

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

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19 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 epiphytic lichen 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 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

20 INTRODUCTION

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

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

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

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

99 Here, we investigate how genetic variation in a foundation tree species determines
100 the structure of a network of interactions among a community of tree associated lichens.
101 Using a long-term (20+ years), common garden experiment with clonally replicated
102 *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001).
103 We focused on a community of 9 epiphytic lichen species, as previous research has
104 demonstrated significant compositional responses of epiphytes to genotypic variation
105 (Winfrey et al., 2011; Zytynska et al., 2011). Applying a probability-theory based
106 network modeling approach (Araújo et al., 2011), we constructed a set of interaction
107 network models for the lichens associated with individual trees. Using these models,
108 we then examined the genetic basis of the structure of these ecological networks via
109 several network metrics that measure different aspects of network structure at the scale
110 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. We hypothesize 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). More specifically, based on the community similarity rule Bangert et al. (2006), we hypothesize that trees will co-vary in functional phenotypic traits, such as bark roughness and chemical composition, and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks.

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, only pure or advanced generation back-crosses of *P. angustifolia* were sampled. 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 lichen present in order to permit the construction of interaction networks.

Bark Lichen and Trait Observations

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

154 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegantula*.

155 The cell size and checkerboard sampling pattern was chosen to isolate the individuals
156 in each cell. In a previous survey of *X. galericulata* thallus size in this common garden
157 (Lamit et al., 2015b), we had observed a median thallus size of $0.12 \pm 0.001 \text{ cm}^2$ (1
158 S.E.) (Supporting Information, Fig. 1). Based on the median thallus size, we expected
159 thalli observed in each cell to generally be spatially independent of thalli present in other
160 cells but exposed to similar micro-environmental conditions created by the bark and
161 the location of the sampling area on an individual tree. Therefore, we were confident
162 in treating the cell-wise observations in quadrats as independent with respect to lichen-
163 lichen interactions. We quantified the texture of the bark in the quadrat is the percent of
164 1 cm^2 cells with rough bark. In addition to bark roughness, we also measured several
165 bark chemistry traits by taking bark samples immediately adjacent to each quadrat using
166 the methods of Lamit et al. (2011): including, the concentration of condensed tannins,
167 pH and carbon and nitrogen concentrations and pH.

168 Lichen Network Modeling

169 For each tree, repeated observations of lichen were made in order to construct replicated
170 interaction networks for each genotype. We conducted a modified sampling procedure
171 originally developed by Lamit et al. (2015b) with the addition that we quantified the
172 presence of lichen in the 1 cm^2 cells on individual trees of *P. angustifolia*. Unipartite
173 networks were generated using the conditional probabilities of each species pair, i.e., the
174 probability of observing one species given an observation of another species $P(S_i|S_j)$,
175 based on the method developed by Araújo et al. (2011). To calculate conditional
176 probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and
177 the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species
178 and their co-occurrences. We were then able to calculate the conditional probabilities of
179 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
180 a matrix that could possibly be asymmetric, i.e., $P(S_i|S_j)$ does not have to be equal to
181 $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was
182 equal to one for all species present and zero for species that were not observed in any
183 cell.

184 We then applied an analytical procedure to remove non-significant links between
185 species. This procedure determines if the joint probability of a species pair (i.e., $P(S_i, S_j)$)
186 is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as
187 $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences
188 $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of
189 each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the
190 expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability
191 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
192 the observed number of co-occurrence falls outside of the confidence interval, the
193 joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual
194 probabilities (i.e., $P(S_i)P(S_j)$), and the conditional probability reduces to the individual
195 probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair
196 falls outside the confidence interval, the probability that the observation of one species
197 given the other is no different than simply observing that species alone. This enables us
198 to remove links from a given network by re-scaling the resulting conditional probabilities

199 by subtracting the individual probabilities from the conditional probabilities (i.e., how
200 different the conditional probability is from the independent probability), which makes
201 any species with a non-significant conditional probability zero.

