

# 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 ecosystems whereby natural selection  
2 defines the structure of ecological networks. Therefore, elucidating  
3 the genetic basis to ecological network structure is fundamental to  
4 understanding evolution. Although previous work has demonstrated  
5 that genetic variation can influence food webs and trophic chains,  
6 we are unaware of a study that quantified the contribution of pheno-  
7 typic variation to heritable variation in network structure. To examine  
8 this, in a 20+ year common garden we observed nine epiphytic lichen  
9 species associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation species. We constructed and  
10 conducted genetic analyses of signed, weighted, directed lichen inter-  
11 action networks. We found three primary results. First, genotype  
12 identity significantly predicted lichen network similarity; i.e., replicates  
13 of the same genotype supported more similar lichen networks  
14 than different genotypes. Second, broad sense heritability estimates  
15 showed that plant genotype explained network similarity ( $H^2 = 0.41$ ),  
16 degree ( $H^2 = 0.32$ ) and centralization ( $H^2 = 0.33$ ). Third, of several  
17 tree phenotypic traits examined, bark roughness was both heritable  
18 ( $H^2 = 0.32$ ) and significantly correlated with lichen network simi-  
19 larity ( $R^2 = 0.26$ ). These results support a mechanistic, genetic pathway  
20 from variation in a heritable tree trait to ecological network structure  
21 and demonstrate that evolution can act at the community level to in-  
22 fluence not only abundances of organisms but also interactions at  
23 the scale of entire networks. Given that network structure has deter-  
24 mines system-wide stability and resilience, our findings have impor-  
25 tant implications for how evolution acts in ecosystems.  
26

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 ecosystems by modulating  
5 and stabilizing local conditions (1), plays a significant  
6 role in defining distinct communities of interacting  
7 organisms: such as, endophytes, pathogens, lichens,  
8 arthropods, and soil microbes (2–4). Multiple studies  
9 have now demonstrated that genetic variation influ-  
10 ences numerous functional traits (e.g., phytochemi-  
11 cal, phenological, morphological) that in combination  
12 result in a multivariate functional trait phenotype  
13 (5) in which individual plant genotypes support dif-

ferent communities and ecosystem processes (6, 7).  
14 Recently, the importance of genetic variation in struc-  
15 turing ecological systems was reviewed, and not only  
16 were many instances of strong genetic effects found  
17 in many ecosystems but the effect of intraspecific  
18 variation was at times greater than inter-specific vari-  
19 ation (8). There is now evidence to support that  
20 selection, acting on this heritable variation, tends to  
21

## Significance Statement

Evolution occurs in the context of ecosystems com-  
prised of complex ecological networks. Research at  
the interface of ecology and evolution has primarily  
focused on pairwise interactions among species and  
have rarely included a genetic component to net-  
work structure. Here, we used a 20+ year common  
garden experiment to reveal the effect that geno-  
typic variation can have on networks of lichens that  
colonize the bark of a foundation tree species. We  
found that lichen interaction network structure is ge-  
netically based and primarily driven by bark rough-  
ness. These findings demonstrate the importance  
of genetic variation and evolutionary dynamics in  
shaping ecological networks as evolved traits. In  
particular, this study points to the importance of as-  
sessing the effect of foundation species genetics on  
the structure of species interactions that can gen-  
erate 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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22 occur among groups of species (9) and that genetic  
23 variation and phylogenetic relatedness contribute to  
24 variation in community assembly (10) and species  
25 interactions (6, 11, 12), which shape the structure of  
26 ecological interaction networks (13–15).

27 The development of interspecific indirect genetic  
28 effects (IIGE) theory (16) in evolutionary biology  
29 points to the importance of studying the genetic ba-  
30 sis of interaction network structure because genetic  
31 based differences in network structure among indi-  
32 viduals can be acted upon by natural selection when  
33 there are fitness consequences of different networks of  
34 IIGEs that can result in community evolution (17).  
35 For example, although the analysis was of abun-  
36 dances rather than interaction networks, (18, 19)  
37 found that the mycorrhizal communities on the roots  
38 of drought tolerant and intolerant trees are domi-  
39 nated by different orders of ectomycorrhizal fungal  
40 mutualists that also differ in the benefits they provide  
41 that enhance tree performance. Because drought tol-  
42 erant genotypes are three times more likely to survive  
43 record droughts, selection acts both on the tree and  
44 its fungal community and with increased drought the  
45 community phenotype has changed over time. Also,  
46 in an antagonistic interaction context, (2) found that  
47 with the addition of a damaging leaf pathogen to cot-  
48 tonwoods in a common garden, the impacts of these  
49 strong interactors results in a different and dimin-  
50 ished community of arthropods relative to control  
51 trees. Thus, selection acting on the tree may alter  
52 the network structure of associated communities in  
53 which different networks of communities are most  
54 likely to survive pathogen outbreaks. Regardless of  
55 whether the IIGE is unilateral (i.e., tree affects the  
56 community) or reciprocal (i.e., the community also af-  
57 fects the relative fitness of the tree), selection on tree,  
58 community or both can change network structure  
59 (17) and thereby alter community dynamics. Net-  
60 work theory and evidence from empirical studies in  
61 ecology have demonstrated that indirect effects can  
62 lead to self-organization, producing sign-changing,  
63 amplifying and/or dampening effects (20, 21), and  
64 evolutionary applications have demonstrated that in-  
65 direct effects of interactions among species can lead  
66 to network structures that amplify or dampen the  
67 effects of selection, such as the formation of star-like  
68 structures in which there is a “central” species or  
69 group of species that interact with other, peripheral  
70 species, can amplify selection events (22).

In this 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, (23) 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 (24) 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*) (25–29) 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 (30, 31) 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.

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 lichens. Using a long-term (20+ years), common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic identity (32). We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (33, 34). 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. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (30, 31, 35, 36). More specifically, based on community genetics theory, particularly the community similarity rule (23), 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. 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.

## Materials and Methods

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**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 intensively sampled in this system and provide an ideal community in which to observe and model interaction networks, as their sessile nature permits accurate identification of individuals and their highly localized, direct contact interactions and slow population turnover rates facilitate the assessment of interactions among lichen species on individual trees (37).

