**Tree genotype mediates covariance among functionally and taxonomically divergent communities**

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1. The importance of plant genetics in structuring associated communities has been widely demonstrated. However, community genetics studies have focused narrowly on specific communities (e.g., foliar arthropods), limiting our understanding of how the ecological and evolutionary dynamics of one community may be constrained or modulated by its underlying genetic connections to another community.

2. Using data from multiple studies conducted within a single common garden, we tested for evidence of community-level genetic covariation (community-genetic correlations) among divergent, often taxonomically distinct communities (e.g., endophytes, pathogens, lichens, arthropods) associated with replicated genotypes of *Populus angustifolia* (narrowleaf cottonwood). Next, we evaluated whether resource similarity, taxonomic similarity, time between sampling communities and foundation species within communities explained variation in the strength of correlations.

3. Three main results emerged. First, pair-wise Mantel tests between communities revealed moderate to strong (rho ≥ 0.2) community-genetic correlations in almost half of the comparisons, with nearly 30% of tests being statistically significant (*P*≤0.05); correlations among canopy endophyte, pathogen and arthropod communities were the most robust. Second, resource similarity rather than taxonomic similarity or time between sampling communities determined the strength of community-genetic correlations, supporting the *resource similarity hypothesis*. Third, consistent with the *interacting foundation species hypothesis*, the most abundant species drove many of the stronger correlations, although there were important exceptions.

4. *Synthesi*s. The field of community genetics has shown that plant-associated communities can display heritable variation among plant genotypes, where related plant genotypes support similar communities. Here, we add to our understanding of the genetic basis to community structure by showing that functionally and taxonomicallydiverse communities can covary among plant genotypes. Because communities may constrain and modulate each other through ecological interactions or other mechanisms whereby they are attracted to the same genotypes, but do not necessarily interact, the ecological and evolutionary dynamics of a diverse array of associated species will be mediated by shared connections at the genetic level. These findings have important implications for our understanding of the relationships between ecological and evolutionary process, and the genetically based, non-neutral organization of biodiversity.

Key words: Community-genetic correlations, community phenotype, community networks, interacting foundation species hypothesis, community evolution, common garden, Mantel test, *Populus*

**INTRODUCTION**

Individual plant genotypes and the genetic structure of plant species play an important role in defining community structure and ecosystem processes. A series of reviews in community genetics have established these relationships in diverse systems around the world (Whitham, Young & Martinsen *et al*. 2003; Whitham, Bailey & Schweitzer *et al.* 2006; Johnson and Stinchcombe 2007; Wade 2007; Haolin & Strauss 2008; Hughes; Inouye & Johnson *et al*. 2008; Bailey, Schweitzer & Úbeda *et al*. 2009; Genung, Schweitzer & Úbeda *et al*. 2011; Wymore, Keeley & Yturralde *et al*. 2011; Hersch-Green, Turley & Johnson 2011; Rountree, Shuker & Preziosi 2011; Schweitzer, Bailey & Fischer *et al*. 2012; Whitham, Gehring & Lamit *et al*. 2012; Fischer, Chapman & Classen *et al*. 2014; Woolbright, Whitham & Gehring *et al*. 2014). Studies cited in the above reviews demonstrate that related individuals support similar communities and rates of ecosystem processes, such that a plant genotype can be viewed as having its own community and ecosystem phenotypes (*sensu* Whitham, Bailey & Schweitzer *et al*. 2006), which are heritable (e.g., Keith, Bailey & Whitham 2010 – insects; Lamit, Lau & Næsborg *et al.* 2014 – lichens). Thus, as plants respond ecologically and evolutionarily to biotic and abiotic selection pressures, their associated communities can change with them (e.g., Johnson, Vellend & Stinchcombe 2009; Gehring, Flores-Rentería & Sthultz *et al*. 2014).

A community phenotype is the product of interactions among an individual plant genotype, a community of associated organisms and the environment. Diverse community members are commonly influenced by plant phenotypes (e.g., Wimp, Wooley and Bangert *et al*. 2007; Crutsinger, Rodriguez-Cabal & Roddy *et al*. 2014; Bernhardsson, Robinson, Abreu *et al.* 2013; Lamit, Lau & Næsborg *et al*. 2014), including phytochemical, ontogenetic, induced, phenological, and morphological traits. In combination, these result in a multivariate plant phenotype (*sensu* Holeski, Hillstrom & Whitham *et al.* 2012) that results in different plant genotypes supporting different communities (i.e., the community phenotype). The influence of plant trait variation on communities also alters interactions between species within a community (Gassman & Hare 2005; Johnson 2008; Mooney & Agrawal 2008; Lamit, Lau & Næsborg *et al.* 2014; Busby, Lamit & Keith *et al*. in press), and *their* fitness and phenotypes (Shuster, Lonsdorf & Wimp *et al*. 2006; Smith, Bailey & Shuster *et al*. 2010), which further shape the character of a community phenotype. These effects may produce important selection pressures that lead to local adaptation of community members to individual plant genotypes or populations (Capelle & Neema 2005; Shuster, Lonsdorf & Wimp *et al*. 2006; Evans, Allan & Shuster *et al*. 2008; Smith, Bailey & Shuster *et al*. 2010) that can cascade to higher trophic levels (Stireman, Nason & Heard *et al*. 2006), and may feed back to act as selective forces on plants (Lankau & Strauss 2007; Smith, Schweitzer & Turk *et al*. 2012; Gehring, Flores-Rentería & Sthultz *et al*. 2014).

