

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

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

**6 <sup>1</sup>Department of Biological Sciences and Merriam-Powell Center for Environmental  
7 Research, Northern Arizona University, Flagstaff, AZ 86011, USA**

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

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

**11 <sup>4</sup>Cheadle Center for Biodiversity and Restoration, University of California Santa  
12 Barbara, Santa Barbara, CA 93106, USA**

**13 <sup>5</sup>Department of Biology and Marine Biology, University of North Carolina Wilmington,  
14 601 South College Road, Wilmington, NC, 28403, USA**

**15 <sup>6</sup>School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA**

## **16 ABSTRACT**

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

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

## 17 INTRODUCTION

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

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

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

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

importance of network structures that have focal or “central” nodes (e.g., species) (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. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (Lau et al., 2015; Keith et al., 2017; Thompson, 2013; Bascompte et al., 2006). More specifically, based on the community similarity rule Bangert et al. (2006), we hypothesize that trees will co-vary in functional phenotypic traits, such as bark roughness and chemical composition, and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks.

## MATERIALS AND METHODS

### Study System

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

A long-term, common garden experiment was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated with each individual and spatial autocorrelation. Established in 1992, asexually propagated clones of genotyped *P. angustifolia* individuals were obtained from wild collections and planted in fully randomized design at the Ogden Nature Center, Ogden, UT. From the population of established individuals in the common garden, we chose a total of ten genotypes, replicated between 3 and 8 times each, for sampling.

### Bark Lichen and Trait Observations

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

151 The cell size and checkerboard sampling pattern was chosen to isolate the individuals  
152 in each cell. In a previous survey of lichen thallus size in this common garden, we had  
153 observed a median thallus size of  $0.12 \pm 0.001 \text{ cm}^2$  (1 S.E.) (Supporting Information,  
154 Fig. 1). Based on the median thallus size, we expected thalli observed in each cell to  
155 generally be spatially independent of thalli present in other cells but exposed to similar  
156 micro-environmental conditions created by the bark and the location of the sampling area  
157 on an individual tree. Therefore, we were confident in treating the cell-wise observations  
158 in quadrats as independent with respect to lichen-lichen interactions. We quantified  
159 the texture of the bark in the quadrat is the percent of  $1 \text{ cm}^2$  cells with rough bark. In  
160 addition to bark roughness, we also measured several bark chemistry traits by taking  
161 bark samples immediately adjacent to each quadrat using the methods of Lamit et al.  
162 (2011): including, the concentration of condensed tannins, pH and carbon and nitrogen  
163 concentrations and pH.

#### 164 **Lichen Network Modeling and Analysis**

165 For each tree, repeated observations of lichen were made in order to construct replicated  
166 interaction networks for each genotype. We conducted a modified sampling procedure  
167 originally developed by Lamit et al. (2015b) with the addition that we quantified the  
168 presence of lichen in the  $1 \text{ cm}^2$  cells on individual trees of *P. angustifolia*. Unipartite  
169 networks were generated using the conditional probabilities of each species pair, i.e., the  
170 probability of observing one species given an observation of another species  $P(S_i|S_j)$ ,  
171 based on the method developed by Araújo et al. (2011). To calculate conditional  
172 probabilities, we quantified the individual probabilities of species occurrences  $P(S_i)$  and  
173 the joint probability of co-occurrences  $P(S_i, S_j)$  using the frequencies of each species  
174 and their co-occurrences. We were then able to calculate the conditional probabilities of  
175 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  
176 a matrix that could possibly be asymmetric, i.e.,  $P(S_i|S_j)$  does not have to be equal to  
177  $P(S_j|S_i)$ . Another important property of this matrix is that the diagonal,  $P(S_i|S_i)$ , was  
178 equal to one for all species present and zero for species that were not observed in any  
179 cell.

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

196 different the conditional probability is from the independent probability), which makes  
197 any species with a non-significant conditional probability zero.

198 The resulting matrix ( $\mathbf{D} = D_{ij}$ ) can be interpreted as one species' impact on another  
199 with zero being no effect and values less than or greater than zero being negative and  
200 positive effects, respectively. Here, we will refer to  $\mathbf{D}$  as a signed, weighted interaction  
201 matrix. As such,  $\mathbf{D}$  has the properties that it can be asymmetric (i.e.,  $D_{ij}$  does not  
202 necessarily equal  $D_{ji}$ ) and it scales between -1 and 1, and, therefore, does not have the  
203 mathematical properties of a probabilistic network (Poisot et al., 2016). Also, as the  
204 method does not track individuals within species and interactions such as competitive  
205 exclusion or facilitation within species would result in the same species being observed.  
206 Therefore, the results of intra-specific interactions always results in the same species  
207 being observed and a resulting  $D_{ii} = 0$ .

## 208 Network Metrics

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

## 222 Statistical Analyses, Software and Data

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

231 For multivariate response variables, such as lichen community composition and  
232 network structure, we used distance based multivariate statistical approaches, including  
233 Permutational Analysis of Variance (PERMANOVA) and Mantel tests. To quantify  
234 the similarity of lichen networks among individual trees, we calculated the pairwise  
235 Euclidean distance of the  $\mathbf{D}$  interaction matrices among all pairs of trees. For visualization  
236 of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS)  
237 (Goslee and Urban, 2007) to produce dimensionally reduced ordinations of these multi-  
238 variate responses and fitted vectors for continuous predictor variables to the ordinated  
239 values (Oksanen et al., 2019). Using random initial configurations with a maximum of

240 500 iterations and a change in stress threshold of less than  $10^{-12}$ . Final configurations  
241 has the lowest stress with at most a stress level of 0.10.

242 For each network, we also calculated metrics that measure different structural aspects.  
243 Although there are many other metrics, for the sake of simplicity we focus on a subset  
244 that represent several interesting features of network structure (see Lau et al. (2017)).  
245 We calculated the number of interactions or “links” in each network, which provides  
246 a measure of the size of the network Lau et al. (2015); Borrett and Lau (2014). We  
247 also calculated the centralization of each network, which measures the evenness of  
248 the distribution of interactions among the species in the network (Butts, 2019). In a  
249 network with a low level of centralization species have similar amount of interaction in  
250 the network, while a network with a high level of centralization tends to have one or  
251 small number of species that interact with other species. We used a related function to  
252 calculate the centrality of each species (i.e., node level centrality) in each network as  
253 well. To calculate separate metrics for positive and negative links, we applied methods  
254 for calculating the centrality accounting for the sign differences (Everett and Borgatti,  
255 2014) using the `signnet` package (Schoch, 2020).

256 For all tests where genotype was used as a predictor, we quantified the heritability  
257 of the response variable. Because the trees in the garden were clonal replicates of each  
258 genotype, we calculated broad-sense heritability, which is the genotypic variance divided  
259 by the total phenotypic variance (Conner and Hartl, 2004). This can be interpreted as a  
260 measure of the phenotypic variance due to genotypic variation. We also apply this to  
261 the community genetics context as the variance in *extended* phenotypic variance due to  
262 genotypic variation (Whitham et al., 2006, 2012; Crutsinger, 2016). For the multivariate  
263 analyses, where we employ PERMANOVA, we followed the methods of Shuster et al.  
264 (2006) to adjust the degrees of freedom for unbalanced genotype replicates.

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

## 269 RESULTS

270 Tree genotype influenced lichen network structure and multiple lichen network metrics  
271 were heritable. Tree genotype significantly predicted the structural similarity of lichen  
272 networks (PERMANOVA: Pseudo- $F_{9,27} = 3.58$ ,  $H^2 = 0.41$ ,  $p\text{-value} = 0.0537$ ) (Fig. 4).  
273 Overall network level metrics responded significantly to tree genotype (Table 1), in-  
274 cluding network degree ( $RLRT = 3.52$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0255$ ) and centralization  
275 including both in-coming and out-going links ( $RLRT = 4.04$ ,  $H^2 = 0.33$ ,  $p\text{-value} =$   
276 0.0184) or when separated into in-coming only ( $RLRT = 3.9852$ ,  $H^2 = 0.3309$ ,  $p\text{-value} =$   
277 0.0190) or out-going only ( $RLRT = 3.8615$ ,  $H^2 = 0.3193$ ,  $p\text{-value} = 0.0205$ ). Metrics  
278 including only positive links also showed a significant effect of tree genotype, including  
279 positive degree ( $RLRT = 3.6925$ ,  $H^2 = 0.3242$ ,  $p\text{-value} = 0.0229$ ), positive in-going  
280 centralization ( $RLRT = 4.4812$ ,  $H^2 = 0.3487$ ,  $p\text{-value} = 0.0142$ ) Metrics calculated with  
281 negative links were not significant, including degree (negative) ( $RLRT = 0.0327$ ,  $H^2 =$   
282 0.0318,  $p\text{-value} = 0.3859$ ) and both in-coming (negative) ( $RLRT = 0.3304$ ,  $H^2 = 0.1057$ ,  
283  $p\text{-value} = 0.2508$ ) and out-going centralization (negative) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ ,

284  $p$ -value = 0.3446).

