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Contrasting effects of space and environment on functional and phylogenetic dissimilarity in a tropical forest

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Abstract

Aims

The evolutionary history and functional traits of species can illuminate ecological processes supporting coexistence in diverse forest communities. However, little has been done in decoupling the relative importance of these mechanisms on the turnover of phylogenetic and functional characteristics across life stages and spatial scales. Therefore, this study aims to estimate the contribution of environment and dispersal on the turnover of phylogenetic and functional diversity across life stages and spatial scales, in order to build a coherent picture of the processes responsible for species coexistence.

Methods

We conducted the study in Xishuangbanna Forest Dynamics Plot in Yunnan Province, southwest China. We used four different spatial point process models to estimate the relative importance of dispersal limitation and environmental filtering. The functional traits and phylogenetic relationships of all individual trees were incorporated in the analyses to generate measures of dissimilarity in terms of pairwise and nearest-neighbor phylogenetic and functional characteristics across life stages and spatial scales.

Important Findings

We found non-random patterns of phylogenetic and functional turnover across life stages and spatial scales. Environmental filtering structured pairwise phylogenetic and functional beta diversity across spatial scales, while dispersal limitation alone, and in combination with environment filtering, shaped nearest neighbor phylogenetic and functional beta diversity. The relative importance of dispersal limitation and environmental filtering appeared to change with life stage but not with spatial scale. Our findings suggest that phylogenetic and functional beta diversity help to reveal the ecological processes responsible for evolutionary and functional assembly and highlight the importance of using a range of different metrics to gain full insights into these processes.

Keywords: community assembly, functional beta diversity, life stage, phylogenetic beta diversity, spatial point pattern

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INTRODUCTION

It is widely accepted that a combination of niche-based deterministic processes and dispersal-based stochastic processes are responsible for structuring plant communities (Brown *et al.* 2013; Myers *et al.* 2013). Both types of process have their own particular influence on community spatial structure, making them potentially detectable through a range of spatial statistics (Brown *et al.* 2016; May *et al.* 2015). However, while the statistical techniques and census data necessary for estimating underlying processes are now widely available (Law *et al.* 2009; Velázquez *et al.* 2016; Wiegand and Moloney 2014), several important ecological questions remain unresolved. In particular, disentangling the roles of different ecological mechanisms is a key step towards understanding community assembly rules. One way to achieve this is to test the importance of evolutionary history and functional traits for community spatial structure.

Indeed, the spatial turnover of tree communities is a major focus of ecological research. Species beta diversity has long been used to extend knowledge and make inferences about the driving forces of community composition (Condit *et al.* 2002; Kraft *et al.* 2011; Legendre *et al.* 2005; Myers *et al.* 2013; Yuan *et al.* 2011). For instance, Condit *et al.* (2002) used species beta diversity to explore the roles of habitat filtering and dispersal limitation in shaping species turnover in tropical forests, while Wang *et al.* (2011) applied a spatial point pattern approach to analyze species beta diversity in two temperate forests to identify the signals of different ecological processes. Moreover, De Cáceres *et al.* (2012) analyzed species turnover at larger scales to partition the variation explained by the environment and dispersal limitation along a latitudinal range. Nevertheless, species beta diversity has been criticized for its neglect of information about evolution and functional traits that might illuminate structuring mechanisms (McGill *et al.* 2006). As a result, the concept of species beta diversity has recently been integrated with evolutionary and functional information to explore whether spatial changes in phylogenetic and functional assemblages indicate the action of particular ecological mechanisms in different forest types (Mi *et al.* 2016; Wang *et al.* 2015). Therefore, spatial patterns of phylogenetic and functional turnover could provide important signals of evolutionary and functional-based assembly processes.

Functional and phylogenetic approaches have been increasingly used to make adequate inferences about the relative importance of assembly mechanisms on species coexistence (Kraft and Ackerly 2010). The incorporation of these evolutionary and trait data in community assembly analyses not only help to partition the contribution of ecological processes, but also how these processes vary with the degree of species relatedness and similarity (Emerson and Gillespie 2008). Furthermore, they help to explore how relatedness in the evolution and function of the species affects the species turnover in space (Fine and Kembel 2011). However, such studies of evolutionary and functional beta diversity have so far been rare, particularly using advanced spatial statistical methods (Illian *et al.* 2008; Wiegand and Moloney 2014), and/or considering variations across spatial scales and life stages (Swenson *et al.* 2007). These methods more often used the spatial structure of individual trees based on their exact locations to link patterns with underlying processes (Wiegand and Moloney 2014). Most previous studies of functional and phylogenetic turnover lack this explicit spatial information of trees to make inferences about driving forces (Wang *et al.* 2015).

It is also known that the relative importance of ecological mechanisms varies considerably across life stages of trees (Lasky *et al.* 2015) and, that community assembly mechanisms vary greatly in strength across spatial scales (Cavender-Bares *et al.* 2006; Swenson *et al.* 2006; Vamosi *et al.* 2009). For a tropical forest community in southwest China, trees at early life stages have been found to be phylogenetically clustered, while those at later stages have been found to be phylogenetically overdispersed (Yang *et al.* 2014). Similar overdispersion occurs in the functional distribution of trees at small spatial scales, while at large spatial scales trees of all life stages show functional clustering in the same tree community (Yang *et al.* 2014). Clustering of both phylogenetic and functional strategies was also found along different niche axes (Asefa *et al.* 2017). These functional and phylogenetic alpha distribution patterns imply corresponding changes in functional and phylogenetic beta diversity that have been little investigated but which may hold important clues about the roles of mechanisms such as environmental filtering and dispersal limitation in community structures (Swenson *et al.* 2012; Yang *et al.* 2015).

We hypothesized that environmental homogeneity makes dispersal limitation most important at small scales and early life stages, with environmental filtering becoming stronger at larger, more environmentally heterogeneous scales and later life stages. In order to test this hypothesis, we analyzed phylogenetic- and functional-based turnover of trees across life stages and spatial scales using a spatial point pattern approach in the seasonal tropical forest in Xishuangbanna, southwest China. Specifically, we used spatial point process models to estimate the relative importance of random placement, environmental filtering, dispersal limitation and the joint-effect of environmental filtering and dispersal limitation on the structure of phylogenetic and functional beta diversity across stem sizes and three spatial scales (20 m × 20 m, 50 m × 50 m and 100 m × 100 m) in the tree community.

METHODS

Study area

We conducted this study in the 20-ha Xishuangbanna Forest Dynamics Plot (FDP) in Yunnan Province, southwest China (21°37′08″ N, 101°35′07″ E) (see online supplementary Fig. S1) that represents a seasonal tropical rainforest with *Parashorea chinensis* (Dipterocarpaceae), *Pittosporopsis kerrii* (Icacinaceae) and *Garcinia cowa (*Clusiaceae) as dominant species. It is mainly characterized by warm-wet air masses from the Indian Ocean and continental air masses from the sub-tropical regions in summer and winter respectively, which results in an alternation of dry and rainy seasons with a typical monsoon climate. The mean annual rainfall and temperature are 1 493 mm and 21.8°C, respectively (Cao *et al.* 2006). The topography of the plot is heterogeneous with an elevational range from 709 m to 869 m. The plot is trisected by three perennial streams that join in the southwest of the plot (Lan *et al.* 2009). The first census was held in 2007. The measurement, mapping and identification of the species were carried out for all the freestanding woody stems ≥ 1 cm in diameter at 130 cm from the ground (diameter at breast height [DBH]) (Condit 1998).

