

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

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1 Biological evolution occurs in the context of complex ecosystems of
2 interacting species in which natural selection defines the structure
3 of ecological networks. Fundamental to understanding evolutionary
4 processes is illuminating the genetic basis to ecological network
5 structure. Although previous work has demonstrated that genotypic
6 variation in foundation species contributes to interaction network
7 structure, we are not aware of a study that has quantified the genetic
8 contribution to network structure. To examine this we observed
9 epiphytic lichens associated with genotypes of (*Populus angustifolia*), a foundation species of riparian ecosystems. We constructed
10 signed, weighted, directed interaction networks for the lichens and
11 conducted genetic analyses of whole network similarity and network
12 degree and centralization. We found three primary results. First,
13 tree genotype significantly predicted lichen network similarity, i.e.
14 clonal replicates of the same genotype tended to support more similar
15 lichen networks, using multiple network metrics. Third, one of
16 the examined tree traits, bark roughness, was both predicted by tree
17 genotype and correlated with lichen network similarity, supporting a
18 mechanistic pathway from variation in a heritable tree trait and the
19 genetically based variation in lichen network structure. We conclude
20 that tree genotype can influence not only the relative abundances of
21 organisms but also the interaction network structure of associated
22 organisms. Given that variation in network structure can have consequences
23 for the dynamics of communities through altering the stability of the system and modulating or amplifying perturbations, these
24 results have important implications for the evolutionary dynamics of
25 ecosystems.

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

1 Evolution occurs in the context of complex ecological networks. Community genetics studies
2 have shown that genetic variation in foundation species, which have large effects on communities
3 and ecosystems by modulating and stabilizing local conditions (1), plays a significant role in defining distinct
4 communities of interacting organisms: such as, endophytes, pathogens, lichens, arthropods, and soil
5 microbes (2–4). Multiple studies have now demonstrated that genetic variation influences numerous
6 functional traits (e.g., phytochemical, phenological, morphological) produces a multivariate phenotype

(5) that contributes to variation in associated communities (6). The importance of genetic variation in structuring ecological systems was recently reviewed (7), 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

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 analyses. Here, we use a long-term common garden experiment to reveal the effect that genotypic variation can have on networks of lichens that occur on the bark of a foundation tree species. We found that lichen interaction network structure is genetically based and primarily driven by a tree trait, 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 interactions, given that interaction network structure has systems-level properties that could affect the response of these communities to selection.

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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support that selection, acting on this heritable variation, tends to occur among groups of species (8) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly (9) and species interactions (6, 10, 11), shaping the structure of ecological interaction networks (12–14).

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, (15) observed that individuals of a foundation species, such as cottonwoods, that are more genetically similar will tend to have similar 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 (16); and, community genetics studies have primarily focused on community composition in terms of the abundance of species (7). There are studies that have examined the effects of genetic variation on trophic chains, such as several in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (17–21) 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 (22, 23) and both found that genotypic diversity generates increased network modularity (i.e. compartmentalization). However, both of these studies were at the scale of forest stands, rather than 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.

What are the potential issues/concerns of not considering 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 (24, 25). The development of indirect genetic effects (IGE) and its community-level extension, inter-specific indirect genetic effects (IIGE) (26) NEED TO ADD WHITHAM2020 in evolutionary biology point to the importance of

studying the genetic basis of interaction network structure. IGE and IIGE theory develop a quantitative framework that demonstrates the importance of the indirect effect of genetic variation of one individual on other individuals of the same (IGE) or different species (IIGE). Evolutionary applications of network theory have demonstrated that, at least at the population scale, indirect effects of interactions can lead to network structures that can amplify or dampen the effects of selection (27). 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 greatly 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 (28) NEED TO ADD BASCOMPTE2014. Therefore, observing not only *if* but *how* networks of genetically similar individuals are more similar, is essential to fully understanding evolutionary dynamics in real ecosystems.

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 (29). 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 replicated individuals of known genetic identity and a naturally established stand of *Populus angustifolia*. We focused on a model community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (30, 31). In addition, the life-history characteristics of lichens, having highly localized, direct contact interactions and slow population turnover rates, facilitated the assessment of interactions among lichen species on individual trees. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (22, 23, 28, 32). If correct, we expect to find that network structure is genetically based in which different plant genotypes support different interaction networks and that these interactions net-

118 works can function as indicators of ecological dynamics
119 important for conserving biodiversity. Applying a
120 probability-theory based network modeling approach,
121 we constructed a set of interaction network models
122 for the lichens associated with individual trees. Using
123 these models, we then examined the genetic basis of
124 the structure of these ecological networks via several
125 network metrics that measures different aspects of
126 network structure at the scale of individual species
127 (i.e. nodes) or the entire network observed on each
128 tree. In particular, we focus the metric of centrality
129 for individual species and centralization for whole
130 networks, which measures how much a species is con-
131 nected in the network relative to other species. Based
132 on previous community genetics studies, particularly
133 the community similarity rule (15), we hypothesize
134 that trees will vary in some phenotypic traits and
135 those trees of the same genotype will tend to have
136 similar traits leading to similarities in lichen network
137 structure.

138 Materials and Methods

139

140 **Study System.** The study was conducted along the We-
141 ber River, UT (USA), which is a cottonwood (*Populus*
142 spp.) dominated riparian ecosystem. Although two native
143 species, *Populus angustifolia* (James) and *Populus fremontii*
144 (S. Watson), occur here and are known to hybridize,
145 only pure or advanced generation backcrosses of *P. angusti-
146 folia* were sampled. Bark lichens have been extensively
147 studied in this system and provide an ideal system in
148 which to observe and model lichen interaction networks,
149 as their sessile nature permits accurate identification of
150 individuals (33).

