

# Tree genotype mediates covariance among communities from microbes to lichens and arthropods

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## Summary

**1.** Community genetics studies frequently focus on individual communities associated with individual plant genotypes, but little is known about the genetically based relationships among taxonomically and spatially disparate communities. We integrate studies of a wide range of communities living on the same plant genotypes to understand how the ecological and evolutionary dynamics of one community may be constrained or modulated by its underlying genetic connections to another community.

**2.** We use pre-existing data sets collected from *Populus angustifolia* (narrowleaf cottonwood) growing in a common garden to test the hypothesis that the composition of pairs of distinct communities (e.g. endophytes, pathogens, lichens, arthropods, soil microbes) covary across tree genotypes, such that individual plant genotypes that support a unique composition of one community are more likely to support a unique composition of another community. We then evaluate the hypotheses that physical proximity, taxonomic similarity, time between sampling (time attenuation), and interacting foundation species within communities explain the strength of correlations.

**3.** Three main results emerged. First, Mantel tests between communities revealed moderate to strong ( $\rho = 0.25\text{--}0.85$ ) community–genetic correlations in almost half of the comparisons; correlations among phyllosphere endophyte, pathogen and arthropod communities were the most robust. Secondly, physical proximity determined the strength of community–genetic correlations, supporting a *physical proximity hypothesis*. Thirdly, consistent with the *interacting foundation species hypothesis*, the most abundant species drove many of the stronger correlations. Other hypotheses were not supported.

**4. Synthesis.** The field of community genetics demonstrates that the structure of communities varies among plant genotypes; our results add to this field by showing that disparate communities covary among plant genotypes. Eco-evolutionary dynamics between plants and their associated organisms may therefore be mediated by the shared connections of different communities to plant genotype, indicating that the organization of biodiversity in this system is genetically based and non-neutral.

**Key-words:** common garden, community assembly theory, community evolution, community networks, community phenotype, community–genetic correlations, ecological genetics and ecogenomics, interacting foundation species hypothesis, physical proximity hypothesis, *Populus*

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## Introduction

Individual plant genotypes and the genetic structure of plant populations play important roles in defining community structure. A series of reviews on community genetics outline these relationships in diverse systems around the world (e.g. Whitham *et al.* 2006, 2012; Johnson & Stinchcombe 2007; Haloin & Strauss 2008; Rowntree, Shuker & Preziosi 2011; Fischer *et al.* 2014). Studies cited in these reviews demonstrate that related individuals support similar communities, such that different plant genotypes can be viewed as having different community phenotypes (*sensu* Whitham *et al.* 2006) and these phenotypes are heritable (e.g. Keith, Bailey & Whitham 2010; Lamit *et al.* 2014). Genetic variation is the raw material for evolution; the existence of community phenotypes, and the growing acknowledgement that ecology and evolution shape each other in real-time (Fussmann, Loreau & Abrams 2007; Thompson 2013), suggests an eco-evolutionary coupling of plants with their associated communities that has far reaching consequences (Genung *et al.* 2011).

A community phenotype is the product of interactions among an individual plant genotype, a community of associated organisms and the environment. Community members can be influenced by phytochemical, ontogenetic, phenological and morphological traits (e.g. Wimp *et al.* 2007; Bernhardsson *et al.* 2013; Crutsinger *et al.* 2014; Lamit *et al.* 2014) that comprise a multivariate plant phenotype (*sensu* Holeski *et al.* 2012), resulting in different plant genotypes supporting different communities (i.e. the community phenotype). The influence of genetically based plant trait variation on communities alters interactions among species within a community (Johnson 2008; Mooney & Agrawal 2008; Lamit *et al.* 2014; Busby *et al.* 2015), and their fitness and phenotypes (Shuster *et al.* 2006; Smith *et al.* 2010). These dynamics may produce selection pressures leading to local adaptation of community members to individual plant genotypes or populations (Capelle & Neema 2005; Shuster *et al.* 2006; Evans *et al.* 2008; Smith *et al.* 2012) that can cascade to higher trophic levels (Stireman *et al.* 2006), and may feedback to act as selective forces on plants (Madritch & Lindroth 2011; Smith *et al.* 2012; Gehring *et al.* 2014).

Community genetics studies typically focus on single communities and do not explore how plant genes link different community phenotypes (but see Korkama *et al.* 2007; Crutsinger *et al.* 2014). There is abundant evidence that different types of communities are sensitive to genotypic differences within the same plant species (Whitham *et al.* 2012). For example, communities of litter invertebrates and epiphytic plants are influenced by the genotype of a tropical forest tree (Zytynska *et al.* 2011). If communities are linked by common connections to plant genotype, such relationships should be detectable as *community–genetic correlations*, which we define as changes in the composition of one community among plant genotypes that are mirrored by changes in the composition of another community. Verifying

the presence of community–genetic correlations, and identifying factors that shape them, are important steps towards disentangling the complex effects of plant genetic variation on biodiversity and understanding how evolutionary changes in plants affect the ecology and evolution of disparate communities.

