

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

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## **20 ABSTRACT**

Elucidating the genetic basis to ecological network structure is fundamental to understanding evolution in complex ecosystems. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that quantified the contribution of phenotypic variation to heritable variation in network structure. To examine this, in a 20+ year old common garden we observed epiphytic lichens associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation species. We constructed and conducted genetic analyses of signed, weighted, directed lichen interaction networks on individual trees. We found three primary results. First, genotype identity significantly predicted lichen network similarity; i.e., replicates of the same genotype supported more similar lichen networks than different genotypes. Second, broad sense heritability estimates showed that plant genotype explained network similarity ( $H^2 = 0.41$ ), degree ( $H^2 = 0.32$ ) and centralization ( $H^2 = 0.33$ ). Third, of several tree phenotypic traits examined, bark roughness was both heritable ( $H^2 = 0.32$ ) and significantly predicted by lichen network similarity ( $R^2 = 0.26$ ). These results support a mechanistic, genetic pathway from variation in a heritable tree trait to ecological network structure and demonstrate that evolution can act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks. Given that network structure can influence system-wide stability and resilience, our findings have important implications for how evolution acts in ecosystems.

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

## 21 INTRODUCTION

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

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

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

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

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

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

## MATERIALS AND METHODS

### Study System

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

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

### Bark Lichens and Trait Observations

On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm<sup>2</sup> cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens,

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

165 The cell size and checkerboard sampling pattern was chosen to isolate the individuals  
166 in each cell. *Xanthomendoza galericulata* thallus size in this common garden, we had  
167 observed a median thallus size of  $0.12 \pm 0.001\text{ cm}^2$  (1 S.E.) (Supporting Information,  
168 Fig. 1). Based on the median thallus size, we expected thalli observed in each cell to  
169 generally be spatially independent of thalli present in other cells but exposed to similar  
170 micro-environmental conditions created by the bark and the location of the sampling area  
171 on an individual tree. Therefore, we were confident in treating the cell-wise observations  
172 in quadrats as independent with respect to lichen-lichen interactions. We quantified  
173 the texture of the bark in the quadrat is the percent of  $1\text{ cm}^2$  cells with rough bark. In  
174 addition to bark roughness, we also examined several bark chemistry traits by taking  
175 bark samples immediately adjacent to each quadrat. We used previously collected  
176 phytochemical data from Lamit et al. (2011), including the concentration of condensed  
177 tannins, carbon and nitrogen. Additionally, we quantified bark pH for each tree. Bark  
178 samples were collected in June 2011 by excavating adjacent to the quadrat down to a  
179 depth of 2 mm. Bark pieces were air dried for storage. In May of 2019, samples were  
180 processed for pH measurements by crushing with a mortar and pestle until all pieces  
181 were  $\approx 0.5\text{ cm}$  in diameter, creating equivalent surface areas among samples. 0.5 g of  
182 crushed bark was placed in a 15 ml Falcon collection tube with 5 ml of deionized water.  
183 Tubes were capped and let sit for 24 hrs prior to pH measurement. **pH instrument?**

#### 184 **Lichen Network Modeling**

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

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

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

## 232 Analyses, Software and Data

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

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

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

## 282 RESULTS

283 In support of our first hypotheses, we found that tree genotype influenced lichen net-  
284 work structure and that multiple lichen network metrics were heritable. Tree genotype  
285 significantly predicted the structural similarity of lichen networks and, overall, network-  
286 level metrics responded significantly to tree genotype, including network degree and  
287 centralization including both in-coming and out-going links or when separated into  
288 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 correlated with network similarity and other lichen network metrics, including negative correlations with overall network degree ( $df = 35$ ,  $t = -2.13$ ,  $r = -0.34$ ,  $p\text{-value} = 0.04$ ) and centralization ( $df = 35$ ,  $t = -2.52$ ,  $r = -0.39$ ,  $p\text{-value} = 0.02$ ). In other words, trees with more similar levels of bark roughness tended to have lichen interaction networks

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

## 325 DISCUSSION

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

## 340 Implications of Ecological Network Heritability

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

350 integrate intraspecific variation to the species level (Maliet et al., 2020), even though  
351 recent syntheses have pointed to the importance of processes operating across scales of  
352 organization (Guimarães, 2020). There are two important functional ramifications of  
353 genetically based variation in network structure.

