

Genotypic variation in a foundation tree results in heritable ecological network structure

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ABSTRACT

Elucidating the genetic basis to ecological network structure is fundamental to understanding evolution in complex ecosystems. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that has quantified the heritability of network structure of a foundation species associated. To examine this, in a 20+ year old common garden we observed epiphytic lichens associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation species. We constructed and conducted genetic analyses of signed, weighted, directed lichen interaction networks on individual trees. 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 predicted by 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 has the potential to act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks.

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

²² **INTRODUCTION**

²³ Evolution occurs in the context of complex ecological networks. Community genetics
²⁴ studies have shown that genetic variation in foundation species, which have large effects
²⁵ on ecosystems by modulating and stabilizing local conditions (Ellison et al., 2005),
²⁶ plays a significant role in defining distinct communities of interacting organisms: such
²⁷ as endophytes, pathogens, lichens, arthropods, and soil microbes (Busby et al., 2015;
²⁸ Barbour et al., 2009; Lamit et al., 2015a). Multiple studies have now demonstrated
²⁹ that genetic variation influences numerous functional traits (e.g., phytochemical, phe-
³⁰ nological, morphological) that in combination result in a multivariate functional trait
³¹ phenotype (Holeski et al., 2012) in which individual plant genotypes support differ-
³² ent communities and ecosystem processes (Bailey et al., 2009; Whitham et al., 2012).
³³ Recently, the importance of genetic variation in structuring ecological systems was
³⁴ reviewed, and not only were many instances of strong genetic effects found in many
³⁵ ecosystems but the effect of intraspecific variation was at times greater than inter-specific
³⁶ variation (Des Roches et al., 2018). There is now evidence to support that selection
³⁷ occurs among groups of species (Wade, 2007) and that genetic variation and phyloge-
³⁸ netic relatedness contribute to variation in community assembly (Crutsinger, 2016) and
³⁹ species interactions (Whitham et al., 2006; Bailey et al., 2009; Moya-Laraño, 2011).
⁴⁰ These evolutionary dynamics have the potential to shape the structure of ecological
⁴¹ interaction networks (Rezende et al., 2007; Guimarães et al., 2007; Gómez et al., 2009).

⁴² Empirical and theoretical work in network ecology and evolutionary biology point
⁴³ to the need for examinations of the genetic basis of ecological network structure. Anal-
⁴⁴ yses of ecological networks have demonstrated that indirect effects can lead to self-
⁴⁵ organization, producing sign-changing, amplifying and/or dampening effects (Fath and
⁴⁶ Patten, 1998; Newman, 2006; Sole and Bascompte, 2006), and other studies have demon-
⁴⁷ strated that indirect effects of interactions among species can lead to network structures
⁴⁸ that amplify or dampen the effects of selection, such as the formation of star-like struc-
⁴⁹ tures in which there is a “central” species or group of species that interact with other
⁵⁰ peripheral species can amplify selection events (Lieberman et al., 2005). Also, work by
⁵¹ Toju et al. (2014, 2016, 2017) observed consistent patterns of centralized interactions of
⁵² species modules (i.e., groups of species that interact more strongly within their group
⁵³ than with other species) focused around hubs of plant-fungal interactions. In other words,
⁵⁴ a small number of plant and fungal symbionts tended to have disproportionate numbers
⁵⁵ of interactions with other species and likely are the drivers in determining community
⁵⁶ assembly, structure and dynamics. Interspecific indirect genetic effects (IIGE) theory
⁵⁷ (*sensu* Shuster et al. (2006)) in evolutionary biology also point to the importance of
⁵⁸ studying the genetics of interaction network structure. Genetically based differences in
⁵⁹ network structure among individuals can be acted upon by natural selection when there
⁶⁰ are fitness consequences of different networks of IIGEs, leading to community evolution
⁶¹ per Whitham et al. (2020) and, by extension, network evolution. For example, although
⁶² the analysis was of abundances rather than interaction networks, Gehring et al. (2014,
⁶³ 2017) found that the mycorrhizal communities on the roots of drought tolerant and intol-
⁶⁴ erant trees are dominated by different orders of ectomycorrhizal fungal mutualists that
⁶⁵ also differ in the benefits they provide that enhance tree performance. Because drought
⁶⁶ tolerant genotypes are three times more likely to survive record droughts, selection acts

67 both on the tree and its fungal community and with increased drought the community
68 phenotype has changed over time. Also, in an antagonistic interaction context, Busby
69 et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods in
70 a common garden, the impacts of these strong interactors results in a different and di-
71 minished community of arthropods relative to control trees. These examples collectively
72 support the possibility that selection acting on the tree may alter the network structure of
73 associated communities in which different networks of communities are most likely to
74 survive drought and pathogen outbreaks, respectively. Regardless of whether the IIQE
75 is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also
76 affects the relative fitness of the tree), selection at the level of the tree population or
77 its community, or both, can change network structure and alter community dynamics
78 (Whitham et al., 2020).

79 In this context, the “genetic similarity rule” of community genetics provides a
80 useful framework we can apply to interaction networks at the nexus of ecological
81 and evolutionary dynamics. In a study combining experimental common gardens and
82 landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and
83 arthropods, Bangert et al. (2006) observed that individual genotypes that are more
84 genetically similar will tend to have similar phytochemical traits and thus tend to have
85 similar interactions with other species. Although this is likely to have consequences for
86 interactions and network structure, studies in the network ecology literature generally
87 do not include a genetic component (Lau et al., 2017) and community genetics studies
88 have primarily focused on community composition in terms of the abundance of
89 species (Des Roches et al., 2018). Some studies have examined the effects of genetic
90 variation on trophic chains in plant-associated communities (including *Populus*, *Sol-*
91 *idago*, *Oenothera*, *Salix*) (Bailey et al., 2005; Johnson, 2008; Smith et al., 2011, 2015;
92 Barbour et al., 2016) and generally found that increasing genotypic diversity leads to
93 increased trophic complexity. We are aware of only two studies that explicitly examined
94 the effect of genotypic variation on interaction networks between tree individuals and
95 associated herbivores using ecological network metrics (Lau et al., 2016a; Keith et al.,
96 2017). Both found that genotypic diversity generates increased network modularity
97 (i.e., compartmentalization); however, both were examining networks at the scale of
98 forest stands, rather than networks associated with individual trees; therefore, neither
99 was able to observe replicated networks in order to statistically test for genetic effects
100 on network structure and quantify the genetic component (i.e., heritable variation) in
101 network structure.