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

216 **Analyses, Software and Data**

217 To quantify the structural variation of lichen networks we calculated several metrics at
218 both the level of node and whole networks. Although there are many other metrics, for
219 the sake of simplicity we focus on a subset that represent the primary interesting features
220 of network structure (see Lau et al. (2017)). We calculated the number of interactions or
221 “links” in each network (degree), which provides a measure of the size of the network
222 (Lau et al., 2016a; Borrett and Lau, 2014). We also calculated the centralization of each
223 network using Freeman's centrality, which measures the evenness of the distribution of
224 interactions among the species in the network, using the `sna` package (Butts, 2019). In
225 a network with a low level of centralization species have similar amount of interaction
226 in the network, while a network with a high level of centralization tends to have one or
227 small number of species that interact with other species. We used a related function to
228 calculate the centrality of each species (i.e., node level centrality) in each network as well.
229 To calculate separate metrics for positive and negative links, as the networks contained
230 not only positive and negative connections but also directional connections (both in-
231 coming and out-going), we calculated the same network metrics for all combinations of
232 these types of connections using recently developed methods for signed, weighted and
233 directed networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch,
234 2020).

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

243 For multivariate response variables, such as lichen community composition and

network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the **D** interaction matrices among all pairs of trees. For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of these multivariate responses and fitted vectors for continuous predictor variables to the ordinated values (Oksanen et al., 2019). Using random initial configurations with a maximum of 500 iterations and a change in stress threshold of less than 10^{-12} . Final configurations has the lowest stress with at most a stress level of 0.10.

For all tests where genotype was used as a predictor, we quantified the heritability of the response variable. Because the trees in the garden were clonal replicates of each genotype, we calculated broad-sense heritability, which is the genotypic variance divided by the total phenotypic variance (Conner and Hartl, 2004). This can be interpreted as a measure of the phenotypic variance due to genotypic variation.

All analyses were conducted using R version 3.6.1 (R Development Core Team 2019). Code and data for the project are openly available as a reproducible workflow using drake (Landau, 2018), which is archived via Zenodo zenodo.com/doiXXXXXX.

RESULTS

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

Response	df	RLRT	H ²	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.

272 The genetic response of network centralization was driven by variation in *Caloplaca*
 273 *holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$,
 274 $p\text{-value} < 0.0001$). *Caloplaca holocarpa* centrality was the main species to exhibit
 275 a significant response to tree genotype in terms of positive centrality for both the in-
 276 incoming ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, H^2
 277 = 0.30, $p\text{-value} = 0.0327$) perspectives, but not for either negative centrality metrics
 278 in-coming ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} =$
 279 0.4543). None of the other species' centralities showed a genotypic response (Supporting
 280 Information, Fig. 2) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value}$
 281 = 0.0375); however, the centrality of *X. montana* was much lower overall relative to *C.*
 282 *holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes
 283 (Fig. 5).

284 Genotype indirectly influenced lichen network centralization via the genetically
 285 based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$,
 286 $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$,
 287 $p\text{-value} = 0.0343$) both displayed significant responses to tree genotype. None of the
 288 other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen
 289 ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response
 290 to tree genotype and none other than bark roughness was correlated with network
 291 similarity (Table 2); therefore, we focused our subsequent analyses on the indirect
 292 effect of genotype on lichen network structure via bark roughness. We found that bark
 293 roughness was significantly correlated with network similarity and other lichen network
 294 metrics, including negative correlations with overall network degree ($df = 35$, $t = -2.13$,
 295 $r = -0.34$, $p\text{-value} = 0.04$) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, $p\text{-value}$
 296 = 0.02). In other words, trees with more similar levels of bark roughness tended to
 297 have lichen interaction networks with similar structure. To quantify the genetic bases
 298 of this effect of bark roughness on network structure, we used the residual values from
 299 regressions of network degree and centralization in tests of the effect of tree genotype
 300 and found no significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 =$
 301 0.00, $p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$),
 302 suggesting that the observed relationship between bark roughness and lichen network
 303 structure was largely genetically based (Fig. 6).

	df	SS	R^2	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.

304 **DISCUSSION**

305 We found that tree genotype influenced the network structure of lichen communities
306 associated with narrowleaf cottonwoods in a riparian forest ecosystem. Network simi-
307 larity and metrics of network structure tended to be more similar on trees of the same
308 genotype. Generally, this genetic effect was manifested in positive interactions and
309 largely driven by *C. holocarpa*. The genetically based trait, bark roughness, was the
310 only trait observed to effect network variation, largely via shifts in positive in-coming
311 and out-going interactions. Chemistry traits, whether genetically based, such as tannin
312 concentration, or not, were not significantly correlated with lichen network structure.
313 Bark roughness has been demonstrated previously to be under strong genetic control
314 (Bdeir et al., 2017), and bark roughness has also been shown to be an important tree trait
315 influencing bark lichens (Lamit et al., 2015b); however this is the first demonstration of
316 a link from genetics to lichen network structure. As such these results have important
317 implications for the potential influence of genetically based variation in ecosystems with
318 networks of interacting species.

