

# **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 cm<sup>2</sup> 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 cm<sup>2</sup> 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  $1 \text{ cm}^2$  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  $1 \text{ cm}^2$  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

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](https://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).

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* ( $RLRT = 2.92$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0375$ ); however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent cover of rough bark ( $RLRT = 4.8526$ ,  $H^2 = 0.3221$ ,  $p\text{-value} = 0.0113$ ) and condensed tannins ( $RLRT = 3.0522$ ,  $H^2 = 0.3205$ ,

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.

*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).

	df	SS	$R^2$	Pseudo- <i>F</i>	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.

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 cm<sup>2</sup> cells, which could over-estimate cover depending on  
365 the frequency at which actual thallus size was less than 1 cm<sup>2</sup>, 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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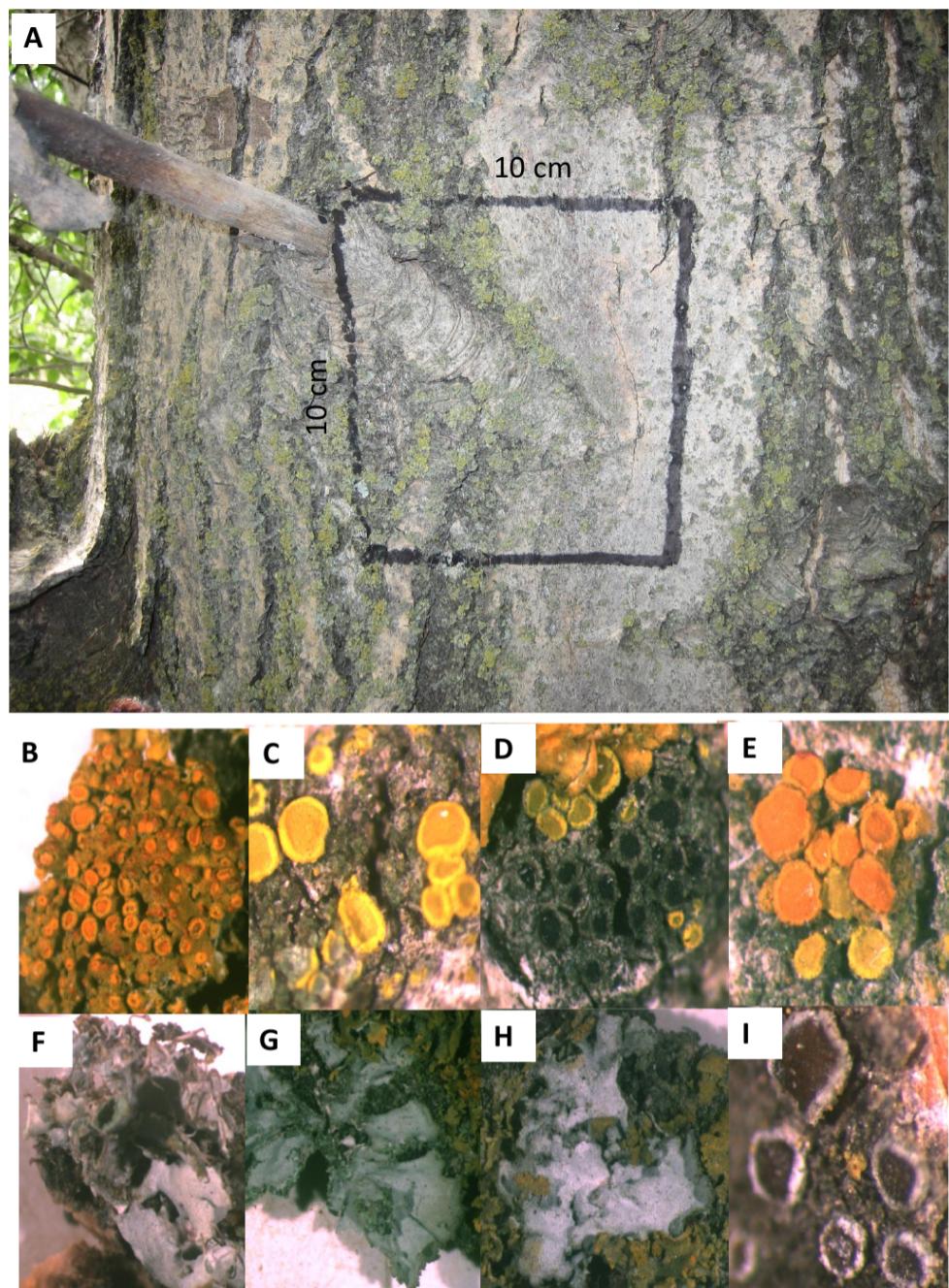
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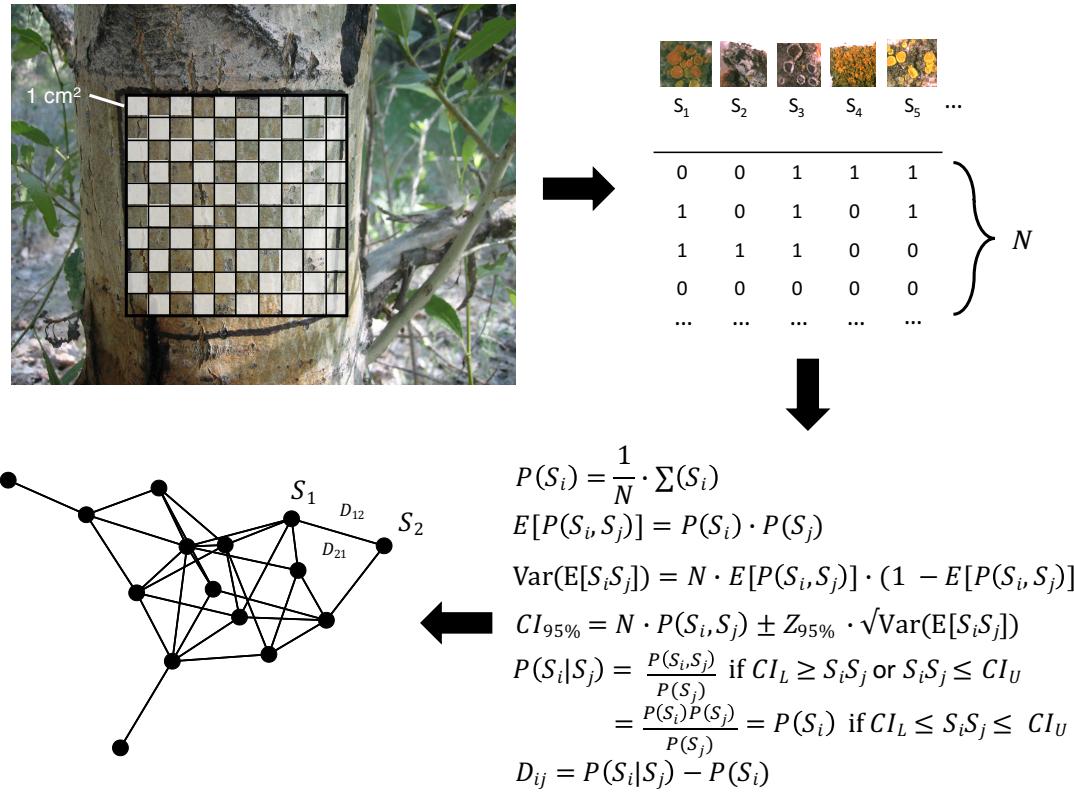
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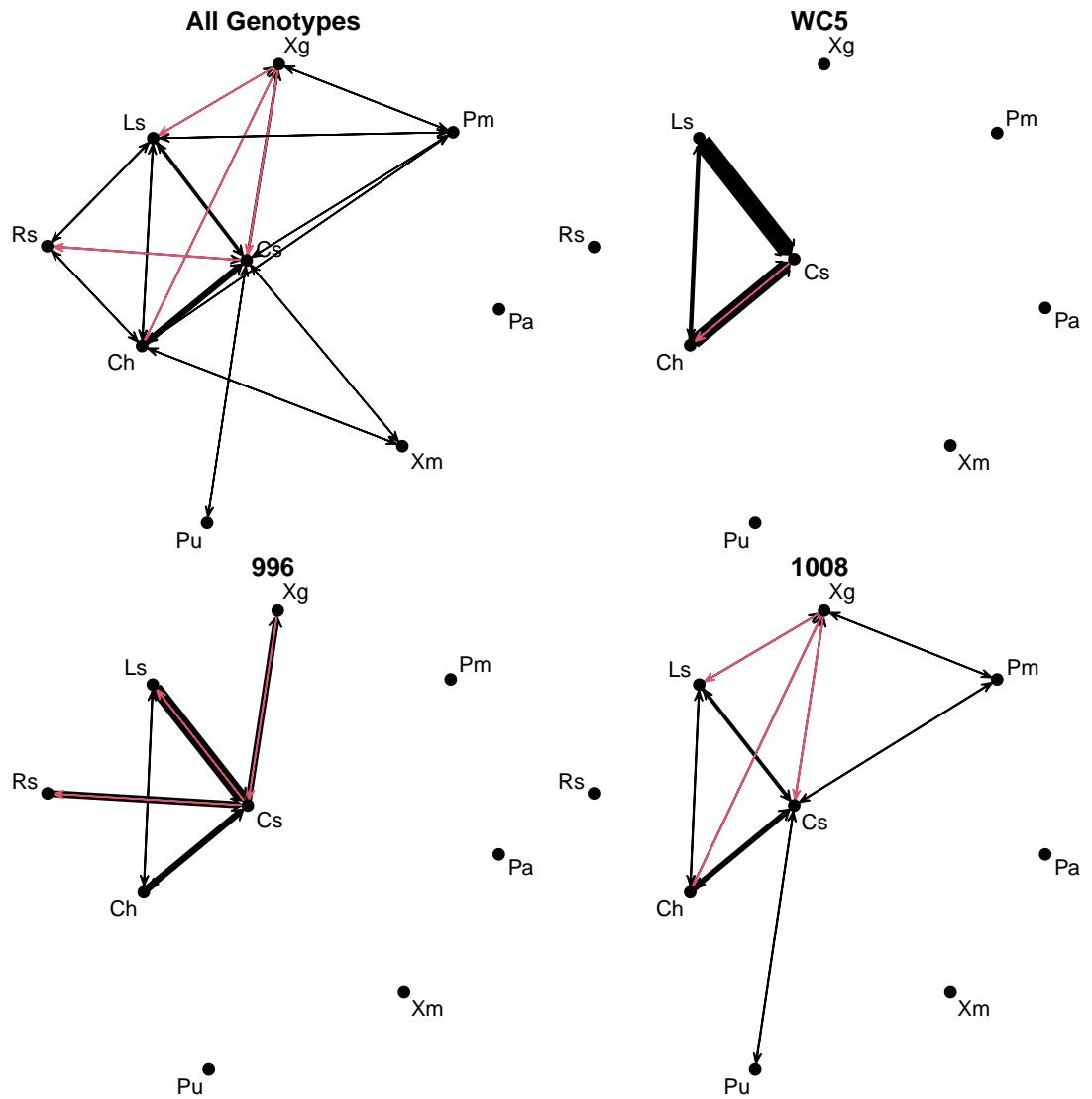
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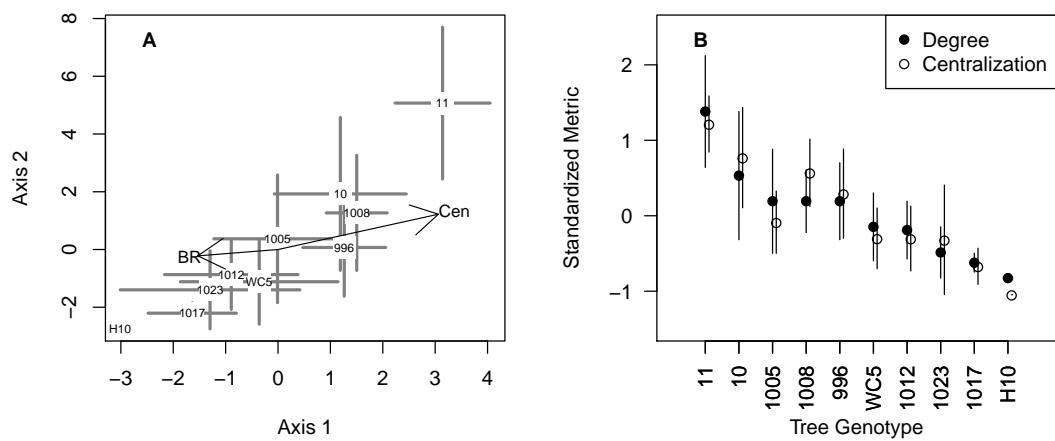
**Figure 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *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).



