

# Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats

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## Summary

1. Increasingly, ecologists are using functional and phylogenetic approaches to quantify the relative importance of stochastic, abiotic filtering and biotic filtering processes shaping the pattern of species co-occurrence. A remaining challenge in functional and phylogenetic analyses of tropical tree communities is to successfully integrate the functional and phylogenetic structure of tree communities across spatial and size scales and habitats in a single analysis.

2. We analysed the functional and phylogenetic structure of tree assemblages in a 20-ha tropical forest dynamics plot in south-west China. Because the influence of biotic interactions may become more apparent as cohorts age, on local scales, and in resource-rich environments, we perform our analyses across three size classes, six spatial scales and six distinct habitat types, using 10 plant functional traits and a molecular phylogeny for the > 400 tree taxa found in the plot.

3. All traits, except leaf area and stem-specific resistance, had significant, albeit weak phylogenetic signal. For canopy species, phylogenetic clustering in small and medium size classes turned to phylogenetic overdispersion in the largest size class and this change in dispersion with size was found in each habitat type and across all spatial scales. On fine spatial scales, functional dispersion changed from clustering to overdispersion with increasing size classes. However, on larger spatial scales assemblages were functionally clustered for all size classes and habitats.

4. Phylogenetic and functional structure across spatial and size scales and habitats gave strong support for a deterministic model of species co-occurrence rather than for a neutral model. The results also support the hypothesis that abiotic determinism is more important at larger scales, while biotic determinism is more important on smaller scales within habitats.

**Key-words:** deterministic processes, functional and phylogenetic dispersion, functional traits, neutral processes, phylogenetic signal, spatial scales

## Introduction

Understanding the mechanisms underlying community assembly and species co-occurrence is a continuing topic of debate in ecology. The mechanistic models often debated generally fall into two classes – neutral models

and deterministic niche-based models. Neutral models invoke the relative importance of dispersal limitation and stochastic demography, but not the importance of the ecological or evolutionary differentiation between species (Hubbell 2001). A neutral model therefore predicts the structure of a community should be random with respect to functional traits and phylogeny aside from that expected from spatial autocorrelation (i.e. dispersal limitation). Deterministic models on the other hand assert the

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overriding importance of the ecological and evolutionary differentiation between species. Thus, deterministic models predict that community structure should be non-random with respect to functional traits and phylogeny (e.g. Swenson & Enquist 2009; Kraft & Ackerly 2010; Swenson *et al.* 2012). Specifically, biotic interactions (e.g. competitive exclusion or facilitation) should drive the overdispersion of functional traits and relatedness if the traits involved in the biotic interactions have phylogenetic signal. Conversely, abiotic interactions (e.g. environmental filtering) should drive the underdispersion or clustering of functional traits and relatedness if the traits involved in the abiotic interactions have phylogenetic signal (Swenson & Enquist 2009).

Previous trait- and phylogenetically based studies have focused on spatial scale dependency (e.g. Cavender-Bares, Keen & Miles 2006; Swenson *et al.* 2007, 2012; Swenson & Enquist 2009; Kraft & Ackerly 2010) and size class dependency (Swenson *et al.* 2007; Letcher & Chazdon 2009; Swenson & Enquist 2009; Gonzalez *et al.* 2010; Kraft & Ackerly 2010). Spatial scale has been a focus of investigation because the imprint of biotic interactions on the composition of tree assemblages is likely to be most evident on the spatial scales on which individuals interact, whereas the imprint of abiotic filtering should be more evident on larger spatial scales (Weiher & Keddy 1995). Size class has been a focus of investigation because it is expected that as cohorts or groups of similarly sized individuals grow in an assemblage similar species are likely to be excluded due to biotic interactions generating an increase in dissimilarity with size class (Swenson *et al.* 2007).

Most of these studies in the tropics have analysed the spatial scale dependency by dividing large tree plots into multiple equally sized quadrats from fine to large spatial scales and have found that the degree of trait or phylogenetic dispersion generally decrease as the spatial scale increases indicating the importance of biotic interactions on local scales (e.g. Cavender-Bares, Keen & Miles 2006; Swenson *et al.* 2007, 2012). Also in these studies, size classes have been used as crude proxies for life stages to test how phylogenetic dispersion change as ontogeny progresses (Swenson 2013). For example, Swenson *et al.* (2007) have found that phylogenetic overdispersion increases with the size classes (1–2.9 cm, 3–4.9 cm, 5–9.9 cm, 10–14.9 cm, and 15 cm and above) for canopy species indicating the increasing importance of biotic interactions as cohorts or groups of similarly sized individuals grow. Lastly, trait and phylogenetic dispersion has also been found to vary across habitat types often with habitats considered resource poor containing phylogenetically or functionally clustered assemblages indicating the importance of abiotic filtering (Kress *et al.* 2009; Pei *et al.* 2011; Katabuchi *et al.* 2012; Liu *et al.* 2012b).

Despite all of the above results from various assemblages, a remaining challenge in functional and phylogenetic analyses of tropical tree communities is to successfully integrate the functional and phylogenetic

structure of these communities across spatial and size scales and habitats in a single analysis of an assemblage. Given that the relative importance of biotic and abiotic interactions (e.g. competitive exclusion vs. environmental filtering) is expected to vary across spatial and size scales and habitats, we expect the phylogenetic and trait dispersion in assemblages to be predictable. For example, biotic interactions should be more pronounced than abiotic filtering at finer spatial scales within habitats and at later stages of ontogeny due to a local thinning of similar individuals or an accumulation of this effect through time. Thus, we predict phylogenetic and functional overdispersion increases with increasing size classes at finer spatial scales. In contrast, at larger spatial scales where biotic interactions are expected to play a reduced role, we expect environmental filtering to be more pronounced. Thus, we predict phylogenetic and functional clustering to increase at larger spatial scales particularly in more stressful habitats such as habitats with low soil nutrient and water availability (e.g. high elevations in the present study plot). If there is no phylogenetic signal in trait data, we do not expect the phylogenetic and functional results to align across scales or habitats, signifying that other unmeasured traits may also be important for structuring the assemblage or that phylogeny is not a relevant predictor of species performance.

