

# 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 ge-

netic 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). 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. 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 (32). As such differences in network structure could occur without observable differences in species richness or community composition, which have been the primary focus of almost all previous community

genetics studies. Thus, it is important to quantify how network structure changes in response to genetic variation in order to fully understand evolutionary dynamics in complex communities.

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 (33). 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 clonally replicated *Populus angustifolia* individuals of known genetic identity. We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (34, 35). 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. manuscript We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (23, 24, 36, 37). If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks. Applying a probability-theory based network modeling approach, we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks via several network metrics that measures different aspects of network structure at the scale of individual species (i.e., nodes) or the entire network observed on each tree genotype. In particular, we focus the metric of centrality for individual species and centralization for whole networks, which measures how much a species is connected in the network relative to other species. Based on previous community genetics theory, particularly the community similarity rule (16), we hypothesize that trees will co-vary in functional phenotypic traits such as bark roughness and chemical composition and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. This work is important because it provides a mechanistic basis for understanding how community

network theory is intimately associated with the evolutionary process and how human alterations of the environment (e.g., climate change, invasive species, pollution) may have cascading, indirect effects that alter network structure and evolution.

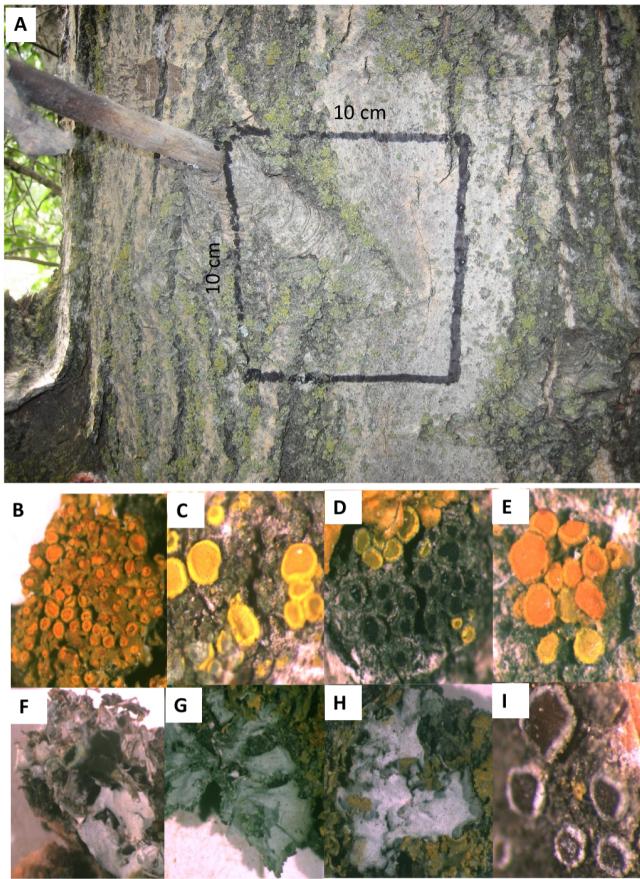
## Materials and Methods

**Study System.** The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled. Bark lichens have been extensively studied in this system and provide an ideal system in which to observe and model lichen interaction networks, as their sessile nature permits accurate identification of individuals (38).

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

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

The cell size and checkerboard sampling pattern was chosen to isolate the individuals in each cell. In a previous survey of lichen thallus size in this common garden, we had observed a median thallus size of 0.12 ± 0.001 cm<sup>2</sup> (1



**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).

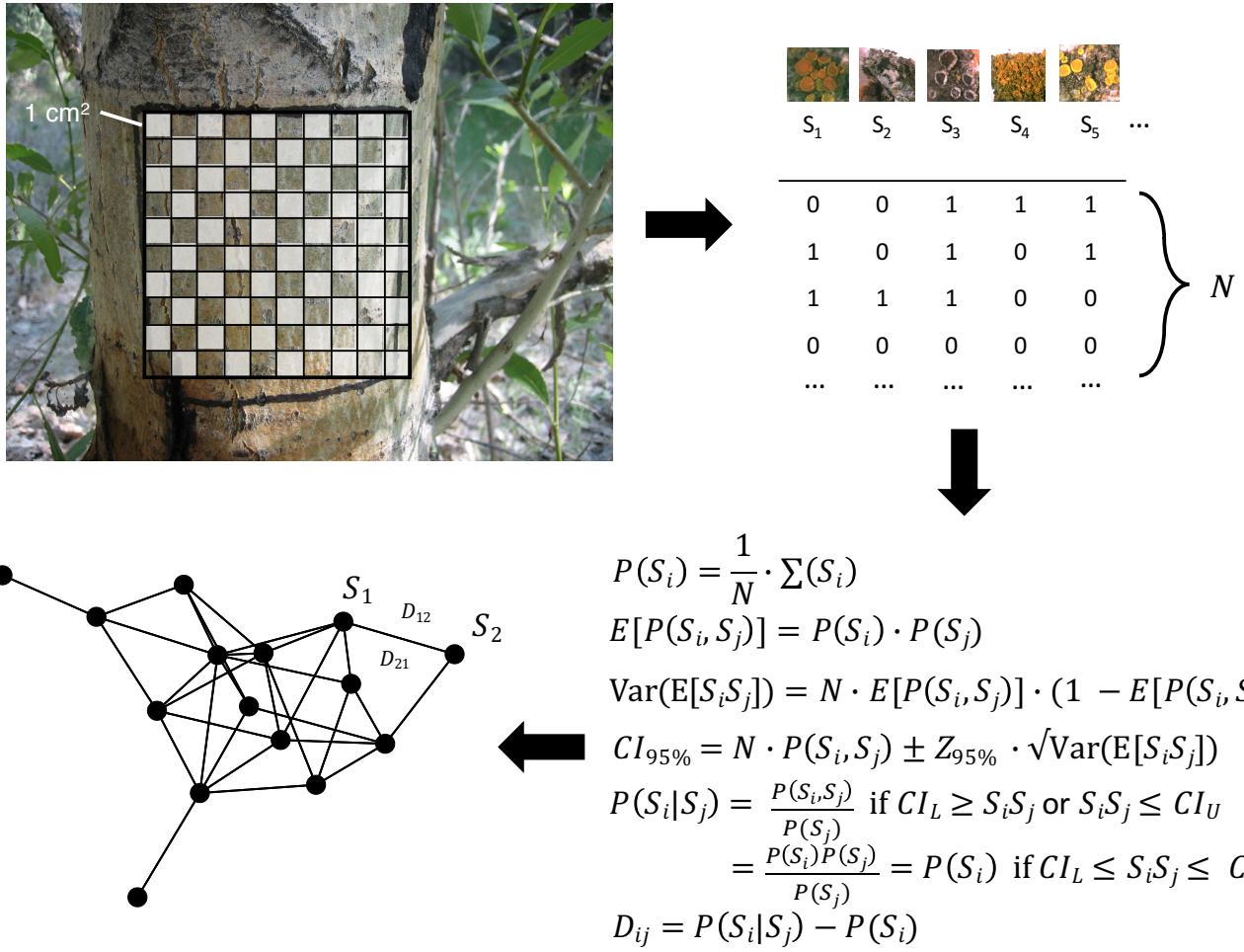
S.E.) (see Supporting Information). Based on the median thallus size, we expected thalli observed in each cell to generally be spatially independent of thalli present in other cells but exposed to similar micro-environmental conditions created by the bark and the location of the sampling area on an individual tree. Therefore, we were confident in treating the cell-wise observations in quadrats as independent with respect to lichen-lichen interactions. We quantified the texture of the bark in the quadrat as the percent of  $1 \text{ cm}^2$  cells with rough bark. In addition to bark roughness, we also measured several bark chemistry traits by taking bark samples immediately adjacent to each quadrat using the methods of (38): including, the concentration of condensed tannins, pH and carbon and nitrogen concentrations and pH.