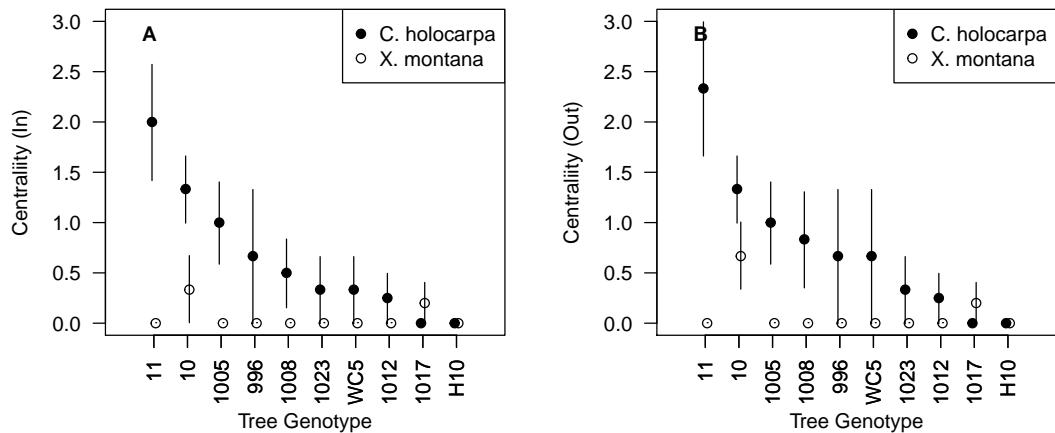
**Figure 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence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