Environmental data

We included soil variables and topography as environmental factors in our analysis. Based on the protocols indicated in John *et al.* (2007), soils data were previously collected as described in Hu *et al.* (2012). These data include measures of soil pH, organic matter content, total nitrogen, total phosphorus, total potassium, available nitrogen, available phosphorus, available potassium, soil bulk density and soil moisture. Soil samples were collected from a regular grid of 30 × 30 m in the 20-ha plot. We used 252 nodes from these grids as sampling points. Two additional sampling points were created at random combinations of 2 and 5 m, 2 and 15 m or 5 and 15 m along a random compass bearing away from each grid point. We removed the litter and humus layer from these sampling points and collected 500 g topsoil at a depth of 10 cm. We collected 756 fresh soil samples and transported them to the Biogeochemistry Laboratory at the Xishuangbanna Tropical Botanical Garden.

Elevation, convexity, slope and aspect were also measured in each of the 500 20 m × 20 m quadrats in the full plot. Elevation was calculated as the mean of the four corners of each 20 m × 20 m subplot and convexity as the elevation of each quadrat minus the mean elevation of the eight surrounding quadrats (in the case of edge quadrats, convexity was calculated as the elevation of the center minus mean elevation of the four corners of the quadrat) (Valencia *et al.* 2004). Slope was calculated as the average angular deviation from horizontal of each of the four triangular planes produced by connecting three of the corners of each quadrat (Harms *et al.* 2001).

Aspect was calculated as:

$$Aspect = 180 - \arctan\left(\frac{fy}{fx}\right) \times \left(\frac{180}{\pi}\right) + 90 \times \left(\frac{fy}{|fx|}\right) \qquad (1)$$

where fx is the elevation difference from east to west in the quadrat and fy is the elevation difference from north to south.

To estimate the relative importance of ecological processes on phylogenetic and functional beta diversity at different spatial scales, we divided the full plot into square quadrats with different sizes: 20 m × 20 m ($n = 500$), 50 m × 50 m ($n = 80$) and 100 m × 100 m ($n = 20$). We indicated the plot layout of the 20-ha Xishuangbanna FDP (Fig. 1).

Trait selection and measurement

We collected vegetation samples in the plot to get trait data for the tree species (Cornelissen *et al.* 2003). Eleven functional traits were selected that are expected to reflect the trade-offs in the function of leaves, wood and seeds of the trees (Westoby 1998; Westoby *et al.* 2002). We measured leaf area (cm^2), specific leaf area (SLA, $cm^2\ g^{-1}$), leaf chlorophyll content ($g\ cm^{-1}$), leaf thickness (mm), water content of the leaf, leaf mass, leaf weight, wood resistance ($g\ cm^{-3}$), maximum tree height (m), seed dry mass (g) and maximum

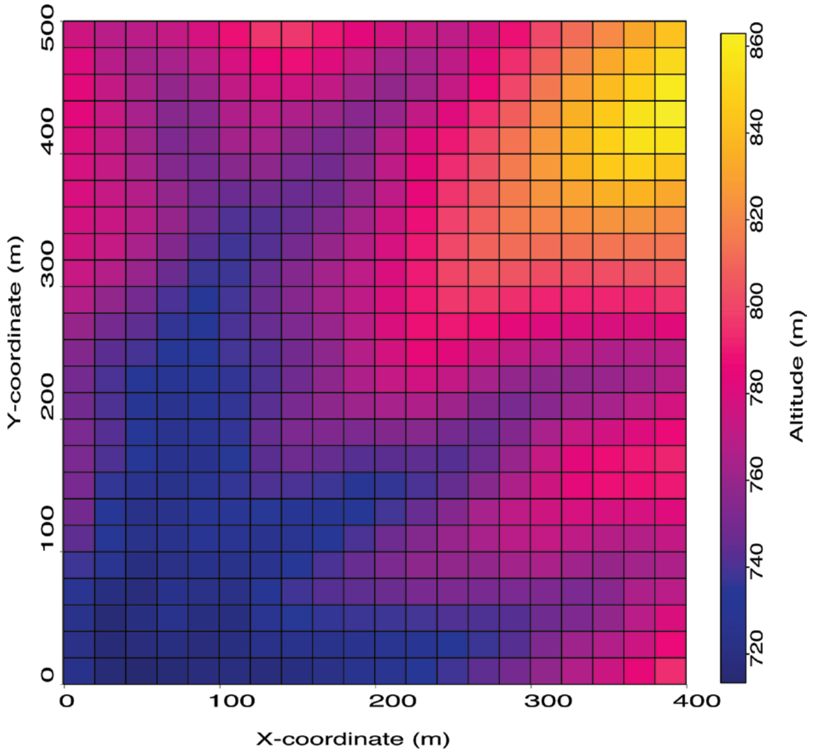

Figure 1: plot layout of the 20-ha Xishuangbanna FDP. The 20-ha plot was divided into 500 20 × 20 m square quadrats (each square is 20 m × 20 m). All trees in each quadrat were recorded. Soil and topographical variables were measured in each quadrat as described above.

tree diameter at breast height (cm). For leaf traits measurement, we selected adult trees with a height of ten meters for the collection of sun-exposed outer canopy matured leaves. However, for those species less than 10 m tall, shade-tolerance was assumed and shade leaves were collected.

We collected at least three leaves with no large cover of epiphylls from each of five individuals of each species belonging to 428 taxa. The collected leaves were checked for any apparent symptoms of pathogen and herbivore attack (Cornelissen *et al.* 2003). We measured wood-specific resistance using Resistograph (Isik and Li 2003) on the five largest individuals for each of the 428 taxa. For those species that do not reach 10 m in height, we used main branch material. Using traits from adult trees alone could limit the effort to disentangle the driving forces for community structure, given that traits could vary across life stages of a species (Spasojevic *et al.* 2014). However, this variation is expected to be small (Wright *et al.* 2010), and adult traits better reflect the variation of species in evolutionary history, functional strategies and demographic structure among the species. Therefore, we took adult traits as representative across life stages, and used the mean trait values of each species for analysis. Based on the covariance matrix of species mean trait values (log-transformed), we constructed a trait dendrogram using hierarchical clustering of the Unweighted Pair Group Method, and used this to compute a distance matrix between species.

Phylogenetic tree reconstruction

A phylogenetic tree was reconstructed for 428 species using the commonly used DNA barcode markers: - *rbcL, matK and trnH-psbA* which were derived from the chloroplast genomic material. In addition, the nuclear ribosomal internal transcribed spacer (ITS) has also been used to generate a DNA supermatrix (Kress *et al.* 2009). According to Kress *et al.* (2010), a global multiple sequence alignment was implemented for the *rbcL* and *matK* DNA markers whereas, for the *trnH-psbA* and *ITS* markers, due to high rate variation of sequences, SATé was utilized for the family-based alignment (Liu *et al.* 2012). The DNA supermatrix was then created by concatenated all the aforementioned alignments. The maximum likelihood (ML) analysis was carried out using RA x ML software to analyze the DNA supermatrix (Stamatakis 2006) for the best search of phylogenetic tree using the APG III phylogenetic tree as a guide tree which enables to fix the deep evolutionary relationship of species (Kress *et al.* 2010). Bootstrap analysis was undertaken in order to estimate node support for which 50% cutoff was taken. Nodes with less than 50% support being collapsed into soft polytomies. We ultimately applied the non-parametric rate smoothing method in *r8s* software package to produce ultrametric phylogenetic tree (Sanderson 2003).

