

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, positive interactions of one lichen**
17 **species, *Caloplaca holocarpa* drove the genetically based variation**
18 **in network structure. Third, bark roughness was both predicted by**
19 **tree genotype and correlated with lichen network similarity. We con-**
20 **clude that tree genotype can influence not only the relative abun-**
21 **dances of organisms but also the interaction network structure of**
22 **associated organisms. Given that variation in network structure can**
23 **have consequences for the dynamics of communities through alter-**
24 **ing the stability of the system and modulating or amplifying perturba-**
25 **tions, these results have important implications for the evolutionary**
26 **dynamics of ecosystems.**

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

1 **E**volution occurs in the context of complex ecolog-
2 **ical networks. Initially, evolution in a community**
3 **context was focused on examples of highly co-evolved**
4 **pairs of species (e.g. Darwin's famous prediction of**
5 **the Sphinx Moth and Christmas Orchid) (?). How-**
6 **ever, studies of diffuse co-evolution (*sensu* (?)) (? ?**
7 **?), geographic mosaics of co-evolution (?) and com-**
8 **munity genetics (?) have provided an in-road for**
9 **ecological network approaches (8? ?) to illuminate**
10 **a more complex perspective of the interface between**
11 **ecological and evolutionary dynamics. There is now**
12 **evidence to support that selection tends to occur**
13 **among groups of species (? ? ?) favoring the de-**
14 **velopment of small webs (? ? ?) and that genetic**

15 variation and phylogenetic relatedness contributes
16 to variation in community assembly (1) and species
17 interactions (? ? ?), which shapes the ecological
18 interaction networks (2).

19 Community genetics studies (3) have shown that
20 genetic variation in foundation species (4) plays a
21 significant role in defining distinct communities of in-
22 teracting organisms: such as, endophytes, pathogens,
23 lichens, arthropods, and soil microbes. Multiple stud-
24 ies have now demonstrated that genetic variation
25 influences numerous functional traits (e.g., phyto-
26 chemical, phenological, morphological) produces a

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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27 multivariate phenotype (5) that contributes to variation
28 in associated communities (6). The importance
29 of genetic variation in structuring ecological systems
30 was recently reviewed by Des Roches et al. (2018).

31 Additional work has provided support for the hypothesis
32 that not only does composition vary among genetically distinct genotypes of foundation species,
33 it also impacts the structure of the network of species interactions in these communities. Two studies have
34 demonstrated conceptually (7) and empirically (8).
35 However, studies in the network ecology literature generally do not include a genetic component (see
36 review by Borrett et al. 2014) and community genetics papers do not have data on network structure of
37 associated communities. Currently, we are aware of
38 only one paper that empirically examines the genetic basis of network structure of a community (?).

- 44 • DesRoches 2017 The ecological importance of
45 intraspecific variation. Synthesis: Our results
46 show that intraspecific effects are often comparable to, and sometimes stronger than, species
47 effects.
- 48 • Barbour 2018 Trait plasticity is more important
49 than genetic variation in determining species
50 richness of associated communities. Synthesis:
51 These results indicate that trait plasticity can be
52 a dominant driver of above- and below-ground
53 biodiversity.
- 54 • Barbour 2016 Genetic specificity of a plant-insect foodweb. Synthesis: Taken together, our
55 results indicate that intraspecific genetic variation
56 can play a key role in structuring ecological networks, which may in turn affect network persistence.
- 60 • Barbour 2015 Multiple plant traits shape the genetic basis of herbivore community assembly.
61 Synthesis: Taken together, our results support
62 that the genetic basis of herbivore community
63 assembly occurs through a suite of plant traits
64 for different herbivore species and feeding guilds.
- 68 • Busby 2019 Contingency rules for pathogen competition and antagonism in a genetically based, plant defense hierarchy. Synthesis: Our results point to a *Populus* defense hierarchy with resistance genes on top, followed by pathogen competition, and finally pathogen antagonism

69 by endophytes. We expect these rules will help
70 to explain the variation in pathogen antagonism
71 that is currently attributed to context dependency.

72 • Barker 2019 Linking plant genes to insect communities: Identifying the genetic bases of plant
73 traits and community composition. Synthesis:
74 These findings support the concept that particular
75 plant traits are the mechanistic link between
76 plant genes and the composition of associated
77 insect communities.

78 • Cooper 2018 Genotypic variation in phenological
79 plasticity: Reciprocal common gardens reveal
80 adaptive responses to warmer springs but not to
81 fall frost. Synthesis: Trees transferred to warmer
82 climates generally showed small to moderate
83 shifts in an adaptive direction, a hopeful result
84 for climate change. Trees experiencing cooler
85 climates exhibited large, non-adaptive changes,
86 suggesting smaller transfer distances for assisted
87 migration.

88 • Whipple 2018 Epigenetic inheritance across the
89 landscape. Synthesis: Transgenerational epigenetic
90 variation may alter the interpretation
91 of landscape genomic studies that rely upon
92 phenotypic analyses, but should have less influence
93 on landscape genomic approaches that rely upon
94 outlier analyses or genome-environment
95 associations.

96 Here, we investigate how genetic variation in a
97 foundation tree species determines the structure of
98 a network of interactions among a community of
99 tree associated lichen species. Previous studies have
100 examined aspects of networks but to date, no studies
101 have examined the genetic basis of networks of interacting
102 species (?). Here we examine the genetic
103 basis of network structure on a community of sessile
104 lignicolous (i.e. bark) lichen on cottonwood trees.
105 Using a long-term (20+ years), common garden experiment
106 with replicated individuals of known genetic
107 identity and a naturally established stand of *Populus*
108 *angustifolia*. We focused on a model community of
109 9 epiphytic lichen species, as previous research has
110 demonstrated significant compositional responses of
111 epiphytes to genotypic variation (9, 10). In addition,
112 the life-history characteristics of lichens, having
113 highly localized, direct contact interactions and slow
114 growth rates, make them well suited for this approach.
115 We used a combination of common garden and
116 reciprocal common garden experiments to test
117 whether lichen species composition is influenced by
118 genetic variation in the host tree. We found that
119 lichen species composition was significantly influenced
120 by host tree genotype, and that this effect was
121 consistent across all nine lichen species. This
122 finding provides the first evidence that genetic variation
123 in a foundation tree species influences the structure
124 of a network of interactions among a community of
125 tree associated lichen species.

population turnover rates, allowed us to assess interactions among lichen species on individual trees. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (7, 8, 11, 12). If correct, we expect to find that network structure is genetically based in which different plant genotypes support different interaction networks and that these interactions networks can function as indicators of ecological dynamics important for conserving biodiversity. Applying a probability-theory based network modeling approach, we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks. Based on previous community genetics studies, such as Bangert et al. (2005) which proposed the community similarity rule, we hypothesize that trees will vary in some phenotypic traits and those trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure.

