

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

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ABSTRACT

Biological evolution occurs in ecosystems whereby natural selection defines the structure of ecological networks. Therefore, elucidating the genetic basis to ecological network structure is fundamental to understanding evolution. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that quantified the contribution of phenotypic variation to heritable variation in network structure. To examine this, in a 20+ year old 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 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 by lichen network similarity ($R^2 = 0.26$). These results support a mechanistic, genetic pathway from variation in a heritable tree trait to ecological network structure and demonstrate that evolution can act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks. Given that network structure can influence system-wide stability and resilience, our findings have important implications for how evolution acts in ecosystems.

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

21 **INTRODUCTION**

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

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

its fungal community and with increased drought the community phenotype has changed over time. Also, in an antagonistic interaction context, Busby et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods in a common garden, the impacts of these strong interactors results in a different and diminished community of arthropods relative to control trees. This effect was dependent on the hybrid cross-type of the tree and was, therefore, determined by tree genetics. These examples collectively support the possibility that selection acting on the tree may alter the network structure of associated communities in which different networks of communities are most likely to survive pathogen outbreaks. Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative fitness of the tree), selection at the level of the tree population or its community, or both, can change network structure and thereby alter community dynamics (Whitham et al., 2020).

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

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of tree associated lichens. Using a long-term (20+ years), common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001). We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (Winfrey et al., 2011; Zytynska et al., 2011). Applying a probability-theory based network modeling approach (Araújo et al., 2011), we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks via several network metrics that measure different aspects of network structure at the scale

of individual species (i.e., nodes) or the entire network observed on each tree genotype. Given the potential importance of focal or “central” nodes (e.g., species) for determining network dynamics (Lieberman et al., 2005), we focused on network metrics that measure centrality for individual species and centralization for whole networks. Both of these metrics measure how much a species is connected in the network relative to other species. As there is a preponderance of evidence that in natural systems evolution occurs in communities comprised of networks of interacting species (Lau et al., 2016a; Keith et al., 2017; Thompson, 2013; Bascompte et al., 2006), we set out to test two hypotheses. First, per the community similarity rule (Bangert et al., 2006) and IIGE theory (Whitham et al., 2020), we hypothesize that trees of the same genotype (i.e., clones) will support more similar lichen interaction networks relative to less related genotypes. In other words, epiphytic lichen network structure is heritable, which can be calculated via comparisons of within and among group variation in network structure. Second, heritability of lichen network structure is the result of underlying phenotypic covariation in tree traits important to interactions between trees and lichens and among lichens. Evidence that such trait covariance generates variation in interactions among community members provides an intermediate genetics-based mechanism for the underlying factors determining lichen distribution and abundance. In combination, evaluating these two hypotheses is fundamental to understanding variation and dynamics of network structure and evolution.

MATERIALS AND METHODS

Study System

The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, in order to focus on intra-specific genetic variation we only sampled pure or advanced generation back-crosses of *P. angustifolia*. 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 lichens present in order to permit the construction of interaction networks.

Bark Lichen and Trait Observations

On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm² cells arrayed in a checkerboard pattern. Given the small size and sessile nature

of lichens, we were able to rapidly assess lichen interactions by quantifying thalli of different species occurring in close proximity. Sampling was restricted to the northern aspect of the trunk to maximize the abundance of lichen and control for the effect of trunk aspect. Two adjacent 100 cm^2 quadrats centered at 50 cm and 95 cm from ground level were sampled (Fig 1). The observed lichen community included (abbreviations are given for species present in study): Ah = *Athallia holocarpa*, Cs = *Candelariella subdeflexa*, Mh = *Myriolecis hagenii*, Rf = *Rinodina freyi*, Pa = *Physcia adscendens*, Pm = *Physciella melanochra*, Pu = *Physcia undulata*, Xg = *Xanthomendoza galericulata*, Xm = *X. montana*. Several other species were not observed in the present study but are known to occur in this region: *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanohalea subolivacea*, *Melanohalea elegantula*.

