**Correlated communities from microbes to arthropods: tree genotype mediates the structure of covariance among functionally and taxonomically divergent communities**

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Summary

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 connection to another community.

2. Using data from multiple studies conducted within a single common garden, we tested for genetic covariation among divergent, often taxonomically distinct communities (e.g., endophytes, pathogens, lichens, arthropods) associated with replicated genotypes of *Populus angustifolia*. Next, we evaluated whether resource similarity, taxonomic similarity, time be between sampling communities and numerically dominant 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) genetic correlations in almost half 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 community sampling determined the strength of genetic correlations. Third, the absolute abundances of the most common species drove many of the stronger correlations, supporting the interacting foundation species hypothesis, although there were important exceptions.

4. *Synthesi*s. We show that in addition to communities expressing heritable variation, they also covary among plant genotypes. Communities may constrain and modulate each other through these genetic correlations, such that the ecological and evolutionary dynamics of a diverse array of associated species is 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 organization of biodiversity.

Key words: Genetic correlations, community phenotype, foundation species, dominant species, 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 *et al*. 2003, Wade 2007, Haolin & Strauss 2008, Hughes *et al*. 2008, Bailey *et al*. 2009, Genung *et al*. 2011, Wymore *et al*. 2011, Hersch-Green *et al*. 2011, Rountree *et al*. 2011, Schweitzer *et al*. 2012, Whitham *et al*. 2012, Fischer *et al*. 2014, Woolbright *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 phenotype (*sensu* Whitham *et al*. 2006). Thus, as plants respond ecologically and evolutionarily to biotic and abiotic selection pressures, their associated communities can change with them (e.g., Johnson *et al*. 2009, Gehring *et al*. 2014).

A community phenotype is the product of interactions between an individual plant genotype and its interacting community of associated organisms and the environment. Plant associated organisms are sensitive to genetic variation in plant traits that influence their abundances through interactions or indirectly through modification of the local plant environment (e.g., Bangert *et al*. 2006, Crutsinger *et al*. 2014, Lamit *et al*. 2014, in press). Because many associated species are sensitive to multiple plant traits, their interactions with the multivariate phenotype (Holeski *et al*. 2012) of an individual plant genotype are the foundational cause of community phenotypes. The influence of genetic variation in plant traits cascades to alter complex interactions among community members (Gassman & Hare 2005, Johnson 2008, Mooney *et al*. 2008, Lamit *et al*. 2014, Busby *et al*. in press), and shape the phenotypes of associated organisms (e.g., aphid gall size and fecundity, Smith *et al*. 2010). These effects may produce important selection pressures that lead to local adaptation of community members to individual plant genotypes or populations (Shuster *et al*. 2006, Evans *et al*. 2008, Smith *et al*. 2010, Stireman *et al*. 2006) that can cascade to higher trophic levels (Stireman *et al*. 2006), and may also feed back to act as selective forces on plants (Lankau & Strauss 2007, Smith *et al*. 2012, Gehring *et al*. 2014). The community phenotype is therefore the extended consequences of: 1) genetically based plant traits directly affecting abundances and fitness of community members, 2) genotype-specific modulation of interactions among community members, 3) interspecific indirect genetic effects (IIGEs), where the phenotype of an individual in one species is, in part, due to the expression of genes in one or more different species (Shuster *et al*. 2006, Wade 2007, Allan *et al*. 2012), and 4) local adaptation of dependent species to plant genotypes.

Eco-evolutionary studies of the interactions between plants and their associated communities have typically focused on single communities (e.g., arthropods). However, because plant genes can link diverse groups of plant-associated species (e.g., Dickson & Whitham 1996, Ahlholm *et al*. 2003, Tagu *et al*. 2005, Sthultz *et al*. 2009), entire communities of distantly related, spatially disjunct species are likely linked by common connections to plant genotype. For example, Zytynska *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 direct and indirect effects of plant genetic variation on communities, and understanding how ecological and evolutionary change in plants affects the dynamics and biodiversity of plant-associated communities as a whole.

