

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

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ABSTRACT

Elucidating the genetic basis to ecological network structure is fundamental to understanding evolution in complex ecosystems. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that has quantified the heritability of network structure of a foundation species associated community. To examine this, in a 20+ year old common garden we observed epiphytic lichens associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation tree species. We constructed and conducted genetic analyses of signed, weighted, directed lichen interaction networks on individual trees. 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 predicted 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 has the potential to act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks.

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

INTRODUCTION

Evolution occurs in the context of complex ecological networks. Community genetics studies have shown that genetic variation in foundation species, which have large effects on ecosystems by modulating and stabilizing local conditions (Ellison et al., 2005), plays a significant role in defining distinct communities of interacting organisms: such as endophytes, pathogens, lichens, arthropods, and soil microbes (Busby et al., 2015; Barbour et al., 2009; Lamit et al., 2015a). Multiple studies have now demonstrated that genetic variation influences numerous functional traits (e.g., phytochemical, phenological, morphological)

29 that in combination result in a multivariate functional trait phenotype (Holeski et al., 2012) in which
30 individual plant genotypes support different communities and ecosystem processes (Bailey et al., 2009;
31 Whitham et al., 2012). Recently, the importance of genetic variation in structuring ecological systems
32 was reviewed, and 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 (Des Roches et al.,
34 2018). There is now evidence to support that selection occurs among groups of species (Wade, 2007)
35 and that genetic variation and phylogenetic relatedness contribute to variation in community assembly
36 (Crutsinger, 2016) and species interactions (Whitham et al., 2006; Bailey et al., 2009; Moya-Laraño,
37 2011). These evolutionary dynamics have the potential to shape the structure of ecological interaction
38 networks (Rezende et al., 2007; Guimarães et al., 2007; Gómez et al., 2009).

39 Empirical and theoretical work in network ecology and evolutionary biology point to the need for
40 examinations of the genetic basis of ecological network structure. Analyses of ecological networks have
41 demonstrated that indirect effects can lead to self-organization, producing sign-changing, amplifying
42 and/or dampening effects (Fath and Patten, 1998; Newman, 2006; Sole and Bascompte, 2006) and other
43 studies have demonstrated that indirect effects of interactions among species can lead to network structures
44 that amplify or dampen the effects of selection, such as the formation of star-like structures in which there
45 is a “central” species or core group of species (Lieberman et al., 2005). Also, work by Toju et al. (2014,
46 2016, 2017) observed consistent patterns of centralized interactions of species modules (i.e., groups of
47 species that interact more strongly within their group than with other species) focused around hubs of
48 plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have
49 disproportionate numbers of interactions with other species and likely are the drivers in determining
50 community assembly, structure and dynamics. Interspecific indirect genetic effects (IIGE) theory (*sensu*
51 Shuster et al. (2006)) in evolutionary biology also points to the importance of studying the genetics of
52 interaction network structure. Genetically based differences in network structure among individuals
53 can be acted upon by natural selection when there are fitness consequences of different networks of
54 IIGEs, leading to community evolution per Whitham et al. (2020) and, by extension, interaction network
55 evolution. For example, although the analysis was of abundances rather than interaction networks, Gehring
56 et al. (2014, 2017) found that the mycorrhizal communities on the roots of drought tolerant and intolerant
57 trees are dominated by different orders of ectomycorrhizal fungal mutualists that also differ in the benefits
58 they provide that enhance tree performance. Because drought tolerant genotypes are three times more
59 likely to survive record droughts, selection acts both on the tree and its fungal community and with
60 increased drought the community phenotype has changed over time. Also, in an antagonistic interaction
61 context, Busby et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods in a
62 common garden, the impacts of these strong interactors results in a different and diminished community
63 of arthropods relative to control trees. These examples collectively support the possibility that selection
64 acting on the tree may alter the network structure of associated communities in which different networks
65 are more likely to survive drought and pathogen outbreaks, respectively. Regardless of whether the IIGE
66 is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative
67 fitness of the tree), selection at the level of the tree population or its community, or both, can change
68 network structure and alter community dynamics (Whitham et al., 2020).

69 In this context, the “genetic similarity rule” of community genetics provides a useful framework
70 we can apply to interaction networks at the nexus of ecological and evolutionary dynamics. In a study
71 combining experimental common gardens and landscape-scale observations of interactions between
72 *Populus* spp. (cottonwoods) and arthropods, Bangert et al. (2006) observed that individual genotypes
73 that are more genetically similar will tend to have similar phytochemical traits and thus tend to have
74 similar interactions with other species. Although this is likely to have consequences for interactions and
75 network structure, studies in the network ecology literature generally do not include a genetic component
76 (Lau et al., 2017) and community genetics studies have primarily focused on community composition
77 in terms of the abundance of species (Des Roches et al., 2018). Some studies have examined the effects
78 of genetic variation on trophic chains in plant-associated communities (including *Populus*, *Solidago*,
79 *Oenothera*, *Salix*) (Bailey et al., 2005; Johnson, 2008; Smith et al., 2011, 2015; Barbour et al., 2016) and
80 generally found that increasing genotypic diversity leads to increased trophic complexity. We are aware
81 of only two studies that explicitly examined the effect of genotypic variation on interaction networks
82 between tree individuals and associated herbivores using ecological network metrics (Lau et al., 2016a;
83 Keith et al., 2017). Both found that genotypic diversity generates increased network modularity (i.e.,

