

# 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 Evolution 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.

The authors have no conflicts of interest.

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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 (20); 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  $1\text{ cm}^2$  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  $100\text{ cm}^2$  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.

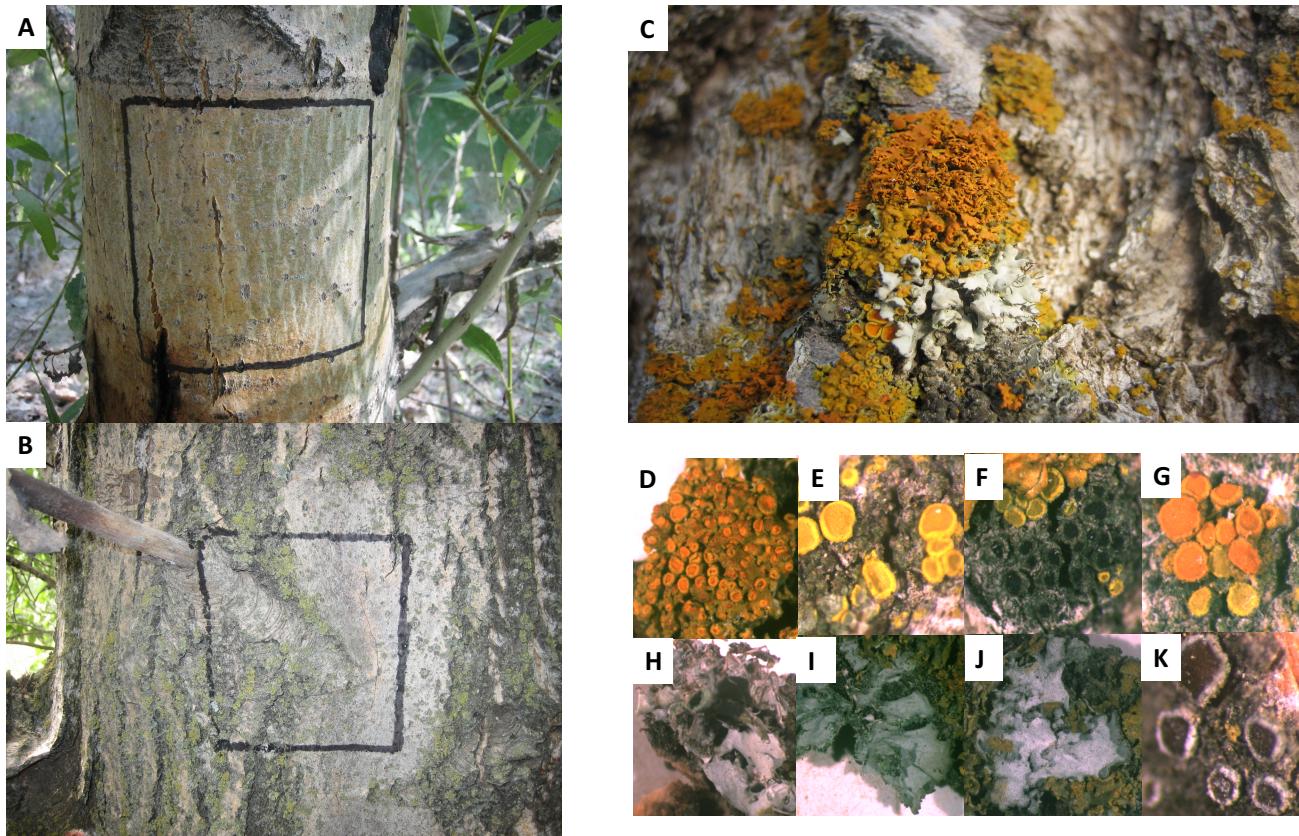
We also measured several bark traits for each tree: including, bark roughness, condensed tannin, carbon and nitrogen concentrations and pH. **ADD METHODS FROM JAMIE.**

**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  $1\text{ cm}^2$  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 ( $100 \text{ cm}^2$ ) 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

- 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) (34) to



**Fig. 2.** Lichen interaction networks were constructed by conducting field observations in  $1 \text{ cm}^2$  cells within a  $100 \text{ cm}^2$  grid on each tree using a checkerboard pattern (grey cells). Thus, a set of  $N$  total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (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 (35). 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.

