

## Negative relationship between interspecies spatial association and trait dissimilarity

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**Decision date:** 25-Oct-2018

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/oik.05876].

## Abstract

Species' response to environmental site conditions and neighborhood interactions are among the important drivers of species' spatial distributions and the resultant interspecific spatial association. The importance of competition to interspecific spatial association can be inferred from a high degree of trait dissimilarity of the associated species, and vice versa for environmental filtering. However, because the importance of environmental filtering and competition in structuring plant communities often vary with spatial scale and with plant life stage, the species' spatial association – trait dissimilarity relationship should vary accordingly. We tested these assumptions in a fully mapped 50-ha subtropical evergreen forest of China, where we assessed the degrees of interspecific spatial associations between adult trees and between saplings at two different spatial scales (10 m versus 40 m) and measured the degrees of trait dissimilarity of the associated species using six traits (leaf area, specific leaf area, leaf dry-matter content, wood density, wood dry-matter content and maximum height). Consistent across spatial scales and plant life stages, the degree of interspecific spatial association and the degree of overall trait dissimilarity (i.e. all six traits together) was negatively correlated, suggesting that environmental filtering might help assemble functionally similar species in our studied communities. However, when we looked into the spatial association – trait dissimilarity relationship for individual traits, we found that the relationships between interspecific spatial associations and the dissimilarity of wood density and dry-matter content were significant for adults but not for saplings, suggesting the importance of wood traits in species' survival during ontogeny. We conclude that processes shaping interspecific spatial association are spatial scale and plant life stage dependent, and that the distributions of functional traits offer useful insights into the processes underlying community spatial structure.

*Keywords:* competition, environmental filtering, life stage, scale dependency, point pattern

## Introduction

Species' response to environmental site conditions and neighborhood interactions are governed by species' functional traits (Kraft, et al. 2014, Lasky, et al. 2014). And relevant processes (e.g., environmental filtering and competition) often leave their signatures on the spatial structure of plant populations and communities (Biswas, et al. 2016, Seabloom, et al. 2005). Linking spatial analyses of species with community trait structure may thus help understand processes underlying community spatial structure (Bartlett, et al. 2015, Biswas, et al. 2016, Velázquez, et al. 2016). Interspecies spatial association (hereafter called "species association"), in which some pairs of species co-occur at a particular spatial scale more or less frequently than expected by chance, is a key dimension of community spatial structure (Wang, et al. 2010, Wiegand, et al. 2007, Wiegand, et al. 2012). Species association is ubiquitous in nature, but processes shaping species association and their relevance to community trait structure are still poorly understood (Velázquez, et al. 2016).

Theory suggests that environmental site conditions act as a primary filter to determine the establishment success of a particular phenotype; hence, species with similar phenotypes often coexist (Lasky, et al. 2013, Southwood 1977, Weiher, et al. 1998). This means, in a spatially explicit context, that species with similar phenotypes (or traits) are expected to co-occur at the scale of environmental patchiness. The theory of limiting similarity, by contrast, suggests that co-occurring species should be dissimilar in their resource utilization and related phenotypes (MacArthur and Levins 1967, Wilson and Stubbs 2012). That is, species with dissimilar phenotypes (or traits)

are expected to co-occur at the scale of neighborhood. Alternatively, if species association is shaped by random dispersal, then there may be a lack of predictable trait similarity (or dissimilarity) of the associated species (Hubbell 2005, Wiegand, et al. 2012).

Such importance of environmental filtering and competition in structuring plant communities often vary with spatial scale (Bartlett, et al. 2015, Wiens 1989, Zhang, et al. 2018). Environmental filtering, which produces spatially aggregated pattern, is typically important at a larger spatial scale; whereas, competition, which produces spatially segregated pattern, is important at a smaller spatial scale (Biswas, et al. 2017, Biswas, et al. 2016, HilleRisLambers, et al. 2012). Therefore, a high degree of trait similarity of the associated species—which is the signature of environmental filtering—is expected to be associated with positive spatial association (i.e. aggregation) at a larger spatial scale. Whereas, a high degree of trait dissimilarity of the associated species—which is the signature of competition—is expected to be associated with negative spatial association (i.e. segregation) at a smaller spatial scale. Functional traits may further mediate plants' demographic performances during ontogeny. For instance, higher wood density promotes individual's survival after establishment, while adult stature (i.e. maximum height) promotes individual's survival at late life stages (Visser, et al. 2016). In addition, the negative effects of trait similarity between neighboring trees on their growth is often stronger in older than younger trees (Lasky, et al. 2015). A sapling cohort should pass through environmental and competitive filtering before recruiting into the adult stage. In the long run, saplings with traits that do not favor a species to withstand a particular environmental regime and/or

competitive pressure are typically excluded, resulting in an adult tree assemblage with a particular suite of traits. That is, the signatures of processes causing individual's mortality (environmental filtering and competition) embodied in community trait structure and the resultant relationship between interspecific trait similarity and species associations are expected to be stronger in adult than sapling communities.

