

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 dy-
4 namics in structuring communities and ecosys-
5 tems
- 6 • Community composition, ecosystem processes
7 have been shown to vary in response to the
8 genetic variation of foundation species
- 9 • Previous studies have examined aspects of net-
10 works but to date, no studies have examined the
11 genetic basis of networks of interacting species
- 12 • Here we examine the genetic basis of network
13 structure on a community of sessile lignicolous

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

- 16 1. Lichen do not move among trees, although
17 asexual propagules could move to other
18 trees in the garden
- 19 2. Is not unapproachably complex
- 20 3. Is comprised of distinct individuals that
21 are small enough for an entire community
22 to occur on a single tree but not too small
23 to be quantified easily

Significance Statement

Evolution occurs in the context of ecosystems com-
prised of complex ecological networks. Research
at the interface of ecology and evolution has primar-
ily focused on pairwise interactions among species
and have rarely included a genetic component to
analyses. Here, we use a long-term common gar-
den 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 genet-
ically based and is correlated with heritable bark
traits, including roughness and condensed tannins.
These findings demonstrate the importance of ge-
netic 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 cm²
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 cm² 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 cm² (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 cm² 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 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. Naesbour (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

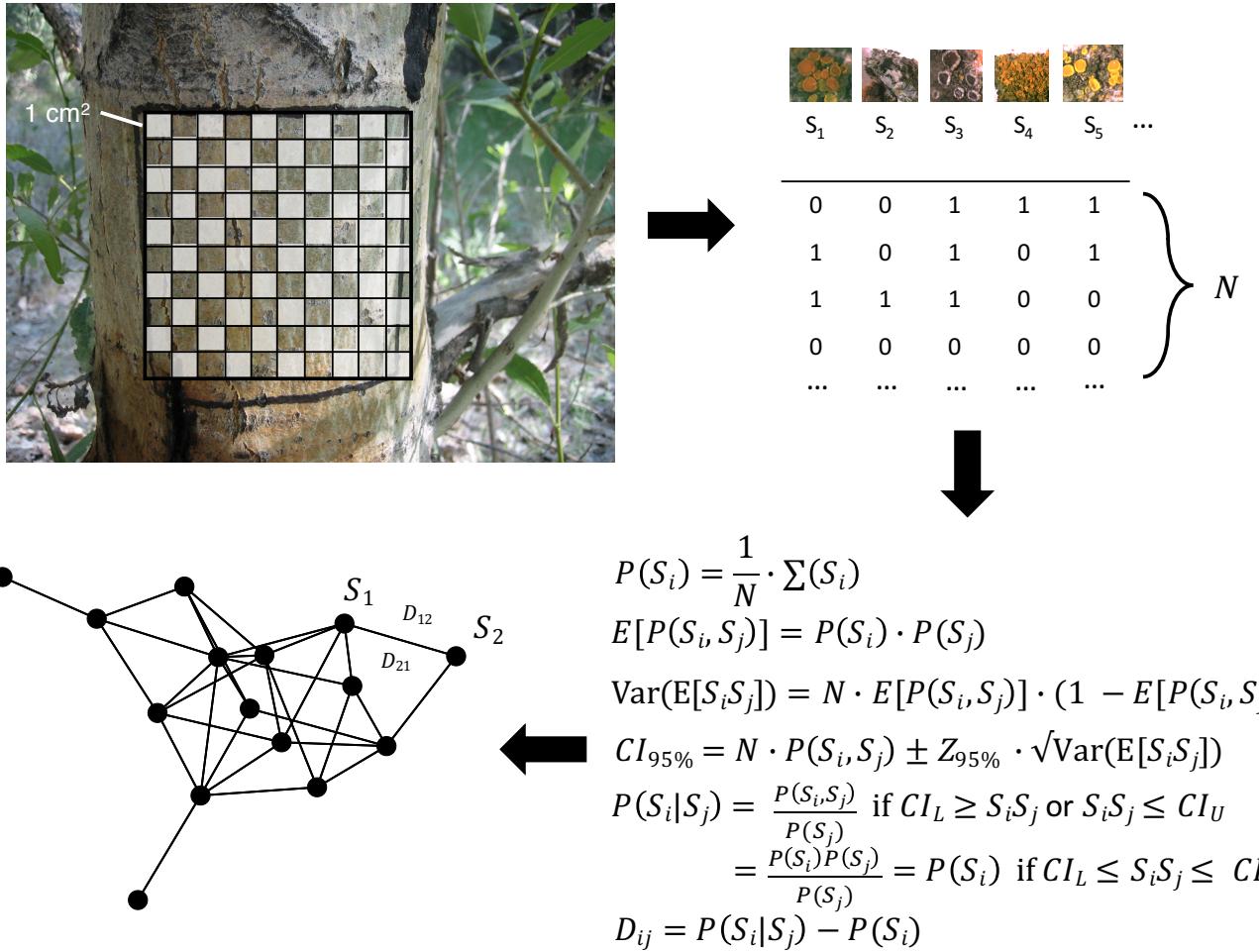


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 10 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded 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. The project is also archived via Zenodo at zenodo.com/doiXXXXXX. 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 ($RLRT = ?$, $H^2 = 0.33$, $p\text{-value} = 0.0196$).
- Networks were dominated by positive links (mean + SE), and in general we observed far fewer negative links among lichen species (mean + SE).
- Only positive links responded to tree genotype (see h2-net.tex)
- Tree genotype significantly predicted both in-degree ($RLRT = ?$, $H^2 = 0.35$, $p\text{-value} = 0.0157$) and out-degree ($RLRT = ?$, $H^2 = 0.30$, $p\text{-value} = 0.0160$).

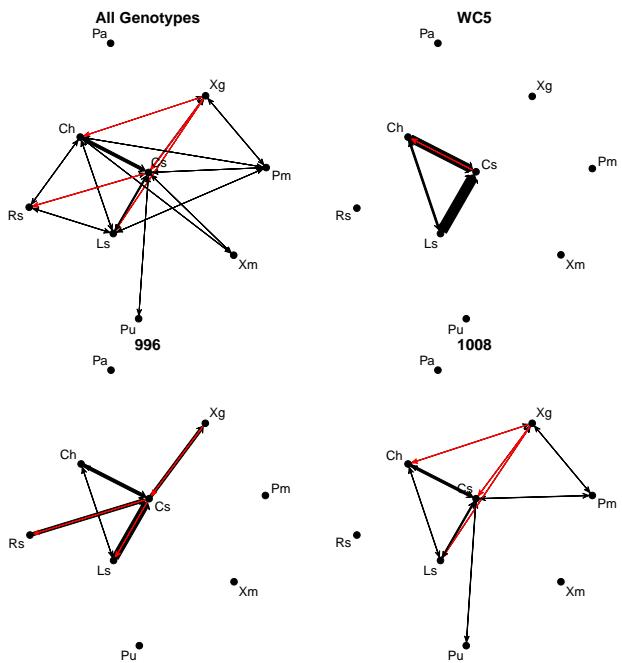


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) 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.

$= 0.33$, $p\text{-value} = 0.0195$) centralization.

