

1 Genotypic variation in a foundation tree 2 results in heritable ecological network 3 structure

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20 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 quantified the contribution of phenotypic variation to heritable variation in network structure. 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 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 can influence 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

21 INTRODUCTION

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

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

66 both on the tree and its fungal community and with increased drought the community
67 phenotype has changed over time. Also, in an antagonistic interaction context, Busby
68 et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods
69 in a common garden, the impacts of these strong interactors results in a different and
70 diminished community of arthropods relative to control trees. This effect was dependent
71 on the hybrid cross-type of the tree and was, therefore, determined by tree genetics.
72 These examples collectively support the possibility that selection acting on the tree may
73 alter the network structure of associated communities in which different networks of
74 communities are most likely to survive pathogen outbreaks. Regardless of whether the
75 IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community
76 also 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 useful
80 framework we can apply to interaction networks at the nexus of ecological and evolution-
81 ary dynamics. In a study combining experimental common gardens and landscape-
82 scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods,
83 Bangert et al. (2006) observed that individual genotypes that are more genetically similar
84 will tend to have similar phytochemical traits and thus tend to have similar interactions
85 with other species. Although this is likely to have consequences for interactions and
86 network structure, studies in the network ecology literature generally do not include a
87 genetic component (Lau et al., 2017) and community genetics studies have primarily
88 focused on community composition in terms of the abundance of species (Des Roches
89 et al., 2018). Some studies have examined the effects of genetic variation on trophic
90 chains in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*)
91 (Bailey et al., 2005; Johnson, 2008; Smith et al., 2011, 2015; Barbour et al., 2016) and
92 generally found that increasing genotypic diversity leads to increased trophic complexity.
93 Only two other studies, that we are aware of, have explicitly examined the effect of
94 genotypic variation on the structure of interaction networks between tree individuals and
95 associated herbivores (Lau et al., 2016a; Keith et al., 2017) and both found that genotypic
96 diversity generates increased network modularity (i.e., compartmentalization). However,
97 both of these studies were examining networks at the scale of forest stands, rather
98 than networks associated with individual trees; therefore, neither was able to observe
99 replicated networks in order to statistically test for genetic effects on network structure
100 and quantify the genetic component (i.e., heritable variation) in network structure.

101 Here, we investigate how genetic variation in a foundation tree species determines
102 the structure of a network of interactions among a community of tree associated lichens.
103 Using a long-term (20+ years), common garden experiment with clonally replicated
104 *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001).
105 We focused on a community of 9 epiphytic lichen species, as previous research has
106 demonstrated significant compositional responses of epiphytes to genotypic variation
107 (Winfrey et al., 2011; Zytynska et al., 2011). Applying a probability-theory based
108 network modeling approach (Araújo et al., 2011), we constructed a set of interaction
109 network models for the lichens associated with individual trees. Using these models,
110 we then examined the genetic basis of the structure of these ecological networks via
111 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 less related 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.

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, in order to focus on intra-specific genetic variation we only sampled pure or advanced generation back-crosses of *P. angustifolia*. 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., 2015b).

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. We selected tree genotypes that generally had lichens present in order to permit the construction of interaction networks.

Bark Lichens 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,

155 we were able to rapidly assess lichen interactions by quantifying thalli of different
156 species occurring in close proximity. Sampling was restricted to the northern aspect
157 of the trunk to maximize the abundance of lichens and control for the effect of trunk
158 aspect. Two adjacent 100 cm^2 quadrats centered at 50 cm and 95 cm from ground level
159 were sampled (Fig 1). The observed lichen community included: *Athallia holocarpa*,
160 *Candelariella subdeflexa*, *Myriolecis hagenii*, *Rinodina freyi*, *Physcia adscendens*,
161 *Physciella melanchra*, *Physcia undulata*, *Xanthomendoza galericulata*, *Xanthomendoza*
162 *montana*. Several other species were not observed in the present study but are known to
163 occur in this region: *Melanohalea elegantula*, *Melanohalea subolivacea*, *Phaeophyscia*
164 *ciliata* and *Phaeophyscia orbicularis*.

