

Genotypic variation in foundation trees generates ecological network structure

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ABSTRACT

Biological evolution is argued to occur in the context of complex networks of interacting species in which natural selection defines the structure of ecological networks^{1,2,3}. However, fundamental to this evolutionary process is the discovery of a genetic basis to ecological network structure, which remains largely unknown. Here, we use both a long-term experimental common garden² with genotyped individuals and a natural riparian forest of the foundation tree species⁴ *Populus angustifolia*, to test how genetic variation contributes to the interaction network structure of a model community comprised of epiphytic lichens. We found three main results: 1) lichen communities showed significant unipartite (i.e., one mode) network structure that was similar between the common garden and a natural stand, 2) individual tree genotype significantly influenced lichen species interactions, which was strongly correlated with bark roughness, a genetically based trait in cottonwoods² known to influence epiphytic lichen², and 3) bipartite (two mode) genotype-species networks, comprised of the foundation species and its associated lichen community, showed significant modular structure in both the common garden and natural stand. In demonstrating a strong genetic component to ecological network structure, selection differentially acting on different tree genotypes will likely alter network structure and vice-versa, selection acting on the network in a community context could feed back to affect plant performance and evolution. Such findings set the stage for quantifying community evolution and the evolution of Darwin's 'entangled bank', a metaphor that characterizes the complexity and interconnectedness of complex communities in nature.

¹ Abstract is still not showing in rich text mode and I've changed the last two lines to better reflect what I think is
² novel and important

Introduction

Evolution occurs in the context of complex networks of interacting species. In ecological communities, community dynamics depend on key interactions⁵ that occur in species interaction networks, such as: trophic⁶ and mutualistic⁷ interaction networks. Phylogenetic patterns in ecological networks support the importance of evolutionary processes in shaping species interactions, community structure and ecosystem processes^{2,1,8}. Community genetics studies⁹ have shown that genetic variation in foundation species⁴ plays a significant role in defining distinct communities of interacting organisms: such as, endophytes, pathogens, lichens, arthropods, and soil microbes. Multiple studies have now demonstrated that genetic variation influences numerous functional traits (e.g., phytochemical, phenological, morphological) produces a multivariate phenotype¹¹ that contributes to variation in associated communities¹⁰. Additional work has provided support for the hypothesis that not only does composition vary among genetically distinct genotypes of foundation species but it also impacts the structure of the network of species interactions in these communities^{2,2}.

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Lau, M.K., A.R. Keith, S.R. Borrett, S.M. Shuster, and T.G. Whitham. 2016. Genotypic variation in foundation species generates network structure that may drive community dynamics and evolution. *Ecology* 97:733-742.

Crutsinger, G.M., 2016 A community genetics perspective: opportunities for the coming decade. *New Phytologist*, 210, 65-70.

Last, previous work has indicated that

add newer lit studies here.

- Daves 2016 paper
- Jamie's 2016 paper
- McKnight's paper: ecological networks are connected across aquatic and terrestrial systems and impact evolutionary processes
- Nat Eco Evo 2017:
- Liza and Amy 2017:
- Ghering 2017: Tree genetics defines fungal partner communities that may confer drought tolerance
- Bothwell 2017: Precipitation gradients and river networks drive genetic connectivity and diversity in a foundation riparian tree
- Poisot

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 that might be least expected to support different interaction networks on different tree genotypes. 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^{15,16}. 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^{?,?,?.?}. If correct, we should expect to find that network structure is genetically based in which different plant genotypes support different interaction

66 networks and that these interactions networks can function as indicators of ecological dynamics important for conserving
67 biodiversity. Applying a dual-scale (lichen-lichen and genotype-lichen interactions) network analysis approach, we then
68 examined the genetically based impacts of *P. angustifolia* on network structure.

69 Results

70 Tree Genotype Influences Ecological Network Structure

71 In both the experimental garden and the natural stand, we discovered that genotypic variation in a *P. angustifolia* predictably
72 influenced the structure of the lichen species interaction network and contributed to the formation of evolutionary modules
73 comprised of tree genotypes and the lichen community. We focused our network analysis on modularity (i.e. the formation
74 of compartments) and nestedness (i.e. the overlap in sets of interactions among species) both of which are of interest in the
75 context of the interplay between ecological and evolutionary dynamics as have established theoretical and empirical support as
76 relevant structural metrics of ecological dynamics and can serve as indicators of the units of evolution in a community context.
77 We observed significant unipartite (one-mode) network structure¹⁷ in the lichen species interaction networks that was similar
78 between the experimental garden and the natural stand (Fig. 1a and 1b; Garden: $z = -6.31$, $p = 0.0002$; Natural: $z = -3.15$, $p =$
79 0.002). The two networks displayed high multivariate structural similarity (Mantel $R = 0.51$, $p = 0.029$).

