

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

**4 Matthew K. Lau<sup>1,2</sup>, Louis J. Lamit<sup>1,3,4</sup>, Rikke Reese Næsborg<sup>1,5</sup>, Stuart R.  
5 Borrett<sup>6</sup>, Matthew A. Bowker<sup>7</sup>, and Thomas G. Whitham<sup>1,8</sup>**

**6 <sup>1</sup>Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011,  
7 USA**

**8 <sup>2</sup>Harvard Forest, Harvard University, 324 N Main St, Petersham, MA 01366, USA**

**9 <sup>3</sup>Department of Biology, State University of New York College of Environmental  
10 Sciences, Syracuse University, 107 College Place Syracuse, NY 13244, USA**

**11 <sup>4</sup>Department of Environmental Forest Biology and Forestry, Syracuse, NY 13210, USA**

**12 <sup>5</sup>Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105**

**13 <sup>6</sup>Department of Biology and Marine Biology, University of North Carolina Wilmington,  
14 601 South College Road, Wilmington, NC 28403, USA**

**15 <sup>7</sup>Duke Network Analysis Center, Duke University, Durham, NC 27708, USA**

**16 <sup>8</sup>School of Forestry, 200 E. Pine Knoll Dr., Northern Arizona University, Flagstaff, AZ  
17 86011, USA**

**18 <sup>9</sup>Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, AZ  
19 86011, USA**

## **20 ABSTRACT**

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

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

21 **INTRODUCTION**

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

41 Empirical and theoretical work in network ecology and evolutionary biology point  
42 to the need for examinations of the genetic basis of ecological network structure. Anal-  
43 yses of ecological networks have demonstrated that indirect effects can lead to self-  
44 organization, producing sign-changing, amplifying and/or dampening effects (Fath and  
45 Patten, 1998; Newman, 2006; Sole and Bascompte, 2006), and other studies have demon-  
46 strated that indirect effects of interactions among species can lead to network structures  
47 that amplify or dampen the effects of selection, such as the formation of star-like struc-  
48 tures in which there is a “central” species or group of species that interact with other  
49 peripheral species can amplify selection events (Lieberman et al., 2005). Also, work by  
50 Toju et al. (2014, 2016, 2017) observed consistent patterns of centralized interactions of  
51 species modules (i.e., groups of species that interact more strongly within their group  
52 than with other species) focused around hubs of plant-fungal interactions. In other words,  
53 a small number of plant and fungal symbionts tended to have disproportionate numbers  
54 of interactions with other species and likely are the drivers in determining community  
55 assembly, structure and dynamics. Interspecific indirect genetic effects (IIGE) theory  
56 (*sensu* Shuster et al. (2006)) in evolutionary biology also point to the importance of  
57 studying the genetics of interaction network structure. Genetically based differences in  
58 network structure among individuals can be acted upon by natural selection when there  
59 are fitness consequences of different networks of IIGEs, leading to community evolution  
60 per Whitham et al. (2020) and, by extension, network evolution. For example, although  
61 the analysis was of abundances rather than interaction networks, Gehring et al. (2014,  
62 2017) found that the mycorrhizal communities on the roots of drought tolerant and intol-  
63 erant trees are dominated by different orders of ectomycorrhizal fungal mutualists that  
64 also differ in the benefits they provide that enhance tree performance. Because drought  
65 tolerant genotypes are three times more likely to survive record droughts, selection acts

66 both on the tree and its fungal community and with increased drought the community  
67 phenotype has changed over time. Also, in an antagonistic interaction context, Busby  
68 et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods in  
69 a common garden, the impacts of these strong interactors results in a different and di-  
70 minished community of arthropods relative to control trees. These examples collectively  
71 support the possibility that selection acting on the tree may alter the network structure of  
72 associated communities in which different networks of communities are most likely to  
73 survive drought and pathogen outbreaks, respectively. Regardless of whether the IIQE  
74 is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also  
75 affects the relative fitness of the tree), selection at the level of the tree population or  
76 its community, or both, can change network structure and alter community dynamics  
77 (Whitham et al., 2020).

78 In this context, the “genetic similarity rule” of community genetics provides a  
79 useful framework we can apply to interaction networks at the nexus of ecological  
80 and evolutionary dynamics. In a study combining experimental common gardens and  
81 landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and  
82 arthropods, Bangert et al. (2006) observed that individual genotypes that are more  
83 genetically similar will tend to have similar phytochemical traits and thus tend to have  
84 similar interactions with other species. Although this is likely to have consequences for  
85 interactions and network structure, studies in the network ecology literature generally  
86 do not include a genetic component (Lau et al., 2017) and community genetics studies  
87 have primarily focused on community composition in terms of the abundance of  
88 species (Des Roches et al., 2018). Some studies have examined the effects of genetic  
89 variation on trophic chains in plant-associated communities (including *Populus*, *Sol-*  
90 *idago*, *Oenothera*, *Salix*) (Bailey et al., 2005; Johnson, 2008; Smith et al., 2011, 2015;  
91 Barbour et al., 2016) and generally found that increasing genotypic diversity leads to  
92 increased trophic complexity. We are aware of only two studies that explicitly examined  
93 the effect of genotypic variation on interaction networks between tree individuals and  
94 associated herbivores using ecological network metrics (Lau et al., 2016a; Keith et al.,  
95 2017). Both found that genotypic diversity generates increased network modularity  
96 (i.e., compartmentalization); however, both were examining networks at the scale of  
97 forest stands, rather than networks associated with individual trees; therefore, neither  
98 was able to observe replicated networks in order to statistically test for genetic effects  
99 on network structure and quantify the genetic component (i.e., heritable variation) in  
100 network structure.

101 Here, we investigate how genetic variation in a foundation tree species determines  
102 the structure of a network of interactions among a community of tree associated lichens.  
103 We used a long-term (20+ years), common garden experiment with clonally replicated  
104 *Populus angustifolia* individuals of known genetic identity (Martinsen et al., 2001).  
105 We focused on a community of epiphytic lichen species, as previous research has  
106 demonstrated significant compositional effects of genotypic variation on lichen in this  
107 system (Lamit et al., 2011, 2015b,a) and epiphytic organisms in other systems (Winfrey  
108 et al., 2011; Zytynska et al., 2011). Applying a probability-theory based network  
109 modeling approach (Araújo et al., 2011), we constructed a set of interaction network  
110 models for the lichens associated with individual trees. Using these models, we then  
111 examined the genetic basis of the structure of these ecological networks via several

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

## 133 MATERIALS AND METHODS

### 134 Study System

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

145 A long-term, common garden experiment was used to isolate the effect of tree geno-  
146 type from the effect of the localized microenvironment associated with each individual  
147 and spatial autocorrelation. Established in 1992, asexually propagated clones of geno-  
148 typed *P. angustifolia* individuals were obtained from wild collections and planted in  
149 fully randomized design at the Ogden Nature Center, Ogden, UT. From the population  
150 of established individuals in the common garden, we chose a total of ten genotypes,  
151 replicated between 3 and 8 times each, for sampling. We selected tree genotypes that  
152 generally had lichens present in order to permit the construction of interaction networks.

153 **Bark Lichens and Trait Observations**

154 On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm<sup>2</sup>  
155 cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens,  
156 we were able to rapidly assess lichen interactions by quantifying thalli of different  
157 species occurring in close proximity. Sampling was restricted to the northern aspect  
158 of the trunk to maximize the abundance of lichens and control for the effect of trunk  
159 aspect. Two adjacent 100 cm<sup>2</sup> quadrats centered at 50 cm and 95 cm from ground level  
160 were sampled (Fig 1). The observed lichen community included: *Athallia holocarpa*,  
161 *Candelariella subdeflexa*, *Myriolecis hagenii*, *Rinodina freyi*, *Physcia adscendens*,  
162 *Physciella melanchra*, *Physcia undulata*, *Xanthomendoza galericulata*, *Xanthomendoza*  
163 *montana*. Several other species were not observed in the present study but are known to  
164 occur in this region: *Melanohalea elegantula*, *Melanohalea subolivacea*, *Phaeophyscia*  
165 *ciliata* and *Phaeophyscia orbicularis*.

