

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 individuals 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., 2015; 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 that network theory applications to evolutionary dynamics have pointed to the importance of network structures that have focal or “central” nodes (e.g., species) (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., 2015; 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 orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegans*.

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

Lichen Network Modeling

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

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

199 to remove links from a given network by re-scaling the resulting conditional probabilities
200 by subtracting the individual probabilities from the conditional probabilities (i.e., how
201 different the conditional probability is from the independent probability), which makes
202 any species with a non-significant conditional probability zero.

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

217 Analyses, Software and Data

218 To quantify the structural variation of lichen networks we calculated several metrics at
219 both the level of node and whole networks. Although there are many other metrics, for
220 the sake of simplicity we focus on a subset that represent the primary interesting features
221 of network structure (see Lau et al. (2017)). We calculated the number of interactions or
222 “links” in each network (degree), which provides a measure of the size of the network
223 (Lau et al., 2015; Borrett and Lau, 2014). We also calculated the centralization of each
224 network using Freeman's centrality, which measures the evenness of the distribution of
225 interactions among the species in the network, using the `sna` package (Butts, 2019). In
226 a network with a low level of centralization species have similar amount of interaction
227 in the network, while a network with a high level of centralization tends to have one or
228 small number of species that interact with other species. We used a related function to
229 calculate the centrality of each species (i.e., node level centrality) in each network as well.
230 To calculate separate metrics for positive and negative links, as the networks contained
231 not only positive and negative connections but also directional connections (both in-
232 coming and out-going), we calculated the same network metrics for all combinations of
233 these types of connections using recently developed methods for signed, weighted and
234 directed networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch,
235 2020).

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

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	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.

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

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

	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.

305 **DISCUSSION**

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

320 **Implications of Ecological Network Heritability**

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

334 First, A genetic basis to network structure suggests that some amount of interaction
335 network complexity is determined and therefore could be predicted. Variation in space
336 and time create variation in ecological networks that influences evolutionary dynamics
337 via shifts in ecological dynamics, such as population demographics (Guimarães, 2020).
338 Given that ecosystems are comprised of hundreds and thousands of species, each having
339 a multitude of interactions, the potential to find traction for making predictions in the
340 context of ecological, let alone evolutionary, dynamics seems daunting. The promise of
341 predictability lies in the presence of asymmetries in ecosystems that contribute to the
342 occurrence of foundation species, such as hierarchy and nestedness created by body size
343 differences or life-history strategies, has been widely observed (Ellison et al., 2005). The
344 second is that heritability (i.e., genetic determination) means that there is structure in the
345 spatial or temporal variation that is created by individuals of foundation species whose
346 traits are in part determined by underlying trait differences. Although this variation
347 is inherently a function of both genetic and environmental effects (Conner and Hartl,
348 2004), the community and network-level effects are also a function of the scale of the

349 interaction (Shuster et al., 2006).

350 Second, even if the composition of the communities is the same among individuals
351 and genotypes, interactions may not be. We didn't observe compositional differences
352 using the same data from which the lichen networks were derived. If we only had our
353 composition dataset from this study, we would have concluded no response of the lichen
354 community to tree genotype, even though the underlying interactions among lichen
355 species does vary among genotypes. As such differences in network structure could
356 occur without observable differences in species richness or community composition,
357 which have been the primary focus of almost all previous community genetics studies
358 (Des Roches et al., 2018). Community composition of lichen has previously been
359 observed to be different among tree genotype in the same experimental garden (Lamit
360 et al., 2011, 2015b), the difference between the present study is likely a result of
361 differences in sampling method and the choice of genotypes leading to overall higher
362 abundances of observed lichens to assure the possibility of observing lichen interactions.
363 The previous study used a visual percent cover estimation, unlike the current study, which
364 observed lichen at the scale of 1 cm² cells, which could over-estimate cover depending on
365 the frequency at which actual thallus size was less than 1 cm², as well as both the northern
366 and southern aspects of each tree. These differences do not negate the findings of either
367 study. The present study's finding of differences in network structure without significant
368 compositional differences points to the importance of quantifying how network structure
369 changes in response to genetic variation in order to fully understand evolutionary
370 dynamics in complex communities. Having not observed a compositional effect of tree
371 genotype without measuring the network structure could lead to the conclusion of no
372 genetic effect on the community, even though differences in network structure are leading
373 to altered, local evolutionary dynamics. It is possible that these underlying differences
374 in interactions among lichen could lead to differences in community composition at
375 a future point in time via there effects on species abundances (Shuster et al., 2006);
376 however, this is not needed for evolutionary dynamics to play out via selection that leads
377 to shifts in trait distributions without shifting species abundance distributions, which is
378 possible under stabilizing, disruptive and directional selection (Conner and Hartl, 2004),
379 so long as the relative abundances of each species is imperceptibly changed. Thus, it is
380 imperative that further community genetics research assess or at least be aware of the
381 potential effects of variation in interactions and not just observe species abundances,
382 otherwise community level genetic effects may be underestimated, especially when
383 cumulative interaction 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 that
386 variation in network structure points to the need to expand IIGEs encompass the structure
387 of interaction networks. Although, IIGE theory provides a quantitative framework within
388 which to approach evolutionary theory at higher levels of biological organization (from
389 populations to communities and ecosystems), this theory has focused on modeling the
390 strong effects of foundation species (Shuster et al., 2006; Whitham et al., 2012, 2020) and
391 has not yet integrated developments from the ecological or evolutionary network theory
392 literature. Thus, it has not developed a way to examine complex interactions among
393 species; however, previous studies have demonstrated this network context is likely to be
394 important, as altering the structure of interaction networks provides a means for genetic

