

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

Matthew K. Lau^{a,b,1}, Louis J. Lamit^b, Rikke R. Naesbourg^c, Stuart R. Borrett^d, Matthew A. Bowker^e, and Thomas G. Whitham^a

^aDepartment of Biological Sciences and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA; ^bHarvard Forest, Harvard University, 324 N Main St, Petersham, MA 01366, USA; ^cDepartment of Biology, Syracuse University, 107 College Place Syracuse, NY 13244, USA; ^eUniversity of California Berkeley, Berkeley, CA, USA; ^fDepartment of Biology and Marine Biology, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC, 28403, USA; ^gSchool of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA; ^hCurrent Address: Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China 00000-00000

This manuscript was compiled on October 13, 2020

1 Biological evolution occurs in the context of complex ecosystems
2 of 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 structure, which is defined by interactions among species. Al-
5 though previous work has demonstrated that genotypic variation in
6 foundation species contributes to interaction network structure, we
7 are not aware of a study that has quantified the genetic contribution
8 to network structure or shown network structure to be a heritable
9 trait. To examine this, in a 20+ year common garden we observed
10 interactions among nine epiphytic lichen species associated with
11 genotypes of (*Populus angustifolia*), a foundation species of ripar-
12 ian ecosystems. We constructed signed, weighted, directed interaction
13 networks for the lichens and conducted genetic analyses of
14 whole network similarity, degree and centralization. We found three
15 primary results. First, using multiple metrics, tree genotype signifi-
16 cantly predicted lichen network structure; i.e., clonal replicates of
17 the same genotype tended to support more similar lichen networks
18 than different genotypes. Second, broad sense heritability estimates
19 show that plant genotype explains network similarity ($H^2 = 0.41$), net-
20 work degree ($H^2 = 0.32$) and network centralization ($H^2 = 0.33$). Third,
21 one of the examined tree traits, bark roughness, was also heritable
22 ($H^2 = 0.32$) and significantly correlated with lichen network similarity
23 ($R^2 = 0.26$), supporting a mechanistic pathway from variation in a her-
24 itable 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.
31
32

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 communi-
6 ties of interacting organisms: such as, endophytes,
7 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
9
10
11
12
13
14
15
16

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.

The authors have no conflicts of interest.

¹Dr. Matthew K. Lau. E-mail: matthewklau@fas.harvard.edu

(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). For example, 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

115 community genetics studies. Thus, it is important to
116 quantify how network structure changes in response
117 to genetic variation in order to fully understand evo-
118 lutionary dynamics in complex communities.

119 Here, we investigate how genetic variation in a
120 foundation tree species determines the structure of
121 a network of interactions among a community of
122 tree associated lichen species. Previous studies have
123 examined aspects of networks (33). Here we examine
124 the genetic basis of network structure on a com-
125 munity of sessile lignicolous (i.e., bark) lichens on
126 cottonwood trees. Using a long-term (20+ years),
127 common garden experiment with clonally replicated
128 *Populus angustifolia* individuals of known genetic
129 identity. We focused on a community of 9 epiphytic
130 lichen species, as previous research has demonstrated
131 significant compositional responses of epiphytes to
132 genotypic variation (34, 35). In addition, the life-
133 history characteristics of lichens, having highly local-
134 ized, direct contact interactions and slow population
135 turnover rates, facilitated the assessment of interac-
136 tions among lichen species on individual trees. We
137 hypothesize that in natural systems evolution occurs
138 in a community context involving interactions of com-
139 plex networks of interacting species (23, 24, 36, 37).
140 If correct, we expect to find that network structure
141 is genetically based, or, in other words, plant geno-
142 types will support different and heritable interaction
143 networks. Applying a probability-theory based net-
144 work modeling approach, we constructed a set of
145 interaction network models for the lichens associated
146 with individual trees. Using these models, we then
147 examined the genetic basis of the structure of these
148 ecological networks via several network metrics that
149 measures different aspects of network structure at
150 the scale of individual species (i.e., nodes) or the
151 entire network observed on each tree genotype. In
152 particular, we focus the metric of centrality for indi-
153 vidual species and centralization for whole networks,
154 which measures how much a species is connected
155 in the network relative to other species. Based on
156 previous community genetics theory, particularly the
157 community similarity rule (16), we hypothesize that
158 trees will co-vary in functional phenotypic traits such
159 as bark roughness and chemical composition and
160 trees of the same genotype will tend to have similar
161 traits leading to similarities in lichen network struc-
162 ture. This work is important because it provides a
163 mechanistic basis for understanding how community

164 network theory is intimately associated with the evo-
165 lutionary process and how human alterations of the
166 environment (e.g., climate change, invasive species,
167 pollution) may have cascading, indirect effects that
168 alter network structure and evolution.

Materials and Methods

169
170
Study System. The study was conducted along the We-
171 ber River, UT (USA), which is a cottonwood (*Populus*
172 spp.) dominated riparian ecosystem. Although two native
173 species, *Populus angustifolia* (James) and *Populus fremontii*
174 (S. Watson), occur here and are known to hybridize,
175 only pure or advanced generation backcrosses of *P. angus-*
176 *tifolia* were sampled. Bark lichens have been extensively
177 studied in this system and provide an ideal system in
178 which to observe and model lichen interaction networks,
179 as their sessile nature permits accurate identification of
180 individuals (38).

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

192
Bark Lichen and Trait Observations. On each tree, pres-
193 ence or absence of each lichen species was assessed in 50
194 total 1 cm² cells arrayed in a checkerboard pattern. Given
195 the small size and sessile nature of lichens, we were able to
196 rapidly assess lichen interactions by quantifying thalli in
197 close contact. Sampling was restricted to the northern aspect
198 of the trunk to maximize the abundance of lichen and
199 control for the effect of trunk aspect. Two adjacent 100
200 cm² quadrats centered at 50 cm and 95 cm from ground
201 level were sampled (Fig 1 A and B). The observed lichen
202 community included (abbreviations are given for species
203 present in study): Xg = *Xanthomendoza galericulata*, Xm
204 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Cande-*
205 *lariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora*
206 *hagenii*, Pm = *Phyciella melanchra*, Pa = *Physcia adscen-*
207 *dens*, Pu = *Physcia undulata*. Several other species were
208 not observed in the present study but are known to occur
209 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia*
210 *ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

211 The cell size and checkerboard sampling pattern was
212 chosen to isolate the individuals in each cell. In a previous
213 survey of lichen thallus size in this common garden, we
214 had observed a median thallus size of 0.12 ± 0.001 cm² (1

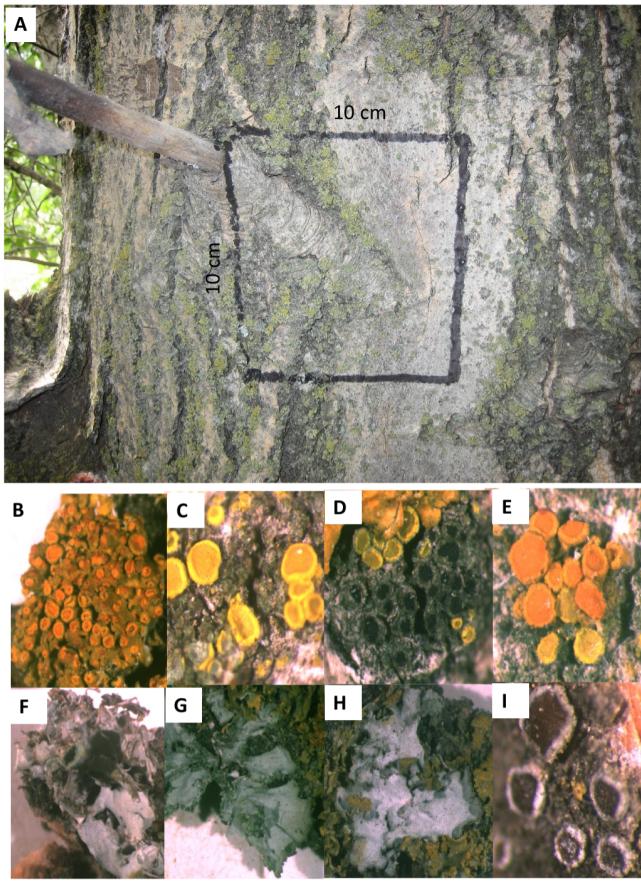


Fig. 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the 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).

ated 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 (S_{ii}) 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 ($D = D_{ij}$) can be interpreted as how one species impacts another with zero being no effect and values less than or greater than zero interpreted as negative and positive effects, respectively. Here, we will refer to this matrix (D) as an interaction matrix with the properties that it can be asymmetric (i.e. P_{ij} does not necessarily equal P_{ji}), and the diagonal (P_{ii}) is zero (i.e. a species does not influence its own probability of being observed).

