

# **1 Genotypic variation in a foundation tree 2 results in heritable ecological network 3 structure of an associated community**

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## **19 ABSTRACT**

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

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

<sup>20</sup> **INTRODUCTION**

<sup>21</sup> Evolution occurs in the context of complex ecological networks. Community genetics  
<sup>22</sup> studies have shown that genetic variation in foundation species, which have large effects  
<sup>23</sup> on ecosystems by modulating and stabilizing local conditions (Ellison et al., 2005),  
<sup>24</sup> plays a significant role in defining distinct communities of interacting organisms: such  
<sup>25</sup> as, endophytes, pathogens, lichens, arthropods, and soil microbes (Busby et al., 2015;  
<sup>26</sup> Barbour et al., 2009; Lamit et al., 2015a). Multiple studies have now demonstrated that  
<sup>27</sup> genetic variation influences numerous functional traits (e.g., phytochemical, phenologi-  
<sup>28</sup> cal, morphological) that in combination result in a multivariate functional trait phenotype  
<sup>29</sup> (Holeski et al., 2012) in which individual plant genotypes support different communities  
<sup>30</sup> and ecosystem processes (Bailey et al., 2009; Whitham et al., 2012). Recently, the  
<sup>31</sup> importance of genetic variation in structuring ecological systems was reviewed, and  
<sup>32</sup> not only were many instances of strong genetic effects found in many ecosystems but  
<sup>33</sup> the effect of intraspecific variation was at times greater than inter-specific variation  
<sup>34</sup> (Des Roches et al., 2018). There is now evidence to support that selection, acting on  
<sup>35</sup> this heritable variation, tends to occur among groups of species (Wade, 2007) and that  
<sup>36</sup> genetic variation and phylogenetic relatedness contribute to variation in community  
<sup>37</sup> assembly (Crutsinger, 2016) and species interactions (Whitham et al., 2006; Bailey et al.,  
<sup>38</sup> 2009; Moya-Laraño, 2011), which shape the structure of ecological interaction networks  
<sup>39</sup> (Rezende et al., 2007; Guimarães et al., 2007; Gómez et al., 2009). Network theory and  
<sup>40</sup> evidence from empirical studies in ecology have demonstrated that indirect effects can  
<sup>41</sup> lead to self-organization, producing sign-changing, amplifying and/or dampening effects  
<sup>42</sup> (Newman, 2006; Sole and Bascompte, 2006), and other studies have demonstrated  
<sup>43</sup> that indirect effects of interactions among species can lead to network structures that  
<sup>44</sup> amplify or dampen the effects of selection, such as the formation of star-like structures in  
<sup>45</sup> which there is a “central” species or group of species that interact with other, peripheral  
<sup>46</sup> species, can amplify selection events (Lieberman et al., 2005). Also, work by Toju et al.  
<sup>47</sup> (2014, 2016, 2017) observed consistent patterns of centralized interactions of species  
<sup>48</sup> modules (i.e., groups of species that interact more strongly within their group than  
<sup>49</sup> with other species) focused around hubs of plant-fungal interactions. In other words, a  
<sup>50</sup> small number of plant and fungal symbionts tended to have disproportionate numbers  
<sup>51</sup> of interactions with other species and likely are the drivers in determining community  
<sup>52</sup> assembly, structure and dynamics.

<sup>53</sup> Interspecific indirect genetic effects (IIGE) theory (*sensu* Shuster et al. (2006)) in  
<sup>54</sup> evolutionary biology supports ecological network studies that point to the importance of  
<sup>55</sup> studying the genetic basis of interaction network structure. Genetic based differences in  
<sup>56</sup> network structure among individuals can be acted upon by natural selection when there  
<sup>57</sup> are fitness consequences of different networks of IIGEs, leading to community evolution  
<sup>58</sup> per Whitham et al. (2020) and, by extension, network evolution. For example, although  
<sup>59</sup> the analysis was of abundances rather than interaction networks, Gehring et al. (2014,  
<sup>60</sup> 2017) found that the mycorrhizal communities on the roots of drought tolerant and intol-  
<sup>61</sup> erant trees are dominated by different orders of ectomycorrhizal fungal mutualists that  
<sup>62</sup> also differ in the benefits they provide that enhance tree performance. Because drought  
<sup>63</sup> tolerant genotypes are three times more likely to survive record droughts, selection acts  
<sup>64</sup> 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.

Hi Matt, In thinking more about your paper, it seems we need more explicit definitions of evolutionary terms and how they relate to networks. The following text is something to consider, which could go into the intro or discussion if you feel it adds to the paper. Cheers, Tom

The demonstration of community evolution requires demonstrating three key elements. First, there must be variation in the structure (composition, abundance, species interactions, diversity) 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. Importantly, this study shows that networks are also heritable traits that greatly increases 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 or 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.

