

Genotypic variation in a foundation tree directs ecological network structure

Matthew K. Lau^{a,b,1}, Louis J. Lamit^b, Rikke R. Naesbourg^c, Stuart R. Borrett^d, Matthew A. Bowker^e, and Thomas G. Whitham^a

^aDepartment of Biological Sciences and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA; ^bHarvard Forest, Harvard University, 324 N Main St, Petersham, MA 01366, USA; ^cUniversity of California Berkeley, Berkeley, CA, USA; ^dDepartment of Biology and Marine Biology, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC, 28403, USA; ^eSchool of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA

This manuscript was compiled on January 31, 2019

1 **Biological evolution occurs in the context of complex networks of**
2 **interacting species in which natural selection defines the structure**
3 **of ecological networks. Fundamental to this evolutionary process**
4 **is the discovery of a genetic basis to ecological network structure.**
5 **Although previous work has demonstrated that tree genotype con-**
6 **tributes to interaction network structure at the scale of forest stands,**
7 **the contribution of tree genetics to localized interaction networks**
8 **at the scale of individual trees has not yet been explored. To test**
9 **the degree to which tree genetics can contribute to network struc-**
10 **ture, we conducted quantitative modeling of interaction network for**
11 **a community of epiphytic lichens in a long-term experimental com-**
12 **mon garden of genotyped trees of a foundation species (*Populus***
13 ***angustifolia*). We found three main results: 1) bark roughness and**
14 **lichen communities displayed significant responses to tree genotype,**
15 **2) tree genotype contributed to lichen network structure, explaining**
16 **a third of the variation in lichen interaction networks, and 3) different**
17 **aspects of lichen network structure, including the number of inter-**
18 **actions and centralization, responded to tree genotype, primarily as**
19 **a function of the number of species present and to a lesser extent**
20 **the abundance of lichen. We conclude that tree genotype influences**
21 **lichen interaction network structure with one potential pathway be-**
22 **ing that bark roughness alters the presence and overall abundance**
23 **of lichen, which determines the nature and magnitude of interactions**
24 **in the community. These results support the hypothesis that vari-**
25 **ation in ecological interaction networks can result from genetically**
26 **based variation in foundation species. This study opens the possibil-**
27 **ity for a genetic basis to both direct and indirect interactions among**
28 **species in complex communities.**

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

1 **E**volution occurs in the context of complex networks of
2 interacting species. In ecological communities, commu-
3 nity dynamics depend on key interactions (1) that occur in
4 species interaction networks, such as: trophic (2–4) and mu-
5 tualistic (5) interaction networks. Phylogenetic patterns in
6 ecological networks support the importance of evolutionary
7 processes in shaping species interactions, community structure
8 and ecosystem processes (6–8).

9 Add a discussion of Des Roches.

10 More on the importance of ecological networks (9–11).

11 Elamo1999 = fungi

12 Community genetics studies (12) have shown that genetic
13 variation in foundation species (13) plays a significant role in
14 defining distinct communities of interacting organisms: such as,
15 endophytes, pathogens, lichens, arthropods, and soil microbes.
16 Multiple studies have now demonstrated that genetic variation
17 influences numerous functional traits (e.g., phytochemical, phe-
18 nological, morphological) produces a multivariate phenotype

(14) that contributes to variation in associated communities (15).

19 Additional work has provided support for the hypothesis
20 that not only does composition vary among genetically distinct
21 genotypes of foundation species but it also impacts the struc-
22 ture of the network of species interaction [these communities
23 (16, 17)]. Also, work by (18–20) observe consistent patterns
24 of centralized interactions of species modules focused around
25 hubs of plant-fungal interactions. In other words, a small
26 number of plant and fungal symbionts tended to have have
27 disproportionate numbers of interactions with other species
28 and likely are the drivers in determining community assembly,
29 structure and dynamics.

30 Here, we investigate how genetic variation in a foundation
31 tree species determines the structure of a network of inter-
32 actions among a community [the associated lichen specie
33 Using a long-term (20+ years), common garden experimen
34 with replicated individuals of known genetic identity and a nat
35 urally established stand of *Populus angustifolia*. We focused on
36 a model community of epiphytic lichens species, as previous
37 research has demonst[red] significant compositional responses
38 of epiphytes to genotypic variation (21, 22). In addition, the
39 life-history characteristics of lichen, having highly localized,
40 direct contact interactions and slow population turnover rates,
41 allowed us to assess interactions among lichen species on indi
42 vidual trees. We hypothesize that in natural systems evolution
43 occurs in a community context involving interactions of com
44 plex networks of interacting species (2, 16, 17, 23). If correct,
45

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. Here, we use a long-term common garden experiment to reveal the effect that genotypic variation can have on networks of lichen communities that occur on the bark of a foundation tree species. We found that lichen interaction networks respond to a genetically based tree trait, which alters network structure both through environmental filtering of species and by changing how species interact. These findings demonstrate the importance of assessing the impacts of genetic variation on the structure and function of ecosystems.

