

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

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This manuscript was compiled on September 23, 2020

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**  
10 **foundation species of riparian ecosystems. We constructed**  
11 **signed, weighted, directed interaction networks for the lichens and**  
12 **conducted genetic analyses of whole network similarity and network**  
13 **degree and centralization. We found three primary results. First,**  
14 **tree genotype significantly predicted lichen network similarity, i.e.**  
15 **clonal replicates of the same genotype tended to support more similar**  
16 **lichen networks, using multiple network metrics. Third, one of**  
17 **the examined tree traits, bark roughness, was both predicted by tree**  
18 **genotype and correlated with lichen network similarity, supporting a**  
19 **mechanistic pathway from variation in a heritable tree trait and the**  
20 **genetically based variation in lichen network structure. We conclude**  
21 **that tree genotype can influence not only the relative abundances of**  
22 **organisms but also the interaction network structure of associated**  
23 **organisms. Given that variation in network structure can have conse-**  
24 **quences for the dynamics of communities through altering the stability**  
25 **of the system and modulating or amplifying perturbations, these**  
26 **results have important implications for the evolutionary dynamics of**  
27 **ecosystems.**

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

1 **E**volution occurs in the context of complex eco-  
2 logical networks. Community genetics studies  
3 have shown that genetic variation in foundation  
4 species, which have large effects on communities  
5 and ecosystems by modulating and stabilizing local  
6 conditions (1), plays a significant role in defining dis-  
7 tinct communities of interacting organisms: such as,  
8 endophytes, pathogens, lichens, arthropods, and soil  
9 microbes (2–4). Multiple studies have now demon-  
10 strated that genetic variation influences numerous  
11 functional traits (e.g., phytochemical, phenological,  
12 morphological) produces a multivariate phenotype  
13 (5) that contributes to variation in associated com-

munities (6). The importance of genetic variation in  
14 structuring ecological systems was recently reviewed  
15 (7), and not only were many instances of strong ge-  
16 netic effects found in many ecosystems but the effect  
17 of intraspecific variation was at times greater than  
18 *inter-specific* variation. There is now evidence to  
19 support that selection, acting on this heritable vari-  
20

## Significance Statement

Evolution occurs in the context of ecosystems com-  
prised of complex ecological networks. Research at  
the interface of ecology and evolution has primarily  
focused on pairwise interactions among species and  
have rarely included a genetic component to anal-  
yses. Here, we use a long-term common garden  
experiment to reveal the effect that genotypic varia-  
tion 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 rough-  
ness. These findings demonstrate the importance  
of genetic variation and evolutionary dynamics in  
shaping ecological networks as evolved traits. In  
particular, this study points to the importance of as-  
sessing the effect of foundation species genetics on  
the structure of 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.

The authors have no conflicts of interest.

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21 ation, tends to occur among groups of species (8)  
22 and that genetic variation and phylogenetic related-  
23 ness contribute to variation in community assembly  
24 (9) and species interactions (6, 10, 11), shaping the  
25 structure of ecological interaction networks (12–14).

## 26 Indirect genetic effects and inter-specific in- 27 direct genetic effects

28 The genetic similarity rule provides a useful frame-  
29 work for approaching the nexus of evolutionary and  
30 community dynamics in the context of complex inter-  
31 action networks. In a study combining experimental  
32 common gardens and landscape-scale observations  
33 of interactions between *Populus* spp. (cottonwoods)  
34 and arthropods, (15) observed that individuals of a  
35 foundation species, such as cottonwoods, that are  
36 more genetically similar will tend to have similar  
37 traits and thus tend to have similar interactions with  
38 other species than individuals that are less similar.  
39 However, studies in the network ecology literature  
40 generally do not include a genetic component (16);  
41 and, community genetics studies have primarily fo-  
42 cused on community composition in terms of the  
43 abundance of species (7). There are studies that have  
44 examined the effects of genetic variation on trophic  
45 chains, such as several in plant-associated communi-  
46 ties (including *Populus*, *Solidago*, *Oenothera*, *Salix*)  
47 (17–21) and generally found that increasing geno-  
48 typic diversity leads to increased trophic complexity.  
49 Only two other studies, that we are aware of, have  
50 explicitly examined the effect of genotypic variation  
51 on the structure of interaction networks between  
52 tree individuals and associated herbivores (22, 23)  
53 and both found that genotypic diversity generates  
54 increased network modularity (i.e. compartmental-  
55 ization). However, both of these studies were at the  
56 scale of forest stands, rather than individual trees;  
57 therefore, neither was able to observe replicated net-  
58 works in order to statistically test for genetic effects  
59 on network structure and quantify the genetic compo-  
60 nent (i.e. heritable variation) in network structure.

61 What are the potential issues/concerns of not con-  
62 sidering network structure? Network theory and  
63 evidence from empirical studies in ecology have  
64 demonstrated that indirect effects can lead to self-  
65 organization, producing sign-changing, amplifying  
66 and/or dampening effects (24, 25). The development  
67 of indirect genetic effects (IGE) and its community-  
68 level extension, inter-specific indirect genetic effects  
69 (IIGE) (26) NEED TO ADD WHITHAM2020

70 in evolutionary biology point to the importance of  
71 studying the genetic basis of interaction network  
72 structure. IGE and IIGE theory develop a quantita-  
73 tive framework that demonstrates the importance of  
74 the indirect effect of genetic variation of one individ-  
75 ual on other individuals of the same (IGE) or different  
76 species (IIGE). Evolutionary applications of network  
77 theory have demonstrated that, at least at the pop-  
78 ulation scale, indirect effects of interactions can lead  
79 to network structures that can amplify or dampen  
80 the effects of selection (27). For example, networks  
81 that form a star-like structure in which there is a  
82 central species or core group of species that interact  
83 with other, peripheral species, can greatly amplify  
84 selection events. Empirically, network analysis of the  
85 structure of bipartite (i.e. two-mode) mutualistic net-  
86 works has shown in multiple cases that nestedness,  
87 or the degree to which species tend to interact with  
88 similar subsets of the community, tends to promote  
89 stability and resilience to disturbances (28) NEED  
90 TO ADD BASCOMPTE2014. Therefore, ob-  
91 serving not only *if* but *how* networks of genetically  
92 similar individuals are more similar, is essential to  
93 fully understanding evolutionary dynamics in real  
94 ecosystems.