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

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

- Centrality varied among species (ANOVA).
 - *Caloplaca holocarpa* centrality was the main species to exhibit a significant response to tree genotype in terms of overall centrality ($RLRT = ?, H^2 = ?, p\text{-value} = ?$), as well as positive centrality for both in- ($RLRT = ?, H^2 = ?, p\text{-value} = ?$) and out-degree ($RLRT = ?, H^2 = ?, p\text{-value} = ?$).
 - Although *X. montana* positive out-degree centrality also varied significantly among tree genotypes ($RLRT = ?, H^2 = ?, p\text{-value} = ?$), this response was small ($H^2 = ?$) and driven by two genotypes.

- Fig 2. dot plot centralization in/out pos/neg 329
 - Supplementary Table: species centrality 331

Genotype indirectly influenced lichen network
centralization via bark roughness 332

333

 - BR Geno (REML), but not other traits (RLRT = ?, $H^2 = 0.32$, *p-value* = 0.0128) 334
 - Net BR (PERMANOVA) ($F_{1,32} = 13.029$, $R^2 = 0.26$, *p-value* = 0.0096) 335
 - Centrality was significantly correlated with bark roughness ($F_{1,32} = ?$, $R^2 = ?$, *p-value* = ?) 336
 - Centrality was significantly correlated with bark roughness ($F_{1,32} = ?$, $R^2 = ?$, *p-value* = ?) 337
 - Bark roughness was significantly correlated with tree genotype ($F_{1,32} = ?$, $R^2 = ?$, *p-value* = ?) 338
 - Bark roughness was significantly correlated with tree genotype ($F_{1,32} = ?$, $R^2 = ?$, *p-value* = ?) 339
 - Bark roughness was significantly correlated with tree genotype ($F_{1,32} = ?$, $R^2 = ?$, *p-value* = ?) 340
 - 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-value* = 0.4219) 341
 - Fig. cross-hair plot Cen BR with trend line 342
 - Fig. cross-hair plot Cen BR with trend line 343
 - Fig. cross-hair plot Cen BR with trend line 344
 - Fig. cross-hair plot Cen BR with trend line 345
 - Fig. cross-hair plot Cen BR with trend line 346
 - Fig. cross-hair plot Cen BR with trend line 347
 - Table: h2-trait.tex 348
 - Supplementary Table: cn-trait-perm.tex 349
 - Supplementary Table: geno-trait-path.tex 350

Network similarity and several tree traits were genetically based. Tree genotype was a significant predictor of network similarity ($H^2 = 0.16$, *p-value* ≤ 0.001). Bark roughness ($H^2 = 0.38$, *p-value* ≤ 0.001) and condensed tannin concentration ($H^2 = 0.28$, *p-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 1) 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-value* = 0.556).

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 2). Bark C:N ratio was also a significant predictor of network similarity, but, as shown previously (see Table ??), there is not sufficient evidence support a genetic basis for it. Bark pH was not a significant

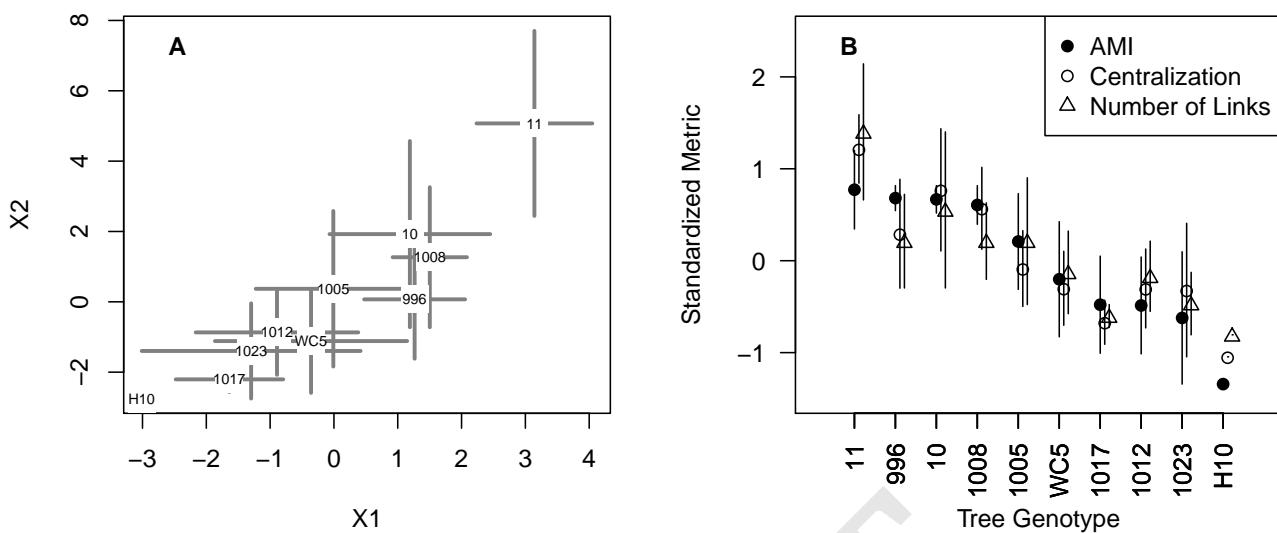


Fig. 4. Tree genotype affected lichen networks and several bark traits. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen networks (± 1 S.E.). Centroids that are closer are more similar in the structure of their lichen networks. B. Plot showing the standardized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

response	statistic	H2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Centralization	4.0444	0.3305	0.0184
Centralization In-Degree	4.4812	0.3487	0.0142
Centralization In-Degree (positive)	3.9852	0.3309	0.0190
Centralization In-Degree (negative)	0.3304	0.1057	0.2508
Centralization Out-Degree	3.8615	0.3193	0.0205
Centralization Out-Degree (positive)	3.5585	0.3119	0.0248
Centralization Out-Degree (negative)	0.0862	0.0513	0.3446
Number of Network Links (Degree)	3.5175	0.3156	0.0255
Degree (positive)	3.6925	0.3242	0.0229
Degree (negative)	0.0327	0.0318	0.3859

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

	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.

- Bark roughness was the primary genetically based trait driving network structure 386
- Lichen networks also varied with cover, richness and diversity of the lichen community, which were not correlated with roughness and primarily driven by one dominant species 387
- What mechanisms could be at play? 388
- Habitat filtering of communities (richness, composition) vs environmental influence on interactions. Likely a combination of both of these factors. 389
- Lichen network structure correlated with species richness, evenness and diversity 390
- Lichen community composition not correlated with network structure 391
- None of these were genetically based 392

374 predictor of lichen network similarity (Table 2). The
375 abundance, richness, evenness and diversity of the
376 bark lichen community, although also not predicted
377 by tree genotype, were all significantly correlated
378 with lichen network structure (Table 2). Lichen com-
379 munity composition was not correlated with lichen
380 network similarity, either when species abundances
381 were relativized (Mantel R = -0.09, p-value = 0.139)
382 or not (Mantel R = -0.03, p-value = 0.573).

