

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 networks of
2 interacting species in which natural selection defines the structure
3 of ecological networks. Fundamental to this evolutionary process
4 is the discovery of a genetic basis to ecological network structure.
5 Although previous work has demonstrated that tree genotype con-
6 tributes to interaction network structure at the scale of forest stands,
7 the contribution of tree genetics to localized interaction networks at
8 the scale of individual trees has not yet been explored. To test the
9 degree to which tree genetics can contribute to network structure
10 we conducted quantitative modeling of interaction networks. We
11 constructed networks of epiphytic lichens associated with individ-
12 ual trees that were a part of a long-term experimental common gar-
13 den of genotypes of (*Populus angustifolia*), a foundation species.
14 We found two primary results. First, tree genotype significantly pre-
15 dicted lichen network similarity, i.e. clonal replicates of the same
16 genotype tended to support more similar lichen networks, using mul-
17 tiple network metrics. Second, although multiple species were ob-
18 served repeatedly in the interaction networks, the effect of tree geno-
19 type was primarily focused on variation of the interactions of one
20 lichen species, *Caloplaca holocarpa*. Third, one of the examined tree
21 traits, bark roughness, was both predicted by tree genotype and cor-
22 related with lichen network similarity, supporting a mechanistic path-
23 way from a variation in a heritable tree trait and the genetically based
24 variation in lichen network structure. We conclude that tree geno-
25 type can influence not only the relative abundances of organisms
26 but also the interaction network structure of associated organisms.
27 Given that variation in network structure can have consequences for
28 the dynamics of communities through altering the stability of the sys-
29 tem and modulating or amplifying perturbations, these results have
30 important implications for the evolutionary dynamics of ecosystems.

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

1 Evolution occurs in the context of complex eco-
2 logical networks. Initially, evolution in a com-
3 munity context was focused on examples of highly
4 co-evolved pairs of species (e.g. Darwin's famous
5 prediction of the Sphinx Moth and Christmas Or-
6 chid) (1). However, studies of diffuse co-evolution
7 (*sensu* (2)) (3, 4), geographic mosaics of co-evolution
8 (5) and community genetics (6) have provided an
9 in-road for ecological network approaches (7–9) to
10 illuminate a more complex perspective of the inter-
11 face between ecological and evolutionary dynamics.

12 There is now evidence to support that selection tends
13 to occur among groups of species (1) favoring the
14 development of small webs (10, 11) and that genetic
15 variation and phylogenetic relatedness contributes
16 to variation in community assembly (12) and species
17 interactions (6, 13, 14), which shapes the ecological
18 interaction networks (15).

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.

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19 *Define foundation species.*

20 Community genetics studies (16) have shown that
21 genetic variation in foundation species, which have
22 large effects on communities and ecosystems by mod-
23 ulating and stabilizing local conditions (17), plays a
24 significant role in defining distinct communities of in-
25 teracting organisms: such as, endophytes, pathogens,
26 lichens, arthropods, and soil microbes. Multiple
27 studies have now demonstrated that genetic varia-
28 tion influences numerous functional traits (e.g., phy-
29 tochemical, phenological, morphological) produces
30 a multivariate phenotype (18) that contributes to
31 variation in associated communities (13). The impor-
32 tance of genetic variation in structuring ecological
33 systems was recently reviewed (19), and not only
34 were many instances of strong genetic effects found
35 in many ecosystems but the effect of intraspecific
36 variation was at times greater than *inter*-specific
37 variation. Additional work has provided support
38 for the hypothesis that not only does composition
39 vary among genetically distinct genotypes of founda-
40 tion species but that it also impacts the structure
41 of species interactions. However, studies in the net-
42 work ecology literature generally do not include a
43 genetic component (20); and, community genetics
44 studies have primarily focused on community com-
45 position in terms of the abundance of species (19).
46 There are studies that have examined the effects of
47 genetic variation on trophic chains, such as several
48 in plant-associated communities (including *Populus*,
49 *Solidago*, *Oenothera*, *Salix*) (7, 21–24) and generally
50 found that increasing genotypic diversity leads to
51 increased trophic complexity. Only two other stud-
52 ies, that we are aware of, have explicitly examined
53 the effect of genotypic variation on the structure of
54 interaction networks between tree individuals and
55 associated herbivores (8, 25) and both found that
56 genotypic diversity generates increased network mod-
57 ularity (i.e. compartmentalization). However, both
58 of these studies were at the scale of forest stands and,
59 therefore, were not able to observe replicated net-
60 works in order to statistically test for genetic effects
61 on network structure.

62 *Make a bigger deal of the application of the genetic*
63 *similarity rule and more similar genotypes supporting*
64 *more similar interaction networks.*

65 Here, we investigate how genetic variation in a
66 foundation tree species determines the structure of
67 a network of interactions among a community of

68 tree associated lichen species. Previous studies have
69 examined aspects of networks (26). Here we examine
70 the genetic basis of network structure on a commu-
71 nity of sessile lignicolous (i.e. bark) lichens on cotton-
72 wood trees. Using a long-term (20+ years), common
73 garden experiment with replicated individuals of
74 known genetic identity and a naturally established
75 stand of *Populus angustifolia*. We focused on a model
76 community of 9 epiphytic lichen species, as previous
77 research has demonstrated significant compositional
78 responses of epiphytes to genotypic variation (27, 28).
79 In addition, the life-history characteristics of lichens,
80 having highly localized, direct contact interactions
81 and slow population turnover rates, facilitated the
82 assessment of interactions among lichen species on
83 individual trees. We hypothesize that in natural
84 systems evolution occurs in a community context
85 involving interactions of complex networks of inter-
86 acting species (5, 8, 25, 29). If correct, we expect
87 to find that network structure is genetically based
88 in which different plant genotypes support different
89 interaction networks and that these interactions net-
90 works can function as indicators of ecological dynam-
91 ics important for conserving biodiversity. Applying a
92 probability-theory based network modeling approach,
93 we constructed a set of interaction network models
94 for the lichens associated with individual trees. Us-
95 ing these models, we then examined the genetic basis
96 of the structure of these ecological networks. Based
97 on previous community genetics studies, particularly
98 the community similarity rule (30), we hypothesize
99 that trees will vary in some phenotypic traits and
100 those trees of the same genotype will tend to have
101 similar traits leading to similarities in lichen network
102 structure.