Network Metrics. To quantify the structural variation of lichen networks we calculated several metrics at both the node and whole-network level. For individual nodes

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 also measured several bark traits for each tree: including, bark roughness, condensed tannin, carbon and nitrogen concentrations and pH. **ADD METHODS FROM JAMIE.**

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 gener-

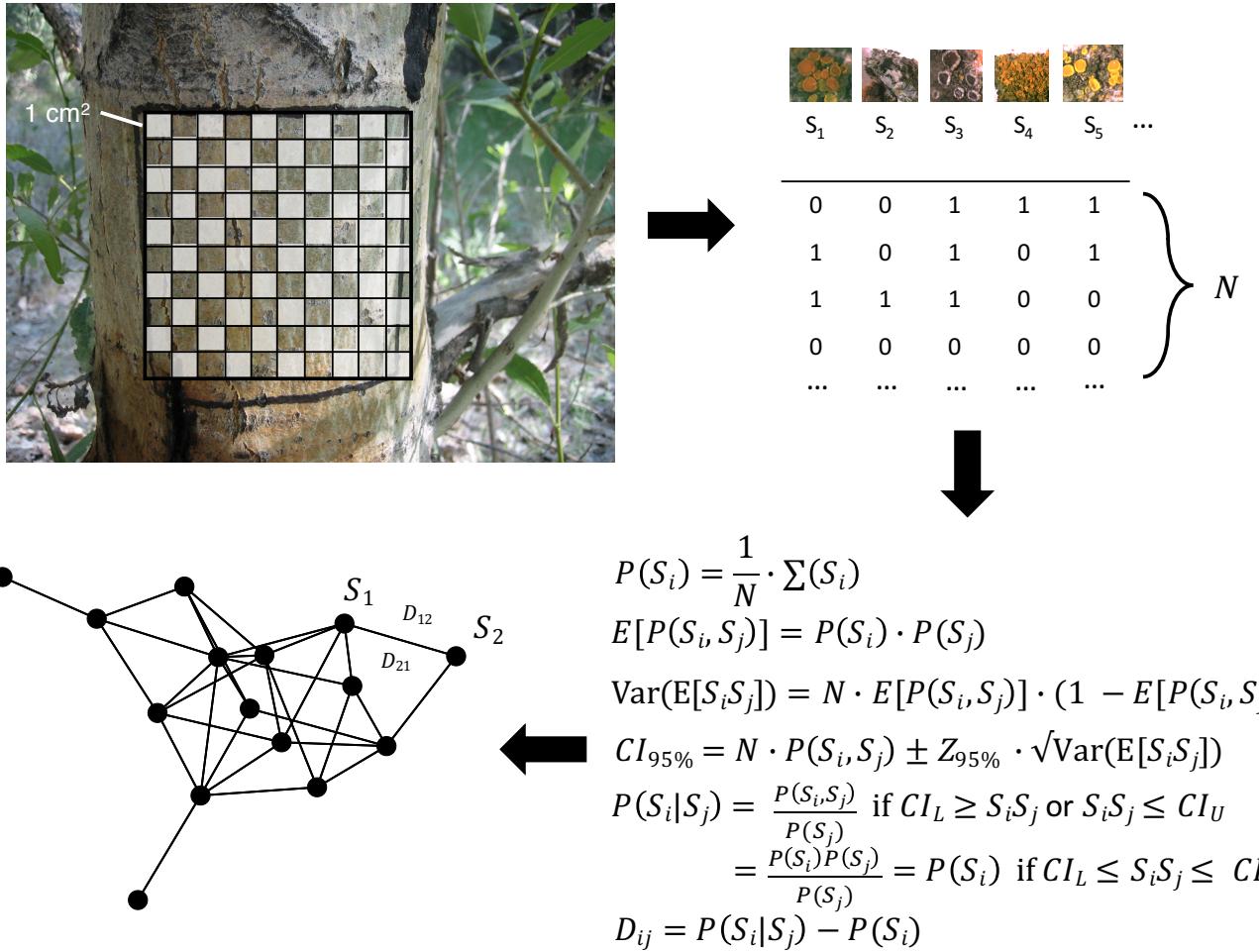


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded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

(i.e. species) in each network, we calculated both the degree Eq. (??) and the centrality. We also calculated two similar global network metrics: degree and centralization. The first was network degree, which is a count of the total number of links in a network. As the networks contained not only positive and negative connections, as well as directional connections (both in-coming and out-going), we calculated the same network metrics for all combinations of these types of connections in each network. Although there are many more possible network metrics that could have been examined, we chose to focus on a restricted set for the sake of clarity. Also, degree and centrality form the basis of many other network metrics. To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (41) using the **signnet** package (42).

Statistical Analyses, Software and Data. We used a combination of parametric and non-parametric, permutation based frequentist statistical analyses to test for the effects of genetic variation on lichen communities and their interaction networks. To assess the effect of genotype on univariate responses, we used additive, random effects models with Restricted Maximum Likelihood (REML). We used a combination of Least Squares Regression, Analysis of Variance (ANOVA) and correlation tests to quantify and test for the relationship among other variables. Bark roughness, lichen cover and species richness were square-root transformed to meet the assumptions of homogeneity of variance and normality for these tests.

For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PERMANOVA) and

324 Mantel tests. To quantify the similarity of lichen net-
 325 works among individual trees, we calculated the pairwise
 326 Euclidean distance of the **D** interaction matrices among
 327 all pairs of trees.

328 For visualization of multivariate patterns, we used
 329 Non-metric Multi-Dimensional Scaling (NMDS) (43) to
 330 produce dimensionally reduced ordinations of these multi-
 331 variate responses and fitted vectors for continuous predictor
 332 variables to the ordinated values (44). Using random
 333 initial configurations with a maximum of 500 iterations
 334 and a change in stress threshold of less than 10^{-12} . Final
 335 configurations has the lowest stress with at most a stress
 336 level of 0.10.

337 For each network, we also calculated metrics that mea-
 338 sure different structural aspects. Although there are many
 339 other metrics, for the sake of simplicity we focus on a
 340 subset that represent several interesting features of net-
 341 work structure (see (17)). We calculated the number of
 342 interactions or “links” in each network, which provides a
 343 measure of the size of the network (23, 45). We also calcu-
 344 lated the centralization of each network, which measures
 345 the evenness of the distribution of interactions among
 346 the species in the network (46). In a network with a
 347 low level of centralization species have similar amount of
 348 interaction in the network, while a network with a high
 349 level of centralization tends to have one or small number
 350 of species that interact with other species. We used a
 351 related function to calculate the centrality of each species
 352 (i.e. node level centrality) in each network as well.

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

366 All code and data for the project are openly avail-
 367 able online. Code and data are available at github.com/
 368 [ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo
 369 at zenodo.com/doi/XXXXXX. All analyses were conducted
 370 using the programming language R version 3.6.1 (R De-
 371 velopment Core Team 2019).