Here, we integrate a diverse collection of existing data sets from a single common garden, to examine patterns of covariation among communities associated with *Populus angustifolia* (narrowleaf cottonwood; Fig. 1a). Our primary goal is to test the hypothesis that disparate communities (e.g. microbes, bark lichens and canopy arthropods) exhibit community–genetic correlations among plant genotypes in a way similar to genetic correlations that are measurable among traits within species (see Simms & Rausher 1992). To address potential factors driving these community–genetic correlations, we evaluate four non-mutually exclusive, mechanistic hypotheses. (i) We define a *physical proximity hypothesis*, which states that communities living in close physical proximity are correlated because they interact with the same genetically determined plant traits and are likely to interact with each other. For example, fungal and arthropod communities associated with *Populus* twigs and leaves may be closely linked by similar source–sink relationships, which are genetically based (e.g. Larson & Whitham 1997; Compson *et al.* 2011). (ii) We define a *taxonomic similarity hypothesis*, which predicts that communities of organisms more closely related to each other are more strongly correlated than communities of organisms more distantly related. For example, ectomycorrhizal and pathogenic fungi should respond more similarly to variation among plant genotypes than ectomycorrhizal fungi and arthropods, because these fungi can have similar genetically based mechanisms of interaction with their host (Tagu *et al.* 2005; Veneault-Fourrey & Martin 2011). (iii) We define a *time attenuation hypothesis*, which posits that the strength of genetically based correlations among communities declines as the time between sampling of each community increases. Time may decouple relationships among communities due to factors such as species turnover, changes in plant trait expression with variation in environmental conditions and ontogenetic shifts, and variation in environmental factors directly affecting community members (e.g. Roche & Fritz 1997; Wimp *et al.* 2007; Yang & Rudolf 2010; Gugerli *et al.* 2013). (iv) The *interacting foundation species hypothesis* argues that strong community–genetic correlations result from interactions of a few influential foundation species (Ellison *et al.* 2005; Keith, Bailey & Whitham 2010; Busby *et al.* 2015). Although addition or removal of potential foundation species is crucial to demonstrate their foundation species status (e.g. Angelini & Silliman 2014), we use abundance as a proxy for their potential to influence members of other communities. Identifying community–genetic correlations and distinguishing among hypotheses explaining their structure are important steps towards elucidating the complexity of eco-evolutionary dynamics between plants and their disparate groups of associated communities.



**Fig. 1.** *Populus angustifolia* (a, scale bar = c. 3 cm relative to the leaf in full view in the centre left of the picture) at the Ogden Nature Center common garden (b, tree in centre = c. 8 m in height). Organisms known to be influenced by tree genotype, including those of the phyllosphere (c = *Pemphigus betae* gall with hemipteran, scale bar = c. 1 cm; d = leaf damage by the fungal leaf pathogens *Mycosphaerella* spp. and *Drepanopeziza populi*, scale bar = c. 1 cm; e = twig endophyte isolates, scale bar = c. 2 cm), lower trunk (f = *Xanthomendoza galericulata* bark lichen, scale bar = c. .5 cm) and soil (g = root tip colonized by an ectomycorrhizal fungus, scale bar = c. 0.025 cm).

## Materials and methods

### STUDY SYSTEM AND COMMON GARDEN

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 (Fig. 1b). *Populus angustifolia* (Salicaceae) is a mid- to upper-elevation foundation tree species of interior western North American riparian habitats, which has become a model species in community genetics (Fig. 1a). Each data set was pre-existing (see references in Table 1), collected to identify the responses of single communities to plant genotype, but data have not yet been integrated with one another as in this study. The garden is located in the geographic centre 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 c. 1 ha garden was planted in 1991, with cuttings clonally propagated from wild *P. angustifolia* growing along a c. 105 km stretch of the Weber River. However, a core set of genotypes present in all data sets in the analyses for this paper originated from a single site located within the lower elevational range of *P. angustifolia* along the Weber River. Trees in the garden were planted four to seven metres apart, with genotypes randomly positioned, and were sexually mature when community data sets were collected. See Lojewski *et al.*

(2009) and Bridgeland *et al.* (2010) for more information on the garden.

### COMMUNITY DATA

Data sets representing a range of communities, both above and below ground, and a variety of functional roles (e.g. primary producers, herbivores, pathogens, mutualists and decomposers), were included in analyses (Fig. 1c–g; Table 1). Each data set contained observations from at least nine replicated *P. angustifolia* genotypes sampled in the ONC north common garden. Data for most of the communities were composed of indicators of abundance of individual species (e.g. % cover of lichens, counts of arthropod galls or other modifications, leaf area damaged by fungal leaf pathogens) or molecular operational taxonomic units (OTUs) approximating species (e.g. colonization of ectomycorrhizal fungi, isolation frequency of endophytic fungi; Table 1). However, soil bacteria and fungi data from Schweitzer *et al.* (2008) were based on phospholipid fatty acid analyses (PLFA) that identified broad taxonomic groups often differing in their effects on soil processes (Table 1). Although the taxonomic resolution of identification differs among data sets, we refer to the members of each community as OTUs for simplicity. Prior to pairing, community data sets included two to 13 OTUs (Table 1). We focused on community composition, which incorporates all individual abundances from OTUs in a multivariate matrix. Compared to reduced metrics, such as



Table 1. Community data used in analyses.