102 Here, we investigate how genetic variation in a foundation tree species determines
103 the structure of a network of interactions among a community of tree associated lichens.
104 We used a long-term (20+ years), common garden experiment with clonally replicated
105 *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001).
106 We focused on a community of epiphytic lichen species, as previous research has
107 demonstrated significant compositional effects of genotypic variation on lichen in this
108 system (Lamit et al., 2011, 2015b,a) and epiphytic organisms in other systems (Winfree
109 et al., 2011; Zytynska et al., 2011). Applying a probability-theory based network
110 modeling approach (Araújo et al., 2011), we constructed a set of interaction network
111 models for the lichens associated with individual trees. Using these models, we then
112 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 the potential importance of focal or “central” nodes (e.g., species) for determining network dynamics (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. As there is a preponderance of evidence that in natural systems evolution occurs in communities comprised of networks of interacting species (Lau et al., 2016a; Keith et al., 2017; Thompson, 2013; Bascompte et al., 2006), we set out to test two hypotheses. First, per the community similarity rule (Bangert et al., 2006) and IIGE theory (Whitham et al., 2020), we hypothesize that trees of the same genotype (i.e., clones) will support more similar lichen interaction networks relative to individuals of other genotypes. In other words, epiphytic lichen network structure is heritable, which can be calculated via comparisons of within and among group variation in network structure. Second, heritability of lichen network structure is the result of underlying phenotypic covariation in tree traits important to interactions between trees and lichens and among lichens. Evidence that such trait covariance generates variation in interactions among community members provides an intermediate genetics-based mechanism for the underlying factors determining lichen distribution and abundance. In combination, evaluating these two hypotheses is fundamental to understanding variation and dynamics of network structure and evolution.

134 MATERIALS AND METHODS

135 Study System

136 The study was conducted along the Weber River, UT (USA), which is a cottonwood
137 (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus*
138 *angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to
139 hybridize, in order to focus on intra-specific genetic variation we only sampled pure or
140 advanced generation back-crosses of *P. angustifolia*. Bark lichens have been intensively
141 sampled in this system and provide an ideal community in which to observe and model
142 interaction networks, as their sessile nature permits accurate identification of individuals
143 and their highly localized, direct contact interactions and slow population turnover rates
144 facilitate the assessment of interactions among lichen species on individual trees (Lamit
145 et al., 2015b).

146 A long-term, common garden experiment was used to isolate the effect of tree geno-
147 type from the effect of the localized microenvironment associated with each individual
148 and spatial autocorrelation. Established in 1992, asexually propagated clones of geno-
149 typed *P. angustifolia* individuals were obtained from wild collections and planted in
150 fully randomized design at the Ogden Nature Center, Ogden, UT. From the population
151 of established individuals in the common garden, we chose a total of ten genotypes,
152 replicated between 3 and 8 times each, for sampling. We selected tree genotypes that
153 generally had lichens present in order to permit the construction of interaction networks.

154 **Bark Lichens and Trait Observations**

155 On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm²
156 cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens,
157 we were able to rapidly assess lichen interactions by quantifying thalli of different
158 species occurring in close proximity. Sampling was restricted to the northern aspect
159 of the trunk to maximize the abundance of lichens and control for the effect of trunk
160 aspect. Two adjacent 100 cm² quadrats centered at 50 cm and 95 cm from ground level
161 were sampled (Fig 1). The observed lichen community included: *Athallia holocarpa*,
162 *Candelariella subdeflexa*, *Myriolecis hagenii*, *Rinodina freyi*, *Physcia adscendens*,
163 *Physciella melanchra*, *Physcia undulata*, *Xanthomendoza galericulata*, *Xanthomendoza*
164 *montana*. Several other species were not observed in the present study but are known to
165 occur in this region: *Melanohalea elegantula*, *Melanohalea subolivacea*, *Phaeophyscia*
166 *ciliata* and *Phaeophyscia orbicularis*.

167 The cell size and checkerboard sampling pattern was chosen to isolate the individuals
168 in each cell. In a survey of *Xanthomendoza galericulata* in the common garden, we had
169 observed a median thallus size of $0.12 \pm 0.001 \text{ cm}^2$ (1 S.E.) (Supporting Information,
170 Fig. 1). This expected thallus size formed the basis for our sampling design, such that
171 lichen observations were spatially independent of thalli present in other cells but exposed
172 to similar micro-environmental conditions created by the bark and the location of the
173 sampling area on an individual tree. Therefore, we were confident in treating the cell-
174 wise observations in quadrats as independent with respect to lichen-lichen interactions.
175 We quantified the texture of the bark in the quadrat as the percent of 1 cm² cells with
176 rough bark. In addition to bark roughness, we also examined several bark chemistry
177 traits by taking bark samples immediately adjacent to each quadrat. We used previously
178 collected phytochemical data from Lamit et al. (2011), including the concentration of
179 condensed tannins, carbon and nitrogen. Additionally, we quantified bark pH for each
180 tree. Bark samples were collected by excavating adjacent to the quadrat down to a depth
181 of 2 mm. Bark pieces were air dried for storage and later processing. Samples were
182 prepped for pH measurements by crushing with a mortar and pestle until all pieces were
183 $\pm 0.5 \text{ cm}$ in diameter, creating equivalent surface areas among samples. 0.5 g of crushed
184 bark was placed in a 15 ml Falcon collection tube with 5 ml of deionized water. Tubes
185 were capped and let sit for 24 hrs prior to pH measurement with a SevenGo™ pH meter
186 (Mettler Toledo).

187 **Lichen Network Modeling**

188 For each tree, repeated observations of lichens were made in order to construct replicated
189 interaction networks for each genotype. We conducted a modified sampling procedure
190 originally developed by Lamit et al. (2015b) with the addition that we quantified the
191 presence of lichens in the 1 cm² cells on individual trees of *P. angustifolia*. Unipartite
192 networks were generated using the conditional probabilities of each species pair, i.e., the
193 probability of observing one species given an observation of another species $P(S_i|S_j)$,
194 based on the method developed by Araújo et al. (2011). To calculate conditional
195 probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and
196 the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species
197 and their co-occurrences. We were then able to calculate the conditional probabilities of
198 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

199 a matrix that could possibly be asymmetric, i.e., $P(S_i|S_j)$ does not have to be equal to
200 $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was
201 equal to one for all species present and zero for species that were not observed in any
202 cell.