319 **Implications of Ecological Network Heritability**

320 Significant heritability of lichen interaction network structure is in line with the genetic
321 similarity rule, networks observed on trees of the same genotype tended to be structurally
322 similar. Although previous studies have examined aspects of networks, such as trophic
323 complexity (Barbour et al., 2016) and forest stand-level interaction network structure
324 (Lau et al., 2016b; Keith et al., 2017), this is the first study that we are aware of to
325 examine the heritability of network structure with replicated networks at the genotype
326 scale. Previous work in the evolution of ecological networks have primarily focused on
327 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,
328 2018; Harmon et al., 2019) or have been simulation based individual-level models that
329 integrate intraspecific variation to the species level (Maliet et al., 2020), even though
330 recent syntheses have pointed to the importance of processes operating across scales of
331 organization (Guimarães, 2020). There are two important functional ramifications of
332 genetically based variation in network structure.

333 First, heritability of network structure suggests that some amount of interaction
334 network complexity is determined and therefore could be predicted by genetic identity.
335 Variation in space and time create variation in ecological networks that influences evolu-
336 tionary dynamics via shifts in ecological dynamics, such as population demographics
337 (Guimarães, 2020). Given that ecosystems are comprised of hundreds and thousands of
338 species, each having a multitude of interactions, the potential to find traction for making
339 predictions in the context of ecological, let alone evolutionary, dynamics seems daunting.
340 The promise of predictability lies in the presence of asymmetries in ecosystems that
341 contribute to the occurrence of foundation species, such as hierarchy and nestedness
342 created by body size differences or life-history strategies, has been widely observed
343 (Ellison et al., 2005). The second is that heritability (i.e., genetic determination) means
344 that there is structure in the spatial or temporal variation that is created by individuals of
345 foundation species whose traits are in part determined by underlying trait differences.
346 Although this variation is inherently a function of both genetic and environmental effects
347 (Conner and Hartl, 2004), the community and network-level effects are also a function

348 of the scale of the interaction (Shuster et al., 2006).

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

384 Furthermore, the demonstration of the heritability of interaction networks, without
385 significant differences in community composition, provides clear empirical evidence
386 that variation in network structure points to the need to expand IIGEs to encompass
387 the structure of interaction networks. Although, IIGE theory provides a quantitative
388 framework within which to approach evolutionary theory at higher levels of biological
389 organization (from populations to communities and ecosystems), this theory has focused
390 on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham
391 et al., 2012, 2020) and has not yet integrated developments from the ecological or
392 evolutionary network theory literature. Thus, it has not developed a way to examine
393 complex interactions among species; however, previous studies have demonstrated this

network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be dampened or magnified within the system of interacting species Smith et al. (2011); Keith et al. (2017). Although such a synthesis necessitates a much greater effort than can be afforded in this paper, it is possible to point to several productive pathways forward. In terms of interaction networks, foundation species are relatively central within the system of interactions, that is their direct and/or indirect effects are greater than other species. So, when the more centralized (foundation) species have genetically based interactions, genetic effects will tend to be magnified in the community. Here, we found that even though more abundant or more centralized (i.e., “important”) species were present in the community, their effects were not the main component responding to genetic effects. Considering the impact of network structure would be a productive path forward for the theoretical development and application of the IIGE concept.

Evolution and Genetically Based Network Structure

The demonstration of evolution at any scale of biological organization requires demonstrating three key elements. First, there must be variation in the structure (composition, abundance, species interactions, diversity, networks) of communities across the landscape. Second, these differences must be genetically based and heritable in which community structure is passed from one generation to the next. For example, numerous studies show that related individuals tend to support the same communities of insects and microbes, and ecosystem processes of biodiversity, nutrient cycling and stability, whereas unrelated individuals support more different communities and ecosystem processes (Des Roches et al., 2018; Whitham et al., 2020). Importantly, the current study shows that networks are also heritable traits that greatly increases its utility as a community phenotype that selection can act upon. Third, selection must act on these differences to favor some communities over others leading to change over time (i.e., community evolution). Since our findings show that networks are heritable, another metric of community evolution is showing how networks change over time in response to an invasive species, climate change, or some other agent of selection.