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.

285 The genetic response of network centralization was driven by variation in *Caloplaca*  
286 *holocarpa*. Centrality varied significantly among species ( $F_{8,324} = 7.99$ ,  $R^2 = 0.16$ ,  
287  $p$ -value < 0.0001). *Caloplaca holocarpa* centrality was the main species to exhibit  
288 a significant response to tree genotype in terms of positive centrality for both the in-  
289 coming ( $RLRT = 3.61$ ,  $H^2 = 0.32$ ,  $p$ -value = 0.0240) and out-going ( $RLRT = 3.13$ ,  $H^2$   
290 = 0.30,  $p$ -value = 0.0327) perspectives, but not for either negative centrality metrics  
291 in-coming ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p$ -value = 1) or out-going ( $RLRT = 0$ ,  $H^2 = 0$ ,  $p$ -value =  
292 0.4543). None of the other species' centralities showed a genotypic response (Supporting  
293 Information, Fig. 2) with the exception of *X. montana* ( $RLRT = 2.92$ ,  $H^2 = 0.32$ ,  $p$ -value  
294 = 0.0375); however, the centrality of *X. montana* was much lower overall relative to *C.*  
295 *holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes  
296 (Fig. 5).

297 Genotype indirectly influenced lichen network centralization via the genetically  
298 based variation in bark roughness. The percent cover of rough bark ( $RLRT = 4.8526$ ,  
299  $H^2 = 0.3221$ ,  $p$ -value = 0.0113) and condensed tannins ( $RLRT = 3.0522$ ,  $H^2 = 0.3205$ ,  
300  $p$ -value = 0.0343) both displayed significant responses to tree genotype. None of the  
301 other bark traits, pH ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p$ -value = 1.0000) or carbon-nitrogen  
302 ratio ( $RLRT = 0.0000$ ,  $H^2 = 0.0000$ ,  $p$ -value = 1.0000), showed a significant response  
303 to tree genotype and none other than bark roughness was correlated with network  
304 similarity (Table 2); therefore, we focused our subsequent analyses on the indirect  
305 effect of genotype on lichen network structure via bark roughness. We found that  
306 bark roughness was significantly correlated with network similarity (PERMANOVA:  
307 Pseudo- $F_{1,32} = 13.029$ ,  $R^2 = 0.26$ ,  $p$ -value = 0.0096) and other lichen network metrics,  
308 including negative correlations with overall network degree ( $df = 35$ ,  $t = -2.13$ ,  $r =$   
309 -0.34,  $p$ -value = 0.04) and centralization ( $df = 35$ ,  $t = -2.52$ ,  $r = -0.39$ ,  $p$ -value = 0.02).  
310 In other words, trees with more similar levels of bark roughness tended to have lichen  
311 interaction networks with similar structure. To quantify the genetic bases of this effect  
312 of bark roughness on network structure, we used the residual values from regressions of  
313 network degree and centralization in tests of the effect of tree genotype and found no

314 significant effect of tree genotype for either degree ( $RLRT = 0.00$ ,  $H^2 = 0.00$ , *p-value*  
 315 = 1.0000) or centralization ( $RLRT = 0.00$ ,  $H^2 = 0.00$ , *p-value* = 1.0000), suggesting  
 316 that the observed relationship between bark roughness and lichen network structure was  
 317 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.

## 318 DISCUSSION

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

### 332 Implications of the Heritability of Interaction Network Structure

333 Significant heritability of lichen interaction network structure is in line with the genetic  
 334 similarity rule, networks observed on trees of the same genotype tended to be struc-  
 335 turally similar. Although previous studies have examined aspects of networks, such  
 336 as trophic (Barbour et al., 2019) and forest stand-level interaction network structure  
 337 (Lau et al., 2016; Keith et al., 2017), this is the first study that we are aware of to  
 338 examine the heritability of network structure with replicated networks at the genotype  
 339 scale. Previous work in the evolution of ecological networks have primarily focused on  
 340 macro-evolutionary dynamics (Rezende et al., 2007; Weber et al., 2017; Valverde et al.,  
 341 2018; Harmon et al., 2019) or have been simulation based individual-level models that  
 342 integrate intraspecific variation to the species level (Maliet et al., 2020), even though  
 343 recent syntheses ave pointed to the importance of processes operating across scales of  
 344 organization (Guimarães, 2020). There are two important functional ramifications of  
 345 genetically based variation in network structure.

346 First, A genetic basis to network structure suggests that some amount of interaction  
347 network complexity is determined and therefore could be predicted. Variation in space  
348 and time create variation in ecological networks that influences evolutionary dynamics  
349 via shifts in ecological dynamics, such as population demographics (Guimarães, 2020).  
350 Given that ecosystems are comprised of hundreds and thousands of species, each having  
351 a multitude of interactions, the potential to find traction for making predictions in the  
352 context of ecological, let alone evolutionary, dynamics seems daunting. The promise  
353 of predictability lies in the presence of assymmetries in ecosystems that contribute to the  
354 occurrence of foundation species, such as hierarchy and nestedness created by body size  
355 differences or life-history strategies, has been widely observed (Ellison et al., 2005).  
356 The second part is that heritability (i.e., genetic determination) means that there is  
357 structure in the spatial or temporal variation that is created by individuals of foundation  
358 species whose traits are in part determined by underlying trait differences. Although this  
359 variation is inherently a function of both genetics and environmental effects (Conner  
360 and Hartl, 2004), the community and network level effects are also a function of the  
361 scale of the interaction (Shuster et al., 2006).

362 Second, even if the composition of the communities is the same among individuals  
363 and genotypes, interactions may not be. We didn't observe compositional differences  
364 using the same data from which the lichen networks were derived. If we only had our  
365 composition dataset from this study, we would have concluded no response of the lichen  
366 community to tree genotype, even though the underlying interactions among lichen  
367 species does vary among genotypes. As such differences in network structure could  
368 occur without observable differences in species richness or community composition,  
369 which have been the primary focus of almost all previous community genetics studies  
370 (Des Roches et al., 2018). Community composition of lichen has previously been  
371 observed to be different among tree genotype in the same experimental garden (Lamit  
372 et al., 2011, 2015b), the difference between the present study is likely a result of  
373 differences in sampling method and the choice of genotypes leading to overall higher  
374 abundances of observed lichens to assure the possibility of observing lichen interactions.  
375 The previous study also used a visual estimation method, unlike the current study, which  
376 observed lichen at the scale of 1 cm<sup>2</sup> cells, which could over-estimate cover depending on  
377 the frequency at which actual thallus size was less than 1 cm<sup>2</sup>, as well as both the northern  
378 and southern aspects of each tree. These differences do not negate the findings of either  
379 study. The present study's finding of differences in network structure without significant  
380 compositional differences points to the importance of quantifying how network structure  
381 changes in response to genetic variation in order to fully understand evolutionary  
382 dynamics in complex communities. Having not observed a compositional effect of tree  
383 genotyp without measuring the network structure could lead to the conclusion of no  
384 genetic effect on the community, even though differences in network structure are leading  
385 to altered, local evolutionary dynamics. It is possible that these underlying differences  
386 in interactions among lichen could lead to differences in community composition at  
387 a future point in time via there effects on species abundances (Shuster et al., 2006);  
388 however, this is not needed for evolutionary dynamics to play out via selection that leads  
389 to shifts in trait distributions without shifting species abundance distributions, which is  
390 possible under stabilizing, disruptive and directional selection (Conner and Hartl, 2004),  
391 so long as the relative abundances of each species is imperceptibly changed. Thus, it is

392 imperative that further community genetics research assess or at least be aware of the  
393 potential effects of variation in interactions and not just observe species abundances,  
394 otherwise community level genetic effects may be underestimated, especially when  
395 cumulative interaction effects are taken into account (Borrett et al., 2007).

