

Trait Dissimilarity and Hierarchy Predict Spatial Co-occurrence Patterns of Tree Species in a Subtropical Forest

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Abstract

1. The dissimilarity and hierarchy of trait values that characterize niche and fitness differences, respectively, have been increasingly applied to infer mechanisms driving community assembly and to explain species co-occurrence patterns. Here, we predict that limiting similarity should result in the spatial segregation of functionally similar species, while functionally similar species will be more likely to co-occur together either due to environmental filtering or competitive exclusion of inferior competitors (hereafter hierarchical competition). 2. We used a fully mapped 50-ha subtropical forest plot in southern China to explore how pairwise spatial associations were influenced by trait dissimilarity and hierarchy between species in order to gain insight into assembly mechanisms. We assessed pairwise spatial associations using two summary statistics of spatial point patterns at different spatial scales and compared the effects of trait dissimilarity and trait hierarchy of different functional traits on the interspecific spatial associations. These comparisons allow us to disentangle the effects of limiting similarity, environmental filtering and hierarchical competition on species co-occurrence. 3. We found that trait dissimilarity was generally negatively correlated with interspecific spatial associations, meaning that species with similar trait values were more likely to co-occur together and thus supporting environmental filtering or hierarchical competition. We further found that leaf area, wood density and maximum height had stronger trait hierarchy effects on the pairwise spatial associations relative to their corresponding trait dissimilarity effects, which suggests that hierarchical competition played a more (or at least equally) important role in structuring our forest community compared to environmental filtering. 4. This study employed a novel method to disentangle the relative importance of multiple assembly mechanisms in structuring co-occurrence patterns, especially the mechanisms of environmental filtering and hierarchical competition, which lead to indistinguishable co-occurrence patterns. This study also reinforced the importance of trait hierarchy rather than trait dissimilarity in driving neighborhood competition.

Introduction

The “entangled bank” metaphor of Darwin has inspired generations of community ecologists to explore the rules governing species coexistence and co-occurrence (Chesson, 2000; Gause, 1934; MacArthur, 1958; Ricklefs & Schluter, 1993; Tilman, 1982). Studies on species co-occurrence in species-rich communities over the past decades have reinforced the importance of the relationship between trait-mediated species differences and spatial distribution patterns among species in understanding the processes underlying coexistence and patterns of biodiversity (Chesson, 2000, 2013; He & Biswas, 2019; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Kraft, Godoy, & Levine, 2015; Laughlin, 2014; Li et al., 2018).

Species differences quantified by trait dissimilarity are frequently used as a proxy for the niche differences among species that are believed to drive species co-occurrence by influencing species’ response to environ-

mental conditions and neighborhood interaction (Burns & Strauss, 2011; Cadotte, Carboni, Si, & Tatsumi, 2019; Cavender-Bares, Kozak, Fine, & Kembel, 2009; Kraft & Ackerly, 2010). With such approaches, the environment is often assumed to act as a filter that selects for species possessing similar traits, leading to aggregated interspecific spatial associations between species with similar traits, while the pairwise spatial repulsion between species with similar traits are thought to result from limiting similarity via competition (Cavender-Bares & Wilczek, 2003; He & Biswas, 2019). However, the assumed link between species differences and co-occurrence only holds when the measured traits dissimilarity actually reflect niche differences and influence neighborhood competition (Cadotte, Davies, & Peres-Neto, 2017). When these assumptions do not hold, for example, neighborhood competition is not driven by trait dissimilarity but by competitive advantage associated with particular trait values (i.e. trait hierarchy) (Kunstler et al., 2016, 2012), the pattern that species with similar functional traits co-occur together could also be the result of competitive exclusion of inferior competitors (hereafter hierarchical competition) in the absence of niche segregation when trait similar species have similarly high fitness -e.g. trees with resource conservative traits (Chesson, 2000; Lasky, Uriarte, Boukili, & Chazdon, 2014; Mayfield & Levine, 2010). Therefore, the relationship between interspecific spatial associations and species differences characterized by trait dissimilarity and trait hierarchy is key for disentangling the relative importance of multiple assembly mechanisms, especially those leading to identical co-occurrence patterns, e.g. environmental filtering and hierarchical competition .

Trait dissimilarity and trait hierarchy can be characterized respectively as absolute and hierarchical (i.e. directional) interspecific trait differences to represent species niche and fitness differences (Kunstler et al., 2012). Bivariate spatial point pattern analysis is a primary tool for estimating the degree of pairwise species co-occurrence patterns departing from independence (Fig. 1a and Fig. 1b), and understanding the underlying processes that cause the departure from independence (He & Duncan, 2000; Wiegand et al., 2007; Wiegand & Moloney, 2014). Associations with trait dissimilarity and trait hierarchy provide the bivariate analysis with a basis for detecting the relative importance of multiple assembly processes (Carmona, de Bello, Azcárate, Mason, & Peco, 2019; Kunstler et al., 2016, 2012; Lasky et al., 2014; Shen, Wiegand, Mi, & He, 2013; Wiegand et al., 2007, 2017). It is notable that the relative importance of different assembly mechanisms and their signatures on spatial associations is highly scale-dependent (Gianuca et al., 2016; Smith, Sandel, Kraft, & Carey, 2013).