395 effects to be dampened or magnified within the system of interacting species Smith et al.
396 (2011); Keith et al. (2017). Although such a synthesis necessitates a much greater effort
397 than can be afforded in this paper, it is possible to point to several productive pathways
398 forward. In terms of interaction networks, foundation species are relatively central
399 within the system of interactions, that is their direct and/or indirect effects are greater
400 than other species. So, when the more centralized (foundation) species have genetically
401 based interactions, genetic effects will tend to be magnified in the community. Here, we
402 found that even though more abundant or more centralized (i.e., “important”) species
403 were present in the community, their effects were not the main component responding to
404 genetic effects. Considering the impact of network structure would be a productive path
405 forward for the theoretical development and application of the IIGE concept.

406 **Evolution and Genetically Based Network Structure**

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

422 Intra-specific, genotypic diversity could be creating lichen metacommunities on
423 individual trees that form interaction modules with different dynamics. When commu-
424 nities are comprised of individuals who’s habitat is primarily determined by another
425 organism, these communities inherently form modules within the larger ecosystem,
426 as they tend to interact more with each other than with other individuals (Lau et al.,
427 2017). Our study demonstrates that the environmental differences determined by the
428 genetic variation within a single species can create differences that not only impacts
429 community composition, as repeatedly demonstrated in other community genetics stud-
430 ies (Whitham et al., 2006; Des Roches et al., 2018), but also the structure of interactions
431 among individuals within these modules. Some network structures are likely to be more
432 stable, either in response to disturbance or via self-organized dynamics. For example,
433 centralized networks, although more efficient, are theorized to be more susceptible to
434 targeted attacks. As mentioned previously, one class of networks that are theorized to
435 have amplifying effects on networks have centralized ”star” shapes with one or a few
436 species at the center and radiating interactions out from the central core (Lieberman
437 et al., 2005). This is structurally what we have observed with the networks that tend
438 to occur on some of the genotypes in our study, i.e., the more centralized networks. It
439 is possible that these networks could function as hot-spots of evolutionary dynamics

440 resulting from the amplifying effect the centralized network structure found on that tree
441 genotype.

442 Ecological network studies have focused on asymmetry and the quantification of
443 its structure in communities, with qualitative discussion of the impacts on evolutionary
444 dynamics (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães et al., 2011;
445 Thompson, 2013). More specific predictions, within a quantitative framework, can
446 be found in applications of evolutionary game theory, and although developed at the
447 population scale, such theory can apply to communities. One seemingly useful direction
448 from evolutionary network developments from game theory is the classification of
449 networks into two general categories, rooted and cyclic, in which rooted networks have
450 interactions in which evolutionary effects emanate from one or multiple origins but these
451 effects do not have connections back to the origins, whereas cyclic networks contain
452 feedbacks to one or more origins. Although it did not explicitly define it in this context,
453 the previous work of Lau et al. (2017) developed the perspective that the structure of the
454 network in the context of a foundation species, such as cottonwoods in which there are
455 demonstrable community level genetic effects, is inherently created when trait variation
456 among genotypes of a foundation species has ecological effects on associated species.