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

397 Intra-specific diversity could be creating lichen metacommunities on individual trees  
398 that form interaction modules with different dynamics. When communities are com-  
399 prised of individuals who's habitat is primarily determined by another organism, these  
400 communities inherently form modules within the larger ecosystem, as they tend to  
401 interact more with each other than with other individuals (Lau et al., 2017). Our study  
402 demonstrates that the environmental differences determined by the genetic variation  
403 within a single species can create differences that not only impacts community composi-  
404 tion, as repeatedly demonstrated in other community genetics studies (Whitham et al.,  
405 2006; Des Roches et al., 2018), but also the structure of interactions among individuals  
406 within these modules. Some network structures are likely to be more stable, either in  
407 response to disturbance or via self-organized dynamics. For example, centralized net-  
408 works, although more efficient, are theorized to be more susceptible to targeted attacks.  
409 As mentioned previously, one class of networks that are theorized to have amplifying  
410 effects on networks have centralized "star" shapes with one or a few species at the center  
411 and radiating interactions out from the central core (Lieberman et al., 2005). This is  
412 structurally what we have observed with the networks that tend to occur on some of the  
413 genotypes in our study, i.e., the more centralized networks. It is possible that these more  
414 centralized networks could function as hot-spots of evolutionary dynamics resulting  
415 from the amplifying effect the centralized network structure found on that tree genotype.

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

431 This builds on many previous studies demonstrating that the community level effects  
432 vary among multiple genotypes. It is not clear what potential there is for feedbacks to  
433 the origins (e.g. the cottonwood genotypes) from the community, and as such it cannot  
434 be determined whether these networks are cyclic or rooted. In terrestrial ecosystems,  
435 lichen play important ecological roles, such as substrate stabilization (Root et al., 2011)  
436 and nutrient fixation (Nelson et al., 2018). In some systems lignicolous lichens can

437 have demonstrable effects on the availability of nutrients for the trees that they are  
438 associated with (Norby and Sigal, 1989), although this has not been measured for  
439 the lichen in the current study's system<sup>q</sup>. Elucidating the absence and/or presence  
440 of and quantifying such feedbacks would allow for the determination of the cyclic  
441 nature and potential evolutionary dynamics of this system. The presence of feedbacks  
442 would provide the potential for non-linear dynamics in which evolutionary effects are  
443 damped or amplified by the structure of the network. For example, a star structure in  
444 which there is a primary or core set of central species with feedbacks from the radiating  
445 species has been demonstrated to be a structure that amplifies evolutionary dynamics  
446 (Lieberman et al., 2005). If such feedbacks do not exist, these sub-networks of the lichen  
447 and tree genotypes are likely to be multi-rooted networks. Such a structure is theorized to  
448 generally promote diversification as variation arising from the shifting distribution of the  
449 "roots", i.e., genotypes; however, loss of genotype/root diversity could lead to fixation  
450 of a single genotype in the population and a decrease in community-wide diversity.  
451 However, such feedbacks to tree fitness are not necessary for evolutionary dynamics to  
452 play out within the lichen networks through the effects of altered network structure on  
453 lichen interaction outcomes, such as competitive exclusion leading to selection.

454 Since lichen are multi-species complexes, there is also the potential for evolutionary  
455 dynamics to shift within the context of the lichen symbiosis. There is substantial  
456 evidence that lichen have served as the "cradle of symbiotic fungal diversification"  
457 (Arnold et al., 2009) and recent research has shown significant network structure of  
458 endolichenic fungi and lichen collected from across North America (Chagnon et al.,  
459 2016). Analysis of the structure of ecological networks has generally supported the  
460 conclusion that nestedness, or the degree to which species tend to interact with similar  
461 subsets of the community, tends to promote stability in mutualistic, primarily bipartite  
462 (i.e., two-mode), networks and modularity contributes to the stabilization of antagonistic  
463 networks (Elias et al., 2013; Grilli et al., 2016). Although there is growing evidence  
464 that the nestedness of mutualistic networks is not necessarily the result of selection for  
465 systems-level properties that promote stability but could be either product of asymptotic  
466 abundance distributions leading to un-even interaction frequencies (Staniczenko et al.,  
467 2013) and/or a by-product of selection and divergence creating network "spandrels" in  
468 ecosystems (Valverde et al., 2018), this does not preclude the functional consequences  
469 of network structure but rather the developmental or evolutionary processes that have  
470 produced the structure. In the present study, we did not examine nestedness or modularity  
471 of the lichen networks as we could not find metrics for analyzing networks that are  
472 not only weighted and directed but also signed. Hopefully future network theoretic  
473 developments will make the appropriate metrics available to conduct these analyses.

#### 474 **Implications for Interspecific Indirect Genetic Effects (IIGEs)**

475 Interspecific indirect genetic effects (IIGE) theory provides a quantitative framework  
476 within which to approach evolutionary theory at higher levels of biological organization:  
477 from populations to communities and ecosystems. To date, this theory has focused  
478 on modeling the strong effects of foundation species (Shuster et al., 2006; Whitham  
479 et al., 2012), but it has not yet integrated developments in the ecological or evolutionary  
480 network theory literature. This is to say that it has not developed a way to examine  
481 complex interactions among species; however, previous studies have demonstrated this

482 network context is likely to be important, as altering the structure of interaction networks  
483 provides a means for genetic effects to be dampened or magnified within the system  
484 of interacting species. For example, Keith et al. (2017) showed that the genetics based  
485 interactions of aphid resistant and aphid susceptible trees resulted in different interaction  
486 networks of their associated arthropod communities composed of 139 species. At the  
487 scale of ecosystems, trophic networks or food webs direct and control the rates of energy  
488 and nutrient flux (Borgatti and Everett, 2006). Furthermore, in a predator-prey-plant  
489 study, Smith et al. (2011) showed that the interactions among species across trophic  
490 levels depended on plant genotype.

491 The results of the current study provides clear empirical evidence that variation  
492 in network structure can be genetically based (i.e., heritable) and points to the need  
493 to expand IIGEs encompass the structure of interaction networks. Although such  
494 a synthesis necessitates a much greater effort than can be afforded in this paper, it  
495 is possible to point to several productive pathways forward. In terms of interaction  
496 networks, foundation species are relatively central within the system of interactions,  
497 that is their direct and/or indirect effects are greater than other species. So, when the  
498 more centralized (foundation) species have genetically based interactions, genetic effects  
499 will tend to be magnified in the community. Here, we found that even though more  
500 abundant or more centralized (i.e., “important”) species were present in the community,  
501 their effects were not the main component responding to genetic effects. Considering  
502 the impact of network structure would be a productive path forward for the theoretical  
503 development and application of the IIGE concept.

#### 504 **Applicability to Other Systems**

505 In attempting to apply these findings to other systems, it is important to consider the  
506 spatial and temporal scaling of genetic effects. In the present study, the sessile nature of  
507 lichens means that individuals, and potentially multiple generations, live their entire lives  
508 on a single tree. As such, our study examines one scaling of a genetic effect, in which  
509 the phenotype of a single tree individual (i.e., tree genotype) has complete influence  
510 on the community with little to no effect of other tree individuals in the population.  
511 The extreme from this would be where the associated community moved among and  
512 interacted with not only other community members but also multiple tree individuals at a  
513 high rate, as would be the case with free-living animals (e.g. flying insects). In the latter  
514 case, the effect of tree genetics would then be the integral effect of all the tree individuals  
515 in the population, and, all other factors being equal, any one tree genotype would have a  
516 lower effect on associated community. In reality, ecosystems are a mixture of species  
517 of different body sizes and life-histories, and, as such, vary in the degree to which  
518 they interact with other organisms, which is the basis of the theory of the geographic  
519 mosaic of co-evolution (Thompson, 2013; Thompson et al., 2013). It is now important to  
520 consider how the impacts of genetic effects on the network structure of sub-groups, such  
521 as lichens, may or may not propagate through the ecosystem to more mobile organisms.  
522 As developed previously, the degree to which a genetic effect influences the community  
523 is a function of the fidelity of the genetic effect (i.e., heritability) and both the frequency  
524 and the intensity of the interaction (Shuster et al., 2006). One possible path forward is for  
525 future work to extend the many previous community genetics studies that have focused  
526 on sessile organisms, such as galling insects (Bailey et al., 2005; Whitham et al., 2006;

527 Crutsinger et al., 2014; Smith et al., 2011; Keith et al., 2017), to quantify the frequency  
528 of these interactions in the context of the larger community. This would provide an  
529 estimate of the relative impact of these focal, often termed foundation, species. In  
530 addition, community genetics theory has only considered first order interactions, i.e.,  
531 between two organisms (Shuster et al., 2006; Whitham et al., 2012, 2020). Given that  
532 network structure could be influenced by genetic effects, as evidenced by the present  
533 study, assessing higher order interactions could provide a path forward for theoretical  
534 advances that could help with identifying important characteristics of sub-groups to  
535 focus on in empirical studies.