203 We then applied an analytical procedure to remove non-significant links between
204 species. This procedure determines if the joint probability of a species pair (i.e., $P(S_i, S_j)$)
205 is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as
206 $CI_{95\%} = E[S_iS_j] * Z_{95\%} * \sqrt{V(S_iS_j)}$, where the expected frequency of co-occurrences
207 $E(S_iS_j)$ is the total number of cells surveyed (N) times the independent probabilities of
208 each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the
209 expected variance of $E(S_iS_j)$ is the total number of cells times the expected probability
210 of S_iS_j and its compliment (i.e., $V(S_iS_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If
211 the observed number of co-occurrence falls outside of the confidence interval, the
212 joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual
213 probabilities (i.e., $P(S_i)\bar{P}(S_j)$), and the conditional probability reduces to the individual
214 probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair
215 falls outside the confidence interval, the probability that the observation of one species
216 given the other is no different than simply observing that species alone. This enables us
217 to remove links from a given network by re-scaling the resulting conditional probabilities
218 through subtraction of the individual probabilities from the conditional probabilities (i.e.,
219 how different the conditional probability is from the independent probability), which
220 makes any species with a non-significant conditional probability zero.

221 The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as one species' impact on another
222 with zero being no effect and values less than or greater than zero being negative and
223 positive effects, respectively. We will refer to \mathbf{D} as a signed, weighted interaction
224 matrix. As such, \mathbf{D} has the properties that it can be asymmetric (i.e., D_{ij} does not
225 necessarily equal D_{ji}) and it scales between -1 and 1, and, therefore, does not have the
226 mathematical properties of a probabilistic network (Poisot et al., 2016). Also, as the
227 method does not track individuals within species and interactions such as competitive
228 exclusion or facilitation within species would result in the same species being observed.
229 Therefore, the results of intra-specific interactions always results in the same species
230 being observed and a resulting $D_{ii} = 0$. In the context of these networks, asymmetry and
231 positive/negative valued connections are distinct quantities. In-coming and out-going
232 connections can be interpreted as “influenced by” and “influenced”, respectively; while
233 positive and negative should be seen as one species increasing or decreasing, respectively,
234 the probability of another species' occurrence.

235 **Analyses, Software and Data**

236 To quantify the structural variation of lichen networks we calculated several metrics at
237 both the level of node and whole networks. Although there are many other metrics, for
238 the sake of simplicity we focus on a subset that represent the primary interesting features
239 of network structure, see Lau et al. (2017). We calculated the number of interactions or
240 “links” in each network (degree), which provides a measure of the size of the network
241 (Lau et al., 2016a; Borrett and Lau, 2014). We also calculated the centralization of each
242 network using Freeman's centrality, which measures the evenness of the distribution of
243 interactions among the species in the network, using the sna package (Butts, 2019).

244 In a network with low centralization species have similar strengths and numbers of
245 interactions. A network with high centralization tends to have one or small number
246 of species that interact with other species. We used a related function to calculate
247 the centrality of each species (i.e., node level centrality) in each network as well. To
248 calculate separate metrics for positive and negative links, as the networks contained not
249 only positive and negative connections but also directional connections (both in-coming
250 and out-going), we calculated the same network metrics for all combinations of these
251 types of connections using recently developed methods for signed, weighted and directed
252 networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch, 2020).

253 We used a combination of parametric and non-parametric, permutation based frequentist
254 statistical analyses to test for the effects of genetic variation on lichen communities
255 and their interaction networks. To assess the effect of genotype on traits as univariate
256 response variables (including the metrics of network structure), we used additive, random
257 effects models with Restricted Maximum Likelihood (REML) conducted in R via the
258 `lme4` and `RLRsim` packages (Bates et al., 2015; Scheipl et al., 2008). To conform to
259 test assumptions, traits were root transformed with the exception of condensed tannin
260 concentration and carbon-nitrogen ratio, which were rank and \log_{10} transformed, respectively.
261 Differences in node level centrality among species was tested using ANOVA and
262 Tukey-HSD multiple comparison tests. Correlations among trait variables and network
263 metrics were quantified and tested using linear correlations of Pearson's r . For multivariate
264 response variables, such as lichen community composition and network structure,
265 we used distance based multivariate statistical approaches. To quantify the similarity of
266 lichen networks among individual trees, we calculated the pairwise Euclidean distance
267 of the \mathbf{D} interaction matrices among all trees (Newman, 2010). To test for the effects of
268 genotype and other predictor variables on network similarity we conducted Permutational
269 Analysis of Variance (PERMANOVA) with `vegan` (Oksanen et al., 2019). For
270 visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling
271 (NMDS) (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of
272 these multivariate responses and fitted vectors for continuous predictor variables to the
273 ordinated values (Oksanen et al., 2019). Using random initial configurations with a
274 maximum of 500 iterations and a change in stress threshold of less than 10^{-12} . This was
275 repeated for one to four dimension configurations, and the configuration with the lowest
276 dimensionality and unexplained variation less than 10% was selected. For all tests
277 where genotype was used as a predictor, we quantified the heritability of the response
278 variable. Because the trees in the garden were clonal replicates of each genotype, we
279 calculated broad-sense heritability, which is the genotypic variance divided by the total
280 phenotypic variance (Conner and Hartl, 2004), which can be interpreted as a measure
281 of the phenotypic variance due to genotypic variation. All analyses were conducted
282 using R version 4.0.2 (R Core Team, 2020). Code and data for the project are openly
283 available as a reproducible workflow using `drake` (Landau, 2018) archived via Zenodo
284 <https://doi.org/10.5281/zenodo.4581639>.

