

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 de-
9 gree to which tree genetics can contribute to network structure, we
10 conducted quantitative modeling of interaction network for a commu-
11 nity of epiphytic lichens in a long-term experimental common garden
12 of genotyped trees of a foundation species (*Populus angustifolia*).
13 We found three main results: 1) bark roughness and lichen commu-
14 nities displayed significant responses to tree genotype, 2) tree geno-
15 type strongly contributed to network structure, explaining a third of
16 the variation in lichen interaction networks, and 3) several metrics of
17 interaction network structure varied in response to genotype, includ-
18 ing the number of interactions and centralization. These results sup-
19 port the hypothesis that variation in ecological interaction networks
20 can result from genetically based variation in foundation species.
21 This study opens the possibility for a genetic basis to both direct
22 and indirect interactions among 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, commu-
3 nity 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 structure
8 and ecosystem processes (4–6).

More on ecological networks

10 Community genetics studies (?) have shown that genetic
11 variation in foundation species (7) plays a significant role in
12 defining distinct communities of interacting organisms: such as,
13 endophytes, pathogens, lichens, arthropods, and soil microbes.
14 Multiple studies have now demonstrated that genetic variation
15 influences numerous functional traits (e.g., phytochemical, phe-
16 nological, morphological) produces a multivariate phenotype
17 (8) that contributes to variation in associated communities (9).

18 Additional work has provided support for the hypothesis
19 that not only does composition vary among genetically distinct
20 genotypes of foundation species but it also impacts the struc-
21 ture of the network of species interactions in these communities
22 (? ?). Also, work by (10 ? ?) observed consistent patterns
23 of centralized interactions of species modules focused around
24 hubs of plant-fungal interactions. In other words, a small
25 number of plant and fungal symbionts tended to have have

disproportionate numbers of interactions with other species
26 and likely are the drivers in determining community assembly,
27 structure and dynamics.

28 Here, we investigate how genetic variation in a foundation
29 tree species determines the structure of a network of inter-
30 actions among a community of tree associated lichen species.
31 Using a long-term (20+ years), common garden experiment
32 with replicated individuals of known genetic identity and a
33 naturally established stand of *Populus angustifolia*. We fo-
34 cused on a model community of 9 epiphytic lichens species,
35 as previous research has demonstrated significant compo-
36 sitional responses of epiphytes to genotypic variation (11, 12).
37 In addition, the life-history characteristics of lichen, having
38 highly localized, direct contact interactions and slow popula-
39 tion turnover rates, allowed us to assess interactions among
40 lichen species on individual trees. We hypothesize that in natu-
41 ral systems evolution occurs in a community context involving
42 interactions of complex networks of interacting species (13)?
43 ? ? ? . If correct, we should expect to find that network
44 structure is genetically based in which different plant geno-
45 types support different interaction networks and that these
46 interactions networks can function as indicators of ecological
47 dynamics important for conserving biodiversity. Applying
48 a probability-theory based network modeling approach, we
49 constructed a set of interaction network models for the lichen
50 associated with individual trees. Using these models, we then
51 examined the genetic basis a foundation tree species on the
52 structure of ecological networks.

Materials and Methods

The study was conducted along the Weber River, UT (USA),
55 which is a cottonwood (*Populus* spp.) dominated riparian ecosystem.
56

Significance Statement

Authors must submit a 120-word maximum statement about
the significance of their research paper written at a level under-
standable to an undergraduate educated scientist outside their
field of speciality. The primary goal of the Significance State-
ment 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 substantively to the conceptual development, T.W. established the common garden. All authors contributed to revisions of the manuscript.

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58 Although two native species, *Populus angustifolia* (James) and *Populus 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 km^2)
 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
 71 each lichen species was assessed in 50 total 1 cm^2 cells arrayed in
 72 a checkerboard pattern. Given the small size and sessile nature
 73 of lichen, we were able to rapidly assess lichen interactions by
 74 quantifying thalli in close contact. Sampling was restricted to
 75 the northern aspect of the trunk to maximize the abundance of
 76 lichen and control for the effect of trunk aspect. Two adjacent
 77 10 cm^2 quadrats centered at 50 cm and 85 cm from ground level
 78 were sampled (Fig 1 A and B). The bark lichen community in this
 79 system is comprised of fourteen species; however, only 9 species
 80 were observed within our study quadrats (Fig 1 C-K). The observed
 81 lichen community included (abbreviations are given for species
 82 present in study): Xg = *Xanthomendoza galericulata*, Xm = *X.*
 83 *montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*,
 84 Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Ls = *Lecanora*
 85 sp., Pm = *Phyciella melanachra*, Pa = *Physcia adscendens*, Pu =
 86 *Physcia undulata*. Several other species were not observed in the
 87 present study but are known to occur in this region: *Phaeophyscia*
 88 *orbicularis*, *Phaeophyscia ciliata*, *Melanelia sublivacea*, *Meanelia*
 89 *elegantula*. Species accumulation curves indicated that communities
 90 in the the common garden were thoroughly sampled and similar in
 91 composition and richness to nearby naturally established cottonwood
 92 stands (Supplementary Materials).