372 Results

373 Tree genotype influenced lichen network structure
 374 and multiple lichen network metrics were herita-
 375 ble. Tree genotype significantly predicted the struc-
 376 tural similarity of lichen networks (PERMANOVA:
 377 Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$)

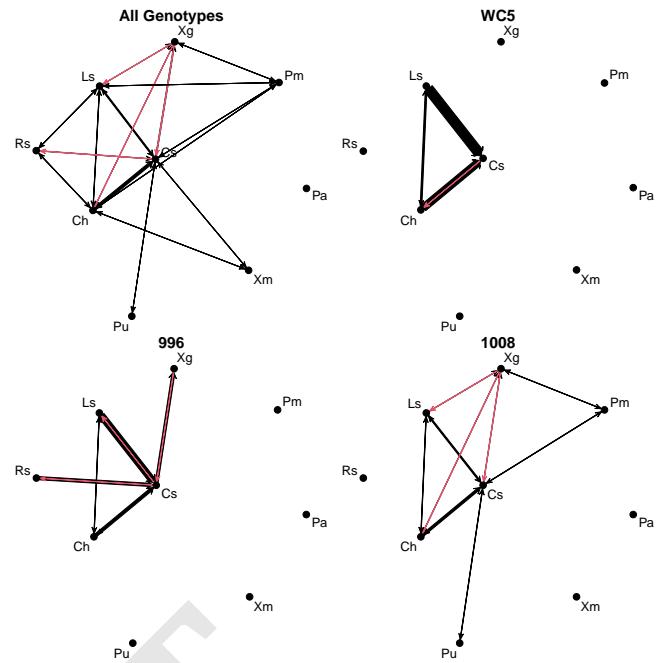


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

(Fig. 4). Overall network level metrics responded
 378 significantly to tree genotype (Table 1), including net-
 379 work degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} =$
 380 0.0255) and centralization including both in-coming
 381 and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} =$
 382 0.0184) or when separated into in-coming
 383 only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} =$
 384 0.0190) or out-going only ($RLRT = 3.8615$, $H^2 =$
 385 0.3193, $p\text{-value} = 0.0205$). Metrics including only
 386 positive links also showed a significant effect of tree
 387 genotype, including positive degree ($RLRT = 3.6925$,
 388 $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
 389 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} =$
 390 0.0142). Metrics calculated with negative
 391 links were not significant, including degree (negative)
 392 ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$)
 393 and both in-coming (negative) ($RLRT = 0.3304$, $H^2 =$
 394 0.1057, $p\text{-value} = 0.2508$) and out-going centraliza-
 395 tion (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$,
 396 $p\text{-value} = 0.3446$).

The genetic response of network centralization was
 397 driven by variation in *Caloplaca holocarpa*. Central-
 398

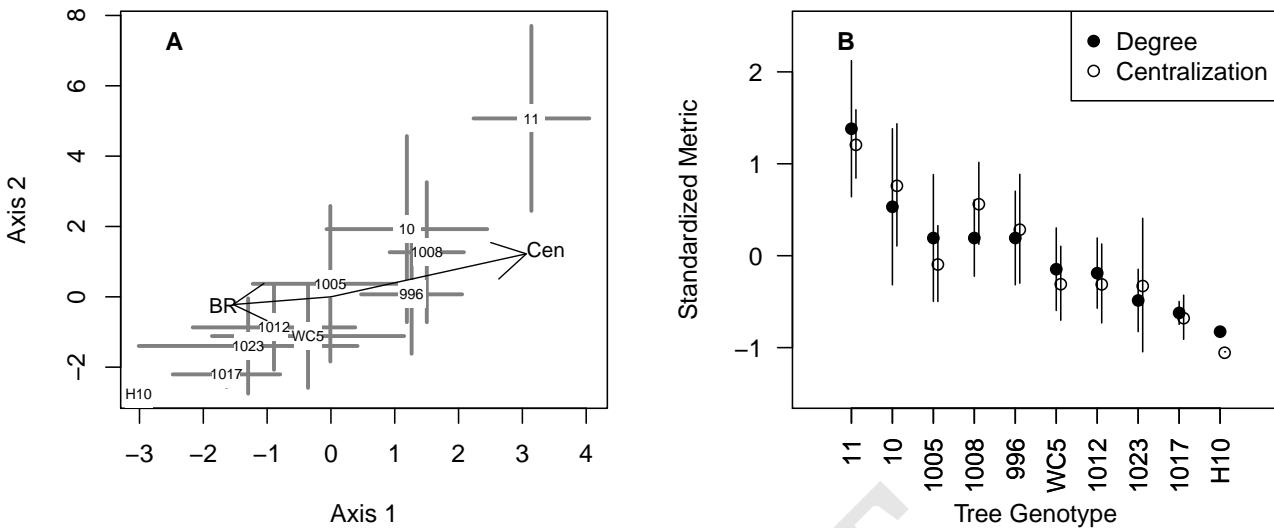


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing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

response	Df	statistic	H2	p-value
Lichen Network Similarity	9.0000	3.5821	0.4130	0.0537
Degree		3.5175	0.3156	0.0255
Degree (positive)		3.6925	0.3242	0.0229
Degree (negative)		0.0327	0.0318	0.3859
Centralization		4.0444	0.3305	0.0184
Centralization In-Degree		4.4812	0.3487	0.0142
Centralization In-Degree (positive)		3.9852	0.3309	0.0190
Centralization In-Degree (negative)		0.3304	0.1057	0.2508
Centralization Out-Degree		3.8615	0.3193	0.0205
Centralization Out-Degree (positive)		3.5585	0.3119	0.0248
Centralization Out-Degree (negative)		0.0862	0.0513	0.3446

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

of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5). Add transformations of variables to methods. Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} = 0.0343$) both displayed significant responses to tree genotype. None of the other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and none other than bark roughness was correlated with network similarity (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

400 ity varied significantly among species ($F_{8,324} = 7.99$,
401 $R^2 = 0.16$, $p\text{-value} < 0.0001$). *Caloplaca holocarpa*
402 centrality was the main species to exhibit a signifi-
403 cant response to tree genotype in terms of positive
404 centrality for both the in-coming ($RLRT = 3.61$, H^2
405 = 0.32, $p\text{-value} = 0.0240$) and out-going ($RLRT =$
406 3.13, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives, but
407 not for either negative centrality metrics in-coming
408 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going
409 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of
410 the other species' centralities showed a genotypic re-
411 sponse (Supplementary Table 3) with the exception

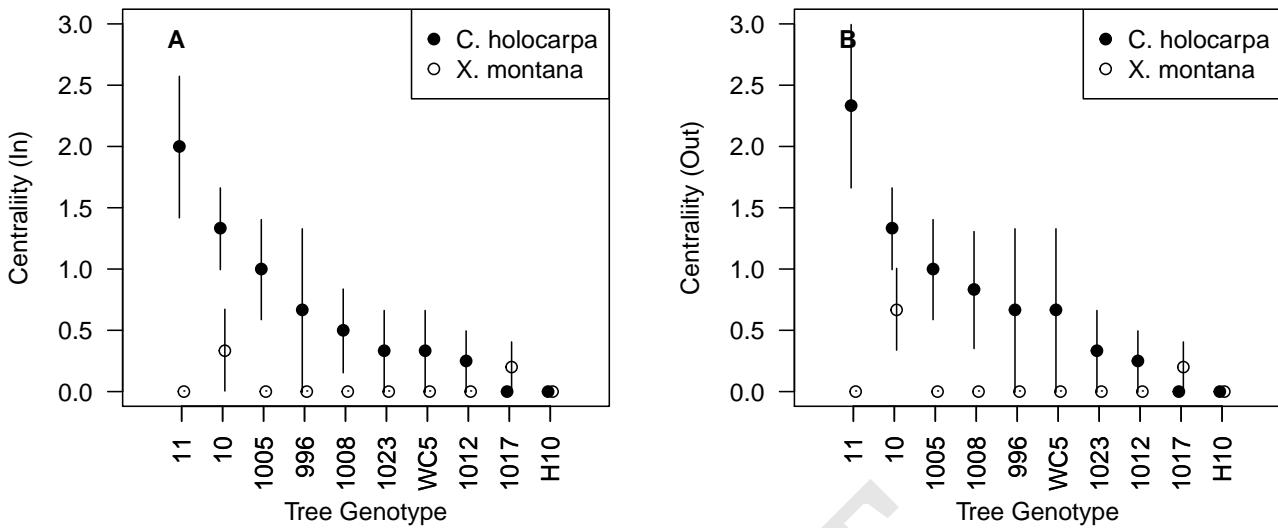


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

437 overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$,
 438 $p\text{-value} = 0.04$) and centralization ($df = 35$, $t = -2.52$,
 439 $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees with
 440 more similar levels of bark roughness tended to have
 441 lichen interaction networks with similar structure.
 442 To quantify the genetic bases of this effect of bark
 443 roughness on network structure, we used the residual
 444 values from regressions of network degree and cen-
 445 tralization in tests of the effect of tree genotype and
 446 found no significant effect of tree genotype for either
 447 degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$)
 448 or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value}$
 449 = 1.0000), suggesting that the observed relationship
 450 between bark roughness and lichen network structure
 451 was largely genetically based (Fig. 6).