Here, we utilize a diverse set of data collected from a single common garden to understand patterns of genetic covariation among communities of organisms associated with *Populus angustifolia* (narrowleaf cottonwood). Our primary goal is to test the hypothesis that communities are genetically correlated with one another across plant genotypes. Next, we evaluate four non-mutually exclusive, mechanistic hypotheses for explaining the patterns of genetic correlations among communities (Table 1). The *resource similarity hypothesis* argues that communities on 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 (CITATION). The *taxonomic similarity hypothesis* predicts that communities of organisms more closely related to each other will be 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 genetic correlations among communities will decline as the time between sampling of each community increases. Time will likely decouple the direct or indirect effects of communities on each other, and be associated with variation in environmental conditions that alter gene expression in the tree. Finally, the *interacting foundation species hypothesis* posits that genetic correlations among communities will be driven by interactions and abundances of a few foundation or dominant species in communities (Keith *et al*. 2010, Busby *et al*. 2014). Dominant species are more likely than rare species to drive genetic correlations among communities because their disproportionate abundance makes them more likely to interact with other dominant species (Ellison *et al*. 2005). While these hypotheses are not mutually exclusive, distinguishing among them will help us to understand how disparate plant-associated communities are modulated by plant genetic variation and address how plant genetics contributes to the assembly of much larger communities of interacting species.

**Methods**

***Study system and common garden***

*Populus angustifolia* is a mid to upper elevation foundation species of interior western North American riparian habitats (Figure 1A). Intraspecific genotypic differences of *P. angustifolia* influence the structures of a variety of communities – foliar arthropods (Keith, Bailey & Whitham 2010), bark lichens (Lamit *et al*. in review), twig endophytes (Lamit *et al*. 2014), foliar pathogens (Busby *et al*. 2013, 2014) and soil bacteria and fungi (Schweitzer *et al*. 2008, Lamit 2013) – and ecosystem processes such as aquatic and terrestrial decomposition, and nutrient mineralization and cycling (Schweitzer *et al*. 2005, LeRoy *et al*. 2007). Genetic influences on communities and ecosystem process are likely due to heritable variation in traits such as foliar chemistry (Bailey *et al*. 2006), productivity (Lamit *et al*. 2014) and source-sink relationships within a tree (Compson *et al*. 2011), although the mechanistic links of *P. angustifolia* genes and functional plant traits to community and ecosystems processes remain largely unresolved. Because *P. angustifolia* is a model species for community genetics research (Whitham *et al*. 2008), it is ideal for examining genetic correlations between associated communities.

All data incorporated into this paper were collected from replicated *P. angustifolia* genotypes growing in the Ogden Nature Center common garden, Ogden, Utah, USA (Figure 1B). The garden is located in the geographic center of the *P. angustifolia*’s latitudinal range, and 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 1.2 hectares garden was planted in 1991 with cuttings clonally propagated from wild *P. angustifolia* growing along an ~105 km stretch of the Weber River. Trees in the garden were planted on 4 m centers, are randomly positioned, and were sexually mature when all community data were collected. Re-analysis of the thirty-five codominant restriction fragment length polymorphism (RFLP) marker dataset from Martinsen *et al*. (2001) indicated that all genotypes used were *P. angustifolia*, with little to no introgression from *P. fremontii* (Lamit *et al*. 2011, Zinkgraf *et al*. unpublished). See Busby *et al*. (2014) for more information on the garden.

***Community data***

Datasets representing a range of communities, both above and belowground, 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 Ogden Nature Center common garden. Datasets were considered community data when they contained information representative of two or more taxonomic groups, which for most datasets corresponds to species-level operational taxonomic units (OTUs). We focused on community composition, which incorporates all individual abundances from OTUs in a multivariate matrix. Compared to reduced metrics, such as species richness, composition contains the most information about community structure, and was shown to vary among genotypes for all of the communities we examined (see references in Table 1). Although the quantification of OTUs in each community was performed with different methods (e.g., % cover of lichens, counts of individual arthropods, pathogen leaf area damage), we considered each of these metrics as indicators of abundance.

Community datasets were merged for pair-wise analyses as follows. 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 communities in a pair 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. Multivariate communities in each of these data contained between 2 and 12 OTUs. Genotype means for each OTU’s abundances 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. 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 test for genetic correlations among communities. This approach identified concomitant shifts in the composition of two communities among a set of genotypes, where, when significant, increasing dissimilarity among genotypes in one community was associated with a similar increase in dissimilarity among genotypes in another community. One-tailed 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. Given the relatively small and uneven number of genotypes in the comparisons, we placed emphasis on the strength of the relationships as indicated by rho-values because some comparisons have low power. We considered rho-values of 0.2 or greater to be of potential importance, however we also report conventional *P*-values. Rho-values from these pair-wise Mantel tests between each community formed a central data used in all subsequent analyses. Analyses were conducted in R 3.0.2 using the package *ecodist* (Goslee and Urban 2007).

