

Genotypic variation in a foundation tree results in heritable ecological network structure of an associated community

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1 Biological evolution occurs in the context of complex ecosystems
2 of interacting species whereby natural selection defines the structure
3 of ecological networks. Fundamental to understanding evolutionary
4 processes is elucidating the genetic basis to ecological network structure, which is defined by interactions among species. Al-
5 though previous work has demonstrated that genotypic variation in
6 foundation species contributes to interaction network structure, we
7 are not aware of a study that has quantified the genetic contribution
8 to network structure or shown network structure to be a heritable
9 trait. To examine this, in a 20+ year common garden we observed
10 interactions among nine epiphytic lichen species associated with
11 genotypes of (*Populus angustifolia*), a foundation species of ripar-
12 ian ecosystems. We constructed signed, weighted, directed interaction
13 networks for the lichens and conducted genetic analyses of
14 whole network similarity, degree and centralization. We found three
15 primary results. First, using multiple metrics, tree genotype signifi-
16 cantly predicted lichen network structure; i.e., clonal replicates of
17 the same genotype tended to support more similar lichen networks
18 than different genotypes. Second, broad sense heritability estimates
19 show that plant genotype explains network similarity ($H^2 = 0.41$), net-
20 work degree ($H^2 = 0.32$) and network centralization ($H^2 = 0.33$). Third,
21 one of the examined tree traits, bark roughness, was also heritable
22 ($H^2 = 0.32$) and significantly correlated with lichen network similarity
23 ($R^2 = 0.26$), supporting a mechanistic pathway from variation in a her-
24 itable tree trait and the genetically based variation in lichen network
25 structure that selection can act upon. We conclude that tree genotype
26 can influence not only the relative abundances of organisms 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 system-wide stability
29 and resilience and modulating perturbations, these results have im-
30 portant implications for the evolutionary dynamics of ecosystems.
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networks | heritability | community | genetics | lichen | cottonwood |
Populus | common garden

1 Evolution occurs in the context of complex ecolog-
2 ical networks. Community genetics studies have
3 shown that genetic variation in foundation species,
4 which have large effects on communities and ecosystems by modulating and stabilizing local conditions
5 (1), plays a significant role in defining distinct communi-
6 ties of interacting organisms: such as, endophytes,
7 pathogens, lichens, arthropods, and soil microbes (2–

4). Multiple studies have now demonstrated that genetic variation influences numerous functional traits (e.g., phytochemical, phenological, morphological) that in combination results in a multivariate functional trait phenotype (5) in which individual plant genotypes support different communities and ecosystem processes (6, 7). The importance of genetic variation in structuring ecological systems was reviewed
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Significance Statement

Evolution occurs in the context of ecosystems comprised of complex ecological networks. Research at the interface of ecology and evolution has primarily focused on pairwise interactions among species and have rarely included a genetic component to network structure. Here, we used a 20+ year common garden experiment to reveal the effect that genotypic variation can have on networks of lichens that colonize the bark of a foundation tree species. We found that lichen interaction network structure is genetically based and primarily driven by bark roughness. 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 assessing the effect of foundation species genetics on the structure of species interactions that can generate heritable network variation that selection can act upon.

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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(8), and not only were many instances of strong genetic effects found in many ecosystems but the effect of intraspecific variation was at times greater than inter-specific variation. There is now evidence to support that selection, acting on this heritable variation, tends to occur among groups of species (9) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly (10) and species interactions (6, 11, 12), which shape the structure of ecological interaction networks (13–15).

In this community-level evolutionary context, the “genetic similarity rule” provides a useful framework for approaching the nexus of evolutionary and community dynamics in the context of complex interaction networks. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, (16) observed that individuals genotypes that are more genetically similar will tend to have similar phytochemical traits and thus tend to have similar interactions with other species than individuals that are less similar. However, studies in the network ecology literature generally do not include a genetic component (17) and community genetics studies have primarily focused on community composition in terms of the abundance of species (8). Some studies have examined the effects of genetic variation on trophic chains in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (18–22) and generally found that increasing genotypic diversity leads to increased trophic complexity. Only two other studies, that we are aware of, have explicitly examined the effect of genotypic variation on the structure of interaction networks between tree individuals and associated herbivores (23, 24) and both found that genotypic diversity generates increased network modularity (i.e., compartmentalization). However, both of these studies were examining networks at the scale of forest stands, rather than networks associated with individual trees; therefore, neither was able to observe replicated networks in order to statistically test for genetic effects on network structure and quantify the genetic component (i.e. heritable variation) in network structure.

Network theory and evidence from empirical studies in ecology have demonstrated that indirect effects can lead to self-organization, producing sign-changing, amplifying and/or dampening effects (25, 26). The development of interspecific indirect

genetic effects (IIGE) theory (27) in evolutionary biology points to the importance of studying the genetic basis of interaction network structure because genetic based differences in network structure among individuals can be acted upon by natural selection when there are fitness consequences of different networks of IIGEs that can result in community evolution (28). For example, although the analysis was of abundances rather than interaction networks, (29, 30) found that the mycorrhizal communities on the roots of drought tolerant and intolerant trees are dominated by different orders of ectomycorrhizal fungal mutualists that also differ in the benefits they provide that enhance tree performance. Because drought tolerant genotypes are 3x more likely to survive record droughts, selection acts both on the tree and its fungal community and with increased drought the community phenotype has changed over time. Also, in an antagonistic interaction context, (2) found that with the addition of a damaging leaf pathogen to cottonwoods in a common garden, the impacts of these strong interactors results in a different and diminished community of arthropods relative to control trees. Thus, selection acting on the tree may alter the network structure of associated communities in which different networks of communities are most likely to survive pathogen outbreaks. Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative fitness of the tree), selection on tree, community or both can change network structure (28) and thereby alter community dynamics. Evolutionary applications of network theory have demonstrated that indirect effects of interactions among species can lead to network structures that amplify or dampen the effects of selection (31). Networks that form a star-like structure in which there is a central species or core group of species that interact with other, peripheral species, can amplify selection events. Empirically, network analysis of the structure of bipartite (i.e., two-mode) mutualistic networks has shown in multiple cases that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability and resilience to disturbances (32) As such differences in network structure could occur without observable differences in species richness or community composition, which have been the primary focus of almost all previous community

genetics studies. Thus, it is important to quantify how network structure changes in response to genetic variation in order to fully understand evolutionary dynamics in complex communities.

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of tree associated lichen species. Previous studies have examined aspects of networks (33). Here we examine the genetic basis of network structure on a community of sessile lignicolous (i.e., bark) lichens on cottonwood trees. Using a long-term (20+ years), common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic identity. We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (34, 35). In addition, the life-history characteristics of lichens, having highly localized, direct contact interactions and slow population turnover rates, facilitated the assessment of interactions among lichen species on individual trees. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (23, 24, 36, 37). If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks. Applying a probability-theory based network modeling approach, we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks via several network metrics that measures different aspects of network structure at the scale of individual species (i.e., nodes) or the entire network observed on each tree genotype. In particular, we focus the metric of centrality for individual species and centralization for whole networks, which measures how much a species is connected in the network relative to other species. Based on previous community genetics theory, particularly the community similarity rule (16), we hypothesize that trees will co-vary in functional phenotypic traits such as bark roughness and chemical composition and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. This work is important because it provides a mechanistic basis for understanding how community

network theory is intimately associated with the evolutionary process and how human alterations of the environment (e.g., climate change, invasive species, pollution) may have cascading, indirect effects that alter network structure and evolution.

Materials and Methods

Study System. The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled. Bark lichens have been extensively studied in this system and provide an ideal system in which to observe and model lichen interaction networks, as their sessile nature permits accurate identification of individuals (38).

A long-term, common garden experiment was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated with each individual and spatial autocorrelation. Established in 1992, asexually propagated clones of genotyped *P. angustifolia* individuals were obtained from wild collections and planted in fully randomized design at the Ogden Nature Center, Ogden, UT. From the population of established individuals in the common garden, we chose a total of 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 cm² cells arrayed in a checkerboard pattern. Given the small size and sessile nature of lichens, we were able to rapidly assess lichen interactions by quantifying thalli in close contact. Sampling was restricted to the northern aspect of the trunk to maximize the abundance of lichen and control for the effect of trunk aspect. Two adjacent 100 cm² 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 sublivacea*, *Meanelia elegantula*.