It is important to consider how network structure itself is a trait that has been selected over time to potentially optimize modules that affect the interactions of mutualists that benefit the plant, while minimizing modules of herbivores and pathogens that negatively impact the plant (I think this deserves more serious thought and it would be good to come up with some predictions). Thus, the combined interactions of communities of interacting species should be reflected in the differences of networks of individual plant genotypes and how they might differ across a landscape in which selection pressures change in response to local biotic and abiotic conditions. Such analyses are also important in helping to identify the modules and species 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 is lacking, a network analysis based upon species occurrence and abundance, could tell researchers which species should be focused on to best understand the dynamics of the system.

110 In this context, the “genetic similarity rule” of community genetics provides a  
111 useful framework we can apply to interaction networks at the nexus of ecological  
112 and evolutionary dynamics. In a study combining experimental common gardens and  
113 landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and  
114 arthropods, Bangert et al. (2006) observed that individuals genotypes that are more genet-  
115 ically similar will tend to have similar phytochemical traits and thus tend to have similar  
116 interactions with other species than individuals that are less similar. Although this is  
117 likely to have consequences for interactions and network structure, studies in the network  
118 ecology literature generally do not include a genetic component (Lau et al., 2017) and  
119 community genetics studies have primarily focused on community composition in terms  
120 of the abundance of species (Des Roches et al., 2018). Some studies have examined the  
121 effects of genetic variation on trophic chains in plant-associated communities (including  
122 *Populus*, *Solidago*, *Oenothera*, *Salix*) (Bailey et al., 2005; Johnson, 2008; Smith et al.,  
123 2011, 2015; Barbour et al., 2016) and generally found that increasing genotypic diversity  
124 leads to increased trophic complexity. Only two other studies, that we are aware of,  
125 have explicitly examined the effect of genotypic variation on the structure of interaction  
126 networks between tree individuals and associated herbivores (Lau et al., 2015; Keith  
127 et al., 2017) and both found that genotypic diversity generates increased network mod-  
128 ularity (i.e., compartmentalization). However, both of these studies were examining  
129 networks at the scale of forest stands, rather than networks associated with individual  
130 trees; therefore, neither was able to observe replicated networks in order to statistically  
131 test for genetic effects on network structure and quantify the genetic component (i.e.,  
132 heritable variation) in network structure.

133 Here, we investigate how genetic variation in a foundation tree species determines  
134 the structure of a network of interactions among a community of tree associated lichens.  
135 Using a long-term (20+ years), common garden experiment with clonally replicated  
136 *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001).  
137 We focused on a community of 9 epiphytic lichen species, as previous research has  
138 demonstrated significant compositional responses of epiphytes to genotypic variation  
139 (Winfrey et al., 2011; Zytynska et al., 2011). Applying a probability-theory based  
140 network modeling approach (Araújo et al., 2011), we constructed a set of interaction  
141 network models for the lichens associated with individual trees. Using these models,  
142 we then examined the genetic basis of the structure of these ecological networks via  
143 several network metrics that measure different aspects of network structure at the scale  
144 of individual species (i.e., nodes) or the entire network observed on each tree genotype.  
145 Given that network theory applications to evolutionary dynamics have pointed to the  
146 importance of network structures that have focal or “central” nodes (e.g., species)  
147 (Lieberman et al., 2005), we focused on network metrics that measure centrality for  
148 individual species and centralization for whole networks. Both of these metrics measure  
149 how much a species is connected in the network relative to other species. We hypothesize  
150 that in natural systems evolution occurs in communities comprised of networks of  
151 interacting species (Lau et al., 2015; Keith et al., 2017; Thompson, 2013; Bascompte  
152 et al., 2006). More specifically, based on the community similarity rule Bangert et al.  
153 (2006), we hypothesize that trees will co-vary in functional phenotypic traits, such as  
154 bark roughness and chemical composition, and trees of the same genotype will tend  
155 to have similar traits leading to similarities in lichen network structure. If correct, we

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

## 158 MATERIALS AND METHODS

### 159 Study System

160 The study was conducted along the Weber River, UT (USA), which is a cottonwood  
161 (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus*  
162 *angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known  
163 to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were  
164 sampled. Bark lichens have been intensively sampled in this system and provide an ideal  
165 community in which to observe and model interaction networks, as their sessile nature  
166 permits accurate identification of individuals and their highly localized, direct contact  
167 interactions and slow population turnover rates facilitate the assessment of interactions  
168 among lichen species on individual trees (Lamit et al., 2015b).