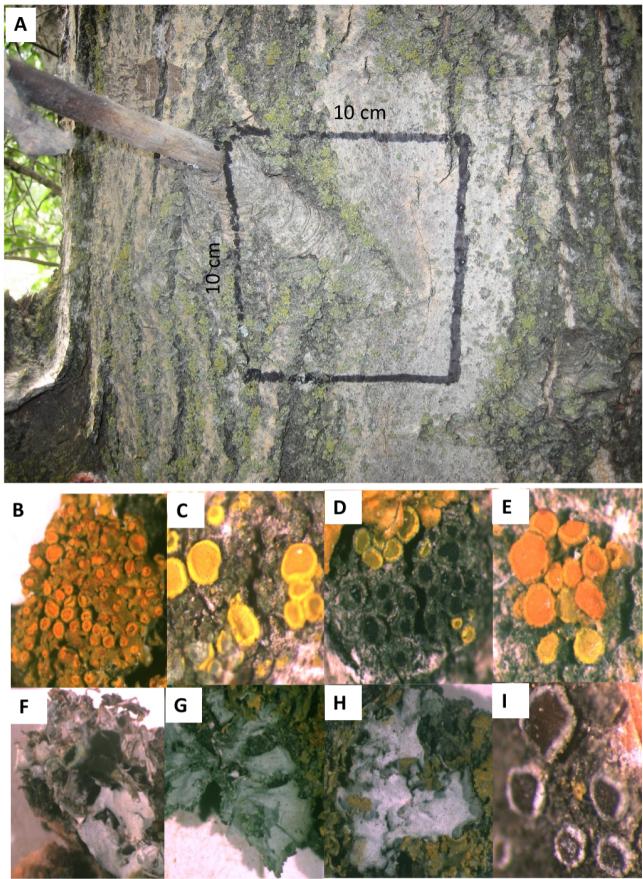
A long-term, common garden experiment was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated with each individual and spatial autocorrelation. Established in 1992, asexually propagated clones of genotyped *P. angustifolia* individuals were obtained 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 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 cm<sup>2</sup> 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 (37): 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 (38) with the addition that we quantified the presence of lichen in the 1 cm<sup>2</sup> 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 (39). 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



**Fig. 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanura*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (B-D) and R.R. Naesbourg (E-I).

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.

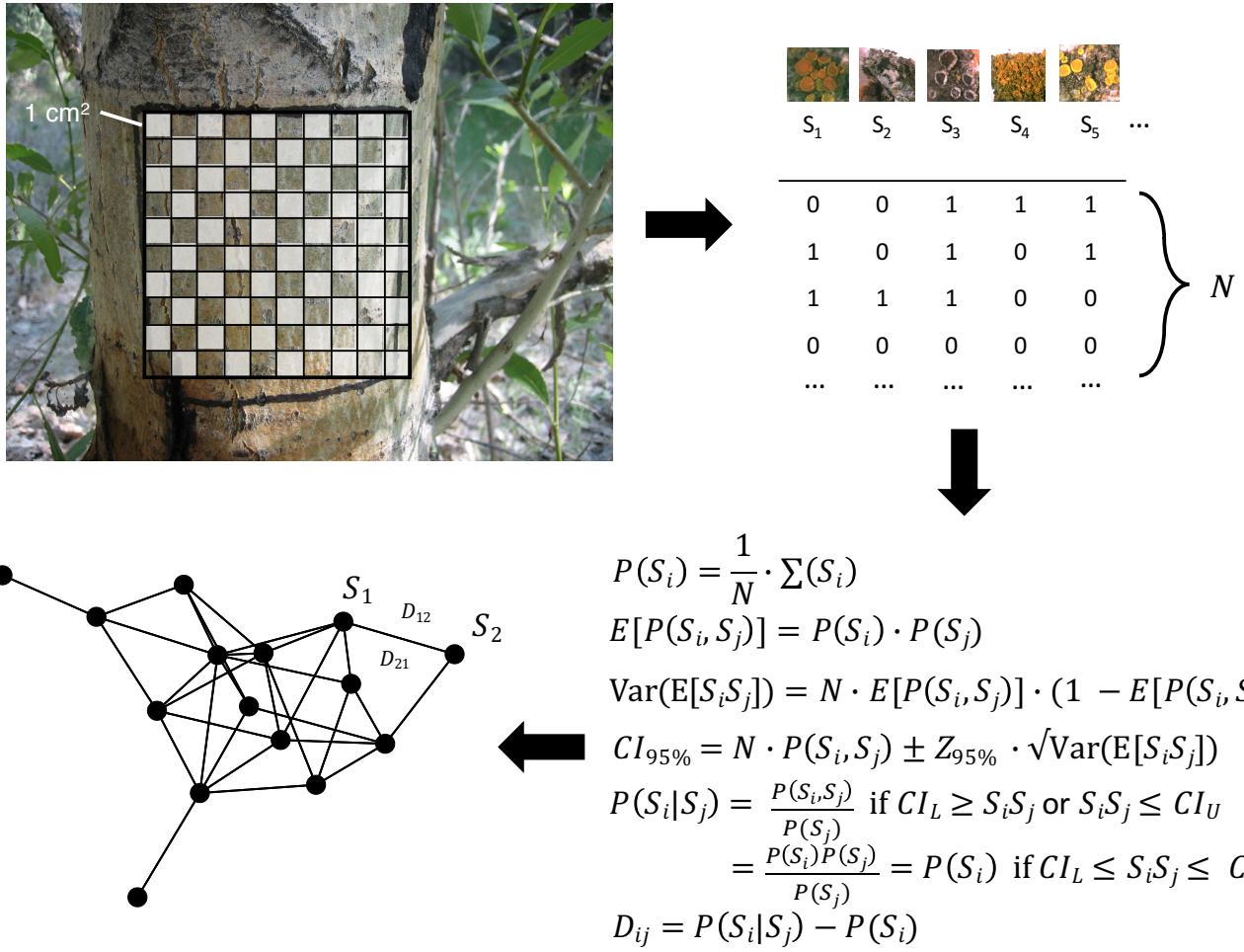
We then applied an analytical procedure to remove non-significant links between species. This procedure determines if the joint probability of a species pair (i.e.  $P(S_i, S_j)$ ) is different from zero (Fig. 2). Here, a confidence interval  $CI_{95\%}$  is calculated as  $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$ , 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 prob-

ability 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 (40). Also, as the method does not track individuals within species and interactions such as competitive exclusion or facilitation within species would result in the same species being observed. Therefore, the results of intra-specific interactions always results in the same species being observed and a resulting  $D_{ii} = 0$ .

**Network Metrics.** To quantify the structural variation of lichen networks we calculated several metrics at both the node and whole-network level. For individual nodes (i.e. species) in each network, we calculated both the degree and the Freeman's centrality (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 but also 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, accounting for differences in sign through the application of recently developed metrics that incorporate sign information from signed, weighted, directed networks (42). 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. In addition, degree and centrality form the basis of many other network metrics.

**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



**Fig. 2.** Lichen interaction networks were constructed by conducting field observations in 1 cm<sup>2</sup> cells within a 100 cm<sup>2</sup> 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 (39), 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.