Materials and Methods

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

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

Bark Lichen Observations. On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm² cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens, we were able to rapidly

assess lichen interactions by quantifying thalli in close contact. Sampling was restricted to the northern aspect of the trunk to maximize the abundance of lichen and control for the effect of trunk aspect. Two adjacent 10 cm² quadrats centered at 50 cm and 85 cm from ground level were sampled (Fig 1 A and B). The observed lichen community included (abbreviations are given for species present in study): Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candeliella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Phyciella melanochra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*. Several other species were not observed in the present study but are known to occur in this region: *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanelia sublivacea*, *Meanelia elegantula*.

The cell size and checkerboard sampling pattern was chosen to isolate the individuals in each cell. In a previous survey of lichen thallus size in this common garden, we had observed a median thallus size of 0.12 ± 0.001 cm² (1 S.E.) (see Supporting Information). Based on the median thallus size, we expected thalli observed in each cell to generally be spatially independent of thalli present in other cells but exposed to similar micro-environmental conditions created by the bark and the location of the sampling area on an individual tree. Therefore, we were confident in treating the cell-wise observations in quadrats as independent with respect to lichen-lichen interactions.

We also measured several bark traits for each tree: including, bark roughness and chemistry. **ADD METHODS FROM JAMIE.**

Lichen Network Modeling and Analysis. For each tree, repeated observations of lichen were made in order to construct replicated interaction networks for each genotype. We quantified the presence of lichen in the 1 cm² cells on individual trees of *P. angustifolia*. Unipartite networks were generated using the conditional probabilities of each species pair, i.e. the probability of observing one species given an observation of another species $P(S_i|S_j)$, based on the method developed by (14). To calculate conditional probabilities, we quantified the individual probabilities of species occurrences $P(S_i)$ and the joint probability of co-occurrences $P(S_i, S_j)$ using the frequencies of each species and their co-occurrences. We were then able to calculate the conditional probabilities of each species pair $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, based on the axioms of probability. This yielded a matrix that could possibly be asymmetric, i.e. $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$. Another important property of this matrix is that the diagonal (S_{ii}) was equal to one for all species present and zero for species that were not observed in any cell.

We then applied an analytical procedure to remove non-significant links between species. This procedure determines if the joint probability of a species pair ($P(S_i, S_j)$) is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as as $CI_{95\%} =$



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).

$E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability of $S_i S_j$ and its compliment (i.e. $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If the observed number of co-occurrence falls outside of the confidence interval, the joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual probabilities (i.e. $P(S_i)P(S_j)$), and the conditional probability reduces to the individual probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair falls outside the confidence interval, the probability that the observation of one species given the other is no different than simply observing that species alone. This enables us to remove links from a given network by re-scaling the resulting conditional probabilities by subtracting the individual probabilities from the conditional probabilities (i.e. how different the conditional probability is from the independent probability), which makes any species with a non-significant conditional probability zero.

The resulting matrix ($\mathbf{D} = D_{ij}$) can be interpreted as how one species impacts another with zero being no effect and values less than or greater than zero interpreted as negative and positive effects, respectively. Here, we will refer to this matrix (\mathbf{D}) as an interaction matrix with the properties that it can be asymmetric (i.e. P_{ij} does not necessarily equal P_{ji}), and the diagonal (P_{ii}) is zero (i.e. species does not influence its own probability of being observed).

234

235 **Network Metrics.** To quantify the structural variation of
236 lichen networks we calculated several metrics at both
237 the node and whole-network level. For individual nodes
238 (i.e. species) in each network, we calculated both the
239 degree Eq. (1) and the centrality. We also calculated two
240 similar global network metrics: degree and centralization.
241 The first was network degree, which is a count of the
242 total number of links in a network. As the networks
243 contained not only positive and negative connections,
244 as well as directional connections (both in-coming and
245 out-going), we calculated the same network metrics for
246 all combinations of these types of connections in each
247 network. Although there are many more possible network
248