80 Node level eigen-centrality¹⁸, a measure of species importance that integrates indirect connections, showed strong correlation
81 between the two stands (Fig. 1c; $r = 0.7$, $t = 2.6135$, $df = 7$, $p = 0.035$). Centrality was also highly correlated with total
82 abundance in both networks (Fig. 1d; Garden: $r = 0.77$, $t = 3.2427$, $df = 7$, $p = 0.014$; Natural: $r = 0.86$, $t = 4.43$, $df = 7$, $p =$
83 0.003). In combination, the similarity of both the whole and node level network structure between the common garden and the
84 wild indicates that the common garden environment captures much of the natural variation that exists in nature and accurately
85 reflects natural processes.

86 Network Response to Tree Trait Variation

87 In the common garden, where the effect of environmental variation was controlled, genotype was an important factor contributing
88 to network structure. Genotype was a significant predictor of interactions on individual trees (Fig. 2a; $F = 3.4213$, num $df =$
89 12.000 , denom $df = 14.668$, $p\text{-value} = 0.01426$). Similar to the effect of a genetically controlled trait (bark roughness) on a
90 dominant lichen⁴, we found that individual tree genotypes with similar levels of bark roughness had similar levels of lichen
91 interactions (Fig. 2a; Mantel $R = 0.08$, $p = 0.013$), which was similar to the correlation observed between bark roughness and
92 lichen interactions in the natural stands (Fig 2b: $r = -0.53$, $p = 0.050$).

93 Genetic Structure Generates Foret-Scale Network Structure

94 We also examined how *P. angustifolia* genotypic differentiation contributes to the formation of groups of tree genotypes and
95 lichen species and found significant modular structure. Using a bipartite (two-mode) network approach in which genotype-
96 species networks were modeled using the species maximum relativized values of each lichen species across all *P. angustifolia*

97 genotypes, we found significant modularity in the common garden stand (Fig. 3a; $z = 9.64$, $p < 0.001$). When using the same
98 analyses on individual trees in the natural stand, we also found significant modularity (Fig. 3b; $z = 7.42$, $p < 0.001$). Furthermore,
99 nestedness of both of these networks was significantly lower than expected under a null model (Garden: $z = -2.30$, $p < 0.001$;
100 Natural Stand: $z = -2.84$, $p < 0.001$), most likely as a result of module formation.

101 Discussion

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

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

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

108 Several lines of evidence support this conclusion. First, the wild stand showed significant interaction network structure (Fig.
109 1a and b); and both tree genotype and the genetically based tree trait, bark roughness, was a strong predictor of co-occurrence
110 patterns (Fig. 2a).

111 **TGW: I THINK WE NEED TO EMPHASIZE THE LONG-TERM NATURE OF OUR COMMON GARDEN**
112 **STUDY AS VERY FEW COMMON GARDEN STUDIES OF LICHENS LIKELY EXIST. ANY REFS ON THIS? IF**
113 **TRUE MIGHT WANT TO MENTION THIS UP FRONT IN INTRO.**

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

115 Second, in a long-term common garden study, network (Fig. 1b) structure showed a high degree of similarity to the wild
116 stand network structure (Fig. 1c and d). Third, tree genotype was a significant predictor of SES values (Fig. 2a), displaying
117 significant correlation with a genetically linked trait, bark roughness, both in the common garden (Fig. 2a) and in a naturally
118 established stand of trees (Fig. 2b). Last, both of the bipartite genotype-species networks in the common garden and natural
119 stand displayed significant modularity, suggesting that genotypic variation is leading to the formation of evolutionarily dynamic
120 compartments within the community. Thus, just as numerous studies have shown that plant genotype can affect species richness,
121 abundance, diversity, and composition and previous work has demonstrated that evolutionary processes shape ecological
122 networks^{2,3}, our study includes genetics in an empirical investigation that combines both experimental common garden findings
123 along with studies in the wild that are in close agreement.