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

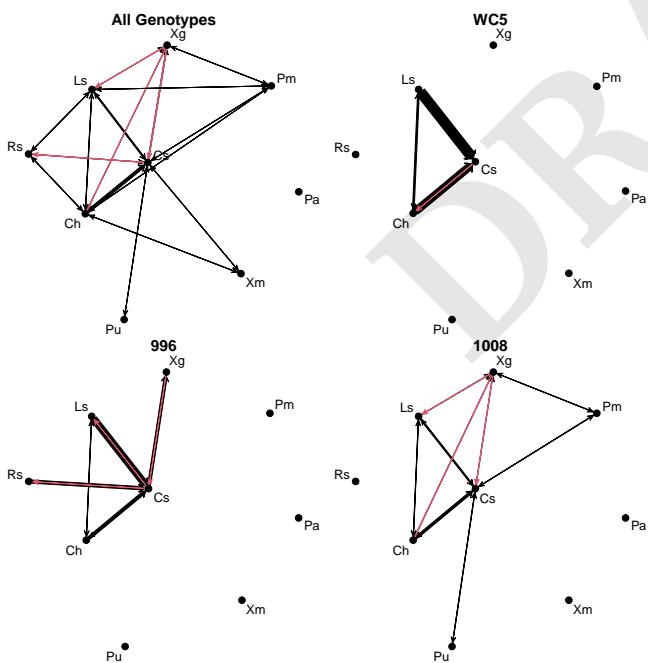
and a change in stress threshold of less than  $10^{-12}$ . Final configurations has the lowest stress with at most a stress level of 0.10.

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 (24)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (30, 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. 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).

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 (16) to adjust the degrees of freedom for unbalanced genotype replicates.

All code and data for the project are openly available online. Code and data are available at [github.com/ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo at [zenodo.com/doi/XXXXXX](https://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.

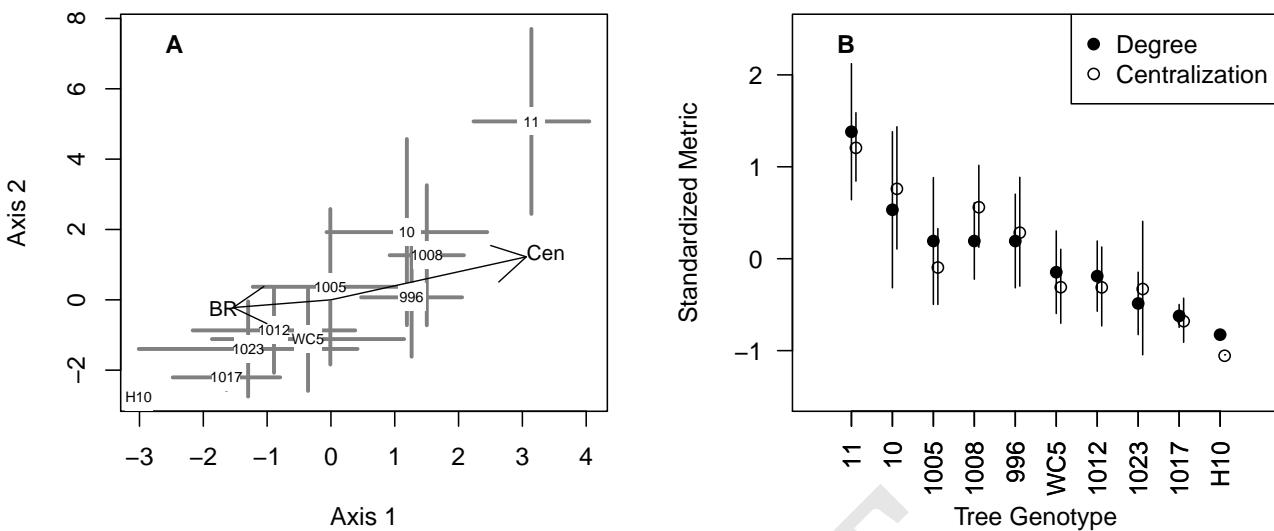
## Results

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-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-value* = 0.0255) and centralization including both in-coming and out-going links ( $RLRT = 4.04$ ,  $H^2 = 0.33$ , *p-value* = 0.0184) or when separated into in-coming only ( $RLRT = 3.9852$ ,  $H^2 = 0.3309$ , *p-value* = 0.0190) or out-going only ( $RLRT = 3.8615$ ,  $H^2 = 0.3193$ , *p-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-value* = 0.0229), positive in-going centralization ( $RLRT = 4.4812$ ,  $H^2 = 0.3487$ , *p-value* = 0.0142). Metrics calculated with negative links were not significant, including degree (negative) ( $RLRT = 0.0327$ ,  $H^2 = 0.0318$ , *p-value* = 0.3859) and both in-coming (negative) ( $RLRT = 0.3304$ ,  $H^2 = 0.1057$ , *p-value* = 0.2508) and out-going centralization (negative) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ , *p-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*. Centrality varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ , *p-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-value* = 0.0240) and out-going ( $RLRT = 3.13$ ,  $H^2 = 0.30$ , *p-value* = 0.0327) perspectives, but not for either negative centrality metrics in-coming



**Fig. 4.** The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ( $R^2 = 0.999$ , stress = 0.008) lichen network similarity ( $\pm 1$  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.

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

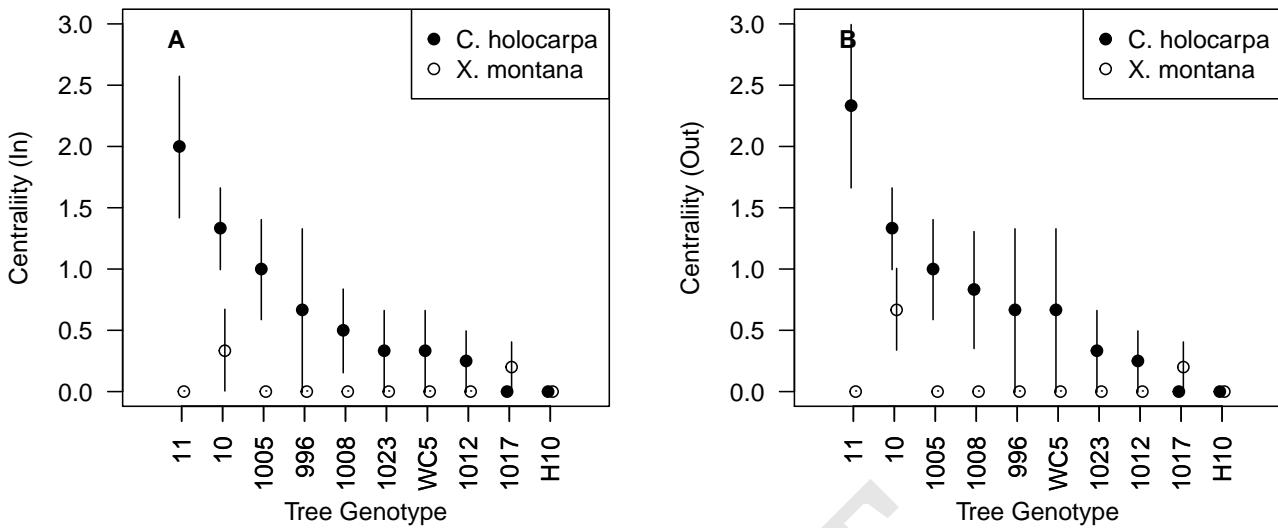
#### 402 Add transformations of variables to methods.

