

Genotypic variation in a foundation tree results in heritable ecological network structure of an associated community

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ABSTRACT

Biological evolution occurs in ecosystems whereby natural selection defines the structure of ecological networks. Therefore, elucidating the genetic basis to ecological network structure is fundamental to understanding evolution. Although previous work has demonstrated that genetic variation can influence food webs and trophic chains, we are unaware of a study that quantified the contribution of phenotypic variation to heritable variation in network structure. To examine this, in a 20+ year common garden we observed nine epiphytic lichen species associated with narrowleaf cottonwood (*Populus angustifolia*), a riparian ecosystem foundation species. We constructed and conducted genetic analyses of signed, weighted, directed lichen interaction networks. We found three primary results. First, genotype identity significantly predicted lichen network similarity; i.e., replicates of the same genotype supported more similar lichen networks than different genotypes. Second, broad sense heritability estimates showed that plant genotype explained network similarity ($H^2 = 0.41$), degree ($H^2 = 0.32$) and centralization ($H^2 = 0.33$). Third, of several tree phenotypic traits examined, bark roughness was both heritable ($H^2 = 0.32$) and significantly correlated with lichen network similarity ($R^2 = 0.26$). These results support a mechanistic, genetic pathway from variation in a heritable tree trait to ecological network structure and demonstrate that evolution can act at the community level to influence not only abundances of organisms but also interactions at the scale of entire networks. Given that network structure has determines system-wide stability and resilience, our findings have important implications for how evolution acts in ecosystems.

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

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) that in combination result in a multivariate functional trait phenotype Holeski et al. (2012) in which individual plant genotypes support different communities and ecosystem processes Bailey et al. (2009); Whitham et al. (2012). Recently, the importance of genetic variation in structuring ecological systems was reviewed, and not only were many instances of strong genetic effects found in many ecosystems but the effect of intraspecific variation was at times greater than inter-specific variation Des Roches et al. (2018). There is now evidence to support that selection, acting on this heritable variation, tends to occur among groups of species Wade (2007) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly Crutsinger (2016) and species interactions Whitham et al. (2006); Bailey et al. (2009); Moya-Laraño (2011), which shape the structure of ecological interaction networks Rezende et al. (2007); Guimarães et al. (2007); Gómez et al. (2009).

The development of interspecific indirect genetic effects (IIGE) theory Shuster et al. (2006) in evolutionary biology points to the importance of studying the genetic basis of interaction network structure because genetic based differences in network structure among individuals can be acted upon by natural selection when there are fitness consequences of different networks of IIGEs that can result in community evolution Whitham et al. (2020). For example, although the analysis was of abundances rather than interaction networks, (Gehring et al., 2014, 2017) found that the mycorrhizal communities on the roots of drought tolerant and intolerant trees are dominated by different orders of ectomycorrhizal fungal mutualists that also differ in the benefits they provide that enhance tree performance. Because drought tolerant genotypes 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. Thus, 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 on tree, community or both can change network structure Whitham et al. (2020) and thereby alter community dynamics. Network theory and evidence from empirical studies in ecology have demonstrated that indirect effects can lead to self-organization, producing sign-changing, amplifying and/or dampening effects Newman (2006); Sole and Bascompte (2006), and evolutionary applications have demonstrated that indirect effects of interactions among species can lead to network structures that

amplify or dampen the effects of selection, such as the formation of star-like structures in which there is a “central” species or group of species that interact with other, peripheral species, can amplify selection events Lieberman et al. (2005).

In this context, the “genetic similarity rule” 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 individuals genotypes that are more genetically similar will tend to have similar phytochemical traits and thus tend to have similar interactions with other species than individuals that are less similar. However, 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. (2015); 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; Zytnyska et al., 2011). Applying a probability-theory based network modeling approach, 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 measures different aspects of network structure at the scale of individual species (i.e., nodes) or the entire network observed on each tree genotype. In particular, we focus the metric of centrality for individual species and centralization for whole networks, which measures how much a species is connected in the network relative to other species. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species Lau et al. (2015); Keith et al. (2017); Thompson (2013); Bascompte et al. (2006). More specifically, based on community genetics theory, particularly the community similarity rule (Bangert et al., 2006), we hypothesize that trees will co-vary in functional phenotypic traits, such as bark roughness and chemical composition, and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. If correct, we expect to

find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks.

MATERIALS AND METHODS

Study System

The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled. Bark lichens have been intensively sampled in this system and provide an ideal community in which to observe and model interaction networks, as their sessile nature permits accurate identification of individuals and their highly localized, direct contact interactions and slow population turnover rates facilitate the assessment of interactions among lichen species on individual trees Lamit et al. (2011).

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.

Bark Lichen and Trait Observations

On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm² cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens, we were able to rapidly assess lichen interactions by quantifying thalli in close contact. Sampling was restricted to the northern aspect of the trunk to maximize the abundance of lichen and control for the effect of trunk aspect. Two adjacent 100 cm² quadrats centered at 50 cm and 95 cm from ground level were sampled (Fig 1 A and B). The observed lichen community included (abbreviations are given for species present in study): Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella melanchra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were not observed in the present study but are known to occur in this region: *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegantula*.