Community	Date collected	Operational taxonomic units (OTUs) in community*	Tree genotypes in full data set (N)	Trees in full data set (N)	Location	Ecological roles	Units of quantification for OTUs	References
Twig endophytes	2006, June	12	10	49	3-yr-old twig tissue of lower canopy	Tree symbionts but function uncertain	Isolation frequency	Lamit <i>et al.</i> (2014)
Ectomycorrhizal fungi	2006, May	13	10	47	Tips of fine roots	Primarily plant mutualists	% of root tips colonized by OTUs clustered at 97% sequence similarity	Lamit (2013)
Soil bacteria	2004, October	12	9	30	Soil beneath tree	Variable, including decomposers	Phospholipid fatty acid concentrations	Schweitzer <i>et al.</i> (2008)
Soil fungi	2004, October	4	9	30	Soil beneath tree	Variable, including decomposer and plant mutualists	Phospholipid fatty acid concentrations	Schweitzer <i>et al.</i> (2008)
Epiphytic lichens	2010, May	9	18	74	Bark of lower trunk	Primary producers	% cover	Lamit <i>et al.</i> (2015a)
Leaf/stem modifying arthropods	2010, July	11	25	75	Leaves and associated branches of lower canopy	Tree herbivores	Counts of galls and other modifications per standardized branch diameter	A.R. Keith, unpubl. data. See methods in Wimp <i>et al.</i> (2007)
Fungal leaf pathogens	2009, September	2	30	104	Leaves of lower canopy	Tree pathogens	% leaf area damaged	Busby <i>et al.</i> (2014)
Fungal leaf pathogens	2010, September	2	25	92	Leaves of lower canopy	Tree pathogens	% leaf area damaged	Busby <i>et al.</i> (2013, 2014)

\*Values for operational taxonomic unit (OTU), genotype and tree numbers are for full data sets, prior to reduction after pairing with other communities.

diversity (e.g. Shannon's H), composition contains the most information about community structure and was shown to vary among genotypes for all of the communities examined (see references in Table 1).

Community data sets were merged for pairwise analyses. Initially, data sets contained 30–104 trees, representing 9–30 genotypes (Table 1). To merge each unique pair of data sets, observations from trees not present in both data sets were removed. Matched data for pair-wise comparisons were composed of 20–92 total trees, representing 6–25 genotypes with 2–9 replicate trees (clones) per genotype, although in the majority of cases, genotypes were represented by three or more trees after matching data sets. Mean values of each OTU associated with each genotype were then calculated from replicate trees of each genotype. OTUs that were associated with 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, distorting mean community composition after averaging its abundances. A total of 28 pairs of matched communities were created.

## STATISTICAL ANALYSES

We used a series of pairwise Mantel tests (Mantel 1967) to examine correlations between communities (i.e. community–genetic correlations). 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 & Fritz 1997). However, because Mantel tests examine correlations of pairwise dissimilarities, their estimate of the strength of the relationship between two communities is not directly comparable to genetic correlation results obtained with univariate traits or abundances. We suggest that this Mantel approach provides a suitable indicator of the relative strength of the pairwise genetic correlation between communities found on clones of host plants grown in a common garden. Given the relatively small and uneven number of tree genotypes in our analyses, we placed emphasis on the strength of the community–genetic correlations as indicated by  $\rho$  values. As a rule of thumb, we considered modest to high  $\rho$  values (0.25 or greater) to be of potential importance. We also reported  $P$ -values but caution their interpretation because power to detect significant relationships, which is highly dependent on sample size (Gotelli & Ellison 2004), varied considerably between comparisons with different pairs of communities. Because  $P$ -values from Mantel tests are generated through an extensive randomization procedure (Mantel 1967), they are exact and do not require adjustment for multiple comparisons.  $\rho$  values from pairwise Mantel tests between communities formed a central data set in all subsequent analyses. All Mantel tests in this paper 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 pairwise 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.

We also used Mantel tests to evaluate overall patterns of community–genetic correlations, with the specific goal of examining whether physical proximity, taxonomic similarity or time influenced their strength. Four triangular matrices were constructed using pairwise values for each comparison between communities (Table S1 in Supporting Information). The *time attenuation* matrix indicated the number of months between the sampling of each pair of communities. The *physical proximity* matrix indicated whether or not two communities occurred in similar locations of a tree. Pairwise relationships were coded as zero if communities were present in the same location and one if present in different locations, with three locations defined: the phyllosphere (including leaves and associated branches), the lower trunk (within 1 m of the ground) and below ground. The *taxonomic similarity* matrix indicated whether or not two communities were within the same broad taxonomic group (fungi, bacteria, arthropods), with pairwise relationships coded as zero if communities were in the same taxonomic group or one if in different taxonomic groups. Additionally, to understand whether variation in sample size influenced the strength of community–genetic correlations, a matrix was created which was composed of the number of genotypes used for each pairwise Mantel test used to estimate community–genetic correlations. The relationship between each of the four matrices described above and the matrix of  $\rho$  values of community–genetic correlations (from Mantel tests described in the first paragraph of this subsection) were initially tested with pairwise Mantel tests using Spearman's  $\rho$ . This was followed by a partial Mantel test that included all four matrices together, using partial Spearman's  $\rho$  to test for a relationship between each of the explanatory matrices and strength of community–genetic correlations, while holding the effect of the other matrices constant. Table S1a–e contains all triangular matrices used in these Mantel tests.