403 Genotype indirectly influenced lichen network centralization via the genetically based variation in bark 404 roughness. The percent cover of rough bark ( $RLRT = 4.8526$ ,  $H^2 = 0.3221$ ,  $p\text{-value} = 0.0113$ ) and 405 condensed tannins ( $RLRT = 3.0522$ ,  $H^2 = 0.3205$ ,  $p\text{-value} = 0.0343$ ) both displayed significant responses 406 to tree genotype. None of the other bark traits, 407 pH ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ) 408 or carbon-nitrogen ratio ( $RLRT = 0.0000$ ,  $H^2 = 409 0.0000$ ,  $p\text{-value} = 1.0000$ ), showed a significant 410 response to tree genotype and none other than bark 411 roughness was correlated with network similarity (Ta- 412 ble 2); therefore, we focused our subsequent analyses 413 on the indirect effect of genotype on lichen network 414 structure via bark roughness. We found that bark 415

roughness was significantly correlated with network 416 similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$ , 417  $R^2 = 0.26$ ,  $p\text{-value} = 0.0096$ ) and other lichen net- 418 work metrics, including negative correlations with 419 overall network degree ( $df = 35$ ,  $t = -2.13$ ,  $r = -0.34$ , 420  $p\text{-value} = 0.04$ ) and centralization ( $df = 35$ ,  $t = -2.52$ , 421  $r = -0.39$ ,  $p\text{-value} = 0.02$ ). In other words, trees with 422 more similar levels of bark roughness tended to have 423 lichen interaction networks with similar structure. 424 To quantify the genetic bases of this effect of bark 425 roughness on network structure, we used the residual 426 values from regressions of network degree and cen- 427 tralization in tests of the effect of tree genotype and 428 found no significant effect of tree genotype for either 429 degree ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ) 430 or centralization ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 431 1.0000$ ), suggesting that the observed relationship 432 between bark roughness and lichen network structure 433 was largely genetically based (Fig. 6). 434

## 435 Discussion

We found that tree genotype influenced lichen net- 436 work structure in the experimental cottonwood forest. 437 Network similarity and metrics of network structure 438 tended to be more similar on trees of the same geno- 439



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

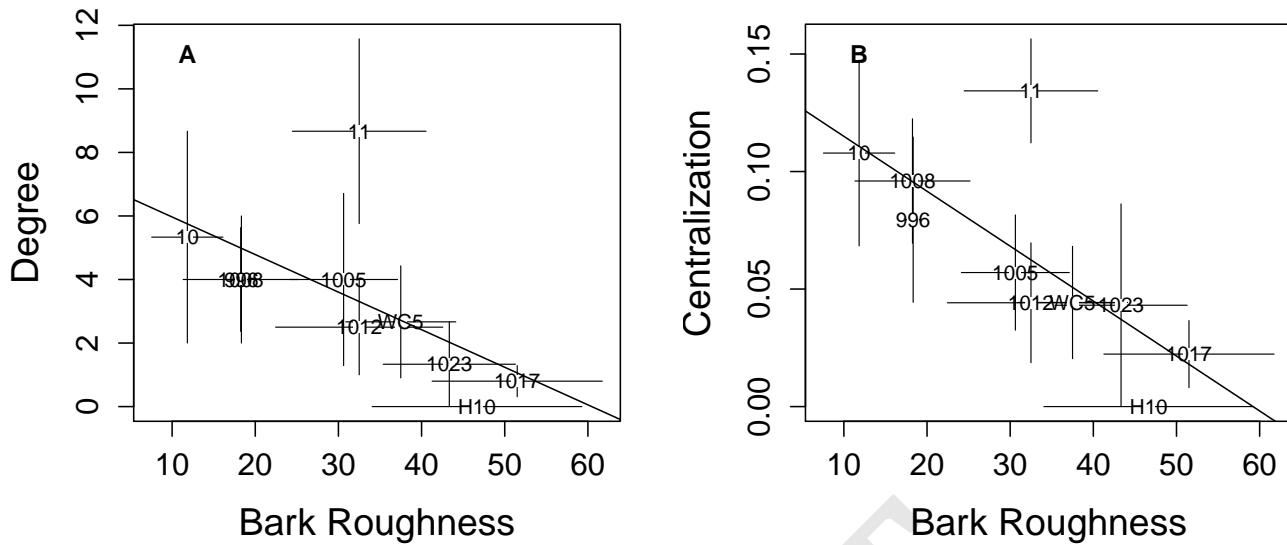
	df	SumOfSqs	R2	F	Pr(>F)
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

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

442 type. Generally, this genetic effect was manifested in  
 443 positive interactions and largely driven by *C. holocarpa*. The genetically based trait, bark roughness,  
 444 was the only trait observed to effect network variation,  
 445 largely via shifts in positive in-coming and  
 446 out-going interactions. Bark roughness has been  
 447 demonstrated previously to be under strong genetic  
 448 control (49), and bark roughness has also previously  
 449 been shown to be an important tree trait influencing  
 450 bark lichens (38); however this is the first demonstra-  
 451 tion of a link from genes to lichen network structure.  
 452 As such these results have important implications  
 453 for the potential influence of genetically based varia-  
 454 tion in ecosystems with networks of interacting  
 455 species. This work is important because it provides  
 456 a mechanistic basis for understanding how commu-  
 457 nity network theory is intimately associated with  
 458

the evolutionary process and how human alterations  
 459 of the environment (e.g., climate change, invasive  
 460 species, pollution) may have cascading, indirect ef-  
 461 fects that alter network structure and evolution.  
 462