165 The cell size and checkerboard sampling pattern was chosen to isolate the individuals
166 in each cell. *Xanthomendoza galericulata* thallus size in this common garden, we had
167 observed a median thallus size of $0.12 \pm 0.001\text{ cm}^2$ (1 S.E.) (Supporting Information,
168 Fig. 1). Based on the median thallus size, we expected thalli observed in each cell to
169 generally be spatially independent of thalli present in other cells but exposed to similar
170 micro-environmental conditions created by the bark and the location of the sampling area
171 on an individual tree. Therefore, we were confident in treating the cell-wise observations
172 in quadrats as independent with respect to lichen-lichen interactions. We quantified
173 the texture of the bark in the quadrat is the percent of 1 cm^2 cells with rough bark. In
174 addition to bark roughness, we also examined several bark chemistry traits by taking
175 bark samples immediately adjacent to each quadrat. We used previously collected
176 phytochemical data from Lamit et al. (2011), including the concentration of condensed
177 tannins, carbon and nitrogen. Additionally, we quantified bark pH for each tree using
178 bark collected adjacent to quadrats, to a depth of 2 mm. Bark pieces were air dried and
179 crushed with a mortar and pestle until all pieces were $\leq 1\text{ mm}$ in diameter. Approximately
180 0.5 g of crushed bark was placed in a 15 ml collection tube with 5 ml of deionized
181 water. Tubes were capped and let sit for 24 hrs prior to pH measurement.

182 **Collection date? pH instrument? Collection tube manufacturer?**

183 **Lichen Network Modeling**

184 For each tree, repeated observations of lichens were made in order to construct replicated
185 interaction networks for each genotype. We conducted a modified sampling procedure
186 originally developed by Lamit et al. (2015b) with the addition that we quantified the
187 presence of lichens in the 1 cm^2 cells on individual trees of *P. angustifolia*. Unipartite
188 networks were generated using the conditional probabilities of each species pair, i.e., the
189 probability of observing one species given an observation of another species $P(S_i|S_j)$,
190 based on the method developed by Araújo et al. (2011). To calculate conditional
191 probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and
192 the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species
193 and their co-occurrences. We were then able to calculate the conditional probabilities of
194 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
195 a matrix that could possibly be asymmetric, i.e., $P(S_i|S_j)$ does not have to be equal to
196 $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was
197 equal to one for all species present and zero for species that were not observed in any
198 cell.

199 We then applied an analytical procedure to remove non-significant links between

200 species. This procedure determines if the joint probability of a species pair (i.e., $P(S_i, S_j)$)
201 is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as
202 $CI_{95\%} = E[S_iS_j] * Z_{95\%} * \sqrt{V(S_iS_j)}$, where the expected frequency of co-occurrences
203 $E(S_iS_j)$ is the total number of cells surveyed (N) times the independent probabilities of
204 each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the
205 expected variance of $E(S_iS_j)$ is the total number of cells times the expected probability
206 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
207 the observed number of co-occurrence falls outside of the confidence interval, the
208 joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual
209 probabilities (i.e., $P(S_i)\bar{P}(S_j)$), and the conditional probability reduces to the individual
210 probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair
211 falls outside the confidence interval, the probability that the observation of one species
212 given the other is no different than simply observing that species alone. This enables us
213 to remove links from a given network by re-scaling the resulting conditional probabilities
214 through subtraction of the individual probabilities from the conditional probabilities (i.e.,
215 how different the conditional probability is from the independent probability), which
216 makes any species with a non-significant conditional probability zero.

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

231 Analyses, Software and Data

232 To quantify the structural variation of lichen networks we calculated several metrics at
233 both the level of node and whole networks. Although there are many other metrics, for
234 the sake of simplicity we focus on a subset that represent the primary interesting features
235 of network structure (see Lau et al. (2017)). We calculated the number of interactions or
236 “links” in each network (degree), which provides a measure of the size of the network
237 (Lau et al., 2016a; Borrett and Lau, 2014). We also calculated the centralization of each
238 network using Freeman's centrality, which measures the evenness of the distribution of
239 interactions among the species in the network, using the `sna` package (Butts, 2019).
240 In a network with low centralization species have similar strengths and numbers of
241 interactions. A network with high centralization tends to have one or small number
242 of species that interact with other species. We used a related function to calculate
243 the centrality of each species (i.e., node level centrality) in each network as well. To
244 calculate separate metrics for positive and negative links, as the networks contained not

245 only positive and negative connections but also directional connections (both in-coming
246 and out-going), we calculated the same network metrics for all combinations of these
247 types of connections using recently developed methods for signed, weighted and directed
248 networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch, 2020).