**Lichen Network Modeling and Analysis.** For each tree, repeated observations of lichen were made in order to construct replicated interaction networks for each genotype. We conducted a modified sampling procedure originally

developed by (39) 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 (40). 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 (?). Also, as the method does not track individuals within species and interactions such as



**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 (40), 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.

291 competitive exclusion or facilitation within species would  
 292 result in the same species being observed. Therefore, the  
 293 results of intra-specific interactions always results in the  
 294 same species being observed and a resulting  $D_{ii} = 0$ .

295 **Network Metrics.** To quantify the structural variation of  
 296 lichen networks we calculated several metrics at both the  
 297 node and whole-network level. For individual nodes (i.e.  
 298 species) in each network, we calculated both the degree  
 299 and the Freeman’s centrality (41). We also calculated two  
 300 similar global network metrics: degree and centralization.  
 301 The first was network degree, which is a count of the  
 302 total number of links in a network. As the networks  
 303 contained not only positive and negative connections,  
 304 as well as directional connections (both in-coming and  
 305 out-going), we calculated the same network metrics for  
 306 all combinations of these types of connections in each

307 network. Although there are many more possible network  
 308 metrics that could have been examined, we chose to focus  
 309 on a restricted set for the sake of clarity. Also, degree and  
 310 centrality form the basis of many other network metrics.  
 311 To calculate separate metrics for positive and negative  
 312 links, we applied methods for calculating the centrality  
 313 accounting for the sign differences (42) using the **signnet**  
 314 package (43).

315 **Statistical Analyses, Software and Data.** We used a com-  
 316 bination of parametric and non-parametric, permutation  
 317 based frequentist statistical analyses to test for the effects  
 318 of genetic variation on lichen communities and their inter-  
 319 action networks. To assess the effect of genotype on uni-  
 320 variate responses, we used additive, random effects models  
 321 with Restricted Maximum Likelihood (REML). We used  
 322 a combination of Least Squares Regression, Analysis of

323 Variance (ANOVA) and correlation tests to quantify and  
 324 test for the relationship among other variables. Bark  
 325 roughness, lichen cover and species richness were square-  
 326 root transformed to meet the assumptions of homogeneity  
 327 of variance and normality for these tests.

328 For multivariate response variables, such as lichen com-  
 329 munity composition and network structure, we used dis-  
 330 tance based multivariate statistical approaches, including  
 331 Permutational Analysis of Variance (PERMANOVA) and  
 332 Mantel tests. To quantify the similarity of lichen net-  
 333 works among individual trees, we calculated the pairwise  
 334 Euclidean distance of the **D** interaction matrices among  
 335 all pairs of trees.

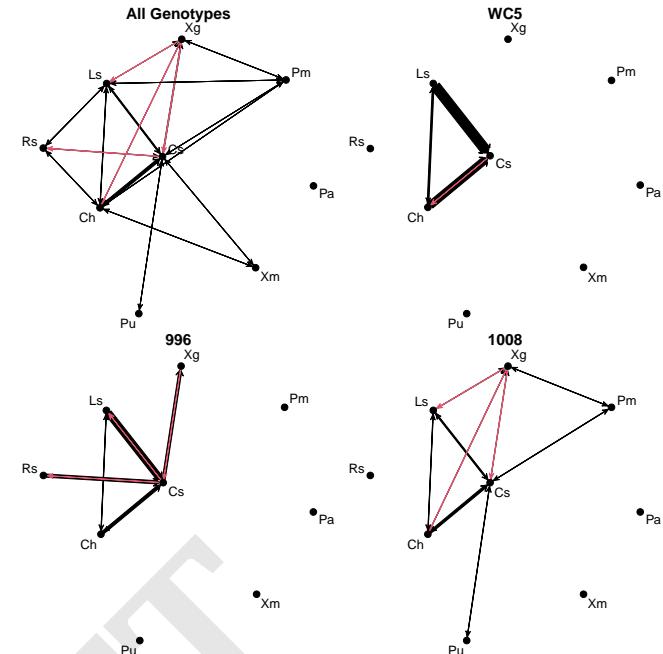
336 For visualization of multivariate patterns, we used  
 337 Non-metric Multi-Dimensional Scaling (NMDS) (44) to  
 338 produce dimensionally reduced ordinations of these multi-  
 339 variate responses and fitted vectors for continuous predi-  
 340 cator variables to the ordinated values (45). Using random  
 341 initial configurations with a maximum of 500 iterations  
 342 and a change in stress threshold of less than  $10^{-12}$ . Final  
 343 configurations has the lowest stress with at most a stress  
 344 level of 0.10.

345 For each network, we also calculated metrics that mea-  
 346 sure different structural aspects. Although there are many  
 347 other metrics, for the sake of simplicity we focus on a  
 348 subset that represent several interesting features of net-  
 349 work structure (see (17)). We calculated the number of  
 350 interactions or “links” in each network, which provides a  
 351 measure of the size of the network (23, 46). We also calcu-  
 352 lated the centralization of each network, which measures  
 353 the evenness of the distribution of interactions among  
 354 the species in the network (41). In a network with a  
 355 low level of centralization species have similar amount of  
 356 interaction in the network, while a network with a high  
 357 level of centralization tends to have one or small number  
 358 of species that interact with other species. We used a  
 359 related function to calculate the centrality of each species  
 360 (i.e. node level centrality) in each network as well.

361 For all tests where genotype was used as a predictor,  
 362 we quantified the heritability of the response variable. Be-  
 363 cause the trees in the garden were clonal replicates of each  
 364 genotype, we calculated broad-sense heritability, which  
 365 is the genotypic variance divided by the total phenotypic  
 366 variance (47). This can be interpreted as a measure of  
 367 the phenotypic variance due to genotypic variation. We  
 368 also apply this to the community genetics context as the  
 369 variance in *extended* phenotypic variance due to genotypic  
 370 variation (48). For the multivariate analyses, where we  
 371 employ PERMANOVA, we followed the methods of (27)  
 372 to adjust the degrees of freedom for unbalanced genotype  
 373 replicates.