169 A long-term, common garden experiment was used to isolate the effect of tree genotype  
170 from the effect of the localized microenvironment associated with each individual  
171 and spatial autocorrelation. Established in 1992, asexually propagated clones of geno-  
172 typed *P. angustifolia* individuals were obtained from wild collections and planted in  
173 fully randomized design at the Ogden Nature Center, Ogden, UT. From the population  
174 of established individuals in the common garden, we chose a total of ten genotypes,  
175 replicated between 3 and 8 times each, for sampling. We selected tree genotypes that  
176 generally had lichen present in order to permit the construction of interaction networks.

### 177 Bark Lichen and Trait Observations

178 On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm<sup>2</sup>  
179 cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens,  
180 we were able to rapidly assess lichen interactions by quantifying thalli in close contact.  
181 Sampling was restricted to the northern aspect of the trunk to maximize the abundance of  
182 lichen and control for the effect of trunk aspect. Two adjacent 100 cm<sup>2</sup> quadrats centered  
183 at 50 cm and 95 cm from ground level were sampled (Fig 1 A and B). The observed  
184 lichen community included (abbreviations are given for species present in study): Xg =  
185 *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs =  
186 *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella*  
187 *melanchra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were  
188 not observed in the present study but are known to occur in this region: *Phaeophyscia*  
189 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegans*.

190 The cell size and checkerboard sampling pattern was chosen to isolate the individuals  
191 in each cell. In a previous survey of *X. galericulata* thallus size in this common garden  
192 (Lamit et al., 2015b), we had observed a median thallus size of  $0.12 \pm 0.001$  cm<sup>2</sup> (1  
193 S.E.) (Supporting Information, Fig. 1). Based on the median thallus size, we expected  
194 thalli observed in each cell to generally be spatially independent of thalli present in other  
195 cells but exposed to similar micro-environmental conditions created by the bark and  
196 the location of the sampling area on an individual tree. Therefore, we were confident  
197 in treating the cell-wise observations in quadrats as independent with respect to lichen-  
198 lichen interactions. We quantified the texture of the bark in the quadrat is the percent of

199 1 cm<sup>2</sup> cells with rough bark. In addition to bark roughness, we also measured several  
200 bark chemistry traits by taking bark samples immediately adjacent to each quadrat using  
201 the methods of Lamit et al. (2011): including, the concentration of condensed tannins,  
202 pH and carbon and nitrogen concentrations and pH.

203 **Lichen Network Modeling and Analysis**

204 For each tree, repeated observations of lichen were made in order to construct replicated  
205 interaction networks for each genotype. We conducted a modified sampling procedure  
206 originally developed by Lamit et al. (2015b) with the addition that we quantified the  
207 presence of lichen in the 1 cm<sup>2</sup> cells on individual trees of *P. angustifolia*. Unipartite  
208 networks were generated using the conditional probabilities of each species pair, i.e., the  
209 probability of observing one species given an observation of another species  $P(S_i|S_j)$ ,  
210 based on the method developed by Araújo et al. (2011). To calculate conditional  
211 probabilities, we quantified the individual probabilities of species occurrences  $P(S_i)$  and  
212 the joint probability of co-occurrences  $P(S_i, S_j)$  using the frequencies of each species  
213 and their co-occurrences. We were then able to calculate the conditional probabilities of  
214 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  
215 a matrix that could possibly be asymmetric, i.e.,  $P(S_i|S_j)$  does not have to be equal to  
216  $P(S_j|S_i)$ . Another important property of this matrix is that the diagonal,  $P(S_i|S_i)$ , was  
217 equal to one for all species present and zero for species that were not observed in any  
218 cell.

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

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

244 exclusion or facilitation within species would result in the same species being observed.  
245 Therefore, the results of intra-specific interactions always results in the same species  
246 being observed and a resulting  $D_{ii} = 0$ . In the context of these networks, asymmetry and  
247 positive/negative valued connections are distinct quantities. In-coming and out-going  
248 connections can be interpreted as “influenced by” and “influenced”, respectively; while  
249 positive and negative should be seen as one species increasing or decreasing, respectively,  
250 the probability of another species’ occurrence.

## 251 **Network Metrics**

252 To quantify the structural variation of lichen networks we calculated several metrics  
253 at both the level of node and whole networks. For individual nodes (i.e., species) in  
254 each network, we calculated both the degree and the Freeman’s centrality (Butts, 2019).  
255 We also calculated two similar global network metrics: degree and centralization. The  
256 first was network degree, which is a count of the total number of links in a network. As  
257 the networks contained not only positive and negative connections but also directional  
258 connections (both in-coming and out-going), we calculated the same network metrics  
259 for all combinations of these types of connections in each network, accounting for  
260 differences in sign through the application of recently developed metrics that incorporate  
261 sign information from signed, weighted, directed networks (Everett and Borgatti, 2014).  
262 Although there are many more possible network metrics that could have been examined,  
263 we chose to focus on a restricted set for the sake of clarity. In addition, degree and  
264 centrality form the basis of many other network metrics.