The cell size and checkerboard sampling pattern was chosen to isolate the individuals in each cell. In a previous survey of lichen thallus size in this common garden, we had observed a median thallus size of 0.12 ± 0.001 cm² (1

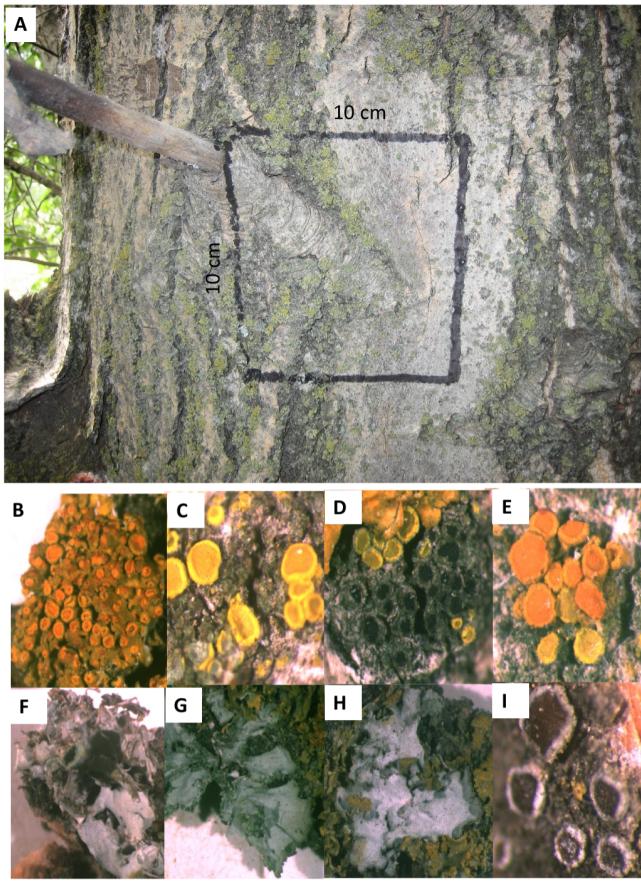


Fig. 1. The communities of bark lichens were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). (A) Lichens were sampled within a fixed area (100 cm^2) on individual trees at two heights, 50cm and 95cm from the ground. (B-I) Close-up photos show the other lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Physciella melanachra*, *Physcia undulata* and *Lecanora hagenii*. Photo Credits: L.J. Lamit (B-D) and R.R. Naesbourn (E-I).

ated 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 (40). 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 $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected frequency of co-occurrences $E(S_i S_j)$ is the total number of cells surveyed (N) times the independent probabilities of each species $P(S_i) * P(S_j)$, $Z_{95\%}$ is the Z-score for 95% from a Z-distribution and the expected variance of $E(S_i S_j)$ is the total number of cells times the expected probability of $S_i S_j$ and its compliment (i.e. $V(S_i S_j) = N * E[P(S_i, S_j)] * (1 - E[P(S_i, S_j)])$). If the observed number of co-occurrence falls outside of the confidence interval, the joint probability $P(S_i, S_j)$ is determined to be equal to the product of the individual probabilities (i.e. $P(S_i)P(S_j)$), and the conditional probability reduces to the individual probability of that species $P(S_i)$. Therefore, unless the co-occurrence of a species pair falls outside the confidence interval, the probability that the observation of one species given the other is no different than simply observing that species alone. This enables us to remove links from a given network by re-scaling the resulting conditional probabilities by subtracting the individual probabilities from the conditional probabilities (i.e. how different the conditional probability is from the independent probability), which makes any species with a non-significant conditional probability zero. The resulting matrix ($D = D_{ij}$) 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 (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.

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 (39) 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 gener-

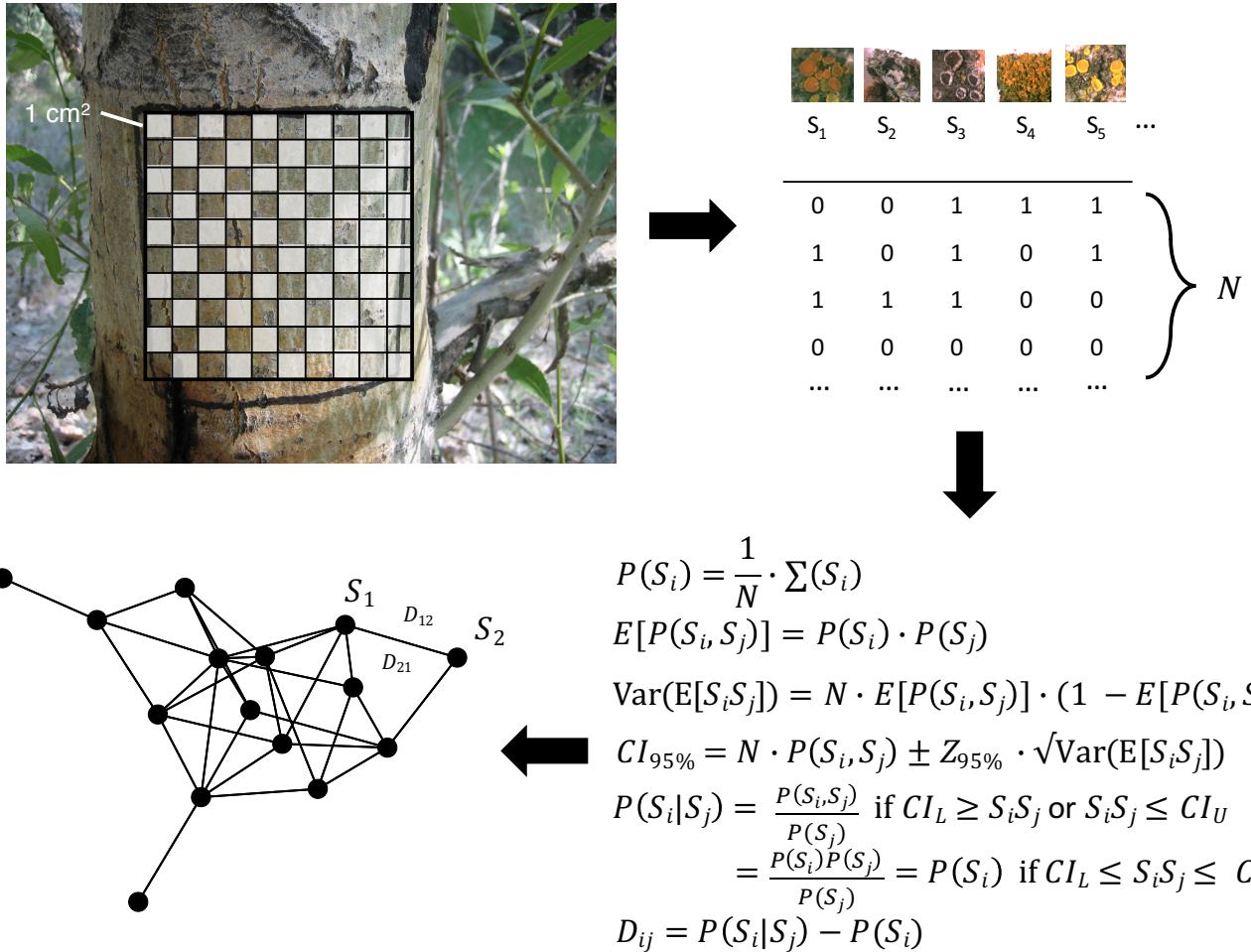


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 100 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (40), 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.

species) in each network, we calculated both the degree and the Freeman’s centrality (41). 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, 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. To calculate separate metrics for positive and negative links, we applied methods for calculating the centrality accounting for the sign differences (42) using the **signnet** package (43).

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

324 Mantel tests. To quantify the similarity of lichen net-
 325 works among individual trees, we calculated the pairwise
 326 Euclidean distance of the **D** interaction matrices among
 327 all pairs of trees.

328 For visualization of multivariate patterns, we used
 329 Non-metric Multi-Dimensional Scaling (NMDS) (44) to
 330 produce dimensionally reduced ordinations of these multi-
 331 variate responses and fitted vectors for continuous predictor
 332 variables to the ordinated values (45). Using random
 333 initial configurations with a maximum of 500 iterations
 334 and a change in stress threshold of less than 10^{-12} . Final
 335 configurations has the lowest stress with at most a stress
 336 level of 0.10.

337 For each network, we also calculated metrics that mea-
 338 sure different structural aspects. Although there are many
 339 other metrics, for the sake of simplicity we focus on a
 340 subset that represent several interesting features of net-
 341 work structure (see (17)). We calculated the number of
 342 interactions or “links” in each network, which provides a
 343 measure of the size of the network (23, 46). We also calcu-
 344 lated the centralization of each network, which measures
 345 the evenness of the distribution of interactions among
 346 the species in the network (41). In a network with a
 347 low level of centralization species have similar amount of
 348 interaction in the network, while a network with a high
 349 level of centralization tends to have one or small number
 350 of species that interact with other species. We used a
 351 related function to calculate the centrality of each species
 352 (i.e. node level centrality) in each network as well.

