Forest tree neighborhoods are structured more by negative conspecific density dependence than by interactions among closely related species

Lei Chen[1], Liza S. Comita[2,3], S. Joseph Wright[3] , Nathan G. Swenson[4],

Jess K. Zimmerman[5], Xiangcheng Mi[1], Zhanqing Hao[6], Wanhui Ye[7],

Stephen P. Hubbell[3,8], W. John Kress[9], Maria Uriarte[10], Jill Thompson[5,11],

Christopher J. Nytch[5], Xugao Wang[6], Juyu Lian[7], Keping Ma[1]

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany,

Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China.

[2]School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511,

USA.

[3]Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa Ancón,

Republic of Panama.

[4]Department of Biology, The University of Maryland, College Park, MD 20742, USA.

[5]Department of Environmental Sciences, University of Puerto Rico, Río Piedras, Puerto

Rico 00931, USA.

[6]Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology,

Chinese Academy of Sciences, Shenyang 110016, China.

[7]Key Laboratory of Plant Resource Conservation and Sustainable Utilization, South

China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China.

[8]Department of Ecology and Evolutionary Biology, University of California, Los

Angeles, CA 90024, USA.

[9]Department of Botany, MRC-166, National Museum of Natural History, Smithsonian

Institution, P.O. Box 37012, Washington, DC 20013-7012,USA.

[10]Department of Ecology, Evolution and Environmental Biology, Columbia University,

New York, NY 10027, USA.

[11]Centre for Ecology & Hydrology; Bush Estate, Penicuik, Midlothan Scotland EH26

0QB, UK.

Corresponding author: Keping Ma, State Key Laboratory of Vegetation and

Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20

Nanxincun, Xiangshan, Beijing 100093, China. E-mail: kpma@ibcas.ac.cn

Abstract

Interactions among neighbors influence the structure of communities of sessile organisms. Closely related species tend to share habitat and resource requirements and to interact with the same mutualists and natural enemies so that the strength of interspecific interactions tends to decrease with evolutionary divergence time. Nevertheless, the degree to which such phylogenetically related ecological interactions structure plant communities remains unclear. Using data from five large mapped forest plots combined with a DNA barcode mega-phylogeny, we employed an individual-based approach to assess the collective effects of focal tree size on neighborhood phylogenetic relatedness. Abundance-weighted average divergence time for all neighbors (ADT_all) and for heterospecific neighbors only (ADT_hetero) were calculated for each individual of canopy tree species. Within local neighborhoods, we found phylogenetic composition changed with focal tree size. Specifically, significant increases in ADT_all with focal tree size were evident at all sites. In contrast, there was no significant change in ADT_hetero with tree size in four of the five sites for both sapling-sized and all neighbors, even at the smallest neighbourhood scale (0-5 m), suggesting a limited role for phylogeny-dependent interactions. However, there were inverse relationships between focal tree size and the proportion of heterospecific neighbors belonging to closely related species at some sites, providing evidence for negative phylogenetic density dependence. Overall, our results indicate that negative interaction with conspecifics had a much greater impact on neighborhood assemblages than interactions among closely related species and could contribute to community structure and diversity maintenance in different forest communities.

Introduction

Since Darwin (1859), ecologists have recognized that closely related species, which tend to share similar phenotypic traits and ecological requirements by common descent, are likely to interact strongly and thus are unlikely to coexist. A wide range of evidence supports the hypothesis that the strength of interspecific interactions declines with evolutionary divergence time (the time since species last shared a common ancestor). Functional traits associated with ecological performance are significantly more similar among closely related species than expected by chance (e.g., Swenson et al. 2007, Lebrija-Trejos et al. 2014). In addition, the probability that two plant species share a common pest species (e.g., pathogens, herbivores) and, hence, the strength of indirect interactions mediated by shared pests, also declines with evolutionary divergence time (Novotny et al. 2002, Gilbert and Webb 2007, Liu et al. 2012, Gilbert et al. 2015). Finally, Darwin's prediction that closely related species are strong competitors has been confirmed experimentally for plants and microbes (Maherali and Klironomos 2007, Burns and Strauss 2011, Violle et al. 2011). Although a number of exceptions have been noted (e.g., Cahill et al. 2008, Araya et al. 2012, Godoy et al. 2014), phylogenetic relatedness remains an informative surrogate for characterizing the similarity of species, particularly when functional trait data are unavailable (Swenson 2013).

