

Genotypic variation in a foundation tree results in heritable ecological network structure of an associated community

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1 Biological evolution occurs in the context of complex ecosystems of
2 interacting species 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 evolutionary context, the “genetic similarity rule” provides a useful framework for approaching the nexus of evolutionary and community dynamics in the context of complex interaction networks. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, (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 3x 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. 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 cm² 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 cm² 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 cm² (1

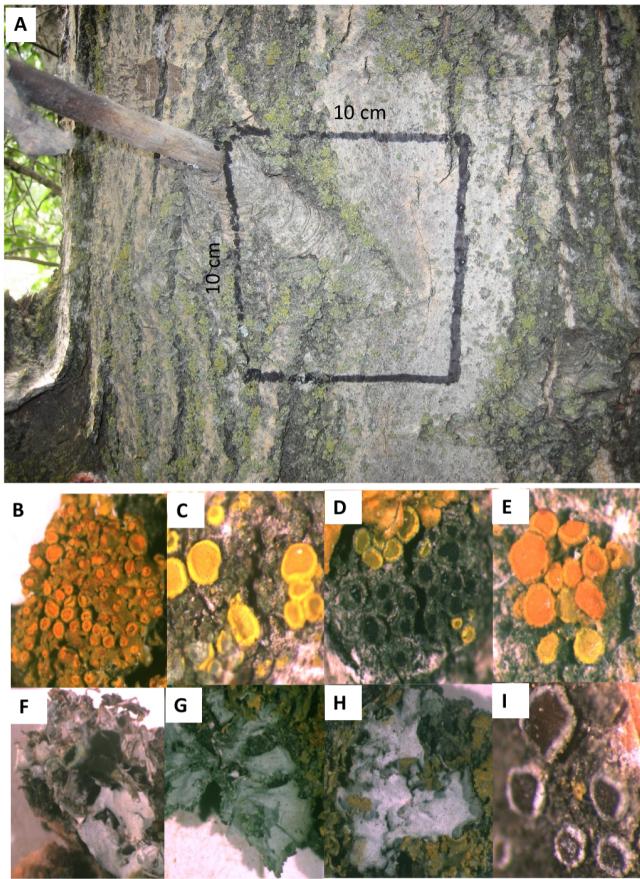


Fig. 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the 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. Naesboung (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 is the percent of 1 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 tannin, 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 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 how one species impacts another with zero being no effect and values less than or greater than zero interpreted as negative and positive effects, respectively. Here, we will refer to this matrix (\mathbf{D}) as an interaction matrix with the properties that it can be asymmetric (i.e. D_{ij} does not necessarily equal D_{ji}). Here, the diagonal (D_{ii}) is zero, 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 ob-



Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 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.

served. 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 (41). We also calculated two similar global network metrics: degree and centralization. The first was network degree, which is a count of the total number of links in a network. As the networks contained not only positive and negative connections, as well as directional connections (both in-coming and out-going), we calculated the same network metrics for all combinations of these types of connections in each network. Although there are many more possible network

metrics that could have been examined, we chose to focus on a restricted set for the sake of clarity. Also, degree and centrality form the basis of many other network metrics. To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (42) using the `signnet` package (43).

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) (44) to produce dimensionally reduced ordinations of these multivariate responses and fitted vectors for continuous predictor variables to the ordinated values (45). Using random initial configurations with a maximum of 500 iterations and a change in stress threshold of less than 10^{-12} . Final configurations has the lowest stress with at most a stress level of 0.10.

For each network, we also calculated metrics that measure different structural aspects. Although there are many other metrics, for the sake of simplicity we focus on a subset that represent several interesting features of network structure (see (17)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (23, 46). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (41). In a network with a low level of centralization species have similar amount of interaction in the network, while a network with a high level of centralization tends to have one or small number of species that interact with other species. We used a related function to calculate the centrality of each species (i.e. node level centrality) in each network as well.