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 average value occurring within its reduced matrix. This relativization places all OTU values on the same scale and down-weights the effect of highly abundant OTUs (McCune & Grace 2002), which, due to their sheer abundances, have the potential to interact more with other community members than rare species. Community–genetic correlations were then estimated using pairwise Mantel tests for each pair of relativized community matrices, using Bray–Curtis dissimilarity and Spearman's  $\rho$ . Permutation-based paired  $t$ -tests were used to test for a decrease in pairwise  $\rho$  values in two ways: (i) using  $\rho$  values from all tests to examine the effect of relativization across all community–genetic correlations and (ii) using only community–genetic correlations of  $\rho \geq 0.25$  prior to relativization to examine the effect of relativization on comparisons that showed the strongest relationships prior to relativization. A network diagram was also used to visualize the structure of correlations between relativized data sets. The *interacting foundation species hypothesis* would be supported if data relativization reduced  $\rho$  values of community–genetic correlations, 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 and keystone species, as well as ecosystem engineers (Ellison *et al.* 2005), and the function of a species as a foundation species must ultimately be confirmed using removal or addition experiments (e.g. Angelini & Silliman 2014; Busby *et al.* 2015). However, we suggest that our test is an important first step that can

**Table 2.** Mantel  $\rho$  values from community–genetic correlations\*

	Twig endophytes 2006	Ectomycorrhizal fungi 2006	Soil Bacteria 2004	Soil Fungi 2004	Epiphytic lichens 2010	Leaf/stem modifying arthropods 2010	Fungal leaf pathogens 2009	Fungal leaf pathogens 2010
Twig endophytes 2006	–	0.040	–0.036	–0.218	–0.189	0.178	<b>0.225</b>	<b>0.327</b>
Ectomycorrhizal fungi 2006	0.192	–	–0.029	0.064	0.120	<b>0.280</b>	<b>0.246</b>	<b>0.234</b>
Soil bacteria 2004	0.032	–0.089	–	<b>0.880</b>	–0.131	–0.069	–0.026	<b>0.347</b>
Soil fungi 2004	<b>0.304</b>	–0.075	<b>0.852</b>	–	–0.039	–0.035	0.115	0.160
Epiphytic lichens 2010	–0.124	–0.094	0.077	0.030	–	0.173	0.102	0.049
Leaf/stem modifying arthropods 2010	<b>0.247</b>	0.149	0.186	0.278	<b>0.262</b>	–	<b>0.270</b>	<b>0.252</b>
Fungal leaf pathogens 2009	<b>0.326</b>	<b>0.544</b>	–0.034	0.091	–0.010	<b>0.297</b>	–	<b>0.555</b>
Fungal leaf pathogens 2010	<b>0.414</b>	<b>0.338</b>	0.209	0.177	–0.066	<b>0.327</b>	<b>0.617</b>	–

Bold =  $0.1 > P < 0.05$ . Bold italics =  $P \leq 0.05$ .

\* $\rho$  values from pairwise Mantel tests conducted with raw, unrelativized data are in the lower left triangle, while  $\rho$  values from Mantel tests conducted with data relativized by operational taxonomic unit maximum values are in the upper right triangle.

indicate whether abundant OTUs, which are candidate foundation species, may be driving community–genetic correlations. Permutation-based paired *t*-tests were conducted in R 3.0.2 using the *BROMAN* package (Broman & Broman 2014) and data relativization was conducted with the package *vegan* (Oksanen *et al.* 2013). Table S1a,f contains the two matrices used to perform these tests.

## Results

### PAIRWISE MANTEL TESTS AND NETWORK ANALYSIS

Pairwise Mantel tests revealed that disparate communities were correlated among *P. angustifolia* genotypes (Table 2). Nearly half of the comparisons (12 out of 28) had  $\rho$  values  $\geq 0.25$  (Table 2). Nine out of 28 (32.1%) of the comparisons were statistically significant ( $P \leq 0.05$ ), with another two comparisons marginally significant ( $0.05 < P < 0.1$ ); this is far more than the 5% (1.4 comparisons) expected by chance at a 0.05 alpha level (Gotelli & Ellison 2004). The communities that most consistently had the highest correlations were fungal leaf pathogens sampled in 2010 (median  $\rho = 0.333$ ) and in 2009 (median  $\rho = 0.312$ ), which were each correlated with multiple other communities (Table 2). In contrast, epiphytic bark lichens (median  $\rho = 0.010$ ) and soil bacteria (median  $\rho = 0.132$ ) tended to be more weakly correlated than other communities overall, although both communities had significant community–genetic correlations with at least one other community (Table 2).

