

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

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

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

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

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

Significance Statement

Evolution occurs in the context of ecosystems comprised of complex ecological networks. Research at the interface of ecology and evolution has primarily focused on pairwise interactions among species and have rarely included a genetic component to network structure. Here, we used a 20+ year common garden experiment to reveal the effect that genotypic variation can have on networks of lichens that colonize the bark of a foundation tree species. We found that lichen interaction network structure is genetically based and primarily driven by bark roughness. These findings demonstrate the importance of genetic variation and evolutionary dynamics in shaping ecological networks as evolved traits. In particular, this study points to the importance of assessing the effect of foundation species genetics on the structure of species interactions that can generate heritable network variation that selection can act upon.

M.L. and L.L. conceived the study, M.L. and L.L. conducted the field work, R.N. assisted in lichen identifications, M.L. wrote the first draft of the manuscript, S.B. and T.W. contributed substantively to the conceptual development, T.W. established the common garden. All authors contributed to revisions of the manuscript.

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(8), and not only were many instances of strong genetic effects found in many ecosystems but the effect of intraspecific variation was at times greater than inter-specific variation. There is now evidence to support that selection, acting on this heritable variation, tends to occur among groups of species (9) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly (10) and species interactions (6, 11, 12), which shape the structure of ecological interaction networks (13–15).

In this community-level context, the “genetic similarity rule” provides a useful framework we can apply to interaction networks at the nexus of ecological and evolutionary dynamics. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, (16) observed that individuals genotypes that are more genetically similar will tend to have similar phytochemical traits and thus tend to have similar interactions with other species than individuals that are less similar. However, studies in the network ecology literature generally do not include a genetic component (17) and community genetics studies have primarily focused on community composition in terms of the abundance of species (8). Some studies have examined the effects of genetic variation on trophic chains in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (18–22) and generally found that increasing genotypic diversity leads to increased trophic complexity. Only two other studies, that we are aware of, have explicitly examined the effect of genotypic variation on the structure of interaction networks between tree individuals and associated herbivores (23, 24) and both found that genotypic diversity generates increased network modularity (i.e., compartmentalization). However, both of these studies were examining networks at the scale of forest stands, rather than networks associated with individual trees; therefore, neither was able to observe replicated networks in order to statistically test for genetic effects on network structure and quantify the genetic component (i.e. heritable variation) in network structure.

Network theory and evidence from empirical studies in ecology have demonstrated that indirect effects can lead to self-organization, producing sign-changing, amplifying and/or dampening effects (25, 26). The development of interspecific indirect ge-

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

Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative fitness of the tree), selection on tree, community or both can change network structure (28) and thereby alter community dynamics. Evolutionary applications of network theory have demonstrated that indirect effects of interactions among species can lead to network structures that amplify or dampen the effects of selection (31). Networks that form a star-like structure in which there is a central species or core group of species that interact with other, peripheral species, can amplify selection events. Empirically, network analysis of the structure of bipartite (i.e., two-mode) mutualistic networks has shown in multiple cases that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability and resilience to disturbances (32). As such differences in network structure could occur without observable differences in species richness or community composition, which have been the primary focus of almost all previous community

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

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of tree associated lichen species. Previous studies have examined aspects of networks (33). Here we examine the genetic basis of network structure on a community of sessile lignicolous (i.e., bark) lichens on cottonwood trees. Using a long-term (20+ years), common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic identity. We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (34, 35). In addition, the life-history characteristics of lichens, having highly localized, direct contact interactions and slow population turnover rates, facilitated the assessment of interactions among lichen species on individual trees. manuscript We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (23, 24, 36, 37). If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks. Applying a probability-theory based network modeling approach, we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks via several network metrics that measures different aspects of network structure at the scale of individual species (i.e., nodes) or the entire network observed on each tree genotype. In particular, we focus the metric of centrality for individual species and centralization for whole networks, which measures how much a species is connected in the network relative to other species. Based on previous community genetics theory, particularly the community similarity rule (16), we hypothesize that trees will co-vary in functional phenotypic traits such as bark roughness and chemical composition and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. This work is important because it provides a mechanistic basis for understanding how community

