

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, which creates potential for selection to act at the community level, 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 drought and pathogen outbreaks, respectively.
75 Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or recipro-
76 cal (i.e., the community also affects the relative fitness of the tree), selection at the level
77 of the tree population or its community, or both, can change network structure and alter
78 community dynamics (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 evolu-
81 tionary 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. In a survey of *Xanthomendoza galericulata* in the 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). This expected thallus size formed the basis for our sampling design, such
169 that lichen observations were spatially independent of thalli present in other cells but
170 exposed to similar micro-environmental conditions created by the bark and the location
171 of the sampling area on an individual tree. Therefore, we were confident in treating
172 the cell-wise observations in quadrats as independent with respect to lichen-lichen
173 interactions. We quantified the texture of the bark in the quadrat is the percent of 1
174 cm^2 cells with rough bark. In addition to bark roughness, we also examined several
175 bark chemistry traits by taking bark samples immediately adjacent to each quadrat. We
176 used previously collected phytochemical data from Lamit et al. (2011), including the
177 concentration of condensed tannins, carbon and nitrogen. Additionally, we quantified
178 bark pH for each tree. Bark samples were collected in June 2011 by excavating adjacent
179 to the quadrat down to a depth of 2 mm. Bark pieces were air dried for storage. In May
180 of 2019, samples were processed for pH measurements by crushing with a mortar and
181 pestle until all pieces were $<0.5\text{ cm}$ in diameter, creating equivalent surface areas among
182 samples. 0.5 g of crushed bark was placed in a 15 ml Falcon collection tube with 5 ml
183 of deionized water. Tubes were capped and let sit for 24 hrs prior to pH measurement.
184

pH instrument?

Lichen Network Modeling

185 For each tree, repeated observations of lichens were made in order to construct replicated
186 interaction networks for each genotype. We conducted a modified sampling procedure
187 originally developed by Lamit et al. (2015b) with the addition that we quantified the
188 presence of lichens in the 1 cm^2 cells on individual trees of *P. angustifolia*. Unipartite
189 networks were generated using the conditional probabilities of each species pair, i.e., the
190 probability of observing one species given an observation of another species $P(S_i|S_j)$,
191 based on the method developed by Araújo et al. (2011). To calculate conditional
192 probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and
193 the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species
194 and their co-occurrences. We were then able to calculate the conditional probabilities of
195 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
196 a matrix that could possibly be asymmetric, i.e., $P(S_i|S_j)$ does not have to be equal to
197 $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was
198 equal to one for all species present and zero for species that were not observed in any
199

200 cell.

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

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

233 Analyses, Software and Data

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

245 the centrality of each species (i.e., node level centrality) in each network as well. To
246 calculate separate metrics for positive and negative links, as the networks contained not
247 only positive and negative connections but also directional connections (both in-coming
248 and out-going), we calculated the same network metrics for all combinations of these
249 types of connections using recently developed methods for signed, weighted and directed
250 networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch, 2020).

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

283 RESULTS

284 In support of our first hypotheses, we found that tree genotype influenced lichen net-
285 work structure and that multiple lichen network metrics were heritable. Tree genotype
286 significantly predicted the structural similarity of lichen networks and, overall, network-
287 level metrics responded significantly to tree genotype, including network degree and
288 centralization including both in-coming and out-going links or when separated into

289 in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive links
 290 also showed a significant effect of tree genotype, including positive degree and positive
 291 in-going centralization. Metrics calculated with negative links were not significant,
 292 including degree (negative) and both in-coming (negative) and out-going centralization
 293 (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.

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

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

318 with more similar levels of bark roughness tended to have lichen interaction networks
 319 with similar structure. To quantify the genetic bases of this effect of bark roughness on
 320 network structure, we used the residual values from regressions of network degree and
 321 centralization in tests of the effect of tree genotype and found no significant effect of tree
 322 genotype for either degree ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or centralization
 323 ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$), suggesting that the observed relationship
 324 between bark roughness and lichen network structure was largely genetically based
 325 (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.