For long-lived, sessile organisms, such as trees, interactions with nearby neighbors are thought to play a critical role in influencing plant performance and thereby structuring community composition and diversity (Janzen 1970, Connell 1971). Ample evidence from tree communities around the world indicates that growth and survival are reduced when neighbors are of the same species (conspecifics) rather than different species (heterospecifics) (e.g., Comita and Hubbell 2009, Bai et al. 2012). More recently, researchers have turned their focus to testing whether the phylogenetic relatedness of heterospecific neighbors also influences tree performance in natural communities, with mixed results (Webb et al. 2006, Metz et al. 2010,

Uriarte et al. 2010, Paine et al. 2012, Lebrija-Trejos et al. 2014). The strength and relative importance of conspecific and phylogenetically-dependent interspecific interactions has been shown to vary with tree life stage (Piao et al. 2013, Zhu et al. 2015). Determining the degree to which these interactions structure diverse natural tree communities therefore requires integration across multiple life stages.

Here, we analyze large-scale, spatially-explicit datasets on tree size and neighborhood composition from a global network of forest plots (Anderson-Teixeira et al. 2015) to determine the influence of conspecific and phylogenetically-dependent interactions on the composition of forest tree communities. We examine how the composition of individuals surrounding focal trees changes with focal tree size. Size asymmetry characterizes interactions among trees (Weiner 1990). Large trees shade their smaller neighbors, dominate the rooting zone, and harbor large populations of pathogens, herbivores and mutualists (e.g., mycorrhizae) (Laliberte et al. 2015). Individual trees often live for centuries, and although age-size relationships can be highly variable (Youngblood et al. 2004, Fulé et al. 2014), larger individuals usually tend to be older than smaller conspecifics in forests that are in stable conditions (Leak 1985). Thus, we used the size of focal trees (diameter at 1.3 m above ground, DBH) as an integrator of the strength and duration of interactions with neighbors and asked whether the phylogenetic composition of neighbors surrounding focal trees shifted with focal tree size. Specifically, abundance-weighted average phylogenetic divergence times (1) between focal trees and all their neighbors, including conspecifics (ADT_all), and (2) between focal trees and only their heterospecific neighbors (ADT_hetero) were modelled as a function of focal tree size in hierarchical models. We also examined shifts in the proportion of conspecifics and closely related heterospecifics (i.e., species that have diverged ≤25 Myr, ≤50 Myr, ≤75 Myr or ≤100 Myr) around focal trees as a function of focal tree size, because phylogenetic signal of interspecific interactions might be obscured when using only average divergence time.

Using the approach described above, we attempt to tease apart the relative importance of the key ecological processes known to influence plant neighborhood composition, specifically seed dispersal, habitat requirements and species interactions (Detto and Muller-Landau 2013, Detto and Muller-Landau 2016). These processes are expected to differentially affect the relationship between focal tree size and our two measures of phylogenetic neighborhood composition (ADT_all and ADT_hetero; Fig. 1). Forest trees begin reproducing at relatively large sizes, levels of seed production tend to increase with tree size, and seed dispersal distances are limited with most seeds landing near their seed-bearing parent (Howe and Smallwood 1982, Wright et al. 2005, Muller-Landau et al. 2008). Limited seed dispersal will contribute to negative relationships between focal tree size and ADT_all because conspecific neighbors have evolutionary divergence times of zero; however, seed dispersal should have no effect on the relationship between focal tree size and phylogenetic neighborhood composition when only heterospecific neighbors are considered (i.e., ADT_hetero; Fig. 1a). Conversely, if closely related species share habitat requirements (Webb 2000, Webb et al. 2002), fitness-related functional traits (i.e., competitive hierarchy; Mayfield and Levine 2010) or mutualists (i.e., phylogenetically dependent positive interactions; van der Heijden and Horton 2009) and therefore thrive in the same micro-habitats, the predicted relationships for both ADT_all and ADT_hetero with focal tree size are negative (Fig. 1b). In contrast, if interactions with closely related neighbors are predominantly negative, due to competition or shared pests (Gilbert and Webb 2007, Burns and Strauss 2011), then we would expect both ADT_all and ADT_hetero to increase with focal tree size, indicating that tree neighborhoods become less related over time (Fig. 1c). However, if plant-plant competitive effects or natural enemies tend to be species-specific, as suggested by the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), there will be a significant positive signal of tree size only for ADT_all (Fig. 1d).

Using this framework, we analysed the relationships between focal tree size and neighborhood composition by using data on the spatial locations of 456,794 individuals of 715 species from five fully mapped forest plots, combined with DNA barcode phylogenies that enabled nearly complete resolution of divergence times. We quantified the strength of neighborhood phylogenetic transitions over tree ontogeny to evaluate the role of phylogenetically dependent interactions at different spatial scales and in distinct forests. Then, we weighed the relative importance of conspecific negative density dependence (CNDD) and phylogenetic-dependent heterospecific interactions in driving shifts in the phylogenetic relatedness of neighborhoods with focal tree size. Overall, our approach sheds light on how the evolutionary history of tree species at a site affects present-day ecological interactions that influence community structure and dynamics.

