

1 Genotypic variation in a foundation tree 2 results in heritable ecological network 3 structure of an associated community

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16 ABSTRACT

Biological evolution occurs in ecosystems whereby natural selection defines the structure of ecological networks. Therefore, elucidating the genetic basis to ecological network structure is fundamental to understanding evolution. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that quantified the contribution of phenotypic variation to heritable variation in network structure. To examine this, in a 20+ year common garden we observed nine epiphytic lichen species associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation species. We constructed and conducted genetic analyses of signed, weighted, directed lichen interaction networks. We found three primary results. First, genotype identity significantly predicted lichen network similarity; i.e., replicates of the same genotype supported more similar lichen networks than different genotypes. Second, broad sense heritability estimates showed that plant genotype explained network similarity ($H^2 = 0.41$), degree ($H^2 = 0.32$) and centralization ($H^2 = 0.33$). Third, of several tree phenotypic traits examined, bark roughness was both heritable ($H^2 = 0.32$) and significantly correlated with lichen network similarity ($R^2 = 0.26$). These results support a mechanistic, genetic pathway from variation in a heritable tree trait to ecological network structure and demonstrate that evolution can act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks. Given that network structure has determines system-wide stability and resilience, our findings have important implications for how evolution acts in ecosystems.

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

17 INTRODUCTION

18 Evolution occurs in the context of complex ecological networks. Community genetics
19 studies have shown that genetic variation in foundation species, which have large effects
20 on ecosystems by modulating and stabilizing local conditions Ellison et al. (2005),
21 plays a significant role in defining distinct communities of interacting organisms: such
22 as, endophytes, pathogens, lichens, arthropods, and soil microbes (Busby et al., 2015;
23 Barbour et al., 2009; Lamit et al., 2015a). Multiple studies have now demonstrated that
24 genetic variation influences numerous functional traits (e.g., phytochemical, phenologi-
25 cal, morphological) that in combination result in a multivariate functional trait phenotype
26 (Holeski et al., 2012) in which individual plant genotypes support different communities
27 and ecosystem processes (Bailey et al., 2009; Whitham et al., 2012). Recently, the
28 importance of genetic variation in structuring ecological systems was reviewed, and
29 not only were many instances of strong genetic effects found in many ecosystems but
30 the effect of intraspecific variation was at times greater than inter-specific variation
31 (Des Roches et al., 2018). There is now evidence to support that selection, acting on
32 this heritable variation, tends to occur among groups of species (Wade, 2007) and that
33 genetic variation and phylogenetic relatedness contribute to variation in community
34 assembly (Crutsinger, 2016) and species interactions (Whitham et al., 2006; Bailey et al.,
35 2009; Moya-Laraño, 2011), which shape the structure of ecological interaction networks
36 (Rezende et al., 2007; Guimarães et al., 2007; Gómez et al., 2009). Network theory and
37 evidence from empirical studies in ecology have demonstrated that indirect effects can
38 lead to self-organization, producing sign-changing, amplifying and/or dampening effects
39 (Newman, 2006; Sole and Bascompte, 2006), and other studies have demonstrated
40 that indirect effects of interactions among species can lead to network structures that
41 amplify or dampen the effects of selection, such as the formation of star-like structures in
42 which there is a “central” species or group of species that interact with other, peripheral
43 species, can amplify selection events (Lieberman et al., 2005). Also, work by Toju et al.
44 (2014, 2016, 2017) observed consistent patterns of centralized interactions of species
45 modules (i.e., groups of species that interact more strongly within their group than
46 with other species) focused around hubs of plant-fungal interactions. In other words, a
47 small number of plant and fungal symbionts tended to have disproportionate numbers
48 of interactions with other species and likely are the drivers in determining community
49 assembly, structure and dynamics.

50 Interspecific indirect genetic effects (IIGE) theory (*sensu* Shuster et al. (2006)) in
51 evolutionary biology supports ecological network studies that point to the importance of
52 studying the genetic basis of interaction network structure. Genetic based differences in
53 network structure among individuals can be acted upon by natural selection when there
54 are fitness consequences of different networks of IIGEs, leading to community evolution
55 per Whitham et al. (2020) and, by extension, network evolution. For example, although
56 the analysis was of abundances rather than interaction networks, Gehring et al. (2014,
57 2017) found that the mycorrhizal communities on the roots of drought tolerant and intol-
58 erant trees are dominated by different orders of ectomycorrhizal fungal mutualists that
59 also differ in the benefits they provide that enhance tree performance. Because drought
60 tolerant genotypes are three times more likely to survive record droughts, selection acts
61 both on the tree and its fungal community and with increased drought the community

phenotype has changed over time. Also, in an antagonistic interaction context, Busby et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods in a common garden, the impacts of these strong interactors results in a different and diminished community of arthropods relative to control trees. Thus, selection acting on the tree may alter the network structure of associated communities in which different networks of communities are most likely to survive pathogen outbreaks. Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative fitness of the tree), selection on tree, community or both can change network structure (Whitham et al., 2020) and thereby alter community dynamics.

In this context, the “genetic similarity rule” of community genetics provides a useful framework we can apply to interaction networks at the nexus of ecological and evolutionary dynamics. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, Bangert et al. (2006) observed that individuals genotypes that are more genetically similar will tend to have similar phytochemical traits and thus tend to have similar interactions with other species than individuals that are less similar. Although this is likely to have consequences for interactions and network structure, studies in the network ecology literature generally do not include a genetic component (Lau et al., 2017) and community genetics studies have primarily focused on community composition in terms of the abundance of species (Des Roches et al., 2018). Some studies have examined the effects of genetic variation on trophic chains in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (Bailey et al., 2005; Johnson, 2008; Smith et al., 2011, 2015; Barbour et al., 2016) and generally found that increasing genotypic diversity leads to increased trophic complexity. Only two other studies, that we are aware of, have explicitly examined the effect of genotypic variation on the structure of interaction networks between tree individuals and associated herbivores (Lau et al., 2015; Keith et al., 2017) and both found that genotypic diversity generates increased network modularity (i.e., compartmentalization). However, both of these studies were examining networks at the scale of forest stands, rather than networks associated with individual trees; therefore, neither was able to observe replicated networks in order to statistically test for genetic effects on network structure and quantify the genetic component (i.e., heritable variation) in network structure.