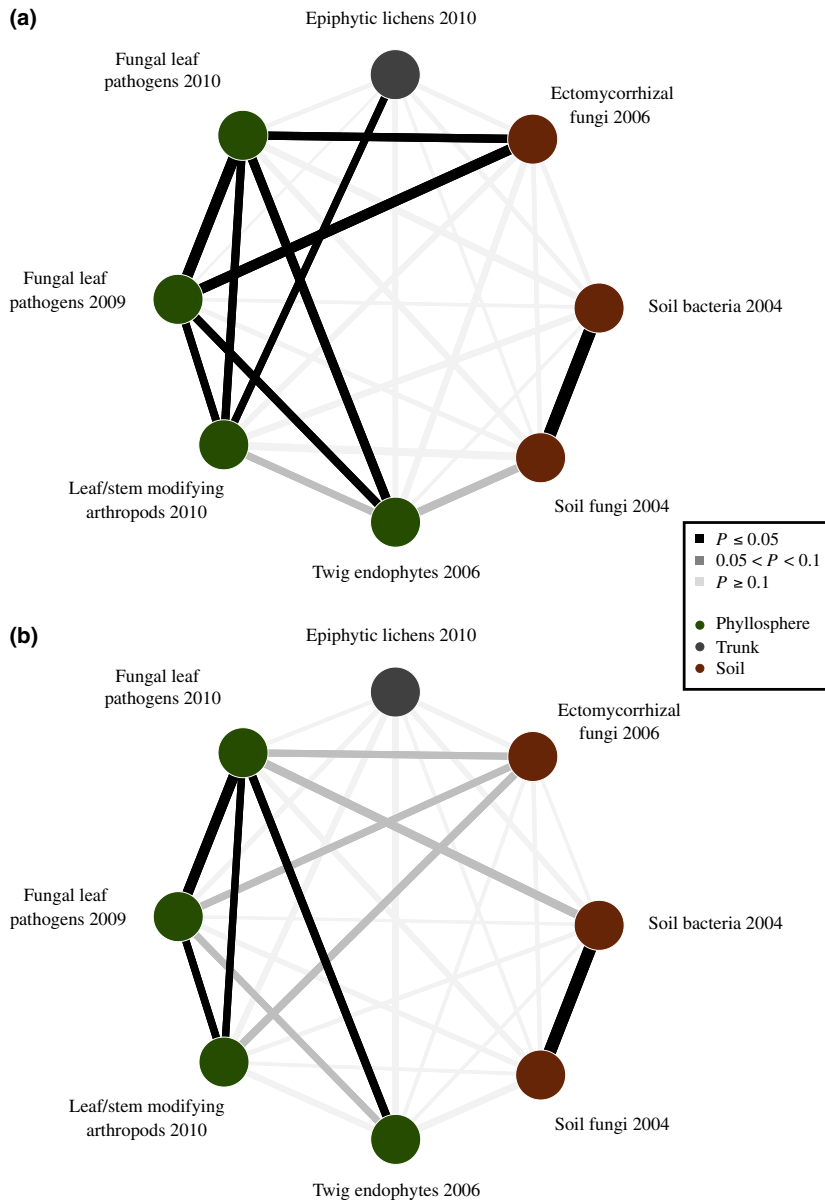
Analysis of the network of community–genetic correlations revealed a non-random structure in which specific communities were more likely to be associated with one another than other communities. The phyllosphere nodes were all directly connected to each other forming a dense cluster, with fewer connections to other communities (Fig. 2a). A second, smaller cluster was composed only of a very strong connection between the soil fungal and bacterial PLFA communities, and this cluster had little connection to outside nodes. Importantly, the one community that was sampled twice, fungal leaf pathogens, showed similar connections with other communities across both sample dates.

### PHYSICAL PROXIMITY, TAXONOMIC SIMILARITY AND TIME ATTENUATION HYPOTHESES

Of these three hypotheses, only the *physical proximity hypothesis*, that communities living in similar locations exhibit stronger community–genetic correlations than communities in different locations, was supported. Using pairwise Mantel tests, this hypothesis was supported by a decrease in  $\rho$  (negative slope) from community–genetic correlations between communities on similar locations compared to  $\rho$  values for community–genetic correlations between communities that occur in very different locations (Mantel  $\rho = -0.364$ ,  $P = 0.044$ ; Fig. 3a). In contrast, no clear effect on the strength of community–genetic correlations due to taxonomic similarity of communities (*taxonomic similarity hypothesis* Mantel  $\rho = 0.058$ ,  $P = 0.532$ ), or the distance in time between sampling communities (*time attenuation hypothesis* Mantel  $\rho = -0.171$ ,  $P = 0.167$ ), was observed. Furthermore, a significant effect of the number of genotypes used to estimate community–genetic correlations on the strength of community–genetic correlations was not detected (Mantel  $\rho = 0.263$ ,  $P = 0.155$ ), although the  $\rho$  value suggests that this factor may be important. When considering the four explanatory matrices together in a partial Mantel analysis, only the *physical proximity hypothesis* was supported, although significance was marginal (*physical proximity hypothesis* partial Mantel  $\rho = -0.315$ ,  $P = 0.071$ ; *taxonomic similarity hypothesis* partial Mantel  $\rho = 0.041$ ,  $P = 0.510$ ; *time attenuation hypothesis* partial Mantel  $\rho = 0.050$ ,  $P = 0.585$ ; number of genotypes used to estimate community–genetic correlations partial Mantel  $\rho = 0.205$ ,  $P = 0.227$ ).

