

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 at**
8 **the scale of individual trees has not yet been explored. To test the**
9 **degree to which tree genetics can contribute to network structure**
10 **we conducted quantitative modeling of interaction networks. We**
11 **constructed networks of epiphytic lichens associated with individ-**
12 **ual trees that were a part of a long-term experimental common gar-**
13 **den of genotypes of (*Populus angustifolia*), a foundation species.**
14 **We found two primary results. First, tree genotype significantly pre-**
15 **dicted lichen network similarity, i.e. clonal replicates of the same**
16 **genotype tended to support more similar lichen networks, using mul-**
17 **tiple network metrics. Second, although multiple species were ob-**
18 **served repeatedly in the interaction networks, the effect of tree geno-**
19 **type was primarily focused on variation of the interactions of one**
20 **lichen species, *Caloplaca holocarpa*. Third, one of the examined tree**
21 **traits, bark roughness, was both predicted by tree genotype and cor-**
22 **related with lichen network similarity, supporting a mechanistic path-**
23 **way from a variation in a heritable tree trait and the genetically based**
24 **variation in lichen network structure. We conclude that tree geno-**
25 **type can influence not only the relative abundances of organisms**
26 **but also the interaction network structure of associated organisms.**
27 **Given that variation in network structure can have consequences for**
28 **the dynamics of communities through altering the stability of the sys-**
29 **tem and modulating or amplifying perturbations, these results have**
30 **important implications for the evolutionary dynamics of ecosystems.**

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

1 **E**volution occurs in the context of complex eco-
2 logical networks. Initially, evolution in a com-
3 munity context was focused on examples of highly
4 co-evolved pairs of species (e.g. Darwin's famous
5 prediction of the Sphinx Moth and Christmas Or-
6 chid) (1). However, studies of diffuse co-evolution
(*sensu* (2)) (3, 4), geographic mosaics of co-evolution
(5) and community genetics (6) have provided an
in-road for ecological network approaches (7–9) to
illuminate a more complex perspective of the inter-
face between ecological and evolutionary dynamics.

12 There is now evidence to support that selection tends
13 to occur among groups of species (1) favoring the
14 development of small webs (10, 11) and that genetic
15 variation and phylogenetic relatedness contributes
16 to variation in community assembly (12) and species
17 interactions (6, 13, 14), which shapes the ecological
18 interaction networks (15).

Significance Statement

Evolution occurs in the context of ecosystems com-
prised of complex ecological networks. Research at
the interface of ecology and evolution has primarily
focused on pairwise interactions among species and
have rarely included a genetic component to anal-
yses. Here, we use a long-term common garden
experiment to reveal the effect that genotypic varia-
tion can have on networks of lichens that occur on
the bark of a foundation tree species. We found that
lichen interaction network structure is genetically
based and primarily driven by a tree trait, bark rough-
ness. These findings demonstrate the importance
of genetic variation and evolutionary dynamics in
shaping ecological networks as evolved traits. In
particular, this study points to the importance of as-
sessing the effect of foundation species genetics on
the structure of interactions, given that interaction
network structure has systems-level properties that
could affect the response of these communities to
selection.

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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19 Define foundation species.

20 Community genetics studies (16) have shown that
21 genetic variation in foundation species (17) plays a
22 significant role in defining distinct communities of in-
23 teracting organisms: such as, endophytes, pathogens,
24 lichens, arthropods, and soil microbes. Multiple
25 studies have now demonstrated that genetic varia-
26 tion influences numerous functional traits (e.g., phy-
27 tochemical, phenological, morphological) produces
28 a multivariate phenotype (18) that contributes to
29 variation in associated communities (13). The impor-
30 tance of genetic variation in structuring ecological
31 systems was recently reviewed (19), and not only
32 were many instances of strong genetic effects found
33 in many ecosystems but the effect of intraspecific
34 variation was at times greater than *inter*-specific
35 variation.

36 Additional work has provided support for the hy-
37 pothesis that not only does composition vary among
38 genetically distinct genotypes of foundation species
39 but that it also impacts the structure of species
40 interactions. However, studies in the network ecol-
41 ogy literature generally do not include a genetic
42 component (34); and, community genetics studies
43 have primarily focused on community composition
44 in terms of the abundance of species (19). There
45 are studies that have examined the effects of genetic
46 variation on trophic chains, such as several in plant-
47 associated communities (including *Populus*, *Solidago*,
48 *Oenothera*, *Salix*) (7, 21–24) and generally found
49 that increasing genotypic diversity leads to increased
50 trophic complexity. Only two other studies, that we
51 are aware of, have explicitly examined the effect of
52 genotypic variation on the structure of interaction
53 networks between tree individuals and associated
54 herbivores (8, 25) and both found that genotypic di-
55 versity generates increased network modularity (i.e.
56 compartmentalization). However, both of these stud-
57 ies were at the scale of forest stands and, therefore,
58 were not able to observe replicated networks in order
59 to statistically test for genetic effects on network
60 structure.

61 Here, we investigate how genetic variation in a
62 foundation tree species determines the structure of
63 a network of interactions among a community of
64 tree associated lichen species. Previous studies have
65 examined aspects of networks (26). Here we examine
66 the genetic basis of network structure on a commu-
67 nity of sessile lignicolous (i.e. bark) lichens on cotton-

68 wood trees. Using a long-term (20+ years), common
69 garden experiment with replicated individuals of
70 known genetic identity and a naturally established
71 stand of *Populus angustifolia*. We focused on a model
72 community of 9 epiphytic lichen species, as previous
73 research has demonstrated significant compositional
74 responses of epiphytes to genotypic variation (27, 28).
75 In addition, the life-history characteristics of lichens,
76 having highly localized, direct contact interactions
77 and slow population turnover rates, facilitated the
78 assessment of interactions among lichen species on
79 individual trees. We hypothesize that in natural
80 systems evolution occurs in a community context
81 involving interactions of complex networks of inter-
82 acting species (5, 8, 25, 29). If correct, we expect
83 to find that network structure is genetically based
84 in which different plant genotypes support different
85 interaction networks and that these interactions net-
86 works can function as indicators of ecological dynam-
87 ics important for conserving biodiversity. Applying a
88 probability-theory based network modeling approach,
89 we constructed a set of interaction network models
90 for the lichens associated with individual trees. Us-
91 ing these models, we then examined the genetic basis
92 of the structure of these ecological networks. Based
93 on previous community genetics studies, particularly
94 (30) which proposed the community similarity rule,
95 we hypothesize that trees will vary in some pheno-
96 typic traits and those trees of the same genotype will
97 tend to have similar traits leading to similarities in
98 lichen network structure.