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of tree associated lichens. Using a long-term (20+ years), common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001). We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (Winfrey et al., 2011; Zytynska et al., 2011). Applying a probability-theory based network modeling approach (Araújo et al., 2011), we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks via several network metrics that measure different aspects of network structure at the scale of individual species (i.e., nodes) or the entire network observed on each tree genotype. Given that network theory applications to evolutionary dynamics have pointed to the

importance of network structures that have focal or “central” nodes (e.g., species) (Lieberman et al., 2005), we focused on network metrics that measure centrality for individual species and centralization for whole networks. Both of these metrics measure how much a species is connected in the network relative to other species. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (Lau et al., 2015; Keith et al., 2017; Thompson, 2013; Bascompte et al., 2006). More specifically, based on the community similarity rule Bangert et al. (2006), we hypothesize that trees will co-vary in functional phenotypic traits, such as bark roughness and chemical composition, and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks.

MATERIALS AND METHODS

Study System

The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled. Bark lichens have been intensively sampled in this system and provide an ideal community in which to observe and model interaction networks, as their sessile nature permits accurate identification of individuals and their highly localized, direct contact interactions and slow population turnover rates facilitate the assessment of interactions among lichen species on individual trees (Lamit et al., 2011).

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

Bark Lichen and Trait Observations

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

151 The cell size and checkerboard sampling pattern was chosen to isolate the individuals
152 in each cell. In a previous survey of lichen thallus size in this common garden, we had
153 observed a median thallus size of $0.12 \pm 0.001 \text{ cm}^2$ (1 S.E.) (Supporting Information,
154 Fig. 1). Based on the median thallus size, we expected thalli observed in each cell to
155 generally be spatially independent of thalli present in other cells but exposed to similar
156 micro-environmental conditions created by the bark and the location of the sampling area
157 on an individual tree. Therefore, we were confident in treating the cell-wise observations
158 in quadrats as independent with respect to lichen-lichen interactions. We quantified
159 the texture of the bark in the quadrat is the percent of 1 cm^2 cells with rough bark. In
160 addition to bark roughness, we also measured several bark chemistry traits by taking
161 bark samples immediately adjacent to each quadrat using the methods of Lamit et al.
162 (2011): including, the concentration of condensed tannins, pH and carbon and nitrogen
163 concentrations and pH.

164 **Lichen Network Modeling and Analysis**

165 For each tree, repeated observations of lichen were made in order to construct replicated
166 interaction networks for each genotype. We conducted a modified sampling procedure
167 originally developed by Lamit et al. (2015b) with the addition that we quantified the
168 presence of lichen in the 1 cm^2 cells on individual trees of *P. angustifolia*. Unipartite
169 networks were generated using the conditional probabilities of each species pair, i.e., the
170 probability of observing one species given an observation of another species $P(S_i|S_j)$,
171 based on the method developed by Araújo et al. (2011). To calculate conditional
172 probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and
173 the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species
174 and their co-occurrences. We were then able to calculate the conditional probabilities of
175 each species pair as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, based on the axioms of probability. This yielded
176 a matrix that could possibly be asymmetric, i.e., $P(S_i|S_j)$ does not have to be equal to
177 $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was
178 equal to one for all species present and zero for species that were not observed in any
179 cell.

180 We then applied an analytical procedure to remove non-significant links between
181 species. This procedure determines if the joint probability of a species pair (i.e., $P(S_i, S_j)$)
182 is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as
183 $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences
184 $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of
185 each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the
186 expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability
187 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
188 the observed number of co-occurrence falls outside of the confidence interval, the
189 joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual
190 probabilities (i.e., $P(S_i)P(S_j)$), and the conditional probability reduces to the individual
191 probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair
192 falls outside the confidence interval, the probability that the observation of one species
193 given the other is no different than simply observing that species alone. This enables us
194 to remove links from a given network by re-scaling the resulting conditional probabilities
195 by subtracting the individual probabilities from the conditional probabilities (i.e., how

196 different the conditional probability is from the independent probability), which makes
197 any species with a non-significant conditional probability zero.

198 The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as one species' impact on another
199 with zero being no effect and values less than or greater than zero being negative and
200 positive effects, respectively. Here, we will refer to \mathbf{D} as a signed, weighted interaction
201 matrix. As such, \mathbf{D} has the properties that it can be asymmetric (i.e., D_{ij} does not
202 necessarily equal D_{ji}) and it scales between -1 and 1, and, therefore, does not have the
203 mathematical properties of a probabilistic network (Poisot et al., 2016). Also, as the
204 method does not track individuals within species and interactions such as competitive
205 exclusion or facilitation within species would result in the same species being observed.
206 Therefore, the results of intra-specific interactions always results in the same species
207 being observed and a resulting $D_{ii} = 0$.

208 Network Metrics

209 To quantify the structural variation of lichen networks we calculated several metrics
210 at both the node and whole-network level. For individual nodes (i.e., species) in each
211 network, we calculated both the degree and the Freeman's centrality (Butts, 2019). We
212 also calculated two similar global network metrics: degree and centralization. The first
213 was network degree, which is a count of the total number of links in a network. As
214 the networks contained not only positive and negative connections but also directional
215 connections (both in-coming and out-going), we calculated the same network metrics
216 for all combinations of these types of connections in each network, accounting for
217 differences in sign through the application of recently developed metrics that incorporate
218 sign information from signed, weighted, directed networks (Everett and Borgatti, 2014).
219 Although there are many more possible network metrics that could have been examined,
220 we chose to focus on a restricted set for the sake of clarity. In addition, degree and
221 centrality form the basis of many other network metrics.

222 Statistical Analyses, Software and Data

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

231 For multivariate response variables, such as lichen community composition and
232 network structure, we used distance based multivariate statistical approaches, including
233 Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify
234 the similarity of lichen networks among individual trees, we calculated the pairwise
235 Euclidean distance of the \mathbf{D} interaction matrices among all pairs of trees. For visualization
236 of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS)
237 (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of these multi-
238 variate responses and fitted vectors for continuous predictor variables to the ordinated
239 values (Oksanen et al., 2019). Using random initial configurations with a maximum of

240 500 iterations and a change in stress threshold of less than 10^{-12} . Final configurations
241 has the lowest stress with at most a stress level of 0.10.

242 For each network, we also calculated metrics that measure different structural aspects.
243 Although there are many other metrics, for the sake of simplicity we focus on a subset
244 that represent several interesting features of network structure (see Lau et al. (2017)).
245 We calculated the number of interactions or “links” in each network, which provides
246 a measure of the size of the network Lau et al. (2015); Borrett and Lau (2014). We
247 also calculated the centralization of each network, which measures the evenness of
248 the distribution of interactions among the species in the network (Butts, 2019). In a
249 network with a low level of centralization species have similar amount of interaction in
250 the network, while a network with a high level of centralization tends to have one or
251 small number of species that interact with other species. We used a related function to
252 calculate the centrality of each species (i.e., node level centrality) in each network as
253 well. To calculate separate metrics for positive and negative links, we applied methods
254 for calculating the centrality accounting for the sign differences (Everett and Borgatti,
255 2014) using the `signnet` package (Schoch, 2020).

