

Genotypic variation in a foundation tree results in heritable ecological network structure

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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 can influence system-wide stability and resilience, our findings have important implications for how evolution acts in ecosystems.

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

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 play a significant role in defining distinct communities of interacting organisms: such
25 as rhizophytes, 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 points to the importance of
56 studying the genetics of interaction network structure. Genetic 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. As there is a preponderance of evidence that in natural systems evolution occurs in communities comprised of networks of interacting species (Lau et al., 2016a; Keith et al., 2017; Thompson, 2013; Bascompte et al., 2006), we set out to test two hypotheses. First, per the community similarity rule (Bangert et al., 2006) and IIGE theory (Whitham et al., 2020), we hypothesize that trees of the same genotype (i.e., clones) will support more similar lichen interaction networks relative to less related genotypes. In other words, epiphytic lichen network structure is heritable, which can be calculated via comparisons of within and among group variation in network structure. Second, heritability of lichen network structure is the result of underlying phenotypic covariation in tree traits important to interactions between trees and lichens and among lichens. Evidence that such trait covariance generates variation in interactions among community members provides an intermediate genetics-based mechanism for the underlying factors determining lichen distribution and abundance. In combination, evaluating these two hypotheses is fundamental to understanding variation and dynamics of network structure and evolution.

MATERIALS AND METHODS

Study System

The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, 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 them 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 cm^2 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 = *Physcia melanochra*, 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*, *Meigenia elegantula*.

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 $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences $E(S_i S_j)$ 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 $E(S_i S_j)$ is the total number of cells times the expected probability 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

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

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

Analyses, Software and Data

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

We used a combination of parametric and non-parametric, permutation based frequentist statistical analyses to test for the effects of genetic variation on lichen communities

and their interaction networks. To assess the effect of genotype on univariate responses, we used additive, random effects models with Restricted Maximum Likelihood (REML). We used a combination of Least Squares Regression, Analysis of Variance (ANOVA) and correlation tests to quantify and test for the relationship among other variables. Bark roughness, lichen cover and species richness were square-root transformed to meet the 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

In support of our first hypotheses, we found that tree genotype influenced lichen network structure as 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).

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

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.

= 0.0375); however, the centrality of *X. montana* was much lower overall relative to *X. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

In support of our second hypothesis, analysis of trait covariation revealed that genotype indirectly influenced lichen network centralization via genetically based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, *p-value* = 0.0113) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, *p-value* = 0.0343) both displayed significant responses to tree genotype. None of the other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, *p-value* = 1.0000) or carbon-nitrogen ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, *p-value* = 1.0000), showed a significant response to tree genotype and none other than bark roughness was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen network structure via bark roughness. We found that bark roughness was significantly correlated with network similarity and other lichen network metrics, including negative correlations with overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$, *p-value* = 0.04) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, *p-value* = 0.02). In other words, trees with more similar levels of bark roughness tended to have lichen interaction networks with similar structure. To quantify the genetic bases of this effect of bark roughness on network structure, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 = 0.00$, *p-value* = 1.0000) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, *p-value* = 1.0000), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

DISCUSSION

We found support for both of our hypotheses. First, tree genotype influenced the network structure of lichen communities associated with narrowleaf cottonwoods in a riparian forest ecosystem. Network similarity and metrics of network structure tended to be more

	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.

similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *holocarpa*. Second, the genetically based trait, bark roughness, was observed to affect network variation, largely via shifts in positive in-going and out-going interactions. Chemistry traits, whether genetically based, such as *thin* concentration, or not, were not significantly correlated with lichen network structure. Bark roughness has been demonstrated previously to be under strong genetic control (Bdeir et al., 2017), and bark roughness has also been shown to be an important tree trait influencing bark lichens (Lamit et al., 2015b); however this is the first demonstration of a link from genetics to lichen network structure. As such, these results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species.