Here, we analyse the functional and phylogenetic structure of tree assemblages in a tropical forest dynamics plot in Xishuangbanna, China. To empirically test those hypotheses above, we measured 10 plant functional traits and generated a molecular phylogeny for the >400 tree taxa in the plot. First, functional trait and phylogenetic data were used to quantify the degree of phylogenetic signal in the trait data to determine whether we should expect the phylogenetic and functional trait dispersion results to align. Phylogenetic signal describes the degree to which phylogenetic similarity predicts functional trait similarity. Thus, if there is phylogenetic signal in trait data, we expect the phylogenetic and functional dispersion results to align. Secondly, we quantified the functional and phylogenetic dispersion of individual co-occurring trees in quadrats across six spatial scales (5 m × 5 m, 10 m × 10 m, 20 m × 20 m, 25 m × 25 m, 50 m × 50 m and 100 m × 100 m) and three size classes (1–5 cm, 5–15 cm, and 15 cm and above) for canopy species. Next, we analysed the dispersion results with respect to six distinct habitat types (valley, low slope, high slope, high gully, high plateau and forest gap) described in the plot. From these analyses, we addressed the following questions. (i) Do functional traits have phylogenetic signal in this diverse tropical tree community? We hypothesize that phylogenetic signal will be found in the trait data in this forest. (ii) Do measurements of phylogenetic signal in trait data underlie the similarity or dissimilarity in the patterns of functional and phylogenetic dispersion in this forest? We hypothesize that if phylogenetic signal is found, the phylogenetic and trait dispersion patterns will be the same.

(iii) Does the functional and phylogenetic structure of assemblages vary across size classes, and is this consistent across the six spatial scales and the six habitat types? We hypothesize that biotic interactions occurring on local scales through time will leave an imprint of increasing overdispersion with size class and on finer spatial scales and in low elevations that are more resource rich and therefore less stressful.

## Materials and methods

### STUDY SITE

The study was performed in the 20-ha Xishuangbanna forest dynamics plot (FDP) located in Yunnan Province, south-west China (21°37'08" N, 101°35'07" E) (Fig. S1). This forest is characterized as a seasonal tropical rain forest and dominated by large individuals of *Parashorea chinensis* (Dipterocarpaceae). Annual rainfall averages 1493 mm, of which 1256 mm (84%) occurs in the wet season (Cao *et al.* 2006). Elevation ranges from 708.2 m to 869.1 m a.s.l. The FDP was established in 2007, and censuses are carried out every 5 years. All free-standing woody stems  $\geq 1$  cm diameter at breast height (dbh), that is, 130 cm from the ground, were measured, tagged, identified and mapped. A detailed description of the climate, geology and flora of Xishuangbanna can be found in Cao *et al.* (2006) and Zhu, Cao & Hu (2006).

### TRAIT SELECTION AND MEASUREMENT

Trait data for the tree species in the plot were derived from vegetation samples collected using standardized protocols (Cornelissen *et al.* 2003) with the exception of leaf chlorophyll content, stem-specific resistance and seed dormancy. In total, we measured 10 functional traits that are believed to represent fundamental functional trade-offs in leaves, wood and seeds among tree species (Westoby 1998; Westoby *et al.* 2002). The traits measured are listed in Table 1. Leaf area has important consequences for the leaf energy and water balance with smaller leaves reducing boundary layer resistance (Cornelissen *et al.* 2003). Specific leaf area

(SLA) represents a trade-off between construction costs and leaf life span (Cornelissen *et al.* 2003; Wright *et al.* 2004). Leaf dry matter content (LDMC) represents a trade-off between rapid assimilation and growth (Garnier *et al.* 2001; Cornelissen *et al.* 2003; Vaieretti *et al.* 2007). Leaf chlorophyll content is directly related to the photosynthetic rate of plants (Gitelson, Gritz & Merzlyak 2003; Coste *et al.* 2010). Leaf thickness is related to leaf life span, litter decomposition and nutrient cycling (Onoda *et al.* 2011; Pérez-Harguindeguy *et al.* 2013). Maximum tree height represents adult size and the adult light niche (Cornelissen *et al.* 2003). Wood density represents a trade-off between volumetric growth rates and mechanical strength and is therefore of interest in tropical tree assemblages, but it is especially time-consuming to quantify for hundreds of species, coring trees in a long-term forest dynamics plot is ill-advised, and finding individuals of rare species outside of forest plots is often very difficult (Isik & Li 2003). Thus, we quantified stem-specific resistance as a proxy for wood density (Isik & Li 2003). Seed dormancy and seed mass are important traits related to the dispersal of species and their regeneration niche (Cornelissen *et al.* 2003; Baskin & Baskin 2004).