383 Discussion

- 384 • We found:
- Lichen networks genetically based

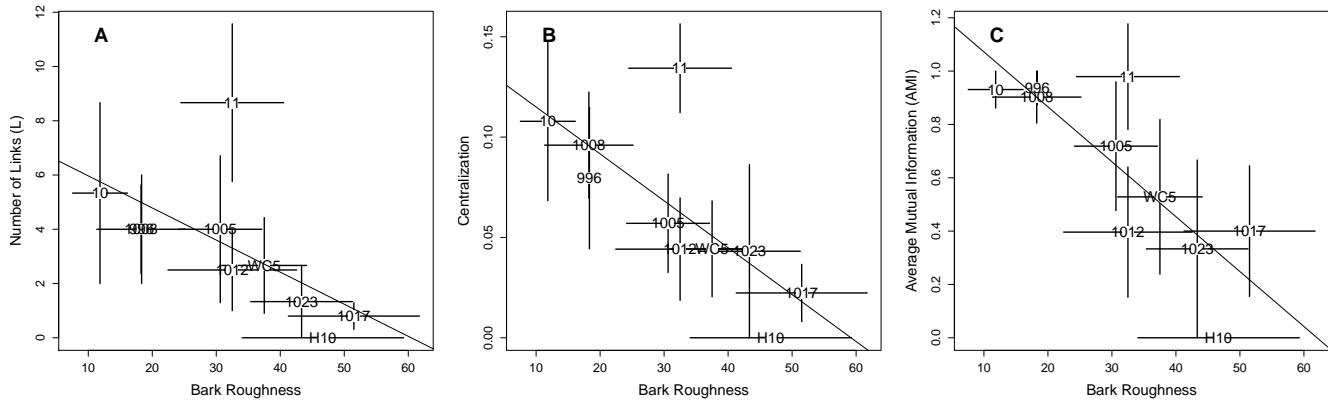


Fig. 5. Bivariate plots of the relationship between bark roughness and three network metrics: A) number of links (L), B) centralization and C) average mutual information (AMI). Each plot displays the genotype mean \pm 1 S.E. for both variables and a least-squares regression calculated using the genotype means.

- 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?

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

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

463	significantly predicted network centrality but only	512
464	marginally predicted the number of network links.	513
465	This latter result could be due to the relationship	514
466	between species richness and the number of links	515
467	in the network, which were significantly correlated	516
468	with each other. We also found that bark roughness	517
469	did not significantly predict either the number of	518
470	links or the centrality of lichen networks, suggesting	519
471	that bark roughness has some other effect on the	520
472	structure of the lichen networks. Taken together,	521
473	these findings support the hypothesis that genotypic	
474	variation in a foundation species contributes to the	
475	structure of a network of interacting species.	
476	LJL: I wonder if you need to have so much	522
477	on richness here. Overall, I think you want to	523
478	focus on the network responses and patterns	524
479	among genotype first, and then go into mech-	525
480	anism later. I think we don't quite have a	526
481	good mechanism yet so I don't think it needs	527
482	to come up in the first paragrpah of the dis-	528
483	cussion.	529
484	These findings point to the importance of under-	530
485	standing the community level effects of genetic vari-	531
486	ation in plant functional traits and highlights the	532
487	potential for indirect effects of genetic variation to	533
488	propagate through networks of interacting species	534
489	and trophic levels.	535
490	This work corroborates previous findings of the	536
491	importance of plant genetics in shaping community	
492	structure and ecosystem processes. citepBangert2008	
493	Altering the structure of interaction networks	537
494	presents a means for genetic effects to be magni-	538
495	fied within the system of interacting species. For	539
496	example, (8) showed that the genetics based interac-	540
497	tions of aphid resistant and aphid susceptible trees	541
498	resulted in different interaction networks of their	542
499	associated arthropod communities composed of 139	543
500	species. At the scale of ecosystems, trophic net-	
501	works or food webs direct and control the rates of	
502	energy and nutrient flux (16). Furthermore, in a	
503	predator-prey-plant study, Smith (17), showed that	
504	the interactions among species across trophic levels	
505	depended on plant genotype.	
506	Also, work by (18–20) observed consistent pat-	544
507	terns of centralized interactions of species modules	545
508	focused around hubs of plant-fungal interactions. In	546
509	other words, a small number of plant and fungal	547
510	symbionts tended to have disproportionate numbers	548
511	of interactions with other species and likely are the	549
	drivers in determining community assembly, struc-	550
	ture and dynamics.	551
	More on the importance of ecological networks	552
	(21, 22).	553
	From Thompson2014	554
	• Pairwise interactions are usually influenced by	555
	other species	556
	• Selection favors the development of small webs	557
	• Evolution of new lifestyles leads to changes in	558
	selection on large and small webs	559
	Specific hypothesis from Thompson2014	560
	LJL: If I recall, the Elamo paper just looks	561
	at genetic correlations between pairwise indi-	562
	vidual abundances. I would suggest maybe it	563
	doesn't deserve to be in this 1st paragraph.	564
	Perhaps it actually should be in the 2nd or	565
	3rd paragraph, just as a reference that points	566
	to the potential for genotype to influence net-	567
	works. Definately our 2015 JOE paper goes	568
	much further, too, since it has whole com-	569
	munities being correlationed. But, again, I	570
	would put both of these as citation in the com-	571
	munity genetics paragraphs (2 of 3) instead	572
	of the first paragrpah, which focuses on the	573
	general network lit.	574
	LJL: It could be useful to point out that	575
	our findings are not related to trophic inter-	576
	actions, which is pretty cool. Also,we talk	577
	about interaction networks but it is not clear	578
	to me if the interactions tend to be positive	579
	or negative. Can we get at that with the ap-	580
	proach used?	581
	TGW: Is there any adaptive component to	582
	the tree in having certain lichen communi-	583
	ties? e.g., can they feed back to affect tree	584
	performance in some way or is this a pas-	585
	sive outcome of a trait that affects bark for	586
	other adaptive reasons and lichens are pas-	587
	sive players that tag along for the ride? I	588
	could envision that lichens covering the bark	589
	of a tree act as a barrier between insects and	590
	pathogens, much like ectomycorrhizae cover	591
	fine roots as a first line of defense by invad-	592
	ing microorganisms. Uptake of N that gets	593
	passed to the tree??	594
	LJL: I agree that there is a general over-	595
	arching theme that evolution occurs in a com-	596

559 munity network context, but I'm not sure
560 that we should state that as our main hypothesis.
561 It seems more that this is a fundamental foundation for our work. The hypothesis
562 is more what we are testing directly, but
563 we don't test this directly. I guess I don't
564 want to give the impression that our communities are necessarily the result of each
565 species evolving into its place in the community on these tree genotypes (although I do
566 understand this as Shuster et al 2006's fundamen-
567 tal explanation for why we see different
568 communities on different genotypes; I don't
569 necessarily agree that this is the only reason we would see different communities on
570 dif genotypes). Most of these are pretty generalist lichens, which could be found on other
571 deciduous trees in the surrounding city or natural areas. I would look at it more like an
572 assembling of lichen species into unique configura-
573 tions on genetically different substrates.
574 There may be some selection for different
575 genotype of lichen during the community as-
576 sembly process but we can't really tell that
577 just by differences in species abundances or
578 coocurneces. I guess to me the evolutionary
579 context that is more direclty related to this
580 work is that the tree genotype is a central
581 controller (indeed a sort of hub species in the
582 network) of network structure. By anchor-
583 ing the lichen network to tree genotype (and
584 variation among networks to variation among
585 tree genotypes), our study highlights the pos-
586 sibility that natural selection acting on the
587 trees may have an extended consequence for
588 the network structure of organisms living on
589 the trees...the extra thing we add to the field
590 is that we show interaction networks are sen-
591 sitive to genotype. I doubt the lichens have
592 a direct effect on tree fitness, but favorabil-
593 ity of some tree genotypes over others during
594 natural selection will then go on to favor and
595 disfavor certain lichen communities of differ-
596 ent network structures. By being sensitive
597 to tree genotype, the lichen community net-
598 works are passive riders on the waves of evolu-
599 tionary dynamics that occur within the tree
600 species they inhabit.