457 This builds on many previous studies demonstrating that the community level effects
458 vary among genotypes. It is not clear what potential there is for feedbacks to the origins
459 (e.g. the cottonwood genotypes) from the community. In terrestrial ecosystems, lichen
460 play important ecological roles, such as substrate stabilization (Root et al., 2011) and
461 nutrient fixation (Nelson et al., 2018). In some systems lignicolous lichens can have
462 demonstrable effects on the availability of nutrients for the trees that they are associated
463 with (Norby and Sigal, 1989), although this has not been measured for the lichen in
464 the current study's system. Elucidating the absence and/or presence of and quantifying
465 such feedbacks would allow for the determination of the cyclic nature and potential
466 evolutionary dynamics of this system (Lieberman et al., 2005). However, such effects of
467 the bark lichen in this system on their tree hosts has not been quantified in this system.

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

486 not only weighted and directed but also signed. Hopefully future network theoretic
487 developments will make the appropriate metrics available to conduct these analyses.

488 **Conclusion**

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

505 One possible path forward is for future work to extend the many previous community
506 genetics studies that have focused on sessile organisms, such as galling insects (Bailey
507 et al., 2005; Whitham et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith
508 et al., 2017), to quantify the frequency of these interactions in the context of the larger
509 community. This would provide an estimate of the relative impact of these focal, often
510 termed foundation, species. In addition, community genetics theory has only considered
511 first order interactions, i.e., between two organisms (Shuster et al., 2006; Whitham
512 et al., 2012, 2020). Given that network structure could be influenced by genetic effects,
513 assessing higher order interactions could provide a path forward for theoretical advances
514 (e.g., IIGEs) that could help with identifying important characteristics of sub-groups
515 to focus on in empirical studies. That is, the combined interactions of communities of
516 interacting species should be reflected in the differences of networks of individual plant
517 genotypes and how they might differ across a landscape in which selection pressures
518 change in response to local biotic and abiotic conditions, leading to the optimization of
519 modules under selective pressures. Network modeling and analysis could prove useful
520 for the identification of species within network modules that are most important to
521 study in systems where little is known about the biology of the system. For example, in
522 systems where background knowledge of the natural history of organisms is lacking,
523 network analyses based on species occurrence and abundance direct researchers to
524 species that could be focused on to best understand the dynamics of the system. Such
525 investigations will bring us closer to understanding the evolutionary drivers of Darwin's
526 entangled bank and the interconnectedness of species in complex communities (Darwin,
527 1859; Dátillo et al., 2016).

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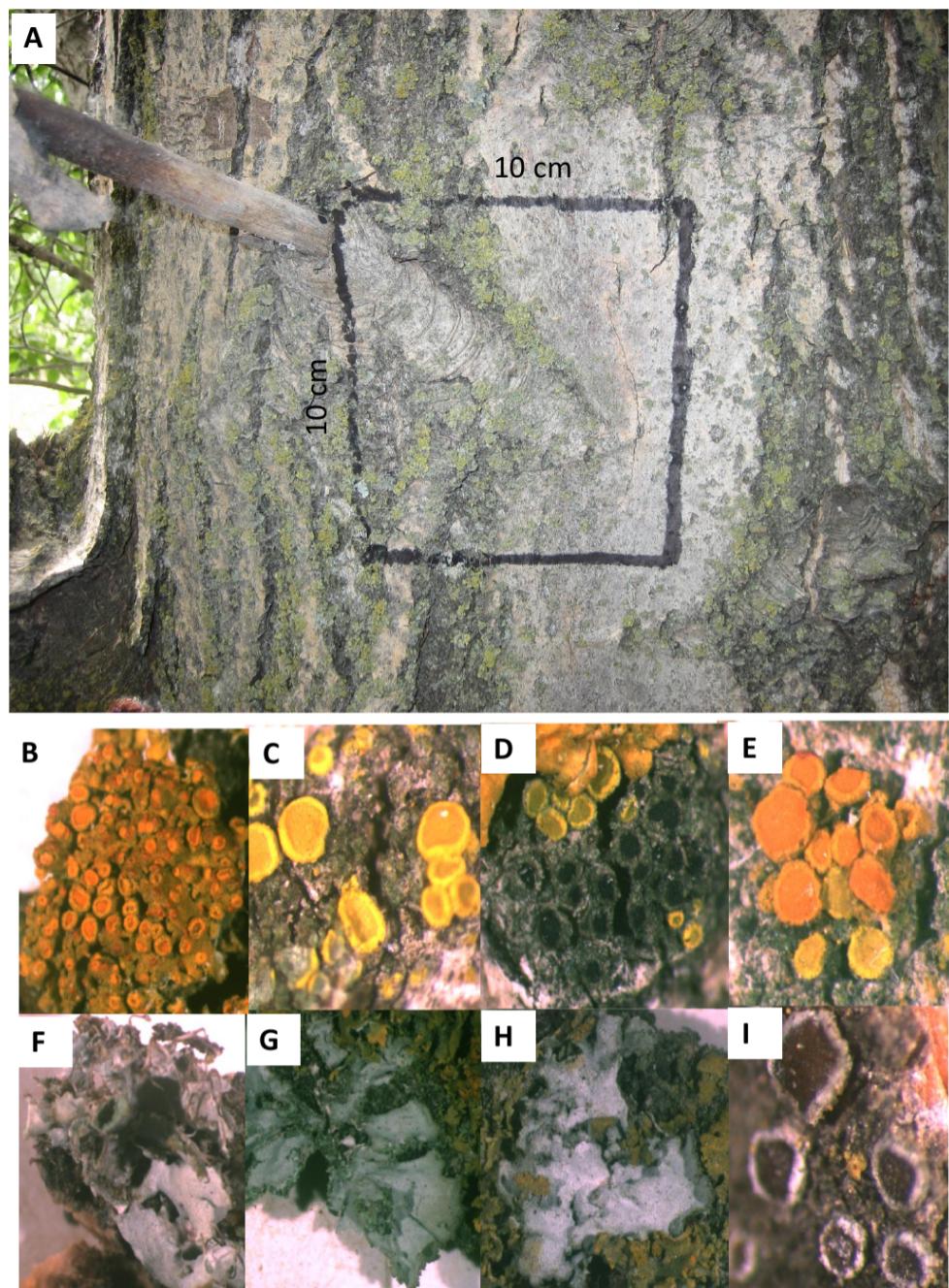


