

# **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.

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 epiphytic lichen species, as previous research has  
106 demonstrated significant compositional effects genotypic variation on lichen in this  
107 system (Lamit et al., 2011, 2015b,a) and epiphytic organisms in other systems (Winfrey  
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

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

## 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  
149 fully randomized design at the Ogden Nature Center, Ogden, UT. From the population  
150 of established individuals in the common garden, we chose a total of ten genotypes,  
151 replicated between 3 and 8 times each, for sampling. We selected tree genotypes that  
152 generally had lichens present in order to permit the construction of interaction networks.

153 **Bark Lichens and Trait Observations**

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

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

186 **Lichen Network Modeling**

187 For each tree, repeated observations of lichens were made in order to construct replicated  
188 interaction networks for each genotype. We conducted a modified sampling procedure  
189 originally developed by Lamit et al. (2015b) with the addition that we quantified the  
190 presence of lichens in the 1 cm<sup>2</sup> cells on individual trees of *P. angustifolia*. Unipartite  
191 networks were generated using the conditional probabilities of each species pair, i.e., the  
192 probability of observing one species given an observation of another species  $P(S_i|S_j)$ ,  
193 based on the method developed by Araújo et al. (2011). To calculate conditional  
194 probabilities, we quantified the individual probabilities of species occurrences  $P(S_i)$  and  
195 the joint probability of co-occurrences  $P(S_i, S_j)$  using the frequencies of each species  
196 and their co-occurrences. We were then able to calculate the conditional probabilities of  
197 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

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

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

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

## 234 Analyses, Software and Data

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

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

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

## 284 RESULTS

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

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

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

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

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

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

316 correlated with network similarity and other lichen network metrics, including negative  
 317 correlations with overall network degree ( $df = 35$ ,  $t = -2.13$ ,  $r = -0.34$ ,  $p\text{-value} = 0.04$ )  
 318 and centralization ( $df = 35$ ,  $t = -2.52$ ,  $r = -0.39$ ,  $p\text{-value} = 0.02$ ). In other words, trees  
 319 with more similar levels of bark roughness tended to have lichen interaction networks  
 320 with similar structure. To quantify the genetic bases of this effect of bark roughness on  
 321 network structure, we used the residual values from regressions of network degree and  
 322 centralization in tests of the effect of tree genotype and found no significant effect of tree  
 323 genotype for either degree ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ) or centralization  
 324 ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ), suggesting that the observed relationship  
 325 between bark roughness and lichen network structure was largely genetically based  
 326 (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.

## 327 DISCUSSION

### 328 Ecological and Evolutionary Importance of Network Heritability

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

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

355 Notably, even if the composition of the communities is the same among individuals  
356 and genotypes, interactions may not be. We didn't observe compositional differences  
357 using the same data from which the lichen networks were derived. If we only had  
358 our composition dataset from this study, we would have concluded no response of the  
359 lichen community to tree genotype, even though the underlying interactions among  
360 lichen species does vary among genotypes. As such differences in network structure  
361 could occur without observable differences in species richness or community com-  
362 position, which have been the primary focus of the majority of community genetics  
363 studies (Whitham et al., 2020). Community composition of lichens has previously been  
364 observed to be different among tree genotypes in the same experimental garden (Lamit  
365 et al., 2011, 2015b). The different results observed in the present study is likely a result  
366 of differences in lichen quantification and the tree genotypes observed leading to overall  
367 higher abundances of observed lichens to assure the possibility of observing lichen inter-  
368 actions. The previous study used a visual percent cover estimation, unlike the current  
369 study, which observed lichens at the scale of 1 cm<sup>2</sup> cells, which could over-estimate  
370 cover depending on the frequency at which actual thallus size was less than 1 cm<sup>2</sup>,  
371 as well as both the northern and southern aspects of each tree. These differences do  
372 not negate the findings of either study. The present study's finding of differences in  
373 network structure without significant compositional differences points to the importance  
374 of quantifying how network structure changes in response to genetic variation in order to  
375 fully understand evolutionary dynamics in complex communities. Having not observed  
376 a compositional effect of tree genotype without measuring the network structure could  
377 lead to the conclusion of no genetic effect on the community, even though differences  
378 in network structure are leading to altered, local evolutionary dynamics. It is possible  
379 that these underlying differences in interactions among lichens could lead to differences  
380 in community composition at a future point in time via their effects on species abun-  
381 dances (Shuster et al., 2006); however, this is not needed for evolutionary dynamics  
382 to occur via selection that leads to shifts in trait distributions without shifting species  
383 abundance distributions, which is possible under stabilizing, disruptive and directional  
384 selection (Conner and Hartl, 2004), so long as the relative abundances of each species is  
385 imperceptibly changed. Thus, it is imperative that further community genetics research  
386 assess or at least be aware of the potential effects of variation in interactions and not  
387 just observe species abundances, otherwise community level genetic effects may be  
388 underestimated, especially when cumulative interaction effects are taken into account  
389 (Borrett et al., 2007, 2010).