Discussion

We found that tree genotype influenced lichen net-
 452 work structure in the experimental cottonwood forest.
 453 Network similarity and metrics of network structure
 454 tended to be more similar on trees of the same geno-
 455 type. Generally, this genetic effect was manifested in
 456 positive interactions and largely driven by *C. holocarpa*.
 457 The genetically based trait, bark roughness,
 458 was the only trait observed to effect network vari-
 459 ation, largely via shifts in positive in-coming and
 460 out-going interactions. Bark roughness has been
 461 demonstrated previously to be under strong genetic
 462 control (49), and bark roughness has also previously
 463 been shown to be an important tree trait influencing
 464 bark lichens (39); however this is the first demon-
 465 stration of a link from genes to lichen network structure.
 466 As such these results have important implications for
 467 the potential influence of genetically based variation
 468 in ecosystems with networks of interacting species.
 469

Heritability of Interaction Network Structure. Re- 471 visit the community similarity rule.

Add more text here on positive and negative inter-
 473 actions of lichen from the literature.

Elaborate on how many species might be supported
 475 by each lichen thallus including the symbionts and
 476 other species.

**Table 2. PERMANOVA Pseudo-F Table of lichen net-
 477 work similarity response to bark traits.**

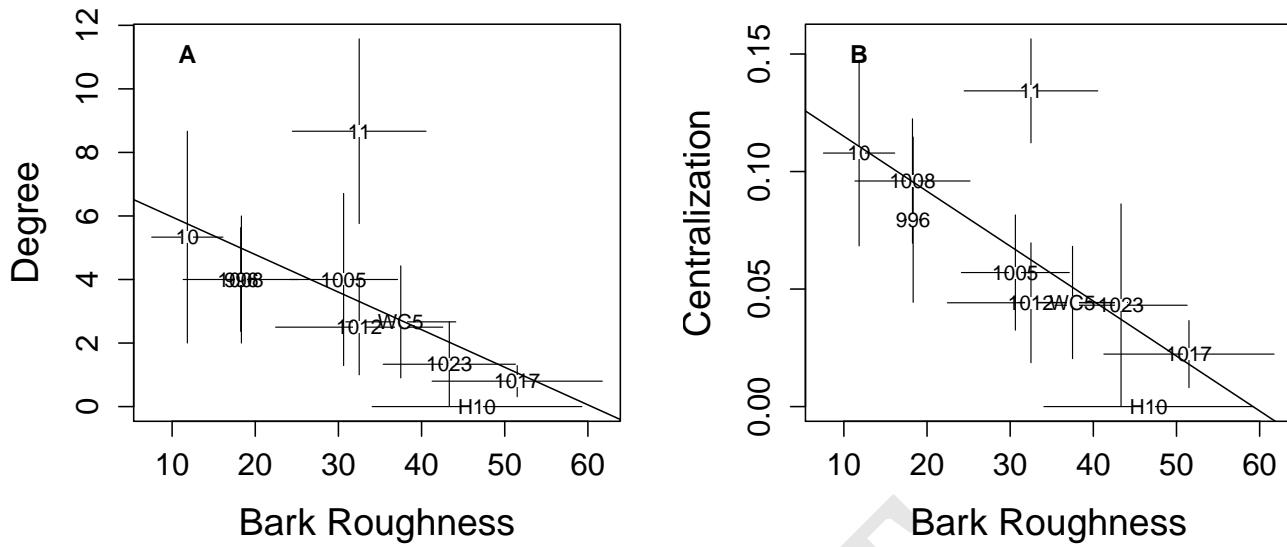


Fig. 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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

478 *Elaborate on the importance of identifying the
479 species/node level patterns in network structure re-
480 sponse to genotype.*

481 *What is the relationship between tree growth, bark
482 roughness and disruption of the lichen community?
483 Tree grow and the bark expands over time, causing
484 furrows.*

485 *Does bark roughness increase habitat and decrease
486 interactions?*

487 There are important functional ramifications of ge-
488 netically based variation in network structure. First,
489 even if the composition of the communities is the
490 same among individuals and genotypes, interactions
491 may not be. We didn't observe compositional dif-
492 ferences using the same data from which the lichen
493 networks were derived. If we only had our compo-
494 sition dataset from this study, we would have con-
495 cluded no response of the lichen community to tree
496 genotype, even though the underlying interactions
497 among lichen species does vary among genotypes.
498 Community composition of lichen has previously
499 been observed to be different among tree genotype
500 in the same experimental garden, though this was
501 observed with a larger sampling of total area and
502 quadrats per tree. Regardless, this could result in a
503 situation in which abundance based investigations
504 of community-level genetic effects may miss impor-

tant variation in the interactions among individuals
505 in these communities, leading to an underestimate of
506 genetic effects in ecosystems. It is possible that these
507 underlying differences in interactions among lichen
508 could lead to differences in community composition
509 at a future point in time, however, this is not needed
510 for evolutionary dynamics to play out.

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

532 out from the central core (Leiberman). This is struc-
533 turally what we have observed with the networks that
534 tend to occur on some of the genotypes in our study,
535 i.e. the more centralized networks. It is possible that
536 these more centralized networks could function as
537 hot-spots of evolutionary dynamics resulting from
538 the amplifying effect the network structure fostered
539 on that tree genotype.

540 There are several important points to consider
541 with regard to the generalization of the observed
542 genetically based response of the lichen networks.
543 Body size and sessile nature of lichen important to
544 observing genotype responses. As bark lichen in-
545 dividuals do not move, but grow in a largely two
546 dimensional plane, these communities and their in-
547 teractions occur in the highly localized context of
548 the tree's bark surface. Lichen individuals are many
549 orders of magnitude smaller than the tree individual
550 and the life-span of a tree is many times that of a
551 lichen. For these reasons, any genetic effects on these
552 communities is not damped by the movement of
553 individuals and the mixing of the effect of different
554 tree genotypes on the lichen community, as might
555 occur for more mobile species (e.g. insects and birds).
556 We only looked at lichen, other species whose distri-
557 bution, abundance or interactions respond to tree
558 genotype, such as epiphytic plants (e.g. moss and
559 liverworts), algae or insects, could be playing a role.
560 Other traits could also be playing a role, such as
561 traits that are correlated with bark roughness, such
562 as micro-aspect, albedo, moisture, etc.

563 Bark roughness could possibly be serving the role
564 that other lichen play in facilitating the success of
565 new propagule attachment and the growth of estab-
566 lishing thalli. This is supported by the patterns over-
567 all being positive, including *C. holocarpa* centrality.
568 We did not observe specific microscopic dynamics,
569 such as photobionts, mycobionts, endolichenic fungi
570 and bacteria, but variation in these underlying in-
571 teractions could also be playing a role. Although we
572 can not rule out the possibility that other unmea-
573 sured tree traits or organisms correlated with bark
574 roughness are underlying the observed patterns in
575 bark lichen network structure, substantial research
576 supports the importance of genetically based tree
577 traits for communities and ecosystems (8), and in
578 particular bark roughness for bark lichen communi-
579 ties (38, 39, 49).

580 In the present study, lichen cover, lichen species

581 richness and composition were not responsive to tree
582 genotype, unlike what was found in (39). This is
583 likely, at least in part, the result of differences in
584 sampling method and the choice of genotypes sam-
585 pled leading to overall higher abundances of observed
586 lichens. In the current study mean % total lichen
587 cover among genotypes ranges from 60-93% cover;
588 whereas the range reported in (39) is 0.86-18.73%.
589 The previous study used a visual estimation method,
590 unlike the current study, which observed lichen at
591 the scale of 1 cm² cells, which could over-estimate
592 cover depending on the frequency at which actual
593 thallus size was less than 1 cm². The previous study
594 used samples from both the northern and southern
595 aspects of each tree; whereas, the current study only
596 observed lichen on the northern aspect. Also, our
597 current results are likely different from the previous
598 study because the current study selected genotypes
599 that tended to have bark lichen, with the interest
600 of focusing on generating networks for comparison.
601 These differences do not negate the findings of either
602 study but is important to explain the differences
603 in the findings, particularly in the community-level
604 effects of tree genotype.

605 **Implications for Interspecific Indirect Genetic Ef-
606 ffects (IIGEs).** Initially, evolution in a community
607 context was focused on examples of highly co-evolved
608 pairs of species (e.g. Darwin's famous prediction
609 of the Sphinx Moth and Christmas Orchid) (9).
610 However, studies of diffuse co-evolution (*sensu* (50))
611 (51, 52), geographic mosaics of co-evolution (36) and
612 community genetics (11) have provided an in-road
613 for ecological network approaches (21, 24, 53) to illu-
614 minate a more complex perspective of the interface
615 between ecological and evolutionary dynamics.