285 RESULTS

286 In support of our first hypotheses, we found that tree genotype influenced lichen net-
287 work structure and that multiple lichen network metrics were heritable. Tree genotype

significantly predicted the structural similarity of lichen networks and, overall, network-level metrics responded significantly to tree genotype, including network degree and centralization including both in-coming and out-going links or when separated into in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree and positive in-going centralization. Metrics calculated with negative links were not significant, including degree (negative) and both in-coming (negative) and out-going centralization (negative).

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

Table 1. Genotypic effects on the associated lichen network structure. *RLRT* is the statistic from the restricted likelihood ratio tests.

The genetic response of network centralization was driven by variation in *Athallia holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$, $p\text{-value} < 0.0001$). The node-level metrics for *A. holocarpa* displayed the strongest response to tree genotype with high levels of heritability of positive centrality for both the in-coming ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives but not for either negative centrality metrics in-coming ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of the other species' centralities showed a genotypic response (Supporting Information, Fig. 2) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however, the centrality of *X. montana* was much lower overall relative to *A. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

In support of our second hypothesis, analysis of trait covariation revealed that genotype indirectly influenced lichen network centralization via genetically based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} = 0.0343$) both displayed significant responses to tree genotype. None of the other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and none other than bark roughness was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen

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

	df	SS	R2	Pseudo-F	p-value
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.

DISCUSSION

Ecological and Evolutionary Importance of Network Heritability

Although previous studies have examined aspects of networks, such as trophic complexity (Barbour et al., 2016) and forest stand level interaction network structure (Lau et al., 2016b; Keith et al., 2017), this is the first study that we are aware of to examine the heritability of network structure with replicated networks at the genotype scale. Previous work in the evolution of ecological networks have primarily focused on macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al., 2018; Harmon et al., 2019) or have been simulation based individual-level models that integrate intraspecific variation to the species level (Maliet et al., 2020), even though recent syntheses have pointed to the importance of processes operating across scales of organization (Guimarães, 2020). There are two important functional ramifications of genetically based variation in network structure. First, heritability of network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted by genetic identity. Variation in space and time create variation in ecological networks that influences evolutionary dynamics via shifts in ecological dynamics, such as population demographics (Guimarães, 2020). Given that ecosystems are comprised of hundreds and thousands of species, each having a multitude of interactions, the potential to find traction for making predictions in the context of ecological, let alone evolutionary, dynamics seems daunting. The promise of predictability lies in the presence of asymmetries in ecosystems, such as hierarchy created by foundation

350 species via differences in body size and/or life-history strategies (Ellison et al., 2005).
351 Second, heritability (i.e., genetic determination) means that there is structure in the
352 spatial or temporal variation that is created by individuals of foundation species whose
353 traits are in part determined by underlying trait differences. Although this variation
354 is inherently a function of both genetic and environmental effects (Conner and Hartl,
355 2004), the community and network-level effects are also a function of the scale of the
356 interaction (Shuster et al., 2006; Lau et al., 2017).

357 Notably, even if the composition of the communities is the same among individuals
358 and genotypes, interactions may not be. We didn't observe compositional differences
359 using the same data from which the lichen networks were derived. If we only had
360 our composition dataset from this study, we would have concluded no response of the
361 lichen community to tree genotype, even though the underlying interactions among
362 lichen species does vary among genotypes. As such differences in network structure
363 could occur without observable differences in species richness or community com-
364 position, which have been the primary focus of the majority of community genetics
365 studies (Whitham et al., 2020). Community composition of lichens has previously been
366 observed to be different among tree genotypes in the same experimental garden (Lamit
367 et al., 2011, 2015b). The different results observed in the present study is likely a result
368 of differences in lichen quantification and the tree genotypes observed leading to overall
369 higher abundances of observed lichens to assure the possibility of observing lichen inter-
370 actions. The previous study used a visual percent cover estimation, unlike the current
371 study, which observed lichens at the scale of 1 cm² cells, which could over-estimate
372 cover depending on the frequency at which actual thallus size was less than 1 cm²,
373 as well as both the northern and southern aspects of each tree. These differences do
374 not negate the findings of either study. The present study's finding of differences in
375 network structure without significant compositional differences points to the importance
376 of quantifying how network structure changes in response to genetic variation in order to
377 fully understand evolutionary dynamics in complex communities. Having not observed
378 a compositional effect of tree genotype without measuring the network structure could
379 lead to the conclusion of no genetic effect on the community, even though differences
380 in network structure are leading to altered, local evolutionary dynamics. It is possible
381 that these underlying differences in interactions among lichens could lead to differences
382 in community composition at a future point in time via their effects on species abun-
383 dances (Shuster et al., 2006); however, this is not needed for evolutionary dynamics
384 to occur via selection that leads to shifts in trait distributions without shifting species
385 abundance distributions, which is possible under stabilizing, disruptive and directional
386 selection (Conner and Hartl, 2004), so long as the relative abundances of each species is
387 imperceptibly changed. Thus, it is imperative that further community genetics research
388 assess or at least be aware of the potential effects of variation in interactions and not
389 just observe species abundances, otherwise community level genetic effects may be
390 underestimated, especially when cumulative interaction effects are taken into account
391 (Borrett et al., 2007, 2010).

392 Furthermore, the demonstration of the heritability of interaction networks, without
393 significant differences in community composition, provides clear empirical evidence
394 that IIGEs need to encompass the structure of interaction networks. Although IIGE
395 theory provides a quantitative framework within which to approach evolutionary the-

ory at higher levels of biological organization (from populations to communities and ecosystems), this theory has focused on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham et al., 2012, 2020) and has not yet integrated developments from the ecological or evolutionary network theory literature. Thus, it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated this network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be damped or magnified within the system of interacting species (Smith et al., 2011; Keith et al., 2017). Although such a synthesis necessitates a much greater effort than can be afforded in this paper, it is possible to point to several productive pathways forward. In terms of interaction networks, foundation species are relatively central within the system of interactions, that is their direct and/or indirect effects are greater than other species. So, when the more centralized (foundation) species have genetically based interactions, genetic effects will tend to be propagated and possibly magnified in the community. Here, we found that even though species with relatively higher abundances (e.g., *X. galericulata*) were present in the community, the response of the network was not predominately due to their interactions. In addition, although there were species that tended to be central within the lichen networks, the similarity of networks showed the highest heritability compared to any of the centrality metrics, which suggests that there are aspects to network structure that are not solely due to the central species. Taken together, these results point to the importance of considering the impact of network structure and that it is a potentially productive path forward for the development and application of IIGE theory.

