

# Genotypic variation in a foundation tree alters ecological network structure of an associated community

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1 Biological evolution occurs in the context of complex networks of  
2 interacting species in which natural selection defines the structure  
3 of ecological networks. Fundamental to this evolutionary process  
4 is the discovery of a genetic basis to ecological network structure.  
5 Although previous work has demonstrated that tree genotype con-  
6 tributes to interaction network structure at the scale of forest stands,  
7 the contribution of tree genetics to localized interaction networks  
8 at the scale of individual trees has not yet been explored. To test  
9 the degree to which tree genetics can contribute to network struc-  
10 ture we conducted quantitative modeling of interaction networks. We  
11 constructed networks of epiphytic lichen associated with individual  
12 trees that were a part of a long-term experimental common garden  
13 of genotypes of (*Populus angustifolia*), a foundation species. We  
14 found three main results. First, tree genotype significantly predicted  
15 lichen network similarity, i.e. trees of the same genotype had more  
16 similar lichen networks. Second, bark roughness and condensed  
17 tannin concentration were both predicted by tree genotype and cor-  
18 related with lichen network similarity. Third, the network metrics, the  
19 number of links and centrality, were both correlated with several tree  
20 traits, including bark roughness and condensed tannin concentra-  
21 tion. We conclude that tree genotype influences lichen interaction  
22 network structure with two potential pathways through bark rough-  
23 ness and condensed tannin concentration. These results provide  
24 evidence that variation in ecological networks can result from genet-  
25 ically based variation in foundation species.

networks | heritability | community | genetics | lichen | cottonwood |  
Populus | common garden

- 1 Evolution occurs in complex ecosystems
- 2 Community genetics studies have demonstrated  
3 the importance of genetics and evolutionary dynamics in structuring communities and ecosystems
- 4 Community composition, ecosystem processes have been shown to vary in response to the genetic variation of foundation species
- 5 Previous studies have examined aspects of networks but to date, no studies have examined the genetic basis of networks of interacting species
- 6 Here we examine the genetic basis of network structure on a community of sessile lignicolous

(i.e. bark) lichen on cottonwood trees. This system is ideal for examining for this kind of study because it:

- 1 Lichen do not move among trees, although  
2 asexual propagules could move to other  
3 trees in the garden
- 4 Is not unapproachably complex
- 5 Is comprised of distinct individuals that  
6 are small enough for an entire community  
7 to occur on a single tree but not too small  
8 to be quantified easily

## Significance Statement

Evolution occurs in the context of ecosystems comprised of complex ecological networks. Research at the interface of ecology and evolution has primarily focused on pairwise interactions among species and have rarely included a genetic component to analyses. Here, we use a long-term common garden experiment to reveal the effect that genotypic variation can have on networks of lichens that occur on the bark of a foundation tree species. We found that lichen interaction network structure is genetically based and is correlated with heritable bark traits, including roughness and condensed tannins. These findings demonstrate the importance of genetic variation and evolutionary dynamics in shaping ecological networks as evolved traits.

M.L. and L.L. conceived the study, M.L. and L.L. conducted the field work, R.N. assisted in lichen identifications, M.L. wrote the first draft of the manuscript, S.B. and T.W. contributed substantively to the conceptual development, T.W. established the common garden. All authors contributed to revisions of the manuscript.

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- 25 • We hypothesize that trees will vary in some  
 26 phenotypic traits, such that trees of the same  
 27 genotype will tend to have similar traits produc-  
 28 ing similarities in lichen network structure. To  
 29 test this hypothesis, we use a common garden  
 30 of cottonwood trees with lichen communities.

31 **E**volution occurs in the context of complex eco-  
 32 logical networks. Initially, evolution in a com-  
 33 munity context was focused on examples of highly  
 34 co-evolved pairs of species (e.g. Darwin's famous  
 35 prediction of the Sphinx Moth and Christmas  
 36 Orchid) citeWade2007. However, studies of dif-  
 37 fuse co-evolution (*sensu* citeJanzen1980) citeStinch-  
 38 combe2002, Strauss2007, Dicke2010, geographic mo-  
 39 saics of co-evolution citeThompson2005 and com-  
 40 munity genetics citeWhitham2006 have provided an  
 41 in-road for ecological network approaches citeFor-  
 42 tuna2009, Keith2017, Lau2016 to illuminate a more  
 43 complex perspective of the interface between eco-  
 44 logical and evolutionary dynamics. There is now  
 45 evidence to support that selection tends to occur  
 46 among groups of species citeWade2007, Pieterse2007,  
 47 Dicke2010 favoring the development of small webs  
 48 citeNuismer2006, Guimaraes2007, Gomez2009 and  
 49 that genetic variation and phylogenetic relatedness  
 50 contributes to variation in community assembly (1)  
 51 and species interactions citeWhitham2006a, Bai-  
 52 ley2009, Moya-Larano2011, which shapes the eco-  
 53 logical interaction networks (2).

54 Community genetics studies (3) have shown that  
 55 genetic variation in foundation species (4) plays a  
 56 significant role in defining distinct communities of in-  
 57 teracting organisms: such as, endophytes, pathogens,  
 58 lichens, arthropods, and soil microbes. Multiple stud-  
 59 ies have now demonstrated that genetic variation  
 60 influences numerous functional traits (e.g., phyto-  
 61 chemical, phenological, morphological) produces a  
 62 multivariate phenotype (5) that contributes to varia-  
 63 tion in associated communities (6). The importance  
 64 of genetic variation in structuring ecological systems  
 65 was recently reviewed by Des Roches et al. (2018).

66 Additional work has provided support for the hy-  
 67 pothesis that not only does composition vary among  
 68 genetically distinct genotypes of foundation species,  
 69 it also impacts the structure of the network of species  
 70 interactions in these communities. Two studies have  
 71 demonstrated conceptually (7) and empirically (8).  
 72 However, studies in the network ecology literature  
 73 generally do not include a genetic component (see

74 review by Borrett et al. 2014) and community genet-  
 75 ics papers do not have data on network structure of  
 76 associated communities. Currently, we are aware of  
 77 only one paper that empirically examines the genetic  
 78 basis of network structure of a community citeBar-  
 79 bour2019.

80 Here, we investigate how genetic variation in a  
 81 foundation tree species determines the structure of a  
 82 network of interactions among a community of tree  
 83 associated lichen species. Using a long-term (20+  
 84 years), common garden experiment with replicated  
 85 individuals of known genetic identity and a naturally  
 86 established stand of *Populus angustifolia*. We focused  
 87 on a model community of 9 epiphytic lichen species,  
 88 as previous research has demonstrated significant  
 89 compositional responses of epiphytes to genotypic  
 90 variation (9, 10). In addition, the life-history char-  
 91 acteristics of lichens, having highly localized, direct  
 92 contact interactions and slow population turnover  
 93 rates, allowed us to assess interactions among lichen  
 94 species on individual trees. We hypothesize that in  
 95 natural systems evolution occurs in a community  
 96 context involving interactions of complex networks  
 97 of interacting species (7, 8, 11, 12). If correct, we  
 98 expect to find that network structure is genetically  
 99 based in which different plant genotypes support  
 100 different interaction networks and that these interac-  
 101 tions networks can function as indicators of ecologi-  
 102 cal dynamics important for conserving biodiveristy.  
 103 Applying a probability-theory based network mod-  
 104 eling approach, we constructed a set of interaction  
 105 network models for the lichens associated with indi-  
 106 vidual trees. Using these models, we then examined  
 107 the genetic basis of the structure of these ecological  
 108 networks.

## Materials and Methods

109 The study was conducted along the Weber River, UT  
 110 (USA), which is a cottonwood (*Populus* spp.) dominated  
 111 riparian ecosystem. Although two native species, *Populus*  
 112 *angustifolia* (James) and *Populus fremontii* (S. Watson),  
 113 occur here and are known to hybridize, only pure or  
 114 advanced generation backcrosses of *P. angustifolia* were  
 115 sampled. Bark lichens have been extensively studied  
 116 in this system and provide an ideal system in which to  
 117 observe and model lichen interaction networks, as their  
 118 sessile nature permits accurate identification of individuals  
 119 (13).

120 A long-term, common garden experiment was used  
 121

123 to isolate the effect of tree genotype from the effect of  
124 the localized microenvironment associated with each individual  
125 and spatial autocorrelation. Established in 1992,  
126 asexually propagated clones of genotyped *P. angustifolia*  
127 individuals were obtained from wild collections and  
128 planted in fully randomized design at the Ogden Nature  
129 Center, Ogden, UT. From the population of established  
130 individuals in the common garden, we chose a total of  
131 thirteen genotypes, replicated between 3 and 8 times each,  
132 for sampling.

