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The variation of tree beta diversity across a global network of forest plots

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ABSTRACT

Aims With the aim of understanding why some of the world's forests exhibit higher tree beta diversity values than others, we asked: (1) what is the contribution of environmentally related variation versus pure spatial and local stochastic variation to tree beta diversity assessed at the forest plot scale; (2) at what resolution are these beta-diversity components more apparent; and (3) what determines the variation in tree beta diversity observed across regions/continents?

Location World-wide.

Methods We compiled an unprecedented data set of 10 large-scale stem-mapping forest plots differing in latitude, tree species richness and topographic variability. We assessed the tree beta diversity found *within* each forest plot separately. The non-directional variation in tree species composition among cells of the plot was our measure of beta diversity. We compared the beta diversity of each plot with the value expected under a null model. We also apportioned the beta diversity into four components: pure topographic, spatially structured topographic, pure spatial and unexplained. We used linear mixed models to interpret the variation of beta diversity values across the plots.

Results Total tree beta diversity within a forest plot decreased with increasing cell size, and increased with tree species richness and the amount of topographic variability of the plot. The topography-related component of beta diversity was correlated with the amount of topographic variability but was unrelated to its species richness. The unexplained variation was correlated with the beta diversity expected under the null model and with species richness.

Main conclusions Because different components of beta diversity have different determinants, comparisons of tree beta diversity across regions should quantify not only overall variation in species composition but also its components. Global-scale patterns in tree beta diversity are largely coupled with changes in gamma richness due to the relationship between the latter and the variation generated by local stochastic assembly processes.

Keywords

Beta diversity, community composition, latitudinal gradient, spatial variation, stem-mapping forest plots, tree species richness, variation partitioning.

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INTRODUCTION

The spatial distribution of species assemblages is often described using three components of species diversity: alpha or local diversity, beta diversity and gamma or regional diversity (Whittaker, 1960). Alpha and gamma diversities describe the species composition observed within sampling units, and are differentiated only by the scale (sampling unit size) at which species inventories are conducted (Jurasiński *et al.*, 2009; Whittaker *et al.*, 2001). In contrast, the concept of beta diversity describes the variation in species composition observed when comparing sampling units with one another. There are two main approaches to defining beta diversity (Anderson *et al.*, 2011): *directional turnover* and *non-directional variation*. Studies addressing beta diversity as directional turnover measure the change in community composition from one sampling unit to another along a spatial, temporal or environmental gradient (Nekola & White, 1999; Morlon *et al.*, 2008). In contrast, the non-directional variation approach to beta diversity does not define it in relation to any specific spatial or environmental structure, but as the variation in community structure among a set of sampling units within a given spatial extent (Koleff *et al.*, 2003; Legendre *et al.*, 2005; Anderson *et al.*, 2006). In both cases beta diversity plays a pivotal role in linking local and regional diversity and it captures a fundamental facet of the spatial pattern of species assemblages.

Much macroecological research has focused on the description and analysis of the spatial patterns of alpha/gamma species diversity (e.g. Rosenzweig, 1995; Gaston, 2000; Whittaker *et al.*, 2001; Gotelli *et al.*, 2009). Only recently have efforts been made to describe and compare the amount of beta diversity found in different areas (e.g. van Rensburg *et al.*, 2004; Rodríguez & Arita, 2004; Harborne *et al.*, 2006; Gaston *et al.*, 2007; McKnight *et al.*, 2007; Melo *et al.*, 2009) or measured at different scales (e.g. Normand *et al.*, 2006). A limited number of studies have so far specifically investigated the spatial variation of plant beta diversity at large (regional to global) scales (Scheiner & Rey-Benayas, 1994; Condit *et al.*, 2002; Qian *et al.*, 2005; Qian & Ricklefs, 2007; Lenoir *et al.*, 2010). Using angiosperm floras of states/provinces (sampling units of *c.* 10⁵ km²), Qian *et al.* (2005) found larger rates of similarity decay in eastern Asia compared with eastern North America, along both east–west and north–south directions, and Qian & Ricklefs (2007) reported a latitudinal gradient in beta diversity with lower latitudes exhibiting larger rates of decay compared with higher latitudes. Similarly, Lenoir *et al.* (2010) analysed vegetation plot records (sampling units of < 0.1 ha) and found both higher rates of similarity decay and higher values of non-directional variation in the Alps (southern Europe) than in the Scandes (northern Europe).