The cell size and checkerboard sampling pattern was chosen to isolate the individuals in each cell. In a previous survey of lichen thallus size in this common garden, we had observed a median thallus size of 0.12 ± 0.001 cm² (1 S.E.) (see Supporting Information). 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 cm² cells with rough bark. In addition to bark roughness, we also measured several bark chemistry traits by taking

bark samples immediately adjacent to each quadrat using the methods of (Lamit et al., 2011): including, the concentration of condensed tannins, pH and carbon and nitrogen concentrations and pH.

Lichen Network Modeling and Analysis

For each tree, repeated observations of lichen were made in order to construct replicated interaction networks for each genotype. We conducted a modified sampling procedure originally developed by (Lamit et al., 2015b) with the addition that we quantified the presence of lichen in the 1 cm² cells on individual trees of *P. angustifolia*. Unipartite networks were generated using the conditional probabilities of each species pair, i.e. the probability of observing one species given an observation of another species $P(S_i|S_j)$, based on the method developed by (Araújo et al., 2011). To calculate conditional probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species and their co-occurrences. We were then able to calculate the conditional probabilities of each species pair as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, based on the axioms of probability. This yielded a matrix that could possibly be asymmetric, i.e. $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Another important property of this matrix is that the diagonal, $P(S_i|S_i)$, was equal to one for all species present and zero for species that were not observed in any cell.

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

The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as one species' impact on another with zero being no effect and values less than or greater than zero being negative and positive effects, respectively. Here, we will refer to \mathbf{D} as a signed, weighted interaction matrix. As such, \mathbf{D} has the properties that it can be asymmetric (i.e. D_{ij} does not necessarily equal D_{ji}) and it scales between -1 and 1, and, therefore, does not have the mathematical properties of a probabilistic network Poisot et al. (2016). Also, as the method does not track individuals within species and interactions such as competitive exclusion or facilitation within species would result in the same species being observed.

Therefore, the results of intra-specific interactions always results in the same species being observed and a resulting $D_{ii} = 0$.

Network Metrics

To quantify the structural variation of lichen networks we calculated several metrics at both the node and whole-network level. For individual nodes (i.e. species) in each network, we calculated both the degree and the Freeman's centrality Butts (2019). We also calculated two similar global network metrics: degree and centralization. The first was network degree, which is a count of the total number of links in a network. 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 in each network, accounting for differences in sign through the application of recently developed metrics that incorporate sign information from signed, weighted, directed networks Everett and Borgatti (2014). Although there are many more possible network metrics that could have been examined, we chose to focus on a restricted set for the sake of clarity. In addition, degree and centrality form the basis of many other network metrics.

Statistical Analyses, Software and Data

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

For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the \mathbf{D} interaction matrices among all pairs of trees.

For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) Goslee and Urban (2007) to produce dimensionally reduced ordinations of these multi-variate responses and fitted vectors for continuous predictor variables to the ordinated values Oksanen et al. (2019). Using random initial configurations with a maximum of 500 iterations and a change in stress threshold of less than 10^{-12} . Final configurations has the lowest stress with at most a stress level of 0.10.

For each network, we also calculated metrics that measure different structural aspects. Although there are many other metrics, for the sake of simplicity we focus on a subset that represent several interesting features of network structure (see (Lau et al., 2017)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (Lau et al., 2015; Borrett and Lau, 2014). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network Butts (2019). In a network with a low level of centralization species have similar amount of interaction in

the network, while a network with a high level of centralization tends to have one or small number of species that interact with other species. We used a related function to calculate the centrality of each species (i.e. node level centrality) in each network as well. To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences Everett and Borgatti (2014) using the `signnet` package Schoch (2020).

For all tests where genotype was used as a predictor, we quantified the heritability of the response variable. Because the trees in the garden were clonal replicates of each genotype, we calculated broad-sense heritability, which is the genotypic variance divided by the total phenotypic variance Conner and Hartl (2004). This can be interpreted as a measure of the phenotypic variance due to genotypic variation. We also apply this to the community genetics context as the variance in *extended* phenotypic variance due to genotypic variation Whitham et al. (2006, 2012); Crutsinger (2016). For the multivariate analyses, where we employ PERMANOVA, we followed the methods of (Shuster et al., 2006) to adjust the degrees of freedom for unbalanced genotype replicates.

All code and data for the project are openly available online. Code and data are available at github.com/ecgen/comgen. The project is also archived via Zenodo at zenodo.com/doi/XXXXXX. All analyses were conducted using the programming language R version 3.6.1 (R Development Core Team 2019).

RESULTS

Tree genotype influenced lichen network structure and multiple lichen network metrics were heritable. Tree genotype significantly predicted the structural similarity of lichen networks (PERMANOVA: Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$) (Fig. 4). Overall network level metrics responded significantly to tree genotype (Table 1), including network degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} = 0.0255$) and centralization including both in-coming and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} = 0.0184$) or when separated into in-coming only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} = 0.0190$) or out-going only ($RLRT = 3.8615$, $H^2 = 0.3193$, $p\text{-value} = 0.0205$). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree ($RLRT = 3.6925$, $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} = 0.0142$). Metrics calculated with negative links were not significant, including degree (negative) ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$) and both in-coming (negative) ($RLRT = 0.3304$, $H^2 = 0.1057$, $p\text{-value} = 0.2508$) and out-going centralization (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$, $p\text{-value} = 0.3446$).