### INTERACTING FOUNDATION SPECIES HYPOTHESIS

Our results are consistent with the *interacting foundation species hypothesis* (Table 2, Figs 2 and 3b), which predicts that community–genetic correlations are driven by foundation species. Using matrices relativized by OTU maximum, 8 out of 28 comparisons had positive  $\rho$  values  $\geq 0.25$ . Five comparisons (17.9%) were statistically significant ( $P \leq 0.05$ ),



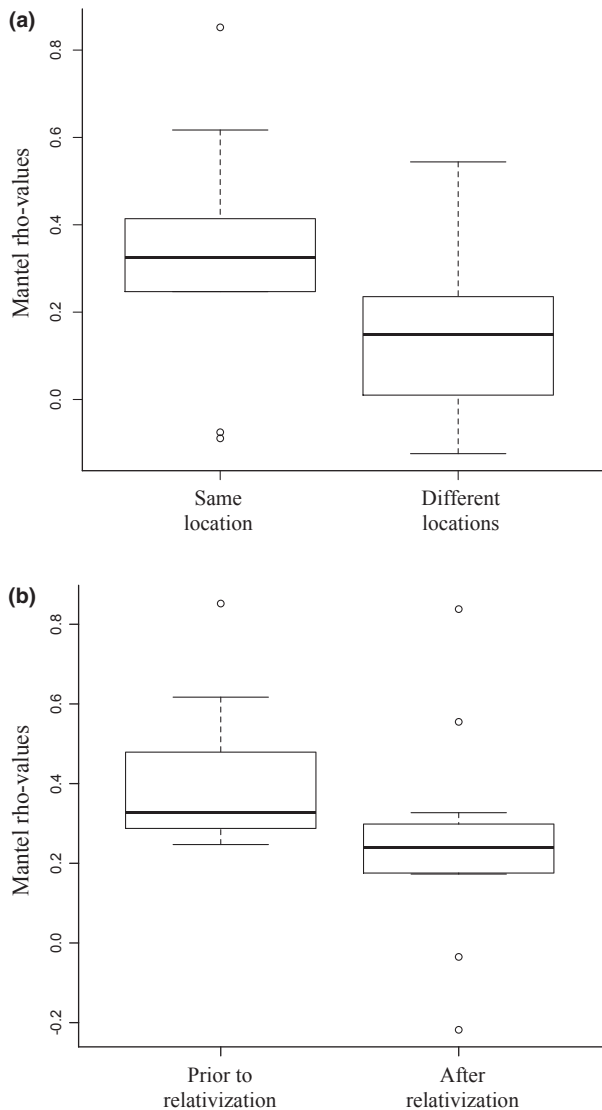
**Fig. 2.** Communities associated with *Populus angustifolia* display significant community–genetic correlations, shown here as community networks for (a) unrelativized and (b) relativized matrices with communities (nodes labelled with the year of sample collection) connected by edges scaled by the magnitude of the pairwise Mantel  $\rho$  values. Two important results are evident: phyllosphere communities are the most consistently interconnected communities, and several community–genetic correlations disappear or change when the influence of the most abundant species is down-weighted with relativization.

with another five comparisons being marginally significant ( $0.05 < P < 0.1$ ; Table 2, Fig. 2b). Considering all comparisons,  $\rho$  values from community–genetic correlations estimated with relativized matrices were lower than those from community–genetic correlations estimated with unrelativized community matrices ( $N = 28$ ,  $t = 1.955$ ,  $P = 0.030$ ;  $Q_1$ , median and  $Q_3$  for Mantel  $\rho$  with unrelativized data = 0.020, 0.189, 0.310;  $Q_1$ , median and  $Q_3$  for Mantel  $\rho$  with relativized data = –0.031, 0.118, 0.248). When considering only  $\rho$  values that were  $\geq 0.25$  for community–genetic correlations conducted with unrelativized data, there was a similar drop in the median  $\rho$  value after Mantel tests were rerun with their matrices relativized ( $N = 12$ ,  $t = 3.355$ ,  $P = 0.001$ ;  $Q_1$ , median and  $Q_3$  for Mantel  $\rho$  with unrelativized data = 0.292, 0.327, 0.446;  $Q_1$ , median and  $Q_3$  for Mantel  $\rho$  with relativized data = 0.177, 0.240, 0.284), indicating that the strongest community–genetic correlations estimated with unrelativized data dropped substantially after the most abundant OTUs

were down-weighted (Fig. 3b). In contrast, a small number of correlations became stronger after relativization (Table 2; Fig. 2).