616 Interspecific indirect genetic effects (IIGE) theory
617 as provided a quantitative framework within which
618 to approach evolutionary theory at higher levels of
619 biological organization: from populations to com-
620 munities and ecosystems. To date, this theory has
621 focused on modeling the strong effects of foundation
622 species (7, 27), but it has not yet integrated devel-
623 opments in the ecological or evolutionary network
624 theory literature. This is to say that it has not devel-
625 oped a way to examine complex interactions among
626 species; however, previous studies have demonstrated
627 that this network context is likely to be important, as
628 altering the structure of interaction networks pro-
629 vides a means for genetic effects to be damped or

630 magnified within the system of interacting species.
631 For example, (24) showed that the genetics based
632 interactions of aphid resistant and aphid susceptible
633 trees resulted in different interaction networks of
634 their associated arthropod communities composed
635 of 139 species. At the scale of ecosystems, trophic
636 networks or food webs direct and control the rates
637 of energy and nutrient flux (54). Furthermore, in a
638 predator-prey-plant study, Smith (20), showed that
639 the interactions among species across trophic levels
640 depended on plant genotype. Also, work by (55–57)
641 observed consistent patterns of centralized interactions
642 of species modules focused around hubs of
643 plant-fungal interactions. In other words, a small
644 number of plant and fungal symbionts tended to
645 have disproportionate numbers of interactions with
646 other species and likely are the drivers in determining
647 community assembly, structure and dynamics.

648 The results of the current study provides clear em-
649 perical evidence that networks points to the need to
650 expand IIGEs encompass the structure of interaction
651 networks. Although such a synthesis necessitates
652 a much greater effort than can be afforded in this
653 paper, it is possible to point to several productive
654 pathways forward. In terms of interaction networks,
655 foundation species are relatively central within the
656 system of interactions, that is their direct and/or
657 indirect effects are greater than other species. So,
658 when the more centralized (foundation) species have
659 genetically based interactions, genetic effects will
660 tend to be magnified in the community. Here, we
661 found that even though more abundant or more cen-
662 tralized (i.e. “important”) species were present in
663 the community, their effects were not the main com-
664 ponent responding to genetic effects. Considering
665 the impact of network structure would be a produc-
666 tive path forward for the theoretical development
667 and application of the IIGE concept.

668 With regard to the evolutionary implications of
669 network structure, ecological network studies have
670 focused on asymmetry and the quantification of
671 its structure in communities, with qualitative dis-
672 cussion of the impacts on evolutionary dynamics
673 (36, 37, 58, 59). More specific predictions, with a
674 quantitative framework, can be found in applications
675 of evolutionary game theory, and although developed
676 at the population scale, such theory can apply to
677 communities. One seemingly useful direction from game the-

678 ory is the classification of networks into two genreal
679 categories, rooted and cyclic, in which rooted net-
680 works have interactions in which evolutionary effects
681 emanate from one or multiple origins but these effects
682 do not have connections back to the origins, whereas
683 cyclic networks contain feedbacks to one or more ori-
684 gins. Although it did not explicitly define it in this
685 context, the previous work (17), developed that the
686 structure of the network in the context of a founda-
687 tion species, such as cottonwoods in which there are
688 demonstrable community level genetic effects, is that
689 of a multiple origin network. This builds on many
690 previous studies demonstrating that the community
691 level effects vary among multiple genotypes. It is not
692 clear what potential there is for feedbacks there are
693 to the origins (e.g. the cottonwood genotypes) from
694 the community, and as such it cannot be determined
695 whether these networks are cyclic or rooted. In other
696 systems, lignicolous lichens can have demonstrable
697 positive effects on the availability of nutrients for the
698 trees that they are associated with, but this has not
699 been measured in the current system. Illucidating
700 the absence and/or presence and quantifying such
701 feedbacks would allow for the determination of the
702 cyclic nature and potential evolutionary dynamics of
703 this system. The presence of feedbacks would provide
704 the potential for non-linear dynamics in which evo-
705 lutionary effects are dampened or amplified by the
706 struture of the network. For example, a star struc-
707 ture in which there is a primary or core set of central
708 species with feedbacks from the radiating species has
709 been demonstrated to be a structure that amplifies
710 evolutionary dynamics (31). If such feedbacks do
711 not exist, and these sub-networks of the lichen and
712 tree genotypes are likely to be multi-rooted networks.
713 Such a structure is theorized to generally promote
714 diversification as variation arising from the shifting
715 distribution of the “roots”, i.e. genotypes; however,
716 loss of genotype/root diversity could lead to fixation
717 of a single genotype in the population and a decrease
718 in community-wide diversity.

719
Conclusion. Although our study was conducted with
720 a community of lichens, these results should be gen-
721 eralized to other groups of diverse organisms around
722 the world that also exhibit significant genetic signals
723 at the community level (7, 60). In the face of the
724 high degree of complexity and potential context de-
725 pendancy of ecological processes, the current study
726 points to the utility of considering the spatial and

728 temporal scales of interactions, as discussed to some
729 in previous studies (16, 61, 62). In the present study,
730 we found that community assembly processes, such
731 as environmental filtering and species interactions,
732 are genetically based. This is likely due, in part,
733 to the large difference in the differences in size and
734 longevity of the lichen and cottonwood individuals
735 with the trees determining the environment in which
736 the lichen occur. We suggest that future work would
737 be aided by determining these modules within the
738 biotic community that include species with similar
739 differences in body-size and time-scales. As heritable
740 variation is the raw material for natural selection
741 to act upon, a genetic basis for interaction network
742 structure indicates evolutionary dynamics should be
743 considered at the community level and that con-
744 serving genetic variation is important to consider in
745 efforts to restore or preserve complex species interac-
746 tions and their associated ecosystem functions (63).
747 With such findings, it appears that we are closer to
748 understanding the evolutionary drivers of Darwin's
749 entangled bank and the interconnectedness of species
750 in complex communities.

751 Future work should consider the potential influ-
752 ence on evolutionary dynamics of the associated com-
753 munities. The network of interactions of species that
754 are strongly influenced by a foundation species, could
755 amplify the effects of genotype, this serves as a means
756 for genetic effects to increase rather than diffuse
757 through an ecosystem either through space or over
758 time, as has been proposed in the construction of the
759 genetic diffusion hypothesis. Altered abundances can
760 lead to differences in interactions. Genotype effects
761 on abundances of individual abundances may cancel
762 out. Specifically for asexually reproducing species,
763 such as many lichen are, shifting interaction frequen-
764 cies could lead to evolutionary outcomes, given the
765 potential to take-up symbionts and genetic material
766 from thalli that they come into contact with. Alter-
767 ing interaction frequencies could result in differences
768 in rates of the exchange of genetic materials among
769 lichen that could then be passed on to vegetative
770 and possibly sexually produced reproductive propa-
771 gules. The larger scale (stand or region) effects of
772 these "evolutionary units" on each tree would de-
773 pend on the connectivity and rate of movement of
774 propagules among trees per the geographic mosaic
775 of co-evolution hypothesis (3, 36).

776 Add evolutionary unit to the larger narrative. That

is mainly that identifying how evolution might be
777 acting on multiple species is useful for conservation
778 and management.

779 Discuss the impacts of *P. betae* removal on net-
780 work structure per Lau 2016 and Keith 2017. Also,
781 what about Barbour 2016.

783 Other studies that should be discussed::

- 784 • Multiple plant traits shape the genetic basis
785 of herbivore community assembly. Synthesis:
786 Taken together, our results support that the
787 genetic basis of herbivore community assembly
788 occurs through a suite of plant traits for different
789 herbivore species and feeding guilds (Barbour
790 2015). Also discuss Lamit 2015 and Holeski's
791 multivarite phenotype paper.
- 792 • Linking plant genes to insect communities: Iden-
793 tifying the genetic bases of plant traits and com-
794 munity composition. Synthesis: These findings
795 support the concept that particular plant traits
796 are the mechanistic link between plant genes
797 and the composition of associated insect com-
798 munities (Barker 2019).

799 **ACKNOWLEDGMENTS.** This work was supported by
800 the National Science Foundation grant (DEB-0425908)
801 and Integrative Graduate Research Traineeship (IGERT)
802 fellowships for M.L. and L.L. The Ogden Nature Center
803 staff helped to maintain the common gardens. Lichen
804 sampling was supported by Todd Wojtowicz, Luke Evans
805 and David Solance Smith.