536 Although our study was conducted with a community of lichens, these results can  
537 be generalized to other groups of diverse organisms around the world that also exhibit  
538 significant genetic signals at the community level (Rowntree et al., 2011; Whitham  
539 et al., 2012). However, there are important points to consider when extending the  
540 observed genetically based response of the lichen networks to other systems. As  
541 bark lichen individuals do not move, but grow in a primarily two dimensional plane,  
542 these communities and their interactions occur in the highly localized context of the  
543 tree's bark surface. Lichen individuals are also many orders of magnitude smaller  
544 than the tree individual in this system (Lamit et al., 2011). For these reasons, the  
545 genetic effects on these communities is not damped by the movement of individuals  
546 and the mixing of the effect of different tree genotypes on the lichen community, as  
547 might occur for more mobile species (e.g. insects and birds). Relatedly, we only  
548 examined lichen in this study, and other species whose distributions, abundances and/or  
549 interactions vary in their response to tree genotype, such as animals that may also impact  
550 lichen communities, could be playing a role that we did not examine. For example, an  
551 analysis of the multivariate correlations of different components of the community in  
552 this system demonstrated significant patterns of genetic co-responses to tree genotype,  
553 supporting the non-mutually exclusive possibilities of shared responses to tree genotype  
554 or tree genotypic effects on interactions among these sub-communities (Lamit et al.,  
555 2015a). As such, although we can not rule out the possibility that other unmeasured  
556 tree traits or organisms correlated with bark roughness are underlying the observed  
557 patterns, substantial research supports the importance of genetically based tree traits for  
558 communities and ecosystems (Des Roches et al., 2018), and in particular bark roughness  
559 for bark lichen communities (Bdeir et al., 2017; Lamit et al., 2011, 2015b).

560 These findings also have implications for our understanding of community assembly.  
561 Models based on neutral theory have been developed that can reconstruct interactions  
562 networks with similar structural characteristics to those observed in real ecosystems  
563 (Coelho and Rangel, 2018). The findings of our study support the possibility that,  
564 although communities and their interaction networks may assemble as a result of  
565 conditions that are entirely agnostic to functional variation, if there are strong ecological  
566 assymmetries, such as the case in foundation species systems, then spatial and temporal  
567 variation in network structure will arise as a result of trait variation within the foundation  
568 species. Taking even the extreme case, even when such genetically based variation is the  
569 result of "neutral" evolutionary processes (e.g., genetic drift), as long as resulting genetic  
570 diversity produces ecological relevant phenotypic diversity, then network structure will  
571 still have a genetic basis. Given that ecosystems with large assymmetries seem to be  
572 the rule rather than the exception for ecosystems (Ellison et al., 2005; Santamaría and

573 Rodríguez-Gironés, 2007; Staniczenko et al., 2013; Dormann et al., 2017; Coelho and  
574 Rangel, 2018), the results of our study are likely to be broadly applicable and provides  
575 further support for the conclusion that the community context of evolutionary dynamics  
576 at either micro- or macro-evolutionary scales (Weber et al., 2017; Harmon et al., 2019)  
577 should not be ignored. As genetic variation is inherent to biological systems, it would  
578 now seem that the adage “you can’t be neutral on a moving train” might well apply to  
579 the evolutionary dynamics of ecosystems that are comprised of networks of interacting  
580 species.

## 581 Conclusion

582 In the face of the high degree of complexity and potential context dependency of  
583 ecological processes, the current study points to the utility of considering the spatial  
584 and temporal scales of interactions, as discussed in previous studies (Bangert et al.,  
585 2006; Zook et al., 2010; Zytnyska et al., 2012). In the present research, we found that  
586 the assembly of ecological networks can have a measurable genetic basis depending  
587 on the spatial scale of interactions, due in part, to assymetries in size and longevity of  
588 organisms. The importance of the scale of network organization to create hierarchical  
589 structure (Guimarães, 2020) and the potential for foundation species to create this  
590 structure in the vast majority of ecosystems (Ellison et al., 2005; Whitham et al., 2006)  
591 suggests that future work would be aided by determining these modules within the biotic  
592 community that include species with large differences in body-size and longevity. Also,  
593 as heritable variation is the raw material for natural selection to act upon, a genetic basis  
594 for interaction network structure indicates evolutionary dynamics should be considered  
595 at the community level and that conserving genetic variation is important to consider in  
596 efforts to restore or preserve complex species interactions and their associated ecosystem  
597 functions (Evans et al., 2013). Such findings will bring us closer to understanding the  
598 evolutionary drivers of Darwin’s entangled bank and the interconnectedness of species  
599 in complex communities.

## 600 Acknowledgements

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

## 605 Citations

## 606 REFERENCES

- 607 Araújo, M. B., Rozenfeld, A., Rahbek, C., and Marquet, P. A. (2011). Using species  
608 co-occurrence networks to assess the impacts of climate change. *Ecography*, 34:897–  
609 908.
- 610 Arnold, A. E., Miadlikowska, J., Higgins, K. L., Sarvate, S. D., Gugger, P., Way, A.,  
611 Hofstetter, V., Kauff, F., and Lutzoni, F. (2009). A phylogenetic estimation of trophic  
612 transition networks for ascomycetous Fungi: Are lichens cradles of symbioticrophic  
613 Fungal diversification? *Systematic Biology*, 58(3):283–297.
- 614 Bailey, J. K., Schweitzer, J. A., Ubeda, F., Koricheva, J., LeRoy, C. J., Madritch, M. D.,  
615 Rehill, B. J., Bangert, R. K., Fischer, D. G., Allan, G. J., and Whitham, T. G. (2009).