Despite recognition of the extended effects of plant genes on a variety of interacting plant-associated communities, eco-evolutionary studies of the interactions between plants and their associated organisms typically focus on single communities (e.g., arthropods). However, because plant genes can link diverse groups of associated species (e.g., Dickson & Whitham 1996; Ahlholm, Helander & Elamo *et al*. 2003; Tagu, Bastien & Faivre-Rampant 2005; Sthultz, Whitham & Kennedy *et al*. 2009), entire communities of distantly related, spatially disjunct species are likely linked by common connections to plant genotype. For example, Zytynska, Fay & Penny *et al*. (2011) show that different genotypes of a tropical forest tree affect both their associated epiphytic plants and invertebrate communities. These diverse communities may be genetically correlated among plant genotypes, in which shifts in the composition of one community among genotypes are mirrored by similar shifts in the composition of another community. Establishing such connections is important for disentangling the effects of plant genetic variation on communities, and understanding how ecological and evolutionary changes in plants resulting from climate change and other agents of selection can affect the ecological and evolutionary dynamics of communities.

Here, we utilize a diverse set of data collected from a single common garden to examine the patterns of community-genetic covariation among communities of organisms associated with the narrowleaf cottonwood tree, *Populus angustifolia*. Our primary goal is to test the hypothesis that very different communities (e.g., lichens and canopy arthropods) tend to co-vary among plant genotypes in a way that is analogous to genetic correlations that are measurable among traits within species. We refer to these genetically based, inter-specific correlations as “community-genetic correlations.” Next, we evaluate four non-mutually exclusive, mechanistic hypotheses for explaining the observed patterns of such genetically based correlations among communities (Table 1). The *resource similarity hypothesis* argues that communities associated with similar resource types (e.g., soil versus leaves) are more strongly correlated than those on different resources. Species connected through the same local food web are more likely to interact through direct encounters (e.g., competition) or indirectly through plant trait modulation, and be sensitive to genetic variation in the same plant traits. The *taxonomic similarity hypothesis* predicts that communities of organisms more closely related to each other are more strongly correlated than communities of organisms distantly related. This hypothesis is based on the assumption that the phenotypic expression of gene(s) will be more likely to influence related organisms than unrelated organisms. Third, the *time attenuation hypothesis* posits that the strength of genetically based correlations among communities declines as the time between sampling of each community increases. Time likely decouples the effects of communities on each other, and allows for variation in environmental conditions that may alter gene expression in the tree. Finally, the *interacting foundation species hypothesis* posits that a few highly interactive species can define much larger communities (Keith, Bailey & Whitham 2010; Busby, Newcombe & Dirzo *et al*. 2014). We hypothesize that an implication of this hypothesis is that genetically based correlations among communities are driven by a small number of abundant and interacting foundation species in communities (we use term to include keystone, dominant, ecosystem engineers or other species of large effect; Ellison, Bank & Clinton *et al*. 2005). While these hypotheses are not mutually exclusive, distinguishing among them is important to understand how disparate plant genotype-associated communities are modulated by plant genetic variation and address how plant genetics contributes to the assembly of much larger communities of interacting species. We also discuss how our findings relate to neutral theory and other largely untested hypotheses that our data do not allow us to address.

**Methods**

***Study system and common garden***

*Populus angustifolia* is a mid to upper elevation foundation species of interior western North American riparian habitats, which has become an important model species in community genetics (Figure 1A; Whitham, DiFazio & Schweitzer *et al*. 2008). Intraspecific genotypic differences of *P. angustifolia* influence the structure of a variety of communities (Figure 1C-G), including foliar arthropods (Keith, Bailey & Whitham 2010), bark lichens (Lamit, Lau & Næsborg *et al*. 2014), twig endophytes (Lamit, Lau & Sthultz *et al*. 2014), foliar pathogens (Busby, Newcombe & Dirzo *et al*. 2013, 2014) and soil bacteria and fungi (Schweitzer, Bailey & Fischer *et al*. 2008; Lamit 2013). Additionally, interspecific genotypic variation in *P. angustifolia* influences ecosystem processes, such as aquatic and terrestrial decomposition, and nutrient mineralization and cycling (Schweitzer, Bailey & Hart *et al*. 2005; LeRoy; Whitham & Wooley *et al*. 2007). Genetic influences on communities and ecosystem process are likely due to heritable variation in traits, such as foliar chemistry (Bailey, Wooley & Lindroth *et al*. 2006), productivity (Lamit, Lau & Næsborg *et al*. 2014) and source-sink relationships within a tree (Compson, Larson & Zinkgraf *et al*. 2011), although mechanisms by which *P. angustifolia* genes and functional plant traits influence community and ecosystems processes remain largely unresolved.

All data incorporated into this paper were collected from replicated *P. angustifolia* genotypes growing in the Ogden Nature Center (ONC) north common garden, Ogden, Utah, USA (Figure 1B). The garden is located in the geographic center of *P. angustifolia*’s latitudinal range, at the lower end of the species’ elevational distribution along the nearby Weber and Ogden Rivers (latitude = 41.248146, longitude = -111.999830, elevation = 1302 m). The ~1 hectare garden was planted in 1991 with cuttings clonally propagated from wild *P. angustifolia* growing along a ~105 km stretch of the Weber River. However, a core set of genotypes present in all datasets in the analyses originated from a single site located along the lower elevational range of *P. angustifolia* in the Weber River. Trees in the garden were planted with 4 m spacing, with genotypes randomly positioned, and were sexually mature when community datasets were collected. See Busby, Newcombe & Dirzo *et al*. (2014) for more information on the garden.