## 265 **Statistical Analyses, Software and Data**

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

274 For multivariate response variables, such as lichen community composition and  
275 network structure, we used distance based multivariate statistical approaches, including  
276 Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify  
277 the similarity of lichen networks among individual trees, we calculated the pairwise  
278 Euclidean distance of the **D** interaction matrices among all pairs of trees. For visualization  
279 of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS)  
280 (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of these multi-  
281 variate responses and fitted vectors for continuous predictor variables to the ordinated  
282 values (Oksanen et al., 2019). Using random initial configurations with a maximum of  
283 500 iterations and a change in stress threshold of less than  $10^{-12}$ . Final configurations  
284 has the lowest stress with at most a stress level of 0.10.

285 For each network, we also calculated metrics that measure different structural aspects.  
286 Although there are many other metrics, for the sake of simplicity we focus on a subset  
287 that represent several interesting features of network structure (see Lau et al. (2017)).

288 We calculated the number of interactions or “links” in each network, which provides  
289 a measure of the size of the network (Lau et al., 2015; Borrett and Lau, 2014). We  
290 also calculated the centralization of each network, which measures the evenness of  
291 the distribution of interactions among the species in the network (Butts, 2019). In a  
292 network with a low level of centralization species have similar amount of interaction in  
293 the network, while a network with a high level of centralization tends to have one or  
294 small number of species that interact with other species. We used a related function to  
295 calculate the centrality of each species (i.e., node level centrality) in each network as  
296 well. To calculate separate metrics for positive and negative links, we applied methods  
297 for calculating the centrality accounting for the sign differences (Everett and Borgatti,  
298 2014) using the `signnet` package (Schoch, 2020).

299 For all tests where genotype was used as a predictor, we quantified the heritability  
300 of the response variable. Because the trees in the garden were clonal replicates of each  
301 genotype, we calculated broad-sense heritability, which is the genotypic variance divided  
302 by the total phenotypic variance (Conner and Hartl, 2004). This can be interpreted as a  
303 measure of the phenotypic variance due to genotypic variation. We also apply this to  
304 the community genetics context as the variance in *extended* phenotypic variance due to  
305 genotypic variation (Whitham et al., 2006, 2012; Crutsinger, 2016).

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

## 310 RESULTS

311 Tree genotype influenced lichen network structure and multiple lichen network metrics  
312 were heritable. Tree genotype significantly predicted the structural similarity of lichen  
313 networks and, overall, network-level metrics responded significantly to tree genotype,  
314 including network degree and centralization including both in-coming and out-going  
315 links or when separated into in-coming only or out-going only (Table 1, Fig. 4). Metrics  
316 including only positive links also showed a significant effect of tree genotype, including  
317 positive degree and positive in-going centralization. Metrics calculated with negative  
318 links were not significant, including degree (negative) and both in-coming (negative)  
319 and out-going centralization (negative).

320 The genetic response of network centralization was driven by variation in *Caloplaca*  
321 *holocarpa*. Centrality varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ ,  
322  $p\text{-value} < 0.0001$ ). *Caloplaca holocarpa* centrality was the main species to exhibit  
323 a significant response to tree genotype in terms of positive centrality for both the in-  
324 coming ( $RLRT = 3.61$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0240$ ) and out-going ( $RLRT = 3.13$ ,  $H^2$   
325 = 0.30,  $p\text{-value} = 0.0327$ ) perspectives, but not for either negative centrality metrics  
326 in-coming ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 1$ ) or out-going ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} =$   
327 0.4543). None of the other species’ centralities showed a genotypic response (Supporting  
328 Information, Fig. 2) with the exception of *X. montana* ( $RLRT = 2.92$ ,  $H^2 = 0.32$ ,  $p\text{-value}$   
329 = 0.0375); however, the centrality of *X. montana* was much lower overall relative to *C.*  
330 *holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes  
331 (Fig. 5).

	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.

