “cradle of symbiotic fungal diversification” (62)  
670 and recent research has shown significant network  
671 structure of endolichenic fungi and lichen collected  
672 from across North America (63). Analysis of the  
673 structure of ecological networks has generally sup-  
674 ported the conclusion that nestedness, or the degree  
675 to which species tend to interact with similar sub-  
676 sets of the community, tends to promote stability in  
677 mutualistic, primarily bipartite (i.e., two-mode), net-  
678 works and modularity contributes to the stabilization  
679 of antagonistic networks (64, 65). Although there is

680 growing evidence that the nestedness of mutualistic  
681 networks is not necessarily the result of selection for  
682 systems-level properties that promote stability but  
683 could be either product of asymptotic abundance dis-  
684 tributions leading to un-even interaction frequencies  
685 (66) and/or a by-product of selection and divergence  
686 creating network “spandrels” in ecosystems (52), this  
687 does not preclude the functional consequences of net-  
688 work structure but rather the developmental or evo-  
689 lutionary processes that have produced the structure.  
690 In the present study, we did not examine nestedness  
691 or modularity of the lichen networks as we could not  
692 find metrics for analyzing networks that are not only  
693 weighted and directed but also signed. Hopefully  
694 future network theoretic developments will make  
695 the appropriate metrics available to conduct these  
696 analyses.

697 **Implications for Interspecific Indirect Genetic Ef-  
698 ffects (IIGEs).** Interspecific indirect genetic effects  
699 (IIGE) theory provides a quantitative framework  
700 within which to approach evolutionary theory at  
701 higher levels of biological organization: from pop-  
702 ulations to communities and ecosystems. To date,  
703 this theory has focused on modeling the strong ef-  
704 ffects of foundation species (7, 27), but it has not  
705 yet integrated developments in the ecological or evo-  
706 lutionary network theory literature. This is to say  
707 that it has not developed a way to examine com-  
708 plex interactions among species; however, previous  
709 studies have demonstrated this network context is  
710 likely to be important, as altering the structure of  
711 interaction networks provides a means for genetic  
712 effects to be damped or magnified within the sys-  
713 tem of interacting species. For example, (24) showed  
714 that the genetics based interactions of aphid resis-  
715 tant and aphid susceptible trees resulted in different  
716 interaction networks of their associated arthropod  
717 communities composed of 139 species. At the scale  
718 of ecosystems, trophic networks or food webs direct  
719 and control the rates of energy and nutrient flux (67).  
720 Furthermore, in a predator-prey-plant study, Smith  
721 (20), showed that the interactions among species  
722 across trophic levels depended on plant genotype.  
723 Also, work by (68–70) observed consistent patterns  
724 of centralized interactions of species modules focused  
725 around hubs of plant-fungal interactions. In other  
726 words, a small number of plant and fungal symbionts  
727 tended to have disproportionate numbers of interac-  
728 tions with other species and likely are the drivers

729 in determining community assembly, structure and  
730 dynamics.

731 The results of the current study provides clear empirical evidence that variation in network structure  
732 can be genetically based (i.e. heritable) and points to  
733 the need to expand IIGEs encompass the structure  
734 of interaction networks. Although such a synthesis  
735 necessitates a much greater effort than can be afforded in this paper, it is possible to point to several  
736 productive pathways forward. In terms of interaction  
737 networks, foundation species are relatively central  
738 within the system of interactions, that is their direct  
739 and/or indirect effects are greater than other species.  
740 So, when the more centralized (foundation) species  
741 have genetically based interactions, genetic effects  
742 will tend to be magnified in the community. Here,  
743 we found that even though more abundant or more  
744 centralized (i.e. “important”) species were present in  
745 the community, their effects were not the main component responding to genetic effects. Considering the  
746 impact of network structure would be a productive  
747 path forward for the theoretical development and  
748 application of the IIGE concept. These results also  
749 provide insights into the dynamics of real ecosystems  
750 and the potential inter-play of ecology and evolution  
751 with regard to empirical and theoretical support for  
752 neutral theory, as models have been developed that  
753 can reconstruct interactions networks with similar  
754 structural characteristics to those observed in real  
755 ecosystems (71). The findings of our study support  
756 the possibility that, although communities and their  
757 interaction networks may assemble as a result of  
758 conditions that are entirely agnostic to functional  
759 variation, if there are strong ecological asymmetries,  
760 such as the case in foundation species systems, then  
761 spatial and temporal variation in network structure  
762 will arise as a result of trait variation within the  
763 foundation species. Taking even the extreme case,  
764 even when such genetically based variation is the result  
765 of “neutral” evolutionary processes (e.g., genetic drift),  
766 as long as resulting genetic diversity produces  
767 ecological relevant phenotypic diversity, then network  
768 structure will still have a genetic basis. Given  
769 that ecosystems with large asymmetries seem to be  
770 the rule rather than the exception for ecosystems  
771 (1, 66, 71–73), the results of our study are likely to  
772 be broadly applicable and provides further support  
773 for the conclusion that the community context of  
774 evolutionary dynamics at either micro- or macro-