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

Materials and Methods

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

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

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

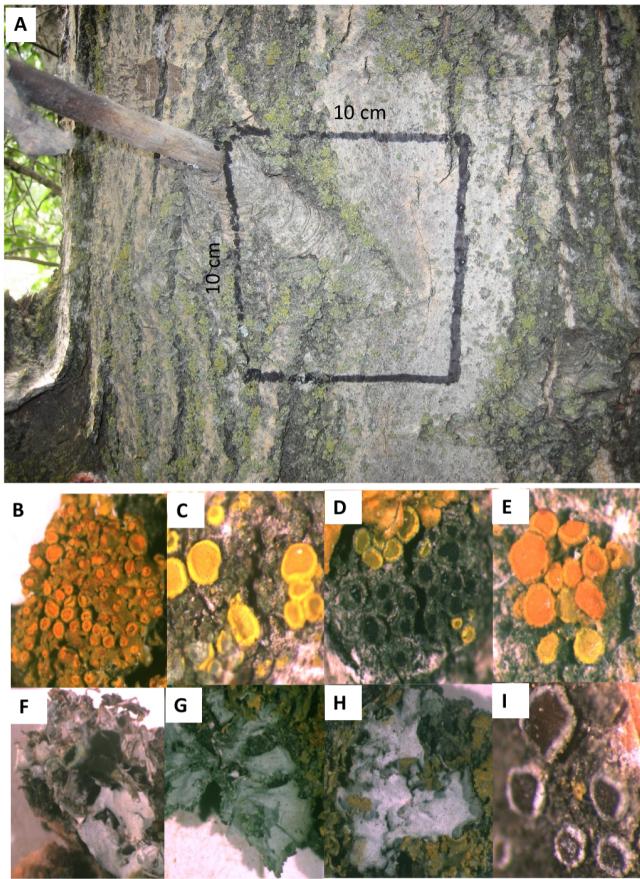


Fig. 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the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

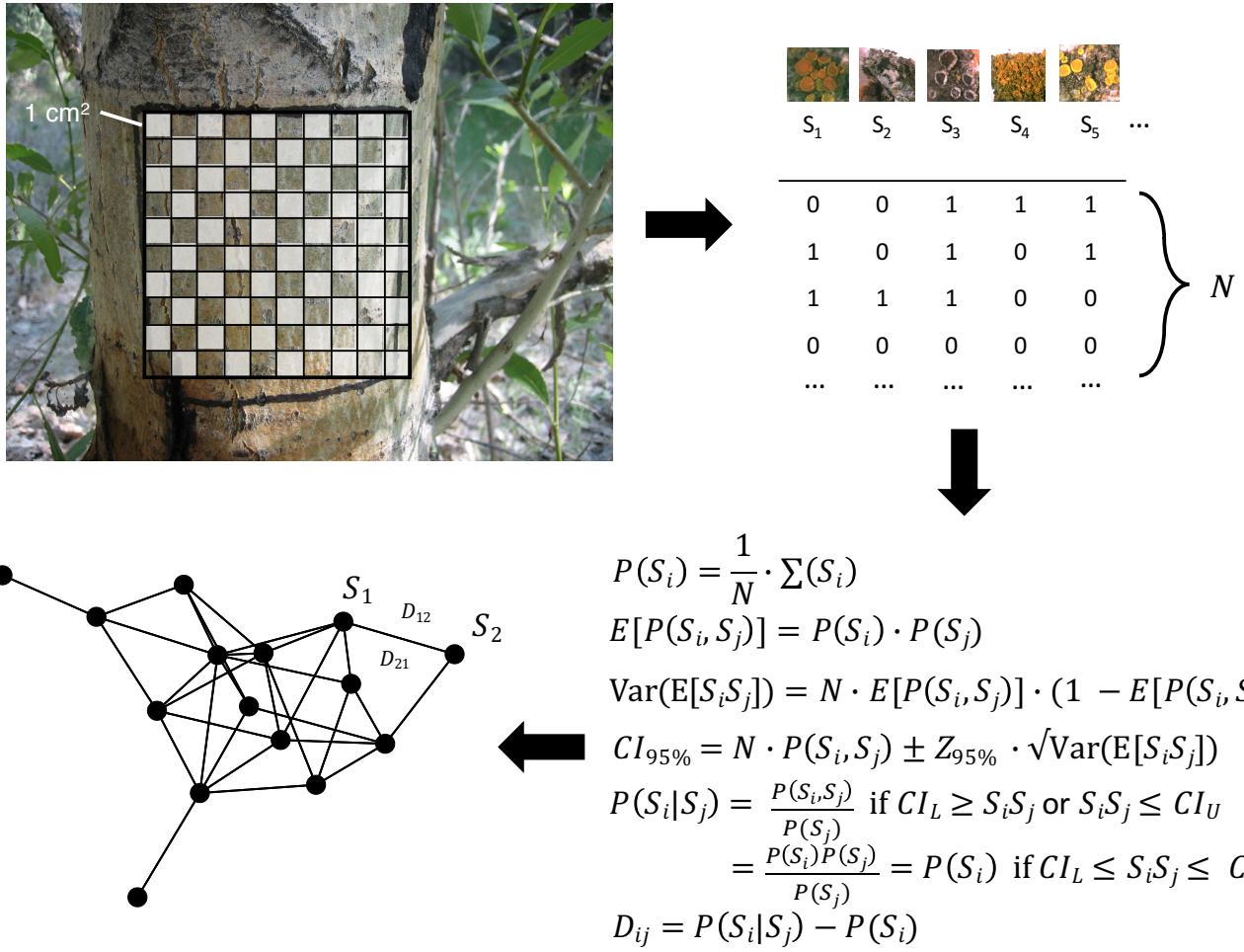


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded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