332 Genotype indirectly influenced lichen network centralization via the genetically  
 333 based variation in bark roughness. The percent cover of rough bark ( $RLRT = 4.8526$ ,  
 334  $H^2 = 0.3221$ ,  $p\text{-value} = 0.0113$ ) and condensed tannins ( $RLRT = 3.0522$ ,  $H^2 = 0.3205$ ,  
 335  $p\text{-value} = 0.0343$ ) both displayed significant responses to tree genotype. None of the  
 336 other bark traits, pH ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ) or carbon-nitrogen  
 337 ratio ( $RLRT = 0.0000$ ,  $H^2 = 0.0000$ ,  $p\text{-value} = 1.0000$ ), showed a significant response  
 338 to tree genotype and none other than bark roughness was correlated with network  
 339 similarity (Table 2); therefore, we focused our subsequent analyses on the indirect  
 340 effect of genotype on lichen network structure via bark roughness. We found that bark  
 341 roughness was significantly correlated with network similarity and other lichen network  
 342 metrics, including negative correlations with overall network degree ( $df = 35$ ,  $t = -2.13$ ,  
 343  $r = -0.34$ ,  $p\text{-value} = 0.04$ ) and centralization ( $df = 35$ ,  $t = -2.52$ ,  $r = -0.39$ ,  $p\text{-value}$   
 344 = 0.02). In other words, trees with more similar levels of bark roughness tended to  
 345 have lichen interaction networks with similar structure. To quantify the genetic bases  
 346 of this effect of bark roughness on network structure, we used the residual values from  
 347 regressions of network degree and centralization in tests of the effect of tree genotype  
 348 and found no significant effect of tree genotype for either degree ( $RLRT = 0.00$ ,  $H^2 =$   
 349 0.00,  $p\text{-value} = 1.0000$ ) or centralization ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ),  
 350 suggesting that the observed relationship between bark roughness and lichen network  
 351 structure was largely genetically based (Fig. 6).

	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.

352 **DISCUSSION**

353 We found that tree genotype influenced lichen network structure in the experimental  
354 cottonwood forest. Network similarity and metrics of network structure tended to be  
355 more similar on trees of the same genotype. Generally, this genetic effect was manifested  
356 in positive interactions and largely driven by *C. holocarpa*. The genetically based trait,  
357 bark roughness, was the only trait observed to effect network variation, largely via shifts  
358 in positive in-coming and out-going interactions. Chemistry traits, whether genetically  
359 based, such as tannin concentration, or not, were not significantly correlated with lichen  
360 network structure. Bark roughness has been demonstrated previously to be under strong  
361 genetic control (Bdeir et al., 2017), and bark roughness has also been shown to be an  
362 important tree trait influencing bark lichens (Lamit et al., 2015b); however this is the first  
363 demonstration of a link from genetics to lichen network structure. As such these results  
364 have important implications for the potential influence of genetically based variation in  
365 ecosystems with networks of interacting species.

366 **Implications of the Heritability of Interaction Network Structure**

367 Significant heritability of lichen interaction network structure is in line with the genetic  
368 similarity rule, networks observed on trees of the same genotype tended to be structurally  
369 similar. Although previous studies have examined aspects of networks, such as trophic  
370 complexity (Barbour et al., 2016) and forest stand-level interaction network structure  
371 (Lau et al., 2016; Keith et al., 2017), this is the first study that we are aware of to  
372 examine the heritability of network structure with replicated networks at the genotype  
373 scale. Previous work in the evolution of ecological networks have primarily focused on  
374 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,  
375 2018; Harmon et al., 2019) or have been simulation based individual-level models that  
376 integrate intraspecific variation to the species level (Maliet et al., 2020), even though  
377 recent syntheses ave pointed to the importance of processes operating across scales of  
378 organization (Guimarães, 2020). There are two important functional ramifications of  
379 genetically based variation in network structure.

380 First, A genetic basis to network structure suggests that some amount of interaction  
381 network complexity is determined and therefore could be predicted. Variation in space  
382 and time create variation in ecological networks that influences evolutionary dynamics  
383 via shifts in ecological dynamics, such as population demographics (Guimarães, 2020).  
384 Given that ecosystems are comprised of hundreds and thousands of species, each having  
385 a multitude of interactions, the potential to find traction for making predictions in the  
386 context of ecological, let alone evolutionary, dynamics seems daunting. The promise  
387 of predictability lies in the presence of assymetries in ecosystems that contribute to the  
388 occurrence of foundation species, such as hierarchy and nestedness created by body size  
389 differences or life-history strategies, has been widely observed (Ellison et al., 2005). The  
390 second is that heritability (i.e., genetic determination) means that there is structure in the  
391 spatial or temporal variation that is created by individuals of foundation species whose  
392 traits are in part determined by underlying trait differences. Although this variation  
393 is inherently a function of both genetic and environmental effects (Conner and Hartl,  
394 2004), the community and network-level effects are also a function of the scale of the  
395 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 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 lichen interactions. The previous study used a visual percent cover estimation, unlike the current study, which observed lichen at the scale of 1 cm<sup>2</sup> cells, which could over-estimate cover depending on the frequency at which actual thallus size was less than 1 cm<sup>2</sup>, 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 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), 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).