775 evolutionary scales (51, 53) cannot safely be ignored.  
776 As genetic variation is inherent to biological systems,  
777 it would now seem that the adage “you can’t  
778 be neutral on a moving train” might well apply to  
779 ecosystems that are comprised of interacting species.  
780

781 **Applicability to Other Systems.** In attempting to apply  
782 these findings to other systems, it is important to  
783 consider the spatial and temporal scaling of genetic  
784 effects. In the present study, the sessile nature of  
785 lichens means that individuals, and potentially multiple  
786 generations, live their entire lives on a single tree.  
787 As such, our study examines one scaling of a genetic  
788 effect, in which the phenotype of a single tree individual  
789 (i.e., tree genotype) has complete influence on  
790 the community with little to no effect of other tree  
791 individuals in the population. The extreme from this  
792 would be where the associated community moved  
793 among and interacted with not only other community  
794 members but also multiple tree individuals at a high  
795 rate, as would be the case with free-living animals  
796 (e.g. flying insects). In the latter case, the effect of  
797 tree genetics would then be the integral effect of all  
798 the tree individuals in the population, and, all other  
799 factors being equal, any one tree genotype would  
800 have a lower effect on associated community. In reality,  
801 ecosystems are a mixture of species of different  
802 body sizes and life-histories, and, as such, vary in the  
803 degree to which they interact with other organisms,  
804 which is the basis of the theory of the geographic  
805 mosaic of co-evolution (34, 74). It is now important  
806 to consider how the impacts of genetic effects on  
807 the network structure of sub-groups, such as lichens,  
808 may or may not propagate through the ecosystem  
809 to more mobile organisms. As developed previously,  
810 the degree to which a genetic effect influences the  
811 community is a function of the fidelity of the genetic  
812 effect (i.e., heritability) and both the frequency and  
813 the intensity of the interaction (27). One possible  
814 path forward is for future work to extend the many  
815 previous community genetics studies that have focused  
816 on sessile organisms, such as gallin insects  
817 (11, 18, 20, 24, 75), to quantify the frequency of these  
818 interactions in the context of the larger community.  
819 This would provide an estimate of the relative impact  
820 of these focal, often termed foundation, species.  
821 In addition, community genetics theory has only  
822 considered first order interactions, i.e., between two  
823 organisms (7, 27, 28). Given that network structure  
824 could be influenced by genetic effects, as evidenced  
825 by our study, this is an area that requires further  
826 investigation.

827 by the present study, assessing higher order interactions  
828 could provide a path forward for theoretical  
829 advances that could help with identifying important  
830 characteristics of sub-groups to focus on in empirical  
831 studies.