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

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

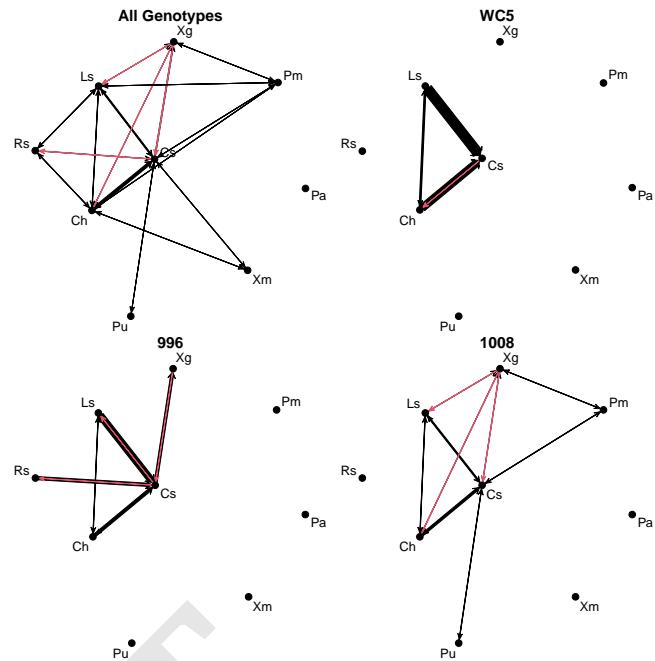


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species (abbreviated by the first letter of the genus and specific epithet), which are scaled by their magnitude. The sign of the interaction is indicative of greater (positive) or lesser (negative) paired occurrences than expected relative to the overall frequency of occurrence of each species. Ecologically, the links in the network are likely the product of multiple types of interactions (e.g. mutualism, parasitism, competition, facilitation) that could vary over both space and time.

Results

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

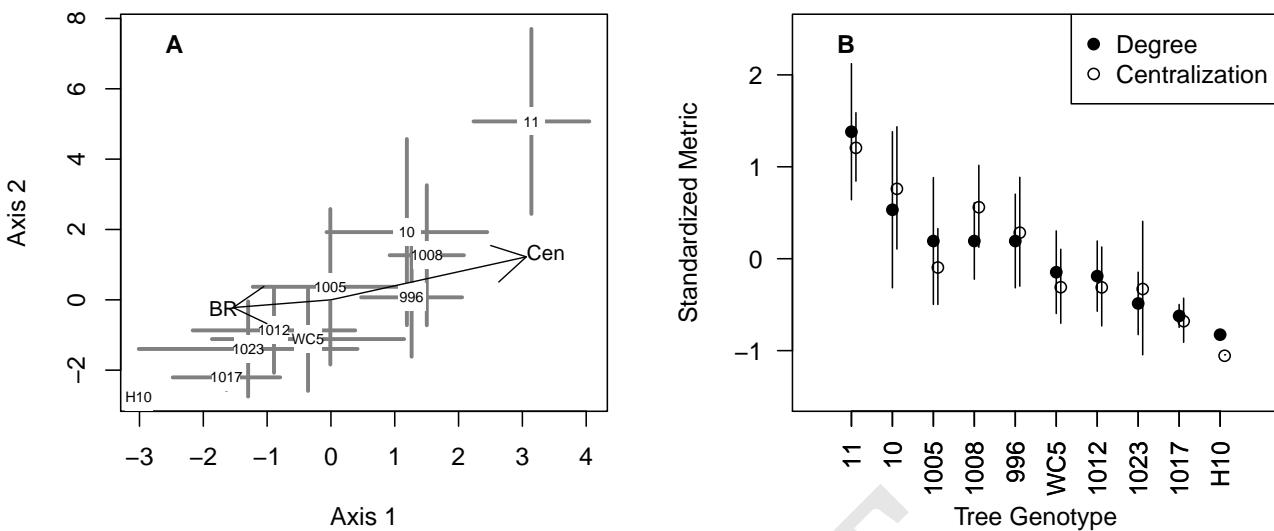


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing 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 (± 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.

($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$) 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 centralization 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).

= 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 roughness was correlated with network similarity (Ta-