256 For all tests where genotype was used as a predictor, we quantified the heritability
257 of the response variable. Because the trees in the garden were clonal replicates of each
258 genotype, we calculated broad-sense heritability, which is the genotypic variance divided
259 by the total phenotypic variance (Conner and Hartl, 2004). This can be interpreted as a
260 measure of the phenotypic variance due to genotypic variation. We also apply this to
261 the community genetics context as the variance in *extended* phenotypic variance due to
262 genotypic variation (Whitham et al., 2006, 2012; Crutsinger, 2016). For the multivariate
263 analyses, where we employ PERMANOVA, we followed the methods of Shuster et al.
264 (2006) to adjust the degrees of freedom for unbalanced genotype replicates.

265 All code and data for the project are openly available online. Code and data are
266 available at github.com/ecgen/comgen. The project is also archived via Zenodo
267 at zenodo.com/doi/XXXXXX. All analyses were conducted using the programming
268 language R version 3.6.1 (R Development Core Team 2019).

269 RESULTS

270 Tree genotype influenced lichen network structure and multiple lichen network metrics
271 were heritable. Tree genotype significantly predicted the structural similarity of lichen
272 networks (PERMANOVA: Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$) (Fig. 4).
273 Overall network level metrics responded significantly to tree genotype (Table 1), in-
274 cluding network degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} = 0.0255$) and centralization
275 including both in-coming and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} =$
276 0.0184) or when separated into in-coming only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} =$
277 0.0190) or out-going only ($RLRT = 3.8615$, $H^2 = 0.3193$, $p\text{-value} = 0.0205$). Metrics
278 including only positive links also showed a significant effect of tree genotype, including
279 positive degree ($RLRT = 3.6925$, $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
280 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} = 0.0142$) Metrics calculated with
281 negative links were not significant, including degree (negative) ($RLRT = 0.0327$, $H^2 =$
282 0.0318, $p\text{-value} = 0.3859$) and both in-coming (negative) ($RLRT = 0.3304$, $H^2 = 0.1057$,
283 $p\text{-value} = 0.2508$) and out-going centralization (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$,

284 p -value = 0.3446).

response	df	statistic	H2	p-value
Lichen Network Similarity	9	3.5821	0.41	0.0537
Degree		3.5175	0.32	0.0255
Degree (positive)		3.6925	0.32	0.0229
Degree (negative)		0.0327	0.03	0.3859
Centralization		4.0444	0.33	0.0184
Centralization In-Degree		4.4812	0.35	0.0142
Centralization In-Degree (positive)		3.9852	0.33	0.0190
Centralization In-Degree (negative)		0.3304	0.11	0.2508
Centralization Out-Degree		3.8615	0.32	0.0205
Centralization Out-Degree (positive)		3.5585	0.31	0.0248
Centralization Out-Degree (negative)		0.0862	0.05	0.3446

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

285 The genetic response of network centralization was driven by variation in *Caloplaca*
286 *holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$,
287 p -value < 0.0001). *Caloplaca holocarpa* centrality was the main species to exhibit
288 a significant response to tree genotype in terms of positive centrality for both the in-
289 coming ($RLRT = 3.61$, $H^2 = 0.32$, p -value = 0.0240) and out-going ($RLRT = 3.13$, H^2
290 = 0.30, p -value = 0.0327) perspectives, but not for either negative centrality metrics
291 in-coming ($RLRT = 0$, $H^2 = 0$, p -value = 1) or out-going ($RLRT = 0$, $H^2 = 0$, p -value =
292 0.4543). None of the other species' centralities showed a genotypic response (Supporting
293 Information, Fig. 2) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, p -value
294 = 0.0375); however, the centrality of *X. montana* was much lower overall relative to *C.*
295 *holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes
296 (Fig. 5).

297 Genotype indirectly influenced lichen network centralization via the genetically
298 based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$,
299 $H^2 = 0.3221$, p -value = 0.0113) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$,
300 p -value = 0.0343) both displayed significant responses to tree genotype. None of the
301 other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, p -value = 1.0000) or carbon-nitrogen
302 ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, p -value = 1.0000), showed a significant response
303 to tree genotype and none other than bark roughness was correlated with network
304 similarity (Table 2); therefore, we focused our subsequent analyses on the indirect
305 effect of genotype on lichen network structure via bark roughness. We found that
306 bark roughness was significantly correlated with network similarity (PERMANOVA:
307 Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, p -value = 0.0096) and other lichen network metrics,
308 including negative correlations with overall network degree ($df = 35$, $t = -2.13$, $r =$
309 -0.34, p -value = 0.04) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, p -value = 0.02).
310 In other words, trees with more similar levels of bark roughness tended to have lichen
311 interaction networks with similar structure. To quantify the genetic bases of this effect
312 of bark roughness on network structure, we used the residual values from regressions of
313 network degree and centralization in tests of the effect of tree genotype and found no

314 significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 = 0.00$, *p-value*
 315 = 1.0000) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, *p-value* = 1.0000), suggesting
 316 that the observed relationship between bark roughness and lichen network structure was
 317 largely genetically based (Fig. 6).

	df	SumOfSqs	R2	F	Pr(>F)
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

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

318 DISCUSSION

319 We found that tree genotype influenced lichen network structure in the experimental
 320 cottonwood forest. Network similarity and metrics of network structure tended to be
 321 more similar on trees of the same genotype. Generally, this genetic effect was manifested
 322 in positive interactions and largely driven by *C. holocarpa*. The genetically based trait,
 323 bark roughness, was the only trait observed to effect network variation, largely via shifts
 324 in positive in-coming and out-going interactions. Chemistry traits, whether genetically
 325 based, such as tannin concentration, or not, were not significantly correlated with lichen
 326 network structure. Bark roughness has been demonstrated previously to be under strong
 327 genetic control (Bdeir et al., 2017), and bark roughness has also been shown to be an
 328 important tree trait influencing bark lichens (Lamit et al., 2015b); however this is the first
 329 demonstration of a link from genetics to lichen network structure. As such these results
 330 have important implications for the potential influence of genetically based variation in
 331 ecosystems with networks of interacting species.