832 Although our study was conducted with a com-  
833 munity of lichens, these results can be generalized to  
834 other groups of diverse organisms around the world  
835 that also exhibit significant genetic signals at the  
836 community level (7, 76). However, there are impor-  
837 tant points to consider when extending the observed  
838 genetically based response of the lichen networks  
839 to other systems. As bark lichen individuals do not  
840 move, but grow in a primarily two dimensional plane,  
841 these communities and their interactions occur in  
842 the highly localized context of the tree's bark sur-  
843 face. Lichen individuals are also many orders of  
844 magnitude smaller than the tree individual in this  
845 system (36). For these reasons, the genetic effects  
846 on these communities is not dampened by the move-  
847 ment of individuals and the mixing of the effect of  
848 different tree genotypes on the lichen community, as  
849 might occur for more mobile species (e.g. insects and  
850 birds). Relatedly, we only examined lichen in this  
851 study, and other species whose distributions, abun-  
852 dances and/or interactions vary in their response to  
853 tree genotype, such as animals that may also impact  
854 lichen communities, could be playing a role that we  
855 did not examine. For example, an analysis of the mul-  
856 tivariate correlations of different components of the  
857 community in this system demonstrated significant  
858 patterns of genetic co-responses to tree genotype,  
859 supporting the non-mutually exclusive possibilities  
860 of shared responses to tree genotype or tree genotypic  
861 effects on interactions among these sub-communities  
862 (4). As such, although we can not rule out the possi-  
863 bility that other unmeasured tree traits or organisms  
864 correlated with bark roughness are underlying the  
865 observed patterns, substantial research supports the  
866 importance of genetically based tree traits for com-  
867 munities and ecosystems (8), and in particular bark  
868 roughness for bark lichen communities (36, 37, 48).

869 **Conclusion.** In the face of the high degree of com-  
870 plexity and potential context dependency of ecologi-  
871 cal processes, the current study points to the utility  
872 of considering the spatial and temporal scales of in-  
873 teractions, as discussed to some in previous studies  
874 (16, 77, 78). In the present study, we found that  
875 community assembly processes, such as environmen-

tal filtering and species interactions, are genetically  
876 based. This is likely due, in part, to the large differ-  
877 ence in the differences in size and longevity of the  
878 lichen and cottonwood individuals with the trees de-  
879 termining the environment in which the lichen occur.  
880 The importance of the scale of network organization  
881 to create hierarchical structure (55) and the poten-  
882 tial for foundation species to create this structure in  
883 the vast majority of ecosystems (1, 11) suggests that  
884 future work would be aided by determining these  
885 modules within the biotic community that include  
886 species with similar differences in body-size and time-  
887 scales. Also, as heritable variation is the raw material  
888 for natural selection to act upon, a genetic basis for  
889 interaction network structure indicates evolutionary  
890 dynamics should be considered at the community  
891 level and that conserving genetic variation is im-  
892 portant to consider in efforts to restore or preserve  
893 complex species interactions and their associated  
894 ecosystem functions (79). Such findings will bring us  
895 closer to understanding the evolutionary drivers of  
896 Darwin's entangled bank and the interconnectedness  
897 of species in complex communities.

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1077 **Supplementary Materials**

1078 **Tables.**

	df	SS	R2	F	p-value
geno	9.00	44078.13	0.54	3.58	0.05
Residual	27.00	36915.46	0.46		
Total	36.00	80993.59	1.00		

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

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	response	df	statistic	H2	p-value
Lichen Network Similarity		9	3.5821	0.41	0.0537
Average Mutual Information			3.5235	0.31	0.0254
Centralization			4.0444	0.33	0.0184
Centralization In-Degree			4.4812	0.35	0.0142
Centralization Out-Degree			3.8615	0.32	0.0205
Centralization In-Degree (positive)			3.9852	0.33	0.0190
Centralization In-Degree (negative)			0.3304	0.11	0.2508
Centralization Out-Degree (positive)			3.5585	0.31	0.0248
Centralization Out-Degree (negative)			0.0862	0.05	0.3446
Degree			3.5175	0.32	0.0255
Degree (positive)			3.6925	0.32	0.0229
Degree (negative)			0.0327	0.03	0.3859
Percent Lichen Cover			0.0000	0.00	1.0000
Lichen Species Diversity			0.0000	0.00	0.4543
Lichen Species Richness			0.0000	0.00	0.4543
Lichen Species Evenness			0.0000	0.00	0.4543
Percent Rough Bark			4.8526	0.32	0.0113
pH			0.0000	0.00	1.0000
Carbon-Nitrogen Ratio			0.0000	0.00	1.0000
Condensed Tannins			3.0522	0.32	0.0343
BR-L Residuals			0.0000	0.00	1.0000
BR-Cen Residuals			0.0000	0.00	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	Df	SumOfSqs	R2	F	Pr(>F)	
BR									-0.34	-0.39	geno	9.0000	1.5049	0.2001	0.7507	0.8878
CT									0.34		Residual	27.0000	6.0143	0.7999		
pH											Total	36.0000	7.5193	1.0000		
CN																
PC																
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**