353 For all tests where genotype was used as a predictor,
 354 we quantified the heritability of the response variable. Be-
 355 cause the trees in the garden were clonal replicates of each
 356 genotype, we calculated broad-sense heritability, which
 357 is the genotypic variance divided by the total phenotypic
 358 variance (47). This can be interpreted as a measure of
 359 the phenotypic variance due to genotypic variation. We
 360 also apply this to the community genetics context as the
 361 variance in *extended* phenotypic variance due to genotypic
 362 variation (48). For the multivariate analyses, where we
 363 employ PERMANOVA, we followed the methods of (27)
 364 to adjust the degrees of freedom for unbalanced genotype
 365 replicates.

366 All code and data for the project are openly avail-
 367 able online. Code and data are available at [github.com/
 368 ecgen/comgen](https://github.com/ecgen/comgen). The project is also archived via Zenodo
 369 at zenodo.com/doi/XXXXXX. All analyses were conducted
 370 using the programming language R version 3.6.1 (R De-
 371 velopment Core Team 2019).

372 Results

373 Tree genotype influenced lichen network structure
 374 and multiple lichen network metrics were herita-
 375 ble. Tree genotype significantly predicted the struc-
 376 tural similarity of lichen networks (PERMANOVA:
 377 Pseudo- $F_{9,27} = 3.58$, $H^2 = 0.41$, $p\text{-value} = 0.0537$)

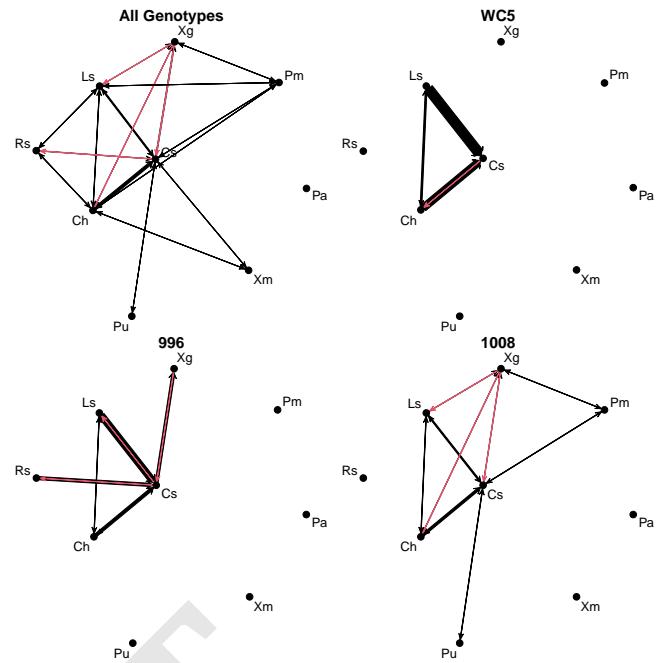


Fig. 3. Lichen networks varied in structure among tree genotypes. Network diagrams of the mean lichen interaction matrices averaged for all trees and for several individual genotypes (996, WC5 and 1008) showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, 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.

(Fig. 4). Overall network level metrics responded
 378 significantly to tree genotype (Table 1), including net-
 379 work degree ($RLRT = 3.52$, $H^2 = 0.32$, $p\text{-value} =$
 380 0.0255) and centralization including both in-coming
 381 and out-going links ($RLRT = 4.04$, $H^2 = 0.33$, $p\text{-value} =$
 382 0.0184) or when separated into in-coming
 383 only ($RLRT = 3.9852$, $H^2 = 0.3309$, $p\text{-value} =$
 384 0.0190) or out-going only ($RLRT = 3.8615$, $H^2 =$
 385 0.3193, $p\text{-value} = 0.0205$). Metrics including only
 386 positive links also showed a significant effect of tree
 387 genotype, including positive degree ($RLRT = 3.6925$,
 388 $H^2 = 0.3242$, $p\text{-value} = 0.0229$), positive in-going
 389 centralization ($RLRT = 4.4812$, $H^2 = 0.3487$, $p\text{-value} =$
 390 0.0142). Metrics calculated with negative
 391 links were not significant, including degree (negative)
 392 ($RLRT = 0.0327$, $H^2 = 0.0318$, $p\text{-value} = 0.3859$)
 393 and both in-coming (negative) ($RLRT = 0.3304$, $H^2 =$
 394 0.1057, $p\text{-value} = 0.2508$) and out-going centraliza-
 395 tion (negative) ($RLRT = 0.0862$, $H^2 = 0.0513$,
 396 $p\text{-value} = 0.3446$).

The genetic response of network centralization was
 397 driven by variation in *Caloplaca holocarpa*. Central-
 398

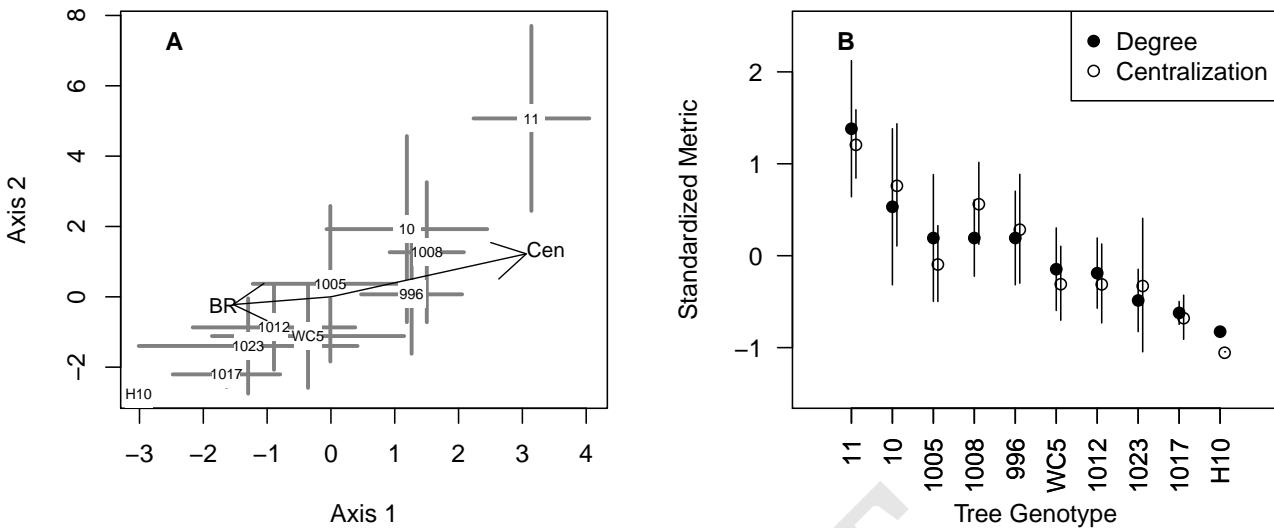


Fig. 4. The similarity of lichen networks varied among tree genotypes. A. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.008) lichen network similarity (± 1 S.E.). Genotype centroids that are closer together tend to have more similar lichen network structure. Arrows showing the direction (arrowhead) and magnitude (length) of the vectors of correlation between bark roughness (BR) and network centralization (Cen) and the ordinated network similarity. 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.

response	df	statistic	H2	p-value
Lichen Network Similarity	9	3.5821	0.41	0.0537
Degree		3.5175	0.32	0.0255
Degree (positive)		3.6925	0.32	0.0229
Degree (negative)		0.0327	0.03	0.3859
Centralization		4.0444	0.33	0.0184
Centralization In-Degree		4.4812	0.35	0.0142
Centralization In-Degree (positive)		3.9852	0.33	0.0190
Centralization In-Degree (negative)		0.3304	0.11	0.2508
Centralization Out-Degree		3.8615	0.32	0.0205
Centralization Out-Degree (positive)		3.5585	0.31	0.0248
Centralization Out-Degree (negative)		0.0862	0.05	0.3446

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

of *X. montana* ($RLRT = 2.92$, $H^2 = 0.32$, *p*-value = 412
 0.0375); however, the centrality of *X. montana* was 413
 much lower overall relative to *C. holocarpa* and the 414
 variation in *X. montana* centrality was restricted to 415
 two genotypes (Fig. 5). 416

Add transformations of variables to methods.