332 Implications of the Heritability of Interaction Network Structure

333 Significant heritability of lichen interaction network structure is in line with the genetic
 334 similarity rule, networks observed on trees of the same genotype tended to be struc-
 335 turally similar. Although previous studies have examined aspects of networks, such
 336 as trophic (Barbour et al., 2019) and forest stand-level interaction network structure
 337 (Lau et al., 2016; Keith et al., 2017), this is the first study that we are aware of to
 338 examine the heritability of network structure with replicated networks at the genotype
 339 scale. Previous work in the evolution of ecological networks have primarily focused on
 340 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,
 341 2018; Harmon et al., 2019) or have been simulation based individual-level models that
 342 integrate intraspecific variation to the species level (Maliet et al., 2020), even though
 343 recent syntheses ave pointed to the importance of processes operating across scales of
 344 organization (Guimarães, 2020). There are two important functional ramifications of
 345 genetically based variation in network structure.

346 First, A genetic basis to network structure suggests that some amount of interaction
347 network complexity is determined and therefore could be predicted. Variation in space
348 and time create variation in ecological networks that influences evolutionary dynamics
349 via shifts in ecological dynamics, such as population demographics (Guimarães, 2020).
350 Given that ecosystems are comprised of hundreds and thousands of species, each having
351 a multitude of interactions, the potential to find traction for making predictions in the
352 context of ecological, let alone evolutionary, dynamics seems daunting. The promise
353 of predictability lies in the presence of assymmetries in ecosystems that contribute to the
354 occurrence of foundation species, such as hierarchy and nestedness created by body size
355 differences or life-history strategies, has been widely observed (Ellison et al., 2005).
356 The second part is that heritability (i.e., genetic determination) means that there is
357 structure in the spatial or temporal variation that is created by individuals of foundation
358 species whose traits are in part determined by underlying trait differences. Although this
359 variation is inherently a function of both genetics and environmental effects (Conner
360 and Hartl, 2004), the community and network level effects are also a function of the
361 scale of the interaction (Shuster et al., 2006).

362 Second, even if the composition of the communities is the same among individuals
363 and genotypes, interactions may not be. We didn't observe compositional differences
364 using the same data from which the lichen networks were derived. If we only had our
365 composition dataset from this study, we would have concluded no response of the lichen
366 community to tree genotype, even though the underlying interactions among lichen
367 species does vary among genotypes. As such differences in network structure could
368 occur without observable differences in species richness or community composition,
369 which have been the primary focus of almost all previous community genetics studies
370 (Des Roches et al., 2018). Community composition of lichen has previously been
371 observed to be different among tree genotype in the same experimental garden (Lamit
372 et al., 2011, 2015b), the difference between the present study is likely a result of
373 differences in sampling method and the choice of genotypes leading to overall higher
374 abundances of observed lichens to assure the possibility of observing lichen interactions.
375 The previous study also used a visual estimation method, unlike the current study, which
376 observed lichen at the scale of 1 cm² cells, which could over-estimate cover depending on
377 the frequency at which actual thallus size was less than 1 cm², as well as both the northern
378 and southern aspects of each tree. These differences do not negate the findings of either
379 study. The present study's finding of differences in network structure without significant
380 compositional differences points to the importance of quantifying how network structure
381 changes in response to genetic variation in order to fully understand evolutionary
382 dynamics in complex communities. Having not observed a compositional effect of tree
383 genotype without measuring the network structure could lead to the conclusion of no
384 genetic effect on the community, even though differences in network structure are leading
385 to altered, local evolutionary dynamics. It is possible that these underlying differences
386 in interactions among lichen could lead to differences in community composition at
387 a future point in time via there effects on species abundances (Shuster et al., 2006);
388 however, this is not needed for evolutionary dynamics to play out via selection that leads
389 to shifts in trait distributions without shifting species abundance distributions, which is
390 possible under stabilizing, disruptive and directional selection (Conner and Hartl, 2004),
391 so long as the relative abundances of each species is imperceptibly changed. Thus, it is

392 imperative that further community genetics research assess or at least be aware of the
393 potential effects of variation in interactions and not just observe species abundances,
394 otherwise community level genetic effects may be underestimated, especially when
395 cumulative interaction effects are taken into account (Borrett et al., 2007).

396 **Evolutionary Implications of a Genetic Basis to Network Structure**

397 Intra-specific diversity could be creating lichen metacommunities on individual trees
398 that form interaction modules with different dynamics. When communities are com-
399 prised of individuals who's habitat is primarily determined by another organism, these
400 communities inherently form modules within the larger ecosystem, as they tend to
401 interact more with each other than with other individuals (Lau et al., 2017). Our study
402 demonstrates that the environmental differences determined by the genetic variation
403 within a single species can create differences that not only impacts community composi-
404 tion, as repeatedly demonstrated in other community genetics studies (Whitham et al.,
405 2006; Des Roches et al., 2018), but also the structure of interactions among individuals
406 within these modules. Some network structures are likely to be more stable, either in
407 response to disturbance or via self-organized dynamics. For example, centralized net-
408 works, although more efficient, are theorized to be more susceptible to targeted attacks.
409 As mentioned previously, one class of networks that are theorized to have amplifying
410 effects on networks have centralized "star" shapes with one or a few species at the center
411 and radiating interactions out from the central core (Lieberman et al., 2005). This is
412 structurally what we have observed with the networks that tend to occur on some of the
413 genotypes in our study, i.e., the more centralized networks. It is possible that these more
414 centralized networks could function as hot-spots of evolutionary dynamics resulting
415 from the amplifying effect the centralized network structure found on that tree genotype.

416 Ecological network studies have focused on asymmetry and the quantification of
417 its structure in communities, with qualitative discussion of the impacts on evolutionary
418 dynamics (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães et al., 2011;
419 Thompson, 2013). More specific predictions, within a quantitative framework, can
420 be found in applications of evolutionary game theory, and although developed at the
421 population scale, such theory can apply to communities. One seemingly useful direction
422 from evolutionary network developments from game theory is the classification of
423 networks into two general categories, rooted and cyclic, in which rooted networks have
424 interactions in which evolutionary effects emanate from one or multiple origins but these
425 effects do not have connections back to the origins, whereas cyclic networks contain
426 feedbacks to one or more origins. Although it did not explicitly define it in this context,
427 the previous work of Lau et al. (2017) developed the perspective that the structure of the
428 network in the context of a foundation species, such as cottonwoods in which there are
429 demonstrable community level genetic effects, is inherently created when trait variation
430 among genotypes of a foundation species has ecological effects on associated species.