607 MKL: In response to Lamit's comment

608 above, I agree that it is not required that
609 there is co-evolution. Another, perhaps sim-
610 pler, explanation is that there is variation in
611 environmental filtering of lichen individuals
612 created in part by genetic variation in tree
613 individuals.

614 TGW: might be good to cite papers on
615 competition in lichens or other organizing fac-
616 tors to back up the least expected statement.
617 as epiphytes we might not expect them to
618 care.

619 TGW: I think we need to emphasize the
620 long-term nature of our common garden
621 study as very few common garden studies of
622 lichens likely exist. Any refs on this? If true
623 might want to mention this up front in intro.

624 MKL: Environmental filtering is evidenced
625 by species richness, but also possibly species
626 interaction varying based on environment as
627 networks varied in terms of sign and magni-
628 tude as well.

629 MKL: The effect of bark roughness on
630 network similarity was primarily genetically
631 based, and there are likely other factors at
632 play.

633 Discussion of network implications for sta-
634 bility with genetics.

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

638 Although our study was conducted with a commu-
639 nity of lichens, these results should be generalized
640 to other groups of diverse organisms around the
641 world that also exhibit significant genetic signals at
642 the community level (24, 25). In the face of the
643 high degree of complexity and potential context de-
644 pendancy of ecological processes, the current study
645 points to the utility of considering the spatial and
646 temporal scales of interactions, as discussed to some
647 in previous studies (26–28). In the present study,
648 we found that community assembly processes, such
649 as environmental filtering and species interactions,
650 are genetically based. This is likely due, in part,
651 to the large difference in the differences in size and
652 longevity of the lichen and cottonwood individuals
653 with the trees determining the environment in which
654 the lichen occur. We suggest that future work would
655 be aided by determining these modules within the
656 biotic community that include species with similar

657 differences in body-size and time-scales. As heritable
 658 variation is the raw material for natural selection
 659 to act upon, a genetic basis for interaction network
 660 structure indicates evolutionary dynamics should be
 661 considered at the community level and that con-
 662 serving genetic variation is important to consider in
 663 efforts to restore or preserve complex species inter-
 664 actions and their associated ecosystem functions (29).
 665 With such findings, it appears that we are closer to
 666 understanding the evolutionary drivers of Darwin's
 667 entangled bank and the interconnectedness of species
 668 in complex communities.

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 670 the National Science Foundation grant (DEB-0425908)
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 674 sampling was supported by Todd Wojtowicz, Luke Evans
 675 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.

	PC	SR	SD	SE	BR	L	L.pos	L.neg	Cen	Cen.
736	mean	69.78	4.32	0.66	0.46	32.16	3.24	2.54	0.70	0.06
737	se	4.24	0.23	0.05	0.02	3.16	0.65	0.50	0.18	0.01
738										
739	response	statistic	H2	p-value						
740	Lichen Network Similarity	3.5821	0.4130	0.0537						
741	Average Mutual Information	3.5235	0.3101	0.0254						
742	Centralization	4.0444	0.3305	0.0184						
743	Centralization In-Degree	4.4812	0.3487	0.0142						
744	Centralization Out-Degree	3.8615	0.3193	0.0205						
745	Centralization In-Degree (positive)	3.9852	0.3309	0.0190						
746	Centralization In-Degree (negative)	0.3304	0.1057	0.2508						
747	Centralization Out-Degree (positive)	3.5585	0.3119	0.0248						
748	Centralization Out-Degree (negative)	0.0862	0.0513	0.3446						
749	Number of Network Links (Degree)	3.5175	0.3156	0.0255						
750	Degree (positive)	3.6925	0.3242	0.0229						
751	Degree (negative)	0.0327	0.0318	0.3859						
752	Percent Lichen Cover	0.0000	0.0000	1.0000						
753	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
	Lichen Network Similarity	3.5821	0.4130	0.0537
	Centralization	4.0444	0.3305	0.0184
	Centralization In-Degree	4.4812	0.3487	0.0142
	Centralization In-Degree (positive)	3.9852	0.3309	0.0190
	Centralization In-Degree (negative)	0.3304	0.1057	0.2508
	Centralization Out-Degree	3.8615	0.3193	0.0205
	Centralization Out-Degree (positive)	3.5585	0.3119	0.0248
	Centralization Out-Degree (negative)	0.0862	0.0513	0.3446
	Number of Network Links (Degree)	3.5175	0.3156	0.0255
	Degree (positive)	3.6925	0.3242	0.0229
	Degree (negative)	0.0327	0.0318	0.3859

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

	r	p-value
Bark Roughness	0.451	0.030
Number of Links	0.974	0.010
Centralization	0.961	0.010
AMI	0.903	0.010

Table 3. Correlation tests for vectors displayed in NMDS ordination of network similarity.

	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 4. Genotypic effects on tree traits and residuals from trait regressions of lichen network structure.

Figures.

	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

Table 5. Tests of the correlation between tree bark traits and lichen network structure

	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 6. 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 7. 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. melanochra	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. melanochra	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. melanochra	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. melanochra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0			

Table 8. REML tests of the effect of tree genotype on lichen species centrality.

	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 10. Pseudo-F Table of lichen community similarity PERMANOVA.

	BR	CT	pH	CN	PC	SR	SE	SD	L	Cen	AMI
BR								-0.34	-0.39	-0.36	
CT					-0.34			0.34			
pH											
CN											
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											

Table 9. Matrix of correlations among tree traits, lichen community metrics and network metrics