84 compartmentalization); however, both were examining networks at the scale of forest stands, rather than
85 networks associated with individual trees; therefore, neither was able to observe replicated networks in
86 order to statistically test for genetic effects on network structure and quantify the genetic component (i.e.,
87 heritable variation) in network structure.

88 Here, we investigate how genetic variation in a foundation tree species determines the structure of a
89 network of interactions among a community of tree associated lichens. We used a long-term (20+ years),
90 common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic
91 identity (Martinsen et al., 2001). We focused on a community of epiphytic lichen species, as previous
92 research has demonstrated significant compositional effects of genotypic variation on lichen in this system
93 (Lamit et al., 2011, 2015b,a) and epiphytic organisms in other systems (Winfree et al., 2011; Zytynska
94 et al., 2011). Applying a probability-theory based network modeling approach (Araújo et al., 2011), we
95 constructed a set of interaction network models for the lichens associated with individual trees. Using
96 these models, we then examined the genetic basis of the structure of these ecological networks via several
97 network metrics that measure different aspects of network structure at the scale of individual species (i.e.,
98 nodes) or the entire network observed on each tree genotype. Given the potential importance of focal or
99 “central” nodes (e.g., species) for determining network dynamics (Lieberman et al., 2005), we focused on
100 network metrics that measure centrality for individual species and centralization for whole networks. Both
101 of these metrics measure how much a species is connected in the network relative to other species. As
102 there is a preponderance of evidence that in natural systems evolution occurs in communities comprised
103 of networks of interacting species (Lau et al., 2016a; Keith et al., 2017; Thompson, 2013; Bascompte
104 et al., 2006), we set out to test two hypotheses. First, per the genetic similarity rule (Bangert et al., 2006)
105 and IIGE theory (Whitham et al., 2020), we hypothesize that trees of the same genotype (i.e., clones) will
106 support more similar lichen interaction networks relative to individuals of other genotypes. In other words,
107 epiphytic lichen network structure is heritable, which can be calculated via comparisons of within and
108 among group variation in network structure. Second, heritability of lichen network structure is the result
109 of underlying phenotypic covariation in tree traits important to interactions between trees and lichens and
110 among lichens. Evidence that such trait covariance generates variation in interactions among community
111 members provides an intermediate genetics-based mechanism for the underlying factors determining
112 lichen distribution and abundance. In combination, evaluating these two hypotheses is fundamental to
113 understanding variation and dynamics of network structure and evolution.

114 MATERIALS AND METHODS

115 Study System

116 The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.)
117 dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus*
118 *fremontii* (S. Watson), occur here and are known to hybridize, in order to focus on intra-specific genetic
119 variation we only sampled pure or advanced generation back-crosses of *P. angustifolia*. Bark lichens
120 have been intensively sampled in this system and provide an ideal community in which to observe and
121 model interaction networks, as their sessile nature permits accurate identification of individuals and their
122 highly localized, direct contact interactions and slow population turnover rates facilitate the assessment of
123 interactions among lichen species on individual trees (Lamit et al., 2015b).

124 A long-term, common garden experiment was used to isolate the effect of tree genotype from the
125 effect of the localized microenvironment associated with each individual and spatial autocorrelation.
126 Established in 1992, asexually propagated clones of genotyped *P. angustifolia* individuals were obtained
127 from wild collections and planted in a fully randomized design at the Ogden Nature Center, Ogden, UT.
128 From the population of established individuals in the common garden, we sampled a total of ten genotypes,
129 replicated between 3 and 8 times each. These individuals comprised a set of tree genotypes with lichen
130 communities that have been well studied by previous investigations (Lamit et al., 2011, 2015b,a).

131 Bark Lichens and Trait Observations

132 We conducted a modified sampling procedure originally developed by Lamit et al. (2015b). On each
133 tree, presence or absence of each lichen species was assessed in a total of 50 1 cm² cells arrayed in
134 a 10 cm² checkerboard pattern. Given the small size and sessile nature of lichens, we were able to
135 rapidly assess lichen interactions by quantifying thalli of different species occurring in close proximity.
136 Sampling was restricted to the northern aspect of the trunk to maximize the abundance of lichens 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). The observed lichen community included: *Athallia holocarpa*, *Candelariella subdeflexa*, *Myriolecis hagenii*, *Rinodina freyi*, *Physcia adscendens*, *Physciella melanachra*, *Physcia undulata*, *Xanthomendoza galericulata*, *Xanthomendoza montana*. Several other species were not observed in the present study but are known to occur in this region: *Melanohalea elegantula*, *Melanohalea subolivacea*, *Phaeophyscia ciliata* and *Phaeophyscia orbicularis*.