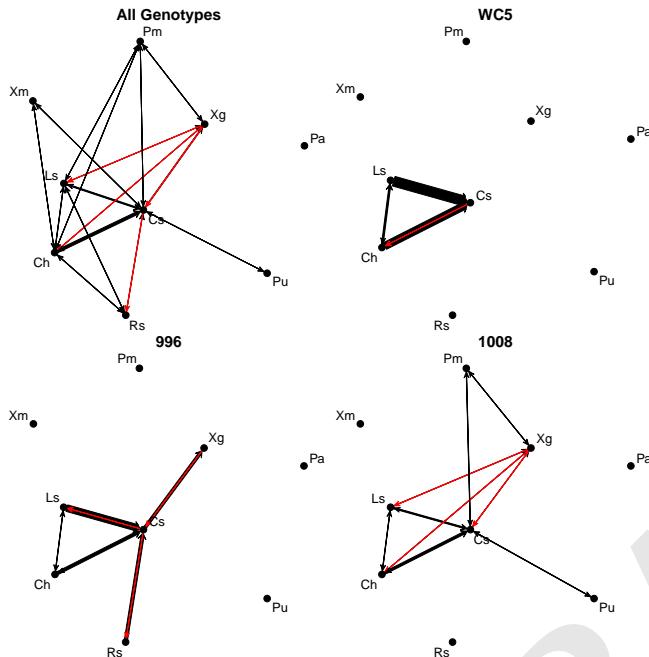
For each network, we also calculated metrics that measure different structural aspects. Although there are many other metrics, for the sake of simplicity we focus on a subset that represent several interesting features of network structure (see (20)). We calculated the number of interactions or “links” in each network, which provides a measure of the size of the network (25, 36). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (37). 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 (38). 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 (39). For the multivariate analyses, where we employ PERMANOVA, we followed the methods of (40)

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

304 All code and data for the project are openly available online. Code and data are available at [github.com/ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo at [zenodo.com/doi/XXXXXX](https://zenodo.com/doi/XXXXXX). All analyses were conducted  
305 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 (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species (abbreviated by the first letter of the genus and specific epithet), which are scaled by their magnitude. The sign of the interaction is indicative of greater (positive) or lesser (negative) paired occurrences than expected relative to the overall frequency of occurrence of each species. Ecologically, the links in the network are likely the product of multiple types of interactions (e.g. mutualism, parasitism, competition, facilitation) that could vary over both space and time.

## 310 Results

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

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 ( $RLRT = 4.4812$ ,  $H^2 = 0.3487$ ,  $p\text{-value} = 0.0142$ ) Metrics calculated with negative  
328 links were not significant, including degree (negative)  
329 ( $RLRT = 0.0327$ ,  $H^2 = 0.0318$ ,  $p\text{-value} = 0.3859$ )  
330 and both in-coming (negative) ( $RLRT = 0.3304$ ,  $H^2$   
331 = 0.1057,  $p\text{-value} = 0.2508$ ) and out-going central-  
332 ization (negative) ( $RLRT = 0.0862$ ,  $H^2 = 0.0513$ ,  
333  $p\text{-value} = 0.3446$ ).

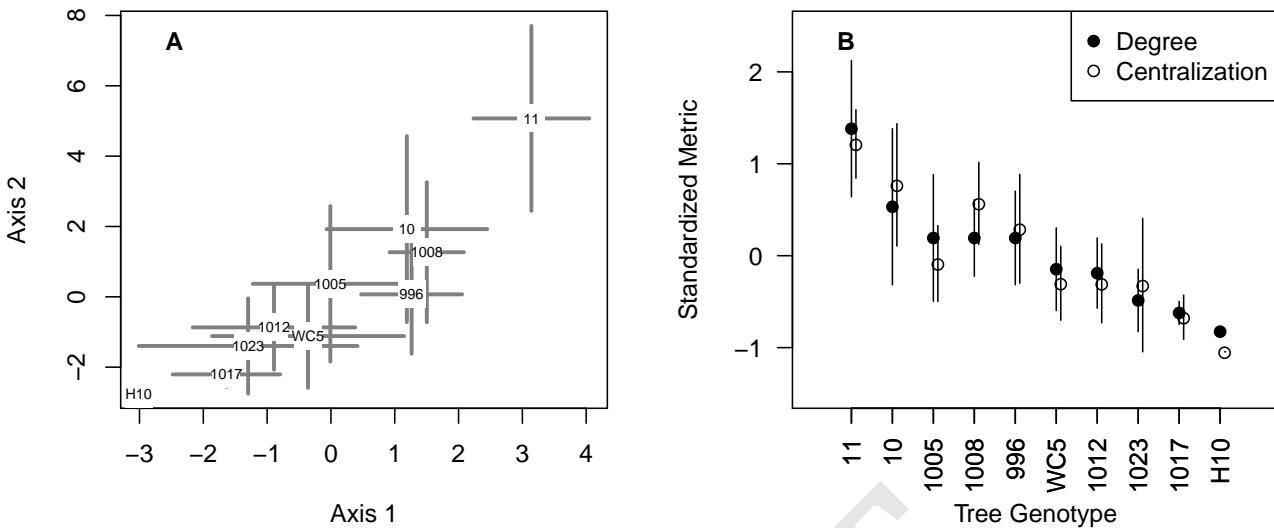
response	statistic	$H^2$	p-value
Lichen Network Similarity	3.5821	0.4130	0.0537
Degree	3.5175	0.3156	0.0255
Degree (positive)	3.6925	0.3242	0.0229
Degree (negative)	0.0327	0.0318	0.3859
Centralization	4.0444	0.3305	0.0184
Centralization In-Degree	4.4812	0.3487	0.0142
Centralization In-Degree (positive)	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 centrality 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 4) 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).

