

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

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ABSTRACT

Elucidating the genetic basis to ecological network structure is fundamental to understanding evolution in complex ecosystems. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that has quantified the heritability of network structure of a foundation species associated community. To examine this, in a 20+ year old common garden we observed epiphytic lichens associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation tree 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 lichen network similarity ($R^2 = 0.26$). These results support a mechanistic, genetic pathway from variation in a heritable tree trait to ecological network structure and demonstrate that evolution has the potential to act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks.

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

22 INTRODUCTION

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

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

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

78 In this context, the “genetic similarity rule” of community genetics provides a
79 useful framework we can apply to interaction networks at the nexus of ecological
80 and evolutionary dynamics. In a study combining experimental common gardens and
81 landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and
82 arthropods, Bangert et al. (2006) observed that individual genotypes that are more
83 genetically similar will tend to have similar phytochemical traits and thus tend to have
84 similar interactions with other species. Although this is likely to have consequences for
85 interactions and network structure, studies in the network ecology literature generally
86 do not include a genetic component (Lau et al., 2017) and community genetics stud-
87 ies have primarily focused on community composition in terms of the abundance of
88 species (Des Roches et al., 2018). Some studies have examined the effects of genetic
89 variation on trophic chains in plant-associated communities (including *Populus*, *Sol-*
90 *idago*, *Oenothera*, *Salix*) (Bailey et al., 2005; Johnson, 2008; Smith et al., 2011, 2015;
91 Barbour et al., 2016) and generally found that increasing genotypic diversity leads to
92 increased trophic complexity. We are aware of only two studies that explicitly examined
93 the effect of genotypic variation on interaction networks between tree individuals and
94 associated herbivores using ecological network metrics (Lau et al., 2016a; Keith et al.,
95 2017). Both found that genotypic diversity generates increased network modularity
96 (i.e., compartmentalization); however, both were examining networks at the scale of
97 forest stands, rather than networks associated with individual trees; therefore, neither
98 was able to observe replicated networks in order to statistically test for genetic effects
99 on network structure and quantify the genetic component (i.e., heritable variation) in
100 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 We used 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 epiphytic lichen species, as previous research has
106 demonstrated significant compositional effects of genotypic variation on lichen in this
107 system (Lamit et al., 2011, 2015b,a) and epiphytic organisms in other systems (Winfree
108 et al., 2011; Zytynska et al., 2011). Applying a probability-theory based network
109 modeling approach (Araújo et al., 2011), we constructed a set of interaction network
110 models for the lichens associated with individual trees. Using these models, we then
111 examined the genetic basis of the structure of these ecological networks via several
112 network metrics that measure different aspects of network structure at the scale of

113 individual species (i.e., nodes) or the entire network observed on each tree genotype.
114 Given the potential importance of focal or “central” nodes (e.g., species) for determining
115 network dynamics (Lieberman et al., 2005), we focused on network metrics that measure
116 centrality for individual species and centralization for whole networks. Both of these
117 metrics measure how much a species is connected in the network relative to other species.
118 As there is a preponderance of evidence that in natural systems evolution occurs in
119 communities comprised of networks of interacting species (Lau et al., 2016a; Keith
120 et al., 2017; Thompson, 2013; Bascompte et al., 2006), we set out to test two hypotheses.
121 First, per the community similarity rule (Bangert et al., 2006) and IIGE theory (Whitham
122 et al., 2020), we hypothesize that trees of the same genotype (i.e., clones) will support
123 more similar lichen interaction networks relative to individuals of other genotypes. In
124 other words, epiphytic lichen network structure is heritable, which can be calculated
125 via comparisons of within and among group variation in network structure. Second,
126 heritability of lichen network structure is the result of underlying phenotypic covariation
127 in tree traits important to interactions between trees and lichens and among lichens.
128 Evidence that such trait covariance generates variation in interactions among community
129 members provides an intermediate genetics-based mechanism for the underlying factors
130 determining lichen distribution and abundance. In combination, evaluating these two
131 hypotheses is fundamental to understanding variation and dynamics of network structure
132 and evolution.