326 DISCUSSION

327 Ecological and Evolutionary Importance of Network Heritability

328 Although previous studies have examined aspects of networks, such as trophic com-
 329 plexity (Barbour et al., 2016) and forest stand-level interaction network structure (Lau
 330 et al., 2016b; Keith et al., 2017), this is the first study that we are aware of to ex-
 331 amine the heritability of network structure with replicated networks at the genotype
 332 scale. Previous work in the evolution of ecological networks have primarily focused on
 333 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,
 334 2018; Harmon et al., 2019) or have been simulation based individual-level models that
 335 integrate intraspecific variation to the species level (Maliet et al., 2020), even though
 336 recent syntheses have pointed to the importance of processes operating across scales of
 337 organization (Guimarães, 2020). There are two important functional ramifications of
 338 genetically based variation in network structure. First, heritability of network structure
 339 suggests that some amount of interaction network complexity is determined and there-
 340 fore could be predicted by genetic identity. Variation in space and time create variation
 341 in ecological networks that influences evolutionary dynamics via shifts in ecological
 342 dynamics, such as population demographics (Guimarães, 2020). Given that ecosystems
 343 are comprised of hundreds and thousands of species, each having a multitude of interac-
 344 tions, the potential to find traction for making predictions in the context of ecological,
 345 let alone evolutionary, dynamics seems daunting. The promise of predictability lies in
 346 the presence of asymmetries in ecosystems, such as hierarchy created by foundation
 347 species via differences in body size and/or life-history strategies (Ellison et al., 2005).
 348 Second, heritability (i.e., genetic determination) means that there is structure in the
 349 spatial or temporal variation that is created by individuals of foundation species whose
 350 traits are in part determined by underlying trait differences. Although this variation

351 is inherently a function of both genetic and environmental effects (Conner and Hartl,
352 2004), the community and network-level effects are also a function of the scale of the
353 interaction (Shuster et al., 2006; Lau et al., 2017).

354 Notably, even if the composition of the communities is the same among individuals
355 and genotypes, interactions may not be. We didn't observe compositional differences
356 using the same data from which the lichen networks were derived. If we only had our
357 composition dataset from this study, we would have concluded no response of the lichen
358 community to tree genotype, even though the underlying interactions among lichen
359 species does vary among genotypes. As such differences in network structure could
360 occur without observable differences in species richness or community composition,
361 which have been the primary focus of almost all previous community genetics studies
362 (Des Roches et al., 2018). Community composition of lichens has previously been
363 observed to be different among tree genotypes in the same experimental garden (Lamit
364 et al., 2011, 2015b). The different results observed in the present study is likely a
365 result of differences in lichen quantification and the tree genotypes observed leading
366 to overall higher abundances of observed lichens to assure the possibility of observing
367 lichen interactions. The previous study used a visual percent cover estimation, unlike
368 the current study, which observed lichens at the scale of 1 cm² cells, which could
369 over-estimate cover depending on the frequency at which actual thallus size was less
370 than 1 cm², as well as both the northern and southern aspects of each tree. These
371 differences do not negate the findings of either study. The present study's finding of
372 differences in network structure without significant compositional differences points
373 to the importance of quantifying how network structure changes in response to genetic
374 variation in order to fully understand evolutionary dynamics in complex communities.
375 Having not observed a compositional effect of tree genotype without measuring the
376 network structure could lead to the conclusion of no genetic effect on the community,
377 even though differences in network structure are leading to altered, local evolutionary
378 dynamics. It is possible that these underlying differences in interactions among lichens
379 could lead to differences in community composition at a future point in time via their
380 effects on species abundances (Shuster et al., 2006); however, this is not needed for
381 evolutionary dynamics to occur via selection that leads to shifts in trait distributions
382 without shifting species abundance distributions, which is possible under stabilizing,
383 disruptive and directional selection (Conner and Hartl, 2004), so long as the relative
384 abundances of each species is imperceptibly changed. Thus, it is imperative that further
385 community genetics research assess or at least be aware of the potential effects of
386 variation in interactions and not just observe species abundances, otherwise community
387 level genetic effects may be underestimated, especially when cumulative interaction
388 effects are taken into account (Borrett et al., 2007, 2010).