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

281 RESULTS

282 In support of our first hypotheses, we found that tree genotype influenced lichen network
283 structure and that multiple lichen network metrics were heritable. Tree genotype
284 significantly predicted the structural similarity of lichen networks and, overall, network-level
285 metrics responded significantly to tree genotype, including network degree and
286 centralization including both in-coming and out-going links or when separated into
287 in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive links
288 also showed a significant effect of tree genotype, including positive degree and positive

289 in-going centralization. Metrics calculated with negative links were not significant,
 290 including degree (negative) and both in-coming (negative) and out-going centralization
 291 (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.

292 The genetic response of network centralization was driven by variation in *Athallia*
 293 *holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$,
 294 $p\text{-value} < 0.0001$). *Athallia holocarpa* was the main species to exhibit a significant
 295 response to tree genotype in terms of positive centrality for both the in-coming ($RLRT =$
 296 3.61 , $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, $H^2 = 0.30$, $p\text{-value} =$
 297 0.0327) perspectives, but not for either negative centrality metrics in-coming ($RLRT = 0$,
 298 $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of the
 299 other species' centralities showed a genotypic response (Supporting Information, Fig. 2)
 300 with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however,
 301 the centrality of *X. montana* was much lower overall relative to *A. holocarpa* and the
 302 variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

303 In support of our second hypothesis, analysis of trait covariation revealed that geno-
 304 type indirectly influenced lichen network centralization via genetically based variation in
 305 bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} =$
 306 0.0113) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} = 0.0343$)
 307 both displayed significant responses to tree genotype. None of the other bark traits, pH
 308 ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT = 0.0000$,
 309 $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and
 310 none other than bark roughness was correlated with network similarity (Table 2); there-
 311 fore, we focused our subsequent analyses on the indirect effect of genotype on lichen
 312 network structure via bark roughness. We found that bark roughness was significantly
 313 correlated with network similarity and other lichen network metrics, including negative
 314 correlations with overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$, $p\text{-value} = 0.04$)
 315 and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees
 316 with more similar levels of bark roughness tended to have lichen interaction networks
 317 with similar structure. To quantify the genetic bases of this effect of bark roughness on

318 network structure, we used the residual values from regressions of network degree and
 319 centralization in tests of the effect of tree genotype and found no significant effect of tree
 320 genotype for either degree ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or centralization
 321 ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$), suggesting that the observed relationship
 322 between bark roughness and lichen network structure was largely genetically based
 323 (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.

324 DISCUSSION

325 We found support for both of our hypotheses. First, tree genotype influenced the network
 326 structure of lichen communities associated with narrowleaf cottonwoods in a riparian
 327 forest ecosystem. Network similarity and metrics of network structure tended to be more
 328 similar on trees of the same genotype. Generally, this genetic effect was manifested
 329 in positive interactions and largely driven by *A. holocarpa*. Second, the genetically
 330 based trait, bark roughness, was observed to affect network variation, largely via shifts
 331 in positive in-coming and out-going interactions. Chemistry traits, whether genetically
 332 based (e.g., tannin concentration) or not, were not significantly correlated with lichen
 333 network structure. Bark roughness has been demonstrated previously to be under strong
 334 genetic control (Bdeir et al., 2017), and bark roughness has also been shown to be an
 335 important tree trait influencing bark lichens (Lamit et al., 2015b); however this is the
 336 first demonstration of a link from genetics to lichen network structure. As such, these
 337 results have important implications for the influence of genetically based variation in
 338 ecosystems with networks of interacting species.