In this study, we predict that limiting similarity should result in functionally similar species occupying segregated areas (i.e. functionally similar-spatial repulsive pattern), leading to a positive relationship between the absolute functional trait distance (trait dissimilarity) and pairwise spatial associations (Fig. 1c). While, at the same time, functionally similar species would co-occur together more likely (i.e. forming functionally similar-spatial aggregated pattern) resulting from either environmental filtering or hierarchical competition (HilleRisLambers et al., 2012; Mayfield & Levine, 2010), leading to a negative relationship between the absolute functional trait distance and spatial associations Fig. 1d). To disentangle which of these two processes in the case of Fig. 1d , environmental filtering and hierarchical competition, is responsible for the functionally similar-spatial aggregated pattern, it is necessary to simultaneously test and compare the relative strengths of trait dissimilarity and trait hierarchy on pairwise spatial associations. If environmental filtering prevails, we would expect that the strength of trait dissimilarity should be greater than that of trait hierarchy (Fig. 1e), and if hierarchical competition drives the community assemblage, the effects of trait hierarchy are expected to be stronger than that of trait dissimilarity (Fig. 1f).

To link forest assembly mechanisms to trait difference- spatial association relationships and test the three hypotheses above (Fig. 1c, d, e and f), we addressed the following questions about spatial associations: (1) How are pairwise spatial associations correlated with trait dissimilarity and trait hierarchy? (2) Do the spatial pattern-trait difference relationships remain consistent across different spatial scales? Moreover, little attention has been paid to variation in abundances among the focal tree species and relative importance of different assembly mechanisms. In this study, we explored how the magnitude that the hierarchical competition effects outcompete the environmental filtering effects was related to the abundance of each focal species when trait hierarchy effects were detected.

To address these questions, we analyzed the bivariate spatial associations of 80 common species in a fully mapped 50 ha (1000 × 500 m) plot in Heishiding nature reserve in southern China using spatial point pattern analysis. To reveal how trait dissimilarity and hierarchy determine species co-occurrence patterns in the study forest, we evaluated the support for the three hypotheses by assessing the spatial pattern-trait difference relationships across different spatial scales. We then related the relative strengths of trait hierarchy and trait dissimilarity on spatial associations to the abundance of each focal species to better understand the underlying mechanisms.

Materials and methods

Dataset

The study area is located in the Heishiding Nature Reserve (HSD; 111°52 E, 23°27 N), Guangdong Province, China. Stems with diameters at breast height (DBH) > 1 cm were measured, identified and mapped in a 50 ha plot established in 2013, providing us with the distribution and abundance of 213 tree/shrub species with 213,969 individuals in total (Yin & He, 2014). The HSD plot is one of the sites of the CTFS-Forest Global Earth Observatory, which is a worldwide network dedicated to advancing long-term study of the world's forests (<http://www.ctfs.si.edu>; Anderson-Teixeira et al., 2015).

We chose adult trees for analysis in this study because the spatial distributions of adults would better reflect the effect of ecological processes (e.g. dispersal limitation, environmental filtering and biotic interactions) on their growth and survival over time. To obtain a sufficiently large sample size for point pattern analyses, in this study we included 80 common tree species (each with at least 50 individuals with DBH > 10 cm) including a total of 27,453 individuals in 52 genera and 33 families.

Spatial point pattern analysis of pairwise species association

We test the null hypothesis that species pairs are spatially independent, as opposed to showing patterns of attraction or repulsion. If two species show attraction in their spatial distributions, we will find more points of species j within the neighborhood of species i than expected under independence of the two species. Conversely, if the two species show segregation, we will find fewer points of species j within the neighborhood of species i than expected. To assess pairwise spatial associations, we used seminal techniques of bivariate point pattern analysis based on the distributions of distances of all pairs of points between the two species (Lotwick & Silverman, 1982; Wiegand & Moloney, 2014; Wiegand et al., 2017). Two summary statistics, bivariate pair-correlation function (pcf) $g_{ij}(r)$ and bivariate distribution function $D_{ij}(r)$ of nearest neighbor distances, were used in this analysis. The bivariate pair-correlation function $g_{ij}(r)$ can be estimated using the quantity $\lambda_j \gamma_{ij}(r)$, where λ_j is intensity (i.e. density) of species j in the whole study area, measuring the mean density of trees of species j at distance r away from a tree of the focal species i (Ripley, 1981; Stoyan & Stoyan, 1994). $D_{ij}(r)$ could be defined as the probability that trees of the focal species i have their nearest species j neighbor(s) within distance r (Diggle, 1983). $D_{ij}(r)$ can provide additional information of the spatial patterns that is not provided by the bivariate pair-correlation function $g_{ij}(r)$, especially in the extremely heterogeneous cases for focal species, e.g., many individuals of focal species i have no species j neighbor but few have many species j neighbors (Wang et al., 2010; Wiegand et al., 2007).