### 354 Add transformations of variables to methods.

355 Genotype indirectly influenced lichen network cen-  
356 tralization via the genetically based variation in bark  
357 roughness. The percent cover of rough bark ( $RLRT$   
358



**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 ( $\pm 1 \text{ S.E.}$ ). 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 ( $\pm 1 \text{ S.E.}$ ) 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.

= 4.8526,  $H^2 = 0.3221$ ,  $p\text{-value} = 0.0113$ ) and condensed tannins ( $RLRT = 3.0522$ ,  $H^2 = 0.3205$ ,  $p\text{-value} = 0.0343$ ) both displayed significant responses to tree genotype. None of the other bark traits, 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 (Table 3); 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 ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ )

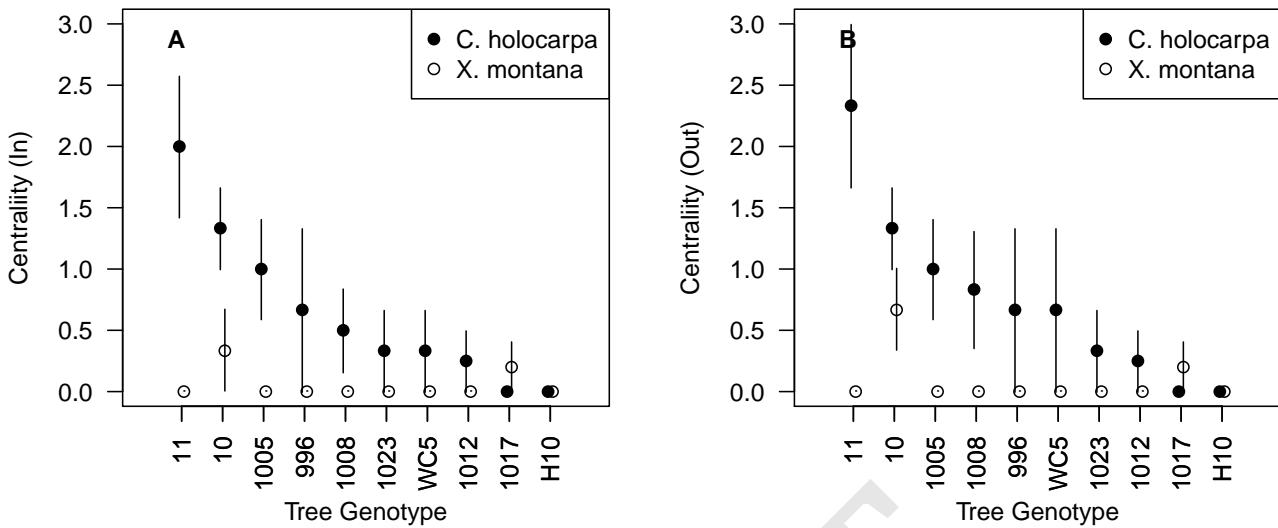
or centralization ( $RLRT = 0.00$ ,  $H^2 = 0.00$ ,  $p\text{-value} = 1.0000$ ), suggesting that the observed relationship between bark roughness and lichen network structure was largely genetically based (Fig. 6).