The cell size and checkerboard sampling pattern was chosen to isolate the individuals in each cell. In a survey of *Xanthomendoza galericulata* in the common garden, we had observed a median thallus size of $0.12 \pm 0.001\text{ cm}^2$ (1 S.E.) (Supporting Information, Fig. 1). This expected thallus size formed the basis for our sampling design, such that lichen observations were 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 tree traits inside or in close proximity to the lichen quadrats. Selected traits have been demonstrated previously to be under strong genetic control in cottonwoods (Bdeir et al., 2017) and other foundation tree species, such as *Eucalyptus* (Nantongo et al., 2020), and previous work has provided evidence for effects on lichen communities of some of these traits (Lamit et al., 2011). We assessed bark texture/structure, hereafter referred to as roughness, in the quadrat as the percent of 1 cm^2 cells with “rough” bark, i.e., bark containing a fractured surface. In addition, we also examined several bark chemistry traits by taking bark samples immediately adjacent to each quadrat. We used previously collected phytochemical data from Lamit et al. (2011), including the concentration of condensed tannins, carbon and nitrogen. Additionally, we quantified bark pH for each tree. Bark samples were collected by excavating adjacent to the quadrat down to a depth of 2 mm. Bark pieces were air dried for storage and later processing. Samples were prepped for pH measurements by crushing with a mortar and pestle until all pieces were approximately 0.5 cm in diameter, creating equivalent surface areas among samples. 0.5 g of crushed bark was placed in a 15 ml Falcon collection tube with 5 ml of deionized water. Tubes were capped and let sit for 24 hrs prior to pH measurement with a SevenGo™ pH meter (Mettler Toledo).

Lichen Network Modeling

For each tree, the repeated observations of lichens were used to construct replicated interaction networks, i.e. one for each individual tree. 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. Using the axioms of probability, we can calculate the conditional probabilities of each species pair as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$. This yields a matrix that could possibly be asymmetrical, i.e., $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Also, the diagonal, $P(S_i|S_i)$, is 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 within the confidence interval, the joint probability $P(S_i, S_j)$ is concluded 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 through subtraction of 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 that 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; therefore, the “intra-specific” observations are the same species being counted across the cells of the grid 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 are within this study interpreted 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 network 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 low centralization species have similar strengths and numbers of interactions. A network with high centralization tends to have one or a 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 traits as univariate response variables (including the metrics of network structure), we used additive, random effects models with Restricted Maximum Likelihood (REML) conducted in R via the `lme4` and `RLRsim` packages (Bates et al., 2015; Scheipl et al., 2008). To conform to test assumptions, traits were root transformed with the exception of condensed tannin concentration and carbon-nitrogen ratio, which were rank and \log_{10} transformed, respectively. Differences in node level centrality among species was tested using ANOVA and Tukey-HSD multiple comparison tests. Correlations among trait variables and network metrics were quantified and tested using linear correlations of Pearson’s r . For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches. To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the \mathbf{D} interaction matrices among all trees (Newman, 2010). For community composition we applied Bray-Curtis similarity to a matrix of species abundances obtained by aggregating the gridded observations by summing over the binary cell-wise species presence-absences. To test for the effects of genotype and other predictor variables on community and network similarity we conducted Permutational Analysis of Variance (PERMANOVA) with `vegan` (Oksanen et al., 2019) using 100000 permutations. 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 100 random initial configurations with a maximum of 1000 iterations and a change in stress threshold of less than 10^{-12} . This was repeated for one to four dimension configurations, and the configuration with the lowest dimensionality and an unexplained variation less than 10% was selected. 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), which can be interpreted as a measure of the phenotypic variance due to genotypic variation. All analyses were conducted using R version 4.0.2 (R Core Team, 2020). Code and data for the project

245 are openly available as a reproducible workflow using `drake` (Landau, 2018) archived via Zenodo
246 <https://doi.org/10.5281/zenodo.4581639>.

247 RESULTS

248 In support of our first hypotheses, we found that tree genotype influenced lichen network structure and
249 that multiple lichen network metrics were heritable. Tree genotype significantly predicted the structural
250 similarity of lichen networks and, overall, network-level metrics responded significantly to tree genotype,
251 including network degree and centralization including both in-coming and out-going links or when
252 separated into in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive
253 links also showed a significant effect of tree genotype, including positive degree and positive in-going
254 centralization. Metrics calculated with negative links were not significant, including degree (negative)
255 and both in-coming (negative) and out-going centralization (negative). Interestingly, although network
256 similarity and multiple network metrics were significantly predicted by tree genotype, we did not observe
257 a significant genotypic effect for community composition ($\text{Pseudo-}F_{9,27} = 0.751$, $R^2 = 0.20$, $p\text{-value} = 0.888$).
258

	Response	df	RLRT	H2	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.