The cell size and checkerboard sampling pattern was chosen to isolate the individuals in each cell. *Xanthomendoza galericulata* thallus size in this 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). 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 is the percent of 1 cm^2 cells with rough bark. In addition to bark roughness, 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 data from dried bark samples collected in XXXX L JL INPUT. Samples were soaked in XX ml of XXX water for XX hours and pH was measured using a XX L JL INPUT.

Lichen Network Modeling

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

We then applied an analytical procedure to remove non-significant links between species. This procedure determines if the joint probability of a species pair (i.e., $P(S_i, S_j)$) is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as

200 $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences
 201 $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of
 202 each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the
 203 expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability
 204 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
 205 the observed number of co-occurrence falls outside of the confidence interval, the
 206 joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual
 207 probabilities (i.e., $P(S_i)P(S_j)$), and the conditional probability reduces to the individual
 208 probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair
 209 falls outside the confidence interval, the probability that the observation of one species
 210 given the other is no different than simply observing that species alone. This enables us
 211 to remove links from a given network by re-scaling the resulting conditional probabilities
 212 through subtraction of the individual probabilities from the conditional probabilities (i.e.,
 213 how different the conditional probability is from the independent probability), which
 214 makes any species with a non-significant conditional probability zero.

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

229 Analyses, Software and Data

230 To quantify the structural variation of lichen networks we calculated several metrics at
 231 both the level of node and whole networks. Although there are many other metrics, for
 232 the sake of simplicity we focus on a subset that represent the primary interesting features
 233 of network structure (see Lau et al. (2017)). We calculated the number of interactions or
 234 "links" in each network (degree), which provides a measure of the size of the network
 235 (Lau et al., 2016a; Borrett and Lau, 2014). We also calculated the centralization of each
 236 network using Freeman's centrality, which measures the evenness of the distribution of
 237 interactions among the species in the network, using the `sna` package (Butts, 2019).
 238 In a network with low centralization species have similar strengths and numbers of
 239 interactions. A network with high centralization tends to have one or small number
 240 of species that interact with other species. We used a related function to calculate
 241 the centrality of each species (i.e., node level centrality) in each network as well. To
 242 calculate separate metrics for positive and negative links, as the networks contained not
 243 only positive and negative connections but also directional connections (both in-coming
 244 and out-going), we calculated the same network metrics for all combinations of these

245 types of connections using recently developed methods for signed, weighted and directed
246 networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch, 2020).

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

255 For multivariate response variables, such as lichen community composition and
256 network structure, we used distance based multivariate statistical approaches, including
257 Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify
258 the similarity of lichen networks among individual trees, we calculated the pairwise
259 Euclidean distance of the **D** interaction matrices among all pairs of trees. For visualiza-
260 tion of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS)
261 (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of these multi-
262 variate responses and fitted vectors for continuous predictor variables to the ordinated
263 values (Oksanen et al., 2019). Using random initial configurations with a maximum
264 of 500 iterations and a change in stress threshold of less than 10^{-12} . This was re-
265 peated for one to four dimension configurations, and the configuration with the lowest
266 dimensionality and unexplained variation less than 10% was selected.

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

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

275 RESULTS

276 In support of our first hypotheses, we found that tree genotype influenced lichen net-
277 work structure and that multiple lichen network metrics were heritable. Tree genotype
278 significantly predicted the structural similarity of lichen networks and, overall, network-
279 level metrics responded significantly to tree genotype, including network degree and
280 centralization including both in-coming and out-going links or when separated into
281 in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive links
282 also showed a significant effect of tree genotype, including positive degree and positive
283 in-going centralization. Metrics calculated with negative links were not significant,
284 including degree (negative) and both in-coming (negative) and out-going centralization
285 (negative).

286 The genetic response of network centralization was driven by variation in *Athallia*
287 *holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$,
288 $p\text{-value} < 0.0001$). *Athallia holocarpa* centrality was the main species to exhibit a

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.