133 **Bark Lichen Observations.** On each tree, presence or absence  
134 of each lichen species was assessed in 50 total 1 cm<sup>2</sup>  
135 cells arrayed in a checkerboard pattern. Given the small  
136 size and sessile nature of lichens, we were able to rapidly  
137 assess lichen interactions by quantifying thalli in close  
138 contact. Sampling was restricted to the northern aspect  
139 of the trunk to maximize the abundance of lichen and  
140 control for the effect of trunk aspect. Two adjacent 10  
141 cm<sup>2</sup> quadrats centered at 50 cm and 85 cm from ground  
142 level were sampled (Fig 1 A and B). The observed lichen  
143 community included (abbreviations are given for species  
144 present in study): Xg = *Xanthomendoza galericulata*, Xm  
145 = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candeliella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella melanchra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were  
149 not observed in the present study but are known to occur  
150 in this region: *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

152 The cell size and checkerboard sampling pattern was  
153 chosen to isolate the individuals in each cell. In a previous  
154 survey of lichen thallus size in this common garden, we  
155 had observed a median thallus size of 0.12 ± 0.001 cm<sup>2</sup> (1  
156 S.E.) (see Supporting Information). Based on the median  
157 thallus size, we expected thalli observed in each cell to  
158 generally be spatially independent of thalli present in  
159 other cells but exposed to similar micro-environmental  
160 conditions created by the bark and the location of the  
161 sampling area on an individual tree. Therefore, we were  
162 confident in treating the cell-wise observations in quadrats  
163 as independent with respect to lichen-lichen interactions.

164 We also measured several bark traits for each tree:  
165 including, bark roughness and chemistry. **INSERT  
166 FROM LAMIT.**

167 **Lichen Network Modeling and Analysis.** For each tree,  
168 repeated observations of lichen were made in order to construct  
169 replicated interaction networks for each genotype.  
170 We quantified the presence of lichen in the 1 cm<sup>2</sup> cells on  
171 individual trees of *P. angustifolia*. Unipartite networks  
172 were generated using the conditional probabilities of each  
173 species pair, i.e. the probability of observing one species  
174 given an observation of another species  $P(S_i|S_j)$ , based on  
175 the method developed by (14). To calculate conditional  
176 probabilities, we quantified the individual probabilities

177 of species occurrences  $P(S_i)$  and the joint probability  
178 of co-occurrences  $P(S_i, S_j)$  using the frequencies of each  
179 species and their co-occurrences. We were then able to  
180 calculate the conditional probabilities of each species pair  
181 as  $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$ , based on the axioms of probability.  
182 This yielded a matrix that could possibly be asymmetric, i.e.  
183  $P(S_i|S_j)$  does not have to be equal to  $P(S_j|S_i)$ . Another  
184 important property of this matrix is that the diagonal  
185 ( $S_{ii}$ ) was equal to one for all species present and zero for  
186 species that were not observed in any cell.

187 We then applied an analytical procedure to remove  
188 non-significant links between species. This procedure  
189 determines if the joint probability of a species pair  
190 (i.e.  $P(S_i, S_j)$ ) is different from zero (Fig. 2). Here, a  
191 confidence interval  $CI_{95\%}$  is calculated as  $CI_{95\%} =$   
192  $E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$ , where the expected  
193 frequency of co-occurrences  $E(S_i S_j)$  is the total number  
194 of cells surveyed ( $N$ ) times the independent probabilities  
195 of each species  $P(S_i) * P(S_j)$ ,  $Z_{95\%}$  is the Z-score  
196 for 95% from a Z-distribution and the expected variance  
197 of  $E(S_i S_j)$  is the total number of cells times the  
198 expected probability of  $S_i S_j$  and its compliment (i.e.  
199  $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$ ). If the  
200 observed number of co-occurrence falls outside of the  
201 confidence interval, the joint probability  $P(S_i, S_j)$  is de-  
202 termined to be equal to the product of the individual  
203 probabilities (i.e.  $P(S_i) * P(S_j)$ ), and the conditional prob-  
204 ability reduces to the individual probability of that species  
205  $P(S_i)$ . Therefore, unless the co-occurrence of a species  
206 pair falls outside the confidence interval, the probabil-  
207 ity that the observation of one species given the other  
208 is no different than simply observing that species alone.  
209 This enables us to remove links from a given network by  
210 re-scaling the resulting conditional probabilities by sub-  
211 tracting the individual probabilities from the conditional  
212 probabilities (i.e. how different the conditional probability  
213 is from the independent probability), which makes any  
214 species with a non-significant conditional probability zero.  
215 The resulting matrix ( $\mathbf{D} = D_{ij}$ ) can be interpreted as  
216 how one species impacts another with zero being no effect  
217 and values less than or greater than zero interpreted as  
218 negative and positive effects, respectively. Here, we will  
219 refer to this matrix ( $\mathbf{D}$ ) as an interaction matrix with  
220 the properties that it can be asymmetric (i.e.  $P_{ij}$  does not  
221 necessarily equal  $P_{ji}$ ), and the diagonal ( $P_{ii}$ ) is zero (i.e.  
222 a species does not influence its own probability of being  
223 observed).

224 **Statistical Analyses, Software and Data.** We used a com-  
225 bination of parametric and non-parametric, permutation  
226 based frequentist statistical analyses to test for the effects  
227 of genetic variation on lichen communities and their inter-  
228 action networks. To assess the effect of genotype on uni-  
229 partite responses, we used additive, random effects models  
230 with Restricted Maximum Likelihood (REML). We used  
231 a combination of Least Squares Regression, Analysis of



**Fig. 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). Lichens were sampled within a fixed area ( $10 \text{ cm}^2$ ) on individual trees at two heights, 40cm and 80cm from the ground (A and B, respectively). (C) a photo of a typical community of bark lichen species interacting on the trunk of a cottonwood tree, including one of the more abundant species, *Xanthomendoza galericulata*, in the center. (D-K) shows 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 (A-C) and R.R. Naesbourn (D-K).

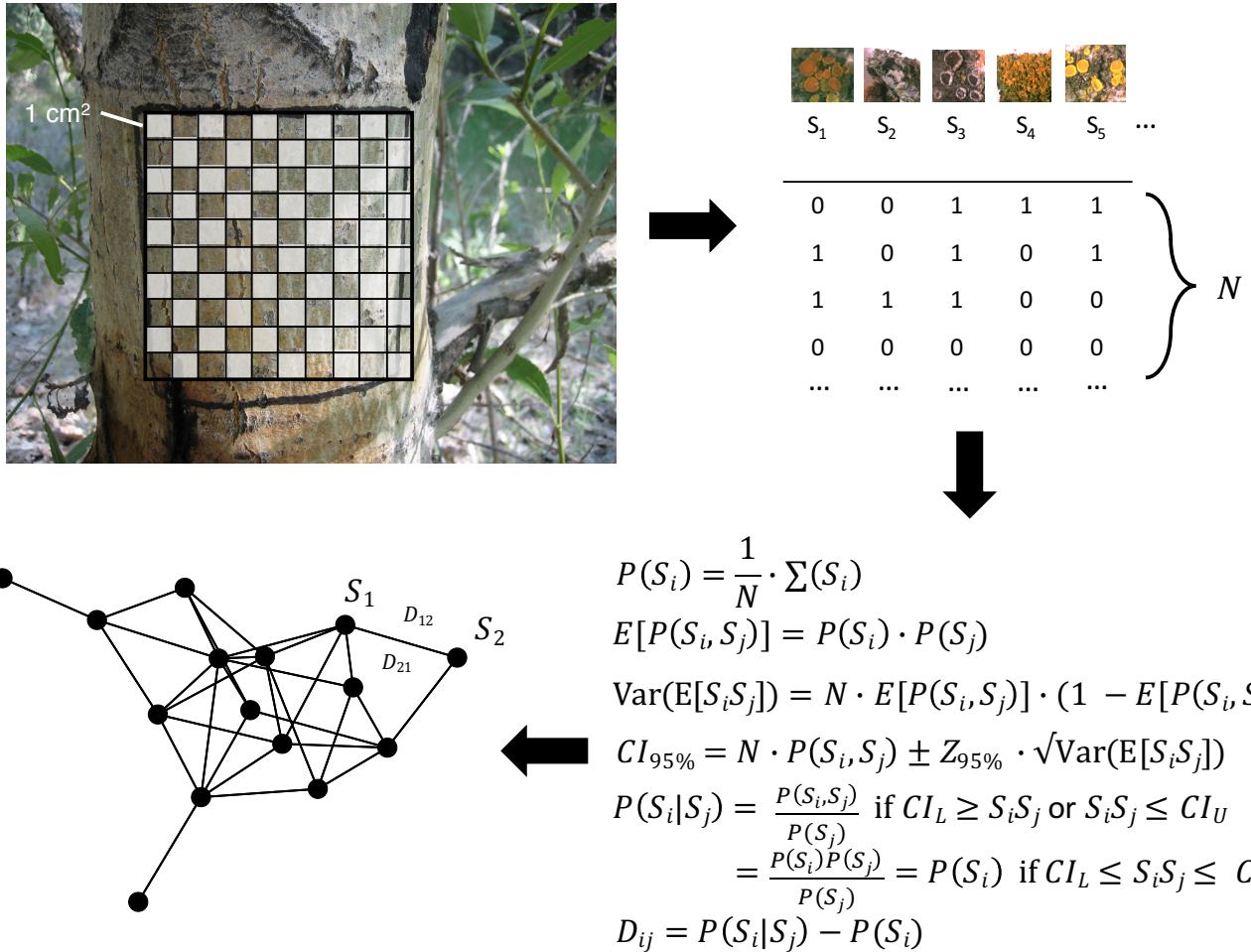
232 Variance (ANOVA) and correlation tests to quantify and  
 233 test for the relationship among other variables. Bark  
 234 roughness, lichen cover and species richness were square-  
 235 root transformed to meet the assumptions of homogeneity  
 236 of variance and normality for these tests.