The independence of bivariate spatial point patterns is examined through the comparison of the summary statistics of the observed bivariate patterns with those of the null model, i.e., the observed patterns are compared against the simulated null model to test whether the hypothesis holds. In this study, we implemented the null model by keeping the locations of the focal species i unchanged while randomizing the distribution of species j by the method of Toroidal shift, which maintains most of structure of species j (Lotwick & Silverman, 1982). The null model of Toroidal shift removes the effects of environmental heterogeneity and the interspecific interactions, while retains the spatial structures of individual species. If a summary statistic of the observed bivariate spatial pattern significantly differs from the expectation of the null model, it is reasonable to conclude that the departure results from species interactions or environmental heterogeneity.

To assess the magnitude of departures from the null model, for each species pair and for each observed

summary statistic $S_0(r)$ (i.e., $g_{ij}(r)$ or $D_{ij}(r)$), we computed their standardized effect size $z(r)$ as:

$$z(r) = \frac{S_0(r) - \mu_{\text{null}}(r)}{\sigma_{\text{null}}(r)}, \quad (1)$$

where $S_0(r)$ is the observed summary function (either $g_{ij}(r)$ or $D_{ij}(r)$), and $\mu_{\text{null}}(r)$ and $\sigma_{\text{null}}(r)$ are respectively the average and the standard deviation of the summary functions for 999 bivariate patterns simulated according to the null models (Chanthorn, Wiegand, Getzin, Brockelman, & Nathalang, 2018; Wang et al., 2018; Wiegand, Grabarnik, & Stoyan, 2016). For a given distance r , the hypothesis of independence for a species pair can then be accepted if $-z_\alpha(r) < z(r) < z_\alpha(r)$ at a given pointwise significance level of α . For $\alpha = 0.05$, $z_\alpha = 1.96$, which is equivalent to testing whether the observed summary statistic is located within the 2.5th and 97.5th percentiles of the corresponding null model distribution. When $z(r) > 1.96$, the observed summary statistic is larger than the expectation of the null model with error rate $\alpha = 0.025$, and the species pairs are spatially attracted at distance r . While $z(r) < -1.96$ suggests repulsion at distance r . The distance r in this study was chosen to be 5, 30 and 50 m to test the effect of scale on spatial patterns. Because the association between two species might be asymmetric, we analyzed the spatial patterns between two species twice with each species serving as the focal species, i.e. species i versus species j and species j versus species i . Specifically, we examined the interspecific spatial associations of $80 \times 79 = 6320$ species pairs in this study for two different summary statistics of bivariate spatial point pattern analysis: $g_{ij}(r)$ and $D_{ij}(r)$. All the spatial association analyses were conducted in R (R Core Team, 2018) and using the package of “spatstat” (Version 1.62-2, Baddeley, Rubak, & Turner, 2015).

Species Trait Dissimilarity and Hierarchy

We focused on six key functional traits here: leaf area (LA; cm^2), specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$, calculated as leaf area/dry mass), leaf dry matter content (LDMC; g g^{-1} , calculated as leaf dry mass/fresh mass), wood density (WD; g cm^{-3} , calculated as trunk wood dry mass/fresh volume), wood dry matter content (WDMC; g g^{-1} , calculated as dry wood mass/fresh wood mass) and tree maximum height (H_{max} ; m) for each of the 80 species in this study. These traits represent leading axes of ecological variation among tree species that have been previously implicated in interspecific variation in resource use efficiency, species interactions, and life history strategies and are frequently used in analyses of the functional structure of forest communities (Kraft & Ackerly, 2010; Kunstler et al., 2016; Li et al., 2018). Specifically, LA is important for energy balance and hydraulic architecture (Ackerly & Cornwell, 2007). SLA and WDMC are key elements of the leaf and wood economic spectrum and correlate with procurement of resources (Chave et al., 2009; Wright et al., 2004). LDMC is indicative of a plant species’ resource use strategy that links to the trade-off between a rapid assimilation and growth (Díaz et al., 2004). WD is significant in relation to growth, stress-tolerance and survival rates (Chave et al., 2006). H_{max} is a key determinant of light competition (Westoby, Falster, Moles, Vesk, & Wright, 2002). Data on these traits on species-level were collected and measured from the HSD plot (He, Chen, Zhao, Cornelissen, & Chu, 2018), in which H_{max} was estimated by averaging the top 1% tallest trees for each species in the plot.

We calculated two kinds of species differences based on each single trait: absolute trait distance and hierarchical trait distance, to evaluate the effects of trait dissimilarity and trait hierarchy on interspecific spatial associations, respectively (Kunstler et al., 2012). Absolute trait distance between species i and j was calculated as $|t_i - t_j|$ where t_i and t_j are the functional trait values of the respective species, whilst hierarchical trait distance was calculated as $t_i - t_j$. In both trait distance measures, species i is the focal species in correspondence to that in the spatial point pattern analysis. As species’ niche dissimilarity might be better measured by a multi-trait than by a single trait approach (Kraft et al., 2015), we also computed species absolute distance in a multidimensional space defined by the 6 (centered and standardized) functional traits.