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1.0000	20850.0933	0.2574	12.9234	0.0101
CT	1.0000	5993.6629	0.0740	3.7150	0.0813
pH	1.0000	1273.1905	0.0157	0.7892	0.3712
CN	1.0000	3896.1754	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

**Table 2. PERMANOVA Pseudo-F Table of lichen network similarity response to bark traits.**

## 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 only trait observed to effect network variation, largely via shifts in positive in-coming and out-going interactions. Bark roughness has been



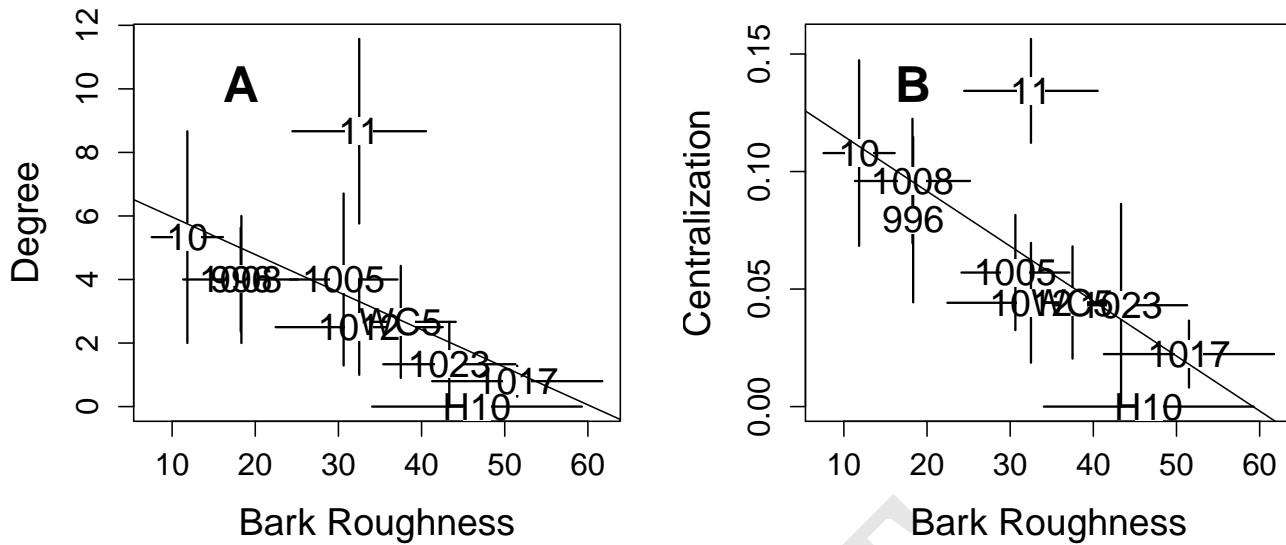
**Fig. 5.** Dot-plots showing the mean (dot) and  $\pm 1$  SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero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

demonstrated previously to be under strong genetic control (41), 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 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.

In the present study, lichen cover, lichen species richness and composition were not responsive to tree genotype, unlike what was found in (16). This is likely, at least in part, the result of differences in sampling method and the choice of genotypes sampled leading to overall higher abundances of observed lichens. In the current study mean % total lichen cover among genotypes ranges from 60-93% cover; whereas the range reported in (16) is 0.86-18.73%. The previous study used a visual estimation method, unlike the current study, which observed lichen at the scale of  $1\text{ cm}^2$  cells, which could over-estimate cover depending on the frequency at which actual thallus size was less than  $1\text{ cm}^2$ . The previous study used samples from both the northern and southern aspects of each tree; whereas, the current study only observed lichen on the northern aspect. Also, our current results are likely different from the previous study because the current study selected genotypes that tended to have bark lichen, with the interest of focusing on generating networks for comparison.



**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.

These differences do not negate the findings of either study but is important to explain the differences in the findings, particularly in the community-level effects of tree genotype.

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.

**Implications for Interspecific Indirect Genetic Effects (IIGEs).** Interspecific indirect genetic effects (IIGE) theory as provided a quantitative framework within which to approach evolutionary theory at higher levels of biological organization: from populations to communities and ecosystems. To date, this theory has focused on modeling the strong effects of foundation species (40, 47), but it has not yet integrated developments in the ecological or evolutionary network theory literature. This is to say that it has not developed a way to examine complex interactions among species; however, previous studies have demonstrated this network context is likely to be important, as altering the structure of interaction networks provides a means for genetic effects to be dampened or magnified within the system of interacting species. For example, (8) showed that the genetics based interactions of aphid resistant and aphid susceptible trees resulted in different interaction networks of their associated arthropod communities composed of 139 species. At the scale of ecosystems, trophic networks or food webs direct

508 and control the rates of energy and nutrient flux (42).  
509 Furthermore, in a predator-prey-plant study, Smith  
510 (23), showed that the interactions among species  
511 across trophic levels depended on plant genotype.  
512 Also, work by (43–45) observed consistent patterns  
513 of centralized interactions of species modules focused  
514 around hubs of plant-fungal interactions. In other  
515 words, a small number of plant and fungal symbionts  
516 tended to have disproportionate numbers of interac-  
517 tions with other species and likely are the drivers  
518 in determining community assembly, structure and  
519 dynamics.