Earlier studies on the relationship between interspecific trait dissimilarity and spatial associations at varying spatial scales have offered useful insights into the processes underlying spatial structure (Bartlett, et al. 2015, Velázquez, et al. 2015). However, the dependence of the species association-trait similarity relationship on plant life stage remains somewhat unclear. To advance the understanding of demographic processes involving environmental and competitive filtering (Palow, et al. 2012, Poorter 2007), a comparison of the role of trait dissimilarity in shaping species association across life stages would be valuable.

Based on an explicit stem-mapping dataset plus intensive trait sampling in a 50-ha subtropical evergreen forest, here we aim to assess the relationship between species associations and trait similarity at two spatial scales (small versus large scale) and across two life stages (sapling versus adult). We hypothesize that species pairs with high trait similarity are spatially aggregated at a larger scale of environmental variation, but these species pairs are segregated at a neighborhood scale due to competition. We further hypothesize that species association – trait similarity relationship is stronger in adult than in sapling life stage.

## **Methods**

### *Study site*

This study was conducted in the Heishiding Forest Dynamic Plot (23.455°N, 111.908°E; elevation: 435 – 698 m), one of the monitoring sites of the global network of CTFs-ForestGEO (Anderson-Teixeira, et al. 2015). The study plot (size 50 ha) was located in Guangdong province of southern China. This area experiences a subtropical monsoon climate, with mean annual temperature of ~19.6 °C and mean precipitation of ~1740 mm. The plot has a rough terrain with slopes ranging from 6.89° to 74.6°. The floristic composition of the plot was characteristic of evergreen broadleaf forests, and about a half of species were mesophanerophytes (i.e., height between 8 m and 30 m). The dominant canopy species were *Cryptocarya concinna* (Lauraceae), *Neolitsea phanerophlebia* (Lauraceae) and *Altingia chinensis* (Hamamelidaceae); and the most abundant understory species were represented by *Lindera chunii* (Lauraceae) and *Antidesma venosum* (Euphorbiaceae).

#### *Data collection and analytical steps*

To assess the relationship between species associations and trait similarity, we first conducted a forest census to identify the species and to record all individuals present in the study area. We then distinguished the recorded individuals into saplings and adult categories based on a predefined diameter threshold. Subsequently, a subset of species from both adult and sapling categories was selected according to whether their abundance are appropriate to quantify species associations using the pair-correlation function. On the other hand, species-specific traits for the selected species were measured either in the field or collected from trait database. Trait dissimilarity of the spatially associated species were then computed using Euclidean or Mahalanobis distance. In the final step, we

assessed the correlation between species association and trait dissimilarity of the associated species using Mantel tests. These data collection analytical steps are outlined in Fig. 1 and described in detail below.

#### 1) Forest census

During 2011-2013, we conducted a plot census following the field protocol of the CTFS-forestGEO network (<http://www.forestgeo.si.edu/>). All free-standing plants with diameter at breast height (dbh) > 1 cm were identified to species level, and they were measured, tagged and mapped within a geographical coordinate frame (500 × 1000 m). There were 218 518 plants representing 214 species, 129 genus and 60 families recorded. There were 17 hyper-dominant species (> 4000 plants) accounting for about a half of total abundance and 141 species (> 200 plants) accounting for 98%.

#### 2) Classifying saplings and adult trees

Individuals with dbh > 10 cm were classified as adults and individuals with dbh < 3 cm were classified as saplings (e.g., Baldeck, et al. 2013, Velázquez, et al. 2015). That is, adults represent a well-established life stage, and saplings represent a recruiting stage that is vulnerable to environmental hazards and/or competitive pressure.

For some species with only few individuals, stochasticity would have precluded meaningful spatial point pattern analyses (Velázquez, et al. 2015). Thus, we set the criteria of minimum 50 individuals per species to include a species in species' spatial association analyses. There were 141 species with more than 50 individuals per species present in the sapling sub-community (157 620 individuals in total) and 77 species with more than 50 individuals per species in the adult sub-community (27 076 individuals in total); and all of these species were included in our analyses. Our selected species

accounted for 84.5% of total individuals in the plot. These selected species were well interspersed across the study area (Appendix A).