### **Evolutionary Implications of a Genetic Basis to Network Structure**

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 who's 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 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

441 response to disturbance or via self-organized dynamics. For example, centralized net-  
442 works, although more efficient, are theorized to be more susceptible to targeted attacks.  
443 As mentioned previously, one class of networks that are theorized to have amplifying  
444 effects on networks have centralized "star" shapes with one or a few species at the center  
445 and radiating interactions out from the central core (Lieberman et al., 2005). This is  
446 structurally what we have observed with the networks that tend to occur on some of the  
447 genotypes in our study, i.e., the more centralized networks. It is possible that these more  
448 centralized networks could function as hot-spots of evolutionary dynamics resulting  
449 from the amplifying effect the centralized network structure found on that tree genotype.

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

465 This builds on many previous studies demonstrating that the community level effects  
466 vary among genotypes. It is not clear what potential there is for feedbacks to the origins  
467 (e.g. the cottonwood genotypes) from the community. In terrestrial ecosystems, lichen  
468 play important ecological roles, such as substrate stabilization (Root et al., 2011) and  
469 nutrient fixation (Nelson et al., 2018). In some systems lignicolous lichens can have  
470 demonstrable effects on the availability of nutrients for the trees that they are associated  
471 with (Norby and Sigafoos, 1989), although this has not been measured for the lichen in  
472 the current study's system. Elucidating the absence and/or presence of and quantifying  
473 such feedbacks would allow for the determination of the cyclic nature and potential  
474 evolutionary dynamics of this system (Lieberman et al., 2005). However, such effects of  
475 the bark lichen in this system on their tree hosts has not been quantified in this system.

476 Since lichen are multi-species complexes, there is also the potential for evolutionary  
477 dynamics to shift within the context of the lichen symbiosis. There is substantial  
478 evidence that lichen have served as the "cradle of symbiotic fungal diversification"  
479 (Arnold et al., 2009) and recent research has shown significant network structure of  
480 endolichenic fungi and lichen collected from across North America (Chagnon et al.,  
481 2016). Analysis of the structure of ecological networks has generally supported the  
482 conclusion that nestedness, or the degree to which species tend to interact with similar  
483 subsets of the community, tends to promote stability in mutualistic, primarily bipartite  
484 (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic  
485 networks (Elias et al., 2013; Grilli et al., 2016). Although there is growing evidence  
486 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 et al. (2011) showed that the interactions among species across trophic levels depended on plant genotype.

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.

#### 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 in previous studies (Bangert et al., 2006; Zook et al., 2010; Zytynska et al., 2012). In the present research, we found that

531 the assembly of ecological networks can have a measurable genetic basis depending  
532 on the spatial scale of interactions, due in part, to assymetries in size and longevity of  
533 organisms. The importance of the scale of network organization to create hierarchical  
534 structure (Guimarães, 2020) and the potential for foundation species to create this  
535 structure in the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006)  
536 suggests that future work would be aided by determining these modules within the biotic  
537 community that include species with large differences in body-size and longevity. Also,  
538 as heritable variation is the raw material for natural selection to act upon, a genetic basis  
539 for interaction network structure indicates evolutionary dynamics should be considered  
540 at the community level and that conserving genetic variation is important to consider in  
541 efforts to restore or preserve complex species interactions and their associated ecosystem  
542 functions (Evans et al., 2013).

543 One possible path forward is for future work to extend the many previous community  
544 genetics studies that have focused on sessile organisms, such as galling insects (Bailey  
545 et al., 2005; Whitham et al., 2006; Crutsinger et al., 2014; Smith et al., 2011; Keith  
546 et al., 2017), to quantify the frequency of these interactions in the context of the larger  
547 community. This would provide an estimate of the relative impact of these focal, often  
548 termed foundation, species. In addition, community genetics theory has only considered  
549 first order interactions, i.e., between two organisms (Shuster et al., 2006; Whitham  
550 et al., 2012, 2020). Given that network structure could be influenced by genetic effects,  
551 assessing higher order interactions could provide a path forward for theoretical advances  
552 that could help with identifying important characteristics of sub-groups to focus on in  
553 empirical studies. Such findings will bring us closer to understanding the evolutionary  
554 drivers of Darwin's entangled bank and the interconnectedness of species in complex  
555 communities (??).