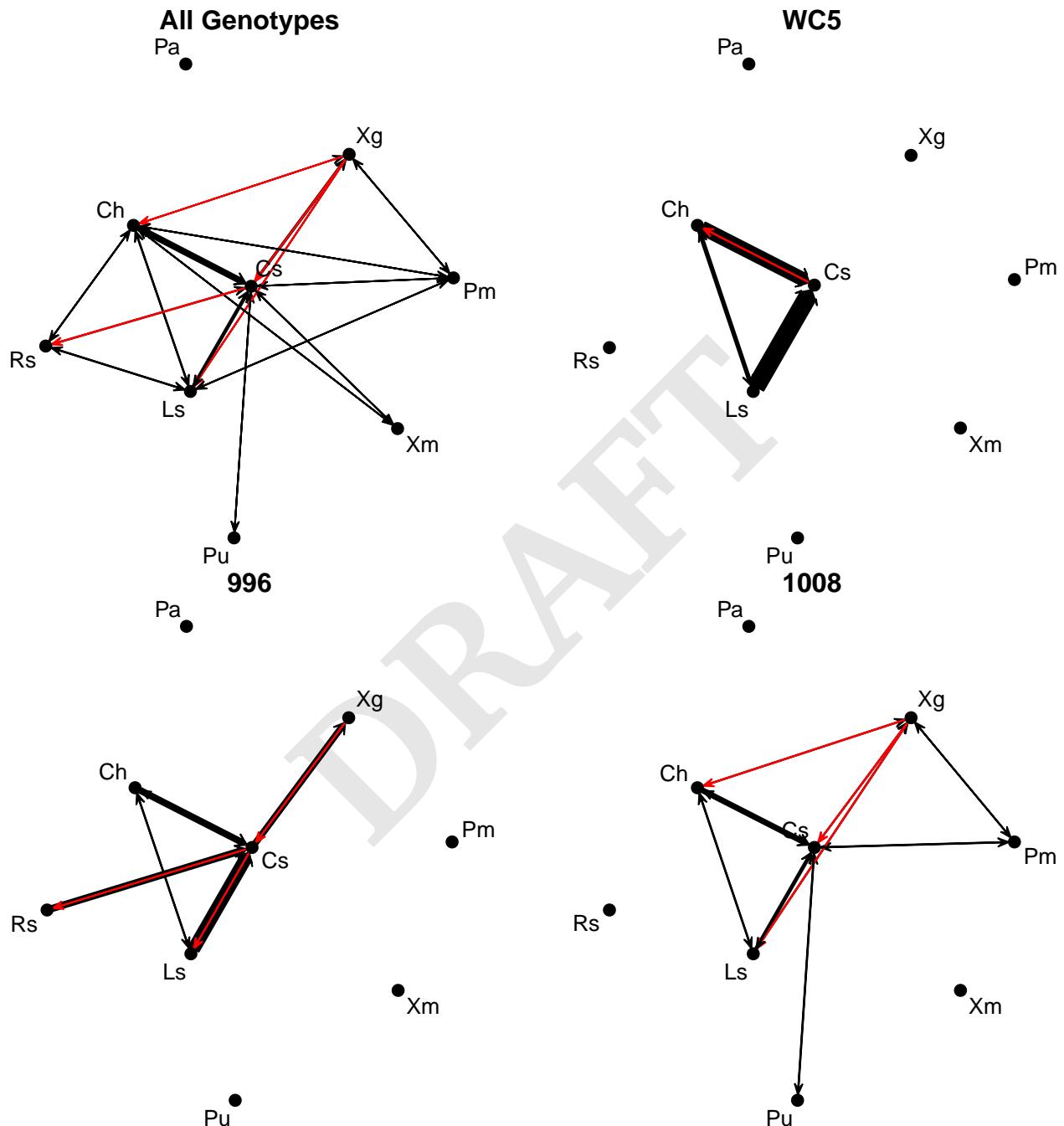


Fig. 1

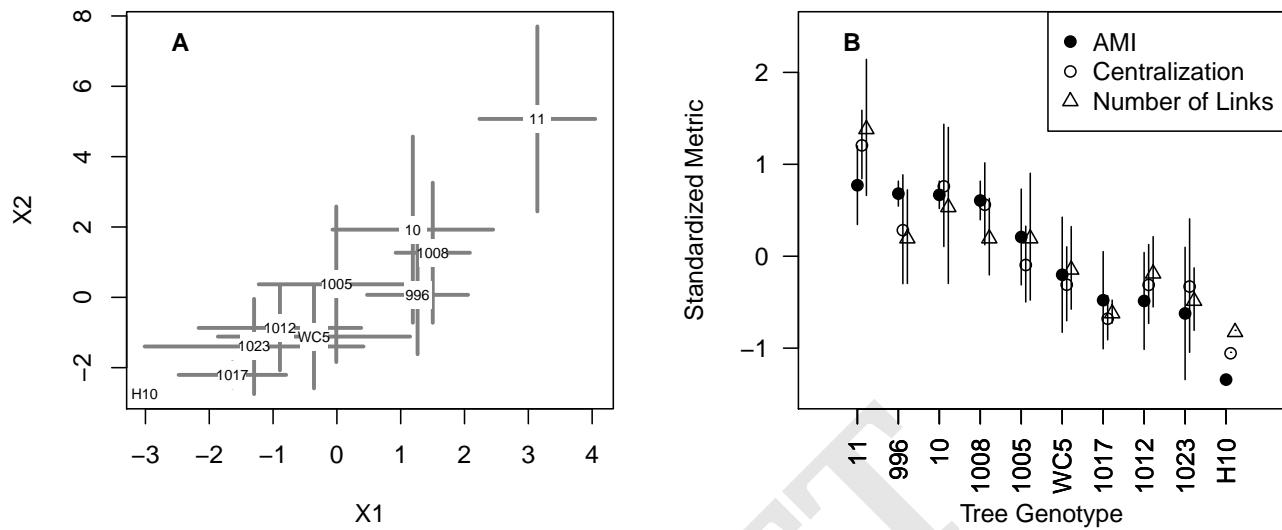


Fig. 2

