

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

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

Materials and Methods

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

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

Bark Lichen and Trait Observations. On each tree, presence or absence of each lichen species was assessed in 50 total 1 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

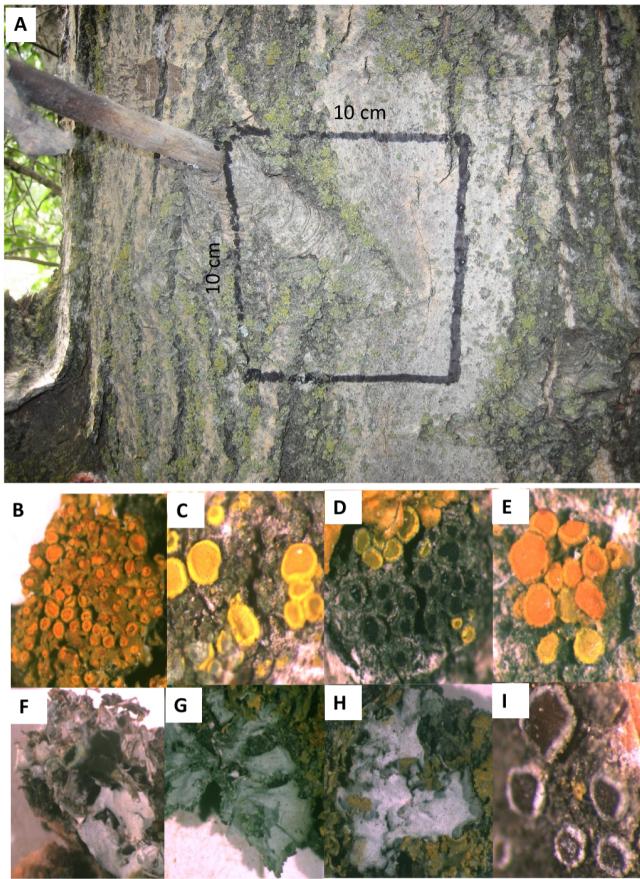


Fig. 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the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

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

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

developed by (39) with the addition that we quantified the presence of lichen in the 1 cm^2 cells on individual trees of *P. angustifolia*. Unipartite networks were generated using the conditional probabilities of each species pair, i.e. the probability of observing one species given an observation of another species $P(S_i|S_j)$, based on the method developed by (40). To calculate conditional probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species and their co-occurrences. We were then able to calculate the conditional probabilities of each species pair as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, based on the axioms of probability. This yielded a matrix that could possibly be asymmetric, i.e. $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was equal to one for all species present and zero for species that were not observed in any cell.

We then applied an analytical procedure to remove non-significant links between species. This procedure determines if the joint probability of a species pair (i.e. $P(S_i, S_j)$) is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability of $S_i S_j$ and its compliment (i.e. $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If the observed number of co-occurrence falls outside of the confidence interval, the joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual probabilities (i.e. $P(S_i)P(S_j)$), and the conditional probability reduces to the individual probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair falls outside the confidence interval, the probability that the observation of one species given the other is no different than simply observing that species alone. This enables us to remove links from a given network by re-scaling the resulting conditional probabilities by subtracting the individual probabilities from the conditional probabilities (i.e. how different the conditional probability is from the independent probability), which makes any species with a non-significant conditional probability zero.

The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as one species' impact on another with zero being no effect and values less than or greater than zero being negative and positive effects, respectively. Here, we will refer to \mathbf{D} as a signed, weighted interaction matrix. As such, \mathbf{D} has the properties that it can be asymmetric (i.e. D_{ij} does not necessarily equal D_{ji}) and it scales between -1 and 1, and, therefore, does not have the mathematical properties of a probabilistic network (?). Also, as the method does not track individuals within species and interactions such as