95 Here, we investigate how genetic variation in a  
96 foundation tree species determines the structure of  
97 a network of interactions among a community of  
98 tree associated lichen species. Previous studies have  
99 examined aspects of networks (29). Here we examine  
100 the genetic basis of network structure on a commu-  
101 nity of sessile lignicolous (i.e. bark) lichens on cotton-  
102 wood trees. Using a long-term (20+ years), common  
103 garden experiment with replicated individuals of  
104 known genetic identity and a naturally established  
105 stand of *Populus angustifolia*. We focused on a model  
106 community of 9 epiphytic lichen species, as previous  
107 research has demonstrated significant compositional  
108 responses of epiphytes to genotypic variation (30, 31).  
109 In addition, the life-history characteristics of lichens,  
110 having highly localized, direct contact interactions  
111 and slow population turnover rates, facilitated the  
112 assessment of interactions among lichen species on  
113 individual trees. We hypothesize that in natural  
114 systems evolution occurs in a community context  
115 involving interactions of complex networks of inter-  
116 acting species (22, 23, 28, 32). If correct, we expect  
117 to find that network structure is genetically based  
118 in which different plant genotypes support different

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

## 140 Materials and Methods

141

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

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

164 **Bark Lichen and Trait Observations.** On each tree, pres-  
165 ence or absence of each lichen species was assessed in 50  
166 total 1 cm<sup>2</sup> cells arrayed in a checkerboard pattern. Given  
167 the small size and sessile nature of lichens, we were able to  
168 rapidly assess lichen interactions by quantifying thalli in

169 close contact. Sampling was restricted to the northern as-  
170 pect of the trunk to maximize the abundance of lichen and  
171 control for the effect of trunk aspect. Two adjacent 100  
172 cm<sup>2</sup> quadrats centered at 50 cm and 95 cm from ground  
173 level were sampled (Fig 1 A and B). The observed lichen  
174 community included (abbreviations are given for species  
175 present in study): Xg = *Xanthomendoza galericulata*, Xm  
176 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Cande-*  
177 *lariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora*  
178 *hagenii*, Pm = *Phyciella melanochra*, Pa = *Physcia adscen-*  
179 *dens*, Pu = *Physcia undulata*. Several other species were  
180 not obesrvd in the present study but are known to occur  
181 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia*  
182 *ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

183 The cell size and checkerboard sampling pattern was  
184 chosen to isolate the individuals in each cell. In a previous  
185 survey of lichen thallus size in this common garden, we  
186 had observed a median thallus size of 0.12 ± 0.001 cm<sup>2</sup> (1  
1 S.E.) (see Supporting Information). Based on the median  
187 thallus size, we expected thalli observed in each cell to  
188 generally be spatially independent of thalli present in  
189 other cells but exposed to similar micro-environmental  
190 conditions created by the bark and the location of the  
191 sampling area on an individual tree. Therefore, we were  
192 confident in treating the cell-wise observations in quadrats  
193 as independent with respect to lichen-lichen interactions.  
194

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

199 **Lichen Network Modeling and Analysis.** For each tree,  
200 repeated observations of lichen were made in order to con-  
201 struct replicated interaction networks for each genotype.  
202 We conducted a modified sampling procedure originally  
203 developed by (34) with the addition that we quantified  
204 the presence of lichen in the 1 cm<sup>2</sup> cells on individual  
205 trees of *P. angustifolia*. Unipartite networks were gener-  
206 ated using the conditional probabilities of each species  
207 pair, i.e. the probability of observing one species given  
208 an observation of another species  $P(S_i|S_j)$ , based on  
209 the method developed by (35). To calculate conditional  
210 probabilities, we quantified the individual probabilities  
211 of species occurrences  $P(S_i)$  and the joint probability  
212 of co-occurrences  $P(S_i, S_j)$  using the frequencies of each  
213 species and their co-occurrences. We were then able to  
214 calculate the conditional probabilities of each species pair  
215 as  $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$ , based on the axioms of probability.  
216 This yielded a matrix that could possibly be asymmetric, i.e.  
217  $P(S_i|S_j)$  does not have to be equal to  $P(S_j|S_i)$ . Another  
218 important property of this matrix is that the diagonal  
219 ( $S_{ii}$ ) was equal to one for all species present and zero for  
220 species that were not observed in any cell.

221 We then applied an analytical procedure to remove  
222 non-significant links between species. This procedure  
223 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). Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 500cm and 95cm from the ground (A and B, respectively). (C) a photo of a typical community of bark lichen species interacting on the trunk of a cottonwood tree, including one of the more abundant species, *Xanthomendoza galericulata*, in the center. (D-K) shows the other lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanchra*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (A-C) and R.R. Naesbourg (D-K).

(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



**Fig. 2.** Lichen interaction networks were constructed by conducting field observations in 1 cm<sup>2</sup> cells within a 100 cm<sup>2</sup> grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (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.

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 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

298 of variance and normality for these tests.

299 For multivariate response variables, such as lichen com-  
300 munity composition and network structure, we used dis-  
301 tance based multivariate statistical approaches, including  
302 Permutational Analysis of Variance (PERMANOVA) and  
303 Mantel tests. To quantify the similarity of lichen net-  
304 works among individual trees, we calculated the pairwise  
305 Euclidean distance of the **D** interaction matrices among  
306 all pairs of trees.

307 For visualization of multivariate patterns, we used  
308 Non-metric Multi-Dimensional Scaling (NMDS) (37) to  
309 produce dimensionally reduced ordinations of these multi-  
310 variate responses and fitted vectors for continuous predi-  
311 cator variables to the ordinated values (38). Using random  
312 initial configurations with a maximum of 500 iterations  
313 and a change in stress threshold of less than  $10^{-12}$ . Final  
314 configurations has the lowest stress with at most a stress  
315 level of 0.10.