389 Furthermore, the demonstration of the heritability of interaction networks, without
390 significant differences in community composition, provides clear empirical evidence
391 that variation in network structure points to the need to expand IIIGEs to encompass
392 the structure of interaction networks. Although IIIGE theory provides a quantitative
393 framework within which to approach evolutionary theory at higher levels of biological
394 organization (from populations to communities and ecosystems), this theory has focused
395 on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham
396 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 dampened 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 more abundant or more centralized (i.e., “important”) species were present in the community, their effects were not the singularly responding to genetic effects, rather the similarity of the whole network depending on interactions among multiple species. Considering the impact of network structure would be a productive path forward for the theoretical development and application of the IIGE concept.

Network Structure and Levels Selection

Multilevel selection theory argues that selection can occur simultaneously at individual, group and community levels (?Whitham et al., 2006, 2020) and the demonstration of evolution at any scale requires demonstrating three key elements (Conner and Hartl, 2004). 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; 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). Since our findings show that networks are heritable, another metric of community evolution is showing how networks change over time in response to an invasive species, climate change, or some other agent of selection. The differential survival and performance of individual tree genotypes will simultaneously result in selection occurring on the lichen community it supports.

The current study points to 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; Zytynska 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

442 form modules within the larger ecosystem, as they tend to interact more with each other
443 than with other individuals (Lau et al., 2017). Our study demonstrates that the localized
444 environmental differences determined by the genetic variation within a single tree
445 species can not only impact community composition, as repeatedly demonstrated in
446 other community genetics studies (Whitham et al., 2006; Des Roches et al., 2018), but
447 also shape the structure of interactions among individuals. Some network structures
448 are likely to be more stable, either in response to disturbance or via self-organized
449 dynamics. For example, centralized networks, although more efficient, are theorized
450 to be more susceptible to targeted “attacks” in the terminology of defense networks.
451 As mentioned previously, one class of networks that are theorized to have amplifying
452 effects on networks have centralized “star” shapes with one or a few species at the
453 center and radiating interactions out from the central core (Lieberman et al., 2005).
454 This is structurally what we have observed with the networks that tend to occur on
455 some of the genotypes in our study, i.e., the more centralized networks. It is likely that
456 these networks could function as hot-spots of evolutionary dynamics resulting from
457 the amplifying effect the centralized network structure found on that tree genotype, as
458 multiple studies have found significant impacts of the removal of foundation species
459 in different systems (Keith et al., 2017; Des Roches et al., 2018). The importance of
460 the scale of network organization to create hierarchical structure (Guimarães, 2020)
461 and the potential for foundation species to create this structure in the vast majority of
462 ecosystems (Ellison et al., 2005; Whitham et al., 2006) suggests that future work would
463 be aided by determining species with large differences in body-size and longevity, which
464 could be contributing to interaction network structure (e.g., modules and centralized
465 species). As heritable variation is the raw material for natural selection to act upon, a
466 genetic basis for interaction network structure indicates that conserving genetic variation
467 is important to consider in efforts to restore or preserve complex species interactions and
468 their associated ecosystem functions (Whitham et al., 2012; Evans et al., 2013; Whitham
469 et al., 2020).