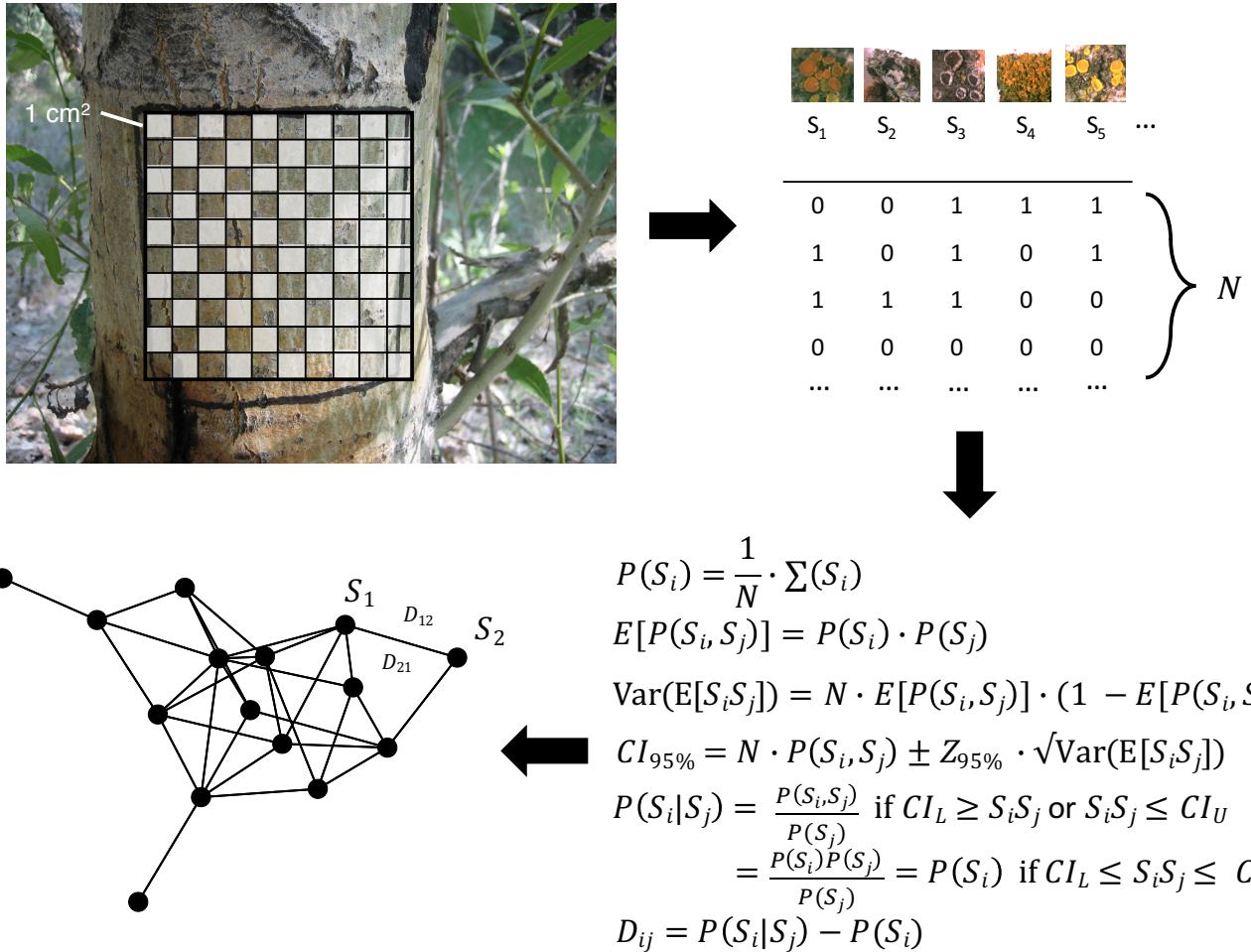


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 10 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded 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, $S_i S_j$, to that expected due to chance alone, $E[P(S_i S_j)] = P(S_i) P(S_j)$, and $P(S_i | S_j)$ reduces to $P(S_i)$, the observed individual probability of species S_i . In the context of these networks, asymmetry and positive/negative valued connections are distinct quantities. In-coming and out-going connections can be interpreted as “influenced by” and “influenced”, respectively; while positive and negative should be seen as one species increasing or decreasing, respectively, the probability of another species’ occurrence.

metrics that could have been examined, we chose to focus on a restricted set for the sake of clarity. Also, degree and centrality form the basis of many other network metrics.

ADD EQUATIONS FOR METRICS

$$\sum x_i$$

- Node degree
- Node centrality
- Network degree
- Centralization
- In vs out
- Pos vs neg

To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (7 and Borgatti 2014).

We used the `signnet` package version ????, which is available at ???.

[1] 274
286 **Statistical Analyses, Software and Data.** We used a combination of parametric and non-parametric, permutation 287 275 based frequentist statistical analyses to test for the effects 288 276 of genetic variation on lichen communities and their inter- 289 277 action networks. To assess the effect of genotype on uni- 290 278 variate responses, we used additive, random effects models 291 279 with Restricted Maximum Likelihood (REML). We used 292 280 a combination of Least Squares Regression, Analysis of 293 281 Variance (ANOVA) and correlation tests to quantify and 294 282 test for the relationship among other variables. Bark 295 283 roughness, lichen cover and species richness were square- 296 284

root transformed to meet the assumptions of homogeneity of variance and normality for these tests.

For multivariate response variables, such as lichen community composition and network structure, we used distance based multivariate statistical approaches, including Permutational Analysis of Variance (PERMANOVA) and Mantel tests. For some analyses, community composition was relativized by species maxima to reduce the effect of the highly abundant *X. galericulata*. For community composition we used Bray-Curtis dissimilarity, which has optimal performance with count data (?). To quantify the similarity of lichen networks among individual trees, we calculated the pairwise Euclidean distance of the **D** interaction matrices among all pairs of trees.

For visualization of multivariate patterns, we used Non-metric Multi-Dimensional Scaling (NMDS) (?) to produce dimensionally reduced ordinations of these multivariate responses and fitted vectors for continuous predictor variables to the ordinated values (?). Using 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.

For each network, we also calculated metrics that measure different structural aspects. Although there are many other metrics, for the sake of simplicity we focus on a subset that represent several interesting features of network structure (see (15)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (? ?). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (?). In a network with a low level of centralization species have similar amount of interaction in the network, while a network with a high level of centralization tends to have one or small number of species that interact with other species. We used a related function to calculate the centrality of each species (i.e. node level centrality) in each network as well. The modularity of each network was also quantified using a weighted algorithm (?), which measures the degree to which a given network is divided into groups of species more connected to each other than 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/doi/XXXXXX. All analyses were conducted using the programming language R version 3.6.1 (R Development Core Team 2019).

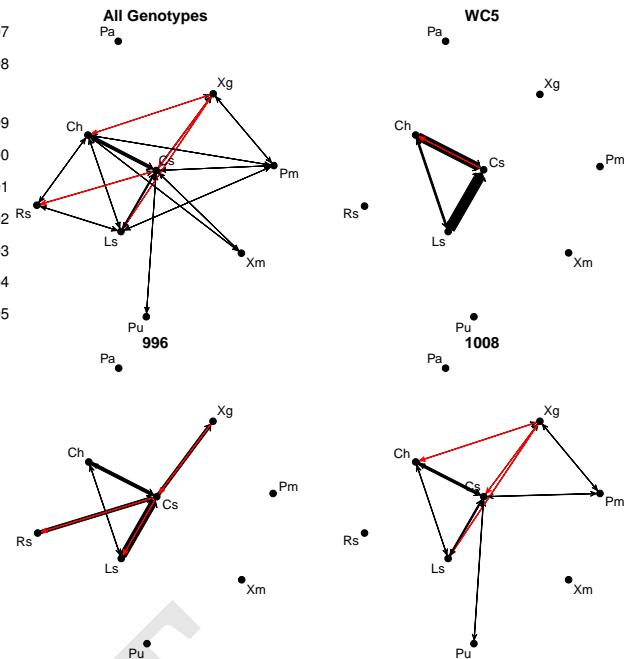


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive)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

Results

Tree genotype influenced lichen network structure.