Relationships between pairwise spatial associations and trait dissimilarity and hierarchy

The pairwise spatial associations (estimated as SES of $g_{ij}(r)$ and $D_{ij}(r)$), represented as z_{ij} below) was modeled as a function of trait dissimilarity and trait hierarchy between species i and j , in a linear mixed model using the ‘lmer’ in the R package ‘lme4’ (Bates, Mächler, Bolker, & Walker, 2015), in which the focal

species were treated as random intercept allowing intercepts to vary among each focal species and we used each explanatory predictor as random slopes to evaluate the effects of each predictor on spatial associations for different focal species. The model takes the general form:

$$z_{ij} = a + a_i + \sum_{m=1}^n (b_m + b_{im}) x_{mij} + \varepsilon_{ij}, \quad (2)$$

where z_{ij} represents the spatial associations between species i and species j with the focal species i , x_{mij} represents the m^{th} explanatory predictors of trait distance (with n predictors in total), which could either be absolute or hierarchical trait distances, a is the fixed intercept and b_m is fixed slope of the m^{th} explanatory predictor for the overall regression, while a_i is the random intercept for the focal species i and b_{im} is the random slope for the m^{th} explanatory predictor for the focal species i .

We first exclusively applied the absolute trait distances of six individual traits: LA, SLA, LDMC, WD, WDMC and H_{\max} in equation (2) to evaluate the effects of absolute trait distances on the pairwise spatial associations to distinguish the assembly mechanisms of limiting similarity (Fig. 1c) and environmental filtering or hierarchical completion (Fig. 1d). If absolute trait distances have positive effects on pairwise spatial associations, it suggests functionally similar species tend to be spatially repulsive and indicates the operation of competition via limiting similarity in the forest (Fig. 1c). If absolute trait distance have negative effects on pairwise spatial associations, it indicates functionally similar species tend to co-occur together, presumably caused by either environmental filtering or hierarchical competition (Fig. 1d) that needs to be further tested. In addition, we also applied absolute trait distances estimated by multiple traits separately to equation (2) to test the effects of trait dissimilarity on pairwise spatial association because of the collinearity between absolute trait distances of individual and multiple traits.

To further test the mechanisms of environmental filtering and hierarchical competition when absolute trait distances have negative effects on pairwise spatial associations (Fig. 1d), we simultaneously included variables of both absolute and hierarchical trait distances and tested the relative importance of absolute and hierarchical trait distances in explaining the pairwise spatial associations by comparing the absolute values of the coefficients of the absolute trait distances and their corresponding hierarchical trait distances for each focal species. To do this, we compared the differences in the 95% confidence intervals of the coefficients (absolute values) of each absolute trait distance and its corresponding hierarchical trait distance for each focal species and we then grouped species into three categories, which are (1) hierarchical trait distances had stronger effects, (2) absolute trait distances had stronger effects and (3) hierarchical trait distances had comparable effects to absolute trait distances.

Relating the magnitude that trait hierarchy effects outcompete trait dissimilarity effects to the abundance of focal species

We measured the magnitude that trait hierarchy effects outcompete trait dissimilarity effects (MHD) by the differences in the absolute values of coefficients of hierarchical trait distances and absolute trait distances in the full model in equation (2) for different functional traits and for each focal species. If trait hierarchy had stronger effects than trait dissimilarity, MHD is supposed to be significantly larger than 0; If trait dissimilarity had stronger effects than trait hierarchy, MHD is expected to be smaller than 0. We then assessed the relationship between MHD and the abundance of each focal species to explore how the effects of different mechanisms vary among species with different abundance.

Results

Pairwise spatial associations

The pairwise spatial associations assessed by $g_{ij}(r)$ indicate that interspecific spatial independence ($-1.96 < z(r) < 1.96$) was the dominant pattern across the three different spatial scales (accounting for 82.09%, 83.05% and 85.30%, respectively) (Table 1). There were 315, 375 and 346 repulsion cases ($z(r) < -1.96$) out of the 6320 pairs (accounting for 4.98%, 5.93% and 5.47%) at the spatial scales of 5, 30 and 50 m, respectively. Attraction was more commonly observed with 817, 696 and 583 cases ($z(r) > 1.96$) (accounting for 12.93% 11.01% and 9.22%) than repulsion cases at the three scales. The same trends

were also found in the spatial association evaluated by the summary statistic of $D_{ij}(r)$, in which, spatial independence was also the dominating pattern between species (Table 1).

Relationships between spatial pattern and absolute trait distances

By fitting the linear mixed regression model (2) using absolute trait distances of individual traits exclusively, we found statistical support for negative effects of the absolute trait distances measured by individual traits on pairwise spatial associations assessed by the two summary statistics ($g_{ij}(r)$ and $D_{ij}(r)$) across different spatial scales (Fig. 2). The coefficients of absolute trait distances of individual traits of LA, WD and H_{\max} were consistently negative for both summary statistics across spatial scales. SLA (at $r = 5$ m) and WDMC showed slightly negative effects on pairwise spatial associations, while LDMC did not show significant effects. As for absolute trait distances based on multiple traits, negative effects on spatial associations were also observed consistently across summary statistics and spatial scales (Fig. S1).