Network Structure and Levels of Selection

The demonstration of evolution at any scale requires demonstrating three key elements (Conner and Hartl, 2004), which multilevel selection theory posits can occur simultaneously at multiple levels of ecological organization (Whitham et al., 2003, 2020). First, there must be variation in the structure (composition, abundance, species interactions, diversity, interaction network structure) of communities. Second, these differences must be genetically based and heritable in which community structure is passed from one generation to the next. For example, numerous studies show that related individuals tend to support the same communities of insects and microbes, and ecosystem processes of biodiversity, nutrient cycling and stability, whereas unrelated individuals support more different communities and ecosystem processes (Bangert et al., 2006, 2008; Barbour et al., 2009; Whitham et al., 2020). Importantly, the current study shows that networks are also heritable traits that greatly increases its utility as a community phenotype that selection can act upon. Third, selection must act on these differences to favor some communities over others leading to change over time (i.e., community evolution). The differential survival and performance of individual tree genotypes will simultaneously result in selection occurring on the lichen community and network structure that it supports. Since our findings show that networks are heritable, another metric of community evolution would be to quantify how networks change over time in response to an invasive species, climate change, or some other agent of selection, which represents a frontier for future ecological network studies.

The current study shows the utility of considering the spatial and temporal scales of

ecological and evolutionary dynamics. In line with previous empirical studies (Bangert et al., 2006; Zook et al., 2010; Zytnyska et al., 2012), we found that the assembly of ecological networks can have a measurable genetic basis depending on the spatial scale of interactions, due in part, to asymmetries in size and longevity of organisms. Intra-specific, genotypic diversity among cottonwood trees appears to be a major factor in the creation of meta-communities of lichens on individual trees that form interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily determined by another organism, these communities inherently form modules within the larger ecosystem, as they tend to interact more with each other than with other individuals (Lau et al., 2017). Our study demonstrates that the localized environmental differences determined by the genetic variation within a single tree species can not only impact community composition, as repeatedly demonstrated in other community genetics studies (Whitham et al., 2006; Des Roches et al., 2018), but also shape the structure of interactions among individuals. Some network structures are likely to be more stable, either in response to disturbance or via self-organized dynamics. For example, centralized networks, although more efficient, are theorized to be more susceptible to targeted “attacks” in the terminology of defense networks. As mentioned previously, one class of networks that are theorized to have amplifying effects on networks have centralized “star” shapes with one or a few species at the center and radiating interactions out from the central core (Lieberman et al., 2005). This is structurally what we have observed with the networks that tend to occur on some of the genotypes in our study, i.e., the more centralized networks. It is likely that these networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the centralized network structure found on that tree genotype, as multiple studies have found significant impacts of the removal of foundation species in different systems (Keith et al., 2017; Des Roches et al., 2018). The importance of the scale of network organization to create hierarchical structure (Guimarães, 2020) and the potential for foundation species to create this structure in the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006) suggests that future work would be aided by determining species with large differences in body-size and longevity, which could be contributing to interaction network structure (e.g., modules and centralized species). As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (Whitham et al., 2012; Evans et al., 2013; Whitham et al., 2020).

Ecological network studies have focused on asymmetry and the quantification of its structure in communities, which can arise at different scales in space, time or ecological organization. The impacts of asymmetry on evolution from community dynamics have primarily produced qualitative discussion (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific predictions can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities (Lieberman et al., 2005). One seemingly useful direction 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 feedbacks to the origin,

whereas cyclic networks contain feedbacks to one or more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in the context of IIGE theory (Whitham et al., 2020). As we do not have an estimate of the effect of the lichen at the larger scale of the fitness of the tree they occur on, we can not determine whether the lichen networks in this system are cyclic or not. In terrestrial ecosystems, lichens play important ecological roles, such as substrate stabilization (Root et al., 2011) and nitrogen fixation (Nelson et al., 2018). Some epiphytic lichens can have demonstrable effects on the availability of nutrients for the trees that they are associated with (Norby and Sigal, 1989). Although none of the lichens the present study’s system is known to fix nitrogen, it is possible that they might add micro-nutrients or provide some other unobserved benefit to their host trees. Elucidating the presence of and quantifying such feedbacks would allow for the determination of the cyclic nature and potential evolutionary dynamics. If there are positive effects of lichens on host trees that might increase their ability to respond to environmental stress, then selection could enhance tree performance and trees with superior communities are more likely to survive. Gehring et al. (2014, 2017) showed this with ectomycorrhizal communities in which trees with superior mutualist communities were more likely to survive drought and community evolution occurred (Whitham et al., 2020). However, such feedbacks to the higher level of the foundation species are not a requirement for evolution, and, regardless of whether networks are rooted (no feedbacks) or cyclic (feedbacks present), selection at the community level leading to evolution can still occur. Specifically within the context of the current study, even if lichens and their interactions do not feed back to affect the performance and ultimate fitness of the tree on which they reside, non-random death of trees, such as those observed for drought in arid systems Sthultz et al. (2009); Gehring et al. (2017), can still result in selection at the community level and evolution. For example, when a tree dies from some event (e.g., a drought, fire, storm, etc.), its lichen network is selected against while intact networks persist on other trees that survive this selection event.

Last, it is worth considering the ecological and evolutionary dynamics at the scale of the lichen individuals. Since lichens are multi-species complexes, there is also the potential for evolutionary dynamics to shift within the context of the lichen symbiosis. There is substantial evidence that lichens have served as the “cradle of symbiotic fungal diversification” (Arnold et al., 2009) and recent research has shown significant network structure of endolichenic fungi and lichens collected from across North America (Chagnon et al., 2016). Analysis of the structure of ecological networks has generally supported the conclusion that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability in mutualistic, primarily bipartite (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic networks (Elias et al., 2013; Grilli et al., 2016). Although there is growing evidence that the nestedness of mutualistic networks is not necessarily the result of selection for systems-level properties that promote stability but could be either product of asymptotic abundance distributions leading to uneven interaction frequencies (Staniczenko et al., 2013) and/or a by-product of selection and divergence creating network “spandrels” in ecosystems (Valverde et al., 2018), this does not preclude the functional consequences of network structure but rather the developmental or evolutionary processes that have produced the structure. In the present study system, we did not examine nestedness or modularity of the lichen networks as we could not find metrics for

533 analyzing networks that are not only weighted and directed but also signed. Hopefully
534 future network theoretic developments will make the appropriate metrics available to
535 conduct these analyses.