Tree genotype significantly predicted the structural similarity of lichen networks (PERMANOVA: Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$) (Fig. 4). Overall network level metrics responded significantly to tree genotype (Table 1), including network degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} = 0.0255$) and centralization including both in-coming and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} = 0.0184$) or when separated into in-coming only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} = 0.0190$) or out-going only ($RLRT = 3.8615$, $H^2 = 0.3193$, $p\text{-value} = 0.0205$). Metrics including only positive links also showed a significant effect of tree genotype, including positive degree ($RLRT = 3.6925$, $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} = 0.0142$) Metrics calculated with negative links were not significant, including degree (negative) ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$) and both in-coming (negative) ($RLRT = 0.3304$, $H^2 = 0.3200$, $p\text{-value} = 0.3859$).

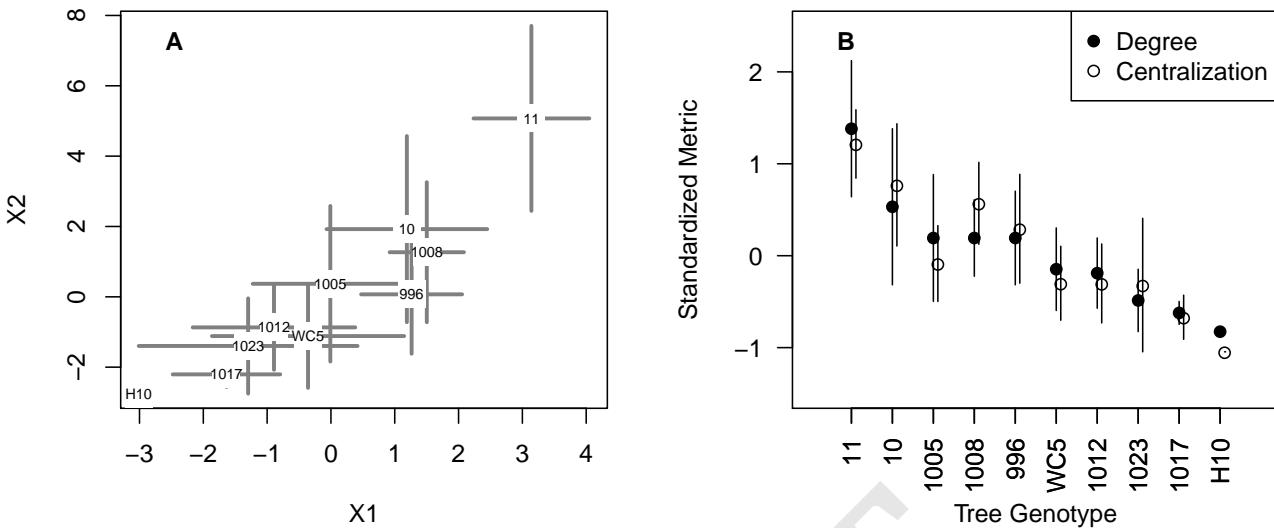


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen networks (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. B. Plot showing the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

372 = 0.1057, *p-value* = 0.2508) and out-going centralization (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$, *p-value* = 0.3446).

($RLRT = 0$, $H^2 = 0$, *p-value* = 1) or out-going ($RLRT = 0$, $H^2 = 0$, *p-value* = 0.4543). None of the other species' centralities showed a genotypic response (Supplementary Table 6) with the exception of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, *p-value* = 0.0375); however, the centrality of *X. montana* was much lower overall relative to *C. holocarpa* and the variation in *X. montana* centrality was restricted to two genotypes (Fig. 5).

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent of rough bark was the only tree trait that displayed a significant response to genotype ($RLRT = 4.8526$, $H^2 = 0.3221$, *p-value* = 0.0113). None of the other bark traits, condensed tannins ($RLRT = 0.0007$, $H^2 = 0.0041$, *p-value* = 0.4439), pH ($RLRT = 0.00$, $H^2 = 0.00$, *p-value* = 1.0000) or carbon-nitrogen Ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, *p-value* = 1.0000), showed a significant response to tree genotype and none other than bark roughness were correlated with network similarity (Supplementary Table 5); therefore, we focused our analysis on bark roughness. We found that bark roughness was significantly correlated with network similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, *p-value* = 0.0096) and other lichen net-

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

The genetic response of network centralization was driven by variation in *Caloplaca holocarpa*. Centrality varied significantly among species ($F_{8,324} = 7.99$, $R^2 = 0.16$, *p-value* << 0.0001). *Caloplaca holocarpa* centrality was the main species to exhibit a significant response to tree genotype in terms of positive centrality for both the in-coming ($RLRT = 3.61$, $H^2 = 0.32$, *p-value* = 0.0240) and out-going ($RLRT = 3.13$, $H^2 = 0.30$, *p-value* = 0.0327) perspectives, but not for either negative centrality metrics in-coming

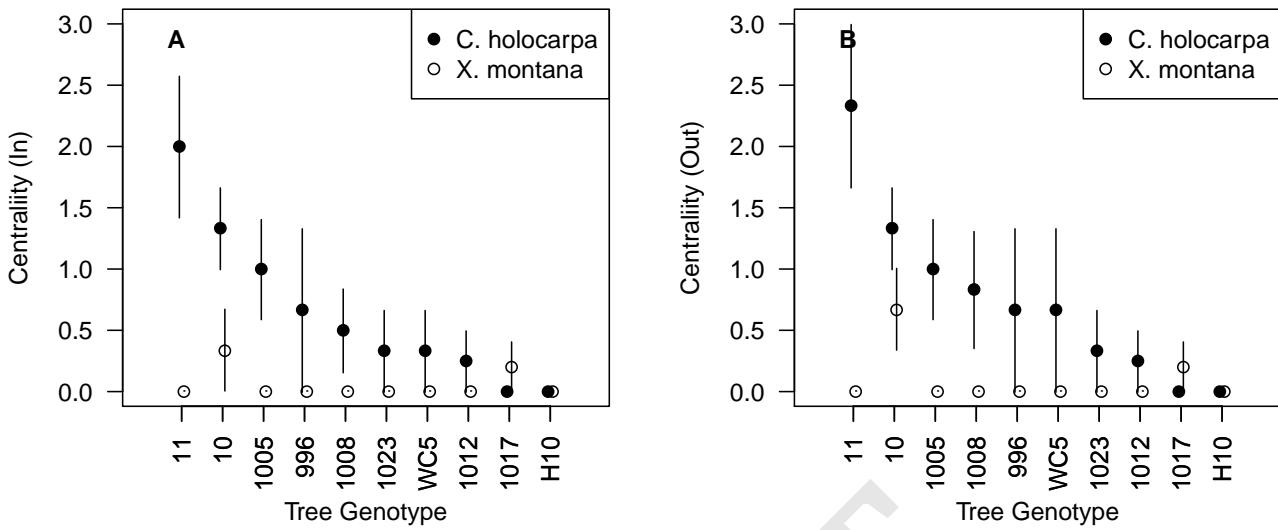


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

work metrics, including negative correlations with overall network degree ($df = 35, t = -2.13, r = -0.34, p\text{-value} = 0.04$) and centralization ($df = 35, t = -2.52, r = -0.39, p\text{-value} = 0.02$). To determine how much of the effect of bark roughness was genetically based, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00, H^2 = 0.00, p\text{-value} = 1.0000$), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