Tree DBH-size

In order to make inferences about the importance of tree life stages for species distributions, we made comparisons between trees at different stem sizes. Based on the diameter size distribution of stems, we divided stem diameters into three size classes: low, medium and high DBH, used to represent different life stages (Bagchi *et al.* 2011). We used one-third quantiles of the DBH-size of stems for each species to make sure that a sufficient number of stems was included in each of the three DBH-size classes, and species composition and abundances in each size class were nearly equivalent. For each of the DBH-size classes, species with abundances of at least 30 individuals were included in the point process models (described below), and as a result a total of 144 tree species were included in our analysis (see online supplementary Appendix A2). We also combined the DBH-size classes together (labeled as ‘all DBH-size class’) to explore the effect of ecological mechanisms without categorizing trees into different stem sizes.

Spatial point process models

We used a spatial point pattern approach based on the exact location of trees (Illian *et al.* 2008; Wiegand and Moloney 2014) to test the relative importance of different ecological processes for phylogenetic and functional beta diversity. We used four point process models: the Homogeneous Poisson process, Inhomogeneous Poisson process, Homogeneous Thomas process, and Inhomogeneous Thomas process (Detailed explanations are given for each spatial point process model in the supporting information; online supplementary Appendix A1). These were used as null models to estimate the role of random effect, environmental filtering, dispersal limitation and joint-effect of dispersal limitation and environmental filtering, respectively on the species area curve (Shen *et al.* 2009). We separately fitted these point process models to the observed distribution pattern of each species, and generated a realization of the fitted model for each species in each DBH-size class. Finally, we independently superimposed the generated patterns of all species to produce one null community in each DBH-size class. Each of the models was used to generate 100 null communities for each DBH-size class. We then calculated the average phylogenetic and functional beta diversity across the null communities, and compared it to the observed phylogenetic and functional beta diversity. The simulation process and computation of phylogenetic and functional beta diversity is illustrated in Fig. 2.

We estimated the parameters of the four process models for each species based on the method of Waagepetersen and Guan (2009). The maximum likelihood method was applied for estimation of the intensity function $\lambda(s)$ using environmental variables for inhomogeneous Poisson process model. The minimum contrast method was used to estimate dispersal-related parameters for the Thomas models.

Goodness of fit of the models

To evaluate the performance of the null models, we used two methods.

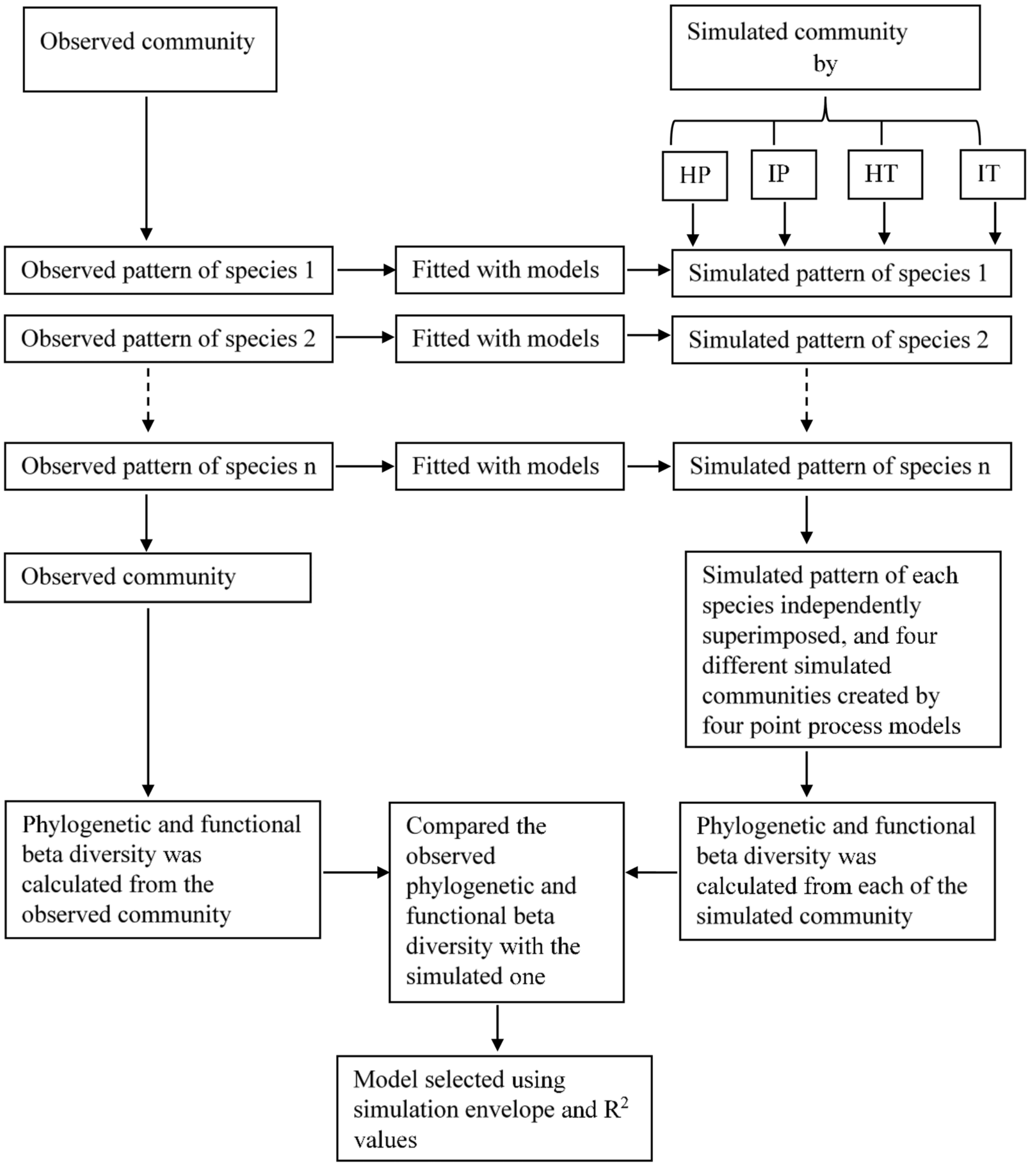

Figure 2: a diagram illustrating the simulation process by the four point process models and the respective analysis of phylogenetic and functional beta diversity. HP = Homogeneous Poisson process model; HT = Homogeneous Thomas process model; IP = Inhomogeneous Poisson process model; IT = Inhomogeneous Thomas process model.

Firstly, we constructed the 95% simulation envelope for each model, and if the observed phylogenetic and functional beta diversity values fell within the 95% simulation envelope the model was considered adequate, and otherwise rejected (Wang *et al.* 2011; Wiegand and Moloney 2014). Secondly, we identified the best-fit model using the R-squared statistic which is used to explain the contribution of each model for phylogenetic and functional beta diversity.

$$R^2 = 1 - SSE / SST,$$

where

$$SSE = \sum_r [D_{obs}(r) - D_{pre}(r)]^2,$$

and

$$SST = \sum_r [D_{obs}(r) - mean(D_{obs})]^2.$$

$D_{pre}(r)$ is the predicted phylogenetic or functional beta diversity value, $D_{obs}(r)$ is the observed phylogenetic or functional beta diversity value and $mean(D_{obs})$ is the mean value of the observed phylogenetic or functional value over all the distances analyzed (Wang *et al.* 2015).

Analyzing phylogenetic and functional beta diversity

We analyzed the phylogenetic and functional beta diversity for the observed and each simulated null community for each

DBH-size class across spatial scales. We log-transformed the functional trait data and constructed a Euclidean trait distance matrix. A trait dendrogram which is a representation of traits similarity among taxa (Swenson *et al.* 2011), was then constructed from this matrix using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) hierarchical clustering method (Swenson 2014).