Leaf traits were quantified from randomly collected mature outer canopy leaf samples from adult trees. In most cases, outer canopy leaves were sun leaves collected from individuals 15–25 metres tall that have reached the forest canopy, though may not have reached their absolute maximum possible height. However, in the case of small shade-tolerant species, outer canopy leaves were necessarily shade leaves collected from individuals less than ten metres tall given that these species do not occupy gaps or reach the forest canopy. We assured that the leaves collected did not have any obvious symptoms of pathogen or herbivore attack and were without substantial cover of epiphylls (Cornelissen *et al.* 2003). More than five leaves were sampled from each of five individuals of each taxon belonging to 462 of the 468 taxa. The functional traits of rare species were collected outside of the 20-ha Xishuangbanna FDP. Each leaf (without petiole or rachis) was scanned, and leaf area (cm<sup>2</sup>) was measured using IMAGEJ software (Abramoff, Magelhaes & Ram 2004). Each leaf (including petiole or rachis) was cut from the stem and dried to a constant weight at 60 °C. LDMC (mg g<sup>-1</sup>) was the oven-dry mass of a leaf divided by its fresh mass (Cornelissen *et al.* 2003). SLA (cm<sup>2</sup> g<sup>-1</sup>) was the ratio of one-sided of a fresh leaf excluding the petiole or rachis to oven-dry mass. Leaf thickness (mm) was measured at the centre of the leaf lamina to avoid major leaf veins with electronic digital micrometer (CANY Co., Shanghai, China) on fresh leaves (Seelig, Stoner & Linden 2012). Relative leaf chlorophyll content was measured using a hand-held 'SPAD-502 Chl meter' (Minolta Camera Co., Osaka, Japan). Three readings were taken from the widest portion of the leaf blade to the narrow portion at about 15 mm from the leaf margin (Uddling *et al.* 2007; Marengo, Antezana-Vera & Nascimento 2009). We positioned the adaxial leaf surface towards the emitting lens of the instrument to avoid the major veins. Stem-specific resistance (N) was measured on the five largest individuals for each of 420 taxa using a Resistograph (Rinntech Co., Germany). Maximum tree height (m) was from the data base of Flora of China (Wu & Raven 2012) and Flora of Yunnan (Wu 2008). Seed mass (g) was the oven-dry mass of one thousand seeds of a species. We removed any wings, comas, pappus and fruit flesh, dried the seeds at 80 °C for at least 48 h and then weighed them. The seed mass was measured for each of 232 species from seeds collected in seed traps inside the FDP (Yang 2010). The seed mass of the remaining 200 species was measured from specimens in the Germplasm Bank of Xishuangbanna Tropical Botanic Gardens and the China Germplasm Bank of Wild Species of Kunming Institute of Botany. Classes of seed dormancy (*sensu* Baskin & Baskin 2004) were determined/inferred from information in the literature for all 467 species in the plot. Specifically, dormancy class (or non-dormancy) was determined for 173 species based on actual data and for 294 species inferred from

**Table 1.** The ranges of functional traits and phylogenetic signal tests using Blomberg's *K* statistic for the continuous functional traits and parsimony Sankoff scores for the categorical functional traits

Traits	Ranges	<i>K</i>	Sankoff	n	<i>P</i>
Leaf area (cm <sup>2</sup> )	1.86–239.526	0.27	–	426	0.419
SLA (cm <sup>2</sup> g <sup>-1</sup> )	14.48–394.34	0.17	–	426	<b>0.049</b>
Leaf chlorophyll content (SPAD)	24.98–67.12	0.13	–	426	<b>0.045</b>
LDMC (mg g <sup>-1</sup> )	0.035–0.851	0.19	–	426	<b>0.015</b>
Leaf thickness (mm)	0.11–0.63	0.27	–	426	<b>0.001</b>
Maximum height (m)	2–60	0.24	–	428	<b>0.001</b>
Stem specific resistance (N)	11.22–362.73	0.24	–	420	0.203
Seed mass (g)	0.01–22990	0.49	–	412	<b>0.001</b>
Life-form		–	171	428	<b>0.001</b>
Seed dormancy		–	79	412	<b>0.001</b>

Key to abbreviations: SLA, specific leaf area; LDMC, leaf dry mass content; n, the number of species with trait data represented in the given phylogeny; – means this trait was not been tested. *P* values < 0.05 are shown in bold.

studies of other species in the genus or family. See Baskin & Baskin (1998) for procedures used to assign a dormancy class to a species for which actual data on dormancy/germination are not available and to a species for which dormancy is inferred from data at the genus or family level.

Leaf thickness, area, chlorophyll content, LDMC and SLA, stem-specific resistance, maximum tree height and seed mass were log<sub>10</sub>-transformed prior to analyses to meet the assumption of normality in the data. Next, a principle components analysis (PCA) was conducted to reduce the trait data to major orthogonal axes of function. The first three PCA axes accounted for over 95% of the variation (Table S1) and were used to compute a distance matrix. A functional trait dendrogram was generated using both the three-axis PCA matrix and the raw trait distance matrix and hierarchical clustering. All analyses were conducted using both dendrograms, and the results were similar. Therefore, only the results from the raw trait distance matrix are presented.

#### PHYLOGENETIC TREE RECONSTRUCTION

We reconstructed a community phylogeny representing 428 of the taxa in the Xishuangbanna FDP (Fig. S2, Table S2). A DNA supermatrix was generated from three chloroplast sequence regions – *rbcL*, *matK*, *trnH-psbA* and the nuclear ribosomal internal transcribed spacer (ITS) (Kress *et al.* 2009). The *rbcL* and *matK* regions were globally aligned following the methods described in Kress *et al.* (2009, 2010). The *trnH-psbA* and ITS regions were aligned within families using software package SATÉ (Liu *et al.* 2012a) and then concatenated to the *rbcL* and *matK* alignments. The DNA supermatrix was then analysed using RAxML (Stamatakis 2006) via the CIPRES supercomputer cluster (Miller *et al.* 2009) to infer a maximum likelihood (ML) phylogeny using the APG III phylogenetic tree as a constraint or guide tree as described in Kress *et al.* (2010). A constraint tree approach helps assure the basal topology of a molecular community phylogeny is consistent with the global working hypothesis for the angiosperm basal topology. Node support was estimated using bootstrap values with nodes with less than 50% support being collapsed into soft polytomies. Finally, an ultrametric tree was obtained using the nonparametric rate smoothing approach in the r8s software package (Sanderson 2003).