520 The results of the current study of lichen interac-  
521 tion networks provides clear empirical evidence that  
522 networks points to the need to expand IIGEs encom-  
523 pass the structure of interaction networks. Although  
524 such a synthesis necessitates a much greater effort  
525 than can be afforded in this paper, it is possible to  
526 point to several productive pathways forward. In  
527 terms of interaction networks, foundation species are  
528 relatively central within the system of interactions,  
529 that is their direct and/or indirect effects are greater  
530 than other species. So, when the more centralized  
531 (foundation) species have genetically based interac-  
532 tions, genetic effects will tend to be magnified in  
533 the community. Here, we found that even though  
534 more abundant or more centralized (i.e. “impor-  
535 tant”) species were present in the community, their  
536 effects were not the main component responding to  
537 genetic effects. Considering the impact of network  
538 structure (e.g. Nowak 2015) would be a productive  
539 path forward for the theoretical development and  
540 application of the IIGE concept. Previous work has  
541 classified several network structures that can impact  
542 the evolutionary dynamics. Although developed at  
543 the population scale, such theory can apply to com-  
544 munities. This theory provides a means to classify  
545 networks into two general categories, rooted and  
546 cyclic, in which rooted networks have interactions  
547 in which evolutionary effects emanate from one or  
548 multiple origins but these effects do not have con-  
549 nections back to the origins, whereas cyclic networks  
550 contain feedbacks to one or more origins. Although  
551 it did not explicitly define it in this context, the  
552 previous work (?), developed that the structure of  
553 the network in the context of a foundation species,  
554 such as cottonwoods in which there are demonstrable  
555 community level genetic effects, is that of a multi-  
556 ple origin network. This builds on many previous

557 studies demonstrating that the community level ef-  
558 fects vary among multiple genotypes. It is not clear  
559 what potential there is for feedbacks there are to  
560 the origins (e.g. the cottonwood genotypes) from  
561 the community, and as such it cannot be determined  
562 whether these networks are cyclic or rooted. In other  
563 systems, lignicolous lichens can have demonstrable  
564 positive effects on the availability of nutrients for the  
565 trees that they are associated with, but this has not  
566 been measured in the current system. Illucidating  
567 the absence and/or presence and quantifying such  
568 feedbacks would allow for the determination of the  
569 cyclic nature and potential evolutionary dynamics of  
570 this system. The presence of feedbacks would provide  
571 the potential for non-linear dynamics in which evo-  
572 lutionary effects are dampened or amplified by the  
573 struture of the network. For example, a star struc-  
574 ture in which there is a primary or core set of central  
575 species with feedbacks from the radiating species has  
576 been demonstrated to be a structure that amplifies  
577 evolutionary dynamics (?). If such feedbacks do  
578 not exist, and these sub-networks of the lichen and  
579 tree genotypes are likely to be multi-rooted networks.  
580 Such a structure is theorized to generally promote  
581 diversification as variation arising from the shifting  
582 distribution of the “roots”, i.e. genotypes; however,  
583 loss of genotype/root diversity could lead to fixation  
584 of a single genotype in the population and a decrease  
585 in community-wide diversity.

586 *Make a bigger deal of the application of the genetic  
587 similarity rule and more similar genotypes supporting  
588 more similar interaction networks.*

589 There are several important points to consider  
590 with regard to the generalization of the observed  
591 genetically based response of the lichen networks.  
592 Body size and sessile nature of lichen important to  
593 observing genotype responses. As bark lichen  
594 individuals do not move, but grow in a largely two  
595 dimensional plane, these communities and their in-  
596 teractions occur in the highly localized context of  
597 the tree’s bark surface. Lichen individuals are many  
598 orders of magnitude smaller than the tree individual  
599 and the life-span of a tree is many times that of a  
600 lichen. For these reasons, any genetic effects on these  
601 communities is not dampened by the movement of  
602 individuals and the mixing of the effect of different  
603 tree genotypes on the lichen community, as might  
604 occur for more mobile species (e.g. insects and birds).  
605 We only looked at lichen, other species whose distri-

bution, 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.

