

1 Genotypic variation in a foundation tree 2 results in heritable ecological network 3 structure of an associated community

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16 ABSTRACT

Biological evolution occurs in ecosystems whereby natural selection defines the structure of ecological networks. Therefore, elucidating the genetic basis to ecological network structure is fundamental to understanding evolution. 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 common garden we observed nine epiphytic lichen species associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation species. We constructed and conducted genetic analyses of signed, weighted, directed lichen interaction networks. 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 correlated with 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 has determines 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

17 **INTRODUCTION**

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

37 The development of interspecific indirect genetic effects (IIGE) theory Shuster
38 et al. (2006) in evolutionary biology points to the importance of studying the genetic
39 basis of interaction network structure because genetic based differences in network
40 structure among individuals can be acted upon by natural selection when there are fitness
41 consequences of different networks of IIGEs that can result in community evolution
42 Whitham et al. (2020). For example, although the analysis was of abundances rather
43 than interaction networks, (Gehring et al., 2014, 2017) found that the mycorrhizal
44 communities on the roots of drought tolerant and intolerant trees are dominated by
45 different orders of ectomycorrhizal fungal mutualists that also differ in the benefits they
46 provide that enhance tree performance. Because drought tolerant genotypes are three
47 times more likely to survive record droughts, selection acts both on the tree and its fungal
48 community and with increased drought the community phenotype has changed over time.
49 Also, in an antagonistic interaction context, (Busby et al., 2015) found that with the
50 addition of a damaging leaf pathogen to cottonwoods in a common garden, the impacts
51 of these strong interactors results in a different and diminished community of arthropods
52 relative to control trees. Thus, selection acting on the tree may alter the network structure
53 of associated communities in which different networks of communities are most likely
54 to survive pathogen outbreaks. Regardless of whether the IIGE is unilateral (i.e., tree
55 affects the community) or reciprocal (i.e., the community also affects the relative fitness
56 of the tree), selection on tree, community or both can change network structure Whitham
57 et al. (2020) and thereby alter community dynamics. Network theory and evidence from
58 empirical studies in ecology have demonstrated that indirect effects can lead to self-
59 organization, producing sign-changing, amplifying and/or dampening effects Newman
60 (2006); Sole and Bascompte (2006), and evolutionary applications have demonstrated
61 that indirect effects of interactions among species can lead to network structures that

62 amplify or dampen the effects of selection, such as the formation of star-like structures in
63 which there is a “central” species or group of species that interact with other, peripheral
64 species, can amplify selection events Lieberman et al. (2005).

65 In this context, the “genetic similarity rule” provides a useful framework we can
66 apply to interaction networks at the nexus of ecological and evolutionary dynamics. In
67 a study combining experimental common gardens and landscape-scale observations
68 of interactions between *Populus* spp. (cottonwoods) and arthropods, (Bangert et al.,
69 2006) observed that individuals genotypes that are more genetically similar will tend
70 to have similar phytochemical traits and thus tend to have similar interactions with
71 other species than individuals that are less similar. However, studies in the network
72 ecology literature generally do not include a genetic component Lau et al. (2017) and
73 community genetics studies have primarily focused on community composition in terms
74 of the abundance of species Des Roches et al. (2018). Some studies have examined the
75 effects of genetic variation on trophic chains in plant-associated communities (including
76 *Populus*, *Solidago*, *Oenothera*, *Salix*) Bailey et al. (2005); Johnson (2008); Smith et al.
77 (2011, 2015); Barbour et al. (2016) and generally found that increasing genotypic
78 diversity leads to increased trophic complexity. Only two other studies, that we are
79 aware of, have explicitly examined the effect of genotypic variation on the structure
80 of interaction networks between tree individuals and associated herbivores Lau et al.
81 (2015); Keith et al. (2017) and both found that genotypic diversity generates increased
82 network modularity (i.e., compartmentalization). However, both of these studies were
83 examining networks at the scale of forest stands, rather than networks associated with
84 individual trees; therefore, neither was able to observe replicated networks in order
85 to statistically test for genetic effects on network structure and quantify the genetic
86 component (i.e. heritable variation) in network structure.

87 Here, we investigate how genetic variation in a foundation tree species determines
88 the structure of a network of interactions among a community of tree associated lichens.
89 Using a long-term (20+ years), common garden experiment with clonally replicated
90 *Populus angustifolia* individuals of known genetic identity Martinsen et al. (2001).
91 We focused on a community of 9 epiphytic lichen species, as previous research has
92 demonstrated significant compositional responses of epiphytes to genotypic variation
93 (Winfrey et al., 2011; Zytnyska et al., 2011). Applying a probability-theory based
94 network modeling approach, we constructed a set of interaction network models for
95 the lichens associated with individual trees. Using these models, we then examined the
96 genetic basis of the structure of these ecological networks via several network metrics
97 that measures different aspects of network structure at the scale of individual species
98 (i.e., nodes) or the entire network observed on each tree genotype. In particular, we focus
99 the metric of centrality for individual species and centralization for whole networks,
100 which measures how much a species is connected in the network relative to other
101 species. We hypothesize that in natural systems evolution occurs in a community context
102 involving interactions of complex networks of interacting species Lau et al. (2015);
103 Keith et al. (2017); Thompson (2013); Bascompte et al. (2006). More specifically, based
104 on community genetics theory, particularly the community similarity rule (Bangert et al.,
105 2006), we hypothesize that trees will co-vary in functional phenotypic traits, such as bark
106 roughness and chemical composition, and trees of the same genotype will tend to have
107 similar traits leading to similarities in lichen network structure. If correct, we expect to

108 find that network structure is genetically based, or, in other words, plant genotypes will
109 support different and heritable interaction networks.

110 MATERIALS AND METHODS

111 Study System

112 The study was conducted along the Weber River, UT (USA), which is a cottonwood
113 (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus*
114 *angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known
115 to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were
116 sampled. Bark lichens have been intensively sampled in this system and provide an ideal
117 community in which to observe and model interaction networks, as their sessile nature
118 permits accurate identification of individuals and their highly localized, direct contact
119 interactions and slow population turnover rates facilitate the assessment of interactions
120 among lichen species on individual trees Lamit et al. (2011).