166 The cell size and checkerboard sampling pattern was chosen to isolate the individuals  
167 in each cell. In a survey of *Xanthomendoza galericulata* in the common garden, we had  
168 observed a median thallus size of  $0.12 \pm 0.001 \text{ cm}^2$  (1 S.E.) (Supporting Information,  
169 Fig. 1). This expected thallus size formed the basis for our sampling design, such that  
170 lichen observations were spatially independent of thalli present in other cells but exposed  
171 to similar micro-environmental conditions created by the bark and the location of the  
172 sampling area on an individual tree. Therefore, we were confident in treating the cell-  
173 wise observations in quadrats as independent with respect to lichen-lichen interactions.  
174 We quantified the texture of the bark in the quadrat as the percent of 1 cm<sup>2</sup> cells with  
175 rough bark. In addition to bark roughness, we also examined several bark chemistry  
176 traits by taking bark samples immediately adjacent to each quadrat. We used previously  
177 collected phytochemical data from Lamit et al. (2011), including the concentration of  
178 condensed tannins, carbon and nitrogen. Additionally, we quantified bark pH for each  
179 tree. Bark samples were collected by excavating adjacent to the quadrat down to a depth  
180 of 2 mm. Bark pieces were air dried for storage and later processing. Samples were  
181 prepped for pH measurements by crushing with a mortar and pestle until all pieces were  
182  $\leq 0.5 \text{ cm}$  in diameter, creating equivalent surface areas among samples. 0.5 g of crushed  
183 bark was placed in a 15 ml Falcon collection tube with 5 ml of deionized water. Tubes  
184 were capped and let sit for 24 hrs prior to pH measurement with a SevenGo™ pH meter  
185 (Mettler Toledo).

186 **Lichen Network Modeling**

187 For each tree, repeated observations of lichens were made in order to construct replicated  
188 interaction networks for each genotype. We conducted a modified sampling procedure  
189 originally developed by Lamit et al. (2015b) with the addition that we quantified the  
190 presence of lichens in the 1 cm<sup>2</sup> cells on individual trees of *P. angustifolia*. Unipartite  
191 networks were generated using the conditional probabilities of each species pair, i.e., the  
192 probability of observing one species given an observation of another species  $P(S_i|S_j)$ ,  
193 based on the method developed by Araújo et al. (2011). To calculate conditional  
194 probabilities, we quantified the individual probabilities of species occurrences  $P(S_i)$  and  
195 the joint probability of co-occurrences  $P(S_i, S_j)$  using the frequencies of each species  
196 and their co-occurrences. We were then able to calculate the conditional probabilities of  
197 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

198 a matrix that could possibly be asymmetric, i.e.,  $P(S_i|S_j)$  does not have to be equal to  
199  $P(S_j|S_i)$ . Another important property of this matrix is that the diagonal,  $P(S_i|S_i)$ , was  
200 equal to one for all species present and zero for species that were not observed in any  
201 cell.

202 We then applied an analytical procedure to remove non-significant links between  
203 species. This procedure determines if the joint probability of a species pair (i.e.,  $P(S_i, S_j)$ )  
204 is different from zero (Fig. 2). Here, a confidence interval  $CI_{95\%}$  is calculated as as  
205  $CI_{95\%} = E[S_iS_j] * Z_{95\%} * \sqrt{V(S_iS_j)}$ , where the expected frequency of co-occurrences  
206  $E(S_iS_j)$  is the total number of cells surveyed ( $N$ ) times the independent probabilities of  
207 each species  $P(S_i) * P(S_j)$ ,  $Z_{95\%}$  is the Z-score for 95% from a Z-distribution and the  
208 expected variance of  $E(S_iS_j)$  is the total number of cells times the expected probability  
209 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  
210 the observed number of co-occurrence falls outside of the confidence interval, the  
211 joint probability  $P(S_i, S_j)$  is determined to be equal to the product of the individual  
212 probabilities (i.e.,  $P(S_i)\bar{P}(S_j)$ ), and the conditional probability reduces to the individual  
213 probability of that species  $P(S_i)$ . Therefore, unless the co-occurrence of a species pair  
214 falls outside the confidence interval, the probability that the observation of one species  
215 given the other is no different than simply observing that species alone. This enables us  
216 to remove links from a given network by re-scaling the resulting conditional probabilities  
217 through subtraction of the individual probabilities from the conditional probabilities (i.e.,  
218 how different the conditional probability is from the independent probability), which  
219 makes any species with a non-significant conditional probability zero.

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

## 234 Analyses, Software and Data

235 To quantify the structural variation of lichen networks we calculated several metrics at  
236 both the level of node and whole networks. Although there are many other metrics, for  
237 the sake of simplicity we focus on a subset that represent the primary interesting features  
238 of network structure, see Lau et al. (2017). We calculated the number of interactions or  
239 “links” in each network (degree), which provides a measure of the size of the network  
240 (Lau et al., 2016a; Borrett and Lau, 2014). We also calculated the centralization of each  
241 network using Freeman's centrality, which measures the evenness of the distribution of  
242 interactions among the species in the network, using the sna package (Butts, 2019).

243 In a network with low centralization species have similar strengths and numbers of  
244 interactions. A network with high centralization tends to have one or small number  
245 of species that interact with other species. We used a related function to calculate  
246 the centrality of each species (i.e., node level centrality) in each network as well. To  
247 calculate separate metrics for positive and negative links, as the networks contained not  
248 only positive and negative connections but also directional connections (both in-coming  
249 and out-going), we calculated the same network metrics for all combinations of these  
250 types of connections using recently developed methods for signed, weighted and directed  
251 networks (Everett and Borgatti, 2014) using the `signnet` package (Schoch, 2020).

252 We used a combination of parametric and non-parametric, permutation based frequentist  
253 statistical analyses to test for the effects of genetic variation on lichen communities  
254 and their interaction networks. To assess the effect of genotype on traits as univariate response  
255 variables (including the metrics of network structure), we used additive, random effects models with Restricted Maximum Likelihood (REML) conducted in R via the  
256 `lme4` and `RLRsim` packages (Bates et al., 2015; Scheipl et al., 2008). To conform to  
257 test assumptions, traits were root transformed with the exception of condensed tannin  
258 concentration and carbon-nitrogen ratio, which were rank and  $\log_{10}$  transformed, respectively. Differences in node level centrality among species was tested using ANOVA and  
259 Tukey-HSD multiple comparison tests. Correlations among trait variables and network  
260 metrics were quantified and tested using linear correlations of Pearson's  $r$ . For multivariate  
261 response variables, such as lichen community composition and network structure,  
262 we used distance based multivariate statistical approaches. To quantify the similarity of  
263 lichen networks among individual trees, we calculated the pairwise Euclidean distance  
264 of the  $\mathbf{D}$  interaction matrices among all trees (Newman, 2010). To test for the effects of  
265 genotype and other predictor variables on network similarity we conducted Permutational  
266 Analysis of Variance (PERMANOVA) with `vegan` (Oksanen et al., 2019). For  
267 visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling  
268 (NMDS) (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of  
269 these multivariate responses and fitted vectors for continuous predictor variables to the  
270 ordinated values (Oksanen et al., 2019). Using random initial configurations with a  
271 maximum of 500 iterations and a change in stress threshold of less than  $10^{-12}$ . This was  
272 repeated for one to four dimension configurations, and the configuration with the lowest  
273 dimensionality and unexplained variation less than 10% was selected. For all tests  
274 where genotype was used as a predictor, we quantified the heritability of the response  
275 variable. Because the trees in the garden were clonal replicates of each genotype, we  
276 calculated broad-sense heritability, which is the genotypic variance divided by the total  
277 phenotypic variance (Conner and Hartl, 2004), which can be interpreted as a measure of  
278 the phenotypic variance due to genotypic variation. All analyses were conducted using  
279 R version 4.0.2 (R Core Team, 2020). Code and data for the project are openly available  
280 as a reproducible workflow using `drake` (Landau, 2018), which is archived via Zenodo  
281 [zenodo.com/doi/XXXXXX](https://zenodo.com/doi/XXXXXX).

## 284 RESULTS

285 In support of our first hypotheses, we found that tree genotype influenced lichen net-  
286 work structure and that multiple lichen network metrics were heritable. Tree genotype

significantly predicted the structural similarity of lichen networks and, overall, network-level metrics responded significantly to tree genotype, including network degree and centralization including both in-coming and out-going links or when separated into in-coming only or out-going only (Table 1, Fig. 4). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree and positive in-going centralization. Metrics calculated with negative links were not significant, including degree (negative) and both in-coming (negative) and out-going centralization (negative).

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

**Table 1.** Genotypic effects on the associated lichen network structure. *RLRT* is the statistic from the restricted likelihood ratio tests.