259 The genetic response of network centralization was driven by variation in *Athallia holocarpa*. Cen-
260 tralinity varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$, $p\text{-value} < 0.0001$). The node-level
261 metrics for *A. holocarpa* displayed the strongest response to tree genotype with high levels of heritability
262 of positive centrality for both the in-coming ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going
263 ($RLRT = 3.13$, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives but not for either negative centrality metrics
264 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
265 of the other species' centralities showed a genotypic response (Supporting Information, Fig. 2) with
266 the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$); however, the centrality of *X.*
267 *montana* was much lower overall relative to *A. holocarpa* and the variation in *X. montana* centrality was
268 restricted to two genotypes (Fig. 5).

269 In support of our second hypothesis, analysis of trait covariation revealed that genotype indirectly
270 influenced lichen network centralization via genetically based variation in bark roughness. The percent
271 cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and condensed tannins ($RLRT =$
272 3.0522 , $H^2 = 0.3205$, $p\text{-value} = 0.0343$) both displayed significant responses to tree genotype. None of
273 the other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT$
274 = 0.0000 , $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and none
275 other than bark roughness was correlated with network similarity (Table 2); therefore, we focused our
276 subsequent analyses on the indirect effect of genotype on lichen network structure via bark roughness. We
277 found that bark roughness was significantly correlated with network similarity and other lichen network
278 metrics, including negative correlations with overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$, $p\text{-value}$
279 = 0.04) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees with more
280 similar levels of bark roughness tended to have lichen interaction networks with similar structure (Fig. 6).
281 To quantify the genetic bases of this effect of bark roughness on network structure, we used the residual

values from regressions of the network metrics and bark roughness in subsequent tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$), and, thus, the bulk of the genetically based variation in the network metrics can be explained by bark roughness.

	df	SS	R2	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.

DISCUSSION

Evolutionary Importance of Ecological Network Heritability

The demonstration of evolution by natural selection requires three key elements (Conner and Hartl, 2004), which multilevel selection theory posits can occur simultaneously at multiple levels of ecological organization (Whitham et al., 2003, 2020). First, there must be variation, which at the community level means variation in species abundance, richness, interactions and/or interaction network structure. Second, these differences must be genetically based and heritable in which community structure is passed from one generation to the next. For example, numerous studies show that related individuals tend to support the same communities of insects and microbes, and ecosystem processes of biodiversity, nutrient cycling and stability, whereas unrelated individuals support more different communities and ecosystem processes, per the genetic similarity rule (Bangert et al., 2006, 2008; Barbour et al., 2009; Whitham et al., 2020). Third, selection must favor some communities over other. Given these conditions, selection will lead to community level change over time (i.e., community evolution). This is consistent with holobiont theory and empirical studies (Zilber-Rosenberg and Rosenberg, 2008; Gilbert et al., 2012) in which the holobiome (usually a multicellular host and its symbionts) is the primary unit of selection (Bordenstein and Theis, 2015; Johnson and Gibson, 2021).

Most notably, the current study shows that the structure of lichen networks on individual trees are heritable traits, which the important mechanism for selection to act. There are two important functional ramifications of genetically based variation in network structure. First, heritability (i.e., genetic determination) means that there is structure in the spatial or temporal variation that is created by individuals of foundation species whose traits are in part determined by underlying trait differences. Although this variation is inherently a function of both genetic and environmental effects (Conner and Hartl, 2004), the community and network-level effects are also a function of the scale of the interaction (Shuster et al., 2006; Lau et al., 2017). Second, heritability of network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted by genetic identity. Thus, variation in foundation species traits in space and time create variation in ecological networks that influences evolutionary dynamics via shifts in ecological dynamics, such as population demographics and interactions (Guimarães, 2020).

An important implication of this latter point is that intraspecific variation in a foundation species inherently creates variation in network structure, whether or not there are feedbacks from the foundation species to the associated organisms, as suggested previously by Lau et al. (2016a). Thus, the differential survival and performance of individual tree genotypes will simultaneously result in selection occurring on the lichen community and network structure that it supports. Although previous studies have examined aspects of ecological 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

325 (Maliet et al., 2020), even though recent syntheses have pointed to the importance of processes operating
326 across scales of organization (Guimarães, 2020).

327 **Network Structure and Scaling**

328 Our study demonstrates that the localized environmental differences determined by the genetic variation
329 within a single tree species can not only impact community composition, as repeatedly demonstrated in
330 other community genetics studies (Whitham et al., 2006; Des Roches et al., 2018), but also shape the
331 structure of interactions among individuals. Some network structures are likely to be more stable, either
332 in response to disturbance or via self-organized dynamics. For example, centralized networks, although
333 more efficient, are theorized to be more susceptible to targeted “attacks” in the terminology of defense
334 networks. As mentioned previously, one class of networks that are theorized to have amplifying effects on
335 networks have centralized “star” shapes with one or a few species at the center and radiating interactions
336 out from the central core (Lieberman et al., 2005). This is structurally what we have observed with the
337 networks that tend to occur on some of the genotypes in our study, i.e., the more centralized networks.
338 It is likely that these networks could function as hot-spots of evolutionary dynamics resulting from the
339 amplifying effect of the centralized network structure found on that tree genotype, as multiple studies
340 have found significant impacts of the removal of foundation species in different systems (Keith et al.,
341 2017; Des Roches et al., 2018).