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 substantially 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.

¹Dr. Matthew K. Lau. E-mail: matthewklau@fas.harvard.edu

we should expect to find that network structure is genetically based in which different plant genotypes support different interaction networks and that these interactions networks can function as indicators of ecological dynamics important for conserving biodiversity. Applying a probability-theory based network modeling approach, we constructed a set of interaction network models for the lichen associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks.

Materials and Methods

The study was conducted along the Weber River, UT (USA), which is a cottonwood (*Populus* spp.) dominated riparian ecosystem. Although two native species, *Populus angustifolia* (James) and *Populus fremontii* (S. Watson), occur here and are known to hybridize, only pure or advanced generation backcrosses of *P. angustifolia* were sampled in order to avoid the effect of the hybridization between these two species (?). Bark lichen have been extensively studied in this system previously, and provide an ideal system in which to observe and model lichen interaction networks, as their sessile nature permits accurate identification of individuals (24).

Need to add more citations of Lamits or other lichen studies.

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 randomly in a single field (0.025 km²) at the Ogden Nature Center, Ogden, UT. From the population of established individuals in the common garden, we chose a total of thirteen genotypes, replicated between 3 and 8 times each, for sampling. In this study, we use the genotype notations previously published in (?).

Bark Lichen Observations. On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm² cells arranged in a checkerboard pattern. Given the small size and sessile nature of lichen, we were able to rapidly assess lichen interactions by quantifying thalli in close contact. Sampling was restricted to the northern aspect of the trunk to maximize the abundance of lichen and control for the effect of trunk aspect. Two adjacent 10 cm² quadrats centered at 50 cm and 85 cm from ground level were sampled (Fig 1 A and B). The bark lichen community in this system is comprised of fourteen species; however, only 9 species were observed within our study quadrats (Fig 1 C-K). The observed lichen community included (abbreviations given for species present in study): Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Pm = *Physciella melanocarpa*, 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*. Species accumulation curves indicated that communities in the common garden were thoroughly sampled and similar in composition (richness to nearby naturally established cottonwood stands) (see Supplementary Materials).

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 (S.E.) (see Supplementary Fig 1). Based on this, we expected thalli observed in each cell to generally be spatially independent of the other cells in the quadrat 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.

As bark roughness had previously been shown to be an important, genetically based tree trait impacting bark lichen, we measured the percentage of rough bark on each tree following the methods of (24). Briefly, the number of cells containing disrupted, fissured bark were

counted within each quadrat on each tree. The number of rough bark containing cells were then summed and divided by the total number of cells surveyed. This was done for all quadrats on all trees in which lichen communities were also observed.

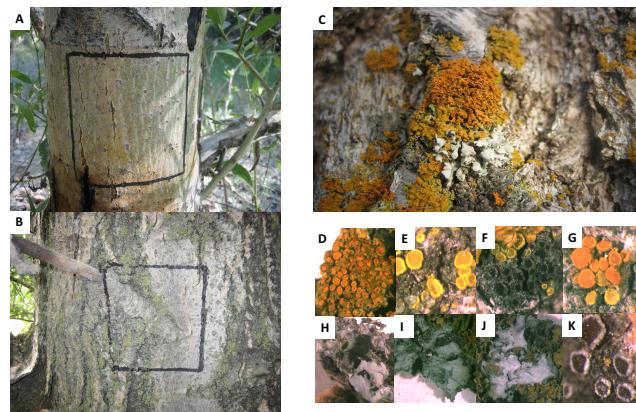


Fig. 1. The communities of bark lichen were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). Lichen were sampled within a fixed area (10 cm²) on individual trees (A and B). (C) a photo of a typical community 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 main lichen species observed, respectively: *X. montana*, *Candelariella subdeflexa*, *Rinodina* sp., *Caloplaca holocarpa*, *Physcia adscendens*, *Physciella melanocarpa*, *Physcia undulata* and *Lecanora hagenii*.