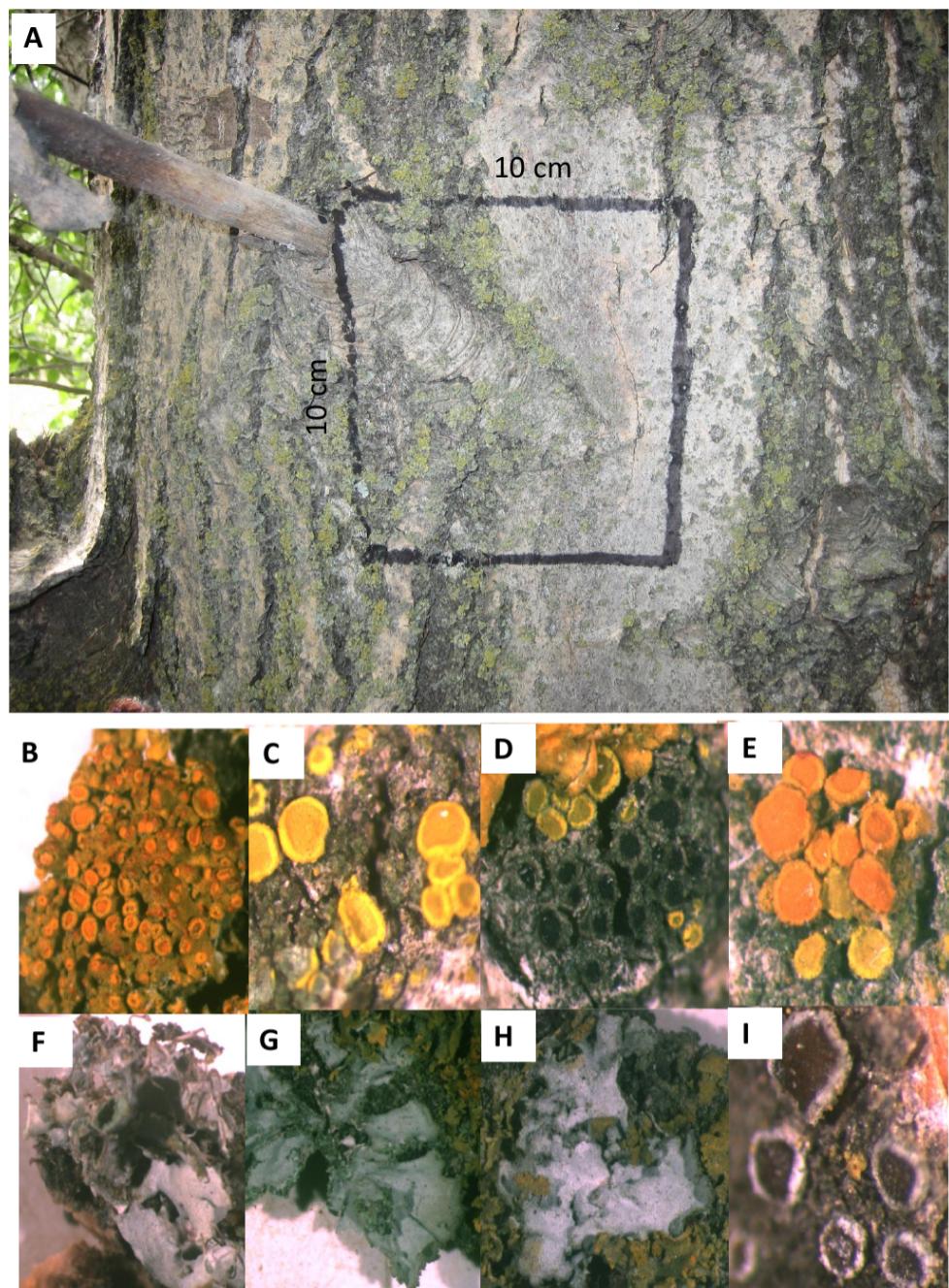
- 616 From genes to ecosystems: a synthesis of the effects of plant genetic factors across  
617 levels of organization. *Philosophical transactions of the Royal Society of London.*  
618 *Series B, Biological sciences*, 364(1523):1607–16.
- 619 Bailey, J. K., Wooley, S. C., Lindroth, R. L., and Whitham, T. G. (2005). Importance  
620 of species interactions to community heritability: a genetic basis to trophic-level  
621 interactions. *Ecology Letters*, 0(0):051122062725008.
- 622 Bangert, R. K., Turek, R. J., Rehill, B., Wimp, G. M., Schweitzer, J. A., Allan, G. J.,  
623 Bailey, J. K., Martinsen, G. D., Keim, P., Lindroth, R. L., and Whitham, T. G. (2006).  
624 A genetic similarity rule determines arthropod community structure. *Molecular  
ecology*, 15:1379–1391.
- 625 Barbour, M. A., Erlandson, S., Peay, K., Locke, B., Jules, E. S., and Crutsinger, G. M.  
626 (2019). Trait plasticity is more important than genetic variation in determining species  
627 richness of associated communities. *Journal of Ecology*, 107(1):350–360.
- 628 Barbour, M. A., Fortuna, M. A., Bascompte, J., Nicholson, J. R., Julkunen-Tiitto, R.,  
629 Jules, E. S., and Crutsinger, G. M. (2016). Genetic specificity of a plant-insect food  
630 web: Implications for linking genetic variation to network complexity. *Proceedings of  
631 the National Academy of Sciences of the United States of America*, 113(8):2128–2133.
- 632 Barbour, R. C., O'Reilly-Wapstra, J. M., Little, D. W. D., Jordan, G. J., Steane, D. A.,  
633 Humphreys, J. R., Bailey, J. K., Whitham, T. G., Potts, B. M., De Little, D. W., Jordan,  
634 G. J., Steane, D. A., Humphreys, J. R., Bailey, J. K., Whitham, T. G., and Potts, B. M.  
635 (2009). A geographic mosaic of genetic variation within a foundation tree species  
636 and its community-level consequences. *Ecology*, 90(7):1762–1772.
- 637 Bascompte, J., Jordano, P., and Olesen, J. M. (2006). Asymmetric Coevolutionary  
638 Networks Facilitate Biodiversity Maintenance \r10.1126/science.1123412. *Science*,  
639 312:431–433.
- 640 Bdeir, R., Muchero, W., Yordanov, Y., Tuskan, G. A., Busov, V., and Gailing, O. (2017).  
641 Quantitative trait locus mapping of Populus bark features and stem diameter. *BMC  
642 Plant Biology*.
- 643 Borgatti, S. P. and Everett, M. G. (2006). A Graph-theoretic perspective on centrality.  
644 *Social Networks*, 28:466–484.
- 645 Borrett, S. R., Fath, B. D., and Patten, B. C. (2007). Functional integration of ecological  
646 networks through pathway proliferation. *Journal of Theoretical Biology*, 245(1):98–  
647 111.
- 648 Borrett, S. R. and Lau, M. K. (2014). enaR: An R package for Ecosystem Network  
649 Analysis. *Methods in Ecology and Evolution*, 5(11):1206–1213.
- 650 Busby, P. E., Lamit, L. J., Keith, A. R., Newcombe, G., Gehring, C. A., Whitham, T. G.,  
651 and Dirzo, R. (2015). Genetics-based interactions among plants, pathogens, and  
652 herbivores define arthropod community structure. *Ecology*, 96(7):1974–1984.
- 653 Butts, C. T. (2019). *sna: Tools for Social Network Analysis*. R package version 2.5.
- 654 Chagnon, P. L., U'Ren, J. M., Miadlikowska, J., Lutzoni, F., and Elizabeth Arnold,  
655 A. (2016). Interaction type influences ecological network structure more than local  
656 abiotic conditions: evidence from endophytic and endolichenic fungi at a continental  
657 scale. *Oecologia*, 180(1):181–191.
- 658 Coelho, M. T. P. and Rangel, T. F. (2018). Neutral community dynamics and the  
659 evolution of species interactions. *American Naturalist*, 191(4):421–434.
- 660 Conner, K. and Hartl, D. L. (2004). *A Primer of Ecological Genetics: a textbook*.

- 662 Sinauer Associates, Inc., Sunderland, Massachusetts, 1st edition.
- 663 Crutsinger, G. M. (2016). A community genetics perspective: Opportunities for the  
664 coming decade. *New Phytologist*.
- 665 Crutsinger, G. M., Rudman, S. M., Rodriguez-Cabal, M. A., McKown, A. D., Sato,  
666 T., MacDonald, A. M., Heavyside, J., Geraldes, A., Hart, E. M., LeRoy, C. J., and  
667 El-Sabaawi, R. W. (2014). Testing a ‘genes-to-ecosystems’ approach to understanding  
668 aquatic-terrestrial linkages. *Molecular Ecology*, 23(23):5888–5903.
- 669 Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison,  
670 M. T., Schweitzer, J. A., and Palkovacs, E. P. (2018). The ecological importance of  
671 intraspecific variation. *Nature Ecology and Evolution*, 2(1):57–64.
- 672 Díaz-Castelazo, C., Guimarães, P. R., Jordano, P., Thompson, J. N., Marquis, R. J., and  
673 Rico-Gray, V. (2010). Changes of a mutualistic network over time: Reanalysis over a  
674 10-year period. *Ecology*.
- 675 Dormann, C. F., Fründ, J., and Schaefer, H. M. (2017). Identifying Causes of Patterns  
676 in Ecological Networks: Opportunities and Limitations. *Annual Review of Ecology,*  
677 *Evolution, and Systematics*, 48(1):559–584.
- 678 Elias, M., Fontaine, C., and Frank Van Veen, F. J. (2013). Evolutionary history and  
679 ecological processes shape a local multilevel antagonistic network. *Current Biology*,  
680 23(14):1355–1359.
- 681 Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R.,  
682 Foster, D. R., Kloeppe, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig,  
683 D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M.,  
684 Thompson, J., Von Holle, B., and Webster, J. R. (2005). Loss of foundation species:  
685 consequences for the structure and dynamics of forested ecosystems. *Frontiers in*  
686 *Ecology and the Environment*, 3(9):479–486.
- 687 Evans, D. M., Pocock, M. J. O., and Memmott, J. (2013). The robustness of a network  
688 of ecological networks to habitat loss. *Ecology letters*, 16:844–52.
- 689 Everett, M. G. and Borgatti, S. P. (2014). Networks containing negative ties. *Social*  
690 *Networks*, 38(1):111–120.
- 691 Gehring, C., Flores-Rentería, D., Sthultz, C. M., Leonard, T. M., Flores-Rentería,  
692 L., Whipple, A. V., and Whitham, T. G. (2014). Plant genetics and interspecific  
693 competitive interactions determine ectomycorrhizal fungal community responses to  
694 climate change. *Molecular Ecology*, 23(6):1379–1391.
- 695 Gehring, C. A., Sthultz, C. M., Flores-Rentería, L., Whipple, A. V., and Whitham, T. G.  
696 (2017). Tree genetics defines fungal partner communities that may confer drought  
697 tolerance. *Proceedings of the National Academy of Sciences*.
- 698 Gómez, J. M., Abdelaziz, M., Camacho, J. P. M., Muñoz-Pajares, A. J., and Perfectti, F.  
699 (2009). Local adaptation and maladaptation to pollinators in a generalist geographic  
700 mosaic. *Ecology Letters*, 12(7):672–682.
- 701 Goslee, S. C. and Urban, D. L. (2007). The ecodist package for dissimilarity-based  
702 analysis of ecological data. *Journal of Statistical Software*, 22:1–19.
- 703 Grilli, J., Rogers, T., and Allesina, S. (2016). Modularity and stability in ecological  
704 communities. *Nature Communications*, 7.
- 705 Guimarães, P. R. (2020). The Structure of Ecological Networks Across Levels of  
706 Organization. *Annual Review of Ecology, Evolution, and Systematics*, 51(1).
- 707 Guimarães, P. R., Jordano, P., and Thompson, J. N. (2011). Evolution and coevolution