### 3) Quantifying interspecific spatial association

We characterized interspecies spatial association for a total of 9870 (i.e.,  $C_{141}^2$ ) species pairs in the sapling community and a total of 2926 (i.e.,  $C_{77}^2$ ) species pairs in the adult community. To quantify the spatial association of a given pair of species  $i$  and  $j$  at a distance  $r$ , we used the cross-pair correlation function  $g_{ij}(r)$  (Diggle 1983). The function  $g_{ij}(r)$  is defined as the point density within radius  $r$  around location  $x$ , divided by the square of the average point density of the area (Fig. 2a), and the function  $g_{ij}(r)$  was calculated as follows:

$$g_{ij}(r) = \frac{1}{\lambda_i \lambda_j} \frac{1}{2\pi r A} \sum_{m=1}^M \sum_{n=1}^N w_{ij}^{-1} k_h(\|x_i - x_j\| - r)$$

Where  $\lambda_i$  and  $\lambda_j$  are the average point density of species  $i$  and species  $j$  in the area  $A$  (i.e., intensity function),  $x_i$  and  $x_j$  are the locations of species  $i$  and species  $j$ , respectively;  $M$  and  $N$  represent the plant number of species  $i$  and  $j$ , respectively;  $w_{ij}$  is the weighting function that accounts for the edge effects created by the unobservable points outside the study area. Here edge effects are corrected in such a way that if a point  $x$  is located nearer the edge than its neighboring point  $y$ , then the inverse of the inside proportion of the perimeter of the circle centered on  $x$  and passing through  $y$  was used as a correction factor (Ripley 1977). The term  $k_h$  is a kernel function that is used to estimate point density; and the kernel is specified by bandwidth  $h$  that defines the size of the radius neighborhood that will receive weighting. Points lying outside the bandwidth is not considered in the calculation of point density at the radius. We used the Epanechnikov



kernel (i.e., the function provides greater weight to points near the radius and less weight to points further away) to estimate point density and adjusted the bandwidth  $h$  according to Stoyan and Stoyan (1994).

The function  $g_{ij}(r)$  is interpreted in such a way that if  $g_{ij}(r) = 1$ , then the two species are independent from each other; if  $g_{ij}(r) > 1$ , then the two species are spatially aggregated; and if  $g_{ij}(r) < 1$ , then then the two species are spatially segregated (Diggle 1983). To test if the observed spatial association ( $g_{ij}$ ) is significantly different from expected by chance (i.e., random pattern), we compared the observed  $g_{ij}$  with those generated by a null model. For each species pair, we generated 999 of random patterns and at each time we computed the  $g_{ij}$  statistic (i.e., random  $g_{ij}$ ). We then derived the range and mean of randomly generated  $g_{ij}$ . The observed  $g_{ij}$  was then compared with the random  $g_{ij}$  to judge the statistical significance of spatial aggregation and segregation.

We used a homogeneous Poisson model for large scale pattern, and inhomogeneous Poisson model for small scale pattern. In the homogeneous Poisson model, the locations of the individuals of the focal species (e.g., species  $i$ ) remained unchanged while those of neighboring species (e.g. species  $j$ ) were distributed randomly and independently of the location of the focal species  $i$ . The intensity function  $\lambda$  was estimated as a constant under the assumption of homogeneity. In the heterogeneous Poisson model, by contrast, the locations of individuals of the focal species (species  $i$ ) were fixed, but the locations of the individuals of the second species (species  $j$ ) were randomized in accordance with its local point density. The intensity function  $\lambda(x)$  varied with locations (i.e., the area is divided into several small blocks according to the bandwidth), and the mean intensity is the integral of the location-specific intensities

over the specified area with a radius  $r$  around  $x$ . This procedure (i.e., inhomogeneous pair function) can account for the confounding effects of large scale environmental heterogeneity on fine-scale patterns (Wiegand, et al. 2007) and thus suitable for this study.

The area under the cross-pair correlation function ( $A_{ij}$ , (Brown, et al. 2013, Law, et al. 2009) were then used to summarize the dominant spatial relationship of the species pairs up to a distance  $R$  (fig. 2a). Where  $A_{ij}$  was computed as:

$$A_{ij}(R) = \int_0^R \log(g_{ij}(r))dr$$

Here, an increasingly larger value of  $A_{ij}$  indicates a stronger spatial association between species  $i$  and  $j$ ; and a positive value of  $A_{ij}$  indicates spatial aggregation, while a negative value of  $A_{ij}$  indicates spatial segregation.

To characterize the interspecific spatial association for large and small spatial scales, we set the values of  $R$  to 40 m and 10 m, respectively. This is because topographic and edaphic patch size (i.e., the scale of habitat patchiness) in this forest plot was  $\sim 40$  m in radius (He 2016, Zhou 2015), and because 10 m radius is relevant for neighborhood effects (Velázquez, et al. 2015). Therefore, these two scales are relevant to capture the effects of environmental filtering and competition on species association, respectively.