Implications of Ecological Network Heritability

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

First, heritability of network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted by genetic identity. Variation in space and time create variation in ecological networks that influences evolutionary dynamics via shifts in ecological dynamics, such as population demographics (Guimarães, 2020). Given that ecosystems are comprised of hundreds and thousands of species, each having a multitude of interactions, the potential to find traction for making predictions in the context of ecological, let alone evolutionary, dynamics seems daunting. The promise of predictability lies in the presence of asymmetries in ecosystems that contribute to the occurrence of foundation species, such as hierarchy and nestedness

350 created by body size differences or life-history strategies, has been widely observed
351 (Ellison et al., 2005). The second is that heritability (i.e., genetic determination) means
352 that there is structure in the spatial or temporal variation that is created by individuals of
353 foundation species whose traits are in part determined by underlying trait differences.
354 Although this variation is inherently a function of both genetic and environmental effects
355 (Conner and Hartl, 2004), the community and network-level effects are also a function
356 of the scale of the interaction (Shuster et al., 2006).

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

392 Furthermore, the demonstration of the heritability of interaction networks, without
393 significant differences in community composition, provides clear empirical evidence
394 that variation in network structure points to the need to expand IIGEs to encompass
395 the structure of interaction networks. Although IIGE theory provides a quantitative

framework within which to approach evolutionary theory at higher levels of biological organization (from populations to communities and ecosystems), this theory has focused on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham et al., 2012, 2020) and has not yet integrated developments from the ecological or evolutionary network theory literature. Thus, it has not developed a way to examine 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  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.

415 **Evolution and Genetically Based Network Structure**

416 The demonstration of evolution at any scale of biological organization requires demonstrating three key elements. First, there must be variation in the structure (composition, 417 abundance, species interactions, diversity, networks) of communities across the landscape. Second, these differences must be genetically based and heritable in which 418 community structure is passed from one generation to the next. For example, numerous 419 studies show that related individuals tend to support the same communities of insects 420 and microbes, and ecosystem processes of biodiversity, nutrient cycling and stability, 421 whereas unrelated individuals support more different communities and ecosystem 422 processes (Des Roches et al., 2018; Whitham et al., 2020). Importantly, the current 423 study shows that networks are also heritable traits that greatly increases its utility as a 424 community phenotype that selection can act upon. Third, selection must act on these 425 differences to favor some communities over others leading to change over time (i.e., 426 community evolution). Since our findings show that networks are heritable, another 427 metric of community evolution is showing how networks change over time in response 428 to an invasive species, climate change, or some other agent of selection.

429 Intra-specific, genotypic diversity could be creating lichen metacommunities  individual trees that form interaction modules with different dynamics. When 430 communities are comprised of individuals whose habitat is primarily determined by another 431 organism, these communities inherently form modules within the larger ecosystem, 432 as they tend to interact more with each other than with other individuals (Lau et al., 433 2017). Our study demonstrates that the environmental differences determined by  genetic variation within a single species  create differences that not only impact 434 community composition, as repeatedly demonstrated in other community genetics studies 435 (Whitham et al., 2006; Des Roches et al., 2018), but also the structure of interactions 436 among individuals within these modules. Some network structures are likely to be more 437 438 439 440

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

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

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

487 ecosystems (Valverde et al., 2018), this does not preclude the functional consequences
488 of network structure but rather the developmental or evolutionary processes that have
489 produced the structure. In the present study, we did not examine nestedness or modularity
490 of the lichen networks as we could not find metrics for analyzing networks that are
491 not only weighted and directed but also signed. Hopefully future network theoretic
492 developments will make the appropriate metrics available to conduct these analyses.

493 Conclusion



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

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

532 entangled bank and the interconnectedness of species in complex communities (Darwin,
533 1859; Dátilo et al., 2016).