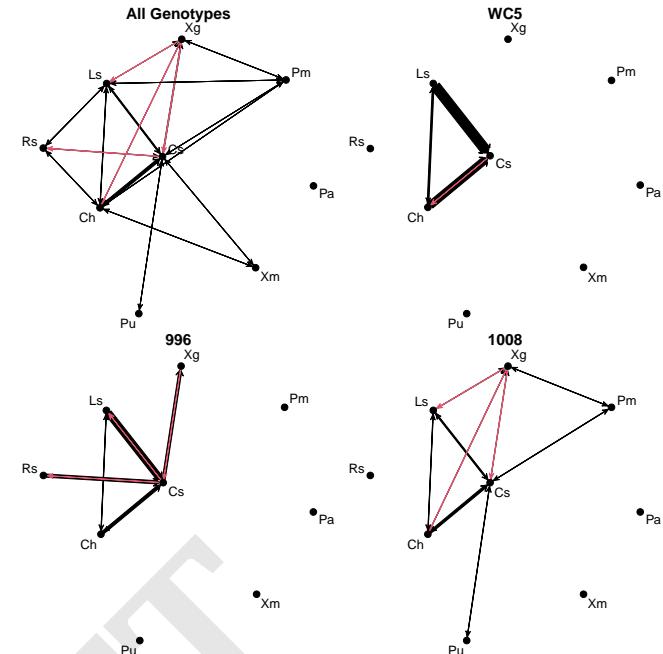


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

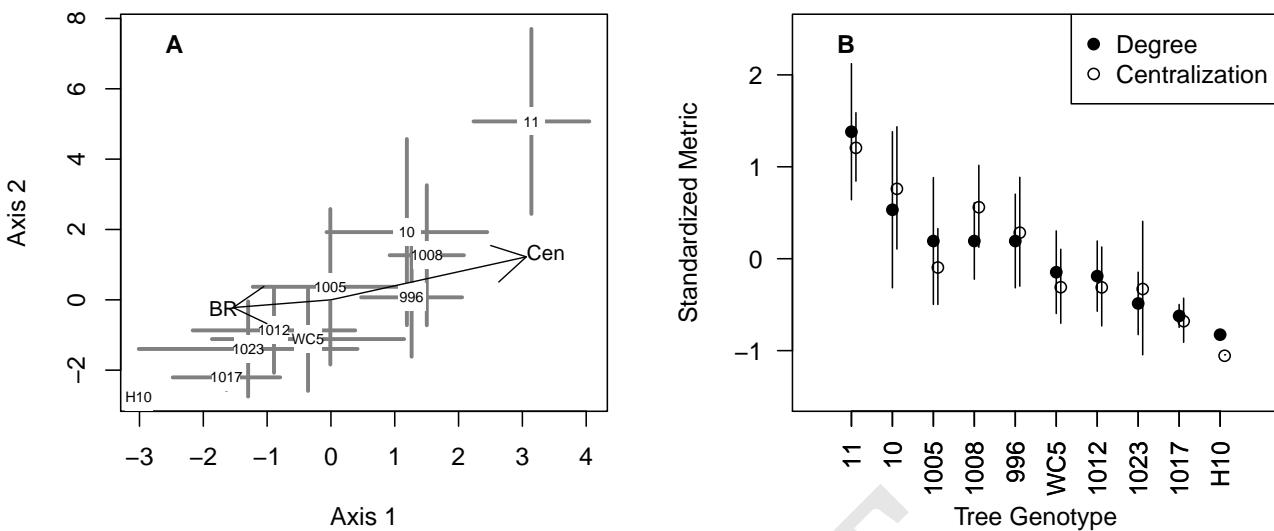


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing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