237 For multivariate response variables, such as lichen com-  
 238 munity composition and network structure, we used dis-  
 239 tance based multivariate statistical approaches, including  
 240 Permutational Analysis of Variance (PERMANOVA) and  
 241 Mantel tests. For some analyses, community composition  
 242 was relativized by species maxima to reduce the effect  
 243 of the highly abundant *X. galericulata*. For community  
 244 composition we used Bray-Curtis dissimilarity, which has  
 245 optimal performance with count data citepMinchen1998.  
 246 To quantify the similarity of lichen networks among indi-  
 247 vidual trees, we calculated the pairwise Euclidean distance  
 248 of the **D** interaction matrices among all pairs of trees.

249 For visualization of multivariate patterns, we used Non-  
 250 metric Multi-Dimensional Scaling (NMDS) citeecodist  
 251 to produce dimensionally reduced ordinations of these  
 252 multi-variate responses and fitted vectors for continuous  
 253 predictor variables to the ordinated values citevegan. Us-  
 254 ing random initial configurations with a maximum of 500

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

255 For each network, we also calculated metrics that mea-  
 256 sure different structural aspects. Although there are many  
 257 other metrics, for the sake of simplicity we focus on a sub-  
 258 set that represent several interesting features of network  
 259 structure (see (15)). We calculated the number of interac-  
 260 tions or “links” in each network, which provides a measure  
 261 of the size of the network citepLau2015, Borrett2014. We  
 262 also calculated the centralization of each network, which  
 263 measures the evenness of the distribution of interactions  
 264 among the species in the network citeButts2005. In a net-  
 265 work with a low level of centralization species have similar  
 266 amount of interaction in the network, while a network  
 267 with a high level of centralization tends to have one or  
 268 small number of species that interact with other species.  
 269 We used a related function to calculate the centrality of  
 270 each species (i.e. node level centrality) in each network  
 271 as well. The modularity of each network was also quanti-  
 272 fied using a weighted algorithm citeBeckett2016, which  
 273 measures the degree to which a given network is divided  
 274 into groups of species more connected to each other than  
 275



**Fig. 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $10 \text{ cm}^2$  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 (14), 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,  $S_iS_j$ , 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  $S_i$ .

other species. As with the other response variables, the number of links was log-transformed and both modularity and centralization scores were fourth-root transformed to meet variance and normality assumptions.

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

## Results

### 1. Genotype influenced lichen network structure

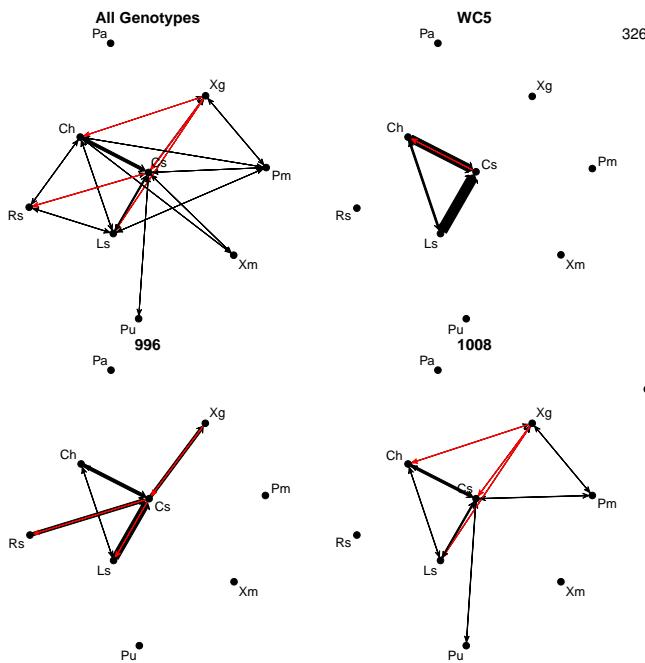
- Tree genotype significantly predicted the similarity of lichen networks ( $\text{Pseudo-}F_{9,27} = 3.58$ ,  $H^2 = 0.41$ ,  $p\text{-value} = 0.0537$ ).

- All network metrics examined responded significantly to tree genotype: including the number of links ( $RLRT = ?$ ,  $H^2 = 0.32$ ,  $p\text{-value} = 0.0269$ ), AMI ( $RLRT = ?$ ,  $H^2 = 0.31$ ,  $p\text{-value} = 0.0268$ ) and degree centralization ( $RLRT = ?$ ,  $H^2 = 0.33$ ,  $p\text{-value} = 0.0196$ ).

- Fig 1. NMDS crosshair with vectors
- Supplementary Table. Vectors
- Supplementary Table. h2-net

### 2. Genotype impacts were on positive interactions mainly driven by Ch

- Tree genotype significantly predicted both in-degree ( $RLRT = ?$ ,  $H^2 = 0.35$ ,  $p\text{-value} = 0.0196$ ).



**Fig. 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 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.

= 0.0157) and out-degree ( $RLRT = ?, H^2 = 0.33$ ,  $p\text{-value} = 0.0195$ ) centralization.

- *Caloplaca holocarpa* centrality was the only species to exhibit a significant response to tree genotype ( $RLRT = ?, H^2 = ?, p\text{-value} = ?$ ).
- Fig 2. dot plot centralization in/out pos/neg
- REFER table: h2-net
- Supplementary Table: species centrality

### 3. Genotype indirectly influenced lichen network centralization via bark roughness

- BR Geno (REML), but not other traits ( $RLRT = ?, H^2 = 0.32$ ,  $p\text{-value} = 0.0128$ )
- Net BR (PERMANOVA) ( $F_{1,32} = 13.029$ ,  $R^2 = 0.26$ ,  $p\text{-value} = 0.0096$ )
- Centrality was significantly correlated with bark roughness ( $F_{1,32} = ?, R^2 = ?, p\text{-value} = ?$ )

- However, tree genotype did not significantly predict the variation in the residuals from the regression of centrality and bark roughness ( $RLRT = ?, H^2 = 0.011$ ,  $p\text{-value} = 0.4219$ )

- Fig. cross-hair plot Cen BR with trend line
- Table: h2\_trait.texSupplementaryTable : cn - trait - perm.tex

- Supplementary Table: geno-trait-path.tex

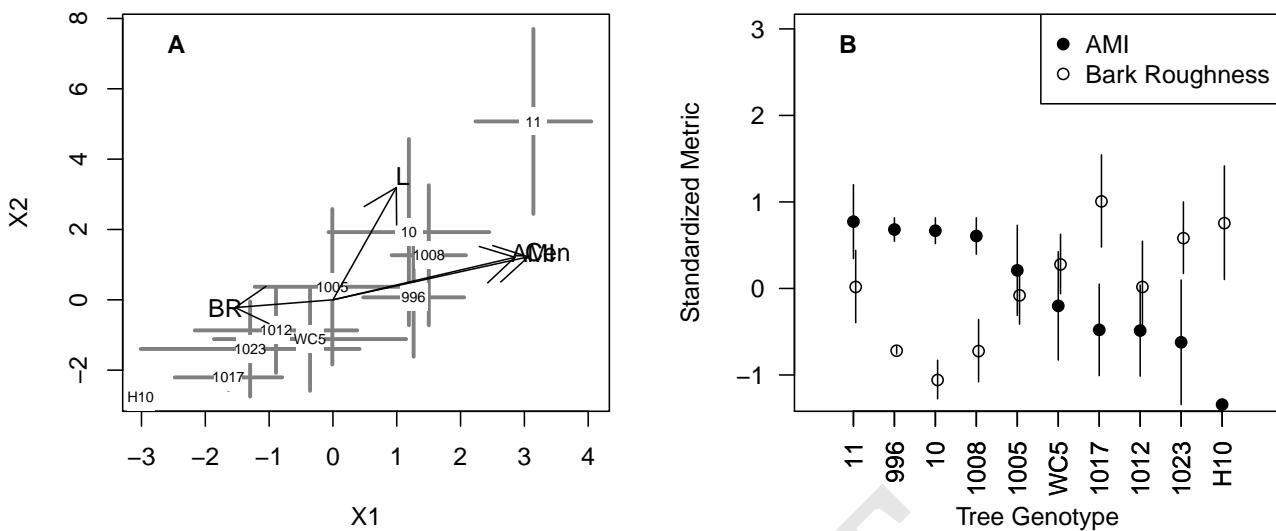
### 4. Net(sim) Other lichen variation (LM) not genetically based (PERMANOVA)

Network similarity and several tree traits were genetically based. Tree genotype was a significant predictor of network similarity ( $H^2 = 0.16$ ,  $p\text{-value} \leq 0.001$ ). Bark roughness ( $H^2 = 0.38$ ,  $p\text{-value} \leq 0.001$ ) and condensed tannin concentration ( $H^2 = 0.28$ ,  $p\text{-value} = 0.014$ ) also showed a signature of tree genotype (Fig. 4); however, this was not the case for other tree traits, bark pH and carbon to nitrogen ratio. Also, none of the lichen network metrics were significantly predicted by tree genotype, either at the scale of the entire network (Table 2) or for individual species (see Supporting Information). Although both showed a response to tree genotype, bark roughness and condensed tannins were not correlated (Pearson's  $r = 0.084$ ,  $p\text{-value} = 0.556$ ).