*Add more text here on positive and negative interactions of lichen from the literature.*

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

*Elaborate on the importance of identifying the species/node level patterns in network structure response to genotype.*

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

*Does bark roughness increase habitat and decrease interactions?*

Bark roughness could possibly be 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* centrality. We did not observe specific microscopic dynamics, such as photobionts, mycobionts, endolichenic fungi and bacteria, but variation in these underlying interactions could also be playing a role. Although we can not rule out the possibility that other unmeasured tree traits or organisms correlated with bark roughness are underlying the observed patterns in bark lichen network structure, substantial research supports the importance of genetically based tree traits for communities and ecosystems (19), and in particular bark roughness for bark lichen communities (16, 31, 41).

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 (46, 47). 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 (30, 48, 49). 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 (50). 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 frequencies 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 result in differences in rates of 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 (5, 51).

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

*Discuss the impacts of *P. betae* removal on net-*

work structure per Lau 2016 and Keith 2017. Also, what about Barbour 2016.

## Other studies that should be discussed:

- 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 (Barbour 2015). Also discuss Lamit 2015 and Holeski's multivarite phenotype paper.
- 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 (Barker 2019).

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837 **Supplementary Materials**

838 **Tables.**

	df	SS	R2	F	p-value
geno	9.0000	44078.1324	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	3.0522	0.3205	0.0343
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.

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1.0000	20850.0933	0.2574	12.9234	0.0101
CT	1.0000	5993.6629	0.0740	3.7150	0.0813
pH	1.0000	1273.1905	0.0157	0.7892	0.3712
CN	1.0000	3896.1754	0.0481	2.4150	0.1890
Residual	32.0000	51627.3270	0.6374		
Total	36.0000	80993.5932	1.0000		

**Table 3.** 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 4. 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 5. 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 6. Pseudo-F Table of lichen community similarity  
PERMANOVA.**