470 Ecological network studies have focused on asymmetry and the quantification of
471 its structure in communities. The impacts of asymmetry on evolution from community
472 dynamics have primarily produced qualitative discussion (Bascompte et al., 2006;
473 Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific
474 predictions can be found in applications of evolutionary game theory, and although
475 developed at the population scale, such theory can apply to communities (Lieberman
476 et al., 2005). One seemingly useful direction is the classification of networks into
477 two general categories, rooted and cyclic, in which rooted networks have interactions
478 in which evolutionary effects emanate from one or multiple origins but these effects
479 do not have feedbacks to the origin, whereas cyclic networks contain feedbacks to
480 one or more origins. This is equivalent to “unidirectional” and “reciprocal” genetic
481 effects in the context of IIGE theory (Whitham et al., 2020). As we do not have an
482 estimate of the effect of the lichen on the fitness of the tree they occur on, we can not
483 determine whether the lichen networks in this system are cyclic or not. In terrestrial
484 ecosystems, lichens play important ecological roles, such as substrate stabilization (Root
485 et al., 2011) and nitrogen fixation (Nelson et al., 2018). Some epiphytic lichens can
486 have demonstrable effects on the availability of nutrients for the trees that they are
487 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 are not a requirement for evolution, and, regardless of whether networks are rooted (no feedbacks) or cyclic (feedbacks present), selection at the community level and evolution can still occur. Even if lichens and their interactions do not feed back to affect tree performance, non-random death of trees, such as those observed for drought in an arid system ?, 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.

Since lichen individuals 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, we did not examine nestedness or modularity of the lichen networks as we could not find metrics for analyzing networks that are not only weighted and directed but also signed. Hopefully future network theoretic developments will make the appropriate metrics available to conduct these analyses.

Conclusion

We found support for both of our hypotheses. First, tree genotype influenced the network structure of lichen communities associated with narrowleaf cottonwoods in a riparian forest ecosystem. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *A. holocarpa*. Second, the genetically based trait, bark roughness, was observed to affect network variation, largely via shifts

in positive in-coming and out-going interactions. Chemistry traits, whether genetically based (e.g., tannin concentration) or not, were not significantly correlated with lichen network structure. Bark roughness has been demonstrated previously to be under strong genetic control (Bdeir et al., 2017), and bark roughness has also been shown to be an important tree trait influencing bark lichens (Lamit et al., 2015b); however this is the first demonstration of a link from genetics to lichen network structure. As such, these results have important implications for the influence of genetically based variation in ecosystems with networks of interacting species. Going forward, future work could extend the many previous community genetics studies that have focused on sessile organisms, such as galling insects (Bailey et al., 2005; Whitham et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify the frequency of these interactions in the context of the larger community. Network modeling and analysis will provide useful tools for the identification of species within network modules that are most important to study in systems where little is known about the natural history of organisms in an ecosystem is lacking. Such investigations will bring us closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species 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) 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).