response	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Average Mutual Information	3.5235	0.3101	0.0254
Degree Centralization	4.0444	0.3305	0.0184
In-degree Centralization	4.4812	0.3487	0.0142
In-Positive Centralization	3.9852	0.3309	0.0190
In-Negative Centralization	0.3304	0.1057	0.2508
Out-degree Centralization	3.8615	0.3193	0.0205
Out-Positive Centralization	3.5585	0.3119	0.0248
Out-Negative Centralization	0.0862	0.0513	0.3446
Number of Network Links	3.5175	0.3156	0.0255

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

Tree traits and lichen community metrics were correlated with lichen networks. The genetically based traits, bark roughness and condensed tannins were both significant predictors of network similarity (Table 4). Bark C:N ratio was also a significant predictor of network similarity, but, as shown previously (see Table 1), there is not sufficient evidence support a genetic basis for it. Bark pH was not a significant



**Fig. 4.** Tree genotype affected lichen networks and several bark traits. A. The plot shows genotype centroids of NMDS ordinated ( $R^2 = 0.999$ , stress = 0.008) lichen networks ( $\pm 1$  S.E.). Centroids that are closer are more similar in the structure of their lichen networks. B. Plot showing the standardized ( $\frac{x - \bar{x}}{\sigma}$ ) means ( $\pm 1$  S.E.) for the two genetically based tree traits: tree bark roughness and condensed tannin concentration.

predictor of lichen network similarity (Table 4). The abundance, richness, evenness and diversity of the bark lichen community, although also not predicted by tree genotype, were all significantly correlated with lichen network structure (Table 4). Lichen community composition was not correlated with lichen network similarity, either when species abundances were relativized (Mantel R = -0.09, *p*-value = 0.139) or not (Mantel R = -0.03, *p*-value = 0.573).

	df	SS	R2	F	p-value
geno	9.0000	44078.1327	0.5442	3.5821	0.0537
Residual	27.0000	36915.4605	0.4558		
Total	36.0000	80993.5932	1.0000		

**Table 2.** PERMANOVA Pseudo-F Table of lichen network similarity to genotype.

## Discussion

- We found:
    - Lichen networks genetically based
    - Bark roughness was the primary genetically based trait driving network structure
    - Lichn networks also varied with cover, richness and diversity of the lichen community, which were not correlated with rough-

ness and primarily driven by one dominant species

- What mechanisms could be at play?
  - Habitat filtering of communities (richness, composition) vs environmental influence on interactions. Likely a combination of both of these factors.
    - Lichen network structure correlated with species richness, evenness and diversity
    - Lichen community composition not correlated with network structure
    - None of these were genetically based
  - An important consequence for diversity is that genotypes could be supporting unique communities, even if the composition of the communities is the same among individuals and genotypes.
  - Genetic diversity could be influencing the stability of communities through the effects on interactions. Some network structures are likely to be more stable, either in response to disturbance or via self-organized dynamics. Although, none of the metrics examined, such as the number of links, modularity or centrality, showed a genetic signature.

- Important factors to consider in studies of other ecological networks:
    - Relative body size
    - Mobility
    - Reproductive isolation
  - Future work should consider the potential influence on evolutionary dynamics of communities
    - Network structure influences network stability
    - Are the communities nested subsets?

410 TGW: I think window is too vague and this  
411 topic sentence needs to be much stronger for  
412 a journal like PNAS. Might be stronger by  
413 saying "Our findings argue there is a genetic  
414 component to network structure, which im-  
415 plies that network structure could be subject  
416 to selection and networks can evolve."

417 TGW: Could we also make the comparison  
418 that genetically more similar trees also have  
419 more similar communities? We've done this  
420 in the past and it has worked, e.g., Randy's  
421 genetic similarity rule.

- Genetic assembly rule = similar genetics will have more similar communities
  - What we don't know is whether or not these interactions will also lead to similar interactions among other species.
  - Thus, it would be possible for genetics to not only influence other species directly, but also indirectly by influencing the interactions among other species.

We observed significant lichen interaction structure that varied among genotypes of a foundation tree species, narrowleaf cottonwood (*P. angustifolia*). We found that a genetically based trait, bark roughness, partially explained the variation in lichen interaction networks. Some of this variation in lichen networks was related to both the overall abundance and species richness of lichen; though, statistically controlling for the effect of genotype on these variables indicates that a significant portion of the variance in lichen species richness is due to a factor<sup>10</sup> other than tree genotype. By using network metrics,

we were also able to probe for specific characteristics of how these networks were responding to tree genotype. We found that both number of links and the centralization of the networks were highly correlated with network similarity and that tree genotype significantly predicted network centrality but only marginally predicted the number of network links. This latter result could be due to the relationship between species richness and the number of links in the network, which were significantly correlated with each other. We also found that bark roughness did not significantly predict either the number of links or the centrality of lichen networks, suggesting that bark roughness has some other effect on the structure of the lichen networks. Taken together, these findings support the hypothesis that genotypic variation in a foundation species contributes to the structure of a network of interacting species.

LJL: I wonder if you need to have so much on richness here. Overall, I think you want to focus on the network responses and patterns among genotype first, and then go into mechanism later. I think we don't quite have a good mechanism yet so I don't think it needs to come up in the first paragraph of the discussion.

These findings point to the importance of understanding the community level effects of genetic variation in plant functional traits and highlights the potential for indirect effects of genetic variation to propagate through networks of interacting species and trophic levels.

This work corroborates previous findings of the importance of plant genetics in shaping community structure and ecosystem processes. citepBangert2008

Altering the structure of interaction networks  
presents a means for genetic effects to be magnified  
within the system of interacting species. For  
example, (8) showed that the genetics based interactions  
of aphid resistant and aphid susceptible trees  
resulted in different interaction networks of their  
associated arthropod communities composed of 139  
species. At the scale of ecosystems, trophic networks  
or food webs direct and control the rates of  
energy and nutrient flux (16). Furthermore, in a  
predator-prey-plant study, Smith (17), showed that  
the interactions among species across trophic levels  
depended on plant genotype.

<sup>442</sup> Also, work by (18–20) observed consistent pat-

492 terns of centralized interactions of species modules  
493 focused around hubs of plant-fungal interactions. In  
494 other words, a small number of plant and fungal  
495 symbionts tended to have disproportionate numbers  
496 of interactions with other species and likely are the  
497 drivers in determining community assembly, struc-  
498 ture and dynamics.

499 More on the importance of ecological networks  
500 (21, 22).

501 From Thompson2014

- 502 • Pairwise interactions are usually influenced by  
503 other species
- 504 • Selection favors the development of small webs
- 505 • Evolution of new lifestyles leads to changes in  
506 selection on large and small webs

507 Specific hypothesis from Thompson2014

508 **LJL:** If I recall, the Elamo paper just looks  
509 at genetic correlations between pairwise individ-  
510 ual abundances. I would suggest maybe it  
511 doesn't deserve to be in this 1st paragraph.  
512 Perhaps it actually should be in the 2nd or  
513 3rd paragraph, just as a reference that points  
514 to the potential for genotype to influence net-  
515 works. Definately our 2015 JOE paper goes  
516 much further, too, since it has whole com-  
517 munities being correlated. But, again, I  
518 woudl put both of these as citation in the com-  
519 munity genetics paragraphs (2 of 3) instead  
520 of the first paragrphah, which focuses on the  
521 general network lit.

522 **LJL:** It could be useful to point out that  
523 our findings are not related to trophic inter-  
524 actions, which is pretty cool. Also,we talk  
525 about interaction networks but it is not clear  
526 to me if the interactions tend to be positive  
527 or negative. Can we get at that with the ap-  
528 proach used?

529 **TGW:** Is there any adaptive component to  
530 the tree in having certain lichen communi-  
531 ties? e.g., can they feed back to affect tree  
532 performance in some way or is this a pas-  
533 sive outcome of a trait that affects bark for  
534 other adaptive reasons and lichens are pas-  
535 sive players that tag along for the ride? I  
536 could envision that lichens covering the bark  
537 of a tree act as a barrier between insects and  
538 pathogens, much like ectomycorrhizae cover-

539 fine roots as a first line of defense by invad-  
540 ing microorganisms. Uptake of N that gets  
541 passed to the tree??