Methods

Study sites and forest plot data

We used datasets from one site in temperate North Asia (CBS), two from subtropical Asia (GTS and DHS), and two from the neotropics (LUQ and BCI), ranging from 9-18 °N in the Americas to 23-42 °N in Asia, with mean annual temperature ranging from 3.3 to 27.0 °C and mean annual precipitation from 672 to 3500 mm (Table 1). At each site there is a large, fully enumerated Forest Dynamics Plot (FDP) in which all free-standing woody stems ≥1 cm DBH have been measured, mapped to the nearest 0.5 m and identified to species using standardized protocols (Condit 1998, Anderson-Teixeira et al. 2015). Molecular phylogenies were constructed for woody species in these FDPs using three barcode loci (*rbcL, matK* and *trnH-psbA*) (Kress et al. 2009, Kress et al. 2010, Pei et al. 2011). In this study, we used a single dated mega-phylogeny that was constructed simultaneously based on the DNA barcode sequence data in different ForestGEO plots (Erickson et al. 2014). Most species without

barcoding data are rare species and only account for a limited proportion of trees in each plot. Thus, taking into account the large amount of data, we excluded species that lacked the *rbcL, matK* and *trnH-psbA* sequences from the analysis (Table 1). At all five study sites, there was evidence of phylogenetic signals in key plant functional traits (i.e., closely related species have more similar trait values than expected by chance; Supplementary material Appendix 1, Table A1).

Phylogenetic relatedness of neighbors

We calculated abundance-weighted average divergence time between individual *i* of focal species *j* and all its neighbors (ADT_all) and heterospecific neighbors only (ADT_hetero) as follows:

$$ADT\_all_{ij}(r) = \sum_{n=1}^{s} f_n \times DT_{nj} \quad \text{and} \quad ADT\_hetero_{ij}(r) = \sum_{n \neq j}^{s} f_n \times DT_{nj} \qquad (1)$$

S represents the number of species, f_n the frequency of neighbor species *n*, DT_{nj} the divergence time between species *j* and *n*, and *r* the neighborhood annulus. Distance *r* refers to 5-m annuli centred on the focal tree, ranging from 0 to 30m (i.e., 0-5m, 5-10m, … 25-30m).To avoid edge effects, all focal individuals were located > 30 m from the nearest plot edge. Because gymnosperms were absent from the tropical FDPs, we standardized divergence times to range from 0 (conspecifics) to 1 (most distantly related species in the plot) to facilitate comparisons among FDPs. Gymnosperms can have a large effect on average relatedness values even though they are relatively rare in these communities. So in addition, we tested whether the results were consistent when gymnosperms were excluded from our temperate and subtropical plots.

Statistical analyses

We restricted our analyses to 236 focal species that have the potential to become large canopy tree species to ensure that a full size range of saplings, poles and reproductive adults

were potentially available for each focal species. Determination of large canopy tree species was based on site-specific criteria related to tree architecture and maximum height (Little et al. 1974, Hubbell and Foster 1986). We performed separate analyses for neighbors of all sizes (DBH ≥ 1 cm) and for the subset of sapling-sized neighbors (1 cm ≤ DBH < 5 cm) because we expected size asymmetric interactions to impact these smaller neighbors most strongly.

Tree size is log-normally distributed, and maximum size varies widely among species. We therefore standardized the DBH of focal individual (*i*) of species (*j*) by species within sites, as:

$$D_{ij} = \frac{log(DBH_{ij}) - \overline{log(DBH_{.j})}}{sd(log(DBH_{.j}))} \qquad \textbf{(2)}$$

For all focal tree species with ≥10 individuals, we used linear mixed models to evaluate the relationships between focal tree size and ADT_all or ADT_hetero as follows:

$$ADT\_all_{ij}(r) \; or \; ADT\_hetero_{ij}(r) = \beta_{0j} + \beta_{1j} \times D_{ij} + \Phi_p + \varepsilon_{ij}$$

$$\varepsilon_{ij} \sim N(0, \sigma^2) \qquad \textbf{(3)}$$

Where $\beta_{0j} = \gamma_{00} + \pi_{0j}$, $\beta_{1j} = \gamma_{10} + \pi_{1j}$, γ_{00} and γ_{10} are the community-level intercept and slope, respectively, and π_{0j} and π_{1j} are random species-level effects on the intercept and slope, respectively. To control for spatial autocorrelation, we include a random effect for tree subplot (20-by-20 m plots) ($\Phi_p \sim$ Normal (0, σ_ϕ)) because preliminary analyses using variograms showed that ADT_all and ADT_hetero for each focal trees tended to be correlated within 20 m (Dormann et al. 2007, Jones and Comita 2010).