342 Game theoretic applications to ecological networks provide a theoretical basis that relates to the
343 heritability of network centralization found in the present study. Although developed at the population
344 scale, this theory could be applied at the community scale as well (Lieberman et al., 2005). One seemingly
345 useful direction is the classification of networks into two general categories, rooted and cyclic, in which
346 rooted networks have interactions in which evolutionary effects emanate from one or multiple origins but
347 these effects do not have feedbacks to the origin, whereas cyclic networks contain feedbacks to one or
348 more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in the context of IIGE
349 theory (Whitham et al., 2020). As we do not have an estimate of the effect of the lichen at the larger scale
350 of the fitness of the tree they occur on, we can not determine whether the lichen networks in this system
351 are cyclic or not. In terrestrial ecosystems, lichens play important ecological roles, such as substrate
352 stabilization (Root et al., 2011) and nitrogen fixation (Nelson et al., 2018). Some epiphytic lichens can
353 have demonstrable effects on the availability of nutrients for the trees that are associated with (Norby
354 and Siga, 1989). Although none of the lichens the present study’s system is known to fix nitrogen, it is
355 possible that they might add micro-nutrients or provide some other unobserved benefit to their host trees.

356 Elucidating the presence of and quantifying such feedbacks would permit the determination of the
357 cyclic nature evolutionary dynamics. If there are positive effects of lichens on host trees that might
358 increase their ability to respond to environmental stress, then selection could enhance tree performance
359 and trees with superior communities are more likely to survive. Gehring et al. (2014, 2017) showed this
360 with ectomycorrhizal communities in which trees with superior mutualist communities were more likely
361 to survive drought and community evolution occurred (Whitham et al., 2020). However, such feedbacks to
362 the higher level of the foundation species are not a requirement for evolution, and, regardless of whether
363 networks are rooted (no feedbacks) or cyclic (feedbacks present), selection at the community level leading
364 to evolution can still occur. Specifically within the context of the current study, even if lichens and their
365 interactions do not feed back to affect the performance and ultimate fitness of the tree on which they
366 reside, non-random death of trees, such as those observed for drought in arid systems Sthultz et al. (2009);
367 Gehring et al. (2017), can still result in selection at the community level and evolution. For example,
368 when a tree dies from some event (e.g., a drought, fire, storm, etc.), its lichen network is selected against
369 while intact networks persist on other trees that survive this selection event.

370 The importance of the scale of network organization to create hierarchical structure (Guimarães, 2020)
371 and the potential for foundation species to create this structure in the vast majority of ecosystems (Ellison
372 et al., 2005; Whitham et al., 2006) suggests that future work would be aided by determining species
373 with large differences in body-size and longevity. Such differences are likely contributing to interaction
374 network structure (e.g., modules and centralized species). Many ecological network studies that have an
375 evolutionary context have focused on asymmetry (e.g., nestedness) and the quantification of its structure
376 in communities (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson,
377 2013). Although there is growing evidence that the nestedness of mutualistic networks is not necessarily
378 the result of selection for systems-level properties but could be either the numerical result 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 ecosystems (Valverde et al., 2018), the findings of these studies have generally supported the hypothesis that nestedness (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 that modularity contributes to the stabilization of antagonistic networks (Elias et al., 2013; Grilli et al., 2016). We were not able to examine nestedness or modularity of the lichen networks in the current study, as metrics for analyzing weighted, directed *and* signed networks could not be found. Future network theoretic developments will hopefully produce the appropriate metrics to conduct these analyses.

Community Composition and Quantifying Network Structure

Our findings point to the importance of quantifying interactions and not simply using community composition as a proxy. We did not observe compositional differences using the same data from which the lichen networks were derived. Thus, if we only had analyzed the composition data, we would have concluded no response of the lichen community to tree genotype, even though the interactions among lichen species vary among genotypes. Community composition of lichens has previously been observed to be different among tree genotypes in the same experimental garden (Lamit et al., 2011, 2015b). The different results observed in the present study is likely a result of differences in lichen quantification and the tree genotypes observed leading to overall higher abundances of observed lichens to assure the possibility of observing lichen interactions. Thus, the findings of the current study do not negate the previous study, as the quantification methods were different for community composition, but they do support the conclusion that composition is not a proxy for interactions in complex communities.