#### SPATIAL SCALES, HABITAT TYPES AND TREE SIZE CLASSIFICATION

To test whether the average phylogenetic and functional dispersion of local tree communities depended on spatial scale, we divided the plot into square quadrats with variable areas: 5 m × 5 m quadrats ( $n = 8000$ ), 10 m × 10 m quadrats ( $n = 2000$ ), 20 m × 20 m quadrats ( $n = 500$ ), 25 m × 25 m quadrats ( $n = 320$ ), 50 m × 50 m quadrats ( $n = 80$ ) and 100 m × 100 m quadrats ( $n = 20$ ).

For habitat analyses, the 20-ha plot was divided into six habitat types. At first, we sorted each 20 m × 20 m quadrat by similarity into five topographical habitats including valley, low slope, high slope, high gully and high plateau which were classified by using the topographical variables including slope, elevation and convexity (Hu 2010). Previous work has shown that soil nutrient concentrations are lowest at high elevations in the plot (Hu 2010), and we therefore predicted that the high-slope, high-gully and high-plateau habitats are more stressful and have phylogenetically and functionally clustered assemblages. The detailed classification scheme for topographical habitats is given in Table S3. After assigning each 20 m × 20 m quadrat to one of the five topographical habitats, some of 500 20 m × 20 m quadrats were assigned as ‘forest gap’ in place of previous topographical habitats. This was

determined by dividing each 20 m × 20 m quadrat into 16 sub-quadrats of 5 m × 5 m each. When the subquadrat consisted of open canopy and the average tree height was less than 10 m, the subquadrat was classified as a ‘gap’. If 70% or more of the 16 sub-quadrats in a 20 m × 20 m quadrat were ‘gaps’, the 20 m × 20 m quadrat was assigned as a ‘forest gap’ habitat (Hu *et al.* 2012). Ultimately, valley, low-slope, high-slope, high-gully, high-plateau and forest gap habitats have 140, 91, 89, 59, 90 and 31 quadrats of 20 m × 20 m, respectively.

To test whether the average phylogenetic and functional dispersion through different life stages depends on spatial scales and habitats, we used the size class as a crude surrogate for life stages. We deemed any tree species in Xishuangbanna FDP that has an individual reaching ≥15 cm dbh as a canopy species (Swenson *et al.* 2007) and divided all individuals of these species into small (1–5 cm dbh), medium (5–15 cm dbh) and large (15 cm dbh and above) size classes (Table S4, Hu *et al.* 2012). We also analysed the phylogenetic and functional dispersion for all stems ≥1 cm dbh whether belonging to a canopy species or not.

Lastly, we compared the phylogenetic and functional dispersion in quadrats varying in soil properties. Soil samples were collected and analysed following the standardized protocols described in John *et al.* (2007). Fresh soil samples were placed into pre-labelled plastic bags and shipped to the Biogeochemistry Laboratory at the Xishuangbanna Tropical Botanical Garden. We obtained the spatial maps of 9 variables of soil fertility (pH, total N, total P, total K, available N, extractable P, extractable K, total C, bulk density) in the plot by using ordinary kriging parameterized using the variable values at the sampling locations. Detailed information regarding the soil data collection and measurement can be found in Hu *et al.* (2012). A principal components analysis (PCA) was used to extract orthogonal axes of soil fertility from the nine soil nutrients measured and to reduce information redundancy. The first three principal components accounted for over 95% of the variation and were used to characterize soil fertility for subsequent analyses (Table S5).

#### PHYLOGENETIC SIGNAL TESTS

To quantify the degree to which the phylogenetic tree estimates trait similarity of species, we quantified the phylogenetic signal in the trait data. For continuous traits, the phylogenetic signal was quantified using the *K* statistic (Blomberg, Garland & Ives 2003). For the categorical traits, we quantified the parsimony Sankoff score for the traits arrayed on the community phylogeny (Maddison & Slatkin 1991). To test for significance for both *K* and the Sankoff score, we randomly arrayed the trait data on the community phylogeny 999 times to generate a null distribution from which a *p* value could be calculated. The calculation of the *K* statistic and the randomizations were implemented in the R package ‘phytools’ (R Development Core Team 2012).

#### PHYLOGENETIC ANALYSES OF COMMUNITY STRUCTURE

To determine whether the observed phylogenetic alpha diversity differs from that expected by chance, we implemented a frequently used null model, randomly shuffling taxa names across the tips of the phylogeny 999 times to randomize phylogenetic relationships among species, given a tree topology and branch lengths. This algorithm randomizes the relatedness of species to one another, but it maintains species occurrence frequency and abundances. During each of the 999 shufflings, a null phylogenetic alpha diversity is produced. The 999 null values constituted a null distribution to which the observed value is compared. All null models were performed at the plot scale and not at the quadrat scale. In

other words, we did not do 999 randomizations for each quadrat. The phylogenetic dispersion of assemblages was determined using the net relatedness index (NRI). NRI is the standardized effect size (S.E.S.) for the mean pairwise phylogenetic distance (MPD) for all individuals in each quadrat, which is abundance-weighted calculation relative to the previous calculation (e.g. Webb 2000; Swenson *et al.* 2007). NRI was calculated using the following equations.

$$\text{NRI} = -1 \times (\text{MPD}_{\text{obs}} - \text{mean}(\text{MPD}_{\text{null}})) / \text{sd}(\text{MPD}_{\text{null}})$$

MPD is the mean pairwise phylogenetic distance between all individuals within a local sample. The  $\text{MPD}_{\text{obs}}$  is the observed value of mean pairwise phylogenetic distances. The mean ( $\text{MPD}_{\text{null}}$ ) is the mean value from a null distribution where species names were randomly shuffled on the tips of the community phylogeny 999 times, and the MPD values were calculated each time for each quadrat. The  $\text{sd}(\text{MPD}_{\text{null}})$  is the standard deviation of the null distribution. A negative NRI indicates that a community is phylogenetically overdispersed, whereas a positive NRI indicates that a community is phylogenetically clustered. The tip shuffling null model was used as it only randomizes relatedness and does not randomize any spatial or size data. Therefore, it allows us to ask address-specific hypotheses regarding whether relatedness alone is non-random in an assemblage while fixing the observed spatial and size patterns in the assemblages.