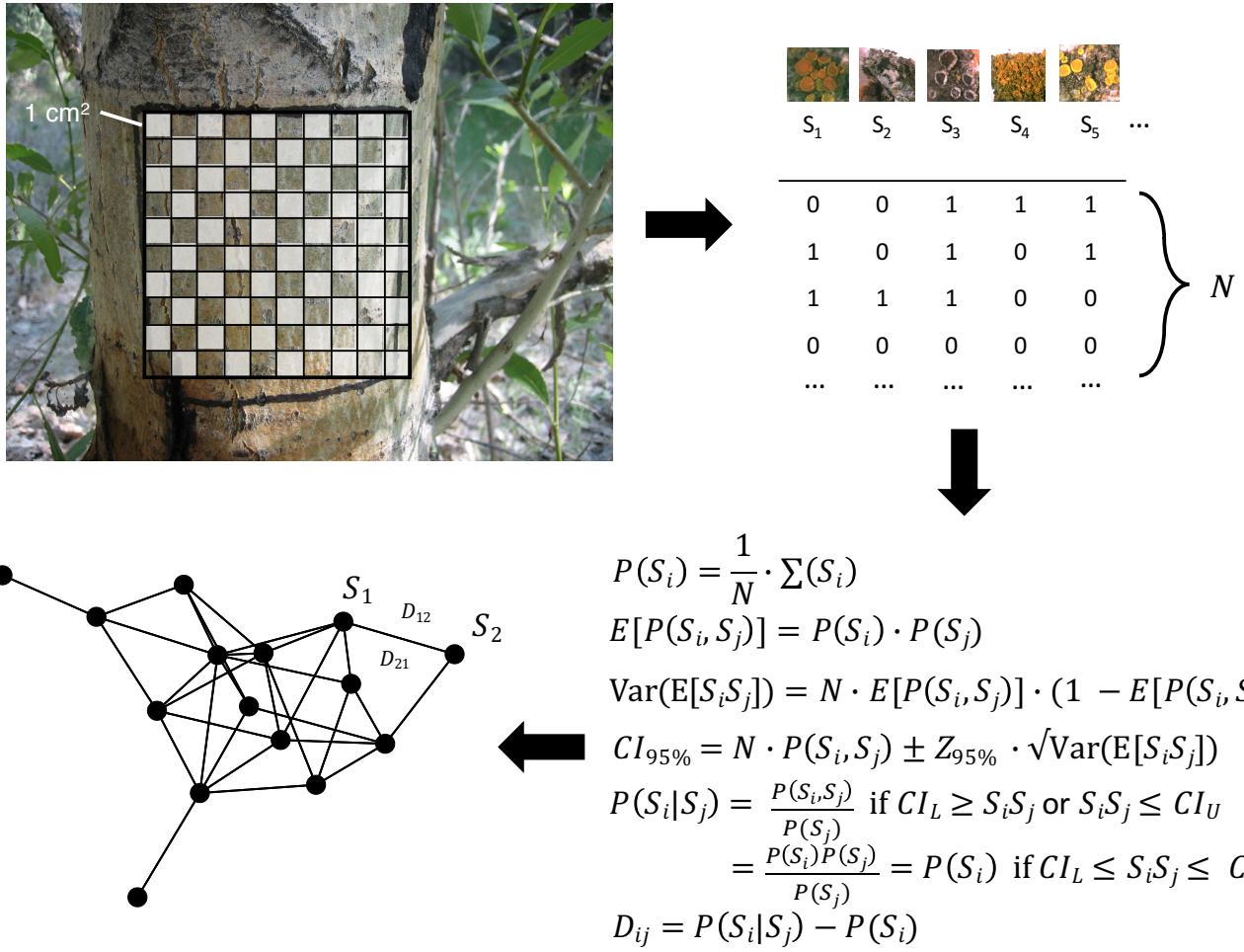


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded 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.

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

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

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

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

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

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

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

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

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

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

379 velopment Core Team 2019).

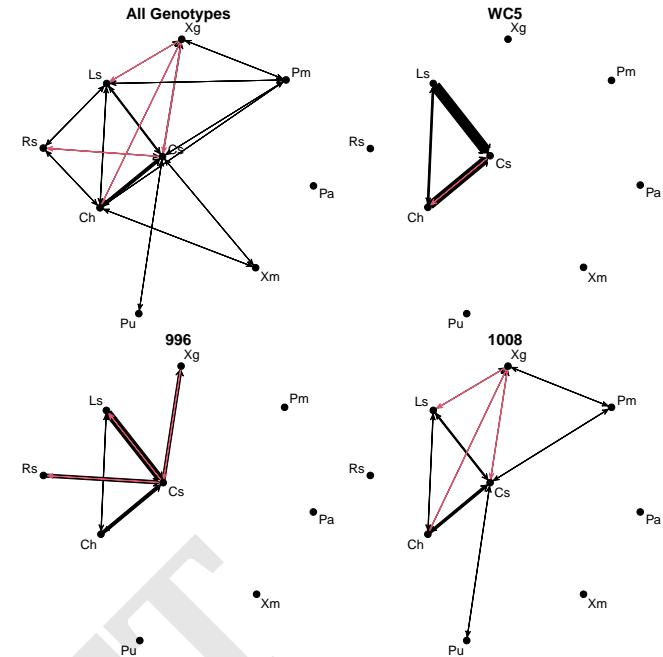


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

Results

Tree genotype influenced lichen network structure and multiple lichen network metrics were heritable. Tree genotype significantly predicted the structural similarity of lichen networks (PERMANOVA: $Pseudo-F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$) (Fig. 4). Overall network level metrics responded significantly to tree genotype (Table 1), including network degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} = 0.0255$) and centralization including both in-coming and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} = 0.0184$) or when separated into in-coming only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} = 0.0190$) or out-going only ($RLRT = 3.8615$, $H^2 = 0.3193$, $p\text{-value} = 0.0205$). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree ($RLRT = 3.6925$, $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} = 0.0142$). Metrics calculated with negative

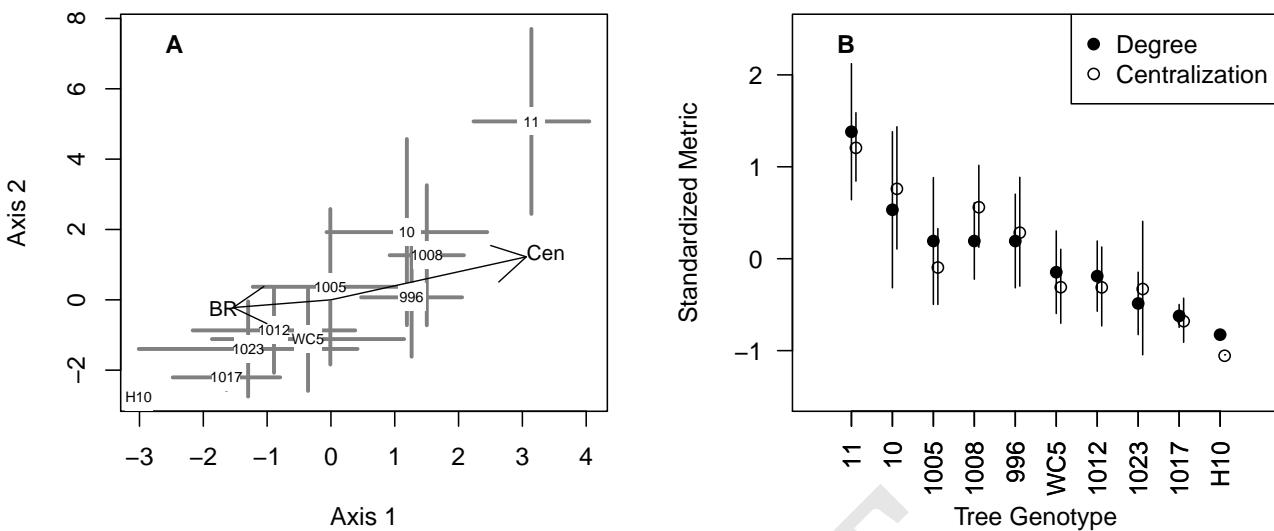


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing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

links were not significant, including degree (negative) ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$) and both in-coming (negative) ($RLRT = 0.3304$, $H^2 = 0.1057$, $p\text{-value} = 0.2508$) and out-going centralization (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$, $p\text{-value} = 0.3446$).