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

369 Second, even if the composition of the communities is the same among individuals  
370 and genotypes, interactions may not be. We didn't observe compositional differences  
371 using the same data from which the lichen networks were derived. If we only had our  
372 composition dataset from this study, we would have concluded no response of the lichen  
373 community to tree genotype, even though the underlying interactions among lichen  
374 species does vary among genotypes. As such differences in network structure could  
375 occur without observable differences in species richness or community composition,  
376 which have been the primary focus of almost all previous community genetics studies  
377 (Des Roches et al., 2018). Community composition of lichens has previously been  
378 observed to be different among tree genotypes in the same experimental garden (Lamit  
379 et al., 2011, 2015b). The different results observed in the present study is likely a  
380 result of differences in lichen quantification and the tree genotypes observed leading  
381 to overall higher abundances of observed lichens to assure the possibility of observing  
382 lichen interactions. The previous study used a visual percent cover estimation, unlike  
383 the current study, which observed lichens at the scale of 1 cm<sup>2</sup> cells, which could  
384 over-estimate cover depending on the frequency at which actual thallus size was less  
385 than 1 cm<sup>2</sup>, as well as both the northern and southern aspects of each tree. These  
386 differences do not negate the findings of either study. The present study's finding of  
387 differences in network structure without significant compositional differences points  
388 to the importance of quantifying how network structure changes in response to genetic  
389 variation in order to fully understand evolutionary dynamics in complex communities.  
390 Having not observed a compositional effect of tree genotype without measuring the  
391 network structure could lead to the conclusion of no genetic effect on the community,  
392 even though differences in network structure are leading to altered, local evolutionary  
393 dynamics. It is possible that these underlying differences in interactions among lichens  
394 could lead to differences in community composition at a future point in time via their  
395 effects on species abundances (Shuster et al., 2006); however, this is not needed for

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

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

## 427 **Evolution and Genetically Based Network Structure**

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

441 metric of community evolution is showing how networks change over time in response  
442 to an invasive species, climate change, or some other agent of selection.

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

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

486 Since lichen individuals are multi-species complexes, there is also the potential for

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

## Conclusion

In the face of the high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed in previous studies (Bangert et al., 2006; Zook et al., 2010; Zytynska et al., 2012). In the present research, we found that the assembly of ecological networks can have a measurable genetic basis depending on the spatial scale of interactions, due in part, to asymmetries in size and longevity of organisms. 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 these modules that include species with large differences in body-size and longevity. 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). Going forward, future work could extend the many previous community genetics studies that have focused on sessile organisms, such as galling insects (Bailey et al., 2005; Whitham et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify the frequency of these interactions in the context of the larger community. Network modeling and analysis will provide useful tools for the identification of species within network modules that are most important to study in systems where little is known about the natural history of organisms in an ecosystem is lacking. Such investigations will bring us closer to understanding the evolutionary drivers of Darwin’s entangled bank and the interconnectedness of species in complex communities (Darwin, 1859; Dátilo

532 et al., 2016).