374 All code and data for the project are openly avail-  
 375 able online. Code and data are available at [github.com/  
 376 ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo  
 377 at [zenodo.com/doi/XXXXXX](https://zenodo.com/doi/XXXXXX). All analyses were conducted  
 378 using the programming language R version 3.6.1 (R De-

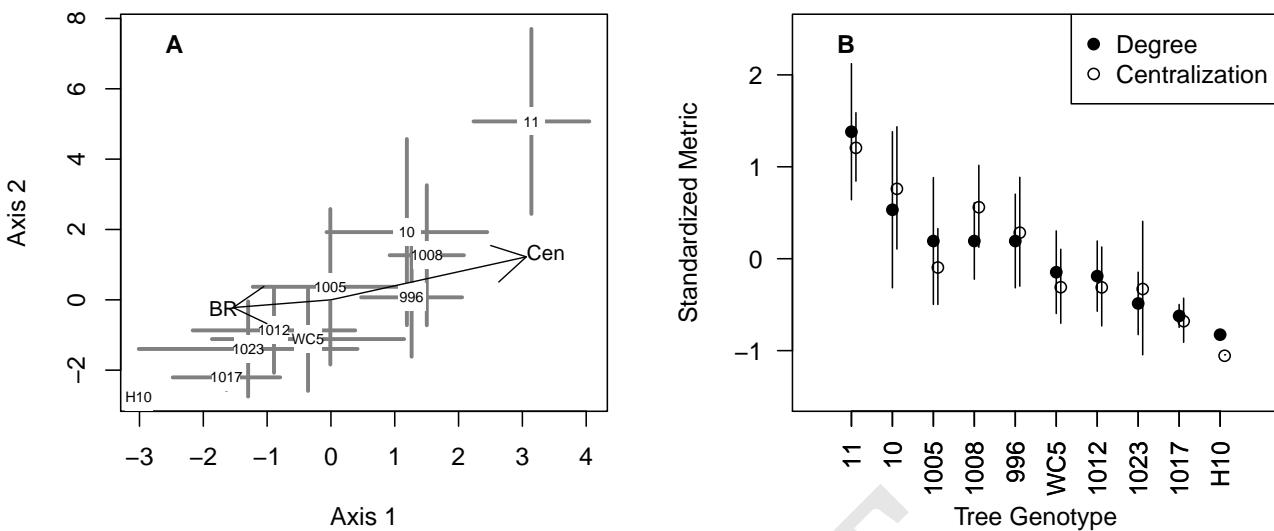
379 velopment Core Team 2019).



**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



**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.

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                             | 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  |

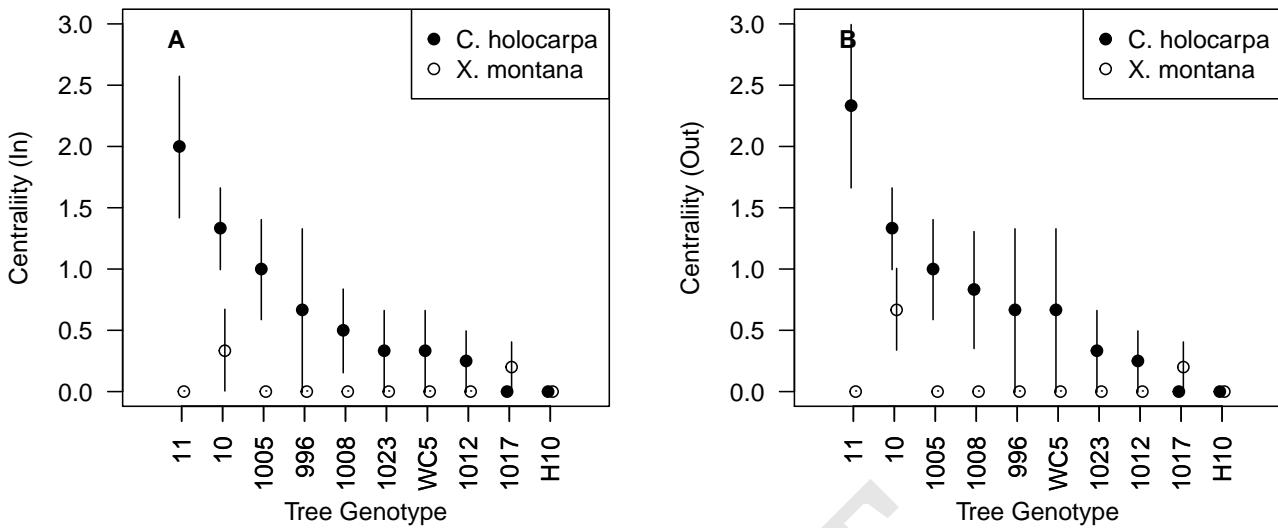
**Table 1. Genotypic effects on the associated lichen network structure.**

The genetic response of network centralization was driven by variation in *Caloplaca holocarpa*. Centralization varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ ,  $p\text{-value} < 0.0001$ ). *Caloplaca holocarpa* centrality was the main species to exhibit a significant response to tree genotype in terms of positive

centrality for both the in-coming ( $RLRT = 3.61$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0240$ ) and out-going ( $RLRT = 3.13$ ,  $H^2 = 0.30$ ,  $p\text{-value} = 0.0327$ ) perspectives, but not for either negative centrality metrics in-coming ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 1$ ) or out-going ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 0.4543$ ). None of the other species' centralities showed a genotypic response (Supplementary Table 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



**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.

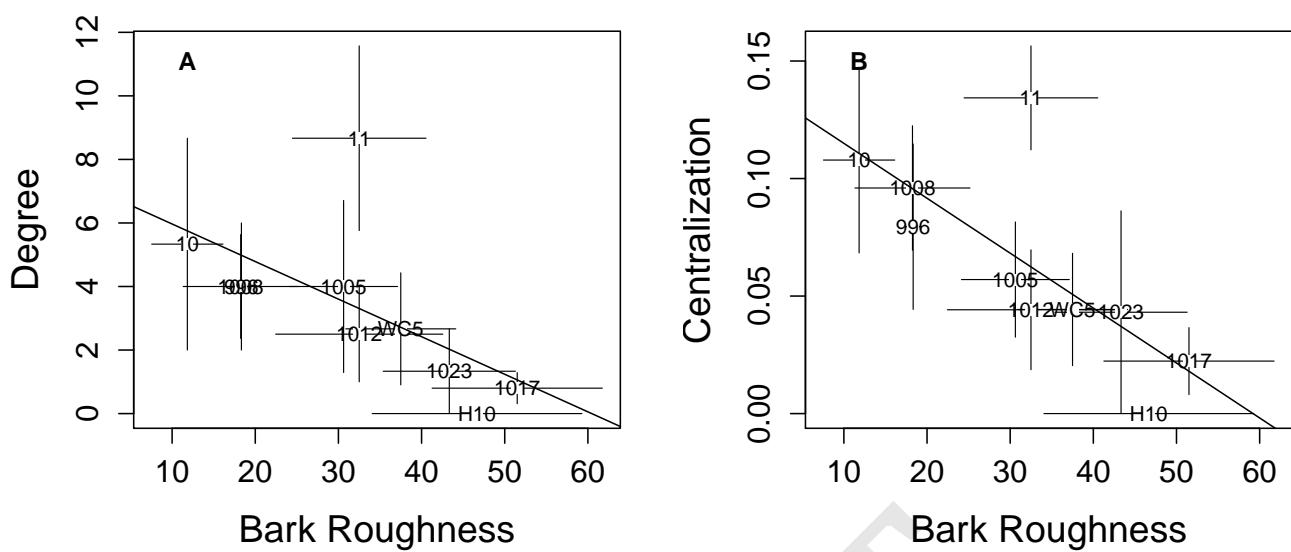
roughness was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen network structure via bark roughness. We found that bark roughness was significantly correlated with network similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$ ,  $R^2 = 0.26$ ,  $p\text{-value} = 0.0096$ ) 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 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).