542 **LJL:** I agree that there is a general overar-  
543 ching theme that evolution occurs in a com-  
544 munity network context, but I'm not sure  
545 that we should state that as our main hypoth-  
546 esis. It seems more that this is a fundamen-  
547 tal foundation for our work. The hypoth-  
548 esis is more what we are testing directly, but  
549 we don't test this directly. I guess I don't  
550 want to give the impresison that our com-  
551 munities are necessarily the result of each  
552 species evolving into its place in the commu-  
553 nity on these tree genotypes (although I do  
554 understand this as Shuster et al 2006's funda-  
555 mental explanation for why we see different  
556 communities on different genotypes; I don't  
557 necessarily agree that this is the only rea-  
558 son we woudl see different communities on  
559 dif genotypes). Most of these are pretty gen-  
560 eralist lichens, which could be found on other  
561 decidous trees in the surrounding city or nat-  
562 ural areas. I would look at it more like an  
563 assembling of lichen species into unique con-  
564 figurations on genetically different substrates.  
565 There may be some selection for different  
566 genotype of lichen during the community as-  
567 sembly process but we can't really tell that  
568 just by differences in species abundances or  
569 coocurneces. I guess to me the evolutionary  
570 context that is more direclty related to this  
571 work is that the tree genotype is a central  
572 controller (indeed a sort of hub species in the  
573 network) of network structure. By anchor-  
574 ing the lichen network to tree genotype (and  
575 variation among networks to variation among  
576 tree genotypes) , our study highlights the poss-  
577 ibility that natural selection acting on the  
578 trees may have an extended consequence for  
579 the network structure of organisms living on  
580 the trees...the extra thing we add to the field  
581 is that we show interaction networks are sen-  
582 sitive to genotype. I doubt the lichens have  
583 a direct effect on tree fitness, but favorabil-  
584 ity of some tree genotypes over others during  
585 natural selection will then go on to favor and  
586 disfavor certain lichen communities of differ-  
587 ent network structures. By being sensitive

588 to tree genotype, the lichen community net-  
589 works are passive riders on the waves of evolu-  
590 tionary dynamics that occur within the tree  
591 species they inhabit.

592 **MKL:** In response to Lamit's comment  
593 above, I agree that it is not required that  
594 there is co-evolution. Another, perhaps sim-  
595 pler, explanation is that there is variation in  
596 environmental filtering of lichen individuals  
597 created in part by genetic variation in tree  
598 individuals.

599 **TGW:** might be good to cite papers on  
600 competition in lichens or other organizing fac-  
601 tors to back up the least expected statement.  
602 as epiphytes we might not expect them to  
603 care.

604 **TGW:** I think we need to emphasize the  
605 long-term nature of our common garden  
606 study as very few common garden studies of  
607 lichens likely exist. Any refs on this? If true  
608 might want to mention this up front in intro.

609 **MKL:** Environmental filtering is evidenced  
610 by species richness, but also possibly species  
611 interaction varying based on environment as  
612 networks varied in terms of sign and magni-  
613 tude as well.

614 **MKL:** The effect of bark roughness on  
615 network similarity was primarily genetically  
616 based, and there are likely other factors at  
617 play.

#### 618 Discussion of network implications for sta- 619 bility with genetics.

620 Bark roughness had previously been shown to be  
621 an important tree trait influencing bark lichens (13)  
622 that is under strong genetic control (23).

623 Although our study was conducted with a commu-  
624 nity of lichens, these results should be generalized  
625 to other groups of diverse organisms around the  
626 world that also exhibit significant genetic signals at  
627 the community level (24, 25). In the face of the  
628 high degree of complexity and potential context de-  
629 pendence of ecological processes, the current study  
630 points to the utility of considering the spatial and  
631 temporal scales of interactions, as discussed to some  
632 in previous studies (26–28). In the present study,  
633 we found that community assembly processes, such  
634 as environmental filtering and species interactions  
635 are genetically based. This is likely due, in part  
636 to the large difference in the differences in size and

637 longevity of the lichen and cottonwood individuals  
638 with the trees determining the environment in which  
639 the lichen occur. We suggest that future work would  
640 be aided by determining these modules within the  
641 biotic community that include species with similar  
642 differences in body-size and time-scales. As heritable  
643 variation is the raw material for natural selection  
644 to act upon, a genetic basis for interaction network  
645 structure indicates evolutionary dynamics should be  
646 considered at the community level and that con-  
647 serving genetic variation is important to consider in  
648 efforts to restore or preserve complex species interac-  
649 tions and their associated ecosystem functions (29).  
650 With such findings, it appears that we are closer to  
651 understanding the evolutionary drivers of Darwin's  
652 entangled bank and the interconnectedness of species  
653 in complex communities.

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660 and David Solance Smith.

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## Assessment and Results

- Network similarity not genetically based
- Genetically based number of links and centrality but not modularity
- Lichen cover, richness, evenness, diversity and composition not genetically based
- Roughness genetically based but not bark condensed tannins, CN or pH
- Bark roughness correlation with number of links (yes) and centrality (yes)? <- TODO add figure A = mdc.plot(L, Cen), B = (ch.plot(L,Cen,geno), BR vector))
- Centrality values for species <- censpp.pdf
- Redo haritability calculations
- Jamie double check genotype network permanova in PRIMER
- Jamie double check reml's in R

## Tables.

738

response	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Average Mutual Information	3.5235	0.3101	0.0254
Degree Centralization	4.0444	0.3305	0.0184
In-degree Centralization	4.4812	0.3487	0.0142
Out-degree Centralization	3.8615	0.3193	0.0205
In-Positive Centralization	3.9852	0.3309	0.0190
In-Negative Centralization	0.3304	0.1057	0.2508
Out-Positive Centralization	3.5585	0.3119	0.0248
Out-Negative Centralization	0.0862	0.0513	0.3446
Number of Network Links	3.5175	0.3156	0.0255
Percent Lichen Cover	0.0000	0.0000	1.0000
Lichen Species Diversity	0.0000	0.0000	0.4543
Lichen Species Richness	0.0000	0.0000	0.4543
Lichen Species Evenness	0.0000	0.0000	1.0000
Percent Rough Bark	4.8526	0.3221	0.0113
pH	0.0000	0.0000	1.0000
Carbon-Nitrogen (CN) Ratio	0.0000	0.0000	1.0000
Condensed Tannins (CT)	0.0007	0.0041	0.4439
BR-L Residuals	0.0000	0.0000	1.0000
BR-Cen Residuals	0.0000	0.0000	1.0000
BR-AMI Residuals	0.0000	0.0000	1.0000

**Table 1. Genotypic effects on tree traits and bark lichen.**

response	statistic	H2	p-value
Percent Rough Bark	4.8526	0.3221	0.0113
pH	0.0000	0.0000	1.0000
Carbon-Nitrogen (CN) Ratio	0.0000	0.0000	1.0000
Condensed Tannins (CT)	0.0007	0.0041	0.4439
BR-L Residuals	0.0000	0.0000	1.0000
BR-Cen Residuals	0.0000	0.0000	1.0000
BR-AMI Residuals	0.0000	0.0000	1.0000

**Table 3. Genotypic effects on tree traits and residuals from trait regressions of lichen network structure.**

	r	R2	estimate	SE	t	p-value
br_L	-0.34	0.11	-0.07	0.03	-2.13	0.04
br_Cen	-0.39	0.15	-0.00	0.00	-2.52	0.02
br_AMI	-0.36	0.13	-0.01	0.00	-2.27	0.03
ct_L	0.34	0.11	0.57	0.27	2.13	0.04
ct_Cen	0.08	0.01	0.00	0.00	0.46	0.65
ct_AMI	0.02	0.00	0.00	0.03	0.12	0.91
ph_L	0.08	0.01	0.67	1.41	0.48	0.64
ph_Cen	0.13	0.02	0.02	0.02	0.78	0.44
ph_AMI	-0.04	0.00	-0.04	0.17	-0.21	0.83
cn_L	0.06	0.00	50.19	145.84	0.34	0.73
cn_Cen	0.16	0.03	2.14	2.18	0.98	0.33
cn_AMI	0.13	0.02	12.84	17.10	0.75	0.46

response	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Average Mutual Information	3.5235	0.3101	0.0254
Degree Centralization	4.0444	0.3305	0.0184
In-degree Centralization	4.4812	0.3487	0.0142
In-Positive Centralization	3.9852	0.3309	0.0190
In-Negative Centralization	0.3304	0.1057	0.2508
Out-degree Centralization	3.8615	0.3193	0.0205
Out-Positive Centralization	3.5585	0.3119	0.0248
Out-Negative Centralization	0.0862	0.0513	0.3446
Number of Network Links	3.5175	0.3156	0.0255

**Table 2. Genotypic effects on the associated lichen network structure.**

## Figures.

739

	df	SS	R2	F	p-value
geno	9.0000	44078.1327	0.5442	3.5821	0.0537
Residual	27.0000	36915.4605	0.4558		
Total	36.0000	80993.5932	1.0000		

**Table 4. PERMANOVA Pseudo-F Table of lichen network similarity to genotype.**

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1.0000	21021.8765	0.2595	13.0299	0.0096
CT	1.0000	2349.3142	0.0290	1.4562	0.2016
pH	1.0000	2098.8999	0.0259	1.3010	0.2899
CN	1.0000	3896.1757	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

**Table 5. PERMANOVA Pseudo-F Table of lichen network similarity response to bark traits.**

lichen species	mean	statistic	H2	p-value
Positive				
In-Degree				
X. galericulata	0.2703	0	0	1
C. subdeflexa	0.8919	2.1926	0.2158	0.0595
L. spp.	0.4324	0	0	1
C. holocarpa	0.5946	3.6146	0.3241	0.024
X. montana	0.0541	0	0	0.4543
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.1351	2.049	0.2613	0.0656
Out-Degree				
X. galericulata	0.027	0	0	0.4543
C. subdeflexa	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4246
C. holocarpa	0.7027	3.1318	0.2981	0.0327
X. montana	0.0811	2.9228	0.3163	0.0375
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.2973	0.1505	0.0612	0.3119
Negative				
In-Degree				
X. galericulata	0			
C. subdeflexa	0.1892	0	0	0.4543
L. spp.	0.1892	0.0015	0.0057	0.4398
C. holocarpa	0.1351	0	0	1
X. montana	0.027	0.0377	0.0394	0.3807
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0.1622	0	0	1
Out-Degree				
X. galericulata	0.2432	0	0	1
C. subdeflexa	0.4054	0	0	0.4543
L. spp.	0.027	0	0	0.4543
C. holocarpa	0.027	0	0	0.4543
X. montana	0			
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0			