93 The cell size and checkerboard sampling pattern was chosen to
 94 isolate the individuals in each cell. In a previous survey of lichen
 95 thallus size in this common garden, we had observed a median thallus
 96 size of $0.12 \pm 0.001 \text{ cm}^2$ (S.E.) (?). Based on this, we expected
 97 thalli observed in each cell to generally be spatially independent
 98 of the other cells in the quadrat but exposed to similar micro-
 99 environmental conditions created by the bark and the location of the
 100 sampling area on an individual tree. Therefore, we were confident
 101 in treating the cell-wise observations in quadrats as independent
 102 with respect to lichen-lichen interactions.

103 As bark roughness had previously been shown to be an important,
 104 genetically based tree trait impacting bark lichen, we measured the
 105 percentage of rough bark on each tree following the methods of (?).
 106 Briefly, the number of cells containing disrupted, fissured bark
 107 were counted within each quadrat on each tree. The number of
 108 rough bark containing cells were then summed and divided by the
 109 total number of cells surveyed. This was done for all quadrats on
 110 all trees in which lichen communities were also observed.

111 **Lichen Network Modeling and Analysis.** We used the observations of
 112 lichen in the 1cm^2 cells on individual trees of *P. angustifolia*. Uni-
 113 partite networks were generated using the conditional probabilities
 114 of each species pair, i.e. the probability of observing one species
 115 given an observation of another species ($P(A|B)$), based on the
 116 method developed by (14). To calculate conditional probabilities,
 117 we quantified the individual probabilities of species occurrences
 118 ($P(A)$) and the joint probability of co-occurrences ($P(A, B)$) using
 119 the frequencies of each species and their co-occurrences. We were
 120 then able to calculate the conditional probabilities of each species
 121 pair as $P(A|B) = \frac{P(A, B)}{P(B)}$, based on the axioms of probability. This
 122 yielded an asymmetric matrix, that is $P(A|B)$ does not have to be
 123 equal to $P(B|A)$ with a trace equal to the identity matrix (i.e.
 124 $P(A|A) = 1$).

125 Once these network matrices were constructed using the condi-
 126 tional probabilities of species pairs, we then applied an analytical
 127 procedure to remove non-significant links between species (Fig. 2).
 128 This procedure determines if the joint probability of a species

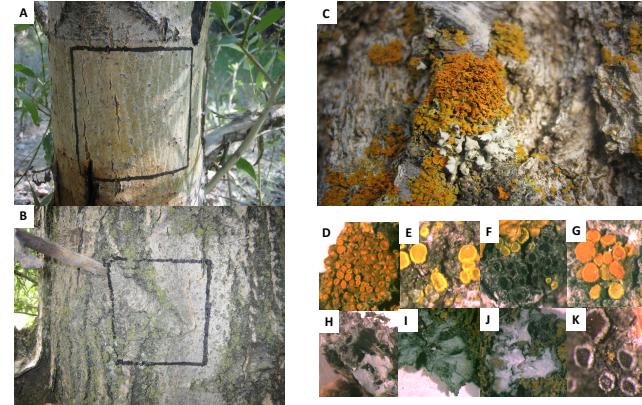


Fig. 1. The communities of bark lichen were observed in a common garden of replicated genotypes of narrowleaf cottonwood trees (*P. angustifolia*) at the Ogden Nature Center (Ogden, UT). Lichen were sampled within a fixed area ($10\text{cm} \times 10\text{cm}$) on individual trees (A and B). (C) a photo 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*, *Phyciella melanachra*, *Physcia undulata* and *Lecanora hagenii*.