To aid in the interpretation of changes in ADT_all and ADT_hetero with focal tree size, we conducted two additional analyses. First, we tested for a relationship between focal tree size and the proportion of neighbors that were conspecific (vs. heterospecific). We used this analysis to confirm that differing relationships with focal tree size for ADT_all (all neighbors) vs. ADT_hetero (only heterospecific neighbors) were due to changes in the frequency of conspecifics in the local neighborhood. Second, we separated heterospecific neighbors into closely related vs. distantly relatedly species and tested for a relationship between focal tree

size and the proportion of heterospecific neighbors that were closely related (vs. distantly related). For this analysis, we tried four different cut-offs for close vs. distant divergence times: ≤25 Myr, ≤50 Myr, ≤75 Myr and ≤100 Myr. This analysis was used to detect shifts in phylogenetic neighborhood composition driven by interactions between only the most closely related species, which may be obscured when using average divergence time of all heterospecific neighbors. Relationships between focal tree size and the proportion of neighbors that were conspecifics or that were closely related heterospecifics were tested by using a generalized linear mixed model (Crawley 2013):

$$log(Odds(k)) = log\left(\frac{f_{ij(k)}}{1 - f_{ij(k)}}\right) = \beta_{0j} + \beta_{1j} \times D_{ij} + \Phi_p \qquad (4)$$

Where $f_{ij(k)}$ represents the frequency of neighbors in category k around focal individual i of species j, and all other terms are as defined above for Eq. 3 (e.g., $\beta_{1j} = \gamma_{10} + \pi_{1j}$). Separate models were run for each of the five categories (i.e., conspecifics, and heterospecifics: ≤25 Myr, ≤50 Myr, ≤75 Myr and ≤100 Myr).

All analyses were conducted in R 3.3.2 (R Development Core Team) and the mixed models were fitted using the lme4 package (Bates et al. 2015). To determine the significance of each term in these models, LRtest significance (likelihood ratio test) was determined by parametric bootstrapping (PBtest) to compare the full model with the simpler model using the pbkrtest package (Halekoh and Højsgaard 2014). Model fit was evaluated based on the conditional R^2 (i.e., variance explained by both fixed and random effects) using the MuMIn package (Nakagawa and Schielzeth 2013, Barton 2016).

Results

The effects of focal tree size on neighborhood phylogenetic relatedness (ADT_all and ADT_hetero)

When examining average divergence times between focal individuals and their neighbors including conspecifics (ADT_all), we found that the ADT_all of sapling sized neighbors (< 5 cm DBH) increased significantly with focal tree size at all five sites for 5 m neighborhood annuli (and up to 10 m at four sites, 15 m at two site and 25 m at one site; Fig. 2, Supplementary material Appendix 1, Table A2). A similar trend was found for all neighbors ≥ 1 cm DBH, but was only significant for four of the five plots at the 0-5 m neighborhood scale and one plot up to 15 m scale (Supplementary material Appendix 1, Table A2). In contrast, when examining average divergence times of only heterospecific neighbors (ADT_hetero), we only detected a significant relationship between focal tree size and ADT_hetero at two sites, and only for sapling-sized neighbors at CBS and all neighbors at LUQ in the smallest annulus (0-5 m) (Fig. 2, Supplementary material Appendix 1, Table A2). There was no qualitative difference when gymnosperms were excluded for the two subtropical plots (GTS and DHS). However, for the temperate plot (CBS), the focal tree size effects on both ADT_all and ADT_hetero were stronger when gymnosperms were excluded (Supplementary material Appendix 1, Table A2).

Change in proportion of individuals in the neighborhood with increasing focal tree size

At the community level, we found significant decreases in the proportion of conspecific sapling-sized neighbors (1 cm ≤ DBH < 5 cm) with focal tree size at all five sites for neighborhood annuli up to 20-30 m (Fig. 3). The strength of conspecific effects varied widely among species but was overwhelmingly negative (Supplementary material Appendix 1, Fig. A1). When examining all neighbors ≥1 cm DBH, however, only one plot (BCI) showed significant negative relationships between focal tree size and proportion of conspecific neighbors (Supplementary material Appendix 1, Fig. A2) and fewer species were interpreted as experiencing conspecific negative dependence (Supplementary material Appendix 1, Fig.

A1).

In our analysis of closely related heterospecific neighbors, we did detect significant declines in proportion of closely related heterospecific neighbors with increasing tree size. However, patterns varied widely among plots and depended on the cut-off for defining closely related species and the spatial scale (Fig. 3, Supplementary material Appendix 1, Table A4 and Fig. A1–A2). When closely-related heterospecific neighbors were defined as those that diverged ≤ 25 Myr or ≤ 50 Myr, significant declines in proportion of closely related neighbors with tree size were only detected at the 5-15 m scale in one plot (BCI). For heterospecific neighbors that diverged ≤ 75 Myr or ≤ 100 Myr, we detected much more prevalent negative relationships between focal tree size and proportion of close relatives, especially for the two Neotropical sites (Fig. 3, Supplementary material Appendix 1, Fig. A1–A2).