Interspecific interactions could also be asymmetric (Velázquez, et al. 2015, Wiegand, et al. 2012). Therefore, we considered reciprocal relationships of species pair  $i-j$  and  $j-i$  at the neighborhood scale. Our analyses reveal that  $A_{ij}$  and  $A_{ji}$  are closely related (Mantel test,  $r = 0.996$ ,  $P < 0.001$  for saplings,  $r = 0.998$ ,  $P < 0.001$  for adult trees), indicating a

symmetric co-occurrence pattern. Thus, we did not deal with reciprocal relationships of species pairs in subsequent analyses.

#### 4) Measuring functional traits and quantifying trait dissimilarity

We considered six traits (leaf area, specific leaf area, leaf dry-matter content, wood density, wood dry-matter content and maximum height) for this study. These traits reflect important photosynthetic, hydraulic and mechanic functions (Baraloto, et al. 2010, Pérez-Harguindeguy, et al. 2013, Thomas and Bazzaz 1999). For each of 141 species present in the sapling sub-community, we randomly selected 20-30 individuals for trait measurement. Selected individuals were well interspersed across the 50-ha plot (He, et al. 2018).

From each plant, we detached 20 healthy looking fully developed leaves from outer canopy. We followed Pérez-Harguindeguy, et al. (2013) to measure leaf area (LA), specific leaf area (SLA) and leaf dry-matter content (LDMC). For wood density and wood dry-matter content (the ratio of dry to fresh wood mass), we cut a segment of twig with diameter < 1 cm at a distance ca. 30–50 cm back from the terminal branch and without the current-year shootings (He and Deane 2016). Wood density and wood dry-matter content of twigs were measured according to Osazuwa-Peters, et al. (2011).

Individual-level measurements were averaged at the level of species to represent the species-specific trait values. Finally, we collected species specific maximum height ( $H_{\max}$ ) for all species from Flora Republicae Popularis Sinicae (<http://foc.eflora.cn>). Note that, although it would be ideal to conduct trait measurements for saplings and adults separately, our trait sampling was largely conducted on individuals with dbh < 6 cm due to the difficulty in accessing leaves and branches in the upper canopy. However, variance

partitioning analyses revealed that interspecific variation was the main source of trait variation in our data set (75% variance attributed to species vs. 0.1% variance attributed to individual size, Table 1). Therefore, species-specific trait data measured on small sized individuals should not be a major problem in our study.

For each species pairs, we calculated multivariate trait dissimilarity (six traits collectively) using Mahalanobis (1936) distance and univariate trait dissimilarity (each trait separately) using Euclidean distance (Fig. 2b).

### *Statistical analyses*

The correlations between interspecies spatial association  $A_{ij}$  and trait dissimilarity  $Td_{ij}$  were evaluated by Mantel (1967) tests, separately for large and small spatial scales and for adult and sapling life stages. We permuted the matrix  $A_{ij}$  10 000 times and calculated the correlation statistic between  $A_{ij}$  and  $Td_{ij}$  for each permutation. The original statistic (Mantel  $r$ ) was compared with the distribution of the test statistics from the permutations to generate a  $P$ -value.

Since we performed multiple tests (7 trait dissimilarity indices  $\times$  2 life stages  $\times$  2 spatial scales = 28 tests in total) over the same dataset, we adjusted the  $P$ -value to control false discovery rate (i.e., type I error) by following Benjamini and Hochberg (1995). That is, instead of an overall  $P$ -value of 0.05 to reject the null hypothesis, we set a critical value of 0.032 to reject a family of 28 null hypotheses (Appendix B).

Because there were more species in the sapling sub-community, we randomly sampled 77 species pairs to calculate the correlation between  $A_{ij}$  and  $Td_{ij}$  999 times so as to compare with that in the adult sub-community. All analyses were conducted in the

statistical program R, using packages “spatstat” (Baddeley and Turner 2005) and “ecodist” (Goslee and Urban 2007).

## Results

### *Interspecific spatial association*

At a larger spatial scale of 40 m, 36.2% pairs in the sapling sub-community were significantly aggregated and 46.0% species pairs were significantly segregated (Fig.3a,b); and the dominant spatial associations ( $\underline{A}_{ij}$ ) up to 40 m were positive for 49.0% species pairs and negative for 51.0% species pairs. At the same spatial scale, 28.0% pairs in the adult sub-community were significantly aggregated and 36.2% species pairs were significantly segregated; and the dominant spatial associations ( $\underline{A}_{ij}$ ) up to 40 m were positive for 42.9% species pairs and negative for 57.1% species pairs (Fig.3c, d).

