

Genotypic variation in a foundation tree directs ecological network structure

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1 **Biological evolution occurs in the context of complex networks of**
2 **interacting species in which natural selection defines the structure**
3 **of ecological networks. Fundamental to this evolutionary process**
4 **is the discovery of a genetic basis to ecological network structure.**
5 **Although previous work has demonstrated that tree genotype con-**
6 **tributes to interaction network structure at the scale of forest stands,**
7 **the contribution of tree genetics to localized interaction networks at**
8 **the scale of individual trees has not yet been explored. To test the**
9 **degree to which tree genetics can contribute to network structure**
10 **across scales from trees to stands, we conducted quantitative mod-**
11 **eling of interaction network for a community of epiphytic lichens in**
12 **a long-term experimental common garden of genotyped trees of a**
13 **foundation species (*Populus angustifolia*). We found three main re-**
14 **sults: 1) Tree genotype strongly contributed to network structure ex-**
15 **plaining over a third of the variation in lichen interaction networks, 2)**
16 **Multiple aspects of interaction network structure varied in response**
17 **to genotype, including network size, the number of interactions, link-**
18 **age density and connectance, 3) At the stand scale, we also found**
19 **significant modular structure of plant-lichen networks resulting in**
20 **part from the combination of trees of the same genotype tending to**
21 **have similar community compositions and supporting similar lichen**
22 **interaction networks dominated by positive interactions. These re-**
23 **sults support the hypothesis that variation in ecological interaction**
24 **networks can result from genetically based variation in foundation**
25 **species. Although these results are for a community of sessile or-**
26 **ganisms in close proximity to the tree, this study opens the possibil-**
27 **ity for a genetic basis to both direct and indirect interactions among**
28 **species in complex communities.**

Keyword 1 | Keyword 2 | Keyword 3 | ...

1 **E**volution occurs in the context of complex networks of
2 interacting species. In ecological communities, community
3 dynamics depend on key interactions (1) that occur in
4 species interaction networks, such as: trophic (2) and mu-
5 tualistic (3) interaction networks. Phylogenetic patterns in
6 ecological networks support the importance of evolutionary
7 processes in shaping species interactions, community struc-
8 ture and ecosystem processes (13? ?). Community genetics
9 studies (?) have shown that genetic variation in foundation
10 species (4) plays a significant role in defining distinct commu-
11 nities of interacting organisms: such as, endophytes, pathogens,
12 lichens, arthropods, and soil microbes. Multiple studies have
13 now demonstrated that genetic variation influences numerous
14 functional traits (e.g., phytochemical, phenological, morpho-
15 logical) produces a multivariate phenotype (5) that contributes
16 to variation in associated communities (6).

17 Additional work has provided support for the hypothesis
18 that not only does composition vary among genetically distinct
19 genotypes of foundation species but it also impacts the struc-

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

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of lichen species. Using a long-term (20 years+), common garden experiment with replicated individuals of known genetic identity and a naturally established stand of *P. angustifolia*. We focused on a model community of 9 epiphytic lichens species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (7, 8). In addition, the life-history characteristics of lichen, having highly localized, direct contact interactions and slow population turnover rates, allowed us to assess interactions among lichen species on individual trees. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (9? ? ? ?). If correct, 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 dual-scale (lichen-lichen and genotype-lichen interactions) network modeling and analyses, we then examined the genetically based impacts of *P. angustifolia* on network structure.

Significance Statement

Authors must submit a 120-word maximum statement about the significance of their research paper written at a level understandable to an undergraduate educated scientist outside their field of speciality. The primary goal of the Significance Statement is to explain the relevance of the work in broad context to a broad readership. The Significance Statement appears in the paper itself and is required for all research papers.

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.