121 A long-term, common garden experiment was used to isolate the effect of tree genotype
122 from the effect of the localized microenvironment associated with each individual
123 and spatial autocorrelation. Established in 1992, asexually propagated clones of geno-
124 typed *P. angustifolia* individuals were obtained from wild collections and planted in
125 a fully randomized design at the Ogden Nature Center, Ogden, UT. From the population
126 of established individuals in the common garden, we chose a total of ten genotypes,
127 replicated between 3 and 8 times each, for sampling.

128 Bark Lichen and Trait Observations

129 On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm²
130 cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens,
131 we were able to rapidly assess lichen interactions by quantifying thalli in close contact.
132 Sampling was restricted to the northern aspect of the trunk to maximize the abundance of
133 lichen and control for the effect of trunk aspect. Two adjacent 100 cm² quadrats centered
134 at 50 cm and 95 cm from ground level were sampled (Fig 1 A and B). The observed
135 lichen community included (abbreviations are given for species present in study): Xg
136 = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs =
137 *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella*
138 *melanchra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were
139 not observed in the present study but are known to occur in this region: *Phaeophyscia*
140 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegantula*.

141 The cell size and checkerboard sampling pattern was chosen to isolate the individuals
142 in each cell. In a previous survey of lichen thallus size in this common garden, we
143 had observed a median thallus size of 0.12 ± 0.001 cm² (1 S.E.) (see Supporting
144 Information). Based on the median thallus size, we expected thalli observed in each cell
145 to generally be spatially independent of thalli present in other cells but exposed to similar
146 micro-environmental conditions created by the bark and the location of the sampling area
147 on an individual tree. Therefore, we were confident in treating the cell-wise observations
148 in quadrats as independent with respect to lichen-lichen interactions. We quantified
149 the texture of the bark in the quadrat is the percent of 1 cm² cells with rough bark. In
150 addition to bark roughness, we also measured several bark chemistry traits by taking

151 bark samples immediately adjacent to each quadrat using the methods of (Lamit et al.,
152 2011): including, the concentration of condensed tannins, pH and carbon and nitrogen
153 concentrations and pH.

154 **Lichen Network Modeling and Analysis**

155 For each tree, repeated observations of lichen were made in order to construct replicated
156 interaction networks for each genotype. We conducted a modified sampling procedure
157 originally developed by (Lamit et al., 2015b) with the addition that we quantified the
158 presence of lichen in the 1 cm² cells on individual trees of *P. angustifolia*. Unipartite
159 networks were generated using the conditional probabilities of each species pair, i.e. the
160 probability of observing one species given an observation of another species $P(S_i|S_j)$,
161 based on the method developed by (Araújo et al., 2011). To calculate conditional
162 probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and
163 the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species
164 and their co-occurrences. We were then able to calculate the conditional probabilities of
165 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
166 a matrix that could possibly be asymmetric, i.e. $P(S_i|S_j)$ does not have to be equal to
167 $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was
168 equal to one for all species present and zero for species that were not observed in any
169 cell.

170 We then applied an analytical procedure to remove non-significant links between
171 species. This procedure determines if the joint probability of a species pair (i.e. $P(S_i, S_j)$)
172 is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as
173 $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences
174 $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of
175 each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the
176 expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability
177 of $S_i S_j$ and its compliment (i.e. $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If
178 the observed number of co-occurrence falls outside of the confidence interval, the
179 joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual
180 probabilities (i.e. $P(S_i) * P(S_j)$), and the conditional probability reduces to the individual
181 probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair
182 falls outside the confidence interval, the probability that the observation of one species
183 given the other is no different than simply observing that species alone. This enables us
184 to remove links from a given network by re-scaling the resulting conditional probabilities
185 by subtracting the individual probabilities from the conditional probabilities (i.e. how
186 different the conditional probability is from the independent probability), which makes
187 any species with a non-significant conditional probability zero.

188 The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as one species' impact on another
189 with zero being no effect and values less than or greater than zero being negative and
190 positive effects, respectively. Here, we will refer to \mathbf{D} as a signed, weighted interaction
191 matrix. As such, \mathbf{D} has the properties that it can be asymmetric (i.e. D_{ij} does not
192 necessarily equal D_{ji}) and it scales between -1 and 1, and, therefore, does not have the
193 mathematical properties of a probabilistic network Poisot et al. (2016). Also, as the
194 method does not track individuals within species and interactions such as competitive
195 exclusion or facilitation within species would result in the same species being observed.

196 Therefore, the results of intra-specific interactions always results in the same species
197 being observed and a resulting $D_{ii} = 0$.

198 **Network Metrics**

199 To quantify the structural variation of lichen networks we calculated several metrics
200 at both the node and whole-network level. For individual nodes (i.e. species) in each
201 network, we calculated both the degree and the Freeman's centrality Butts (2019). We
202 also calculated two similar global network metrics: degree and centralization. The first
203 was network degree, which is a count of the total number of links in a network. As
204 the networks contained not only positive and negative connections but also directional
205 connections (both in-coming and out-going), we calculated the same network metrics
206 for all combinations of these types of connections in each network, accounting for
207 differences in sign through the application of recently developed metrics that incorporate
208 sign information from signed, weighted, directed networks Everett and Borgatti (2014).
209 Although there are many more possible network metrics that could have been examined,
210 we chose to focus on a restricted set for the sake of clarity. In addition, degree and
211 centrality form the basis of many other network metrics.

212 **Statistical Analyses, Software and Data**

213 We used a combination of parametric and non-parametric, permutation based frequentist
214 statistical analyses to test for the effects of genetic variation on lichen communities and
215 their interaction networks. To assess the effect of genotype on univariate responses, we
216 used additive, random effects models with Restricted Maximum Likelihood (REML).
217 We used a combination of Least Squares Regression, Analysis of Variance (ANOVA)
218 and correlation tests to quantify and test for the relationship among other variables. Bark
219 roughness, lichen cover and species richness were square-root transformed to meet the
220 assumptions of homogeneity of variance and normality for these tests.

221 For multivariate response variables, such as lichen community composition and
222 network structure, we used distance based multivariate statistical approaches, including
223 Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify
224 the similarity of lichen networks among individual trees, we calculated the pairwise
225 Euclidean distance of the \mathbf{D} interaction matrices among all pairs of trees.

226 For visualization of multivariate patterns, we used Non-metric Multi-Dimensional
227 Scaling (NMDs) Goslee and Urban (2007) to produce dimensionally reduced ordinations
228 of these multi-variate responses and fitted vectors for continuous predictor variables to
229 the ordinated values Oksanen et al. (2019). Using random initial configurations with a
230 maximum of 500 iterations and a change in stress threshold of less than 10^{-12} . Final
231 configurations has the lowest stress with at most a stress level of 0.10.