316 For each network, we also calculated metrics that mea-  
317 sure different structural aspects. Although there are many  
318 other metrics, for the sake of simplicity we focus on a  
319 subset that represent several interesting features of net-  
320 work structure (see (16)). We calculated the number of  
321 interactions or “links” in each network, which provides a  
322 measure of the size of the network (22, 39). We also calcu-  
323 lated the centralization of each network, which measures  
324 the evenness of the distribution of interactions among  
325 the species in the network (40). In a network with a  
326 low level of centralization species have similar amount of  
327 interaction in the network, while a network with a high  
328 level of centralization tends to have one or small number  
329 of species that interact with other species. We used a  
330 related function to calculate the centrality of each species  
331 (i.e. node level centrality) in each network as well.

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

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

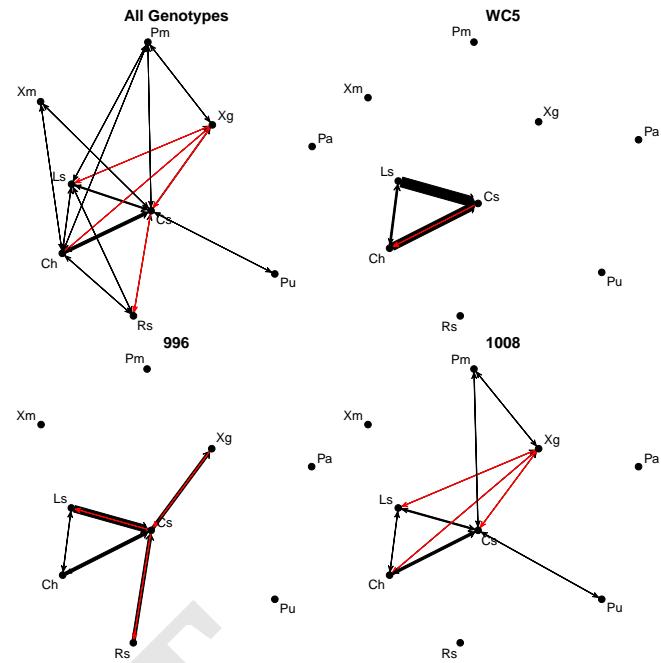
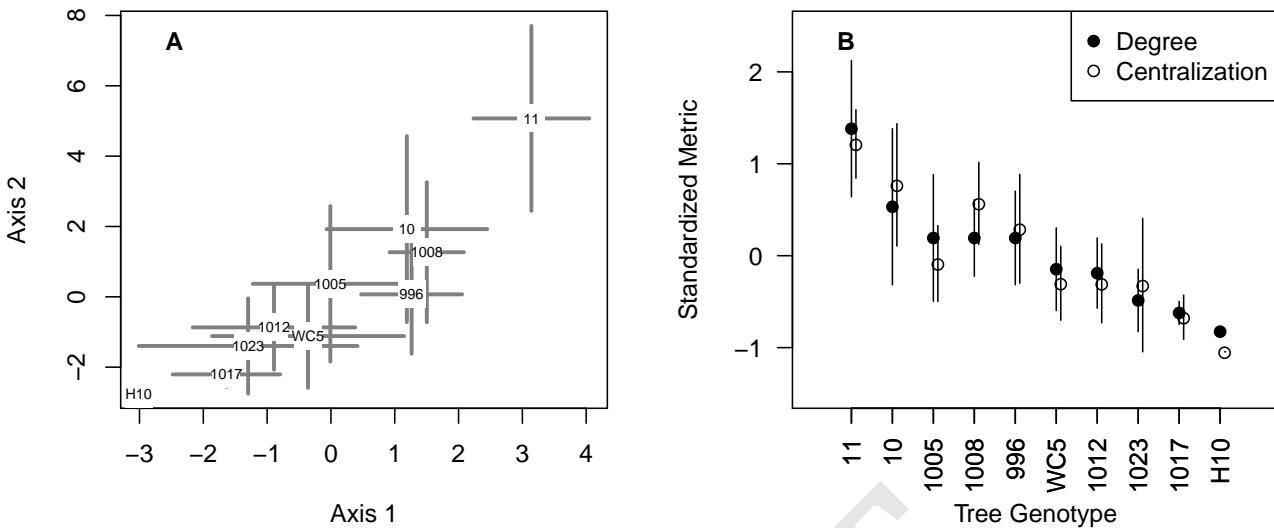


Fig. 3. Lichen networks varied in structure among tree genotypes. Network dia-  
grams of the mean lichen interaction matrices averaged for all trees and for several  
individual genotypes (996, WC5 and 1008) showing a range of interaction network  
structure. Directionality (arrowheads) and sign (red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

## Results

Tree genotype influenced lichen network structure and multiple lichen network metrics were heritable. Tree genotype significantly predicted the structural similarity of lichen networks (PERMANOVA:  $Pseudo-F_{9,27} = 3.58$ ,  $H^2 = 0.41$ ,  $p\text{-value} = 0.0537$ ) (Fig. 4). Overall network level metrics responded significantly to tree genotype (Table 1), including network degree ( $RLRT = 3.52$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0255$ ) and centralization including both in-coming and out-going links ( $RLRT = 4.04$ ,  $H^2 = 0.33$ ,  $p\text{-value} = 0.0184$ ) or when separated into in-coming only ( $RLRT = 3.9852$ ,  $H^2 = 0.3309$ ,  $p\text{-value} = 0.0190$ ) or out-going only ( $RLRT = 3.8615$ ,  $H^2 = 0.3193$ ,  $p\text{-value} = 0.0205$ ). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree ( $RLRT = 3.6925$ ,  $H^2 = 0.3242$ ,  $p\text{-value} = 0.0229$ ), positive in-going centralization ( $RLRT = 4.4812$ ,  $H^2 = 0.3487$ ,  $p\text{-value} = 0.0142$ ). Metrics calculated with negative links were not significant, including degree (negative)