|                       | 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 variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control (49), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (39); however this is the first demonstration of a link from genes to lichen network structure. As such these results have important implications for



**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.

477 the potential influence of genetically based variation  
478 in ecosystems with networks of interacting species.

479 **Implications of the Heritability of Interaction Net-  
480 work Structure.**

481 The patterns of interaction in individual-  
482 based networks depart from these theo-  
483 retical benchmarks, revealing the role of  
484 variability in space, time, traits, and pre-  
485 ferences in shaping ecological interactions  
486 (Araújo et al. 2008).

487 Space and time create templates for ecolog-  
488 ical interactions (Cantor et al. 2018) that  
489 favor departures from homogeneous and  
490 abundance-based network patterns. The  
491 spatial configuration of an environment may  
492 foster the rise of modules of interacting in-  
493 dividuals (Fortuna et al. 2009, Tur et al.  
494 2015). Similarly, temporal variation in the  
495 availability of partners affects the network  
496 structure on different time scales (Dátillo  
497 et al. 2014b, Valverde et al. 2016). For  
498 example, networks describing interactions  
499 among individual insects and different plant  
500 species show temporal modularity, with dif-  
501 ferent individuals sharing pollen resources

502 at different times in the flowering season  
503 (Tur et al. 2015). Space and time may  
504 therefore promote spatiotemporal variation  
505 in the network structure by affecting the  
506 likelihood of potential interactions. Even  
507 so, the macroscopic properties of individual-  
508 based networks may show structural con-  
509 stancy. For example, networks of inter-  
510 actions among protective ant species and  
511 individual plants show daily turnover in ant  
512 species, while maintaining nestedness and  
513 average levels of reciprocal specialization  
514 (Dátillo et al. 2014b).

515 Space and time set the scales in which  
516 individual-based networks occur, but the  
517 interaction patterns are further modified  
518 by variation in individual traits. For ex-  
519 ample, the numbers of individual honey-  
520 bees (*Apis mellifera*, Apidae) visiting this-  
521 tle (*Cirsium arvense*, Asteraceae) flowers  
522 increase with the number of flower heads  
523 and the height of the inflorescences on  
524 individual plants (Dupont et al. 2011).  
525 Network description of intraspecific varia-  
526 tion in dietary niches uncovers subtle as-  
527 sociations between traits and resource use

528 that go beyond the number of resources  
529 used. For example, in a monomorphic  
530 population of three-spine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae), differ-  
531 ences in trait combinations (e.g., body and  
532 snout shapes) were associated with dietary  
533 modules, i.e., groups of individuals feed-  
534 ing on similar prey (Araújo et al. 2008).  
535 Similarly, networks describing diet overlap  
536 among thick-billed murres (*Uria lomvia*,  
537 Alcidae) revealed sexbased dietary groups  
538 (Provencher et al. 2013). Network analyses  
539 can therefore reveal how patterns of interac-  
540 tion across individuals are associated with  
541 variation in individual traits.

543 A disconnected network structure implies  
544 that the dynamical consequences of eco-  
545 logical interactions are limited to pairs  
546 or to small groups of interacting species  
547 (e.g., Guimarães et al. 2007). In con-  
548 trast, a connected network structure im-  
549 plies that trophic cascades, trait-based cas-  
550 cades, and eco-evolutionary feedbacks can  
551 propagate across multiple species in the  
552 community. For example, indirect effects  
553 generated by the decline in sea otters in  
554 the Aleutian Archipelago propagated across  
555 trophic chains, resulting in a dietary shift  
556 in bald eagles (Anthony et al. 2008). In  
557 fact, most of the classic empirical exam-  
558 ples of keystone species shaping ecological  
559 communities due to indirect effects show  
560 species with either (a) generalist diets or  
561 (b) generalism at the species level emerging  
562 due to intrapopulation variation in traits or  
563 preferences (Estes et al. 2003, Paine 1966).  
564 From a network perspective, at least some  
565 keystone species can be viewed as highly  
566 connected species that shift the community-  
567 level dynamics by promoting connectedness  
568 in ecological networks.

569 Highly connected species may also connect  
570 modules generated by trait variation across  
571 potentially interacting species (Donatti et  
572 al. 2011, Schleuning et al. 2014). High trait  
573 variation across species may lead to the for-  
574 mation of modules due to specialization  
575 (Poisot et al. 2013), intervality (Guimerà et  
576 al. 2010, Stouffer et al. 2006), interspecific

577 competition (Dalerum et al. 2016, Valverde  
578 et al. 2020), trade-offs in resource use (Pin-  
579 heiro et al. 2019), and the combination of  
580 multiple ecological and evolutionary factors  
581 (Rezende et al. 2009). However, the impact  
582 of trait variation on species interactions is  
583 not straightforward, being dependent on  
584 the rules connecting traits of interacting  
585 species (Gibert DeLong 2017, Gravel et al.  
586 2016). If trait variation hinders the emer-  
587 gence of highly connected species, loosely  
588 connected networks should emerge in which  
589 some modules may present internal nested  
590 patterns due to differences in species abun-  
591 dance and forbidden links (Lewinsohn et  
592 al. 2006, Pinheiro et al. 2019, Vacher et al.  
593 2008). If, however, some highly connected  
594 species are able to interact with partners  
595 with disparate traits, then different modules  
596 will be connected to each other through the  
597 pathways created by these highly connected  
598 species (Olesen et al. 2007, Schleuning et  
599 al. 2014). Therefore, the presence of highly  
600 connected species shapes the cohesiveness  
601 of ecological communities, markedly affect-  
602 ing different aspects of their network struc-  
603 ture.