Materials and Methods

99
100
Study System. The study was conducted along the We-
101 ber River, UT (USA), which is a cottonwood (*Populus*
102 spp.) dominated riparian ecosystem. Although two native
103 species, *Populus angustifolia* (James) and *Populus fremontii*
104 (S. Watson), occur here and are known to hybridize,
105 only pure or advanced generation backcrosses of *P. angus-
106 tifolia* were sampled. Bark lichens have been extensively
107 studied in this system and provide an ideal system in
108 which to observe and model lichen interaction networks,
109 as their sessile nature permits accurate identification of
110 individuals (31).

111 A long-term, common garden experiment was used
112 to isolate the effect of tree genotype from the effect of
113 the localized microenvironment associated with each indi-
114 vidual and spatial autocorrelation. Established in 1992,
115 asexually propagated clones of genotyped *P. angustifo-*
116

lia individuals were obtained from wild collections and planted in fully randomized design at the Ogden Nature Center, Ogden, UT. From the population of established individuals in the common garden, we chose a total of ten genotypes, replicated between 3 and 8 times each, for sampling.

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

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 $0.12 \pm 0.001\text{ cm}^2$ (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, condensed tannin, carbon and nitrogen concentrations and pH. **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 conducted a modified sampling procedure originally developed by (16) with the addition that we quantified the presence of lichen in the 1 cm^2 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 (32). 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 as $P(S_i|S_j) = \frac{P(S_i, S_j)}{P(S_j)}$, 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 (i.e. $P(S_i, S_j)$) is different from zero (Fig. 2). Here, a confidence interval $CI_{95\%}$ is calculated as $CI_{95\%} = E[S_iS_j] * Z_{95\%} * \sqrt{V(S_iS_j)}$, where the expected frequency of co-occurrences $E(S_iS_j)$ 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 $E(S_iS_j)$ is the total number of cells times the expected probability of S_iS_j and its compliment (i.e. $V(S_iS_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If 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. $P(S_i)\dot{P}(S_j)$), 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. a species does not influence its own probability of being observed).

Network Metrics. To quantify the structural variation of lichen networks we calculated several metrics at both the node and whole-network level. For individual nodes (i.e. species) in each network, we calculated both the degree Eq. (1) and the centrality. We also calculated two similar global network metrics: degree and centralization. The first was network degree, which is a count of the total number of links in a network. As the networks contained not only positive and negative connections,



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 (100 cm^2) on individual trees at two heights, 500cm and 95cm 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. Naesbørg (D-K).

as well as directional connections (both in-coming and out-going), we calculated the same network metrics for all combinations of these types of connections in each network. Although there are many more possible network 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

$$\sum x_i \quad [1]$$

- 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 (33). We used the **signnet** package version ????, which is available at ???.

Statistical Analyses, Software and Data. We used a combination of parametric and non-parametric, permutation based frequentist statistical analyses to test for the effects of genetic variation on lichen communities and their interaction networks. To assess the effect of genotype on univariate responses, we used additive, random effects models with Restricted Maximum Likelihood (REML). We used a combination of Least Squares Regression, Analysis of Variance (ANOVA) and correlation tests to quantify and test for the relationship among other variables. Bark roughness, lichen cover and species richness were square-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. 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