Under the assumption of inhomogeneous poisson intensity (i.e., the confounding effects of large-scale environmental heterogeneity on small scale pattern was removed), only 8.9% species pairs in the sapling sub-community were significantly aggregated and most species pairs (61.9 %) tended to be significantly segregated at a smaller spatial scale of 10 m (Fig. 3e, f). However, less than a half of species pairs (39.6 %) in the adult sub-community tended to be significantly segregated at a scale of 10 m (Fig.3g, h). When modelled through inhomogeneous poisson process, the dominant spatial relationships up to 10 m in the sapling sub-community was overwhelmed by negative associations (84.8%), and in adult sub-community the proportion of negative associations was close to 90% (Fig. 3e, g). That is, the general pattern of species association in the adult sub-community was similar to the pattern in sapling sub-community, but with a slightly lower proportion of positive associations (Fig. 3).

*Correlation between interspecific spatial association and trait dissimilarity*

Consistent across spatial scales and plant life stages, the degree of interspecific spatial association and the degree of overall trait dissimilarity (i.e., all six traits together) was negatively correlated (Mantel correlation coefficients ranged from -0.22 – -0.29,  $P < 0.01$ ; Fig. 4), suggesting that environmental filtering might help assemble functionally similar species in our studied communities. When we looked into the spatial association – trait dissimilarity relationship for individual traits, we found that dissimilarity in leaf area, specific leaf area and maximum height were consistently negatively correlated with interspecies spatial association across plant life stage and spatial scale. Leaf dry-matter content, however, did not show any significant correlation with interspecies spatial association in any cases (Fig. 4). Interestingly, life stage-dependent variation of the spatial association - trait dissimilarity relationship was evident mostly in woody traits. Trait distances in wood density and dry-matter content were significantly correlated with the degrees of interspecific spatial association for adult trees (Fig. 4b, d), but such relationships were not found for saplings (Fig.4a, c).

**Discussion**

Our results indicate that species pairs with similar functional traits are likely to co-occur at a scale of 40 m, which is the spatial scale of environmental patchiness (e.g., light and soil nutrients) in our study. This result is consistent with an earlier study in an adjacent forest (Zhang, et al. 2018) and reinforces the idea that trait-mediated environmental filtering is an important process shaping the large-scale spatial structure in tropical or subtropical forest communities (Bartlett, et al. 2015, Velázquez, et al. 2015).

However, it should be noted that different processes may create similar spatial association and similar processes may create different spatial associations (Cale, et al. 1989, Dale and Fortin 2014); and accordingly, different processes may create similar spatial association-trait dissimilarity relationship. While we did not focus on species' dispersal pattern, patchy dispersal could also create spatially aggregated pattern (Biswas and Wagner 2015) and corresponding spatial association-trait dissimilarity relationship. On the other hand, if the environmental filtering is the one and only reason for the observed species association-trait dissimilarity relationship, then one could expect no such relationship above the scale of environmental patchiness. Surprisingly, the relationship between species association and overall trait dissimilarity continue to prevail even up to the scale of 200 m (Mantel  $r = -0.07$ ,  $P = 0.02$ ; and for adults, Mantel  $r = -0.17$ ,  $P < 0.001$ ), perhaps due to patchy dispersal and/or broader environmental gradient (e.g., topography). It would be helpful to conduct further studies by considering species' dispersal strategies and broader environmental gradient to elucidate the processes or relative importance of processes underlying the species association-trait dissimilarity relationship.

We did not detect the signal of competition (i.e., greater degree of trait dissimilarity for species pairs with lower degree of spatial segregation) at a neighbourhood scale of 10 m. Instead, we detect the signal of environmental filtering at a neighbourhood scale. Perhaps, environmental filtering played a stronger role than competition in structuring our studied communities, and large-scale environmental heterogeneity might confounded the weaker effect of competition at a neighbourhood scale (Uriarte, et al. 2010). Alternatively, our chosen traits might be more responsive to environmental

gradients indicating  $\beta$  niche (i.e., differences among positions along environmental gradients, Silvertown, et al. 2006) than  $\alpha$  niche (i.e., differences among co-occurring species within a competitive milieu).

We found partial support for our hypothesis that the relationship between interspecific trait dissimilarity and spatial associations would be stronger for adults than saplings. The dissimilarity of wood density and dry-matter content were significantly negatively correlated with spatial associations for adult trees, but not for saplings. In a tropical forest, Visser, et al. (2016) also found that the survival of small sized individuals ( $\sim 7$  cm dbh) was closely associated with wood density. That is, trees with low wood density and wood dry-matter content might experience high mortality risk during the transition from sapling to adult. However, unlike the wood traits, the life stage dependent variations in the species association - trait dissimilarity relationship was less clear for leaf traits such as LA and SLA. Perhaps, individual mortality after sapling stage was random with respect to leaf traits (Visser, et al. 2016). Poorter (2007) found that adult leaf traits were more strongly associated with habitat conditions at a species' regeneration phase than with its adults' own conditions, suggesting a long-lasting effect of regeneration niche. The spatial structure of adult trees in our studied community to some extent inherited the patterns of saplings (Mantel correlations between species associations for saplings and adults,  $r = 0.17$ ,  $P < 0.001$  at the scale of 40 m), and the spatial association - trait dissimilarity relationships were roughly the same for the 72 species present in both stages. These results suggest that mortality risk is relatively low for saplings once they pass through a critical stage (Baldeck, et al. 2013).