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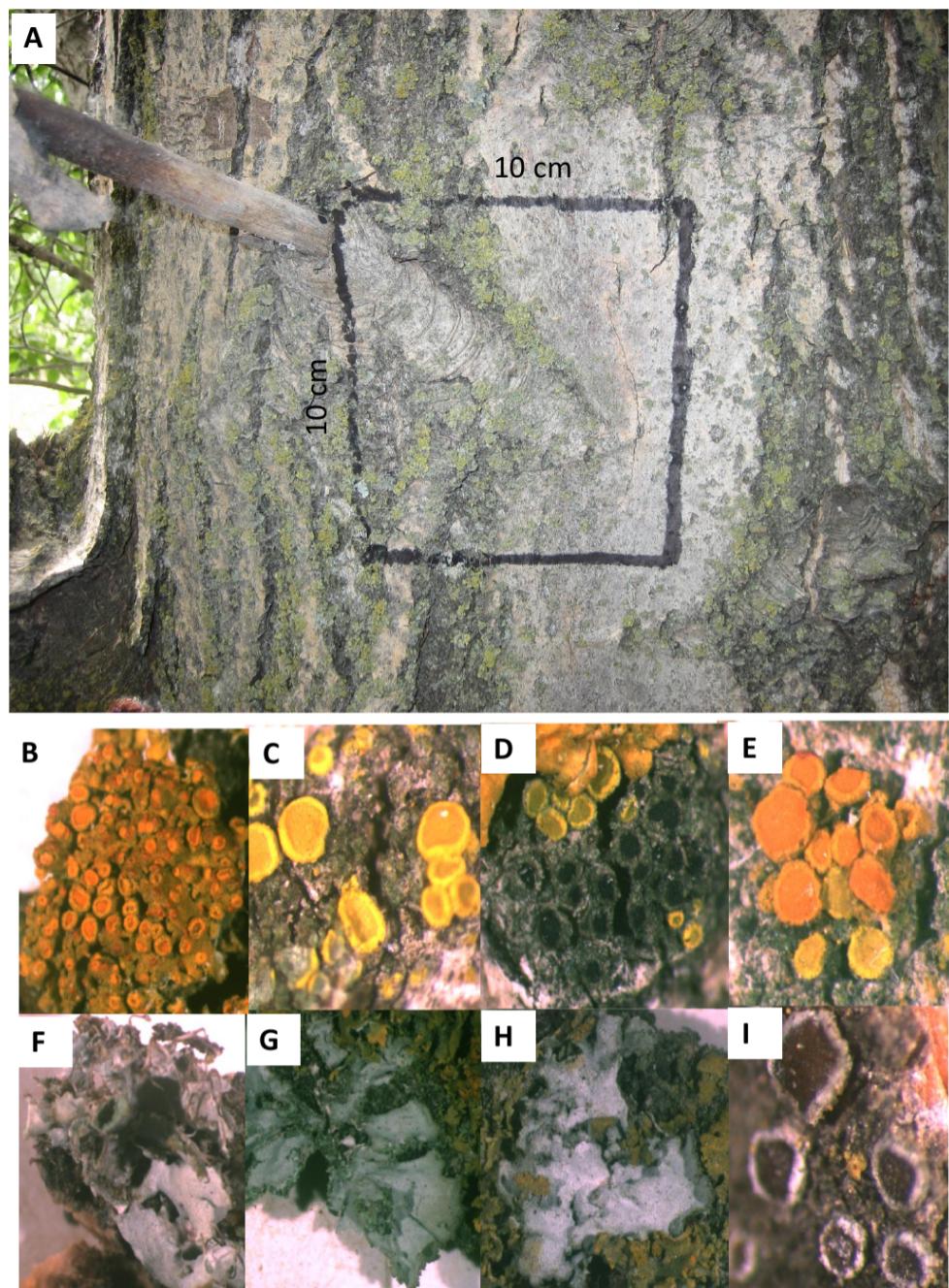


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from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