For the 80 focal species, we found that the effects of absolute trait distances were non-significant for most of the focal species on their pairwise spatial associations as the 95% confidence intervals of coefficients intercepted 0 (Fig. 2). While for the remaining focal species, in general, more focal species' spatial associations were negatively correlated to absolute trait distances than those were positively correlated (Fig. 2).

Comparison between the strengths of trait dissimilarity and hierarchy on spatial patterns

As the absolute trait distances of individual traits used in this study generally had negative effects on pairwise spatial associations, which supports environmental filtering or hierarchical competition (Fig. 1d), we compared the strengths between trait hierarchy and trait dissimilarity on pairwise spatial associations by simultaneously including explanatory predictors of both absolute and hierarchical trait distances in equation (2) to distinguish these two mechanisms. For the 80 focal species in this study, we found that LA, WD, and H_{\max} consistently showed stronger trait hierarchy effects on pairwise spatial associations than trait dissimilarity effects for more focal species across different summary statistics and spatial scales (Fig. 3 and Fig. S2-S6). For SLA and WDMC under situations where we observed negative relationships between trait dissimilarity and spatial associations, the strengths of trait hierarchy did not vary significantly from the strengths of trait dissimilarity effects (Fig. 3 and Fig. S3, Fig. S4 and Fig. S6).

The relationship between the magnitude that trait hierarchy effect outcompetes trait dissimilarity effect and the abundance of focal species

Overall, LA, WD and H_{\max} showed stronger trait hierarchy effects than trait dissimilarity effects on their pairwise spatial associations for the 80 focal species. For LA and WD, we observed a positive relationship between the magnitude that trait hierarchy effects outcompete trait dissimilarity effects (MHD) and the abundance of each focal species, while for the trait of H_{\max} , the MHD decreased with the abundance of focal species (Fig. 4).

Discussion

Trait dissimilarity effects were widely considered to explain species co-occurrence and coexistence over the past decade (Burns & Strauss, 2011; He & Biswas, 2019; Kraft & Ackerly, 2010). Consistent to the findings in He & Biswas (2019), we observed negative relationships between trait dissimilarity and pairwise spatial associations in this study across different summary statistics and spatial scales for individual and multiple functional traits (Fig. 2), except LDMC that showed non-significant effects on pairwise spatial associations. However, while necessary, this evidence is not sufficient to support that environmental filtering is the dominant mechanism. Instead of simply interpreting this negative relationship as a result of environmental filtering and absence of competition (He and Biswas 2019), we pointed out that hierarchical competition that selects species with traits conferring competitive advantages (i.e. hierarchical competition) could also be able to produce a negative relationship between trait dissimilarity and pairwise spatial associations, which is identical to the result of environmental filtering (Fig. 1d).

By comparing the relative strengths of trait dissimilarity and hierarchy on pairwise spatial associations,

we demonstrated that competitive hierarchies captured by the traits of LA, WD and H_{\max} better explained species co-occurrence than trait dissimilarity (Fig. 3 and Fig. S2-6), which supports the hypothesis that hierarchical competition contributes to the co-occurrence patterns. As for the trait of SLA and WDMC, we observed that the effects of trait dissimilarity and hierarchy were comparable on the pairwise spatial associations.

Taking together the effects of both trait dissimilarity and trait hierarchy on pairwise spatial associations, we infer that except LDMC, other traits showed either stronger (e.g. LA, WD and H_{\max}) or comparable (SLA and WDMC) trait hierarchy effects relative to trait dissimilarity effects on interspecific spatial associations, indicating that the effects of hierarchical competition on the co-occurrence patterns in our forest plot were greater than or comparable to the effects of environmental filtering. Other traits may show stronger effects of environmental filtering or limiting similarity in structuring the forest community, but we currently lack the trait data to capture such effects.

This study provides a novel method to disentangle the relative importance of multiple assembly mechanisms in structuring co-occurrence patterns by assessing the effects of trait hierarchy and trait dissimilarity on pairwise spatial associations. By linking the pairwise spatial associations, which reflect signatures left by different assembly mechanisms to the effects of trait dissimilarity and trait hierarchy, our study provides alternative perspectives and better understanding in the underlying mechanisms that govern the co-occurrence pattern (He & Duncan, 2000; Wiegand et al., 2007; Wiegand & Moloney, 2014).

The negative relationship between trait dissimilarity and pairwise spatial associations was typically interpreted as evidence for no signal of competition and inferred as a result of environmental filtering (He & Biswas 2019). However, this interpretation could be misleading because the negative relationship between trait dissimilarity and pairwise spatial associations could also be caused by neighborhood competition that selects species with particular trait values independent of environmental filtering (Carmona et al., 2019; HilleRisLambers et al., 2012; Mayfield & Levine, 2010). In this study, we found support for the hypothesis that hierarchical competition leads to the negative relationship between trait dissimilarity and pairwise spatial associations as well.