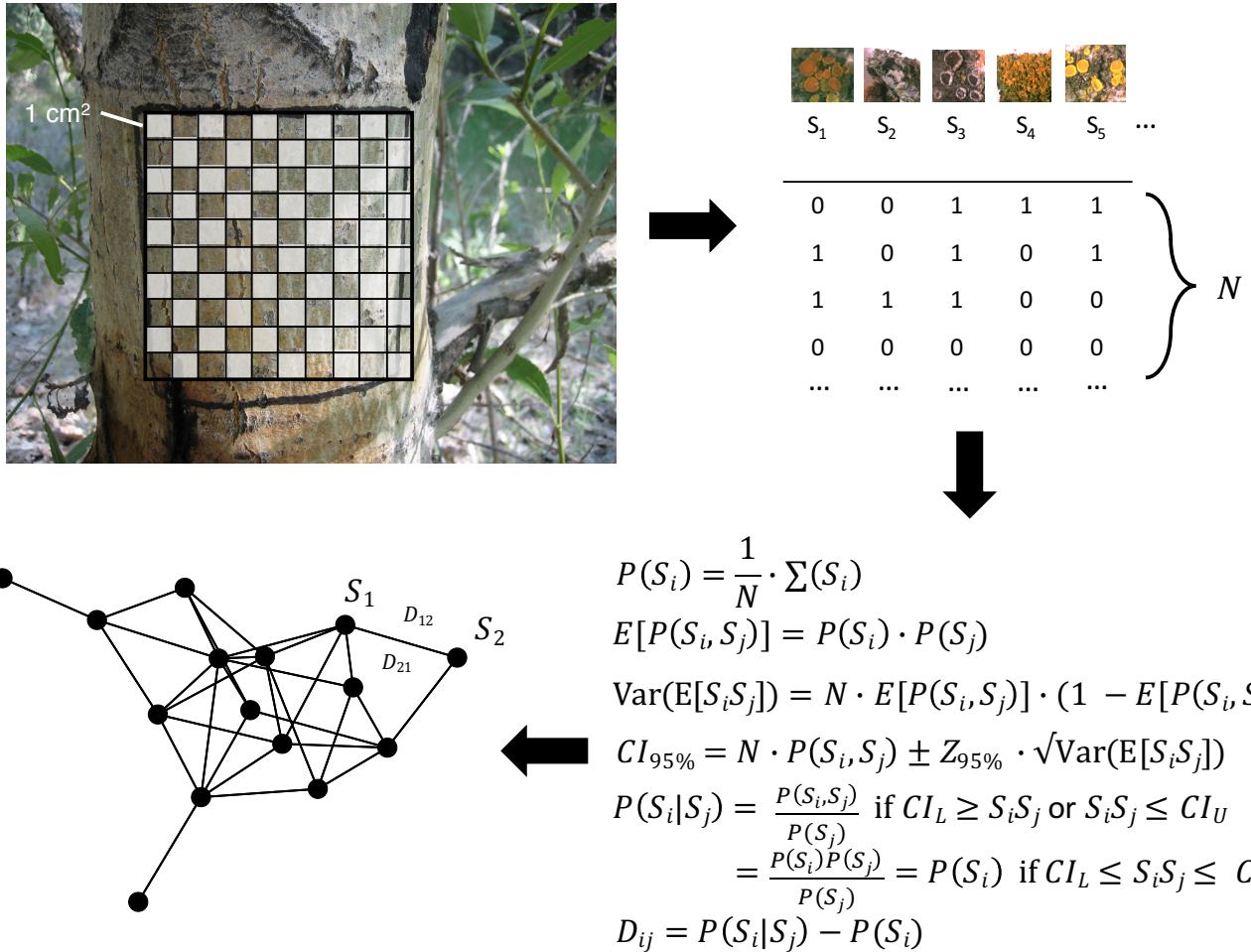


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (32), 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.

produce dimensionally reduced ordinations of these multi-variate 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 (34)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (20, 25). 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.

For all tests where genotype was used as a predictor, we quantified the heritability of the response variable. Because the trees in the garden were clonal replicates of each genotype, we calculated broad-sense heritability, which is the genotypic variance divided by the total phenotypic variance (35). This can be interpreted as a measure of the phenotypic variance due to genotypic variation. We also apply this to the community genetics context as the variance in *extended* phenotypic variance due to genotypic variation (36). For the multivariate analyses, where we employ PERMANOVA, we followed the methods of (37)

302 to adjust the degrees of freedom for unbalanced genotype
303 replicates.

304 All code and data for the project are openly available
305 online. Code and data are available at github.com/
306 ecgen/comgen. The project is also archived via Zenodo
307 at zenodo.com/doiXXXXXX. All analyses were conducted
308 using the programming language R version 3.6.1 (R De-
309 velopment Core Team 2019).

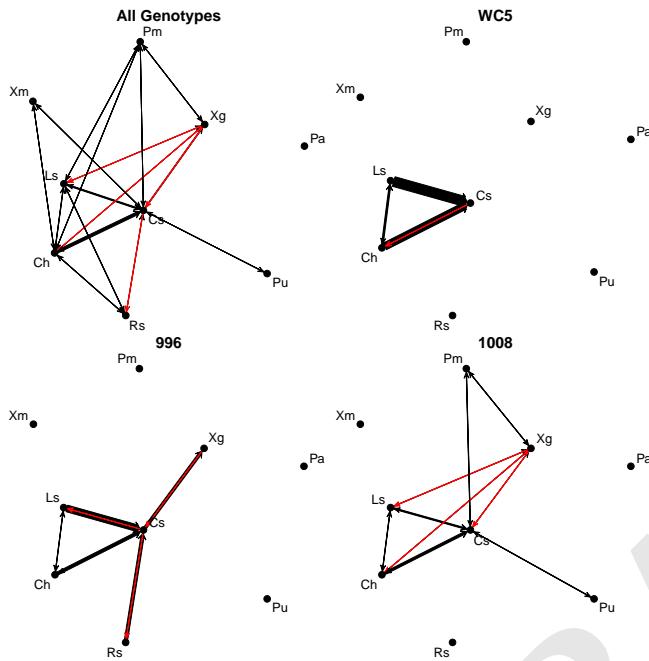


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive)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

310 Tree genotype influenced lichen network structure
311 and multiple lichen network metrics were heritable.
312 Tree genotype significantly predicted the struc-
313 tural similarity of lichen networks (PERMANOVA:
314 Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$)
315 (Fig. 4). Overall network level metrics responded
316 significantly to tree genotype (Table 1), including net-
317 work degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} =$
318 0.0255) and centralization including both in-coming
319 and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} =$
320 0.0184) or when separated into in-coming only
321 ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} =$
322 0.0190) or out-going only ($RLRT = 3.8615$, $H^2 =$

323 0.3193, $p\text{-value} = 0.0205$). Metrics including only
324 positive links also showed a significant effect of tree
325 genotype, including positive degree ($RLRT = 3.6925$,
326 $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
327 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} =$
328 0.0142). Metrics calculated with negative
329 links were not significant, including degree (negative)
330 ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$)
331 and both in-coming (negative) ($RLRT = 0.3304$, $H^2 =$
332 0.1057, $p\text{-value} = 0.2508$) and out-going centraliza-
333 tion (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$,
334 $p\text{-value} = 0.3446$).

response	statistic	H^2	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Degree	3.5175	0.3156	0.0255
Degree (positive)	3.6925	0.3242	0.0229
Degree (negative)	0.0327	0.0318	0.3859
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

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

The genetic response of network centralization was
336 driven by variation in *Caloplaca holocarpa*. Central-
337 ization varied significantly among species ($F_{8,324} = 7.99$,
338 $R^2 = 0.16$, $p\text{-value} < 0.0001$). *Caloplaca holocarpa*
339 centrality was the main species to exhibit a signifi-
340 cant response to tree genotype in terms of positive
341 centralization for both the in-coming ($RLRT = 3.61$, $H^2 =$
342 0.32, $p\text{-value} = 0.0240$) and out-going ($RLRT =$
343 3.13, $H^2 = 0.30$, $p\text{-value} = 0.0327$) perspectives, but
344 not for either negative centrality metrics in-coming
345 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 1$) or out-going
346 ($RLRT = 0$, $H^2 = 0$, $p\text{-value} = 0.4543$). None of
347 the other species' centralities showed a genotypic re-
348 sponse (Supplementary Table 6) with the exception
349 of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, $p\text{-value} =$
350 0.0375); however, the centrality of *X. montana* was
351 much lower overall relative to *C. holocarpa* and the
352 variation in *X. montana* centrality was restricted to
353 two genotypes (Fig. 5).