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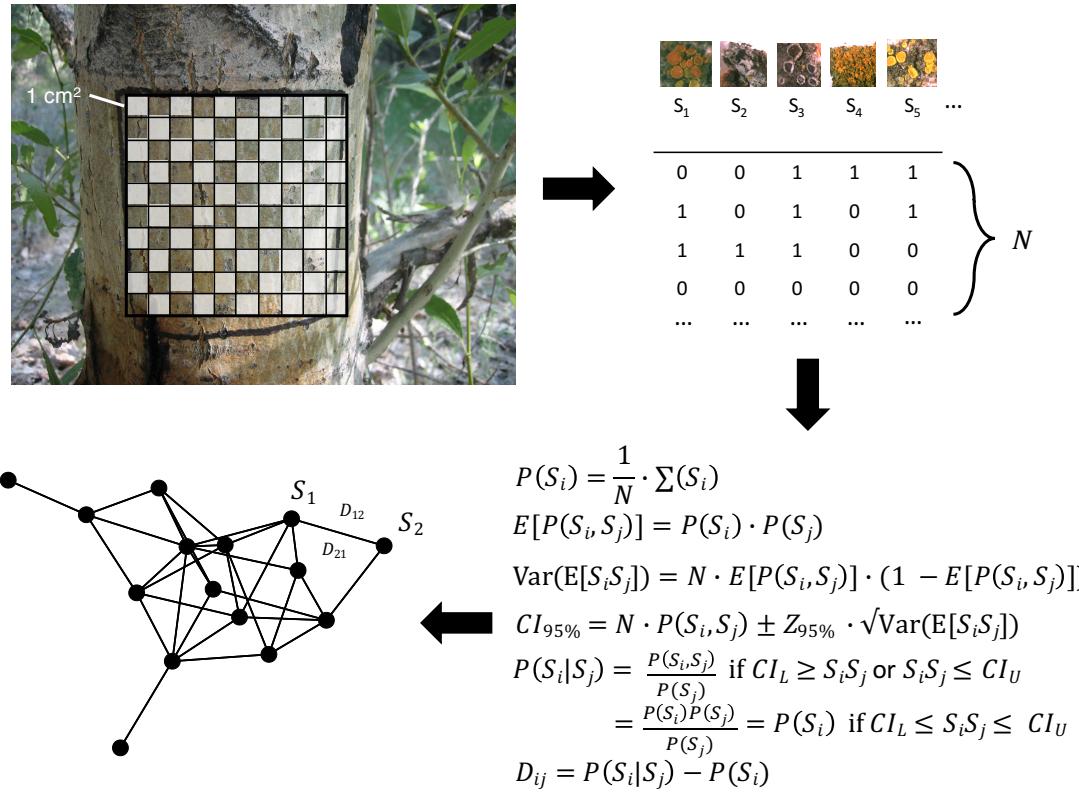
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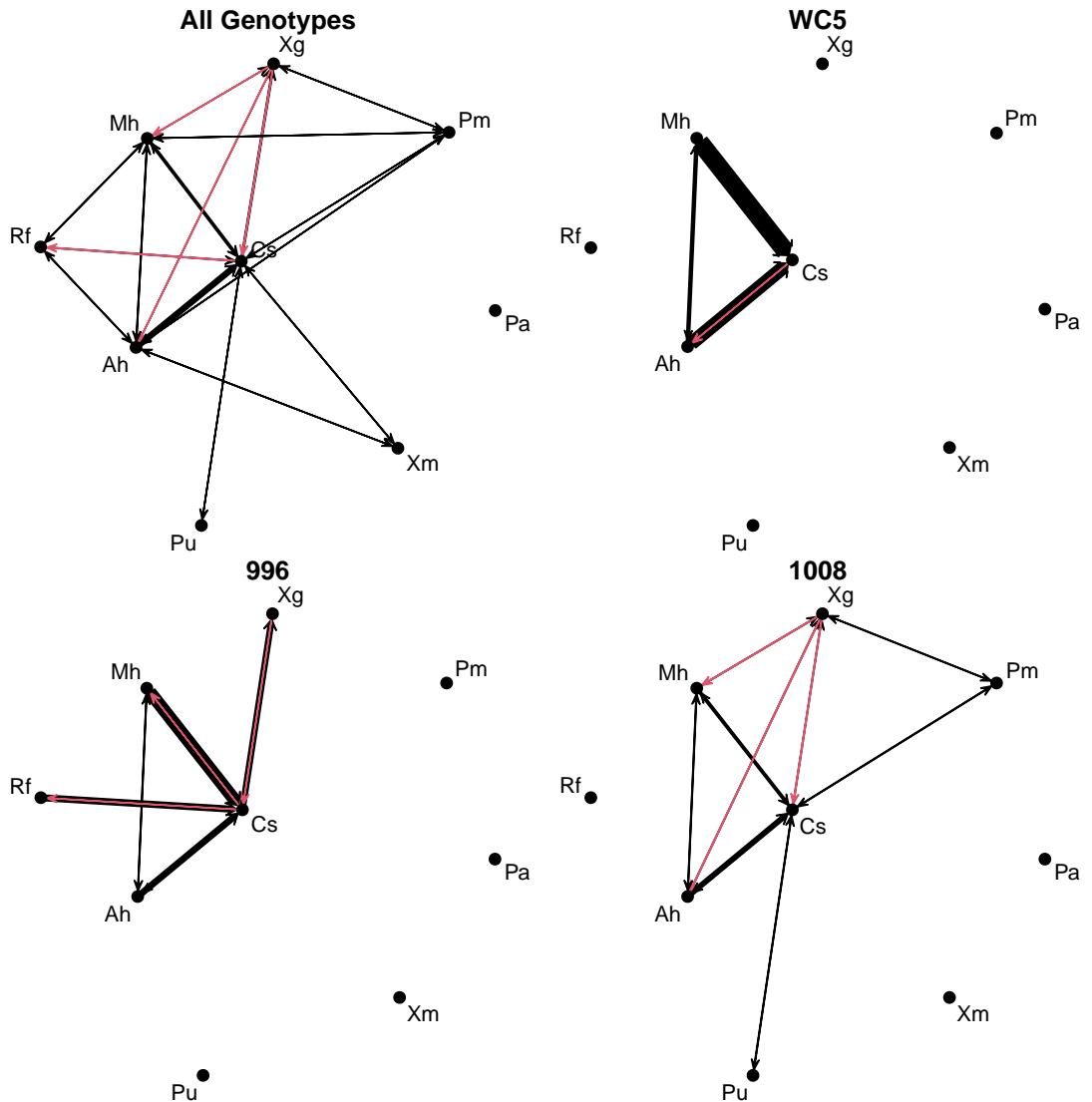
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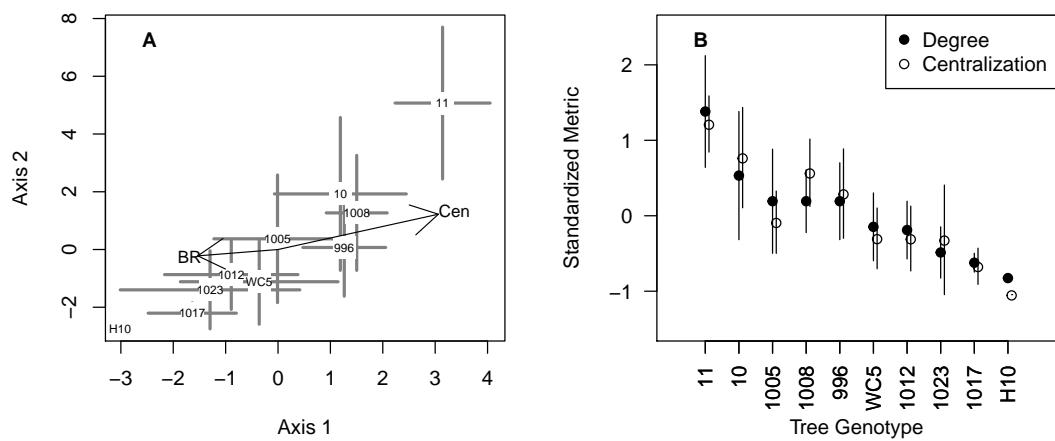
**Figure 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm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