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

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

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

centrality for both the in-coming ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives, but not for either negative centrality metrics in-coming ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of the other species' centralities showed a genotypic response (Supplementary Table 3) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

Add transformations of variables to methods.

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} = 0.0343$) both displayed significant responses to tree genotype. None of the other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and none other than bark

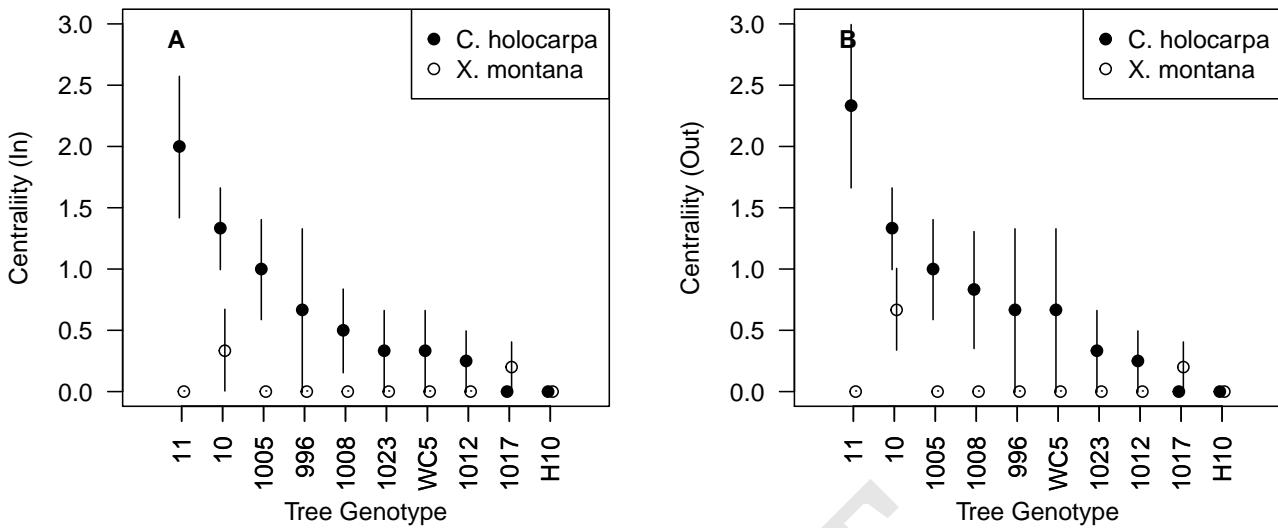


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

roughness was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen network structure via bark roughness. We found that bark roughness was significantly correlated with network similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, $p\text{-value} = 0.0096$) and other lichen network metrics, including negative correlations with overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$, $p\text{-value} = 0.04$) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees with more similar levels of bark roughness tended to have lichen interaction networks with similar structure. To quantify the genetic bases of this effect of bark roughness on network structure, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

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

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

Discussion

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *C. holocarpa*. The genetically based trait, bark roughness, was the only trait observed to effect network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control (49), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (39); however this is the first demonstration of a link from genes to lichen network structure. As such these results have important implications for

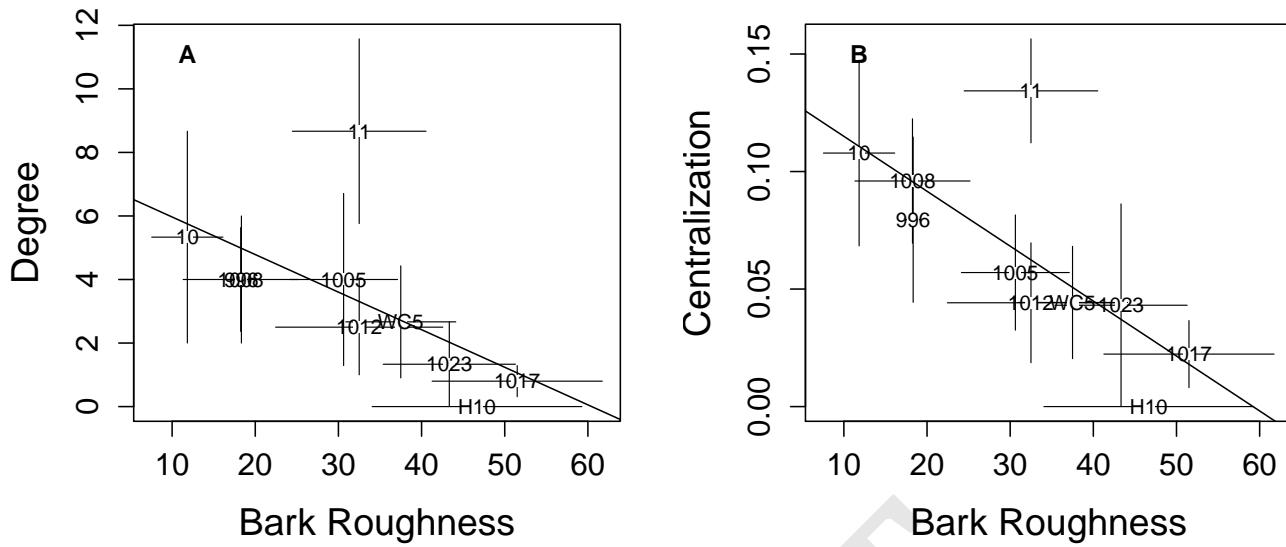


Fig. 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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

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

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

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-

turally what we have observed with the networks that tend to occur on some of the genotypes in our study, i.e. the more centralized networks. It is possible that these more centralized networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the network structure fostered on that tree genotype.