604 We found significant heritability of lichen inter-  
605 action network structure, and, in line with the ge-  
606 netic similarity rule, networks observed on trees of  
607 the same genotype tended to be structurally sim-  
608 ilar. This is the first study that we are aware of  
609 to examine the heritability of network structure in  
610 a real ecosystem. Previous work in the evolution  
611 of ecological networks have primarily focused on  
612 macro-evolutionary dynamics (13? ? ) or have been  
613 simulation based individual-level models that inte-  
614 grate intraspecific variation to the species level (?  
615 ), even though recent syntheses ave pointed to the  
616 importance of processes operating across scales of  
617 organization (? ). There are several important func-  
618 tional ramifications of genetically based variation  
619 in network structure. First, intra-specific diversity  
620 could be creating lichen interaction modules with  
621 different dynamics. When communities are com-  
622 prised of individuals whose habitat is primarily the  
623 determined by another organism, these communities  
624 inherently form modules within the larger ecosystem,  
625 as they tend to interact more with each other than

626 with other individuals (? ? ?). Our study demon-  
627 strates that the environmental differences determined  
628 by the genetic variation within a single species can  
629 create differences that not only impacts community  
630 composition, as repeatedly demonstrated in other  
631 community genetics studies (8?), but also the struc-  
632 ture of interactions among individuals within these  
633 modules. Some network structures are likely to be  
634 more stable, either in response to disturbance or via  
635 self-organized dynamics. For example, centralized  
636 networks, although more efficient, are theorized to  
637 be more susceptible to targeted attacks on the center  
638 of the network. For example, consider a forest with  
639 two genotypes that support lichen communities that  
640 are similar in total abundances of each species but  
641 differ in terms of the structure. Extensions of game  
642 theory to evolutionary biology have demonstrated  
643 that network structure can lead to variation in evo-  
644 lutionary dynamics. Some structures tend toward  
645 dominance and dampening of selection, while others  
646 lead to amplification of selection. One class of net-  
647 works that are theorized to have amplifying effects  
648 on networks have "star" shapes with one or a few  
649 species at the center and radiating interactions out  
650 from the central core (?). This is structurally what  
651 we have observed with the networks that tend to  
652 occur on some of the genotypes in our study, i.e.  
653 the more centralized networks. It is possible that  
654 these more centralized networks could function as  
655 hot-spots of evolutionary dynamics resulting from  
656 the amplifying effect the network structure fostered  
657 on that tree genotype.

658 Second, a genetic basis to network structure sug-  
659 gests that some amount of interaction network com-  
660 plexity is determined and therefore could be pre-  
661 dicted. Variation in space and time create variation  
662 in ecological networks that influences evolutionary  
663 dynamics via shifts in ecological dynamics, such as  
664 population demographics (?). The promise of pre-  
665 dictability is that the presence of assymmetries in  
666 ecosystems that contribute to the occurrence of foun-  
667 dation species, such as hierarchy and nestedness cre-  
668 ated by body size differences or life-history strategies,  
669 has been widely observed (1). The second part is  
670 that heritability (i.e., genetic determination) means  
671 that there is structure in the spatial or temporal  
672 variation that is created by individuals of foundation  
673 species whose traits are in part determined by un-  
674 derlying trait differences. Although this variation is

675 inherently a function of both genetics and environ-  
676 mental effects (47), the community and network level  
677 effects are also a function of the scale of the inter-  
678 action (27). Self-organization of the dynamics within  
679 these communities also points to a mechanism for  
680 strong community and ecosystem effects of genetic  
681 variation, contributing to what may seem unlikely  
682 magnitudes of genetic effects as has been observed in  
683 some systems, such as forest in riparian ecosystems  
684 (16).

685 Third, even if the composition of the communi-  
686 ties is the same among individuals and genotypes,  
687 interactions may not be. We didn't observe compo-  
688 sitional differences using the same data from which  
689 the lichen networks were derived. If we only had  
690 our composition dataset from this study, we would  
691 have concluded no response of the lichen commu-  
692 nity to tree genotype, even though the underlying  
693 interactions among lichen species does vary among  
694 genotypes. Community composition of lichen has  
695 previously been observed to be different among tree  
696 genotype in the same experimental garden (38, 39),  
697 though this was observed with a larger sampling of  
698 total area and quadrats per tree. Regardless, this  
699 could result in a situation in which abundance based  
700 investigations of community-level genetic effects may  
701 miss important variation in the interactions among  
702 individuals in these communities, leading to an un-  
703 derestimate of genetic effects in ecosystems. It is  
704 possible that these underlying differences in inter-  
705 actions among lichen could lead to differences in  
706 community composition at a future point in time via  
707 there effects on species abundances (27); however,  
708 this is not needed for evolutionary dynamics to play  
709 out. This points to the need to assess or be aware  
710 of the potential effects of interactions and not just  
711 observe species abundances.

712 **Evolutionary Implications of a Genetic Basis to**  
713 **Network Structure.** With regard to the evolution-  
714 ary implications of network structure, ecological net-  
715 work studies have focused on asymmetry and the  
716 quantification of its structure in communities, with  
717 qualitative discussion of the impacts on evolutionary  
718 dynamics (36, 37, 54, 55). More specific predication,  
719 with a quantitative framework, can be found in ap-  
720 plications of evolutionary game theory, and although  
721 developed at the population scale, such theory can  
722 apply to communities. One seemingly useful direc-  
723 tion 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 of (17) developed the perspective 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 inherently created when trait variation among genotypes of a foundation species has ecological effects on associated species.

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. Elucidating 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 (31). 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.

**Implications for Interspecific Indirect Genetic Effects (IIGEs).** Interspecific indirect genetic effects (IIGE) theory provides a quantitative framework within which to approach evolutionary theory at higher levels of biological organization: from pop-

ulations to communities and ecosystems. To date, this theory has focused on modeling the strong effects of foundation species (7, 27), 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 damped or magnified within the system of interacting species. For example, (24) 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 (50). Furthermore, in a predator-prey-plant study, Smith (20), showed that the interactions among species across trophic levels depended on plant genotype. Also, work by (51–53) 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 variation in network structure can be genetically based (i.e. heritable) and 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. These results also provide insights into the dynamics of real ecosystems and the potential inter-play of ecology and evolution with regard to empirical and theoretical support for neutral theory. Empirical (?) and theoretical work (?) have provided evidence for the applicability of functional equivalence of species in communities; and recently, models have also been developed that can reconstruct interactions networks with similar structural characteristics to those observed in real ecosystems (?). The findings of our study support the possibility that, although communities and their interaction networks may assemble as a result of conditions that are entirely agnostic to functional variation, if there are strong ecological assymmetries, such as the case in foundation species systems, then spatial and temporal variation in network structure will arise as a results of trait variation within the foundtion species. Taking even the extreme case, even when such genetically based variation is the result of “neutral” evolutionary processes (e.g., genetic drift), as long as resulting genetic diversity produces ecological relevant phenotypic diversity, then network structure will still have a genetic basis. Given that ecosystems with large assymmetries seem to be the rule rather than the exception for ecosystems (1? ? ? ?), the results of our study are likely to be broadly applicable and provides further support for the conclusion that the community context of evolutionary dynamics at either micro- or macro-evolutionary scales (?) can not be safely ignored. As genetic variation is inherent to biological systems, it would now seem that the adage “you can’t be neutral on a moving train” might well apply to ecosystems that are comprised of interacting species.