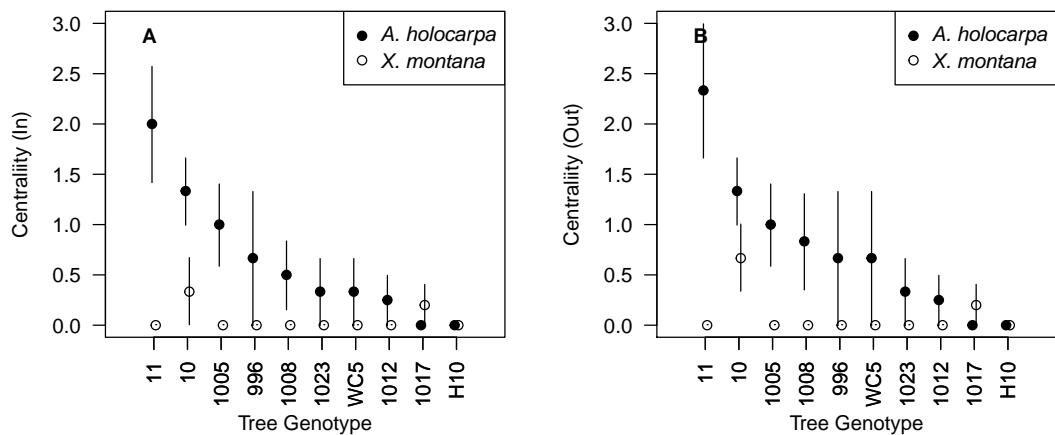
**Figure 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence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