A network approach was used to visualize and interpret the structure of correlations among the different 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. [refs here?]

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

We used partial-Mantel tests to evaluate whether resource similarity, taxonomic similarity and/or time influence the strength of genetic correlations between communities (i.e., the size of rho-values from pair-wise Mantel tests described in the previous subsection). For these analyses,three additional matrices were constructed using pair-wise values for each comparison between communities (Table 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 test (described in the previous subsection) while holding the effect of the other matrices constant.

*Testing the interacting foundation species hypothesis*

We used data relativization 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 reduces the effect of highly abundant, dominant or foundation species (McCune and Grace 2002). Pair-wise Mantel tests were then repeated for each pair of communities, using Bray-Curtis dissimilarity and Spearman’s rho. The *interacting foundation species hypothesis* would be supported if data relativization reduced rho-values from pair-wise Mantel tests, and if significant relationships prior to relativization became insignificant with relativized data. Wilcoxon signed-rank tests were used to test for a decreases in the median pair-wise rho-values using rho from all tests, and then with only those from pair-wise Mantel tests with rho ≥ 0.2 to examine the effect of relativization on only those comparisons that showed moderate to strong community correlations. A network diagram was also used to visualize the structure of correlations between relativized datasets.

**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).

Visual examination of the network of pair-wise relationships between communities (as indicated by Mantel rho-values from pair-wise tests) provided additional resolution on the structure of genetic correlations between communities. The largest clusters of correlated communities was centered on the phyllosphere with some connections to communities in other locations (Figure 2A). In the phyllosphere-centered cluster, no community was more than three connections (edges) away from any other, although not all had a direct correlation. A second, small group 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 with both years of its data. In all cases, it is important to note that these connections may not represent direct ecological interactions; the tree may also act as an intermediary for indirect interactions, or the connections may represent shared responses to the same or correlated quantitative tree traits.

*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 hypothesis* were not supported by the partial-Mantel analysis (Figure 3A).

*Interacting foundation species hypothesis*

Our results suggest tentative support for the *interacting foundation species hypothesis* (Table 3, Figure 2) that genetic correlations among communities are driven by abundances of a few dominant or 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 appears to be as much related to an increase in variance among rho-values after relativization, as it does to differences in median values (Figure 3b). In contrast, a small number of correlations became stronger, or were only significant, after relativization (Table 2; Figure 2).

**Discussion**

*Support for correlated communities*

Individual plants are centers of biodiversity and species interaction for diverse organisms. Results from our study indicate that such disparate plant-associated communities can be linked by the plant’s underlying genetic identity. The interplay between ecological and evolutionary processes in plant-associated communities are, therefore, more complex than studies with organisms in a single, taxonomically defined community may reveal. As with traditional plant phenotypes, the same genes may influence a plant’s interactions with two different communities (pleiotropy), or each community may be influenced by different genes that have non-random associations (linkage-disequilibrium; Simms & Rausher, 1992, Conner & Hartl, 2004). Multivariate communities interact with multivariate suites of genetically based plant traits, as well as with other communities, such that the mechanisms, causal factors, and implications of genetic correlations among community phenotypes are likely more complicated than those for traditional phenotypes.

The community phenotypes that we have shown to be correlated – particularly endophytes, pathogens and arthropods – represent the extended consequences the multivariate plant phenotype, direct and indirect plant genetic effects, and interactions with the environment. In particular, manipulative experimental studies in the same common garden from which our correlated community analyses emerged illustrate that pathogens and arthropod communities of *Populus angustifolia* are connected by underlying genetic variation in plant resistance (Busby 2014 Ecology). Moreover, abiotic (Busby 2014 J Ecol) and biotic environmental factors (i.e., foliar endophytes, Busby Ecosophere) can modulate genetic interactions among plants and pathogens. Thus the endophyte-pathogen-arthropod example clearly illustrates how our understanding the far-reaching impacts of plant genetic variation on communities and ecosystems requires accounting for the complex of communities that are ecologically directly and/or indirectly linked by individual plant genotypes.