103 **Materials and Methods**

104

105 **Study System.** The study was conducted along the We-
106 ber River, UT (USA), which is a cottonwood (*Populus*
107 spp.) dominated riparian ecosystem. Although two native
108 species, *Populus angustifolia* (James) and *Populus fremontii*
109 (S. Watson), occur here and are known to hybridize,
110 only pure or advanced generation backcrosses of *P. angus-*
111 *tifolia* were sampled. Bark lichens have been extensively
112 studied in this system and provide an ideal system in
113 which to observe and model lichen interaction networks,
114 as their sessile nature permits accurate identification of
115 individuals (31).

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

127 **Bark Lichen and Trait Observations.** On each tree, presence
128 or absence of each lichen species was assessed in 50
129 total 1 cm² cells arrayed in a checkerboard pattern. Given
130 the small size and sessile nature of lichens, we were able to
131 rapidly assess lichen interactions by quantifying thalli in
132 close contact. Sampling was restricted to the northern aspect
133 of the trunk to maximize the abundance of lichen and
134 control for the effect of trunk aspect. Two adjacent 100
135 cm² quadrats centered at 50 cm and 95 cm from ground
136 level were sampled (Fig 1 A and B). The observed lichen
137 community included (abbreviations are given for species
138 present in study): Xg = *Xanthomendoza galericulata*, Xm
139 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were
143 not observed in the present study but are known to occur
144 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegans*.

146 The cell size and checkerboard sampling pattern was
147 chosen to isolate the individuals in each cell. In a previous
148 survey of lichen thallus size in this common garden, we
149 had observed a median thallus size of 0.12 ± 0.001 cm² (1
150 S.E.) (see Supporting Information). Based on the median
151 thallus size, we expected thalli observed in each cell to
152 generally be spatially independent of thalli present in
153 other cells but exposed to similar micro-environmental
154 conditions created by the bark and the location of the
155 sampling area on an individual tree. Therefore, we were
156 confident in treating the cell-wise observations in quadrats
157 as independent with respect to lichen-lichen interactions.

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

162 **Lichen Network Modeling and Analysis.** For each tree,
163 repeated observations of lichen were made in order to construct
164 replicated interaction networks for each genotype.
165 We conducted a modified sampling procedure originally
166 developed by (16) with the addition that we quantified
167 the presence of lichen in the 1 cm² cells on individual
168 trees of *P. angustifolia*. Unipartite networks were generated
169 using the conditional probabilities of each species

170 pair, i.e. the probability of observing one species given
171 an observation of another species $P(S_i|S_j)$, based on
172 the method developed by (32). To calculate conditional
173 probabilities, we quantified the individual probabilities
174 of species occurrences $P(S_i)$ and the joint probability
175 of co-occurrences $P(S_i, S_j)$ using the frequencies of each
176 species and their co-occurrences. We were then able to
177 calculate the conditional probabilities of each species pair
178 as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, based on the axioms of probability.
179 This yielded a matrix that could possibly be asymmetric, i.e.
180 $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Another
181 important property of this matrix is that the diagonal
182 (S_{ii}) was equal to one for all species present and zero for
183 species that were not observed in any cell.

184 We then applied an analytical procedure to remove
185 non-significant links between species. This procedure
186 determines if the joint probability of a species pair
187 (i.e. $P(S_i, S_j)$) is different from zero (Fig. 2). Here, a
188 confidence interval $CI_{95\%}$ is calculated as as $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected
189 frequency of co-occurrences $E(S_i S_j)$ is the total number
190 of cells surveyed (N) times the independent probabilities
191 of each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score
192 for 95% from a Z-distribution and the expected variance
193 of $E(S_i S_j)$ is the total number of cells times the
194 expected probability of $S_i S_j$ and its compliment (i.e.
195 $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If the
196 observed number of co-occurrence falls outside of the
197 confidence interval, the joint probability $P(S_i, S_j)$ is de-
198 termined to be equal to the product of the individual
199 probabilities (i.e. $P(S_i)P(S_j)$), and the conditional prob-
200 ability reduces to the individual probability of that species
201 $P(S_i)$. Therefore, unless the co-occurrence of a species
202 pair falls outside the confidence interval, the probability
203 that the observation of one species given the other
204 is no different than simply observing that species alone.
205 This enables us to remove links from a given network by
206 re-scaling the resulting conditional probabilities by sub-
207 tracting the individual probabilities from the conditional
208 probabilities (i.e. how different the conditional probability
209 is from the independent probability), which makes any
210 species with a non-significant conditional probability zero.
211 The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as
212 how one species impacts another with zero being no effect
213 and values less than or greater than zero interpreted as
214 negative and positive effects, respectively. Here, we will
215 refer to this matrix (\mathbf{D}) as an interaction matrix with
216 the properties that it can be asymmetric (i.e. P_{ij} does not
217 necessarily equal P_{ji}), and the diagonal (P_{ii}) is zero (i.e.
218 a species does not influence its own probability of being
219 observed).

221 **Network Metrics.** To quantify the structural variation of
222 lichen networks we calculated several metrics at both
223 the node and whole-network level. For individual nodes
224 (i.e. species) in each network, we calculated both the



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 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. Naesbourn (D-K).

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

$$238 \quad \sum x_i \quad [1]$$

- 239 • Node degree
- 240 • Node centrality
- 241 • Network degree
- 242 • Centralization
- 243 • 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 (33). 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 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



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 (32), 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.

266 Mantel tests. To quantify the similarity of lichen net-
267 works among individual trees, we calculated the pairwise
268 Euclidean distance of the \mathbf{D} interaction matrices among
269 all pairs of trees.