289 significant response to tree genotype in terms of positive centrality for both the in-
 290 incoming ($RLRT = 3.61, H^2 = 0.32, p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13, H^2$
 291 = 0.30, $p\text{-value} = 0.0327$) perspectives, but not for either negative centrality metrics
 292 in-coming ($RLRT = 0, H^2 = 0, p\text{-value} = 1$) or out-going ($RLRT = 0, H^2 = 0, p\text{-value} =$
 293 0.4543). None of the other species' centralities showed a genotypic response (Supporting
 294 Information, Fig. 2) with the exception of *X. montana* ($RLRT = 2.92, H^2 = 0.32, p\text{-value}$
 295 = 0.0375); however, the centrality of *X. montana* was much lower overall relative to *A.*
 296 *holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes
 297 (Fig. 5).

298 In support of our second hypothesis, analysis of trait covariation revealed that geno-
 299 type indirectly influenced lichen network centralization via genetically based variation in
 300 bark roughness. The percent cover of rough bark ($RLRT = 4.8526, H^2 = 0.3221, p\text{-value}$
 301 = 0.0113) and condensed tannins ($RLRT = 3.0522, H^2 = 0.3205, p\text{-value} = 0.0343$)
 302 both displayed significant responses to tree genotype. None of the other bark traits, pH
 303 ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT = 0.0000,$
 304 $H^2 = 0.0000, p\text{-value} = 1.0000$), showed a significant response to tree genotype and
 305 none other than bark roughness was correlated with network similarity (Table 2); there-
 306 fore, we focused our subsequent analyses on the indirect effect of genotype on lichen
 307 network structure via bark roughness. We found that bark roughness was significantly
 308 correlated with network similarity and other lichen network metrics, including negative
 309 correlations with overall network degree ($df = 35, t = -2.13, r = -0.34, p\text{-value} = 0.04$)
 310 and centralization ($df = 35, t = -2.52, r = -0.39, p\text{-value} = 0.02$). In other words, trees
 311 with more similar levels of bark roughness tended to have lichen interaction networks
 312 with similar structure. To quantify the genetic bases of this effect of bark roughness on
 313 network structure, we used the residual values from regressions of network degree and
 314 centralization in tests of the effect of tree genotype and found no significant effect of tree
 315 genotype for either degree ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or centralization
 316 ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$), suggesting that the observed relationship
 317 between bark roughness and lichen network structure was largely genetically based
 318 (Fig. 6).

	df	SS	R ²	Pseudo-F	p-value
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

Table 2. PERMANOVA Pseudo-*F* Table of lichen network similarity response to bark traits.

DISCUSSION

We found support for both of our hypotheses. First, tree genotype influenced the network structure of lichen communities associated with narrowleaf cottonwoods in a riparian forest ecosystem. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *A. holocarpa*. Second, the genetically based trait, bark roughness, was observed to affect network variation, largely via shifts in positive in-coming and out-going interactions. Chemistry traits, whether genetically based (e.g., tannin concentration) or not, were not significantly correlated with lichen network structure. Bark roughness has been demonstrated previously to be under strong genetic control (Bdeir et al., 2017), and bark roughness has also been shown to be an important tree trait influencing bark lichens (Lamit et al., 2015b); however this is the first demonstration of a link from genetics to lichen network structure. As such, these results have important implications for the influence of genetically based variation in ecosystems with networks of interacting species.

Implications of Ecological Network Heritability

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

First, heritability of network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted by genetic identity. Variation in space and time create variation in ecological networks that influences evolutionary dynamics via shifts in ecological dynamics, such as population demographics

(Guimarães, 2020). Given that ecosystems are comprised of hundreds and thousands of species, each having a multitude of interactions, the potential to find traction for making predictions in the context of ecological, let alone evolutionary, dynamics seems daunting. The promise of predictability lies in the presence of asymmetries in ecosystems, such as hierarchy created by foundation species via differences in body size and/or life-history strategies (Ellison et al., 2005). The second is that 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).