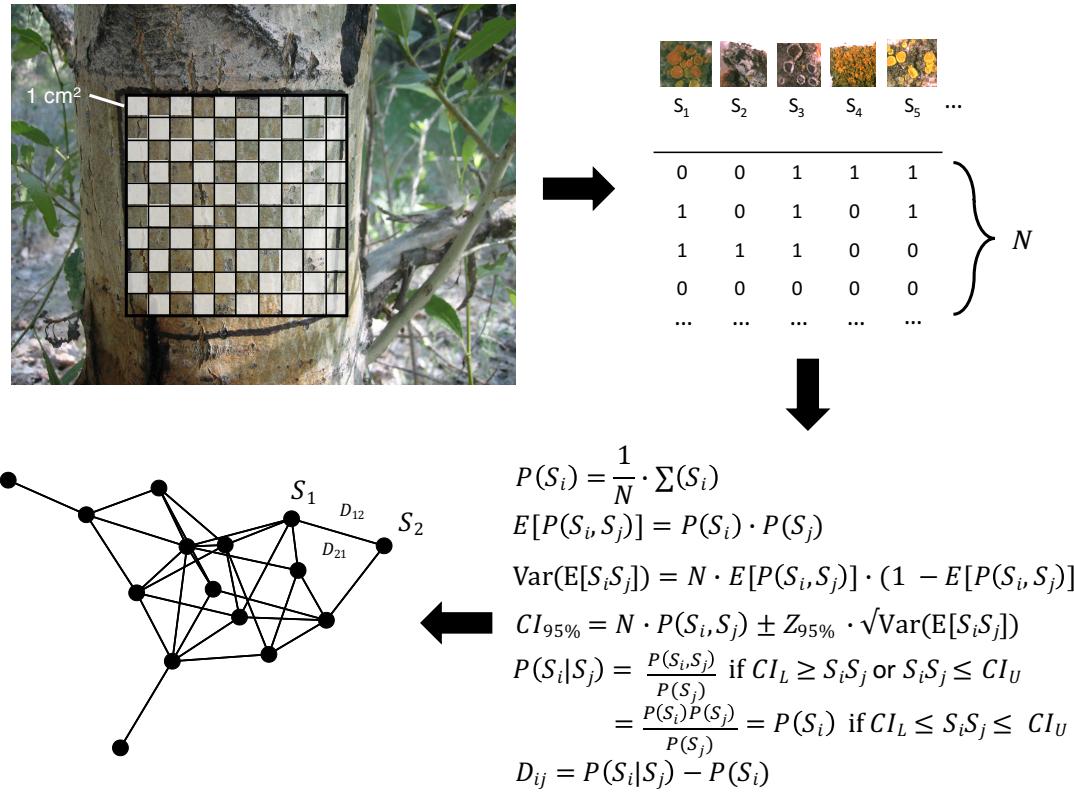


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (Araújo et al., 2011), we calculated the conditional probabilities, $P(S_i | S_j)$, for all species pairs and removed (i.e., set equal to zero) species pairs whose joint probabilities, $P(S_i S_j)$, were not significant using a confidence interval based comparison of their observed co-occurrence frequency, $S_i S_j$, to that expected due to chance alone, $E[P(S_i S_j)] = P(S_i) P(S_j)$, and $P(S_i | S_j)$ reduces to $P(S_i)$, the observed individual probability of species S_i .