270 For visualization of multivariate patterns, we used
271 Non-metric Multi-Dimensional Scaling (NMDS) (34) to
272 produce dimensionally reduced ordinations of these multi-
273 variate responses and fitted vectors for continuous predictor
274 variables to the ordinated values (35). Using random
275 initial configurations with a maximum of 500 iterations
276 and a change in stress threshold of less than 10^{-12} . Final
277 configurations has the lowest stress with at most a stress
278 level of 0.10.

279 For each network, we also calculated metrics that mea-
280 sure different structural aspects. Although there are many
281 other metrics, for the sake of simplicity we focus on a
282 subset that represent several interesting features of net-

work structure (see (20)). We calculated the number of
283 interactions or “links” in each network, which provides a
284 measure of the size of the network (25, 36). We also calcu-
285 lated the centralization of each network, which measures
286 the evenness of the distribution of interactions among
287 the species in the network (37). In a network with a
288 low level of centralization species have similar amount of
289 interaction in the network, while a network with a high
290 level of centralization tends to have one or small number
291 of species that interact with other species. We used a
292 related function to calculate the centrality of each species
293 (i.e. node level centrality) in each network as well.

294 For all tests where genotype was used as a predictor,
295 we quantified the heritability of the response variable. Be-
296 cause the trees in the garden were clonal replicates of each
297 genotype, we calculated broad-sense heritability, which
298 is the genotypic variance divided by the total phenotypic

300 variance (38). This can be interpreted as a measure of
 301 the phenotypic variance due to genotypic variation. We
 302 also apply this to the community genetics context as the
 303 variance in *extended* phenotypic variance due to genotypic
 304 variation (39). For the multivariate analyses, where we
 305 employ PERMANOVA, we followed the methods of (40)
 306 to adjust the degrees of freedom for unbalanced genotype
 307 replicates.

308 All code and data for the project are openly available
 309 online. Code and data are available at github.com/ecgen/comgen. The project is also archived via Zenodo
 310 at zenodo.com/doi/XXXXXX. All analyses were conducted
 311 using the programming language R version 3.6.1 (R De-
 312 velopment Core Team 2019).

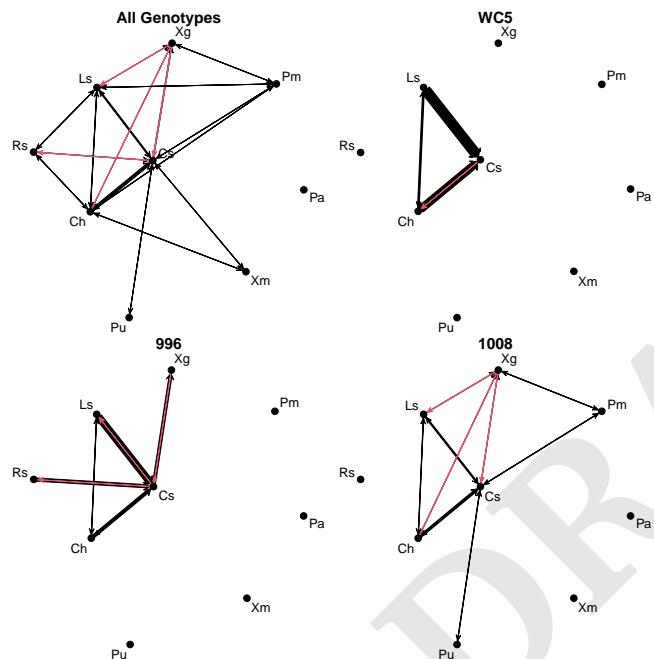


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

314 Results

315 Tree genotype influenced lichen network structure
 316 and multiple lichen network metrics were heritable.
 317 Tree genotype significantly predicted the struc-
 318 tural similarity of lichen networks (PERMANOVA:
 319 Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$)
 320 (Fig. 4). Overall network level metrics responded
 321 significantly to tree genotype (Table 1), including net-

work degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} = 0.0255$) and centralization including both in-coming
 322 and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} = 0.0184$) or when separated into in-coming
 323 and out-going 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
 324 positive links also showed a significant effect of tree
 325 genotype, including positive degree ($RLRT = 3.6925$,
 326 $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
 327 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} = 0.0142$) Metrics calculated with negative
 328 links were not significant, including degree (negative)
 329 ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$)
 330 and both in-coming (negative) ($RLRT = 0.3304$, $H^2 = 0.1057$, $p\text{-value} = 0.2508$) and out-going centralization
 331 (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
 340 driven by variation in *Caloplaca holocarpa*. Central-
 341 ization varied significantly among species ($F_{8,324} = 7.99$,
 342 $R^2 = 0.16$, $p\text{-value} < 0.0001$). *Caloplaca holocarpa*
 343 centrality was the main species to exhibit a signif-
 344 icant response to tree genotype in terms of positive
 345 centralization for both the in-coming ($RLRT = 3.61$, H^2
 346 = 0.32, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives, but
 347 not for either negative centrality metrics in-coming
 348 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going
 349 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of
 350 the other species' centralities showed a genotypic re-
 351 sponse (Supplementary Table 3) with the exception
 352 of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however, the centrality of *X. montana* was
 353 much lower overall relative to *C. holocarpa* and the
 354 variation in *X. montana* centrality was restricted to
 355 356 357