133 MATERIALS AND METHODS

134 Study System

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

145 A long-term, common garden experiment was used to isolate the effect of tree geno-
146 type from the effect of the localized microenvironment associated with each individual
147 and spatial autocorrelation. Established in 1992, asexually propagated clones of geno-
148 typed *P. angustifolia* individuals were obtained from wild collections and planted in a
149 fully randomized design at the Ogden Nature Center, Ogden, UT. From the population
150 of established individuals in the common garden, we sampled a total of ten genotypes,
151 replicated between 3 and 8 times each. These individuals comprised a set of tree geno-
152 types with lichen communities that have been well studied by previous investigations
153 (Lamit et al., 2011, 2015b,a).

154 **Bark Lichens and Trait Observations**

155 We conducted a modified sampling procedure originally developed by Lamit et al.
156 (2015b). On each tree, presence or absence of each lichen species was assessed in
157 a total of 50 1 cm² cells arrayed in a 10 cm² checkerboard pattern. Given the small
158 size and sessile nature of lichens, we were able to rapidly assess lichen interactions
159 by quantifying thalli of different species occurring in close proximity. Sampling was
160 restricted to the northern aspect of the trunk to maximize the abundance of lichens and
161 control for the effect of trunk aspect. Two adjacent 100 cm² quadrats centered at 50 cm
162 and 95 cm from ground level were sampled (Fig 1). The observed lichen community
163 included: *Athallia holocarpa*, *Candelariella subdeflexa*, *Myriolecis hagenii*, *Rinodina*
164 *freyi*, *Physcia adscendens*, *Physciella melanachra*, *Physcia undulata*, *Xanthomendoza*
165 *galericulata*, *Xanthomendoza montana*. Several other species were not observed in
166 the present study but are known to occur in this region: *Melanohalea elegantula*,
167 *Melanohalea subolivacea*, *Phaeophyscia ciliata* and *Phaeophyscia orbicularis*.

168 The cell size and checkerboard sampling pattern was chosen to isolate the individuals
169 in each cell. In a survey of *Xanthomendoza galericulata* in the common garden, we had
170 observed a median thallus size of 0.12 ± 0.001 cm² (1 S.E.) (Supporting Information,
171 Fig. 1). This expected thallus size formed the basis for our sampling design, such
172 that lichen observations were spatially independent of thalli present in other cells but
173 exposed to similar micro-environmental conditions created by the bark and the location
174 of the sampling area on an individual tree. Therefore, we were confident in treating
175 the cell-wise observations in quadrats as independent with respect to lichen-lichen
176 interactions.

177 We quantified tree traits inside or in close proximity to the lichen quadrats. We
178 assessed bark texture/structure in the quadrat as the percent of 1 cm² cells with “rough”
179 bark, i.e., bark with fractured surface. In addition, we also examined several bark
180 chemistry traits by taking bark samples immediately adjacent to each quadrat. We
181 used previously collected phytochemical data from Lamit et al. (2011), including the
182 concentration of condensed tannins, carbon and nitrogen. Additionally, we quantified
183 bark pH for each tree. Bark samples were collected by excavating adjacent to the quadrat
184 down to a depth of 2 mm. Bark pieces were air dried for storage and later processing.
185 Samples were prepped for pH measurements by crushing with a mortar and pestle until
186 all pieces were approximately 0.5 cm in diameter, creating equivalent surface areas
187 among samples. 0.5 g of crushed bark was placed in a 15 ml Falcon collection tube
188 with 5 ml of deionized water. Tubes were capped and let sit for 24 hrs prior to pH
189 measurement with a SevenGo™ pH meter (Mettler Toledo).

190 **Lichen Network Modeling**

191 For each tree, the repeated observations of lichens were used to construct replicated
192 interaction networks, i.e. one for each individual tree. Unipartite networks were
193 generated using the conditional probabilities of each species pair, i.e., the probability
194 of observing one species given an observation of another species $P(S_i|S_j)$, based on
195 the method developed by Araújo et al. (2011). To calculate conditional probabilities,
196 we quantified the individual probabilities of species occurrences $P(S_i)$ and the joint
197 probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species and their
198 co-occurrences. Using the axioms of probability, we can calculate the conditional

probabilities of each species pair as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$. This yields a matrix that could possibly be asymmetrical, i.e., $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Also, the diagonal, $P(S_i|S_i)$, is equal to one for all species present and zero for species that were not observed in any cell.

