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

Biological evolution occurs in the context of complex ecosystems of interacting species whereby natural selection defines the structure of ecological networks. Fundamental to understanding evolutionary processes is elucidating the genetic basis to ecological network structure, which is defined by interactions among species. Although previous work has demonstrated that genotypic variation in foundation species contributes to interaction network structure, we are not aware of a study that has quantified the genetic contribution to network structure or shown network structure to be a heritable trait. To examine this, in a 20+ year common garden we observed interactions among nine epiphytic lichen species associated with genotypes of (*Populus angustifolia*), a foundation species of riparian ecosystems. We constructed signed, weighted, directed interaction networks for the lichens and conducted genetic analyses of whole network similarity, degree and centralization. We found three primary results. First, using multiple metrics, tree genotype significantly predicted lichen network structure; i.e., clonal replicates of the same genotype tended to support more similar lichen networks than different genotypes. Second, broad sense heritability estimates show that plant genotype explains network similarity (H2 = 0.41), network degree (H2 = 0.32) and network centralization (H2 = 0.33). Third, one of the examined tree traits, bark roughness, was also heritable (H2 = 0.32) and significantly correlated with lichen network similarity (R2 = 0.26), supporting a mechanistic pathway from variation in a heritable tree trait and the genetically based variation in lichen network structure that selection can act upon. We conclude that tree genotype can influence not only the relative abundances of organisms but also the interaction network structure of associated organisms. Given that variation in network structure can have consequences for the dynamics of communities through altering system-wide stability and resilience and modulating perturbations, these results have important implications for the evolutionary dynamics of ecosystems.

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

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

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Evolution occurs in the context of complex ecological networks. Community genetics studies have shown that genetic variation in foundation species, which have large effects on communities and ecosystems by modulating and stabilizing local conditions (1), plays a significant role in defining distinct communities of interacting organisms: such as, endophytes, pathogens, lichens, arthropods, and soil microbes (2–4). Multiple studies have now demonstrated that genetic variation influences numerous functional traits (e.g., phytochemical, phenological, morphological) that in combination results in a multivariate functional trait phenotype (5) in which individual plant genotypes support different communities and ecosystem processes (6, 48). The importance of genetic variation in structuring ecological systems was recently reviewed (7), and not only were many instances of strong genetic effects found in many ecosystems but the effect of intraspecific variation was at times greater than inter-specific variation. There is now evidence to support that selection, acting on this heritable variation, tends to occur among groups of species (8) and that genetic variation and phylogenetic relatedness contribute to variation in community assembly (9) and species interactions (6, 10, 11), which shape the structure of ecological interaction networks (12–14).

In this community-level evolutionary context, the “genetic similarity rule” provides a useful framework for approaching the nexus of evolutionary and community dynamics in the context of complex interaction networks. In a study combining experimental common gardens and landscape-scale observations of interactions between *Populus* spp. (cottonwoods) and arthropods, (15) observed that individuals genotypes that are more genetically similar will tend to have similar phytochemical traits and thus tend to have similar interactions with other species than individuals that are less similar. However, studies in the network ecology literature generally do not include a genetic component (16) and community genetics studies have primarily focused on community composition in terms of the abundance of species (7). Some studies have examined the effects of genetic variation on trophic chains in plant-associated communities (including *Populus*, *Solidago*, *Oenothera*, *Salix*) (17–21) and generally found that increasing genotypic diversity leads to increased trophic complexity. Only two other studies, that we are aware of, have explicitly examined the effect of genotypic variation on the structure of interaction networks between tree individuals and associated herbivores (22, 23) and both found that genotypic diversity generates increased network modularity (i.e., compartmentalization). However, both of these studies were examining networks at the scale of forest stands, rather than networks associated with individual trees; therefore, neither was able to observe replicated networks in order to statistically test for genetic effects on network structure and quantify the genetic component (i.e. heritable variation) in network structure.