*Tested mechanisms for correlated communities*

In support of the *resource similarity hypothesis*, we found that the strongest predictor of genetic correlations between community phenotypes was a shared resource; communities utilizing the same or nearby plant resource on a tree were more strongly correlated than communities utilizing different resources on a tree. This mechanism could explain the observed linkages between canopy pathogens [these are necrotrophs], endophytic fungi [these are biotrophs] and arthropods [insect herbivores] that share a food source, the tree’s carbon. We also found correlation between some phyllosphere communities and ectomycorrhizal fungi, a root-associated community that also obtains its energy from the tree. Even across different regions of a plant, these communities could be connected either directly by their responses to variation the shared resource, or indirectly through modulation of the plant resource. For example, mycorrhizal abundance can alter plant defenses, which influence herbivore performance (Vannette and Hunter J Ecol 2013); and leaf feeding herbivores can affect both root feeding herbivores (Moran and Whitham 1990)and mycorrhizae (Gehring et al. 1997, Arnold et al. 2003, Lamit and Gehring 2011). Determining whether communities are correlated as a result of direct plant genetic effects (i.e., similar responses to genetic variation in a plant resource) or indirect plant genetic effects (i.e., one community modulating another) represents a major research goal moving forward.

While the *taxonomic similarity hypothesis* did not receive strong support in our analyses, future tests of this hypothesis incorporating more detailed information on the phylogenetic relationships among community members will be poised to ….

*Evolutionary in a community context*

Correlated communities linked by plant genetics suggest the potential for evolutionary consequences. In particular, our results raise the possibility that plant genotypes can act as a selective environments on associated communities through the direct effect of genetically based plant traits, or through augmentation of intraspecific interactions within an associated community, both of which can have fitness consequences for community members (Shuster et al. 2006, Smith et al. 2010, XXXXX). One community may modulate the selective effect of plant genotype on different communities, either through genotype-specific direct interactions or indirect interactions through plant-trait modulation. For example xxx

Because plant genetics modulates correlations among different communities, selection acting on a plant not only has extended consequences for its associated communities (e.g., Johnson *et al*. 2009?), it has the potential for cascading effects from one community to another, though direct and indirect community interactions, as well as for feedbacks among communities. Directional selection from outside forces, such as climate-change induced drought (citations), should lead to the community phenotypes of some plant genotypes being favored over those of less fit genotypes. For example, record drought resulted in differential mortality among genotypes in pinyon pine, *Pinus edulis* (Sthultz et al. 2009). Drought tolerant and intolerant plants varied in their associations with both shrub neighbors and communities of ectomycorrhizal fungi that likely contributed to performance differences (Gehring et al. 2014). However, feedbacks and selection may also be imposed by the associated community comprising the community phenotype… The community phenotypes of some genotypes may provide fitness benefits relative to the community phenotypes of other plant genotypes. In our case, leaf pathogens and leaf modifying arthropods may impose selection pressures on the trees, the strength of which depends on the composition of the community. Of key importance in these scenarios is that one community will be simultaneously influenced by factors affecting a genetically correlated community, or by the direct fitness consequences of a correlated community.

Evolution in a community context

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Relative importance of genetic, ontogenetic, induction,

and seasonal variation in producing a multivariate

defense phenotype in a foundation tree species

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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. |

Notes: The pair-wise matrices for each variable are presented in Appendix XX

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

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Community | Date collected | Taxonomic groups in community | Tree genotypes in full dataset (N) | Trees in full data set (N) | Location | Units of quantification for each OTU | Reference |
| Soil bacteria | 2004, Oct. | 12 | 8 | 27 | Soil beneath tree | Phospholipid fatty acid concentrations | Schweitzer et al. 2008 |
| Soil fungi | 2004, Oct. | 4 | 8 | 27 | Soil beneath tree | Phospholipid fatty acid concentrations | Schweitzer et al. 2008 |
| Twig fungal endophytes | 2006, June | 12 | 10 | 49 | 3-yr-old twig tissue of lower canopy | Isolation frequency | Lamit et al. 2014 |
| Ectomycorrhizal fungi | 2006, May | 8 | 10 | 48 | Tips of fine roots | % of root tips colonized | Lamit 2013 |
| Epiphytic bark lichens | 2010, May | 9 | 18 | 74 | Bark of lower trunk | % cover | Lamit et al. in review. |
| Necrotrophic fungal pathogens | 2009, Aug/Sept | 2 | 30 | 104 | Leaves of lower canopy | % leaf area damaged | Busby et al. 2014 J Ecol |
| Leaf modifying arthropods | 2010, July | 11 | 25 | 75 | Leaves and young twigs of lower canopy | Counts of galls and other modifications per 100 leaf shoots | Keith et al., unpublished. See methods in Bangert et al. 2006. |
| Necrotrophic fungal pathogens | 2010, Aug/ Sept | 2 | 25 | 92 | Leaves of lower canopy | % leaf area damaged | Busby et al. 2013 J Ecol, 2014 J Ecol |