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51 **Materials and Methods**

52

- Statistical analyses and software

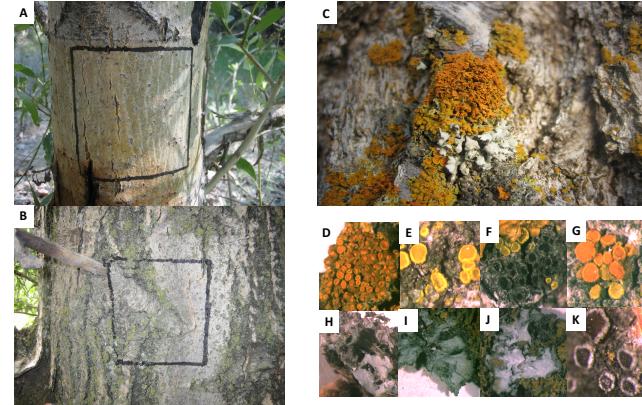
54 **Field observations in common garden and natural riparian forest**
 55 **stands.** The study was conducted along the Weber River, UT (USA),
 56 which is a cottonwood (*Populus* spp.) dominated riparian ecosystem.
 57 Although two native species, *Populus angustifolia* (James) and *Pop-*
 58 *ulus fremontii* (S. Watson), occur here and are known to hybridize,
 59 only pure or advanced generation backcrosses of *P. angustifolia* were
 60 sampled in order to avoid the effect of the hybridization between
 61 these two species.

62 A common garden was used to isolate the effect of tree genotype
 63 from the effect of the localized microenvironment associated with
 64 each individual and spatial autocorrelation. Asexually propagated
 65 clones of genotyped *P. angustifolia* individuals were obtained from
 66 wild collections and planted randomly in a single field (0.025 km²)
 67 at the Ogden Nature Center, Ogden, UT in 1992. A total of thirteen
 68 genotypes replicated between 3 and 8 times each, were chosen for
 69 sampling. Genotype names were previously published in (?).

70 **Bark Lichen Observations.** On each tree, presence or absence of each
 71 lichen species was assessed in 50 total 1 cm² cells arrayed in a
 72 checkerboard pattern. Sampling was restricted to the northern
 73 aspect of the trunk to maximize the abundance of lichen and control
 74 for the effect of trunk aspect. Two adjacent 10 cm² quadrats
 75 centered at 50 cm and 85 cm from ground level were sampled (Fig 1
 76 A and B). The checkerboard sampling pattern was chosen to isolate
 77 each cell based on an average thallus size of 1 cm² (Supplementary
 78 Materials). The thalli in each cell are expected to be spatially
 79 independent of the other cells in the quadrat, but exposed to similar
 80 micro-environmental conditions created by the bark and the location
 81 of the sampling area on an individual tree. The bark lichen commu-
 82 nity in this system is comprised of fourteen species; however, only 9
 83 species were observed within our study quadrats (Fig 1 C-K). The
 84 observed lichen community included (abbreviations are given for
 85 species present in study): Xg = *Xanthomendoza galericulata*, Xm =
 86 *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subde-*
 87 *flexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Ls = *Lecanora*
 88 sp., Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu =
 89 *Physcia undulata*. Several other species were not observed in the
 90 present study but are known to occur in this region: *Phaeophyscia*
 91 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia sublivacea*, *Meanelia*
 92 *elegantula*. We were able to rapidly assess lichen interactions by
 93 quantifying thalli in closed contact as assessed using 1cm² cells.
 94 Species accumulation curves showed that communities in the wild
 95 and the common garden were thoroughly sampled and with very
 96 similar species richness (Supplementary Materials). As bark rough-
 97 ness had previously been shown to be an important, genetically
 98 based, tree trait impacting this lichen community, we measured the
 99 percentage of rough bark on each tree following the methods of (?).
 100 Briefly, the number of cells containing disrupted, fissured bark were
 101 counted within each quadrat on each tree. The number of rough
 102 bark containing cells were then summed and divided by the total
 103 number of cells surveyed.