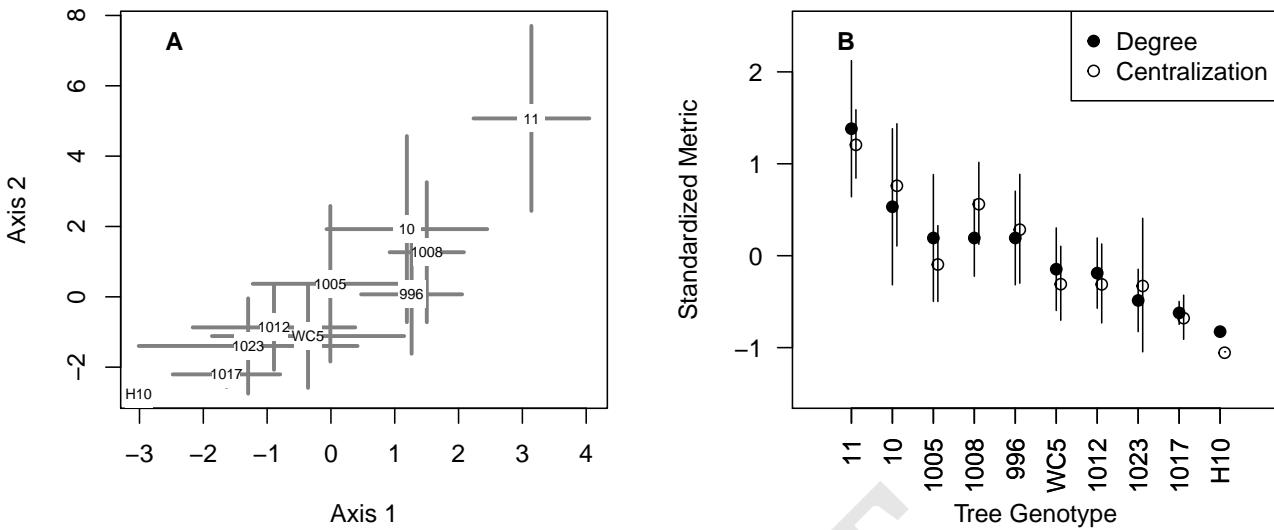


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen networks (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. B. Plot showing the standardized ($\frac{x - \bar{x}}{\sigma}$) means (± 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.

58 two genotypes (Fig. 5).

59 Add transformations of variables to methods.

60 Genotype indirectly influenced lichen network centralization via the genetically based variation in bark 61 roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and 62 condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} = 0.0343$) both displayed significant responses 63 to tree genotype. None of the other bark traits, 64 pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) 65 or carbon-nitrogen Ratio ($RLRT = 0.0000$, $H^2 = 66 0.0000$, $p\text{-value} = 1.0000$), showed a significant re- 67 sponse to tree genotype and none other than bark 68 roughness were correlated with network similarity 69 (Table 2); therefore, we focused our analysis on bark 70 roughness. We found that bark roughness was sig- 71 nificantly correlated with network similarity (PER- 72 MANOVA: Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, $p\text{-} 73 value = 0.0096$) and other lichen network metrics, 74 including negative correlations with overall network 75 degree ($df = 35$, $t = -2.13$, $r = -0.34$, $p\text{-value} = 76 0.04$) and centralization ($df = 35$, $t = -2.52$, $r = 77 -0.39$, $p\text{-value} = 0.02$). In other words, trees with 78 more similar levels of bark roughness tended to have 79 lichen interaction networks with similar structure. 80 To quantify the genetic bases of this effect of bark 81

82 roughness on network structure, we used the residual 83 values from regressions of network degree and cen- 84 tralization in tests of the effect of tree genotype and 85 found no significant effect of tree genotype for either 86 degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) 87 or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 88 1.0000$), suggesting that the observed relationship 89 between bark roughness and lichen network structure 90 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.

Discussion

We found that tree genotype influenced lichen net- 394 work structure in the experimental cottonwood forest. 395 Network similarity and metrics of network structure 396 tended to be more similar on trees of the same geno- 397 type. Generally, this genetic effect was manifested in 398

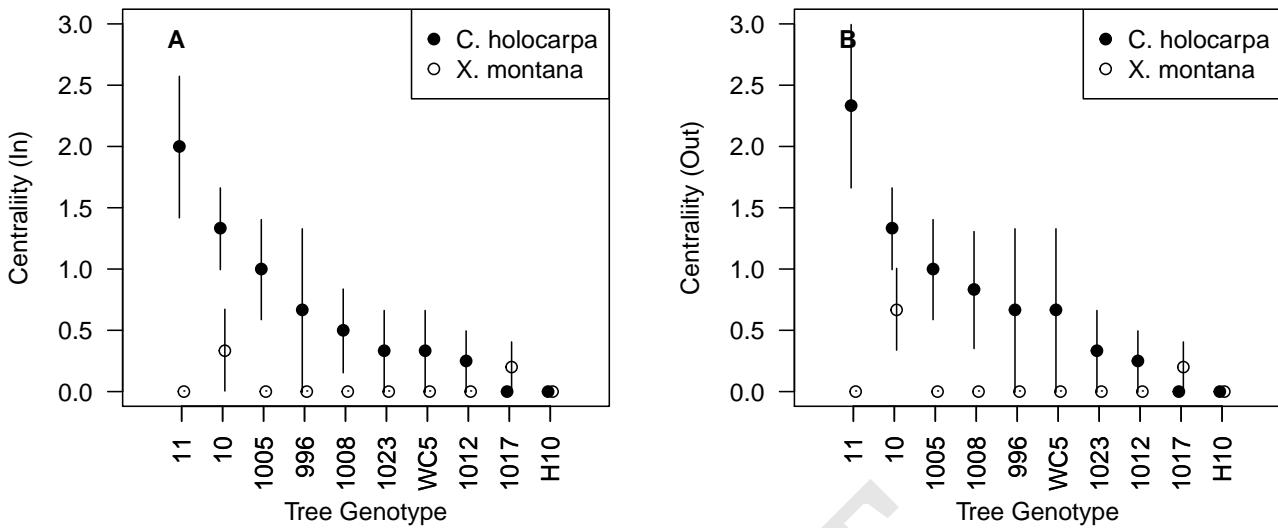


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

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 (41), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (16); 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.

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

Elaborate on the importance of identifying the species/node level patterns in network structure response to genotype.

What is the relationship between tree growth, bark roughness and disruption of the lichen community? Tree grow and the bark expands over time, causing

furrows.