We used two metrics (the mean pairwise (D_{pw}') and the mean nearest neighbor (D_{nn}') phylogenetic or trait distance) to compute the phylogenetic and functional beta diversity between subplots on the basis of abundance-weighted data from the molecular phylogenetic tree and trait dendrogram in the Xishuangbanna FDP (Rao 1982; Ricotta and Burrascano 2008). D_{pw}' and D_{nn}', respectively are the 'basal' and 'terminal' metrics of phylogenetic and/or trait beta diversity (Swenson 2011):

$$D_{pw}' = \frac{\sum_{i=1}^{n_{k_1}} f_i \bar{\delta}_{ik_2} + \sum_{j=1}^{n_{k_2}} f_j \bar{\delta}_{jk_1}}{2} \qquad (2)$$

$$D_{nn}' = \frac{\sum_{i=1}^{n_{k_1}} f_i \min \delta_{ik_2} + \sum_{j=1}^{n_{k_2}} f_j \min \delta_{jk_1}}{2} \qquad (3)$$

where $\bar{\delta}_{ik_2}$ is the mean pairwise phylogenetic or trait distance between species i in community k_1 to all species in community k_2; and $\bar{\delta}_{jk_1}$ is the mean pairwise phylogenetic or trait distance between species j in community k_2 to all species in community k_1; $\min \delta_{ik_2}$ is the nearest neighbor phylogenetic or trait distance between species i in community k_1 to all species in community k_2; and $\min \delta_{jk_1}$ is the nearest neighbor phylogenetic or trait distance between species j in community k_2 to all species in community k_1; and f_i and f_j are the relative abundance of species i in community k_1 and species j in community k_2 (Yang *et al.* 2015). We conducted the analyses using the 'ecodist' (Goslee and Urban 2007), 'vegan' (Oksanen *et al.* 2016) and 'picante' (Kembel *et al.* 2010) packages in R software.

Since phylogenetic and functional beta diversity measures are different in their sensitivity to the depth of phylogenetic and dendrogram turnover (Swenson 2011), we used both the pairwise and nearest neighbor distance metrics. The pairwise metric computes the phylogenetic and functional distances between each pair of species in the two communities from all levels of the phylogenetic tree and dendrogram (Swenson 2014; Webb *et al.* 2008). Therefore, it provides an overall picture of the phylogenetic and functional turnover at all levels of the phylogeny and dendrogram. The nearest neighbor metric however, calculates the phylogenetic and functional distance from each species to its closest relatives in the communities between plots, and each community is largely composed of the same phylogenetic components (Swenson 2011; Webb *et al.* 2008). It ignores the distances of the species from the deep basal part of the phylogeny, and so is ideal for detecting subtle turnover in composition between communities of each plot that may not be detected with pairwise metrics, and thus provides information on the turnover of species at the tip level of the phylogenetic tree/dendrogram (Swenson *et al.* 2012). We compared the phylogenetic and functional beta diversity of all plots with other plots for each spatial scale considered (20 m × 20 m, 50 m × 50 m and 100 m × 100 m).

RESULTS

Phylogenetic beta diversity

We used a spatial point pattern based approach to explore the importance of different ecological mechanisms for phylogenetic and functional turnover in a tropical forest. We found that the random point process model (representing random distribution) produced a poor approximation to the observed phylogenetic beta diversity across all DBH-size classes and spatial scales (Figs 3 and 4). Interestingly, we found that the performance of point process models depended strongly on the metric of measurement used to estimate phylogenetic and functional beta diversity. The inhomogeneous Poisson process model (representing environmental filtering) produced good predictions of mean pairwise phylogenetic beta diversity (Fig. 3), but the homogeneous Thomas model (representing dispersal limitation) performed better for nearest neighbor phylogenetic beta-diversity patterns for the early life stage (Fig. 4). We also found that the inhomogeneous Thomas process (dispersal + environment) performed well in reproducing the nearest neighbor phylogenetic beta diversity for later life stages. Our results in general show that the dissimilarity of observed communities increased with distance, as expected.

Functional beta diversity

The random point process model (random effect) was also found to give the poorest fit to functional beta diversity across all DBH-size classes and spatial scales (Figs 5 and 6). Once again, the inhomogeneous Poisson (representing for environmental filtering) and the homogeneous Thomas process (representing for dispersal limitation) models better reproduced the mean pairwise and nearest neighbor functional beta diversity, respectively (Figs 5 and 6). Moreover, the inhomogeneous Thomas process model (dispersal + environment) also provided good predictions of the nearest neighbor functional turnover of species.

Life stage and spatial scale

Varying the DBH-size class under analysis for nearest neighbor phylogenetic and functional beta diversity produced differences in the relative ranking of point process models. Dispersal limitation primarily structured the lower-DBH size class, while dispersal and environment jointly structured the remaining life stages across spatial scales (Figs 4 and 6; Tables 1 and 2). However, this mixed role of ecological mechanisms across life stages was not observed for pairwise phylogenetic and functional beta diversity, where the inhomogeneous Poisson process (representing environmental filtering) remained most successful in filtering the phylogenetic and functional beta

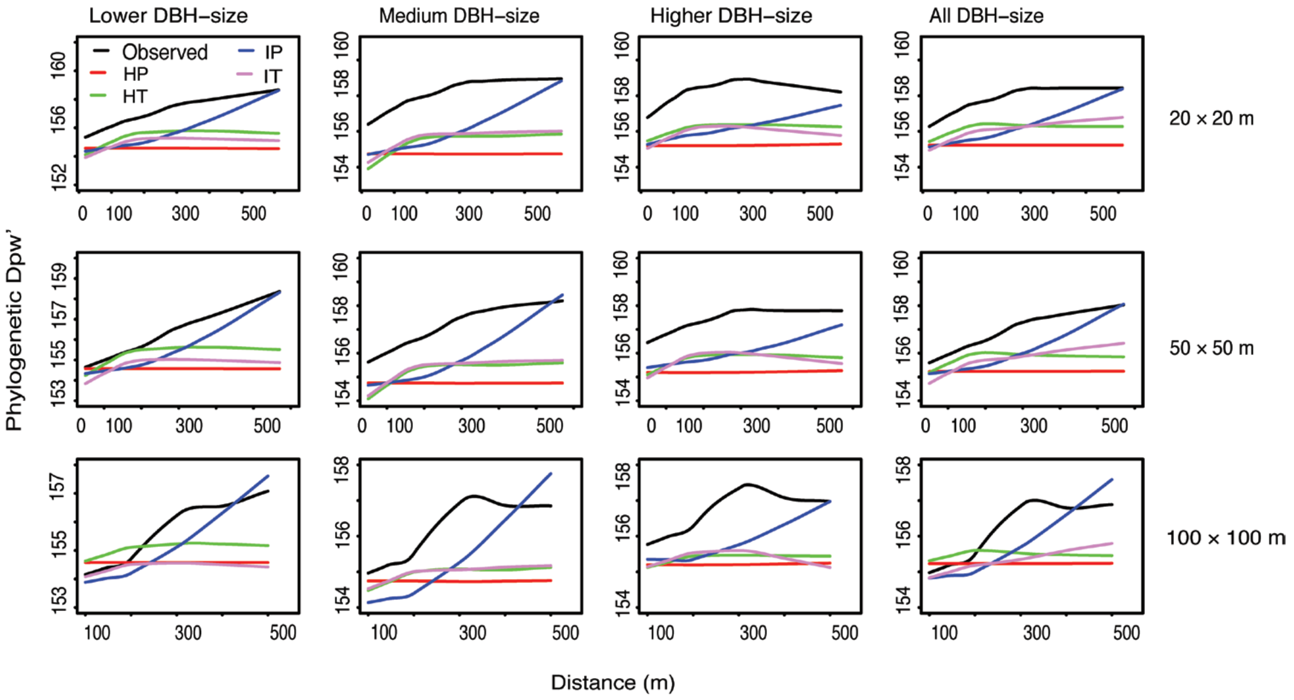

Figure 3: plots of the observed and simulated pairwise phylogenetic beta diversity across DBH-size classes at different spatial scales in Xishuangbanna FDP. HP, HT, IP and IT represent Homogeneous Poisson model, Homogeneous Thomas model, Inhomogeneous Poisson model and Inhomogeneous Thomas model, respectively.