The genetic response of network centralization was driven by variation in *Athallia holocarpa*. Centrality varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ ,  $p\text{-value} < 0.0001$ ). The node-level metrics for *A. holocarpa* displayed the strongest response to tree genotype with high levels of heritability of positive centrality for both the in-coming ( $RLRT = 3.61$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0240$ ) and out-going ( $RLRT = 3.13$ ,  $H^2 = 0.30$ ,  $p\text{-value} = 0.0327$ ) perspectives but not for either negative centrality metrics in-coming ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 1$ ) or out-going ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p\text{-value} = 0.4543$ ). None of the other species' centralities showed a genotypic response (Supporting Information, Fig. 2) with the exception of *X. montana* ( $RLRT = 2.92$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0375$ ); however, the centrality of *X. montana* was much lower overall relative to *A. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

In support of our second hypothesis, analysis of trait covariation revealed that genotype indirectly influenced lichen network centralization via 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 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).

	df	SS	R2	Pseudo-F	p-value
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

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

## DISCUSSION

### Ecological and Evolutionary Importance of Network Heritability

Although previous studies have examined aspects of networks, such as trophic complexity (Barbour et al., 2016) and forest stand level interaction network structure (Lau et al., 2016b; Keith et al., 2017), this is the first study that we are aware of to examine the heritability of network structure with replicated networks at the genotype scale. Previous work in the evolution of ecological networks have primarily focused on macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al., 2018; Harmon et al., 2019) or have been simulation based individual-level models that integrate intraspecific variation to the species level (Maliet et al., 2020), even though recent syntheses have pointed to the importance of processes operating across scales of organization (Guimarães, 2020). There are two important functional ramifications of genetically based variation in network structure. First, heritability of network structure suggests that some amount of interaction network complexity is determined and therefore could be predicted by genetic identity. Variation in space and time create variation in ecological networks that influences evolutionary dynamics via shifts in ecological dynamics, such as population demographics (Guimarães, 2020). Given that ecosystems are comprised of hundreds and thousands of species, each having a multitude of interactions, the potential to find traction for making predictions in the context of ecological, let alone evolutionary, dynamics seems daunting. The promise of predictability lies in the presence of asymmetries in ecosystems, such as hierarchy created by foundation

349 species via differences in body size and/or life-history strategies (Ellison et al., 2005).  
350 Second, heritability (i.e., genetic determination) means that there is structure in the  
351 spatial or temporal variation that is created by individuals of foundation species whose  
352 traits are in part determined by underlying trait differences. Although this variation  
353 is inherently a function of both genetic and environmental effects (Conner and Hartl,  
354 2004), the community and network-level effects are also a function of the scale of the  
355 interaction (Shuster et al., 2006; Lau et al., 2017).

356 Notably, even if the composition of the communities is the same among individuals  
357 and genotypes, interactions may not be. We didn't observe compositional differences  
358 using the same data from which the lichen networks were derived. If we only had  
359 our composition dataset from this study, we would have concluded no response of the  
360 lichen community to tree genotype, even though the underlying interactions among  
361 lichen species does vary among genotypes. As such differences in network structure  
362 could occur without observable differences in species richness or community com-  
363 position, which have been the primary focus of the majority of community genetics  
364 studies (Whitham et al., 2020). Community composition of lichens has previously been  
365 observed to be different among tree genotypes in the same experimental garden (Lamit  
366 et al., 2011, 2015b). The different results observed in the present study is likely a result  
367 of differences in lichen quantification and the tree genotypes observed leading to overall  
368 higher abundances of observed lichens to assure the possibility of observing lichen inter-  
369 actions. The previous study used a visual percent cover estimation, unlike the current  
370 study, which observed lichens at the scale of 1 cm<sup>2</sup> cells, which could over-estimate  
371 cover depending on the frequency at which actual thallus size was less than 1 cm<sup>2</sup>,  
372 as well as both the northern and southern aspects of each tree. These differences do  
373 not negate the findings of either study. The present study's finding of differences in  
374 network structure without significant compositional differences points to the importance  
375 of quantifying how network structure changes in response to genetic variation in order to  
376 fully understand evolutionary dynamics in complex communities. Having not observed  
377 a compositional effect of tree genotype without measuring the network structure could  
378 lead to the conclusion of no genetic effect on the community, even though differences  
379 in network structure are leading to altered, local evolutionary dynamics. It is possible  
380 that these underlying differences in interactions among lichens could lead to differences  
381 in community composition at a future point in time via their effects on species abun-  
382 dances (Shuster et al., 2006); however, this is not needed for evolutionary dynamics  
383 to occur via selection that leads to shifts in trait distributions without shifting species  
384 abundance distributions, which is possible under stabilizing, disruptive and directional  
385 selection (Conner and Hartl, 2004), so long as the relative abundances of each species is  
386 imperceptibly changed. Thus, it is imperative that further community genetics research  
387 assess or at least be aware of the potential effects of variation in interactions and not  
388 just observe species abundances, otherwise community level genetic effects may be  
389 underestimated, especially when cumulative interaction effects are taken into account  
390 (Borrett et al., 2007, 2010).

391 Furthermore, the demonstration of the heritability of interaction networks, without  
392 significant differences in community composition, provides clear empirical evidence  
393 that IIGEs need to encompass the structure of interaction networks. Although IIGE  
394 theory provides a quantitative framework within which to approach evolutionary the-

ory at higher levels of biological organization (from populations to communities and ecosystems), this theory has focused on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham et al., 2012, 2020) and has not yet integrated developments from the ecological or evolutionary network theory literature. Thus, it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated this network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be damped or magnified within the system of interacting species (Smith et al., 2011; Keith et al., 2017). Although such a synthesis necessitates a much greater effort than can be afforded in this paper, it is possible to point to several productive pathways forward. In terms of interaction networks, foundation species are relatively central within the system of interactions, that is their direct and/or indirect effects are greater than other species. So, when the more centralized (foundation) species have genetically based interactions, genetic effects will tend to be propagated and possibly magnified in the community. Here, we found that even though more abundant or more centralized (i.e., “important”) species were present in the community, their effects were not the singularly responding to genetic effects, rather the similarity of the whole network depending on interactions among multiple species. Considering the impact of network structure would be a productive path forward for the theoretical development and application of the IIGE concept.

#### Network Structure and Levels of Selection

The demonstration of evolution at any scale requires demonstrating three key elements (Conner and Hartl, 2004), which multilevel selection theory posits can occur simultaneously multiple levels of ecological organization (Whitham et al., 2003, 2020). First, there must be variation in the structure (composition, abundance, species interactions, diversity, interaction network structure) of communities. 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 (Bangert et al., 2006, 2008; Barbour et al., 2009; Whitham et al., 2020). Importantly, the current 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 (i.e., community evolution). The differential survival and performance of individual tree genotypes will simultaneously result in selection occurring on the lichen community and network structure that it supports. Since our findings show that networks are heritable, another metric of community evolution would be to quantify how networks change over time in response to an invasive species, climate change, or some other agent of selection, which represents a frontier for future ecological network studies.

The current study shows the utility of considering the spatial and temporal scales of ecological and evolutionary dynamics. In line with previous empirical studies (Bangert et al., 2006; Zook et al., 2010; Zytynska et al., 2012), we found that the assembly of ecological networks can have a measurable genetic basis depending on the spatial

scale of interactions, due in part, to asymmetries in size and longevity of organisms. Intra-specific, genotypic diversity among cottonwood trees appears to be a major factor in the creation of meta-communities of lichens on individual trees that form interaction modules with different dynamics. When communities are comprised of individuals whose habitat is primarily determined by another organism, these communities inherently form modules within the larger ecosystem, as they tend to interact more with each other than with other individuals (Lau et al., 2017). Our study demonstrates that the localized environmental differences determined by the genetic variation within a single tree species can not only impact community composition, as repeatedly demonstrated in other community genetics studies (Whitham et al., 2006; Des Roches et al., 2018), but also shape the structure of interactions among individuals. 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” in the terminology of defense networks. As mentioned previously, one class of networks that are theorized to have amplifying effects on networks have centralized “star” shapes with one or a few species at the center and radiating interactions out from the central core (Lieberman 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 likely that these networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the centralized network structure found on that tree genotype, as multiple studies have found significant impacts of the removal of foundation species in different systems (Keith et al., 2017; Des Roches et al., 2018). 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 species with large differences in body-size and longevity, which could be contributing to interaction network structure (e.g., modules and centralized species). As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (Whitham et al., 2012; Evans et al., 2013; Whitham et al., 2020).