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

162 **Bark Lichen and Trait Observations.** On each tree, pres-
163 ence or absence of each lichen species was assessed in 50
164 total 1 cm² cells arrayed in a checkerboard pattern. Given
165 the small size and sessile nature of lichens, we were able to
166 rapidly assess lichen interactions by quantifying thalli in

167 close contact. Sampling was restricted to the northern as-
168 pect of the trunk to maximize the abundance of lichen and
169 control for the effect of trunk aspect. Two adjacent 100
170 cm² quadrats centered at 50 cm and 95 cm from ground
171 level were sampled (Fig 1 A and B). The observed lichen
172 community included (abbreviations are given for species
173 present in study): Xg = *Xanthomendoza galericulata*, Xm
174 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Cande-*
175 *lariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora*
176 *hagenii*, Pm = *Phyciella melanochra*, Pa = *Physcia adscen-*
177 *dens*, Pu = *Physcia undulata*. Several other species were
178 not obesrvd in the present study but are known to occur
179 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia*
180 *ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

181 The cell size and checkerboard sampling pattern was
182 chosen to isolate the individuals in each cell. In a previous
183 survey of lichen thallus size in this common garden, we
184 had observed a median thallus size of 0.12 ± 0.001 cm² (1
185 S.E.) (see Supporting Information). Based on the median
186 thallus size, we expected thalli observed in each cell to
187 generally be spatially independent of thalli present in
188 other cells but exposed to similar micro-environmental
189 conditions created by the bark and the location of the
190 sampling area on an individual tree. Therefore, we were
191 confident in treating the cell-wise observations in quadrats
192 as independent with respect to lichen-lichen interactions.

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

197 **Lichen Network Modeling and Analysis.** For each tree,
198 repeated observations of lichen were made in order to con-
199 struct replicated interaction networks for each genotype.
200 We conducted a modified sampling procedure originally
201 developed by (34) with the addition that we quantified
202 the presence of lichen in the 1 cm² cells on individual
203 trees of *P. angustifolia*. Unipartite networks were gener-
204 ated using the conditional probabilities of each species
205 pair, i.e. the probability of observing one species given
206 an observation of another species $P(S_i|S_j)$, based on
207 the method developed by (35). To calculate conditional
208 probabilities, we quantified the individual probabilities
209 of species occurrences $P(S_i)$ and the joint probability
210 of co-occurrences $P(S_i, S_j)$ using the frequencies of each
211 species and their co-occurrences. We were then able to
212 calculate the conditional probabilities of each species pair
213 as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, based on the axioms of probability.
214 This yielded a matrix that could possibly be asymmetric, i.e.
215 $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Another
216 important property of this matrix is that the diagonal
217 (S_{ii}) was equal to one for all species present and zero for
218 species that were not observed in any cell.

219 We then applied an analytical procedure to remove
220 non-significant links between species. This procedure
221 determines if the joint probability of a species pair

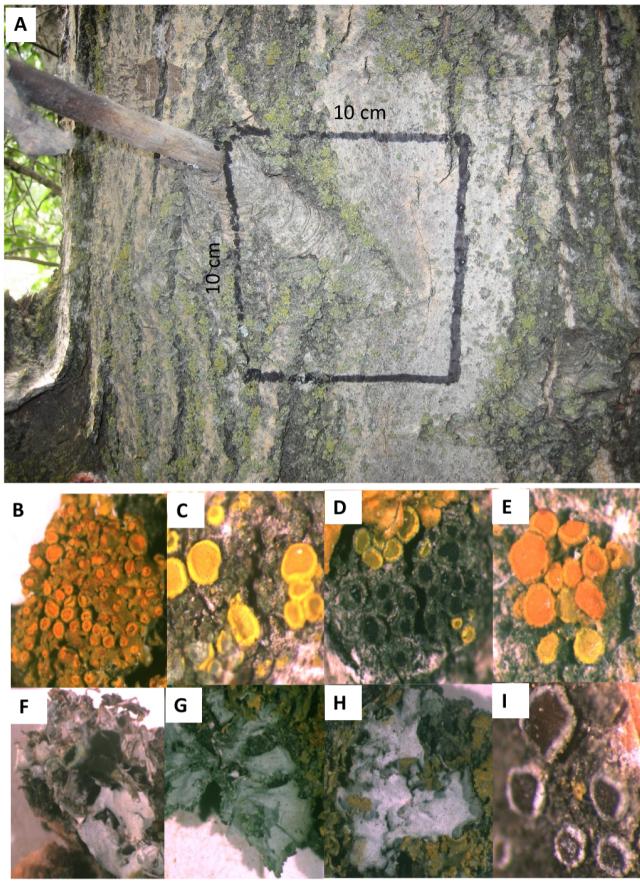


Fig. 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the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

(i.e. $P(S_i, S_j)$) is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability of $S_i S_j$ and its compliment (i.e. $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If the observed number of co-occurrence falls outside of the confidence interval, the joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual probabilities (i.e. $P(S_i)P(S_j)$), and the conditional probability reduces to the individual probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair falls outside the confidence interval, the probability that the observation of one species given the other is no different than simply observing that species alone.

This enables us to remove links from a given network by re-scaling the resulting conditional probabilities by subtracting the individual probabilities from the conditional probabilities (i.e. how different the conditional probability is from the independent probability), which makes any species with a non-significant conditional probability zero. The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as how one species impacts another with zero being no effect and values less than or greater than zero interpreted as negative and positive effects, respectively. Here, we will refer to this matrix (\mathbf{D}) as an interaction matrix with the properties that it can be asymmetric (i.e. 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 (i.e. species) in each network, we calculated both the degree Eq. (1) 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.

ADD EQUATIONS FOR METRICS

$$\sum x_i \quad [1]$$

- Node degree
- Node centrality
- Network degree
- Centralization
- In vs out
- Pos vs neg

To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (36). We used the `signnet` package version ????, which is available at ???.

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



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 (35), 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.

with Restricted Maximum Likelihood (REML). We used a combination of Least Squares Regression, Analysis of Variance (ANOVA) and correlation tests to quantify and test for the relationship among other variables. Bark roughness, lichen cover and species richness were square-root transformed to meet the assumptions of homogeneity of variance and normality for these tests.

For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the \mathbf{D} interaction matrices among all pairs of trees.

For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (37) to

produce dimensionally reduced ordinations of these multi-variate responses and fitted vectors for continuous predictor variables to the ordinated values (38). Using random initial configurations with a maximum of 500 iterations and a change in stress threshold of less than 10^{-12} . Final configurations has the lowest stress with at most a stress level of 0.10.

For each network, we also calculated metrics that measure different structural aspects. Although there are many other metrics, for the sake of simplicity we focus on a subset that represent several interesting features of network structure (see (16)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (22, 39). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (40). In a network with a

324 low level of centralization species have similar amount of
 325 interaction in the network, while a network with a high
 326 level of centralization tends to have one or small number
 327 of species that interact with other species. We used a
 328 related function to calculate the centrality of each species
 329 (i.e. node level centrality) in each network as well.