431 This builds on many previous studies demonstrating that the community level effects
432 vary among multiple genotypes. It is not clear what potential there is for feedbacks to
433 the origins (e.g. the cottonwood genotypes) from the community, and as such it cannot
434 be determined whether these networks are cyclic or rooted. In terrestrial ecosystems,
435 lichen play important ecological roles, such as substrate stabilization (Root et al., 2011)
436 and nutrient fixation (Nelson et al., 2018). In some systems lignicolous lichens can

437 have demonstrable effects on the availability of nutrients for the trees that they are
438 associated with (Norby and Sigal, 1989), although this has not been measured for
439 the lichen in the current study's system^q. Elucidating the absence and/or presence
440 of and quantifying such feedbacks would allow for the determination of the cyclic
441 nature and potential evolutionary dynamics of this system. The presence of feedbacks
442 would provide the potential for non-linear dynamics in which evolutionary effects are
443 damped or amplified by the structure of the network. For example, a star structure in
444 which there is a primary or core set of central species with feedbacks from the radiating
445 species has been demonstrated to be a structure that amplifies evolutionary dynamics
446 (Lieberman et al., 2005). If such feedbacks do not exist, these sub-networks of the lichen
447 and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to
448 generally promote diversification as variation arising from the shifting distribution of the
449 "roots", i.e., genotypes; however, loss of genotype/root diversity could lead to fixation
450 of a single genotype in the population and a decrease in community-wide diversity.
451 However, such feedbacks to tree fitness are not necessary for evolutionary dynamics to
452 play out within the lichen networks through the effects of altered network structure on
453 lichen interaction outcomes, such as competitive exclusion leading to selection.

454 Since lichen are multi-species complexes, there is also the potential for evolutionary
455 dynamics to shift within the context of the lichen symbiosis. There is substantial
456 evidence that lichen have served as the "cradle of symbiotrophic fungal diversification"
457 (Arnold et al., 2009) and recent research has shown significant network structure of
458 endolichenic fungi and lichen collected from across North America (Chagnon et al.,
459 2016). Analysis of the structure of ecological networks has generally supported the
460 conclusion that nestedness, or the degree to which species tend to interact with similar
461 subsets of the community, tends to promote stability in mutualistic, primarily bipartite
462 (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic
463 networks (Elias et al., 2013; Grilli et al., 2016). Although there is growing evidence
464 that the nestedness of mutualistic networks is not necessarily the result of selection for
465 systems-level properties that promote stability but could be either product of asymptotic
466 abundance distributions leading to un-even interaction frequencies (Staniczenko et al.,
467 2013) and/or a by-product of selection and divergence creating network "spandrels" in
468 ecosystems (Valverde et al., 2018), this does not preclude the functional consequences
469 of network structure but rather the developmental or evolutionary processes that have
470 produced the structure. In the present study, we did not examine nestedness or modularity
471 of the lichen networks as we could not find metrics for analyzing networks that are
472 not only weighted and directed but also signed. Hopefully future network theoretic
473 developments will make the appropriate metrics available to conduct these analyses.

474 **Implications for Interspecific Indirect Genetic Effects (IIGEs)**

475 Interspecific indirect genetic effects (IIGE) theory provides a quantitative framework
476 within which to approach evolutionary theory at higher levels of biological organization:
477 from populations to communities and ecosystems. To date, this theory has focused
478 on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham
479 et al., 2012), but it has not yet integrated developments in the ecological or evolutionary
480 network theory literature. This is to say that it has not developed a way to examine
481 complex interactions among species; however, previous studies have demonstrated this

482 network context is likely to be important, as altering the structure of interaction networks
483 provides a means for genetic effects to be dampened or magnified within the system
484 of interacting species. For example, Keith et al. (2017) showed that the genetics based
485 interactions of aphid resistant and aphid susceptible trees resulted in different interaction
486 networks of their associated arthropod communities composed of 139 species. At the
487 scale of ecosystems, trophic networks or food webs direct and control the rates of energy
488 and nutrient flux (Borgatti and Everett, 2006). Furthermore, in a predator-prey-plant
489 study, Smith et al. (2011) showed that the interactions among species across trophic
490 levels depended on plant genotype.

491 The results of the current study provides clear empirical evidence that variation
492 in network structure can be genetically based (i.e., heritable) and points to the need
493 to expand IIGEs encompass the structure of interaction networks. Although such
494 a synthesis necessitates a much greater effort than can be afforded in this paper, it
495 is possible to point to several productive pathways forward. In terms of interaction
496 networks, foundation species are relatively central within the system of interactions,
497 that is their direct and/or indirect effects are greater than other species. So, when the
498 more centralized (foundation) species have genetically based interactions, genetic effects
499 will tend to be magnified in the community. Here, we found that even though more
500 abundant or more centralized (i.e., “important”) species were present in the community,
501 their effects were not the main component responding to genetic effects. Considering
502 the impact of network structure would be a productive path forward for the theoretical
503 development and application of the IIGE concept.

504 **Applicability to Other Systems**

505 In attempting to apply these findings to other systems, it is important to consider the
506 spatial and temporal scaling of genetic effects. In the present study, the sessile nature of
507 lichens means that individuals, and potentially multiple generations, live their entire lives
508 on a single tree. As such, our study examines one scaling of a genetic effect, in which
509 the phenotype of a single tree individual (i.e., tree genotype) has complete influence
510 on the community with little to no effect of other tree individuals in the population.
511 The extreme from this would be where the associated community moved among and
512 interacted with not only other community members but also multiple tree individuals at a
513 high rate, as would be the case with free-living animals (e.g. flying insects). In the latter
514 case, the effect of tree genetics would then be the integral effect of all the tree individuals
515 in the population, and, all other factors being equal, any one tree genotype would have a
516 lower effect on associated community. In reality, ecosystems are a mixture of species
517 of different body sizes and life-histories, and, as such, vary in the degree to which
518 they interact with other organisms, which is the basis of the theory of the geographic
519 mosaic of co-evolution (Thompson, 2013; Thompson et al., 2013). It is now important to
520 consider how the impacts of genetic effects on the network structure of sub-groups, such
521 as lichens, may or may not propagate through the ecosystem to more mobile organisms.
522 As developed previously, the degree to which a genetic effect influences the community
523 is a function of the fidelity of the genetic effect (i.e., heritability) and both the frequency
524 and the intensity of the interaction (Shuster et al., 2006). One possible path forward is for
525 future work to extend the many previous community genetics studies that have focused
526 on sessile organisms, such as galling insects (Bailey et al., 2005; Whitham et al., 2006;

527 Crutsinger et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify the frequency
528 of these interactions in the context of the larger community. This would provide an
529 estimate of the relative impact of these focal, often termed foundation, species. In
530 addition, community genetics theory has only considered first order interactions, i.e.,
531 between two organisms (Shuster et al., 2006; Whitham et al., 2012, 2020). Given that
532 network structure could be influenced by genetic effects, as evidenced by the present
533 study, assessing higher order interactions could provide a path forward for theoretical
534 advances that could help with identifying important characteristics of sub-groups to
535 focus on in empirical studies.