Genotype indirectly influenced lichen network centralization via the genetically based variation in bark roughness. The percent cover of rough bark ($RLRT = 4.8526$, $H^2 = 0.3221$, *p*-value = 0.0113) and condensed tannins ($RLRT = 3.0522$, $H^2 = 0.3205$, *p*-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*-value = 1.0000) or carbon-nitrogen ratio ($RLRT = 0.0000$, $H^2 = 0.0000$, *p*-value = 1.0000), showed a significant response to tree genotype and none other than bark roughness was correlated with network similarity (Table 2); therefore, we focused our subsequent analyses on the indirect effect of genotype on lichen network structure via bark roughness. We found that bark roughness was significantly correlated with network similarity (PERMANOVA: Pseudo- $F_{1,32} = 13.029$, $R^2 = 0.26$, *p*-value = 0.0096) and other lichen network metrics, including negative correlations with

400 ity varied significantly among species ($F_{8,324} = 7.99$,
 401 $R^2 = 0.16$, *p*-value < 0.0001). *Caloplaca holocarpa*
 402 centrality was the main species to exhibit a signifi-
 403 cant response to tree genotype in terms of positive
 404 centrality for both the in-coming ($RLRT = 3.61$, H^2
 405 = 0.32, *p*-value = 0.0240) and out-going ($RLRT =$
 406 3.13, $H^2 = 0.30$, *p*-value = 0.0327) perspectives, but
 407 not for either negative centrality metrics in-coming
 408 ($RLRT = 0$, $H^2 = 0$, *p*-value = 1) or out-going
 409 ($RLRT = 0$, $H^2 = 0$, *p*-value = 0.4543). None of
 410 the other species' centralities showed a genotypic re-
 411 sponse (Supplementary Table 3) with the exception

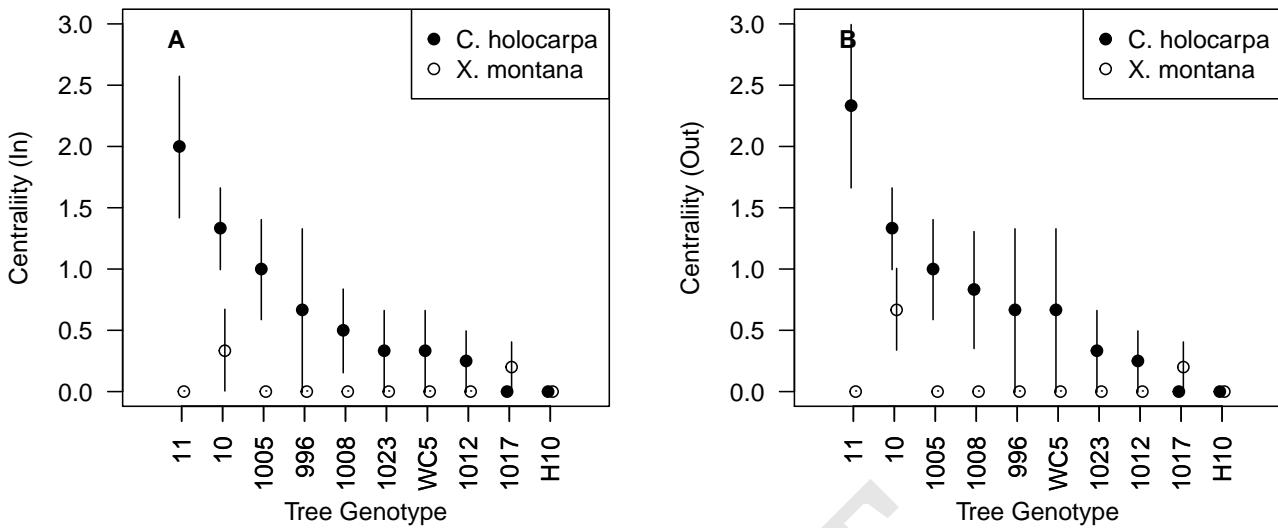


Fig. 5. Dot-plots showing the mean (dot) and ± 1 SE of in-degree (A) and out-degree (B) centrality for two species, *C. holocarpa* and *X. montana*. *Caloplaca holocarpa* centrality was highly variable among genotypes. *Xanthomendoza montana* centrality, both in- and out-degree, was only non-zero for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

437 overall network degree ($df = 35$, $t = -2.13$, $r = -0.34$,
 438 $p\text{-value} = 0.04$) and centralization ($df = 35$, $t = -2.52$,
 439 $r = -0.39$, $p\text{-value} = 0.02$). In other words, trees with
 440 more similar levels of bark roughness tended to have
 441 lichen interaction networks with similar structure.
 442 To quantify the genetic bases of this effect of bark
 443 roughness on network structure, we used the residual
 444 values from regressions of network degree and cen-
 445 tralization in tests of the effect of tree genotype and
 446 found no significant effect of tree genotype for either
 447 degree ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value} = 1.0000$)
 448 or centralization ($RLRT = 0.00$, $H^2 = 0.00$, $p\text{-value}$
 449 = 1.0000), suggesting that the observed relationship
 450 between bark roughness and lichen network structure
 451 was largely genetically based (Fig. 6).

Discussion

- Revisit the community similarity rule. 452
- Add more text here on positive and negative 453 interactions of lichen from the literature, lichen 454 could fix nitrogen 455
- Elaborate on how many species might be sup- 456 ported by each lichen thallus including the sym- 457 bionts and other species. 458
- Elaborate on the importance of identifying the 459 species/node level patterns in network structure 460
- What is the relationship between tree growth, 461 bark roughness and disruption of the lichen com- 462 munity? Tree grow and the bark expands over 463 time, causing furrows. 464
- Does bark roughness increase habitat and de- 465 crease interactions? 466
- Differences in network structure could occur 467 without observable differences in species richness 468 or community composition 469
- Discuss the recent meta-analysis of plant traits 470 and ecosystem property prediction (Nature 471 2020?) 472

	df	SumOfSqs	R2	F	Pr(>F)
Bark Roughness	1	20850.09	0.26	12.9234	0.0101
Condensed Tannins	1	5993.66	0.07	3.7150	0.0813
pH	1	1273.19	0.02	0.7892	0.3712
Carbon:Nitrogen Ratio	1	3896.18	0.05	2.4150	0.1890
Residual	32	51627.33	0.64		
Total	36	80993.59	1.00		

Table 2. PERMANOVA Pseudo-F Table of lichen net- 473 work similarity response to bark traits.

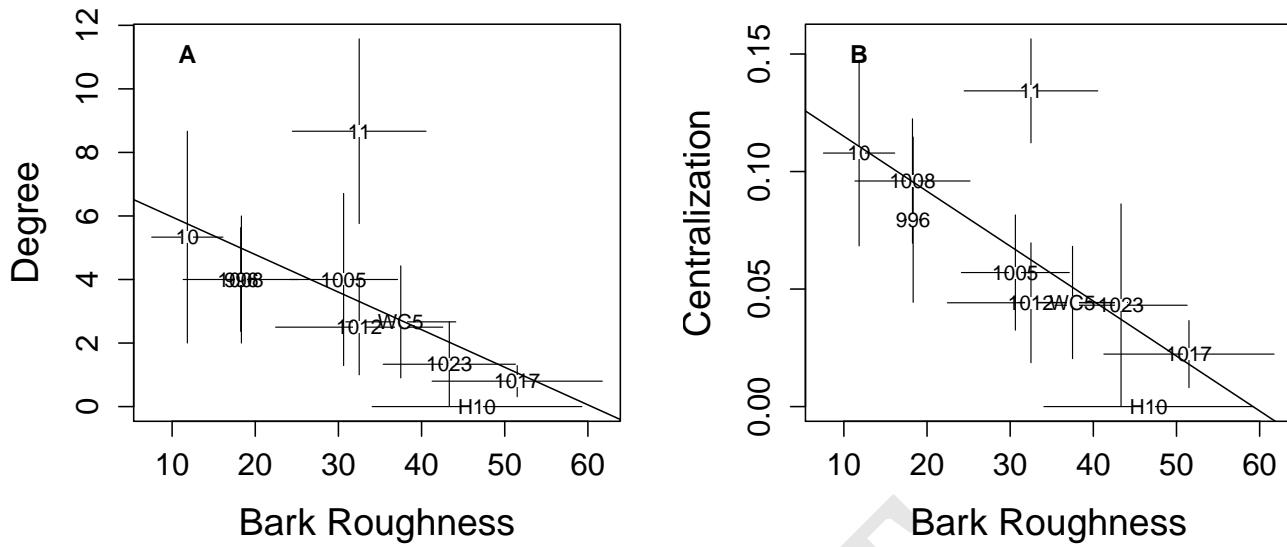


Fig. 6. Bivariate plots of the negative relationship between bark roughness and two network metrics: A) degree and B) centralization. Each plot displays the genotype mean (± 1 S.E.) for both variables and a least-squares regression line calculated using the genotype means. Generally, as roughness increased the number of interactions (degree) and dominance of those interactions decreased.