This study also strongly suggests that trait dissimilarity has little effects on neighborhood competition and that neighborhood competition is more likely to be driven by trait hierarchy, which is consistent to the findings in Kunstler et al. (2012; 2016) and Carmona et al. (2019). If trait dissimilarity was positively correlated to pairwise spatial associations, we would infer that trait dissimilarity affects the neighborhood competition and leads species with similar trait occupying segregated areas. However, which is not the case in this study. Now that the positive relationship between trait dissimilarity and spatial associations was absent and effects of hierarchical competition that exclude inferior competitors were found, we therefore speculate that neighborhood competition in our forest plot was more likely to be driven by trait hierarchy but not by trait dissimilarity as presumed (Carmona et al., 2019; Kunstler et al., 2012).

The two metrics summarizing spatial point patterns ($g_{ij}(r)$ and $D_{ij}(r)$) that we used in this study showed no significant differences in the effects of trait dissimilarity and trait hierarchy on spatial associations for each trait (Fig. 2 and Fig. 3). We therefore speculate that extreme heterogeneity of species distributions were not prevalent in our forest plot (Wiegand et al., 2007). Since these two summary statistics respectively characterize the mean number of individuals and the nearest neighbors of the second species around the focal species, the findings that these two summary statistics of spatial point patterns reveal similar trait effects suggest that the neighborhood interspecific competitive effects on the focal trees come from both the average neighbor density and the nearest neighbors of the other species at least within the scale of 50 m.

By linking the magnitude that trait hierarchy effects outcompete trait dissimilarity effects (MHD) on pairwise spatial associations to the abundance of focal species, we found inconsistency among the three traits LA, WD and H_{\max} that all showed trait hierarchy effects on population fitness (Fig. 4). This inconsistency suggests that different fitness components, e.g., growth, survival and reproduction of each species, might be unequally influenced by traits and a trait might positively affect one component but negatively affects another, e.g.,

growth-survival trade-off and reproduction-survival trade-off (Laughlin, Gremer, Adler, Mitchell, & Moore, 2020). These unequal effects on different components of fitness and trade-offs might therefore influence the abundance of the focal species and lead to variations in the relationships between MHD and focal species abundance for different traits.

In conclusion, we disentangled the assembly mechanisms of limiting similarity, environmental filtering and hierarchical completion in structuring our forest community by assessing and comparing the effects of trait dissimilarity and trait hierarchy on pairwise spatial associations in this study. More specifically, we found that limiting similarity was weak or absent and hierarchical competition played a more (or at least equally) important role than environmental filtering in structuring the co-occurrence patterns in our forest community. This study also reinforced the importance of trait hierarchy, rather than trait dissimilarity, in driving interspecific competition.

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Author contributions: DY, MWC and FH designed the study. DY led the analyses. DY, MWC and FH wrote the manuscript with contribution from all authors.

Conflict of Interest: The authors declare no conflict of interest.

Data Availability Statement

The data of species distribution of HSD plot and functional traits used in this article will be deposited in Dryad (doi:10.5061/dryad.9kd51c5ft) once this paper is published in the journal.

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Table 1. The number and percentages of different types of pairwise spatial point patterns assessed by the standardized effect size (SES) of two different summary statistics, bivariate pair-correlation function ($g_{ij}(r)$) and bivariate distribution function of nearest neighbor ($D_{ij}(r)$), at three spatial scales.

Summary statistics (SES)	Spatial scale (m)	Distribution	Distribution	Distribution
		Repulsion	Independence	Attraction
$g_{ij}(r)$	5	315 (4.98%)	5188 (82.09%)	817 (12.93%)
	30	375 (5.93%)	5249 (83.05%)	696 (11.01%)
	50	346 (5.47%)	5391 (85.30%)	583 (9.22%)
$D_{ij}(r)$	5	250 (3.96%)	5393 (85.33 %)	677 (10.71%)
	30	608 (9.62%)	5039 (79.73%)	673 (10.65%)
	50	617 (9.76%)	5326 (84.27%)	377 (5.97%)

Figure Legends

Figure 1 . Conceptual framework to illustrate hypotheses of this study. (a) and (b) respectively show spatial associations of repulsion and attraction between two species at coarse spatial scale. (c) and (d) show the predicted relationships between pairwise spatial associations and absolute trait distance under different processes of community assembly: (c) limiting similarity, if absolute trait distance has positive effects on pairwise spatial associations; and (d) environmental filtering or hierarchical competition, if absolute trait distance has negative effects on pairwise spatial associations. In the case of (d), if absolute trait distance has stronger effects on pairwise spatial association than hierarchical trait distance, we infer that environmental filtering mainly drives the co-occurrence pattern (e); if the hierarchical trait distance has stronger effects on pairwise spatial associations than absolute trait distance, the effect of hierarchical competition is thought to drive the co-occurrence pattern (f). Abbreviation: SA= pairwise spatial associations.