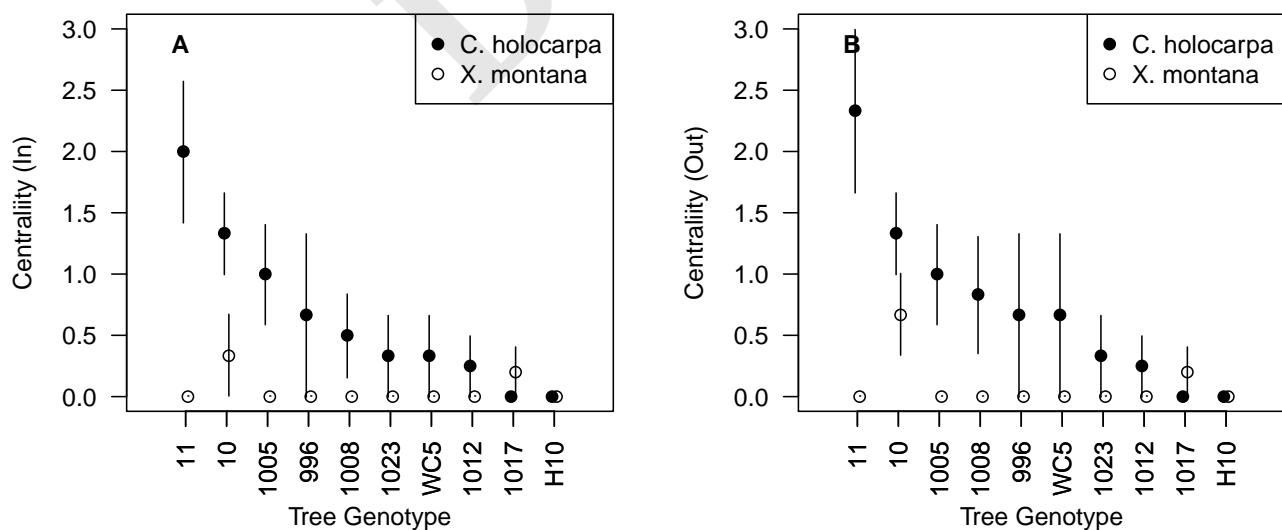


Fig. 3

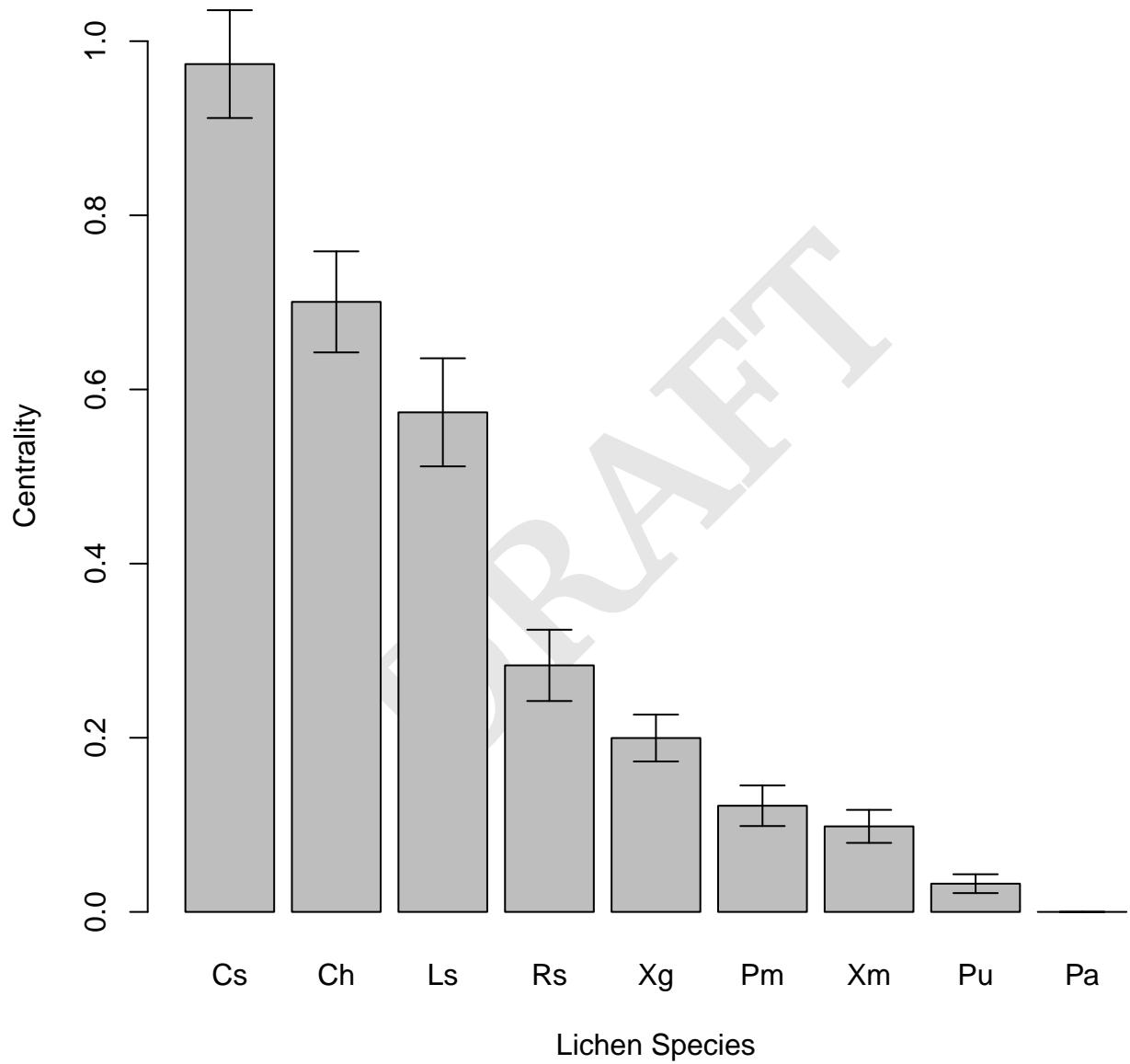


Fig. 4

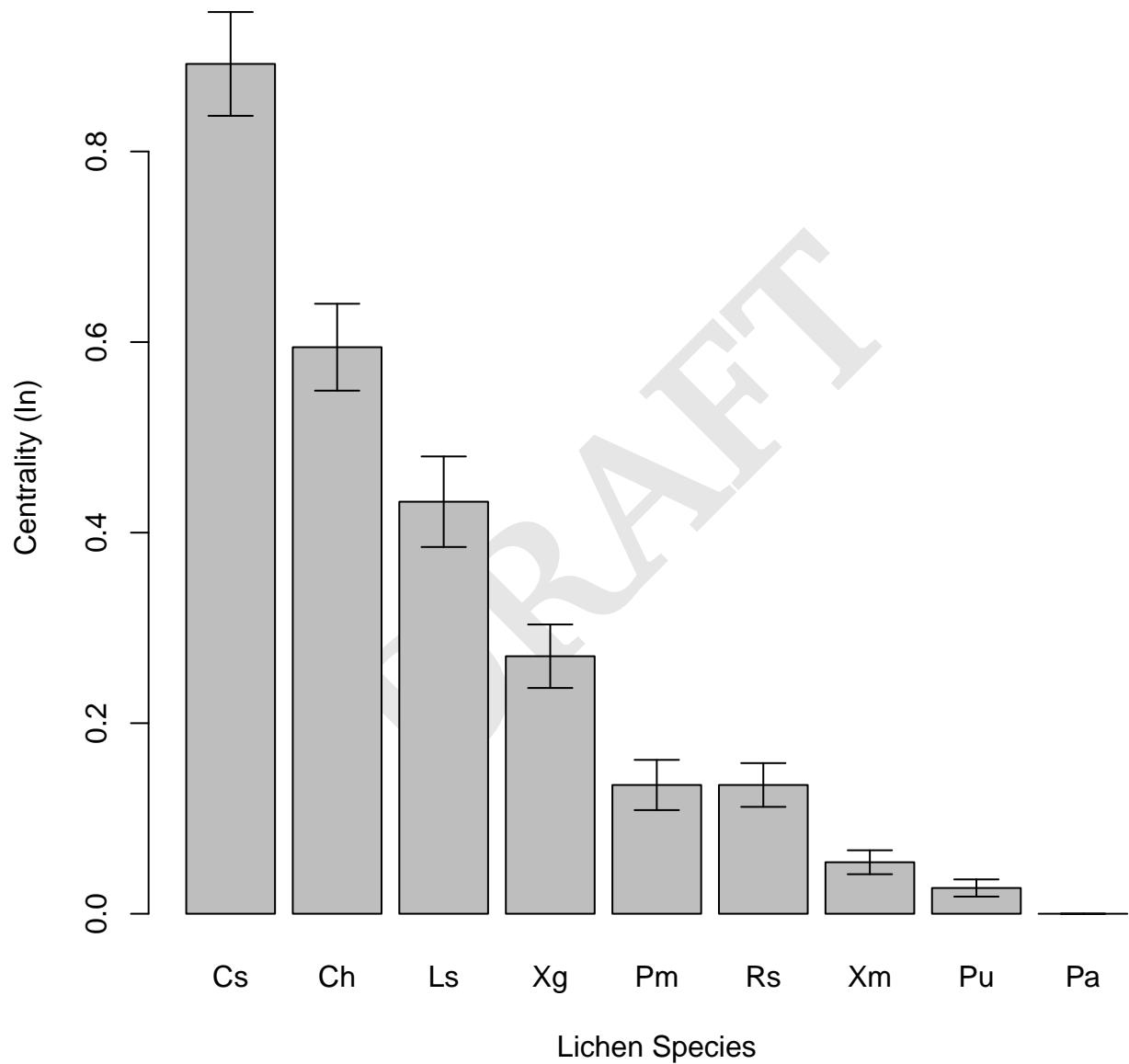