The genetic response of network centralization was driven by variation in *Caloplaca holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$, $p\text{-value} < 0.0001$). *Caloplaca holocarpa* centrality was the main species to exhibit a significant response to tree genotype in terms of positive centrality for both the in-coming ($RLRT = 3.61$, $H^2 = 0.32$, $p\text{-value} = 0.0240$) and out-going ($RLRT = 3.13$, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives, but not for either negative centrality metrics in-coming ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of the other species' centralities showed a genotypic response (Supplementary Table ??) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} = 0.0375$);

	response	df	statistic	H2	p-value
Lichen Network Similarity		9	3.5821	0.41	0.0537
Degree			3.5175	0.32	0.0255
Degree (positive)			3.6925	0.32	0.0229
Degree (negative)			0.0327	0.03	0.3859
Centralization			4.0444	0.33	0.0184
Centralization In-Degree			4.4812	0.35	0.0142
Centralization In-Degree (positive)			3.9852	0.33	0.0190
Centralization In-Degree (negative)			0.3304	0.11	0.2508
Centralization Out-Degree			3.8615	0.32	0.0205
Centralization Out-Degree (positive)			3.5585	0.31	0.0248
Centralization Out-Degree (negative)			0.0862	0.05	0.3446

Table 1. Genotypic effects on the associated lichen network structure.

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

Add transformations of variables to methods.

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} = 0.0113$) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, $p\text{-value} = 0.0343$) both displayed significant responses to tree genotype. None of the other bark traits, pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and none other than bark roughness was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen network structure via bark roughness. We found that bark roughness was significantly correlated with network similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, $p\text{-value} = 0.0096$) and other lichen network metrics, including negative correlations with overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$, $p\text{-value} = 0.04$) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees with more similar levels of bark roughness tended to have lichen interaction networks with similar structure. To quantify the genetic bases of this effect of bark roughness on network structure, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

DISCUSSION

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest. 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 *C. holocarpa*. The genetically based trait,

	df	SumOfSqs	R2	F	Pr(>F)
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

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

bark roughness, was the only trait observed to effect network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control Bdeir et al. (2017), and bark roughness has also previously 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 genes to lichen network structure. As such these results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species. This work is important because it provides a mechanistic basis for understanding how community network theory is intimately associated with the evolutionary process and how human alterations of the environment (e.g., climate change, invasive species, pollution) may have cascading, indirect effects that alter network structure and evolution.

Implications of the Heritability of Interaction Network Structure

We found significant heritability of lichen interaction network structure, and, 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 Barbour et al. (2019) and forest stand-level interaction network structure Lau et al. (2016); 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 ave pointed to the importance of processes operating across scales of organization Guimarães (2020). There are several important functional ramifications of genetically based variation in network structure. First, intra-specific diversity could be creating lichen interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily the 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 variation within a single species can create differences that not only impacts community composition, as repeatedly demonstrated in other community genetics studies Whitham et al. (2006); Des Roches et al. (2018), but also the structure of interactions among individuals within these modules. Some network structures are likely to be more

stable, either in response to disturbance or via self-organized dynamics. For example, centralized networks, although more efficient, are theorized to be more susceptible to targeted attacks on the center of the network. For example, consider a forest with two genotypes that support lichen communities that are similar in total abundances of each species but differ in terms of the structure. Extensions of game theory to evolutionary biology have demonstrated that network structure can lead to variation in evolutionary dynamics. Some structures tend toward dominance and dampening of selection, while others lead to amplification of selection. One class of networks that are theorized to have amplifying effects on networks have "star" shapes with one or a few species at the center and radiating interactions out from the central core Lleberman et al. (2005). This is structurally what we have observed with the networks that tend to occur on some of the genotypes in our study, i.e. the more centralized networks. It is possible that these more centralized networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the network structure that is found on that tree genotype.

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 lichen has previously been observed to be different among tree genotype in the same experimental garden Lamit et al. (2011, 2015b), the difference between the present study is likely a result of differences in sampling method and the choice of genotypes leading to overall higher abundances of observed lichens to assure the possibility of observing xlichen interactions. The previous study also used a visual estimation method, unlike the current study, which observed lichen 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 important variation in network structure are leading to evolutionary dynamics. It is possible that these underlying differences in interactions among lichen could lead to differences in community composition at a future point in time via there effects on species abundances Shuster et al. (2006); however, this is not needed for evolutionary dynamics to play out 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). 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.

Evolutionary Implications of a Genetic Basis to Network Structure

A genetic basis to network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted. 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 assymmetries in ecosystems that contribute to the occurrence of foundation species, such as hierarchy and nestedness created by body size differences or life-history strategies, has been widely observed Ellison et al. (2005). The second part 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 genetics 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). Self-orgnization of the dynamics within these communities also points to a mechanism for strong community and ecosystem effects of genetic variation, contributing to what may seem unlikely magnitudes of genetic effects as has been observed in some systems, such as forest in riparian ecosystems Bangert et al. (2006).