pair (i.e. $P(S_i S_j)$) is different from zero. If the frequency of co-
 130 occurrences ($S_i S_j$) falls outside of the interval ($CI_{95\%}$), the joint
 131 probability is inferred to be non-zero. Here, $CI_{95\%}$ is calculated
 132 as $CI_{95\%} = E[S_i S_j] * Z_{95\%} * \sqrt{V(S_i S_j)}$, where the expected
 133 frequency of co-occurrences ($E(S_i S_j)$) is the total number of cells
 134 surveyed (N) times the independent probabilities of each species
 135 ($P(S_i) * P(S_j)$), $Z_{95\%}$ is the Z-score for 95% from a Z-distribution
 136 and the expected variance of $E(S_i S_j)$ is the total number of cells
 137 times the expected probability of $S_i S_j$ and its compliment (i.e.
 138 $V(S_i S_j) = N * E[P(S_i S_j)] * (1 - E[P(S_i S_j)])$). If the observed
 139 number of co-occurrence falls outside of the confidence interval,
 140 the joint probability ($P(S_i S_j)$) is determined to be equal to the
 141 product of the individual probabilities (i.e. $P(S_i)P(S_j)$), and the
 142 conditional probability reduces to the individual probability of that
 143 species ($P(S_i)$). Therefore, unless the co-occurrence of a species
 144 pair falls outside the confidence interval, the probability that the
 145 observation of one species given the other is no different than simply
 146 observing that species alone. This enables us to remove links from
 147 a given network by re-scaling the resulting conditional probabilities
 148 by subtracting the individual probabilities from the conditional
 149 probabilities (i.e. how different the conditional probability is from
 150 the independent probability), which makes any species with a non-
 151 significant conditional probability zero. The resulting matrix (D_{ij})
 152 can be interpreted as how one species impacts another with zero
 153 being no effect and values less than or greater than zero interpreted
 154 as negative and positive effects, respectively.

155 **Statistical Analyses, Software and Data.** We used a combination of
 156 parametric and non-parametric, permutation based frequentist statistical
 157 analyses to test for the effects of genetic variation on lichen
 158 communities and their interaction networks.

- REML 160
- Least squares models 161
- Multivariate 162
 - Distance Metrics = Euclidean and Bray-Curtis 163
 - PerMANOVA 164
 - Mantel tests 165
- Network metrics 166
 - Number of edges 167
 - Centralization 168

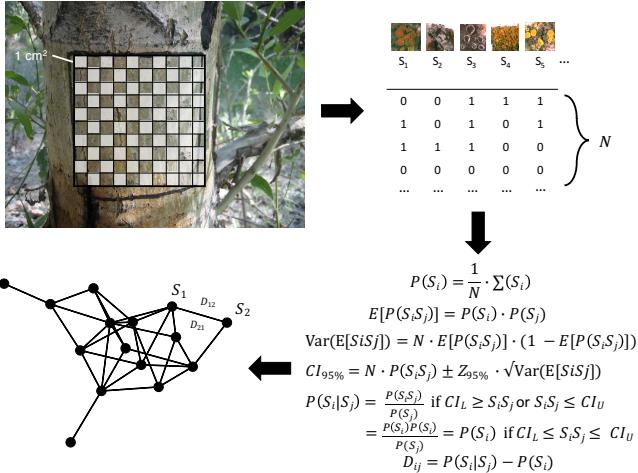


Fig. 2. Lichen interaction networks were constructed by conducting field observations in 1 cm^2 cells within a 10 cm^2 grid on each tree using a checkerboard pattern (grey cells). Thus, a set of N total cell observations were recorded for each tree with the presence or absence of each species recorded for each cell. Applying the probability-based network modeling method adapted from (14), 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 .

206

— Centrality

169 • Code and data available via github and zenodo

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

173 Results

Bark roughness and some lichen community characteristics responded to tree genotype. Percent rough bark varied significantly among genotypes (REML RLRT = 10.69, p-value = 3e-04), as did total lichen cover (REML RLRT = 2.9627, p-value = 0.0375) and community composition (PerMANOVA $R^2 = 0.243$, F 12 = 1.8221, p-value = 0.0029). However, lichen species richness did not show a significant response to genotype (REML RLRT = 0.13047, p-value = 0.3134). Community composition was correlated with lichen cover (PerMANOVA $R^2 = 0.236$, F 1 = 21.2661, p-value = 9.999e-05) and richness (PerMANOVA spr.onc $R^2 = 0.054$, F 1 = 4.9036, p-value = 0.0011) after controlling for tree genotype effects (Fig. 3). Roughness did not predict community composition (PerMANOVA $R^2 = 0.011$, F 1 = 0.9938, p-value = 0.3841) even though it was correlated with total lichen cover (ANOVA $F_{1,55} = 6.797$, p-value = 0.01173). Roughness was not correlated with lichen species richness (ANOVA $F_{1,55} = 1.509$, p-value = 0.2246).