Genotype indirectly influenced lichen network cen-
355 tralization via the genetically based variation in bark
356 roughness. The percent of rough bark was the only
357 tree trait that displayed a significant response to
358 genotype ($RLRT = 4.8526$, $H^2 = 0.3221$, $p\text{-value} =$
359

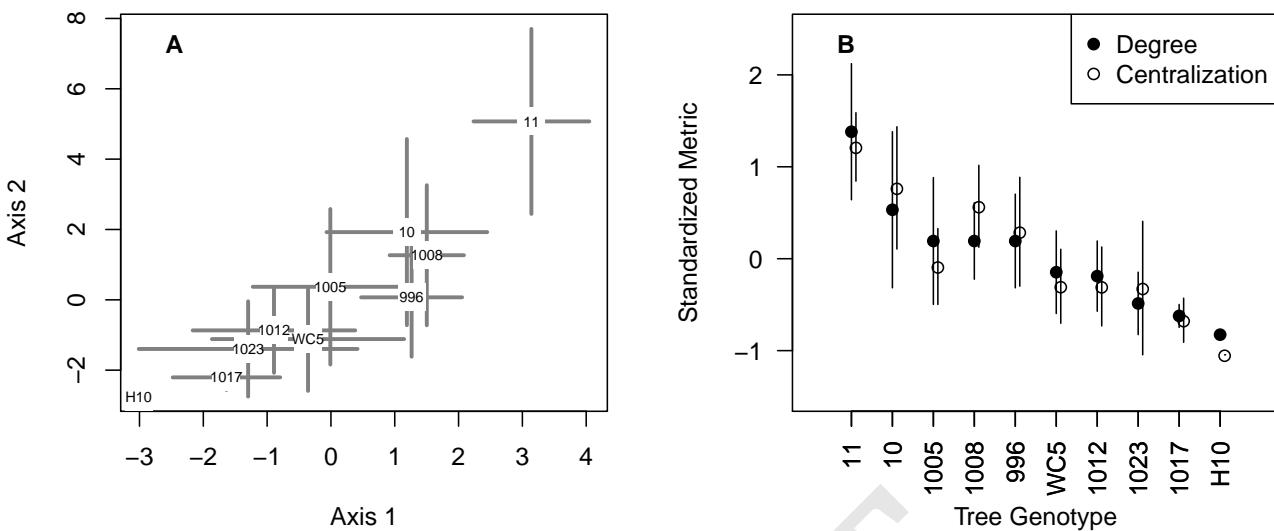


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen networks (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. B. Plot showing the 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.

0.0113). None of the other bark traits, condensed tannins ($RLRT = 0.0007$, $H^2 = 0.0041$, $p\text{-value} = 0.4439$), pH ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or carbon-nitrogen Ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, $p\text{-value} = 1.0000$), showed a significant response to tree genotype and none other than bark roughness 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- $F_{1,32} = 13.029$, $R^2 = 0.26$, $p\text{-value} = 0.0096$) and other lichen network metrics, including negative correlations with overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$, $p\text{-value} = 0.04$) and centralization ($df = 35$, $t = -2.52$, $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees with more similar levels of bark roughness tended to have lichen interaction networks with similar structure. To quantify the genetic bases of this effect of bark roughness on network structure, we used the residual values from regressions of network degree and centralization in tests of the effect of tree genotype and found no significant effect of tree genotype for either degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$) or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$), suggesting that the observed relationship

between bark roughness and lichen network structure was largely genetically based (Fig. 6).

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*. The genetically based trait, bark roughness, was the main driver of network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been demonstrated previously to be under strong genetic control (38), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (16); however this is the first demonstration of a link from genes to lichen network structure. As such these results have important implications for the potential influence of genetically based variation in ecosystems with networks of interacting species.