Lichen Network Modeling and Analysis. We used the observations of lichen in the 1cm² cells on individual trees of *P. angustifolia*. Uni-partite 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 (25). 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 an asymmetric matrix, that is $P(S_i|S_j)$ does not have to be equal to $P(S_j|S_i)$, that also had a diagonal S_{ii} equal to one for all species present and zero for species that were not observed on the tree.

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 ($\mathbf{D} = D_{ij}$) 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).

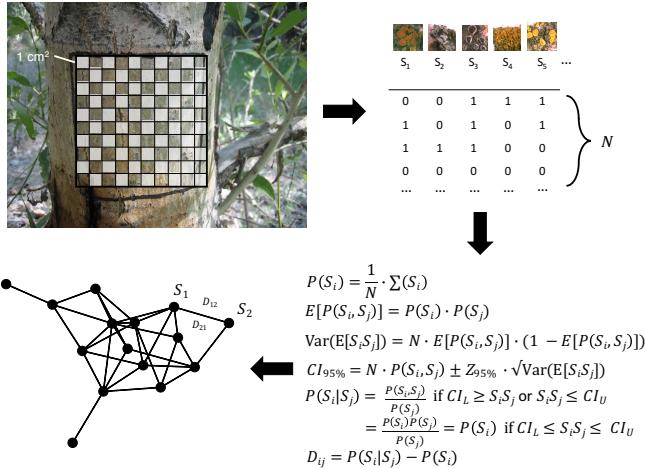


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 10 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (25), 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 .

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. Roughness, lichen cover and species richness were square-root transformed to meet the assumptions of heterogeneity of variance and heteroskedasticity for these tests.

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

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

For each network, we also calculated two network metrics that measure different structural aspects. We calculated the number of

interactions or “links” in each network, which provides a measure of the size of the network (26?). We also calculated the centralization of each network, which measures the evenness of the distribution of interactions among the species in the network (?). In a network with a low level of centralization species have similar amount of interaction in the network, while a network with a high level of centralization tends to one or small subset of species that interact with other species. We used a related function to calculate the centrality of each species in each network as well. Although there are many other metrics, see (27), we focus on a subset for the sake of simplicity and because some metrics are not appropriate for our relatively small communities. In particular, we do not present analysis of the modularity (i.e. the degree of sub-grouping) because our community has relatively few species to form modules. As with the other response variables, the number of links was log-transformed and centralization scores were square-root transformed to meet variance and normality assumptions.

We have made all code and data available online. Code is available at github.com/communitygenetics/lcn. Data is available via the Harvard Dataverse (needs project ID). The project is also archived via Zenodo at zenodo.com/doi/XXXXXX. All analyses were conducted using the programming language R version 3.4.2 (R Development Core Team 2018).

Results

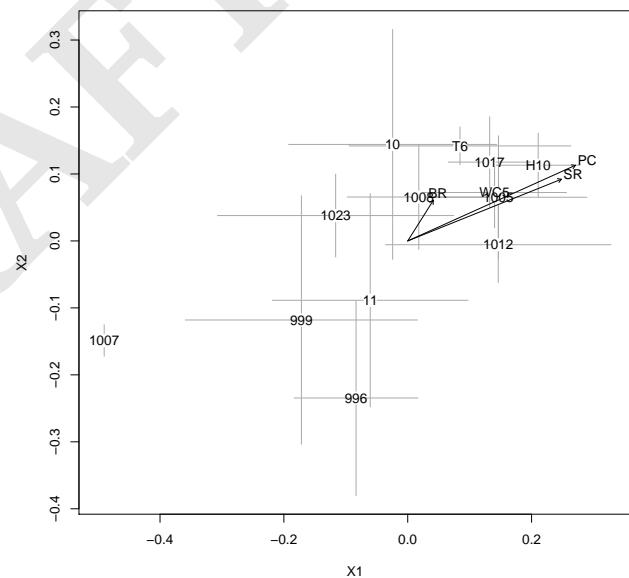


Fig. 3. Lichen community composition varied among genotypes. Plot of the ordinated centroids ($\pm 1 \text{ S.E.}$) from the NMDS ordination ($R^2 = 0.935$, stress = 0.101) community composition of each genotype (indicated by centroid labels). Centroids that are closer together have more similar lichen communities. Arrows show the direction and magnitude of correlation between bark roughness (BR), percent lichen colonization (PC) and lichen species richness (SR) and the ordinated community scores.x