**Table 5. Pseudo-F Table of lichen community similarity PERMANOVA.**

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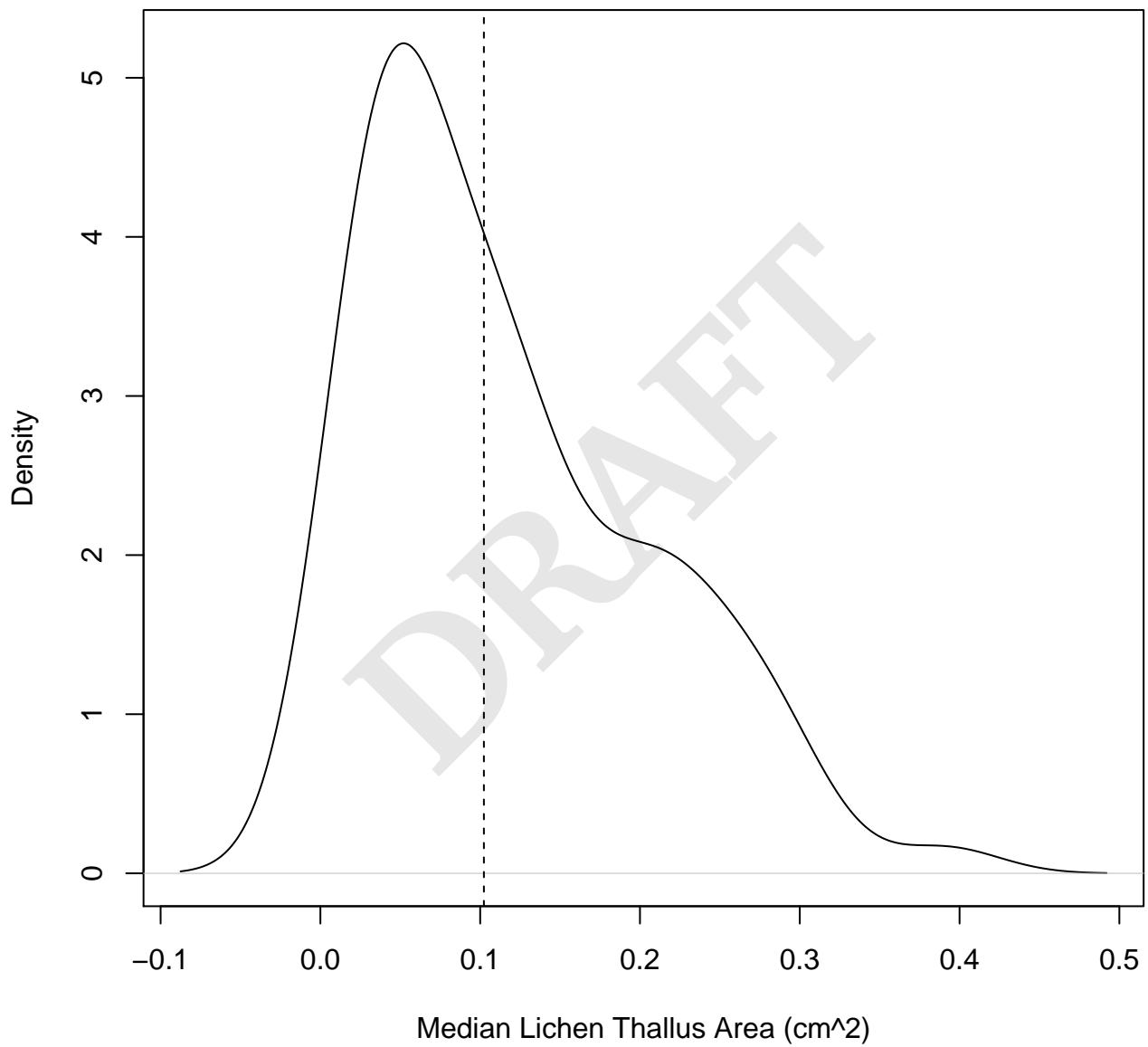
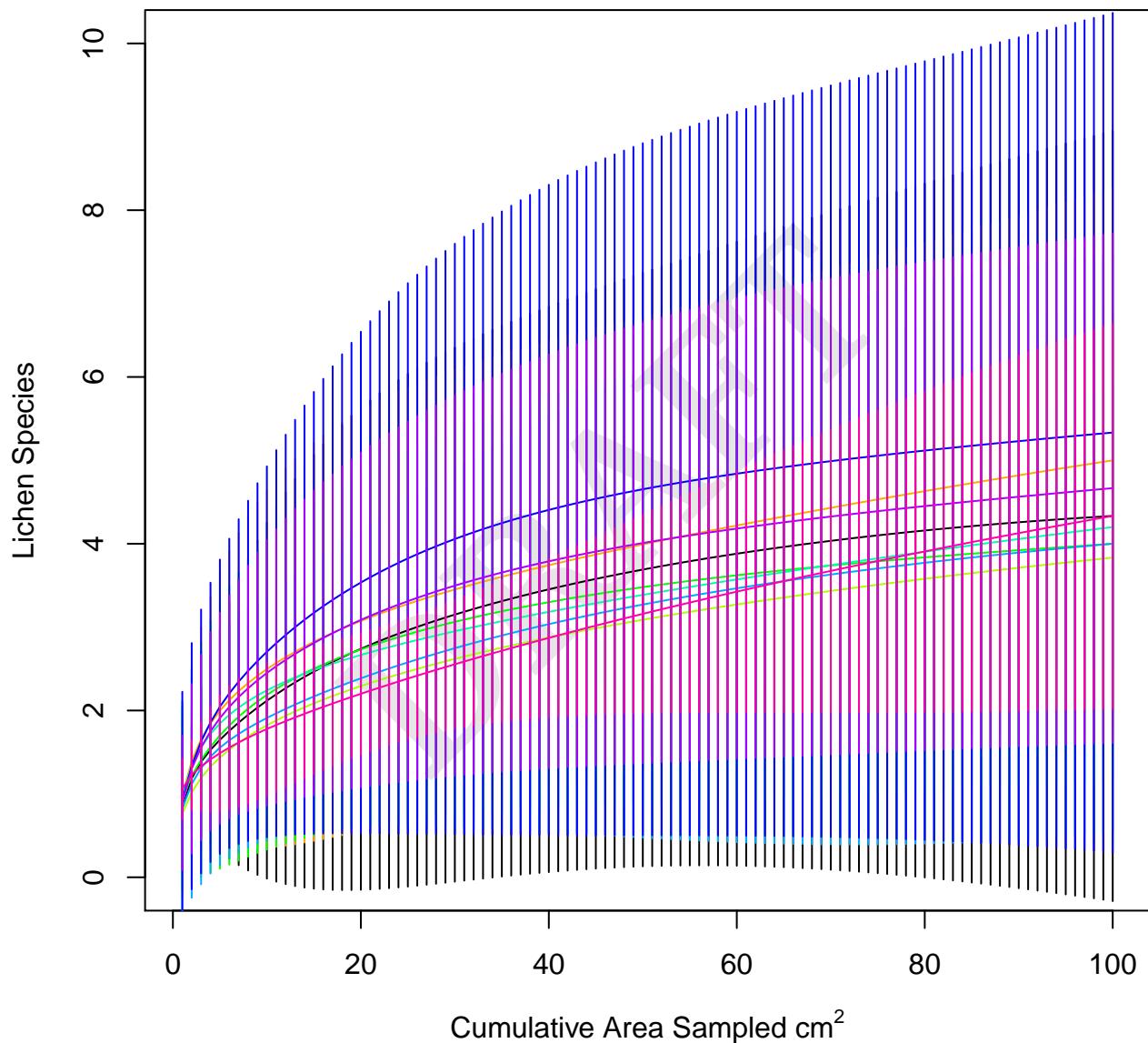