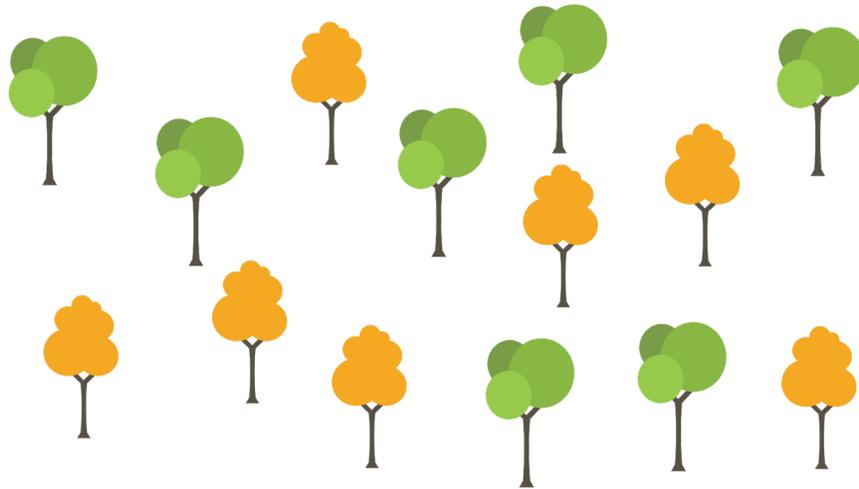
Figure 2 . Effects of absolute trait distances on the pairwise spatial associations in equation 2 that only includes the absolute trait distances as explanatory predictors. The left panels show coefficients of each

variable of absolute trait distances with variance. The right panels present percentages of the 80 focal species whose spatial associations are positively (brown circles), negatively (blue circles) and non-significantly (gray circles) correlated with each variable of absolute trait distances. The panels from Row 1-6 represent the results for spatial associations assessed by bivariate pair-correlation function ($g_{ij}(r)$, pcf) across different spatial scales at $r = 5$ m, 30 m and 50 m and bivariate distribution function of nearest neighbor ($D_{ij}(r)$) at $r = 5$ m, 30 m and 50 m, respectively. Abbreviation: LA=leaf area, SLA=specific leaf area, LDMC=leaf dry matter content, WD=wood density and H_{\max} =maximum height, abdist means absolute trait distance.

Figure 3. Comparison between the strengths of hierarchical and absolute trait distances on spatial associations for the 80 focal species. The strengths of hierarchical and absolute trait distances were respectively given by the absolute values of the coefficients of the variables of hierarchical and absolute trait distances of different functional traits in the full model of equation 2. Each circle represents one focal species. Brown, blue and gray circles respectively represent that hierarchical trait distances had stronger, weaker and non-significantly different effects on the pairwise spatial associations relative to their corresponding absolute trait distances. The results presented here are for spatial associations assessed by bivariate pair-correlation function ($g_{ij}(r)$, pcf) at $r = 50$ m.

Figure 4. The relationships between the abundance of focal species and the magnitude that the effects of trait hierarchy outcompete trait dissimilarity (MHD). MHD was given by the differences in the coefficients (absolute values) of hierarchical trait distances of each trait and their corresponding coefficients (absolute values) of absolute trait distances in the full model of equation 2. Each circle represents one focal species. Brown, blue and gray circles respectively represent that hierarchical trait distances of had stronger, weaker and non-significantly different effects on the spatial associations relative to their corresponding absolute trait distances. The results presented here are for spatial associations assessed by bivariate pair-correlation function ($g_{ij}(r)$, pcf) at $r = 50$ m.