Tree genotype influenced lichen network similarity. 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. hagenii* (0.40). The centralization of the remaining species were *R. sp.* (0.18), *X. galericulata* (0.14), *P. melanochra* (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. Interactions tended to be positive (QUANTIFY!!!); however, *X. galericulata*, although not the most central species, frequently tended to decrease the presence of other species.

Lichen networks observed on trees of the same genotype tended to be similar in structure. Tree genotype significantly predicted

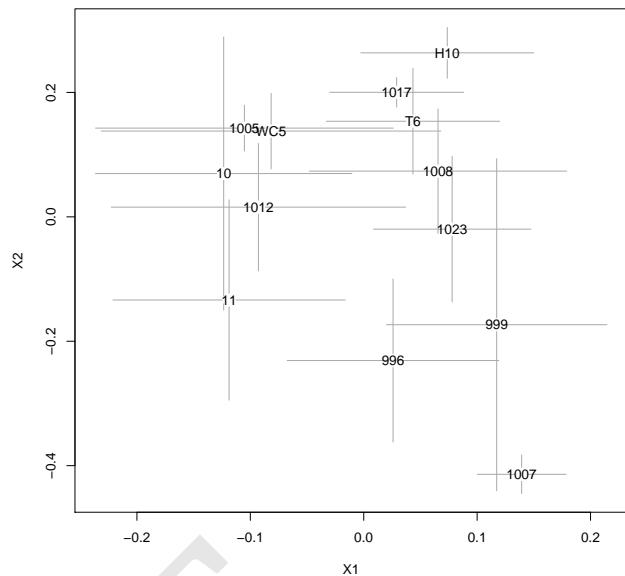


Fig. 3

the similarity of lichen interaction networks (PerMANOVA $R^2 = 0.33795$, F 12 = 2.5379, p-value = 0.0050). Lichen species richness was also a significant predictor of network similarity after controlling for genotype (PerMANOVA $R^2 = 0.3413$, F 1 = 2.5417, p-value = 0.00739); however, neither total cover (PerMANOVA $R^2 = 0.023$, F 1 = 2.0628, p-value = 0.1487) nor roughness (PerMANOVA $R^2 = 0.011$, F 1 = 0.0497, p-value = 0.3394) predicted network similarity (Fig. 5). 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 (Fig. ??). Total cover was correlated with the number of links (ANOVA F 1 = 6.867, p-value = 0.0114) and centrality (ANOVA F 1 = 8.093, p-value = 0.0063). Lichen species richness was also correlated with the number of links (ANOVA F 1 = 29.436, p-value = 1.46e-06) and centrality (ANOVA F 1 = 39.488, p-value = 6.38e-08). Bark roughness, however, did not significantly predict the number of links (ANOVA F 1 = 2.897, p-value = 0.0946) nor the centrality (ANOVA F 1 = 2.591, p-value = 0.1134) of lichen networks. The number of network links (PerMANOVA $R^2 = 0.392$, F 1 = 72.4348, p-value = 0.001) and network centrality (PerMANOVA $R^2 = 0.309$, F 1 = 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
-
- Supplementary: Stats tables

Discussion

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

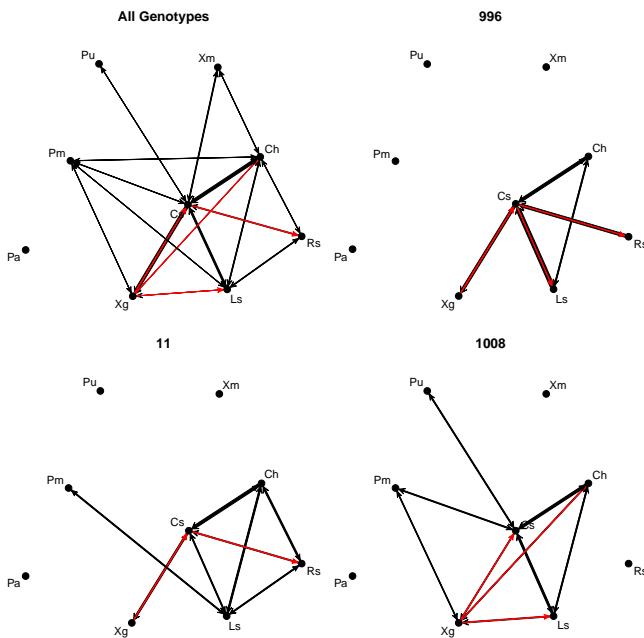


Fig. 4. Significant lichen interaction networks across genotypes.