536 Conclusion

537 We found support for both of our hypotheses. First, tree genotype influenced the network
538 structure of lichen communities associated with narrowleaf cottonwoods in a riparian
539 forest ecosystem. Network similarity and metrics of network structure tended to be more
540 similar on trees of the same genotype. Generally, this genetic effect was manifested
541 in positive interactions and largely driven by *A. holocarpa*. Second, the genetically
542 based trait, bark roughness, was observed to affect network variation, largely via shifts
543 in positive in-coming and out-going interactions. Chemistry traits, whether genetically
544 based (e.g., tannin concentration) or not, were not significantly correlated with lichen
545 network structure. Bark roughness has been demonstrated previously to be under strong
546 genetic control in cottonwoods (Bdeir et al., 2017) and other foundation tree species,
547 such as *Eucalyptus* (Nantongo et al., 2020). Bark roughness has also been shown to
548 be an important tree trait influencing bark lichens (Lamit et al., 2015b); however this
549 is the first demonstration of a link from genetics to lichen network structure. As such,
550 these results have important implications for the influence of genetically based variation
551 in ecosystems with networks of interacting species. Going forward, future work could
552 extend the many previous community genetics studies that have focused on sessile
553 organisms, such as galling insects (Bailey et al., 2005; Whitham et al., 2006; Crutsinger
554 et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify the frequency of these
555 interactions in the context of the larger community. Network modeling and analysis will
556 provide useful tools for the identification of species within network modules that are
557 most important to study in systems where little is known about the natural history of
558 organisms in an ecosystem. Such investigations will bring us closer to understanding the
559 evolutionary drivers of Darwin's entangled bank and the interconnectedness of species
560 in complex communities (Darwin, 1859; Dátilo et al., 2016).

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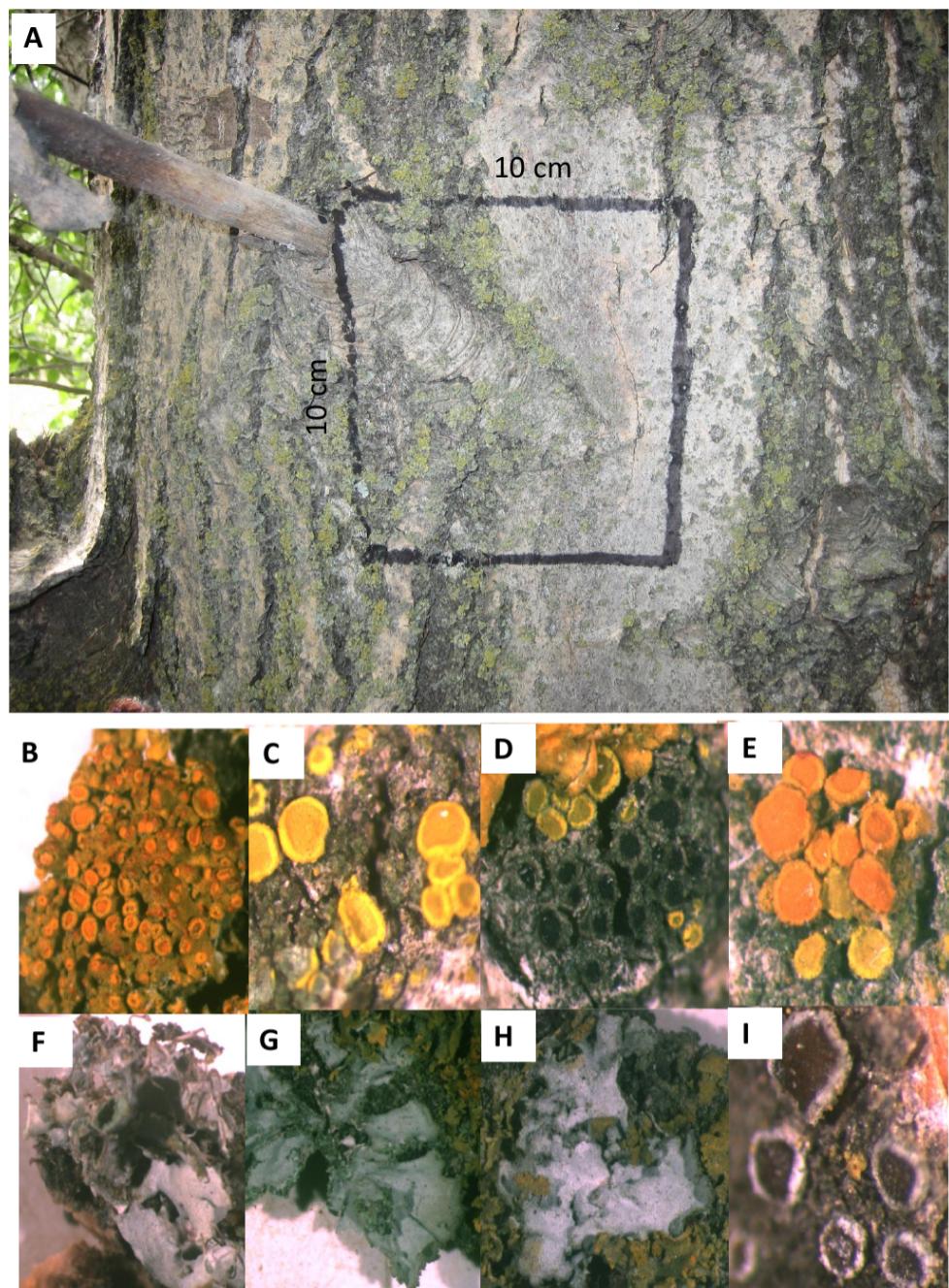


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Photos showing lichen species observed, respectively: *Xanthomendoza montana*, *Candelariella subdeflexa*, *Rinodina freyi*, *Athallia holocarpa*, *Physcia adscendens*, *Physciella melanochra*, *Physcia undulata* and *Myriolecis hagenii*. Photo Credits: L.J. Lamit (B-D) and R. Reese Næsborg (E-I).