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

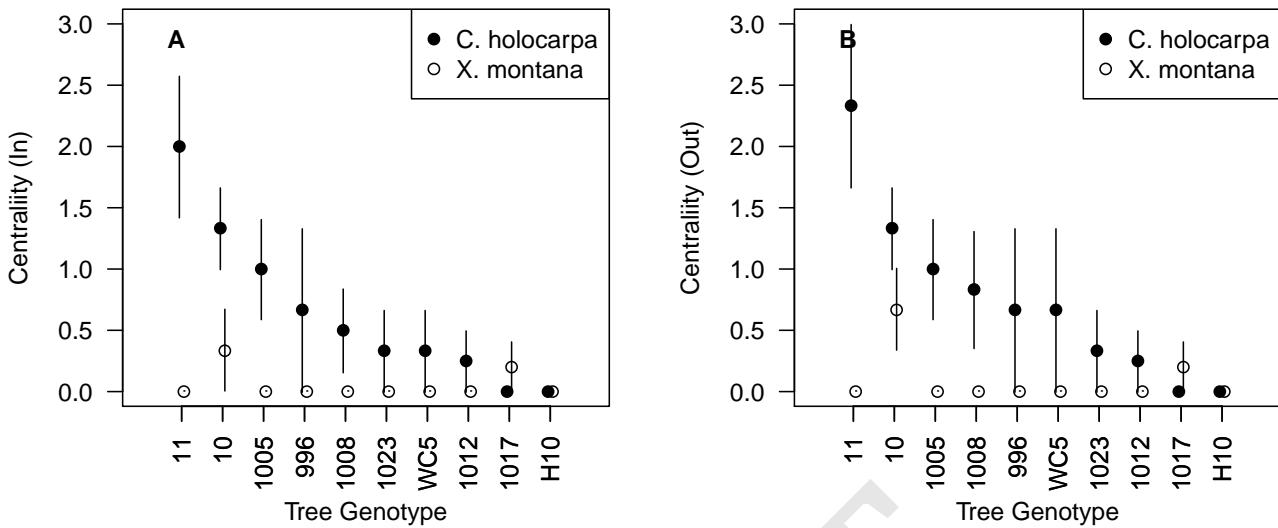


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

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 previously been observed to be different among tree genotype in the same experimental garden, 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 within the system of interacting species. For example, (8) showed that the genetics based interactions of aphid resistant and aphid susceptible trees

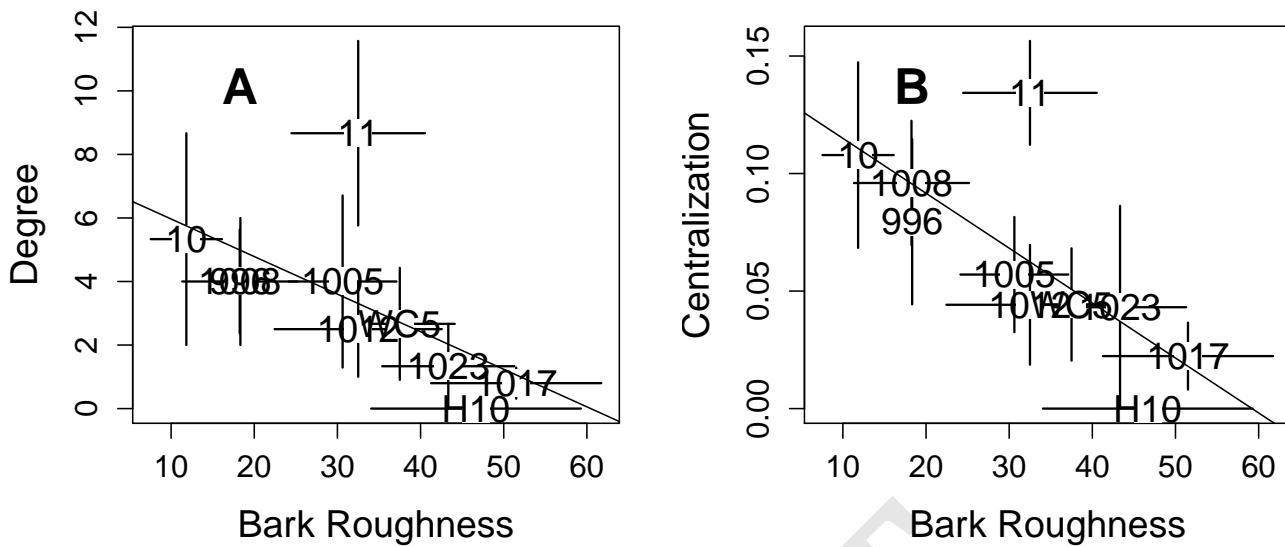


Fig. 6. Bivariate plots of the relationship between bark roughness and three network metrics: A) degree and B) centralization. Each plot displays the genotype mean \pm 1 S.E. for both variables and a least-squares regression calculated using the genotype means.

465 resulted in different interaction networks of their
466 associated arthropod communities composed of 139
467 species. At the scale of ecosystems, trophic net-
468 works or food webs direct and control the rates of
469 energy and nutrient flux (39). Furthermore, in a
470 predator-prey-plant study, Smith (23), showed that
471 the interactions among species across trophic levels
472 depended on plant genotype. Also, work by (40–42)
473 observed consistent patterns of centralized interac-
474 tions of species modules focused around hubs of
475 plant-fungal interactions. In other words, a small
476 number of plant and fungal symbionts tended to
477 have disproportionate numbers of interactions with
478 other species and likely are the drivers in determining
479 community assembly, structure and dynamics.

480 *Review papers that use network analysis to identify
481 foundation species.*

482 *Make a bigger deal of the application of the genetic
483 similarity rule and more similar genotypes supporting
484 more similar interaction networks.*

485 There are several important points to consider
486 with regard to the generalization of the observed
487 genetically based response of the lichen networks.
488 Body size and sessile nature of lichen important to
489 observing genotype responses. As bark lichen
490 individuals do not move, but grow in a largely two
491 dimensional plane, these communities and their in-

teractions occur in the highly localized context of
492 the tree's bark surface. Lichen individuals are many
493 orders of magnitude smaller than the tree individual
494 and the life-span of a tree is many times that of a
495 lichen. For these reasons, any genetic effects on these
496 communities is not dampened by the movement of
497 individuals and the mixing of the effect of different
498 tree genotypes on the lichen community, as might
499 occur for more mobile species (e.g. insects and birds).
500 We only looked at lichen, other species whose distri-
501 bution, abundance or interactions respond to tree
502 genotype, such as epiphytic plants (e.g. moss and
503 liverworts), algae or insects, could be playing a role.
504 Other traits could also be playing a role, such as
505 traits that are correlated with bark roughness, such
506 as micro-aspect, albedo, moisture, etc.

507 *Add more text here on positive and negative inter-
508 actions of lichen from the literature.*

509 *Elaborate on how many species might be supported
510 by each lichen thallus including the symbionts and
511 other species.*

512 *Elaborate on the importance of identifying the
513 species/node level patterns in network structure re-
514 sponse to genotype.*

515 *What is the relationship between tree growth, bark
516 roughness and disruption of the lichen community?
517 Tree grow and the bark expands over time, causing*

519 furrows.