Second, even if the composition of the communities is the same among individuals and genotypes, interactions may not be. We didn't observe compositional differences using the same data from which the lichen networks were derived. If we only had our composition dataset from this study, we would have concluded no response of the lichen community to tree genotype, even though the underlying interactions among lichen species does vary among genotypes. As such differences in network structure could occur without observable differences in species richness or community composition, which have been the primary focus of almost all previous community genetics studies (Des Roches et al., 2018). 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. The previous study used a visual percent cover estimation, unlike the current study, which observed lichens at the scale of 1 cm² cells, which could over-estimate cover depending on the frequency at which actual thallus size was less than 1 cm², as well as both the northern and southern aspects of each tree. These differences do not negate the findings of either study. The present study's finding of differences in network structure without significant compositional differences points to the importance of quantifying how network structure changes in response to genetic variation in order to fully understand evolutionary dynamics in complex communities. Having not observed a compositional effect of tree genotype without measuring the network structure could lead to the conclusion of no genetic effect on the community, even though differences in network structure are leading to altered, local evolutionary dynamics. 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 leads to shifts in trait distributions without shifting species abundance distributions, which is possible under stabilizing, disruptive and directional selection (Conner and Hartl, 2004), so long as the relative abundances of each species is imperceptibly changed. 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).

Furthermore, the demonstration of the heritability of interaction networks, without significant differences in community composition, provides clear empirical evidence that variation in network structure points to the need to expand IIGEs 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). Although such a synthesis necessitates a much greater effort than can be afforded in this paper, it is possible to point to several productive pathways forward. In terms of interaction networks, foundation species are relatively central within the system of interactions, that is their direct and/or indirect effects are greater than other species. So, when the more centralized (foundation) species have genetically based interactions, genetic effects will tend to be propagated and possibly magnified in the community. Here, we found that even though more abundant or more centralized (i.e., “important”) species were present in the community, their effects were not the main component responding to genetic effects. Considering the impact of network structure would be a productive path forward for the theoretical development and application of the IIGE concept.

Evolution and Genetically Based Network Structure

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

Intra-specific, genotypic diversity could be creating lichen metacommunities on individual trees that form interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily determined by another organism, these communities inherently form modules within the larger ecosystem, as they tend to interact more with each other than with other individuals (Lau et al., 2017). Our study demonstrates that the environmental differences determined by the genetic

443 variation within a single species can create differences that not only impact community
444 composition, as repeatedly demonstrated in other community genetics studies (Whitham
445 et al., 2006; Des Roches et al., 2018), but also the structure of interactions among
446 individuals within these modules. Some network structures are likely to be more stable,
447 either in response to disturbance or via self-organized dynamics. For example, central-
448 ized networks, although more efficient, are theorized to be more susceptible to targeted
449 “attacks” in the terminology of defense networks. As mentioned previously, one class
450 of networks that are theorized to have amplifying effects on networks have centralized
451 “star” shapes with one or a few species at the center and radiating interactions out from
452 the central core (Lieberman et al., 2005). This is structurally what we have observed
453 with the networks that tend to occur on some of the genotypes in our study, i.e., the
454 more centralized networks. It is likely that these networks could function as hot-spots
455 of evolutionary dynamics resulting from the amplifying effect the centralized network
456 structure found on that tree genotype, as multiple studies have found significant impacts
457 of the removal of foundation species in different systems (Keith et al., 2017; Des Roches
458 et al., 2018).

459 Ecological network studies have focused on asymmetry and the quantification of
460 its structure in communities. The impacts of asymmetry on evolution from community
461 dynamics have primarily produced qualitative discussion (Bascompte et al., 2006;
462 Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific
463 predictions can be found in applications of evolutionary game theory, and although
464 developed at the population scale, such theory can apply to communities (Lieberman
465 et al., 2005). One seemingly useful direction is the classification of networks into two
466 general categories, rooted and cyclic, in which rooted networks have interactions in
467 which evolutionary effects emanate from one or multiple origins but these effects do
468 not have feedbacks to the origin, whereas cyclic networks contain feedbacks to one or
469 more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in
470 the context of IIGE theory (Whitham et al., 2020). As we do not have an estimate of the
471 effect of the lichen on the fitness of the tree they occur on, we can not determine whether
472 the lichen networks in this system are cyclic or not. In terrestrial ecosystems, lichen
473 play important ecological roles, such as substrate stabilization (Root et al., 2011) and
474 nitrogen fixation (Nelson et al., 2018). Some epiphytic lichens can have demonstrable
475 effects on the availability of nutrients for the trees that they are associated with (Norby
476 and Sigal, 1989). Although none of the lichens the present study’s system is known to
477 fix nitrogen, it is possible that they might add micro-nutrients or provide some other
478 un-observed benefit to their host trees. Elucidating the presence of and quantifying
479 such feedbacks would allow for the determination of the cyclic nature and potential
480 evolutionary dynamics.