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

This builds on many previous studies demonstrating that the community level effects vary among multiple genotypes. It is not clear what potential there is for feedbacks there are to the origins (e.g. the cottonwood genotypes) from the community, and as such it cannot be determined whether these networks are cyclic or rooted. In terrestrial ecosystems, lichen play important ecological roles, such as substrate stabilization Root et al. (2011) and nutrient fixation Nelson et al. (2018). In some systems lignicolous lichens can have demonstrable effects on the availability of nutrients for the trees that they are associated with Norby and Sigal (1989), although this has not been measured for the lichen in the current study's systemq. Elucidating the absence and/or presence of and quantifying such feedbacks would allow for the determination of the cyclic

nature and potential evolutionary dynamics of this system. The presence of feedbacks would provide the potential for non-linear dynamics in which evolutionary effects are damped or amplified by the structure of the network. For example, a star structure in which there is a primary or core set of central species with feedbacks from the radiating species has been demonstrated to be a structure that amplifies evolutionary dynamics Lieberman et al. (2005). If such feedbacks do not exist, these sub-networks of the lichen and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to generally promote diversification as variation arising from the shifting distribution of the “roots”, i.e. genotypes; however, loss of genotype/root diversity could lead to fixation of a single genotype in the population and a decrease in community-wide diversity. However, such feedbacks to tree fitness are not necessary for evolutionary dynamics to play out within the lichen networks through the effects of altered network structure on lichen interaction outcomes, such as competitive exclusion leading to selection.

Since lichen are multi-species complexes, there is also the potential for evolutionary dynamics to shift within the context of the lichen symbiosis. There is substantial evidence that lichen have served as the “cradle of symbiotic fungal diversification” Arnold et al. (2009) and recent research has shown significant network structure of endolichenic fungi and lichen collected from across North America Chagnon et al. (2016). Analysis of the structure of ecological networks has generally supported the conclusion that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability in mutualistic, primarily bipartite (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic networks Elias et al. (2013); Grilli et al. (2016). Although there is growing evidence that the nestedness of mutualistic networks is not necessarily the result of selection for systems-level properties that promote stability but could be either product of asymptotic abundance distributions leading to un-even interaction frequencies Staniczenko et al. (2013) and/or a by-product of selection and divergence creating network “spandrels” in ecosystems Valverde et al. (2018), this does not preclude the functional consequences of network structure but rather the developmental or evolutionary processes that have produced the structure. In the present study, we did not examine nestedness or modularity of the lichen networks as we could not find metrics for analyzing networks that are not only weighted and directed but also signed. Hopefully future network theoretic developments will make the appropriate metrics available to conduct these analyses.

Implications for Interspecific Indirect Genetic Effects (IIGEs)

Interspecific indirect genetic effects (IIGE) theory provides a quantitative framework within which to approach evolutionary theory at higher levels of biological organization: from populations to communities and ecosystems. To date, this theory has focused on modeling the strong effects of foundation species Shuster et al. (2006); Whitham et al. (2012), but it has not yet integrated developments in the ecological or evolutionary network theory literature. This is to say that 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 damped or magnified within the system of interacting species. For example, (Keith et al., 2017) showed that the genetics based interactions of aphid resistant and aphid susceptible trees resulted in different interaction

networks of their associated arthropod communities composed of 139 species. At the scale of ecosystems, trophic networks or food webs direct and control the rates of energy and nutrient flux Borgatti and Everett (2006). Furthermore, in a predator-prey-plant study, Smith Smith et al. (2011), showed that the interactions among species across trophic levels depended on plant genotype. Also, work by (Toju et al., 2017, 2016, 2014) observed consistent patterns of centralized interactions of species modules focused around hubs of plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have disproportionate numbers of interactions with other species and likely are the drivers in determining community assembly, structure and dynamics.

The results of the current study provides clear empirical evidence that variation in network structure can be genetically based (i.e. heritable) and points to the need to expand IIGEs encompass the structure of interaction networks. 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 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. These results also provide insights into the dynamics of real ecosystems and the potential inter-play of ecology and evolution with regard to empirical and theoretical support for neutral theory, as models have been developed that can reconstruct interactions networks with similar structural characteristics to those observed in real ecosystems Coelho and Rangel (2018). The findings of our study support the possibility that, although communities and their interaction networks may assemble as a result of conditions that are entirely agnostic to functional variation, if there are strong ecological assymmetries, such as the case in foundation species systems, then spatial and temporal variation in network structure will arise as a results of trait variation within the foundation species. Taking even the extreme case, even when such genetically based variation is the result of “neutral” evolutionary processes (e.g., genetic drift), as long as resulting genetic diversity produces ecological relevant phenotypic diversity, then network structure will still have a genetic basis. Given that ecosystems with large assymmetries seem to be the rule rather than the exception for ecosystems Ellison et al. (2005); Santamaría and Rodríguez-Gironés (2007); Staniczenko et al. (2013); Dormann et al. (2017); Coelho and Rangel (2018), the results of our study are likely to be broadly applicable and provides further support for the conclusion that the community context of evolutionary dynamics at either micro- or macro-evolutionary scales Weber et al. (2017); Harmon et al. (2019) cannot safely be ignored. As genetic variation is inherent to biological systems, it would now seem that the adage “you can’t be neutral on a moving train” might well apply to ecosystems that are comprised of interacting species.