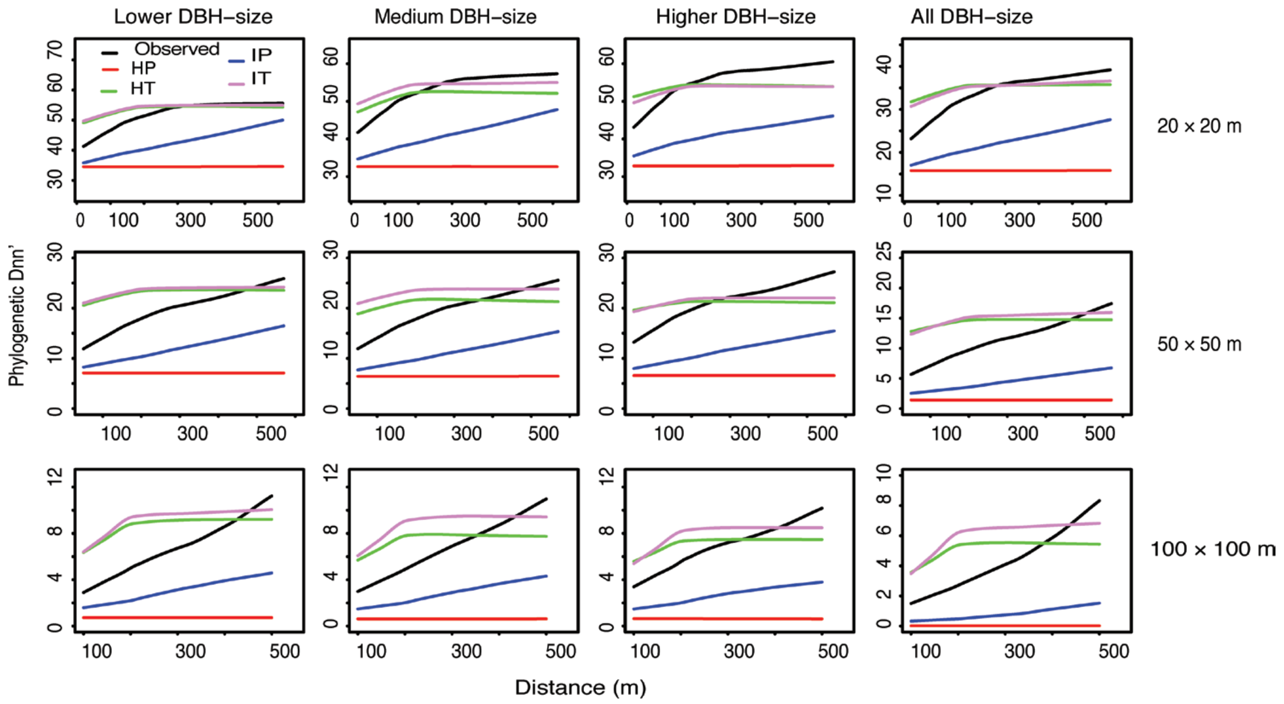

Figure 4: plots of the observed and simulated nearest neighbor phylogenetic beta diversity across DBH-size classes at different spatial scales in Xishuangbanna FDP. HP, HT, IP and IT represent Homogeneous Poisson model, Homogeneous Thomas model, Inhomogeneous Poisson model and Inhomogeneous Thomas model, respectively.

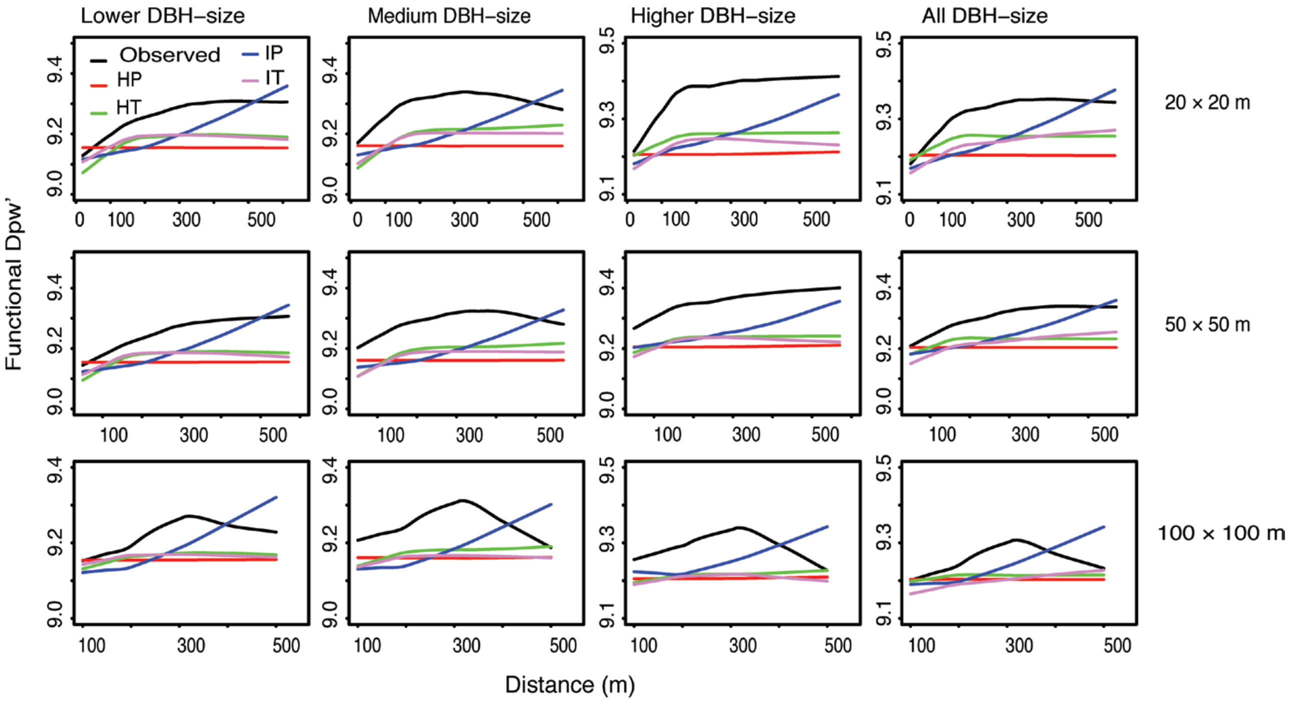

Figure 5: plots of the observed and simulated pairwise functional beta diversity across DBH-size classes at different spatial scales in Xishuangbanna FDP. HP, HT, IP and IT represent Homogeneous Poisson model, Homogeneous Thomas model, Inhomogeneous Poisson model and Inhomogeneous Thomas model, respectively.