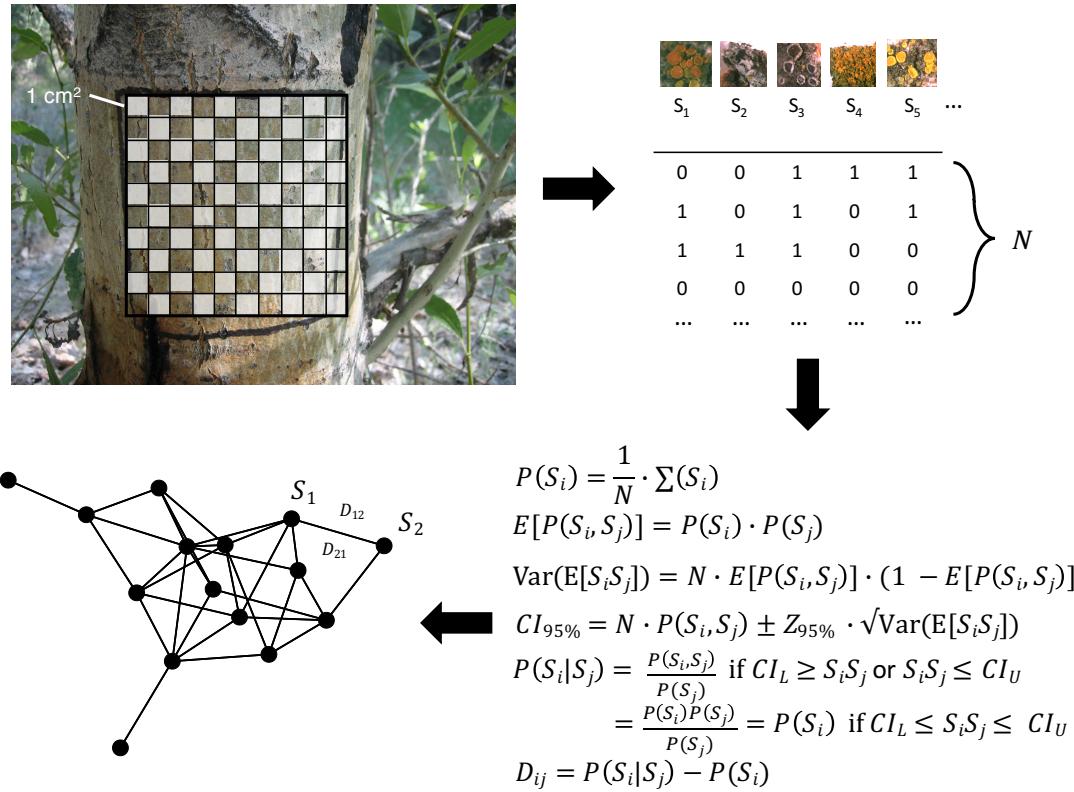


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (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, $P(S_iS_j)$, were not significant using a confidence interval based comparison of their observed co-occurrence frequency, S_iS_j , to that expected due to chance alone, $E[P(S_iS_j)] = P(S_i)P(S_j)$, and $P(S_i|S_j)$ reduces to $P(S_i)$, the observed individual probability of species S_i .