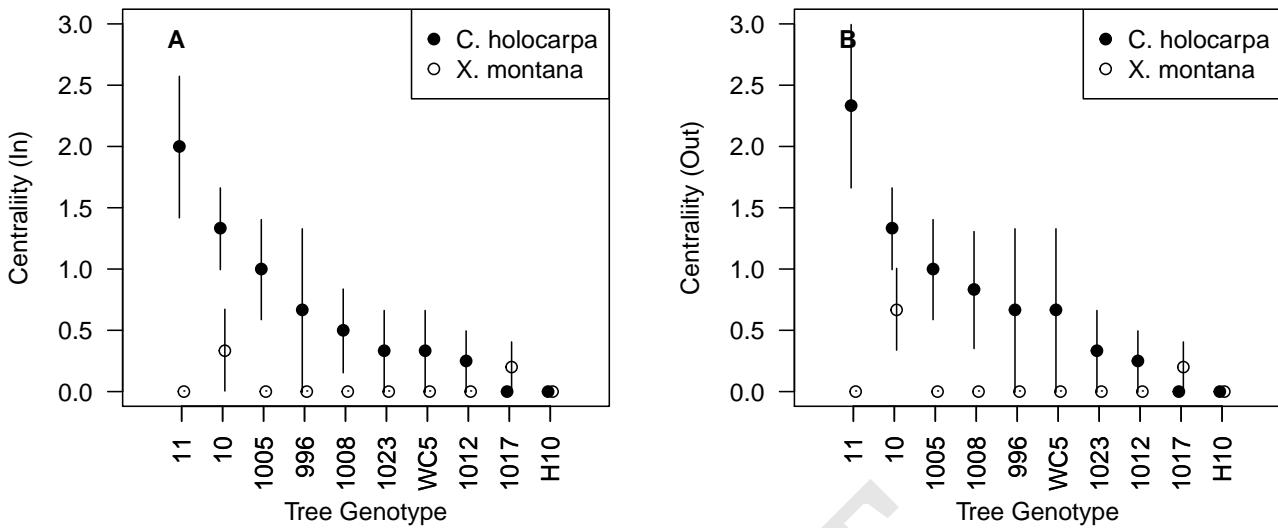


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

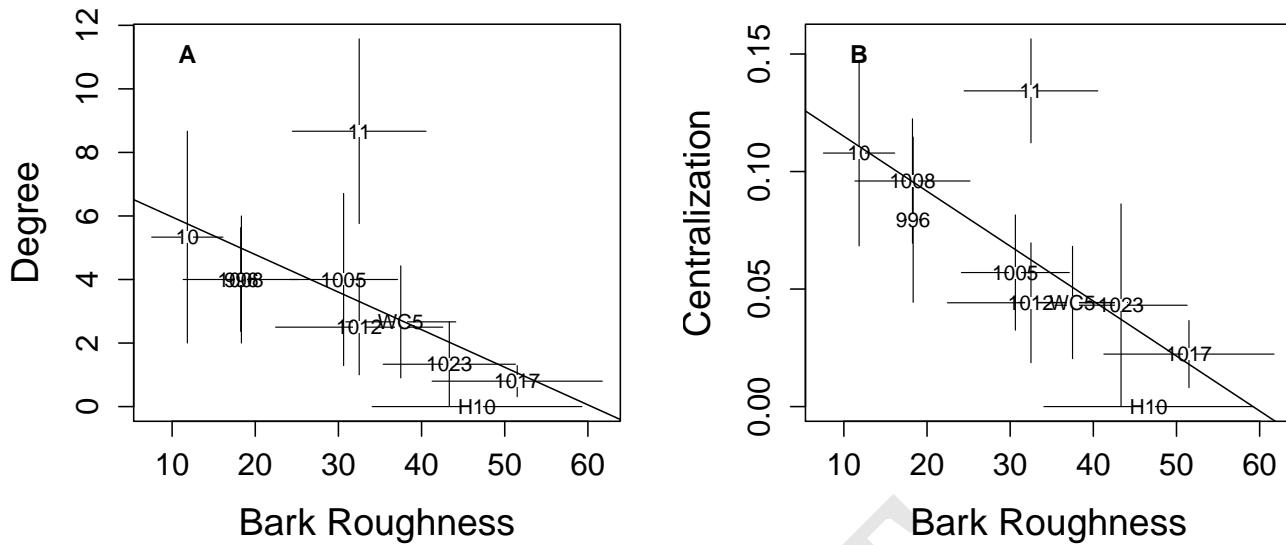


Fig. 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased 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 **Modularity and the Heritability of Interaction Networks.** We found significant heritability of lichen interaction network structure, and, in line with the
480 genetic similarity rule, networks observed on trees
481 of the same genotype tended to be structurally similar.
482 There are important functional ramifications of
483 genetically based variation in network structure.
484

485 The patterns of interaction in individual-based networks depart from these theoretical benchmarks, revealing the role of variability in space, time, traits, and preferences in shaping ecological interactions
486 (Araújo et al. 2008).

487 Space and time create templates for ecological interactions (Cantor et al. 2018) that favor departures from homogeneous and abundance-based network patterns. The spatial configuration of an environment may foster the rise of modules of interacting individuals (Fortuna et al. 2009, Tur et al. 2015). Similarly, temporal variation in the availability of partners affects the network structure on different time scales (Dátillo

et al. 2014b, Valverde et al. 2016). For example, networks describing interactions among individual insects and different plant species show temporal modularity, with different individuals sharing pollen resources at different times in the flowering season (Tur et al. 2015). Space and time may therefore promote spatiotemporal variation in the network structure by affecting the likelihood of potential interactions. Even so, the macroscopic properties of individual-based networks may show structural constancy. For example, networks of interactions among protective ant species and individual plants show daily turnover in ant species, while maintaining nestedness and average levels of reciprocal specialization (Dátillo et al. 2014b).

Space and time set the scales in which individual-based networks occur, but the interaction patterns are further modified by variation in individual traits. For example, the numbers of individual honeybees (*Apis mellifera*, Apidae) visiting thistle (*Cirsium arvense*, Asteraceae) flowers increase with the number of flower heads

and the height of the inflorescences on individual plants (Dupont et al. 2011). Network description of intraspecific variation in dietary niches uncovers subtle associations between traits and resource use that go beyond the number of resources used. For example, in a monomorphic population of three-spine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae), differences in trait combinations (e.g., body and snout shapes) were associated with dietary modules, i.e., groups of individuals feeding on similar prey (Araújo et al. 2008). Similarly, networks describing diet overlap among thick-billed murres (*Uria lomvia*, Alcidae) revealed sexbased dietary groups (Provencher et al. 2013). Network analyses can therefore reveal how patterns of interaction across individuals are associated with variation in individual traits.

First, intra-specific diversity could be creating lichen interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily the determined by another organism, these communities inherently form modules within the larger ecosystem, as they tend to interact more with each other than with other individuals (? ? ?). Our study demonstrates that the environmental differences determined by the genetic variation within a single species can create differences that not only impacts community composition, as repeatedly demonstrated in other community genetics studies (8?), but also the structure of interactions among individuals within these modules. Some network structures are likely to be more stable, either in response to disturbance or via self-organized dynamics. For example, centralized networks, although more efficient, are theorized to be more susceptible to targeted attacks on the center of the network. For example, consider a forest with two genotypes that support lichen communities that are similar in total abundances of each species but differ in terms of the structure. Extensions of game theory to evolutionary biology have demonstrated that network structure can lead to variation in evolutionary dynamics. Some structures tend toward dominance and dampening of selection, while others lead to amplification of selection. One class of networks that are theorized to have amplifying effects

on networks have "star" shapes with one or a few species at the center and radiating interactions out from the central core (?). This is structurally what we have observed with the networks that tend to occur on some of the genotypes in our study, i.e. the more centralized networks. It is possible that these more centralized networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the network structure fostered on that tree genotype.