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, 27), but it has not yet integrated developments in the ecological or evolutionary network theory literature. This is to say that it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated this network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be dampened or magnified within the system of interacting species. For example, (24) showed that the genetics based interactions of aphid resistant and aphid susceptible trees resulted in different interaction networks of their associated arthropod communities composed of 139 species. At the scale of ecosystems, trophic networks or food webs direct and control the rates of energy and nutrient flux (50). Furthermore, in a predator-prey-plant study, Smith (20), showed that the interactions among species across trophic levels depended on plant genotype. Also, work by (51–53) observed consistent patterns of centralized interactions of species modules focused around hubs of plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have disproportionate numbers of interactions with other species and likely are the drivers in determining community assembly, structure and dynamics.

The results of the current study provides clear empirical evidence that variation in network structure can be genetically based (i.e. heritable) and points to the need to expand IIGEs encompass the structure of interaction networks. Although such a synthesis necessitates a much greater effort than can be afforded in this paper, it is possible to point to several productive pathways forward. In terms of interaction

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

Evolutionary Implications of a Genetic Basis to Network Structure. With regard to the evolutionary implications of network structure, ecological network studies have focused on asymmetry and the quantification of its structure in communities, with qualitative discussion of the impacts on evolutionary dynamics (36, 37, 54, 55). More specific predictions, with a quantitative framework, can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities. One seemingly useful direction from evolutionary network developments from game theory is the classification of networks into two general categories, rooted and cyclic, in which rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but these effects do not have connections back to the origins, whereas cyclic networks contain feedbacks to one or more origins. Although it did not explicitly define it in this context, the previous work of (17) developed the perspective that the structure of the network in the context of a foundation species, such as cottonwoods in which there are demonstrable community level genetic effects, is inherently created when trait variation among genotypes of a foundation species has ecological effects on associated species.

This builds on many previous studies demonstrating that the community level effects vary among multiple genotypes. It is not clear what potential there is for feedbacks there are to the origins (e.g. the cottonwood genotypes) from the community, and as such it cannot be determined whether these networks are cyclic or rooted. In other systems, lignicolous lichens can have demonstrable positive effects on the availability of nutrients for the trees that they are associated with, but this has not been measured in

628 the current system. Elucidating the absence and/or
629 presence and quantifying such feedbacks would allow
630 for the determination of the cyclic nature and
631 potential evolutionary dynamics of this system. The
632 presence of feedbacks would provide the potential
633 for non-linear dynamics in which evolutionary effects
634 are damped or amplified by the structure of the network.
635 For example, a star structure in which there is a primary or core set of central species
636 with feedbacks from the radiating species has been demonstrated to be a structure that amplifies evolutionary dynamics (31). If such feedbacks do not exist, and these sub-networks of the lichen and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to generally promote diversification as variation arising from the shifting distribution of the “roots”, i.e. genotypes; however, loss of genotype/root diversity could lead to fixation of a single genotype in the population and a decrease in community-wide diversity.

648 **Applicability to Other Systems.** Although our study
649 was conducted with a community of lichens, these results can be generalized to other groups of diverse organisms around the world that also exhibit significant genetic signals at the community level (7, 56). However, there are important points to consider when extending the observed genetically based response of the lichen networks to other systems. As bark lichen individuals do not move, but grow in a primarily two dimensional plane, these communities and their interactions occur in the highly localized context of the tree’s bark surface. Lichen individuals are also many orders of magnitude smaller than the tree individual in this system (38). For these reasons, the genetic effects on these communities is not dampened by the movement of individuals and the mixing of the effect of different tree genotypes on the lichen community, as might occur for more mobile species (e.g. insects and birds). Relatedly, we only examined lichen in this study, and other species whose distributions, abundances and/or interactions vary in their response to tree genotype, such as animals that may also impact lichen communities, could be playing a role that we did not examine. For example, an analysis of the multivariate correlations of different components of the community in this system demonstrated significant patterns of genetic co-responses to tree genotype, supporting the non-mutually exclusive possibilities of shared responses

677 to tree genotype or tree genotypic effects on interactions among these sub-communities (4). As such,
678 although we can not rule out the possibility that
679 other unmeasured tree traits or organisms correlated
680 with bark roughness are underlying the observed patterns,
681 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).

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

715 In attempting to apply these findings to other
716 systems, it is important to consider the spatial and
717 temporal scaling of genetic effects. In the present
718 study, the sessile nature of lichens means that indi-
719 viduals, and potentially multiple generations, live
720 their entire lives on a single tree. As such, our study
721 examines one scaling of a genetic effect, in which
722 the phenotype of a single tree individual (i.e., tree
723 genotype) has complete influence on the community
724 with little to no effect of other tree individuals in
725 the population. The extreme from this would be

726 where the associated community moved among and
 727 interacted with not only other community members
 728 but also multiple tree individuals at a high rate, as
 729 would be the case with free-living animals (e.g. fly-
 730 ing insects). In the latter case, the effect of tree
 731 genetics would then be the integral effect of all the
 732 tree individuals in the population, and, all other fac-
 733 tors being equal, any one tree genotype would have
 734 a lower effect on associated community. In reality,
 735 ecosystems are a mixture of species of different body
 736 sizes and life-histories, and, as such, vary in the de-
 737 gree to which they interact with other organisms,
 738 which is the basis of the theory of the geographic
 739 mosaic of co-evolution (36, 57). It is now important
 740 to consider how the impacts of genetic effects on
 741 the network structure of sub-groups, such as lichens,
 742 may or may not propagate through the ecosystem
 743 to more mobile organisms. As developed previously,
 744 the degree to which a genetic effect influences the
 745 community is a function of the fidelity of the genetic
 746 effect (i.e., heritability) and both the frequency and
 747 the intensity of the interaction (27). One possible
 748 path forward is for future work to extend the many
 749 previous community genetics studies that have fo-
 750 cused on sessile organisms, such as gallin insects
 751 (11, 18, 24, 58?), to quantify the frequency of these
 752 interactions in the context of the larger community.
 753 This would provide an estimate of the relative im-
 754 pact of these focal, often termed foundation, species.
 755 In addition, community genetics theory has only
 756 considered first order interactions, i.e., between two
 757 organisms (7, 27, 28). Given that network structure
 758 could be influenced by genetic effects, as evidenced
 759 by the present study, assessing higher order interac-
 760 tions could provide a path forward for theoretical
 761 advances that could help with identifying important
 762 characteristics of sub-groups to focus on in empirical
 763 studies.