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from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

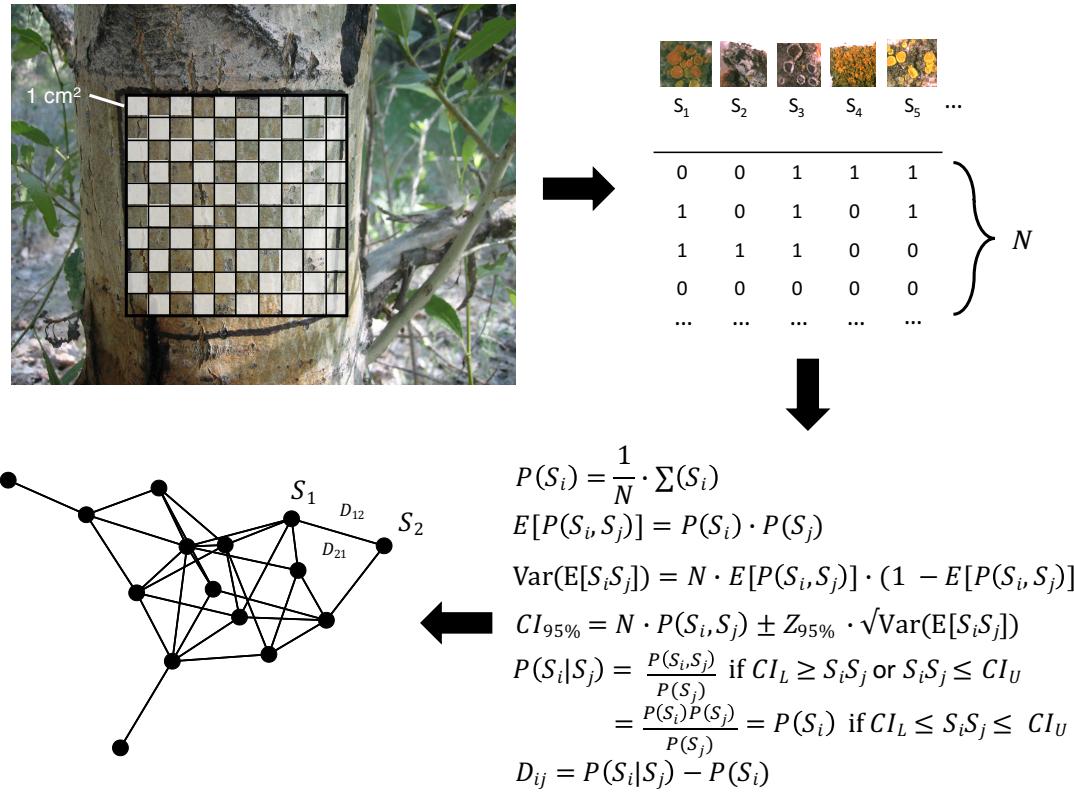


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded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