***Community data***

Datasets representing a range of communities, both above- and belowground, with a variety of functional roles (e.g., primary producers, herbivores, pathogens, mutualists, and decomposers), were included in analyses (Figure 1C-G, Table 2). As criteria for inclusion, datasets contained observations from at least six replicated *P. angustifolia* genotypes sampled in the north section of the ONC common garden. Most communities were composed of indicators of abundance of individual species (e.g., % cover of lichens, counts of individual arthropods, pathogen leaf area damage) or species-level molecular OTUs that approximate species (e.g., % colonization of ectomycorrhizal fungi, isolation frequency of endophytic fungi). However, soil bacteria and fungi from Schweitzer, Bailey & Fischer *et al.* (2008) were based on phospholipid fatty acid analyses (PLFA) that identified broad taxonomic groups that typically differ in terms of their effects on soil processes (Table 2). Although the levels of identification differ among datasets, throughout the remainder of the paper we refer to the members of each community as OTUs for simplicity. Prior to pairing, community datasets included two to twelve OTUs (Table 2). We focused on community composition, which incorporates all individual abundances from OTUs in a multivariate matrix. Compared to reduced metrics, such as diversity (e.g., Shannon’s H), composition contains the most information about community structure, and it was shown to vary among genotypes for all of the communities examined (see references in Table 1).

Community datasets were merged for pair-wise analyses. Initially, datasets contained 27 to 104 trees, representing 8 to 30 genotypes (Table 2). To pair datasets, observations from trees that were not present in both datasets were removed. Matched data for pair-wise comparisons were composed of 20 to 92 total trees, representing 6 to 25 genotypes with 2 to 9 trees per genotype. Genotype mean abundances of each OTU were then calculated from replicate trees of each genotype. OTUs that occurred in only one or two trees in the matched data were removed prior to calculating mean values because extremely rare OTUs provide little information about their affinity to a genotype, but can have disproportionate effects on composition analyses (McCune & Grace 2002). Furthermore, extremely rare OTUs are more likely to occur by chance on genotypes with larger numbers of replicate trees, thus distorting a genotype’s mean community composition after averaging its abundances. A total of 28 pairs of matched communities were created.

***Statistical Analyses***

*Pair-wise Mantel tests and network analysis*

We used a series of bivariate Mantel tests to examine correlations between communities. This approach identified concomitant shifts in the composition of two communities among a set of tree genotypes, where, when significant, increasing dissimilarity among tree genotypes in one community was associated with a similar increase in dissimilarity among tree genotypes in another community. Mantel tests using Bray-Curtis dissimilarity were performed with each pair of matrices of mean OTU abundances to test for a positive slope based on Spearman’s rho. This Mantel-based approach bears similarities to quantitative genetic methods for documenting the existence of genetic correlations of traits within species (see Simms & Rausher 1992), and between abundances of individual species on plant genotypes (e.g., Maddox & Root 1990; Roche and Fritz 1997). Because Mantel tests examine correlations of pair-wise distances, their estimate of the strength of relationship between two communities is not directly comparable to genetic correlation results obtained with univariate traits or abundances. However, we suggest that our measure of Spearman’s rho provides a suitable indicator of the strength of the pair-wise genetic correlation between communities found on clones of host plants grown in common gardens. We call these associations *community-genetic correlations*. Given the relatively small and uneven number of tree genotypes in our analyses, we placed emphasis on the strength of the relationships as indicated by rho-values. We considered rho-values of 0.2 or greater to be of potential importance. However, we also report conventional *P*-values but caution their interpretation because power to detect significant relationships, which is highly dependent on sample size, varied considerably between comparisons with different pairs of communities. Rho-values from pair-wise Mantel tests between communities formed a central dataset in all subsequent analyses. Analyses were conducted in R 3.0.2 using the package *ecodist* (Goslee & Urban 2007).

A network approach was used to visualize and interpret the structure of correlations among communities. This analysis used rho-values from the pair-wise community Mantel tests. Nodes (individual points) in the networks represent each of the communities, while edges (lines connecting points) represent correlations between communities and are scaled by the magnitude of their associated Mantel rho-value.

*Testing the resource similarity, taxonomic similarity and time attenuation hypotheses*

We used partial-Mantel tests to evaluate whether resource similarity, taxonomic similarity, or time influenced the strength of community-genetic correlations. For these analyses,three additional matrices were constructed using pair-wise values for each comparison between communities (Table 1; Supplement 1). The *resource similarity* matrix indicated whether or not two communities occur in similar locations of a tree, the *taxonomic similarity* matrix indicated whether or not two communities were within the same general taxonomic group (i.e., fungi, bacteria, arthropods), and the *time attenuation* matrix indicated the number of months between the sampling of the two communities*.* As a control for variation in sample size among pair-wise tests between communities, an additional matrix, corresponding to the number of genotypes that were used for each pair-wise Mantel test, was included in the analysis. The partial-Mantel test using partial Pearson’s correlation coefficients tested the linear relationship between each of the explanatory matrices and the rho-values from pair-wise Mantel tests (described in the previous subsection), while holding the effect of the other matrices constant.