Response	H2	R2	p-value
Percent Rough Bark	0.37835	0.37835	3e-04
Network Centrality	0.20166	0.20166	0.04132
Percent Lichen Cover	0.17279	0.17279	0.0358
Number of Network Links	0.17016	0.17016	0.0636
Lichen Community Composition	0.16093	0.24287	0.0028
Lichen Network	0.10067	0.27469	0.0137
Network Modularity	0.05731	0.05731	0.2863
Lichen Species Richness	0.03578	0.03578	0.3241

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

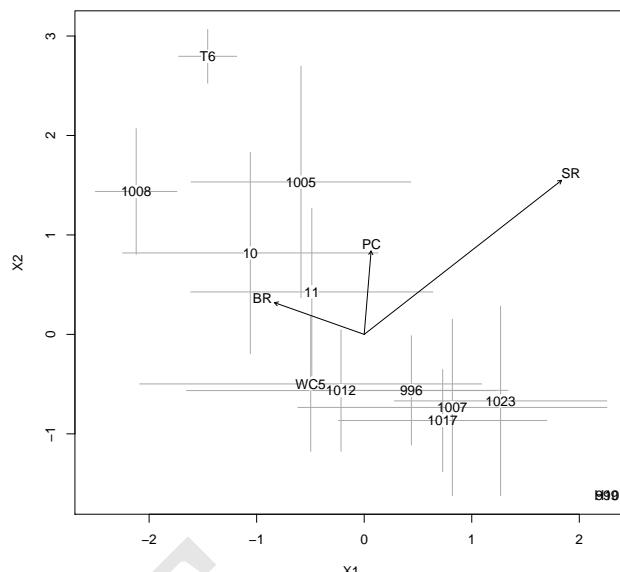


Fig. 5. Significant lichen interaction network structure resulting from tree genotypic variation was observed in the common garden. The plot shows genotype centroids (points) of NMDS ordinated lichen networks (± 1 S.E.). Centroids that are closer in ordination space are more similar in the structure 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).

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.

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

Second, in a long-term common garden study, network (Fig. 1b) structure showed a high degree of similarity to the wild stand network structure (Fig. 1c and d). Third, tree genotype was a significant predictor of SES values (Fig. 2a), displaying significant correlation with a genetically linked trait, bark roughness, both in the common garden (Fig. 2a) and in a naturally established stand of trees (Fig. 2b). Last, both of the bipartite genotype-species networks in the common garden and natural stand displayed significant modularity, suggesting that genotypic variation is leading to the formation of evolutionarily dynamic compartments within the community. Thus, just as numerous studies have shown that plant genotype can affect species richness, abundance, diversity, and composition and previous work has demonstrated that evolutionary processes shape ecological networks (15, 16), 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 (6). This study highlights the potential for indirect effects of genetic varia-

- Indirect effects of genotypes (G - rough - cover - richness - links - networks)
- Importance of indirect effects and complexity and relevance to IIIGEs
- Conclusion

Trait variation + assembly + ecosystem function

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

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

MKL: This is a job for Lamit and Rikke.

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

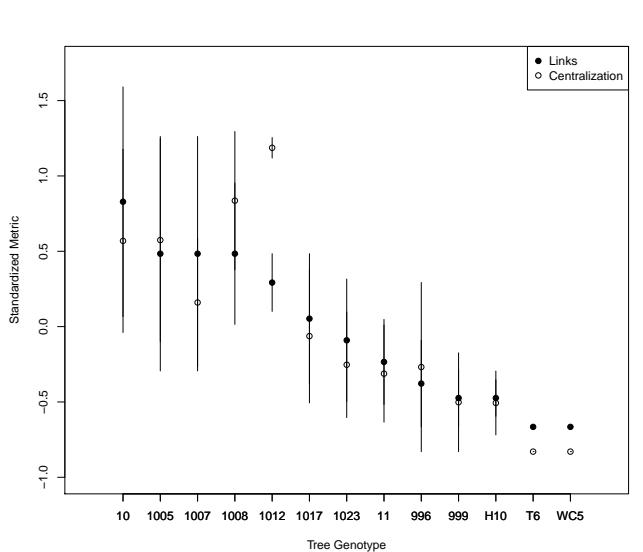


Fig. 6. The impact of tree genotype on lichen network structure was indicative of variation in both the number variation in lichen interactions among species. This Cleveland plot shows the means and standard errors (SE) for two lichen network metrics (number of links and centralization) for all genotypes. Both metrics are presented as standardized scores ($\frac{x-\bar{x}}{\sigma}$).