Consistent with earlier studies (Bartlett, et al. 2015, Velázquez, et al. 2015), we found that the correlation between interspecific trait dissimilarity and spatial associations was quite weak ( $|r| < 0.3$ ) across life stages. One possible explanation is that we might missed other important functional traits relevant to habitat filtering and limiting similarity such as root traits and reproductive traits (Kleyer and Minden 2015). Alternatively, stochastic forces in species-rich tropical and subtropical forest systems (Velázquez, et al. 2015, Wiegand, et al. 2012) could also weaken the trait dissimilarity and spatial associations relationship.

To conclude, species pairs with high trait similarity tended to be spatially aggregated across spatial scales, suggesting that environmental filtering might help assemble functionally similar species in our studied communities. However, the relationship between species associations and trait dissimilarity could also vary with species traits and with plant life stage. These results suggest that processes shaping species association is spatial scale and plant life stage dependent, and that the distributions of functional traits offer useful insights into the processes underlying community spatial structure.

*Acknowledgements* – We thank Fangliang He for valuable advice on the project, Guo-Chun Shen and Jian Zhou for assistance with computer-intensive works, and Ian McFadden and two anonymous reviewers for comments on an earlier version of this manuscript. We also thank the volunteers from Sun Yat-Sen University and South China for their assistance in fieldwork.

*Funding* – This research was supported by a 1000 Plan Grant to FH and a Zijiang Professorship start-up fund of East China Normal University to SRB (13903-120215-10407).

*Author contributions* – DH conceived the ideas, collected and analyzed the data. Both authors designed methodology, prepared the manuscript and gave final approval for publication.

*Conflict of interest* – Both authors declare that they have no conflict of interest.

*Data accessibility* – Upon acceptance, data will be archived and released at the website of ECNU-Alberta Joint Lab for Biodiversity Conservation (<http://biodiversity.ecnu.edu.cn/>)

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## Figure legends

Fig. 1 A schematic diagram of data collection and analytical steps in this study.