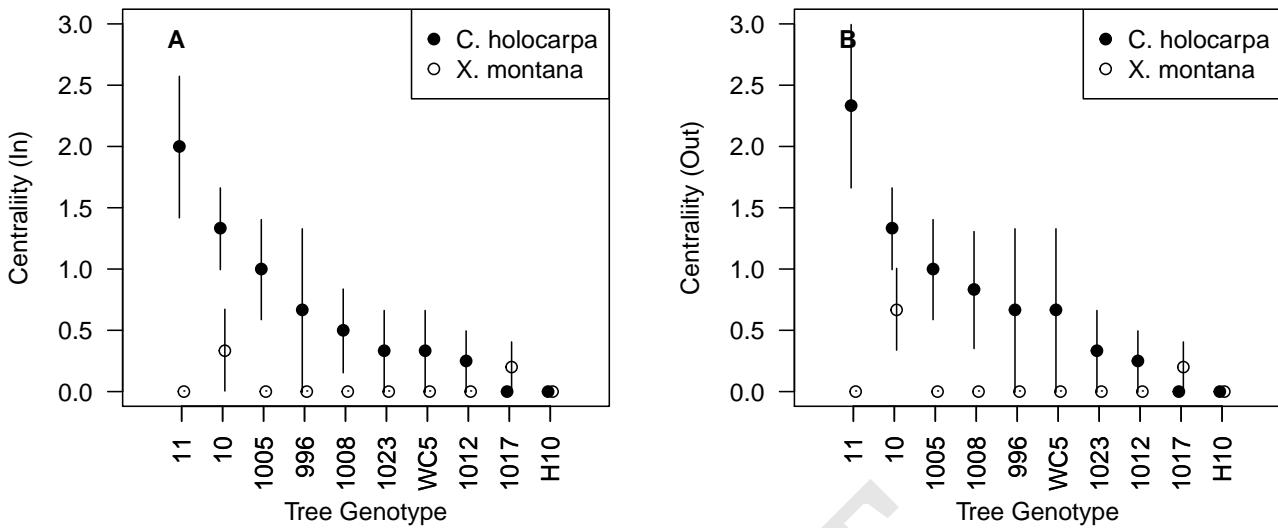


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

ble 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).

Discussion

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest

| | 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.

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

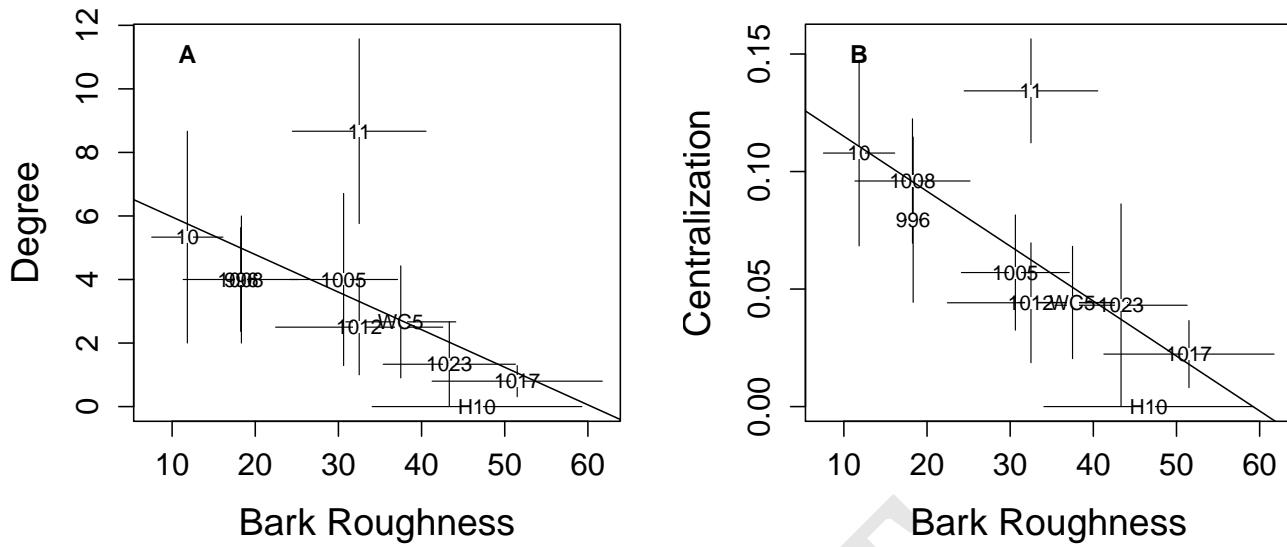


Fig. 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased the number of interactions (degree) and dominance of those interactions decreased.

478 **Heritability of Interaction Network Structure.** We
 479 found significant heritability of lichen interaction
 480 network structure, and, in line with the genetic simi-
 481 larity rule, networks observed on trees of the same
 482 genotype tended to be structurally similar. There
 483 are important functional ramifications of genetically
 484 based variation in network structure. First, even
 485 if the composition of the communities is the same
 486 among individuals and genotypes, interactions may
 487 not be. We didn't observe compositional differences
 488 using the same data from which the lichen networks
 489 were derived. If we only had our composition dataset
 490 from this study, we would have concluded no re-
 491 sponse of the lichen community to tree genotype,
 492 even though the underlying interactions among lichen
 493 species does vary among genotypes. Community com-
 494 position of lichen has previously been observed to
 495 be different among tree genotype in the same ex-
 496 perimental garden, though this was observed with a
 497 larger sampling of total area and quadrats per tree.
 498 Regardless, this could result in a situation in which
 499 abundance based investigations of community-level
 500 genetic effects may miss important variation in the
 501 interactions among individuals in these communi-
 502 ties, leading to an underestimate of genetic effects
 503 in ecosystems. It is possible that these underlying
 504 differences in interactions among lichen could lead

505 to differences in community composition at a fu-
 506 ture point in time, however, this is not needed for
 507 evolutionary dynamics to play out.