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

( $RLRT = 0.0327$ ,  $H^2 = 0.0318$ ,  $p\text{-value} = 0.3859$ ) and both in-coming (negative) ( $RLRT = 0.3304$ ,  $H^2 = 0.1057$ ,  $p\text{-value} = 0.2508$ ) and out-going centralization (negative) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ ,  $p\text{-value} = 0.3446$ ).

response	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

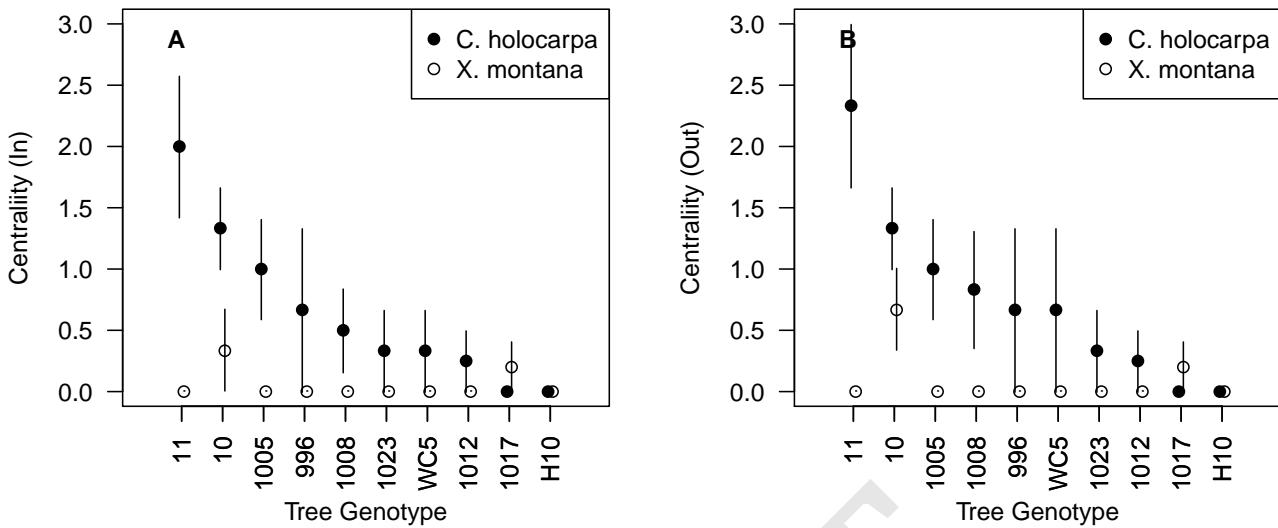
**Table 1. Genotypic effects on the associated lichen network structure.**

The genetic response of network centralization was driven by variation in *Caloplaca holocarpa*. Centralization varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ ,  $p\text{-value} < 0.0001$ ). *Caloplaca holocarpa* centrality was the main species to exhibit a significant response to tree genotype in terms of positive centrality for both the in-coming ( $RLRT = 3.61$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0240$ ) and out-going ( $RLRT =$

$3.13$ ,  $H^2 = 0.30$ ,  $p\text{-value} = 0.0327$ ) perspectives, but not for either negative centrality metrics in-coming ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 1$ ) or out-going ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 0.4543$ ). None of the other species' centralities showed a genotypic response (Supplementary Table 4) 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 3); therefore, we focused our analysis on bark roughness. We found that bark roughness was sign-



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

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

## Discussion

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in

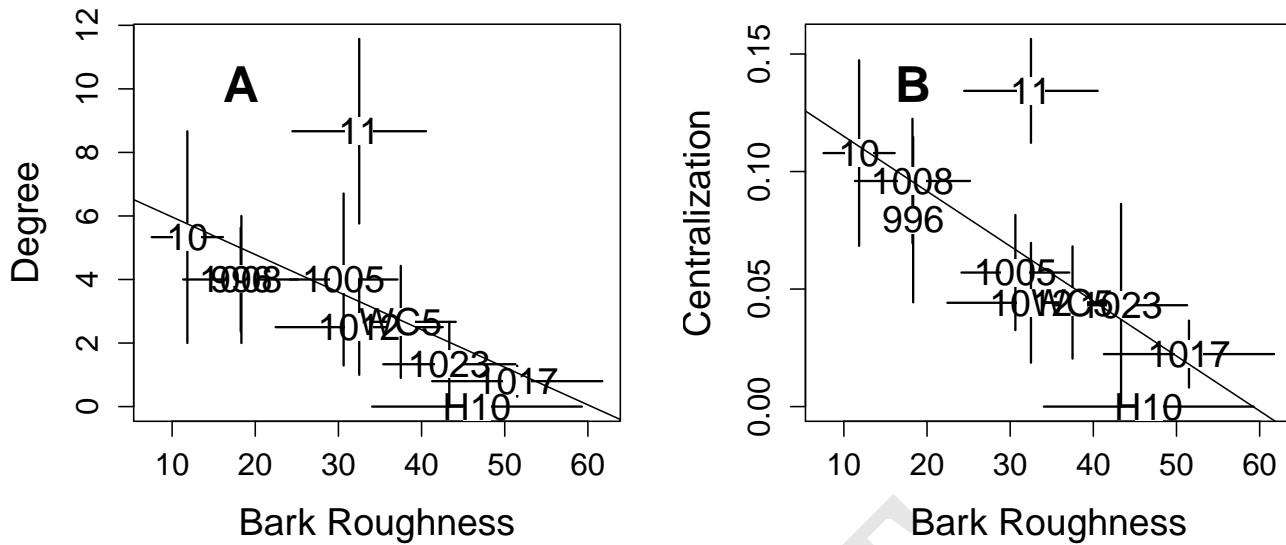
	Df	SumOfSqs	R2	F	Pr(>F)
BR	1.0000	20850.0933	0.2574	12.9234	0.0101
CT	1.0000	5993.6629	0.0740	3.7150	0.0813
pH	1.0000	1273.1905	0.0157	0.7892	0.3712
CN	1.0000	3896.1754	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

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

positive interactions and largely driven by *C. holocarpa*. The genetically based trait, bark roughness, was the only trait observed to effect network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control (43), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (34); however this is the first demonstration of a link from genes to lichen network structure. As such these results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species.