Intra-specific, genotypic diversity could be creating lichen metacommunities on individual trees that form interaction modules with different dynamics. When communities are comprised of individuals who’s habitat is primarily determined by another organism, these communities inherently form modules within the larger ecosystem, as they tend to interact more with each other than with other individuals (Lau et al., 2017). Our study demonstrates that the 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. As mentioned previously, one class of networks that are theorized to have amplifying effects on networks have centralized “star” shapes with one or a few species at the center and radiating interactions out from the central core (Lieberman et al., 2005). This is structurally what we have observed with the networks that tend to

439 occur on some of the genotypes in our study, i.e., the more centralized networks. It is
440 likely that these networks could function as hot-spots of evolutionary dynamics resulting
441 from the amplifying effect the centralized network structure found on that tree genotype,
442 as multiple studies have found significant impacts of the removal of foundation species
443 in different systems (Keith et al., 2017; Des Roches et al., 2018).

444 Ecological network studies have focused on asymmetry and the quantification of
445 its structure in communities. The impacts of asymmetry on evolution from community
446 dynamics have primarily produced qualitative discussion (Bascompte et al., 2006;
447 Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific
448 predictions can be found in applications of evolutionary game theory, and although
449 developed at the population scale, such theory can apply to communities (Lieberman
450 et al., 2005). One seemingly useful direction is the classification of networks into
451 two general categories, rooted and cyclic, in which rooted networks have interactions
452 in which evolutionary effects emanate from one or multiple origins but these effects
453 do not have feedbacks to the origin, whereas cyclic networks contain feedbacks to
454 one or more origins. This is equivalent to “unidirectional” and “reciprocal” genetic
455 effects in the context of IIGE theory (Whitham et al., 2020). As we do not have an
456 estimate of the effect of the lichen on the fitness of the tree they occur on, we can not
457 determine whether the lichen networks in this system are cyclic or not. In terrestrial
458 ecosystems, lichen play important ecological roles, such as substrate stabilization (Root
459 et al., 2011) and nutrient fixation (Nelson et al., 2018). In some systems lignicolous
460 lichens can have demonstrable effects on the availability of nutrients for the trees that
461 they are associated with (Norby and Sigal, 1989), although this has not been measured
462 for the lichen in the current study’s system. Elucidating the presence of and quantifying
463 such feedbacks would allow for the determination of the cyclic nature and potential
464 evolutionary dynamics.

465 Since lichen are multi-species complexes, there is also the potential for evolutionary
466 dynamics to shift within the context of the lichen symbiosis. There is substantial
467 evidence that lichen have served as the “cradle of symbiotrophic fungal diversification”
468 (Arnold et al., 2009) and recent research has shown significant network structure of
469 endolichenic fungi and lichen collected from across North America (Chagnon et al.,
470 2016). Analysis of the structure of ecological networks has generally supported the
471 conclusion that nestedness, or the degree to which species tend to interact with similar
472 subsets of the community, tends to promote stability in mutualistic, primarily bipartite
473 (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic
474 networks (Elias et al., 2013; Grilli et al., 2016). Although there is growing evidence
475 that the nestedness of mutualistic networks is not necessarily the result of selection for
476 systems-level properties that promote stability but could be either product of asymptotic
477 abundance distributions leading to uneven interaction frequencies (Staniczenko et al.,
478 2013) and/or a by-product of selection and divergence creating network “spandrels” in
479 ecosystems (Valverde et al., 2018), this does not preclude the functional consequences
480 of network structure but rather the developmental or evolutionary processes that have
481 produced the structure. In the present study, we did not examine nestedness or modularity
482 of the lichen networks as we could not find metrics for analyzing networks that are
483 not only weighted and directed but also signed. Hopefully future network theoretic
484 developments will make the appropriate metrics available to conduct these analyses.

485 **Conclusion**

486 In the face of the high degree of complexity and potential context dependency of
487 ecological processes, the current study points to the utility of considering the spatial and
488 temporal scales of interactions, as discussed in previous studies (Bangert et al., 2006;
489 Zook et al., 2010; Zytnyska et al., 2012). In the present research, we found that the
490 assembly of ecological networks can have a measurable genetic basis depending on
491 the spatial scale of interactions, due in part, to asymmetries in size and longevity of
492 organisms. The importance of the scale of network organization to create hierarchical
493 structure (Guimarães, 2020) and the potential for foundation species to create this
494 structure in the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006)
495 suggests that future work would be aided by determining these modules within the biotic
496 community that include species with large differences in body-size and longevity. Also,
497 as heritable variation is the raw material for natural selection to act upon, a genetic basis
498 for interaction network structure indicates evolutionary dynamics should be considered
499 at the community level and that conserving genetic variation is important to consider in
500 efforts to restore or preserve complex species interactions and their associated ecosystem
501 functions (Evans et al., 2013).