Discussion

We found that tree genotype influenced lichen network structure in the experimental cottonwood forest. Network similarity and metrics of network structure tended to be more similar on trees of the same genotype. Generally, this genetic effect was manifested in positive interactions and largely driven by *C. holocarpa*. Bark roughness was the primary genetically based trait driving network structure. The genetically based trait, bark roughness, was the main driver of network variation. Not only was bark roughness

the only trait observed to be genetically based, it was correlated with network structure and residual variation from this correlation was not explained by tree genotype. These results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species.

Differences in distributions below the quadrat scale are leading to shifting patterns of interactions among lichen species, largely increased positive incoming and out-going interactions. It could also be that some other variable correlated with bark roughness is altering the quality (i.e. how) the lichen species are interacting, that is as opposed to simply the "quantity" of interactions. Bark roughness effect was negative, possibly serving the role that other lichen play in facilitating the success of new propagule attachment and the growth of establishing thalli. This is supported by the patterns overall being positive, including *C. holocarpa*'s centrality being positive both in and out. We don't know specific microscopic dynamics, such as photobionts, mycobionts, endolichenic fungi and bacteria, but variation in these underlying interactions could also be playing a role. Also, bark roughness had previously been shown to be an important tree trait influencing bark lichens (13) that is under strong genetic control (23).

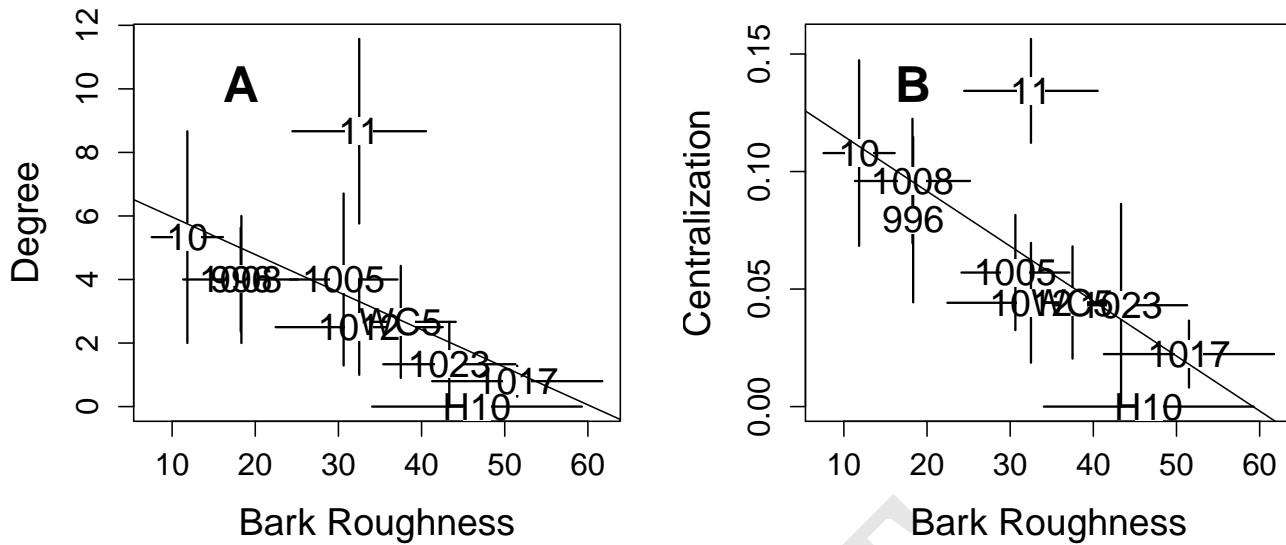


Fig. 6. Bivariate plots of the relationship between bark roughness and three network metrics: A) degree and B) centralization. Each plot displays the genotype mean \pm 1 S.E. for both variables and a least-squares regression calculated using the genotype means.

There are important functional ramifications of genetically based variation in network structure. First, even if the composition of the communities is the same among individuals and genotypes, interactions may not be. We didn't observe compositional differences using the same data from which the lichen networks were derived. If we only had our composition dataset from this study, we would have concluded no response of the lichen community to tree genotype, even though the underlying interactions among lichen species does vary among genotypes. Community composition of lichen has been observed to be different among these trees, though this was observed with a larger sampling of total area and quadrats per tree. Regardless, this could result in a situation in which abundance based investigations of community-level genetic effects may miss important variation in the interactions among individuals in these communities, leading to an underestimate of genetic effects in ecosystems. It is possible that these underlying differences in interactions among lichen could lead to differences in community composition at a future point in time, however, this is not needed for evolutionary dynamics to play out.

Second, following on the previous point, genetic diversity could be influencing the stability of communities through the effects on the structure of interactions. Some network structures are likely to be more stable, either in response to disturbance or via self-organized dynamics. For example, centralized networks, although more efficient, are theorized to be more susceptible to targeted attacks on the center of the network. For example, consider a forest with two genotypes that support lichen communities that are similar in total abundances of each species but differ in terms of the structure. Extensions of game theory to evolutionary biology have demonstrated that network structure can lead to variation in evolutionary dynamics. Some structures tend toward dominance and dampening of selection, while others lead to amplification of selection (Newman). One class of networks that are theorized to have amplifying effects on networks have "star" shapes with one or a few species at the center and radiating interactions out from the central core (Leiberman). This is structurally what we have observed with the networks that tend to occur on some of the genotypes in our study, i.e. the more centralized networks. It is possible that these more centralized networks could function as hot-spots of evolutionary dynamics resulting from the amplifying effect the network structure fostered on that tree genotype.

Altering the structure of interaction networks presents a means for genetic effects to be magnified.

fied 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. Also, work by (18–20) observed consistent patterns of centralized interactions of species modules focused around hubs of plant-fungal interactions. In other words, a small number of plant and fungal symbionts tended to have disproportionate numbers of interactions with other species and likely are the drivers in determining community assembly, structure and dynamics.