339 Implications of Ecological Network Heritability

340 Significant heritability of lichen interaction network structure is in line with the genetic
 341 similarity rule, networks observed on trees of the same genotype tended to be structurally
 342 similar. Although previous studies have examined aspects of networks, such as trophic
 343 complexity (Barbour et al., 2016) and forest stand-level interaction network structure
 344 (Lau et al., 2016b; Keith et al., 2017), this is the first study that we are aware of to
 345 examine the heritability of network structure with replicated networks at the genotype
 346 scale. Previous work in the evolution of ecological networks have primarily focused on
 347 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,
 348 2018; Harmon et al., 2019) or have been simulation based individual-level models that
 349 integrate intraspecific variation to the species level (Maliet et al., 2020), even though

350 recent syntheses have pointed to the importance of processes operating across scales of
351 organization (Guimarães, 2020). There are two important functional ramifications of
352 genetically based variation in network structure.

353 First, heritability of network structure suggests that some amount of interaction
354 network complexity is determined and therefore could be predicted by genetic identity.
355 Variation in space and time create variation in ecological networks that influences evolu-
356 tionary dynamics via shifts in ecological dynamics, such as population demographics
357 (Guimarães, 2020). Given that ecosystems are comprised of hundreds and thousands of
358 species, each having a multitude of interactions, the potential to find traction for making
359 predictions in the context of ecological, let alone evolutionary, dynamics seems daunting.
360 The promise of predictability lies in the presence of asymmetries in ecosystems, such as
361 hierarchy created by foundation species via differences in body size and/or life-history
362 strategies (Ellison et al., 2005). The second is that heritability (i.e., genetic determina-
363 tion) means that there is structure in the spatial or temporal variation that is created
364 by individuals of foundation species whose traits are in part determined by underlying
365 trait differences. Although this variation is inherently a function of both genetic and
366 environmental effects (Conner and Hartl, 2004), the community and network-level
367 effects are also a function of the scale of the interaction (Shuster et al., 2006).

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

396 without shifting species abundance distributions, which is possible under stabilizing,
397 disruptive and directional selection (Conner and Hartl, 2004), so long as the relative
398 abundances of each species is imperceptibly changed. Thus, it is imperative that further
399 community genetics research assess or at least be aware of the potential effects of
400 variation in interactions and not just observe species abundances, otherwise community
401 level genetic effects may be underestimated, especially when cumulative interaction
402 effects are taken into account (Borrett et al., 2007, 2010).

403 Furthermore, the demonstration of the heritability of interaction networks, without
404 significant differences in community composition, provides clear empirical evidence
405 that variation in network structure points to the need to expand IIGEs to encompass
406 the structure of interaction networks. Although IIGE theory provides a quantitative
407 framework within which to approach evolutionary theory at higher levels of biological
408 organization (from populations to communities and ecosystems), this theory has focused
409 on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham
410 et al., 2012, 2020) and has not yet integrated developments from the ecological or
411 evolutionary network theory literature. Thus, it has not developed a way to examine
412 complex interactions among species; however, previous studies have demonstrated
413 this network context is likely to be important, as altering the structure of interaction
414 networks provides a means for genetic effects to be damped or magnified within
415 the system of interacting species (Smith et al., 2011; Keith et al., 2017). Although
416 such a synthesis necessitates a much greater effort than can be afforded in this paper,
417 it is possible to point to several productive pathways forward. In terms of interaction
418 networks, foundation species are relatively central within the system of interactions, that
419 is their direct and/or indirect effects are greater than other species. So, when the more
420 centralized (foundation) species have genetically based interactions, genetic effects will
421 tend to be propagated and possibly magnified in the community. Here, we found that
422 even though more abundant or more centralized (i.e., “important”) species were present
423 in the community, their effects were not the main component responding to genetic
424 effects. Considering the impact of network structure would be a productive path forward
425 for the theoretical development and application of the IIGE concept.

426 **Evolution and Genetically Based Network Structure**

427 The demonstration of evolution at any scale of biological organization requires demon-
428 strating three key elements. First, there must be variation in the structure (composition,
429 abundance, species interactions, diversity, networks) of communities across the land-
430 scape. Second, these differences must be genetically based and heritable in which
431 community structure is passed from one generation to the next. For example, numerous
432 studies show that related individuals tend to support the same communities of insects
433 and microbes, and ecosystem processes of biodiversity, nutrient cycling and stabili-
434 ty, whereas unrelated individuals support more different communities and ecosystem
435 processes (Des Roches et al., 2018; Whitham et al., 2020). Importantly, the current
436 study shows that networks are also heritable traits that greatly increases its utility as a
437 community phenotype that selection can act upon. Third, selection must act on these
438 differences to favor some communities over others leading to change over time (i.e.,
439 community evolution). Since our findings show that networks are heritable, another
440 metric of community evolution is showing how networks change over time in response

441 to an invasive species, climate change, or some other agent of selection.