1. Ellison AM, et al. (2005) Loss of foundation species: consequences for the structure and 806 dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9):479–486.
807
2. Busby PE, et al. (2015) Genetics-based interactions among plants, pathogens, and herbivores define arthropod community structure. *Ecology* 96(7):1974–1984.
808
3. Barbour RC, et al. (2009) A geographic mosaic of genetic variation within a foundation tree 809 species and its community-level consequences. *Ecology* 90(7):1762–1772.
810
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.
812
5. Holeski LM, Hillstrom ML, Whitham TG, Lindroth RL (2012) Relative importance of genetic, 814 ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype
815 in a foundation tree species. *Oecologia* 170:695–707.
816
6. Bailey JK, et al. (2009) From genes to ecosystems: a synthesis of the effects of plant genetic 817 factors across levels of organization. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 364(1523):1607–16.
818
7. Whitham TG, et al. (2012) Community specificity: Life and afterlife effects of genes.
820
8. Des Roches S, et al. (2018) The ecological importance of intraspecific variation. *Nature Ecology and Evolution* 2(1):57–64.
821
9. Wade MJ (2007) The co-evolutionary genetics of ecological communities.
823
10. Crutsinger GM (2016) A community genetics perspective: Opportunities for the coming 824 decade. *New Phytologist*.
825
11. Whitham TG, et al. (2006) A framework for community and ecosystem genetics: from genes 826 to ecosystems. *Nature reviews. Genetics* 7:510–523.
827
12. Moya-Laraño J (2011) Genetic variation, predator-prey interactions and food web structure. 828 *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 366(1569):1425–37.
829
13. Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J (2007) Non-random 831 co-extinctions in phylogenetically structured mutualistic networks. *Nature* 448(7156):925–8.
832
14. Guimarães PR, et al. (2007) Interaction Intimacy Affects Structure and Coevolutionary Dy- 833 namics in Mutualistic Networks. *Current Biology* 17(20):1797–1803.
834

- 835 15. Gómez JM, Abdelaziz M, Camacho JPM, Muñoz-Pajares AJ, Perfectti F (2009) Local adaptation
836 and maladaptation to pollinators in a generalist geographic mosaic. *Ecology Letters*
837 12(7):672–682.
- 838 16. Bangert RK, et al. (2006) A genetic similarity rule determines arthropod community structure.
839 *Molecular ecology* 15:1379–1391.
- 840 17. Lau MK, Borrett SR, Baiser B, Gotelli NJ, Ellison AM (2017) Ecological network metrics:
841 opportunities for synthesis. *Ecosphere* 8(8):e01900.
- 842 18. Bailey JK, Wooley SC, Lindroth RL, Whitham TG (2005) Importance of species interactions
843 to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters*
844 0(0):051122062725008.
- 845 19. Johnson MTJ (2008) Bottom-up effects of plant genotype on aphids, ants, and predators.
846 *Ecology*.
- 847 20. Smith DS, Bailey JK, Shuster SM, Whitham TG (2011) A geographic mosaic of trophic interactions
848 and selection: trees, aphids and birds. *Journal of evolutionary biology* 24(2):422–9.
- 849 21. Smith DS, et al. (2015) Introduced elk alter traits of a native plant and its plant-associated
850 arthropod community. *Acta Oecologica* 67:8–16.
- 851 22. Barbour MA, et al. (2016) Genetic specificity of a plant-insect food web: Implications for
852 linking genetic variation to network complexity. *Proceedings of the National Academy of
853 Sciences of the United States of America* 113(8):2128–2133.
- 854 23. Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG (2015) Genotypic variation in foun-
855 dation species generates network structure that may drive community dynamics and evolution.
856 *Ecology* 97(3):15–0600.
- 857 24. Keith AR, Bailey JK, Lau MK, Whitham TG (2017) Genetics-based interactions of foundation
858 species affect community diversity, stability and network structure. *Proceedings of the Royal
859 Society B: Biological Sciences* 284(1854):20162703.
- 860 25. Newman MEJ (2006) Modularity and community structure in networks. *Proceedings of the
861 National Academy of Sciences of the United States of America* 103(23):8577–82.
- 862 26. Sole R, Bascompte J (2006) *Self-Organization in Complex Ecosystems*. (Princeton Univer-
863 sity Press, Princeton, N.J.).
- 864 27. Shuster SM, Lonsdorf EV, Wimp GM, Bailey JK, Whitham TG (2006) COMMUNITY HERI-
865 TABILITY MEASURES THE EVOLUTIONARY CONSEQUENCES OF INDIRECT GENETIC
866 EFFECTS ON COMMUNITY STRUCTURE. *Evolution* 60(5):991.
- 867 28. Whitham TG, Allan GJ, Cooper HF, Shuster SM (2020) Intraspecific Genetic Variation and
868 Species Interactions Contribute to Community Evolution. *Annual Review of Ecology, Evolu-
869 tion, and Systematics* 51(1).
- 870 29. Gehring C, et al. (2014) Plant genetics and interspecific competitive interactions determine ectomycorrhizal fungal community responses to climate change. *Molecular Ecology*
871 23(6):1379–1391.
- 872 30. Gehring CA, Stultz CM, Flores-Rentería L, Whipple AV, Whitham TG (2017) Tree genetics
873 defines fungal partner communities that may confer drought tolerance. *Proceedings of the
874 National Academy of Sciences*.
- 875 31. Lieberman E, Hauert C, Nowak MA (2005) Evolutionary dynamics on graphs. *Nature*
876 433(7023):312–316.
- 877 32. Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems.
878 *Science* 345(6195).
- 879 33. Barbour MA, et al. (2019) Trait plasticity is more important than genetic variation in determin-
880 ing species richness of associated communities. *Journal of Ecology* 107(1):350–360.
- 881 34. Winfree R, Gross BJ, Kremen C (2011) Valuing pollination services to agriculture. *Ecological
882 Economics* 71:80–88.
- 883 35. Zytnyska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree
884 species influences the associated epiphytic plant and invertebrate communities in a com-
885 plex forest ecosystem. *Philosophical transactions of the Royal Society of London. Series B,
886 Biological sciences* 366:1329–1336.
- 887 36. Thompson JN (2013) *Relentless Evolution*. (University of Chicago Press), p. 499.
- 888 37. Bascompte J, Jordano P, Olesen JM (2006) Asymmetric Coevolutionary Networks Facilitate
889 Biodiversity Maintenance!10.1126/science.1123412. *Science* 312:431–433.
- 890 38. Lamit L, et al. (2011) Genetically-based trait variation within a foundation tree species influ-
891 ences a dominant bark lichen. *Fungal Ecology* 4(1):103–109.
- 892 39. Lamit LJ, et al. (2015) Genotype variation in bark texture drives lichen community assembly
893 across multiple environments. *Ecology* 96(4):960–971.
- 894 40. Araújo MB, Rozenfeld A, Rahbek C, Marquet PA (2011) Using species co-occurrence net-
895 works to assess the impacts of climate change. *Ecography* 34:897–908.
- 896 41. Everett MG, Borgatti SP (2014) Networks containing negative ties. *Social Networks*
897 38(1):111–120.
- 898 42. Schoch D (2020) *signnet: An R package to analyze signed networks*.
- 899 43. Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecolog-
900 ical data. *Journal of Statistical Software* 22(7):1–19.
- 901 44. Oksanen J, et al. (2019) *vegan: Community Ecology Package*. R package version 2.5-6.
- 902 45. Borrett SR, Lau MK (2014) *enaR: An R package for Ecosystem Network Analysis*. *Methods
903 in Ecology and Evolution* 5(11):1206–1213.
- 904 46. Butts CT (2019) *sna: Tools for Social Network Analysis*. R package version 2.5.
- 905 47. Conner K, Hartl DL (2004) *A Primer of Ecological Genetics: a textbook*. (Sinauer Associates,
906 Inc., Sunderland, Massachusetts), 1st edition, p. All.
- 907 48. Dawkins R (year?) *The extended phenotype : the long reach of the gene*, p. 468.
- 908 49. Bdeir R, et al. (2017) Quantitative trait locus mapping of *Populus* bark features and stem
909 diameter. *BMC Plant Biology*.
- 910 50. Janzen DH (1980) Specificity of Seed-Attacking Beetles in a Costa Rican Deciduous Forest.
911 *The Journal of Ecology* 68(3):929.
- 912 51. Stinchcombe JR (year?) Can tolerance traits impose selection on herbivores?, Technical
913 report.
- 914 52. Strauss SY, Lau JA, Schoener TW, Tiffin P (2008) Evolution in ecological field experiments:
915 Implications for effect size.
- 916 53. Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG (2016) Genotypic variation in foun-
917 dation species generates network structure that may drive community dynamics and evolu-
918 tion. *Ecology*.
- 919 54. Borgatti SP, Everett MG (2006) A Graph-theoretic perspective on centrality. *Social Networks*
920 28:466–484.
- 921 55. Toju H, et al. (2017) Species-rich networks and eco-evolutionary synthesis at the metacom-
922 munity level.
- 923 56. Toju H, Yamamoto S, Tanabe AS, Hayakawa T, Ishii HS (2016) Network modules and hubs
924 in plant-root fungal biomes. *Journal of the Royal Society Interface*.
- 925 57. Toju H, Guimarães PR, Olesen JM, Thompson JN (2014) Assembly of complex plant-fungus
926 networks. *Nature Communications*.
- 927 58. Diaz-Castelazo C, et al. (2010) Changes of a mutualistic network over time: Reanalysis over
928 a 10-year period. *Ecology*.
- 929 59. Guimarães PR, Jordano P, Thompson JN (2011) Evolution and coevolution in mutualistic
930 networks. *Ecology letters* 14(9):877–85.
- 931 60. Rowntree JK, Shuker DM, Preziosi RF (2011) Forward from the crossroads of ecology and
932 evolution. *Philosophical transactions of the Royal Society of London. Series B, Biological
933 sciences* 366(1569):1322–8.
- 934 61. Zook AE, Eklof A, Jacob U, Allesina S (2010) Food webs: Ordering species according to
935 body size yields high degree of intervalty. *Journal of theoretical biology* 271(1):106–113.
- 936 62. Zytnyska SE, Khudr MS, Harris E, Preziosi RF (2012) No Title. *Oecologia* 170(2).
- 937 63. Evans DM, Pocock MJO, Memmott J (2013) The robustness of a network of ecological net-
938 works to habitat loss. *Ecology letters* 16:844–52.
- 939