One final point to discuss is that in the present study lichen cover, species richness and composition were not significantly responsive to tree genotype, unlike what has been previously observed for lichen (39) and multiple taxa in this and other systems (8). This is likely the result of differences in sampling method and the choice of genotypes leading to overall higher abundances of observed lichens to assure the possibility of observing lichen interactions. In the current study mean percent total lichen cover among genotypes ranges from 60-93% cover; whereas the range reported in (39) 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 and the general applicability to future studies.

**Applicability to Other Systems.** In attempting to apply these findings to other systems, it is important to consider the spatial and temporal scaling of genetic effects. In the present study, the sessile nature of lichens means that individuals, and potentially multiple generations, live their entire lives on a single tree. As such, our study examines one scaling of a genetic effect, in which the phenotype of a single tree individual (i.e., tree genotype) has complete influence on the community with little to no effect of other tree individuals in the population. The extreme from this would be where the associated community moved among and interacted with not only other community members but also multiple tree individuals at a high rate, as would be the case with free-living animals (e.g. flying insects). In the latter case, the effect of tree genetics would then be the integral effect of all the tree individuals in the population, and, all other factors being equal, any one tree genotype would have a lower effect on associated community. In reality, ecosystems are a mixture of species of different body sizes and life-histories, and, as such, vary in the degree to which they interact with other organisms, which is the basis of the theory of the geographic mosaic of co-evolution (36, 57). It is now important to consider how the impacts of genetic effects on the network structure of sub-groups, such as lichens, may or may not propagate through the ecosystem to more mobile organisms. As developed previously, the degree to which a genetic effect influences the community is a function of the fidelity of the genetic effect (i.e., heritability) and both the frequency and the intensity of the interaction (27). One possible path forward is for future work to extend the many

920 previous community genetics studies that have fo-  
921 cused on sessile organisms, such as galling insects  
922 (11, 18, 24, 58? ), to quantify the frequency of these  
923 interactions in the context of the larger community.  
924 This would provide an estimate of the relative im-  
925 pact of these focal, often termed foundation, species.  
926 In addition, community genetics theory has only  
927 considered first order interactions, i.e., between two  
928 organisms (7, 27, 28). Given that network structure  
929 could be influenced by genetic effects, as evidenced  
930 by the present study, assessing higher order interac-  
931 tions could provide a path forward for theoretical  
932 advances that could help with identifying important  
933 characteristics of sub-groups to focus on in empirical  
934 studies.

935 Although our study was conducted with a com-  
936 munity of lichens, these results can be generalized to  
937 other groups of diverse organisms around the world  
938 that also exhibit significant genetic signals at the  
939 community level (7, 56). However, there are impor-  
940 tant points to consider when extending the observed  
941 genetically based response of the lichen networks  
942 to other systems. As bark lichen individuals do not  
943 move, but grow in a primarily two dimensional plane,  
944 these communities and their interactions occur in  
945 the highly localized context of the tree's bark sur-  
946 face. Lichen individuals are also many orders of  
947 magnitude smaller than the tree individual in this  
948 system (38). For these reasons, the genetic effects  
949 on these communities is not damped by the move-  
950 ment of individuals and the mixing of the effect of  
951 different tree genotypes on the lichen community, as  
952 might occur for more mobile species (e.g. insects and  
953 birds). Relatedly, we only examined lichen in this  
954 study, and other species whose distributions, abun-  
955 dances and/or interactions vary in their response to  
956 tree genotype, such as animals that may also impact  
957 lichen communities, could be playing a role that we  
958 did not examine. For example, an analysis of the mul-  
959 tivariate correlations of different components of the  
960 community in this system demonstrated significant  
961 patterns of genetic co-responses to tree genotype,  
962 supporting the non-mutually exclusive possibilities  
963 of shared responses to tree genotype or tree genotypic  
964 effects on interactions among these sub-communities  
965 (4). As such, although we can not rule out the possi-  
966 bility that other unmeasured tree traits or organisms  
967 correlated with bark roughness are underlying the  
968 observed patterns, substantial research supports the

importance of genetically based tree traits for com-  
969 munities and ecosystems (8), and in particular bark  
970 roughness for bark lichen communities (38, 39, 49).  
971

**Conclusion.** In the face of the high degree of com-  
972 plexity and potential context dependency of ecologi-  
973 cal processes, the current study points to the utility  
974 of considering the spatial and temporal scales of in-  
975 teractions, as discussed to some in previous studies  
976 (16, 59, 60). In the present study, we found that  
977 community assembly processes, such as environmental  
978 filtering and species interactions, are genetically  
979 based. This is likely due, in part, to the large differ-  
980 ence in the differences in size and longevity of the  
981 lichen and cottonwood individuals with the trees de-  
982 termining the environment in which the lichen occur.  
983 As developed elsewhere, the importance of founda-  
984 tion species, their interactions and the hierarchical  
985 structures that they create in communities (1? ? )  
986 suggests that future work would be aided by deter-  
987 mining these modules within the biotic community  
988 that include species with similar differences in body-  
989 size and time-scales. Also, as heritable variation is  
990 the raw material for natural selection to act upon,  
991 a genetic basis for interaction network structure in-  
992 dicates evolutionary dynamics should be considered  
993 at the community level and that conserving genetic  
994 variation is important to consider in efforts to restore  
995 or preserve complex species interactions and their  
996 associated ecosystem functions (61). Such findings  
997 will bring us closer to understanding the evolutionary  
998 drivers of Darwin's entangled bank and the intercon-  
999 nectedness of species in complex communities.  
1000