442 Intra-specific, genotypic diversity could be creating lichen meta-communities on
443 individual trees that form interaction modules with different dynamics. When commu-
444 nities are comprised of individuals whose habitat is primarily determined by another
445 organism, these communities inherently form modules within the larger ecosystem,
446 as they tend to interact more with each other than with other individuals (Lau et al.,
447 2017). Our study demonstrates that the environmental differences determined by the
448 genetic variation within a single species can not only impact community composition,
449 as repeatedly demonstrated in other community genetics studies (Whitham et al., 2006;
450 Des Roches et al., 2018), but also shape the structure of interactions among individuals.
451 Some network structures are likely to be more stable, either in response to disturbance
452 or via self-organized dynamics. For example, centralized networks, although more
453 efficient, are theorized to be more susceptible to targeted “attacks” in the terminology of
454 defense networks. As mentioned previously, one class of networks that are theorized to
455 have amplifying effects on networks have centralized “star” shapes with one or a few
456 species at the center and radiating interactions out from the central core (Lieberman
457 et al., 2005). This is structurally what we have observed with the networks that tend to
458 occur on some of the genotypes in our study, i.e., the more centralized networks. It is
459 likely that these networks could function as hot-spots of evolutionary dynamics resulting
460 from the amplifying effect the centralized network structure found on that tree genotype,
461 as multiple studies have found significant impacts of the removal of foundation species
462 in different systems (Keith et al., 2017; Des Roches et al., 2018).

463 Ecological network studies have focused on asymmetry and the quantification of
464 its structure in communities. The impacts of asymmetry on evolution from community
465 dynamics have primarily produced qualitative discussion (Bascompte et al., 2006;
466 Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific
467 predictions can be found in applications of evolutionary game theory, and although
468 developed at the population scale, such theory can apply to communities (Lieberman
469 et al., 2005). One seemingly useful direction is the classification of networks into two
470 general categories, rooted and cyclic, in which rooted networks have interactions in
471 which evolutionary effects emanate from one or multiple origins but these effects do
472 not have feedbacks to the origin, whereas cyclic networks contain feedbacks to one or
473 more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in
474 the context of IIGE theory (Whitham et al., 2020). As we do not have an estimate of the
475 effect of the lichen on the fitness of the tree they occur on, we can not determine whether
476 the lichen networks in this system are cyclic or not. In terrestrial ecosystems, lichens
477 play important ecological roles, such as substrate stabilization (Root et al., 2011) and
478 nitrogen fixation (Nelson et al., 2018). Some epiphytic lichens can have demonstrable
479 effects on the availability of nutrients for the trees that they are associated with (Norby
480 and Sigal, 1989). Although none of the lichens the present study’s system is known to
481 fix nitrogen, it is possible that they might add micro-nutrients or provide some other
482 unobserved benefit to their host trees. Elucidating the presence of and quantifying
483 such feedbacks would allow for the determination of the cyclic nature and potential
484 evolutionary dynamics.

485 Since lichen individuals are multi-species complexes, there is also the potential for
486 evolutionary dynamics to shift within the context of the lichen symbiosis. There is

487 substantial evidence that lichens have served as the “cradle of symbiotic fungal
488 diversification” (Arnold et al., 2009) and recent research has shown significant net-
489 work structure of endolichenic fungi and lichens collected from across North America
490 (Chagnon et al., 2016). Analysis of the structure of ecological networks has generally
491 supported the conclusion that nestedness, or the degree to which species tend to inter-
492 act with similar subsets of the community, tends to promote stability in mutualistic,
493 primarily bipartite (i.e., two-mode), networks and modularity contributes to the stabi-
494 lization of antagonistic networks (Elias et al., 2013; Grilli et al., 2016). Although there
495 is growing evidence that the nestedness of mutualistic networks is not necessarily the
496 result of selection for systems-level properties that promote stability but could be either
497 product of asymptotic abundance distributions leading to uneven interaction frequencies
498 (Staniczenko et al., 2013) and/or a by-product of selection and divergence creating
499 network “spandrels” in ecosystems (Valverde et al., 2018), this does not preclude the
500 functional consequences of network structure but rather the developmental or evolu-
501 tionary processes that have produced the structure. In the present study, we did not
502 examine nestedness or modularity of the lichen networks as we could not find metrics for
503 analyzing networks that are not only weighted and directed but also signed. Hopefully
504 future network theoretic developments will make the appropriate metrics available to
505 conduct these analyses.