tion 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 (17). Furthermore, in a predator-prey-plant study, Smith (18), 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 (19, 20), although spatial scale of interactions should be considered (21) 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 (22). 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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- 328 1. Fontaine C, et al. (2011) The ecological and evolutionary implications of merging different
329 types of networks. *Ecol. Lett.* 14(11):1170–81.
330 2. Bascompte J, Jordano P, Olesen JM (2006) Asymmetric Coevolutionary Networks Facilitate
Biodiversity Maintenance 10.1126/science.1123412. *Science* (80-.). 312:431–433.
331 3. Rafferty NE, Ives AR (2013) Phylogenetic trait-based analyses of ecological networks. *Ecol-*
ogy 94(10):2321–33.
332 4. Crutsinger GM (2016) A community genetics perspective: Opportunities for the coming
decade. *New Phytol.*
333 5. Rezende EL, Lavabre JE, Guimarães PR, Jordano P, Bascompte J (2007) Non-random coex-
334 tinctions in phylogenetically structured mutualistic networks. *Nature* 448(7156):925–8.
335 6. Whitham TG, et al. (2006) A framework for community and ecosystem genetics: from genes
336 to ecosystems. *Nat. Rev. Genet.* 7:510–523.
337 7. 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.
338 8. Holeski LM, Hillstrom ML, Whitham TG, Lindroth RL (2012) Relative importance of genetic,
ontogenetic, induction, and seasonal variation in producing a multivariate defense phenotype
339 in a foundation tree species. *Oecologia* 170:695–707.
340 9. Bailey JK, et al. (2009) From genes to ecosystems: a synthesis of the effects of plant
genetic factors across levels of organization. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*
341 364(1523):1607–16.
342 10. Toju H, Guimarães PR, Olesen JM, Thompson JN (2014) No Title. *Nat. Commun.* 5:5273.
343 11. Winfree R, Gross BJ, Kremen C (2011) Valuing pollination services to agriculture. *Ecol. Econ.*
71:80–88.
344 12. Zytynska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree
345 species influences the associated epiphytic plant and invertebrate communities in a complex
forest ecosystem. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366:1329–1336.
346 13. Thompson JN (2013) *Relentless Evolution.* (University of Chicago Press), p. 499.
347 14. Araújo MB, Rozenfeld A, Rahbek C, Marquet PA (2011) Using species co-occurrence net-
348 works to assess the impacts of climate change. *Ecography (Cop.)*. 34:897–908.
349 15. Guimarães PR, Jordano P, Thompson JN (2011) Evolution and coevolution in mutualistic
350 networks. *Ecol. Lett.* 14(9):877–85.
351 16. Moya-Laraño J (2011) Genetic variation, predator-prey interactions and food web structure.
352 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366(1569):1425–37.
353 17. Borgatti SP, Everett MG (2006) A Graph-theoretic perspective on centrality. *Soc. Networks*
354 28:466–484.
355 18. Smith DS, Bailey JK, Shuster SM, Whitham TG (2011) A geographic mosaic of trophic inter-
actions and selection: trees, aphids and birds. *J. Evol. Biol.* 24(2):422–9.
356 19. Rowntree JK, Shuker DM, Preziosi RF (2011) Forward from the crossroads of ecology and
357 evolution. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366(1569):1322–8.
358 20. Whitham TG, et al. (2012) Community specificity: Life and afterlife effects of genes.
359 21. Zook AE, Eklof A, Jacob U, Allesina S (2010) Food webs: Ordering species according to body
size yields high degree of intervality. *J. Theor. Biol.* 271(1):106–113.
360 22. Evans DM, Pocock MJ, Memmott J (2013) The robustness of a network of ecological net-
361 works to habitat loss. *Ecol. Lett.* 16:844–52.
362