The phylogenetic dispersion values were calculated in 20-ha FDP with analyses being repeated at multiple spatial scales: 5 m × 5 m, 10 m × 10 m, 20 m × 20 m, 25 m × 25 m, 50 m × 50 m and 100 m × 100 m. Because the NRI values in the quadrats were spatially autocorrelated (Table S6), we used simultaneous spatial autoregression (SAR), which uses neighbour matrices to estimate spatially independent data points that can be utilized for analysis. A generalized least squares model with a first-order spatial neighbour SAR in the 'spdep' R package (Bivand 2010) was used. A Student's *t*-test was used to test for significant deviations of NRI from the expectation of zero. The phylogenetic analyses were implemented in the R package 'picante' (Kembel *et al.* 2010).

#### TRAIT-BASED ANALYSES OF COMMUNITY STRUCTURE

As the measure of phylogenetic alpha diversity based on a phylogenetic tree, we measured functional alpha diversity based on the functional trait dendrogram. The dendrogram was calculated from the Euclidean distance matrix of three PCA axes for the continuous functional traits (Table S1) and hierarchical clustering. This allows for direct comparisons between functional and phylogenetic results (Swenson *et al.* 2012; Liu *et al.* 2013). Functional alpha diversity in each quadrat was quantified by the mean pairwise trait distance (PW) from the functional trait dendrogram for all individuals in a quadrat. It is therefore an abundance-weighted metric. A standardized effect size (S.E.S.) PW was used to quantify the functional dispersion of co-occurring species for each scale across tree size. S.E.S. PW was calculated as follows:

$$\text{S.E.S. PW} = -1 \times (\text{PW}_{\text{obs}} - \text{mean}(\text{PW}_{\text{null}})) / \text{sd}(\text{PW}_{\text{null}})$$

A positive S.E.S. PW indicates that traits are clustered in a quadrat, whereas a negative S.E.S. PW indicates that traits are overdispersed in a quadrat. The same null as that used in the phylogenetic analysis was used in the functional trait analysis such that names on the dendrogram were randomized. Because S.E.S. PW values in the quadrats of spatial size scales were spatially autocorrelated (Table S6), we estimated spatially independent S.E.S. PW values within each quadrat using simultaneous spatial autoregression analyses. A generalized least squares model with a first-order spatial neighbour SAR in the 'spdep' R package (Bivand 2010) of R was used. A Student's *t*-test was used to test for significant deviations of S.E.S. PW from the expectation of zero. All functional dispersion analyses were implemented in the R package 'picante' (Kembel *et al.* 2010).

## Results

### PHYLOGENETIC SIGNAL

The *K* values of all continuous functional traits were less than 1 (mean = 0.27; range = 0.13 to 0.49; Table 1), which indicated weaker phylogenetic signal than expected by a Brownian motion model of trait evolution. However, the *P* value from the permutation test was less than 0.05 for all traits except leaf area (*P* = 0.419) and stem-specific resistance (*P* = 0.203) (Table 1), indicating that most functional traits analysed were less labile than expected by random community phylogeny. By comparing the observed parsimony scores to the null parsimony scores, we found significant phylogenetic signal in the two categorical traits (Table 1). Given that most traits had significant phylogenetic signal, close relatives generally share trait values more similar than that expected by chance in the Xishuangbanna 20-ha FDP.

### PHYLOGENETIC DISPERSION

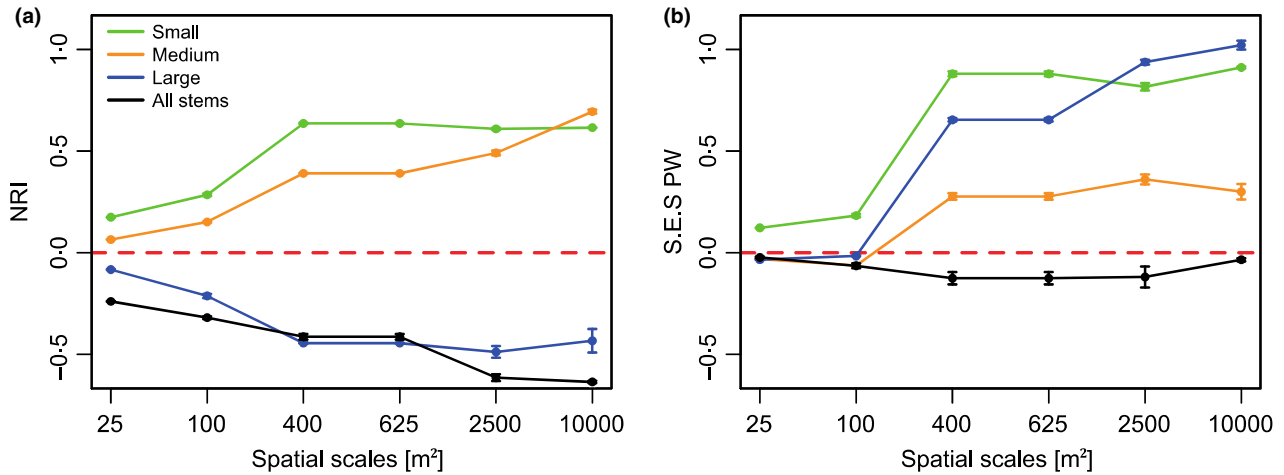
Non-random phylogenetic dispersion was found for each tree size class across all spatial scales and habitat types (Student's *t*-test, *P* < 0.05) (Tables S7 and S8). In each spatial scale and habitat type, phylogenetic clustering was found in small and medium size classes, while phylogenetic overdispersion occurred in large size class (Figs 1a and 2a). For all stems, phylogenetic overdispersion was found in all spatial scales and habitat types (Figs 1a and 2a).