232 For each network, we also calculated metrics that measure different structural aspects.
233 Although there are many other metrics, for the sake of simplicity we focus on a subset
234 that represent several interesting features of network structure (see (Lau et al., 2017)).
235 We calculated the number of interactions or “links” in each network, which provides
236 a measure of the size of the network (Lau et al., 2015; Borrett and Lau, 2014). We
237 also calculated the centralization of each network, which measures the evenness of
238 the distribution of interactions among the species in the network Butts (2019). In a
239 network with a low level of centralization species have similar amount of interaction in

240 the network, while a network with a high level of centralization tends to have one or
241 small number of species that interact with other species. We used a related function to
242 calculate the centrality of each species (i.e. node level centrality) in each network as
243 well. To calculate separate metrics for positive and negative links, we applied methods
244 for calculating the centrality accounting for the sign differences Everett and Borgatti
245 (2014) using the `signnet` package Schoch (2020).

246 For all tests where genotype was used as a predictor, we quantified the heritability
247 of the response variable. Because the trees in the garden were clonal replicates of each
248 genotype, we calculated broad-sense heritability, which is the genotypic variance divided
249 by the total phenotypic variance Conner and Hartl (2004). This can be interpreted as a
250 measure of the phenotypic variance due to genotypic variation. We also apply this to
251 the community genetics context as the variance in *extended* phenotypic variance due to
252 genotypic variation Whitham et al. (2006, 2012); Crutsinger (2016). For the multivariate
253 analyses, where we employ PERMANOVA, we followed the methods of (Shuster et al.,
254 2006) to adjust the degrees of freedom for unbalanced genotype replicates.

255 All code and data for the project are openly available online. Code and data are
256 available at github.com/ecgen/comgen. The project is also archived via Zenodo
257 at zenodo.com/doi/XXXXXX. All analyses were conducted using the programming
258 language R version 3.6.1 (R Development Core Team 2019).

259 RESULTS

260 Tree genotype influenced lichen network structure and multiple lichen network metrics
261 were heritable. Tree genotype significantly predicted the structural similarity of lichen
262 networks (PERMANOVA: Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$) (Fig. 4).
263 Overall network level metrics responded significantly to tree genotype (Table 1), in-
264 cluding network degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} = 0.0255$) and centralization
265 including both in-coming and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} =$
266 0.0184) or when separated into in-coming only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} =$
267 0.0190) or out-going only ($RLRT = 3.8615$, $H^2 = 0.3193$, $p\text{-value} = 0.0205$). Metrics
268 including only positive links also showed a significant effect of tree genotype, including
269 positive degree ($RLRT = 3.6925$, $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
270 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} = 0.0142$) Metrics calculated with
271 negative links were not significant, including degree (negative) ($RLRT = 0.0327$, $H^2 =$
272 0.0318, $p\text{-value} = 0.3859$) and both in-coming (negative) ($RLRT = 0.3304$, $H^2 = 0.1057$,
273 $p\text{-value} = 0.2508$) and out-going centralization (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$,
274 $p\text{-value} = 0.3446$).

275 The genetic response of network centralization was driven by variation in *Caloplaca*
276 *holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$,
277 $p\text{-value} < 0.0001$). *Caloplaca holocarpa* centrality was the main species to exhibit a
278 significant response to tree genotype in terms of positive centrality for both the in-coming
279 ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, $H^2 = 0.30$,
280 $p\text{-value} = 0.0327$) perspectives, but not for either negative centrality metrics in-coming
281 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$).
282 None of the other species' centralities showed a genotypic response (Supplementary
283 Table ??) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$);

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

Table 1. Genotypic effects on the associated lichen network structure.

however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

Add transformations of variables to methods.

Genotype indirectly influenced lichen network centralization via the 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 (PERMANOVA: Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, $p\text{-value} = 0.0096$) 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 with similar structure. To quantify the genetic bases of this effect of bark roughness on network structure, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

DISCUSSION

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *C. holocarpa*. The genetically based trait,

	df	SumOfSqs	R2	F	Pr(>F)
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.

bark roughness, was the only trait observed to effect network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control Bdeir et al. (2017), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens Lamit et al. (2015b); however this is the first demonstration of a link from genes to lichen network structure. As such these results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species. This work is important because it provides a mechanistic basis for understanding how community network theory is intimately associated with the evolutionary process and how human alterations of the environment (e.g., climate change, invasive species, pollution) may have cascading, indirect effects that alter network structure and evolution.

Implications of the Heritability of Interaction Network Structure

We found significant heritability of lichen interaction network structure, and, in line with the genetic similarity rule, networks observed on trees of the same genotype tended to be structurally similar. Although previous studies have examined aspects of networks, such as trophic Barbour et al. (2019) and forest stand-level interaction network structure Lau et al. (2016); Keith et al. (2017), this is the first study that we are aware of to examine the heritability of network structure with replicated networks at the genotype scale. Previous work in the evolution of ecological networks have primarily focused on macro-evolutionary dynamics Rezende et al. (2007); Weber et al. (2017); Valverde et al. (2018); Harmon et al. (2019) or have been simulation based individual-level models that integrate intraspecific variation to the species level Maliet et al. (2020), even though recent syntheses ave pointed to the importance of processes operating across scales of organization Guimarães (2020). There are several important functional ramifications of genetically based variation in network structure. First, intra-specific diversity could be creating lichen interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily the 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 environmental differences determined by the genetic variation within a single species can create differences that not only impacts community composition, as repeatedly demonstrated in other community genetics studies Whitham et al. (2006); Des Roches et al. (2018), but also the structure of interactions among individuals within these modules. 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 on the center of the network. For example, consider a forest with two genotypes that support lichen communities that are similar in total abundances of each species but differ in terms of the structure. Extensions of game theory to evolutionary biology have demonstrated that network structure can lead to variation in evolutionary dynamics. Some structures tend toward dominance and dampening of selection, while others lead to amplification of selection. One class of networks that are theorized to have amplifying effects on networks have "star" shapes with one or a few species at the center and radiating interactions out from the central core Lleberman 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 possible that these more centralized networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the network structure that is found on that tree genotype.