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

The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as one species' impact on another with zero being no effect and values less than or greater than zero being negative and positive effects, respectively. We will refer to \mathbf{D} as a signed, weighted interaction matrix. As such, \mathbf{D} has the properties that it can be asymmetric (i.e., D_{ij} does not necessarily equal D_{ji}) and that it scales between -1 and 1, and, therefore, does not have the mathematical properties of a probabilistic network (Poisot et al., 2016). Also, as the method does not track individuals within species; therefore, the "intra-specific" observations are the same species being counted across the cells of the grid and a resulting $D_{ii} = 0$. In the context of these networks, asymmetry and positive/negative valued connections are distinct quantities. In-coming and out-going connections can be interpreted as "influenced by" and "influenced", respectively; while positive and negative are within this study interpreted as one species increasing or decreasing, respectively, the probability of another species' occurrence.

Analyses, Software and Data

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

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

We used a combination of parametric and non-parametric, permutation based frequentist statistical analyses to test for the effects of genetic variation on lichen communities and their interaction networks. To assess the effect of genotype on traits as univariate response variables (including the metrics of network structure), we used additive, random effects models with Restricted Maximum Likelihood (REML) conducted in R via the `lme4` and `RLRsim` packages (Bates et al., 2015; Scheipl et al., 2008). To conform to test assumptions, traits were root transformed with the exception of condensed tannin concentration and carbon-nitrogen ratio, which were rank and \log_{10} transformed, respectively. Differences in node level centrality among species was tested using ANOVA and Tukey-HSD multiple comparison tests. Correlations among trait variables and network metrics were quantified and tested using linear correlations of Pearson's r . For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches. To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the **D** interaction matrices among all trees (Newman, 2010). For community composition we applied Bray-Curtis similarity to a matrix of species abundances obtained by aggregating the gridded observations by summing over the binary cell-wise species presence-absences. To test for the effects of genotype and other predictor variables on community and network similarity we conducted Permutational Analysis of Variance (PERMANOVA) with `vegan` (Oksanen et al., 2019) using 100000 permutations. For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of these multivariate responses and fitted vectors for continuous predictor variables to the ordinated values (Oksanen et al., 2019), using 100 random initial configurations with a maximum of 1000 iterations and a change in stress threshold of less than 10^{-12} . This was repeated for one to four dimension configurations, and the configuration with the lowest dimensionality and an unexplained variation less than 10% was selected. For all tests where genotype was used as a predictor, we quantified the heritability of the response variable. Because the trees in the garden were clonal replicates of each genotype, we calculated broad-sense heritability, which is the genotypic variance divided by the total phenotypic variance (Conner and Hartl, 2004), which can be interpreted as a measure of the phenotypic variance due to genotypic variation. All analyses were conducted using R version 4.0.2 (R Core Team, 2020). Code and data for the project are openly available as a reproducible workflow using `drake` (Landau, 2018) archived via Zenodo <https://doi.org/10.5281/zenodo.4581639>.

288 **RESULTS**

289 In support of our first hypotheses, we found that tree genotype influenced lichen net-
 290 work structure and that multiple lichen network metrics were heritable. Tree genotype
 291 significantly predicted the structural similarity of lichen networks and, overall, network-
 292 level metrics responded significantly to tree genotype, including network degree and
 293 centralization including both in-coming and out-going links or when separated into
 294 in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive links
 295 also showed a significant effect of tree genotype, including positive degree and positive
 296 in-going centralization. Metrics calculated with negative links were not significant,
 297 including degree (negative) and both in-coming (negative) and out-going centralization
 298 (negative). Interestingly, although network similarity and multiple network metrics were
 299 significantly predicted by tree genotype, we did not observe a significant genotypic
 300 effect for community composition ($\text{Pseudo-}F_{9,27} = 0.751$, $R^2 = 0.20$, $p\text{-value} = 0.888$).

	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.

301 The genetic response of network centralization was driven by variation in *Athallia*
 302 *holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$,
 303 $p\text{-value} < 0.0001$). The node-level metrics for *A. holocarpa* displayed the strongest
 304 response to tree genotype with high levels of heritability of positive centrality for both
 305 the in-coming ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT =$
 306 3.13 , $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives but not for either negative centrality
 307 metrics in-coming ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$,
 308 $p\text{-value} = 0.4543$). None of the other species' centralities showed a genotypic response
 309 (Supporting Information, Fig. 2) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 =$
 310 0.32 , $p\text{-value} = 0.0375$); however, the centrality of *X. montana* was much lower overall
 311 relative to *A. holocarpa* and the variation in *X. montana* centrality was restricted to two
 312 genotypes (Fig. 5).