764 **Conclusion.** In the face of the high degree of com-
 765 plexity and potential context dependency of ecologi-
 766 cal processes, the current study points to the utility
 767 of considering the spatial and temporal scales of in-
 768 teractions, as discussed to some in previous studies
 769 (16, 59, 60). In the present study, we found that
 770 community assembly processes, such as environmen-
 771 tal filtering and species interactions, are genetically
 772 based. This is likely due, in part, to the large dif-
 773 ference in the differences in size and longevity of
 774 the lichen and cottonwood individuals with the trees

775 determining the environment in which the lichen oc-
 776 cur. We suggest that future work would be aided by
 777 determining these modules within the biotic commu-
 778 nity that include species with similar differences in
 779 body-size and time-scales. As heritable variation is
 780 the raw material for natural selection to act upon,
 781 a genetic basis for interaction network structure in-
 782 dicates evolutionary dynamics should be considered
 783 at the community level and that conserving genetic
 784 variation is important to consider in efforts to restore
 785 or preserve complex species interactions and their
 786 associated ecosystem functions (61). With such find-
 787 ings, it appears that we are closer to understanding
 788 the evolutionary drivers of Darwin's entangled bank
 789 and the interconnectedness of species in complex
 790 communities.

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1. Ellison AM, et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9):479–486.
2. Busby PE, et al. (2015) Genetics-based interactions among plants, pathogens, and herbivores define arthropod community structure. *Ecology* 96(7):1974–1984.
3. Barbour RC, et al. (2009) A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* 90(7):1762–1772.
4. Lamit LJ, et al. (2015) Tree genotype mediates covariance among communities from microbes to lichens and arthropods. *Journal of Ecology* 103(4):840–850.
5. Holeski LM, Hillstrom ML, Whitham TG, Lindroth RL (2012) Relative importance of genetic, ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype in a foundation tree species. *Oecologia* 170:695–707.
6. Bailey JK, et al. (2009) From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 364(1523):1607–16.
7. Whitham TG, et al. (2012) Community specificity: Life and afterlife effects of genes.
8. Des Roches S, et al. (2018) The ecological importance of intraspecific variation. *Nature Ecology and Evolution* 2(1):57–64.
9. Wade MJ (2007) The co-evolutionary genetics of ecological communities.
10. Crutsinger GM (2016) A community genetics perspective: Opportunities for the coming decade. *New Phytologist*.
11. Whitham TG, et al. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature reviews. Genetics* 7:510–523.
12. Moya-Laraño J (2011) Genetic variation, predator-prey interactions and food web structure. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 366(1569):1425–37.
13. Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J (2007) Non-random co-extinctions in phylogenetically structured mutualistic networks. *Nature* 448(7156):925–8.
14. Guimarães PR, et al. (2007) Interaction Intimacy Affects Structure and Coevolutionary Dynamics in Mutualistic Networks. *Current Biology* 17(20):1797–1803.
15. Gómez JM, Abdelaziz M, Camacho JPM, Muñoz-Pajares AJ, Perfectti F (2009) Local adaptation and maladaptation to pollinators in a generalist geographic mosaic. *Ecology Letters* 12(7):672–682.
16. Bangert RK, et al. (2006) A genetic similarity rule determines arthropod community structure. *Molecular ecology* 15:1379–1391.
17. Lau MK, Borrett SR, Baisier B, Gotelli NJ, Ellison AM (2017) Ecological network metrics: opportunities for synthesis. *Ecosphere* 8(8):e01900.
18. Bailey JK, Wooley SC, Lindroth RL, Whitham TG (2005) Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters* 8(0):051122062725008.
19. Johnson MTJ (2008) Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology*.
20. Smith DS, Bailey JK, Shuster SM, Whitham TG (2011) A geographic mosaic of trophic interactions and selection: trees, aphids and birds. *Journal of evolutionary biology* 24(2):422–9.