481 Since lichen individuals are multi-species complexes, there is also the potential
482 for evolutionary dynamics to shift within the context of the lichen symbiosis. There
483 is substantial evidence that lichen have served as the “cradle of symbiotic fungal
484 diversification” (Arnold et al., 2009) and recent research has shown significant net-
485 work structure of endolichenic fungi and lichen collected from across North America
486 (Chagnon et al., 2016). Analysis of the structure of ecological networks has generally
487 supported the conclusion that nestedness, or the degree to which species tend to inter-
488 act with similar subsets of the community, tends to promote stability in mutualistic,

489 primarily bipartite (i.e., two-mode), networks and modularity contributes to the stabi-
490 lization of antagonistic networks (Elias et al., 2013; Grilli et al., 2016). Although there
491 is growing evidence that the nestedness of mutualistic networks is not necessarily the
492 result of selection for systems-level properties that promote stability but could be either
493 product of asymptotic abundance distributions leading to uneven interaction frequencies
494 (Staniczenko et al., 2013) and/or a by-product of selection and divergence creating
495 network “spandrels” in ecosystems (Valverde et al., 2018), this does not preclude the
496 functional consequences of network structure but rather the developmental or evolu-
497 tionary processes that have produced the structure. In the present study, we did not
498 examine nestedness or modularity of the lichen networks as we could not find metrics for
499 analyzing networks that are not only weighted and directed but also signed. Hopefully
500 future network theoretic developments will make the appropriate metrics available to
501 conduct these analyses.

502 Conclusion

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

519 One possible path forward is for future work to extend the many previous community
520 genetics studies that have focused on sessile organisms, such as galling insects (Bailey
521 et al., 2005; Whitham et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith
522 et al., 2017), to quantify the frequency of these interactions in the context of the larger
523 community. This would provide an estimate of the relative impact of these focal, often
524 termed foundation, species. In addition, community genetics theory has only quantified
525 first order interactions, i.e., among pairs; therefore, indirect effects from higher order
526 interactions are not explicitly accounted for (Shuster et al., 2006; Whitham et al., 2012,
527 2020). Given that network structure could be influenced by genetic effects, assessing
528 higher order interactions could provide a path forward for theoretical advances (e.g.,
529 IIGEs) that could help with identifying important characteristics of sub-groups to focus
530 on in empirical studies. That is, the combined interactions of communities of interacting
531 species should be reflected in the differences of networks of individual plant genotypes
532 and how they might differ across a landscape in which selection pressures change in
533 response to local biotic and abiotic conditions, leading to the optimization of modules

under different selective pressures. Network modeling and analysis could prove useful for the identification of species within network modules that are most important to study in systems where little is known about the biology of the system. For example, in systems where background knowledge of the natural history of organisms is lacking, network analyses based on species occurrence and abundance direct researchers to species that could be focused on to best understand the dynamics of the system. Such investigations will bring us closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species 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) Close-up photos show the other lichen species observed, respectively: *Xanthomendoza montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Athallia holocarpa*, *Physcia adscendens*, *Physciella melanchra*, *Physcia undulata* and *Myriolecis hagenii*. Photo Credits: L.J. Lamit (B-D) and R. Reese Næsborg (E-I).