*Testing the interacting foundation species hypothesis*

We used data relativizations to test the *interacting foundation species hypothesis*. After pairing community data and averaging individual OTU abundances for each genotype, each OTU was relativized by the maximum value occurring within its reduced matrix. This relativization places all species values on the same scale and down-weights the effect of highly abundant species (McCune & Grace 2002), which have the potential to interact more with other community members than rare species. Pair-wise Mantel tests were then repeated for each pair of communities, using Bray-Curtis dissimilarity and Spearman’s rho. Wilcoxon signed-rank tests were used to test for a decreases in the median pair-wise rho-values in two ways: (1) using rho-values from all tests to examine the effect of relativization across all communities, and (2) using only rho-values from pair-wise Mantel tests with rho ≥ 0.2 to examine the effect of relativization on comparisons that showed moderate to strong community correlations. A network diagram was also used to visualize the structure of correlations between relativized datasets. The *interacting foundation species hypothesis* would be supported if data relativization reduced rho-values from pair-wise Mantel tests, or if significant relationships prior to relativization became insignificant with relativized data. As used elsewhere, the term foundation species encompasses highly interactive species such as dominant, keystone, and ecosystem engineers (Ellison, Bank & Clinton *et al*. 2005), and the function of a species as a foundation species must ultimately be confirmed using removal or addition experiments as in Busby, Lamit, & Keith *et al*. (2014). However, we suggest that our test is an important first step that helps give an indication if abundant species, which are candidate foundation species, may be driving genetic correlations among communities.

**Results**

*Pair-wise Mantel tests and network analysis*

Pair-wise Mantel tests revealed that divergent communities were correlated among individual genotypes of *P. angustifolia* (Table 3). Of the comparisons conducted, nearly half (13 out of 28) had rho-values ≥ 0.20. Eight out of 28 (28.6%) of the comparisons were statistically significant (*P*≤0.05), with another 3 comparisons being marginally significant (0.05<*P*<0.1). The communities that tended to have the highest correlations were leaf pathogens sampled in 2009 (median rho = 0.297) and leaf modifying arthropods (median rho = 0.278), and these were also each correlated with multiple other communities (Table 3). In contrast, bark lichens (median rho = 0.037) and ectomycorrhizal fungi (median rho = 0.076) tended to be more weakly correlated overall, although each of these communities was still significantly correlated with one or more other communities (Table 3).

Analysis of the Mantel rho-value network of pair-wise relationships between communities shows non-random network structure in which specific communities are far more likely to be associated with one another than other communities. The phyllosphere nodes were densely connected with fewer connections to other communities (Figure 2A). In the phyllosphere cluster, no community was more than three connections (edges) away from any other, although not all were directly connected. A second, smaller cluster was composed only of a very strong connection between the soil fungal and bacterial PLFA communities, although soil fungi and bacteria communities were also marginally correlated with twig endophytes and leaf pathogens sampled in 2010, respectively. In most cases, the one community that was sampled twice, necrotrophic foliar pathogens, showed similar connections with communities across both sample dates.

*Resource similarity, taxonomic similarity and time attenuation hypotheses*

Only one of the three hypotheses tested with our Partial-Mantel analysis was supported. The *resource similarity hypothesis* predicts that communities living on similar resources are more strongly genetically correlated than communities associated with different resources. This hypothesis was supported by a decrease in rho (negative slope) from correlations between communities that shared a resource compared to rho-values between communities that did not share a resource (Figure 3A). In contrast, the *taxonomic similarity* and *time attenuation hypotheses* were not supported by the partial-Mantel analysis (Figure 3A).

*Interacting foundation species hypothesis*

Our results are consistent with the *interacting foundation species hypothesis* (Table 3, Figure 2), that genetic correlations among communities are driven by high abundances of a few foundation species. Using matrices relativized by OTU maximum, 8 out of 28 comparisons had positive rho-values ≥ 0.20. Six of these comparisons (21.4%) were statistically significant (*P*≤0.05), with another 2 comparisons being marginally significant (0.05<*P*<0.1). Considering all contrasts, rho-values from pair-wise Mantel tests conducted with relativized matrices were marginally significantly lower than those from pair-wise Mantel tests conducted with unrelativized community matrices (n = 28, V = 262, *P* = 0.093; *Q*1, median and *Q*3 for Mantel rho with unrelativized data = 0.025, 0.182, 0.310; *Q*1, median and *Q*3 for Mantel rho with relativized data = -0.019, 0.120, 0.232). However, when considering only rho-values that were ≥ 0.2 for Mantel tests conducted with unrelativized data, there was a significant drop in the median rho-value after Mantel tests were rerun with their matrices relativized (n = 13, V = 70, *P* = 0.047; *Q*1, median and *Q*3 for Mantel rho with unrelativized data = 0.301, 0.327, 0.453; *Q*1, median and *Q*3 for Mantel rho with relativized data = 0.176, 0.252, 0.454); this effect appeared to be as much related to an increase in variance among rho-values after relativization, as it did to differences in median values (Figure 3B). In contrast, a small number of correlations became stronger after relativization (Table 2; Figure 2).