104 **Lichen Network Modeling and Analysis.** We used the observations of
 105 lichen in the 1cm² cells on individual trees of *P. angustifolia*. Uni-
 106 partite networks were generated using the conditional probabilities
 107 of each species pair, i.e. the probability of observing one species
 108 given an observation of another species ($P(A|B)$), based on the
 109 method developed by (10). To calculate conditional probabilities,
 110 we quantified the individual probabilities of species occurrences
 111 ($P(A)$) and the joint probability of co-occurrences ($P(A, B)$) using
 112 the frequencies of each species and their co-occurrences. We were
 113 then able to calculate the conditional probabilities of each species
 114 pair as $P(A|B) = \frac{P(A,B)}{P(B)}$, based on the axioms of probability. This
 115 yielded an asymmetric matrix, that is $P(A|B)$ does not have to be
 116 equal to $P(B|A)$ with a trace equal to the identity matrix (i.e.
 117 $P(A|A) = 1$).

118 Once these network matrices were constructed using the condi-
 119 tional probabilities of species pairs, we then applied an analytical
 120 procedure to remove non-significant links between species (Fig. 2).



54 **Fig. 1.** The communities of bark lichen were observed in a common garden of
 55 replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden
 56 Nature Center (Ogden, UT). Lichen were sampled within a fixed area (10cm by 10cm)
 57 on individual trees (A and B). (C) a photo of a typical community of bark lichen species
 58 interacting on the trunk of a cottonwood tree, including one of the more abundant
 59 species, *Xanthomendoza galericulata*, in the center. (D-K) shows the other main lichen
 60 species observed, respectively: X. *montana*, *Candelariella subdeflexa*, *Rinodina* sp.,
 61 *Caloplaca holocarpa*, *Physcia adscendens*, *Phyciella melanachra*, *Physcia undulata*
 62 and *Lecanora hagenii*

63 This procedure determines if the joint probability of a species
 64 pair (i.e. $P(S_i S_j)$) is different from zero. If the frequency of co-
 65 occurrences ($S_i S_j$) falls outside of the interval ($CI_{95\%}$), the joint
 66 probability is inferred to be non-zero. Here, $CI_{95\%}$ is calculated
 67 as as $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected
 68 frequency of co-occurrences ($E(S_i S_j)$) is the total number of cells
 69 surveyed (N) times the independent probabilities of each species
 70 ($P(S_i) * P(S_j)$), $Z_{95\%}$ is the Z-score for 95% from a Z-distribution
 71 and the expected variance of $E(S_i S_j)$ is the total number of cells
 72 times the expected probability of $S_i S_j$ and its compliment (i.e.
 73 $V(S_i S_j) = N * E[P(S_i S_j)] * (1 - E[P(S_i S_j)])$). Since the con-
 74 ditional probability is calculated using the joint probability as the
 75 numerator, whenever the joint probability is determined to be zero
 76 the conditional probability is determined to also be zero, since
 77 $P(S_i | S_j) = \frac{P(S_i S_j)}{P(S_j)} = \frac{0}{P(S_j)} = 0$.

78 **Statistical Analyses, Software and Data.** We used a combination of
 79 parametric and non-parametric, permutation based frequentist stat-
 80 istical analyses to test for the effects of genetic variation on lichen
 81 communities and their interaction networks.

- REML
- Least squares models
- PerMANOVA
- Mantel tests
- Code and data available via github and zenodo

82 All analyses were conducted using the programming language R
 83 version 3.4.2 (R Development Core Team 2018).

84 **Results**

85 Figure: Community composition NMDS with vectors

86 Bark roughness and some lichen community characteristics
 87 responded to tree genotype. Percent rough bark varied significantly
 88 among genotypes (REML RLRT = 10.69, p-value = 3e-04), as
 89 did total lichen cover (REML RLRT = 2.9627, p-value = 0.0375)
 90 and community composition (PerMANOVA R2 = 0.243, F 12 =
 91 1.8221, p-value = 0.0029). However, lichen species richness did not
 92 show a significant response to genotype (REML RLRT = 0.13047,
 93 p-value = 0.3134). Community composition was correlated with
 94 lichen cover (PerMANOVA R2 = 0.236, F 1 = 21.2661, p-value =
 95 9.999e-05) and richness (PerMANOVA spr.onc R2 = 0.054, F 1 =
 96 4.9036, p-value = 0.0011) after controlling for tree genotype effects.