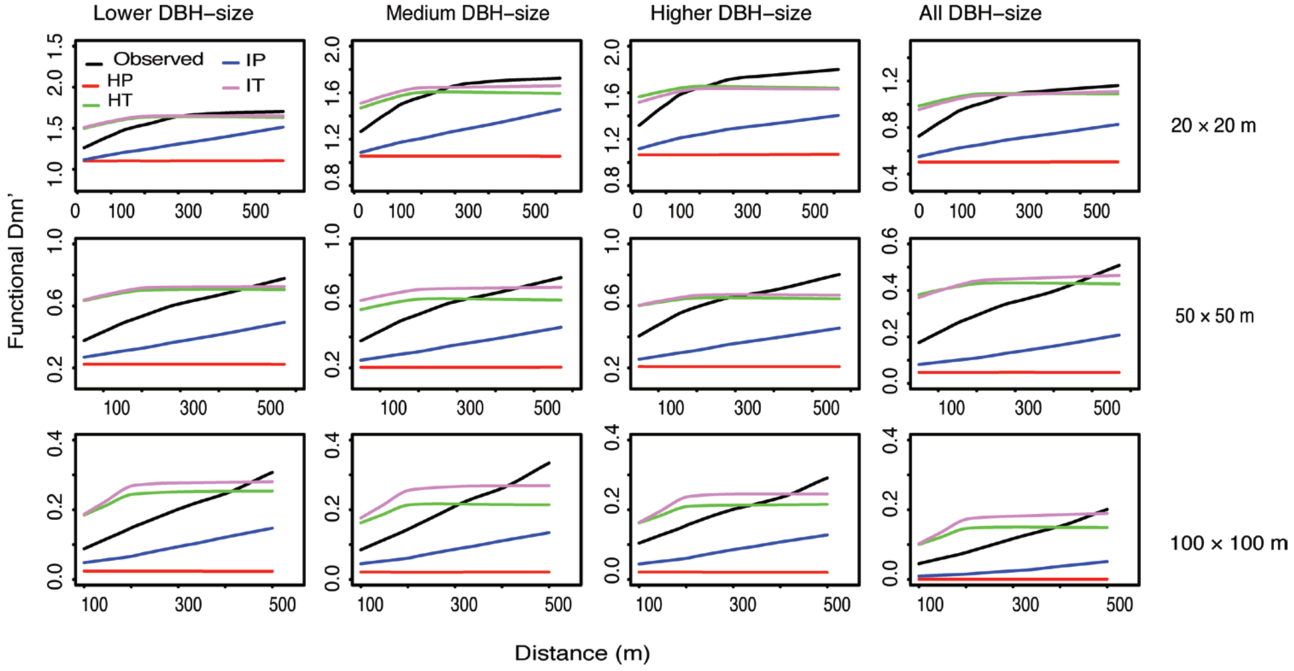

Figure 6: plots of the observed and simulated nearest neighbor functional beta diversity across DBH-size classes at different spatial scales in Xishuangbanna FDP. HP, HT, IP and IT represent Homogeneous Poisson model, Homogeneous Thomas model, Inhomogeneous Poisson model and Inhomogeneous Thomas model, respectively.

Table 1: the proportion of variation (R^2) explained by the point process models for phylogenetic beta diversity at different spatial scales for each DBH-size class in Xishuangbanna FDP

	Spatial scale (m^2)	DBH-size class	HP	HT	IP	IT
Pairwise phylogenetic beta diversity	20 × 20	Lower	0.001	0.004	0.450	0.003
		Medium	0.001	0.002	0.471	0.006
		Higher	0.003	0.014	0.516	0.001
		All	0.0006	0.0003	0.543	0.002
	50 × 50	Lower	0.004	0.004	0.593	0.012
		Medium	0.005	0.006	0.595	0.0062
		Higher	0.042	0.043	0.627	0.0009
		All	0.003	0.001	0.625	0.011
	100 × 100	Lower	0.036	0.017	0.626	0.0005
		Medium	0.210	0.032	0.616	0.0002
		Higher	0.036	0.095	0.595	0.025
		All	0.026	0.030	0.617	0.005
Nearest neighbor phylogenetic beta diversity	20 × 20	Lower	0.0001	0.034	0.006	0.026
		Medium	0.0001	0.021	0.005	0.037
		Higher	0.0002	0.024	0.004	0.023
		All	0.0002	0.035	0.007	0.039
	50 × 50	Lower	0.001	0.084	0.012	0.066
		Medium	0.0001	0.064	0.011	0.065
		Higher	0.0001	0.048	0.012	0.057
		All	0.0007	0.048	0.012	0.054
	100 × 100	Lower	0.017	0.114	0.018	0.109
		Medium	0.0001	0.081	0.017	0.108
		Higher	0.006	0.082	0.018	0.093
		All	0.0004	0.078	0.018	0.076

HP, HT, IP and IT represent Homogeneous Poisson model, Homogeneous Thomas model, Inhomogeneous Poisson model and Inhomogeneous Thomas model, respectively.

diversity expressed as mean pairwise-distance at all spatial scales. Varying the spatial scale of analysis for both pairwise and nearest neighbor phylogenetic and functional beta diversity in general did not produce substantial differences in the relative ranking of point process models suggesting that the role of underlying ecological processes in structuring phylogenetic and functional patterns is more or less consistent across spatial scales, in contrast to our expectation.

DISCUSSION

Phylogenetic and functional beta diversity

We found that the observed phylogenetic and functional beta diversities were strongly non-random, with turnover being more rapid across space than expected by chance (as previously found by, e.g. Yang *et al.* (2015) in the same tropical forest). The random placement model was found to be poor in predicting the phylogenetic and functional turnover as the observed pattern is out of the confidence interval (online supplementary Figs S2–S13). However, such non-random patterns are known to be generated by both deterministic and stochastic forces in tropical forests (Fine and Kembel 2011; Swenson *et al.* 2011). Interestingly, the underlying ecological processes identified as most likely to produce observed phylogenetic and functional turnover were found to depend on the metric of measurement used. Generally, environmental filtering was found to be responsible for pairwise phylogenetic and functional turnover of the community, whereas dispersal limitation alone, and in combination with environmental filtering was found to be responsible for the nearest neighbor phylogenetic and functional turnover.

The role of different ecological processes in structuring phylogenetic and functional turnover is supported by some previous studies. For instance, in tropical tree communities in Panama, Zhang *et al.* (2013) reported that environmental distance determined mean pairwise phylogenetic beta diversity, while geographical distance, which relates to dispersal limitation, influenced the mean nearest neighbor phylogenetic dissimilarity between plots. However, Baldeck *et al.* (2016) showed that the effect of environmental filtering was stronger than dispersal limitation on nearest neighbor phylogenetic beta diversity across eight tropical forest communities, albeit in the context of phylogenetic clustering that is not present in our study plot (Yang *et al.* 2014). Furthermore, Yang *et al.* (2015) found that deterministic-based habitat filtering was the primary process structuring both pairwise and

Table 2: the proportion of variation (R^2) explained by the point process models for functional beta diversity at different spatial scales for each DBH-size class in Xishuangbanna FDP

	Spatial scale (m^2)	DBH-size class	HP	HT	IP	IT
Pairwise functional beta diversity	20 × 20	Lower	0.001	0.006	0.266	0.005
		Medium	0.004	0.0005	0.261	0.0002
		Higher	0.0006	0.010	0.349	0.004
		All	0.0008	0.0001	0.355	0.004
	50 × 50	Lower	0.007	0.008	0.407	0.011
		Medium	0.008	0.0005	0.431	0.004
		Higher	0.014	0.026	0.492	0.001
		All	0.0001	0.0001	0.459	0.003
	100 × 100	Lower	0.005	0.01	0.425	0.0007
		Medium	0.104	0.001	0.458	0.076
		Higher	0.015	0.002	0.481	0.006
		All	0.020	0.018	0.445	0.002
Nearest neighbor functional beta diversity	20 × 20	Lower	0.0007	0.037	0.007	0.023
		Medium	0.0009	0.022	0.006	0.042
		Higher	0.0001	0.029	0.004	0.032
		All	0.0004	0.034	0.006	0.042
	50 × 50	Lower	0.005	0.070	0.010	0.059
		Medium	0.0001	0.066	0.010	0.075
		Higher	0.002	0.062	0.009	0.061
		All	0.0001	0.047	0.010	0.060
	100 × 100	Lower	0.003	0.086	0.020	0.114
		Medium	0.005	0.092	0.017	0.134
		Higher	0.022	0.079	0.018	0.075
		All	0.006	0.073	0.019	0.076

HP, HT, IP and IT represent Homogeneous Poisson model, Homogeneous Thomas model, Inhomogeneous Poisson model, and Inhomogeneous Thomas model, respectively.

nearest neighbor phylogenetic and functional beta-diversity in a tropical tree community.