Ecological network studies have focused on asymmetry and the quantification of its structure in communities, which can arise at different scales in space time or ecological organization. The impacts of asymmetry on evolution from community dynamics have primarily produced qualitative discussion (Bascompte et al., 2006; Díaz-Castelazo et al., 2010; Guimarães et al., 2011; Thompson, 2013). More specific predictions can be found in applications of evolutionary game theory, and although developed at the population scale, such theory can apply to communities (Lieberman et al., 2005). One seemingly useful direction 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 feedbacks to the origin, whereas cyclic networks contain feedbacks to one or more origins. This is equivalent to “unidirectional” and “reciprocal” genetic effects in the context of IIGE theory (Whitham et al., 2020). As we do not have an estimate of the effect of the lichen at the larger scale of

486 the fitness of the tree they occur on, we can not determine whether the lichen networks in  
487 this system are cyclic or not. In terrestrial ecosystems, lichens play important ecological  
488 roles, such as substrate stabilization (Root et al., 2011) and nitrogen fixation (Nelson  
489 et al., 2018). Some epiphytic lichens can have demonstrable effects on the availability of  
490 nutrients for the trees that they are associated with (Norby and Sigal, 1989). Although  
491 none of the lichens the present study's system is known to fix nitrogen, it is possible  
492 that they might add micro-nutrients or provide some other unobserved benefit to their  
493 host trees. Elucidating the presence of and quantifying such feedbacks would allow  
494 for the determination of the cyclic nature and potential evolutionary dynamics. If there  
495 are positive effects of lichens on host trees that might increase their ability to respond  
496 to environmental stress, then selection could enhance tree performance and trees with  
497 superior communities are more likely to survive. Gehring et al. (2014, 2017) showed this  
498 with ectomycorrhizal communities in which trees with superior mutualist communities  
499 were more likely to survive drought and community evolution occurred (Whitham et al.,  
500 2020). However, such feedbacks to the higher level of the foundation species are not a  
501 requirement for evolution, and, regardless of whether networks are rooted (no feedbacks)  
502 or cyclic (feedbacks present), selection at the community level leading to evolution can  
503 still occur. Specifically within the context of the current study, even if lichens and their  
504 interactions do not feed back to affect the performance and ultimate fitness of the tree on  
505 which they reside, non-random death of trees, such as those observed for drought in arid  
506 systems Sthultz et al. (2009); Gehring et al. (2017), can still result in selection at the  
507 community level and evolution. For example, when a tree dies from some event (e.g., a  
508 drought, fire, storm, etc.), its lichen network is selected against while intact networks  
509 persist on other trees that survive this selection event.

510 Last, it is worth considering the ecological and evolutionary dynamics at the scale  
511 of the lichen individuals. Since lichens are multi-species complexes, there is also the  
512 potential for evolutionary dynamics to shift within the context of the lichen symbiosis.  
513 There is substantial evidence that lichens have served as the “cradle of symbiotic  
514 fungal diversification” (Arnold et al., 2009) and recent research has shown significant  
515 network structure of endolichenic fungi and lichens collected from across North America  
516 (Chagnon et al., 2016). Analysis of the structure of ecological networks has generally  
517 supported the conclusion that nestedness, or the degree to which species tend to inter-  
518 act with similar subsets of the community, tends to promote stability in mutualistic,  
519 primarily bipartite (i.e., two-mode), networks and modularity contributes to the stabi-  
520 lization of antagonistic networks (Elias et al., 2013; Grilli et al., 2016). Although there  
521 is growing evidence that the nestedness of mutualistic networks is not necessarily the  
522 result of selection for systems-level properties that promote stability but could be either  
523 product of asymptotic abundance distributions leading to uneven interaction frequencies  
524 (Staniczenko et al., 2013) and/or a by-product of selection and divergence creating  
525 network “spandrels” in ecosystems (Valverde et al., 2018), this does not preclude the  
526 functional consequences of network structure but rather the developmental or evolu-  
527 tionary processes that have produced the structure. In the present study, we did not  
528 examine nestedness or modularity of the lichen networks as we could not find metrics for  
529 analyzing networks that are not only weighted and directed but also signed. Hopefully  
530 future network theoretic developments will make the appropriate metrics available to  
531 conduct these analyses.

532 **Conclusion**

533 We found support for both of our hypotheses. First, tree genotype influenced the network  
534 structure of lichen communities associated with narrowleaf cottonwoods in a riparian  
535 forest ecosystem. Network similarity and metrics of network structure tended to be more  
536 similar on trees of the same genotype. Generally, this genetic effect was manifested  
537 in positive interactions and largely driven by *A. holocarpa*. Second, the genetically  
538 based trait, bark roughness, was observed to affect network variation, largely via shifts  
539 in positive in-coming and out-going interactions. Chemistry traits, whether genetically  
540 based (e.g., tannin concentration) or not, were not significantly correlated with lichen  
541 network structure. Bark roughness has been demonstrated previously to be under strong  
542 genetic control in cottonwoods (Bdeir et al., 2017) and other foundation tree species,  
543 such as *Eucalyptus* (Nantongo et al., 2020). Bark roughness has also been shown to  
544 be an important tree trait influencing bark lichens (Lamit et al., 2015b); however this  
545 is the first demonstration of a link from genetics to lichen network structure. As such,  
546 these results have important implications for the influence of genetically based variation  
547 in ecosystems with networks of interacting species. Going forward, future work could  
548 extend the many previous community genetics studies that have focused on sessile  
549 organisms, such as galling insects (Bailey et al., 2005; Whitham et al., 2006; Crutsinger  
550 et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify the frequency of these  
551 interactions in the context of the larger community. Network modeling and analysis will  
552 provide useful tools for the identification of species within network modules that are  
553 most important to study in systems where little is known about the natural history of  
554 organisms in an ecosystem. Such investigations will bring us closer to understanding the  
555 evolutionary drivers of Darwin's entangled bank and the interconnectedness of species  
556 in complex communities (Darwin, 1859; Dátillo et al., 2016).

557 **Acknowledgments**

558 This work was supported by the National Science Foundation grant (DEB-0425908) and  
559 Integrative Graduate Research Traineeship (IGERT) fellowships for M.L. and L.L. The  
560 Ogden Nature Center staff helped to maintain the common gardens. Lichen sampling  
561 was supported by Todd Wojtowicz, Luke Evans and David Solance Smith.

562 **REFERENCES**

- 563 Araújo, M. B., Rozenfeld, A., Rahbek, C., and Marquet, P. A. (2011). Using species  
564 co-occurrence networks to assess the impacts of climate change. *Ecography*, 34:897–  
565 908.
- 566 Arnold, A. E., Miadlikowska, J., Higgins, K. L., Sarvate, S. D., Gugger, P., Way, A.,  
567 Hofstetter, V., Kauff, F., and Lutzoni, F. (2009). A phylogenetic estimation of trophic  
568 transition networks for ascomycetous Fungi: Are lichens cradles of symbiotrophic  
569 Fungal diversification? *Systematic Biology*, 58(3):283–297.
- 570 Bailey, J. K., Schweitzer, J. A., Ubeda, F., Koricheva, J., LeRoy, C. J., Madritch, M. D.,  
571 Rehill, B. J., Bangert, R. K., Fischer, D. G., Allan, G. J., and Whitham, T. G. (2009).  
572 From genes to ecosystems: a synthesis of the effects of plant genetic factors across  
573 levels of organization. *Philosophical transactions of the Royal Society of London.  
Series B, Biological sciences*, 364(1523):1607–16.