Discussion

Forest communities are structured by a number of ecological processes, including seed dispersal, habitat requirements, and both positive and negative interactions among neighboring individuals (Fig. 1; Detto and Muller-Landau 2013, Detto and Muller-Landau 2016). Using a focal tree approach that combined information on tree size, neighborhood composition, and phylogenetic relatedness, we were able to examine the net outcome of these processes for forest structure at multiple sites. Our results reveal that, of these processes, negative interactions with neighbors play an important role in shaping composition of local tree neighborhoods in both Old World and New World forests, and at neotropical, subtropical and temperate sites. Specifically, strong negative interactions with conspecifics, along with weaker negative interactions with closely related heterospecifics, result in decreasing relatedness of neighbors with increasing focal tree size.

Effect of conspecific neighbors on local composition

We detected significant decreases in the phylogenetic relatedness of neighboring trees with increasing focal tree size at all sites. However, at the majority of sites and spatial scales, this relationship disappeared when we excluded conspecific neighbors from the calculation of neighborhood phylogenetic relatedness. Thus, negative interaction with conspecific neighbors appears to be the dominant mechanism structuring local tree neighborhoods. This is further supported by the fact that the proportion of neighbors that were conspecific declined significantly with focal tree size at all sites, particularly for sapling-sized neighbors. Numerous studies have reported strong conspecific negative density-dependent mortality in both tropical and temperate forests (Augspurger 1984, Terborgh et al. 2008, Uriarte et al. 2004a, Stoll and Newbery 2005, Chen et al. 2010, Swamy and Terborgh 2010, Bai et al. 2012, Comita et al. 2014), particularly at early life stages (e.g., seedling and sapling stages; Zhu et al. 2015). Our results are consistent with these other studies and demonstrate that such density-dependent mortality patterns are strong enough to structure forest composition. Negative interactions with conspecific neighbors can result from strong intraspecific competition for resources, but a large body of literature points to distance/density-responsive, host-specific natural enemies (e.g., pathogens, insect herbivores) as the underlying mechanism, consistent with the Janzen-Connell hypothesis (e.g., Janzen 1970, Connell 1971, Mangan et al. 2010, Bagchi et al. 2014, Comita et al. 2014).

Our analyses also demonstrate that the signature of negative density-dependent interactions with neighbors is strong enough to persist despite other key processes that may have the opposite effects on tree community structure. It is well established that seed dispersal is limited for forest trees (Muller-Landau et al. 2008) and should act to reduce the average divergence time of neighbors by concentrating conspecifics around larger focal trees (Fig.1a). Likewise, shared habitat requirements (Harms et al. 2001), competitive hierarchies (Mayfield

and Levine 2010) and positive interactions among individuals (Waterman et al. 2011) should all act to increase the relatedness of neighboring individuals over time (Fig. 1b). The predicted contributions of these processes are qualitatively similar and mutually reinforcing, yet the observed relationships between focal tree size and community composition were in the opposite direction for all sites (Fig. 2, Supplementary material Appendix 1, Table A2), underscoring the general importance of negative conspecific interactions in structuring tree communities.

Nonetheless, these interactions between focal trees and neighbors appear to have a relatively limited spatial extent in terms of the signature on phylogenetic neighborhood composition. The increase in average divergence time of neighbors with increasing focal tree size was only detected at scales up to 5-25m for sapling-sized neighbors and 5-15 m for neighbors of all sizes (Supplementary material Appendix 1, Table A2). This is somewhat surprising because the focal trees were canopy species that would potentially have accumulated decades of influence on the local environment and trees that established later. However, most other studies of seedling and sapling growth and survival in forests have similarly detected density-dependent effects at scales < 30 m (Curran and Webb 2000, Hubbell et al. 2001, Peters 2003, Uriarte et al. 2004b, Comita and Hubbell 2009, Comita et al. 2010). This limited spatial extent suggests that very localized competition for resources (i.e., roots competing for soil resources) or space-restricted mortality agents (i.e., fungal pathogens, rather than insect or mammalian herbivores) are the main drivers of neighborhood interactions in forests (Terborgh 2012). However, it is important to note that the negative impacts on neighbors may extend further, but could be balanced out by opposing processes at larger scales, namely habitat preferences (e.g., Harms et al. 2001).