Figure 1



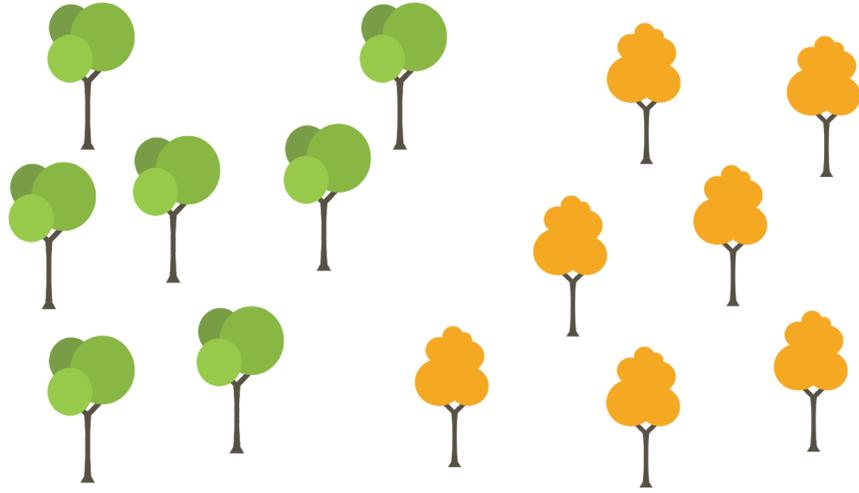


Figure 2

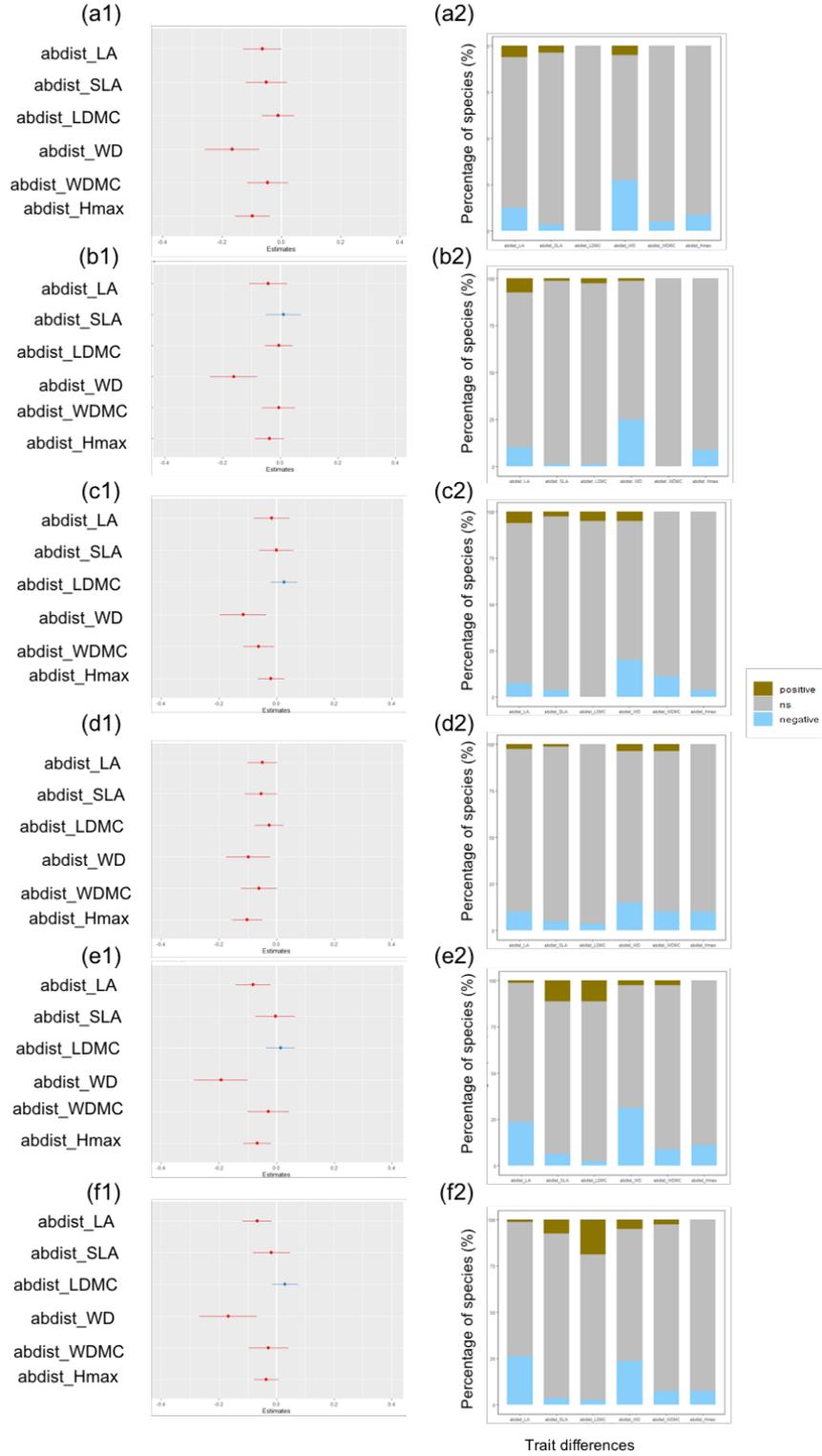


Figure 3

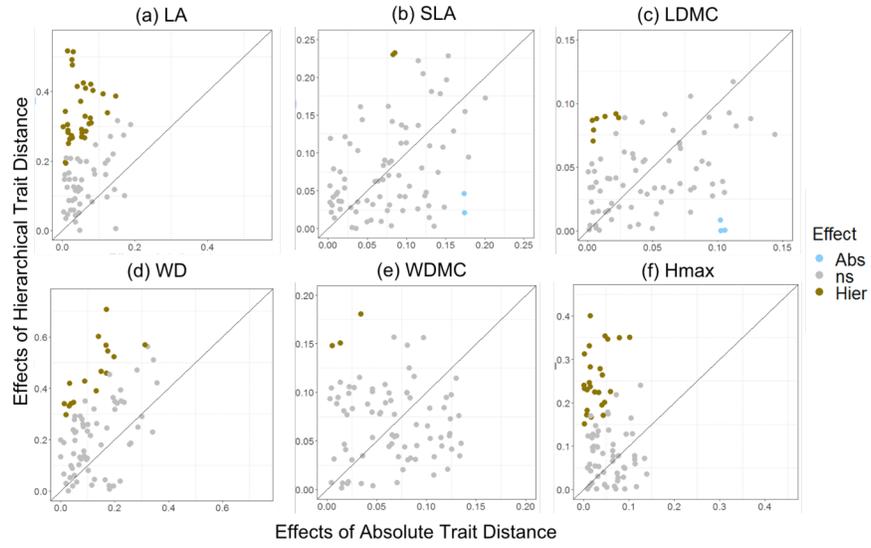


Figure 4