520 *Does bark roughness increase habitat and decrease*
521 *interactions?*

522 Bark roughness could possibly be serving the role
523 that other lichen play in facilitating the success of
524 new propagule attachment and the growth of estab-
525 lishing thalli. This is supported by the patterns over-
526 all being positive, including *C. holocarpa* centrality.
527 We did not observe specific microscopic dynamics,
528 such as photobionts, mycobionts, endolichenic fungi
529 and bacteria, but variation in these underlying inter-
530 actions could also be playing a role. Although we can
531 not rule out the possibility that other unmeasured
532 tree traits or organisms correlated with bark rough-
533 ness are underlying the observed patterns in bark
534 lichen network structure, substantial research sup-
535 ports the importance of genetically based tree traits
536 for communities and ecosystems (19), and in par-
537 ticular bark roughness for bark lichen communities
(16, 31, 38),

538
539 Although our study was conducted with a commu-
540 nity of lichens, these results should be generalized to
541 other groups of diverse organisms around the world
542 that also exhibit significant genetic signals at the
543 community level (43, 44). In the face of the high de-
544 gree of complexity and potential context dependency
545 of ecological processes, the current study points to
546 the utility of considering the spatial and temporal
547 scales of interactions, as discussed to some in pre-
548 vious studies (30, 45, 46). In the present study, we
549 found that community assembly processes, such as
550 environmental filtering and species interactions, are
551 genetically based. This is likely due, in part, to
552 the large difference in the differences in size and
553 longevity of the lichen and cottonwood individuals
554 with the trees determining the environment in which
555 the lichen occur. We suggest that future work would
556 be aided by determining these modules within the
557 biotic community that include species with similar
558 differences in body-size and time-scales. As heritable
559 variation is the raw material for natural selection
560 to act upon, a genetic basis for interaction network
561 structure indicates evolutionary dynamics should be
562 considered at the community level and that con-
563 serving genetic variation is important to consider in
564 efforts to restore or preserve complex species interac-
565 tions and their associated ecosystem functions (47).
566 With such findings, it appears that we are closer to
567 understanding the evolutionary drivers of Darwin's

568 entangled bank and the interconnectedness of species
569 in complex communities.

570 Future work should consider the potential influ-
571 ence on evolutionary dynamics of the associated com-
572 munities. The network of interactions of species that
573 are strongly influenced by a foundation species, could
574 amplify the effects of genotype, this serves as a means
575 for genetic effects to increase rather than diffuse
576 through an ecosystem either through space or over
577 time, as has been proposed in the construction of the
578 genetic diffusion hypothesis. Altered abundances can
579 lead to differences in interactions Genotype effects
580 on abundances of individual abundances may cancel
581 out. Specifically for asexually reproducing species,
582 such as many lichen are, shifting interaction frequen-
583 cies could lead to evolutionary outcomes, given the
584 potential to take-up symbionts and genetic material
585 from thalli that they come into contact with. Alter-
586 ing interaction frequencies could result in differences
587 in rates of the exchange of genetic materials among
588 lichen that could then be passed on to vegetative
589 and possibly sexually produced reproductive propa-
590 gules. The larger scale (stand or region) effects of
591 these "evolutionary units" on each tree would de-
592 pend on the connectivity and rate of movement of
593 propagules among trees per the geographic mosaic
594 of co-evolution hypothesis (5, 48).

595 *Add evolutionary unit to the larger narrative. That*
596 *is mainly that identifying how evolution might be*
597 *acting on multiple species is useful for conservation*
598 *and management.*

599 *Discuss the impacts of *P. betae* removal on net-*
600 *work structure per Lau 2016 and Keith 2017. Also,*
601 *what about Barbour 2016.*

602 **Other studies that should be discussed:**

- Multiple plant traits shape the genetic basis
603 of herbivore community assembly. Synthesis:
604 Taken together, our results support that the
605 genetic basis of herbivore community assembly
606 occurs through a suite of plant traits for different
607 herbivore species and feeding guilds (Barbour
608 2015). Also discuss Lamit 2015 and Holeski's
609 multivarite phenotype paper.
- Linking plant genes to insect communities: Iden-
611 tifying the genetic bases of plant traits and com-
612 munity composition. Synthesis: These findings
613 support the concept that particular plant traits
614 are the mechanistic link between plant genes

616 and the composition of associated insect com-
617 munities (Barker 2019).

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729 **Supplementary Materials**

730 **Tables.**

	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
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	0.4543
Percent Rough Bark	4.8526	0.3221	0.0113
pH	0.0000	0.0000	1.0000
Carbon-Nitrogen Ratio	0.0000	0.0000	1.0000
Condensed Tannins	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				
In-Degree				
X. galericulata	0.2703	0	0	0.4543
C. subdeflexa	0.8919	2.1926	0.2158	0.0595
L. spp.	0.4324	0	0	1
C. holocarpa	0.5946	3.6146	0.3241	0.024
X. montana	0.0541	0	0	0.4543
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.1351	2.049	0.2613	0.0656
Out-Degree				
X. galericulata	0.027	0	0	0.4543
C. subdeflexa	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4246
C. holocarpa	0.7027	3.1318	0.2981	0.0327
X. montana	0.0811	2.9228	0.3163	0.0375
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.2973	0.1505	0.0612	0.3119
Negative				
In-Degree				
X. galericulata	0			
C. subdeflexa	0.1892	0	0	0.4543
L. spp.	0.1892	0.0015	0.0057	0.4398
C. holocarpa	0.1351	0	0	1
X. montana	0.027	0.0377	0.0394	0.3807
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0.1622	0	0	1
Out-Degree				
X. galericulata	0.2432	0	0	1
C. subdeflexa	0.4054	0	0	0.4543
L. spp.	0.027	0	0	0.4543
C. holocarpa	0.027	0	0	0.4543
X. montana	0			
P. melanachra	0			
P. adscendens	0			
P. undulata	0			
R. sp.	0			

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

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

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

	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		

Figures.