Does bark roughness increase habitat and decrease interactions?

There are important functional ramifications of genetically based variation in network structure. First, even if the composition of the communities is the same among individuals and genotypes, interactions may not be. We didn't observe compositional differences using the same data from which the lichen networks were derived. If we only had our composition dataset from this study, we would have concluded no response of the lichen community to tree genotype, even though the underlying interactions among lichen species does vary among genotypes. Community composition of lichen has previously been observed to be different among tree genotype in the same experimental garden, though this was observed with a larger sampling of total area and quadrats per tree. Regardless, this could result in a situation in which abundance based investigations of community-level genetic effects may miss important variation in the interactions among individuals in these communities, leading to an underestimate of genetic effects in ecosystems. It is possible that these underlying differences in interactions among lichen could lead to differences in community composition at a future point in time, however, this is not needed

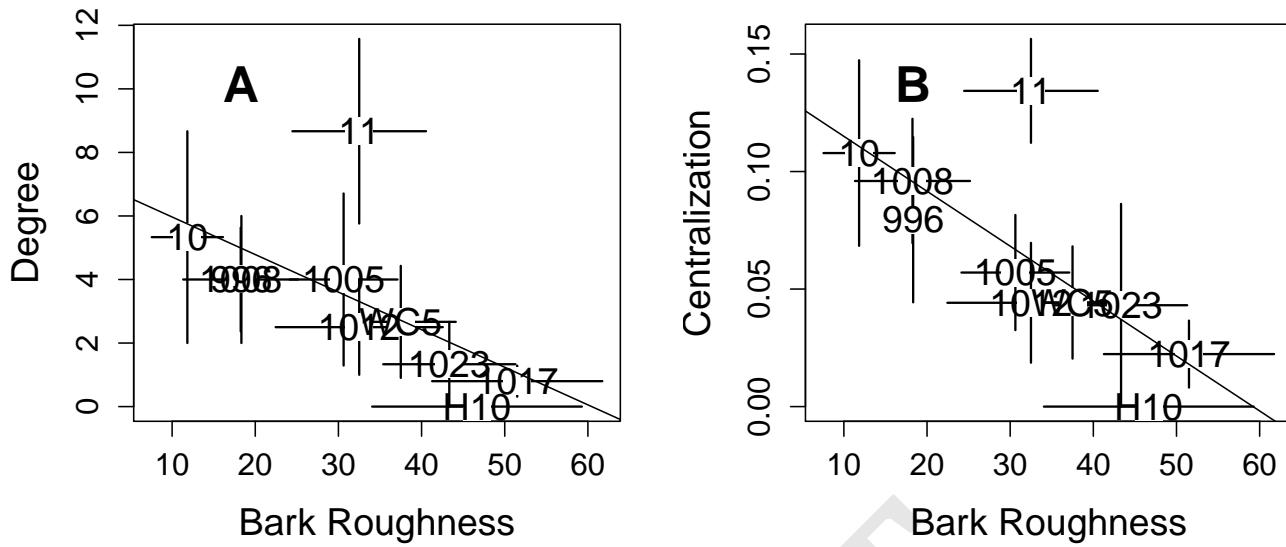


Fig. 6. Bivariate plots of the relationship between bark roughness and three network metrics: A) degree and B) centralization. Each plot displays the genotype mean \pm 1 S.E. for both variables and a least-squares regression calculated using the genotype means.

452 for evolutionary dynamics to play out.

453 Second, following on the previous point, genetic
454 diversity could be influencing the stability of com-
455 munities through the effects on the structure of in-
456 teractions. Some network structures are likely to be
457 more stable, either in response to disturbance or via
458 self-organized dynamics. For example, centralized
459 networks, although more efficient, are theorized to
460 be more susceptible to targeted attacks on the center
461 of the network. For example, consider a forest with
462 two genotypes that support lichen communities that
463 are similar in total abundances of each species but
464 differ in terms of the structure. Extensions of game
465 theory to evolutionary biology have demonstrated
466 that network structure can lead to variation in evo-
467 lutionary dynamics. Some structures tend toward
468 dominance and dampening of selection, while others
469 lead to amplification of selection (Newman). One
470 class of networks that are theorized to have amplifying
471 effects on networks have "star" shapes with one or
472 a few species at the center and radiating interactions
473 out from the central core (Leiberman). This is struc-
474 turally what we have observed with the networks that
475 tend to occur on some of the genotypes in our study,
476 i.e. the more centralized networks. It is possible that
477 these more centralized networks could function as
478 hot-spots of evolutionary dynamics resulting from

479 the amplifying effect the network structure fostered
480 on that tree genotype.

481 There are several important points to consider
482 with regard to the generalization of the observed
483 genetically based response of the lichen networks.
484 Body size and sessile nature of lichen important to
485 observing genotype responses. As bark lichen in-
486 dividuals do not move, but grow in a largely two
487 dimensional plane, these communities and their in-
488 teractions occur in the highly localized context of
489 the tree's bark surface. Lichen individuals are many
490 orders of magnitude smaller than the tree individual
491 and the life-span of a tree is many times that of a
492 lichen. For these reasons, any genetic effects on these
493 communities is not damped by the movement of
494 individuals and the mixing of the effect of different
495 tree genotypes on the lichen community, as might
496 occur for more mobile species (e.g. insects and birds).
497 We only looked at lichen, other species whose distri-
498 bution, abundance or interactions respond to tree
499 genotype, such as epiphytic plants (e.g. moss and
500 liverworts), algae or insects, could be playing a role.
501 Other traits could also be playing a role, such as
502 traits that are correlated with bark roughness, such
503 as micro-aspect, albedo, moisture, etc.