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## Supplementary Materials

### Tables.

|      |          | df    | SS       | R2   | F    | p-value |
|------|----------|-------|----------|------|------|---------|
| 1137 | geno     | 9.00  | 44078.13 | 0.54 | 3.58 | 0.05    |
| 1138 | 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              |        |           |        |         |
| <i>X. galericulata</i> | 0.2703 | 0         | 0      | 1       |
| <i>C. subdeflexa</i>   | 0.8919 | 2.1926    | 0.2158 | 0.0595  |
| <i>L. spp.</i>         | 0.4324 | 0         | 0      | 1       |
| <i>C. holocarpa</i>    | 0.5946 | 3.6146    | 0.3241 | 0.024   |
| <i>X. montana</i>      | 0.0541 | 0         | 0      | 0.4543  |
| <i>P. melanochra</i>   | 0.1351 | 0         | 0      | 1       |
| <i>P. adscendens</i>   | 0      |           |        |         |
| <i>P. undulata</i>     | 0.027  | 0         | 0      | 0.4543  |
| R. sp.                 | 0.1351 | 2.049     | 0.2613 | 0.0656  |
| Out-Degree             |        |           |        |         |
| <i>X. galericulata</i> | 0.027  | 0         | 0      | 0.4543  |
| <i>C. subdeflexa</i>   | 0.6757 | 0         | 0      | 1       |
| <i>L. spp.</i>         | 0.5946 | 0.0061    | 0.0126 | 0.4247  |
| <i>C. holocarpa</i>    | 0.7027 | 3.1318    | 0.2981 | 0.0327  |
| <i>X. montana</i>      | 0.0811 | 2.9228    | 0.3163 | 0.0375  |
| <i>P. melanochra</i>   | 0.1351 | 0         | 0      | 1       |
| <i>P. adscendens</i>   | 0      |           |        |         |
| <i>P. undulata</i>     | 0.027  | 0         | 0      | 0.4543  |
| R. sp.                 | 0.2973 | 0.1505    | 0.0612 | 0.3119  |
| Negative               |        |           |        |         |
| In-Degree              |        |           |        |         |
| <i>X. galericulata</i> | 0      |           |        |         |
| <i>C. subdeflexa</i>   | 0.1892 | 0         | 0      | 0.4543  |
| <i>L. spp.</i>         | 0.1892 | 0.0015    | 0.0057 | 0.4398  |
| <i>C. holocarpa</i>    | 0.1351 | 0         | 0      | 1       |
| <i>X. montana</i>      | 0.027  | 0.0377    | 0.0394 | 0.3807  |
| <i>P. melanochra</i>   | 0      |           |        |         |
| <i>P. adscendens</i>   | 0      |           |        |         |
| <i>P. undulata</i>     | 0      |           |        |         |
| R. sp.                 | 0.1622 | 0         | 0      | 1       |
| Out-Degree             |        |           |        |         |
| <i>X. galericulata</i> | 0.2432 | 0         | 0      | 1       |
| <i>C. subdeflexa</i>   | 0.4054 | 0         | 0      | 0.4543  |
| <i>L. spp.</i>         | 0.027  | 0         | 0      | 0.4543  |
| <i>C. holocarpa</i>    | 0.027  | 0         | 0      | 0.4543  |
| <i>X. montana</i>      | 0      |           |        |         |
| <i>P. melanochra</i>   | 0      |           |        |         |
| <i>P. adscendens</i>   | 0      |           |        |         |
| <i>P. undulata</i>     | 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 |    |    |    | 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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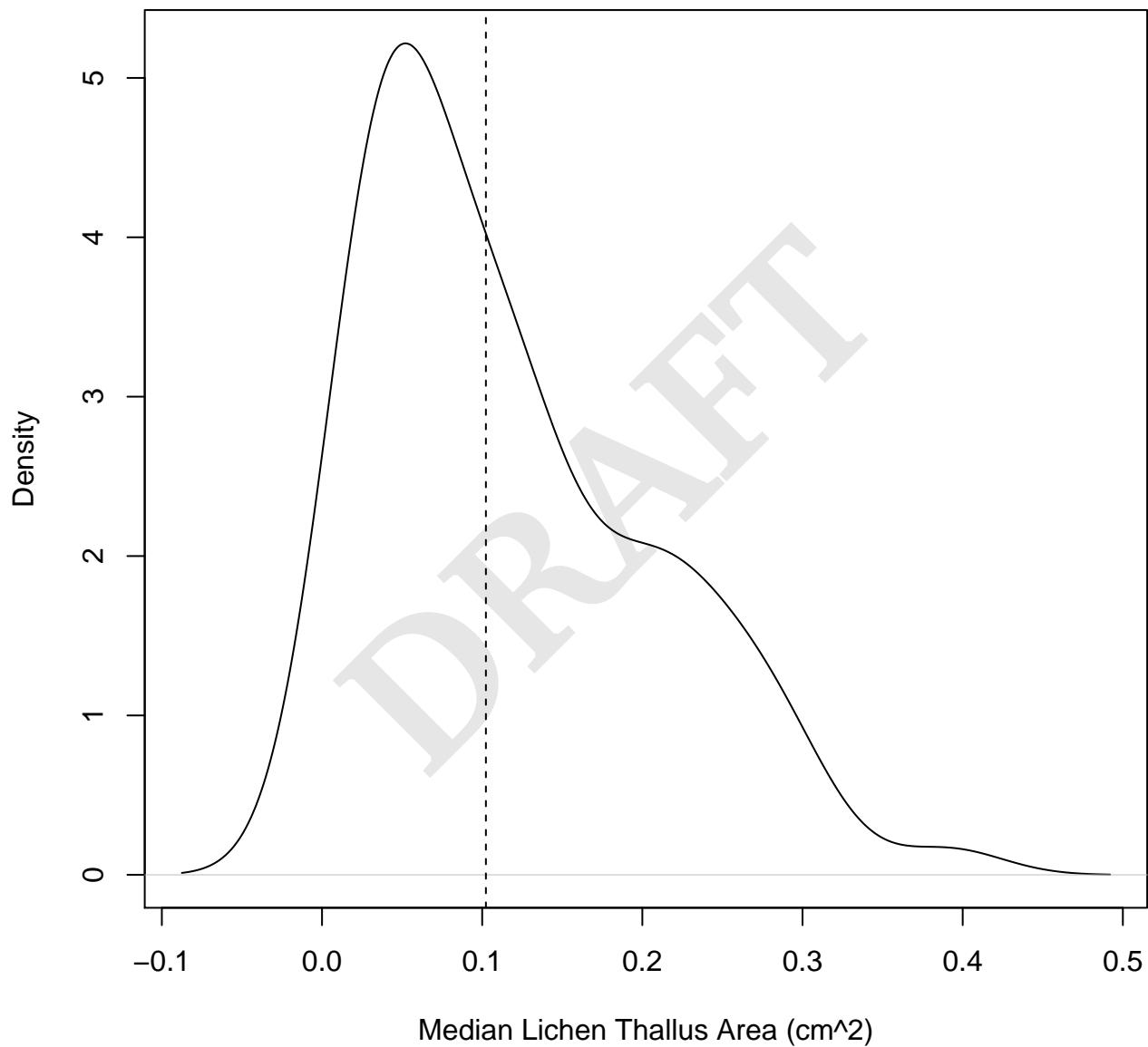
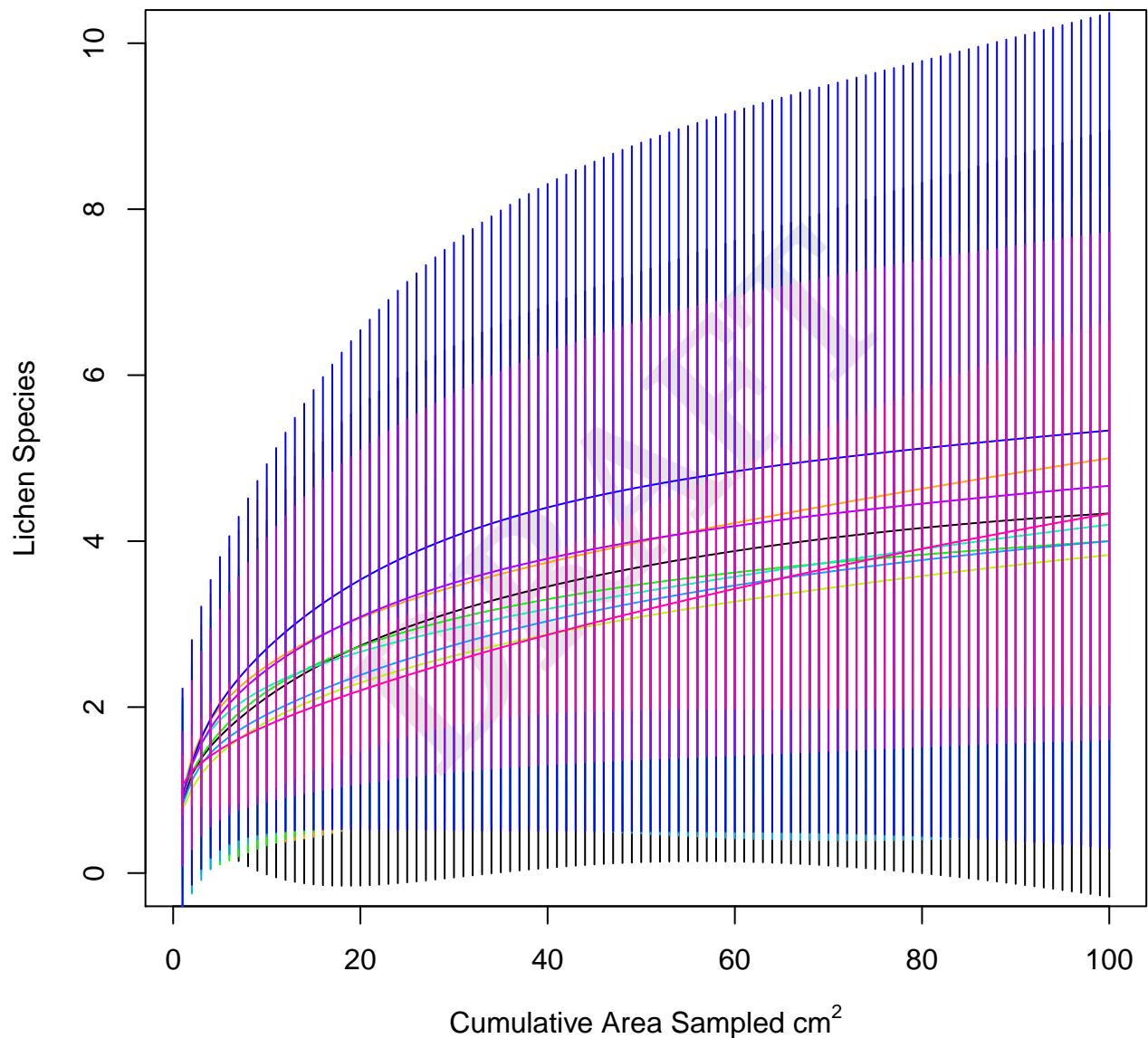