- 841 21. Smith DS, et al. (2015) Introduced elk alter traits of a native plant and its plant-associated
842 arthropod community. *Acta Oecologica* 67:8–16.
- 843 22. Barbour MA, et al. (2016) Genetic specificity of a plant-insect food web: Implications for
844 linking genetic variation to network complexity. *Proceedings of the National Academy of
845 Sciences of the United States of America* 113(8):2128–2133.
- 846 23. Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG (2015) Genotypic variation in foun-
847 dation species generates network structure that may drive community dynamics and evolu-
848 tion. *Ecology* 97(3):15–0600.
- 849 24. Keith AR, Bailey JK, Lau MK, Whitham TG (2017) Genetics-based interactions of foundation
850 species affect community diversity, stability and network structure. *Proceedings of the Royal
851 Society B: Biological Sciences* 284(1854):20162703.
- 852 25. Newman MEJ (2006) Modularity and community structure in networks. *Proceedings of the
853 National Academy of Sciences of the United States of America* 103(23):8577–82.
- 854 26. Sole R, Bascompte J (2006) *Self-Organization in Complex Ecosystems*. (Princeton Univer-
855 sity Press, Princeton, N.J.).
- 856 27. Shuster SM, Lonsdorf EV, Wimp GM, Bailey JK, Whitham TG (2006) COMMUNITY HERI-
857 TABILITY MEASURES THE EVOLUTIONARY CONSEQUENCES OF INDIRECT GENETIC
858 EFFECTS ON COMMUNITY STRUCTURE. *Evolution* 60(5):991.
- 859 28. Whitham TG, Allan GJ, Cooper HF, Shuster SM (2020) Intraspecific Genetic Variation and
860 Species Interactions Contribute to Community Evolution. *Annual Review of Ecology, Evolu-
861 tion, and Systematics* 51(1).
- 862 29. Gehring C, et al. (2014) Plant genetics and interspecific competitive interactions deter-
863 mine ectomycorrhizal fungal community responses to climate change. *Molecular Ecology*
864 23(6):1379–1391.
- 865 30. Gehring CA, Stultz CM, Flores-Renteria L, Whipple AV, Whitham TG (2017) Tree genetics
866 defines fungal partner communities that may confer drought tolerance. *Proceedings of the
867 National Academy of Sciences*.
- 868 31. Lieberman E, Hauert C, Nowak MA (2005) Evolutionary dynamics on graphs. *Nature*
869 433(7023):312–316.
- 870 32. Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems.
871 *Science* 345(6195).
- 872 33. Barbour MA, et al. (2019) Trait plasticity is more important than genetic variation in determin-
873 ing species richness of associated communities. *Journal of Ecology* 107(1):350–360.
- 874 34. Winfree R, Gross BJ, Kremen C (2011) Valuing pollination services to agriculture. *Ecological
875 Economics* 71:80–88.
- 876 35. Zytnyska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree
877 species influences the associated epiphytic plant and invertebrate communities in a com-
878 plex forest ecosystem. *Philosophical transactions of the Royal Society of London. Series B,
879 Biological sciences* 366:1329–1336.
- 880 36. Thompson JN (2013) *Relentless Evolution*. (University of Chicago Press), p. 499.
- 881 37. Bascompte J, Jordano P, Olesen JM (2006) Asymmetric Coevolutionary Networks Facilitate
882 Biodiversity Maintenance<10.1126/science.1123412. *Science* 312:431–433.
- 883 38. Lamit L, et al. (2011) Genetically-based trait variation within a foundation tree species influ-
884 ences a dominant bark lichen. *Fungal Ecology* 4(1):103–109.
- 885 39. Lamit LJ, et al. (2015) Genotype variation in bark texture drives lichen community assembly
886 across multiple environments. *Ecology* 96(4):960–971.
- 887 40. Araújo MB, Rozenfeld A, Rahbek C, Marquet PA (2011) Using species co-occurrence net-
888 works to assess the impacts of climate change. *EcoGraphy* 34:897–908.
- 889 41. Butts CT (2019) *sna: Tools for Social Network Analysis*. R package version 2.5.
- 890 42. Everett MG, Borgatti SP (2014) Networks containing negative ties. *Social Networks*
891 38(1):111–120.
- 892 43. Schoch D (2020) *signnet: An R package to analyze signed networks*.
- 893 44. Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecolog-
894 ical data. *Journal of Statistical Software* 22(7):1–19.
- 895 45. Oksanen J, et al. (2019) *vegan: Community Ecology Package*. R package version 2.5-6.
- 896 46. Borrett SR, Lau MK (2014) *enaR: An R package for Ecosystem Network Analysis*. *Methods
897 in Ecology and Evolution* 5(11):1206–1213.
- 898 47. Conner K, Hartl DL (2004) *A Primer of Ecological Genetics: a textbook*. (Sinauer Associates,
899 Inc., Sunderland, Massachusetts), 1st edition, p. All.
- 900 48. Dawkins R (year?) *The extended phenotype : the long reach of the gene*. p. 468.
- 901 49. Bdeir R, et al. (2017) Quantitative trait locus mapping of *Populus* bark features and stem
902 diameter. *BMC Plant Biology*.
- 903 50. Borgatti SP, Everett MG (2006) A Graph-theoretic perspective on centrality. *Social Networks*
904 28:466–484.
- 905 51. Toju H, et al. (2017) Species-rich networks and eco-evolutionary synthesis at the metacom-
906 munity level.
- 907 52. Toju H, Yamamoto S, Tanabe AS, Hayakawa T, Ishii HS (2016) Network modules and hubs
908 in plant-root fungal biomes. *Journal of the Royal Society Interface*.
- 909 53. Toju H, Guimarães PR, Olesen JM, Thompson JN (2014) Assembly of complex plant-fungus
910 networks. *Nature Communications*.
- 911 54. Diaz-Castelazo C, et al. (2010) Changes of a mutualistic network over time: Reanalysis over
912 a 10-year period. *Ecology*.
- 913 55. Guimarães PR, Jordano P, Thompson JN (2011) Evolution and coevolution in mutualistic
914 networks. *Ecology letters* 14(9):877–85.
- 915 56. Rowntree JK, Shuker DM, Preziosi RF (2011) Forward from the crossroads of ecology and
916 evolution. *Philosophical transactions of the Royal Society of London. Series B, Biological
917 sciences* 366(1569):1322–8.
- 918 57. Thompson JN, Schwind C, Guimaraes PR, Friberg M (2013) Diversification through multitrait
919 evolution in a coevolving interaction. *Proceedings of the National Academy of Sciences*.
- 920 58. Crutsinger GM, et al. (2014) Testing a ‘genes-to-ecosystems’ approach to understanding
921 aquatic-terrestrial linkages. *Molecular Ecology* 23(23):5888–5903.
- 922 59. Zook AE, Eklof A, Jacob U, Allesina S (2010) Food webs: Ordering species according to
923 body size yields high degree of intervality. *Journal of theoretical biology* 271(1):106–113.
- 924 60. Zytnyska SE, Khudr MS, Harris E, Preziosi RF (2012) No Title. *Oecologia* 170(2).

927 **Supplementary Materials**

928 **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.