Phylogenetic relatedness of heterospecific neighbors

In the past decade, there has been a push to integrate phylogeny into community ecology, and a number of recent studies have evaluated whether the phylogenetic relatedness of co-occurring species can be used to understand mechanisms of community assembly (see reviews by Cavender-Bares et al. 2009, Vamosi et al. 2009, Lebrija-Trejos et al. 2014). These studies have primarily used one of two analytical approaches. One approach evaluates relationships between the establishment, growth or survival of focal individuals and the average (or minimum) divergence time of nearby neighbors (Webb et al. 2006, Paine et al. 2012, Lebrija-Trejos et al. 2014, Fortunel et al. 2016). The second approach uses species co-occurrence data and compares observed and randomized values of average (or minimum) divergence times for all pairwise combinations of species present in small quadrats (Webb 2000, Webb et al. 2002). However, these analyses often yield mixed results. In neighborhood analyses, the relationship between focal plant performance and phylogenetic relatedness to neighbors was insignificant, significantly positive and significantly negative in 105, 19 and 21 tests, respectively (Lebrija-Trejos et al. 2014). For studies of phylogenetic dispersion, the full range of phylogenetic community structure has been detected, with phylogenetic composition more similar, more dissimilar or indistinguishable from chance expectation in different 20-by-20-m quadrats at two of our sites (Kress et al. 2009, Pei et al. 2011). A modification of this approach compares a metric of phylogenetic community composition among life stages. Again results were mixed: juveniles can be more closely related or more distantly related than later life stages (Webb et al. 2006, Swenson et al. 2007, Gonzalez et al. 2010, Jin et al. 2015). This mixed evidence has led to numerous critiques of the use of phylogeny as a proxy for the processes of community assembly (e.g., Mayfield and Levine 2010, Araya et al. 2012, HilleRisLambers et al. 2012, Pavoine et al. 2013).

Our study integrates the effects of ecological processes affecting the focal individual and its neighbors over the lifetime of the focal tree, incorporating information on explicit tree

coordinates and species abundances. This approach, with its emphasis on focal individuals instead of quadrats, provides a useful alternative method to detect phylogenetic dependent processes when large, fully mapped forest dynamic plots are available. With this method, we were able to detect a significant decline in phylogenetic relatedness with tree size when including both conspecific and heterospecific neighbors. However, for the majority of sites and spatial scales, this relationship was not significant when only heterospecific neighbors were included, suggesting that phylogenetic relatedness of heterospecific neighbors does not play a critical role in structuring local tree neighborhoods.

Nevertheless, the overall similarity of an individual to its neighbors based on mean phylogenetic distance might average out important information regarding neighborhood interactions. Our finding of significant declines in the proportion of closely related heterospecifics with focal tree size implies that negative interactions between closely related species do play a role in shaping tree neighbourhood composition, particularly in the two Neotropical sites (Fig.3, Supplementary material Appendix 1, Table A3 and Fig. A1–A2). The discrepancy between our results when using average divergence time versus using proportion of closely related neighbors might be due to missing nonlinearities between phylogenetic relatedness of neighborhoods and the strength of interspecific interactions. By focusing on closely related neighbors, our analysis demonstrated that interspecific interactions are phylogenetically constrained. Varying the threshold divergence time used to define close relatives revealed that interactions with heterospecifics appear to be most prevalent when considering neighbors that diverged by ≤ 75 or ≤ 100 Myr, although effects were also found at one site for neighbors that diverged by only ≤ 25 or ≤ 50 Myr. We expect that increasing knowledge of phylogenetic signal in plant-pathogen host range (e.g., Gilbert and Webb 2007) and in shared functional traits (e.g., Swenson and Enquist 2009) will provide a better **understanding** of how different mechanisms structure phylogenetic communities.

Many of the previous studies that have shown effects of phylogenetic neighborhoods have focused on the seedling stage (e.g. Webb et al. 2006, Paine et al. 2012). In our study, we analyzed individuals ≥1cm DBH (i.e. large saplings and adult trees) and therefore may have missed stronger phylogenetic-dependent interactions at earlier life stages. It is possible that phylogenetic neighbor effects are largely due to sharing of natural enemies, to which young plants are particularly vulnerable (Liu et al. 2012). However, for at least one site included in our study (BCI), previous analyses of phylogenetic neighborhood effects found no significant negative effects at the seedling stage (Lebrija-Trejos et al. 2014, Zhu et al. 2015).

Variation among forest sites

Our results highlight the importance of negative density-dependent interactions for neighborhood structure in temperate, subtropical and neotropical forest communities. However, in contrast to recent studies reporting a latitudinal gradient in the strength of conspecific negative density dependence (CNDD) in eastern forests in the United States and across 24 forest plots worldwide (Johnson et al. 2012, LaManna et al. 2017), we found little evidence that CNDD and phylogenetic negative density dependence (PNDD) were more prevalent in diverse tropical forests compared to less diverse subtropical and temperate forests. The lack of latitudinal gradients may be due to the limited number of plots and their locations in different biogeographic realms. The sites included in our study are located in two continents, with the tropical sites located in the Americas and the subtropical and temperate sites located in Asia. As a result, the observed difference between tropical and non-tropical sites might reflect biogeographic, rather than latitudinal differences. However, when looking only at the Asian sites, which have similar evolutionary and biogeographic histories, there was no evidence that CNDD or PNDD were stronger or more prevalent in more diverse subtropical forests (GTS and DHS) compared to a low diversity temperate forest (CBS),

contrary to previously proposed hypotheses and studies (e.g., Janzen 1970, Connell 1971, Givnish 1999, Shuai et al. 2014). In addition, our study focused on community-level patterns and variation among sites. However, variation in the strength of conspecific and phylogenetic neighborhood effects likely occurs within sites, including spatial, temporal, and/or among-species variation (e.g. Comita et al. 2010, Zhu et al. 2015, LaManna et al. 2016). A better understanding of conspecific and phylogenetic neighborhood effects could be gained by future studies examining variation within sites and testing whether interspecific differences in the strength of neighborhood effects are linked to species traits.