506 **Conclusion**

507 In the face of the high degree of complexity and potential context dependency of
508 ecological processes, the current study points to the utility of considering the spatial and
509 temporal scales of interactions, as discussed in previous studies (Bangert et al., 2006;
510 Zook et al., 2010; Zytnyska et al., 2012). In the present research, we found that the
511 assembly of ecological networks can have a measurable genetic basis depending on
512 the spatial scale of interactions, due in part, to asymmetries in size and longevity of
513 organisms. The importance of the scale of network organization to create hierarchical
514 structure (Guimarães, 2020) and the potential for foundation species to create this
515 structure in the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006)
516 suggests that future work would be aided by determining these modules that include
517 species with large differences in body-size and longevity. As heritable variation is the
518 raw material for natural selection to act upon, a genetic basis for interaction network
519 structure indicates that conserving genetic variation is important to consider in efforts
520 to restore or preserve complex species interactions and their associated ecosystem
521 functions (Whitham et al., 2012; Evans et al., 2013; Whitham et al., 2020). Going
522 forward, future work could extend the many previous community genetics studies that
523 have focused on sessile organisms, such as galling insects (Bailey et al., 2005; Whitham
524 et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify
525 the frequency of these interactions in the context of the larger community. Network
526 modeling and analysis will provide useful tools for the identification of species within
527 network modules that are most important to study in systems where little is known about
528 the natural history of organisms in an ecosystem is lacking. Such investigations will
529 bring us closer to understanding the evolutionary drivers of Darwin’s entangled bank
530 and the interconnectedness of species in complex communities (Darwin, 1859; Dátillo
531 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) Close-up photos show the other lichen species observed, respectively: *Xanthomendoza montana*, *Candelariella subdeflexa*, *Rinodina freyi*, *Athallia holocarpa*, *Physcia adscendens*, *Physciella melanchra*, *Physcia undulata* and *Myriolecis hagenii*. Photo Credits: L.J. Lamit (B-D) and R. Reese Næsborg (E-I).