This is a concern, as such differences in network structure could occur without observable differences in species richness or community composition, which has been the primary focus of the majority of community genetics studies (Whitham et al., 2020). It is possible that these underlying differences in interactions among lichens could lead to differences in community composition at a future point in time via their effects on species abundances (Shuster et al., 2006); however, this is not needed for evolutionary dynamics to occur via selection that produces shifts in trait distributions without shifting species abundance distributions, which is possible under stabilizing, disruptive and directional selection (Conner and Hartl, 2004). Thus, it is imperative that further community genetics research assess or at least be aware of the potential effects of variation in interactions and not just observe species abundances, otherwise community level genetic effects may be underestimated, especially when cumulative interaction effects are taken into account (Borrett et al., 2007, 2010). Furthermore, the demonstration of the heritability of interaction networks, without significant differences in community composition, provides clear empirical evidence that IIGEs need to encompass 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). Such a synthesis necessitates a much greater effort than can be afforded in this paper. However, we recommend continued focus on foundation species, which are by definition “central” within the system of interactions and their direct and indirect effects should generally be greater than other species (Ellison et al., 2005). Thus, when the more centralized (foundation) species have genetically based interactions, genetic effects will tend to be propagated and possibly magnified in the community. Identifying central species the modules of species that they interact with provides a promising in-road to understanding ecological complexity, as the presence of asymmetries in ecosystems, such as hierarchy created by foundation species via differences in body size and/or life-history strategies, tend to create directionality in both ecological and evolutionary dynamics (Ellison et al., 2005; Bascompte et al., 2006; Whitham et al., 2020; Guimarães, 2020).

Conclusion

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

433 similarity and metrics of network structure tended to be more similar on trees of the same genotype.
434 Second, the genetically based trait, bark roughness, was observed to affect network variation, largely
435 via shifts in positive in-coming and out-going interactions. Although bark roughness has been shown
436 previously to be an important tree trait influencing bark lichens (Lamit et al., 2015b), this is the first
437 demonstration of a link from plant genetics to lichen network structure via this trait. As heritable variation
438 is the raw material for natural selection to act upon, a genetic basis for interaction network structure
439 indicates that conserving genetic variation is important to consider in efforts to restore or preserve complex
440 species interactions and their associated ecosystem functions (Whitham et al., 2012; Evans et al., 2013;
441 Whitham et al., 2020). Network modeling and analysis will provide useful tools for the identification of
442 species within network modules that are most important to study in systems where little is known about
443 the natural history of organisms in an ecosystem. Collectively, such investigations will bring us closer to
444 understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species
445 in complex communities (Darwin, 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) Photos showing lichen species observed, respectively: *Xanthomendoza montana*, *Candelariella subdeflexa*, *Rinodina freyi*, *Athallia holocarpa*, *Physcia adscendens*, *Physciella melanachra*, *Physcia undulata* and *Myriolecis hagenii*. Photo Credits: L.J. Lamit (B-D) and R. Reese Næsborg (E-I).