Second, even if the composition of the communities is the same among individuals and genotypes, interactions may not be. We didn't observe compositional differences using the same data from which the lichen networks were derived. If we only had our composition dataset from this study, we would have concluded no response of the lichen community to tree genotype, even though the underlying interactions among lichen species does vary among genotypes. As such differences in network structure could occur without observable differences in species richness or community composition, which have been the primary focus of almost all previous community genetics studies Des Roches et al. (2018). Community composition of lichen has previously been observed to be different among tree genotype in the same experimental garden Lamit et al. (2011, 2015b), the difference between the present study is likely a result of differences in sampling method and the choice of genotypes leading to overall higher abundances of observed lichens to assure the possibility of observing xlichen interactions. The previous study also used a visual estimation method, unlike the current study, which observed lichen at the scale of 1 cm² cells, which could over-estimate cover depending on the frequency at which actual thallus size was less than 1 cm², as well as both the northern and southern aspects of each tree. These differences do not negate the findings of either study. The present study's finding of differences in network structure without significant compositional differences points to the importance of quantifying how network structure changes in response to genetic variation in order to fully understand evolutionary dynamics in complex communities. Having not observed a compositional effect of tree genotype without measuring the network structure could lead to the conclusion of no genetic effect on the community, even though important variation in network structure are leading to evolutionary dynamics. It is possible that these underlying differences in interactions among lichen could lead to differences in community composition at a future point in time via there effects on species abundances Shuster et al. (2006); however, this is not needed for evolutionary dynamics to play out via selection that leads to shifts in trait distributions without shifting species abundance distributions, which is possible under stabilizing, disruptive and directional selection Conner and Hartl (2004). Thus, it is imperative that further community genetics research assess or at least be aware of the potential effects of variation in interactions and not just observe species abundances.

393 **Evolutionary Implications of a Genetic Basis to Network Structure**

394 A genetic basis to network structure suggests that some amount of interaction network
395 complexity is determined and therefore could be predicted. Variation in space and time
396 create variation in ecological networks that influences evolutionary dynamics via shifts
397 in ecological dynamics, such as population demographics Guimarães (2020). Given
398 that ecosystems are comprised of hundreds and thousands of species, each having a
399 multitude of interactions, the potential to find traction for making predictions in the
400 context of ecological, let alone evolutionary, dynamics seems daunting. The promise
401 of predictability lies in the presence of assymetries in ecosystems that contribute to the
402 occurrence of foundation species, such as hierarchy and nestedness created by body
403 size differences or life-history strategies, has been widely observed Ellison et al. (2005).
404 The second part is that heritability (i.e., genetic determination) means that there is
405 structure in the spatial or temporal variation that is created by individuals of foundation
406 species whose traits are in part determined by underlying trait differences. Although this
407 variation is inherently a function of both genetics and environmental effects Conner and
408 Hartl (2004), the community and network level effects are also a function of the scale
409 of the interaction Shuster et al. (2006). Self-orgnization of the dynamics within these
410 communities also points to a mechanism for strong community and ecosystem effects of
411 genetic variation, contributing to what may seem unlikely magnitudes of genetic effects
412 as has been observed in some systems, such as forest in riparian ecosystems Bangert
413 et al. (2006).

414 Ecological network studies have focused on asymmetry and the quantification of
415 its structure in communities, with qualitative discussion of the impacts on evolutionary
416 dynamics Bascompte et al. (2006); Díaz-Castelazo et al. (2010); Guimarães et al. (2011);
417 Thompson (2013). More specific predication, within a quantitative framework, can
418 be found in applications of evolutionary game theory, and although developed at the
419 population scale, such theory can apply to communities. One seemingly useful direction
420 from evolutionary network developments from game theory is the classification of
421 networks into two general categories, rooted and cyclic, in which rooted networks have
422 interactions in which evolutionary effects emanate from one or multiple origins but these
423 effects do not have connections back to the origins, whereas cyclic networks contain
424 feedbacks to one or more origins. Although it did not explicitly define it in this context,
425 the previous work of (Lau et al., 2017) developed the perspective that the structure of the
426 network in the context of a foundation species, such as cottonwoods in which there are
427 demonstrable community level genetic effects, is inherently created when trait variation
428 among genotypes of a foundation species has ecological effects on associated species.

429 This builds on many previous studies demonstrating that the community level effects
430 vary among multiple genotypes. It is not clear what potential there is for feedbacks
431 there are to the origins (e.g. the cottonwood genotypes) from the community, and as
432 such it cannot be determined whether these networks are cyclic or rooted. In terrestrial
433 ecosystems, lichen play important ecological roles, such as substrate stabilization Root
434 et al. (2011) and nutrient fixation Nelson et al. (2018). In some systems lignicolous
435 lichens can have demonstrable effects on the availability of nutrients for the trees that
436 they are associated with Norby and Sigal (1989), although this has not been measured
437 for the lichen in the current study's systemq. Elucidating the absence and/or presence
438 of and quantifying such feedbacks would allow for the determination of the cyclic

439 nature and potential evolutionary dynamics of this system. The presence of feedbacks
440 would provide the potential for non-linear dynamics in which evolutionary effects are
441 damped or amplified by the structure of the network. For example, a star structure in
442 which there is a primary or core set of central species with feedbacks from the radiating
443 species has been demonstrated to be a structure that amplifies evolutionary dynamics
444 Lieberman et al. (2005). If such feedbacks do not exist, these sub-networks of the lichen
445 and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to
446 generally promote diversification as variation arising from the shifting distribution of the
447 “roots”, i.e. genotypes; however, loss of genotype/root diversity could lead to fixation
448 of a single genotype in the population and a decrease in community-wide diversity.
449 However, such feedbacks to tree fitness are not necessary for evolutionary dynamics to
450 play out within the lichen networks through the effects of altered network structure on
451 lichen interaction outcomes, such as competitive exclusion leading to selection.