Bark roughness and lichen communities responded to tree genotype. Percent rough bark varied significantly among genotypes (REML $R^2 = 0.378$, RLRT = 10.69, p -value = 0.0001), as did total lichen cover (REML $R^2 = 0.172$, RLRT = 2.9627, p -value = 0.0375). However, lichen species richness did not show a significant response to genotype (REML $R^2 = 0.0981$, RLRT = 1.0001, p -value = 0.1366). Community composition was also affected by tree genotype (PerMANOVA $R^2 = 0.243$, $F_{12} = 1.8221$, p -value = 0.0029). In addition, community composition was correlated with bark roughness (PerMANOVA $R^2 = 0.039$, $F_1 = 3.7408$, p -value = 0.0064), lichen cover (PerMANOVA $R^2 = 0.342$, $F_1 = 32.8482$, p -value = 0.0001) and lichen species richness (PerMANOVA $R^2 = 0.0001$, $F_1 = 0.0001$, p -value = 0.9999).

0.069, $F_1 = 6.5958$, $p\text{-value} = 0.0002$) (Fig. 3). However, after controlling for the effect of tree genotype on community composition, bark roughness did not significantly predict community composition (PerMANOVA $R^2 = 0.011$, $F_1 = 0.9938$, $p\text{-value} = 0.3841$) but lichen cover (PerMANOVA $R^2 = 0.236$, $F_1 = 21.2661$, $p\text{-value} = 0.0001$) and lichen species richness (PerMANOVA $R^2 = 0.054$, $F_1 = 4.9036$, $p\text{-value} = 0.0011$) were still significantly correlated with lichen composition (Supplementary Tables 1 and 2).

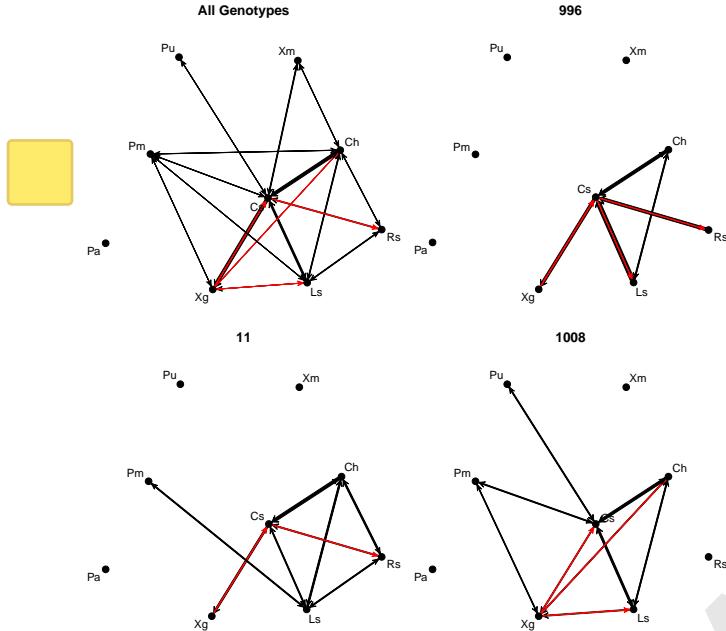


Fig. 4. Lichen networks varied in structure among genotypes. Network diagrams of the mean lichen interaction matrices (i.e. \mathbf{D}) averaged for all trees and for several individual genotypes showing a range of interaction network structure. Directionality (arrowheads) and sign (red = negative, black = positive) of interactions are shown as edges between species (abbreviated by the first letter of the genus and specific epithet), which are scaled by their magnitude.

We observed significant lichen network structure. This structure varied among genotypes (Fig. 4) and lichen species varied in their importance in the network. *Candaleriella subdeflexa* was generally the most central species (i.e. being the most highly connected) having the highest average centrality (0.73), followed by *Ca. holocarpa* (0.54) and *L. hageni* (0.40). The centralization of the remaining species were *R. sp.* (0.18), *X. galericulata* (0.14), *P. melanachra* (0.08), *X. montana* (0.06) and *Ph. undulata* (0.02). *Physcia adscendens* was generally not connected to other species in the networks and had a centralization score of zero.