124 Our results point to the importance of understanding the community level effects of genetic variation and corroborate
125 previous findings of the importance of plant genetics in shaping community structure and ecosystem processes⁸. This study
126 highlights the potential for indirect effects of genetic variation to propagate through networks of interacting species and trophic
127 levels. Altering the structure of interaction networks presents a means for genetic effects to be magnified within the system
128 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 flux¹⁹. Furthermore, in a predator-prey-plant study, Smith², showed that the interactions among species across trophic levels depended on plant genotype.

Tylianakis 2010 Conservation of species interaction networks.

- Functions-Metrics (Figure 2:

- Richness/Connectance = Increased function and function stability
- Nestedness = Buffer extinctions in mutualistic networks
- Compartmentalization = greater stability, slow spread of disturbance (i.e. trophic cascades)
- Proportion of Weak Links = stability, fewer cascades
- Connectivity Distribution = Indicate Assembly, Robustness to 2nd extinctions

- Focus on metrics that saturate quickly with sampling

- Connectivity, Compartmentalization, Nestedness

- Need more research on the impacts of perturbations on these networks

- Networks working at multiple scales re-inforce connectivity

- Gene networks (Zink)

- Community networks (Keith2017, Lau 2016)

- Stand scale (This work)

- Landscape scale (Bothwell2017)

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^{2,20}, although spatial scale of interactions should be considered²¹ 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 functions²². 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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Methods

Field observations in common garden and natural riparian forest stands

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.

A common garden was used to isolate the effect of tree genotype from the effect of the localized microenvironment associated with each individual and spatial autocorrelation. Asexually propagated clones of genotyped *P. angustifolia* individuals⁴ were obtained from wild collections and planted randomly in a single field (0.025 km²) at the Ogden Nature Center, Ogden, UT in 1992. A total of thirteen genotypes replicated between 3 and 8 times each, were chosen for sampling. Genotype names were previously published². Observations were made in the common garden in October 2010 and May 2011.

The natural stand of *P. angustifolia* near the city of Uintah, UT (GPS: N41.13903, W110.94400) was used for the wild stand survey. We conducted sampling of the stand in May 2012. A total of 14 trees were chosen randomly over a 0.10 km² area with a minimal distance of 5.56 m between trees across a range of tree core based ages from 15 to 60 years.

Bark and Lichen Community Observations

On each tree, presence or absence of each lichen species was assessed in 50 total 1 cm² cells arrayed in a checkerboard pattern. Two adjacent 10 cm² quadrats centered at 50 cm and 85 cm from ground level were sampled. The checkerboard sampling pattern was chosen to isolate each cell based on an average thallus size of 1 cm². Samples were restricted to the northern aspect of the trunk to maximize the abundance of lichen and control for the effect of aspect. The thalli in each cell are expected to be spatially independent of the other cells in the quadrat, but exposed to similar micro-environmental conditions. Bark roughness was measured on each tree following¹⁵.

The bark lichen community in this system is comprised of fourteen species; however, only 9 species were observed within our study quadrats. The lichen community included (abbreviations are given for species present in study): Xg = *Xanthomendoza galericulata*, Xm = *X. montana*, Ch = *Caloplaca holocarpa*, Cs = *Candelariella subdeflexa*, Rg = *Rinodina glauca*, Lh = *Lecanora hagenii*, Ls = *Lecanora* (unknown species), Pm = *Phyciella melanchra*, Pa = *Phycia adscendens*, Pu = *Phycia undulata*, *Phaeophyscia orbicularis*, *Phaeophyscia ciliata*, *Melanelia subolivacea*, *Meanelia elegantula*, including both crustose and foliose lichen species that exhibit low inter-annual variation⁹. We were able to rapidly assess lichen interactions by quantifying thalli in closed contact as assessed using 1 cm² cells. Species accumulation curves showed that communities in the wild and the common garden were thoroughly sampled and with very similar species richness (Supplementary Materials).