504 Bark roughness could possibly be serving the role
505 that other lichen play in facilitating the success of

506 new propagule attachment and the growth of establishing thalli. This is supported by the patterns over-
507 all being positive, including *C. holocarpa* centrality.
508 We did not observe specific microscopic dynamics,
509 such as photobionts, mycobionts, endolichenic fungi
510 and bacteria, but variation in these underlying inter-
512 actions could also be playing a role. Although we can
513 not rule out the possibility that other unmeasured
514 tree traits or organisms correlated with bark rough-
515 ness are underlying the observed patterns in bark
516 lichen network structure, substantial research sup-
517 ports the importance of genetically based tree traits
518 for communities and ecosystems (19), and in par-
519 ticular bark roughness for bark lichen communities
(16, 31, 41).

521 In the present study, lichen cover, lichen species
522 richness and composition were not responsive to tree
523 genotype, unlike what was found in (16). This is
524 likely, at least in part, the result of differences in
525 sampling method and the choice of genotypes sam-
526 pled leading to overall higher abundances of observed
527 lichens. In the current study mean % total lichen
528 cover among genotypes ranges from 60-93% cover;
529 whereas the range reported in (16) is 0.86-18.73%.
530 The previous study used a visual estimation method,
531 unlike the current study, which observed lichen at
532 the scale of 1 cm² cells, which could over-estimate
533 cover depending on the frequency at which actual
534 thallus size was less than 1 cm². The previous study
535 used samples from both the northern and southern
536 aspects of each tree; whereas, the current study only
537 observed lichen on the northern aspect. Also, our
538 current results are likely different from the previous
539 study because the current study selected genotypes
540 that tended to have bark lichen, with the interest
541 of focusing on generating networks for comparison.
542 These differences do not negate the findings of either
543 study but is important to explain the differences
544 in the findings, particularly in the community-level
545 effects of tree genotype.

546 **Implications for Interspecific Indirect Genetic Ef-
547 ffects (IIGEs).** Interspecific indirect genetic effects
548 (IIGE) theory as provided a quantitative framework
549 within which to approach evolutionary theory at
550 higher levels of biological organization: from pop-
551ulations to communities and ecosystems. To date,
552 this theory has focused on modeling the strong ef-
553 ffects of foundation species (40, 42), but it has not
554 yet integrated developments in the ecological or evo-

555 lutionary network theory literature. This is to say
556 that it has not developed a way to examine com-
557 plex interactions among species; however, previous
558 studies have demonstrated this network context is
559 likely to be important, as altering the structure of
560 interaction networks provides a means for genetic
561 effects to be dampened or magnified within the sys-
562 tem of interacting species. For example, (8) showed
563 that the genetics based interactions of aphid resis-
564 tant and aphid susceptible trees resulted in different
565 interaction networks of their associated arthropod
566 communities composed of 139 species. At the scale
567 of ecosystems, trophic networks or food webs direct
568 and control the rates of energy and nutrient flux (43).
569 Furthermore, in a predator-prey-plant study, Smith
570 (23), showed that the interactions among species
571 across trophic levels depended on plant genotype.
572 Also, work by (44-46) observed consistent patterns
573 of centralized interactions of species modules focused
574 around hubs of plant-fungal interactions. In other
575 words, a small number of plant and fungal symbionts
576 tended to have disproportionate numbers of interac-
577 tions with other species and likely are the drivers
578 in determining community assembly, structure and
579 dynamics.

580 The results of the current study provides clear em-
581 perical evidence that networks points to the need to
582 expand IIGEs encompass the structure of interaction
583 networks. Although such a synthesis necessitates
584 a much greater effort than can be afforded in this
585 paper, it is possible to point to several productive
586 pathways forward. In terms of interaction networks,
587 foundation species are relatively central within the
588 system of interactions, that is their direct and/or
589 indirect effects are greater than other species. So,
590 when the more centralized (foundation) species have
591 genetically based interactions, genetic effects will
592 tend to be magnified in the community. Here, we
593 found that even though more abundant or more cen-
594 tralized (i.e. “important”) species were present in
595 the community, their effects were not the main com-
596 ponent responding to genetic effects. Considering
597 the impact of network structure would be a produc-
598 tive path forward for the theoretical development
599 and application of the IIGE concept.

600 With regard to the evolutionary implications of
601 network structure, ecological network studies have
602 focused on asymmetry and the quantification of its
603 structure in communities, with qualitative discus-

sion of the impacts on evolutionary dynamics (? ? ?). More specific predictions, with a quantitative framework, can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities. One seemingly useful direction from evolutionary network developments from game theory is the classification of networks into two general categories, rooted and cyclic, in which rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but these effects do not have connections back to the origins, whereas cyclic networks contain feedbacks to one or more origins. Although it did not explicitly define it in this context, the previous work (20), developed that the structure of the network in the context of a foundation species, such as cottonwoods in which there are demonstrable community level genetic effects, is that of a multiple origin network. This builds on many previous studies demonstrating that the community level effects vary among multiple genotypes. It is not clear what potential there is for feedbacks there are to the origins (e.g. the cottonwood genotypes) from the community, and as such it cannot be determined whether these networks are cyclic or rooted. In other systems, lignicolous lichens can have demonstrable positive effects on the availability of nutrients for the trees that they are associated with, but this has not been measured in the current system. Illucidating the absence and/or presence and quantifying such feedbacks would allow for the determination of the cyclic nature and potential evolutionary dynamics of this system. The presence of feedbacks would provide the potential for non-linear dynamics in which evolutionary effects are dampened or amplified by the structure of the network. For example, a star structure in which there is a primary or core set of central species with feedbacks from the radiating species has been demonstrated to be a structure that amplifies evolutionary dynamics (?). If such feedbacks do not exist, and these sub-networks of the lichen and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to generally promote diversification as variation arising from the shifting distribution of the “roots”, i.e. genotypes; however, loss of genotype/root diversity could lead to fixation of a single genotype in the population and a decrease in community-wide diversity.

Conclusion. Although our study was conducted with a community of lichens, these results should be generalized to other groups of diverse organisms around the world that also exhibit significant genetic signals at the community level (42, 47). 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 (30, 48, 49). 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 (50). 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 (5, 51).