536 Although our study was conducted with a community of lichens, these results can
537 be generalized to other groups of diverse organisms around the world that also exhibit
538 significant genetic signals at the community level (Rowntree et al., 2011; Whitham
539 et al., 2012). However, there are important points to consider when extending the
540 observed genetically based response of the lichen networks to other systems. As
541 bark lichen individuals do not move, but grow in a primarily two dimensional plane,
542 these communities and their interactions occur in the highly localized context of the
543 tree's bark surface. Lichen individuals are also many orders of magnitude smaller
544 than the tree individual in this system (Lamit et al., 2011). For these reasons, the
545 genetic effects on these communities is not damped by the movement of individuals
546 and the mixing of the effect of different tree genotypes on the lichen community, as
547 might occur for more mobile species (e.g. insects and birds). Relatedly, we only
548 examined lichen in this study, and other species whose distributions, abundances and/or
549 interactions vary in their response to tree genotype, such as animals that may also impact
550 lichen communities, could be playing a role that we did not examine. For example, an
551 analysis of the multivariate correlations of different components of the community in
552 this system demonstrated significant patterns of genetic co-responses to tree genotype,
553 supporting the non-mutually exclusive possibilities of shared responses to tree genotype
554 or tree genotypic effects on interactions among these sub-communities (Lamit et al.,
555 2015a). As such, although we can not rule out the possibility that other unmeasured
556 tree traits or organisms correlated with bark roughness are underlying the observed
557 patterns, substantial research supports the importance of genetically based tree traits for
558 communities and ecosystems (Des Roches et al., 2018), and in particular bark roughness
559 for bark lichen communities (Bdeir et al., 2017; Lamit et al., 2011, 2015b).

560 These findings also have implications for our understanding of community assembly.
561 Models based on neutral theory have been developed that can reconstruct interactions
562 networks with similar structural characteristics to those observed in real ecosystems
563 (Coelho and Rangel, 2018). The findings of our study support the possibility that,
564 although communities and their interaction networks may assemble as a result of
565 conditions that are entirely agnostic to functional variation, if there are strong ecological
566 assymmetries, such as the case in foundation species systems, then spatial and temporal
567 variation in network structure will arise as a result of trait variation within the foundation
568 species. Taking even the extreme case, even when such genetically based variation is the
569 result of "neutral" evolutionary processes (e.g., genetic drift), as long as resulting genetic
570 diversity produces ecological relevant phenotypic diversity, then network structure will
571 still have a genetic basis. Given that ecosystems with large assymmetries seem to be
572 the rule rather than the exception for ecosystems (Ellison et al., 2005; Santamaría and

573 Rodríguez-Gironés, 2007; Staniczenko et al., 2013; Dormann et al., 2017; Coelho and
574 Rangel, 2018), the results of our study are likely to be broadly applicable and provides
575 further support for the conclusion that the community context of evolutionary dynamics
576 at either micro- or macro-evolutionary scales (Weber et al., 2017; Harmon et al., 2019)
577 should not be ignored. As genetic variation is inherent to biological systems, it would
578 now seem that the adage “you can’t be neutral on a moving train” might well apply to
579 the evolutionary dynamics of ecosystems that are comprised of networks of interacting
580 species.

581 Conclusion

582 In the face of the high degree of complexity and potential context dependency of
583 ecological processes, the current study points to the utility of considering the spatial
584 and temporal scales of interactions, as discussed in previous studies (Bangert et al.,
585 2006; Zook et al., 2010; Zytnyska et al., 2012). In the present research, we found that
586 the assembly of ecological networks can have a measurable genetic basis depending
587 on the spatial scale of interactions, due in part, to assymetries in size and longevity of
588 organisms. The importance of the scale of network organization to create hierarchical
589 structure (Guimarães, 2020) and the potential for foundation species to create this
590 structure in the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006)
591 suggests that future work would be aided by determining these modules within the biotic
592 community that include species with large differences in body-size and longevity. Also,
593 as heritable variation is the raw material for natural selection to act upon, a genetic basis
594 for interaction network structure indicates evolutionary dynamics should be considered
595 at the community level and that conserving genetic variation is important to consider in
596 efforts to restore or preserve complex species interactions and their associated ecosystem
597 functions (Evans et al., 2013). Such findings will bring us closer to understanding the
598 evolutionary drivers of Darwin’s entangled bank and the interconnectedness of species
599 in complex communities.

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605 Citations

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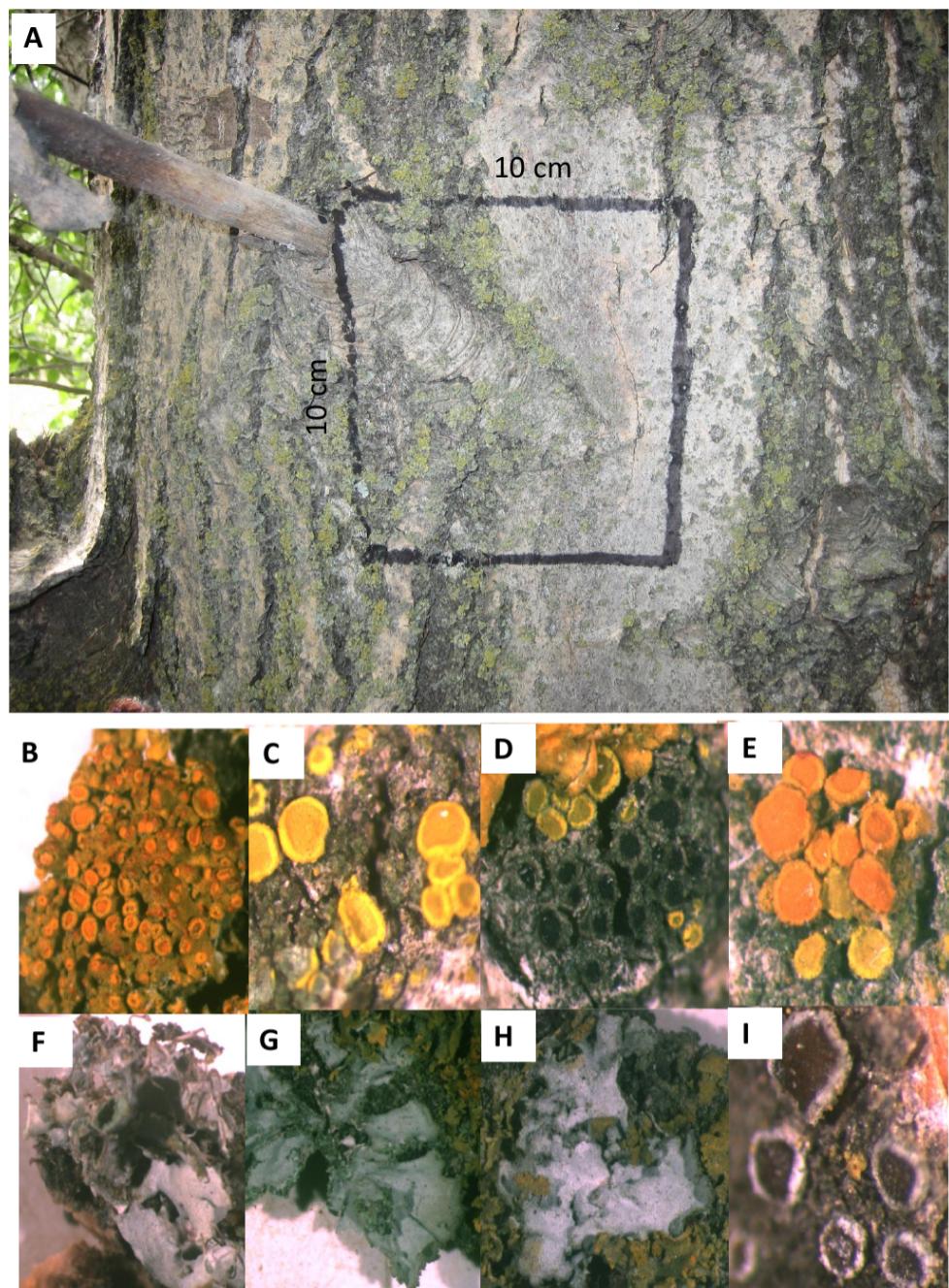