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

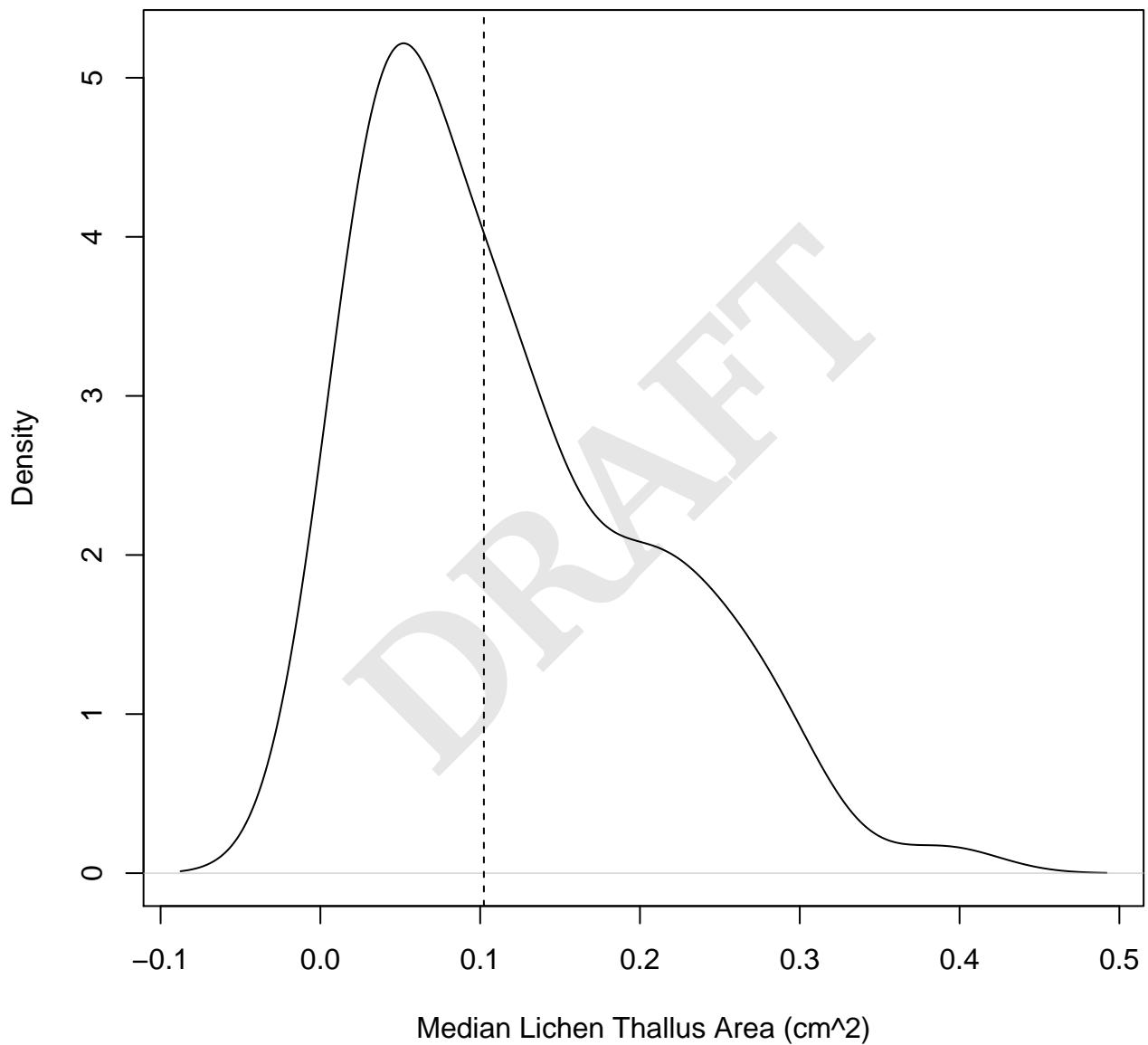


Fig. 1