### FUNCTIONAL DISPERSION

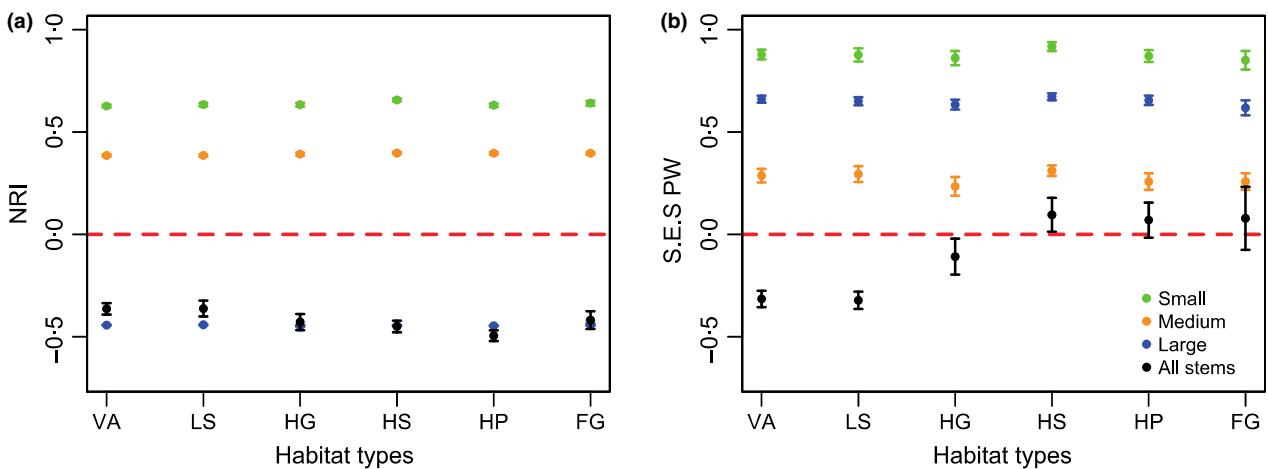
The functional dispersion was significantly different from random for each tree size class across all spatial scales and habitat types (Student's *t*-test, *P* < 0.05) (Tables S7 and S8). On fine spatial scales (5 m × 5 m and 10 m × 10 m), functional clustering was found in small size classes, while functional overdispersion occurred in medium and large size classes (Fig. 1b). On larger spatial scales (20 m × 20 m, 25 m × 25 m, 50 m × 50 m and 100 m × 100 m), all size classes showed functional clustering, especially the medium size class, which was less functionally clustered than the small and large size classes (Fig. 1b). For all stems, functional overdispersion was found in all spatial scales and in three habitat types (valley, low slope and high gully), while functional clustering in high-slope, high-plateau and forest gap habitats (Figs 1b and 2b).

### SOIL FERTILITY AND PHYLOGENETIC AND FUNCTIONAL DISPERSION

The phylogenetic and functional dispersion in 20 m × 20 m quadrats for all individuals was related to the first principal component of soil fertility (Table 2). Across size classes, only the largest trees assemblages had a significant association between phylogenetic and functional dispersion and all



**Fig. 1.** The pattern (Mean  $\pm$  SE) of (a) phylogenetic dispersion (NRI) and (b) functional dispersion (S.E.S PW) for tree communities in quadrats at six spatial scales within the 20-ha Xishuangbanna forest dynamics plot. Positive values indicate phylogenetic or functional clustering, and negative values indicate phylogenetic or functional overdispersion. The pattern was repeated by the following size classes, Small: 1 to <5 cm dbh; Medium: 5 to <15 cm dbh; Large:  $\geq$ 15 cm dbh; All stems: stems  $\geq$ 1 cm dbh no matter if it belongs to canopy species.



**Fig. 2.** The pattern (Mean  $\pm$  SE) of (a) phylogenetic dispersion (NRI) and (b) functional dispersion (S.E.S PW) for tree communities in 20 m  $\times$  20 m quadrats in six habitats within the 20-ha Xishuangbanna forest dynamics plot. Positive values indicate phylogenetic or functional clustering, and negative values indicate phylogenetic or functional overdispersion. The pattern was repeated by the following size classes, Small: 1 to <5 cm dbh; Medium: 5 to <15 cm dbh; Large:  $\geq$ 15 cm dbh; All stems: stems  $\geq$ 1 cm dbh no matter if it belongs to canopy species. VA: valley; LS: low slope; HG: high gully; HS: high slope; HP: high plateau; FG: forest gap.

three principal components of soil fertility (Table 2). In the small size class, the phylogenetic and functional dispersion was significantly associated with the first principal components of soil fertility, while in the medium size class, there is generally no association between phylogenetic and functional dispersion and all the three principal components of soil fertility except that between functional dispersion and the second principal component (Table 2).