**Discussion**

Over the last decade numerous studies have quantified how different plant genotypes can define individual associated communities (see Whitham, Gehring, Lamit *et al*. 2012). Our analyses extend these findings by demonstrating significant community genetic correlations among a diverse range of plant-associated communities (Fig. 2) that have very different functional roles and often occupy different regions of a tree. While slightly less than half of the pair-wise analyses have moderate to strong rho-values and 2/3rds are not significant, given the limitations of the study (e.g., relatively small sample sizes, different years of data collection, different levels of taxonomic identification), our findings are likely conservative. These results indicate that the interplay between ecological and evolutionary processes in plant genotype-associated communities are therefore more complex than studies with organisms in a single, taxonomically defined community may reveal. Below we discuss the ecological and evolutionary implications of our findings.

*Tested hypotheses*

Our results are consistent with the *resource similarity hypothesis* and the *interacting foundation species hypothesis*. We show that the strongest predictor of genetic correlations between community phenotypes is a shared resource; communities utilizing the same or nearby plant resource on a tree are more strongly correlated than communities utilizing different resources on a tree. This support for the *resource similarity hypothesis* may be due to the fact that species living close to each other are more likely to interact or that they respond to genetically similar or correlated plant traits without interacting (see next subsection). The most abundant OTUs, which are candidate foundation species, are also drivers of some of the community-genetic correlations (*interacting foundation species hypothesis*). Removal and addition experiments on replicated plant genotypes (e.g. Busby, Lamit & Keith *et al*. in press) will be required to confirm these OTUs are foundation or highly interactive species that interact across communities. For example, the genotype of tall fescue (*Lolium arundinaceum*) and its systemic endophyte (*Neotyphodium coenophialum*) interact to influence herbivory by mammals and arthropods, and the structure of the surrounding plant community (Rudgers, Fischer & Clay 2010). In this case, the genetically based interactions of two foundation species have strong extended consequences for members of multiple communities.

Neither the *taxonomic similarity hypothesis* or the *time of sampling attenuation hypothesis* receive support by our analyses. Our test of the *taxonomic similarity hypothesis* is admittedly coarse, as it ignores functional diversity within the broad groupings that we classified communities into for the test of this hypothesis. Furthermore, future tests of this hypothesis would benefit from the incorporation phylogenetic information (i.e., a community phylogenetic approach; Cavender-Bares, Kozak & Fine *et al*. 2009) to more adequately represent the relationships among community members. It is more surprising that the *time of sampling attenuation hypothesis* is not supported, as the communities were sampled over a 6 year period and it is well established that environmental variation over time can influence ecological processes (e.g., Wimp, Wooley & Bangert *et al*. 2007). It is possible that communities sampled in one year may give reasonable representations of the average community phenotype in adjacent years. For example, Keith, Bailey & Whitham (2010) show that while different genotypes support different arthropod communities, over a three-year period of repeated censusing, the composition of the arthropod communities remain stable from year to year for individual genotypes. Organisms may also interact across years, for example the effects of ectomycorhizal fungi on tree performance may condition a genotype in such a way as to make it more or less susceptible to attack by herbivores and pathogens in a later year (NEED REF).

*Community-genetic correlations with and without interactions*

Community genetic-correlations may arise from two primary sources – the communities are interacting and affecting each other’s structure, or they are sorting out based on shared responses to the same or correlated plant traits, but not interacting. Experiments such as the addition or removal of foundation species within a specific community or whole communities are essential to differentiate between these hypotheses. For example, experiments conducted in the same garden from which these community-genetic correlations are derived clearly demonstrate strong interactions in which a pathogen and arthropod communities of *P. angustifolia* are connected by underlying genetic variation in tree resistance to a pathogen (Busby, Lamit & Keith *et al*. 2014). Pathogen resistant tree genotypes tend not to lose leaves when inoculated by the common pathogen, *Drepanopeziza populi*, whereas susceptible genotypes lose large quantities of leaves. Genotype specific loss in leaf biomass then alters the structure of foliar arthropod communities. This example represents a case where the interactions between members of two different communities (a pathogen and arthropods) are modulated by the genotypic identity of the host plant. Plant genotypes can be viewed as unique stages that mediate interactions among diverse communities. Consistent variation among plant genotypes in how they modulate interactions between species in different plant-associated communities may lead to community-genetic correlations.

While we argue for the importance of genetically based interactions driving correlations, community sorting by plant traits alone still represents an important alternative. Communities may be correlated due to shared responses to variation in the same genetically based plant traits, or because they each respond to different but correlated traits (i.e., caused by pleiotropy or linkage-disequilibrium; Simms & Rausher 1992; Conner & Hartl 2004), as has been suggested for correlations between individual species among plant genotypes (e.g., Ahlholm, Helander, Elamo *et al*. 2002). These mechanisms may also explain the support for the *resource similarity hypothesis*. For example, the correlated phyllosphere communities (foliar pathogens, endophytic fungi in young twigs and leaf modifying arthropods) may be sensitive to many of the same genetically based plant traits, such as those associated with source-sink carbohydrate dynamics among shoots (Compson, Larson & Zinkgraf *et al*. 2012). More broadly, communities are likely influenced by a multivariate suite of plant phenotypes, many of which are higher composite phenotypes influenced by many genes (e.g., productivity; Lamit, Lau & Sthultz *et al*. 2014). It is likely that a portion of plant genes that influence one community also influence another community, even if the same entire suite of genes does not influence both communities. This contention is supported by the correlation between some phyllosphere communities and ectomycorrhizal fungi forming symbioses with roots. Clearly, genes that influence leaf and shoot traits may have a stronger direct impact on the phyllosphere, whereas genes influencing root traits may more strongly influence ectomycorrhizal fungal communities, but traits associated with whole-plant factors such as carbohydrate dynamics may influence both communities (Wardle, Bardgett & Klironomos *et al*. 2004). Regardless of the relative roles of interactions versus sorting based on plant genetics traits alone, understanding the drivers of community-genetic correlations among plant genotypes represents an important research frontier.