**Implications of the Heritability of Interaction Network Structure.** We found significant heritability of  
 463 lichen interaction network structure, and, in line  
 464 with the genetic similarity rule, networks observed on  
 465 trees of the same genotype tended to be structurally  
 466 similar. Although previous studies have examined  
 467 aspects of networks, such as trophic (50) and for-  
 468 est stand-level interaction network structure (31, 51),  
 469 this is the first study that we are aware of to examine  
 470 the heritability of network structure with replicated  
 471 networks at the genotype scale. Previous work in  
 472 the evolution of ecological networks have primarily  
 473 focused on macro-evolutionary dynamics (13, 52–54)  
 474 or have been simulation based individual-level mod-  
 475 els that integrate intraspecific variation to the species  
 476 level (55), even though recent syntheses ave pointed  
 477 to the importance of processes operating across scales  
 478 of organization (56). There are several important  
 479 functional ramifications of genetically based variation  
 480 in network structure. First, intra-specific diversity  
 481 could be creating lichen interaction modules with  
 482 different dynamics. When communities are com-



**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.

485 prised of individuals whose habitat is primarily the  
 486 determined by another organism, these communities  
 487 inherently form modules within the larger ecosystem,  
 488 as they tend to interact more with each other than  
 489 with other individuals (24). Our study demonstrates  
 490 that the environmental differences determined by  
 491 the genetic variation within a single species can cre-  
 492 ate differences that not only impacts community  
 493 composition, as repeatedly demonstrated in other  
 494 community genetics studies (8, 11), but also the  
 495 structure of interactions among individuals within  
 496 these modules. Some network structures are likely  
 497 to be more stable, either in response to disturbance  
 498 or via self-organized dynamics. For example, central-  
 499 ized networks, although more efficient, are theorized  
 500 to be more susceptible to targeted attacks on the  
 501 center of the network. For example, consider a forest  
 502 with two genotypes that support lichen communi-  
 503 ties that are similar in total abundances of each species  
 504 but differ in terms of the structure. Extensions of  
 505 game theory to evolutionary biology have demon-  
 506 strated that network structure can lead to variation  
 507 in evolutionary dynamics. Some structures tend to-  
 508 toward dominance and dampening of selection, while  
 509 others lead to amplification of selection. One class  
 510 of networks that are theorized to have amplifying  
 511 effects on networks have "star" shapes with one or a

512 few species at the center and radiating interactions  
 513 out from the central core (57). This is structurally  
 514 what we have observed with the networks that tend  
 515 to occur on some of the genotypes in our study, i.e.  
 516 the more centralized networks. It is possible that  
 517 these more centralized networks could function as  
 518 hot-spots of evolutionary dynamics resulting from  
 519 the amplifying effect the network structure that is  
 520 found on that tree genotype.

521 Second, even if the composition of the communi-  
 522 ties is the same among individuals and genotypes,  
 523 interactions may not be. We didn't observe composi-  
 524 tional differences using the same data from which the  
 525 lichen networks were derived. If we only had our com-  
 526 position dataset from this study, we would have con-  
 527 cluded no response of the lichen community to tree  
 528 genotype, even though the underlying interactions  
 529 among lichen species does vary among genotypes.  
 530 As such differences in network structure could occur  
 531 without observable differences in species richness or  
 532 community composition, which have been the pri-  
 533 mary focus of almost all previous community genetics  
 534 studies (8). Community composition of lichen has  
 535 previously been observed to be different among tree  
 536 genotype in the same experimental garden (37, 38),  
 537 the difference between the present study is likely a re-  
 538 sult of differences in sampling method and the choice

of genotypes leading to overall higher abundances of observed lichens to assure the possibility of observing xlichen interactions. The previous study also 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>, as well as both the northern and southern aspects of each tree. These differences do not negate the findings of either study. The present study's finding of differences in network structure without significant compositional differences points to the importance of quantifying how network structure changes in response to genetic variation in order to fully understand evolutionary dynamics in complex communities. Having not observed a compositional effect of tree genotype without measuring the network structure could lead to the conclusion of no genetic effect on the community, even though important variation in network structure are leading to evolutionary dynamics. It is possible that these underlying differences in interactions among lichen could lead to differences in community composition at a future point in time via there effects on species abundances (16); however, this is not needed for evolutionary dynamics to play out via selection that leads to shifts in trait distributions without shifting species abundance distributions, which is possible under stabilizing, disruptive and directional selection (47). Thus, it is imperative that further community genetics research assess or at least be aware of the potential effects of variation in interactions and not just observe species abundances.

**Evolutionary Implications of a Genetic Basis to Network Structure.** A genetic basis to network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted. Variation in space and time create variation in ecological networks that influences evolutionary dynamics via shifts in ecological dynamics, such as population demographics (56). Given that ecosystems are comprised of hundreds and thousands of species, each having a multitude of interactions, the potential to find traction for making predictions in the context of ecological, let alone evolutionary, dynamics seems daunting. The promise of predictability lies in the presence of assymmetries in ecosystems that contribute to the occurrence of foundation species, such as hierarchy and nestedness created by body

size differences or life-history strategies, has been widely observed (1). The second part is that heritability (i.e., genetic determination) means that there is structure in the spatial or temporal variation that is created by individuals of foundation species whose traits are in part determined by underlying trait differences. Although this variation is inherently a function of both genetics and environmental effects (47), the community and network level effects are also a function of the scale of the interaction (16). Self-organization of the dynamics within these communities also points to a mechanism for strong community and ecosystem effects of genetic variation, contributing to what may seem unlikely magnitudes of genetic effects as has been observed in some systems, such as forest in riparian ecosystems (23).

Ecological network studies have focused on asymmetry and the quantification of its structure in communities, with qualitative discussion of the impacts on evolutionary dynamics (35, 36, 58, 59). More specific predication, within a quantitative framework, can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities. One seemingly useful direction from evolutionary network developments from game theory is the classification of networks into two general categories, rooted and cyclic, in which rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but these effects do not have connections back to the origins, whereas cyclic networks contain feedbacks to one or more origins. Although it did not explicitly define it in this context, the previous work of (24) 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 terrestrial ecosystems, lichen play important ecological roles, such as substrate stabilization (60) and nutrient fixation (61). In some

systems lignicolous lichens can have demonstrable effects on the availability of nutrients for the trees that they are associated with (62), although this has not been measured for the lichen in the current study's systemq. Elucidating the absence and/or presence of 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 (22). If such feedbacks do not exist, 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. However, such feedbacks to tree fitness are not necessary for evolutionary dynamics to play out within the lichen networks through the effects of altered network structure on lichen interaction outcomes, such as competitive exclusion leading to selection.