## Discussion

### PHYLOGENETIC SIGNAL OF FUNCTIONAL TRAITS

If the functional traits governing the interactions structuring communities have phylogenetic signal, then the

phylogenetic dispersion of species generally should be indicative of the functional dispersion of species. In this study, we quantified the phylogenetic signal in 10 plant functional traits for the species in our forest plot. All traits, except leaf area and stem-specific resistance, had significant phylogenetic signal when using a permutation test to assess significance (Table 1). The general concordance of the functional and phylogenetic dispersion results is supported by the significant phylogenetic signal in the trait data, but the concordance was not perfect between the two dispersion patterns. This result can be best understood by noting that the  $K$  values (Table 1) for phylogenetic signal were less than one suggesting traits are more labile than expected under a Brownian model of trait evolution. If  $K$  values were higher than one, we may expect a stronger

**Table 2.** Pearson's correlation coefficients between the net relatedness index (NRI) and the standardized effect size of the mean pairwise trait distance (S.E.S PW) in 20 × 20 m quadrats for three size classes of canopy species, and the first three principal components of soil fertility in the 20-ha Xishuangbanna forest dynamics plot

Size classes	NRI			S.E.S. PW		
	PCA1	PCA2	PCA3	PCA1	PCA2	PCA3
Small	−0.285***	−0.020 ns	−0.024 ns	0.311***	−0.043 ns	0.048 ns
Medium	0.010 ns	−0.071 ns	−0.031 ns	0.131 ns	−0.472***	−0.035 ns
Large	0.220***	−0.308***	0.202***	0.249***	−0.313***	−0.019***
All stems	−0.169***	−0.071 ns	0.002 ns	0.369***	−0.559***	0.021 ns

Small: stems 1 to <5 cm dbh; Medium: stems 5 to <15 cm dbh; Large: stems ≥15 cm dbh; All stems: stems ≥1 cm no matter if it belongs to canopy species.

\*\*\* $P < 0.001$ ; ns: not significant.

concordance. Similar results have been reported in other forests where phylogenetic and functional dispersion results align, albeit imperfectly due to weak, but significant, phylogenetic signal in trait data (e.g. Swenson & Enquist 2009; Kraft & Ackerly 2010). Thus, while we can get a rough approximation of functional dispersion from phylogenetic dispersion in this forest, there is not a perfect correlation between the two.

#### PHYLOGENETIC DISPERSION ACROSS SIZE CLASSES, SPATIAL SCALES AND HABITATS

The phylogenetic dispersion among size classes in the Xishuangbanna FDP showed consistent patterns across all spatial scales and habitats. The small and medium size classes were phylogenetically clustered, whereas the large size class was overdispersed (Figs 1a and 2a). Generally, phylogenetic overdispersion increases throughout ontogeny regardless of spatial scales and habitats, as shown by the present phylogenetic-based approach. This is consistent with previous work by Swenson *et al.* (2007) with the general finding that phylogenetic overdispersion increases with the size class analysed. Under the premise that phylogenetic relatedness is a solid proxy for ecological similarity, this lends support to the hypothesis that biotic interactions increase in importance or their accumulation as ontogeny progresses (Swenson 2013).

For all stems ≥1 cm dbh of all species, phylogenetic overdispersion always dominated regardless of spatial scales and habitats (Figs 1a and 2a). The pattern of phylogenetic dispersion for all stems contrasts with previous works focusing on the influence of spatial scaling and habitats. For example, Swenson *et al.* (2006, 2007) in Puerto Rico, Panama and Costa Rica have found that the degree of phylogenetic dispersion decreases as the spatial scale increases, whereas our results showed that the degree of phylogenetic dispersion increases as the spatial scale increases (Fig. 1a). It is likely that the ecological dominance of species from the Fagales in the present forest that are generally less dominant or absent in Central American forests underlies this difference between the present work and results from Central America. While phylogenetic

overdispersion did increase with size class, it did not increase on fine spatial scales or in particular habitats. In particular, phylogenetic overdispersion did not increase in finer spatial scales and phylogenetic overdispersion was found in all habitat types in the forest.

#### FUNCTIONAL DISPERSION ACROSS SIZE CLASSES, SPATIAL SCALES AND HABITATS

Analyses of functional dispersion in tropical tree assemblages are becoming prevalent particularly on tropical trees (Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009; Lebrija-Trejos *et al.* 2010; Paine *et al.* 2011; Swenson, Anglada-Cordero & Barone 2011; Swenson *et al.* 2012; Ding *et al.* 2012; Katabuchi *et al.* 2012). However, many aspects of functional dispersion regarding size, spatial and habitat dependency still remain unknown or have not been integrated. In the present study, the functional dispersion among size classes showed spatial scale dependency. Functional overdispersion increased with size classes at finer spatial scales (e.g. 5 m × 5 m and 10 m × 10 m) (Fig. 1b), which supports our prediction. Specifically, our results demonstrated that at finer spatial scales functional clustering in small size class turned to functional overdispersion in medium and large size classes (Fig. 1b). At large spatial scales (50 m × 50 m and 100 m × 100 m), the large size class showed more clustering than the small and medium size classes (Fig. 1b), which supports our prediction that functional clustering increases with size classes at larger spatial scales where environmental filtering is likely to dominate.

Functional clustering was found in all habitats and across all size classes (Fig. 2b). The results therefore do not support the prediction that the imprint of biotic interactions should become clearer, in the form of trait overdispersion, as size class increases. The results do support that species are filtered into different habitat types and that the abiotic environment rather than the biotic environment plays a stronger role in this process. In sum, tree assemblages in the present forest plot are functionally clustered across size classes, and multiple functionally similar species are packed into habitats in the forest plot. The degree to

which biotic interactions exist within functional strategies is unknown, but the results suggest that the interactions may be diffuse or weak enough to allow coexistence in the same habitat or are indicated by unmeasured traits.