508 Second, following on the previous point, genetic
 509 diversity could be influencing the stability of com-
 510 munities through the effects on the structure of in-
 511 teractions. Some network structures are likely to be
 512 more stable, either in response to disturbance or via
 513 self-organized dynamics. For example, centralized
 514 networks, although more efficient, are theorized to
 515 be more susceptible to targeted attacks on the center
 516 of the network. For example, consider a forest with
 517 two genotypes that support lichen communities that
 518 are similar in total abundances of each species but
 519 differ in terms of the structure. Extensions of game
 520 theory to evolutionary biology have demonstrated
 521 that network structure can lead to variation in evo-
 522 lutionary dynamics. Some structures tend toward
 523 dominance and dampening of selection, while others
 524 lead to amplification of selection (Newman). One
 525 class of networks that are theorized to have amplifying
 526 effects on networks have "star" shapes with one or
 527 a few species at the center and radiating interactions
 528 out from the central core (Leiberman). This is struc-
 529 turally what we have observed with the networks that
 530 tend to occur on some of the genotypes in our study,
 531 i.e. the more centralized networks. It is possible that

532 these more centralized networks could function as
533 hot-spots of evolutionary dynamics resulting from
534 the amplifying effect the network structure fostered
535 on that tree genotype.

536 **Implications for Interspecific Indirect Genetic Ef-
537 ffects (IIGEs).** Interspecific indirect genetic effects
538 (IIGE) theory provides a quantitative framework
539 within which to approach evolutionary theory at
540 higher levels of biological organization: from pop-
541ulations to communities and ecosystems. To date,
542 this theory has focused on modeling the strong ef-
543 ffects of foundation species (7, 27), but it has not
544 yet integrated developments in the ecological or evo-
545 lutionary network theory literature. This is to say
546 that it has not developed a way to examine com-
547 plex interactions among species; however, previous
548 studies have demonstrated this network context is
549 likely to be important, as altering the structure of
550 interaction networks provides a means for genetic
551 effects to be dampened or magnified within the sys-
552 tem of interacting species. For example, (24) showed
553 that the genetics based interactions of aphid resis-
554 tant and aphid susceptible trees resulted in different
555 interaction networks of their associated arthropod
556 communities composed of 139 species. At the scale
557 of ecosystems, trophic networks or food webs direct
558 and control the rates of energy and nutrient flux (50).
559 Furthermore, in a predator-prey-plant study, Smith
560 (20), showed that the interactions among species
561 across trophic levels depended on plant genotype.
562 Also, work by (51–53) observed consistent patterns
563 of centralized interactions of species modules focused
564 around hubs of plant-fungal interactions. In other
565 words, a small number of plant and fungal symbionts
566 tended to have disproportionate numbers of interac-
567 tions with other species and likely are the drivers
568 in determining community assembly, structure and
569 dynamics.

570 The results of the current study provides clear em-
571 perical evidence that variation in network structure
572 can be genetically based (i.e. heritable) and points to
573 the need to expand IIGEs encompass the structure
574 of interaction networks. Although such a synthesis
575 necessitates a much greater effort than can be af-
576 fforded in this paper, it is possible to point to several
577 productive pathways forward. In terms of interaction
578 networks, foundation species are relatively central
579 within the system of interactions, that is their direct
580 and/or indirect effects are greater than other species

581 So, when the more centralized (foundation) species
582 have genetically based interactions, genetic effects
583 will tend to be magnified in the community. Here,
584 we found that even though more abundant or more
585 centralized (i.e. “important”) species were present in
586 the community, their effects were not the main com-
587 ponent responding to genetic effects. Considering
588 the impact of network structure would be a produc-
589 tive path forward for the theoretical development
590 and application of the IIGE concept.

591 **Evolutionary Implications of a Genetic Basis to
592 Network Structure.** With regard to the evolution-
593 ary implications of network structure, ecological net-
594 work studies have focused on asymmetry and the
595 quantification of its structure in communities, with
596 qualitative discussion of the impacts on evolutionary
597 dynamics (36, 37, 54, 55). More specific predication,
598 with a quantitative framework, can be found in appli-
599 cations of evolutionary game theory, and although
600 developed at the population scale, such theory can
601 apply to communities. One seemingly useful direc-
602 tion from evolutionary network developments from
603 game theory is the classification of networks into two
604 general categories, rooted and cyclic, in which rooted
605 networks have interactions in which evolutionary ef-
606 ffects emanate from one or multiple origins but these
607 effects do not have connections back to the origins,
608 whereas cyclic networks contain feedbacks to one or
609 more origins. Although it did not explicitly define it
610 in this context, the previous work of (17) developed
611 the perspective that the structure of the network in
612 the context of a foundation species, such as cotton-
613 woods in which there are demonstrable community
614 level genetic effects, is inherently created when trait
615 variation among genotypes of a foundation species
616 has ecological effects on associated species.