Fig. 1



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

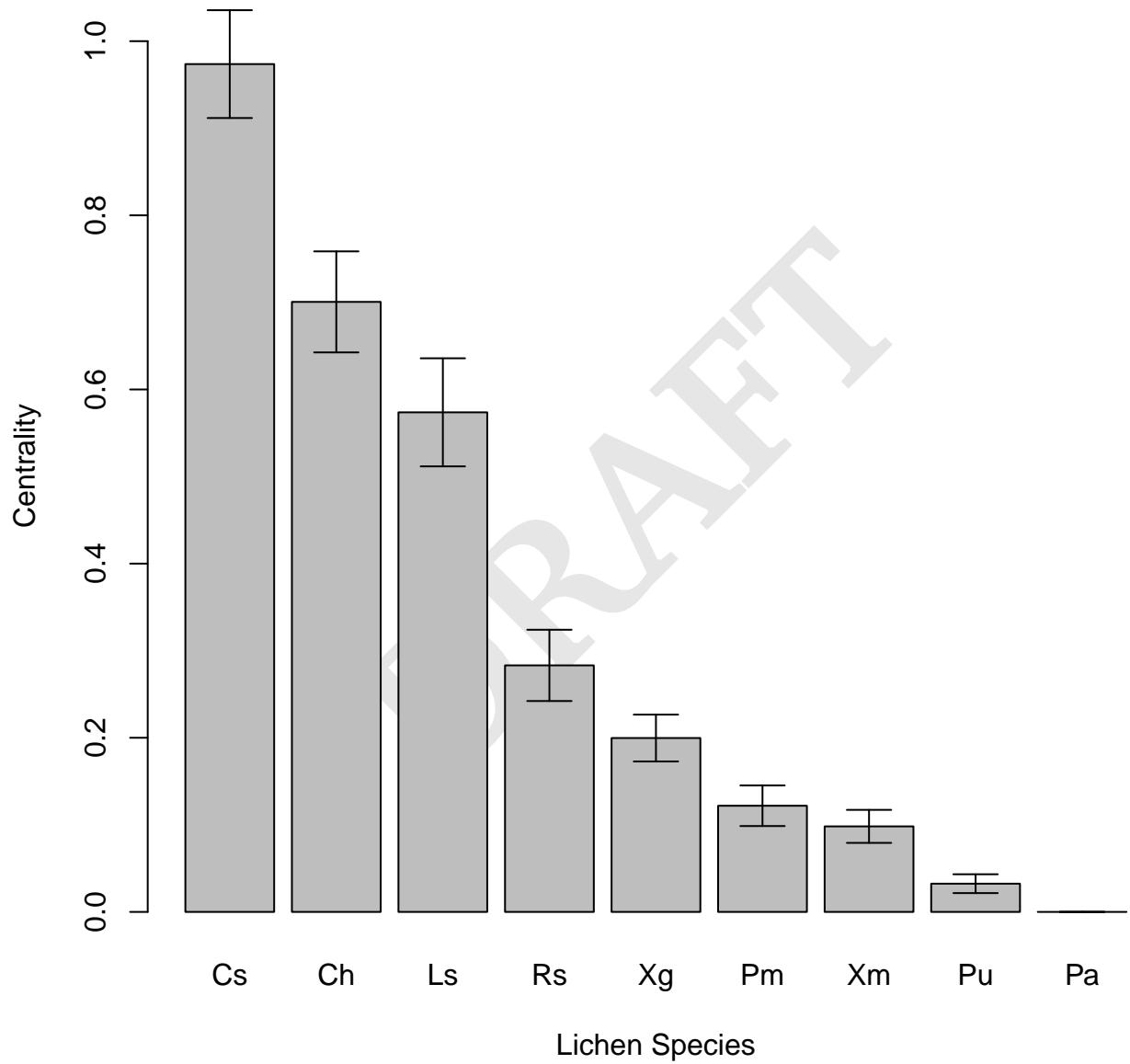


Fig. 3