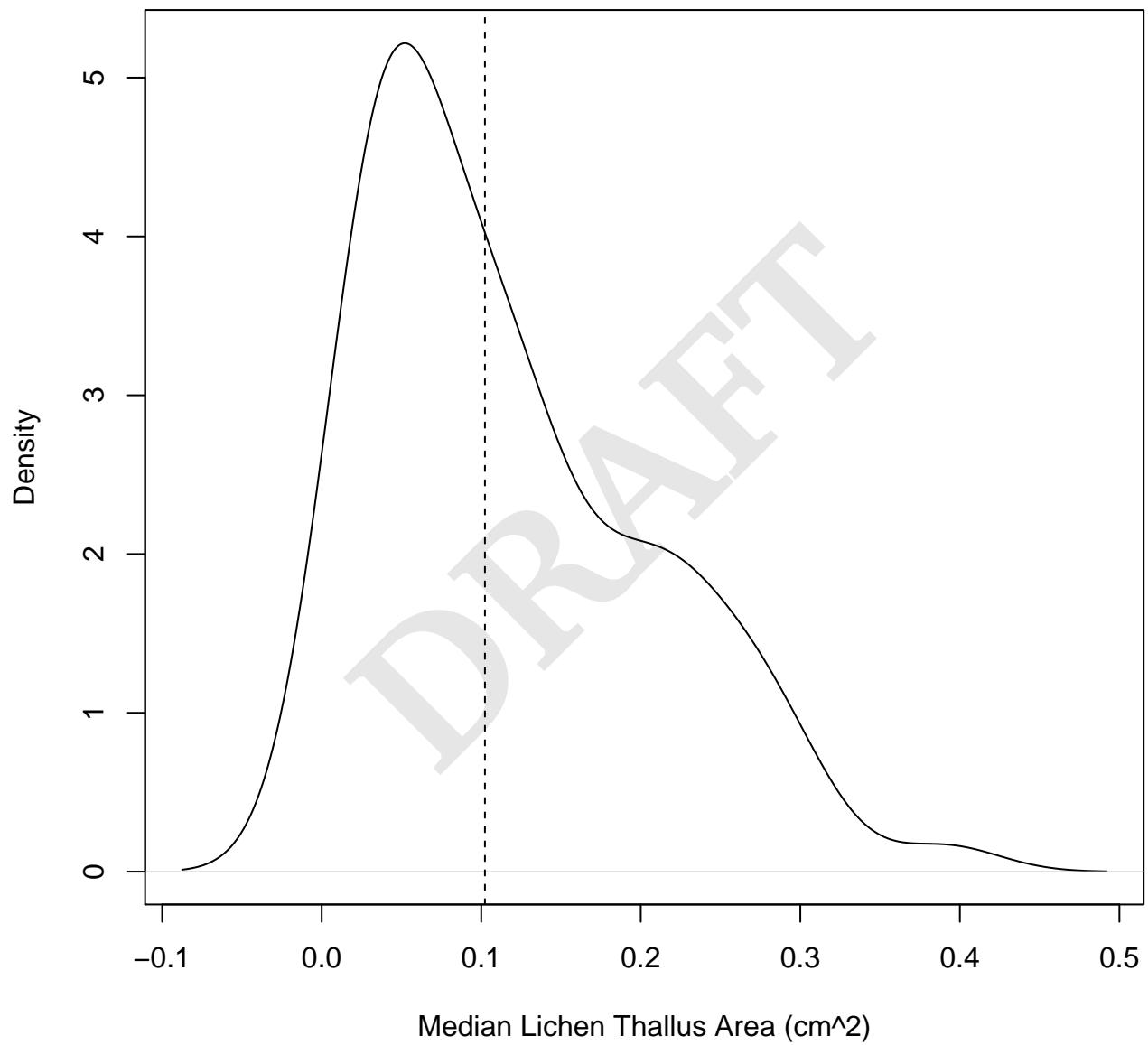
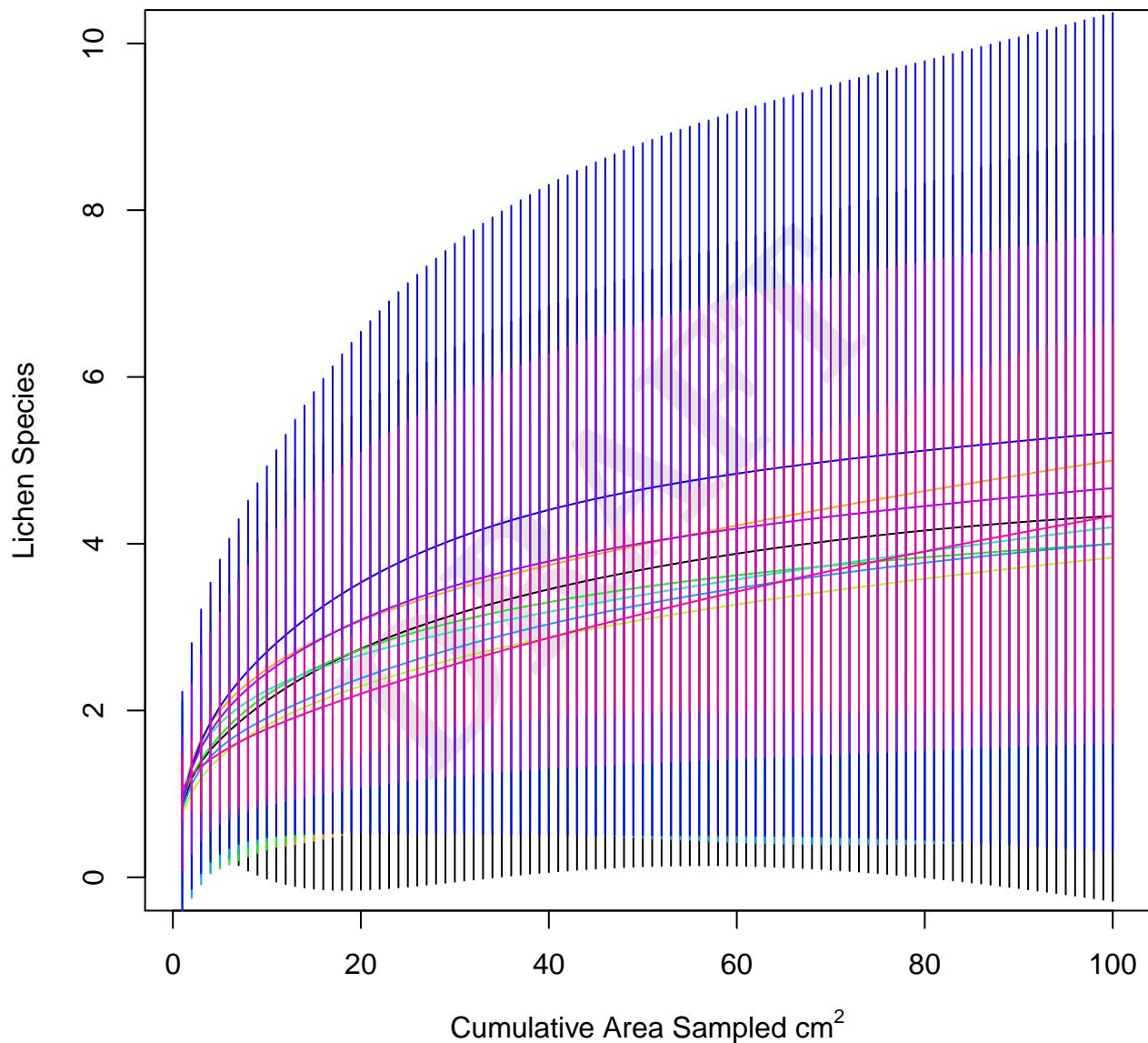