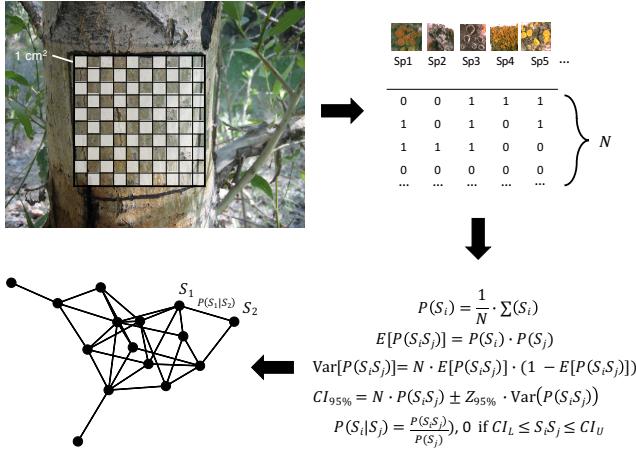


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 10 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded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

Roughness did not predict community composition (PerMANOVA R2 = 0.011, F1 = 0.9938, p-value = 0.3841) even though it was correlated with total lichen cover (ANOVA $F_{1,55} = 6.797$, $p - \text{value} = 0.01173$). Roughness was not correlated with lichen species richness (ANOVA $F_{1,55} = 1.509$, p-value = 0.2246).

Figure: Genotype networks + Genotype network similarity by genotype

Tree genotype influenced lichen network similarity. We observed significant lichen network structure. Lichen species varied in their centralization in the networks with *C. subdeflexa* having the highest average centrality (0.93), followed by *Ca. holocarpa* (0.62). The centralization of the remaining species were *L. hagenii* (0.48), *X. galericulata* (0.23), *R. sp.* (0.21), *P. melanachra* (0.09), *X. montana* (0.07) and *Ph. undulata* (0.02). *Physcia adscendens* was generally not connected to other species in the networks and had a centralization score of zero.

Figure. Networks of several genotypes or individual trees

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 R2 = 0.33795, F12 = 2.5379, p-value = 0.0050). Lichen species richness was also a significant predictor of network similarity after controlling for genotype (PerMANOVA R2 = 0.3413, F1 = 2.5417, p-value = 0.007399); however, neither total cover (PerMANOVA R2 = 0.023, F1 = 2.0628, p-value = 0.1487) nor roughness (PerMANOVA R2 = 0.011, F1 = 0.0497, p-value = 0.3394) predicted network similarity and community similarity was not correlated with network similarity (Mantel Rho spearman = 0.012, p-value = 0.337).

These patterns of structural similarity among networks on similar genotypes could be partially explained by several networks. Tree genotype marginally predicted the number of links (REML RLRT = 2.0221, p-value = 0.0657) and centrality (REML RLRT = 2.0915, p-value = 0.0627) of lichen networks. Total cover was correlated with the number of links (ANOVA F1 = 6.867, p-value = 0.0114) and centrality (ANOVA F1 = 8.093, p-value = 0.0063). Lichen species richness was also correlated with the number of links (ANOVA F1 = 29.436, p-value = 1.46e-06) and centrality (ANOVA F1 = 39.488, p-value = 6.38e-08). Bark roughness, however, did not significantly predict the number of links (ANOVA F1 = 2.897, p-value = 0.0946) nor the centrality (ANOVA F1 = 2.591, p-value = 0.1134) of

lichen networks. The number of network links (PerMANOVA R2 = 0.392, F1 = 72.4348, p-value = 0.001) and network centrality (PerMANOVA R2 = 0.309, F1 = 57.0440, p-value = 0.001) were highly correlated with network similarity.