*Selection and evolution within a community context*

Natural selection occurs when a covariance exists between phenotype and relative fitness. In most cases, genetic variation underlies traits under selection, thus the heritability of the trait, multiplied by the magnitude of the covariance determines the degree of evolutionary change (Wade 2007). When genetic variation in one species underlies traits that influence the variation in relative fitness of other species, “selection within a community context” is possible (Shuster *et al*. 2006). These interactions have been called interspecific indirect genetic effects (IIGEs; Allan et al. 2011), that is, genetic-based interactions that occur among ecologically associated species or whole communities as potentially indicated by the results reporte here. Neutral models of community organization (c.f., Hubbell 2001) suggest that interspecific interactions among species are usually not sufficient to influence community organization, and in particular, as species diversity increases, interspecific interactions become too diffuse to measure. By extension, if all species within a community are interacting at approximately a similar, diffuse level, coherent evolutionary change is unlikely. However, decades of ecological observation in the wild and in common gardens (Whitham, Young & Martinsen *et al*. 2003, Whitham, Bailey & Schweitzer *et al*. 2006) argue that at the community level, the interactions of all species are not equally important, and that the interactions of relatively few species, especially interacting foundation species such as cottonwoods and pathogens (Busby, Lamit & Keith *et al*. 2014) or cottonwoods and aphids (Keith, Bailey & Whitham 2010), can define a much larger community.

These observations generate a simple, testable hypothesis: if genetically based traits in plants have no fitness consequences for species comprising their associated communities, then no differences in the composition of associated communities are expected to appear within or among species associated with distinct plant genotypes (e.g., all cottonwood, eucalypt and every other community heritability study to date). A lack of community organization across plant genotypes would be consistent with neutral models of community organization (Hubbell et al. 2001). However, rejection of this hypothesis, in the form of an observed significant association of particular symbiont communities with individual plant genotypes, provides evidence that selection has occurred within a community context, and that a strong genetic component to community structure exists.

The genetic basis of this interaction is most easily identified as arising from plants (e.g., numerous reviews cited in introduction), but the interpretation of these results is likely to be more complicated. Whether community members respond positively or negatively to plant genotype and its multivariate phenotype (*sensu* Holeski, Hillstrom & Whitham *et al.* 2012) is likely to depend on the genotype of the individual associated organism(s). This expectation is borne out in the observation that individual species and whole communities are not equally represented among all plant genotypes, and hence community heritability, or other covariance measure can be used to show that species associations are nonrandom. Furthermore, the usual measures for documenting the appearance of particular species on plants usually require that individual species are present in all samples. Species that are present in some samples but are lacking in others are excluded from the analysis (e.g., in Bray-Curtis and other dissimilarity procedures). This convention is likely to make dissimilarity measures (as well as covariance matrices such as Mantel tests) conservative, because they include only associated species whose tolerance for plant phytochemical and other traits is exceptionally broad. In species with a high degree of individual specificity for a particular suite of plant traits, individual preferences for plants could be quite specific and result in some plants with large numbers of symbionts and other plants with none. Such patterns may be more easily detected using network analysis as demonstrated in Figure 2.

Our results raise the possibility that one community may complement or modulate the selective effect of plant genotype on members of another community. Plant genotypes can be viewed as unique selective environments that influence the traits and fitness of associated community members (Shuster *et al*. 2006, Wade 2007, Smith *et al*. 2010, XXXXX). Such interspecific indirect genetic effects (IIGEs; *sensu* Shuster *et al*. 2006) could cause local adaptation of community members to specific tree genotypes or populations (Mopper 1996; Capelle & Neema 2005, Evans, Allen, & Shuster *et al*. 2008). However, the phenotypic environment experienced by a focal community on a plant genotype includes both the multivariate suite of traditional phenotypic traits of the plant and the community phenotypes representing other communities on the plant. When community-genetic correlations exist, then the selective effects of one community on another shift in a coordinated fashion across genotypes. Whether the fitness effects arising from such interspecific interactions are sufficient to produce coherent genetic differentiation in community members among plant genotypes, or are mitigated by correlated effects within as well as among species, remains unclear.

Correlations between plant-associated communities suggest that natural selection acting on a plant population can have extended consequences for multiple community phenotypes simultaneously. Johnson, Vellend & Stinchcombe (2009) highlight an important scenario where selection on plant traits such as plant biomass and life history strategy has ecological influences on the structure of arthropod communities associated with different plant genotypes. Accounting for correlations among community phenotypes adds further dimension to this possibility. First, selection on a plant population will influence multiple community phenotypes, if they are genetically correlated. Second, just as with traditional phenotypes, where a trait can constrain the outcome and benefit of selection on a correlated trait (Lande & Arnold 1983, Simms & Rausher 1992), a community phenotype may constrain or modulate the effects of selection on a plant population that influences another community phenotype. In this scenario, communities may not interact in an ecological sense, but because one community is correlated with another through the influence of underlying tree genetics, communities may interact in an evolutionary sense through constraints or modulations of the influence of selection.