617 This builds on many previous studies demonstra-
618 ting that the community level effects vary among
619 multiple genotypes. It is not clear what potential
620 there is for feedbacks there are to the origins (e.g. the
621 cottonwood genotypes) from the community, and as
622 such it cannot be determined whether these networks
623 are cyclic or rooted. In other systems, lignicolous
624 lichens can have demonstrable positive effects on the
625 availability of nutrients for the trees that they are
626 associated with, but this has not been measured in
627 the current system. Illucidating the absence and/or
628 presence and quantifying such feedbacks would al-
629 low for the determination of the cyclic nature and

630 potential evolutionary dynamics of this system. The
631 presence of feedbacks would provide the potential
632 for non-linear dynamics in which evolutionary effects
633 are dampened or amplified by the structure of the net-
634 work. For example, a star structure in which there is
635 a primary or core set of central species with feedbacks
636 from the radiating species has been demonstrated to
637 be a structure that amplifies evolutionary dynamics
638 (31). If such feedbacks do not exist, and these sub-
639 networks of the lichen and tree genotypes are likely
640 to be multi-rooted networks. Such a structure is theo-
641 rized to generally promote diversification as variation
642 arising from the shifting distribution of the “roots”,
643 i.e. genotypes; however, loss of genotype/root diver-
644 sity could lead to fixation of a single genotype in
645 the population and a decrease in community-wide
646 diversity.

647 **Applicability to Other Systems.** Although our study
648 was conducted with a community of lichens, these re-
649 sults can be generalized to other groups of diverse or-
650 ganisms around the world that also exhibit significant
651 genetic signals at the community level (7, 56). How-
652 ever, there are important points to consider when
653 extending the observed genetically based response
654 of the lichen networks to other systems. As bark
655 lichen individuals do not move, but grow in a pri-
656 marily two dimensional plane, these communities
657 and their interactions occur in the highly localized
658 context of the tree’s bark surface. Lichen individu-
659 als are also many orders of magnitude smaller than
660 the tree individual in this system (38). For these
661 reasons, the genetic effects on these communities is
662 not dampened by the movement of individuals and
663 the mixing of the effect of different tree genotypes
664 on the lichen community, as might occur for more
665 mobile species (e.g. insects and birds). Relatedly, we
666 only examined lichen in this study, and other species
667 whose distributions, abundances and/or interactions
668 vary in their response to tree genotype, such as ani-
669 mals that may also impact lichen communities, could
670 be playing a role that we did not examine. For ex-
671 ample, an analysis of the multivariate correlations
672 of different components of the community in this
673 system demonstrated significant patterns of genetic
674 co-responses to tree genotype, supporting the non-
675 mutually exclusive possibilities of shared responses²⁴
676 to tree genotype or tree genotypic effects on interac-²⁵
677 tions among these sub-communities (4). As such,²⁶
678 although we can not rule out the possibility that²⁷

679 other unmeasured tree traits or organisms correlated
680 with bark roughness are underlying the observed pat-
681 terns, substantial research supports the importance
682 of genetically based tree traits for communities and
683 ecosystems (8), and in particular bark roughness for
684 bark lichen communities (38, 39, 49).

685 One final point to discuss is that in the present
686 study lichen cover, species richness and composition
687 were not significantly responsive to tree genotype,
688 unlike what has been previously observed for lichen
689 (39) and multiple taxa in this and other systems (8).
690 This is likely the result of differences in sampling
691 method and the choice of genotypes leading to overall
692 higher abundances of observed lichens to assure the
693 possibility of observing lichen interactions. In the
694 current study mean percent total lichen cover among
695 genotypes ranges from 60-93% cover; whereas the
696 range reported in (39) is 0.86-18.73%. The previous
697 study used a visual estimation method, unlike the
698 current study, which observed lichen at the scale of 1
699 cm² cells, which could over-estimate cover depending
700 on the frequency at which actual thallus size was
701 less than 1 cm². The previous study used samples
702 from both the northern and southern aspects of each
703 tree; whereas, the current study only observed lichen
704 on the northern aspect. Also, our current results
705 are likely different from the previous study because
706 the current study selected genotypes that tended to
707 have bark lichen, with the interest of focusing on
708 generating networks for comparison. These differ-
709 ences do not negate the findings of either study but
710 is important to explain the differences in the find-
711 ings, particularly in the community-level effects of
712 tree genotype and the general applicability to future
713 studies.