330 For all tests where genotype was used as a predictor,
 331 we quantified the heritability of the response variable. Be-
 332 cause the trees in the garden were clonal replicates of each
 333 genotype, we calculated broad-sense heritability, which
 334 is the genotypic variance divided by the total phenotypic
 335 variance (41). This can be interpreted as a measure of
 336 the phenotypic variance due to genotypic variation. We
 337 also apply this to the community genetics context as the
 338 variance in *extended* phenotypic variance due to genotypic
 339 variation (42). For the multivariate analyses, where we
 340 employ PERMANOVA, we followed the methods of (26)
 341 to adjust the degrees of freedom for unbalanced genotype
 342 replicates.

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

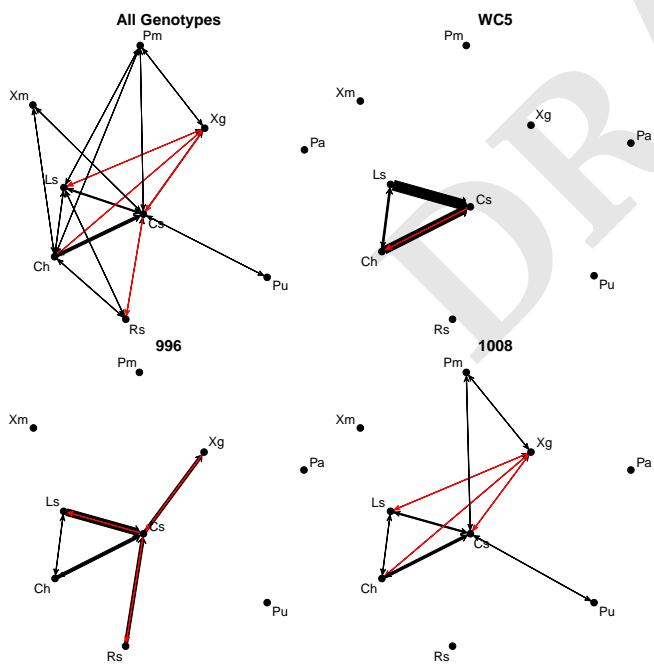


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

349 Tree genotype influenced lichen network structure
 350 and multiple lichen network metrics were herita-
 351 ble. Tree genotype significantly predicted the struc-
 352 tural similarity of lichen networks (PERMANOVA:
 353 Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$)
 354 (Fig. 4). Overall network level metrics responded
 355 significantly to tree genotype (Table 1), including net-
 356 work degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} =$
 357 0.0255) and centralization including both in-coming
 358 and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} =$
 359 0.0184) or when separated into in-coming
 360 only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} =$
 361 0.0190) or out-going only ($RLRT = 3.8615$, $H^2 =$
 362 0.3193, $p\text{-value} = 0.0205$). Metrics including only
 363 positive links also showed a significant effect of tree
 364 genotype, including positive degree ($RLRT = 3.6925$,
 365 $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
 366 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} =$
 367 0.0142). Metrics calculated with negative
 368 links were not significant, including degree (negative)
 369 ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$)
 370 and both in-coming (negative) ($RLRT = 0.3304$, $H^2 =$
 371 0.1057, $p\text{-value} = 0.2508$) and out-going centraliza-
 372 tion (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$,
 373 $p\text{-value} = 0.3446$).

response	statistic	H2	p-value
Lichen Network Similarity	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.

375 The genetic response of network centralization was
 376 driven by variation in *Caloplaca holocarpa*. Central-
 377 ity varied significantly among species ($F_{8,324} = 7.99$,
 378 $R^2 = 0.16$, $p\text{-value} < 0.0001$). *Caloplaca holocarpa*
 379 centrality was the main species to exhibit a signifi-
 380 cant response to tree genotype in terms of positive
 381 centralization for both the in-coming ($RLRT = 3.61$, $H^2 =$
 382 0.32, $p\text{-value} = 0.0240$) and out-going ($RLRT =$
 383 3.13, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives, but
 384 not for either negative centrality metrics in-coming

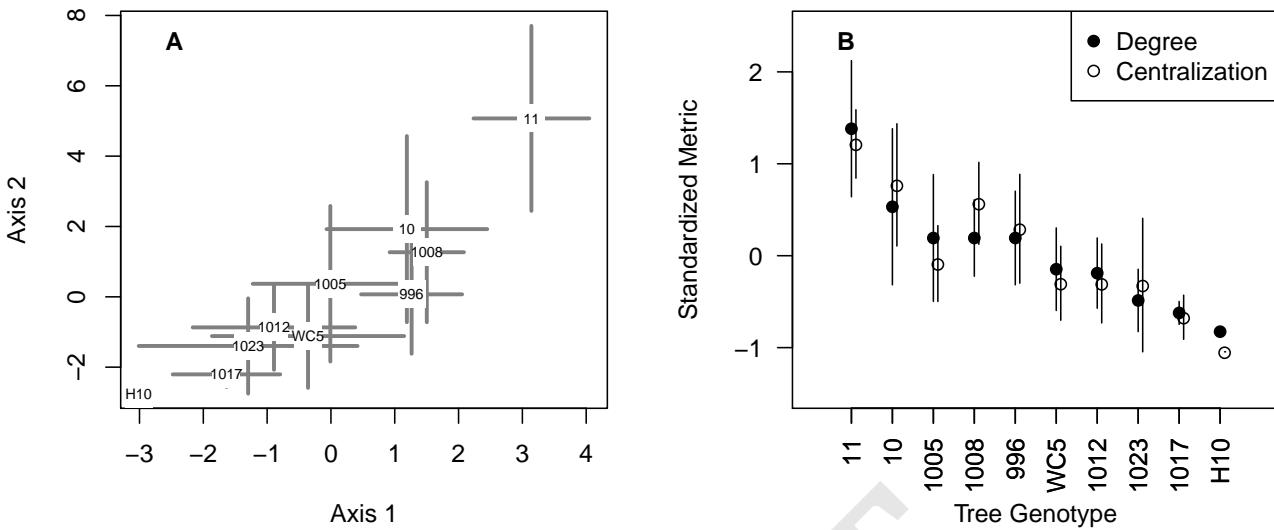


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen networks ($\pm 1 \text{ S.E.}$). Genotype centroids that are closer together tend to have more similar lichen network structure. B. Plot showing the standardized ($\frac{x - \bar{x}}{\sigma}$) means ($\pm 1 \text{ S.E.}$) for the two of the genetically based lichen network metrics: overall degree (i.e. total number of links) and centralization, which is a measure of the dominance of one species in the network.