390 Furthermore, the demonstration of the heritability of interaction networks, without  
391 significant differences in community composition, provides clear empirical evidence  
392 that IIGEs need to encompass the structure of interaction networks. Although IIGE  
393 theory provides a quantitative framework within which to approach evolutionary the-  
394 ory at higher levels of biological organization (from populations to communities and

395 ecosystems), this theory has focused on modeling the strong effects of foundation  
396 species (Shuster et al., 2006; Whitham et al., 2012, 2020) and has not yet integrated  
397 developments from the ecological or evolutionary network theory literature. Thus, it  
398 has not developed a way to examine complex interactions among species; however,  
399 previous studies have demonstrated this network context is likely to be important, as  
400 altering the structure of interaction networks provides a means for genetic effects to  
401 be dampened or magnified within the system of interacting species (Smith et al., 2011;  
402 Keith et al., 2017). Although such a synthesis necessitates a much greater effort than can  
403 be afforded in this paper, it is possible to point to several productive pathways forward.  
404 In terms of interaction networks, foundation species are relatively central within the  
405 system of interactions, that is their direct and/or indirect effects are greater than other  
406 species. So, when the more centralized (foundation) species have genetically based  
407 interactions, genetic effects will tend to be propagated and possibly magnified in the  
408 community. Here, we found that even though more abundant or more centralized (i.e.,  
409 “important”) species were present in the community, their effects were not the singularly  
410 responding to genetic effects, rather the similarity of the whole network depending on  
411 interactions among multiple species. Considering the impact of network structure would  
412 be a productive path forward for the theoretical development and application of the IIGE  
413 concept.

#### 414 **Network Structure and Levels of Selection**

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

433 The current study shows the utility of considering the spatial and temporal scales of  
434 ecological and evolutionary dynamics. In line with previous empirical studies (Bangert  
435 et al., 2006; Zook et al., 2010; Zytnska et al., 2012), we found that the assembly  
436 of ecological networks can have a measurable genetic basis depending on the spatial  
437 scale of interactions, due in part, to asymmetries in size and longevity of organisms.  
438 Intra-specific, genotypic diversity among cottonwood trees appears to be a major factor  
439 in the creation of meta-communities of lichens on individual trees that form interaction

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

Ecological network studies have focused on asymmetry and the quantification of its structure in communities, which can arise at different scales in space time or ecological organization. The impacts of asymmetry on evolution from community dynamics have primarily produced qualitative discussion (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific predictions can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities (Lieberman et al., 2005). One seemingly useful direction is the classification of networks into two general categories, rooted and cyclic, in which rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but these effects do not have feedbacks to the origin, whereas cyclic networks contain feedbacks to one or more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in the context of IIGE theory (Whitham et al., 2020). As we do not have an estimate of the effect of the lichen at the larger scale of the fitness of the tree they occur on, we can not determine whether the lichen networks in this system are cyclic or not. In terrestrial ecosystems, lichens play important ecological roles, such as substrate stabilization (Root et al., 2011) and nitrogen fixation (Nelson