Interestingly, a similar picture emerges from studies outside the tropics. Space (dispersal) and environment were identified as the strongest drivers respectively for terminal and basal turnover of the phylogeny in the Rocky Mountain National Park in Colorado (Jin *et al.* 2015). Environmental filtering was found to affect both the pairwise and nearest neighbor phylogenetic turnover of plants in the Western Swiss Alps (Ndiribe *et al.* 2014) and Southwest Australia (Sander and Wardell-Johnson 2011). In addition to the deterministic functional turnover of plants in North America (Siefert *et al.* 2013), environmental filtering was detected in driving the functional turnover of species in the Mediterranean rangeland (Bernard-Verdier *et al.* 2013).

These apparent contradictions may be explicable by the distinct and partially fluid relationships between phylogeny, functional traits and habitat requirements. The weak effect of environmental filtering that we found on species turnover from the tip phylogeny possibly reflects the wide ecological spectrum of closely related species. Similarly, a recent study in the same plot as ours also reported that the habitat preference of trees was not influenced by evolutionary distance (Zhang *et al.* 2017) suggesting that closely related species could have different functional strategies.

Our findings clearly demonstrate the sensitivity of phylogenetic and functional beta diversity measures to the depth of phylogenetic tree and dendrogram. The mean pairwise phylogenetic/functional beta diversity is sensitive to all levels of the phylogeny and provides an overview of the phylogenetic/functional relationships between communities. In this case, our results suggest that environmental filtering drives phylogenetic and functional turnover among distantly related species. This indicates the influence of evolutionary divergence along environmental axes among distantly related species in regulating their distributions (partially consistent with the findings of Asefa *et al.* (2017) in the same study plot). The mean nearest neighbor phylogenetic/functional beta diversity on the other hand, is sensitive to turnover among recently diverged lineages. In contrast to Qian *et al.* (2013), we found that dispersal limitation alone, and jointly with environment shaped the turnover between closely related species. Consistently, in our study plot, Zhang *et al.* (2017) also found that closely related species did not occupy similar environmental niches suggesting that their structure in space is mainly driven by some other forces, such as dispersal processes.

Life stage and spatial scale

Life stage is considered a very important factor affecting the role of driving mechanisms on tree distributions (Spasojevic *et al.* 2014; Swenson *et al.* 2007). Consistently, we found evidence that the relative importance of ecological processes changes with life stages of trees for nearest neighbor phylogenetic and functional beta diversity, as expected. Dispersal limitation appeared to structure the early life stage (Lower DBH-size), whereas dispersal limitation and environment jointly structured the remaining life stages (Medium and higher DBH-size classes) across spatial scales (Tables 1 and 2). In contrast to this, Wang *et al.* (2015) indicated that the relative importance of ecological processes remained the same across life stages in temperate forests.

However, the relative importance of ecological processes did not change with life stages and spatial scales for phylogenetic and functional beta diversity expressed as a mean pairwise distance. Instead, we found that environmental filtering mainly structured the phylogenetic and functional turnover across life stages and spatial scales, in clear contrast to our expectations. This is consistent with Swenson *et al.*'s (2012) finding that the functional turnover of species expressed as mean pairwise values was strongly influenced by a deterministic abiotic filtering across spatial scales in a tropical forest. Similarly, Yang *et al.* (2015) also reported environmental filtering as the main structuring mechanism for pairwise phylogenetic and functional beta diversity across spatial scales in a tropical forest in southwest China. It is also found to be responsible for the nearest neighbor phylogenetic and functional turnover in their study, which is not true in our case. We found that the relative importance of underlying processes did not change across spatial scales, which is in contrast to Wang *et al.* (2015), who reported that dispersal and environmental effects operate at small and large spatial scales respectively on the structure of phylogenetic and functional dissimilarity of trees in temperate forests.

Although the relative importance of underlying mechanisms did not change with spatial scales, their absolute importance did seem to increase with spatial scale, as indicated by the magnitude of variation explained (Tables 1 and 2). The ability of environmental filtering to structure the mean pairwise functional beta-diversity consistently increased from small to large spatial scales for almost all of the DBH-size classes (Table 2). Similarly, the influence of environmental filtering on pairwise phylogenetic turnover increased from small to intermediate scales for all life stages, and slightly decreased from intermediate to large spatial scales for higher and all DBH-size classes (Table 1). Similar reports have been made that the predictive performance of environmental filtering increased from small to large scales to structure phylogenetic and functional turnover in temperate forests (Wang *et al.* 2015) and tropical forest (Yang *et al.* 2015). We found, however, that dispersal limitation alone, and jointly with environmental filtering showed inconsistent predictive performance across spatial scales for phylogenetic and functional turnover expressed as nearest neighbor values, despite being the dominant process.

To conclude, the present study revealed that the turnover of tree communities is phylogenetically and functionally nonrandom, being structured by both environmental filtering and dispersal limitation. Interestingly, the relative importance of these ecological forces was found to depend upon the metrics used to compute phylogenetic and functional beta diversity. Environmental filtering appears to structure pairwise phylogenetic and functional turnover, whereas dispersal limitation alone, and in combination with environmental filtering, determined the nearest neighbor phylogenetic and functional beta diversity. This suggests the use of different metrics of measurement that are able to detect distinct facets of the phylogenetic and functional structure of plant communities. The relative importance of ecological processes changed with life stages for nearest neighbor (but not for pairwise) phylogenetic and functional turnover: dispersal alone, and jointly with environment, was found to structure early and later life stages respectively. Unexpectedly, varying the spatial scale under analysis did not alter the ranking of point process models applied here, suggesting that the role of underlying processes in assembling the phylogenetic and functional distribution of plants is consistent across spatial scales.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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REFERENCES

Asefa M, Cao M, Zhang G, *et al.* (2017) Environmental filtering structures tree functional traits combination and lineages across space in tropical tree assemblages. *Sci Rep* **7**:132.

Bagchi R, Henrys PA, Brown PE, *et al.* (2011) Spatial patterns reveal negative density dependence and habitat associations in tropical trees. *Ecology* **92**:1723–9.

Baldeck CA, Kembel SW, Harms KE, *et al.* (2016) Phylogenetic turnover along local environmental gradients in tropical forest communities. *Oecologia* **182**:547–57.

Bernard-Verdier M, Flores O, Navas ML, *et al.* (2013) Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. *J Veg Sci* **24**:877–89.

Brown C, Burslem DF, Illian JB, *et al.* (2013) Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proc Biol Sci* **280**:20130502.

Brown C, Illian JB, Burslem DFRP (2016) Success of spatial statistics in determining underlying process in simulated plant communities. *J Ecol* **104**:160–72.

Cao M, Zou X, Warren M, *et al.* (2006) Tropical forests of Xishuangbanna, China. *Biotropica* **38**:306–9.

Cavender-Bares J, Keen A, Miles B (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* **87**:S109–22.

Condit R (1998) Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. TX, USA: Springer-Verlag Berlin Heidelberg and R.G. Landes Georgetown.