This variation in network structure has the consequence of producing differential responses of the communities of lichens, or other species, that are associated with individual tree genotypes. This has consequences in the context of evolutionary dynamics, where either directional or stabilizing selection decreases genotypic richness in the population. As the number of genotypes decreases, the diversity of network structures will also decrease, as a single genotype comes to dominate.

A disconnected network structure implies that the dynamical consequences of ecological interactions are limited to pairs or to small groups of interacting species (e.g., Guimarães et al. 2007). In contrast, a connected network structure implies that trophic cascades, trait-based cascades, and eco-evolutionary feedbacks can propagate across multiple species in the community. For example, indirect effects generated by the decline in sea otters in the Aleutian Archipelago propagated across trophic chains, resulting in a dietary shift in bald eagles (Anthony et al. 2008). In fact, most of the classic empirical examples of keystone species shaping ecological communities due to indirect effects show species with either (a) generalist diets or (b) generalism at the species level emerging due to intrapopulation variation in traits or preferences (Estes et al. 2003, Paine 1966). From a network perspective, at least some keystone species can be viewed as highly connected species that shift the community-level dynamics by promoting connectedness in ecological networks.

Highly connected species may also connect modules generated by trait variation across potentially interacting species (Donatti et

al. 2011, Schleuning et al. 2014). High trait variation across species may lead to the formation of modules due to specialization (Poisot et al. 2013), intervality (Guimerà et al. 2010, Stouffer et al. 2006), interspecific competition (Dalerum et al. 2016, Valverde et al. 2020), trade-offs in resource use (Pinheiro et al. 2019), and the combination of multiple ecological and evolutionary factors (Rezende et al. 2009). However, the impact of trait variation on species interactions is not straightforward, being dependent on the rules connecting traits of interacting species (Gibert DeLong 2017, Gravel et al. 2016). If trait variation hinders the emergence of highly connected species, loosely connected networks should emerge in which some modules may present internal nested patterns due to differences in species abundance and forbidden links (Lewinsohn et al. 2006, Pinheiro et al. 2019, Vacher et al. 2008). If, however, some highly connected species are able to interact with partners with disparate traits, then different modules will be connected to each other through the pathways created by these highly connected species (Olesen et al. 2007, Schleuning et al. 2014). Therefore, the presence of highly connected species shapes the cohesiveness of ecological communities, markedly affecting different aspects of their network structure.

Second, 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 (?). The promise of predictability is that 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 (27). 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 (16).

Third, even if the composition of the communities is the same among individuals and genotypes, interactions may not be. We didn't observe compositional differences using the same data from which the lichen networks were derived. If we only had our composition dataset from this study, we would have concluded no response of the lichen community to tree genotype, even though the underlying interactions among lichen species does vary among genotypes. Community composition of lichen has previously been observed to be different among tree genotype in the same experimental garden (38, 39), though this was observed with a larger sampling of total area and quadrats per tree. Regardless, this could result in a situation in which abundance based investigations of community-level genetic effects may miss important variation in the interactions among individuals in these communities, leading to an underestimate of genetic effects in ecosystems. 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 (27); however, this is not needed for evolutionary dynamics to play out. This points to the need to assess or be aware of the potential effects of interactions and not just observe species abundances.

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

822 in community-wide diversity.

823 **Applicability to Other Systems.** Although our study
824 was conducted with a community of lichens, these re-
825 sults can be generalized to other groups of diverse or-
826 ganisms around the world that also exhibit significant
827 genetic signals at the community level (7, 56). How-
828 ever, there are important points to consider when
829 extending the observed genetically based response
830 of the lichen networks to other systems. As bark
831 lichen individuals do not move, but grow in a pri-
832 marily two dimensional plane, these communities
833 and their interactions occur in the highly localized
834 context of the tree's bark surface. Lichen individ-
835 uals are also many orders of magnitude smaller than
836 the tree individual in this system (38). For these
837 reasons, the genetic effects on these communities is
838 not dampened by the movement of individuals and
839 the mixing of the effect of different tree genotypes
840 on the lichen community, as might occur for more
841 mobile species (e.g. insects and birds). Relatedly, we
842 only examined lichen in this study, and other species
843 whose distributions, abundances and/or interactions
844 vary in their response to tree genotype, such as ani-
845 mals that may also impact lichen communities, could
846 be playing a role that we did not examine. For ex-
847 ample, an analysis of the multivariate correlations
848 of different components of the community in this
849 system demonstrated significant patterns of genetic
850 co-responses to tree genotype, supporting the non-
851 mutually exclusive possibilities of shared responses
852 to tree genotype or tree genotypic effects on inter-
853 actions among these sub-communities (4). As such,
854 although we can not rule out the possibility that
855 other unmeasured tree traits or organisms correlated
856 with bark roughness are underlying the observed pat-
857 terns, substantial research supports the importance
858 of genetically based tree traits for communities and
859 ecosystems (8), and in particular bark roughness for
860 bark lichen communities (38, 39, 49).