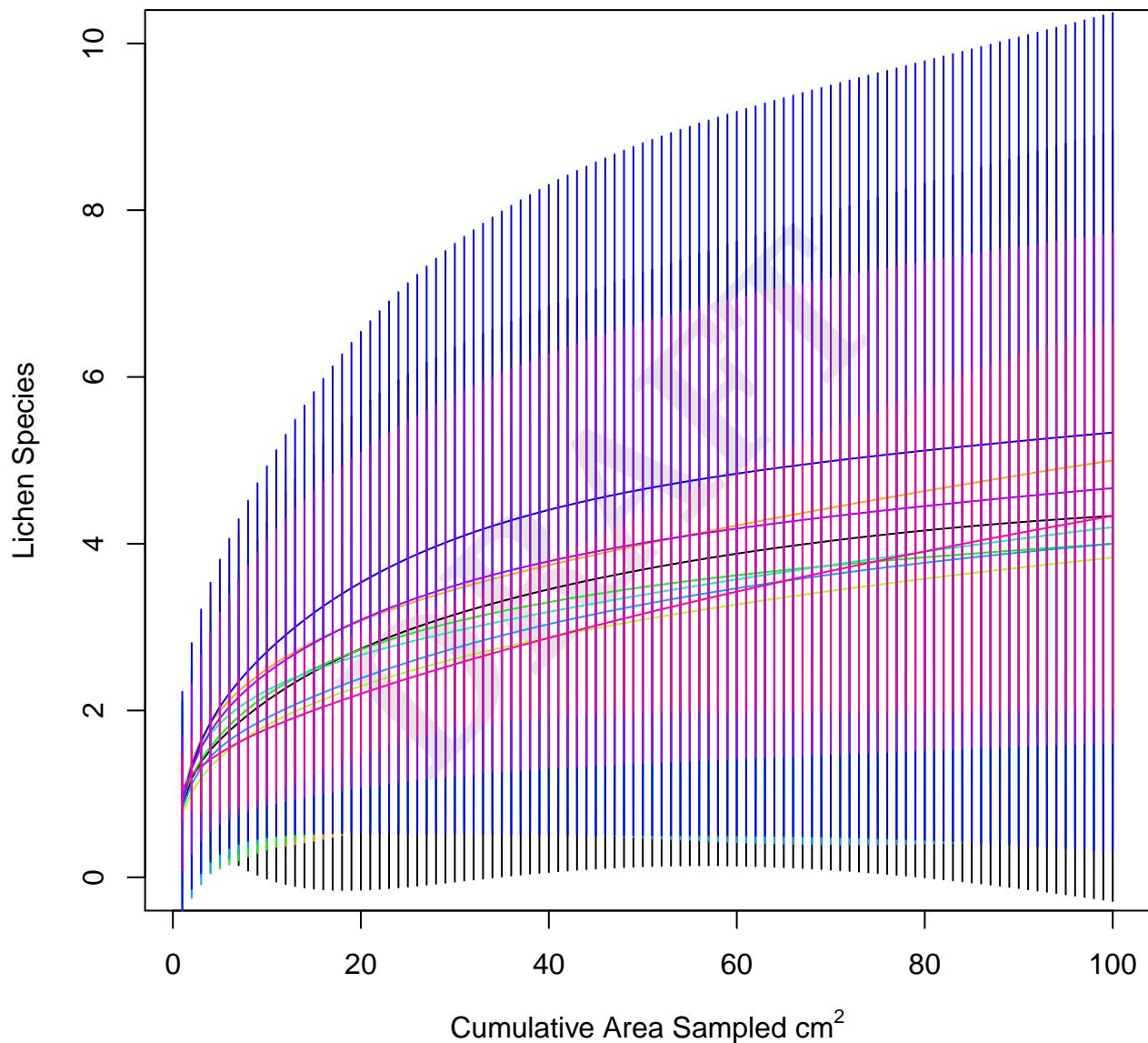


Fig. 2. Species area curve by genotype.

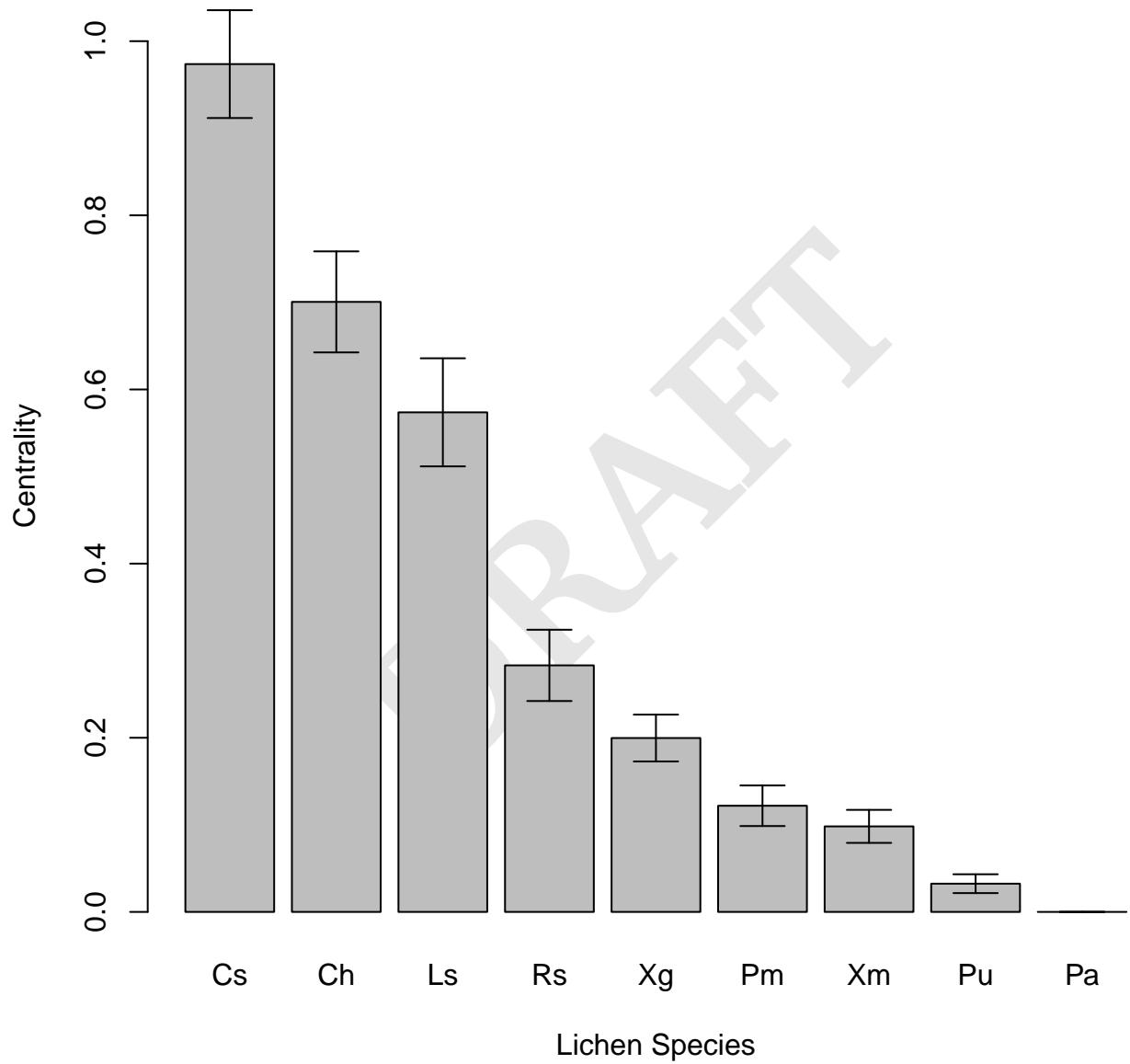


Fig. 3