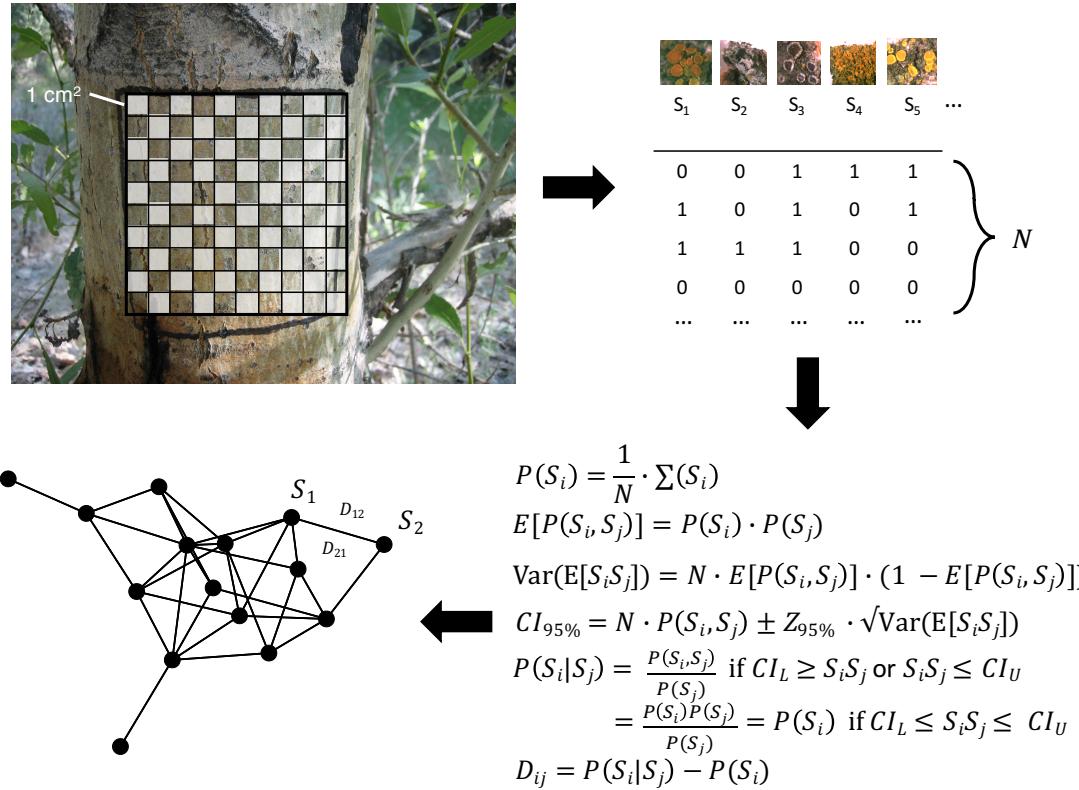
- 708 in mutualistic networks. *Ecology letters*, 14(9):877–85.
- 709 Guimarães, P. R., Rico-Gray, V., Oliveira, P. S., Izzo, T. J., dos Reis, S. F., and Thompson,  
710 J. N. (2007). Interaction Intimacy Affects Structure and Coevolutionary Dynamics in  
711 Mutualistic Networks. *Current Biology*, 17(20):1797–1803.
- 712 Harmon, L. J., Andreazzi, C. S., Débarre, F., Drury, J., Goldberg, E. E., Martins,  
713 A. B., Melián, C. J., Narwani, A., Nuismer, S. L., Pennell, M. W., Rudman, S. M.,  
714 Seehausen, O., Silvestro, D., Weber, M., and Matthews, B. (2019). Detecting the  
715 macroevolutionary signal of species interactions. *Journal of Evolutionary Biology*,  
716 32(8):769–782.
- 717 Holeski, L. M., Hillstrom, M. L., Whitham, T. G., and Lindroth, R. L. (2012). Relative  
718 importance of genetic, ontogenetic, induction, and seasonal variation in producing a  
719 multivariate defense phenotype in a foundation tree species. *Oecologia*, 170:695–707.
- 720 Johnson, M. T. J. (2008). Bottom-up effects of plant genotype on aphids, ants, and  
721 predators. *Ecology*.
- 722 Keith, A. R., Bailey, J. K., Lau, M. K., and Whitham, T. G. (2017). Genetics-based inter-  
723 actions of foundation species affect community diversity, stability and network struc-  
724 ture. *Proceedings of the Royal Society B: Biological Sciences*, 284(1854):20162703.
- 725 Lamit, L., Bowker, M., Holeski, L., Næsborg, R. R., Wooley, S., Zinkgraf, M., Lindroth,  
726 R., Whitham, T., and Gehring, C. (2011). Genetically-based trait variation within a  
727 foundation tree species influences a dominant bark lichen. *Fungal Ecology*, 4(1):103–  
728 109.
- 729 Lamit, L. J., Busby, P. E., Lau, M. K., Compson, Z. G., Wojtowicz, T., Keith, A. R.,  
730 Zinkgraf, M. S., Schweitzer, J. A., Shuster, S. M., Gehring, C. A., and Whitham, T. G.  
731 (2015a). Tree genotype mediates covariance among communities from microbes to  
732 lichens and arthropods. *Journal of Ecology*, 103(4):840–850.
- 733 Lamit, L. J., Lau, M. K., Næsborg, R. R., Wojtowicz, T., Whitham, T. G., and Gehring,  
734 C. A. (2015b). Genotype variation in bark texture drives lichen community assembly  
735 across multiple environments. *Ecology*, 96(4):960–971.
- 736 Lau, M. K., Borrett, S. R., Baiser, B., Gotelli, N. J., and Ellison, A. M. (2017). Ecological  
737 network metrics: opportunities for synthesis. *Ecosphere*, 8(8):e01900.
- 738 Lau, M. K., Keith, A. R., Borrett, S. R., Shuster, S. M., and Whitham, T. G. (2015).  
739 Genotypic variation in foundation species generates network structure that may drive  
740 community dynamics and evolution. *Ecology*, 97(3):15–0600.
- 741 Lau, M. K., Keith, A. R., Borrett, S. R., Shuster, S. M., and Whitham, T. G. (2016).  
742 Genotypic variation in foundation species generates network structure that may drive  
743 community dynamics and evolution. *Ecology*.
- 744 Lieberman, E., Hauert, C., and Nowak, M. A. (2005). Evolutionary dynamics on graphs.  
745 *Nature*, 433(7023):312–316.
- 746 Lieberman, E., Hauert, C., and Nowak, M. A. (2005). Evolutionary dynamics on graphs.  
747 *Nature*, 433(7023):312–316.
- 748 Maliet, O., Loeuille, N., and Morlon, H. (2020). An individual-based model for  
749 the eco-evolutionary emergence of bipartite interaction networks. *Ecology Letters*,  
750 23(11):1623–1634.
- 751 Martinsen, G. D., Whitham, T. G., Turek, R. J., and Keim, P. (2001). Hybrid populations  
752 selectively filter gene introgression between species. *Evolution*, 55(7):1325–1335.
- 753 Moya-Laraño, J. (2011). Genetic variation, predator-prey interactions and food web