Since lichen are multi-species complexes, there is also the potential for evolutionary dynamics to shift within the context of the lichen symbiosis. There is substantial evidence that lichen have served as the "cradle of symbiotic fungal diversification" (63) and recent research has shown significant network structure of endolichenic fungi and lichen collected from across North America (64). Analysis of the structure of ecological networks has generally supported the conclusion that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability in mutualistic, primarily bipartite (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic networks (65, 66). Although there is growing evidence that the nestedness of mutualistic networks is not necessarily the result of selection for systems-level properties that promote stability but could be either product of asymptotic abundance distributions leading to un-even interaction frequencies (67) and/or a by-product of selection and divergence

creating network "spandrels" in ecosystems (53), this does not preclude the functional consequences of network structure but rather the developmental or evolutionary processes that have produced the structure. In the present study, we did not examine nestedness or modularity of the lichen networks as we could not find metrics for analyzing networks that are not only weighted and directed but also signed. Hopefully future network theoretic developments will make the appropriate metrics available to conduct these analyses.

**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 populations to communities and ecosystems. To date, this theory has focused on modeling the strong effects of foundation species (7, 16), 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, (31) 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 (68). Furthermore, in a predator-prey-plant study, Smith (27), showed that the interactions among species across trophic levels depended on plant genotype. Also, work by (69–71) 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, as models have been developed that can reconstruct interactions networks with similar structural characteristics to those observed in real ecosystems (72). 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 asymmetries, such as the case in foundation species systems, then spatial and temporal variation in network structure will arise as a result of trait variation within the foundation 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 asymmetries seem to be the rule rather than the exception for ecosystems (1, 67, 72–74), 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 (52, 54) cannot safely be 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.

**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 (35, 75). 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 (16). 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, 25, 27, 31, 76), 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, 16, 17). 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.

832 Although our study was conducted with a com-  
 833 munity of lichens, these results can be generalized to  
 834 other groups of diverse organisms around the world  
 835 that also exhibit significant genetic signals at the  
 836 community level (7, 77). However, there are impor-  
 837 tant points to consider when extending the observed  
 838 genetically based response of the lichen networks  
 839 to other systems. As bark lichen individuals do not  
 840 move, but grow in a primarily two dimensional plane,  
 841 these communities and their interactions occur in  
 842 the highly localized context of the tree's bark sur-  
 843 face. Lichen individuals are also many orders of  
 844 magnitude smaller than the tree individual in this  
 845 system (37). For these reasons, the genetic effects  
 846 on these communities is not damped by the move-  
 847 ment of individuals and the mixing of the effect of  
 848 different tree genotypes on the lichen community, as  
 849 might occur for more mobile species (e.g. insects and  
 850 birds). Relatedly, we only examined lichen in this  
 851 study, and other species whose distributions, abun-  
 852 dances and/or interactions vary in their response to  
 853 tree genotype, such as animals that may also impact  
 854 lichen communities, could be playing a role that we  
 855 did not examine. For example, an analysis of the mul-  
 856 tivariate correlations of different components of the  
 857 community in this system demonstrated significant  
 858 patterns of genetic co-responses to tree genotype,  
 859 supporting the non-mutually exclusive possibilities  
 860 of shared responses to tree genotype or tree genotypic  
 861 effects on interactions among these sub-communities  
 862 (4). As such, although we can not rule out the possi-  
 863 bility that other unmeasured tree traits or organisms  
 864 correlated with bark roughness are underlying the  
 865 observed patterns, substantial research supports the  
 866 importance of genetically based tree traits for com-  
 867 munities and ecosystems (8), and in particular bark  
 868 roughness for bark lichen communities (37, 38, 49).

869 **Conclusion.** In the face of the high degree of com-  
 870 plexity and potential context dependency of ecologi-  
 871 cal processes, the current study points to the utility  
 872 of considering the spatial and temporal scales of in-  
 873 teractions, as discussed to some in previous studies  
 874 (23, 78, 79). In the present study, we found that  
 875 community assembly processes, such as environmen-  
 876 tal filtering and species interactions, are genetically  
 877 based. This is likely due, in part, to the large differ-  
 878 ence in the differences in size and longevity of the  
 879 lichen and cottonwood individuals with the trees de-  
 880 termining the environment in which the lichen occur.

The importance of the scale of network organization  
 881 to create hierarchical structure (56) and the poten-  
 882 tial for foundation species to create this structure in  
 883 the vast majority of ecosystems (1, 11) suggests that  
 884 future work would be aided by determining these  
 885 modules within the biotic community that include  
 886 species with similar differences in body-size and time-  
 887 scales. Also, as heritable variation is the raw material  
 888 for natural selection to act upon, a genetic basis for  
 889 interaction network structure indicates evolutionary  
 890 dynamics should be considered at the community  
 891 level and that conserving genetic variation is im-  
 892 portant to consider in efforts to restore or preserve  
 893 complex species interactions and their associated  
 894 ecosystem functions (80). Such findings will bring us  
 895 closer to understanding the evolutionary drivers of  
 896 Darwin's entangled bank and the interconnectedness  
 897 of species in complex communities. 898

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1079 **Supplementary Materials**

1080 **Tables.**

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

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

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	response	df	statistic	H2	p-value
Lichen Network Similarity		9	3.5821	0.41	0.0537
Average Mutual Information			3.5235	0.31	0.0254
Centralization			4.0444	0.33	0.0184
Centralization In-Degree			4.4812	0.35	0.0142
Centralization Out-Degree			3.8615	0.32	0.0205
Centralization In-Degree (positive)			3.9852	0.33	0.0190
Centralization In-Degree (negative)			0.3304	0.11	0.2508
Centralization Out-Degree (positive)			3.5585	0.31	0.0248
Centralization Out-Degree (negative)			0.0862	0.05	0.3446
Degree			3.5175	0.32	0.0255
Degree (positive)			3.6925	0.32	0.0229
Degree (negative)			0.0327	0.03	0.3859
Percent Lichen Cover			0.0000	0.00	1.0000
Lichen Species Diversity			0.0000	0.00	0.4543
Lichen Species Richness			0.0000	0.00	0.4543
Lichen Species Evenness			0.0000	0.00	0.4543
Percent Rough Bark			4.8526	0.32	0.0113
pH			0.0000	0.00	1.0000
Carbon-Nitrogen Ratio			0.0000	0.00	1.0000
Condensed Tannins			3.0522	0.32	0.0343
BR-L Residuals			0.0000	0.00	1.0000
BR-Cen Residuals			0.0000	0.00	1.0000