**Heritability of Interaction Network Structure. Revisit the community similarity rule.**

Add more text here on positive and negative interactions of lichen from the literature.



**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.

453     *Elaborate on how many species might be supported  
454     by each lichen thallus including the symbionts and  
455     other species.*

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

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

463     *Does bark roughness increase habitat and decrease  
464     interactions?*

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

480     quadrats per tree. Regardless, this could result in a  
481     situation in which abundance based investigations  
482     of community-level genetic effects may miss impor-  
483     tant variation in the interactions among individuals  
484     in these communities, leading to an underestimate of  
485     genetic effects in ecosystems. It is possible that these  
486     underlying differences in interactions among lichen  
487     could lead to differences in community composition  
488     at a future point in time, however, this is not needed  
489     for evolutionary dynamics to play out.

490     Second, following on the previous point, genetic  
491     diversity could be influencing the stability of com-  
492     munities through the effects on the structure of in-  
493     teractions. Some network structures are likely to be  
494     more stable, either in response to disturbance or via  
495     self-organized dynamics. For example, centralized  
496     networks, although more efficient, are theorized to  
497     be more susceptible to targeted attacks on the center  
498     of the network. For example, consider a forest with  
499     two genotypes that support lichen communities that  
500     are similar in total abundances of each species but  
501     differ in terms of the structure. Extensions of game  
502     theory to evolutionary biology have demonstrated  
503     that network structure can lead to variation in evo-  
504     lutionary dynamics. Some structures tend toward  
505     dominance and dampening of selection, while others  
506     lead to amplification of selection (Newman). One

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

516 There are several important points to consider  
517 with regard to the generalization of the observed  
518 genetically based response of the lichen networks.  
519 Body size and sessile nature of lichen important to  
520 observing genotype responses. As bark lichen individuals do not move, but grow in a largely two  
521 dimensional plane, these communities and their interactions occur in the highly localized context of  
522 the tree's bark surface. Lichen individuals are many orders of magnitude smaller than the tree individual  
523 and the life-span of a tree is many times that of a lichen. For these reasons, any genetic effects on these  
524 communities is not damped by the movement of individuals and the mixing of the effect of different  
525 tree genotypes on the lichen community, as might occur for more mobile species (e.g. insects and birds).  
526 We only looked at lichen, other species whose distribution, abundance or interactions respond to tree  
527 genotype, such as epiphytic plants (e.g. moss and liverworts), algae or insects, could be playing a role.  
528 Other traits could also be playing a role, such as traits that are correlated with bark roughness, such  
529 as micro-aspect, albedo, moisture, etc.

530 Bark roughness could possibly be serving the role  
531 that other lichen play in facilitating the success of  
532 new propagule attachment and the growth of establishing thalli. This is supported by the patterns overall being positive, including *C. holocarpa* centrality.  
533 We did not observe specific microscopic dynamics, such as photobionts, mycobionts, endolichenic fungi and bacteria, but variation in these underlying interactions could also be playing a role. Although we can not rule out the possibility that other unmeasured tree traits or organisms correlated with bark roughness are underlying the observed patterns in bark lichen network structure, substantial research supports the importance of genetically based tree traits for communities and ecosystems (7), and in

534 particular bark roughness for bark lichen communities (33, 34, 43).

535 In the present study, lichen cover, lichen species richness and composition were not responsive to tree genotype, unlike what was found in (34). This is likely, at least in part, the result of differences in sampling method and the choice of genotypes sampled leading to overall higher abundances of observed lichens. In the current study mean % total lichen cover among genotypes ranges from 60-93% cover; whereas the range reported in (34) is 0.86-18.73%. The previous study used a visual estimation method, unlike the current study, which observed lichen at the scale of 1 cm<sup>2</sup> cells, which could over-estimate cover depending on the frequency at which actual thallus size was less than 1 cm<sup>2</sup>. The previous study used samples from both the northern and southern aspects of each tree; whereas, the current study only observed lichen on the northern aspect. Also, our current results are likely different from the previous study because the current study selected genotypes that tended to have bark lichen, with the interest of focusing on generating networks for comparison. These differences do not negate the findings of either study but is important to explain the differences in the findings, particularly in the community-level effects of tree genotype.

536 **Implications for Interspecific Indirect Genetic Effects (IIGEs).** Initially, evolution in a community context was focused on examples of highly co-evolved pairs of species (e.g. Darwin's famous prediction of the Sphinx Moth and Christmas Orchid) (8). However, studies of diffuse co-evolution (*sensu* (44)) (45, 46), geographic mosaics of co-evolution (32) and community genetics (10) have provided an in-road for ecological network approaches (20, 23, 47) to illuminate a more complex perspective of the interface between ecological and evolutionary dynamics.

537 Interspecific indirect genetic effects (IIGE) theory has provided a quantitative framework within which to approach evolutionary theory at higher levels of biological organization: from populations to communities and ecosystems. To date, this theory has focused on modeling the strong effects of foundation species (26, 48), but it has not yet integrated developments in the ecological or evolutionary network theory literature. This is to say that it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated

605 this network context is likely to be important, as  
606 altering the structure of interaction networks pro-  
607 vides a means for genetic effects to be dampened or  
608 magnified within the system of interacting species.  
609 For example, (23) showed that the genetics based  
610 interactions of aphid resistant and aphid suscep-  
611 tible trees resulted in different interaction networks of  
612 their associated arthropod communities composed  
613 of 139 species. At the scale of ecosystems, trophic  
614 networks or food webs direct and control the rates  
615 of energy and nutrient flux (49). Furthermore, in a  
616 predator-prey-plant study, Smith (19), showed that  
617 the interactions among species across trophic levels  
618 depended on plant genotype. Also, work by (50–52)  
619 observed consistent patterns of centralized interac-  
620 tions of species modules focused around hubs of  
621 plant-fungal interactions. In other words, a small  
622 number of plant and fungal symbionts tended to  
623 have disproportionate numbers of interactions with  
624 other species and likely are the drivers in determining  
625 community assembly, structure and dynamics.