861 One final point to discuss is that in the present
862 study lichen cover, species richness and composition
863 were not significantly responsive to tree genotype,
864 unlike what has been previously observed for lichen
865 (39) and multiple taxa in this and other systems (8).
866 This is likely the result of differences in sampling
867 method and the choice of genotypes leading to overall
868 higher abundances of observed lichens to assure the
869 possibility of observing lichen interactions. In the
870 current study mean percent total lichen cover among

genotypes ranges from 60-93% cover; whereas the
871 range reported in (39) is 0.86-18.73%. The previous
872 study used a visual estimation method, unlike the
873 current study, which observed lichen at the scale of 1
874 cm² cells, which could over-estimate cover depending
875 on the frequency at which actual thallus size was
876 less than 1 cm². The previous study used samples
877 from both the northern and southern aspects of each
878 tree; whereas, the current study only observed lichen
879 on the northern aspect. Also, our current results
880 are likely different from the previous study because
881 the current study selected genotypes that tended to
882 have bark lichen, with the interest of focusing on
883 generating networks for comparison. These differ-
884 ences do not negate the findings of either study but
885 is important to explain the differences in the find-
886 ings, particularly in the community-level effects of
887 tree genotype and the general applicability to future
888 studies.

889 In attempting to apply these findings to other
890 systems, it is important to consider the spatial and
891 temporal scaling of genetic effects. In the present
892 study, the sessile nature of lichens means that indi-
893 viduals, and potentially multiple generations, live
894 their entire lives on a single tree. As such, our study
895 examines one scaling of a genetic effect, in which
896 the phenotype of a single tree individual (i.e., tree
897 genotype) has complete influence on the community
898 with little to no effect of other tree individuals in
899 the population. The extreme from this would be
900 where the associated community moved among and
901 interacted with not only other community members
902 but also multiple tree individuals at a high rate, as
903 would be the case with free-living animals (e.g. fly-
904 ing insects). In the latter case, the effect of tree
905 genetics would then be the integral effect of all the
906 tree individuals in the population, and, all other fac-
907 tors being equal, any one tree genotype would have
908 a lower effect on associated community. In reality,
909 ecosystems are a mixture of species of different body
910 sizes and life-histories, and, as such, vary in the de-
911 gree to which they interact with other organisms,
912 which is the basis of the theory of the geographic
913 mosaic of co-evolution (36, 57). It is now important
914 to consider how the impacts of genetic effects on
915 the network structure of sub-groups, such as lichens,
916 may or may not propagate through the ecosystem
917 to more mobile organisms. As developed previously,
918 the degree to which a genetic effect influences the

community is a function of the fidelity of the genetic effect (i.e., heritability) and both the frequency and the intensity of the interaction (27). One possible path forward is for future work to extend the many previous community genetics studies that have focused on sessile organisms, such as galling insects (11, 18, 24, 58?), to quantify the frequency of these interactions in the context of the larger community. This would provide an estimate of the relative impact of these focal, often termed foundation, species. In addition, community genetics theory has only considered first order interactions, i.e., between two organisms (7, 27, 28). Given that network structure could be influenced by genetic effects, as evidenced by the present study, assessing higher order interactions could provide a path forward for theoretical advances that could help with identifying important characteristics of sub-groups to focus on in empirical studies.

Conclusion. In the face of the high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed to some in previous studies (16, 59, 60). In the present study, we found that community assembly processes, such as environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. We suggest that future work would be aided by determining these modules within the biotic community that include species with similar differences in body-size and time-scales. As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (61). With such findings, it appears that we are closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

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Supplementary Materials

Tables.

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1103

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

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

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

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

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

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

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

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

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

Figures.