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

lichen species	mean	statistic	H2	p-value
Positive				
In-Degree				
X. galericulata	0.2703	0	0	1
C. subdeflexa	0.8919	2.1926	0.2158	0.0595
L. spp.	0.4324	0	0	1
C. holocarpa	0.5946	3.6146	0.3241	0.024
X. montana	0.0541	0	0	0.4543
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.1351	2.049	0.2613	0.0656
Out-Degree				
X. galericulata	0.027	0	0	0.4543
C. subdeflexa	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4247
C. holocarpa	0.7027	3.1318	0.2981	0.0327
X. montana	0.0811	2.9228	0.3163	0.0375
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.2973	0.1505	0.0612	0.3119
Negative				
In-Degree				
X. galericulata	0			
C. subdeflexa	0.1892	0	0	0.4543
L. spp.	0.1892	0.0015	0.0057	0.4398
C. holocarpa	0.1351	0	0	1
X. montana	0.027	0.0377	0.0394	0.3807
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0.1622	0	0	1
Out-Degree				
X. galericulata	0.2432	0	0	1
C. subdeflexa	0.4054	0	0	0.4543
L. spp.	0.027	0	0	0.4543
C. holocarpa	0.027	0	0	0.4543
X. montana	0			
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0			

**Table 3. REML tests of the effect of tree genotype on lichen species centrality.**

	BR	CT	pH	CN	PC	SR	SE	SD	L	Cen	Df	SumOfSqs	R2	F	Pr(>F)	
BR									-0.34	-0.39	geno	9.0000	1.5049	0.2001	0.7507	0.8878
CT									0.34		Residual	27.0000	6.0143	0.7999		
pH											Total	36.0000	7.5193	1.0000		
CN																
PC																
SR									0.76	0.47						
SE									0.85	0.45						
SD										0.59	0.33					
L											0.88					
Cen																

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

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

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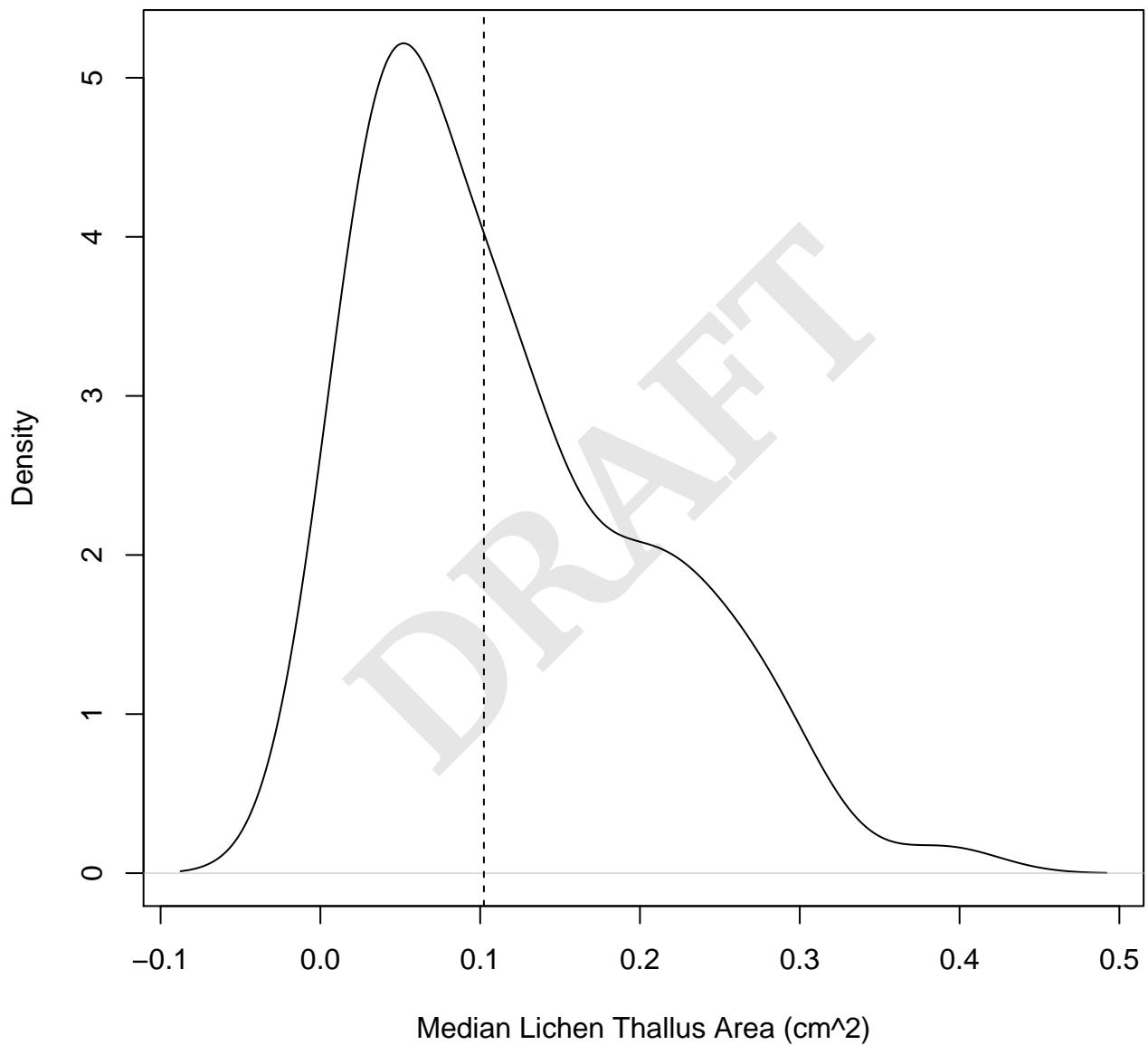
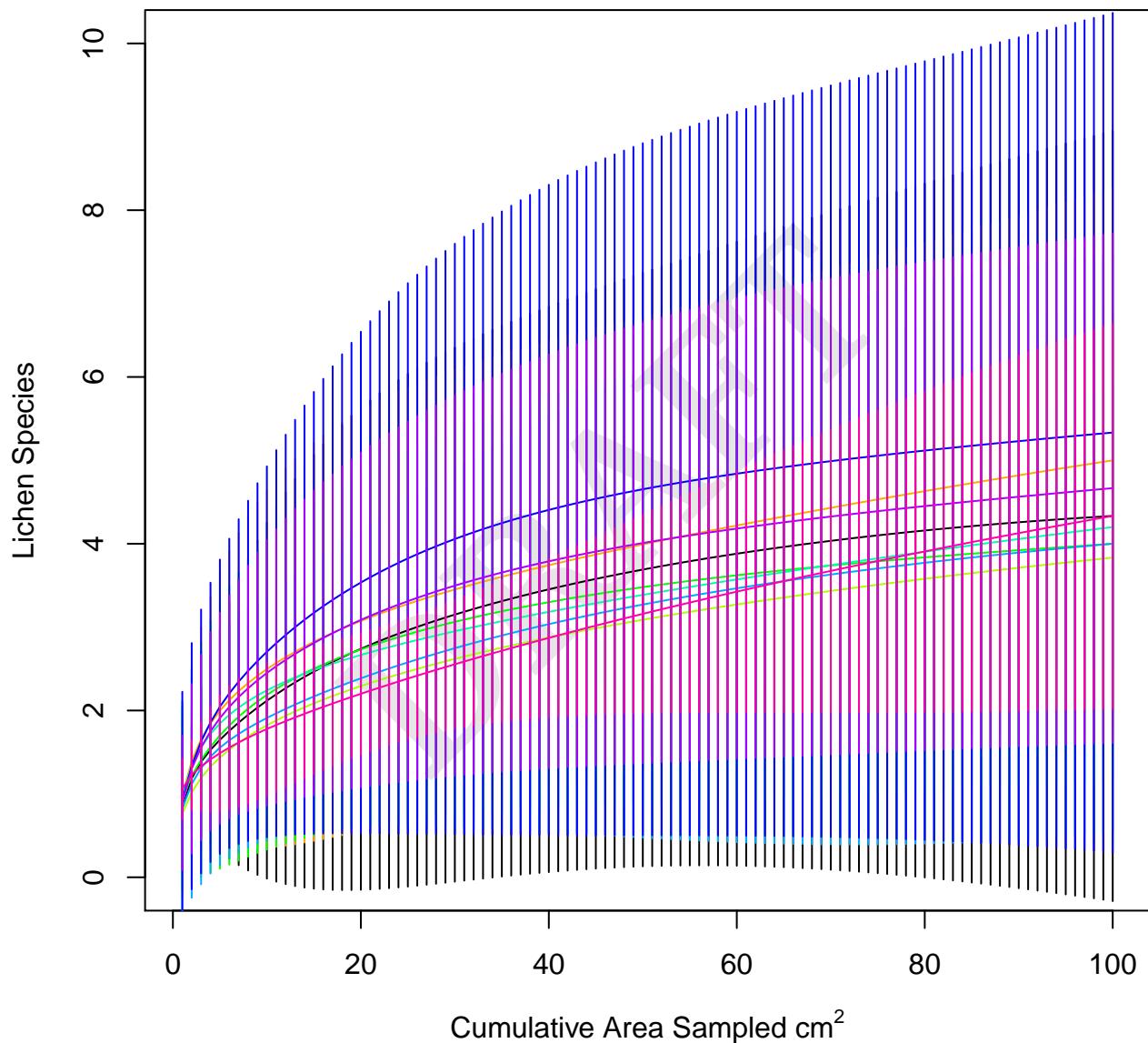