($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of the other species' centralities showed a genotypic response (Supplementary Table 3) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

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 were correlated with network similarity (Table 2); therefore, we focused our analysis on 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 -

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)
BR	1.0000	20850.0933	0.2574	12.9234	0.0101
CT	1.0000	5993.6629	0.0740	3.7150	0.0813
pH	1.0000	1273.1905	0.0157	0.7892	0.3712
CN	1.0000	3896.1754	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

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

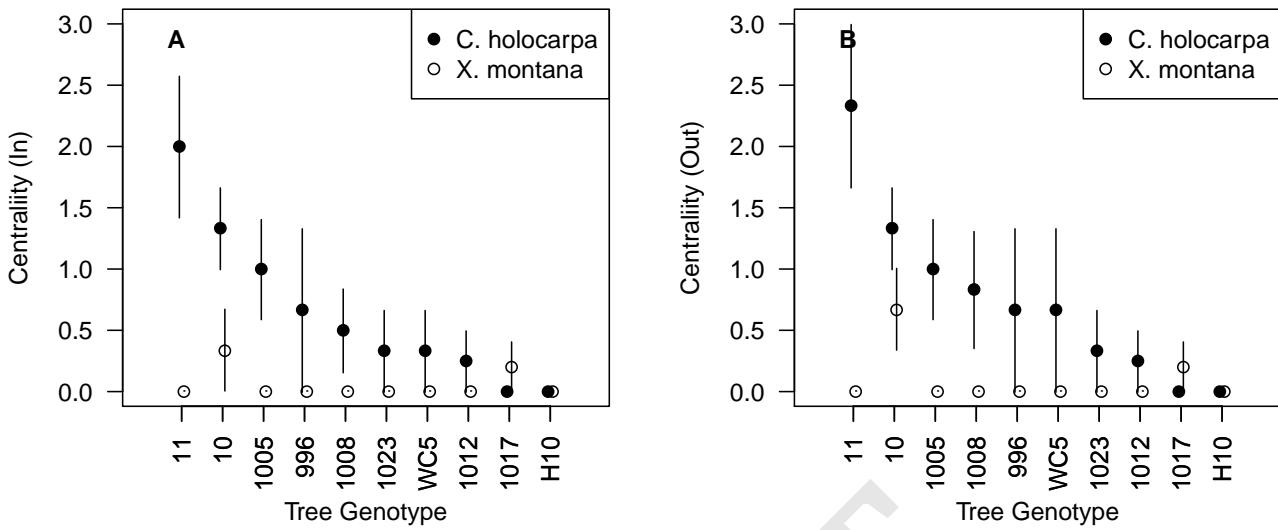


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

428 Discussion

429 We found that tree genotype influenced lichen net-
430 work structure in the experimental cottonwood forest.
431 Network similarity and metrics of network structure
432 tended to be more similar on trees of the same geno-
433 type. Generally, this genetic effect was manifested in
434 positive interactions and largely driven by *C. holocar-
435 pa*. The genetically based trait, bark roughness,
436 was the only trait observed to effect network vari-
437 ation, largely via shifts in positive in-coming and
438 out-going interactions. Bark roughness has been
439 demonstrated previously to be under strong genetic
440 control (43), and bark roughness has also previously
441 been shown to be an important tree trait influencing
442 bark lichens (34); however this is the first demon-
443 stration of a link from genes to lichen network structure.
444 As such these results have important implications for
445 the potential influence of genetically based variation
446 in ecosystems with networks of interacting species.

447 **Heritability of Interaction Network Structure.** Re-
448 visit the community similarity rule.

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

451 Elaborate on how many species might be supported
452 by each lichen thallus including the symbionts and
453 other species.

454 *Elaborate on the importance of identifying the* 454
species/node level patterns in network structure re- 455
sponse to genotype. 456

457 *What is the relationship between tree growth, bark* 457
roughness and disruption of the lichen community? 458
Tree grow and the bark expands over time, causing 459
furrows. 460

461 *Does bark roughness increase habitat and decrease* 461
interactions? 462

463 There are important functional ramifications of ge- 463
genetically based variation in network structure. First, 464
even if the composition of the communities is the 465
same among individuals and genotypes, interactions 466
may not be. We didn't observe compositional dif- 467
ferences using the same data from which the lichen 468
networks were derived. If we only had our compo- 469
sition dataset from this study, we would have con- 470
cluded no response of the lichen community to tree 471
genotype, even though the underlying interactions 472
among lichen species does vary among genotypes. 473
Community composition of lichen has previously 474
been observed to be different among tree genotype 475
in the same experimental garden, though this was 476
observed with a larger sampling of total area and 477
quadrats per tree. Regardless, this could result in a 478
situation in which abundance based investigations 479
of community-level genetic effects may miss impor- 480

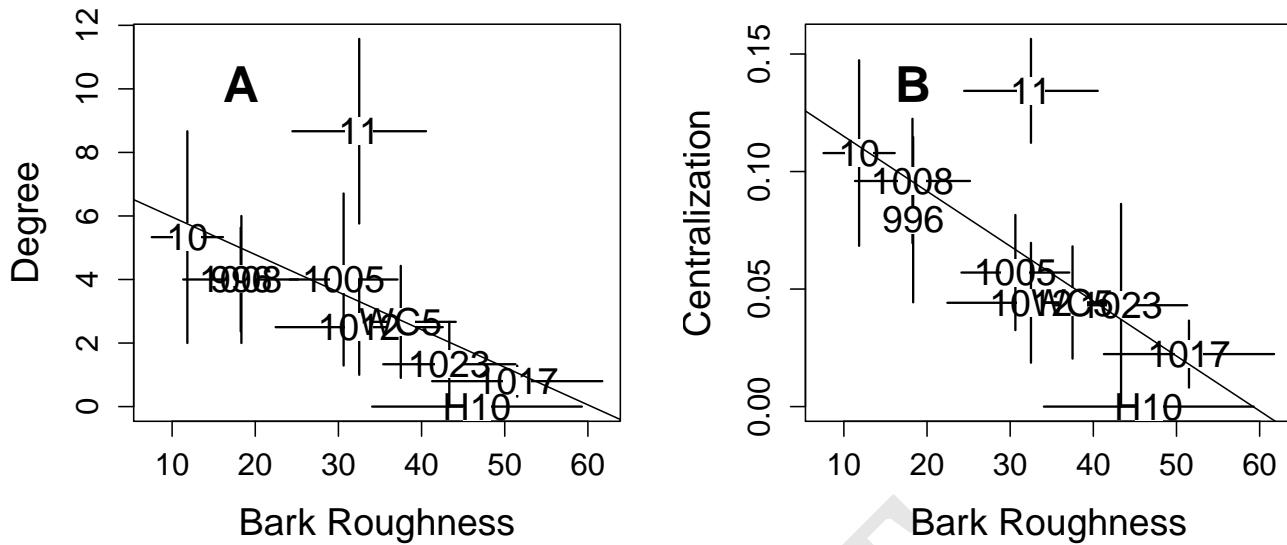


Fig. 6. Bivariate plots of the relationship between bark roughness and three network metrics: A) degree and B) centralization. Each plot displays the genotype mean \pm 1 S.E. for both variables and a least-squares regression calculated using the genotype means.

tant 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, however, this is not needed for evolutionary dynamics to play out.