Conclusions

Our study relied on well resolved barcode phylogenies and large sample sizes enabled by large forest dynamics plots, avoided scale-dependent randomization tests (Swenson et al. 2006), and incorporated information on individual neighbors and the size of focal individuals to examine the relationship between neighborhood phylogenetic structure and compositional change. Our novel approach revealed that shifts in the phylogenetic structure of tree neighborhoods with size do occur, but are largely driven by negative interactions between conspecific neighbors (Volkov et al. 2009; Wang et al. 2016). We did find some evidence for phylogenetic negative density dependence at some sites, but our results revealed that such effects are not likely to strongly influence phylogenetic neighborhood structure in communities. Our study highlights the value of cross-site analyses for providing a broader perspective on the processes structuring tree communities in forests worldwide.

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Table legend

Table 1. Description of the forest dynamics plots. The 2004 census of Changbaishan (CBS) and the 2005 census of the other four FDPs were used in this study. MAT = mean annual temperature; MAP = mean annual precipitation.

Plot	MAT (°C)	MAP (mm)	Location (SW corner)	Area (ha)	Species (analysis/census) [†]	Trees(analysis /census) [†]	Geography	Habitat
Changbaishan, China (CBS)	3.3	672	42.38 N, 128.08 E	25	39/51	36,593/36,894	Asian	Temperate
Gutianshan, China (GTS)	15.3	1964	29.25 N, 118.12 E	24	144/159	135,051/147,000	Asian	Subtropics
Dinghushan, China (DHS)	20.9	1985	23.16 N, 112.51 E	20	162/195	64,903/71,451	Asian	Subtropics
Luquillo, Puerto Rico (LUQ)	22.8	3500	18.33 N, 65.82 W	16	99/122	32,365/37,791	New-world	Neotropics
Barro Colorado Island, Panama (BCI)	27	2600	9.15 N, 79.85 W	50	271/299	187,882/208,387	New-world	Neotropics

[†] analysis/census refers to the number of species and trees with DNA barcodes used in the analysis and the total number present in the census.