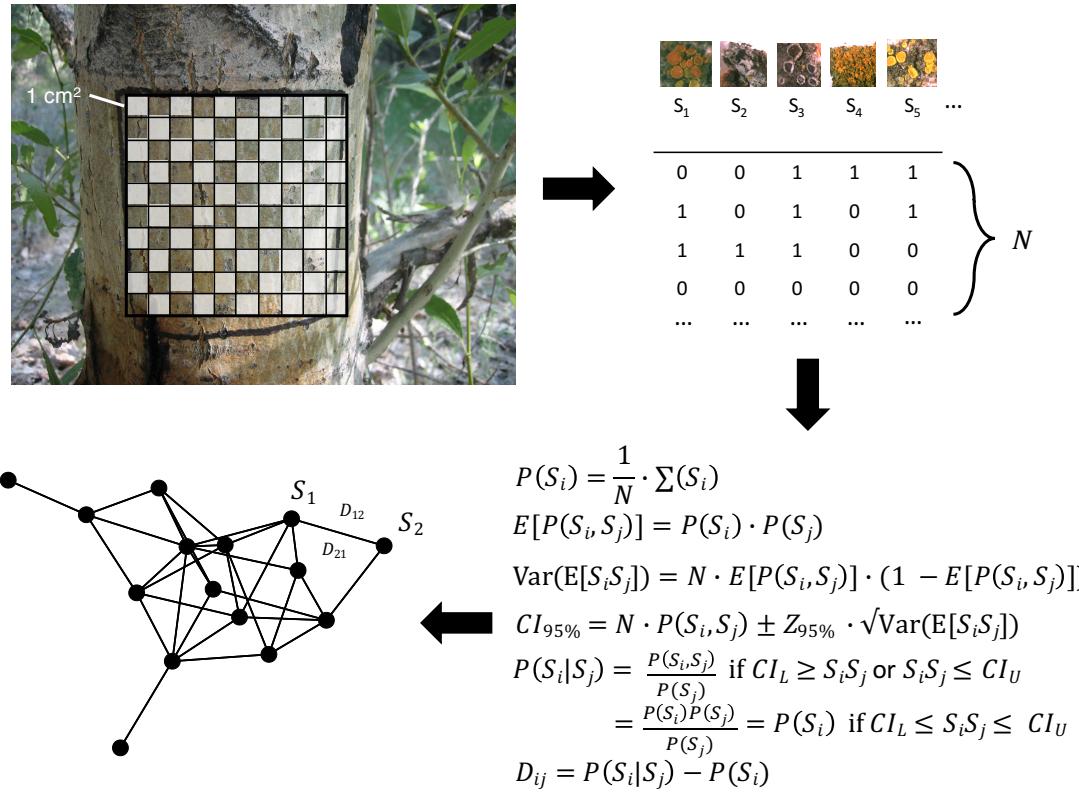


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded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