Second, following on the previous point, genetic diversity could be influencing the stability of communities through the effects on the structure of interactions. 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 (Newman). 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 (Leiberman). 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.

There are several important points to consider with regard to the generalization of the observed genetically based response of the lichen networks. Body size and sessile nature of lichen important to observing genotype responses. As bark lichen individuals do not move, but grow in a largely two dimensional plane, these communities and their interactions occur in the highly localized context of the tree's bark surface. Lichen individuals are many orders of magnitude smaller than the tree individual and the life-span of a tree is many times that of a lichen. For these reasons, any genetic effects on these communities is not dampened by the movement of individuals and the mixing of the effect of different tree genotypes on the lichen community, as might occur for more mobile species (e.g. insects and birds). We only looked at lichen, other species whose distribution, abundance or interactions respond to tree genotype, such as epiphytic plants (e.g. moss and

535 liverworts), algae or insects, could be playing a role.
536 Other traits could also be playing a role, such as
537 traits that are correlated with bark roughness, such
538 as micro-aspect, albedo, moisture, etc.

539 Bark roughness could possibly be serving the role
540 that other lichen play in facilitating the success of
541 new propagule attachment and the growth of estab-
542 lishing thalli. This is supported by the patterns over-
543 all being positive, including *C. holocarpa* centrality.
544 We did not observe specific microscopic dynamics,
545 such as photobionts, mycobionts, endolichenic fungi
546 and bacteria, but variation in these underlying in-
547 teractions could also be playing a role. Although we
548 can not rule out the possibility that other unmea-
549 sured tree traits or organisms correlated with bark
550 roughness are underlying the observed patterns in
551 bark lichen network structure, substantial research
552 supports the importance of genetically based tree
553 traits for communities and ecosystems (7), and in
554 particular bark roughness for bark lichen communi-
555 ties (33, 34, 43).

556 In the present study, lichen cover, lichen species
557 richness and composition were not responsive to tree
558 genotype, unlike what was found in (34). This is
559 likely, at least in part, the result of differences in
560 sampling method and the choice of genotypes sam-
561 pled leading to overall higher abundances of observed
562 lichens. In the current study mean % total lichen
563 cover among genotypes ranges from 60-93% cover;
564 whereas the range reported in (34) is 0.86-18.73%.
565 The previous study used a visual estimation method,
566 unlike the current study, which observed lichen at
567 the scale of 1 cm² cells, which could over-estimate
568 cover depending on the frequency at which actual
569 thallus size was less than 1 cm². The previous study
570 used samples from both the northern and southern
571 aspects of each tree; whereas, the current study only
572 observed lichen on the northern aspect. Also, our
573 current results are likely different from the previous
574 study because the current study selected genotypes
575 that tended to have bark lichen, with the interest
576 of focusing on generating networks for comparison.
577 These differences do not negate the findings of either
578 study but is important to explain the differences
579 in the findings, particularly in the community-level
580 effects of tree genotype.

581 **Implications for Interspecific Indirect Genetic Ef-
582 ffects (IIGEs).** Initially, evolution in a community con-
583 text was focused on examples of highly co-evolved

584 pairs of species (e.g. Darwin's famous prediction
585 of the Sphinx Moth and Christmas Orchid) (8).
586 However, studies of diffuse co-evolution (*sensu* (44))
587 (45, 46), geographic mosaics of co-evolution (32) and
588 community genetics (10) have provided an in-road
589 for ecological network approaches (20, 23, 47) to illu-
590 minate a more complex perspective of the interface
591 between ecological and evolutionary dynamics.

592 Interspecific indirect genetic effects (IIGE) theory
593 as provided a quantitative framework within which
594 to approach evolutionary theory at higher levels of
595 biological organization: from populations to com-
596 munities and ecosystems. To date, this theory has
597 focused on modeling the strong effects of foundation
598 species (26, 48), but it has not yet integrated devel-
599 opments in the ecological or evolutionary network
600 theory literature. This is to say that it has not devel-
601 oped a way to examine complex interactions among
602 species; however, previous studies have demonstrated
603 this network context is likely to be important, as
604 altering the structure of interaction networks pro-
605 vides a means for genetic effects to be dampened or
606 magnified within the system of interacting species.
607 For example, (23) showed that the genetics based
608 interactions of aphid resistant and aphid suscep-
609 tible trees resulted in different interaction networks of
610 their associated arthropod communities composed
611 of 139 species. At the scale of ecosystems, trophic
612 networks or food webs direct and control the rates
613 of energy and nutrient flux (49). Furthermore, in a
614 predator-prey-plant study, Smith (19), showed that
615 the interactions among species across trophic levels
616 depended on plant genotype. Also, work by (50-52)
617 observed consistent patterns of centralized interac-
618 tions of species modules focused around hubs of
619 plant-fungal interactions. In other words, a small
620 number of plant and fungal symbionts tended to
621 have disproportionate numbers of interactions with
622 other species and likely are the drivers in determining
623 community assembly, structure and dynamics.

624 The results of the current study provides clear em-
625 perical evidence that networks points to the need to
626 expand IIGEs encompass the structure of interaction
627 networks. Although such a synthesis necessitates
628 a much greater effort than can be afforded in this
629 paper, it is possible to point to several productive
630 pathways forward. In terms of interaction networks,
631 foundation species are relatively central within the
632 system of interactions, that is their direct and/or

633 indirect effects are greater than other species. So,
634 when the more centralized (foundation) species have
635 genetically based interactions, genetic effects will
636 tend to be magnified in the community. Here, we
637 found that even though more abundant or more cen-
638 tralized (i.e. “important”) species were present in
639 the community, their effects were not the main com-
640 ponent responding to genetic effects. Considering
641 the impact of network structure would be a produc-
642 tive path forward for the theoretical development
643 and application of the IIGE concept.