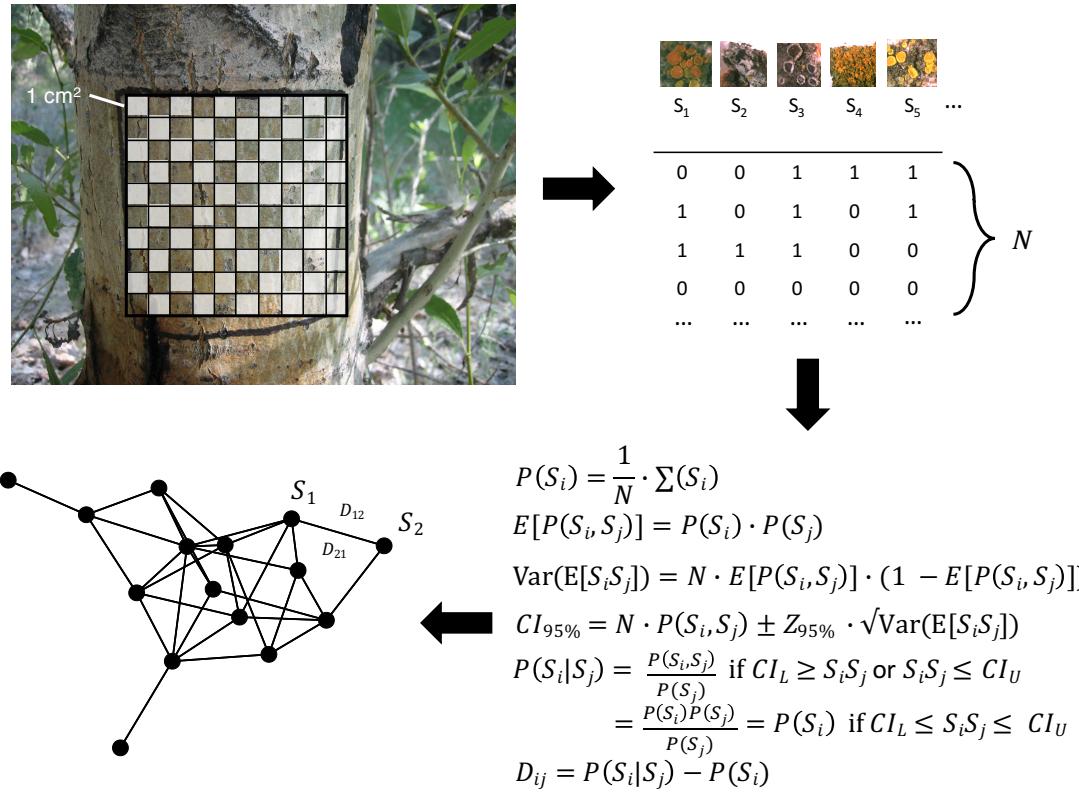


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded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