- 575 Bailey, J. K., Wooley, S. C., Lindroth, R. L., and Whitham, T. G. (2005). Importance  
576 of species interactions to community heritability: a genetic basis to trophic-level  
577 interactions. *Ecology Letters*, 0(0):051122062725008.
- 578 Bangert, R. K., Lonsdorf, E. V., Wimp, G. M., Shuster, S. M., Fischer, D., Schweitzer,  
579 J. A., Allan, G. J., Bailey, J. K., and Whitham, T. G. (2008). Genetic structure of a  
580 foundation species: Scaling community phenotypes from the individual to the region.
- 581 Bangert, R. K., Turek, R. J., Rehill, B., Wimp, G. M., Schweitzer, J. A., Allan, G. J.,  
582 Bailey, J. K., Martinsen, G. D., Keim, P., Lindroth, R. L., and Whitham, T. G. (2006).  
583 A genetic similarity rule determines arthropod community structure. *Molecular  
ecology*, 15:1379–1391.
- 584 Barbour, M. A., Fortuna, M. A., Bascompte, J., Nicholson, J. R., Julkunen-Tiitto, R.,  
585 Jules, E. S., and Crutsinger, G. M. (2016). Genetic specificity of a plant-insect food  
586 web: Implications for linking genetic variation to network complexity. *Proceedings of  
587 the National Academy of Sciences of the United States of America*, 113(8):2128–2133.
- 588 Barbour, R. C., O'Reilly-Wapstra, J. M., Little, D. W. D., Jordan, G. J., Steane, D. A.,  
589 Humphreys, J. R., Bailey, J. K., Whitham, T. G., Potts, B. M., De Little, D. W., Jordan,  
590 G. J., Steane, D. A., Humphreys, J. R., Bailey, J. K., Whitham, T. G., and Potts, B. M.  
591 (2009). A geographic mosaic of genetic variation within a foundation tree species  
592 and its community-level consequences. *Ecology*, 90(7):1762–1772.
- 593 Bascompte, J., Jordano, P., and Olesen, J. M. (2006). Asymmetric Coevolutionary  
594 Networks Facilitate Biodiversity Maintenance \r10.1126/science.1123412. *Science*,  
595 312:431–433.
- 596 Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects  
597 models using lme4. *Journal of Statistical Software*, 67(1):1–48.
- 598 Bdeir, R., Muchero, W., Yordanov, Y., Tuskan, G. A., Busov, V., and Gailing, O. (2017).  
599 Quantitative trait locus mapping of Populus bark features and stem diameter. *BMC  
600 Plant Biology*.
- 601 Borrett, S. R., Fath, B. D., and Patten, B. C. (2007). Functional integration of ecological  
602 networks through pathway proliferation. *Journal of Theoretical Biology*, 245(1):98–  
603 111.
- 604 Borrett, S. R. and Lau, M. K. (2014). enaR: An R package for Ecosystem Network  
605 Analysis. *Methods in Ecology and Evolution*, 5(11):1206–1213.
- 606 Borrett, S. R., Whipple, S. J., and Patten, B. C. (2010). Rapid development of indirect  
607 effects in ecological networks. *Oikos*, 119(7):1136–1148.
- 608 Busby, P. E., Lamit, L. J., Keith, A. R., Newcombe, G., Gehring, C. A., Whitham, T. G.,  
609 and Dirzo, R. (2015). Genetics-based interactions among plants, pathogens, and  
610 herbivores define arthropod community structure. *Ecology*, 96(7):1974–1984.
- 611 Butts, C. T. (2019). *sna: Tools for Social Network Analysis*. R package version 2.5.
- 612 Chagnon, P. L., U'Ren, J. M., Miadlikowska, J., Lutzoni, F., and Elizabeth Arnold,  
613 A. (2016). Interaction type influences ecological network structure more than local  
614 abiotic conditions: evidence from endophytic and endolichenic fungi at a continental  
615 scale. *Oecologia*, 180(1):181–191.
- 616 Conner, K. and Hartl, D. L. (2004). *A Primer of Ecological Genetics: a textbook*.  
617 Sinauer Associates, Inc., Sunderland, Massachusetts, 1st edition.
- 618 Crutsinger, G. M. (2016). A community genetics perspective: Opportunities for the  
619 coming decade. *New Phytologist*.

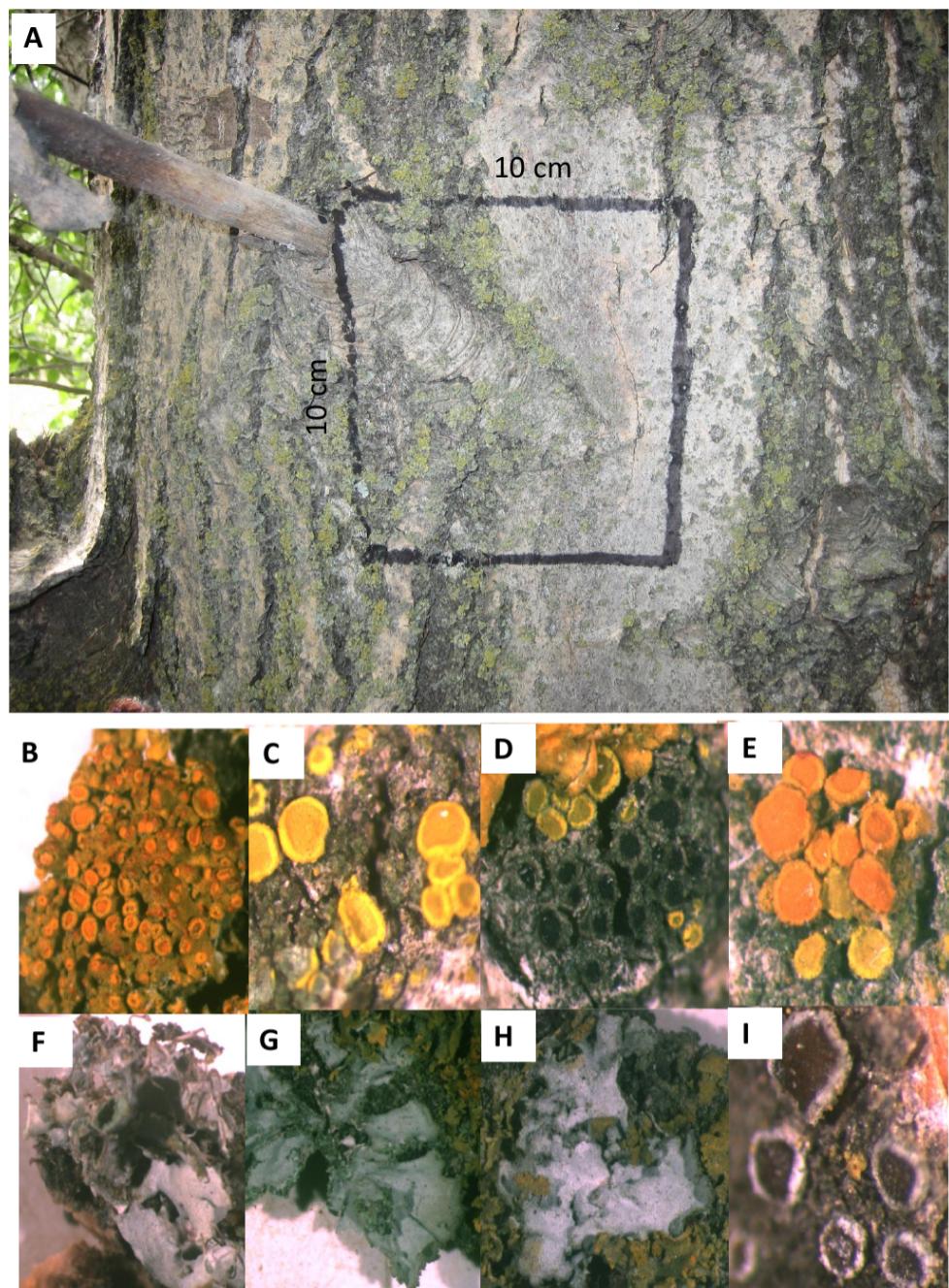
- 621 Crutsinger, G. M., Rudman, S. M., Rodriguez-Cabal, M. A., McKown, A. D., Sato,  
622 T., MacDonald, A. M., Heavyside, J., Geraldes, A., Hart, E. M., LeRoy, C. J., and  
623 El-Sabaawi, R. W. (2014). Testing a ‘genes-to-ecosystems’ approach to understanding  
624 aquatic-terrestrial linkages. *Molecular Ecology*, 23(23):5888–5903.
- 625 Darwin, C. (1859). *On the Origin of Species*. Murray, London.
- 626 Dátilo, W., Lara-Rodríguez, N., Jordano, P., Guimarães, P. R., Thompson, J. N., Marquis,  
627 R. J., Medeiros, L. P., Ortiz-Pulido, R., Marcos-García, M. A., and Rico-Gray,  
628 V. (2016). Unravelling Darwin’s entangled bank: Architecture and robustness of  
629 mutualistic networks with multiple interaction types. *Proceedings of the Royal Society  
B: Biological Sciences*.
- 631 Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison,  
632 M. T., Schweitzer, J. A., and Palkovacs, E. P. (2018). The ecological importance of  
633 intraspecific variation. *Nature Ecology and Evolution*, 2(1):57–64.
- 634 Díaz-Castelazo, C., Guimarães, P. R., Jordano, P., Thompson, J. N., Marquis, R. J., and  
635 Rico-Gray, V. (2010). Changes of a mutualistic network over time: Reanalysis over a  
636 10-year period. *Ecology*.
- 637 Elias, M., Fontaine, C., and Frank Van Veen, F. J. (2013). Evolutionary history and  
638 ecological processes shape a local multilevel antagonistic network. *Current Biology*,  
639 23(14):1355–1359.
- 640 Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R.,  
641 Foster, D. R., Kloeppe, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig,  
642 D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M.,  
643 Thompson, J., Von Holle, B., and Webster, J. R. (2005). Loss of foundation species:  
644 consequences for the structure and dynamics of forested ecosystems. *Frontiers in  
645 Ecology and the Environment*, 3(9):479–486.
- 646 Evans, D. M., Pocock, M. J. O., and Memmott, J. (2013). The robustness of a network  
647 of ecological networks to habitat loss. *Ecology letters*, 16:844–52.
- 648 Everett, M. G. and Borgatti, S. P. (2014). Networks containing negative ties. *Social  
649 Networks*, 38(1):111–120.
- 650 Fath, B. D. and Patten, B. C. (1998). Network synergism: Emergence of positive  
651 relations in ecological systems. *Ecological Modelling*, 107(2):127 – 143.
- 652 Gehring, C., Flores-Rentería, D., Sthultz, C. M., Leonard, T. M., Flores-Rentería,  
653 L., Whipple, A. V., and Whitham, T. G. (2014). Plant genetics and interspecific  
654 competitive interactions determine ectomycorrhizal fungal community responses to  
655 climate change. *Molecular Ecology*, 23(6):1379–1391.
- 656 Gehring, C. A., Sthultz, C. M., Flores-Rentería, L., Whipple, A. V., and Whitham, T. G.  
657 (2017). Tree genetics defines fungal partner communities that may confer drought  
658 tolerance. *Proceedings of the National Academy of Sciences*.
- 659 Gómez, J. M., Abdelaziz, M., Camacho, J. P. M., Muñoz-Pajares, A. J., and Perfectti, F.  
660 (2009). Local adaptation and maladaptation to pollinators in a generalist geographic  
661 mosaic. *Ecology Letters*, 12(7):672–682.
- 662 Goslee, S. C. and Urban, D. L. (2007). The ecodist package for dissimilarity-based  
663 analysis of ecological data. *Journal of Statistical Software*, 22:1–19.
- 664 Grilli, J., Rogers, T., and Allesina, S. (2016). Modularity and stability in ecological  
665 communities. *Nature Communications*, 7.
- 666 Guimarães, P. R. (2020). The Structure of Ecological Networks Across Levels of