644 With regard to the evolutionary implications of
645 network structure, ecological network studies have
646 focused on asymmetry and the quantification of
647 its structure in communities, with qualitative dis-
648 cussion of the impacts on evolutionary dynamics
649 (28, 32, 53, 54). More specific predictions, with a
650 quantitative framework, can be found in applications
651 of evolutionary game theory, and although developed
652 at the population scale, such theory can apply to
653 communities. One seemingly useful direction from
654 evolutionary network developments from game the-
655 ory is the classification of networks into two general
656 categories, rooted and cyclic, in which rooted net-
657 works have interactions in which evolutionary effects
658 emanate from one or multiple origins but these effects
659 do not have connections back to the origins, whereas
660 cyclic networks contain feedbacks to one or more ori-
661 gins. Although it did not explicitly define it in this
662 context, the previous work (16), developed that the
663 structure of the network in the context of a founda-
664 tion species, such as cottonwoods in which there are
665 demonstrable community level genetic effects, is that
666 of a multiple origin network. This builds on many
667 previous studies demonstrating that the community
668 level effects vary among multiple genotypes. It is not
669 clear what potential there is for feedbacks there are
670 to the origins (e.g. the cottonwood genotypes) from
671 the community, and as such it cannot be determined
672 whether these networks are cyclic or rooted. In other
673 systems, lignicolous lichens can have demonstrable
674 positive effects on the availability of nutrients for the
675 trees that they are associated with, but this has not
676 been measured in the current system. Illucidating
677 the absence and/or presence and quantifying such
678 feedbacks would allow for the determination of the
679 cyclic nature and potential evolutionary dynamics of
680 this system. The presence of feedbacks would provide
681 the potential for non-linear dynamics in which evo-

682 lutionary effects are dampened or amplified by the
683 structure of the network. For example, a star struc-
684 ture in which there is a primary or core set of central
685 species with feedbacks from the radiating species has
686 been demonstrated to be a structure that amplifies
687 evolutionary dynamics (27). If such feedbacks do
688 not exist, and these sub-networks of the lichen and
689 tree genotypes are likely to be multi-rooted networks.
690 Such a structure is theorized to generally promote
691 diversification as variation arising from the shifting
692 distribution of the “roots”, i.e. genotypes; however,
693 loss of genotype/root diversity could lead to fixation
694 of a single genotype in the population and a decrease
695 in community-wide diversity.

696 **Conclusion.** Although our study was conducted with
697 a community of lichens, these results should be gen-
698 eralized to other groups of diverse organisms around
699 the world that also exhibit significant genetic signals
700 at the community level (48, 55). In the face of the
701 high degree of complexity and potential context de-
702 pendency of ecological processes, the current study
703 points to the utility of considering the spatial and
704 temporal scales of interactions, as discussed to some
705 in previous studies (15, 56, 57). In the present study,
706 we found that community assembly processes, such
707 as environmental filtering and species interactions,
708 are genetically based. This is likely due, in part,
709 to the large difference in the differences in size and
710 longevity of the lichen and cottonwood individuals
711 with the trees determining the environment in which
712 the lichen occur. We suggest that future work would
713 be aided by determining these modules within the
714 biotic community that include species with similar
715 differences in body-size and time-scales. As heritable
716 variation is the raw material for natural selection
717 to act upon, a genetic basis for interaction network
718 structure indicates evolutionary dynamics should be
719 considered at the community level and that con-
720 serving genetic variation is important to consider in
721 efforts to restore or preserve complex species inter-
722 actions and their associated ecosystem functions (58).
723 With such findings, it appears that we are closer to
724 understanding the evolutionary drivers of Darwin’s
725 entangled bank and the interconnectedness of species
726 in complex communities.

727 Future work should consider the potential influ-
728 ence on evolutionary dynamics of the associated com-
729 munities. The network of interactions of species that
730 are strongly influenced by a foundation species, could

amplify the effects of genotype, this serves as a means for genetic effects to increase rather than diffuse through an ecosystem either through space or over time, as has been proposed in the construction of the genetic diffusion hypothesis. Altered abundances can lead to differences in interactions. Genotype effects on abundances of individual abundances may cancel out. Specifically for asexually reproducing species, such as many lichen are, shifting interaction frequencies could lead to evolutionary outcomes, given the potential to take-up symbionts and genetic material from thalli that they come into contact with. Altering interaction frequencies could result in differences in rates of the exchange of genetic materials among lichen that could then be passed on to vegetative and possibly sexually produced reproductive propagules. The larger scale (stand or region) effects of these "evolutionary units" on each tree would depend on the connectivity and rate of movement of propagules among trees per the geographic mosaic of co-evolution hypothesis (3, 32).

Add evolutionary unit to the larger narrative. That is mainly that identifying how evolution might be acting on multiple species is useful for conservation and management.

Discuss the impacts of P. betae removal on network structure per Lau 2016 and Keith 2017. Also, what about Barbour 2016.

Other studies that should be discussed:

- Multiple plant traits shape the genetic basis of herbivore community assembly. Synthesis: Taken together, our results support that the genetic basis of herbivore community assembly occurs through a suite of plant traits for different herbivore species and feeding guilds (Barbour 2015). Also discuss Lamit 2015 and Holeski's multivarite phenotype paper.
- Linking plant genes to insect communities: Identifying the genetic bases of plant traits and community composition. Synthesis: These findings support the concept that particular plant traits are the mechanistic link between plant genes and the composition of associated insect communities (Barker 2019).

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Supplementary Materials

Tables.