313 In support of our second hypothesis, analysis of trait covariation revealed that geno-
 314 type indirectly influenced lichen network centralization via genetically based variation
 315 in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$,
 316 $p\text{-value} = 0.0113$) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} =$

317 0.0343) both displayed significant responses to tree genotype. None of the other bark
 318 traits, pH ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT =$
 319 $0.0000, H^2 = 0.0000, p\text{-value} = 1.0000$), showed a significant response to tree genotype
 320 and none other than bark roughness was correlated with network similarity (Table 2);
 321 therefore, we focused our subsequent analyses on the indirect effect of genotype on
 322 lichen network structure via bark roughness. We found that bark roughness was signifi-
 323 cantly correlated with network similarity and other lichen network metrics, including
 324 negative correlations with overall network degree ($df = 35, t = -2.13, r = -0.34, p\text{-value}$
 325 $= 0.04$) and centralization ($df = 35, t = -2.52, r = -0.39, p\text{-value} = 0.02$). In other
 326 words, trees with more similar levels of bark roughness tended to have lichen interaction
 327 networks with similar structure (Fig. 6). To quantify the genetic bases of this effect of
 328 bark roughness on network structure, we used the residual values from regressions of the
 329 network metrics and bark roughness in subsequent tests of the effect of tree genotype
 330 and found no significant effect of tree genotype for either degree ($RLRT = 0.00, H^2 =$
 331 $0.00, p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$),
 332 and, thus, the bulk of the genetically based variation in the network metrics can be
 333 explained by bark roughness.

	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.

334 DISCUSSION

335 Ecological and Evolutionary Importance of Network Heritability

336 Although previous studies have examined aspects of networks, such as trophic com-
 337 plexity (Barbour et al., 2016) and forest stand level interaction network structure (Lau
 338 et al., 2016b; Keith et al., 2017), this is the first study that we are aware of to ex-
 339 amine the heritability of network structure with replicated networks at the genotype
 340 scale. Previous work in the evolution of ecological networks have primarily focused on
 341 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,
 342 2018; Harmon et al., 2019) or have been simulation based individual-level models that
 343 integrate intraspecific variation to the species level (Maliet et al., 2020), even though
 344 recent syntheses have pointed to the importance of processes operating across scales of
 345 organization (Guimarães, 2020). There are two important functional ramifications of
 346 genetically based variation in network structure. First, heritability of network structure
 347 suggests that some amount of interaction network complexity is determined and there-
 348 fore could be predicted by genetic identity. Variation in space and time create variation
 349 in ecological networks that influences evolutionary dynamics via shifts in ecological

350 dynamics, such as population demographics (Guimarães, 2020). Given that ecosystems
351 are comprised of hundreds and thousands of species, each having a multitude of interac-
352 tions, the potential to find traction for making predictions in the context of ecological,
353 let alone evolutionary, dynamics seems daunting. The promise of predictability lies in
354 the presence of asymmetries in ecosystems, such as hierarchy created by foundation
355 species via differences in body size and/or life-history strategies (Ellison et al., 2005).
356 Second, heritability (i.e., genetic determination) means that there is structure in the
357 spatial or temporal variation that is created by individuals of foundation species whose
358 traits are in part determined by underlying trait differences. Although this variation
359 is inherently a function of both genetic and environmental effects (Conner and Hartl,
360 2004), the community and network-level effects are also a function of the scale of the
361 interaction (Shuster et al., 2006; Lau et al., 2017).

362 Notably, even if the composition of the communities is the same among individuals
363 and genotypes, interactions may not be. We didn't observe compositional differences
364 using the same data from which the lichen networks were derived. If we only had our
365 composition dataset from this study, we would have concluded no response of the lichen
366 community to tree genotype, even though the underlying interactions among lichen
367 species does vary among genotypes. As such differences in network structure could
368 occur without observable differences in species richness or community composition,
369 which have been the primary focus of the majority of community genetics studies
370 (Whitham et al., 2020). Community composition of lichens has previously been observed
371 to be different among tree genotypes in the same experimental garden (Lamit et al.,
372 2011, 2015b). The different results observed in the present study is likely a result of
373 differences in lichen quantification and the tree genotypes observed leading to overall
374 higher abundances of observed lichens to assure the possibility of observing lichen
375 interactions. The previous study used a visual percent cover estimation, unlike the
376 current study, which observed lichens at the scale of 1 cm² cells, which could over-
377 estimate cover depending on the frequency at which actual thallus size was less than 1
378 cm², as well as both the northern and southern aspects of each tree. These differences
379 do not negate the findings of either study.