Applicability to Other Systems

In attempting to apply these findings to other systems, it is important to consider the spatial and temporal scaling of genetic effects. In the present study, the sessile nature of lichens means that individuals, and potentially multiple generations, live their entire lives on a single tree. As such, our study examines one scaling of a genetic effect, in which the phenotype of a single tree individual (i.e., tree genotype) has complete influence on the community with little to no effect of other tree individuals in the population. The extreme from this would be where the associated community moved among and interacted with not only other community members but also multiple tree individuals at a high rate, as would be the case with free-living animals (e.g. flying insects). In the latter case, the effect of tree genetics would then be the integral effect of all the tree individuals in the population, and, all other factors being equal, any one tree genotype would have a lower effect on associated community. In reality, ecosystems are a mixture of species of different body sizes and life-histories, and, as such, vary in the degree to which they interact with other organisms, which is the basis of the theory of the geographic mosaic of co-evolution Thompson (2013); Thompson et al. (2013). It is now important to consider how the impacts of genetic effects on the network structure of sub-groups, such as lichens, may or may not propagate through the ecosystem to more mobile organisms. As developed previously, the degree to which a genetic effect influences the community is a function of the fidelity of the genetic effect (i.e., heritability) and both the frequency and the intensity of the interaction Shuster et al. (2006). One possible path forward is for future work to extend the many previous community genetics studies that have focused on sessile organisms, such as gallin insects Bailey et al. (2005); Whitham et al. (2006); Crutsinger et al. (2014); Smith et al. (2011); Keith et al. (2017), to quantify the frequency of these interactions in the context of the larger community. This would provide an estimate of the relative impact of these focal, often termed foundation, species. In addition, community genetics theory has only considered first order interactions, i.e., between two organisms Shuster et al. (2006); Whitham et al. (2012, 2020). Given that network structure could be influenced by genetic effects, as evidenced by the present study, assessing higher order interactions could provide a path forward for theoretical advances that could help with identifying important characteristics of sub-groups to focus on in empirical studies.

Although our study was conducted with a community of lichens, these results can be generalized to other groups of diverse organisms around the world that also exhibit significant genetic signals at the community level Rountree et al. (2011); Whitham et al. (2012). However, there are important points to consider when extending the observed genetically based response of the lichen networks to other systems. As bark lichen individuals do not move, but grow in a primarily two dimensional plane, these communities and their interactions occur in the highly localized context of the tree's bark surface. Lichen individuals are also many orders of magnitude smaller than the tree individual in this system Lamit et al. (2011). For these reasons, the genetic effects on these communities is not damped by the movement of individuals and the mixing of the effect of different tree genotypes on the lichen community, as might occur for more mobile species (e.g. insects and birds). Relatedly, we only examined lichen in this study, and other species whose distributions, abundances and/or interactions vary in their response to tree genotype, such as animals that may also impact

lichen communities, could be playing a role that we did not examine. For example, an analysis of the multivariate correlations of different components of the community in this system demonstrated significant patterns of genetic co-responses to tree genotype, supporting the non-mutually exclusive possibilities of shared responses to tree genotype or tree genotypic effects on interactions among these sub-communities Lamit et al. (2015a). As such, although we can not rule out the possibility that other unmeasured tree traits or organisms correlated with bark roughness are underlying the observed patterns, substantial research supports the importance of genetically based tree traits for communities and ecosystems Des Roches et al. (2018), and in particular bark roughness for bark lichen communities Bdeir et al. (2017); Lamit et al. (2011, 2015b).

Conclusion

In the face of the high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed to some in previous studies Bangert et al. (2006); Zook et al. (2010); Zytynska et al. (2012). In the present study, we found that community assembly processes, such as environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. The importance of the scale of network organization to create hierarchical structure Guimarães (2020) and the potential for foundation species to create this structure in the vast majority of ecosystems Ellison et al. (2005); Whitham et al. (2006) suggests that future work would be aided by determining these modules within the biotic community that include species with similar differences in body-size and time-scales. Also, as heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions Evans et al. (2013). Such findings will bring us closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