Figure: (A) Linkage and centrality by genotype and (B) Total cover and species richness predict L and Cen

Heritability estimates for lichen networks. Table: heritability

- Compare all trait heritabilities
-

Response	H2	R2	p-value
Percent Rough Bark	0.37835	0.37835	4e-04
Lichen Network	0.2784	0.3413	0.0074
Percent Lichen Cover	0.17279	0.17279	0.0362
Number of Network Links	0.16892	0.16892	0.0689
Network Centrality	0.17248	0.17248	0.0627
Lichen Community Composition	0.08526	0.27703	0.09529
Network Modularity	0.04511	0.04511	0.2941
Lichen Species Richness	0.03578	0.03578	0.3137

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

Supplementary: Stats tables

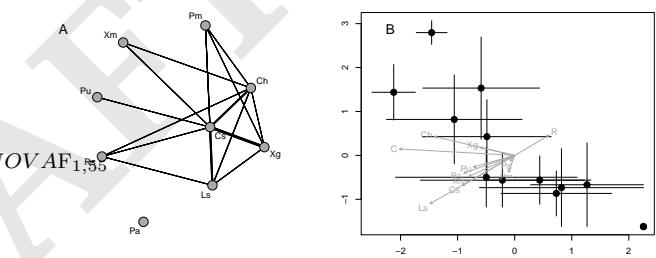


Fig. 3. Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. A) A network diagram showing significant interactions averaged over all trees shown as edges connecting lichen species shown as vertices. B) Genotype centroids (points) of NMDS ordinated lichen networks ($\pm 1 \text{ S.E.}$). Arrows show the magnitude and direction of correlation of the ordinated networks with tree bark roughness (R), network connectance and lichen species abundances (Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rs = *Rinodina* (unknown species), Ls = *Lecanora* (unknown species), Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu = *Physcia undulata*).

Response	Predictor	p-value	H2
Percent Lichen Cover	Tree Genotype	0.0396	0.17
Lichen Species Richness	Tree Genotype	0.1351	0.1
Percent Rough Bark	Tree Genotype	2e-04	0.38
Lichen Network	Genotype	0.0411	0.17
Number of Network Links	Genotype	0.0812	0.15
Network Centrality	Genotype	0.1299	0.12

Table 2. Genotypic effects of cottonwood trees on the associated lichen community.

Discussion

- Rehash of results support hypothesis of genetic basis to network structure
- Genotypic environmental filtering leads to altered interaction network structure and potentially dynamics

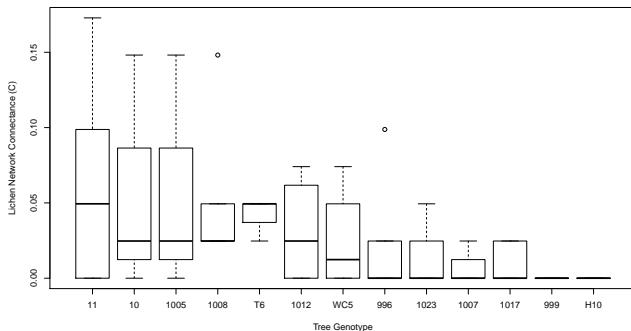


Fig. 4. Connectance significantly varied among genotypes.

- 216 • Indirect effects of genotypes (G -> rough -> cover ->
- 217 richness -> links -> networks)
- 218 • Importance of indirect effects and complexity and relevance
- 219 to IIGEs
- 220 • Conclusion

221 Trait variation + assembly + ecosystem function

222 These findings support the hypothesis that genotypic variation in a foundation species contributes to the structure of a 223 network of interacting species that might be least expected to 224 exhibit such structure.