380 The present study's finding of differences in network structure without significant
381 compositional differences points to the importance of quantifying how network structure
382 changes in response to genetic variation. Having not observed a compositional effect of
383 tree genotype without measuring the network structure could lead to the conclusion of no
384 genetic effect on the community, even though differences in network structure are leading
385 to altered, local evolutionary dynamics. It is possible that these underlying differences
386 in interactions among lichens could lead to differences in community composition at
387 a future point in time via their effects on species abundances (Shuster et al., 2006);
388 however, this is not needed for evolutionary dynamics to occur via selection that leads
389 to shifts in trait distributions without shifting species abundance distributions, which is
390 possible under stabilizing, disruptive and directional selection (Conner and Hartl, 2004),
391 so long as the relative abundances of each species is imperceptibly changed. Thus, it is
392 imperative that further community genetics research assess or at least be aware of the
393 potential effects of variation in interactions and not just observe species abundances,
394 otherwise community level genetic effects may be underestimated, especially when
395 cumulative interaction effects are taken into account (Borrett et al., 2007, 2010).

Furthermore, the demonstration of the heritability of interaction networks, without significant differences in community composition, provides clear empirical evidence that IIGEs need to encompass the structure of interaction networks. Although IIGE theory provides a quantitative framework within which to approach evolutionary theory at higher levels of biological organization (from populations to communities and ecosystems), this theory has focused on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham et al., 2012, 2020) and has not yet integrated developments from the ecological or evolutionary network theory literature. Thus, it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated this network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be 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 species with relatively higher abundances (e.g., *X. galericulata*) were present in the community, the response of the network was not predominately due to their interactions. In addition, although there were species that tended to be central within the lichen networks, the similarity of networks showed the highest heritability compared to any of the centrality metrics, which suggests that there are aspects to network structure that not solely due to the central species. Taken together, these results point to the importance of considering the impact of network structure and that it is a potentially productive path forward for the development and application of IIGE theory.

Network Structure and Levels of Selection

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

441 evolution would be to quantify how networks change over time in response to an invasive
442 species, climate change, or some other agent of selection, which represents a frontier for
443 future ecological network studies.

444 The current study shows the utility of considering the spatial and temporal scales of
445 ecological and evolutionary dynamics. In line with previous empirical studies (Bangert
446 et al., 2006; Zook et al., 2010; Zytynska et al., 2012), we found that the assembly
447 of ecological networks can have a measurable genetic basis depending on the spatial
448 scale of interactions, due in part, to asymmetries in size and longevity of organisms.
449 Intra-specific, genotypic diversity among cottonwood trees appears to be a major factor
450 in the creation of meta-communities of lichens on individual trees that form interaction
451 modules with different dynamics. When communities are comprised of individuals
452 whose habitat is primarily determined by another organism, these communities inherently
453 form modules within the larger ecosystem, as they tend to interact more with each other
454 than with other individuals (Lau et al., 2017). Our study demonstrates that the localized
455 environmental differences determined by the genetic variation within a single tree
456 species can not only impact community composition, as repeatedly demonstrated in
457 other community genetics studies (Whitham et al., 2006; Des Roches et al., 2018), but
458 also shape the structure of interactions among individuals. Some network structures
459 are likely to be more stable, either in response to disturbance or via self-organized
460 dynamics. For example, centralized networks, although more efficient, are theorized
461 to be more susceptible to targeted “attacks” in the terminology of defense networks.
462 As mentioned previously, one class of networks that are theorized to have amplifying
463 effects on networks have centralized “star” shapes with one or a few species at the
464 center and radiating interactions out from the central core (Lieberman et al., 2005).
465 This is structurally what we have observed with the networks that tend to occur on
466 some of the genotypes in our study, i.e., the more centralized networks. It is likely that
467 these networks could function as hot-spots of evolutionary dynamics resulting from
468 the amplifying effect the centralized network structure found on that tree genotype, as
469 multiple studies have found significant impacts of the removal of foundation species in
470 different systems (Keith et al., 2017; Des Roches et al., 2018).