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 demonstrated previously to be under strong genetic control (49), and bark roughness has also previously been shown to be an important tree trait influencing bark lichens (39); 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.

Heritability of Interaction Network Structure. 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.

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

528 two genotypes that support lichen communities that
529 are similar in total abundances of each species but
530 differ in terms of the structure. Extensions of game
531 theory to evolutionary biology have demonstrated
532 that network structure can lead to variation in evo-
533 lutionary dynamics. Some structures tend toward
534 dominance and dampening of selection, while others
535 lead to amplification of selection (Newman). One
536 class of networks that are theorized to have amplifying
537 effects on networks have "star" shapes with one or
538 a few species at the center and radiating interactions
539 out from the central core (Leiberman). This is struc-
540 turally what we have observed with the networks that
541 tend to occur on some of the genotypes in our study,
542 i.e. the more centralized networks. It is possible that
543 these more centralized networks could function as
544 hot-spots of evolutionary dynamics resulting from
545 the amplifying effect the network structure fostered
546 on that tree genotype.

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

570 Bark roughness could possibly be serving the role
571 that other lichen play in facilitating the success of
572 new propagule attachment and the growth of estab-
573 lishing thalli. This is supported by the patterns over-
574 all being positive, including *C. holocarpa* centrality.
575 We did not observe specific microscopic dynamics,
576 such as photobionts, mycobionts, endolichenic fungi²⁵

577 and bacteria, but variation in these underlying in-
578 teractions could also be playing a role. Although we
579 can not rule out the possibility that other unmea-
580 sured tree traits or organisms correlated with bark
581 roughness are underlying the observed patterns in
582 bark lichen network structure, substantial research
583 supports the importance of genetically based tree
584 traits for communities and ecosystems (8), and in
585 particular bark roughness for bark lichen communi-
586 ties (38, 39, 49).

587 In the present study, lichen cover, lichen species
588 richness and composition were not responsive to tree
589 genotype, unlike what was found in (39). This is
590 likely, at least in part, the result of differences in
591 sampling method and the choice of genotypes sam-
592 pled leading to overall higher abundances of observed
593 lichens. In the current study mean % total lichen
594 cover among genotypes ranges from 60-93% cover;
595 whereas the range reported in (39) is 0.86-18.73%.
596 The previous study used a visual estimation method,
597 unlike the current study, which observed lichen at
598 the scale of 1 cm² cells, which could over-estimate
599 cover depending on the frequency at which actual
600 thallus size was less than 1 cm². The previous study
601 used samples from both the northern and southern
602 aspects of each tree; whereas, the current study only
603 observed lichen on the northern aspect. Also, our
604 current results are likely different from the previous
605 study because the current study selected genotypes
606 that tended to have bark lichen, with the interest
607 of focusing on generating networks for comparison.
608 These differences do not negate the findings of either
609 study but is important to explain the differences
610 in the findings, particularly in the community-level
611 effects of tree genotype.

612 **Implications for Interspecific Indirect Genetic Ef-
613 fects (IIGEs).** Initially, evolution in a community
614 context was focused on examples of highly co-evolved
615 pairs of species (e.g. Darwin's famous prediction
616 of the Sphinx Moth and Christmas Orchid) (9).
617 However, studies of diffuse co-evolution (*sensu* (50))
618 (51, 52), geographic mosaics of co-evolution (36) and
619 community genetics (11) have provided an in-road
620 for ecological network approaches (21, 24, 53) to illu-
621 minate a more complex perspective of the interface
622 between ecological and evolutionary dynamics.

623 Interspecific indirect genetic effects (IIGE) theory
624 as provided a quantitative framework within which
625 to approach evolutionary theory at higher levels of

626 biological organization: from populations to com-
627 munities and ecosystems. To date, this theory has
628 focused on modeling the strong effects of foundation
629 species (7, 27), but it has not yet integrated devel-
630 opments in the ecological or evolutionary network
631 theory literature. This is to say that it has not devel-
632 oped a way to examine complex interactions among
633 species; however, previous studies have demonstrated
634 this network context is likely to be important, as
635 altering the structure of interaction networks pro-
636 vides a means for genetic effects to be damped or
637 magnified within the system of interacting species.
638 For example, (24) showed that the genetics based
639 interactions of aphid resistant and aphid suscepti-
640 ble trees resulted in different interaction networks of
641 their associated arthropod communities composed
642 of 139 species. At the scale of ecosystems, trophic
643 networks or food webs direct and control the rates
644 of energy and nutrient flux (54). Furthermore, in a
645 predator-prey-plant study, Smith (20), showed that
646 the interactions among species across trophic levels
647 depended on plant genotype. Also, work by (55–57)
648 observed consistent patterns of centralized interac-
649 tions of species modules focused around hubs of
650 plant-fungal interactions. In other words, a small
651 number of plant and fungal symbionts tended to
652 have disproportionate numbers of interactions with
653 other species and likely are the drivers in determining
654 community assembly, structure and dynamics.

655 The results of the current study provides clear em-
656 prical evidence that networks points to the need to
657 expand IIGEs encompass the structure of interaction
658 networks. Although such a synthesis necessitates
659 a much greater effort than can be afforded in this
660 paper, it is possible to point to several productive
661 pathways forward. In terms of interaction networks,
662 foundation species are relatively central within the
663 system of interactions, that is their direct and/or
664 indirect effects are greater than other species. So,
665 when the more centralized (foundation) species have
666 genetically based interactions, genetic effects will
667 tend to be magnified in the community. Here, we
668 found that even though more abundant or more cen-
669 tralized (i.e. “important”) species were present in
670 the community, their effects were not the main com-
671 ponent responding to genetic effects. Considering
672 the impact of network structure would be a produc-
673 tive path forward for the theoretical development
674 and application of the IIGE concept.

With regard to the evolutionary implications of
network structure, ecological network studies have
focused on asymmetry and the quantification of
its structure in communities, with qualitative dis-
cussion of the impacts on evolutionary dynamics
(36, 37, 58, 59). More specific predictions, with a
quantitative framework, can be found in applications
of evolutionary game theory, and although developed
at the population scale, such theory can apply to
communities. One seemingly useful direction from
evolutionary network developments from game the-
ory is the classification of networks into two general
categories, rooted and cyclic, in which rooted net-
works have interactions in which evolutionary effects
emanate from one or multiple origins but these effects
do not have connections back to the origins, whereas
cyclic networks contain feedbacks to one or more ori-
gins. Although it did not explicitly define it in this
context, the previous work (17), developed that the
structure of the network in the context of a founda-
tion species, such as cottonwoods in which there are
demonstrable community level genetic effects, is that
of a multiple origin network. This builds on many
previous studies demonstrating that the community
level effects vary among multiple genotypes. It is not
clear what potential there is for feedbacks there are
to the origins (e.g. the cottonwood genotypes) from
the community, and as such it cannot be determined
whether these networks are cyclic or rooted. In other
systems, lignicolous lichens can have demonstrable
positive effects on the availability of nutrients for the
trees that they are associated with, but this has not
been measured in the current system. Illucidating
the absence and/or presence and quantifying such
feedbacks would allow for the determination of the
cyclic nature and potential evolutionary dynamics of
this system. The presence of feedbacks would provide
the potential for non-linear dynamics in which evo-
lutionary effects are damped or amplified by the
structure of the network. For example, a star struc-
ture in which there is a primary or core set of central
species with feedbacks from the radiating species has
been demonstrated to be a structure that amplifies
evolutionary dynamics (31). If such feedbacks do
not exist, and these sub-networks of the lichen and
tree genotypes are likely to be multi-rooted networks.
Such a structure is theorized to generally promote
diversification as variation arising from the shifting
distribution of the “roots”, i.e. genotypes; however,

724 loss of genotype/root diversity could lead to fixation
725 of a single genotype in the population and a decrease
726 in community-wide diversity.