Lichen networks observed on trees of the same genotype tended to be similar in structure. Tree genotype significantly predicted the similarity of lichen interaction networks (PerMANOVA $R^2 = 0.33795$, $F_{12} = 2.5379$, $p\text{-value} = 0.0050$) (Fig. 5). Bark roughness (PerMANOVA $R^2 = 0.040$, $F_1 = 4.1680$, $p\text{-value} = 0.03770$) and lichen species richness (PerMANOVA $R^2 = 0.424$, $F_1 = 44.5034$, $p\text{-value} = 9.999e-05$) were significant predictors of lichen network similarity, while total lichen cover was a weak, marginally significant predictor (PerMANOVA $R^2 = 0.032$, $F_1 = 3.3573$, $p\text{-value} = 0.06779$). However, after controlling for the effect of tree genotype on lichen network similarity, only species richness was a significant predictor of lichen network similarity (PerMANOVA $R^2 = 0.300$, $F_1 = 33.3755$, $p\text{-value} = 0.00001$), and neither bark roughness (PerMANOVA $R^2 = 0.019$, $F_1 = 2.0858$, $p\text{-value} = 0.14699$) nor lichen cover (PerMANOVA $R^2 = 0.019$, $F_1 = 2.1504$, $p\text{-value} = 0.14409$) were significant predictors (Supplementary Tables ?? and 4). Community similarity was not correlated with network similarity (Mantel Spearman $\rho = 0.092$, $p\text{-value} = 0.09500$).

The observed genotypic patterns of network similarity could be summarized by several network metrics. The number of links

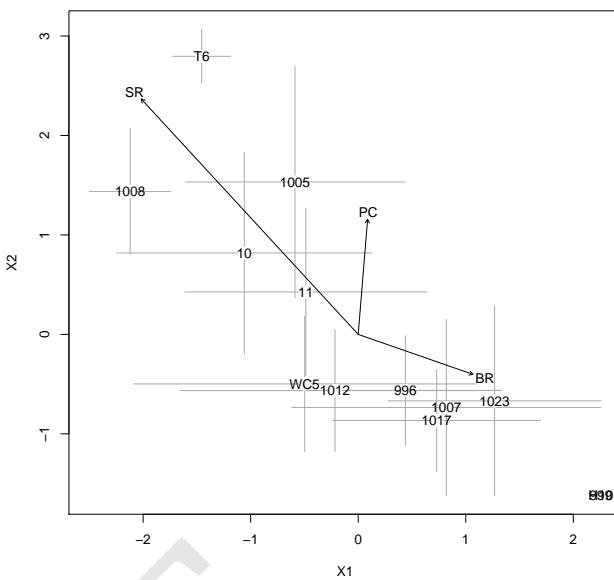


Fig. 5. Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. The plot shows genotype centroids of NMDS ordinated ($R^2 = 0.999$, stress = 0.011) lichen networks (± 1 S.E.). Centroids that are closer are more similar in the structure of their lichen networks. Arrows show the magnitude and direction of correlation of the ordinated networks with tree bark roughness (BR), percent cover of lichens (PC) and lichen species richness (SR).

(PerMANOVA $R^2 = 0.392$, $F_1 = 72.4348$, $p\text{-value} = 0.001$) and network centrality (PerMANOVA $R^2 = 0.309$, $F_1 = 57.0440$, $p\text{-value} = 0.001$) were highly correlated with network similarity. Tree genotype significantly predicted network centrality (REML $R^2 = 0.202$, RLRT = 2.7801, $p\text{-value} = 0.04012$) but marginally predicted the number of links (REML $R^2 = 0.170$, RLRT = 2.0484, $p\text{-value} = 0.065$) (Fig. 6). Total cover was correlated with the number of links (ANOVA $F_1 = 6.867$, $p\text{-value} = 0.0114$) and centrality (ANOVA $F_1 = 8.093$, $p\text{-value} = 0.0063$). Lichen species richness was also correlated with the number of links (ANOVA $F_1 = 29.436$, $p\text{-value} = 0.000015$) and centrality (ANOVA $F_1 = 39.488$, $p\text{-value} < 0.000001$). Bark roughness, however, did not significantly predict either the number of links (ANOVA $F_1 = 2.897$, $p\text{-value} = 0.0946$) or the centrality (ANOVA $F_1 = 2.591$, $p\text{-value} = 0.1134$) of lichen networks (Supplementary Tables 5 and 6).