A plant’s community phenotypes may feed-back to influence its performance and fitness (CITATIONS), and such situations may represent the most clear cases of the evolutionary implications of community-genetic correlations. For example, *Baccharis pilularis* exhibits a genetic polymorphism with shrubs of distinct erect and prostrate architectural morphotypes that have strong effects on associated plant, foliar arthropod and soil bacteria communities (Crutsinger, Strauss & Rudgers 2010; Crutsinger, Rodriguez-Cabal & Roddy *et al*. 2014). The effects on associated communities are linked to the divergent morphologies of the two architectural morphotypes but a variety of correlated plant factors appear to be somewhat independently influencing different communities. However, if one of these community phenotypes (e.g., soil bacteria) provides a greater fitness advantage for one shrub morphotype relative to its effect on the other morphotype, then these selective effects will extend to influence the other community phenotypes that uniquely associate with the different shrub morphotypes (e.g., foliar arthropods). Although this example is hypothetical, these “evolutionary interactions” may occur in the presence or the absence of ecological interactions between the two types of community phenotypes because of community-genetic correlations.

***Conclusions***

A central contribution of community genetics to ecology is to point out that the structure of entire communities predictably varies among different genotypes within a plant species, that these communities can represent heritable traits and that these communities can feed back to affect the fitness of individual plant genotypes. We add to these central tenants of community genetics by showing that communities can genetically covary among plant genotypes. Such community-genetic correlations demonstrate that different plant-associated communities are linked by the underlying genetic identity of individual plants and the traits they express. The genotype is a fundamental unit for both biodiversity and evolution, and the shared genetic connections of disparate communities suggests that the interplay between ecological and evolutionary processes in plant-associated communities in more complex than studies with a single community may reveal.

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**Table 1.** Hypotheses explaining patterns of genetic correlations among communities, with details on our approach to testing them.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Hypothesis** | **Reasoning** | **Our test** | **Notes on our test** | **Result if hypothesis is supported** |
| **Taxonomic similarity hypothesis**: communities more closely related to each other will be more strongly correlated than are distantly related organisms. | A gene will be more likely to influence related organisms than unrelated organisms because related organisms share similar resource needs and functional characteristics. | Explanatory matrix in partial mantel test. | Binned communities into three taxonomic groups: fungi, bacteria, and arthropods. Data matrix coded as: 0 = same taxonomic group, 1 = different taxonomic group. | A negative slope between the strength of pair-wise relationships (rho value) from comparisons between communities within the same group to comparisons between communities of different taxonomic groups. |
| **Time attenuation hypothesis**: the strength of genetic correlations among communities will decline as the time between sampling of each community increases. | A greater time interval between sampling communities will decouple the effects of communities on each other, and variation in environmental conditions may alter tree gene expression between sampling dates. | Explanatory matrix in partial mantel test. | Values in matrix represent approximate number of months between the sampling of two different communities. | A negative slope between the strength (rho value) of pair-wise relationships between communities and the number of months between sampling dates. |
| **Resource similarity hypothesis**: communities associated with similar resources tend to be predictably associated on the same plant genotypes. | Species living in close proximity share habitat and may be connected through the same local food web, so are more likely to interact or be sensitive to genetic variation in the same plant traits. | Explanatory matrix in partial mantel test. | Three resource locations defined: phyllosphere = leaves and young twigs, trunk = lower bole, below ground = litter layer and soil. Data matrix coded as: 0 = communities present in same location, 1 = communities present in different locations. | The strength (rho values) of pair-wise relationships between communities exhibits a negative slope from comparisons between communities in the same location to comparisons of communities in different locations. |

**Table 2.** Community data used in analyses.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Community | Date collected | OTUs in community | Tree genotypes in full dataset (N) | Trees in full data set (N) | Location | Ecological roles | Units of quantification for each OTU | Reference |
| Soil bacteria | 2004, Oct. | 12 | 8 | 27 | Soil beneath tree | Variable, including decomposers | Phospholipid fatty acid concentrations | Schweitzer, Bailey & Fischer *et al*. (2008). |
| Soil fungi | 2004, Oct. | 4 | 8 | 27 | Soil beneath tree | Variable, including decomposer and plant mutualists | Phospholipid fatty acid concentrations | Schweitzer, Bailey & Fischer *et al*. (2008) |
| Twig fungal endophytes | 2006, June | 12 | 10 | 49 | 3-yr-old twig tissue of lower canopy | Tree symbionts but function uncertain | Isolation frequency | Lamit, Lau & Sthultz *et al.* (2014) |
| Ectomycorrhizal fungi | 2006, May | 8 | 10 | 48 | Tips of fine roots | Primarily plant mutualists | % of root tips colonized | Lamit (2013) |
| Epiphytic bark lichens | 2010, May | 9 | 18 | 74 | Bark of lower trunk | Primary producers | % cover | Lamit, Lau & Næsborg *et al.* 2014 |
| Necrotrophic fungal pathogens | 2009, Aug/Sept | 2 | 30 | 104 | Leaves of lower canopy | Tree pathogens | % leaf area damaged | Busby, Newcombe & Dirzo *et al*. (2013) |
| Leaf modifying arthropods | 2010, July | 11 | 25 | 75 | Leaves and young twigs of lower canopy | Tree herbivores | Counts of galls and other modifications per standardized branch diameter | Keith, unpublished. See methods in Wimp, Wooley & Bangert *et al*. (2007). |
| Necrotrophic fungal pathogens | 2010, Aug/ Sept | 2 | 25 | 92 | Leaves of lower canopy | Tree pathogens | % leaf area damaged | Busby, Newcombe & Dirzo *et al*. (2013, 2014). |

\*Values for OTU, genotype and tree numbers represent the counts in the full datasets, prior to reduction after pairing with other communities.