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanchra*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (B-D) and R.R. Naesbourg (E-I).

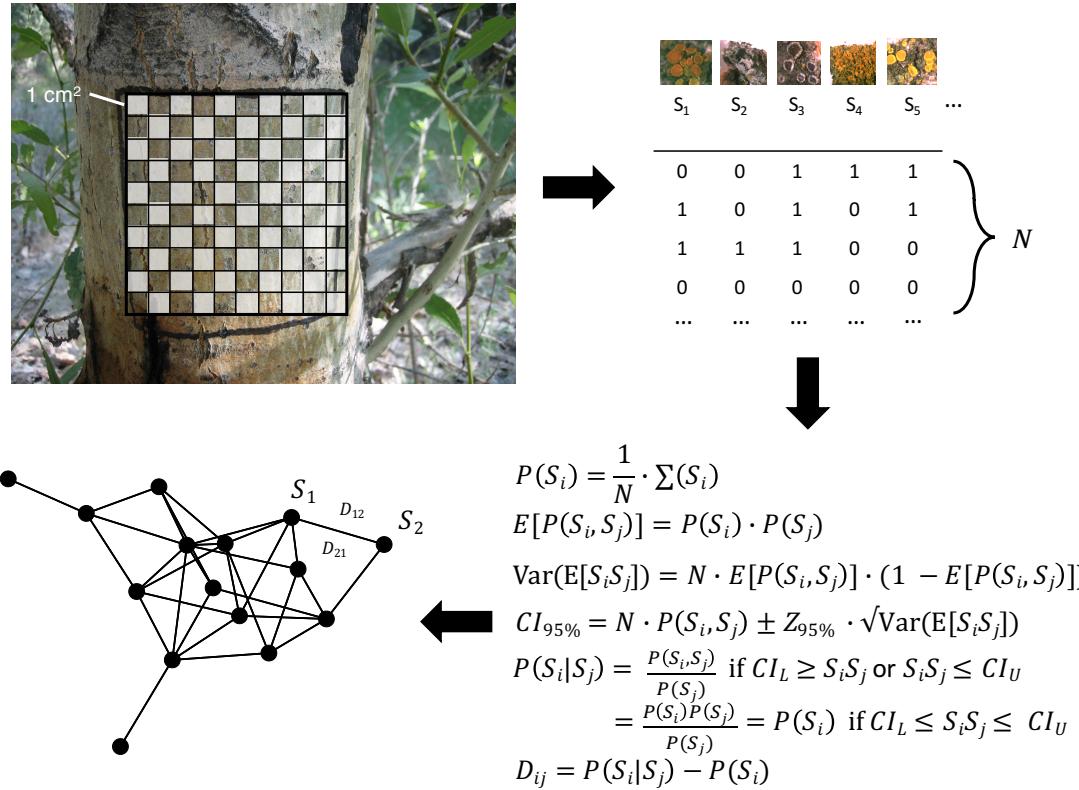


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm² cells within a 100 cm² grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (Araújo et al., 2011), 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.