	BR	CT	PC	SR	SE	SD	L	Cen	AMI
BR							-0.34	-0.39	-0.36
CT							0.34		
PC				0.49				-0.46	
SR					0.76		0.47		
SE					0.85		0.45		
SD						0.59		0.33	
L							0.88		0.38
Cen									0.57
AMI									

	Df	SumOfSqs	R2	F	Pr(>F)
geno	9.0000	1.5049	0.2001	0.7507	0.8878
Residual	27.0000	6.0143	0.7999		
Total	36.0000	7.5193	1.0000		

**Table 6. Pseudo-F Table of lichen community similarity PERMANOVA.**

	r	R2	estimate	SE	t	p-value
br_L	-0.34	0.11	-0.07	0.03	-2.13	0.04
br_Cen	-0.39	0.15	-0.00	0.00	-2.52	0.02
br_AMI	-0.36	0.13	-0.01	0.00	-2.27	0.03
ct_L	0.34	0.11	0.57	0.27	2.13	0.04
ct_Cen	0.08	0.01	0.00	0.00	0.46	0.65
ct_AMI	0.02	0.00	0.00	0.03	0.12	0.91
ph_L	0.08	0.01	0.67	1.41	0.48	0.64
ph_Cen	0.13	0.02	0.02	0.02	0.78	0.44
ph_AMI	-0.04	0.00	-0.04	0.17	-0.21	0.83
cn_L	0.06	0.00	50.19	145.84	0.34	0.73
cn_Cen	0.16	0.03	2.14	2.18	0.98	0.33
cn_AMI	0.13	0.02	12.84	17.10	0.75	0.46