- 754       structure. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366(1569):1425–37.
- 755
- 756       Nelson, P. R., McCune, B., Wheeler, T., Geiser, L. H., and Crisafulli, C. M. (2018).  
757       Lichen community development along a volcanic disturbance gradient at Mount St.  
758       Helens. In *Ecological Responses at Mount St. Helens: Revisited 35 years after the  
759       1980 Eruption*, pages 185–198. Springer New York.
- 760       Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings  
761       of the National Academy of Sciences of the United States of America*, 103(23):8577–  
762       82.
- 763       Norby, R. J. and Sigal, L. L. (1989). Nitrogen fixation in the lichen *Lobaria pulmonaria*  
764       in elevated atmospheric carbon dioxide. *Oecologia*, 79(4):566–568.
- 765       Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin,  
766       P. R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., and  
767       Wagner, H. (2019). *vegan: Community Ecology Package*. R package version 2.5-6.
- 768       Poisot, T., Cirtwill, A. R., Cazelles, K., Gravel, D., Fortin, M., and Stouffer, D. B.  
769       (2016). The structure of probabilistic networks. *Methods in Ecology and Evolution*,  
770       7(3):303–312.
- 771       Rezende, E. L., Lavabre, J. E., Guimarães, P. R., Jordano, P., and Bascompte, J. (2007).  
772       Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*,  
773       448(7156):925–8.
- 774       Root, H. T., Miller, J. E. D., and McCune, B. (2011). Biotic soil crust lichen diversity  
775       and conservation in shrub-steppe habitats of Oregon and Washington. *The Bryologist*,  
776       114(4):796.
- 777       Rowntree, J. K., Shuker, D. M., and Preziosi, R. F. (2011). Forward from the crossroads  
778       of ecology and evolution. *Philosophical transactions of the Royal Society of London.  
779       Series B, Biological sciences*, 366(1569):1322–8.
- 780       Santamaría, L. and Rodríguez-Gironés, M. A. (2007). Linkage rules for plant-pollinator  
781       networks: Trait complementarity or exploitation barriers? *PLoS Biology*, 5(2):0354–  
782       0362.
- 783       Schoch, D. (2020). *signnet: An R package to analyze signed networks*.
- 784       Shuster, S. M., Lonsdorf, E. V., Wimp, G. M., Bailey, J. K., and Whitham, T. G. (2006).  
785       COMMUNITY HERITABILITY MEASURES THE EVOLUTIONARY CONSE-  
786       QUENCES OF INDIRECT GENETIC EFFECTS ON COMMUNITY STRUCTURE.  
787       *Evolution*, 60(5):991.
- 788       Smith, D. S., Bailey, J. K., Shuster, S. M., and Whitham, T. G. (2011). A geographic  
789       mosaic of trophic interactions and selection: trees, aphids and birds. *Journal of  
790       evolutionary biology*, 24(2):422–9.
- 791       Smith, D. S., Lamit, L. J., Lau, M. K., Gehring, C. A., Shuster, S. M., and Whitham,  
792       T. G. (2015). Introduced elk alter traits of a native plant and its plant-associated  
793       arthropod community. *Acta Oecologica*, 67:8–16.
- 794       Sole, R. and Bascompte, J. (2006). *Self-Organization in Complex Ecosystems*. Princeton  
795       University Press, Princeton, N.J.
- 796       Staniczenko, P. P., Kopp, J. C., and Allesina, S. (2013). The ghost of nestedness in  
797       ecological networks. *Nature Communications*, 4(1):1–6.
- 798       Thompson, J. N. (2013). *Relentless Evolution*. University of Chicago Press.
- 799       Thompson, J. N., Schwind, C., Guimaraes, P. R., and Friberg, M. (2013). Diversification

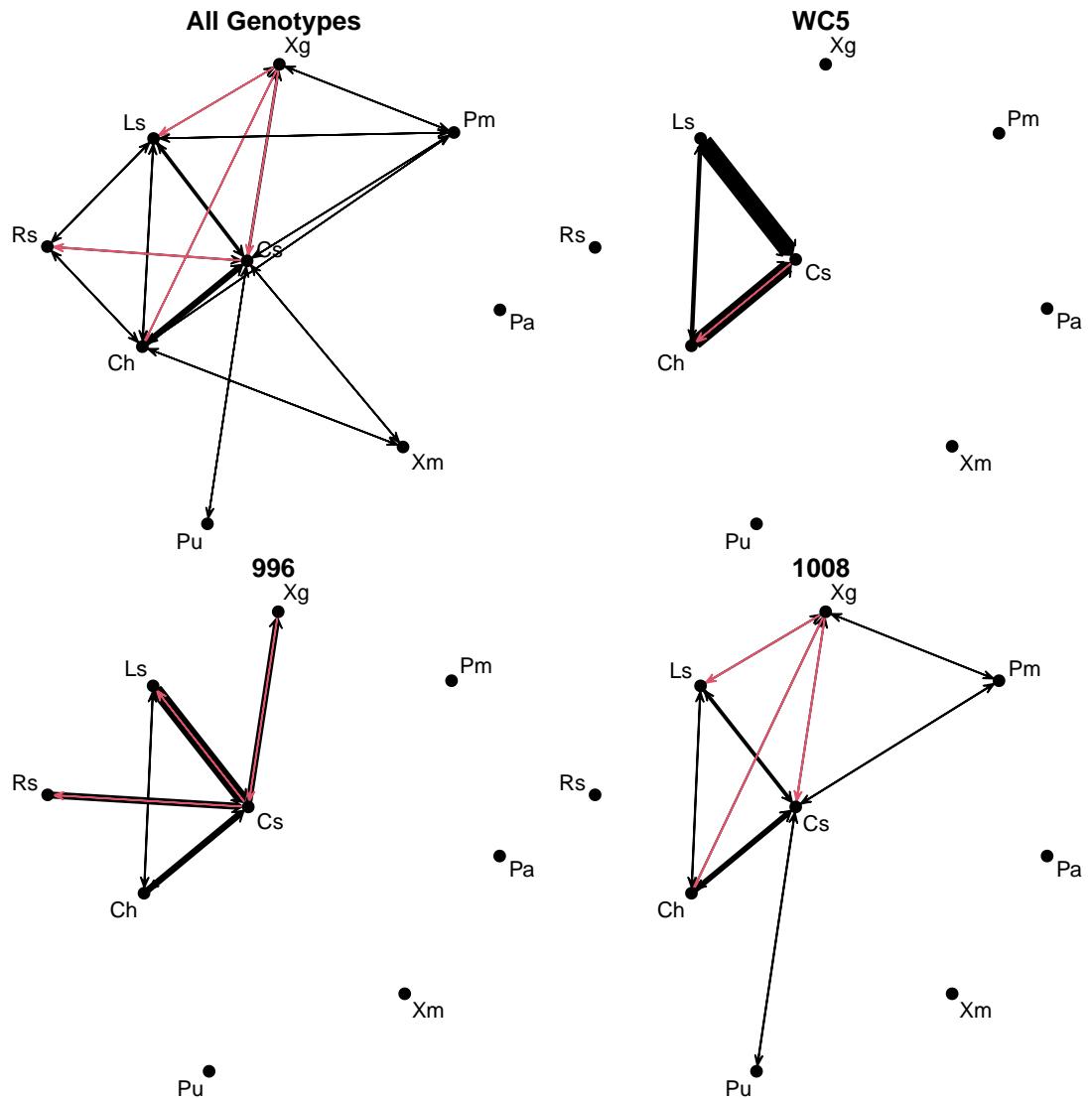
- 800 through multitrait evolution in a coevolving interaction. *Proceedings of the National*  
801 *Academy of Sciences*.
- 802 Toju, H., Guimarães, P. R., Olesen, J. M., and Thompson, J. N. (2014). Assembly of  
803 complex plant-fungus networks. *Nature Communications*.
- 804 Toju, H., Yamamichi, M., Guimarães, P. R., Olesen, J. M., Mougi, A., Yoshida, T., and  
805 Thompson, J. N. (2017). Species-rich networks and eco-evolutionary synthesis at the  
806 metacommunity level.
- 807 Toju, H., Yamamoto, S., Tanabe, A. S., Hayakawa, T., and Ishii, H. S. (2016). Network  
808 modules and hubs in plant-root fungal biomes. *Journal of the Royal Society Interface*.
- 809 Valverde, S., Piñero, J., Corominas-Murtra, B., Montoya, J., Joppa, L., and Solé, R.  
810 (2018). The architecture of mutualistic networks as an evolutionary spandrel. *Nature*  
811 *Ecology and Evolution*, 2(1):94–99.
- 812 Wade, M. J. (2007). The co-evolutionary genetics of ecological communities.
- 813 Weber, M. G., Wagner, C. E., Best, R. J., Harmon, L. J., and Matthews, B. (2017).  
814 Evolution in a Community Context: On Integrating Ecological Interactions and  
815 Macroevolution.
- 816 Whitham, T. G., Allan, G. J., Cooper, H. F., and Shuster, S. M. (2020). Intraspecific Ge-  
817 netic Variation and Species Interactions Contribute to Community Evolution. *Annual*  
818 *Review of Ecology, Evolution, and Systematics*, 51(1).
- 819 Whitham, T. G., Bailey, J. K., Schweitzer, J. A., Shuster, S. M., Bangert, R. K., LeRoy,  
820 C. J., Lonsdorf, E. V., Allan, G. J., DiFazio, S. P., Potts, B. M., Fischer, D. G.,  
821 Gehring, C. A., Lindroth, R. L., Marks, J. C., Hart, S. C., Wimp, G. M., and Wooley,  
822 S. C. (2006). A framework for community and ecosystem genetics: from genes to  
823 ecosystems. *Nature reviews. Genetics*, 7:510–523.
- 824 Whitham, T. G., Gehring, C. A., Lamit, L. J., Wojtowicz, T., Evans, L. M., Keith, A. R.,  
825 and Smith, D. S. (2012). Community specificity: Life and afterlife effects of genes.
- 826 Winfree, R., Gross, B. J., and Kremen, C. (2011). Valuing pollination services to  
827 agriculture. *Ecological Economics*, 71:80–88.
- 828 Zook, A. E., Eklof, A., Jacob, U., and Allesina, S. (2010). Food webs: Ordering species  
829 according to body size yields high degree of intervality. *Journal of theoretical biology*,  
830 271(1):106–113.
- 831 Zytynska, S. E., Fay, M. F., Penney, D., and Preziosi, R. F. (2011). Genetic variation  
832 in a tropical tree species influences the associated epiphytic plant and invertebrate  
833 communities in a complex forest ecosystem. *Philosophical transactions of the Royal*  
834 *Society of London. Series B, Biological sciences*, 366:1329–1336.
- 835 Zytynska, S. E., Khudr, M. S., Harris, E., and Preziosi, R. F. (2012). No Title. *Oecologia*,  
836 170(2).