727 **Conclusion.** Although our study was conducted with
728 a community of lichens, these results should be gen-
729 eralized to other groups of diverse organisms around
730 the world that also exhibit significant genetic signals
731 at the community level (7, 60). In the face of the
732 high degree of complexity and potential context de-
733 pendence of ecological processes, the current study
734 points to the utility of considering the spatial and
735 temporal scales of interactions, as discussed to some
736 in previous studies (16, 61, 62). In the present study,
737 we found that community assembly processes, such
738 as environmental filtering and species interactions,
739 are genetically based. This is likely due, in part,
740 to the large difference in the differences in size and
741 longevity of the lichen and cottonwood individuals
742 with the trees determining the environment in which
743 the lichen occur. We suggest that future work would
744 be aided by determining these modules within the
745 biotic community that include species with similar
746 differences in body-size and time-scales. As heritable
747 variation is the raw material for natural selection
748 to act upon, a genetic basis for interaction network
749 structure indicates evolutionary dynamics should be
750 considered at the community level and that con-
751 serving genetic variation is important to consider in
752 efforts to restore or preserve complex species inter-
753 actions and their associated ecosystem functions (63).
754 With such findings, it appears that we are closer to
755 understanding the evolutionary drivers of Darwin's
756 entangled bank and the interconnectedness of species
757 in complex communities.

758 Future work should consider the potential influ-
759 ence on evolutionary dynamics of the associated com-
760 munities. The network of interactions of species that
761 are strongly influenced by a foundation species, could
762 amplify the effects of genotype, this serves as a means
763 for genetic effects to increase rather than diffuse
764 through an ecosystem either through space or over
765 time, as has been proposed in the construction of the
766 genetic diffusion hypothesis. Altered abundances can
767 lead to differences in interactions. Genotype effects
768 on abundances of individual abundances may cancel
769 out. Specifically for asexually reproducing species,
770 such as many lichen are, shifting interaction frequen-
771 cies could lead to evolutionary outcomes, given the
772 potential to take-up symbionts and genetic material

from thalli that they come into contact with. Alter-
773 ing interaction frequencies could result in differences
774 in rates of the exchange of genetic materials among
775 lichen that could then be passed on to vegetative
776 and possibly sexually produced reproductive propa-
777 gules. The larger scale (stand or region) effects of
778 these "evolutionary units" on each tree would de-
780 pend on the connectivity and rate of movement of
781 propagules among trees per the geographic mosaic
782 of co-evolution hypothesis (3, 36).

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1. Ellison AM, et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9):479–486.
2. Busby PE, et al. (2015) Genetics-based interactions among plants, pathogens, and herbivores define arthropod community structure. *Ecology* 96(7):1974–1984.
3. Barbour RC, et al. (2009) A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* 90(7):1762–1772.
4. Lamit LJ, et al. (2015) Tree genotype mediates covariance among communities from microbes to lichens and arthropods. *Journal of Ecology* 103(4):840–850.
5. Holeski LM, Hillstrom ML, Whitham TG, Lindroth RL (2012) Relative importance of genetic, ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype in a foundation tree species. *Oecologia* 170:695–707.
6. Bailey JK, et al. (2009) From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 364(1523):1607–16.
7. Whitham TG, et al. (2012) Community specificity: Life and afterlife effects of genes.
8. Des Roches S, et al. (2018) The ecological importance of intraspecific variation. *Nature Ecology and Evolution* 2(1):57–64.
9. Wade MJ (2007) The co-evolutionary genetics of ecological communities.
10. Crutsinger GM (2016) A community genetics perspective: Opportunities for the coming decade. *New Phytologist*.
11. Whitham TG, et al. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature reviews. Genetics* 7:510–523.
12. Moya-Laraño J (2011) Genetic variation, predator-prey interactions and food web structure. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 366(1569):1425–37.
13. Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J (2007) Non-random co-extinctions in phylogenetically structured mutualistic networks. *Nature* 448(7156):925–8.
14. Guimarães PR, et al. (2007) Interaction Intimacy Affects Structure and Coevolutionary Dynamics in Mutualistic Networks. *Current Biology* 17(20):1797–1803.
15. Gómez JM, Abdellaziz M, Camacho JPM, Muñoz-Pajares AJ, Perfectti F (2009) Local adaptation and maladaptation to pollinators in a generalist geographic mosaic. *Ecology Letters* 12(7):672–682.
16. Bangert RK, et al. (2006) A genetic similarity rule determines arthropod community structure. *Molecular ecology* 15:1379–1391.
17. Lau MK, Borrett SR, Baiser B, Gotelli NJ, Ellison AM (2017) Ecological network metrics: opportunities for synthesis. *Ecosphere* 8(8):e01900.
18. Bailey JK, Wooley SC, Lindroth RL, Whitham TG (2005) Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters* 8(0):051122062725008.
19. Johnson MTJ (2008) Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology*.
20. Smith DS, Bailey JK, Shuster SM, Whitham TG (2011) A geographic mosaic of trophic interactions and selection: trees, aphids and birds. *Journal of evolutionary biology* 24(2):422–9.
21. Smith DS, et al. (2015) Introduced elk alter traits of a native plant and its plant-associated arthropod community. *Acta Oecologica* 67:8–16.
22. Barbour MA, et al. (2016) Genetic specificity of a plant-insect food web: Implications for linking genetic variation to network complexity. *Proceedings of the National Academy of Sciences of the United States of America* 113(8):2128–2133.
23. Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG (2015) Genotypic variation in foundation species generates network structure that may drive community dynamics and evolution. *Ecology* 97(3):15–0600.
24. Keith AR, Bailey JK, Lau MK, Whitham TG (2017) Genetics-based interactions of foundation species affect community diversity, stability and network structure. *Proceedings of the Royal Society B: Biological Sciences* 284(1854):20162703.

Supplementary Materials

Tables.

- 844 25. Newman MEJ (2006) Modularity and community structure in networks. *Proceedings of the
845 National Academy of Sciences of the United States of America* 103(23):8577–82.
846 26. Sole R, Bascompte J (2006) *Self-Organization in Complex Ecosystems*. (Princeton University
847 Press, Princeton, N.J.).
848 27. Shuster SM, Lonsdorf EV, Wimp GM, Bailey JK, Whitham TG (2006) COMMUNITY HERI-
849 TABILITY MEASURES THE EVOLUTIONARY CONSEQUENCES OF INDIRECT GENETIC
850 EFFECTS ON COMMUNITY STRUCTURE. *Evolution* 60(5):991.
851 28. Whitham TG, Allan GJ, Cooper HF, Shuster SM (2020) Intraspecific Genetic Variation and
852 Species Interactions Contribute to Community Evolution. *Annual Review of Ecology, Evolution,
853 and Systematics* 51(1).
854 29. Gehring C, et al. (2014) Plant genetics and interspecific competitive interactions deter-
855 mine ectomycorrhizal fungal community responses to climate change. *Molecular Ecology*
856 23(6):1379–1391.
857 30. Gehring CA, Stihlitz CM, Flores-Renteria L, Whipple AV, Whitham TG (2017) Tree genetics
858 defines fungal partner communities that may confer drought tolerance. *Proceedings of the
859 National Academy of Sciences*.
860 31. Lieberman E, Hauert C, Nowak MA (2005) Evolutionary dynamics on graphs. *Nature*
861 433(7023):312–316.
862 32. Rohr RP, Saavedra S, Bascompte J (2014) On the structural stability of mutualistic systems.
863 *Science* 345(6195).
864 33. Barbour MA, et al. (2019) Trait plasticity is more important than genetic variation in determin-
865 ing species richness of associated communities. *Journal of Ecology* 107(1):350–360.
866 34. Winfree R, Gross BJ, Kremen C (2011) Valuing pollination services to agriculture. *Ecological
867 Economics* 71:80–88.
868 35. Zytnyska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree
869 species influences the associated epiphytic plant and invertebrate communities in a com-
870 plex forest ecosystem. *Philosophical transactions of the Royal Society of London. Series B,
871 Biological sciences* 366:1329–1336.
872 36. Thompson JN (2013) *Relentless Evolution*. (University of Chicago Press), p. 499.
873 37. Bascompte J, Jordano P, Olesen JM (2006) Asymmetric Coevolutionary Networks Facilitate
874 Biodiversity Maintenance<10.1126/science.1123412. *Science* 312:431–433.
875 38. Lamit L, et al. (2011) Genetically-based trait variation within a foundation tree species influ-
876 ences a dominant bark lichen. *Fungal Ecology* 4(1):103–109.
877 39. Lamit LJ, et al. (2015) Genotype variation in bark texture drives lichen community assembly
878 across multiple environments. *Ecology* 96(4):960–971.
879 40. Araújo MB, Rozenfeld A, Rahbek C, Marquet PA (2011) Using species co-occurrence net-
880 works to assess the impacts of climate change. *Ecography* 34:897–908.
881 41. Butts CT (2019) *sna: Tools for Social Network Analysis*. R package version 2.5.
882 42. Everett MG, Borgatti SP (2014) Networks containing negative ties. *Social Networks*
883 38(1):111–120.
884 43. Schoch D (2020) *signnet: An R package to analyze signed networks*.
885 44. Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological
886 data. *Journal of Statistical Software* 22(7):1–19.
887 45. Oksanen J, et al. (2019) *vegan: Community Ecology Package*. R package version 2.5-6.
888 46. Borrett SR, Lau MK (2014) enaR: An R package for Ecosystem Network Analysis. *Methods
889 in Ecology and Evolution* 5(11):1206–1213.
890 47. Conner K, Hartl DL (2004) *A Primer of Ecological Genetics: a textbook*. (Sinauer Associates,
891 Inc., Sunderland, Massachusetts), 1st edition, p. All.
892 48. Dawkins R (year?) *The extended phenotype : the long reach of the gene*. p. 468.
893 49. Bdeir R, et al. (2017) Quantitative trait locus mapping of *Populus* bark features and stem
894 diameter. *BMC Plant Biology*.
895 50. Janzen DH (1980) Specificity of Seed-Attacking Beetles in a Costa Rican Deciduous Forest.
896 *The Journal of Ecology* 68(3):929.
897 51. Stinchcombe JR (year?) Can tolerance traits impose selection on herbivores?, Technical
898 report.
899 52. Strauss SY, Lau JA, Schoener TW, Tiffen P (2008) Evolution in ecological field experiments:
900 Implications for effect size.
901 53. Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG (2016) Genotypic variation in foun-
902 dation species generates network structure that may drive community dynamics and evolu-
903 tion. *Ecology*.
904 54. Borgatti SP, Everett MG (2006) A Graph-theoretic perspective on centrality. *Social Networks*
905 28:466–484.
906 55. Toju H, et al. (2017) Species-rich networks and eco-evolutionary synthesis at the metacommunity
907 level.
908 56. Toju H, Yamamoto S, Tanabe AS, Hayakawa T, Ishii HS (2016) Network modules and hubs
909 in plant-root fungal biomes. *Journal of the Royal Society Interface*.
910 57. Toju H, Guimarães PR, Olesen JM, Thompson JN (2014) Assembly of complex plant-fungus
911 networks. *Nature Communications*.
912 58. Díaz-Castelazo C, et al. (2010) Changes of a mutualistic network over time: Reanalysis over
913 a 10-year period. *Ecology*.
914 59. Guimarães PR, Jordano P, Thompson JN (2011) Evolution and coevolution in mutualistic
915 networks. *Ecology letters* 14(9):877–85.
916 60. Rountree JK, Shuker DM, Preziosi RF (2011) Forward from the crossroads of ecology and
917 evolution. *Philosophical transactions of the Royal Society of London. Series B, Biological
918 sciences* 366(1569):1322–8.
919 61. Zook AE, Eklof A, Jacob U, Allesina S (2010) Food webs: Ordering species according to
920 body size yields high degree of intervalty. *Journal of theoretical biology* 271(1):106–113.
921 62. Zytnyska SE, Khudr MS, Harris E, Preziosi RF (2012) No Title. *Oecologia* 170(2).
922 63. Evans DM, Pocock MJO, Memmott J (2013) The robustness of a network of ecological net-
works to habitat loss. *Ecology letters* 16:844–52.