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## 561 **Citations**

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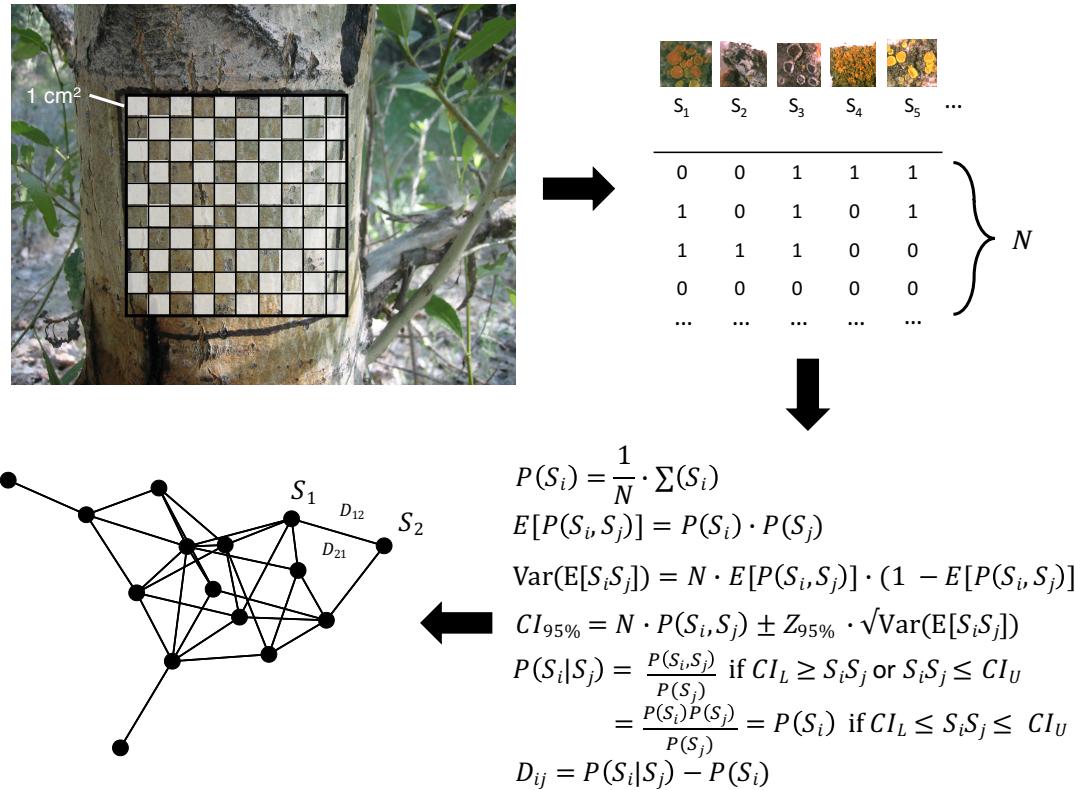
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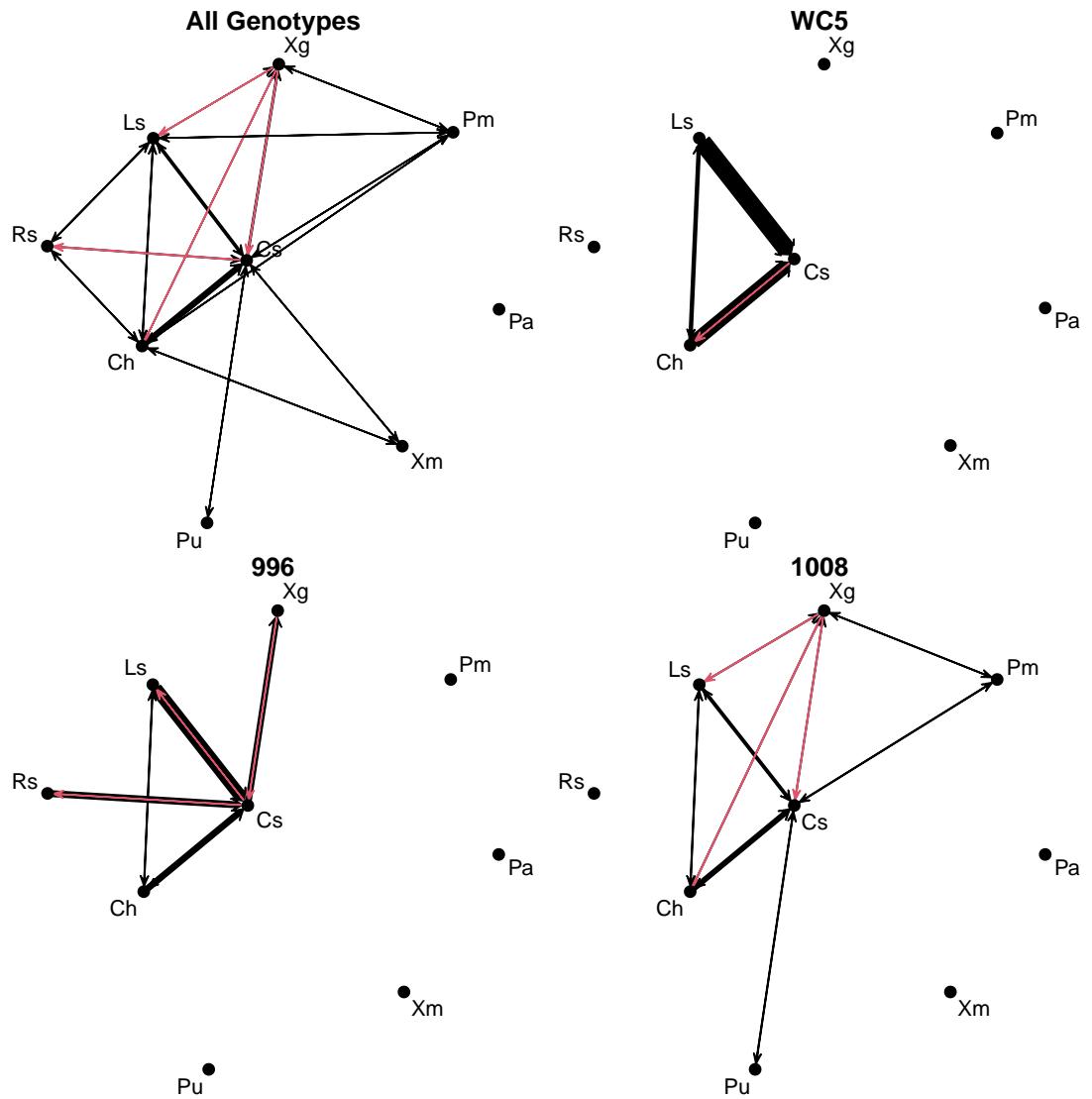
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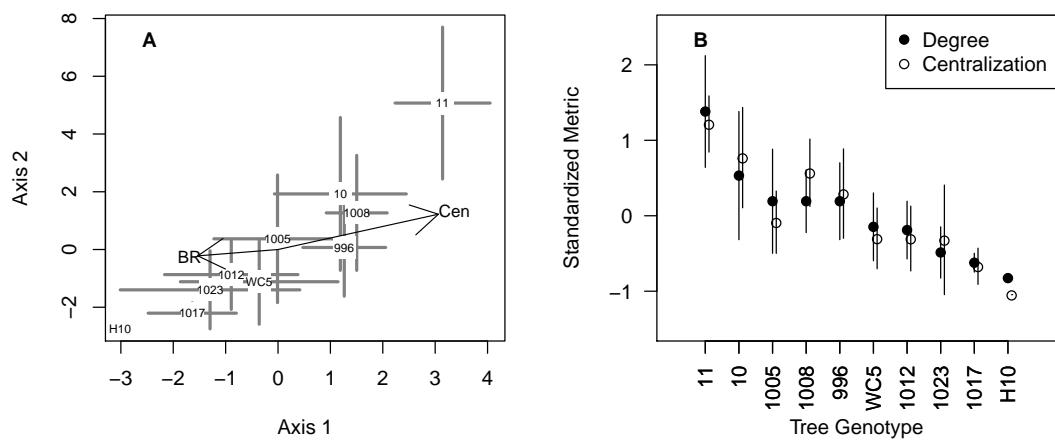
**Figure 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm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