452 Since lichen are multi-species complexes, there is also the potential for evolutionary
453 dynamics to shift within the context of the lichen symbiosis. There is substantial
454 evidence that lichen have served as the “cradle of symbiotic fungal diversification”
455 Arnold et al. (2009) and recent research has shown significant network structure of
456 endolichenic fungi and lichen collected from across North America Chagnon et al.
457 (2016). Analysis of the structure of ecological networks has generally supported the
458 conclusion that nestedness, or the degree to which species tend to interact with similar
459 subsets of the community, tends to promote stability in mutualistic, primarily bipartite
460 (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic
461 networks Elias et al. (2013); Grilli et al. (2016). Although there is growing evidence
462 that the nestedness of mutualistic networks is not necessarily the result of selection for
463 systems-level properties that promote stability but could be either product of asymptotic
464 abundance distributions leading to un-even interaction frequencies Staniczenko et al.
465 (2013) and/or a by-product of selection and divergence creating network “spandrels” in
466 ecosystems Valverde et al. (2018), this does not preclude the functional consequences
467 of network structure but rather the developmental or evolutionary processes that have
468 produced the structure. In the present study, we did not examine nestedness or modularity
469 of the lichen networks as we could not find metrics for analyzing networks that are
470 not only weighted and directed but also signed. Hopefully future network theoretic
471 developments will make the appropriate metrics available to conduct these analyses.

472 **Implications for Interspecific Indirect Genetic Effects (IIGEs)**

473 Interspecific indirect genetic effects (IIGE) theory provides a quantitative framework
474 within which to approach evolutionary theory at higher levels of biological organization:
475 from populations to communities and ecosystems. To date, this theory has focused
476 on modeling the strong effects of foundation species Shuster et al. (2006); Whitham
477 et al. (2012), but it has not yet integrated developments in the ecological or evolutionary
478 network theory literature. This is to say that it has not developed a way to examine
479 complex interactions among species; however, previous studies have demonstrated this
480 network context is likely to be important, as altering the structure of interaction networks
481 provides a means for genetic effects to be damped or magnified within the system of
482 interacting species. For example, (Keith et al., 2017) showed that the genetics based
483 interactions of aphid resistant and aphid susceptible trees resulted in different interaction

484 networks of their associated arthropod communities composed of 139 species. At the
485 scale of ecosystems, trophic networks or food webs direct and control the rates of energy
486 and nutrient flux Borgatti and Everett (2006). Furthermore, in a predator-prey-plant
487 study, Smith Smith et al. (2011), showed that the interactions among species across
488 trophic levels depended on plant genotype. Also, work by (Toju et al., 2017, 2016, 2014)
489 observed consistent patterns of centralized interactions of species modules focused
490 around hubs of plant-fungal interactions. In other words, a small number of plant and
491 fungal symbionts tended to have disproportionate numbers of interactions with other
492 species and likely are the drivers in determining community assembly, structure and
493 dynamics.

494 The results of the current study provides clear empirical evidence that variation
495 in network structure can be genetically based (i.e. heritable) and points to the need
496 to expand IIGEs encompass the structure of interaction networks. Although such
497 a synthesis necessitates a much greater effort than can be afforded in this paper, it
498 is possible to point to several productive pathways forward. In terms of interaction
499 networks, foundation species are relatively central within the system of interactions,
500 that is their direct and/or indirect effects are greater than other species. So, when
501 the more centralized (foundation) species have genetically based interactions, genetic
502 effects will tend to be magnified in the community. Here, we found that even though
503 more abundant or more centralized (i.e. “important”) species were present in the
504 community, their effects were not the main component responding to genetic effects.
505 Considering the impact of network structure would be a productive path forward for
506 the theoretical development and application of the IIGE concept. These results also
507 provide insights into the dynamics of real ecosystems and the potential inter-play of
508 ecology and evolution with regard to empirical and theoretical support for neutral theory,
509 as models have been developed that can reconstruct interactions networks with similar
510 structural characteristics to those observed in real ecosystems Coelho and Rangel (2018).
511 The findings of our study support the possibility that, although communities and their
512 interaction networks may assemble as a result of conditions that are entirely agnostic
513 to functional variation, if there are strong ecological asymmetries, such as the case in
514 foundation species systems, then spatial and temporal variation in network structure will
515 arise as a result of trait variation within the foundation species. Taking even the extreme
516 case, even when such genetically based variation is the result of “neutral” evolutionary
517 processes (e.g., genetic drift), as long as resulting genetic diversity produces ecological
518 relevant phenotypic diversity, then network structure will still have a genetic basis. Given
519 that ecosystems with large asymmetries seem to be the rule rather than the exception for
520 ecosystems Ellison et al. (2005); Santamaría and Rodríguez-Gironés (2007); Staniczenko
521 et al. (2013); Dormann et al. (2017); Coelho and Rangel (2018), the results of our study
522 are likely to be broadly applicable and provides further support for the conclusion that
523 the community context of evolutionary dynamics at either micro- or macro-evolutionary
524 scales Weber et al. (2017); Harmon et al. (2019) cannot safely be ignored. As genetic
525 variation is inherent to biological systems, it would now seem that the adage “you can’t
526 be neutral on a moving train” might well apply to ecosystems that are comprised of
527 interacting species.

528 **Applicability to Other Systems**

529 In attempting to apply these findings to other systems, it is important to consider the
530 spatial and temporal scaling of genetic effects. In the present study, the sessile nature of
531 lichens means that individuals, and potentially multiple generations, live their entire lives
532 on a single tree. As such, our study examines one scaling of a genetic effect, in which
533 the phenotype of a single tree individual (i.e., tree genotype) has complete influence
534 on the community with little to no effect of other tree individuals in the population.
535 The extreme from this would be where the associated community moved among and
536 interacted with not only other community members but also multiple tree individuals at a
537 high rate, as would be the case with free-living animals (e.g. flying insects). In the latter
538 case, the effect of tree genetics would then be the integral effect of all the tree individuals
539 in the population, and, all other factors being equal, any one tree genotype would have a
540 lower effect on associated community. In reality, ecosystems are a mixture of species
541 of different body sizes and life-histories, and, as such, vary in the degree to which they
542 interact with other organisms, which is the basis of the theory of the geographic mosaic
543 of co-evolution Thompson (2013); Thompson et al. (2013). It is now important to
544 consider how the impacts of genetic effects on the network structure of sub-groups, such
545 as lichens, may or may not propagate through the ecosystem to more mobile organisms.
546 As developed previously, the degree to which a genetic effect influences the community
547 is a function of the fidelity of the genetic effect (i.e., heritability) and both the frequency
548 and the intensity of the interaction Shuster et al. (2006). One possible path forward is for
549 future work to extend the many previous community genetics studies that have focused
550 on sessile organisms, such as gallin insects Bailey et al. (2005); Whitham et al. (2006);
551 Crutsinger et al. (2014); Smith et al. (2011); Keith et al. (2017), to quantify the frequency
552 of these interactions in the context of the larger community. This would provide an
553 estimate of the relative impact of these focal, often termed foundation, species. In
554 addition, community genetics theory has only considered first order interactions, i.e.,
555 between two organisms Shuster et al. (2006); Whitham et al. (2012, 2020). Given that
556 network structure could be influenced by genetic effects, as evidenced by the present
557 study, assessing higher order interactions could provide a path forward for theoretical
558 advances that could help with identifying important characteristics of sub-groups to
559 focus on in empirical studies.