940 **Supplementary Materials**

941 **Tables.**

	df	SS	R2	F	p-value
geno	9.0000	44078.1324	0.5442	3.5821	0.0537
Residual	27.0000	36915.4605	0.4558		
Total	36.0000	80993.5932	1.0000		

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

response	Df	statistic	H2	p-value	lichen species	mean	statistic	H2	p-value
Lichen Network Similarity	9.0000	3.5821	0.4130	0.0537	Positive				
Average Mutual Information		3.5235	0.3101	0.0254	In-Degree				
Centralization		4.0444	0.3305	0.0184	<i>X. galericulata</i>	0.2703	0	0	1
Centralization In-Degree		4.4812	0.3487	0.0142	<i>C. subdeflexa</i>	0.8919	2.1926	0.2158	0.0595
Centralization Out-Degree		3.8615	0.3193	0.0205	<i>L. spp.</i>	0.4324	0	0	1
Centralization In-Degree (positive)		3.9852	0.3309	0.0190	<i>C. holocarpa</i>	0.5946	3.6146	0.3241	0.024
Centralization In-Degree (negative)		0.3304	0.1057	0.2508	<i>X. montana</i>	0.0541	0	0	0.4543
Centralization Out-Degree (positive)		3.5585	0.3119	0.0248	<i>P. melanachra</i>	0.1351	0	0	1
Centralization Out-Degree (negative)		0.0862	0.0513	0.3446	<i>P. adscendens</i>	0			
Degree		3.5175	0.3156	0.0255	<i>P. undulata</i>	0.027	0	0	0.4543
Degree (positive)		3.6925	0.3242	0.0229	<i>R. sp.</i>	0.1351	2.049	0.2613	0.0656
Degree (negative)		0.0327	0.0318	0.3859	Out-Degree				
Percent Lichen Cover		0.0000	0.0000	1.0000	<i>X. galericulata</i>	0.027	0	0	0.4543
Lichen Species Diversity		0.0000	0.0000	0.4543	<i>C. subdeflexa</i>	0.6757	0	0	1
Lichen Species Richness		0.0000	0.0000	0.4543	<i>L. spp.</i>	0.5946	0.0061	0.0126	0.4247
Lichen Species Evenness		0.0000	0.0000	0.4543	<i>C. holocarpa</i>	0.7027	3.1318	0.2981	0.0327
Percent Rough Bark		4.8526	0.3221	0.0113	<i>X. montana</i>	0.0811	2.9228	0.3163	0.0375
pH		0.0000	0.0000	1.0000	<i>P. melanachra</i>	0.1351	0	0	1
Carbon-Nitrogen Ratio		0.0000	0.0000	1.0000	<i>P. adscendens</i>	0			
Condensed Tannins		3.0522	0.3205	0.0343	<i>P. undulata</i>	0.027	0	0	0.4543
BR-L Residuals		0.0000	0.0000	1.0000	<i>R. sp.</i>	0.2973	0.1505	0.0612	0.3119
BR-Cen Residuals		0.0000	0.0000	1.0000	Negative				

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

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. melanachra</i>	0			
<i>P. adscendens</i>	0			
<i>P. undulata</i>	0			
<i>R. sp.</i>	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. melanachra</i>	0			
<i>P. adscendens</i>	0			
<i>P. undulata</i>	0			
<i>R. sp.</i>	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