225 **TGW: MIGHT BE GOOD TO CITE PAPERS
ON COMPEPTITION IN LICHENS OR OTHER ORGANIZING FACTORS TO BACK UP THE LEAST EXPECTED STATEMENT. AS EPIPHYTES WE MIGHT NOT EXPECT THEM TO CARE.**

226 **MKL: This is a job for Lamit and Rikke.**

227 Several lines of evidence support this conclusion. First, the 228 wild stand showed significant interaction network structure 229 (Fig. 1a and b); and both tree genotype and the genetically 230 based tree trait, bark roughness, was a strong predictor of 231 co-occurrence patterns (Fig. 2a).

232 **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 IN INTRO.**

233 **MKL: Same here. This is a job for Lamit and Rikke.**

234 Second, in a long-term common garden study, network (Fig. 235 1b) structure showed a high degree of similarity to the wild 236 stand network structure (Fig. 1c and d). Third, tree genotype 237 was a significant predictor of SES values (Fig. 2a), displaying 238 significant correlation with a genetically linked trait, bark 239 roughness, both in the common garden (Fig. 2a) and in a 240 naturally established stand of trees (Fig. 2b). Last, both of the 241 bipartite genotype-species networks in the common garden and 242 natural stand displayed significant modularity, suggesting that 243 genotypic variation is leading to the formation of evolutionarily 244 dynamic compartments within the community. Thus, just as 245 numerous studies have shown that plant genotype can affect 246 species richness, abundance, diversity, and composition and 247 previous work has demonstrated that evolutionary processes 248

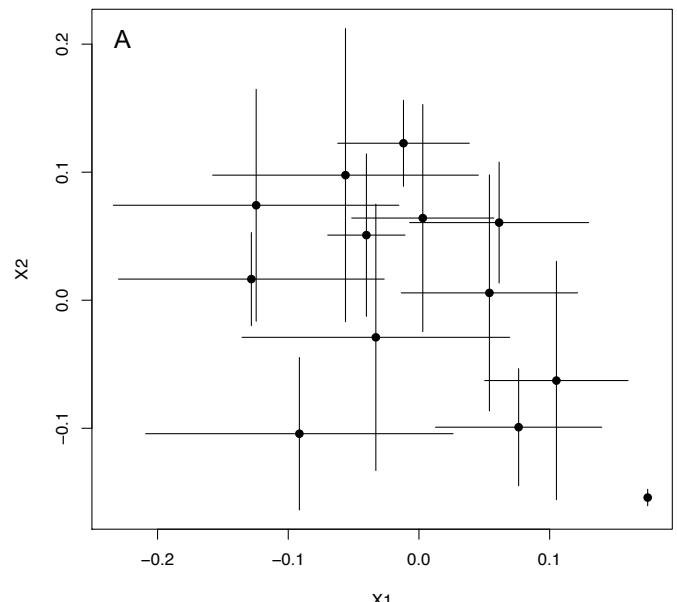


Fig. 5. Tree genotype variation in lichen community composition also contributed to genotype-species bipartite interaction network structure at the scale of the common garden stand. A) Plot of the ordinated community composition scores shown as centroids (± 1 S.E.). B) Bipartite interaction network based on the occurrences of lichen on individual cottonwood trees in the common garden. Edges connecting trees to lichen are scaled by the relative abundance of lichen. Nodes of lichen and trees are colored by their module membership.

- shape ecological networks (11, 12), our study includes genetics in an empirical investigation that combines both experimental common garden findings along with studies in the wild that are in close agreement.
- Our results point to the importance of understanding the community level effects of genetic variation and corroborate previous findings of the importance of plant genetics in shaping community structure and ecosystem processes (13). This study highlights the potential for indirect effects of genetic variation to propagate through networks of interacting species and trophic levels. Altering the structure of interaction networks presents a means for genetic effects to be magnified within the system of interacting species. For example, Keith et al. (2017) 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 (14). Furthermore, in a predator-prey-plant study, Smith (15), showed that the interactions among species across trophic levels depended on plant genotype.
- A. Units of evolutionary potential: Moving beyond species pairs.** 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 (16, 17), although spatial scale of interactions should be considered (18) Bangert et al. 2006. 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 (19). 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.
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