- 667 Organization. *Annual Review of Ecology, Evolution, and Systematics*, 51(1).
- 668 Guimarães, P. R., Jordano, P., and Thompson, J. N. (2011). Evolution and coevolution  
669 in mutualistic networks. *Ecology letters*, 14(9):877–85.
- 670 Guimarães, P. R., Rico-Gray, V., Oliveira, P. S., Izzo, T. J., dos Reis, S. F., and Thompson,  
671 J. N. (2007). Interaction Intimacy Affects Structure and Coevolutionary Dynamics in  
672 Mutualistic Networks. *Current Biology*, 17(20):1797–1803.
- 673 Harmon, L. J., Andreazzi, C. S., Débarre, F., Drury, J., Goldberg, E. E., Martins,  
674 A. B., Melián, C. J., Narwani, A., Nuismer, S. L., Pennell, M. W., Rudman, S. M.,  
675 Seehausen, O., Silvestro, D., Weber, M., and Matthews, B. (2019). Detecting the  
676 macroevolutionary signal of species interactions. *Journal of Evolutionary Biology*,  
677 32(8):769–782.
- 678 Holeski, L. M., Hillstrom, M. L., Whitham, T. G., and Lindroth, R. L. (2012). Relative  
679 importance of genetic, ontogenetic, induction, and seasonal variation in producing a  
680 multivariate defense phenotype in a foundation tree species. *Oecologia*, 170:695–707.
- 681 Johnson, M. T. J. (2008). Bottom-up effects of plant genotype on aphids, ants, and  
682 predators. *Ecology*.
- 683 Keith, A. R., Bailey, J. K., Lau, M. K., and Whitham, T. G. (2017). Genetics-based inter-  
684 actions of foundation species affect community diversity, stability and network struc-  
685 ture. *Proceedings of the Royal Society B: Biological Sciences*, 284(1854):20162703.
- 686 Lamit, L., Bowker, M., Holeski, L., Næsborg, R. R., Wooley, S., Zinkgraf, M., Lindroth,  
687 R., Whitham, T., and Gehring, C. (2011). Genetically-based trait variation within a  
688 foundation tree species influences a dominant bark lichen. *Fungal Ecology*, 4(1):103–  
689 109.
- 690 Lamit, L. J., Busby, P. E., Lau, M. K., Compson, Z. G., Wojtowicz, T., Keith, A. R.,  
691 Zinkgraf, M. S., Schweitzer, J. A., Shuster, S. M., Gehring, C. A., and Whitham, T. G.  
692 (2015a). Tree genotype mediates covariance among communities from microbes to  
693 lichens and arthropods. *Journal of Ecology*, 103(4):840–850.
- 694 Lamit, L. J., Lau, M. K., Næsborg, R. R., Wojtowicz, T., Whitham, T. G., and Gehring,  
695 C. A. (2015b). Genotype variation in bark texture drives lichen community assembly  
696 across multiple environments. *Ecology*, 96(4):960–971.
- 697 Landau, W. M. (2018). The drake r package: a pipeline toolkit for reproducibility and  
698 high-performance computing. *Journal of Open Source Software*, 3(21).
- 699 Lau, M. K., Borrett, S. R., Baiser, B., Gotelli, N. J., and Ellison, A. M. (2017). Ecological  
700 network metrics: opportunities for synthesis. *Ecosphere*, 8(8):e01900.
- 701 Lau, M. K., Keith, A. R., Borrett, S. R., Shuster, S. M., and Whitham, T. G. (2016a).  
702 Genotypic variation in foundation species generates network structure that may drive  
703 community dynamics and evolution. *Ecology*, 97(3):15–0600.
- 704 Lau, M. K., Keith, A. R., Borrett, S. R., Shuster, S. M., and Whitham, T. G. (2016b).  
705 Genotypic variation in foundation species generates network structure that may drive  
706 community dynamics and evolution. *Ecology*.
- 707 Lieberman, E., Hauert, C., and Nowak, M. A. (2005). Evolutionary dynamics on graphs.  
708 *Nature*, 433(7023):312–316.
- 709 Lieberman, E., Hauert, C., and Nowak, M. A. (2005). Evolutionary dynamics on graphs.  
710 *Nature*, 433(7023):312–316.
- 711 Maliet, O., Loeuille, N., and Morlon, H. (2020). An individual-based model for  
712 the eco-evolutionary emergence of bipartite interaction networks. *Ecology Letters*,