**Table 3.** Mantel rho-values from genetic correlations among communities.\*

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Endophyte.06 | EMF.06 | SoilBacteriaPLFA.04 | SoilFungiPLFA.04 | Lichen.10 | LeafModifiers.10 | LeafPaths.09 | LeafPaths.10 |
| Endophyte.06 |  | 0.057 | -0.036 | -0.218 | -0.189 | 0.178 | **0.225** | ***0.797*** |
| EMF.06 | 0.177 |  | 0.086 | 0.182 | 0.125 | ***0.352*** | 0.139 | -0.123 |
| SoilBacteriaPLFA.04 | 0.032 | -0.061 |  | ***0.880*** | -0.105 | 0.069 | -0.026 | **0.347** |
| SoilFungiPLFA.04 | **0.304** | -0.071 | ***0.883*** |  | -0.017 | -0.035 | 0.115 | 0.169 |
| Lichen.10 | -0.124 | 0.076 | 0.081 | 0.037 |  | 0.173 | 0.102 | 0.049 |
| LeafModifiers.10 | **0.247** | ***0.351*** | 0.186 | 0.278 | ***0.262*** |  | ***0.267*** | ***0.252*** |
| LeafPaths.09 | ***0.326*** | **0.329** | -0.034 | 0.091 | -0.010 | ***0.297*** |  | ***0.555*** |
| LeafPaths.10 | ***0.554*** | 0.002 | 0.209 | 0.177 | -0.066 | ***0.327*** | ***0.617*** |  |

\* Rho-values from pair-wise Mantel tests conducted with raw, unrelativized data are in the lower left triangle while rho-values from Mantel tests conducted with data relativized by OTU maximum values are in the upper right triangle. Bold = 0.1 > *P* < 0.05. Bold italics = *P* ≤ 0.05.

**Figure legends**

**Figure 1.** *Populus angustifolia* (A), the Ogden Nature Center Common Garden (B), and *P. angustifolia*-associated organisms known to be influenced by tree genotype, including those of the phyllosphere (C = *Pemphagus batae* gall with hemipteran, D = leaf damage by *Sphaerulina* spp. and *Drepanopeziza populi*, E = twig endophyte isolates), lower trunk (F = *Xanthomendoza galericulata* bark lichen), and soil (G = root tip colonized by ectomycorrhizal fungus).

**Figure 2.** Network diagrams representing the genetic correlation structure among communities associated with *Populus angustifolia*, for analyses conducted with unrelativized (A) and relativized (B) data matrices. Edges (i.e., lines connecting communities) in the networks are scaled by the magnitude of their associated rho-value from pair-wise Mantel tests. Community names are followed by the year in which they were sampled.

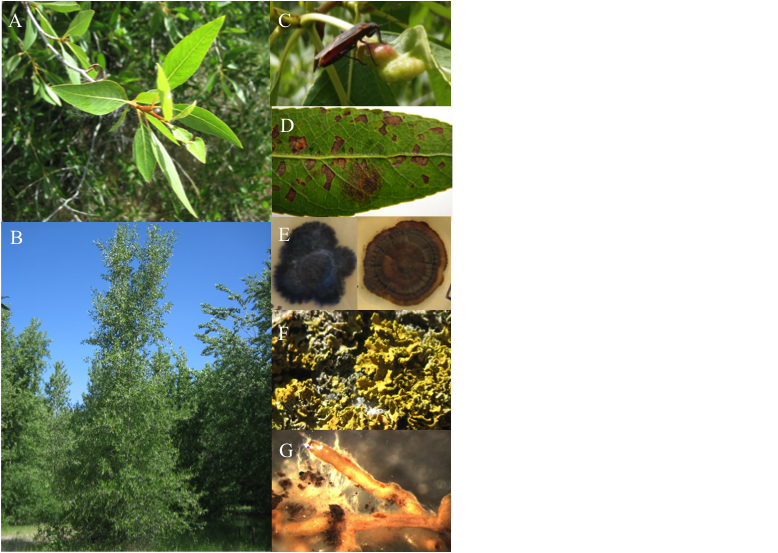
**Figure 3.** Tests of hypotheses about factors affecting the strength (rho from pair-wise Mantel tests) of genetic correlations between communities (see Table 1). A path diagram representing the partial-Mantel test testing the *time attenuation*, *resource similarity* and *taxonomic similarity hypotheses* (A) and a test of the interacting foundation species hypothesis comparing rho-values that were ≥ 0.2 prior to relativization to their values after relativization (B). For the path diagram, each named hypothesis is followed by the specific type of data matrix used in the partial-Mantel model. Arrows are scaled in accordance with their partial-Mantel correlation coefficients (values associated with arrows), dashed arrows represent effects with *P* > 0.05, and the number of genotypes used to generate each rho-value were used as an additional covariate in the analysis.Figure 1.

Figure 2.

Figure 3.