## Discussion

In recent years, numerous studies have quantified how different plant genotypes define individual associated communities (see Whitham *et al.* 2012). These findings point out the importance of intraspecific variation in shaping communities and help set the stage for a more complete integration of community ecology with evolutionary biology and genetics. Our analyses extend these findings by demonstrating community–genetic correlations among a diverse range of plant-associated communities. We observed community–genetic correlations among communities that have different functional roles, sometimes occupy different regions of a tree or may not be in direct contact with the tree (e.g. some soil



**Fig. 3.** Tests of hypotheses about factors affecting the strength ( $\rho$  from pairwise Mantel tests) of community–genetic correlations. A test of the *physical proximity hypothesis* comparing  $\rho$  values from Mantel tests between communities that occupy the same plant tissues to  $\rho$  values from Mantel tests between communities that occupy different plant tissues (a), and a test of the *interacting foundation species hypothesis* comparing  $\rho$  values from Mantel tests that were  $\geq 0.25$  prior to data relativization to  $\rho$  values from Mantel tests conducted for the same pairs of communities after relativization (b). Plots represent median, first and third quartiles, and maximum and minimum (whisker), with black points representing outliers.

microbes). Importantly, we recognize the limitations of our analyses: we use existing data sets sometimes collected in different years or obtained with older methods that may not characterize the full suite of organisms in each community, and unequal sample sizes among data sets created variation in the number of trees and genotypes available for each unique comparison between pairs of communities. Nevertheless, we feel that this synthesis is an important step towards understanding how the genotype of a central organism (a tree in this case) can link a variety of disparate associated communities, and helps direct future work with more comprehensive

(e.g. next-generation sequencing) and coordinated sampling methods.

Community–genetic correlations among *P. angustifolia* genotypes are best explained by the *physical proximity hypothesis*, in which stronger relationships are observed for communities occupying the same or nearby locations on a tree, and the *interacting foundation species hypothesis* (Keith, Bailey & Whitham 2010; Busby *et al.* 2015), in which correlations are, in part, driven by the most abundant OTUs. Our findings regarding foundation species reinforce and expand on their established importance in structuring communities and species interactions (Keith, Bailey & Whitham 2010; Angelini & Silliman 2014; Busby *et al.* 2015). Support for the *physical proximity hypothesis* points to the likelihood that species are more likely to interact across boundaries of closely co-occurring communities or be linked by underlying plant genetic mechanisms (see next subsection), although these are not possible to tease apart in the analysis presented here. In contrast, neither the *taxonomic similarity hypothesis* nor the *time attenuation hypothesis* is supported by our results. The lack of support for the *taxonomic similarity hypothesis* could be methodological, as our broad taxonomic groupings may ignore significant functional diversity. Although taxonomic similarity may not be a broadly applicable predictor of the strength of community–genetic correlations, the consistent correlations between ectomycorrhizal fungi and fungal leaf pathogens, which may both have similar genetically based host interactions (Tagu *et al.* 2005; Veneault-Fourrey & Martin 2011), suggest that this hypothesis is relevant for some groups of organisms. It is more surprising that the *time attenuation hypothesis* is not supported, as the communities were sampled over a 6-year period. However, communities sampled in 1 year may give reasonable representations of the average community phenotype sampled among years. Importantly, community stability can be driven by population stability of a foundation species (Keith, Bailey & Whitham 2010), which may moderate other sources of variation as communities assemble each year and allow for detectable community–genetic correlations across years.

#### SELECTION AND THE SOURCES OF COMMUNITY–GENETIC CORRELATIONS

Genetic correlations arise when the same genes influence two traits (pleiotropy), or when genes influencing different traits have non-random associations (linkage disequilibrium; Simms & Rausher 1992); these factors also underlie community–genetic correlations. Multivariate plant phenotypes can be viewed as ecological filters (see Keddy 1992) influencing the unique assembly of communities on different tree genotypes (Bangert & Whitham 2007; Gugerli *et al.* 2013). Pleiotropy may cause community–genetic correlations when the same suite of genetically variable plant traits imposes filtering effects on two different communities. For example, the community–genetic correlations among fungal leaf pathogens, leaf/stem modifying arthropods and twig endophyte communities that we observed may be caused by shared responses to genetic variation in source–sink carbohydrate dynamics



among shoots (e.g. Larson & Whitham 1997; Compson *et al.* 2011). The existence of significant community–genetic correlations between communities that are unlikely to be influenced by the same set of plant traits (e.g. leaf modifying arthropods and epiphytic lichens) suggests that linkage disequilibrium also plays a role in community–genetic correlations.

Rapid evolution of plants in response to selection pressures influencing one community phenotype (Johnson, Vellend & Stinchcombe 2009) should also influence genetically correlated community phenotypes, no matter whether community–genetic correlations are driven by linkage disequilibrium or pleiotropy. These selection pressures may come from outside forces (e.g. drought; Gehring *et al.* 2014), or directly from a community phenotype (e.g. arthropod herbivory; Agrawal 2005). The evolution of plant traits influencing one community phenotype may be constrained or modulated when a genetically correlated community phenotype has fitness effects, suggesting that selection is diffuse (see Strauss, Sahli & Conner 2005). Importantly, our analyses using Mantel tests only indicate that two community phenotypes exhibit coordinated shifts among plant genotypes. This approach cannot discern negative or positive relationships between communities that would point to trade-offs and constraints, or the evolution of unified strategies for interacting with a full suite of plant-associated communities, respectively. However, the presence of community–genetic correlations between functionally, and sometimes spatially, disparate communities suggests that trade-offs likely exist.