626 The results of the current study provides clear em-  
627 prical evidence that networks points to the need to  
628 expand IIGEs encompass the structure of interaction  
629 networks. Although such a synthesis necessitates  
630 a much greater effort than can be afforded in this  
631 paper, it is possible to point to several productive  
632 pathways forward. In terms of interaction networks,  
633 foundation species are relatively central within the  
634 system of interactions, that is their direct and/or  
635 indirect effects are greater than other species. So,  
636 when the more centralized (foundation) species have  
637 genetically based interactions, genetic effects will  
638 tend to be magnified in the community. Here, we  
639 found that even though more abundant or more cen-  
640 tralized (i.e. “important”) species were present in  
641 the community, their effects were not the main com-  
642 ponent responding to genetic effects. Considering  
643 the impact of network structure would be a produc-  
644 tive path forward for the theoretical development  
645 and application of the IIGE concept.

646 With regard to the evolutionary implications of  
647 network structure, ecological network studies have  
648 focused on asymmetry and the quantification of  
649 its structure in communities, with qualitative dis-  
650 cussion of the impacts on evolutionary dynamics  
651 (28, 32, 53, 54). More specific predictions, with a  
652 quantitative framework, can be found in applications  
653 of evolutionary game theory, and although developed

654 at the population scale, such theory can apply to  
655 communities. One seemingly useful direction from  
656 evolutionary network developments from game the-  
657 ory is the classification of networks into two genreal  
658 categories, rooted and cyclic, in which rooted net-  
659 works have interactions in which evolutionary effects  
660 emanate from one or multiple origins but these effects  
661 do not have connections back to the origins, whereas  
662 cyclic networks contain feedbacks to one or more ori-  
663 gins. Although it did not explicitly define it in this  
664 context, the previous work (16), developed that the  
665 structure of the network in the context of a founda-  
666 tion species, such as cottonwoods in which there are  
667 demonstrable community level genetic effects, is that  
668 of a multiple origin network. This builds on many  
669 previous studies demonstrating that the community  
670 level effects vary among multiple genotypes. It is not  
671 clear what potential there is for feedbacks there are  
672 to the origins (e.g. the cottonwood genotypes) from  
673 the community, and as such it cannot be determined  
674 whether these networks are cyclic or rooted. In other  
675 systems, lignicolous lichens can have demonstrable  
676 positive effects on the availability of nutrients for the  
677 trees that they are associated with, but this has not  
678 been measured in the current system. Illucidating  
679 the absence and/or presence and quantifying such  
680 feedbacks would allow for the determination of the  
681 cyclic nature and potential evolutionary dynamics of  
682 this system. The presence of feedbacks would provide  
683 the potential for non-linear dynamics in which evo-  
684 lutionary effects are dampened or amplified by the  
685 struture of the network. For example, a star struc-  
686 ture in which there is a primary or core set of central  
687 species with feedbacks from the radiating species has  
688 been demonstrated to be a structure that amplifies  
689 evolutionary dynamics (27). If such feedbacks do  
690 not exist, and these sub-networks of the lichen and  
691 tree genotypes are likely to be multi-rooted networks.  
692 Such a structure is theorized to generally promote  
693 diversification as variation arising from the shifting  
694 distribution of the “roots”, i.e. genotypes; however,  
695 loss of genotype/root diversity could lead to fixation  
696 of a single genotype in the population and a decrease  
697 in community-wide diversity.

698 **Conclusion.** Although our study was conducted with  
699 a community of lichens, these results should be gen-  
700 eralized to other groups of diverse organisms around  
701 the world that also exhibit significant genetic signals  
702 at the community level (48, 55). In the face of the

high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed to some in previous studies (15, 56, 57). In the present study, we found that community assembly processes, such as environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. We suggest that future work would be aided by determining these modules within the biotic community that include species with similar differences in body-size and time-scales. As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (58). With such findings, it appears that we are closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

Future work should consider the potential influence on evolutionary dynamics of the associated communities. The network of interactions of species that 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 multivariate 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).

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

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905 **Supplementary Materials**

906 **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	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.**

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

lichen species	mean	statistic	H2	p-value
Positive				
In-Degree				
<i>X. galericulata</i>	0.2703	0	0	0.4543
<i>C. subdeflexa</i>	0.8919	2.1926	0.2158	0.0595
L. spp.	0.4324	0	0	1
<i>C. holocarpa</i>	0.5946	3.6146	0.3241	0.024
<i>X. montana</i>	0.0541	0	0	0.4543
<i>P. melanura</i>	0.1351	0	0	1
<i>P. adscendens</i>	0			
<i>P. undulata</i>	0.027	0	0	0.4543
R. sp.	0.1351	2.049	0.2613	0.0656
Out-Degree				
<i>X. galericulata</i>	0.027	0	0	0.4543
<i>C. subdeflexa</i>	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4246
<i>C. holocarpa</i>	0.7027	3.1318	0.2981	0.0327
<i>X. montana</i>	0.0811	2.9228	0.3163	0.0375
<i>P. melanura</i>	0.1351	0	0	1
<i>P. adscendens</i>	0			
<i>P. undulata</i>	0.027	0	0	0.4543
R. sp.	0.2973	0.1505	0.0612	0.3119
Negative				
In-Degree				
<i>X. galericulata</i>	0			
<i>C. subdeflexa</i>	0.1892	0	0	0.4543
L. spp.	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. melanura</i>	0			
<i>P. adscendens</i>	0			
<i>P. undulata</i>	0			
R. sp.	0.1622	0	0	1
Out-Degree				
<i>X. galericulata</i>	0.2432	0	0	1
<i>C. subdeflexa</i>	0.4054	0	0	0.4543
L. spp.	0.027	0	0	0.4543
<i>C. holocarpa</i>	0.027	0	0	0.4543
<i>X. montana</i>	0			
<i>P. melanura</i>	0			
<i>P. adscendens</i>	0			
<i>P. undulata</i>	0			
R. sp.	0			