There are several important points to consider with regard to the generalization of the observed genetically based response of the lichen networks. Body size and sessile nature of lichen important to observing genotype responses. As bark lichen individuals do not move, but grow in a largely two dimensional plane, these communities and their interactions occur in the highly localized context of the tree's bark surface. Lichen individuals are many orders of magnitude smaller than the tree individual and the life-span of a tree is many times that of a lichen. For these reasons, any genetic effects on these communities is not dampened by the movement of individuals and the mixing of the effect of different tree genotypes on the lichen community, as might occur for more mobile species (e.g. insects and birds). We only looked at lichen, other species whose distribution, abundance or interactions respond to tree genotype, such as epiphytic plants (e.g. moss and liverworts), algae or insects, could be playing a role. Other traits could also be playing a role, such as traits that are correlated with bark roughness, such as micro-aspect, albedo, moisture, etc.

- DesRoches 2017 The ecological importance of intraspecific variation. Synthesis: Our results show that intraspecific effects are often comparable to, and sometimes stronger than, species effects.
- Barbour 2018 Trait plasticity is more important than genetic variation in determining species

richness of associated communities. Synthesis: These results indicate that trait plasticity can be a dominant driver of above- and below-ground biodiversity.

- Barbour 2016 Genetic specificity of a plant-insect foodweb. Synthesis: Taken together, our results indicate that intraspecific genetic variation can play a key role in structuring ecological networks, which may in turn affect network persistence.
- Barbour 2015 Multiple plant traits shape the genetic basis of herbivore community assembly. Synthesis: Taken together, our results support that the genetic basis of herbivore community assembly occurs through a suite of plant traits for different herbivore species and feeding guilds.
- Busby 2019 Contingency rules for pathogen competition and antagonism in a genetically based, plant defense hierarchy. Synthesis: Our results point to a *Populus* defense hierarchy with resistance genes on top, followed by pathogen competition, and finally pathogen antagonism by endophytes. We expect these rules will help to explain the variation in pathogen antagonism that is currently attributed to context dependency.
- Barker 2019 Linking plant genes to insect communities: Identifying the genetic bases of plant traits and community composition. Synthesis: These findings support the concept that particular plant traits are the mechanistic link between plant genes and the composition of associated insect communities.
- Cooper 2018 Genotypic variation in phenological plasticity: Reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost. Synthesis: Trees transferred to warmer climates generally showed small to moderate shifts in an adaptive direction, a hopeful result for climate change. Trees experiencing cooler climates exhibited large, non-adaptive changes, suggesting smaller transfer distances for assisted migration.
- Whipple 2018 Epigenetic inheritance across the landscape. Synthesis: Transgenerational epigenetic variation may alter the interpretation

of landscape genomic studies that rely upon phenotypic analyses, but should have less influence on landscape genomic approaches that rely upon outlier analyses or genome-environment associations.

Although our study was conducted with a community of lichens, these results should be generalized to other groups of diverse organisms around the world that also exhibit significant genetic signals at the community level (24, 25). In the face of the high degree of complexity and potential context dependency of ecological processes, the current study points to the utility of considering the spatial and temporal scales of interactions, as discussed to some in previous studies (26–28). In the present study, we found that community assembly processes, such as environmental filtering and species interactions, are genetically based. This is likely due, in part, to the large difference in the differences in size and longevity of the lichen and cottonwood individuals with the trees determining the environment in which the lichen occur. We suggest that future work would be aided by determining these modules within the biotic community that include species with similar differences in body-size and time-scales. As heritable variation is the raw material for natural selection to act upon, a genetic basis for interaction network structure indicates evolutionary dynamics should be considered at the community level and that conserving genetic variation is important to consider in efforts to restore or preserve complex species interactions and their associated ecosystem functions (29). With such findings, it appears that we are closer to understanding the evolutionary drivers of Darwin's entangled bank and the interconnectedness of species in complex communities.

Future work should consider the potential influence on evolutionary dynamics of the associated communities. The network of interactions of species that are strongly influenced by a foundation species, could amplify the effects of genotype, this serves as a means for genetic effects to increase rather than diffuse through an ecosystem either through space or over time, as has been proposed in the construction of the genetic diffusion hypothesis. Altered abundances can lead to differences in interactions Genotype effects on abundances of individual abundances may cancel out. Specifically for asexually reproducing species, such as many lichen are, shifting interaction frequen-

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ies could lead to evolutionary outcomes, given the potential to take-up symbionts and genetic material from thalli that they come into contact with. Altering interaction frequencies could differences in the frequencies the exchange of genetic materials among lichen that could then be passed on to vegetative and possibly sexually produced reproductive propagules. The larger scale (stand or region) effects of these "evolutionary units" on each tree would depend on the connectivity and rate of movement of propagules among trees per the geographic mosaic of co-evolution hypothesis developed by Thompson.

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Supplementary Materials

Tables.

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| | 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 1. PERMANOVA Pseudo-F Table of lichen network similarity to genotype.

| | response | statistic | H2 | p-value |
|--------------------------------------|----------|-----------|--------|---------|
| Lichen Network Similarity | 3.5821 | 0.4130 | 0.0537 | |
| Average Mutual Information | 3.5235 | 0.3101 | 0.0254 | |
| Centralization | 4.0444 | 0.3305 | 0.0184 | |
| Centralization In-Degree | 4.4812 | 0.3487 | 0.0142 | |
| Centralization Out-Degree | 3.8615 | 0.3193 | 0.0205 | |
| Centralization In-Degree (positive) | 3.9852 | 0.3309 | 0.0190 | |
| Centralization In-Degree (negative) | 0.3304 | 0.1057 | 0.2508 | |
| 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 | |
| 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 | |

Table 2. Genotypic effects on tree traits and bark lichen.

| | 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 |
| 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 |
| 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 |
| 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 |

Table 3. 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 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 | | | | |
| <i>In-Degree</i> | | | | |
| 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 |
| <i>Out-Degree</i> | | | | |
| 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 | | | | |
| <i>In-Degree</i> | | | | |
| 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 |
| <i>Out-Degree</i> | | | | |
| 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 | | | |

Table 6. REML tests of the effect of tree genotype on lichen species centrality.