471 The importance of the scale of network organization to create hierarchical structure
472 (Guimarães, 2020) and the potential for foundation species to create this structure in
473 the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006) suggests
474 that future work would be aided by determining species with large differences in body-
475 size and longevity, which could be contributing to interaction network structure (e.g.,
476 modules and centralized species). As heritable variation is the raw material for natural
477 selection to act upon, a genetic basis for interaction network structure indicates that
478 conserving genetic variation is important to consider in efforts to restore or preserve
479 complex species interactions and their associated ecosystem functions (Whitham et al.,
480 2012; Evans et al., 2013; Whitham et al., 2020). Many ecological network studies that
481 have an evolutionary context have focused on asymmetry and the quantification of its
482 structure in communities (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães
483 et al., 2011; Thompson, 2013). The findings of these studies have generally supported
484 the hypothesis that nestedness (the degree to which species tend to interact with similar
485 subsets of the community) tends to promote stability in mutualistic, primarily bipartite
486 (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 a 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. We were not able to examine nestedness or modularity of the lichen networks as metrics for analyzing weighted, directed *and* signed networks could not be found. Hopefully future network theoretic developments will make the appropriate metrics available to conduct these analyses.

Game theoretic applications to ecological networks provide another theoretical basis that relates more directly to the heritability of network centralization found in the present study. Although developed at the population scale, the network theory could be applied at the community scale as well (Lieberman et al., 2005). One seemingly useful direction is the classification of networks into two general categories, rooted and cyclic, in which rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but these effects do not have feedbacks to the origin, whereas cyclic networks contain feedbacks to one or more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in the context of IIGE theory (Whitham et al., 2020). As we do not have an estimate of the effect of the lichen at the larger scale of the fitness of the tree they occur on, we can not determine whether the lichen networks in this system are cyclic or not. In terrestrial ecosystems, lichens play important ecological roles, such as substrate stabilization (Root et al., 2011) and nitrogen fixation (Nelson et al., 2018). Some epiphytic lichens can have demonstrable effects on the availability of nutrients for the trees that they are associated with (Norby and Sigal, 1989). Although none of the lichens the present study’s system is known to fix nitrogen, it is possible that they might add micro-nutrients or provide some other unobserved benefit to their host trees. Elucidating the presence of and quantifying such feedbacks would permit the determination of the cyclic nature evolutionary dynamics. If there are positive effects of lichens on host trees that might increase their ability to respond to environmental stress, then selection could enhance tree performance and trees with superior communities are more likely to survive. Gehring et al. (2014, 2017) showed this with ectomycorrhizal communities in which trees with superior mutualist communities were more likely to survive drought and community evolution occurred (Whitham et al., 2020). However, such feedbacks to the higher level of the foundation species are not a requirement for evolution, and, regardless of whether networks are rooted (no feedbacks) or cyclic (feedbacks present), selection at the community level leading to evolution can still occur. Specifically within the context of the current study, even if lichens and their interactions do not feed back to affect the performance and ultimate fitness of the tree on which they reside, non-random death of trees, such as those observed for drought in arid systems Sthultz et al. (2009); Gehring et al. (2017), can still result in selection at the community level and evolution. For example, when a tree dies from some event (e.g., a drought, fire, storm, etc.), its lichen network is selected against while intact networks persist on other trees that survive this selection event.