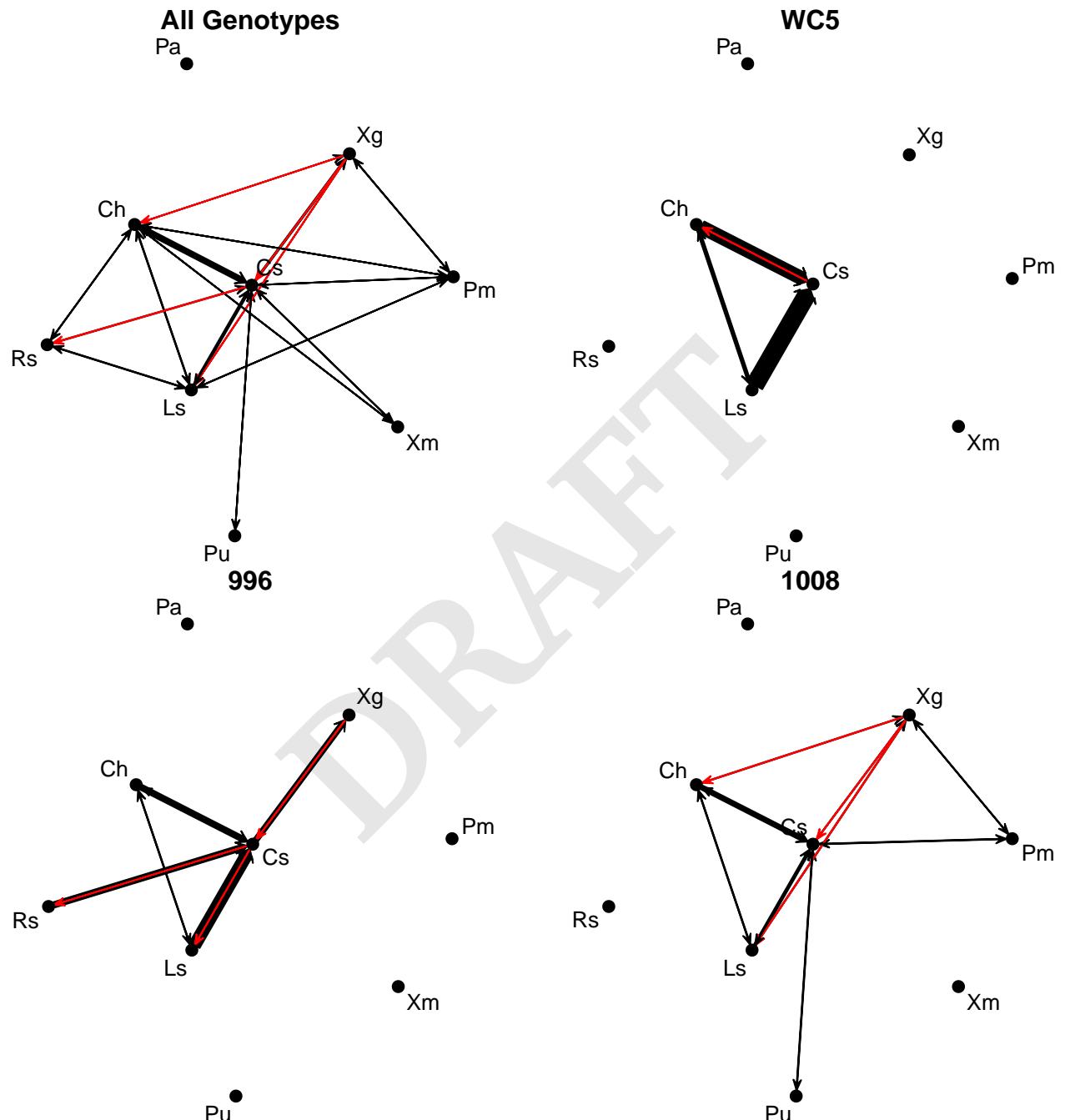


Fig. 1

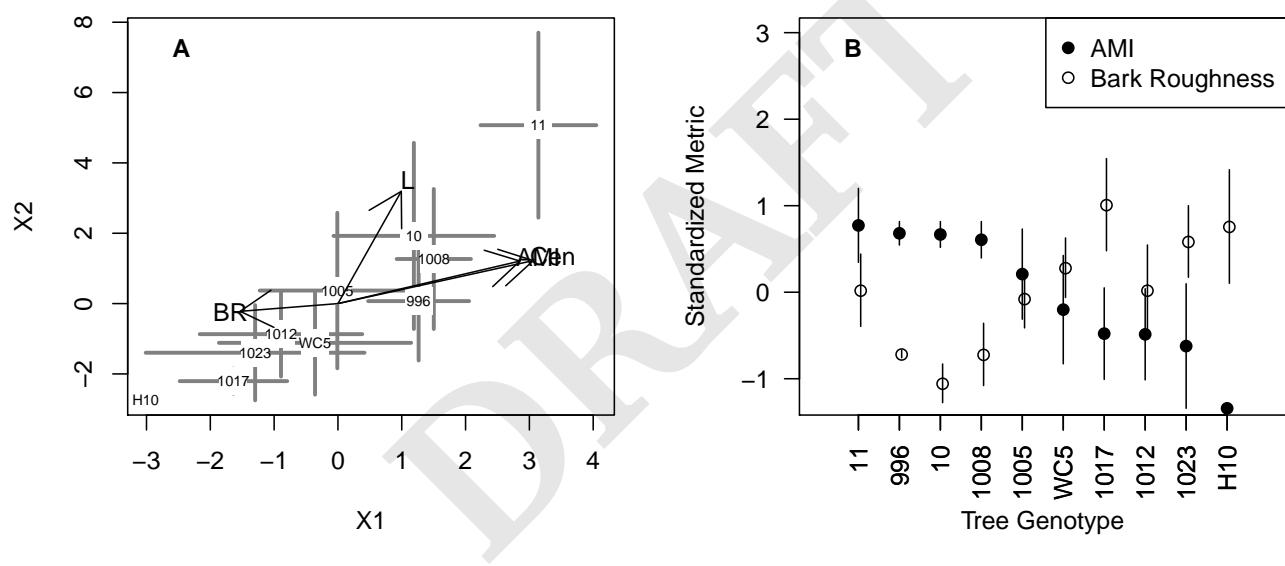


Fig. 2

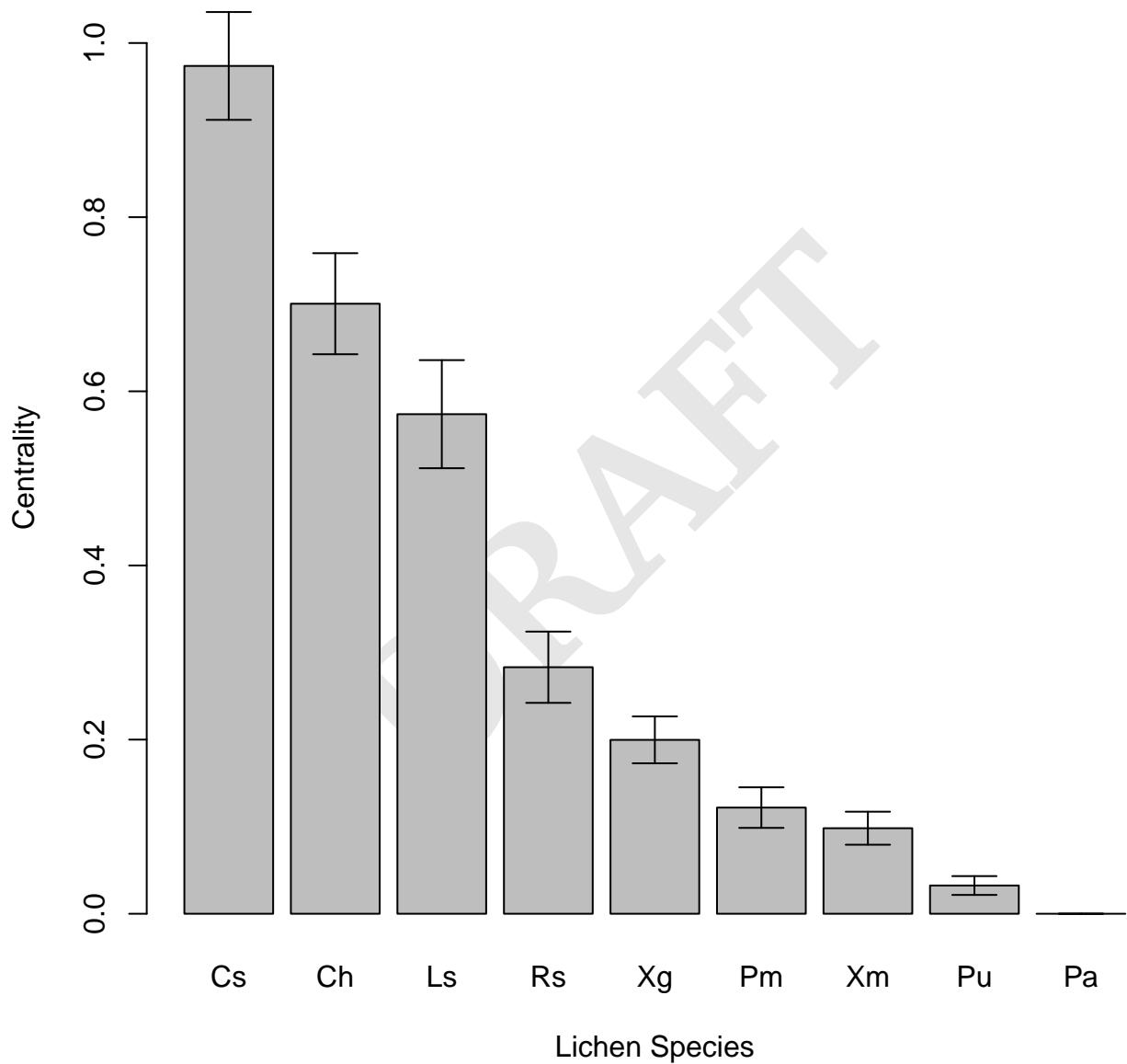


Fig. 3

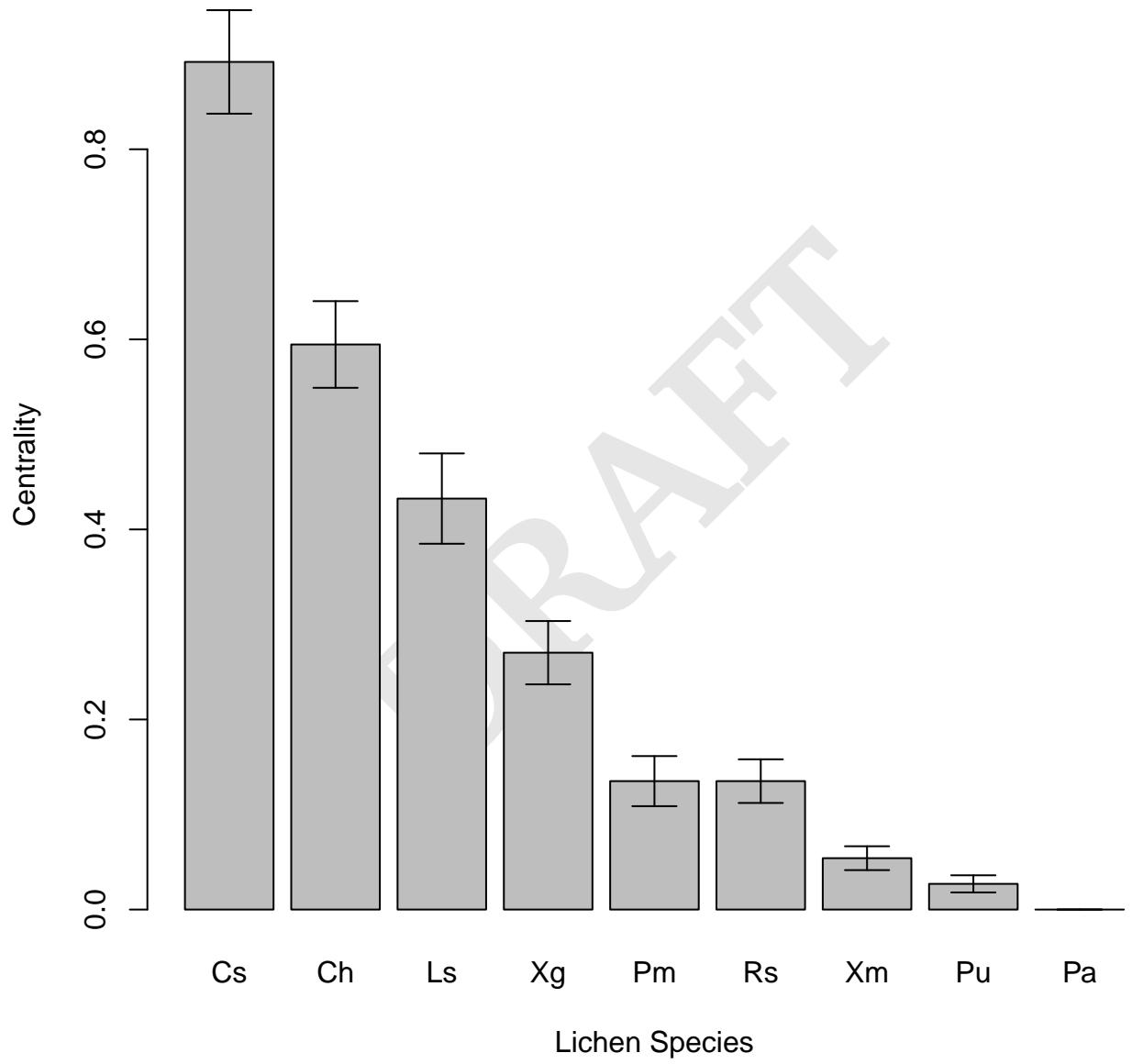