Fig. 1



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

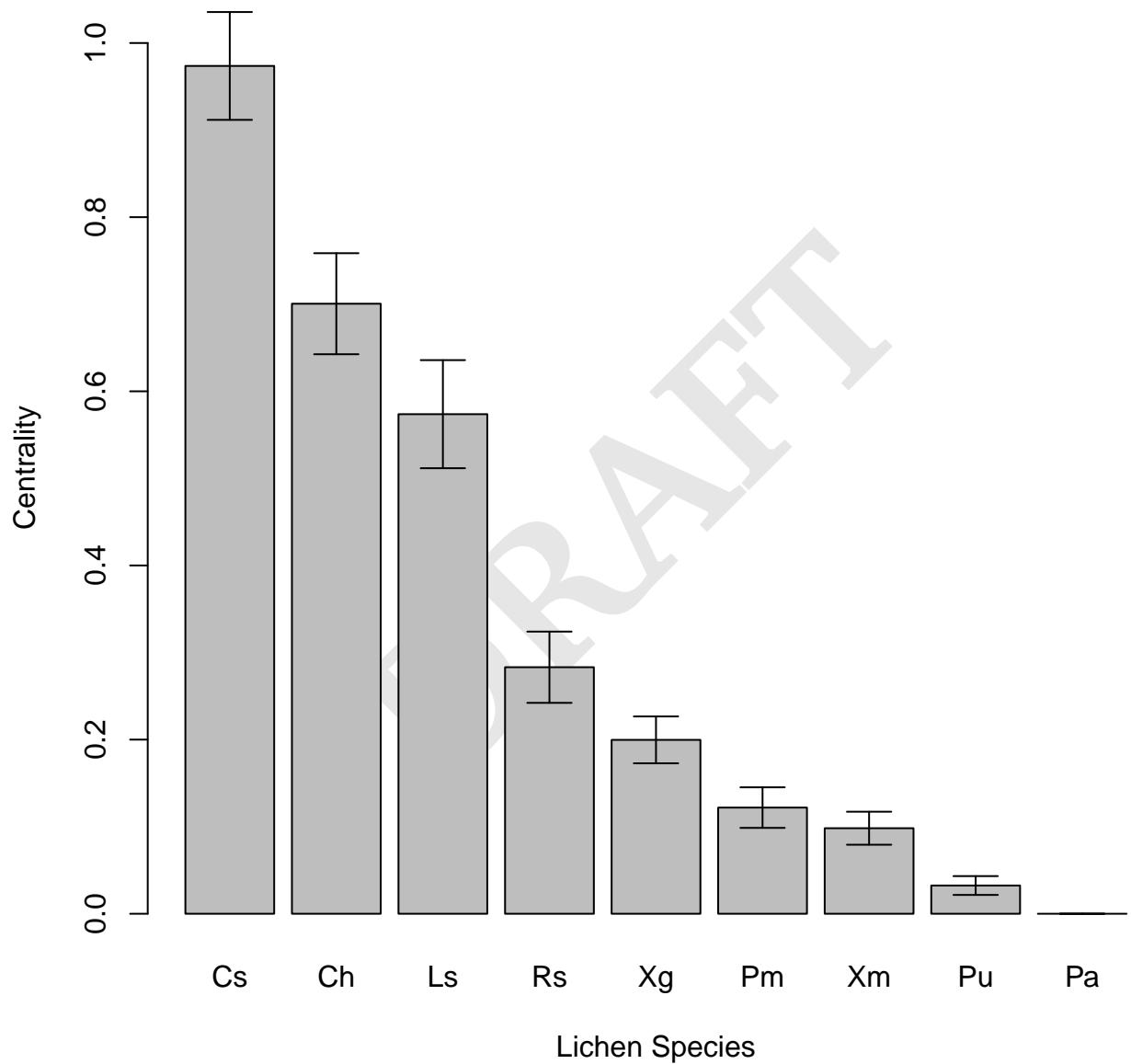


Fig. 3