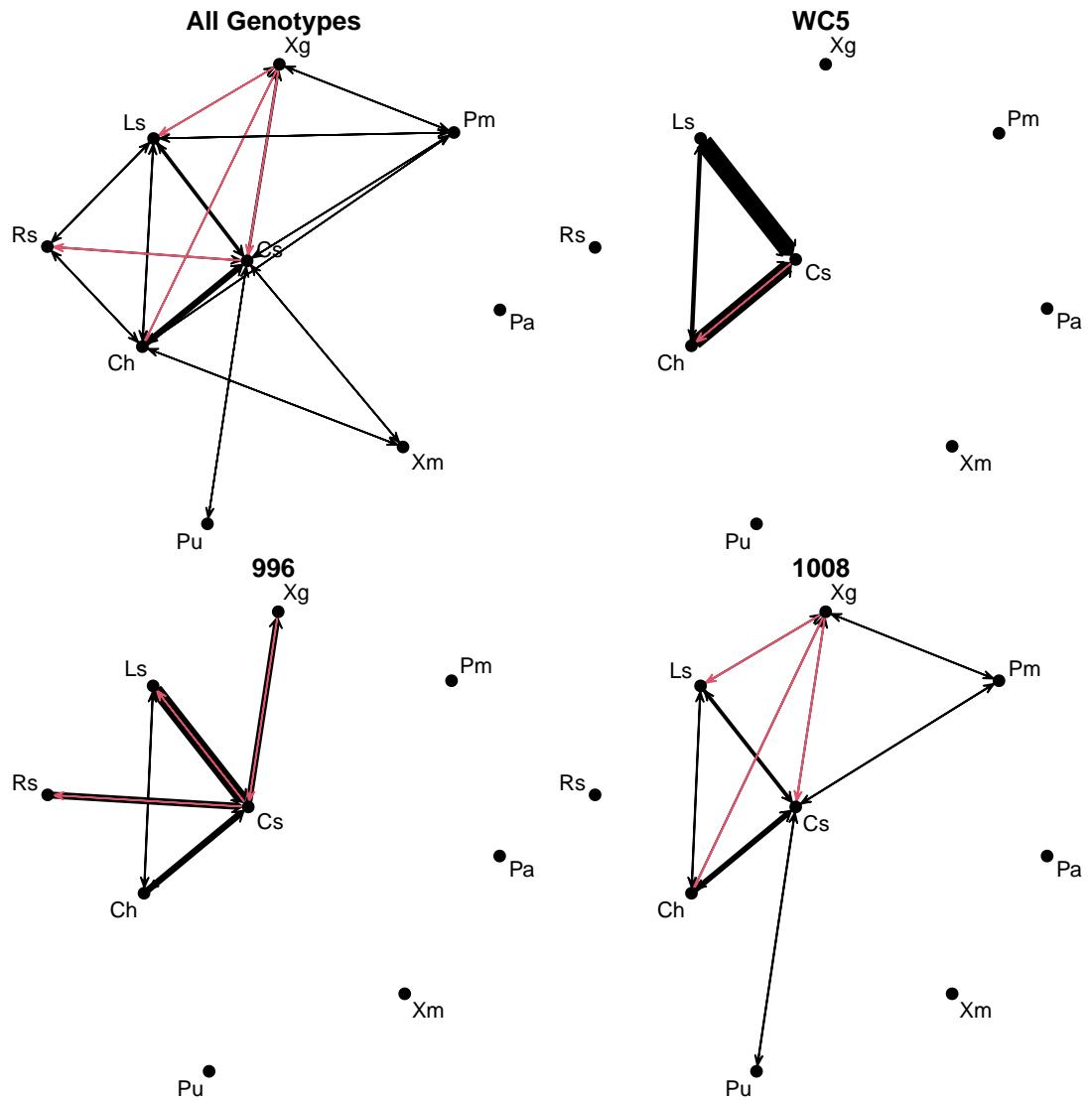


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

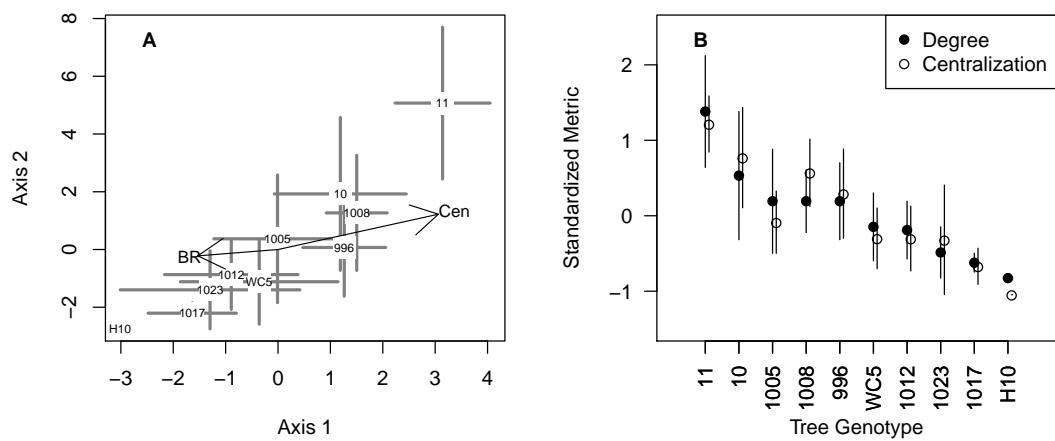


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

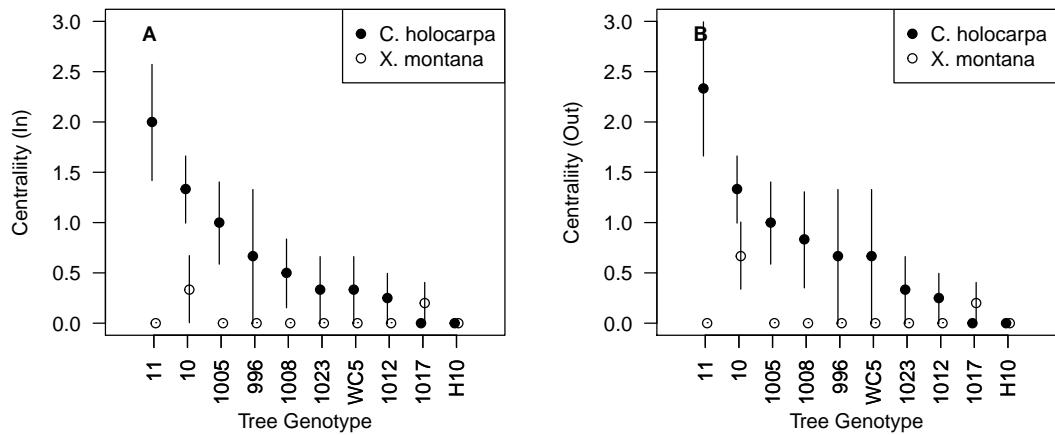