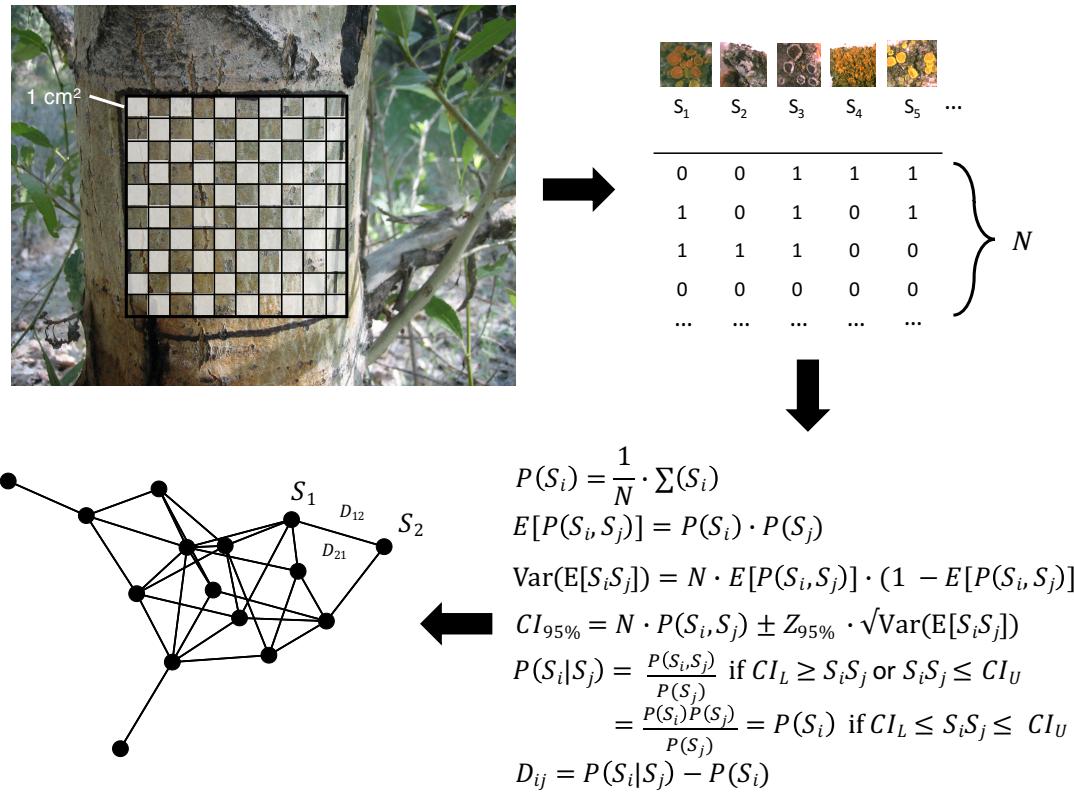


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm² cells within a 100 cm² grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded 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 .

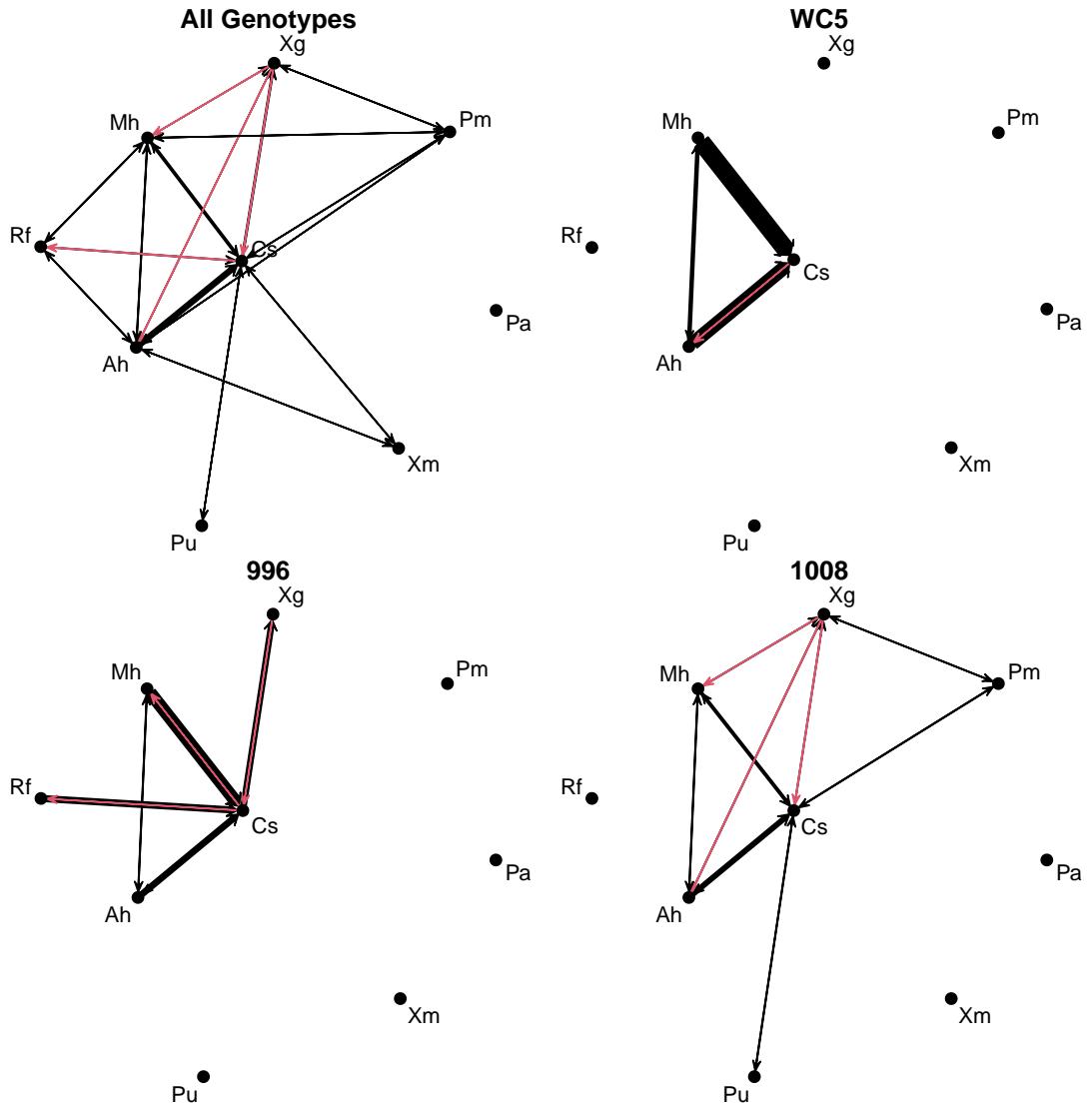


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species, which are scaled by their magnitude. Species names are abbreviated by the first letter of the genus and specific epithet: Ah = *Athallia holocarpa*, Cs = *Candelariella subdeflexa*, Mh = *Myriolecis hagenii*, Rf = *Rinodina freyi*, Pa = *Physcia adscendens*, Pm = *Physciella melanchra*, Pu = *Physcia undulata*, Xg = *Xanthomendoza galericulata*, Xm = *Xanthomendoza montana*. 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.