Network modeling and analyses

We used the observations of lichen in the 1cm² cells on individual trees of *P. angustifolia* both in the common garden and the natural stand. Uni-partite networks were generated using an analytical procedure that removes non-significant interactions

between species¹⁷. We used a null model based approach for all other analyses of network structure. A conservative null model that constrained both the row and column marginal totals was used in order to account for the effects of variation in species' total abundances²⁴. From a total of 5000 null matrices, a standardized score was calculated for each statistic ($z = \frac{x_{obs} - \bar{x}_{sim}}{sd_{sim}}$), including the C-score²³, nestedness²⁴ and modularity²⁵. Here, we follow the convention of the co-occurrence literature and refer to the standardized C-Score as the Standardized Effect Size (SES)².

A correlation test with Pearson's r was used to test for the correlation between the wild and common garden networks. A Welch Analysis of Variance (ANOVA), which relaxes the assumption of homogeneity of variance, was used to test for the effects of genotype on tree scale SES values. A permutation based Mantel Test was used to test for the effect of bark roughness on SES values in the common garden.

Data and Analytical Software Availability

All analyses were conducted using the R statistical programming language². Code for the analyses is available on github and data are available at Figshare.

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273 **Author contributions statement**

274 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
275 the first draft of the manuscript, S.B. and T.W. contributed substantively to the conceptual development, T.W. established the
276 common garden. All authors contributed to revisions of the manuscript.