Fig. 5

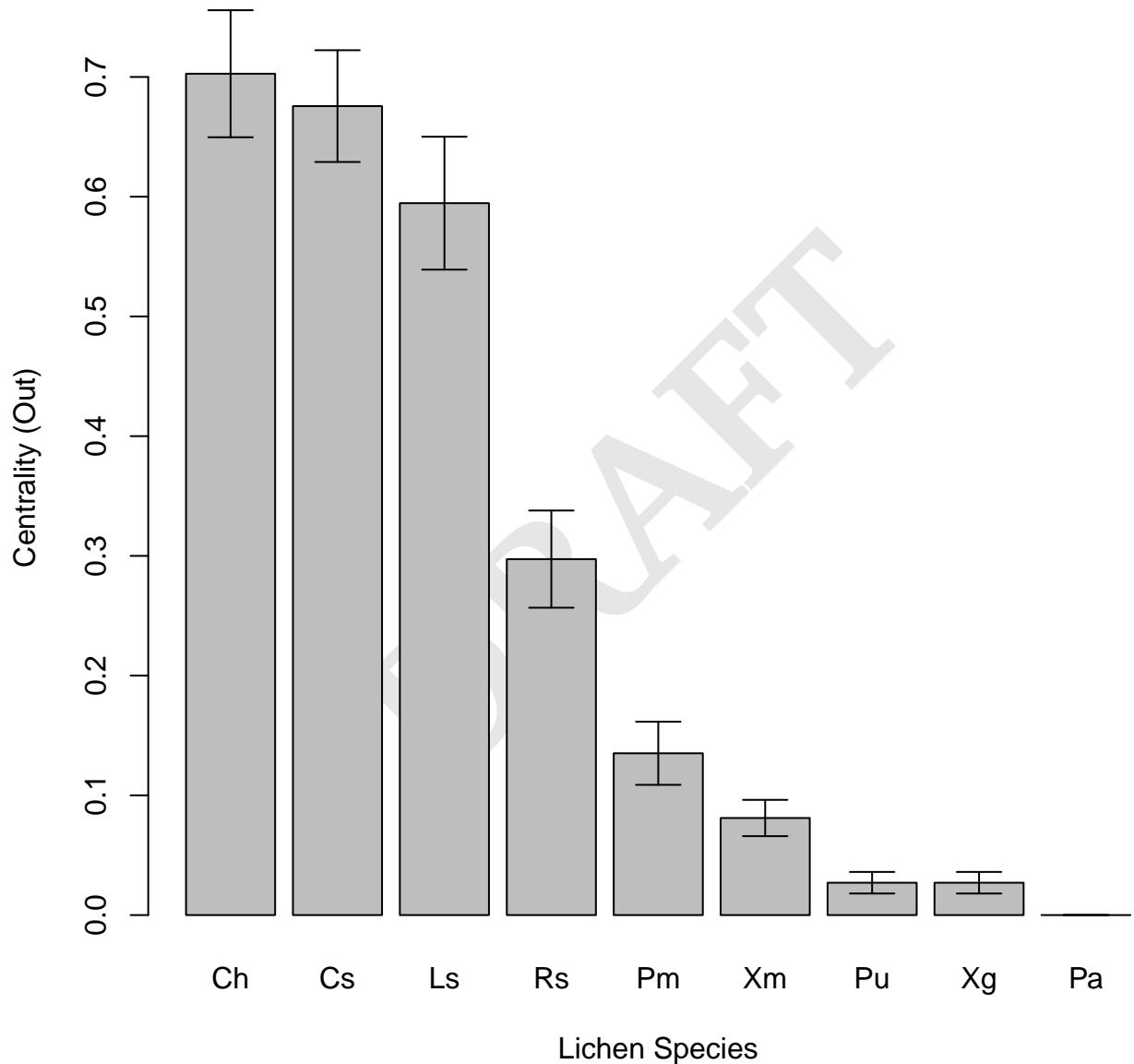


Fig. 6

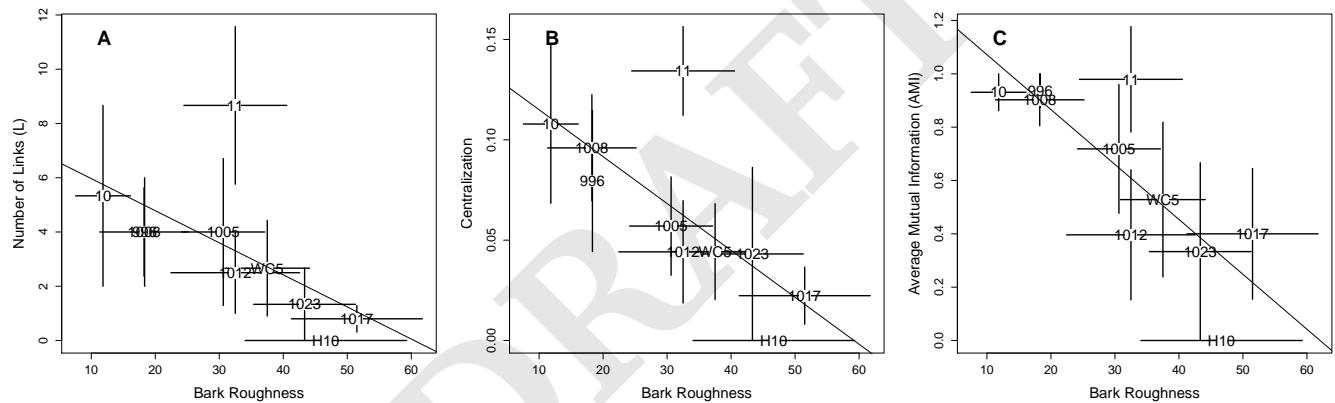


Fig. 7