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.

846

847

DRAFT

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

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

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

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

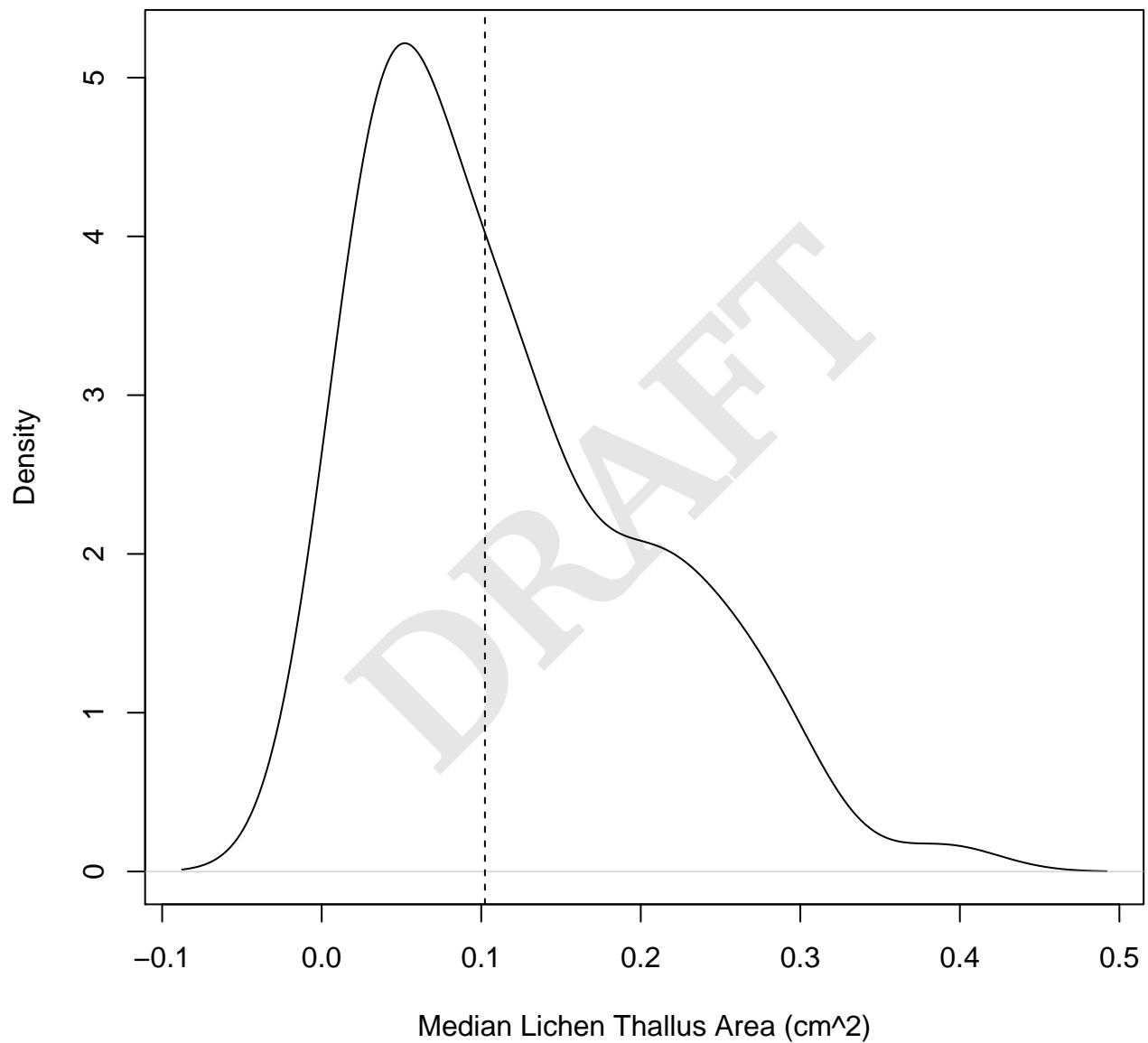


Fig. 1

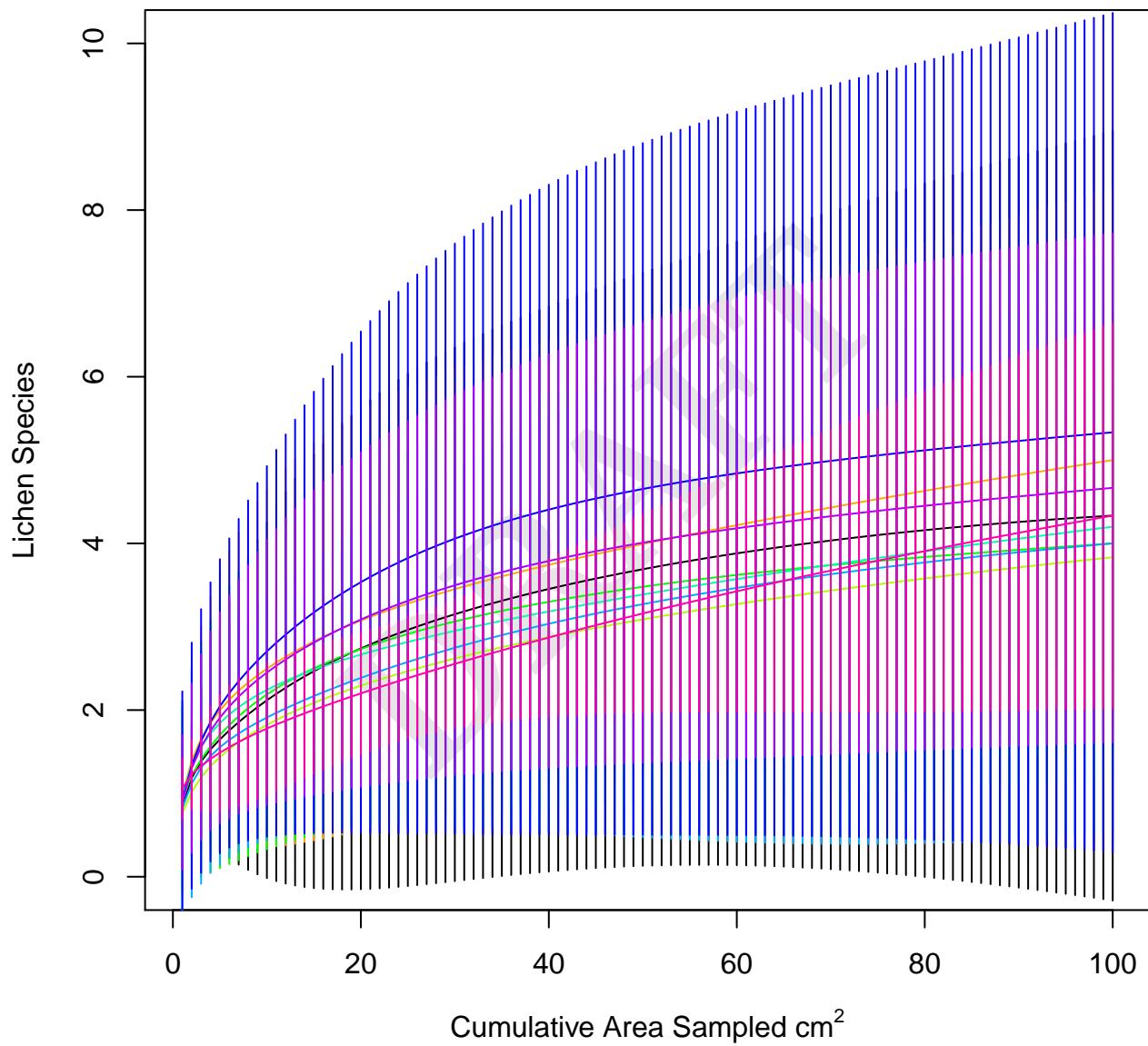


Fig. 2. Species area curve by genotype.

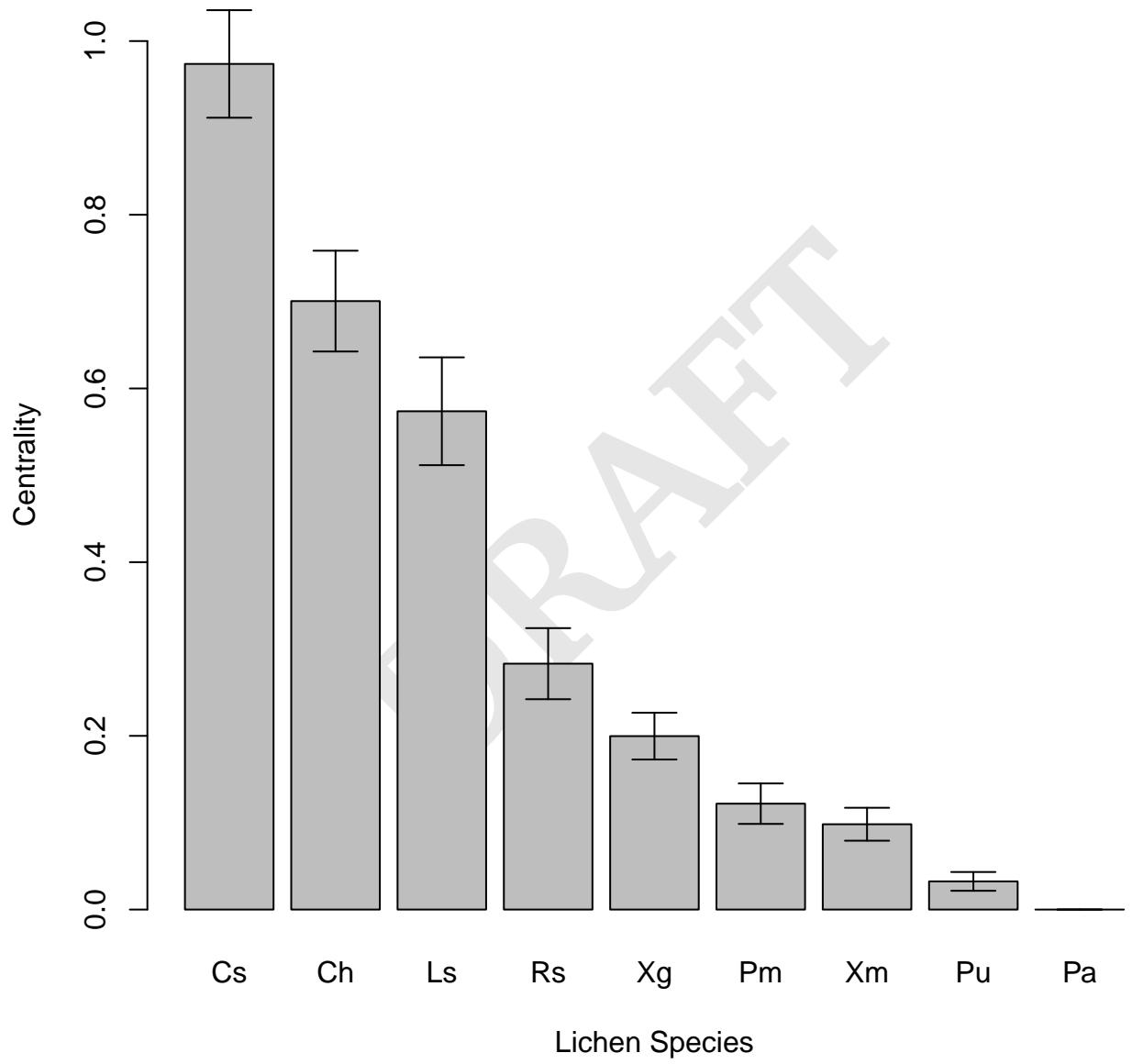


Fig. 3