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Citations

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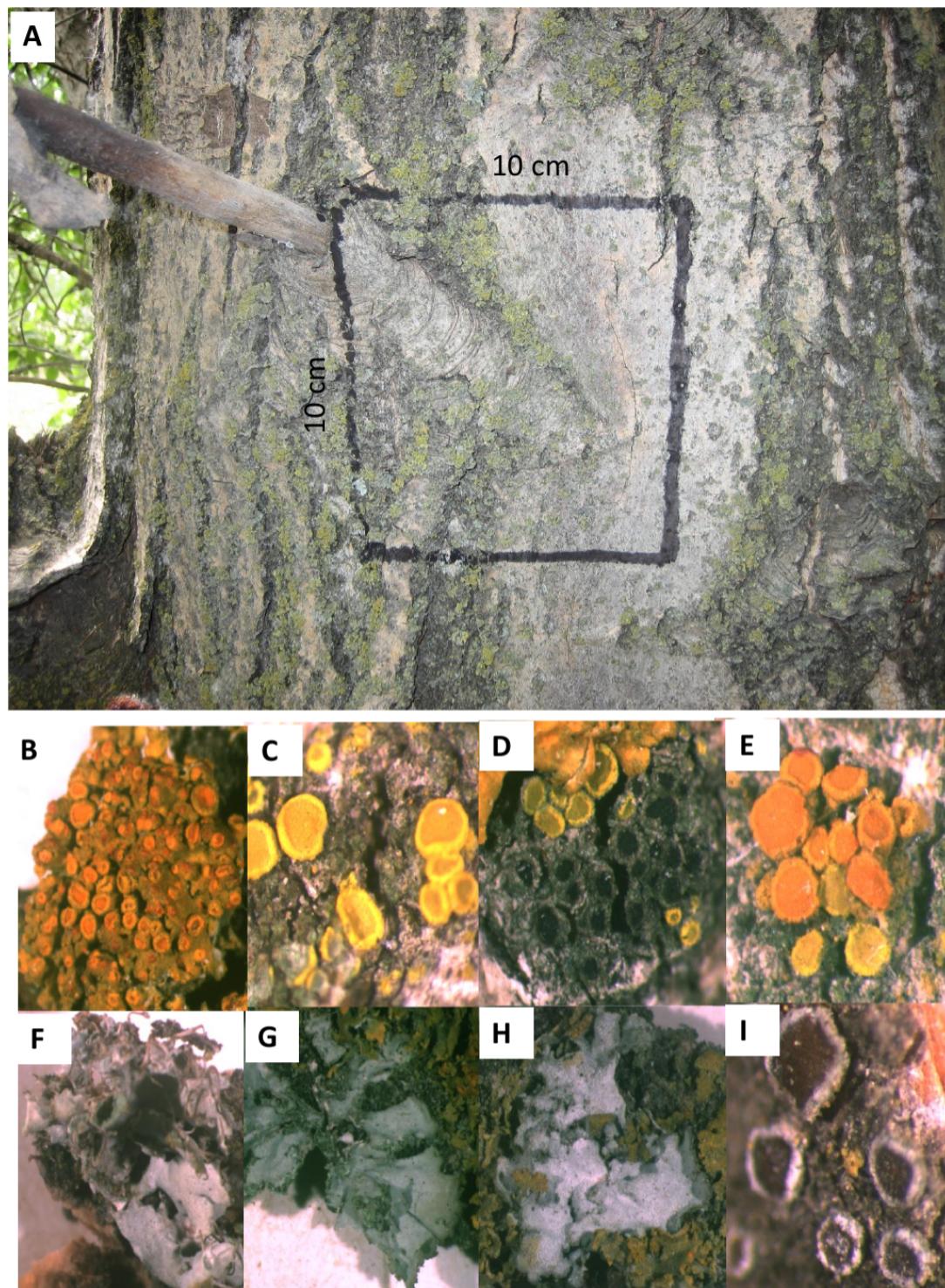


Figure 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from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