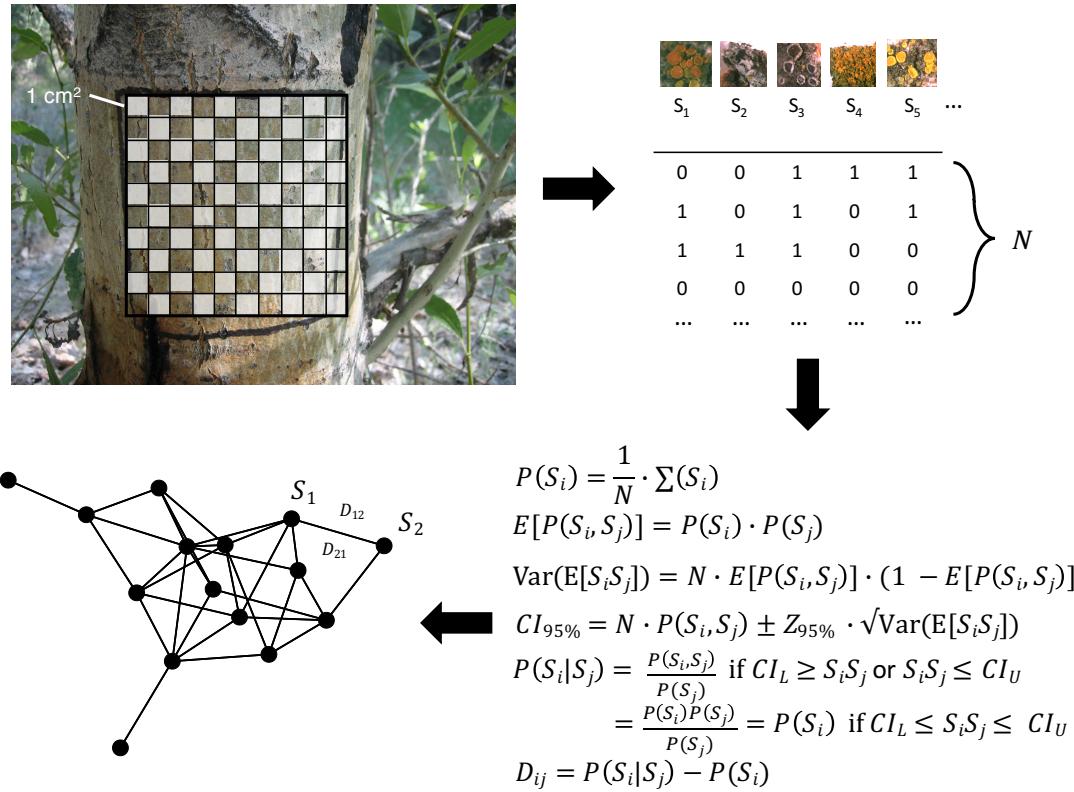
- 713 23(11):1623–1634.
- 714 Martinsen, G. D., Whitham, T. G., Turek, R. J., and Keim, P. (2001). Hybrid populations  
715 selectively filter gene introgression between species. *Evolution*, 55(7):1325–1335.
- 716 Moya-Laraño, J. (2011). Genetic variation, predator-prey interactions and food web  
717 structure. *Philosophical transactions of the Royal Society of London. Series B,  
718 Biological sciences*, 366(1569):1425–37.
- 719 Nantongo, J. S., Potts, B. M., Fitzgerald, H., Newman, J., Elms, S., Aurik, D., Dungey,  
720 H., and O'Reilly-Wapstra, J. M. (2020). Quantitative genetic variation in bark  
721 stripping of pinus radiata. *Forests*, 11(12):1356.
- 722 Nelson, P. R., McCune, B., Wheeler, T., Geiser, L. H., and Crisafulli, C. M. (2018).  
723 Lichen community development along a volcanic disturbance gradient at Mount St.  
724 Helens. In *Ecological Responses at Mount St. Helens: Revisited 35 years after the  
725 1980 Eruption*, pages 185–198. Springer New York.
- 726 Newman, M. (2010). *Networks: An Introduction*. Oxford University Press.
- 727 Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings  
728 of the National Academy of Sciences of the United States of America*, 103(23):8577–  
729 82.
- 730 Norby, R. J. and Sigal, L. L. (1989). Nitrogen fixation in the lichen Lobaria pulmonaria  
731 in elevated atmospheric carbon dioxide. *Oecologia*, 79(4):566–568.
- 732 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin,  
733 P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., and  
734 Wagner, H. (2019). *vegan: Community Ecology Package*. R package version 2.5-6.
- 735 Poisot, T., Cirtwill, A. R., Cazelles, K., Gravel, D., Fortin, M., and Stouffer, D. B.  
736 (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*,  
737 7(3):303–312.
- 738 R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R  
739 Foundation for Statistical Computing, Vienna, Austria.
- 740 Rezende, E. L., Lavabre, J. E., Guimarães, P. R., Jordano, P., and Bascompte, J. (2007).  
741 Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*,  
742 448(7156):925–8.
- 743 Root, H. T., Miller, J. E. D., and McCune, B. (2011). Biotic soil crust lichen diversity  
744 and conservation in shrub-steppe habitats of Oregon and Washington. *The Bryologist*,  
745 114(4):796.
- 746 Scheipl, F., Greven, S., and Kuechenhoff, H. (2008). Size and power of tests for a zero  
747 random effect variance or polynomial regression in additive and linear mixed models.  
748 *Computational Statistics & Data Analysis*, 52(7):3283–3299.
- 749 Schoch, D. (2020). *signnet: An R package to analyze signed networks*.
- 750 Shuster, S. M., Lonsdorf, E. V., Wimp, G. M., Bailey, J. K., and Whitham, T. G. (2006).  
751 COMMUNITY HERITABILITY MEASURES THE EVOLUTIONARY CONSE-  
752 QUENCES OF INDIRECT GENETIC EFFECTS ON COMMUNITY STRUCTURE.  
753 *Evolution*, 60(5):991.
- 754 Smith, D. S., Bailey, J. K., Shuster, S. M., and Whitham, T. G. (2011). A geographic  
755 mosaic of trophic interactions and selection: trees, aphids and birds. *Journal of  
756 evolutionary biology*, 24(2):422–9.
- 757 Smith, D. S., Lamit, L. J., Lau, M. K., Gehring, C. A., Shuster, S. M., and Whitham,  
758 T. G. (2015). Introduced elk alter traits of a native plant and its plant-associated

- 759 arthropod community. *Acta Oecologica*, 67:8–16.
- 760 Sole, R. and Bascompte, J. (2006). *Self-Organization in Complex Ecosystems*. Princeton  
761 University Press, Princeton, N.J.
- 762 Staniczenko, P. P., Kopp, J. C., and Allesina, S. (2013). The ghost of nestedness in  
763 ecological networks. *Nature Communications*, 4(1):1–6.
- 764 Sthultz, C., Gehring, C., and Whitham, T. (2009). Deadly combination of genes and  
765 drought: Increased mortality of herbivore-resistant trees in a foundation species.  
766 *Global Change Biology*, 15(8):1949–1961. Copyright: Copyright 2009 Elsevier B.V.,  
767 All rights reserved.
- 768 Thompson, J. N. (2013). *Relentless Evolution*. University of Chicago Press.
- 769 Toju, H., Guimarães, P. R., Olesen, J. M., and Thompson, J. N. (2014). Assembly of  
770 complex plant-fungus networks. *Nature Communications*.
- 771 Toju, H., Yamamichi, M., Guimarães, P. R., Olesen, J. M., Mougi, A., Yoshida, T., and  
772 Thompson, J. N. (2017). Species-rich networks and eco-evolutionary synthesis at the  
773 metacommunity level.
- 774 Toju, H., Yamamoto, S., Tanabe, A. S., Hayakawa, T., and Ishii, H. S. (2016). Network  
775 modules and hubs in plant-root fungal biomes. *Journal of the Royal Society Interface*.
- 776 Valverde, S., Piñero, J., Corominas-Murtra, B., Montoya, J., Joppa, L., and Solé, R.  
777 (2018). The architecture of mutualistic networks as an evolutionary spandrel. *Nature  
778 Ecology and Evolution*, 2(1):94–99.
- 779 Wade, M. J. (2007). The co-evolutionary genetics of ecological communities.
- 780 Weber, M. G., Wagner, C. E., Best, R. J., Harmon, L. J., and Matthews, B. (2017).  
781 Evolution in a Community Context: On Integrating Ecological Interactions and  
782 Macroevolution.
- 783 Whitham, T., Young, W., Martinsen, G., Gehring, C., Schweitzer, J., Shuster, S., Wimp,  
784 G., Fischer, D., Bailey, J., Lindroth, R., Woolbright, S., and Kuske, C. (2003). Com-  
785 munity and ecosystem genetics: A consequence of the extended phenotype. *Ecology*,  
786 84(3):559–573. Copyright: Copyright 2017 Elsevier B.V., All rights reserved.
- 787 Whitham, T. G., Allan, G. J., Cooper, H. F., and Shuster, S. M. (2020). Intraspecific Ge-  
788 netic Variation and Species Interactions Contribute to Community Evolution. *Annual  
789 Review of Ecology, Evolution, and Systematics*, 51(1).
- 790 Whitham, T. G., Bailey, J. K., Schweitzer, J. A., Shuster, S. M., Bangert, R. K., LeRoy,  
791 C. J., Lonsdorf, E. V., Allan, G. J., DiFazio, S. P., Potts, B. M., Fischer, D. G.,  
792 Gehring, C. A., Lindroth, R. L., Marks, J. C., Hart, S. C., Wimp, G. M., and Wooley,  
793 S. C. (2006). A framework for community and ecosystem genetics: from genes to  
794 ecosystems. *Nature reviews. Genetics*, 7:510–523.
- 795 Whitham, T. G., Gehring, C. A., Lamit, L. J., Wojtowicz, T., Evans, L. M., Keith, A. R.,  
796 and Smith, D. S. (2012). Community specificity: Life and afterlife effects of genes.
- 797 Winfree, R., Gross, B. J., and Kremen, C. (2011). Valuing pollination services to  
798 agriculture. *Ecological Economics*, 71:80–88.
- 799 Zook, A. E., Eklof, A., Jacob, U., and Allesina, S. (2010). Food webs: Ordering species  
800 according to body size yields high degree of intervality. *Journal of theoretical biology*,  
801 271(1):106–113.
- 802 Zytynska, S. E., Fay, M. F., Penney, D., and Preziosi, R. F. (2011). Genetic variation  
803 in a tropical tree species influences the associated epiphytic plant and invertebrate  
804 communities in a complex forest ecosystem. *Philosophical transactions of the Royal*