502 One possible path forward is for future work to extend the many previous community
503 genetics studies that have focused on sessile organisms, such as galling insects (Bailey
504 et al., 2005; Whitham et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith
505 et al., 2017), to quantify the frequency of these interactions in the context of the larger
506 community. This would provide an estimate of the relative impact of these focal, often
507 termed foundation, species. In addition, community genetics theory has only quantified
508 first order interactions, i.e., among pairs; therefore, indirect effects from higher order
509 interactions are not explicitly accounted for (Shuster et al., 2006; Whitham et al., 2012,
510 2020). Given that network structure could be influenced by genetic effects, assessing
511 higher order interactions could provide a path forward for theoretical advances (e.g.,
512 IIGEs) that could help with identifying important characteristics of sub-groups to focus
513 on in empirical studies. That is, the combined interactions of communities of interacting
514 species should be reflected in the differences of networks of individual plant genotypes
515 and how they might differ across a landscape in which selection pressures change in
516 response to local biotic and abiotic conditions, leading to the optimization of modules
517 under different selective pressures. Network modeling and analysis could prove useful
518 for the identification of species within network modules that are most important to
519 study in systems where little is known about the biology of the system. For example, in
520 systems where background knowledge of the natural history of organisms is lacking,
521 network analyses based on species occurrence and abundance direct researchers to
522 species that could be focused on to best understand the dynamics of the system. Such
523 investigations will bring us closer to understanding the evolutionary drivers of Darwin's
524 entangled bank and the interconnectedness of species in complex communities (Darwin,
525 1859; Dátillo et al., 2016).

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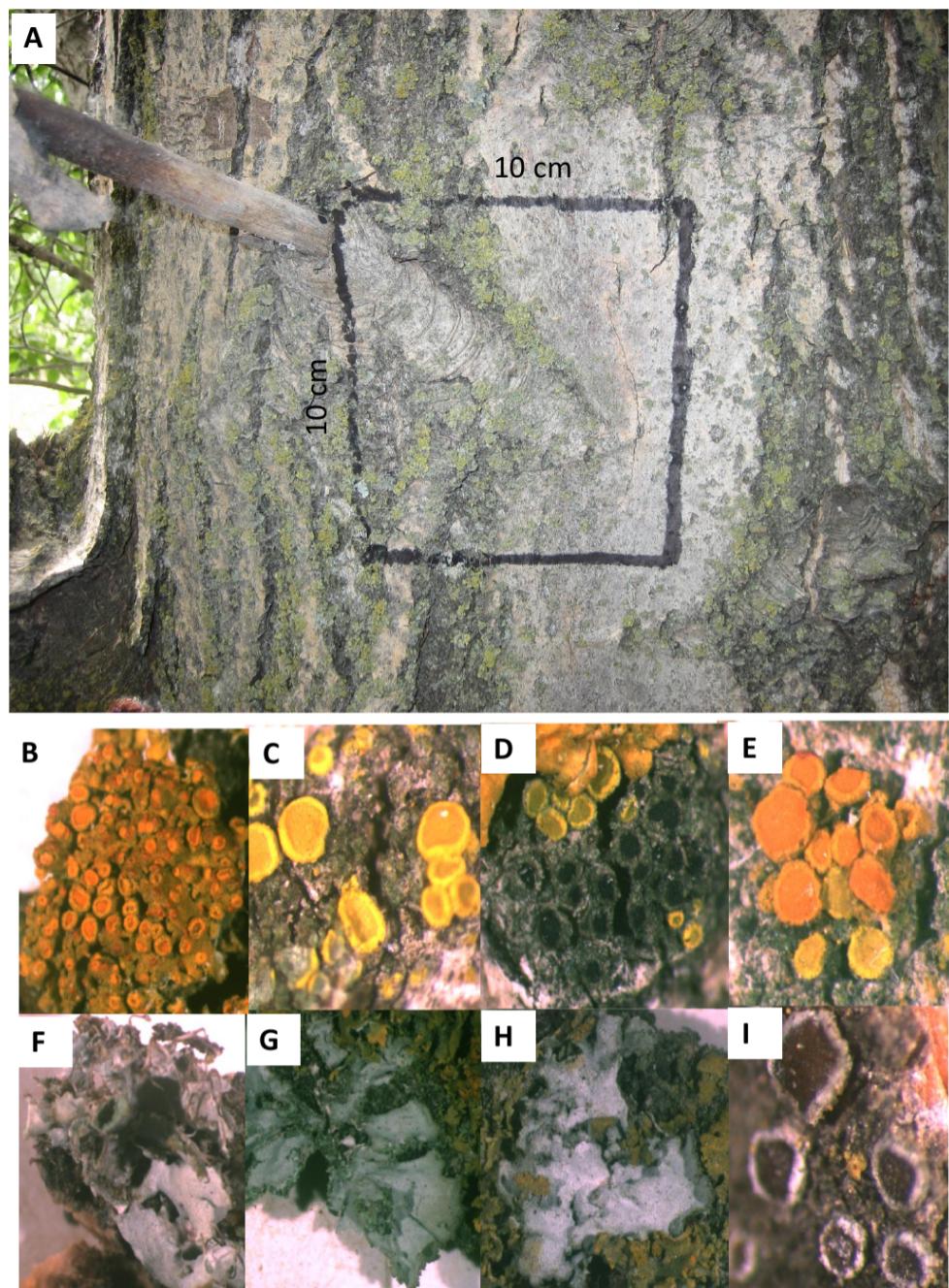