560 Although our study was conducted with a community of lichens, these results can
561 be generalized to other groups of diverse organisms around the world that also exhibit
562 significant genetic signals at the community level Rountree et al. (2011); Whitham
563 et al. (2012). However, there are important points to consider when extending the
564 observed genetically based response of the lichen networks to other systems. As
565 bark lichen individuals do not move, but grow in a primarily two dimensional plane,
566 these communities and their interactions occur in the highly localized context of the
567 tree's bark surface. Lichen individuals are also many orders of magnitude smaller
568 than the tree individual in this system Lamit et al. (2011). For these reasons, the
569 genetic effects on these communities is not damped by the movement of individuals
570 and the mixing of the effect of different tree genotypes on the lichen community, as
571 might occur for more mobile species (e.g. insects and birds). Relatedly, we only
572 examined lichen in this study, and other species whose distributions, abundances and/or
573 interactions vary in their response to tree genotype, such as animals that may also impact

lichen communities, could be playing a role that we did not examine. For example, an analysis of the multivariate correlations of different components of the community in this system demonstrated significant patterns of genetic co-responses to tree genotype, supporting the non-mutually exclusive possibilities of shared responses to tree genotype or tree genotypic effects on interactions among these sub-communities Lamit et al. (2015a). As such, although we can not rule out the possibility that other unmeasured tree traits or organisms correlated with bark roughness are underlying the observed patterns, substantial research supports the importance of genetically based tree traits for communities and ecosystems Des Roches et al. (2018), and in particular bark roughness for bark lichen communities Bdeir et al. (2017); Lamit et al. (2011, 2015b).

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 to some in previous studies Bangert et al. (2006); Zook et al. (2010); Zytynska et al. (2012). In the present study, we found that community assembly processes, such as environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. 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 within the biotic community that include species with similar differences in body-size and time-scales. Also, as heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions Evans et al. (2013). Such findings will bring us closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

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Citations

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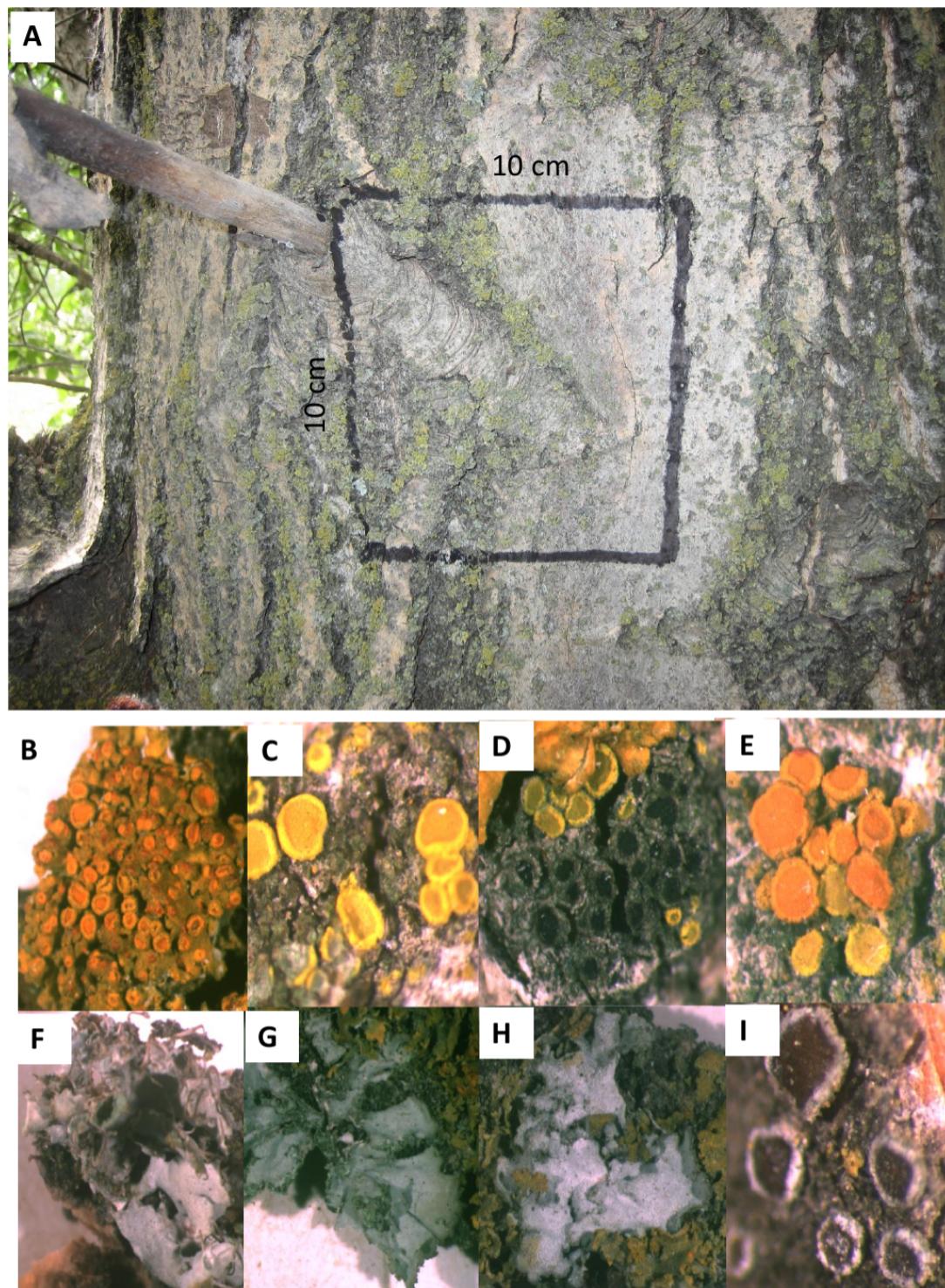


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanchra*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (B-D) and R.R. Naesbourg (E-I).