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

DRAFT

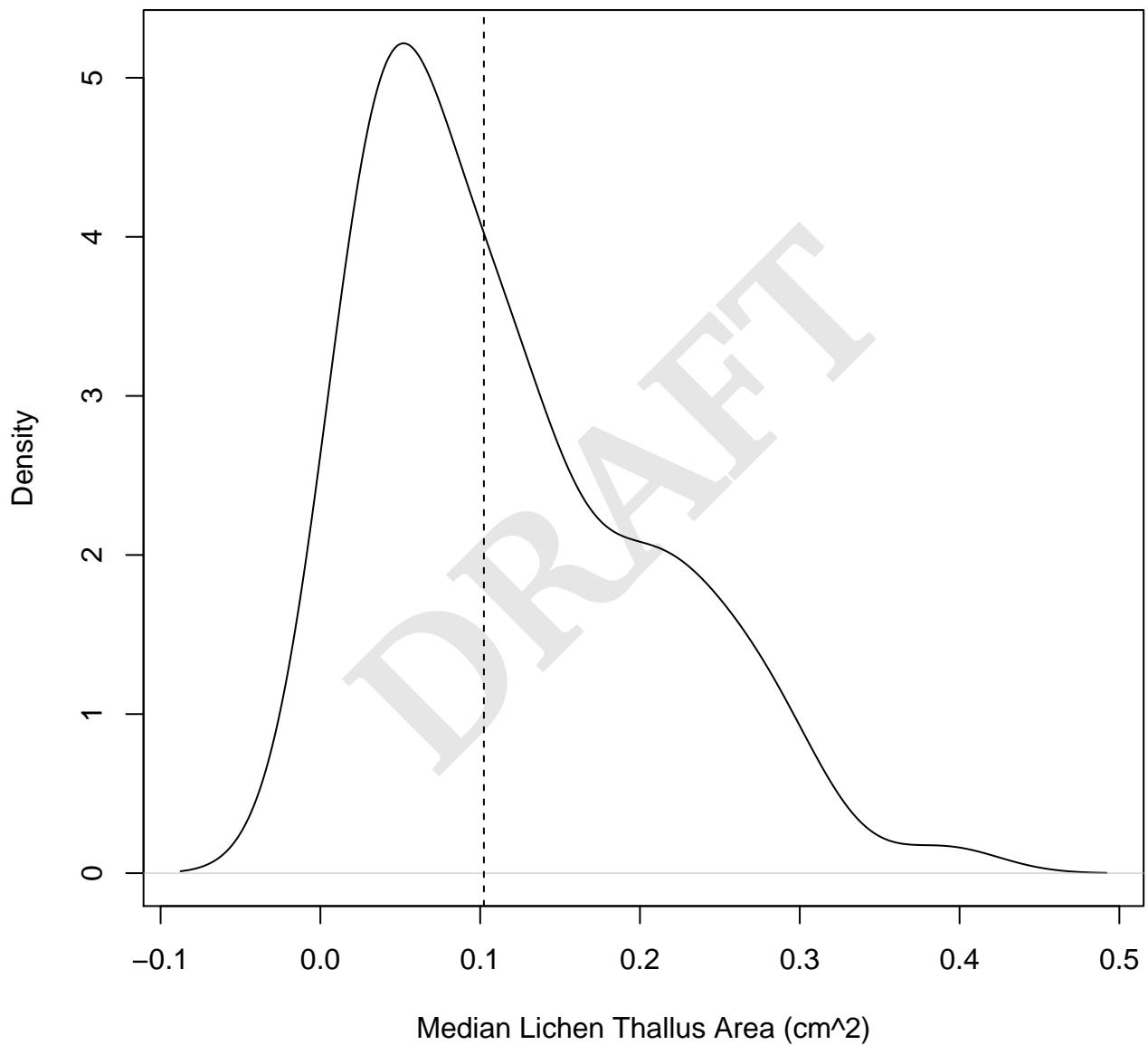


Fig. 1