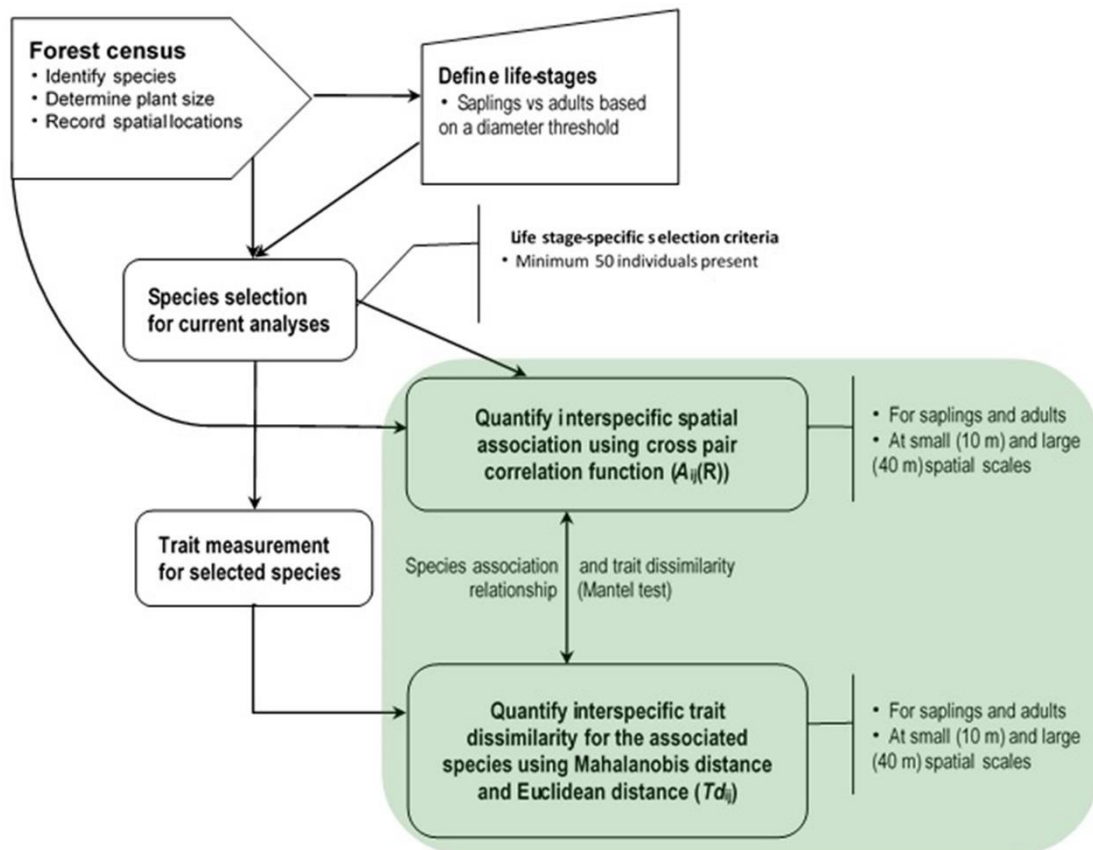


Fig. 2 Conceptual illustrations of interspecific spatial association (a) and trait dissimilarity (b). The top panel (a) shows the spatial distribution of three species on a map, where the kernel density of red species (sp3) is shown by grey shades (Darker grey colors indicate higher density). The spatial association between two species is the sum of kernel density of neighboring species (e.g. sp3) within a given radius  $R$  (e.g.  $R = 40$  m) across all individuals of the focal species (e.g. sp1 or sp2). Here, the sp1-sp3 pair is more strongly associated than the sp2-sp3 pair ( $A_{13}(40) > A_{23}(40)$ ). The bottom panel (b) shows the hypothetical locations of the three species in a multi-trait space. Trait dissimilarity is defined as the distance between two species (i.e., the length of the line segments). Here, sp1 is more similar to sp3 than sp2 (i.e.,  $Td_{13} < Td_{23}$ ).

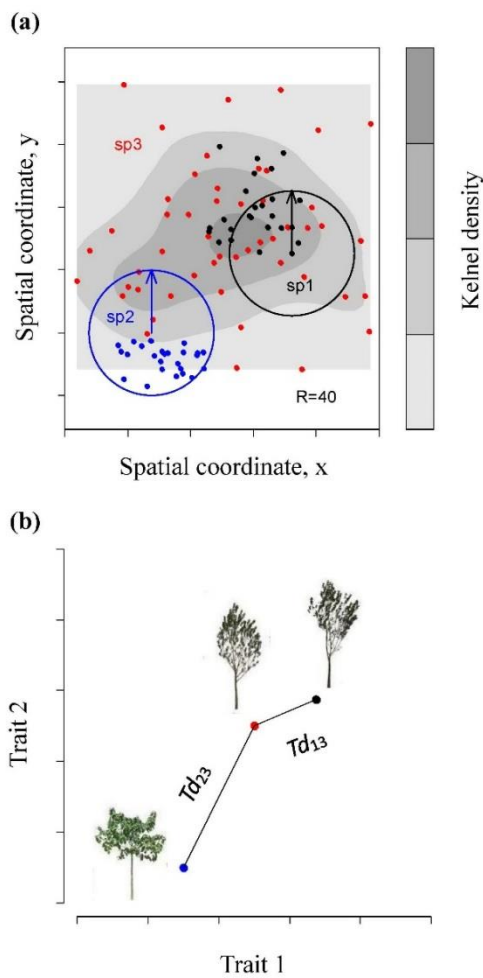




Fig. 3 The distribution of strengths of interspecific spatial association ( $A_{ij}$ ) and the proportion of negative, positive and random association for sapling and adult communities at large (40 m) and small (10 m) spatial scales.  $A_{ij}$  is an integral of pair-correlation function  $g_{ij}(r)$  over an array of  $r$ s up to  $R$  and thus summarizes the dominant relationship of a species pair across multiple scales up to  $R$  (10 m and 40 m in this case). The specific forms of species associations (negative, positive or random) were examined at varying  $r$  (1-100 m). At the large scale of 40 m, homogeneous Poisson processes were employed to model species associations (i.e., the intensity function  $\lambda(x)$  was constant over the study area); at the small scale of 10 m, inhomogeneous Poisson processes were employed to model species associations (i.e., the intensity function  $\lambda(x)$  varied with spatial location). The statistical significance of species association deviating from random expectation were evaluated by using homogeneous or inhomogeneous null models (see texts for details).