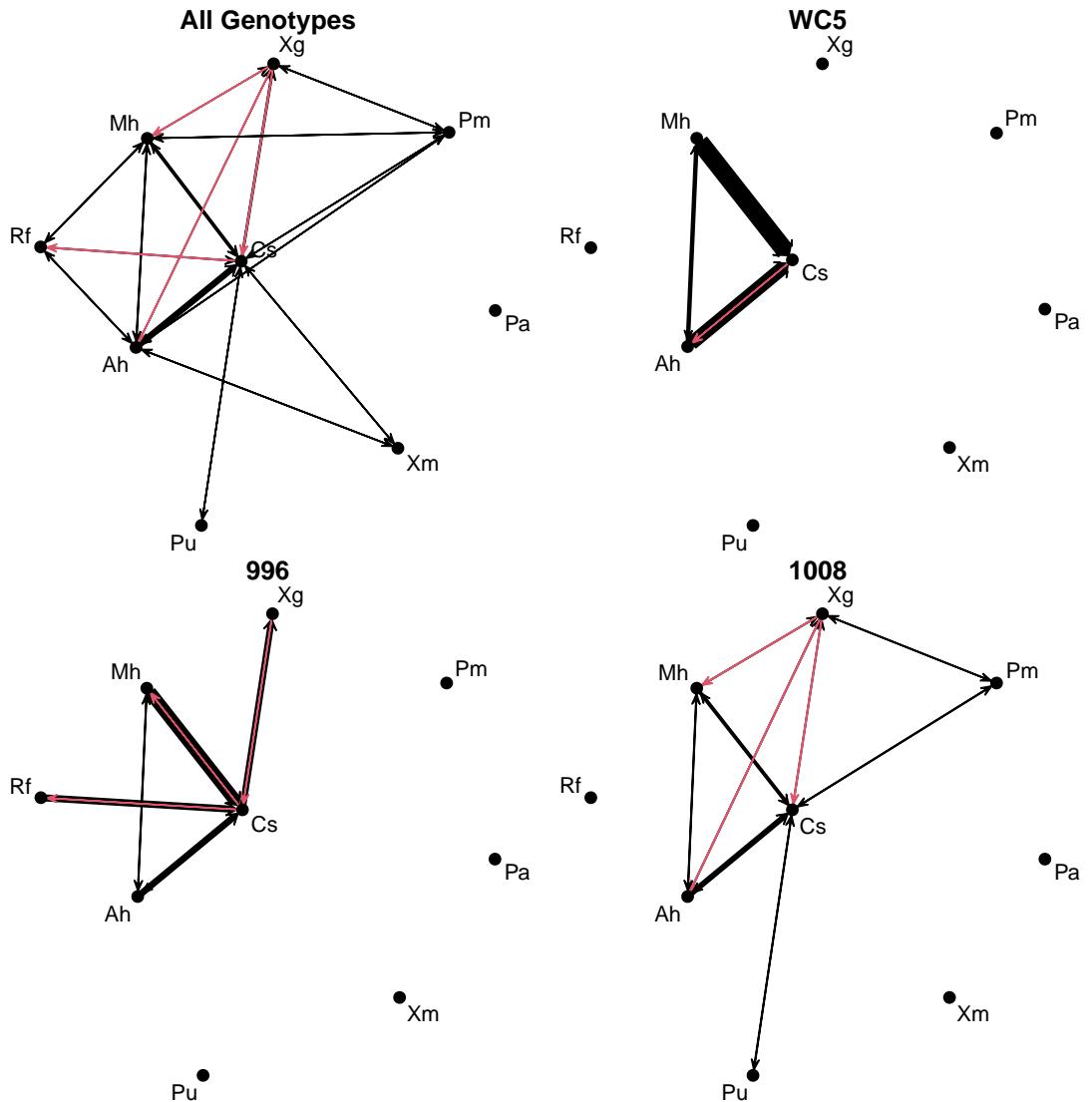


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species, which are scaled by their magnitude. Species names are abbreviated by the first letter of the genus and specific epithet: Ah = *Athallia holocarpa*, Cs = *Candelariella subdeflexa*, Mh = *Myriolecis hagenii*, Rf = *Rinodina freyi*, Pa = *Physcia adscendens*, Pm = *Physciella melanachra*, Pu = *Physcia undulata*, Xg = *Xanthomendoza galericulata*, Xm = *Xanthomendoza montana*. 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.

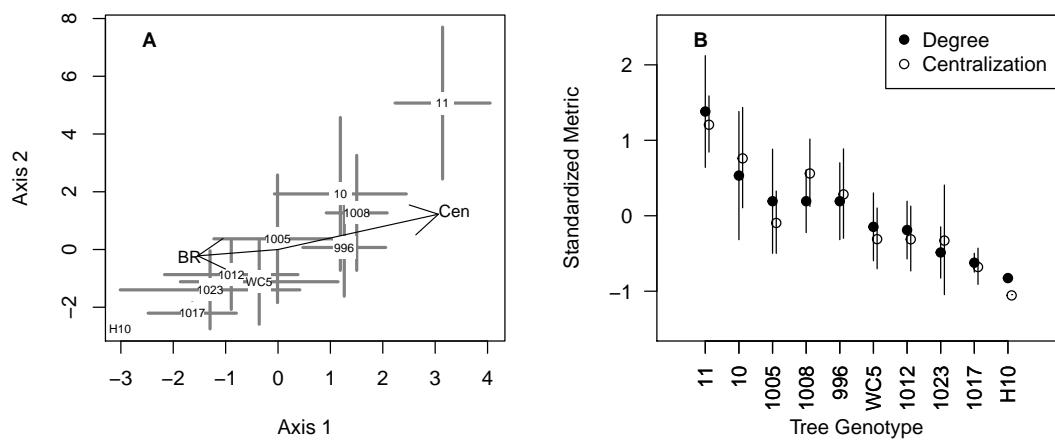


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated networks. 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.

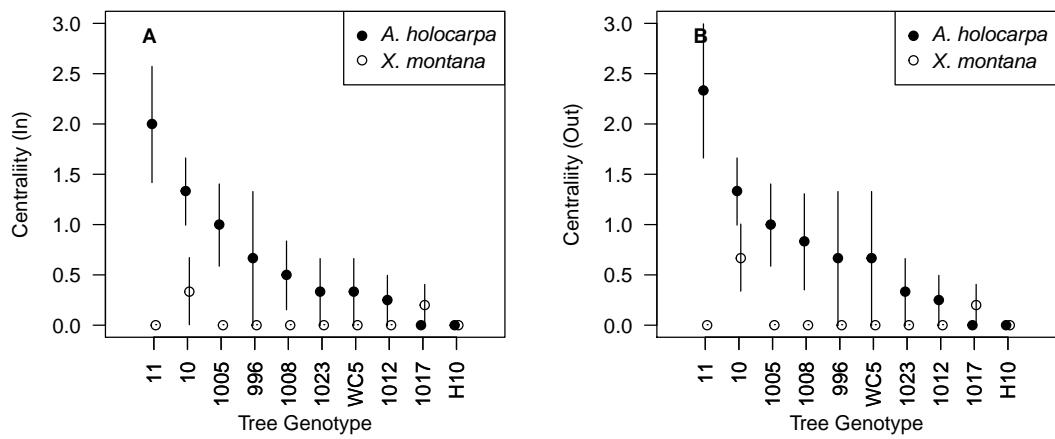


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *A. holocarpa* and *X. montana*. *Athallia holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

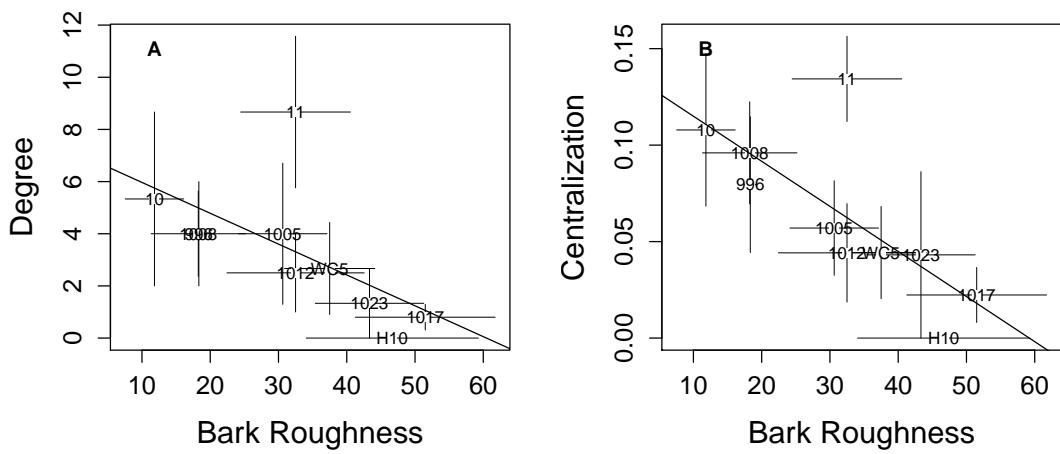


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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