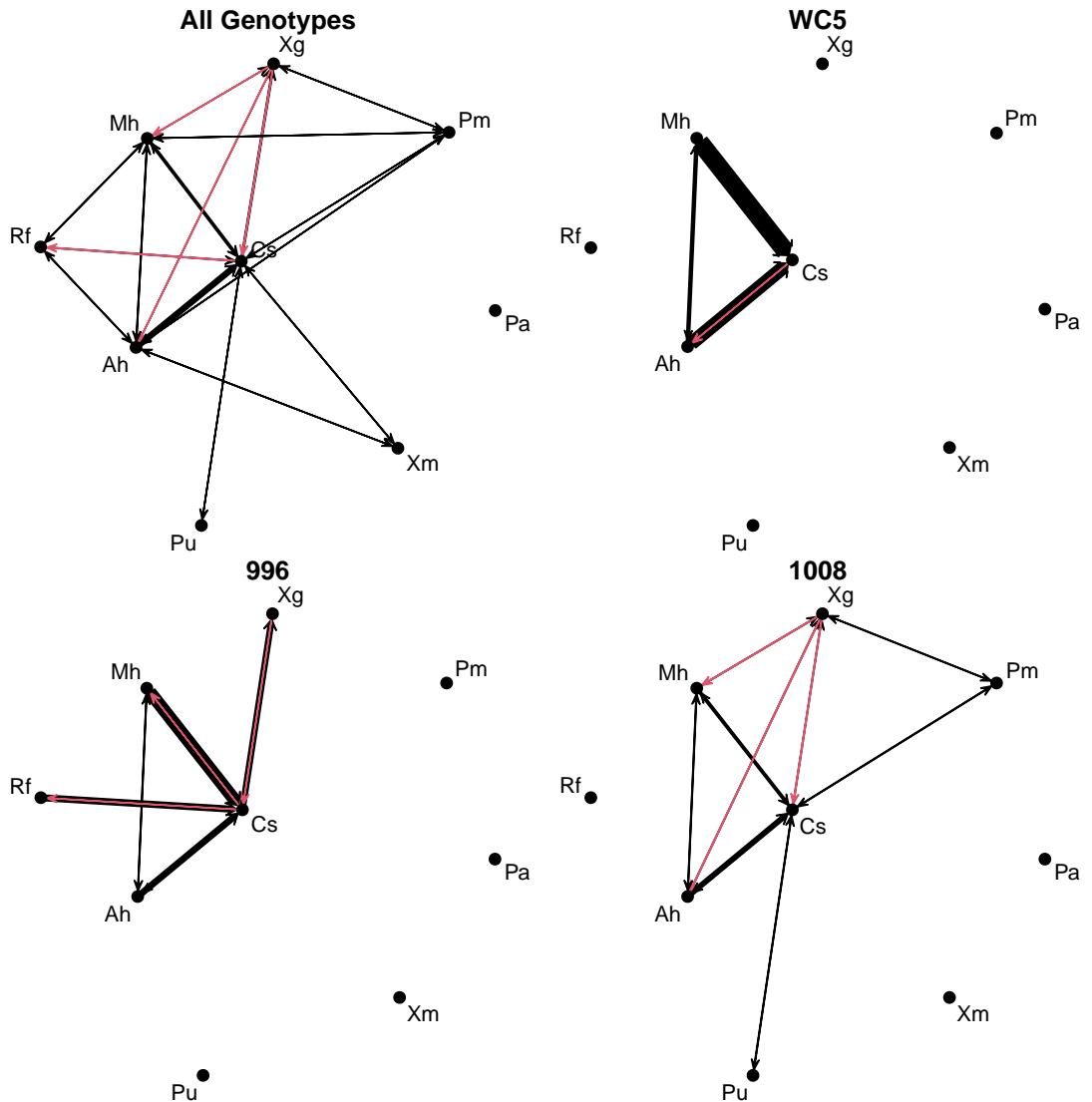


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

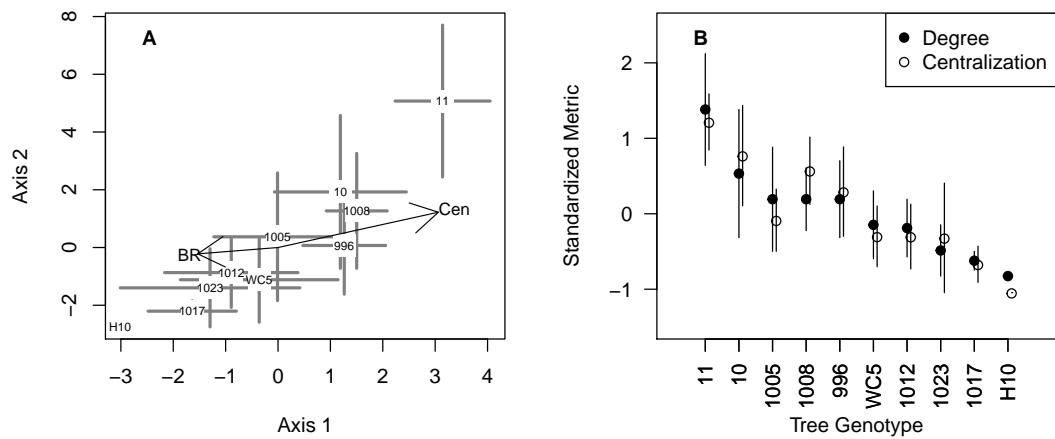


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

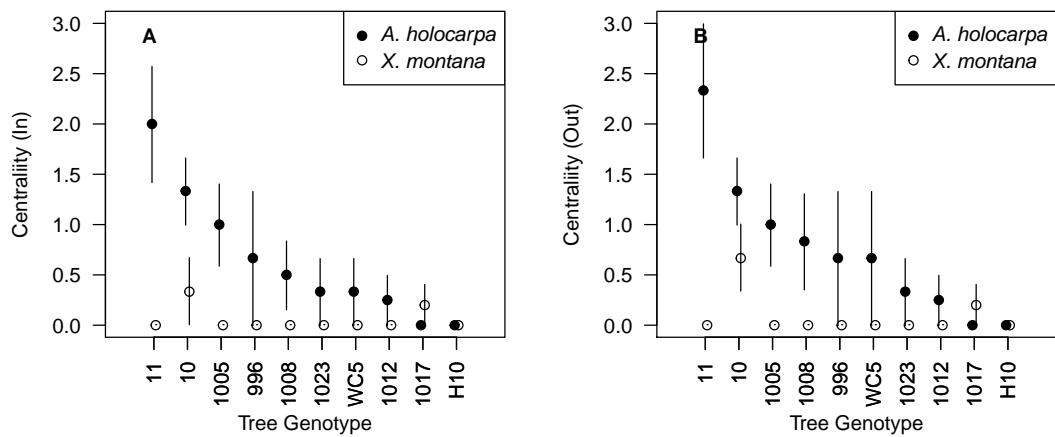


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *A. holocarpa* and *X. montana*. *Athallia holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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