Discussion

Our study provides a window into the genetic underpinnings of an ecological network. We observed significant lichen interaction structure that varied among genotypes of a foundation tree species, narrowleaf cottonwood (*P. angustifolia*). We found that a genetically based trait, bark roughness, partially explained the variation in lichen interaction networks. Some of this variation in lichen networks was related to both the overall abundance and species richness of lichen; though, statistically controlling for the effect of genotype on these variables indicates that a significant portion of the variance in lichen species richness is due to a factor other than tree genotype. By using network metrics, we were also able to probe for specific characteristics of how these networks were responding to tree genotype. We found that both number of links and the centralization of the networks were highly correlated with network similarity and that tree genotype significantly predicted network centrality but only marginally predicted the

in intro.

MKL: Environmental filtering is evidenced by species richness, but also possibly species interaction varying based on environment as networks varied in terms of sign and magnitude as well.

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

Discussion of network implications for stability with genetics.

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 (30, 31). 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 (32–34). 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 (35). 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.

ACKNOWLEDGMENTS. This work was supported by the National Science Foundation grant (DEB-0425908) and Integrative Graduate Research Traineeship (IGERT) fellowships for M.L. and L.L. The Ogden Nature Center staff helped to maintain the common gardens. Lichen sampling was supported by Todd Wojtowicz, Luke Evans and David Solance Smith.

- Fontaine C, et al. (2011) The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14(11):1170–81.
- Bascompte J, Jordano P, Olesen JM (2006) Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science* 312:431–433.
- Johnson MTJ (2008) Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology*.
- Johnson MT, Vellend M, Stinchcombe JR (2009) Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philos. Trans. R. Soc. B Biol. Sci.*
- Rafferty NE, Ives AR (2013) Phylogenetic trait-based analyses of ecological networks. *Ecol. 94(10):2321–33.*
- Crutsinger GM (2016) A community genetics perspective: Opportunities for the coming decade. *New Phytol.*
- Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448(7156):925–8.
- Whitham TG, et al. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7:510–523.
- Guimarães PR, Jordano P, Thompson JN (2011) Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14(9):877–85.
- Moya-Larau J (2011) Genetic variation, predator-prey interactions and food web structure. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366(1569):1425–37.
- Thompson JN, Schwind C, Guimaraes PR, Friberg M (2013) Diversification through multaitrait evolution in a coevolving interaction. *Proc. Natl. Acad. Sci.*
- Lamit LJ, et al. (2015) Genotype variation in bark texture drives lichen community assembly across multiple environments. *Ecology* 96(4):960–971.
- Ellison AM, et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3(9):479–486.

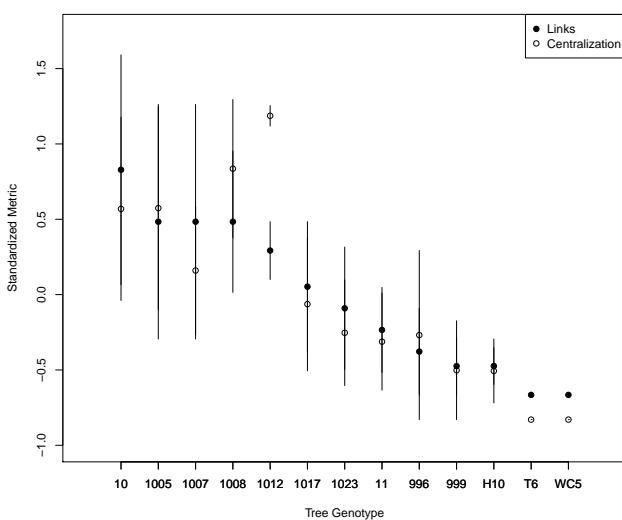


Fig. 6. The impact of tree genotype on lichen network structure was indicative of variation in both the number variation in lichen interactions among species. Plot showing the means (± 1 S.E.) for lichen network metrics, number of links and centralization, for each genotype. Both metrics are presented as standardized scores ($\frac{x-\bar{x}}{\sigma}$).

307 number of network links. This latter result could be due to the
 308 relationship between species richness and the number of links
 309 in the network, which were significantly correlated with each
 310 other. We also found that bark roughness did not significantly
 311 predict either the number of links or the centrality of lichen
 312 networks, suggesting that bark roughness has some other effect
 313 on the structure of the lichen networks. Taken together, these
 314 findings support the hypothesis that genotypic variation in a
 315 foundation species contributes to the structure of a network
 316 of interacting species.