| | BR | CT | pH | CN | PC | SR | SE | SD | L | Cen | Df | SumOfSqs | R2 | F | Pr(>F) | |
|-----|----|----|----|----|-------|----|----|----|-------|-------|----------|----------|--------|--------|--------|--------|
| BR | | | | | | | | | -0.34 | -0.39 | geno | 9.0000 | 1.5049 | 0.2001 | 0.7507 | 0.8878 |
| CT | | | | | -0.34 | | | | 0.34 | | Residual | 27.0000 | 6.0143 | 0.7999 | | |
| pH | | | | | | | | | | | Total | 36.0000 | 7.5193 | 1.0000 | | |
| CN | | | | | | | | | | | | | | | | |
| PC | | | | | | | | | | | | | | | | |
| SR | | | | | | | | | 0.76 | 0.47 | | | | | | |
| SE | | | | | | | | | 0.85 | 0.45 | | | | | | |
| SD | | | | | | | | | 0.59 | 0.33 | | | | | | |
| L | | | | | | | | | | 0.88 | | | | | | |
| Cen | | | | | | | | | | | | | | | | |

Table 7. Matrix of correlations among tree traits, lichen community metrics and network metrics

Table 8. Pseudo-F Table of lichen community similarity PERMANOVA.

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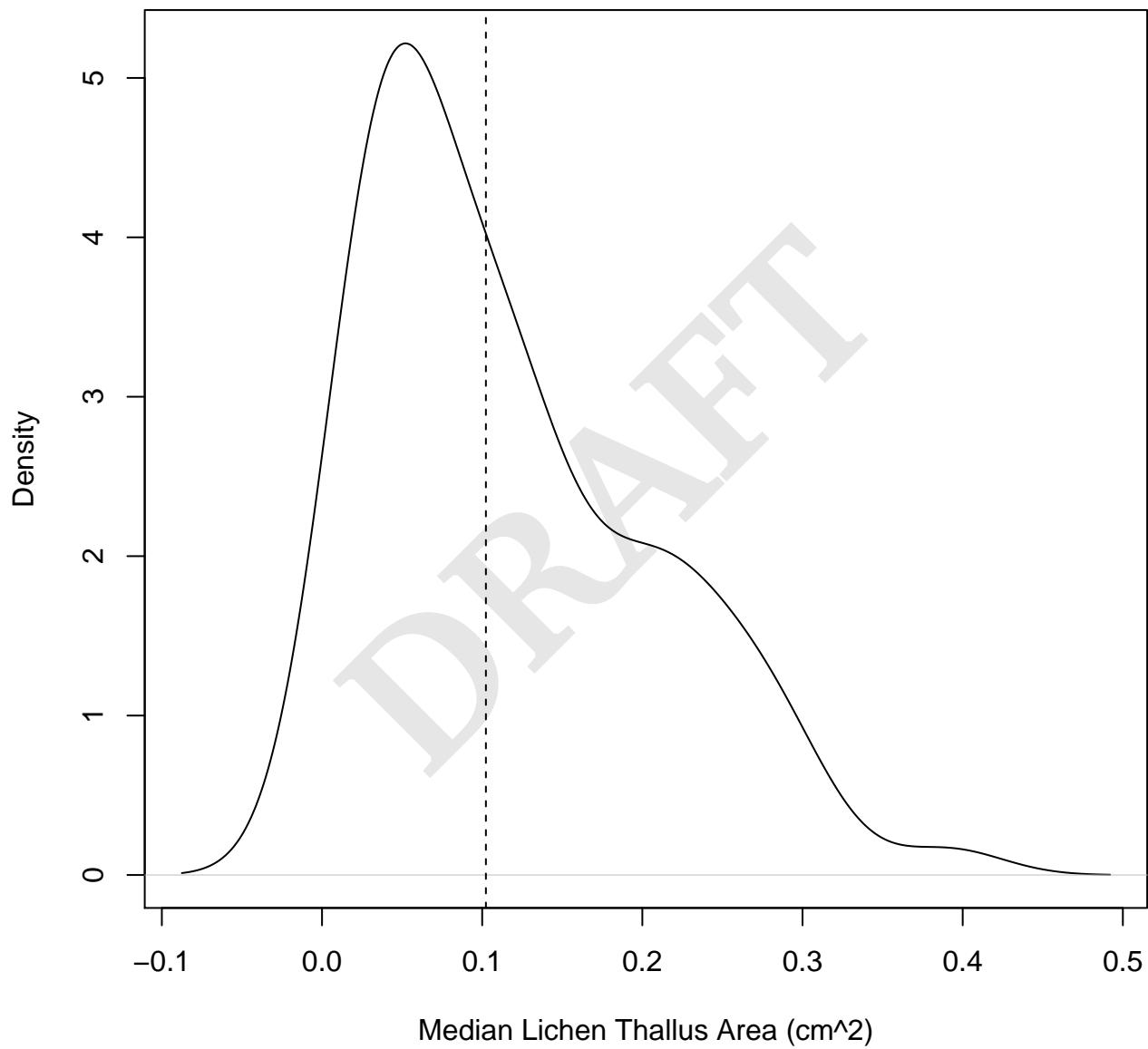