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) 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).

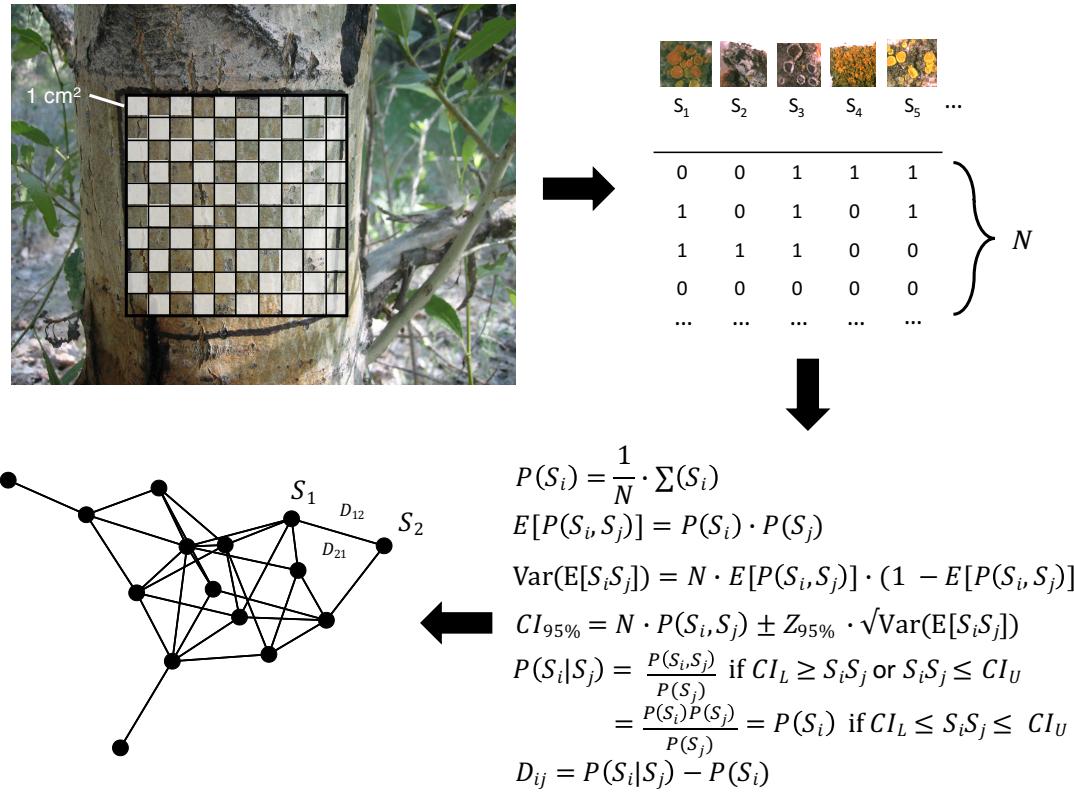


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded 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, $P(S_iS_j)$, were not significant using a confidence interval based comparison of their observed co-occurrence frequency, S_iS_j , to that expected due to chance alone, $E[P(S_iS_j)] = P(S_i)P(S_j)$, and $P(S_i|S_j)$ reduces to $P(S_i)$, the observed individual probability of species S_i .