\*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 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.

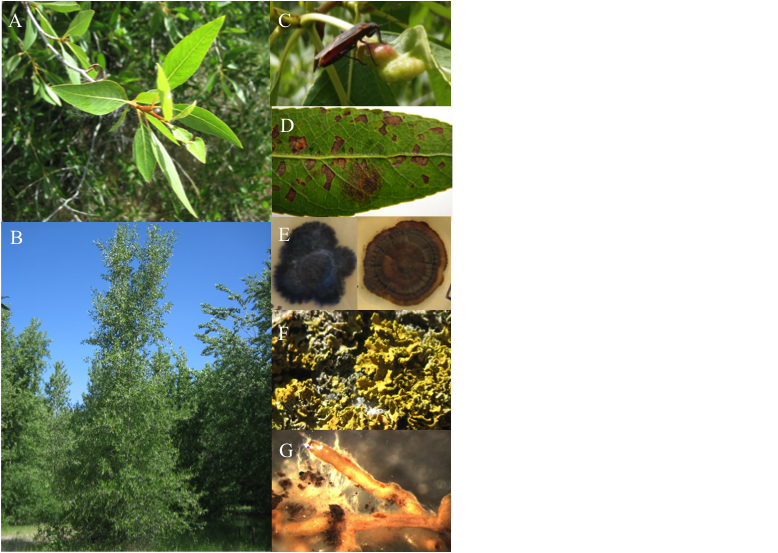
**Figure 3.** Tests of hypotheses about factors affecting the strength (rho from pair-wise Mantel tests) of genetic correlations between communities (see Table 1). A path diagram representing the partial-Mantel test testing the *time attenuation*, *resource similarity* and *taxonomic similarity hypotheses* (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.

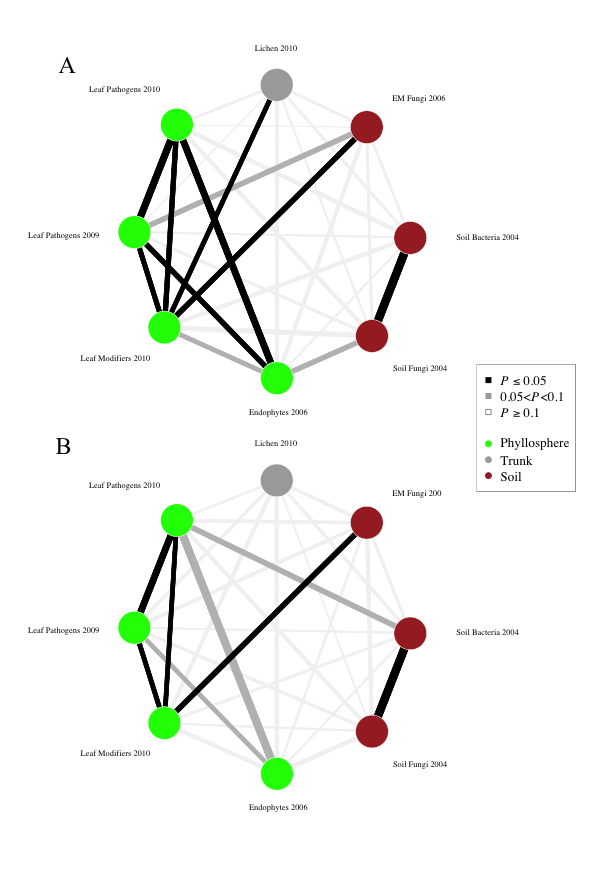


Figure 3.