277 **Additional information**

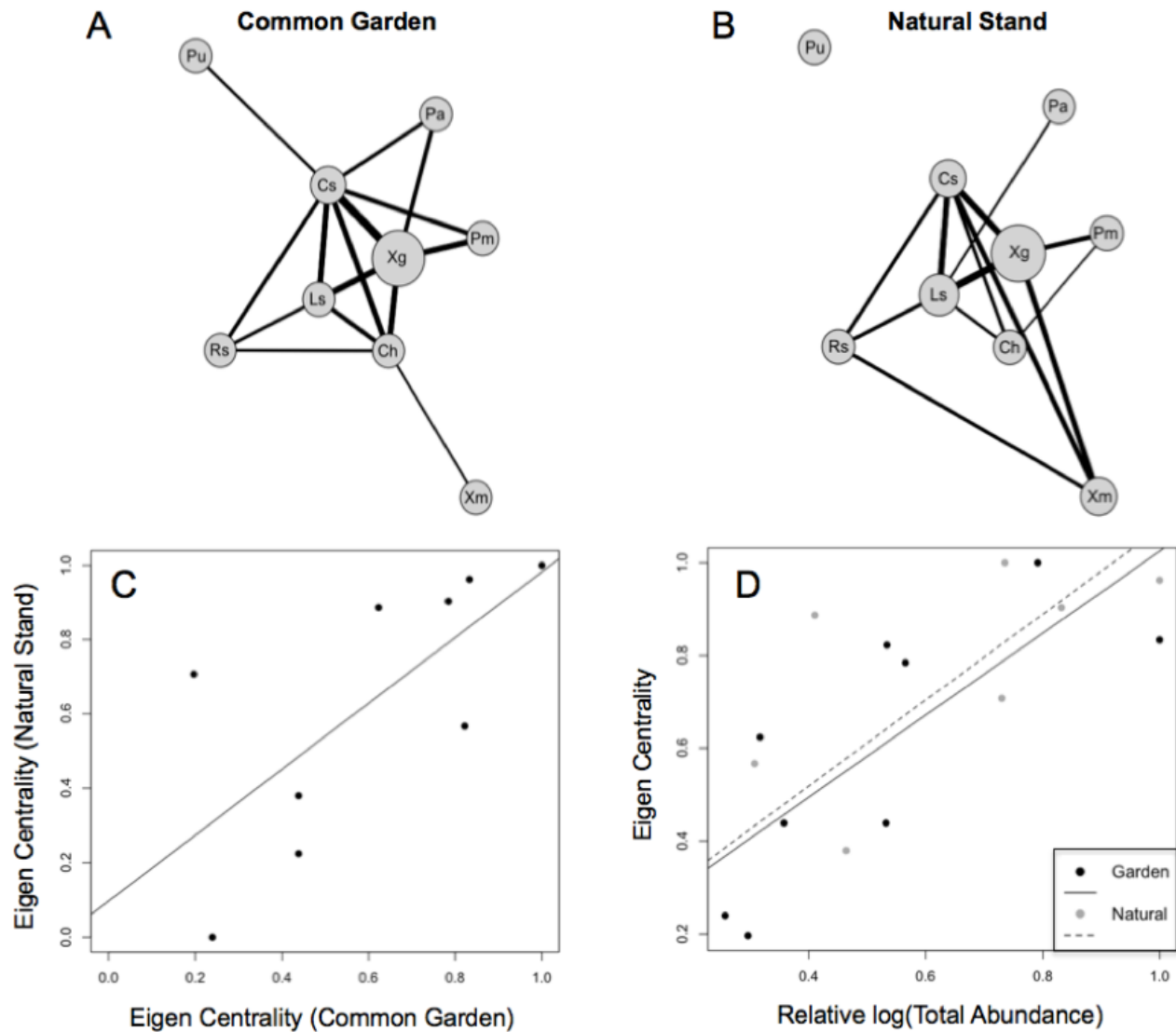


Figure 1. Significant unipartite network structure was observed for epiphytic lichens on trees of known genotype in a common garden (ONC = Ogden Nature Center, Utah, USA) (A) and individual trees in a natural stand (Uintah, Utah, USA) (B) of the foundation species, *Populus angustifolia*. Both networks are shown here with lichen species as nodes (see Methods for complete species names) scaled by the log of their total abundances and significant co-occurrence patterns between species shown as edges scaled by their log frequencies. The bivariate plot (C) shows the significant correlation in Eigen Centrality between the two networks. (D) The total abundance of lichen species was a significant driver of network structure for both networks.