532 **Conclusion**

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

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

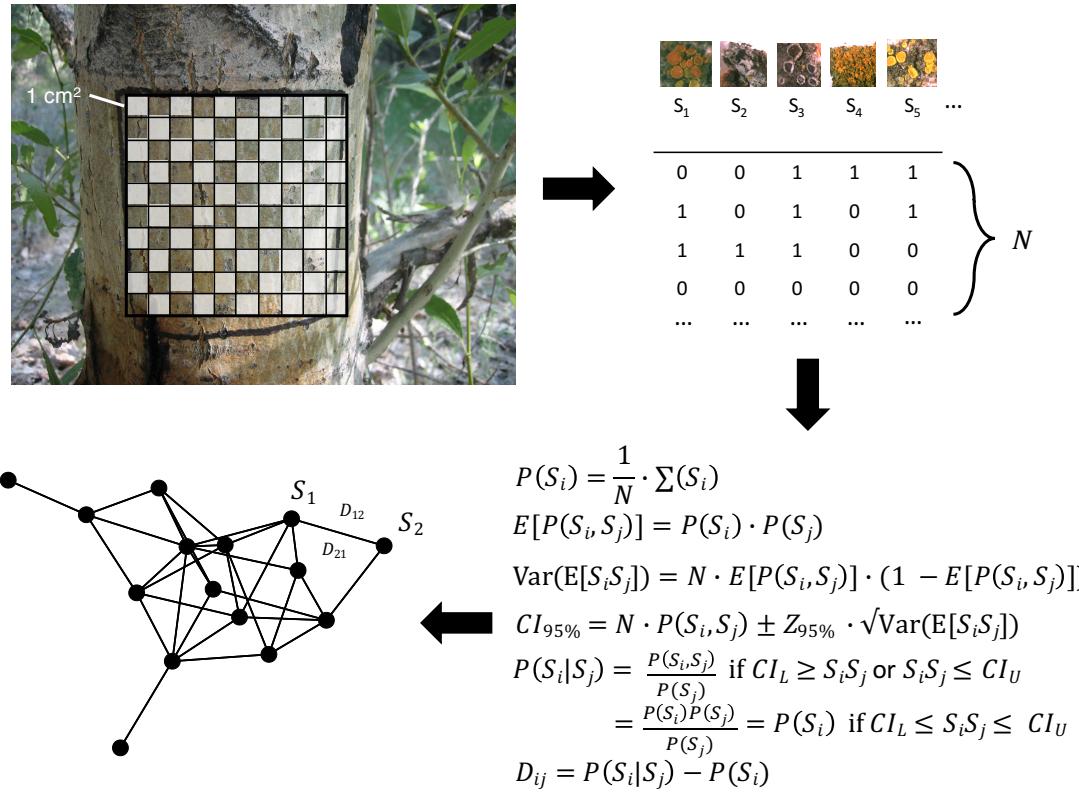


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (Araújo et al., 2011), we calculated the conditional probabilities, $P(S_i | S_j)$, for all species pairs and removed (i.e., set equal to zero) species pairs whose joint probabilities, $P(S_i S_j)$, 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 .