Condit R, Pitman N, Leigh EG Jr, *et al.* (2002) Beta-diversity in tropical forest trees. *Science* **295**:666–9.

Cornelissen J, Lavorel S, Garnier E, *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust J Bot* **51**:335–80.

De Cáceres M, Legendre P, Valencia R, *et al.* (2012) The variation of tree beta diversity across a global network of forest plots. *Global Ecol Biogeogr* **21**:1191–02.

Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol Evol* **23**:619–30.

Fine PVA, Kembel SW (2011) Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. *Ecography* **34**:552–65.

Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. *J Stat Softw* **22**:1–19.

Harms K, Condit R, Hubbell SP, *et al.* (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *J Ecol* **89**:947–59.

Hu Y, Sha L, Blanchet F, *et al.* (2012) Dominant species and dispersal limitation regulate tree species distributions in a 20-ha plot in Xishuangbanna, southwest China. *Oikos* **123**:952–60.

Illian J, Penttinen A, Stoyan H, *et al.* (2008) *Statistical Analysis and Modeling of Spatial Point Patterns*. Chichester, UK: John Wiley & Sons.

Isik F, Li B (2003) Rapid assessment of wood density of live tree using the Resistograph for selection in tree improvement programs. *Can J For Res* **33**:2426–35.

Jin LS, Cadotte MW, Fortin MJ (2015) Phylogenetic turnover patterns consistent with niche conservatism in montane plant species. *J Ecol* **103**:742–9.

John R, Dalling JW, Harms KE, *et al.* (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proc Natl Acad Sci USA* **104**:864–9.

Kembel SW, Cowan PD, Helmus MR, *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**:1463–4.

Kraft N, Ackerly D (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecol Monogr* **80**:401–22.

Kraft NJ, Comita LS, Chase JM, *et al.* (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* **333**:1755–8.

Kress WJ, Erickson DL, Jones FA, *et al.* (2009) Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proc Natl Acad Sci USA* **106**:18621–6.

Kress WJ, Erickson DL, Swenson NG, *et al.* (2010) Advances in the use of DNA barcodes to build a community phylogeny for tropical trees in a Puerto Rican forest dynamics plot. *PLOS ONE* **5**:e15409.

Lan G, Zhu H, Cao M, *et al.* (2009) Spatial dispersion patterns of trees in a tropical rainforest in Xishuangbanna, southwest China. *Ecol Res* **24**:1117–24.

Lasky JR, Bachelot B, Muscarella R, *et al.* (2015) Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology* **96**:2157–69.

Law R, Illian J, Burslem DFRP, *et al.* (2009) Ecological information from spatial patterns of plants: insights from point process theory. *J Ecol* **97**:616–28.

Legendre P, Borcard D, Peres-neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* **75**:435–50.

Liu K, Warnow TJ, Holder MT, *et al.* (2012) SATe-II: very fast and accurate simultaneous estimation of multiple sequence alignments and phylogenetic trees. *Syst Biol* **61**:90–106.

May F, Huth A, Wiegand T (2015) Moving beyond abundance distributions: neutral theory and spatial patterns in a tropical forest. *Proc R Soc B* **282**:0141657.

McGill BJ, Enquist BJ, Weiher E, *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* **21**:178–85.

Mi X, Swenson NG, Jia Q, *et al.* (2016) Stochastic assembly in a subtropical forest chronosequence: evidence from contrasting changes of species, phylogenetic and functional dissimilarity over succession. *Sci Rep* **6**:32596.

Myers JA, Chase JM, Jiménez I, *et al.* (2013) Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol Lett* **16**:151–7.

Ndiribe C, Pellissier L, Dubuis A, *et al.* (2014) Plant functional and phylogenetic turnover correlate with climate and land use in the Western Swiss Alps. *J Plant Ecol* **7**:439–50.

Oksanen FJ, Blanchet G, Friendly M, *et al.* (2016) *Vegan: Community Ecology Package*. http://CRANR-projectorg/package=vegan (5 January 2018, date last accessed).

Qian H, Swenson NG, Zhang J (2013) Phylogenetic beta diversity of angiosperms in North America. *Global Ecol Biogeogr* **22**:1152–61.

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. *Theor Popul Biol* **21**:24–43.

Ricotta C, Burrascano S (2008) Beta diversity for functional ecology. *Preslia* **80**:61–71.

Sander J, Wardell-Johnson G (2011) Fine-scale patterns of species and phylogenetic turnover in a global biodiversity hotspot: implications for climate change vulnerability. *J Veg Sci* **22**:766–80.

Sanderson MJ (2003) r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* **19**:301–2.

Shen G, Yu M, Hu XS, *et al.* (2009) Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. *Ecology* **90**:3033–41.

Siefert A, Ravenscroft C, Weiser MD, *et al.* (2013) Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. *Global Ecol Biogeogr* **22**:682–91.

Spasojevic MJ, Yablon EA, Oberle B, *et al.* (2014) Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* **5**:129.

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**:2688–90.

Swenson NG (2011) Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PLOS ONE* **6**:e21264.

Swenson NG (2014) *Functional and Phylogenetic Ecology in R.* New York: Springer, 64–75.

Swenson NG, Anglada-Cordero P, Barone JA (2011) Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. *Proc Biol Sci* **278**:877–84.

Swenson NG, Enquist BJ, Pither J, *et al.* (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology* **87**:2418–24.

Swenson NG, Enquist BJ, Thompson J, *et al.* (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* **88**:1770–80.

Swenson NG, Erickson DL, Mi XC, *et al.* (2012) Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology* **93**:S112–25.

Valencia R, Foster RB, Villa G, *et al.* (2004) Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J Ecol* **92**:214–29.

Vamosi SM, Heard SB, Vamosi JC, *et al.* (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol Ecol* **18**:572–92.

Velázquez E, Martínez I, Getzin S, *et al.* (2016) An evaluation of the state of spatial point pattern analysis in ecology. *Ecography* **39**:1–14.

Waagepetersen R, Guan Y (2009) Two-step estimation for inhomogeneous spatial point processes. *J R Stat Soc* **71**:685–702.

Wang X, Wiegand T, Swenson NG, *et al.* (2015) Mechanisms underlying local functional and phylogenetic beta diversity in two temperate forests. *Ecology* **96**:1062–73.

Wang XG, Wiegand T, Wolf A, *et al.* (2011) Spatial patterns of tree species richness in two temperate forests. *J Ecol* **99**:1382–93.

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**:2098–100.

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* **199**:213–27.

Westoby M, Falster DS, Moles AT, *et al.* (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Sys* **33**:125–59.

Wiegand T, Moloney KA (2014) *Handbook of Spatial Point-Pattern Analysis in Ecology*. New York, USA: Taylor & Francis Group, LLC.

Wright SJ, Kitajima K, Kraft NJ, *et al.* (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **91**:3664–74.

Yang J, Swenson NG, Zhang G, *et al.* (2015) Local-scale partitioning of functional and phylogenetic beta diversity in a tropical tree assemblage. *Sci Rep* **5**:12731.

Yang J, Zhang GC, Ci XQ, *et al.* (2014) Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. *Funct Ecol* **28**:520–9.

Yuan Z, Gazol A, Wang X, *et al.* (2011) Scale specific determinants of tree diversity in an old growth temperate forest in China. *Basic Appl Ecol* **12**:488–95.

Zhang JL, Swenson NG, Chen SB, *et al.* (2013) Phylogenetic beta diversity in tropical forests: implications for the roles of geographical and environmental distance. *J Syst Evol* **51**:71–85.

Zhang C, Yang J, Sha L, *et al.* (2017) Lack of phylogenetic signals within environmental niches of tropical tree species across life stages. *Sci Rep* **7**:42007.