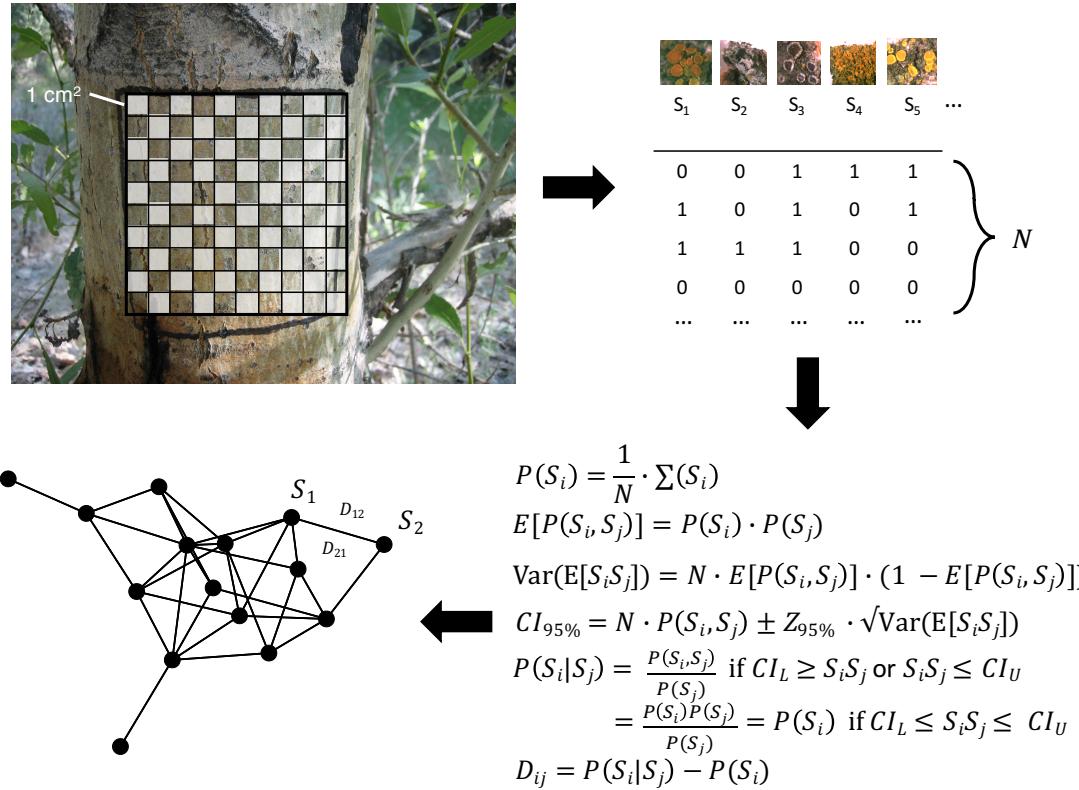


Figure 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from Araújo et al. (2011), we calculated the conditional probabilities, $P(S_i | S_j)$, for all species pairs and removed (i.e. set equal to zero) species pairs whose joint probabilities, $P(S_i S_j)$, 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 . In the context of these networks, asymmetry and positive/negative valued connections are distinct quantities. In-coming and out-going connections can be interpreted as “influenced by” and “influenced”, respectively; while positive and negative should be seen as one species increasing or decreasing, respectively, the probability of another species’ occurrence.

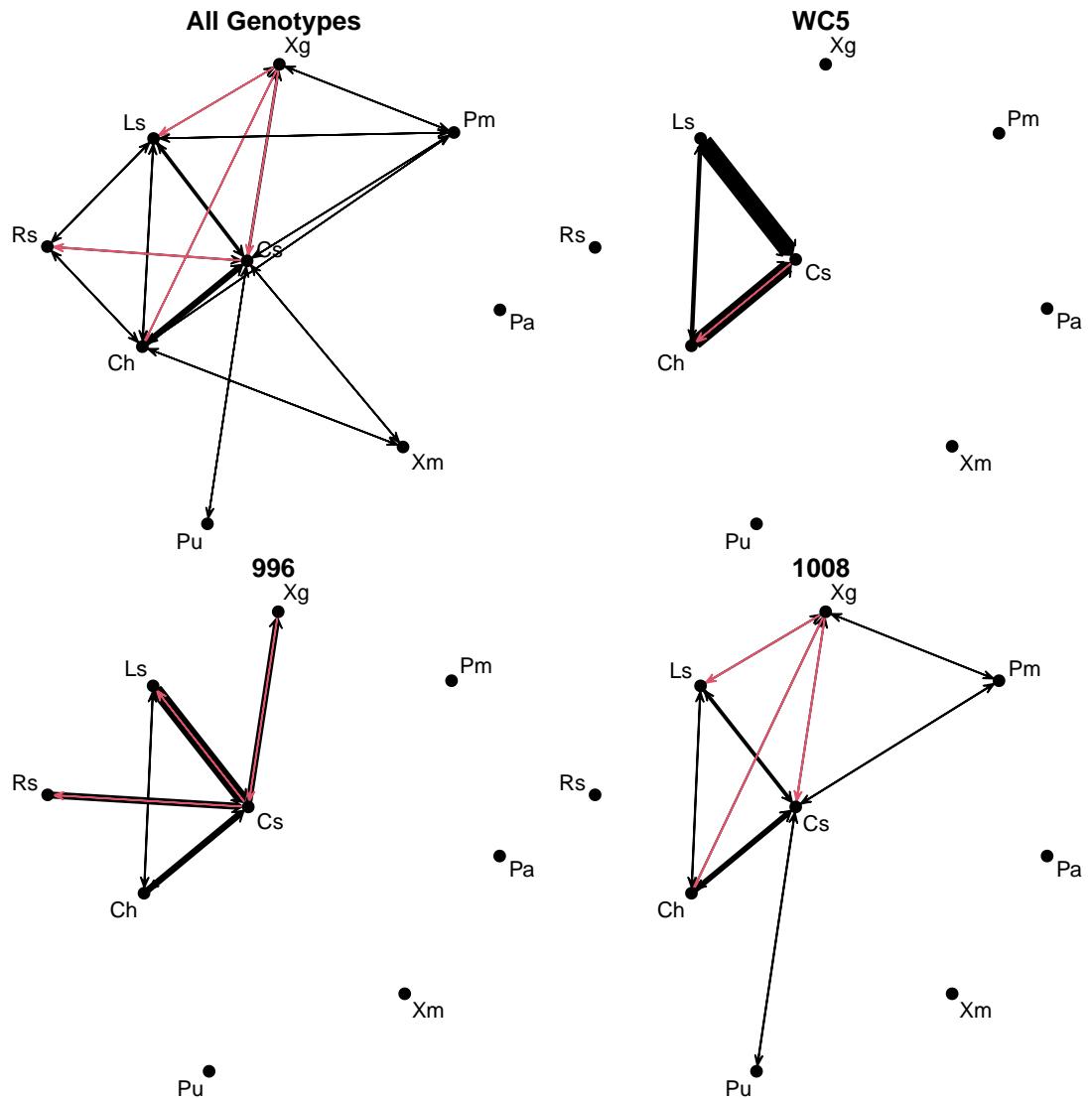


Figure 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative,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