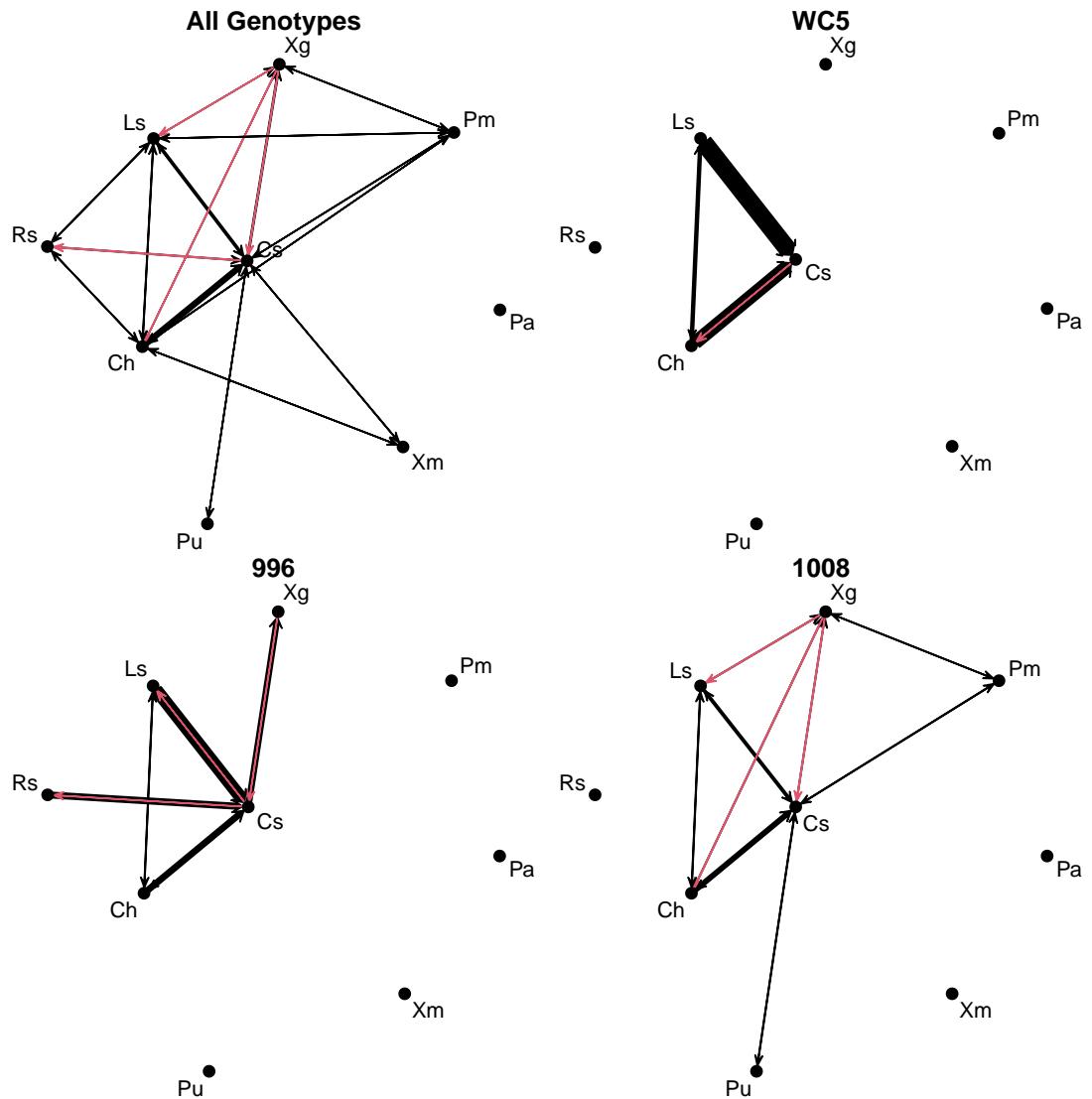


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species (abbreviated by the first letter of the genus and specific epithet), which are scaled by their magnitude. The sign of the interaction is indicative of greater (positive) or lesser (negative) paired occurrences than expected relative to the overall frequency of occurrence of each species. Ecologically, the links in the network are likely the product of multiple types of interactions (e.g. mutualism, parasitism, competition, facilitation) that could vary over both space and time.