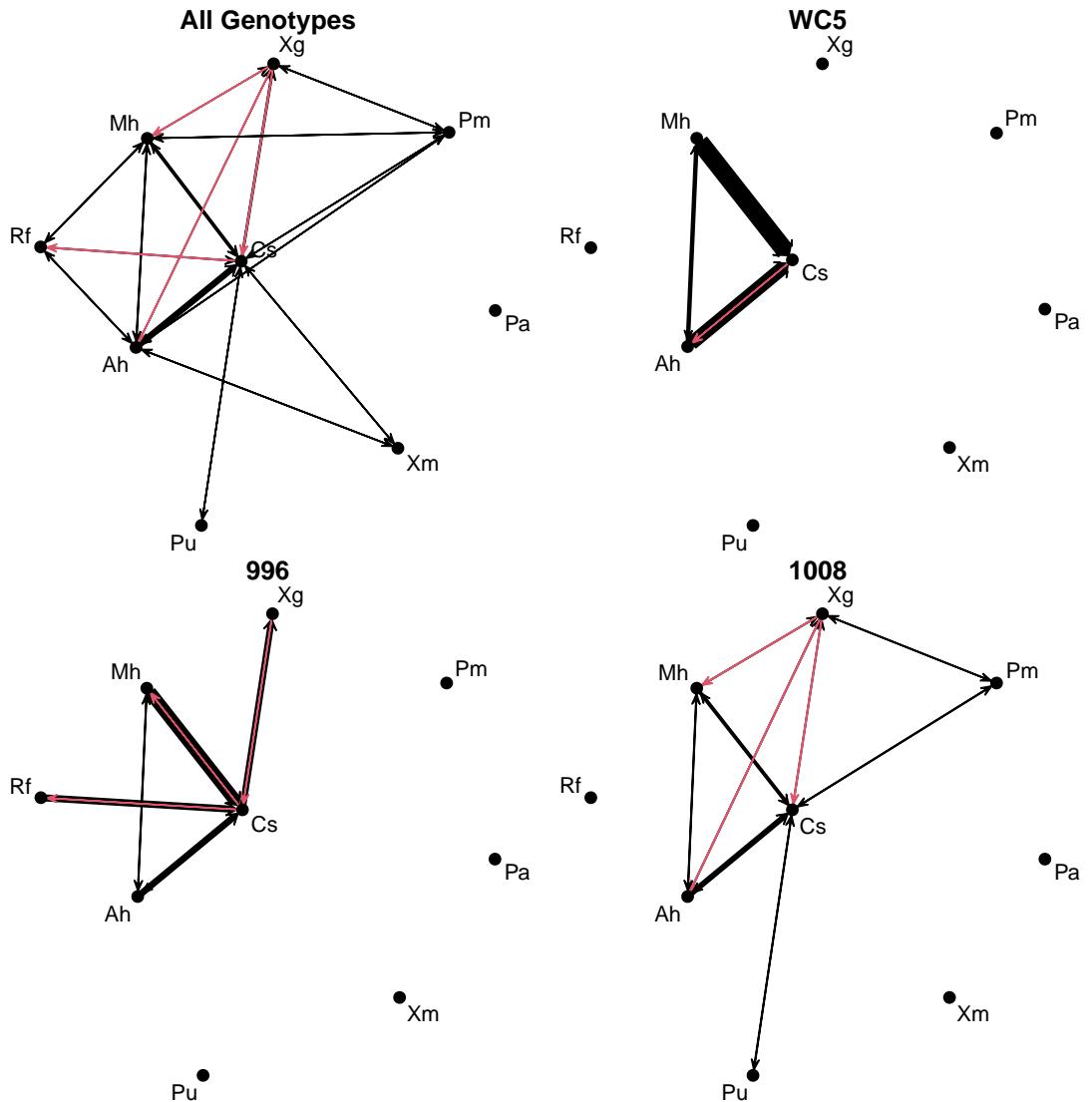
- 805      *Society of London. Series B, Biological sciences*, 366:1329–1336.
- 806      Zytynska, S. E., Khudr, M. S., Harris, E., and Preziosi, R. F. (2012). No Title. *Oecologia*,
- 807      170(2).



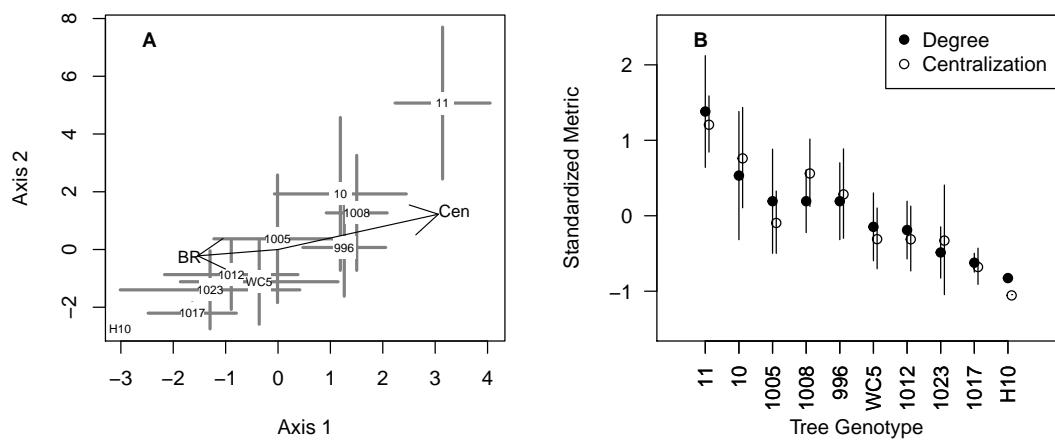
**Figure 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm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



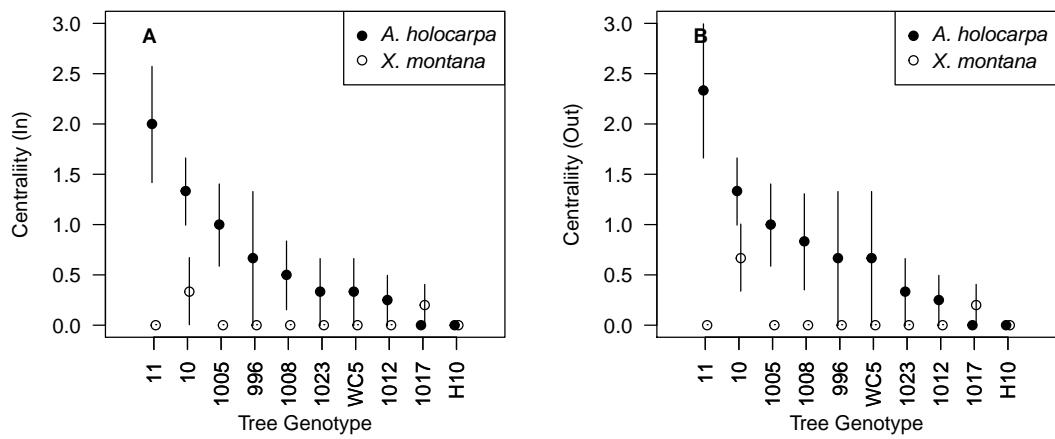
**Figure 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence 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  $S_i$ .



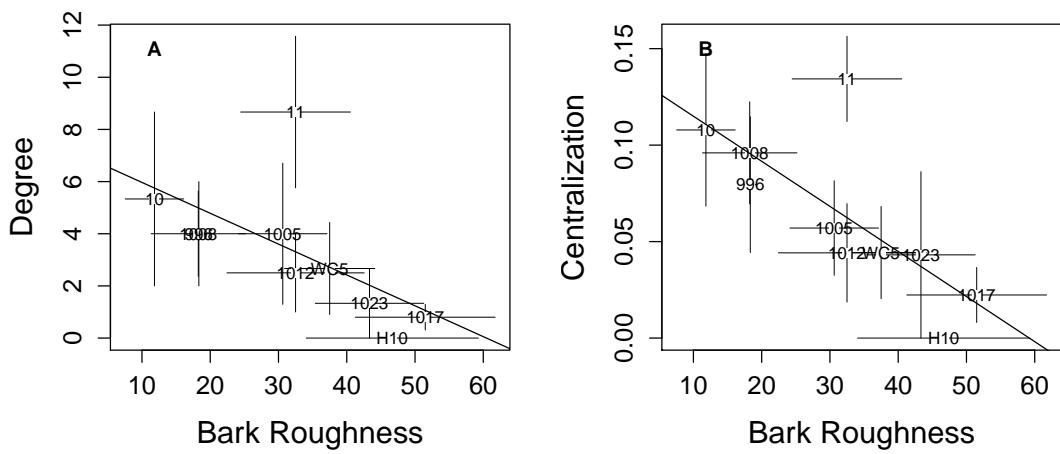
**Figure 3.** Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for illustrative genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species, which are scaled by their magnitude. Species names are abbreviated by the first letter of the genus and specific epithet: Ah = *Athallia holocarpa*, Cs = *Candelariella subdeflexa*, Mh = *Myriolecis hagenii*, Rf = *Rinodina freyi*, Pa = *Physcia adscendens*, Pm = *Physciella melanachra*, Pu = *Physcia undulata*, Xg = *Xanthomendoza galericulata*, Xm = *Xanthomendoza montana*. The sign of the interaction is indicative of greater (positive) or lesser (negative) paired occurrences than expected relative to the overall frequency of occurrence of each species. Ecologically, the links in the network are likely the product of multiple types of interactions (e.g. mutualism, parasitism, competition, facilitation) that could vary over both space and time.



**Figure 4.** The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ( $R^2 = 0.999$ , stress = 0.008) lichen network similarity ( $\pm 1$  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 networks. 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, *A. holocarpa* and *X. montana*. *Athallia holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for two genotypes, and only out-degree centrality displayed a significant response to genotype.



**Figure 6.** Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean ( $\pm 1$  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.