When using all stems  $\geq 1$  cm dbh for all species, the functional overdispersion was consistent across the six spatial scales (Fig. 1b). This result contrasts with the finding by Swenson & Enquist (2009) that at small spatial scales coexisting species are typically functionally clustered. There is still little knowledge on the pattern of functional dispersion across different habitats (but see Kraft, Valencia & Ackerly 2008; Katabuchi *et al.* 2012). Here, we found, functional clustering turns to overdispersion from stressful habitats (high slope and high plateau) to less stressful habitats (valley, low slope and high gully) (Fig. 2b). This is evidence that deterministic biotic interactions may play a dominant role in structuring the tree assemblages in less stressful habitats, and deterministic abiotic filtering is more prevalent in stressful habitats. However, there is an alternative explanation for functional clustering found in high-slope and high-plateau habitats. These two habitats had suffered human cutting disturbance about 40 years ago (Lan *et al.* 2011) and now are in late-successional stages. Some recent studies have shown that disturbed communities contain more clustered traits and closely related species than non-disturbed ones (Helmus *et al.* 2010; Cavender-Bares & Reich 2012; Ding *et al.* 2012), suggesting that species in these disturbed communities are non-randomly filtered on the basis of their functional interactions with the abiotic environmental characteristics of a disturbed habitat.

#### INCONSISTENCY BETWEEN PHYLOGENETIC AND FUNCTIONAL DISPERSION AND ITS IMPLICATIONS

Previous work integrating both phylogenetic and functional analyses has reported the inconsistency between results across spatial and size scales in a neotropical dry-forest community (Swenson & Enquist 2009) and across spatial scales in six forests located in tropical and temperate latitudes (Swenson *et al.* 2012), and the consistency between them across spatial scales in Yasuní FDP (Kraft & Ackerly 2010).

Our results showed a general inconsistency between the phylogenetic and functional dispersion across size classes, spatial scales and habitats. This inconsistency may not be surprising given that the traits analysed were generally more phylogenetically labile than expected given a Brownian motion (i.e. random walk along a branch) model of trait evolution. As many researchers have argued, the limitation of phylogenetic proxies is that phylogenetic distance is not always a good predictor of ecological similarity (Losos 2008) and community assembly studies that only use phylogenetic information may be misleading when coexisting species simultaneously converge and diverge in function (Swenson 2013).

However, divergent phylogenetic and trait results are still of interest particularly because relatedness may still be

representing additional traits that are relevant to the processes being studied (Cadotte, Cardinale & Oakley 2008; Swenson 2013). It is inevitable that some functional traits which are important for species coexistence are not measured in trait-based community ecology studies and that the selected and relatively easy to measure functional traits might not be a full representation of the functional strategies of species. Thus, given the limitations of both phylogenetic and functional-based approaches, it is often better to integrate both of these two approaches into the analysis on the same community. In cases, such as ours where the trait and phylogenetic results are not always consistent, future research into what traits and processes drive the opposing phylogenetic pattern are needed.

#### INTRASPECIFIC VARIATION

A limitation of the trait data used in the present study is that trait data from adult individuals have been used to analyse the functional structure across life stages, since functional trait variation is size-dependent (Niklas 2004; Weiner 2004). Some studies have advocated the important role of intraspecific trait variation in ecological processes underlying community assembly and species coexistence (e.g. Long *et al.* 2011; Courbaud, Vieilledent & Kunstler 2012; Laughlin *et al.* 2012). Some have suggested that incorporating intraspecific variation can improve statistical power for the detection of non-random trait patterns (Jung *et al.* 2010; Swenson, Anglada-Cordero & Barone 2011). Thus, we might have possibly underestimated the deterministic functional dispersion across size classes when we use the trait data from adults across size classes.

#### Conclusion

In the 20-ha Xishuangbanna FDP, both phylogenetic and functional dispersion across size classes, spatial scales and habitats provided strong support for a deterministic model of community assembly rather than for a neutral model. In particular, our results demonstrate that functionally similar species co-occur across spatial and size scales and habitats in the Xishuangbanna FDP indicating the importance of abiotic filtering governing the assembly process. Thus, the results demonstrate how deterministic processes predominate across spatial and size scales and habitat types in unison to result in the assemblage of trees observed in this Chinese forest. Lastly, the research also uncovered weak phylogenetic signal in the selected functional traits, demonstrating how phylogenetic dispersion is not always a reliable predictor of functional dispersion.

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## Supporting Information

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

**Fig. S1.** Geographical location and spatial distribution of the six habitat types in the 20-ha Xishuangbanna forest dynamics plot. Colors represent different habitat types at the spatial scale of 20 m × 20 m.

**Fig. S2.** The phylogenetic tree constructed from DNA barcodes of the 428 taxa in the 20-ha Xishuangbanna forest dynamics plot.

**Table S1.** Principal component analyses for eight continuous functional traits in the 20-ha Xishuangbanna forest dynamics plot.

**Table S2.** The taxa list of phylogenetic tree constructed from DNA barcodes of 428 taxa in the 20-ha Xishuangbanna forest dynamics plot.

**Table S3.** Classification criteria of five topographical habitat types for all 20 m × 20 m quadrats in the 20-ha Xishuangbanna forest dynamics plot.

**Table S4.** The number of taxa, genera and families in each of three size classes for canopy species and for all stems no matter if it belongs to canopy species.

**Table S5.** Principal component analyses for nine variables of soil fertility in the 20-ha Xishuangbanna forest dynamics plot.

**Table S6.** Testing spatial autocorrelation by Moran's *I* for the indices describing phylogenetic and functional dispersion.

**Table S7.** Student's *t* test for whether the means of NRIs and S.E.S PWs across size classes on multiple spatial scales are significantly different from zero.

**Table S8.** Student's *t* test for whether the means of NRIs and S.E.S PWs across size classes in multiple habitats are significantly different from zero.