Fig. 1

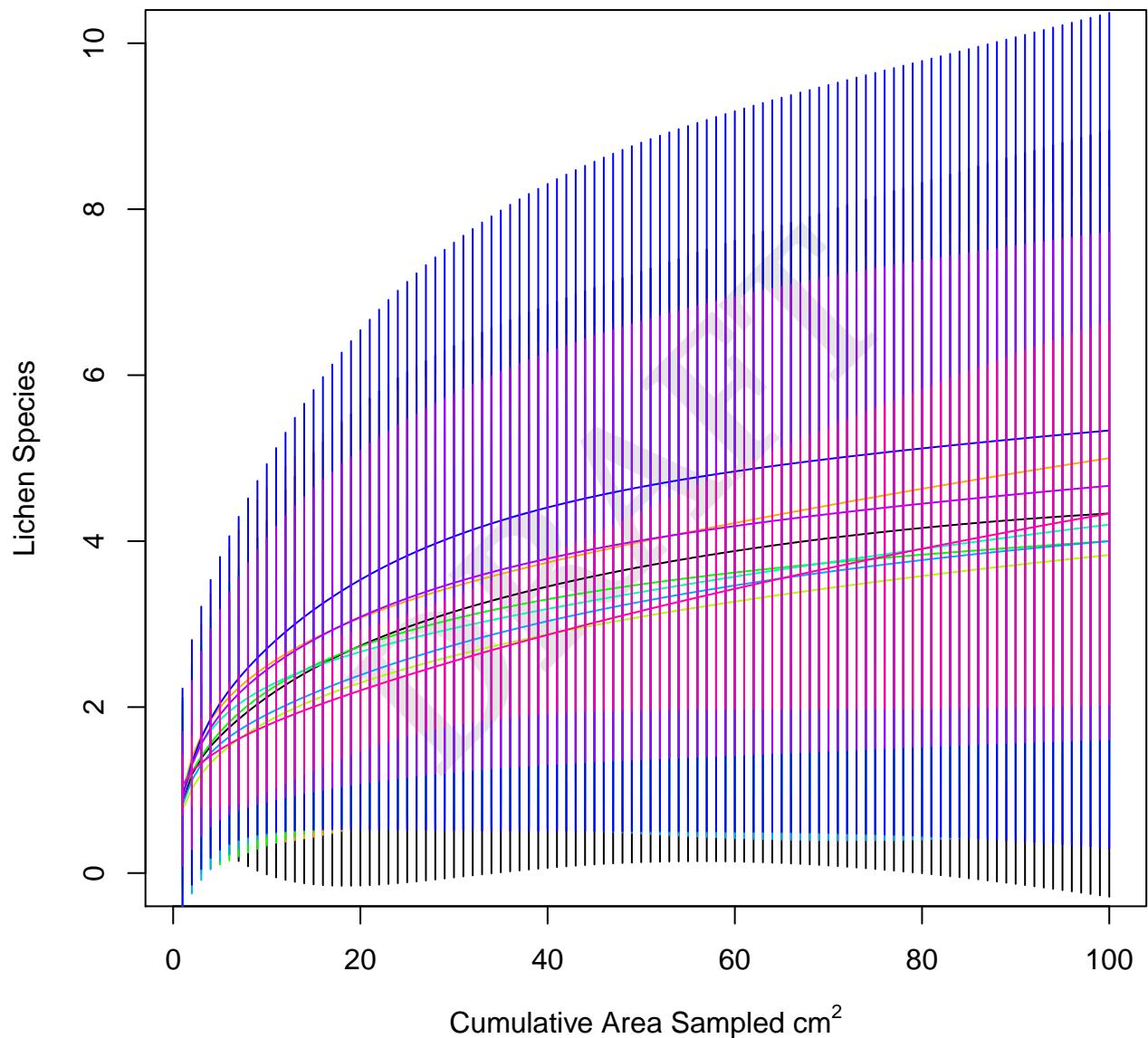


Fig. 2. Species-area curve by genotype.

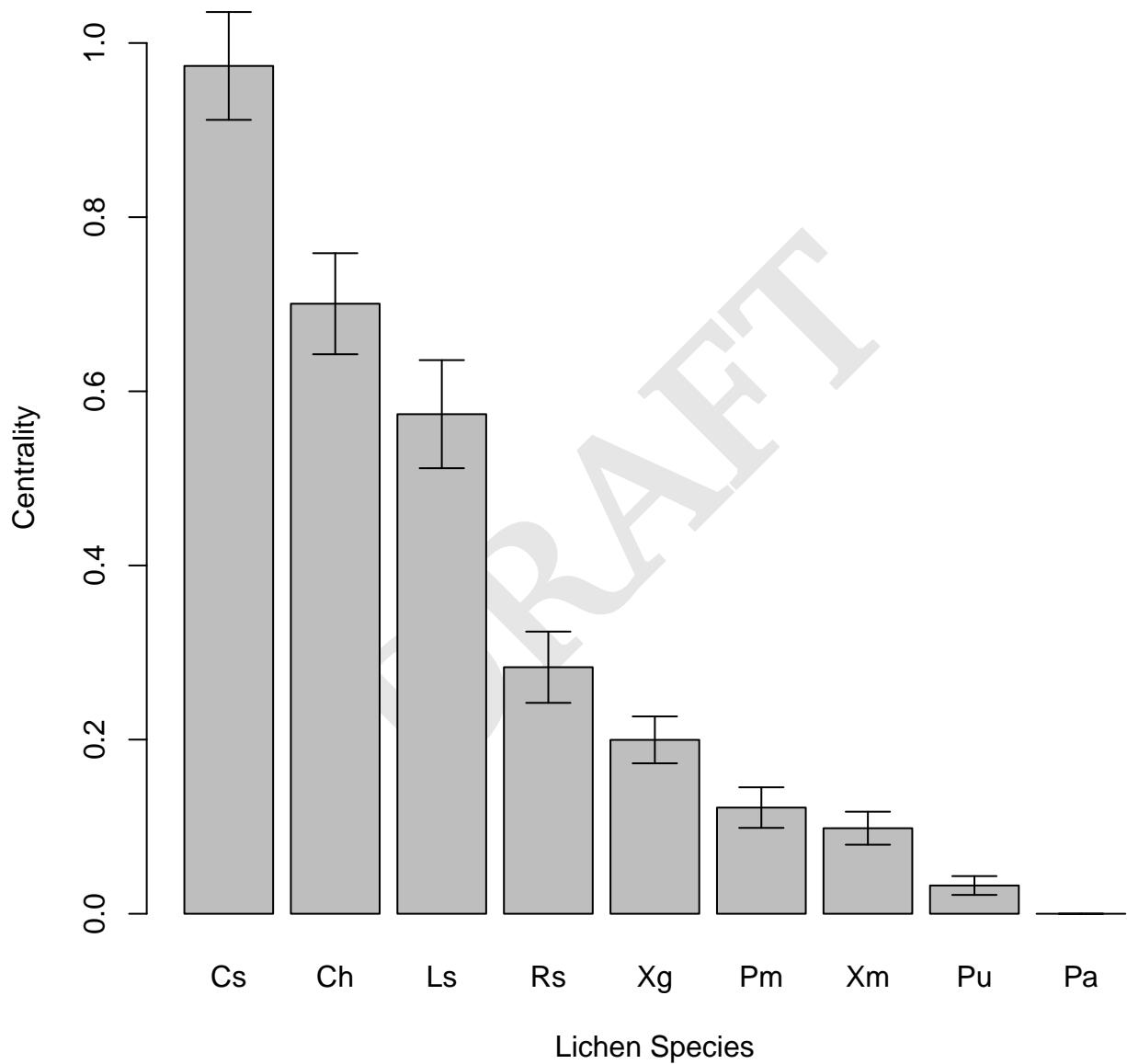


Fig. 3