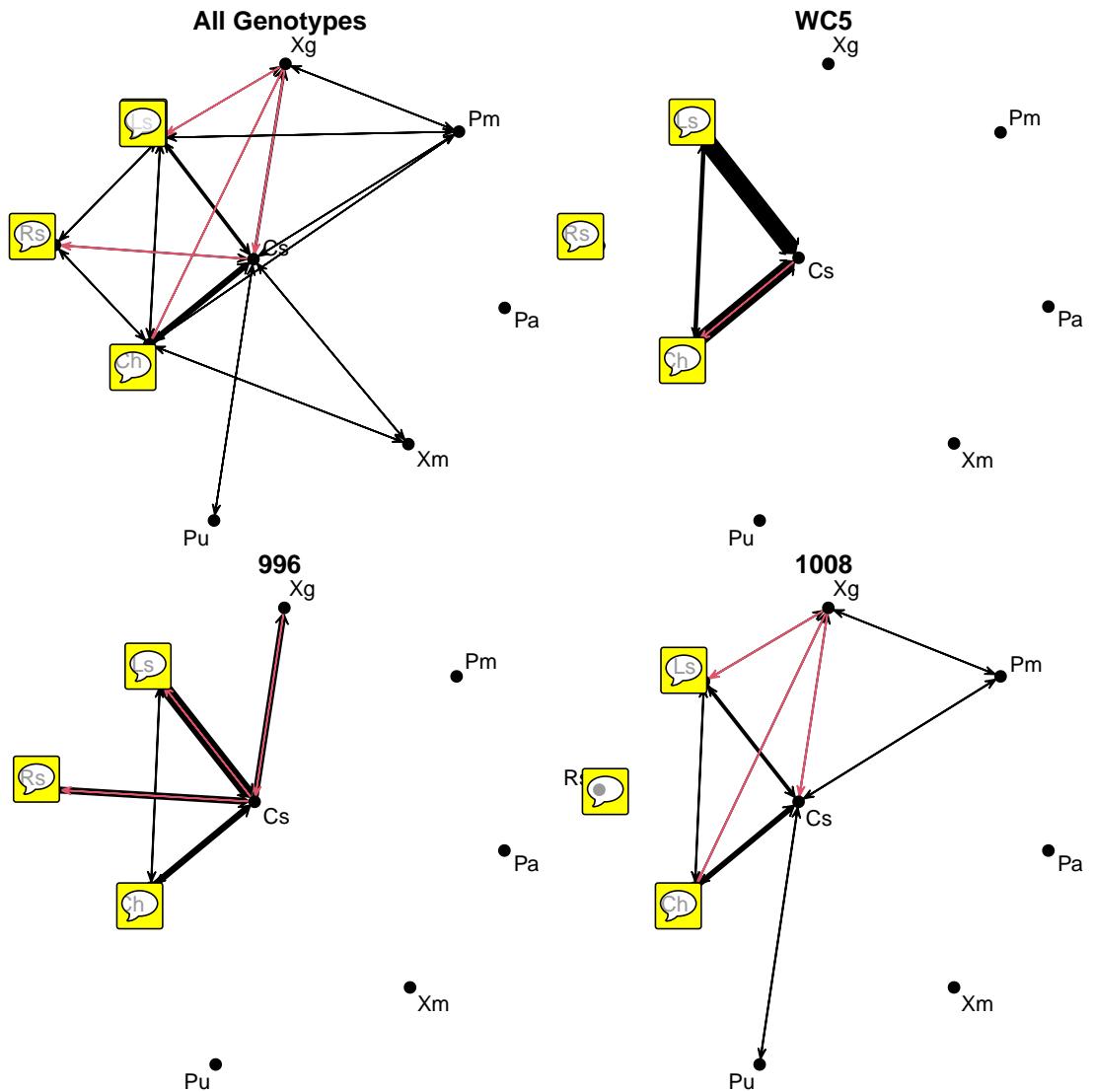


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

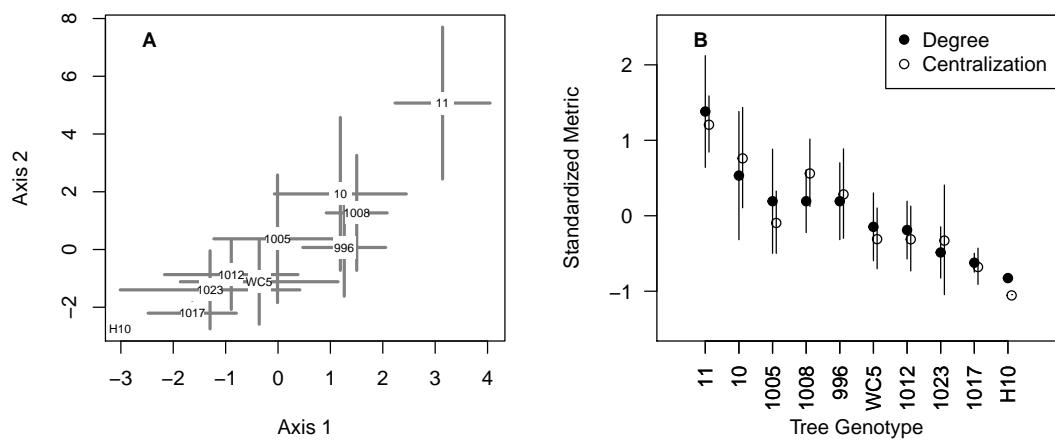


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

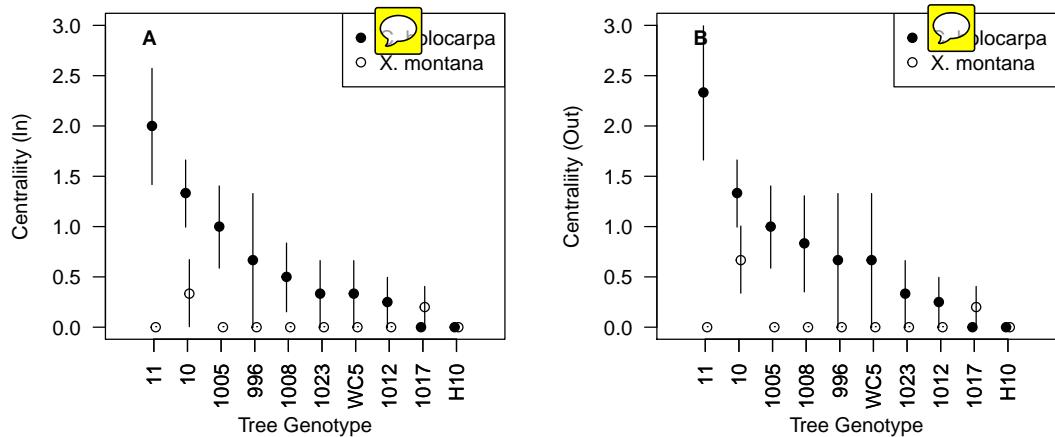


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *Caloplaca holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero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

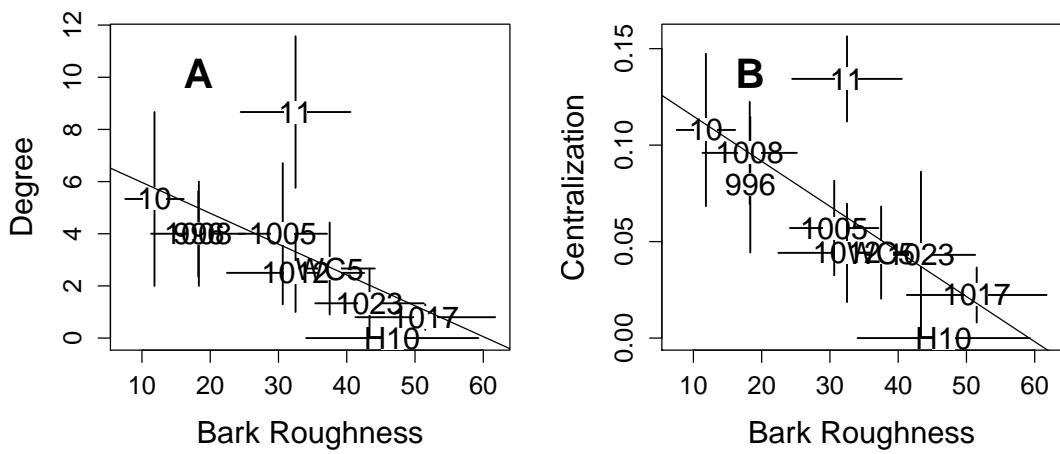


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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