924

925

923

	df	SS	R2	F	p-value
geno	9.00	44078.13	0.54	3.58	0.05
Residual	27.00	36915.46	0.46		
Total	36.00	80993.59	1.00		

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

	response	df	statistic	H2	p-value
Lichen Network Similarity	9	3.5821	0.41	0.0537	
Average Mutual Information		3.5235	0.31	0.0254	
Centralization		4.0444	0.33	0.0184	
Centralization In-Degree		4.4812	0.35	0.0142	
Centralization Out-Degree		3.8615	0.32	0.0205	
Centralization In-Degree (positive)		3.9852	0.33	0.0190	
Centralization In-Degree (negative)		0.3304	0.11	0.2508	
Centralization Out-Degree (positive)		3.5585	0.31	0.0248	
Centralization Out-Degree (negative)		0.0862	0.05	0.3446	
Degree		3.5175	0.32	0.0255	
Degree (positive)		3.6925	0.32	0.0229	
Degree (negative)		0.0327	0.03	0.3859	
Percent Lichen Cover		0.0000	0.00	1.0000	
Lichen Species Diversity		0.0000	0.00	0.4543	
Lichen Species Richness		0.0000	0.00	0.4543	
Lichen Species Evenness		0.0000	0.00	0.4543	
Percent Rough Bark		4.8526	0.32	0.0113	
pH		0.0000	0.00	1.0000	
Carbon-Nitrogen Ratio		0.0000	0.00	1.0000	
Condensed Tannins		3.0522	0.32	0.0343	
BR-L Residuals		0.0000	0.00	1.0000	
BR-Cen Residuals		0.0000	0.00	1.0000	

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

lichen species	mean	statistic	H2	p-value
Positive				
In-Degree				
X. galericulata	0.2703	0	0	1
C. subdeflexa	0.8919	2.1926	0.2158	0.0595
L. spp.	0.4324	0	0	1
C. holocarpa	0.5946	3.6146	0.3241	0.024
X. montana	0.0541	0	0	0.4543
P. melanachra	0.1351	0	0	1
P. adscendens	0			
P. undulata	0.027	0	0	0.4543
R. sp.	0.1351	2.049	0.2613	0.0656
Out-Degree				
X. galericulata	0.027	0	0	0.4543
C. subdeflexa	0.6757	0	0	1
L. spp.	0.5946	0.0061	0.0126	0.4247
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 3. 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 4. 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 5. Pseudo-F Table of lichen community similarity
PERMANOVA.**