Fig. 1



**Fig. 2.** Species area curve by genotype.

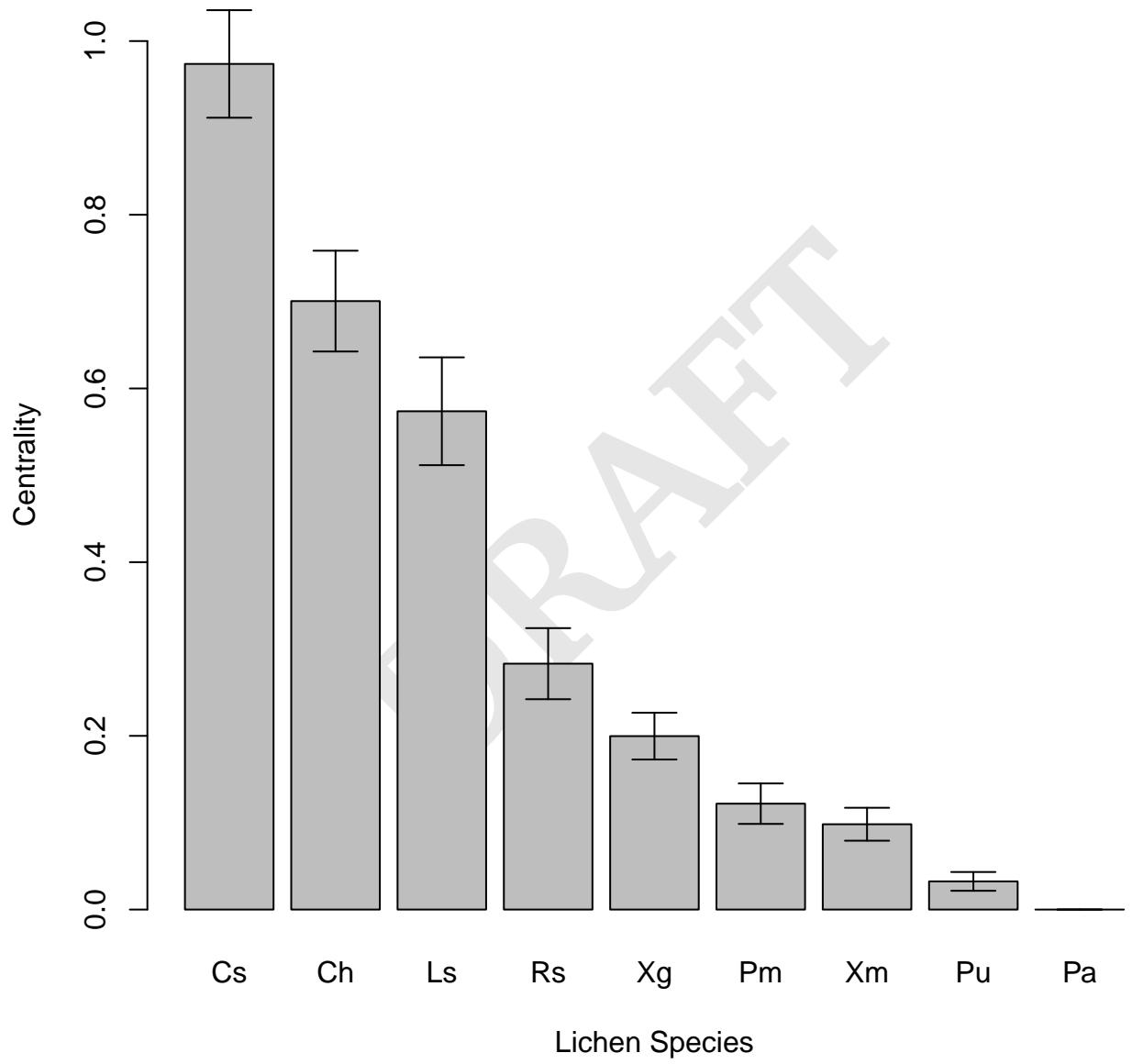


Fig. 3