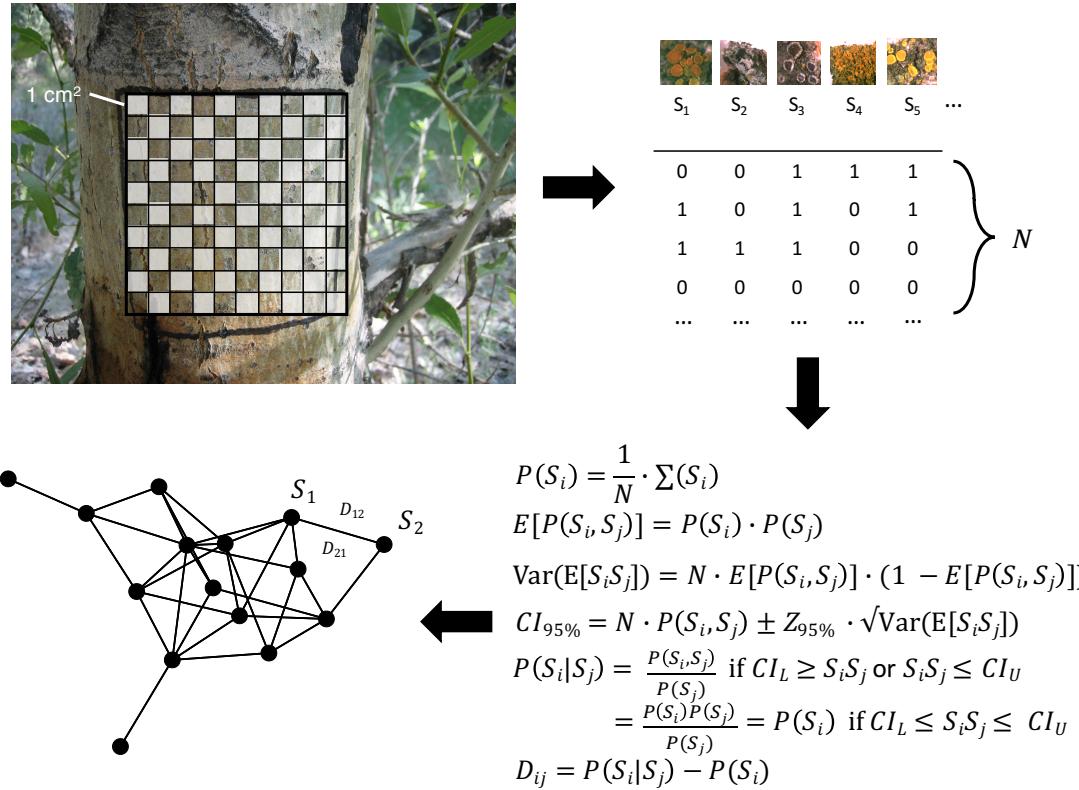


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from Araújo et al. (2011), we calculated the conditional probabilities, $P(S_i | S_j)$, for all species pairs and removed (i.e. set equal to zero) species pairs whose joint probabilities, $P(S_i S_j)$, were not significant using a confidence interval based comparison of their observed co-occurrence frequency, $S_i S_j$, to that expected due to chance alone, $E[P(S_i S_j)] = P(S_i) P(S_j)$, and $P(S_i | S_j)$ reduces to $P(S_i)$, the observed individual probability of species S_i . In the context of these networks, asymmetry and positive/negative valued connections are distinct quantities. In-coming and out-going connections can be interpreted as “influenced by” and “influenced”, respectively; while positive and negative should be seen as one species increasing or decreasing, respectively, the probability of another species’ occurrence.