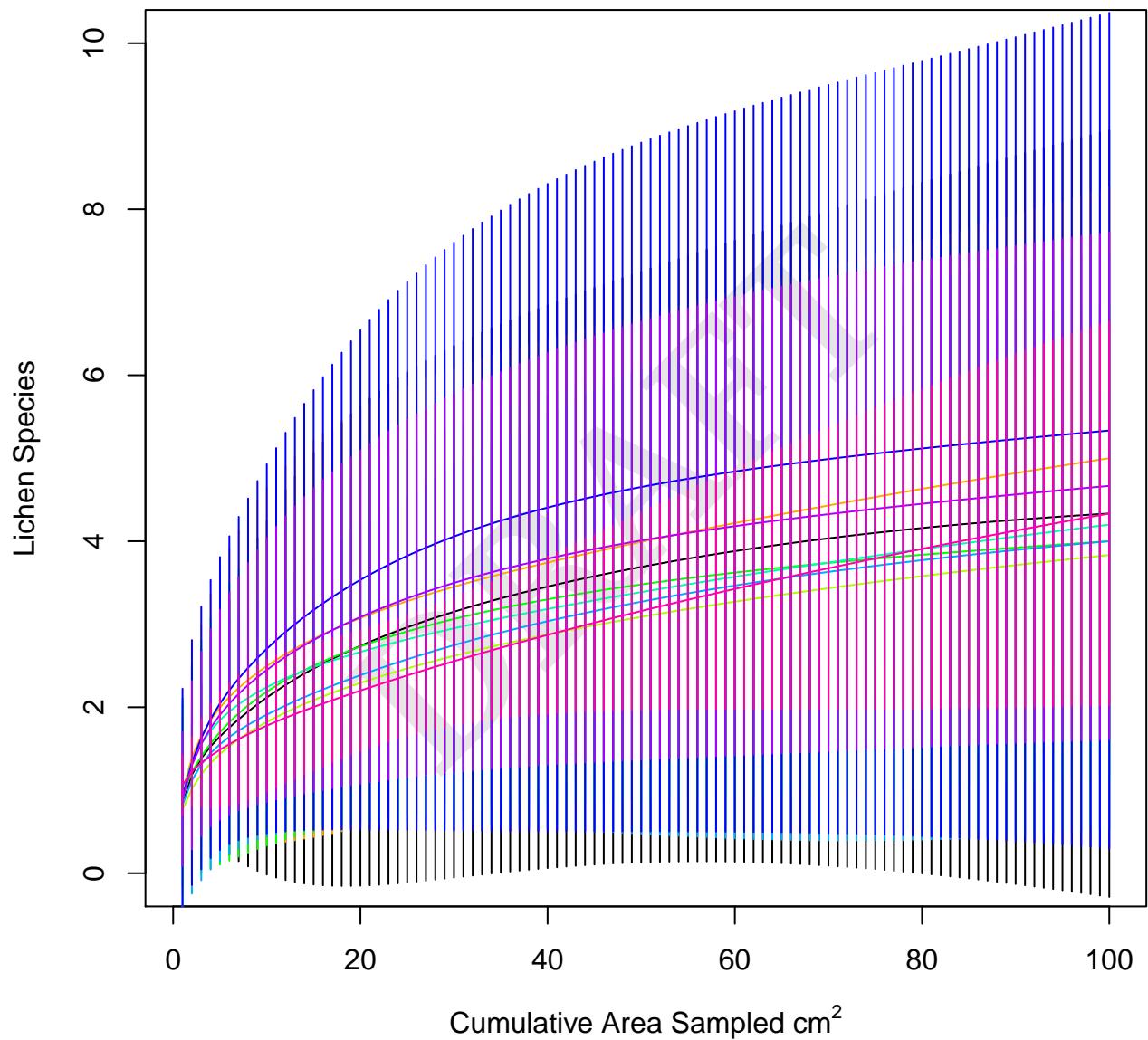


Fig. 8. Species area curve by genotype.

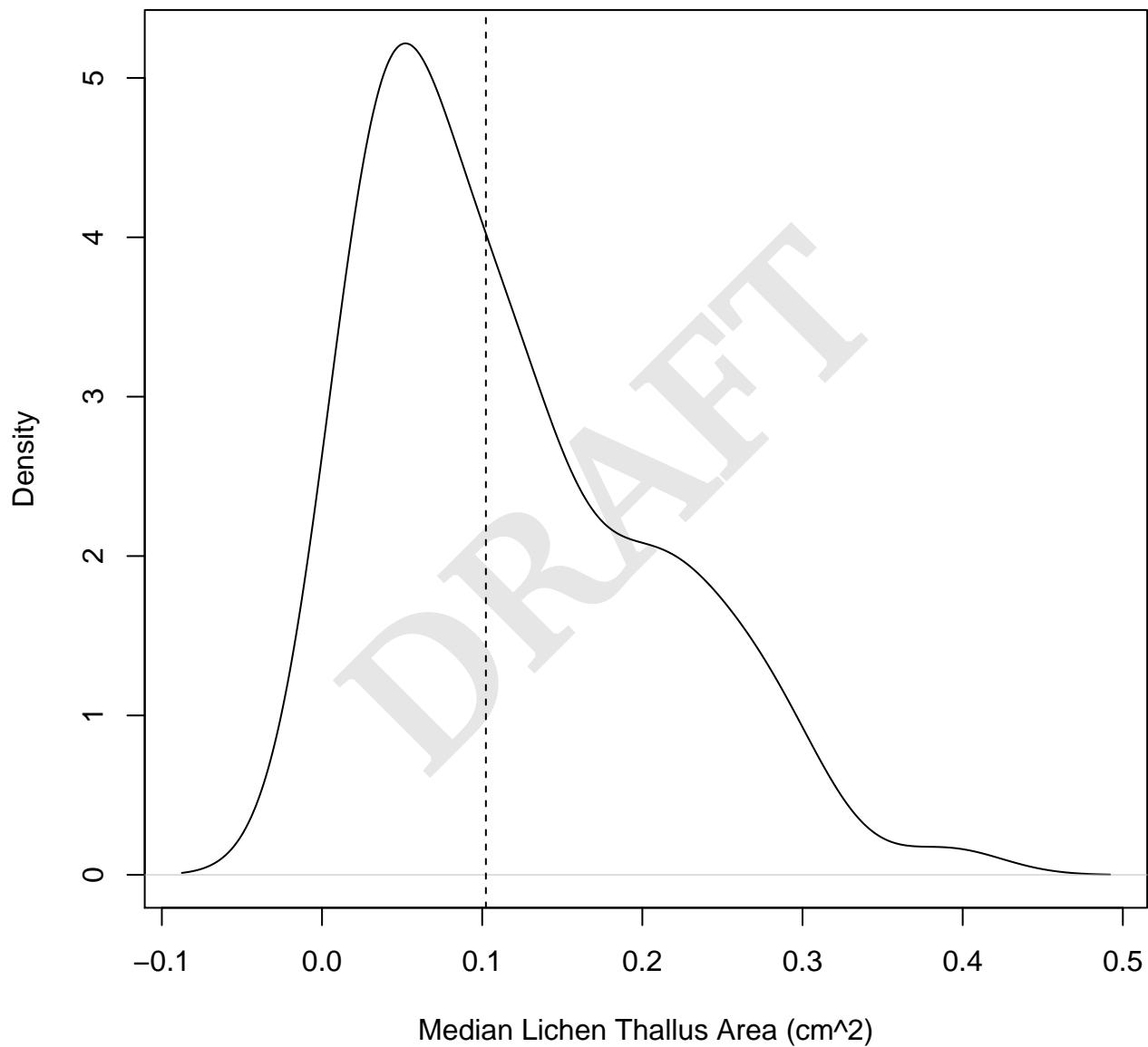


Fig. 9