714 In attempting to apply these findings to other
715 systems, it is important to consider the spatial and
716 temporal scaling of genetic effects. In the present
717 study, the sessile nature of lichens means that indi-
718 viduals, and potentially multiple generations, live
719 their entire lives on a single tree. As such, our study
720 examines one scaling of a genetic effect, in which
721 the phenotype of a single tree individual (i.e., tree
722 genotype) has complete influence on the community
723 with little to no effect of other tree individuals in
724 the population. The extreme from this would be
725 where the associated community moved among and
726 interacted with not only other community members
727 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 previous community genetics studies that have focused on sessile organisms, such as gallin insects (11, 18, 24, 58?), to quantify the frequency of these interactions in the context of the larger community. This would provide an estimate of the relative impact of these focal, often termed foundation, species. In addition, community genetics theory has only considered first order interactions, i.e., between two organisms (7, 27, 28). Given that network structure could be influenced by genetic effects, as evidenced by the present study, assessing higher order interactions could provide a path forward for theoretical advances that could help with identifying important characteristics of sub-groups to focus on in empirical studies.

Conclusion. In the face of the high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed to some in previous studies (16, 59, 60). In the present study, we found that community assembly processes, such as environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. We suggest that future work would be aided by determining these modules within the biotic commu-

nity that include species with similar differences in body-size and time-scales. As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (61). With such findings, it appears that we are closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

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Supplementary Materials

Tables.

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| | 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.

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

Table 4. Matrix of correlations among tree traits, lichen community metrics and network metrics

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

Figures.