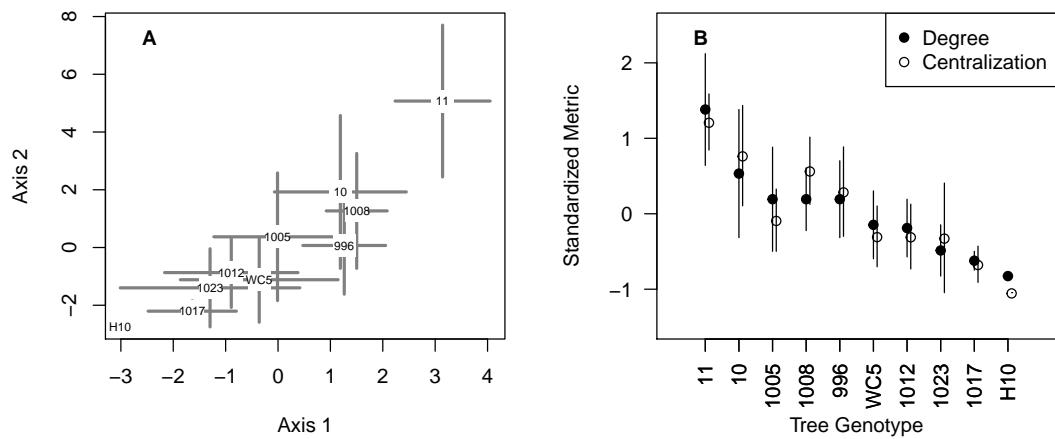


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated network similarity. B. Plot showing the standardized ($\frac{x-\bar{x}}{\sigma}$) means (± 1 S.E.) for the two of the genetically based lichen network metrics: overall degree (i.e., total number of links) and centralization, which is a measure of the dominance of one species in the network.

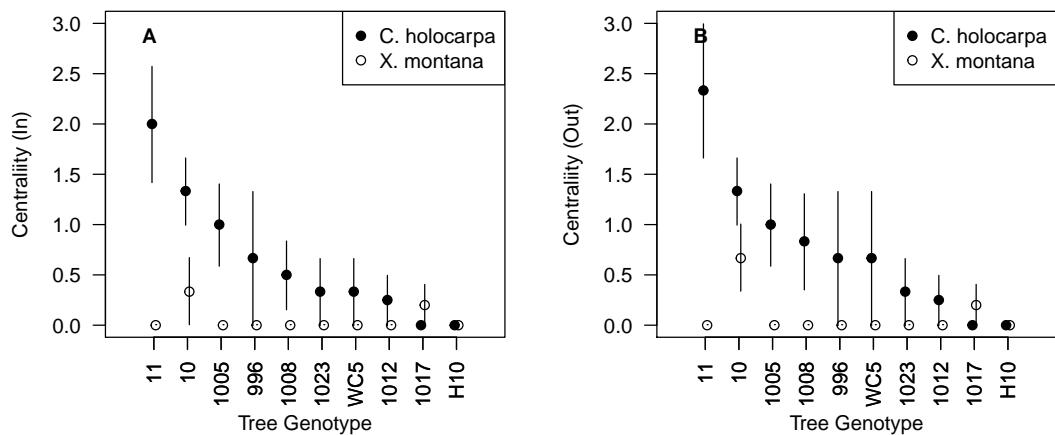


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *A. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

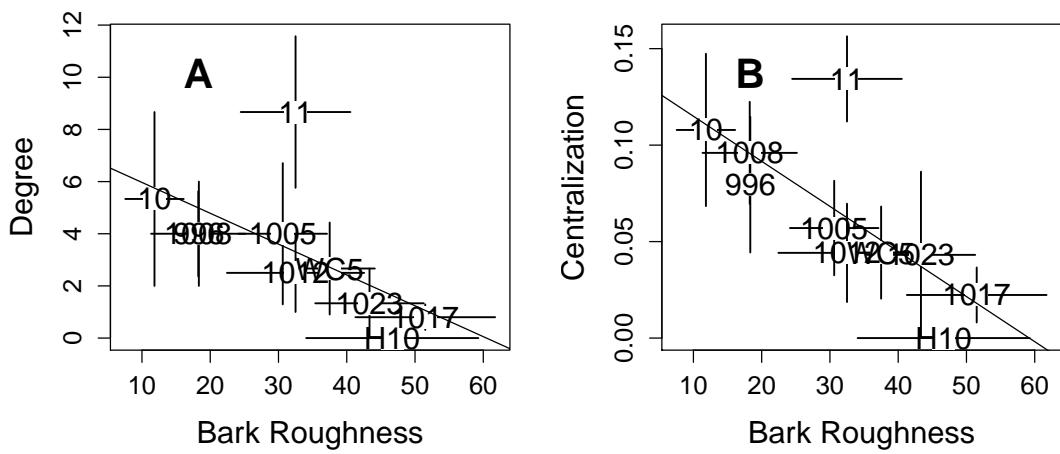


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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