Fig. 1



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

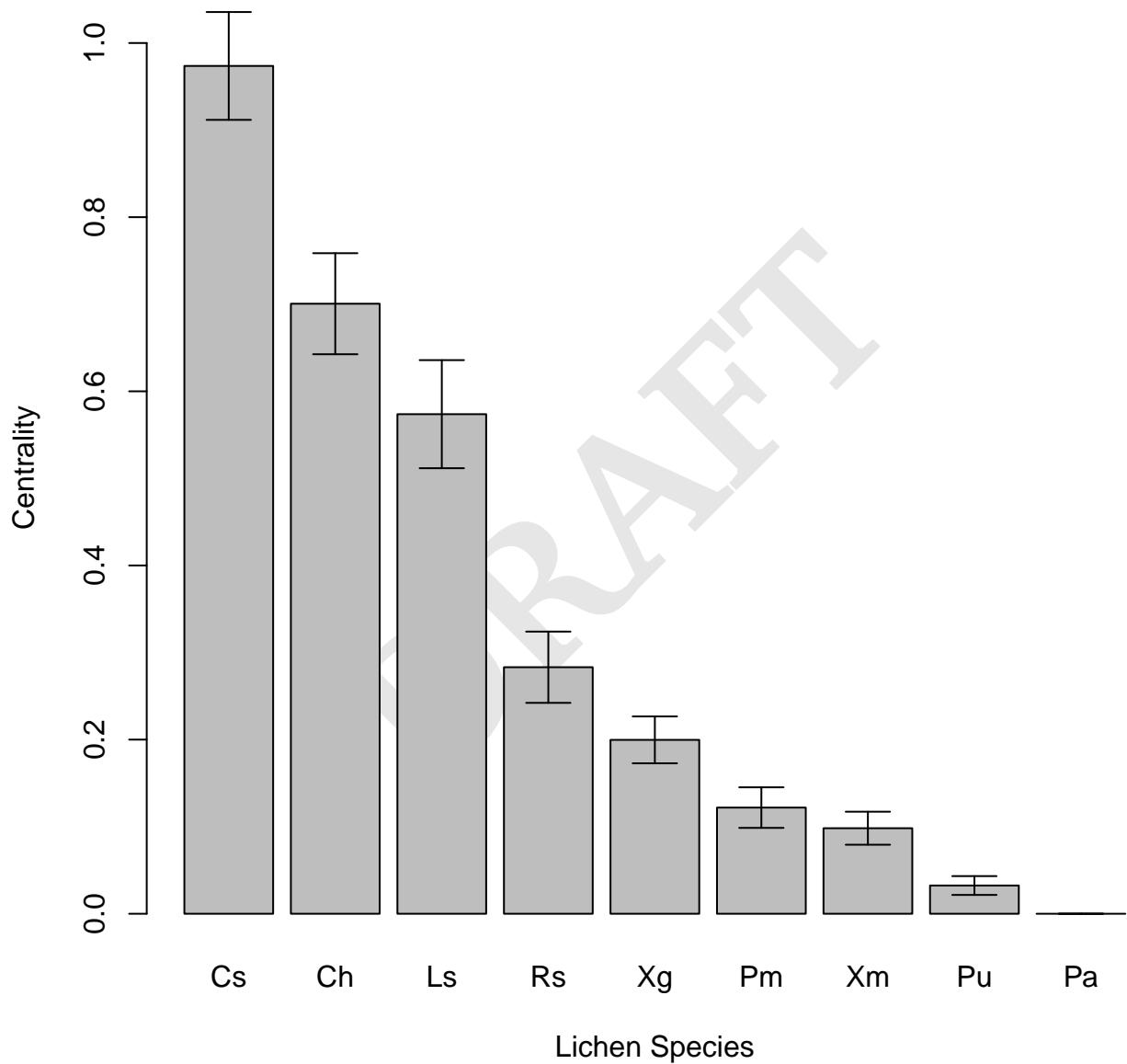


Fig. 3