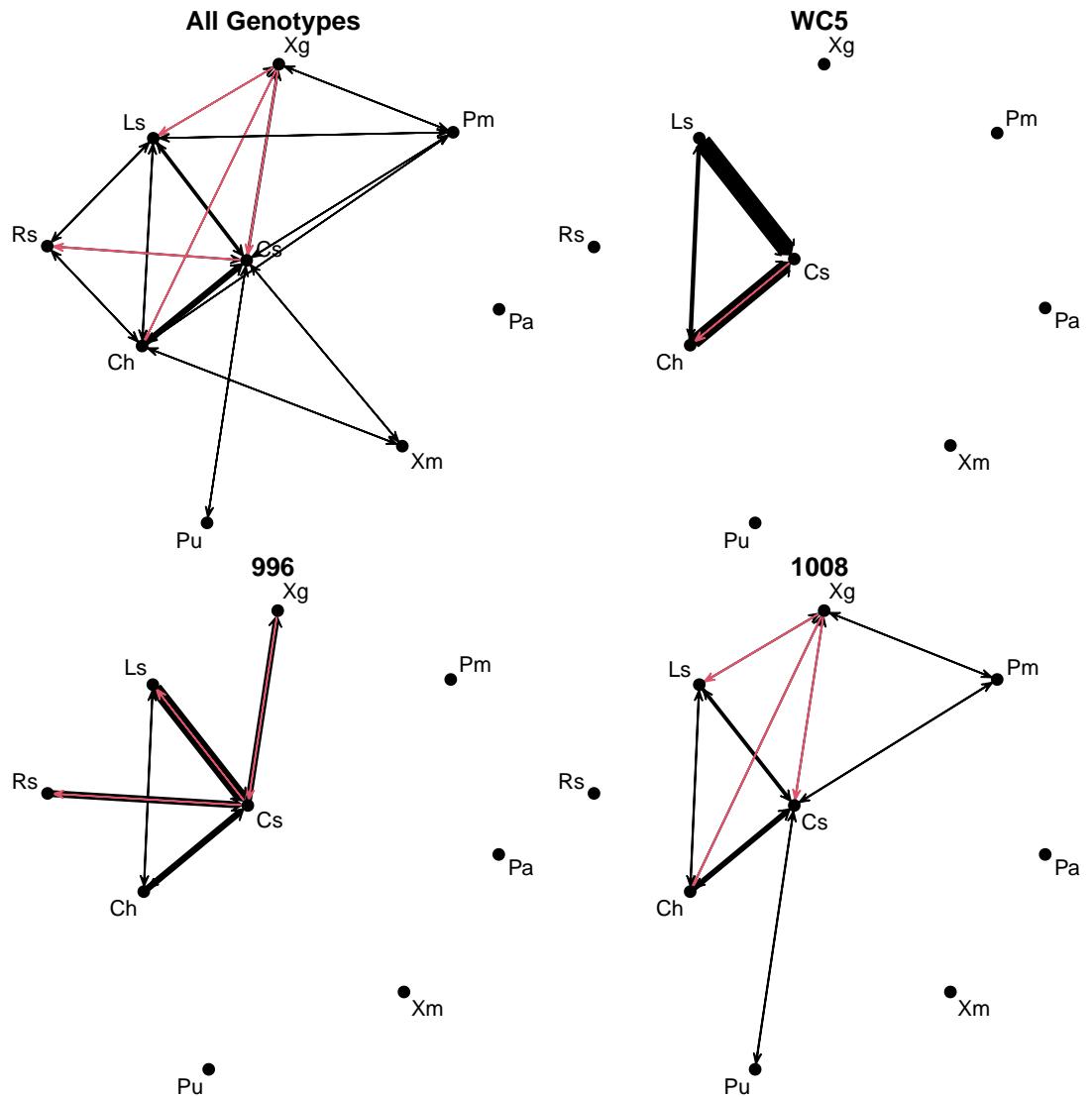


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

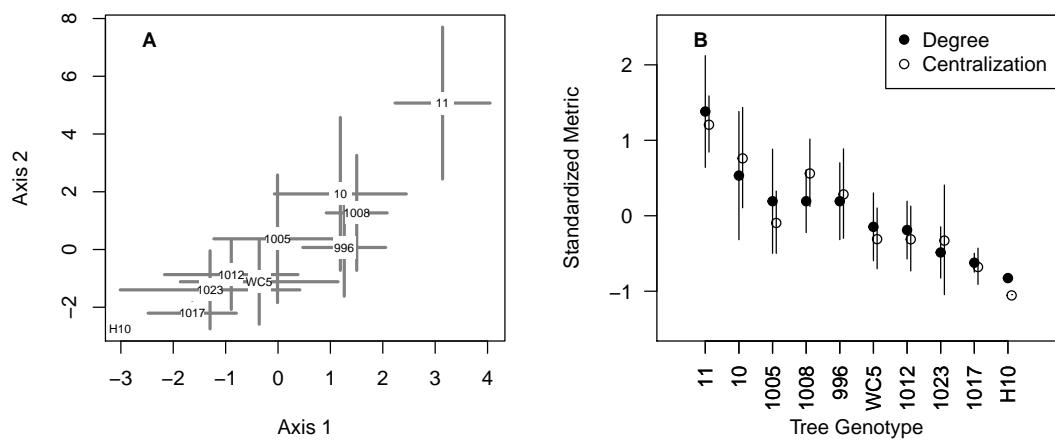


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

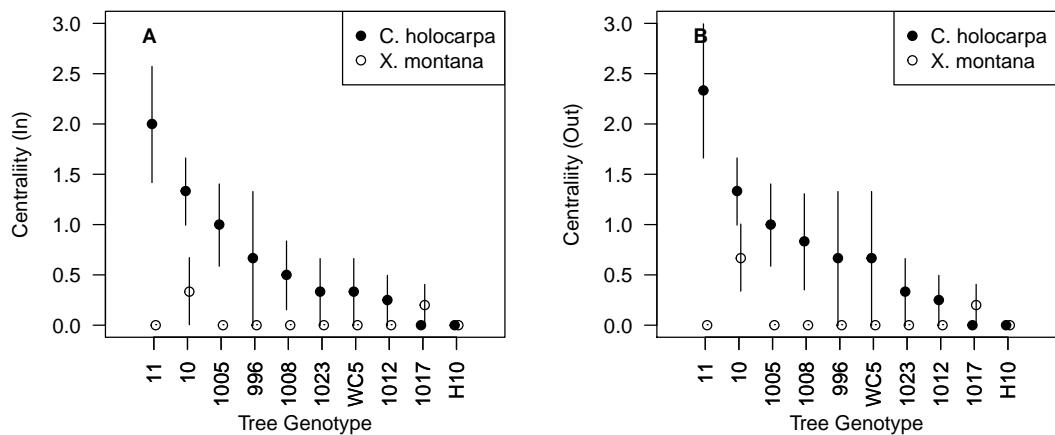