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

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

529 **Conclusion**

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

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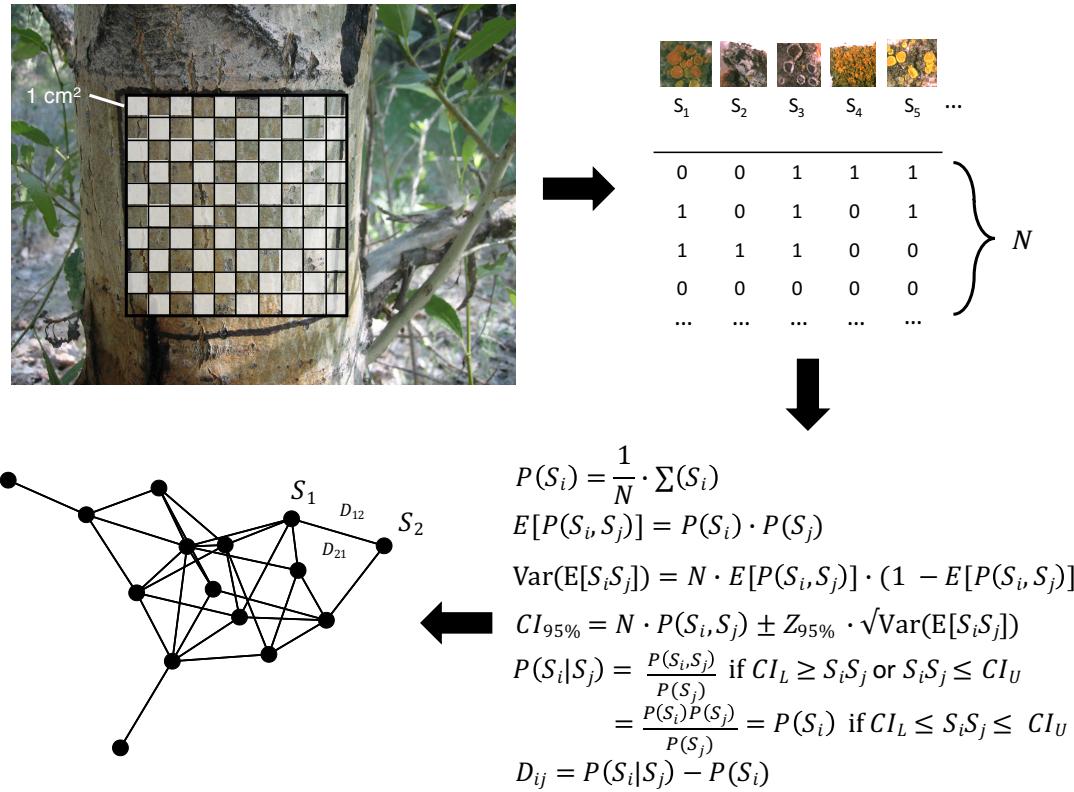
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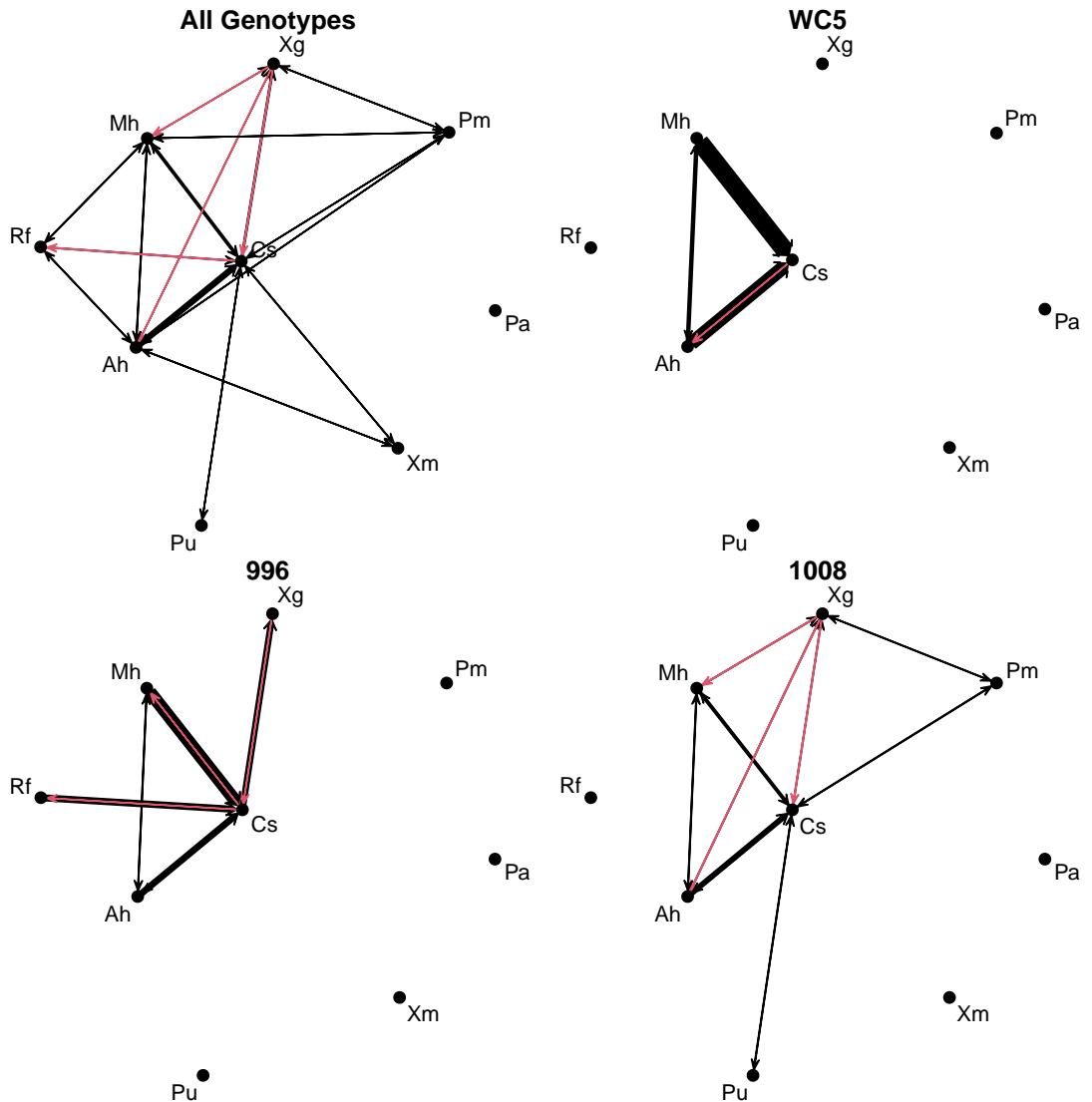
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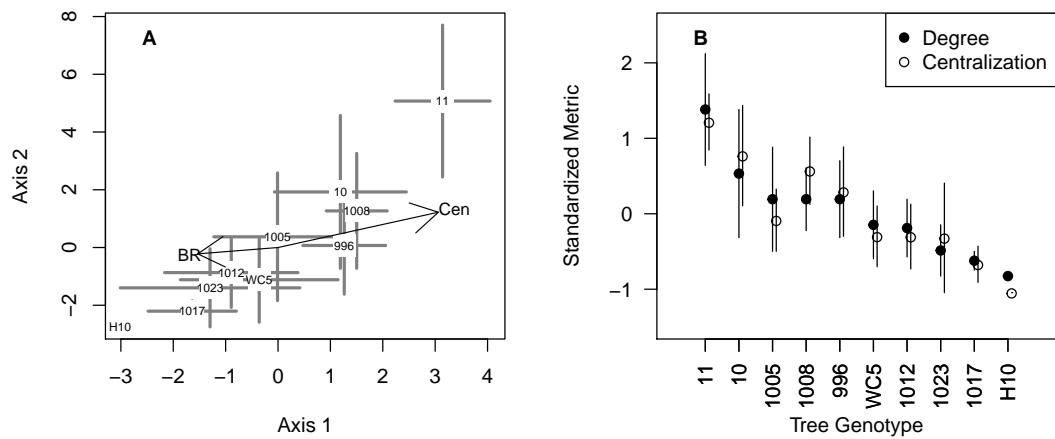
**Figure 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm 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).