**Table 4. 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 5. 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		

**Table 6. Pseudo-F Table of lichen community similarity  
PERMANOVA.**

**Figures.**

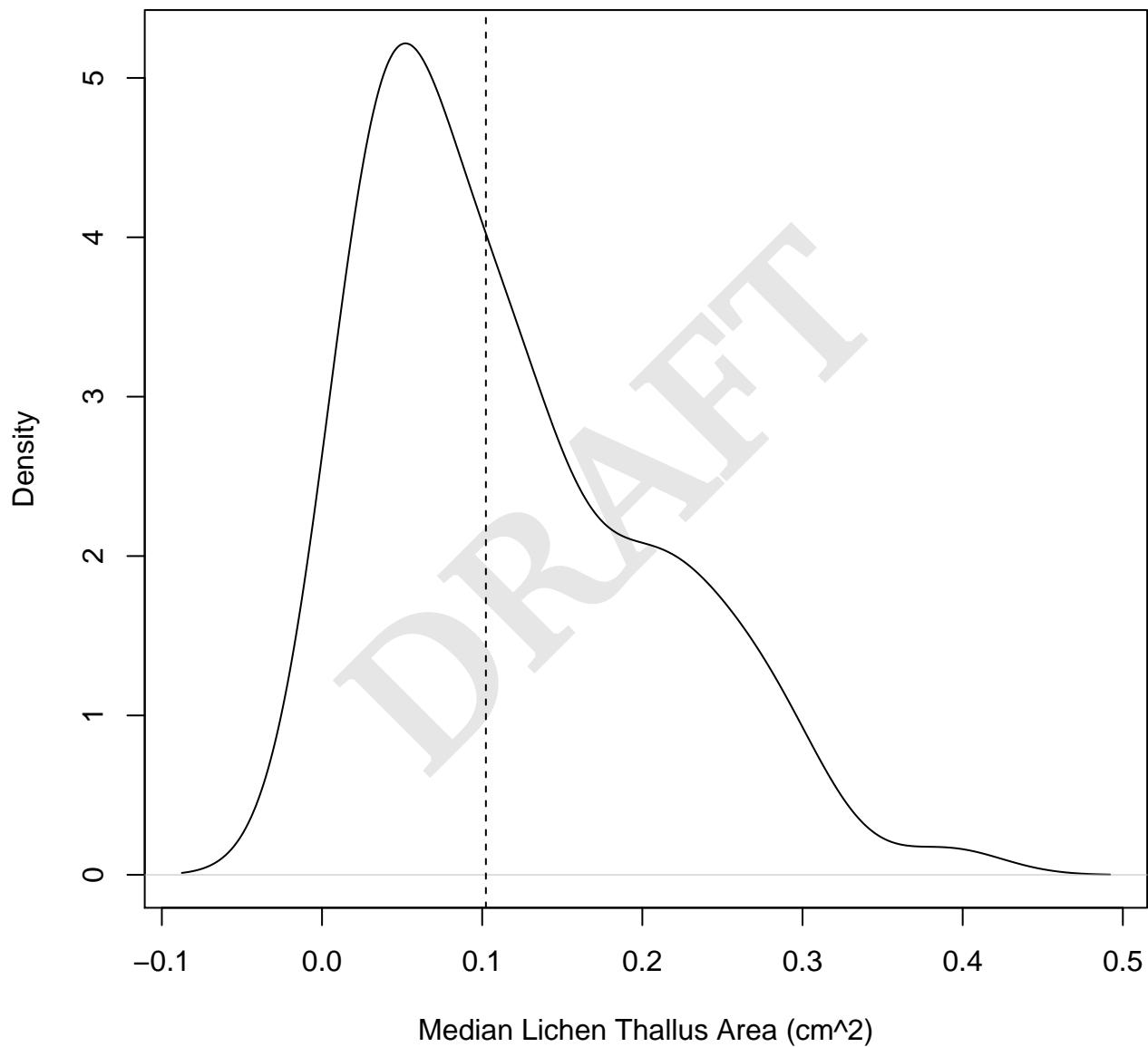
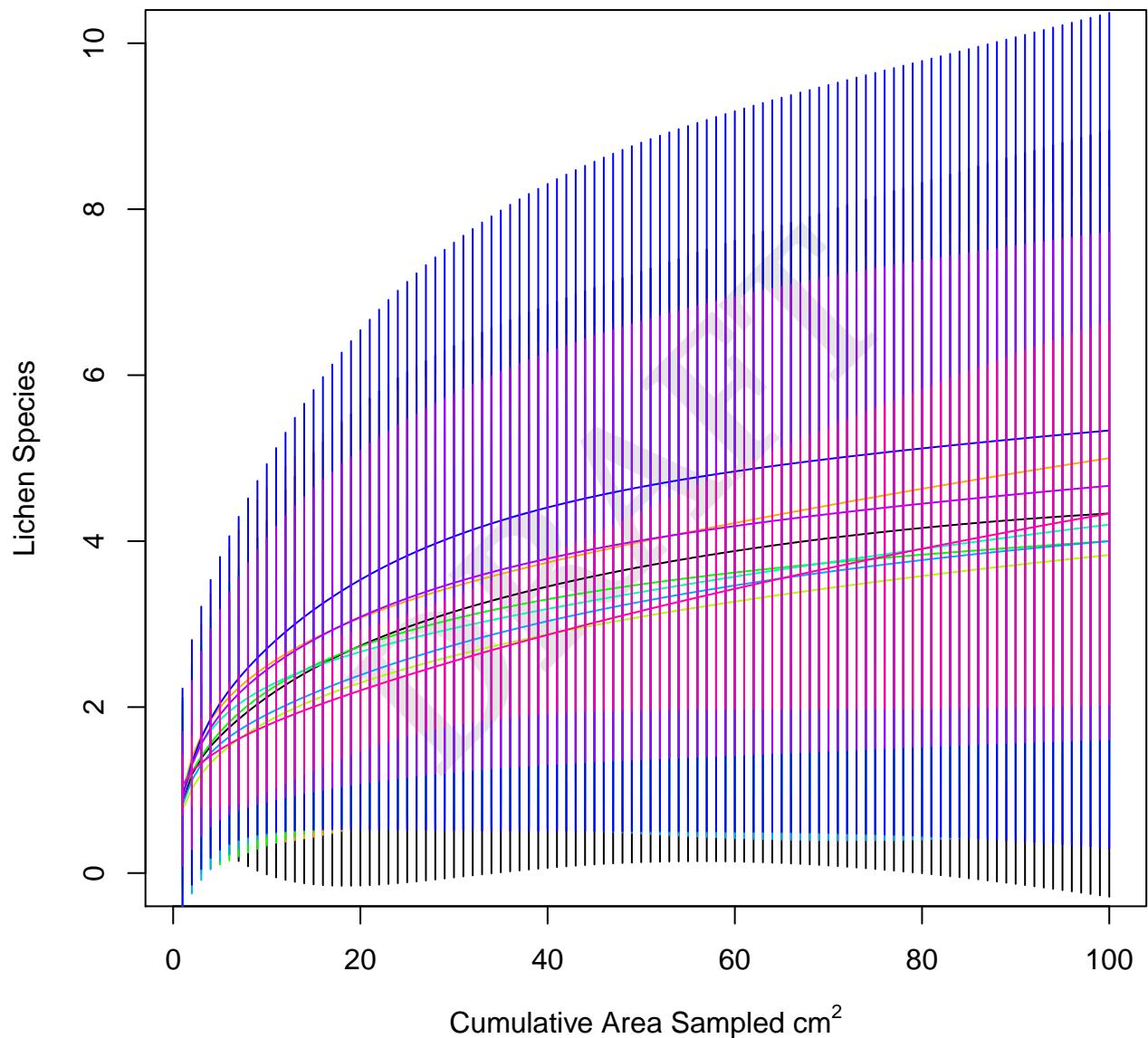