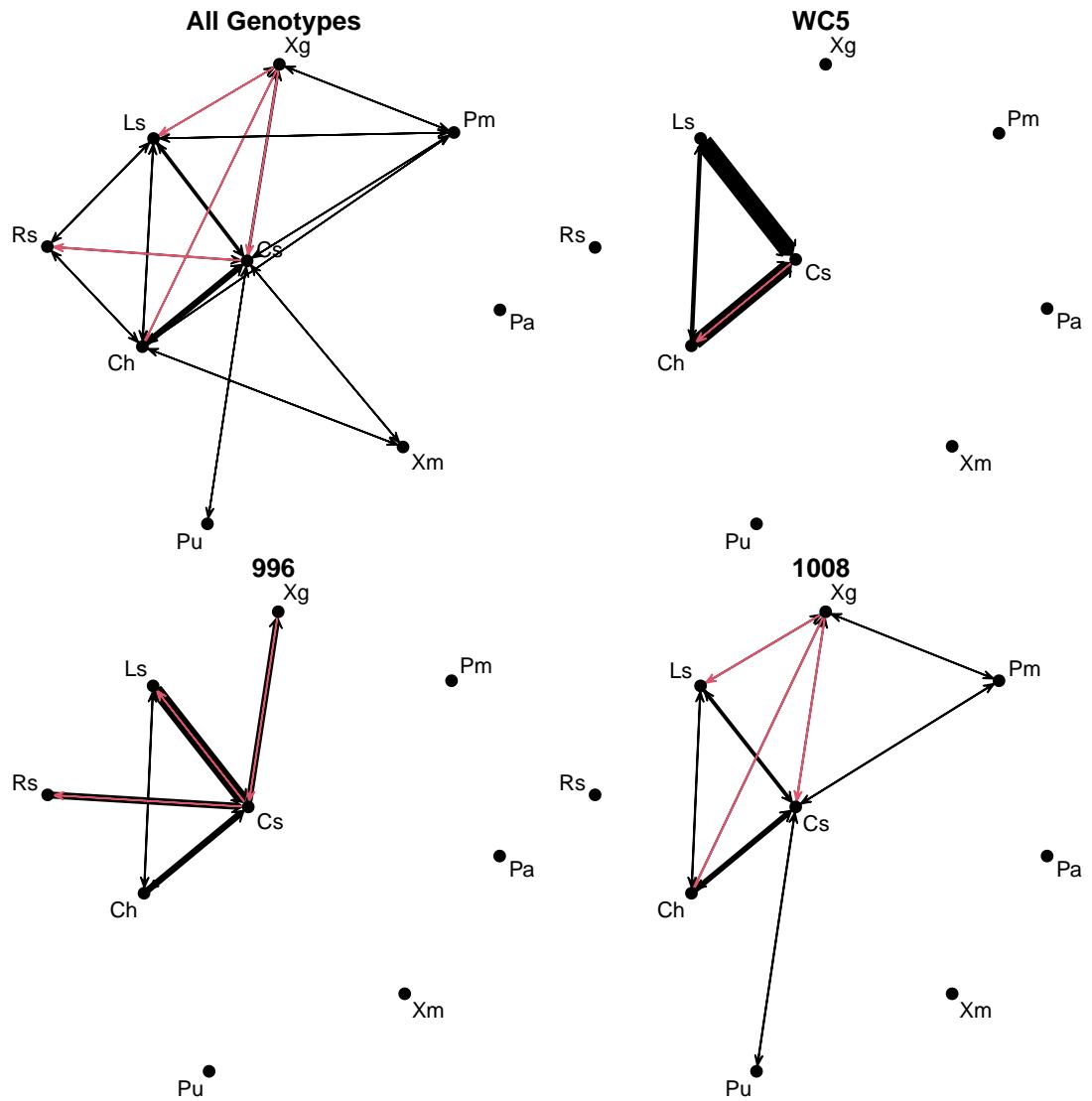


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

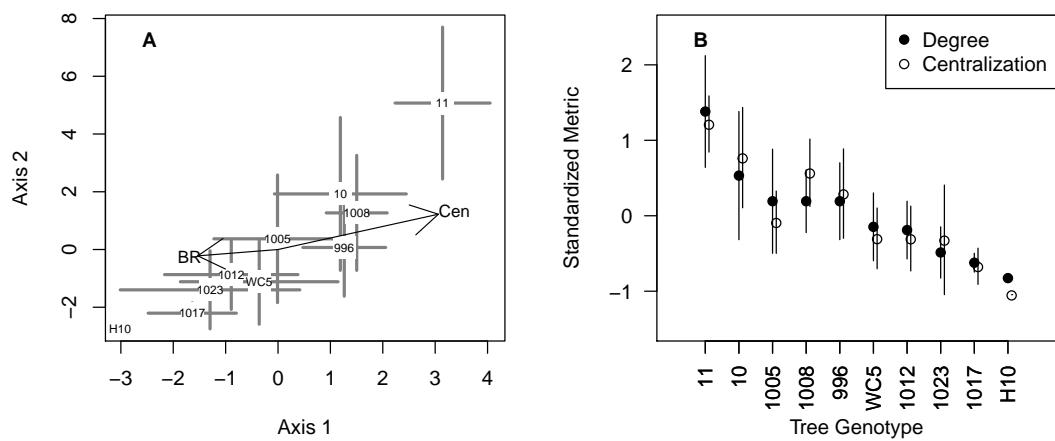


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

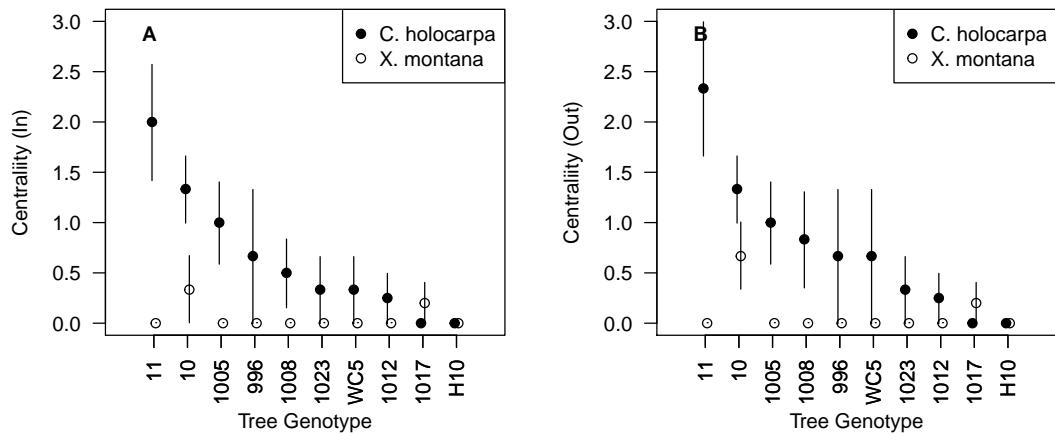


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

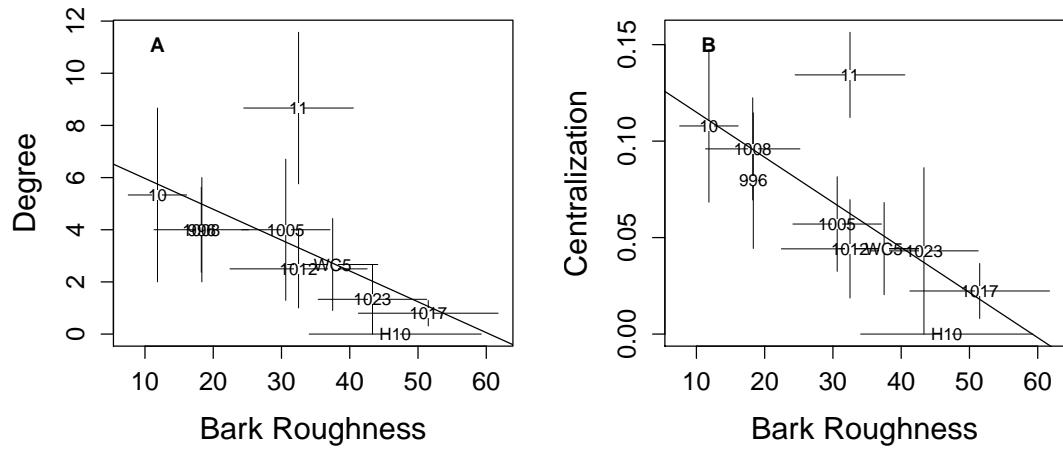


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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