903

904

	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	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537	
Average Mutual Information	3.5235	0.3101	0.0254	
Centralization	4.0444	0.3305	0.0184	
Centralization In-Degree	4.4812	0.3487	0.0142	
Centralization Out-Degree	3.8615	0.3193	0.0205	
Centralization In-Degree (positive)	3.9852	0.3309	0.0190	
Centralization In-Degree (negative)	0.3304	0.1057	0.2508	
Centralization Out-Degree (positive)	3.5585	0.3119	0.0248	
Centralization Out-Degree (negative)	0.0862	0.0513	0.3446	
Degree	3.5175	0.3156	0.0255	
Degree (positive)	3.6925	0.3242	0.0229	
Degree (negative)	0.0327	0.0318	0.3859	
Percent Lichen Cover	0.0000	0.0000	1.0000	
Lichen Species Diversity	0.0000	0.0000	0.4543	
Lichen Species Richness	0.0000	0.0000	0.4543	
Lichen Species Evenness	0.0000	0.0000	0.4543	
Percent Rough Bark	4.8526	0.3221	0.0113	
pH	0.0000	0.0000	1.0000	
Carbon-Nitrogen Ratio	0.0000	0.0000	1.0000	
Condensed Tannins	3.0522	0.3205	0.0343	
BR-L Residuals	0.0000	0.0000	1.0000	
BR-Cen Residuals	0.0000	0.0000	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	0.4543
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	0.4246
C. holocarpa	0.7027	3.1318	0.2981	0.0327
X. montana	0.0811	2.9228	0.3163	0.0375
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.2973	0.1505	0.0612	0.3119
Negative				
In-Degree				
X. galericulata	0			
C. subdeflexa	0.1892	0	0	0.4543
L. spp.	0.1892	0.0015	0.0057	0.4398
C. holocarpa	0.1351	0	0	1
X. montana	0.027	0.0377	0.0394	0.3807
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0.1622	0	0	1
Out-Degree				
X. galericulata	0.2432	0	0	1
C. subdeflexa	0.4054	0	0	0.4543
L. spp.	0.027	0	0	0.4543
C. holocarpa	0.027	0	0	0.4543
X. montana	0			
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0			

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

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

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

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

Figures.