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

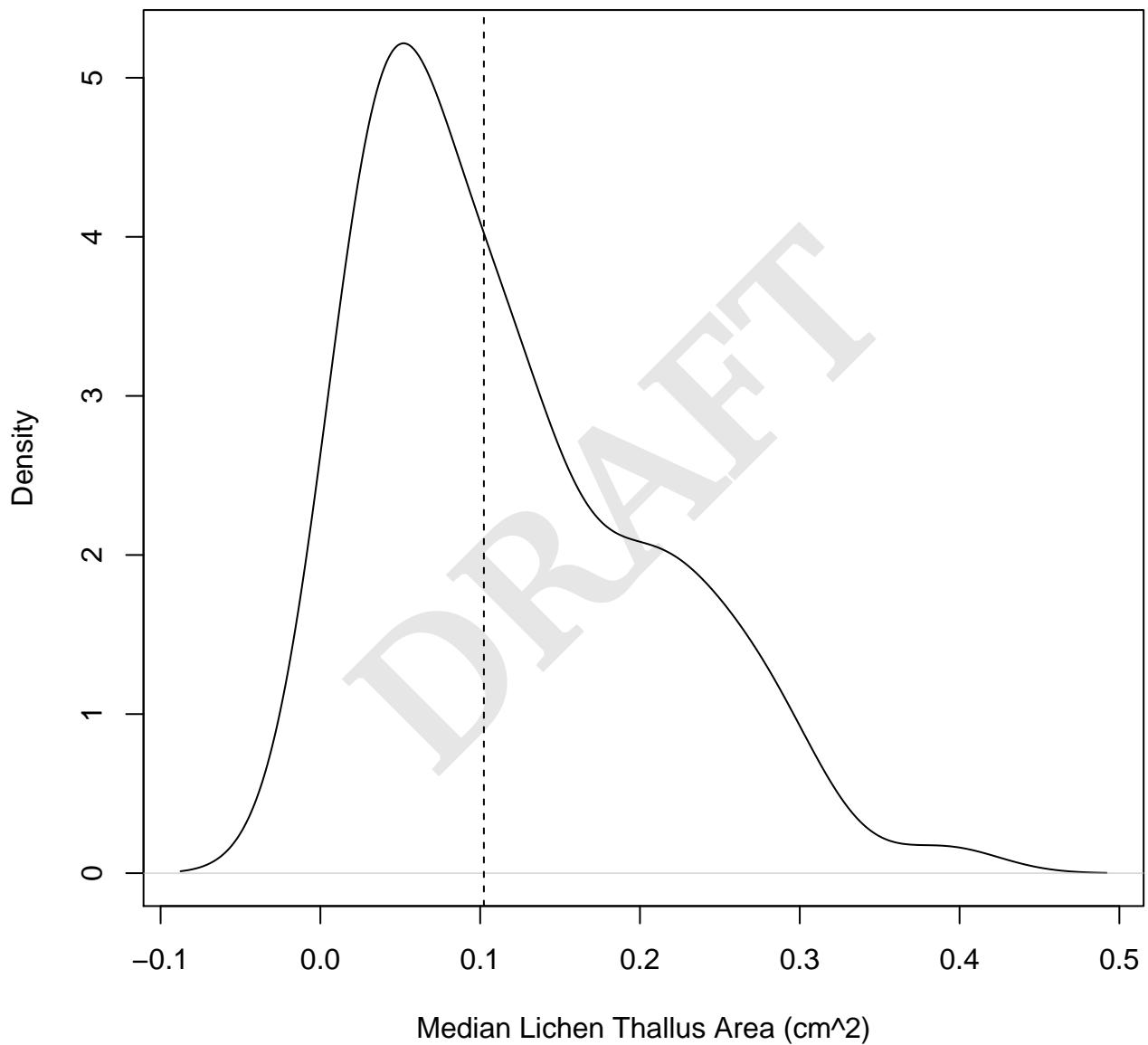


Fig. 1

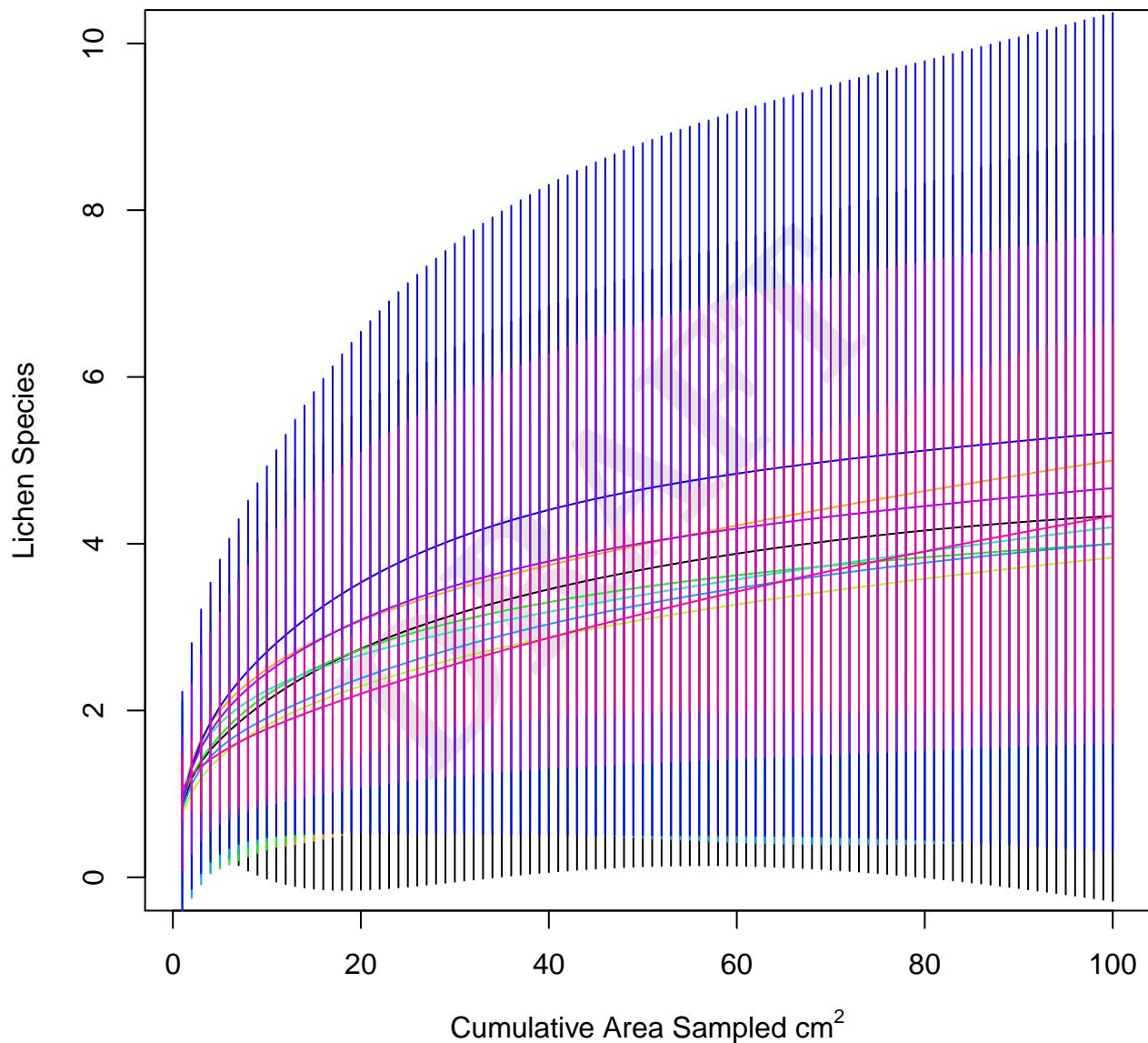


Fig. 2. Species area curve by genotype.