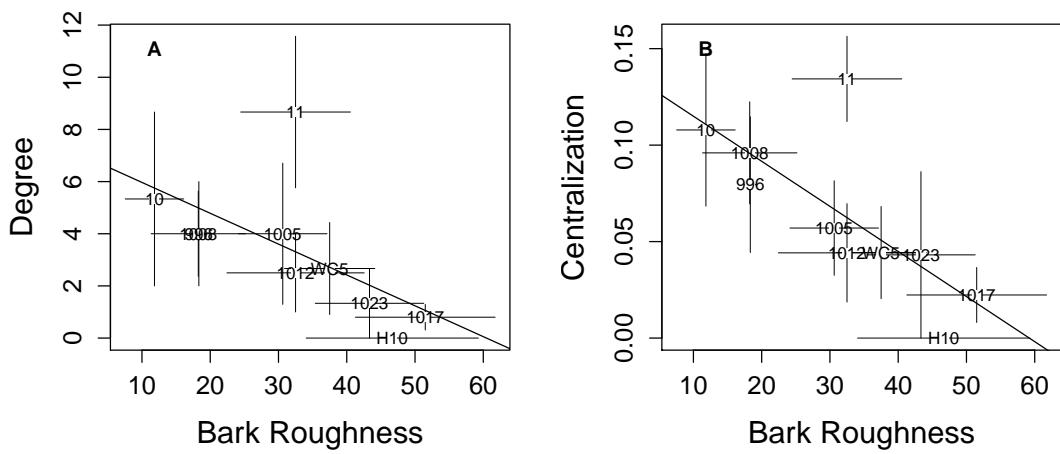
**Figure 3.** Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = 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 ( $\pm 1$  S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated network similarity. B. Plot showing the standardized ( $\frac{x-\bar{x}}{\sigma}$ ) means ( $\pm 1$  S.E.) for the two of the genetically based lichen network metrics: overall degree (i.e., total number of links) and centralization, which is a measure of the dominance of one species in the network.



**Figure 5.** Dot-plots showing the mean (dot) and  $\pm 1$  SE of in-degree (A) and out-degree (B) centrality for two species, *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 ( $\pm 1$  S.E) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased the number of interactions (degree) and dominance of those interactions (centralization) decreased.