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

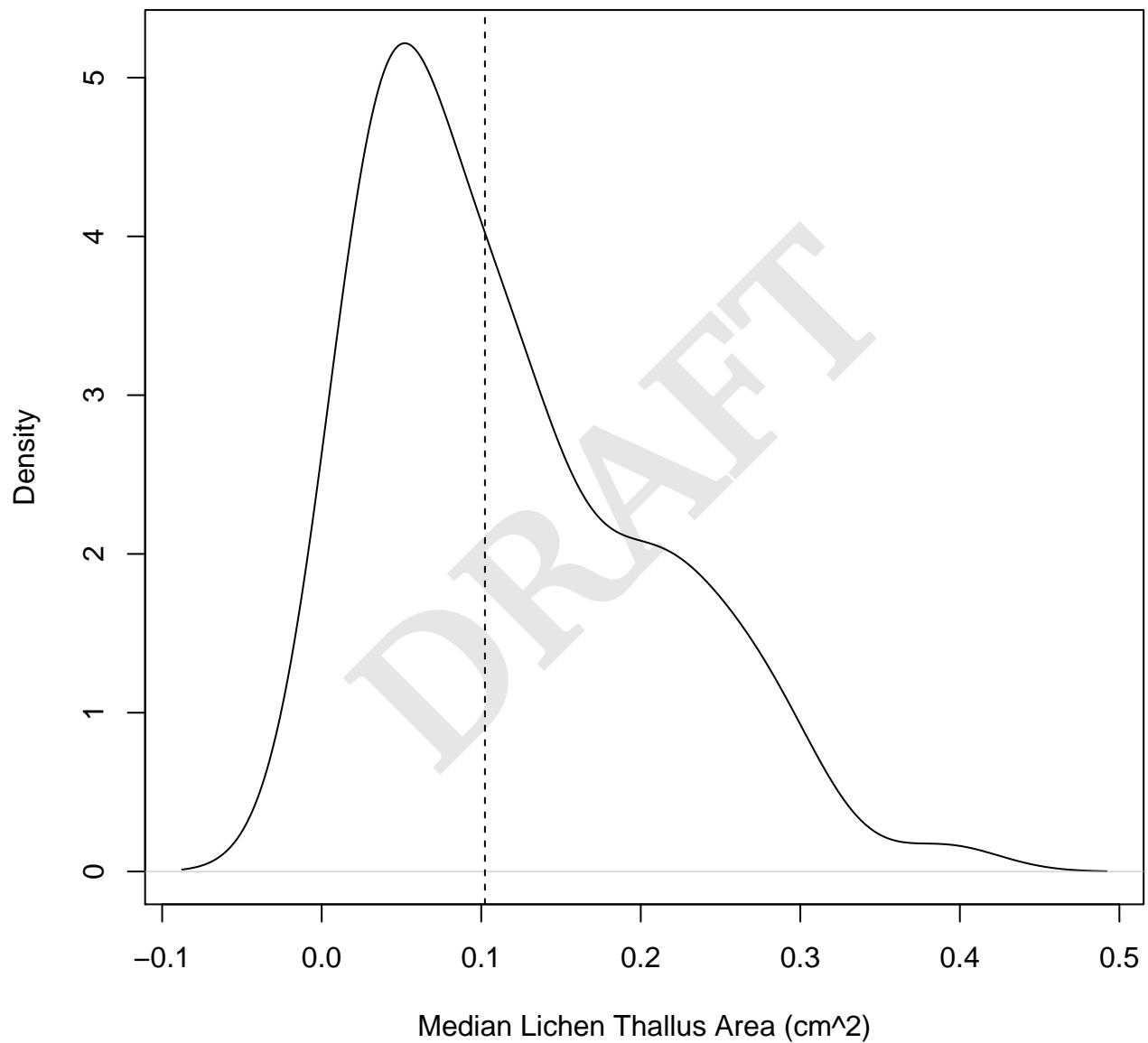


Fig. 1

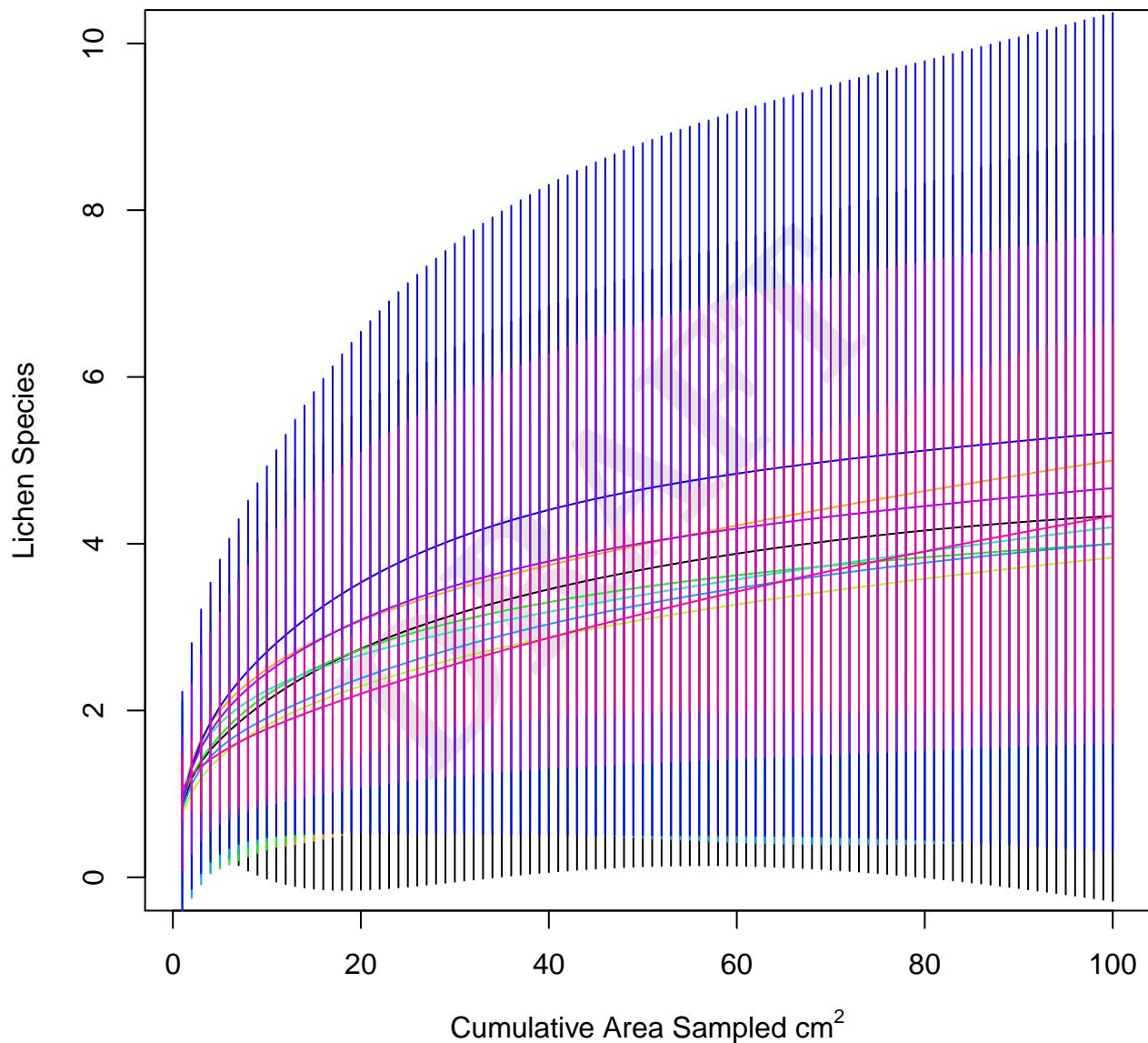


Fig. 2. Species area curve by genotype.

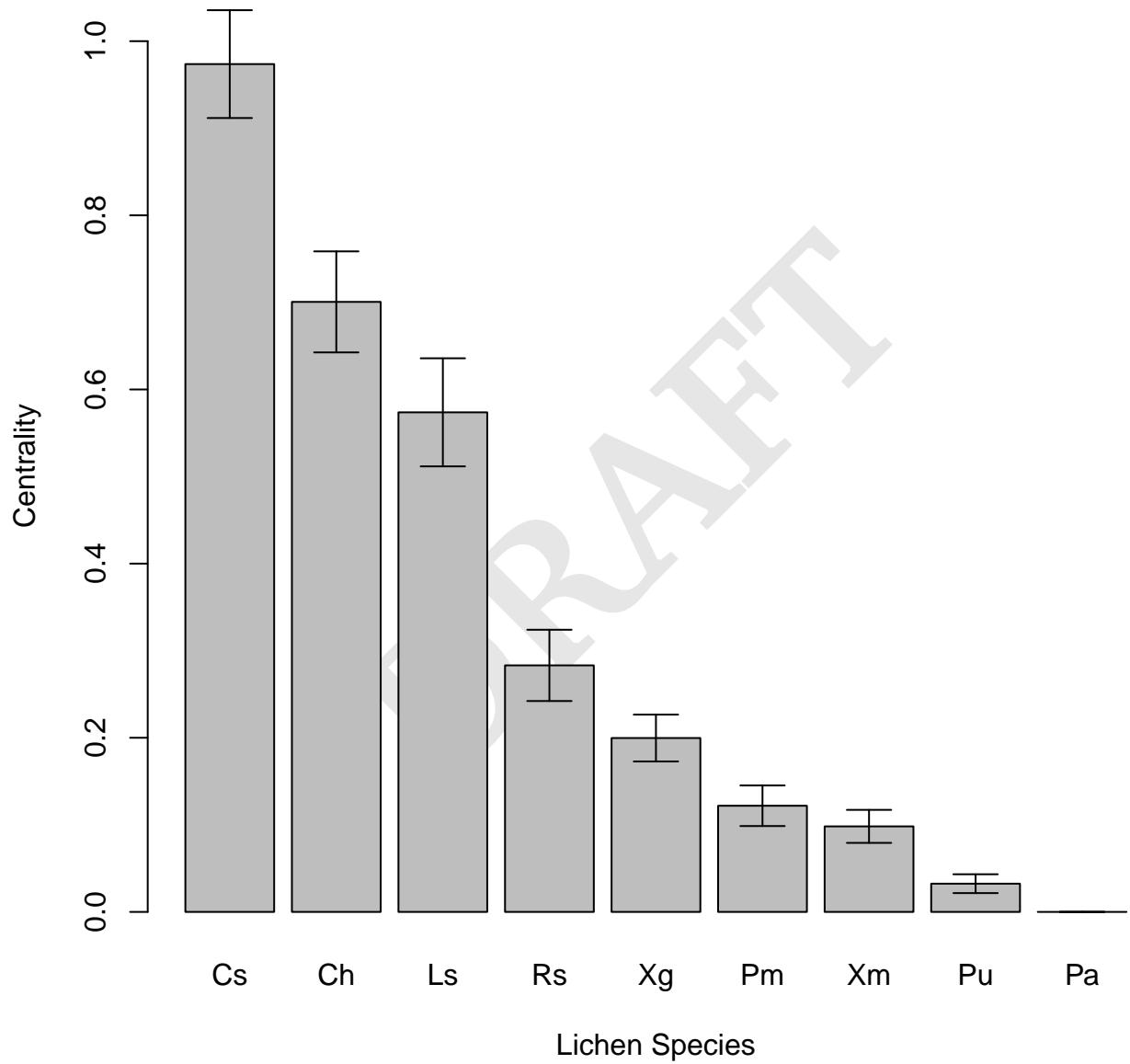


Fig. 3