Figure legends

Figure 1. Predicted relationships between focal tree size and phylogenetic neighborhood composition. Lines represent predicted relationships between focal tree size and average divergence time of neighboring trees, including conspecifics (ADT_all; solid grey line) and with only heterospecific neighbors (ADT_hetero; black dashed line) when different ecological mechanisms are dominant in structuring forest composition: a) seed dispersal; b) phylogenetically-dependent positive interactions, shared habitat requirements or competitive hierarchy; c) phylogenetically-dependent negative interactions; d) Janzen-Connell effects (or conspecific negative density dependence).
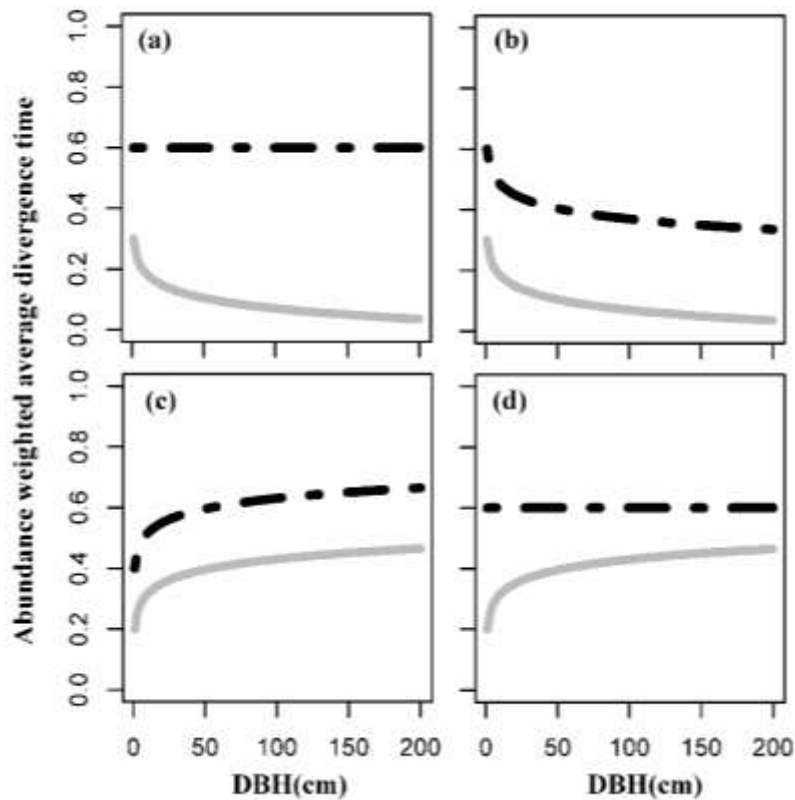
Figure 2. Observed relationships between focal tree size and average divergence time of neighboring trees including conspecifics (ADT_all; green lines) and average divergence time of only heterospecific neighbors (ADT_hetero; redlines) for sapling-sized (1 cm ≤ DBH < 5 cm) neighbors within 0-5 m of the focal tree in the five forest plots. In analyses, focal tree size is log-transformed and standardized by species, and then the results are back-transformed for interpretation. Significant relationships at α=0.05 are shown with solid lines, non-significant relationships with dashed lines, and the shaded area is the 95% confidence interval. Results including all neighbors (≥1 cm DBH), different neighborhood annuli, and conditional R^2 values can be found in Supplementary materials.
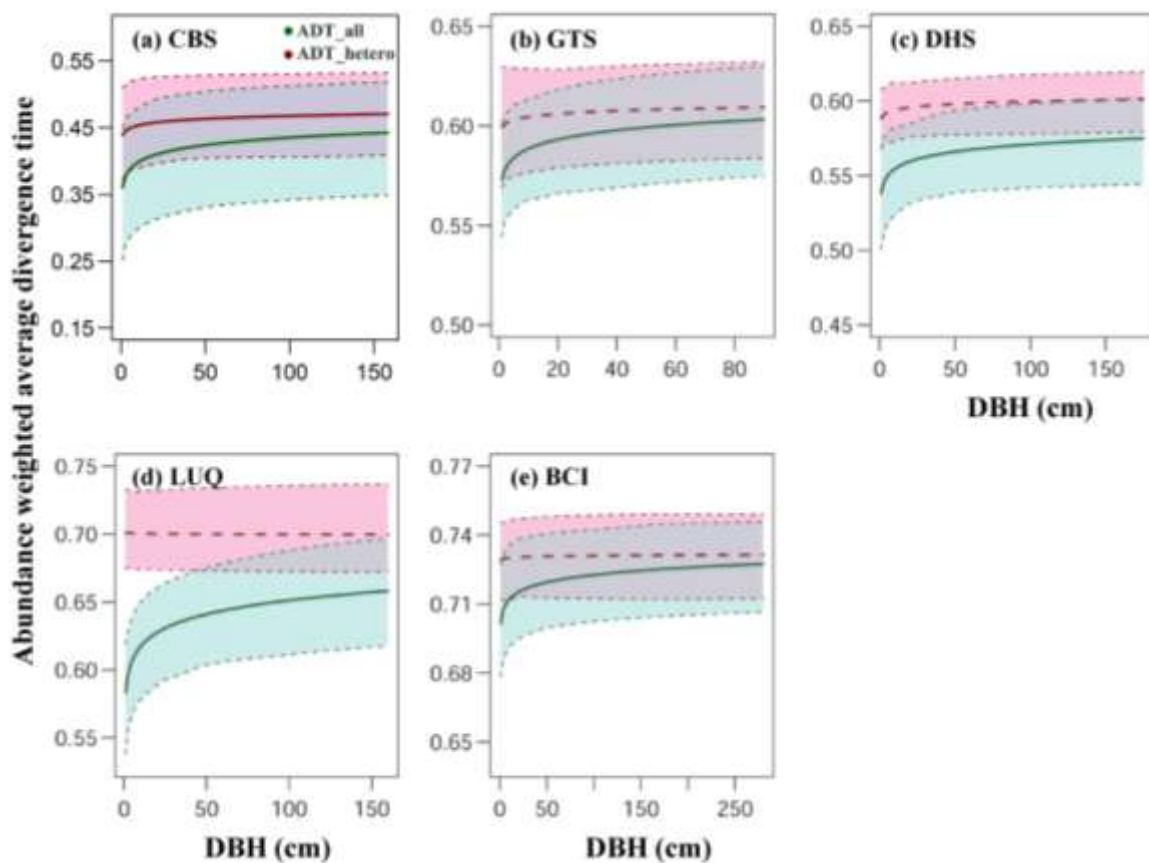
Figure 3. The odds ratios (exp(γ_{10}) in Eq. 4) and 95% confidence intervals of community-level mean relationships between focal tree size and the proportion of sapling sized neighbors (1 cm $\leq$ DBH < 5 cm) in the various phylogenetic categories and at different neighborhood scales at each of the five forest sites. Odds ratios above and below unity indicate positive and negative effects, respectively.