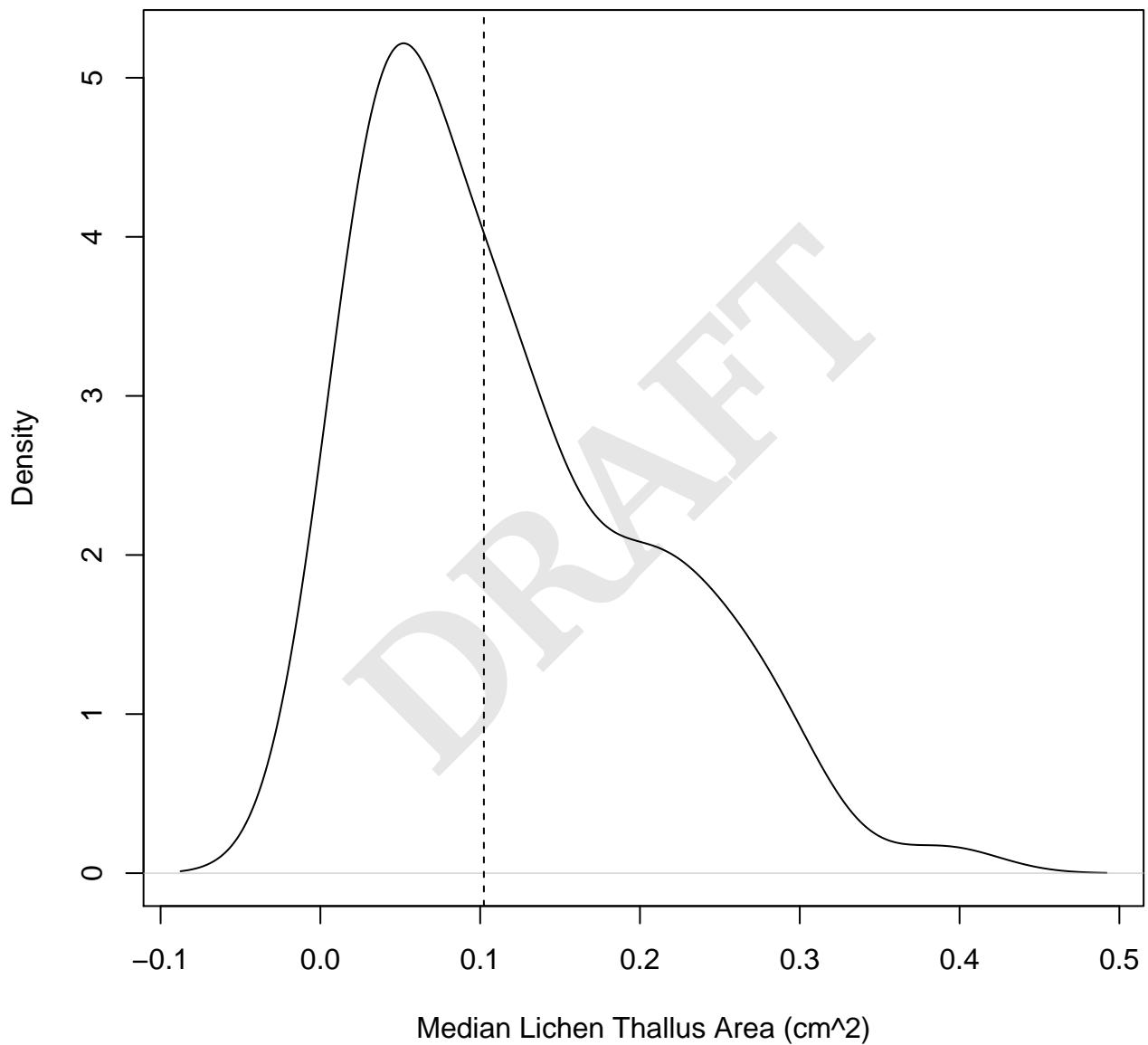


Fig. 1

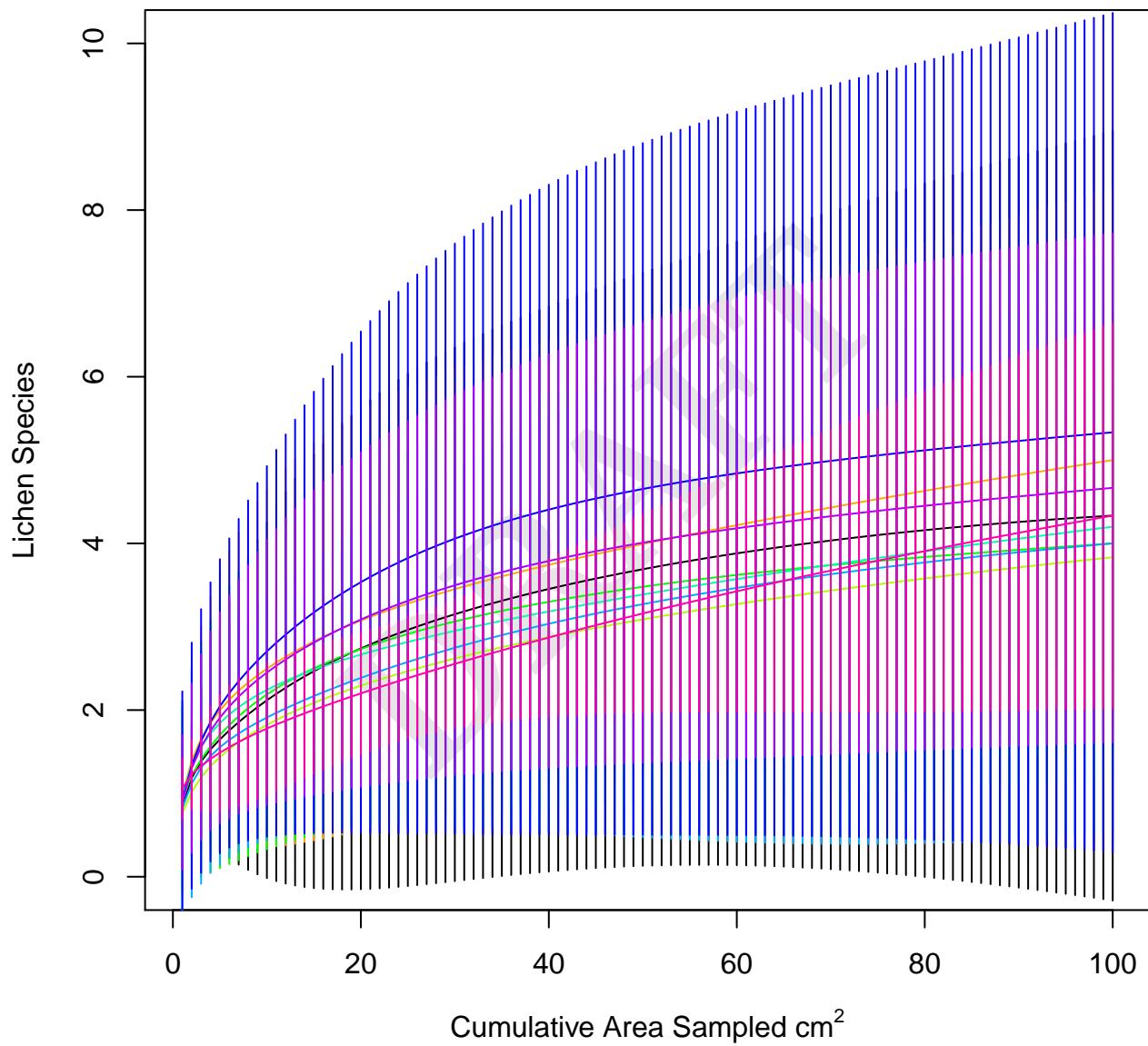


Fig. 2. Species area curve by genotype.

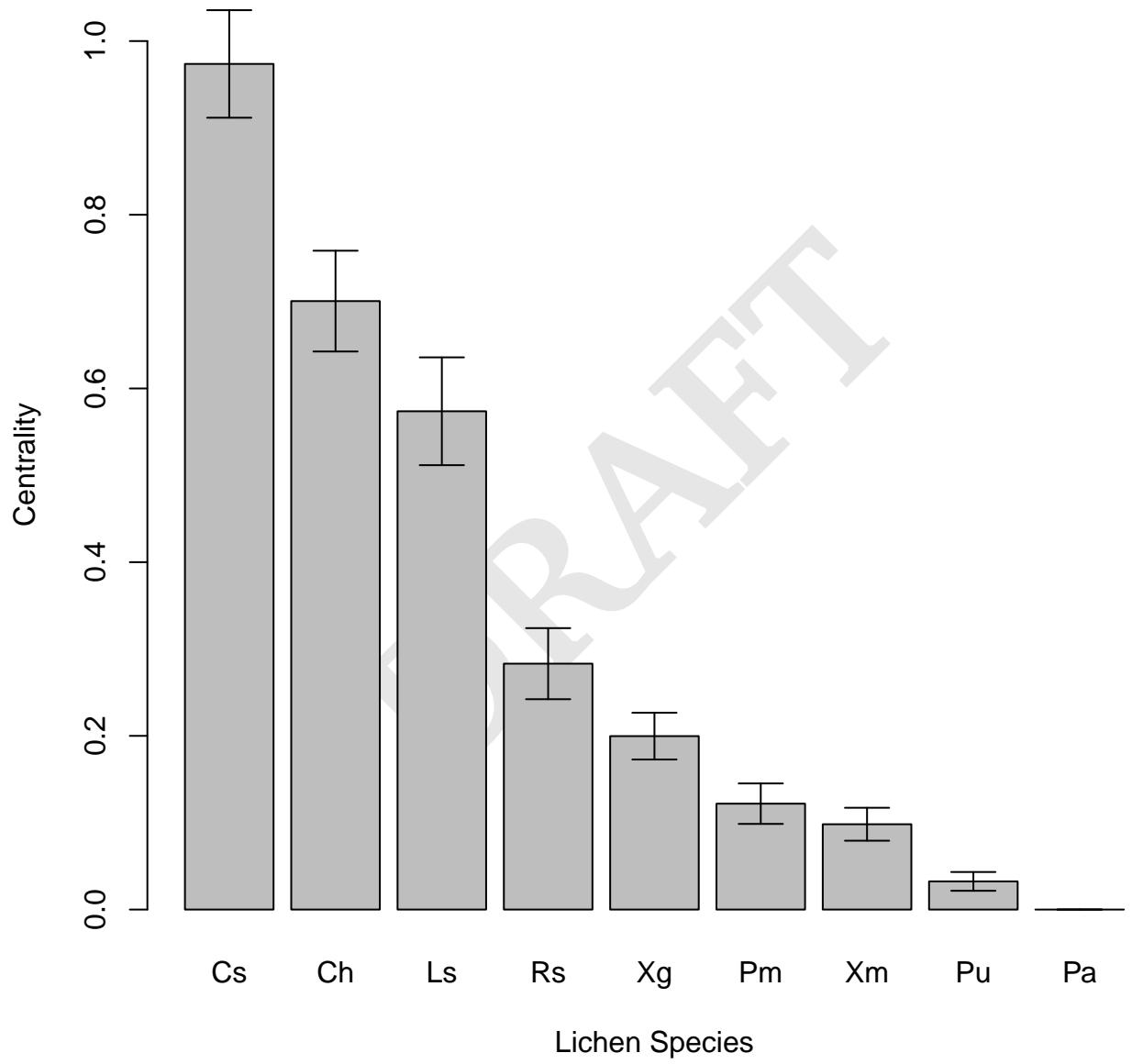


Fig. 3