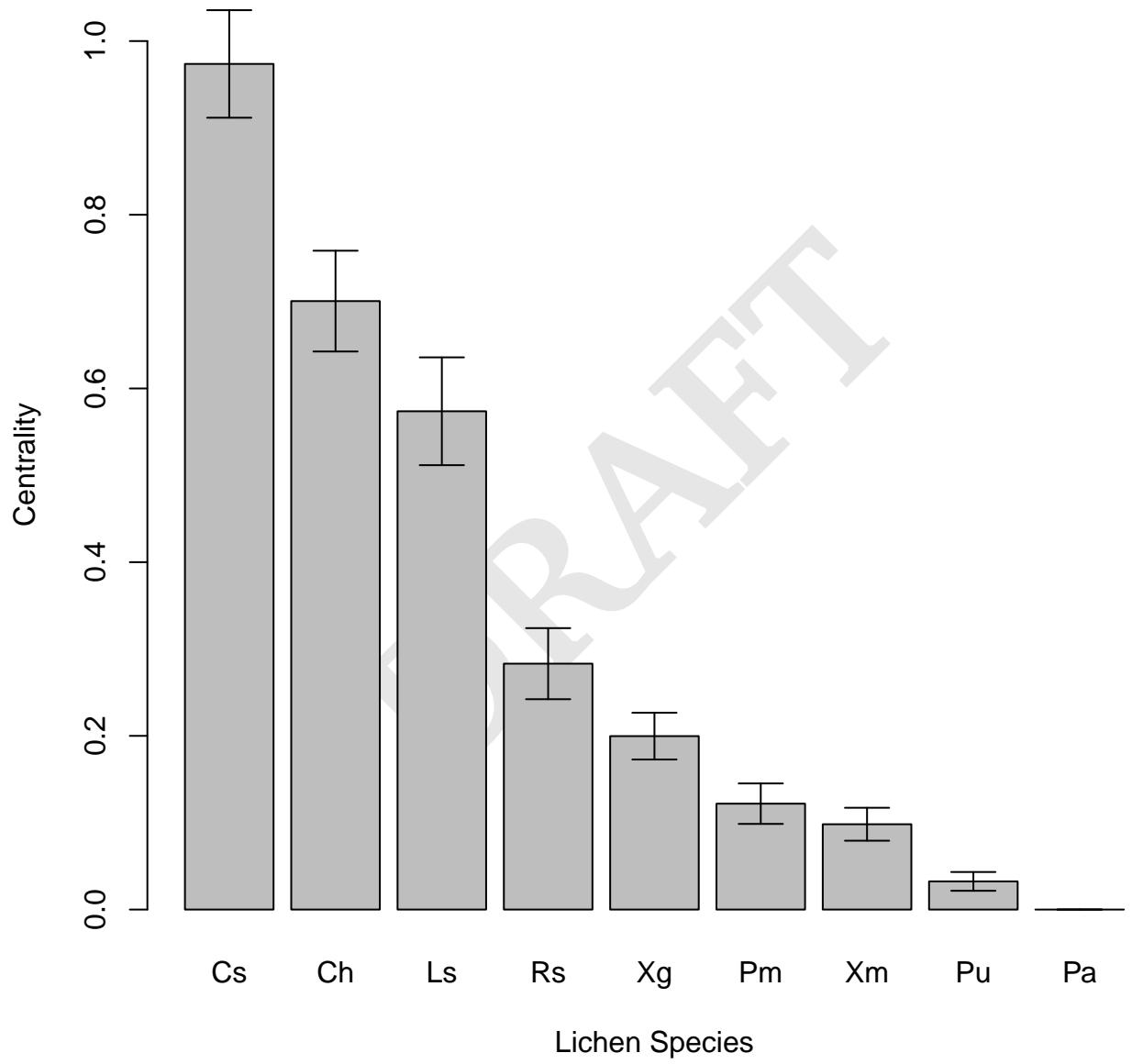


Fig. 3