These findings point to the importance of understanding the community level effects of genetic variation and highlights the potential for indirect effects of genetic variation to propagate through networks of interacting species and trophic levels. This work corroborates previous findings of the importance of plant genetics in shaping community structure and ecosystem processes (8). Altering the structure of interaction networks presents a means for genetic effects to be magnified within the system of interacting species. For example, (16) showed that the genetics based interactions of aphid resistant and aphid susceptible trees resulted in different interaction networks of their associated arthropod communities composed of 139 species. At the scale of ecosystems, trophic networks or food webs direct and control the rates of energy and nutrient flux (28). Furthermore, in a predator-prey-plant study, Smith (29), showed that the interactions among species across trophic levels depended on plant genotype.

TGW: might be good to cite papers on competition in lichens or other organizing factors to back up the least expected statement. as epiphytes we might not expect them to care.

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

- 410 14. Holeski LM, Hillstrom ML, Whitham TG, Lindroth RL (2012) Relative importance of genetics
411 ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype
412 in a foundation tree species. *Oecologia* 170:695–707.
- 413 15. Bailey JK, et al. (2009) From genes to ecosystems: a synthesis of the effects of plant
414 genetic factors across levels of organization. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*
415 364(1523):1607–16.
- 416 16. Keith AR, Bailey JK, Lau MK, Whitham TG (2017) Genetics-based interactions of foundation
417 species affect community diversity, stability and network structure. *Proc. R. Soc. B Biol. Sci.*
418 284(1854):20162703.
- 419 17. Lau MK, Keith AR, Borrett SR, Shuster SM, Whitham TG (2015) Genotypic variation in founda-
420 tion species generates network structure that may drive community dynamics and evolution.
421 *Ecology* 97(3):15–0600.1.
- 422 18. Toju H, et al. (2017) Species-rich networks and eco-evolutionary synthesis at the metacommunity
423 level.
- 424 19. Toju H, Yamamoto S, Tanabe AS, Hayakawa T, Ishii HS (2016) Network modules and hubs in
425 plant-root fungal biomes. *J. R. Soc. Interface*.
- 426 20. Toju H, Guimarães PR, Olesen JM, Thompson JN (2014) Assembly of complex plant-fungus
427 networks. *Nat. Commun.*
- 428 21. Winfree R, Gross BJ, Kremen C (2011) Valuing pollination services to agriculture. *Ecol. Econ.*
429 71:80–88.
- 430 22. Ztynska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree
431 species influences the associated epiphytic plant and invertebrate communities in a complex
432 forest ecosystem. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366:1329–1336.
- 433 23. Thompson JN (2013) *Relentless Evolution*. (University of Chicago Press), p. 499.
- 434 24. Lamit L, et al. (2011) Genetically-based trait variation within a foundation tree species influ-
435 ences a dominant bark lichen. *Fungal Ecol.* 4(1):103–109.
- 436 25. Araújo MB, Rozenfeld A, Rahbeck C, Marquet PA (2011) Using species co-occurrence net-
437 works to assess the impacts of climate change. *Ecography (Cop.)*, 34:897–908.
- 438 26. Lau MK, Borrett SR, Hines DE, Singh P (2015) enaR: Tools for Ecological Network Analysis.
- 439 27. Lau MK, Borrett SR, Baisier B, Gotelli NJ, Ellison AM (2017) Ecological network metrics:
440 opportunities for synthesis. *Ecosphere* 8(8):e01900.
- 441 28. Borgatti SP, Everett MG (2006) A Graph-theoretic perspective on centrality. *Soc. Networks*
442 28:466–484.
- 443 29. Smith DS, Bailey JK, Shuster SM, Whitham TG (2011) A geographic mosaic of trophic inter-
444 actions and selection: trees, aphids and birds. *J. Evol. Biol.* 24(2):422–9.
- 445 30. Rowntree JK, Shuker DM, Preziosi RF (2011) Forward from the crossroads of ecology and
446 evolution. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366(1569):1322–8.
- 447 31. Whitham TG, et al. (2012) Community specificity: Life and afterlife effects of genes.
- 448 32. Bangert RK, et al. (2006) A genetic similarity rule determines arthropod community structure.
Mol. Ecol. 15:1379–1391.
- 449 33. Zook AE, Eklof A, Jacob U, Allesina S (2010) Food webs: Ordering species according to body
450 size yields high degree of intervality. *J. Theor. Biol.* 271(1):106–113.
- 451 34. Ztynska SE, Khudr MS, Harris E, Preziosi RF (2012) No Title. *Oecologia* 170(2).
- 452 35. Evans DM, Pocock MJO, Memmott J (2013) The robustness of a network of ecological net-
453 works to habitat loss. *Ecol. Lett.* 16:844–52.