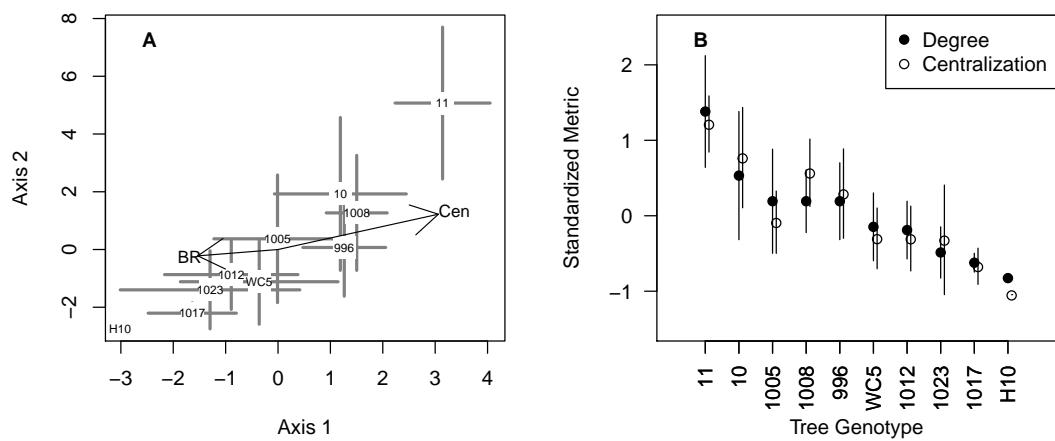
**Figure 1.** The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area ( $100 \text{ cm}^2$ ) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *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).



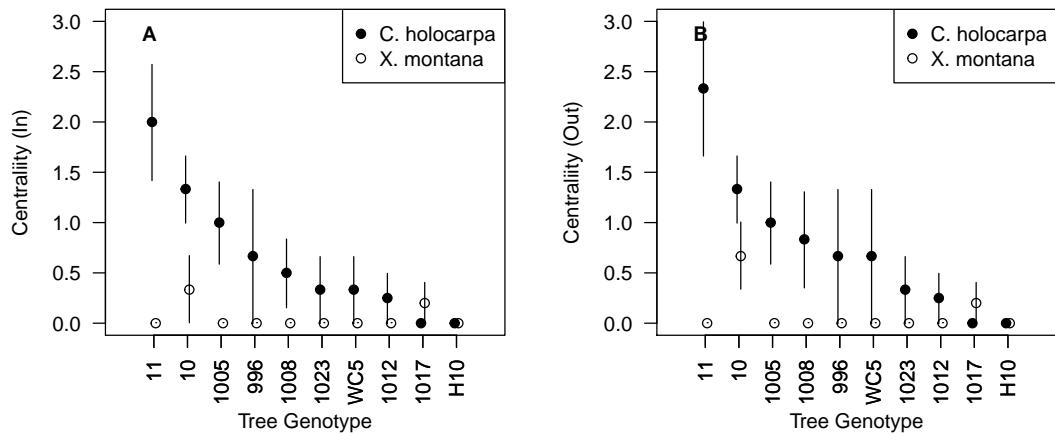
**Figure 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence 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  $S_i$ . In the context of these networks, asymmetry and positive/negative valued connections are distinct quantities. In-coming and out-going connections can be interpreted as “influenced by” and “influenced”, respectively; while positive and negative should be seen as one species increasing or decreasing, respectively, the probability of another species’ occurrence.



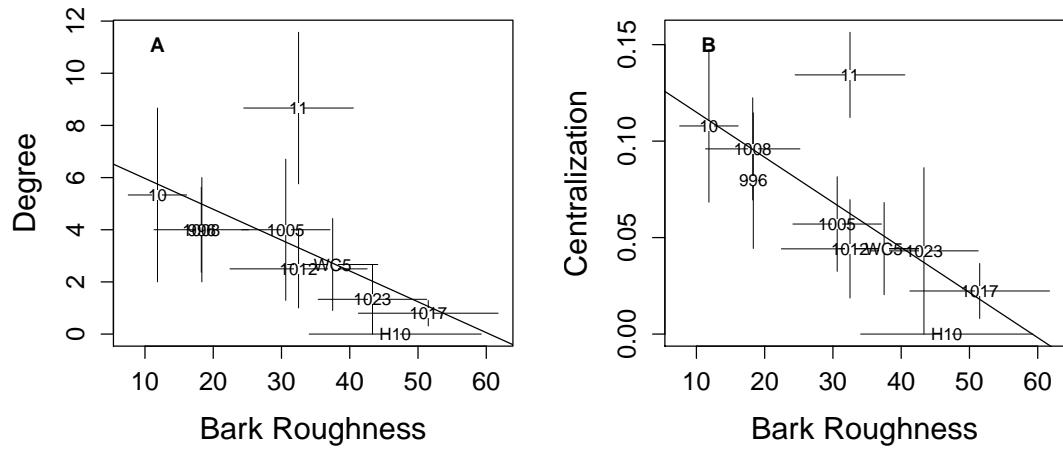
**Figure 3.** Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red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



**Figure 4.** The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ( $R^2 = 0.999$ , stress = 0.008) lichen network similarity ( $\pm 1$  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 decreased.