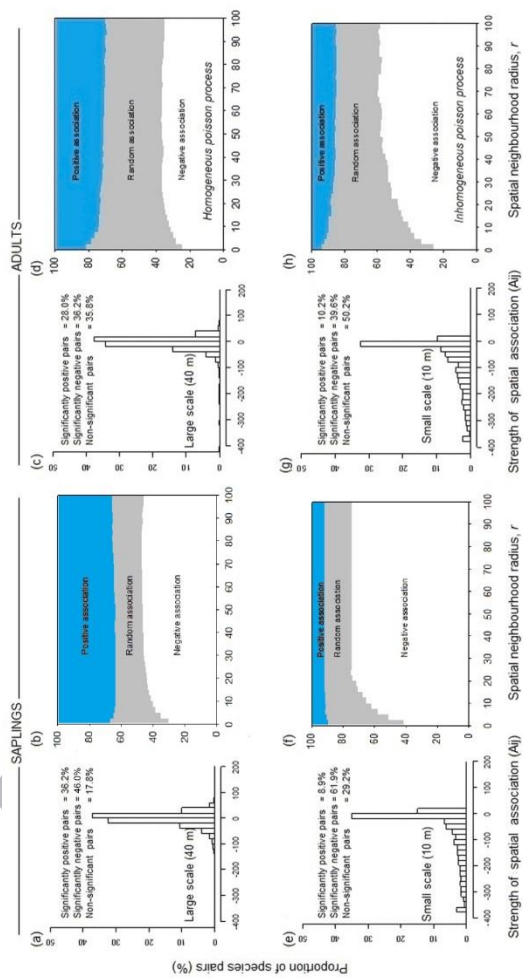
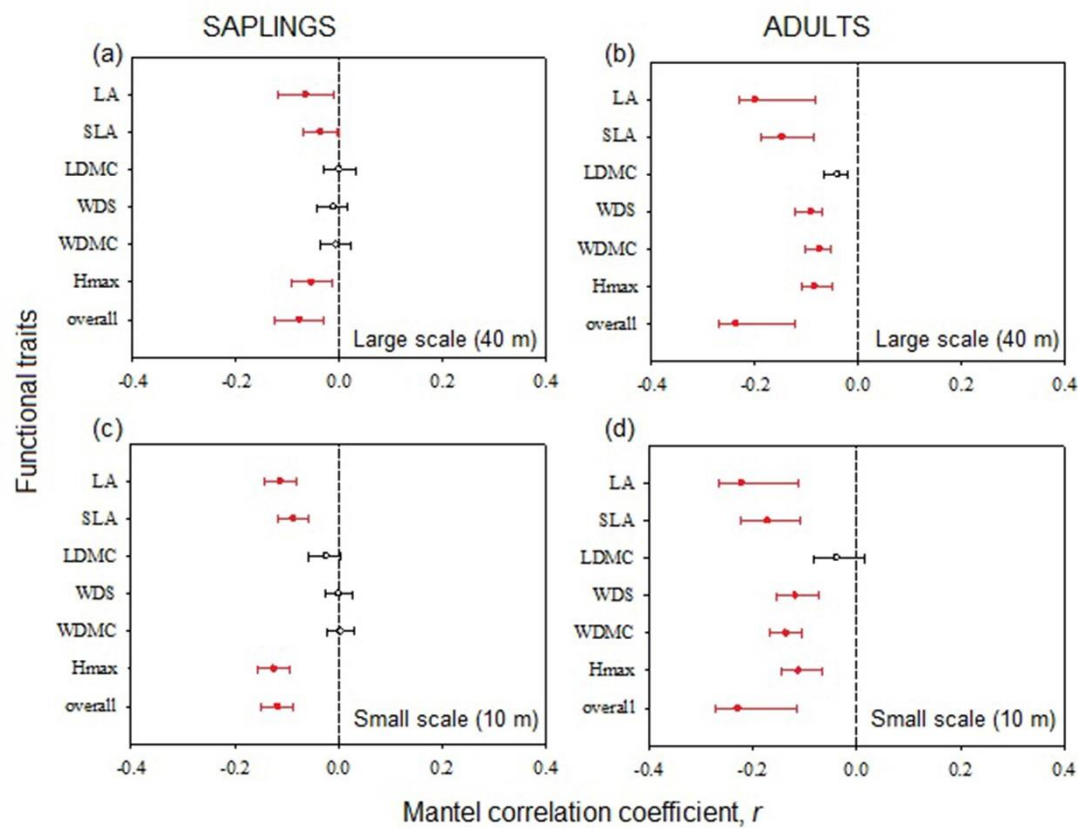


Fig. 4 Mantel correlations between interspecific trait distance and species' spatial association. Correlation coefficients and their 95% confidence limits are shown. Solid dots indicate significant correlations. Trait abbreviations: LA = Leaf area, SLA = specific leaf area, LDMC = leaf dry-matter content, WDS = wood density, WDMC = wood dry-matter content and Hmax = maximum height; overall means all traits together.



**Table Legend****Table 1**

Percentage of variance of functional traits due to species and plant size (i.e., dbh)\*

	Random effect (species)	Fixed effect (dbh)	Residual
LA	80.00%	0.01%	19.99%
SLA	70.68%	0.09%	29.23%
LDMC	69.30%	0.05%	30.65%
WDS	62.48%	0.29%	37.23%
WDMC	49.46%	0.81%	49.73%
H <sub>max</sub>	-	-	-

\* For a focal trait, a mixed effect model of  $T_{ij} = \alpha_0 dbh_{ij} + (1|species)$  was built to decompose its variance.