Fig. 4

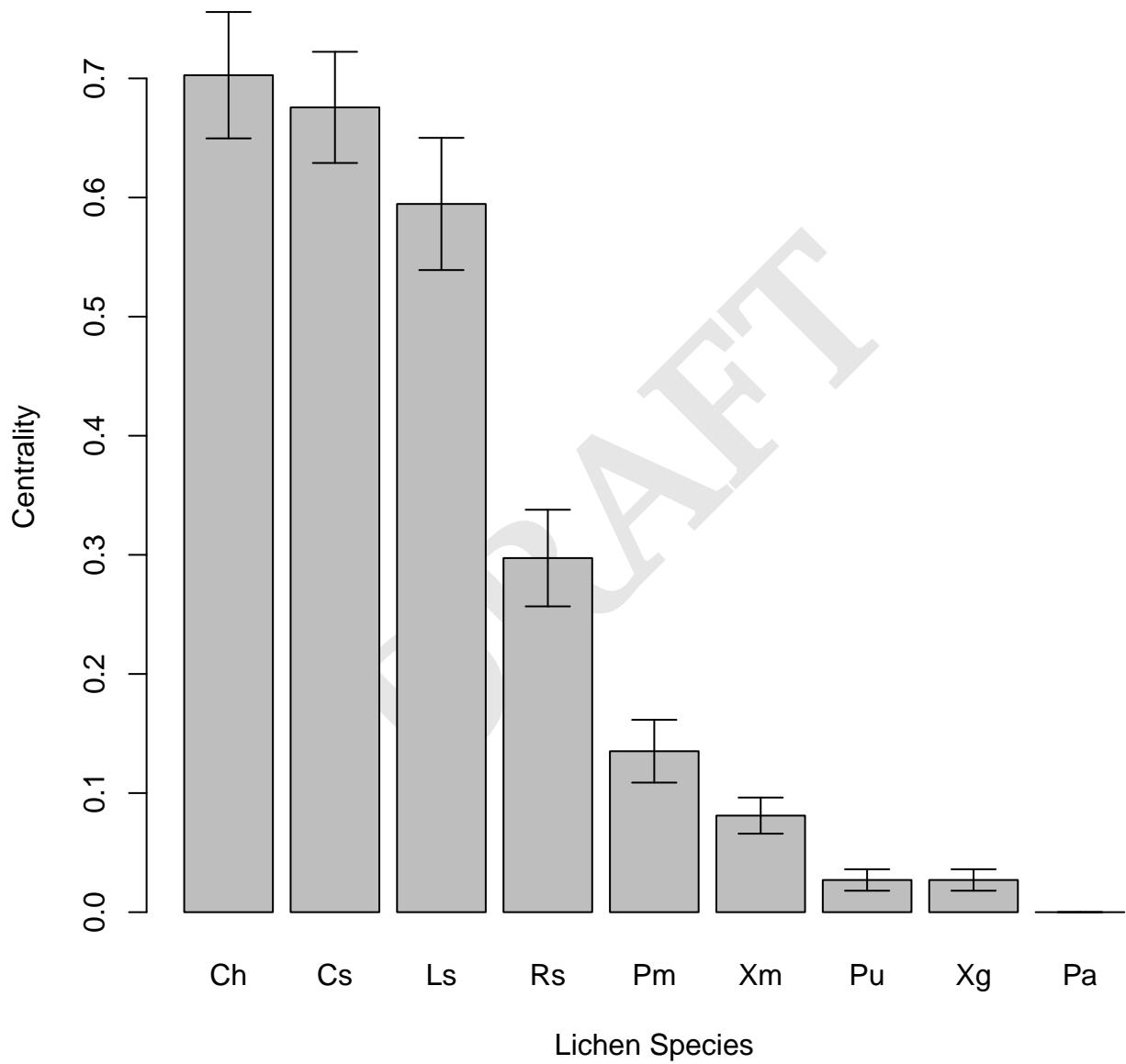
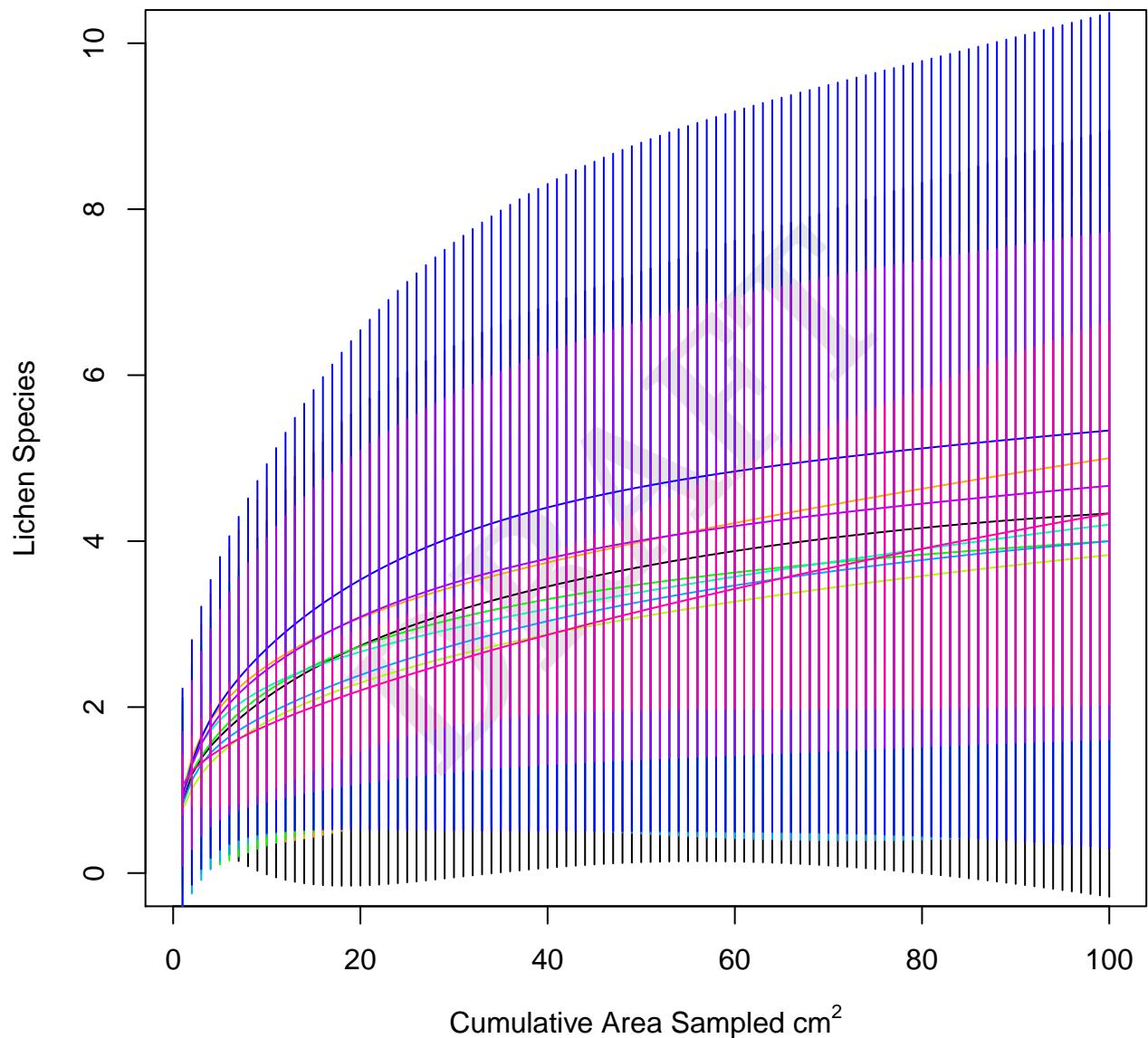


Fig. 5



**Fig. 6.** Species area curve by genotype.

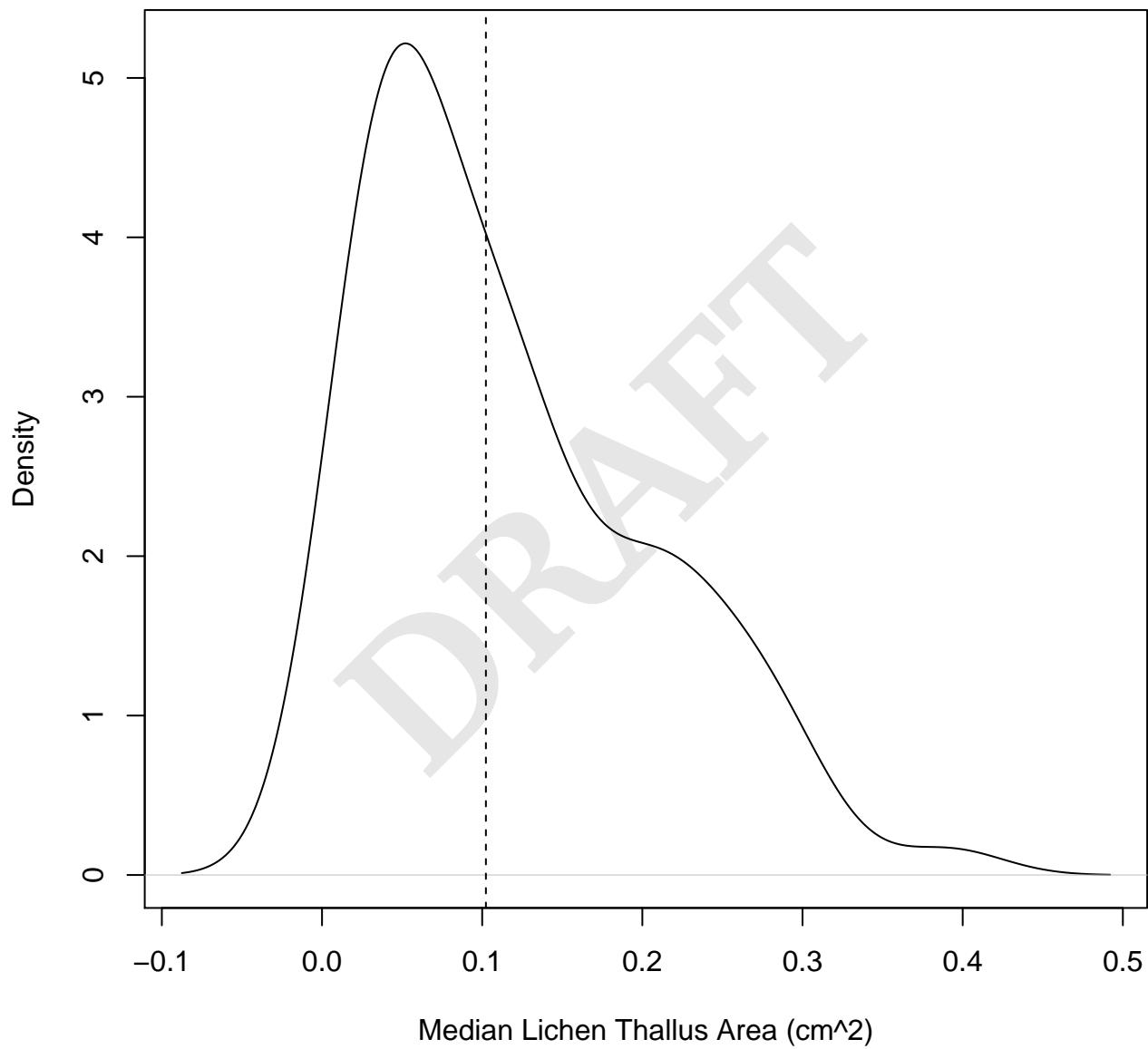


Fig. 7