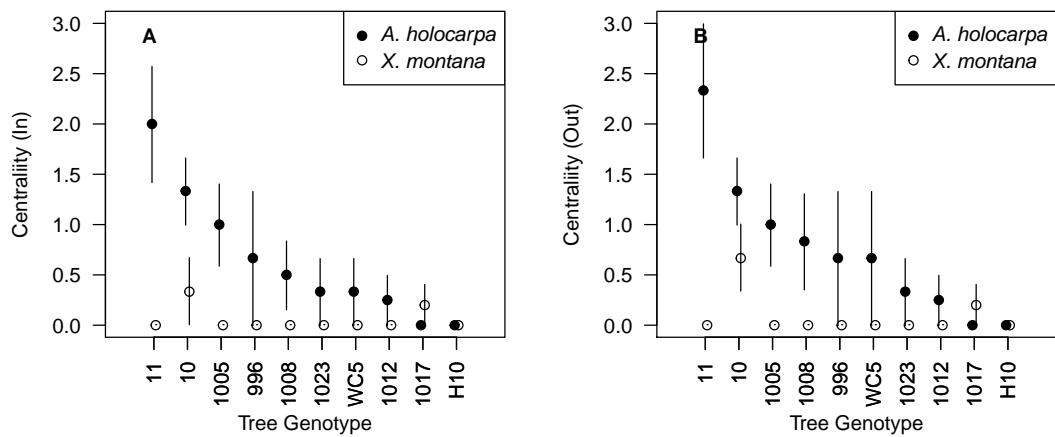
**Figure 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence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