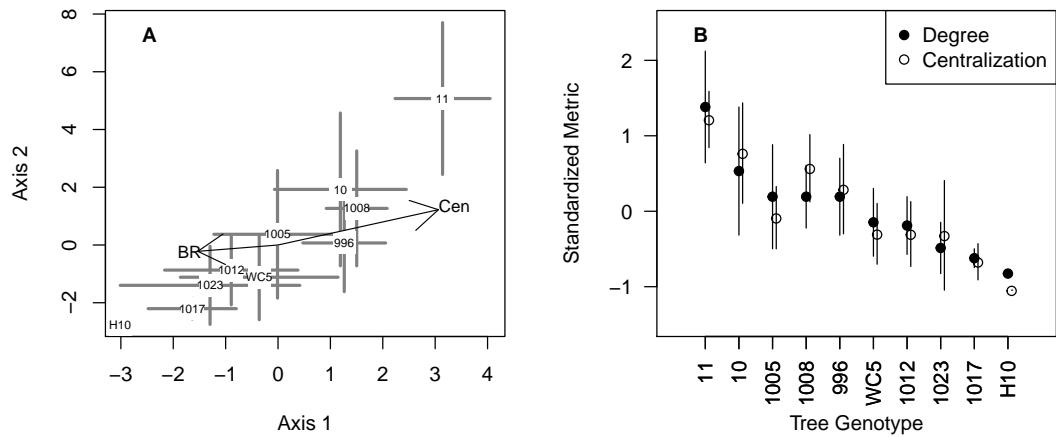


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated networks. 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.

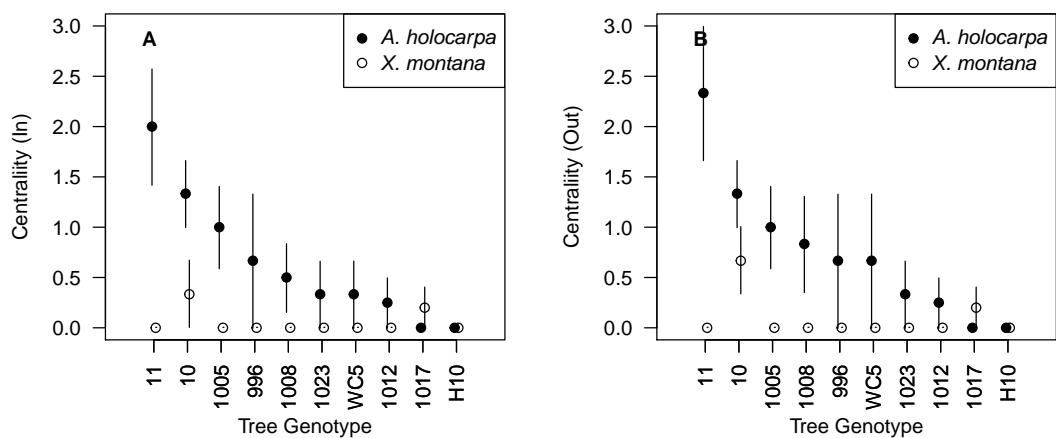


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *A. holocarpa* and *X. montana*. *Athallia holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

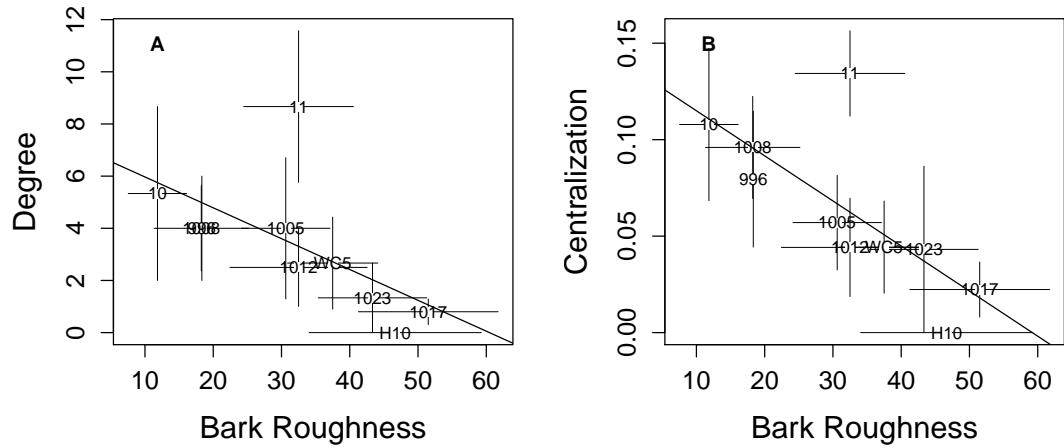


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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