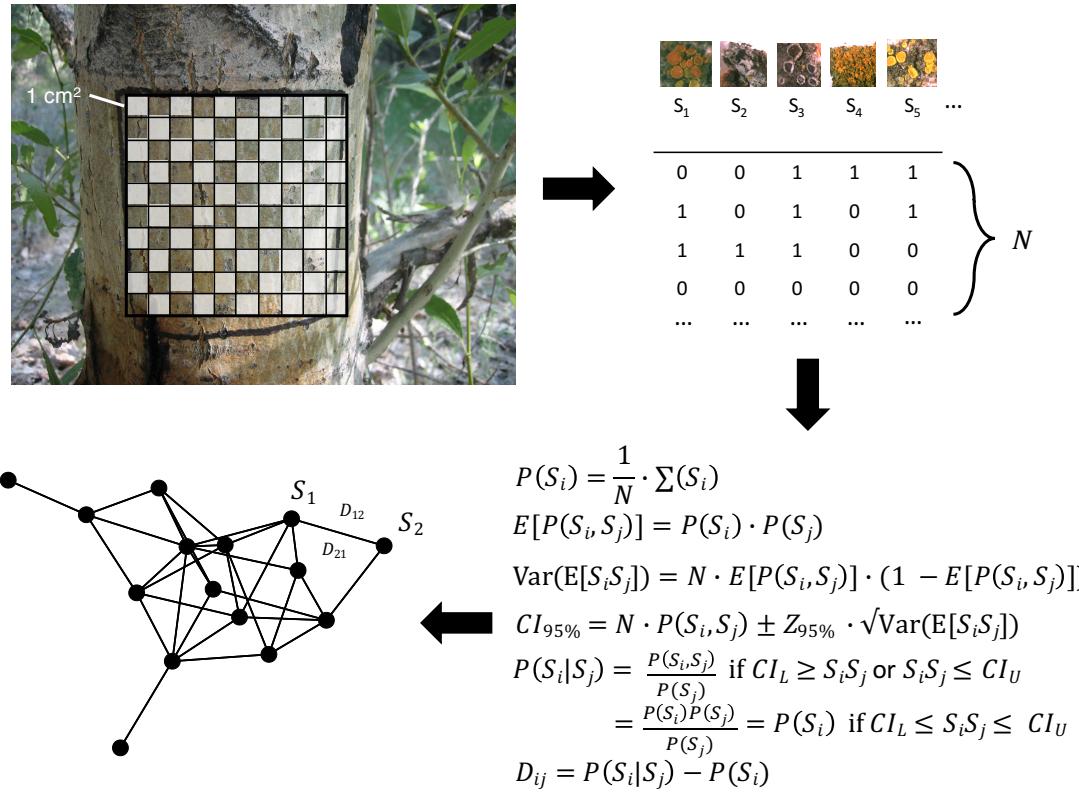


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded 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, $P(S_i S_j)$, 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 .