DRAFT

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

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

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

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

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

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

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

DRAFT

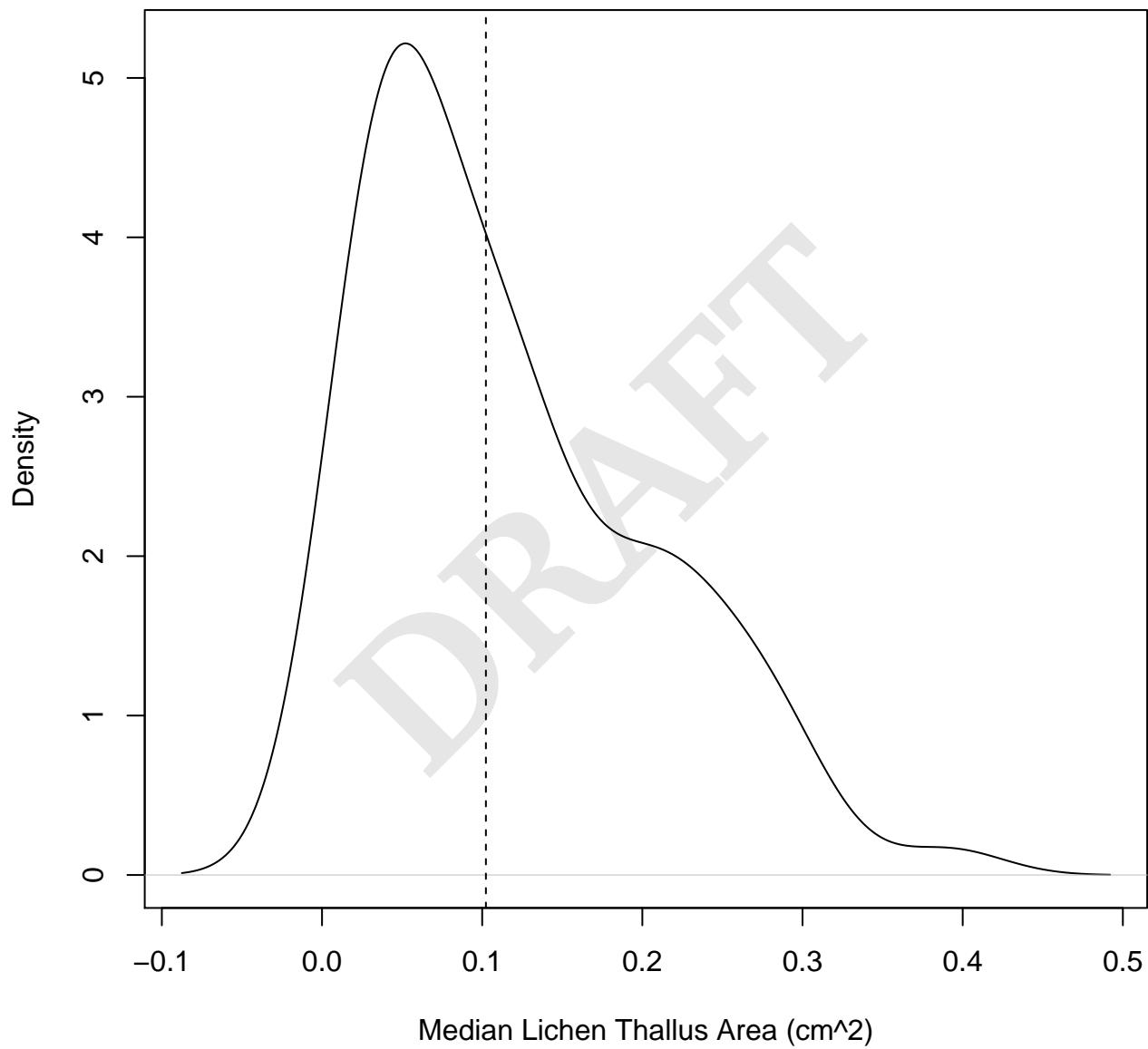


Fig. 1

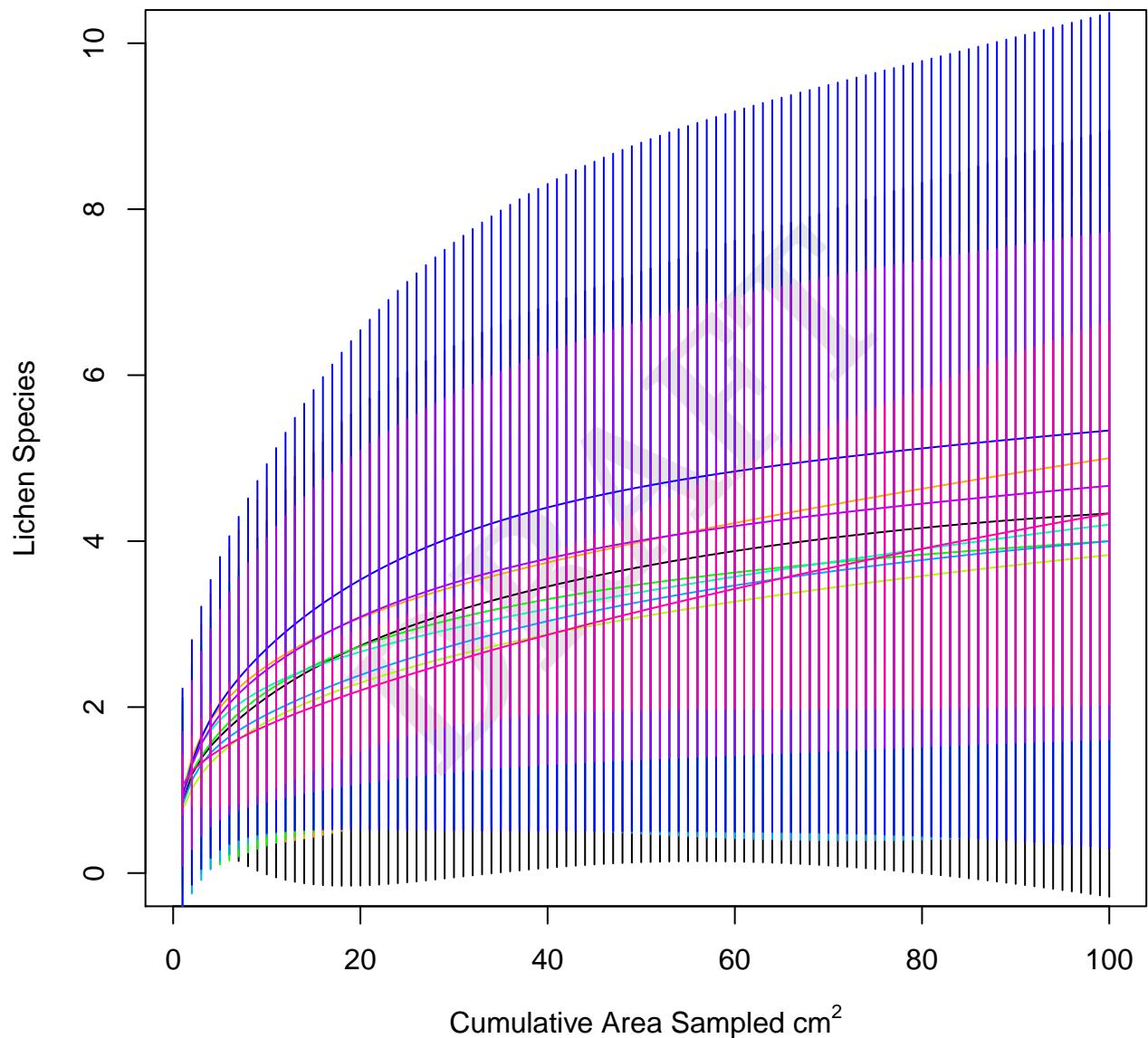


Fig. 2. Species-area curve by genotype.

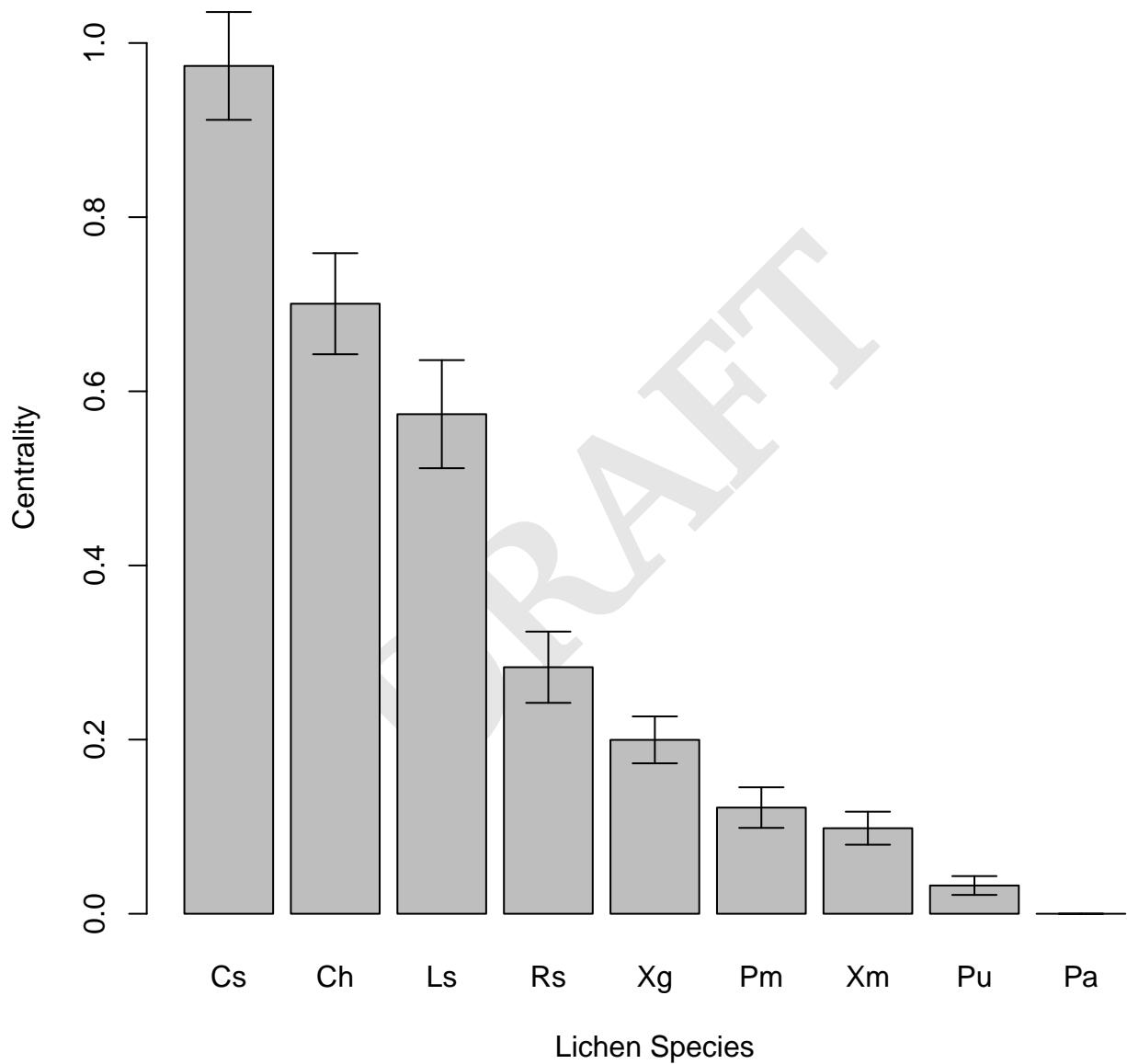


Fig. 3