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

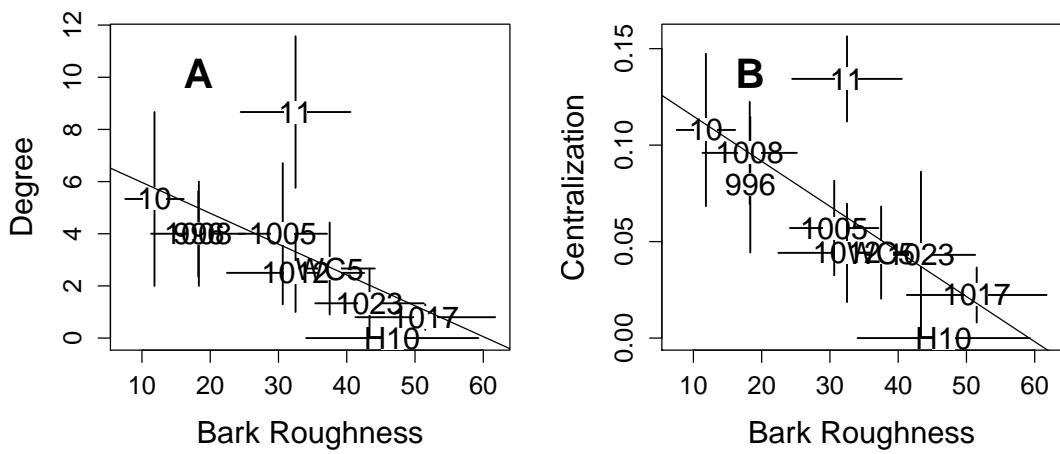


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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