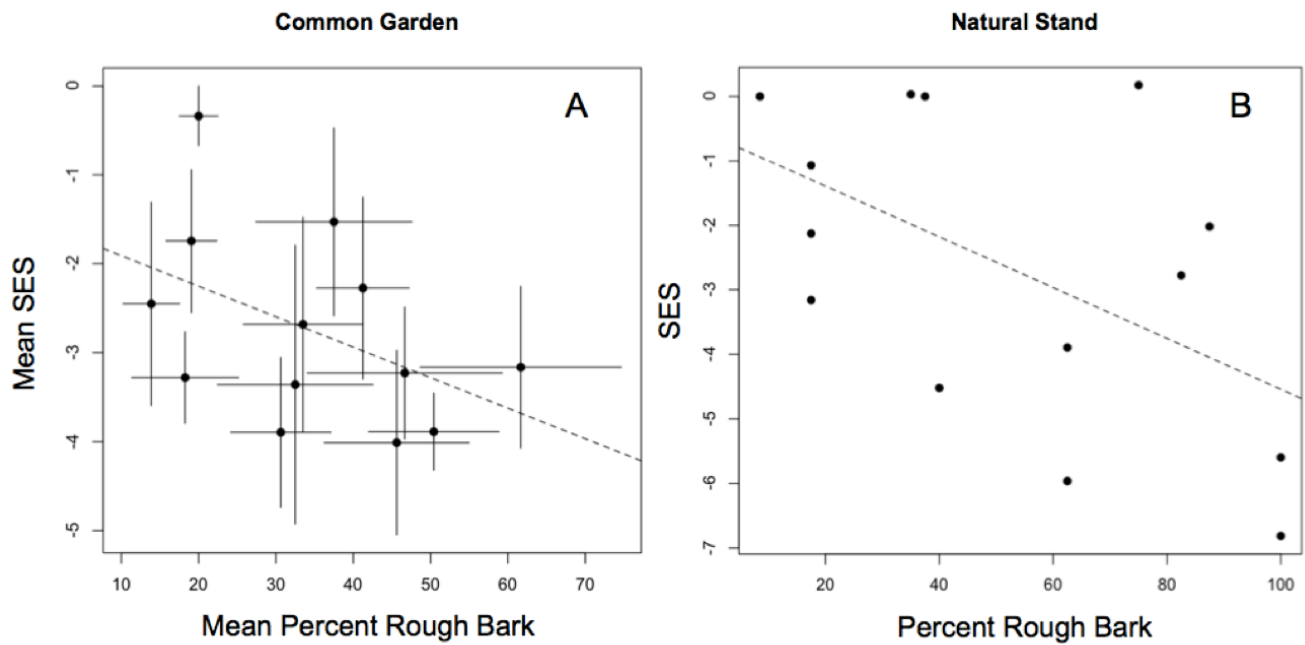


Figure 2. Tree genotype influenced lichen co-occurrence patterns in the common garden and the natural stand through a genetically controlled tree trait. The lichen co-occurrence patterns were highly correlated with the genetically based phenotypic trait; bark roughness (i.e., the percentage of textured bark), in both the common garden and natural stand. The scatterplot (A) shows the mean (± 1 SE) percent rough bark (broad-sense heritability, $H^2 = 0.36$, $\chi^2 = 9.214$, $p = 0.002$) and SES for each genotype for trees in the common garden with SES values becoming more negative (i.e., species interactions increased), indicating stronger co-occurrence patterns, as bark roughness increases. The lichen communities on individual trees in the Unitah natural stand (B) displayed a similar pattern with the SES values becoming increasingly more negative on trees with more rough bark.

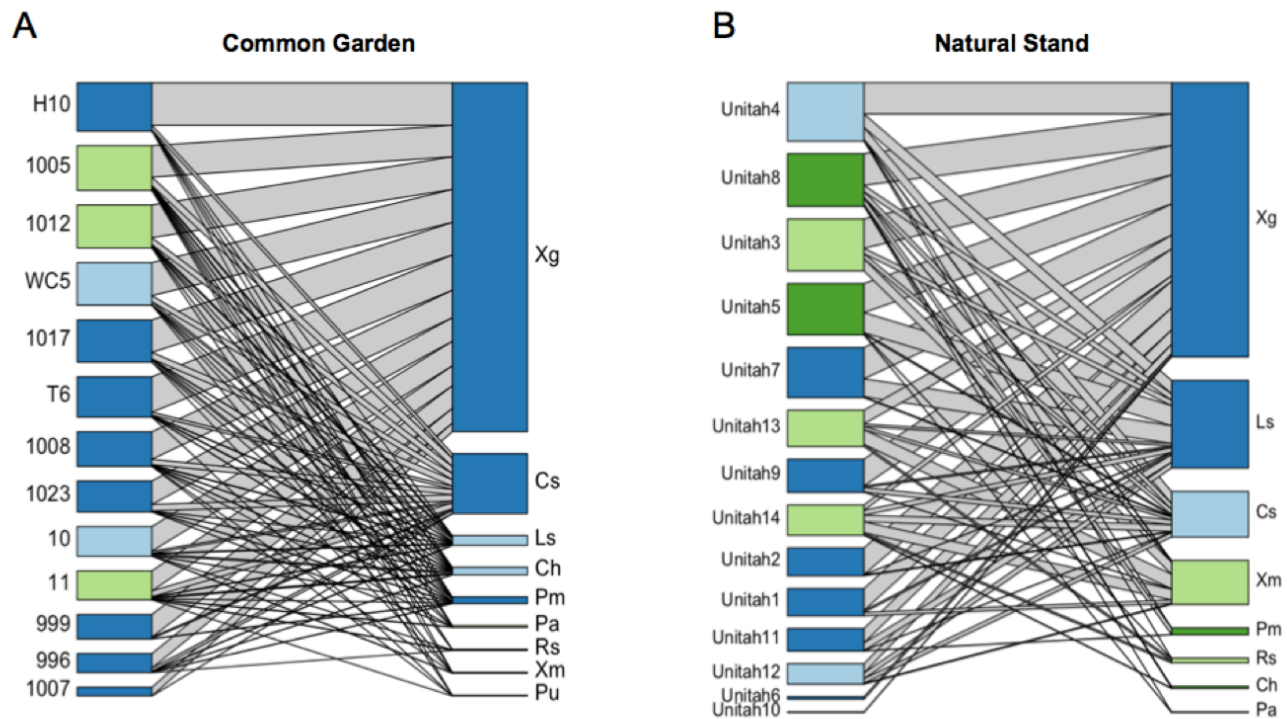


Figure 3. Bipartite networks displayed significant modularity with modules comprised of both genotypes and species. The left most set of nodes shows tree genotypes (see Methods for genotype names) for the common garden (A) or individuals in the natural stand (B) connected to lichen species on the right. Both sets of nodes are scaled by their marginal totals (i.e., total observed individuals for tree nodes and total abundance for lichen species) and arranged by ascending totals from bottom to top. Node color shows the significant module membership for both trees and lichen species with module color having no direct relationship between the two networks, as modules were determined for each network independently.