Community–genetic correlations may also be driven by interactions among communities, similar to the effect of species interactions on genetic correlations among individual herbivore and pathogen species attacking plants (e.g. Maddox & Root 1990; Fritz 1992; Leimu & Koricheva 2006). Experiments such as the addition or removal of foundation species, or whole communities, are essential to establish that community–genetic correlations are influenced by interactions between communities. For example, *P. angustifolia* exhibits genotypic variation in premature leaf abscission when experimentally inoculated with a fungal leaf pathogen, *Drepanopeziza populi*, which alters the structure of foliar arthropod communities (Busby *et al.* 2015). Such trait-mediated interactions are common among plant-associated organisms both among and within communities (Ohgushi, Schmitz & Holt 2012), and genotype-specific modulation of plant traits may drive many of the community–genetic correlations observed in our results (e.g. between fungal leaf pathogens and leaf/stem modifying arthropods). However, other forms of genotype-mediated interactions, including predation, competition and avoidance may also cause community–genetic correlations. Although interactions between communities add an additional layer of complexity to our understanding of the genetic mechanisms that produce community–genetic correlations and the response of community phenotypes to natural selection on plant traits, we posit that interactions among communities are important factors that shape community–genetic correlations.

## EVIDENCE OF COMMUNITY EVOLUTION

The community–genetic correlations of disparate communities observed in this study provide evidence of community evolution. The findings of Goodnight (1990a,b) and Shuster *et al.* (2006) support the definition of community evolution as a ‘genetically based change in the ecological interactions that occur between species over time’. When genetic variation in one species underlies traits influencing the variation in relative fitness of other species, selection occurs within a community context (Shuster *et al.* 2006). These interactions among species have been defined as interspecific indirect genetic effects (IIGEs; Shuster *et al.* 2006), that is genetically based interactions that occur among ecologically associated species or whole communities. Community–genetic correlations are a likely consequence of such selection.

Whitham *et al.* (2006) proposed three lines of evidence that would support a community evolution hypothesis: changes in community heritability in the broad or narrow sense (see Whitham *et al.* 2012), feedback loops between dependent community members and the foundation species (see Fischer *et al.* 2014), and genetic covariance between community members. Our findings address the third line of evidence and represent an essential step justifying genetic analyses of the individual species that comprise the communities associated with a plant, including the complete genome sequencing of foundation species (Whitham *et al.* 2008; Gugerli *et al.* 2013). Where such data exist in the *Populus* system, genetic relationships have been found. For example, the mite, *Aceria parapopuli*, is adapted to individual tree genotypes (Evans *et al.* 2008). Such local adaptations exist because individual plant genotypes often represent unique selective environments influencing the traits and fitness of associated community members (Mopper 1996; Capelle & Neema 2005; Shuster *et al.* 2006; Wade 2007; Evans *et al.* 2008; Smith *et al.* 2010). 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 the fitness effects arising from consistent interspecific interactions between members of different communities (e.g. community–genetic correlations between microbes and arthropods) promote genetic differentiation in other community members among plant genotypes, community evolution has occurred. Although our findings do not demonstrate corresponding genetic changes among species, Shuster *et al.* (2006) argue that community structure based on plant genotype is an expected outcome of genetic correlations among community members.

Because the correlations between communities that we have found in this study are plant genotype dependent, our findings address fundamental theories of community organization that are central to eco-evolutionary approaches (Fussmann, Loreau & Abrams 2007). The classic and prevailing theories of community assembly (e.g. Real & Brown 1991) have largely lacked a genetics framework and an appreciation of how

genetically based multivariate plant phenotypes can structure entire communities and ecosystem processes. However, several reviews call for a synthesis of community ecology and evolutionary biology (e.g. Johnson & Stinchcombe 2007). Our findings of significant community–genetic correlations at the individual plant genotype level are inconsistent with neutral theory and the equivalence of species of Hubbell (2006), as well as the individualistic theory of Gleason (1926), in which species associations are the result of ‘coincidence’ and that every species is a ‘law unto itself’. They do, however, have some elements consistent with the tightly bound communities of Clements (1916), but are more ‘loosely’ bound, as one would expect in a dynamic system. Furthermore, as our findings showing community–genetic correlations are based upon local common garden studies, they also are in opposition to Ricklefs’ (2008) concept of the ‘disintegration’ of local communities in which ‘local coexistence can be understood only in terms of the distributions of species within entire regions’. It appears that the level of community analyses is crucial for detecting significant community structure. By focusing on individual genotypes of the relatively few highly interactive species, which in effect represent community and ecosystem drivers, eco-evolutionary researchers may critically examine the evolution of complex communities.

## 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 tenets of community genetics by showing that whole communities of taxonomically disparate species can 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 suggest that the interplay between ecological and evolutionary processes in plant-associated communities is far more complex than studies with a single community may reveal.

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## Data accessibility

Community data sets used in this paper are available in the archives of the Southwest Experimental Garden Array (Lamit *et al.* 2015b). Table S1 contains all triangular matrices used in analyses to test hypotheses about the factors influencing the strength of community–genetic correlations.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Matrices used to address the time attenuation hypothesis, physical proximity hypothesis, taxonomic similarity hypothesis and interacting foundation species hypothesis.