Supplementary Materials

Response	H2	R2	p-value
Percent Rough Bark	0.37835	0.37835	1e-04
Network Centrality	0.20166	0.20166	0.04076
Percent Lichen Cover	0.17279	0.17279	0.033
Number of Network Links	0.17016	0.17016	0.06602
Lichen Community Composition	0.16093	0.24287	0.0029
Lichen Species Richness	0.09815	0.09815	0.14
Lichen Network	0.06252	0.29111	0.0094
Network Modularity	0.05731	0.05731	0.2809

Table 1. Genotypic effects of cottonwood trees on the associated lichen community.

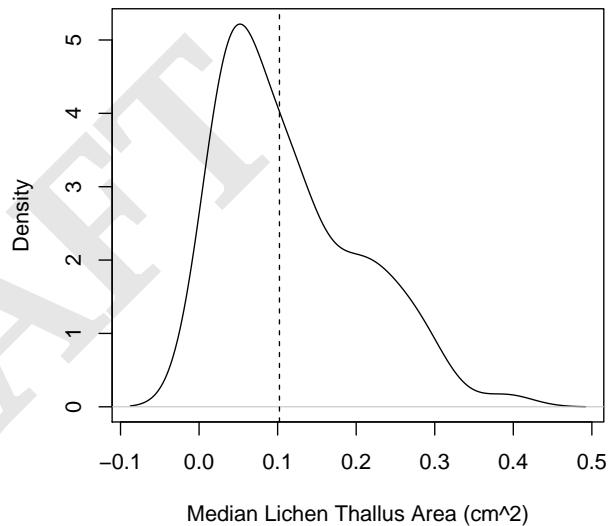


Fig. 1. Density plot of the median lichen thallus area (cm^2).

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1	0.44	0.04	3.74	0.0064
PC	1	3.86	0.34	32.85	0.0001
SR	1	0.78	0.07	6.60	0.0002
Residual	53	6.23	0.55		
Total	56	11.31	1.00		

**Table 1. PerMANOVA Pseudo-F Table showing the predictors of com-
munity similarity.**

	Df	SumOfSqs	R2	F	Pr(>F)
geno	12	2.75	0.24	1.82	0.0029
BR	1	0.12	0.01	0.99	0.3841
PC	1	2.67	0.24	21.27	0.0001
SR	1	0.62	0.05	4.90	0.0011
Residual	41	5.15	0.46		
Total	56	11.31	1.00		

Table 2. PerMANOVA Pseudo-F Table showing the predictors of community similarity.

	Df	SumOfSqs	R2	F	Pr(>F)
BR	1	61.42	0.04	4.17	0.0377
PC	1	49.47	0.03	3.36	0.0678
SR	1	655.76	0.42	44.50	0.0001
Residual	53	780.96	0.50		
Total	56	1547.61	1.00		

Table 3. PerMANOVA Pseudo-F Table showing the predictors of network similarity.

	Df	SumOfSqs	R2	F	Pr(>F)
geno	12	450.52	0.29	2.69	0.0094
BR	1	29.11	0.02	2.09	0.1470
PC	1	30.01	0.02	2.15	0.1441
SR	1	465.78	0.30	33.38	0.0001
Residual	41	572.18	0.37		
Total	56	1547.61	1.00		

Table 4. PerMANOVA Pseudo-F Table showing the predictors of network similarity.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
BR	1	102.25	102.25	2.78	0.1016
PC	1	239.57	239.57	6.50	0.0137
SR	1	956.96	956.96	25.98	0.0000
Residuals	53	1952.23	36.83		

Table 5. ANOVA F Table showing the predictors of the number of network links.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
BR	1	3.77	3.77	2.17	0.1463
PC	1	6.46	6.46	3.72	0.0590
SR	1	56.48	56.48	32.55	0.0000
Residuals	53	91.95	1.73		

Table 6. ANOVA F Table showing the predictors of network centralization.

	Df	SumOfSqs	R2	F	Pr(>F)
L	1	1330.80	0.86	734.67	0.0010
Cen	1	118.99	0.08	65.69	0.0010
Residual	54	97.82	0.06		
Total	56	1547.61	1.00		

Table 7. PERMANOVA Pseudo-F Table showing the predictors of network similarity.