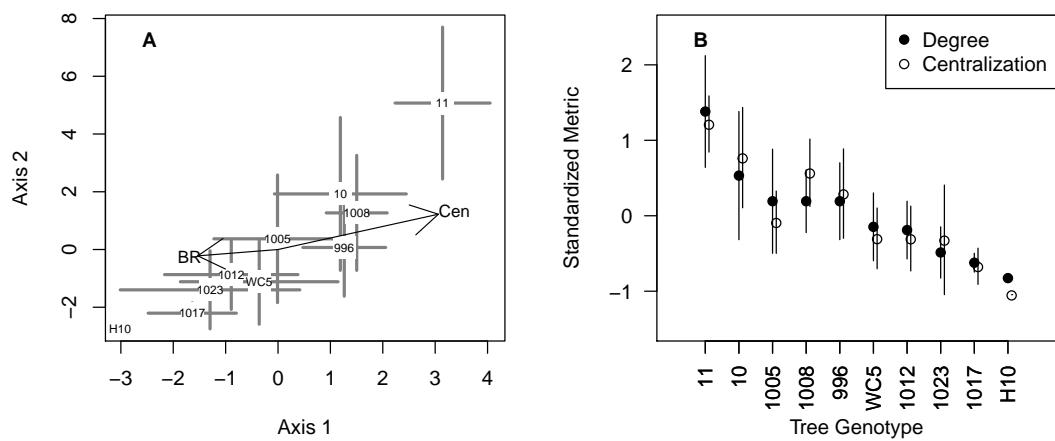


Figure 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows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

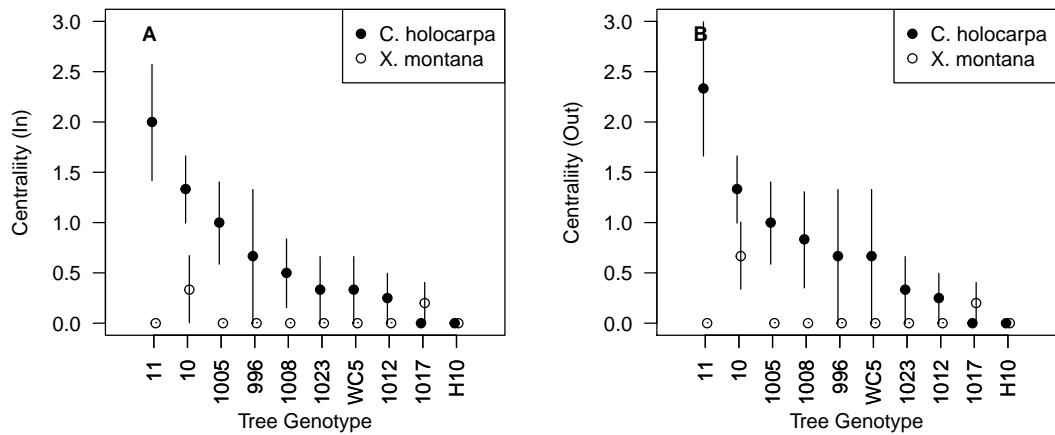


Figure 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

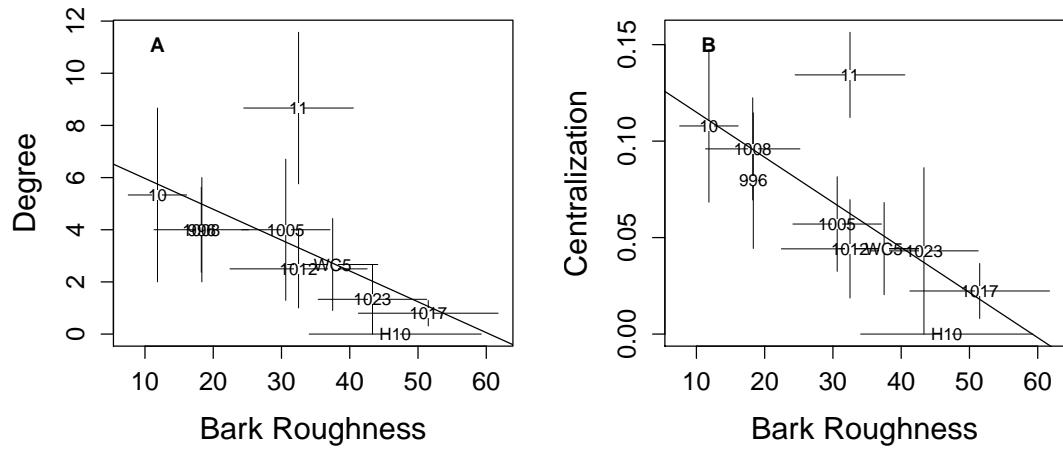


Figure 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased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