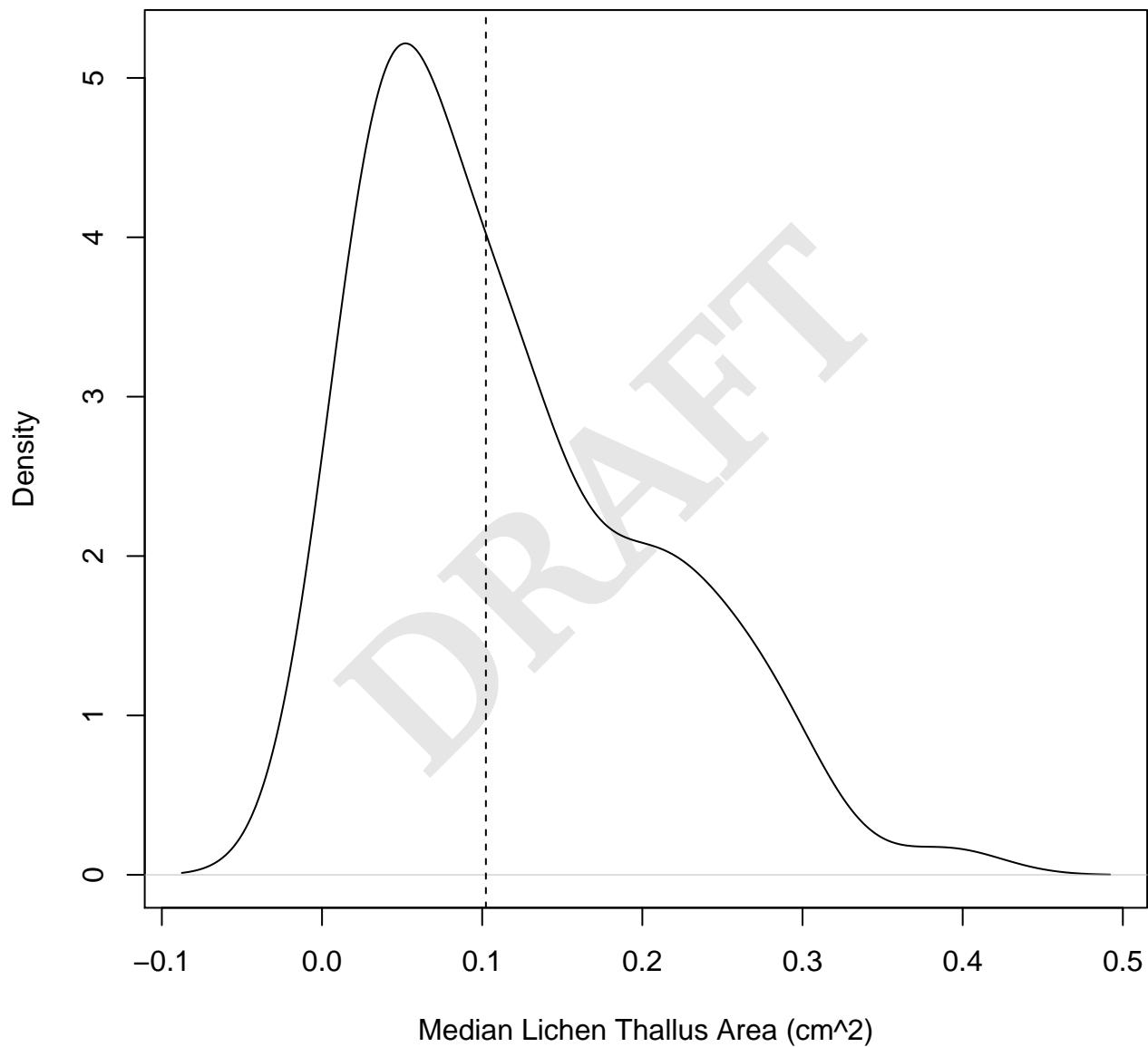


Fig. 1

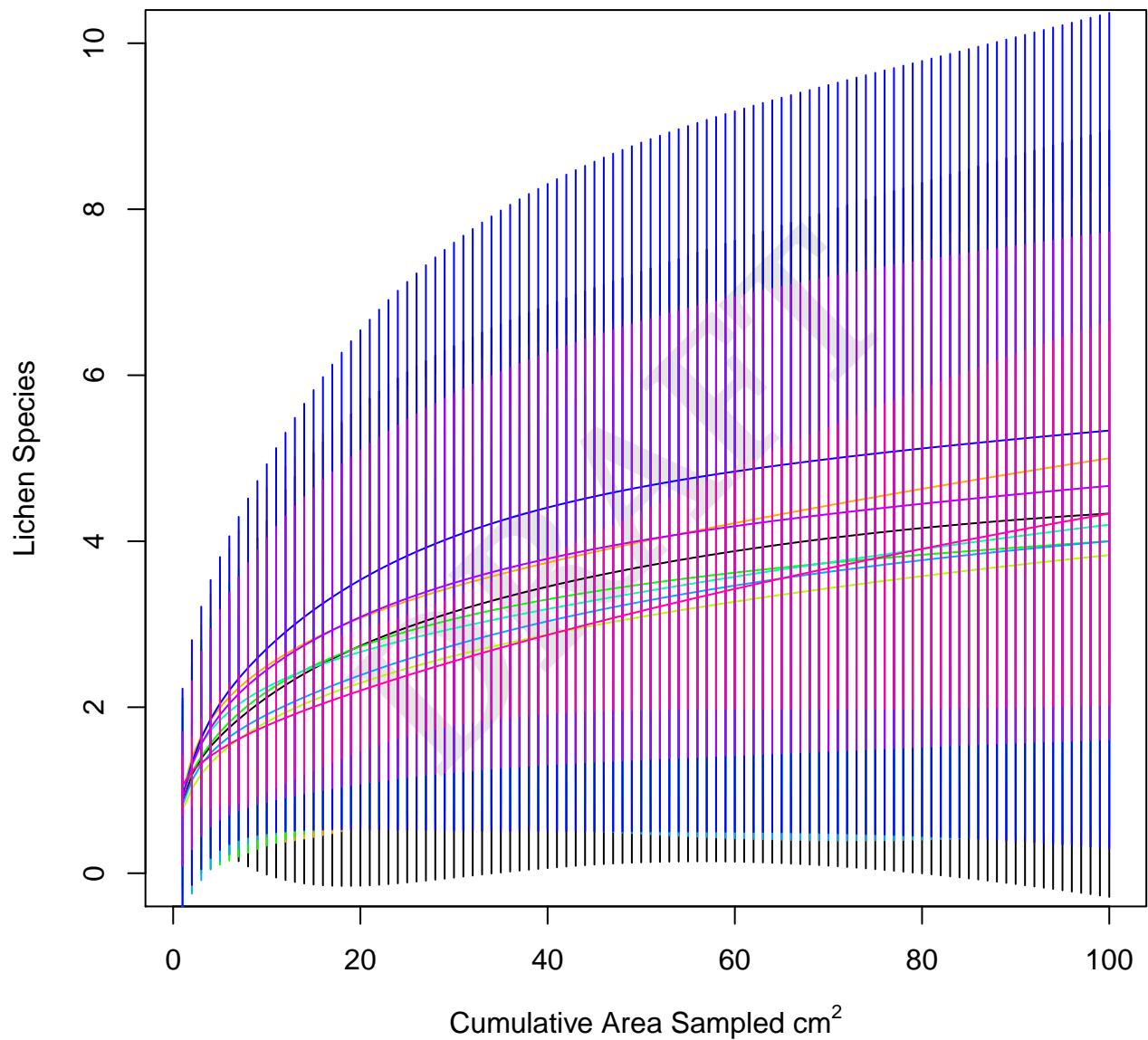


Fig. 2. Species-area curve by genotype.

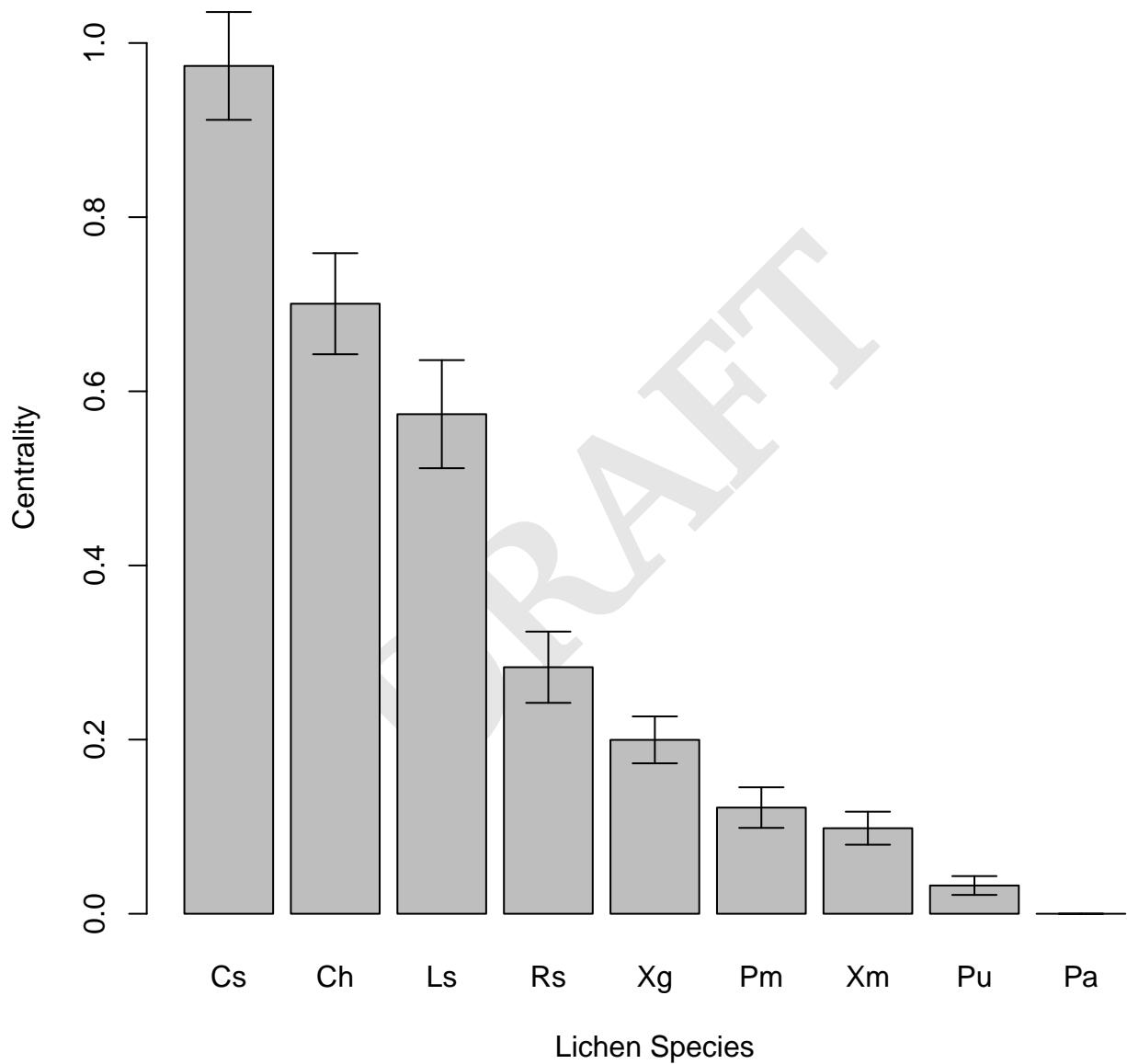


Fig. 3