Network theory and evidence from empirical studies in ecology have demonstrated that indirect effects can lead to self-organization, producing sign-changing, amplifying and/or dampening effects (24, 25). The development of interspecific indirect genetic effects (IIGE) theory (26) in evolutionary biology points to the importance of studying the genetic basis of interaction network structure because genetic based differences in network structure among individuals can be acted upon by natural selection when there are fitness consequences of different networks of IIGEs that can result in community evolution (Whitham et al. 2020). For example, although the analysis was of abundances rather than interaction networks, Gehring et al. (2014, 2017) found that the mycorrhizal communities on the roots of drought tolerant and intolerant trees are dominated by different orders of ectomycorrhizal fungal mutualists that also differ in the benefits they provide that enhance tree performance. Because drought tolerant genotypes are 3x more likely to survive record droughts, selection acts both on the tree and its fungal community and with increased drought the community phenotype has changed over time. Also, in an antagonistic interaction context, Busby et al. (2015) found that with the addition of a damaging leaf pathogen to cottonwoods in a common garden, the impacts of these strong interactors results in a different and diminished community of arthropods relative to control trees. Thus, selection acting on the tree may alter the network structure of associated communities in which different networks of communities are most likely to survive pathogen outbreaks. Regardless of whether the IIGE is unilateral (i.e., tree affects the community) or reciprocal (i.e., the community also affects the relative fitness of the tree), selection on tree, community or both can change network structure (Whitham et al. 2020) and thereby alter community dynamics. Evolutionary applications of network theory have demonstrated that indirect effects of interactions among species can lead to network structures that amplify or dampen the effects of selection (27). For example, networks that form a star-like structure in which there is a central species or core group of species that interact with other, peripheral species, can amplify selection events. Empirically, network analysis of the structure of bipartite (i.e., two-mode) mutualistic networks has shown in multiple cases that nestedness, or the degree to which species tend to interact with similar subsets of the community, tends to promote stability and resilience to disturbances (28) NEED TO ADD BASCOMPTE2014. As such differences in network structure could occur without observable differences in species richness or community composition, which have been the primary focus of almost all previous community genetics studies. Thus, it is important to quantify how network structure changes in response to genetic variation in order to fully understand evolutionary dynamics in complex communities.

Here, we investigate how genetic variation in a foundation tree species determines the structure of a network of interactions among a community of tree associated lichen species. Previous studies have examined aspects of networks (29). Here we examine the genetic basis of network structure on a community of sessile lignicolous (i.e., bark) lichens on cottonwood trees. Using a long-term (20+ years), common garden experiment with clonally replicated *Populus angustifolia* individuals of known genetic identity . We focused on a community of 9 epiphytic lichen species, as previous research has demonstrated significant compositional responses of epiphytes to genotypic variation (30, 31). In addition, the life-history characteristics of lichens, having highly localized, direct contact interactions and slow population turnover rates, facilitated the assessment of interactions among lichen species on individual trees. We hypothesize that in natural systems evolution occurs in a community context involving interactions of complex networks of interacting species (22, 23, 28, 32). If correct, we expect to find that network structure is genetically based, or, in other words, plant genotypes will support different and heritable interaction networks. Applying a probability-theory based network modeling approach, we constructed a set of interaction network models for the lichens associated with individual trees. Using these models, we then examined the genetic basis of the structure of these ecological networks via several network metrics that measures different aspects of network structure at the scale of individual species (i.e., nodes) or the entire network observed on each tree genotype. In particular, we focus the metric of centrality for individual species and centralization for whole networks, which measures how much a species is connected in the network relative to other species. Based on previous community genetics theory, particularly the community similarity rule (15), we hypothesize that trees will co-vary in functional phenotypic traits such as bark roughness and chemical composition and trees of the same genotype will tend to have similar traits leading to similarities in lichen network structure. This work is important because it provides a mechanistic basis for understanding how community network theory is intimately associated with the evolutionary process and how human alterations of the environment (e.g., climate change, invasive species, pollution) may have cascading, indirect effects that alter network structure and evolution.