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

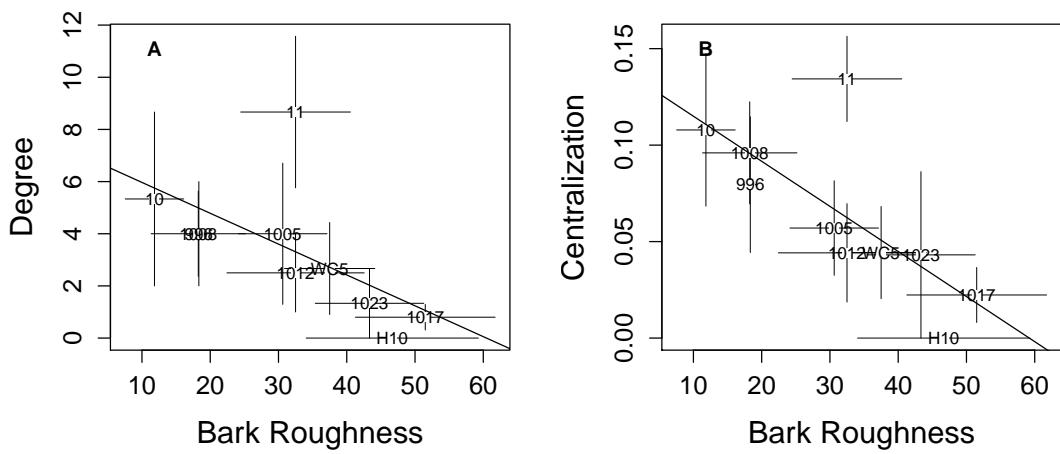


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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