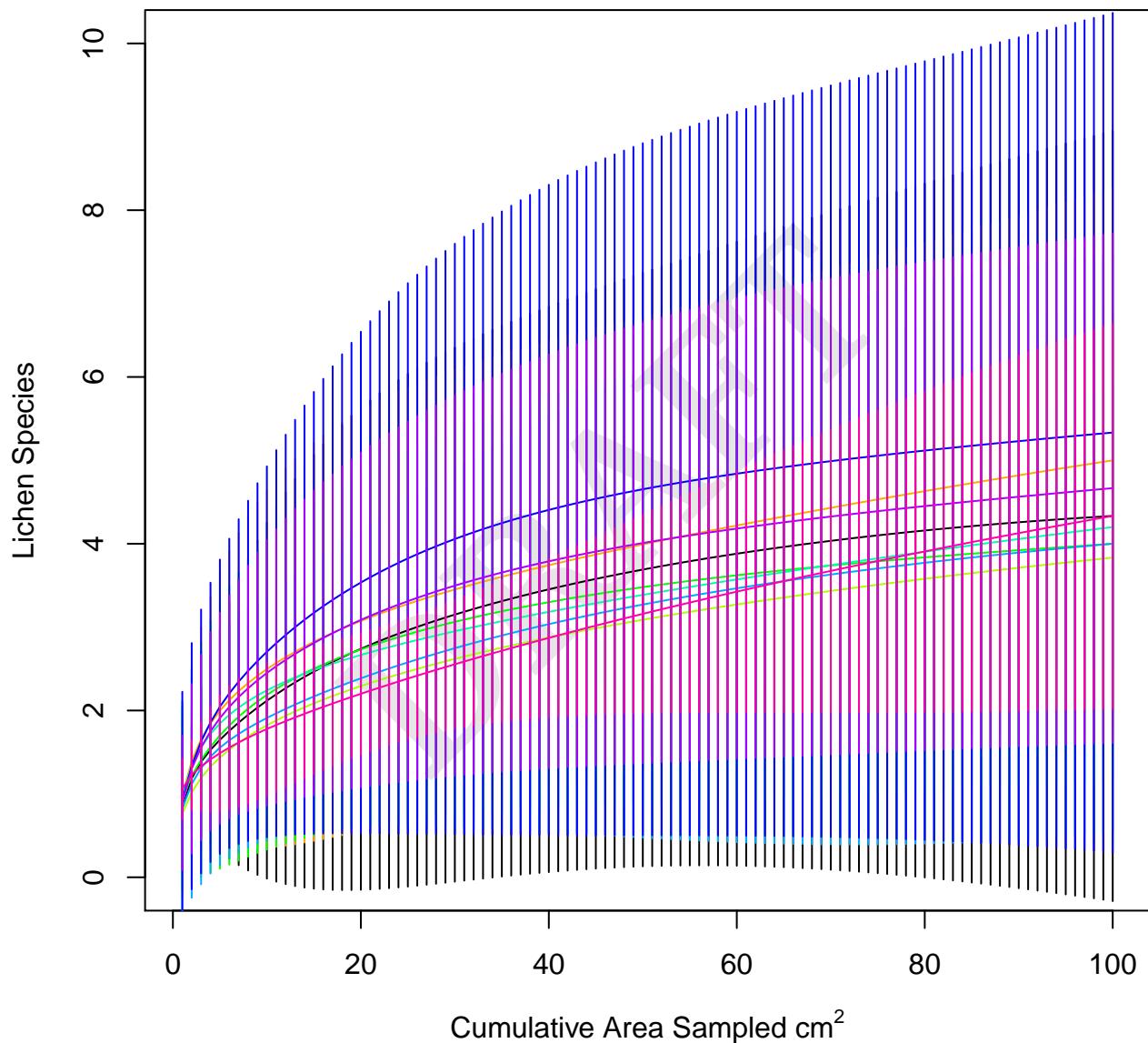


Fig. 2. Species area curve by genotype.

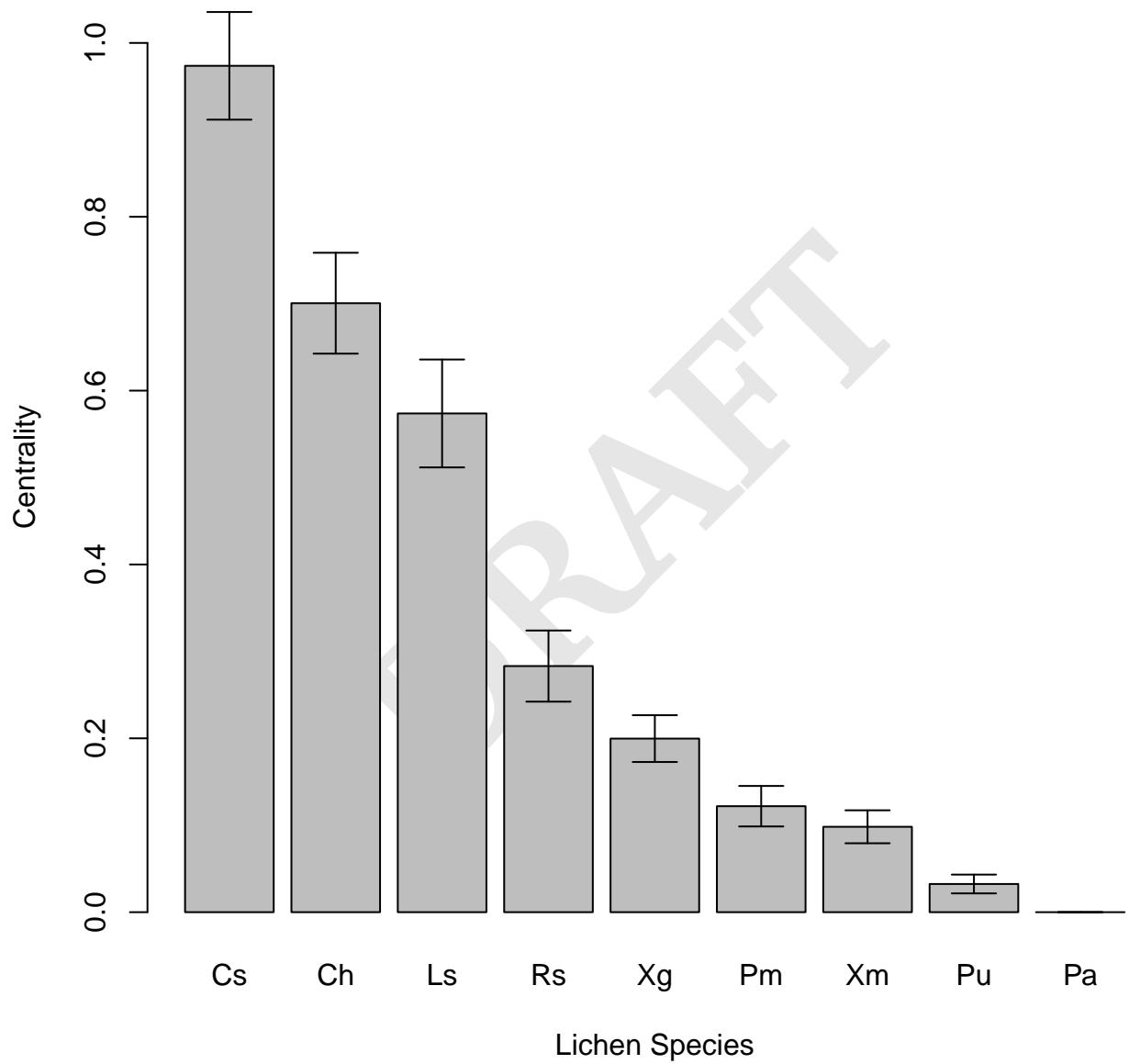


Fig. 3