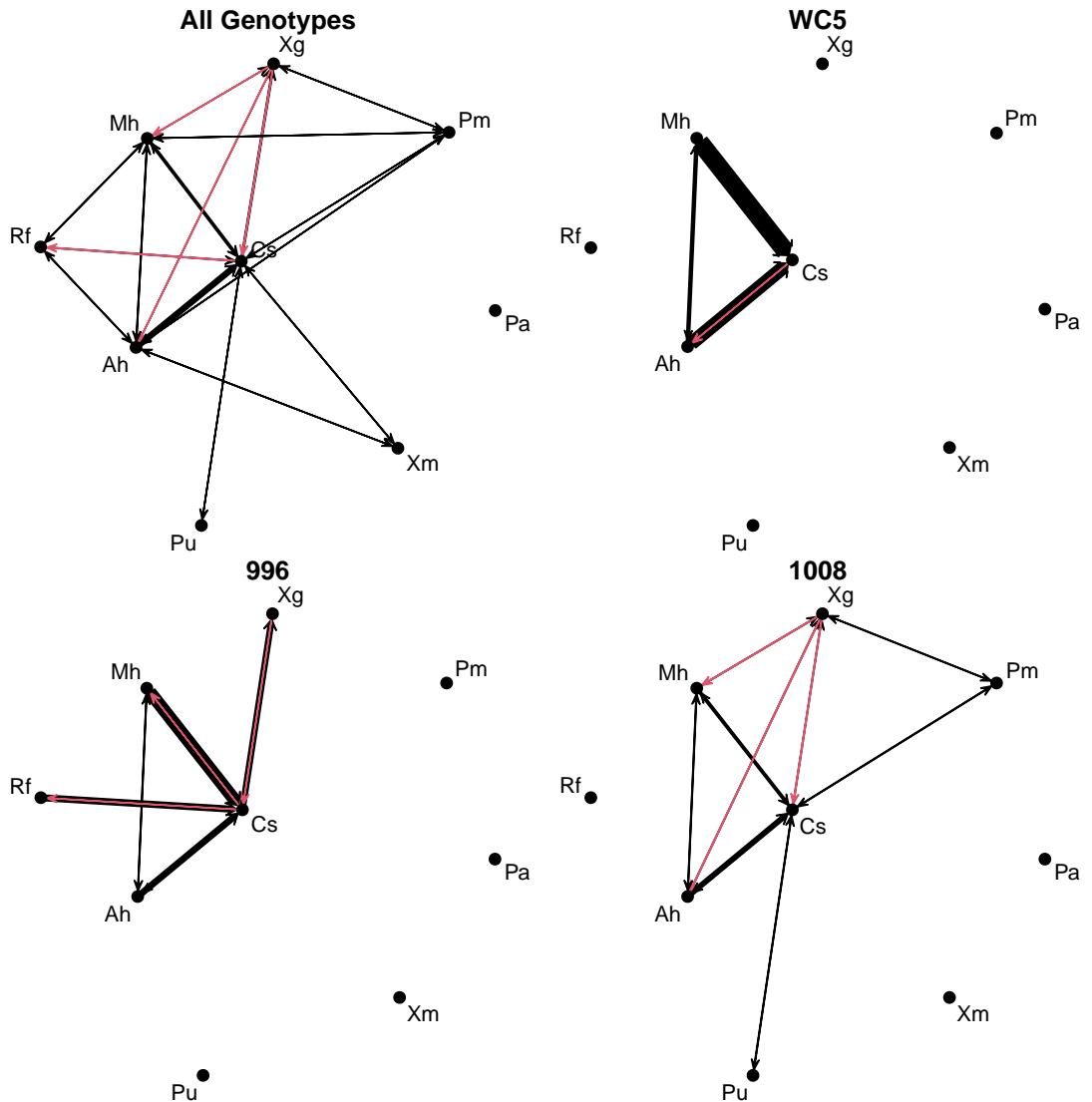


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

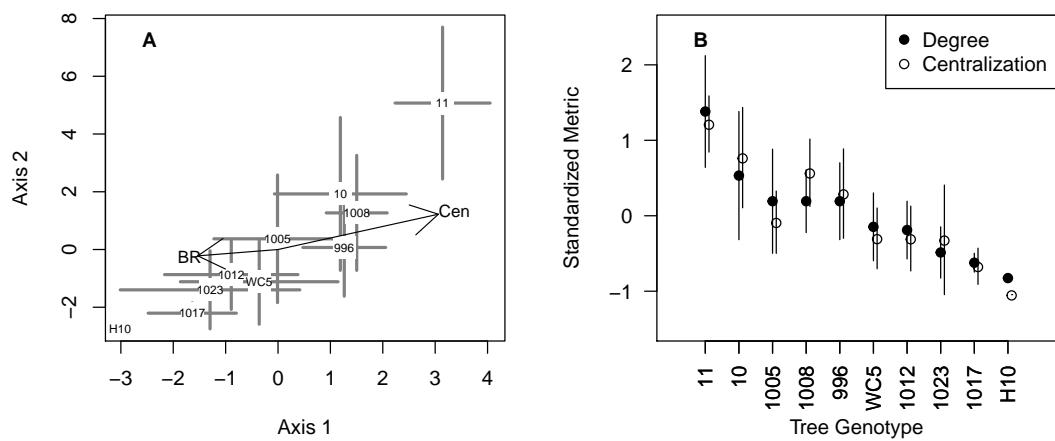


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows 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.

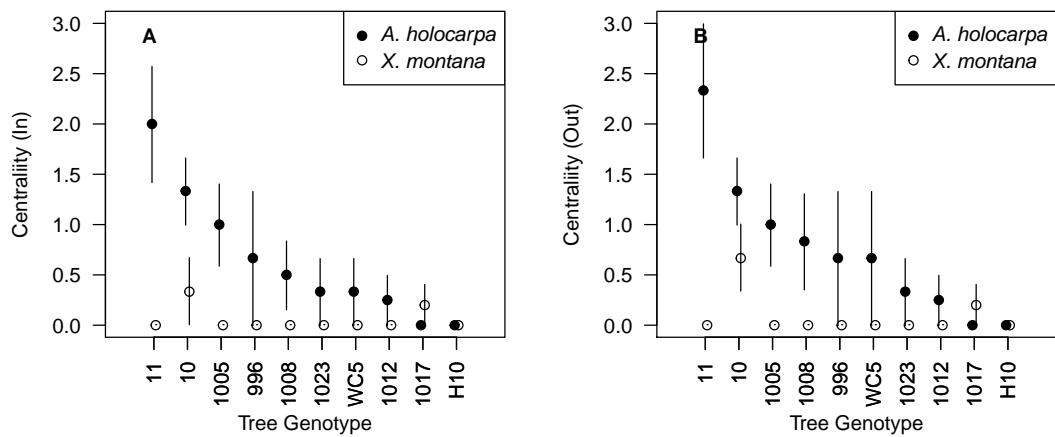


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *A. holocarpa* and *X. montana*. *Athallia holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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