Fig. 1



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

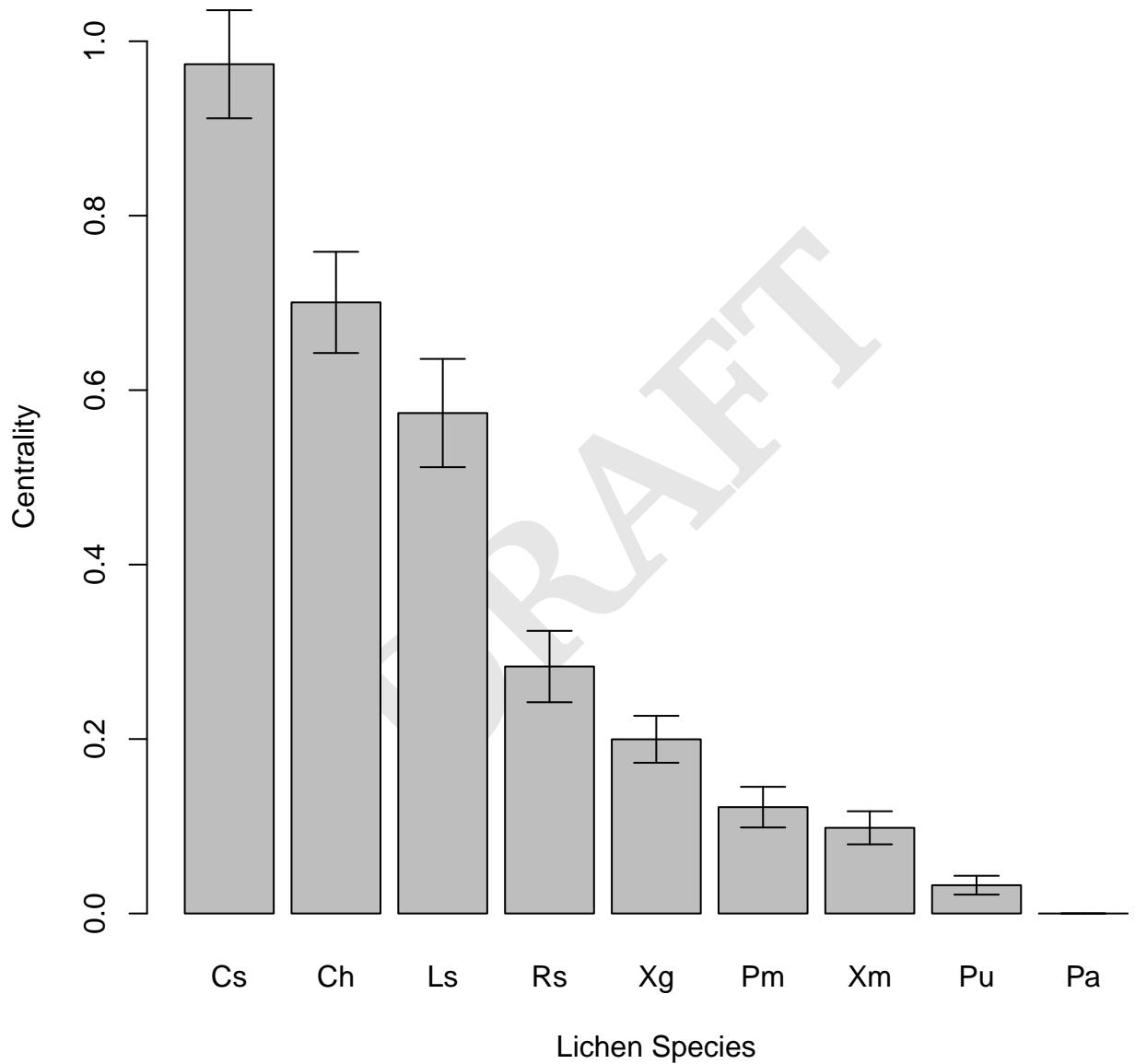


Fig. 3