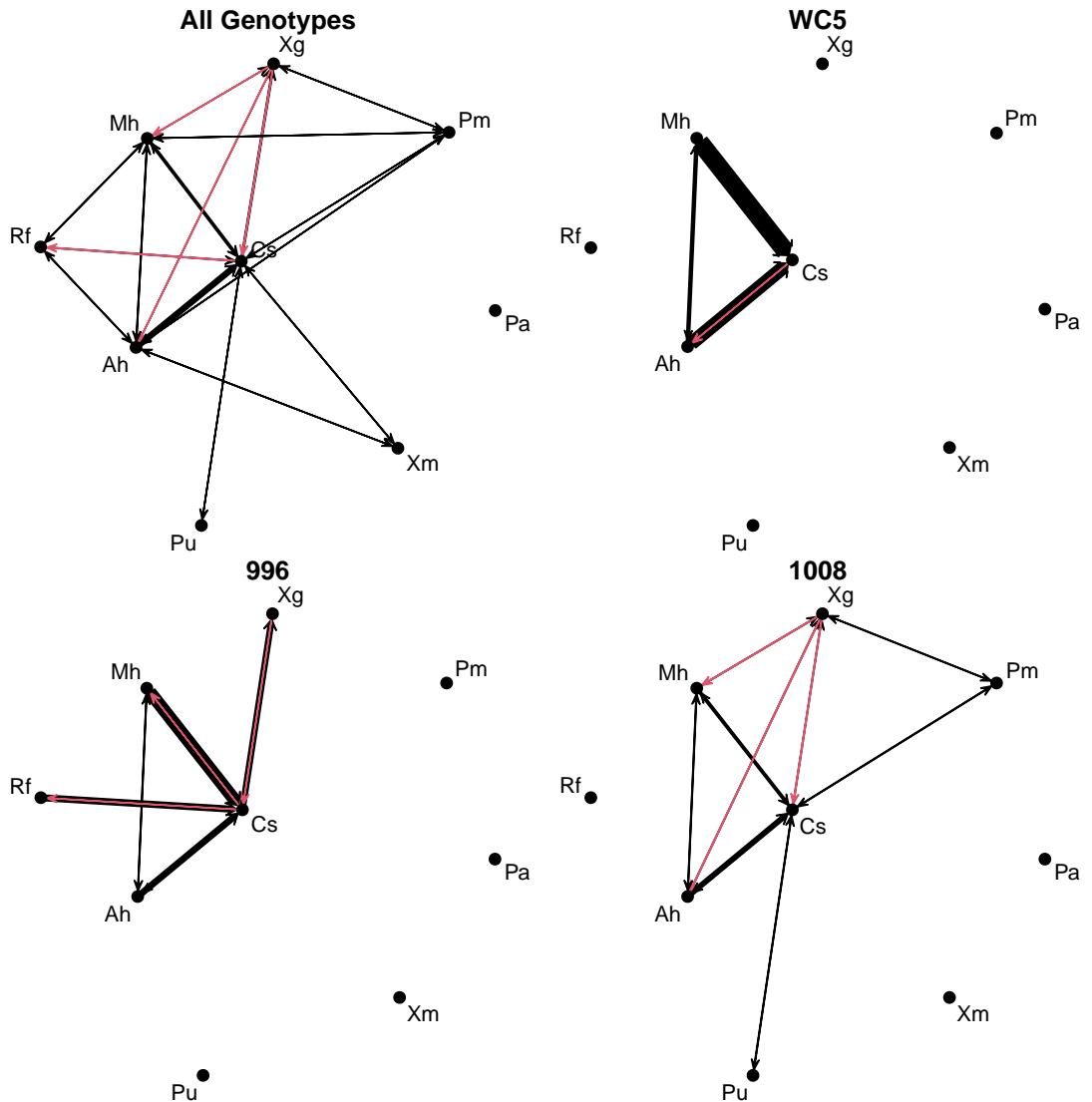


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

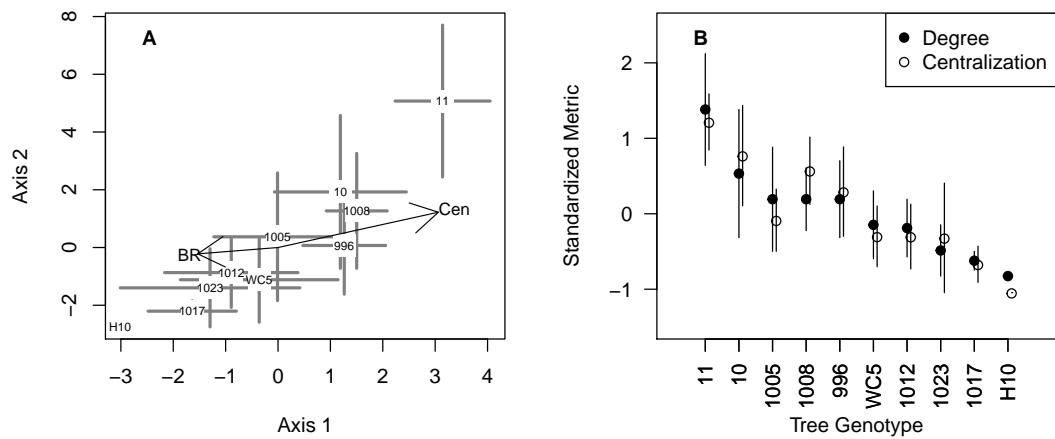


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

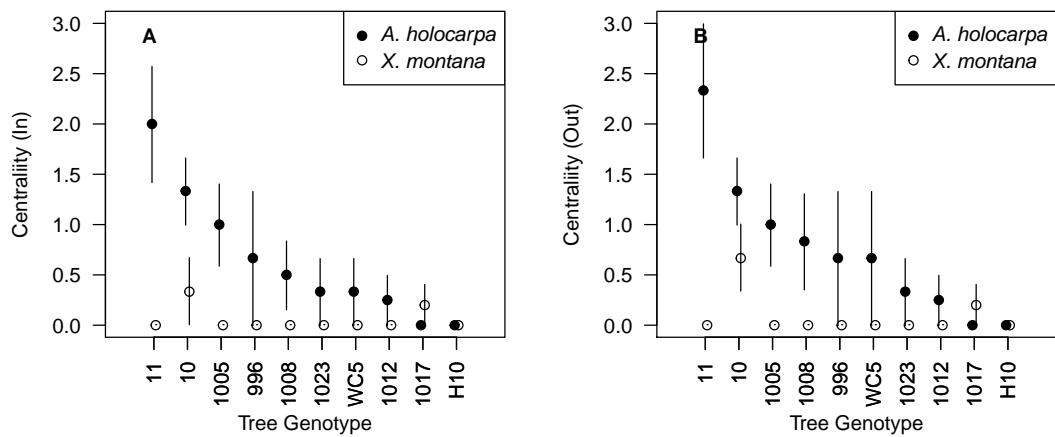


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *A. holocarpa* and *X. montana*. *Athallia holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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