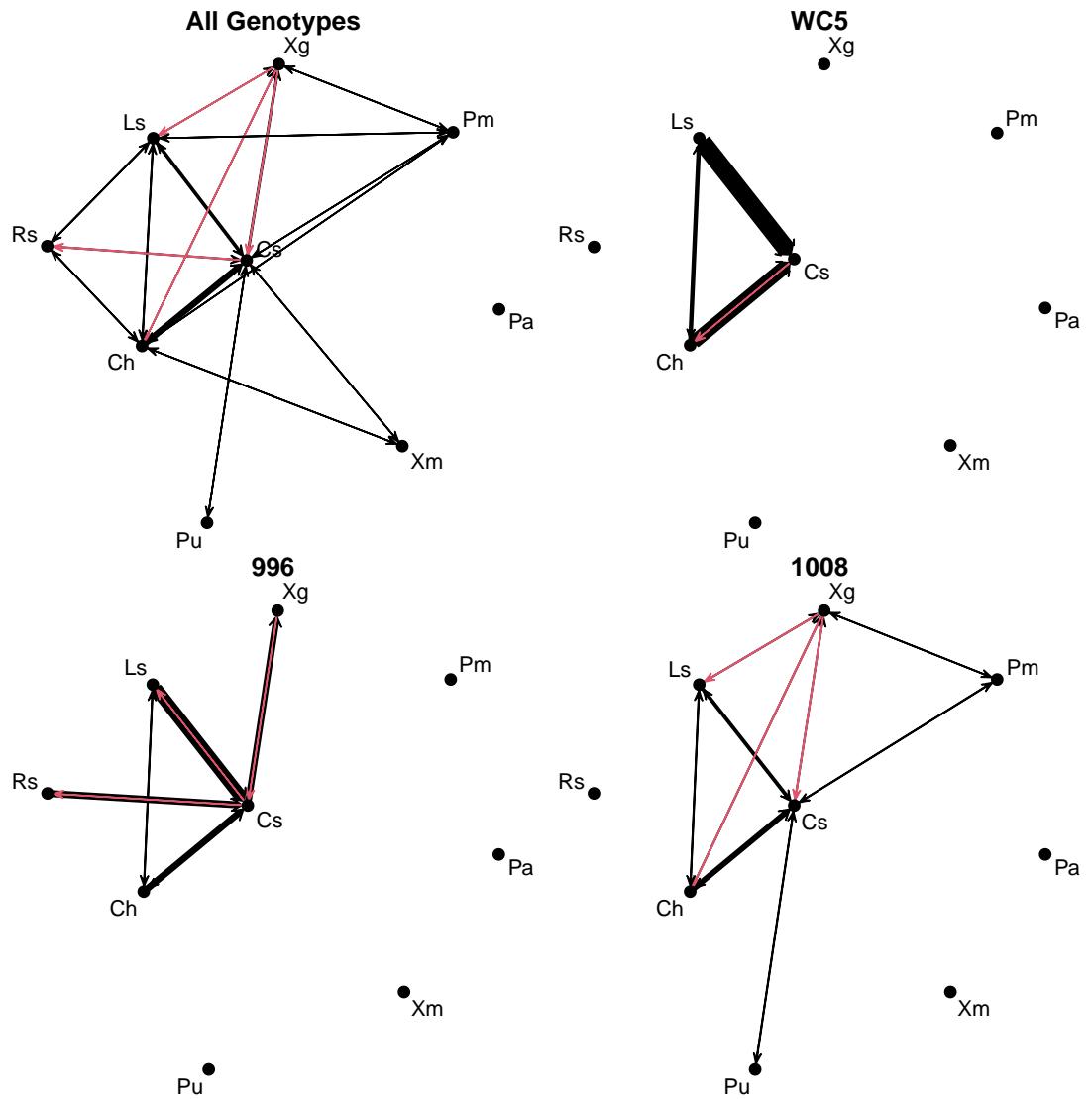


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species (abbreviated by the first letter of the genus and specific epithet), which are scaled by their magnitude. The sign of the interaction is indicative of greater (positive) or lesser (negative) paired occurrences than expected relative to the overall frequency of occurrence of each species. Ecologically, the links in the network are likely the product of multiple types of interactions (e.g. mutualism, parasitism, competition, facilitation) that could vary over both space and time.

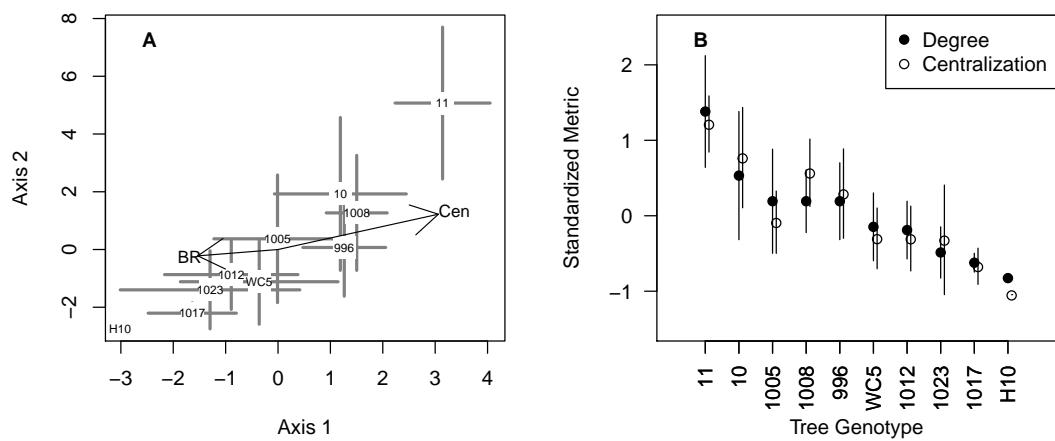


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated network similarity. B. Plot showing the standardized ($\frac{x-\bar{x}}{\sigma}$) means (± 1 S.E.) for the two of the genetically based lichen network metrics: overall degree (i.e. total number of links) and centralization, which is a measure of the dominance of one species in the network.

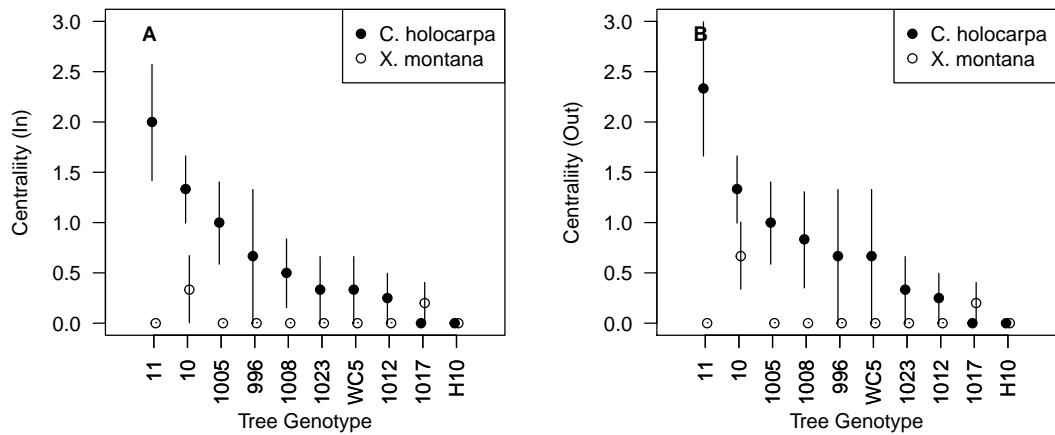


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

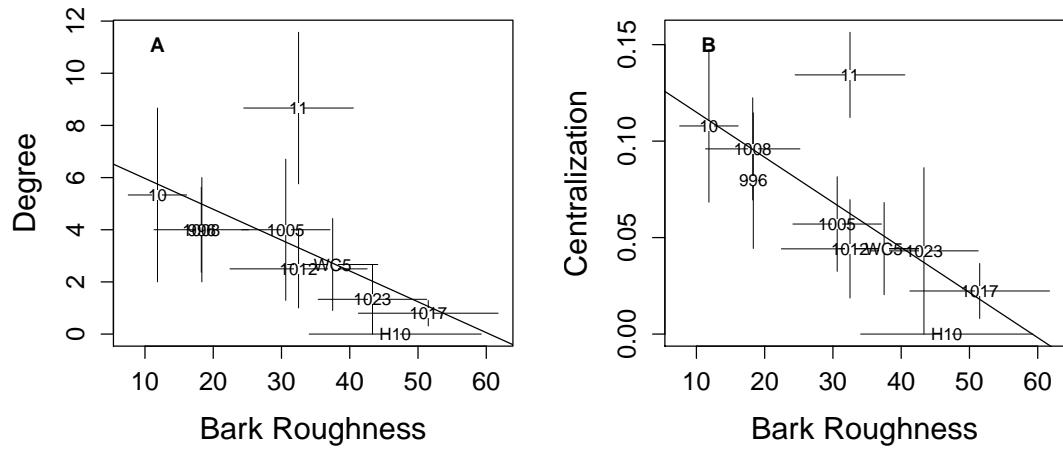


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased the number of interactions (degree) and dominance of those interactions decreased.