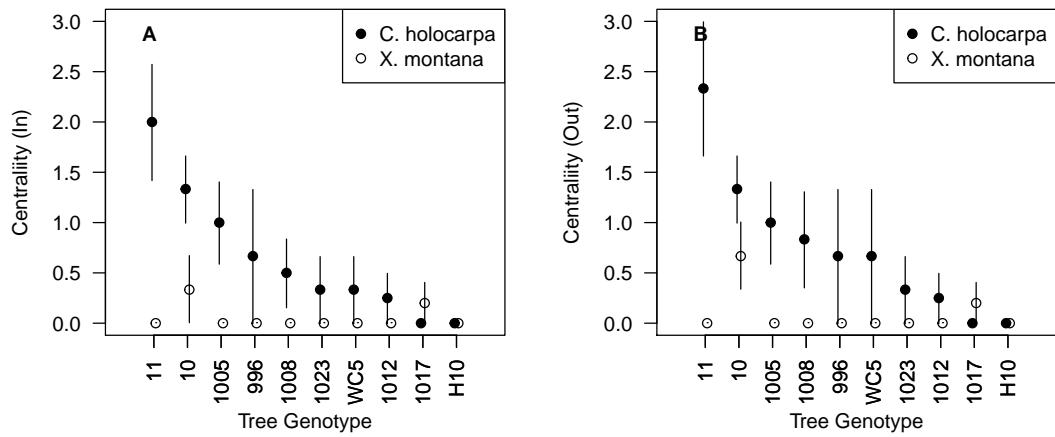
**Figure 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence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



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



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



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



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