Despite these recent efforts to describe and interpret spatial variation in plant beta diversity at the global scale, little is known about the causes of this variation. In addition, the determinants of beta diversity will depend on the scale (i.e. extent and grain) of study (Whittaker *et al.*, 2001). If we restrict our discussion to plant beta diversity assessed at the local (forest plot) scale, several processes can contribute to creating compositional dif-

ferences among local communities, such as environmental filtering, biotic interactions and dispersal limitation. Species composition of local communities will also depend on ecological and evolutionary processes that operate at large spatial scales (regional/continental), such as speciation, extinction or biogeographic dispersal (Whittaker *et al.*, 2001). Although these latter processes are not the main focus of beta-diversity assessments conducted at the local scale, they need to be taken into account when comparing beta-diversity values across regions or continents (Kraft *et al.*, 2011).

In this study we aim at understanding why some forests of the world exhibit higher tree beta-diversity values than others. We ask the following specific questions.

1. What is the contribution of environmentally related variation versus pure spatial and local stochastic variation to tree beta diversity assessed at the scale of the forest plot?
2. At what resolution (i.e. size of sampling unit) are these components of tree beta diversity more apparent?
3. How does tree species richness of the plot affect its beta diversity?
4. What determines the variation in tree beta diversity observed across regions/continents?

To address these questions we compare the tree beta diversity found *within* 10 permanent stem-mapped forest plots that comprise tropical, subtropical and temperate forests distributed world-wide (Table 1, Fig. 1). We divide the surface of each forest plot into cells (i.e. quadrats) of equal size and calculate the tree beta diversity of the plot as the non-directional variation in tree species composition among cells. Because the 10 forest plots are located in regions subjected to different macroclimatic and biogeographic constraints, the plots are drastically different in number of tree species (52 to 1105) and tree density (0.16 to 0.81 individuals/m²) (Table 2). Differences in gamma species richness and the number of individuals per sampling unit may explain differences in beta diversity (Kraft *et al.*, 2011). We therefore compare the tree beta diversity of each forest plot against the beta diversity expected under a null model that assumes random allocation of individuals among plot cells. The difference between the observed and null-model beta diversities should provide evidence of the effect of ecological processes that generate non-random spatial patterns in forest plots. To quantify the spatial variation created by environmental filtering and other ecological processes, we use topographic and spatial descriptors as explanatory variables to partition the total tree beta diversity of each forest plot into four components: pure topographic (i.e. variation fitted by topographic descriptors but not spatial ones), spatially structured topographic (i.e. variation fitted by both spatial and topographic descriptors), pure spatial (i.e. variation fitted by spatial descriptors but not topographic ones) and unexplained (i.e. residual variation). In order to gain insights into the determinants of tree beta diversity and its components, we study the relationship between beta diversity values and three explanatory factors: (1) the tree species richness of the forest plot (a proxy for drivers of diversity acting at spatial scales larger than the forest plot); (2) the altitudinal range spanned in the forest

Table 1 Location, climatic conditions and altitudinal range of the permanent stem-mapping forest plots ordered by latitude.

Forest plot	Coordinates (deg.)		Climate	Rainfall (mm)	Dry season	Temp. (°C)	Alt. range (m)
Yasuní	0.686 S	76.395 W	Tropical	3081	None	21.7–35.0	38
Pasoh	2.982 N	102.313 E	Tropical	1788	Jan.–Feb.	22.7–33.2	25
Korup	5.074 N	8.855 E	Tropical	5272	Dec.–Feb.	22.7–30.6	97
BCI	9.154 N	79.846 W	Tropical	2600	Dec.–Apr.	23.2–31.1	39
Xishuangbanna	21.612 N	101.574 E	Tropical	1493	Nov.–Apr.	21.8	156
Dinghushan	23.156 N	112.511 E	Sub-tropical	1985	Dec.–Jan.	20.9	237
Lienhuachi	23.914 N	120.879 E	Sub-tropical	2285	Oct.–Feb.	14.8–25.2	164
Fushan	24.761 N	121.555 E	Sub-tropical	4271	None	11.8–24.0	121
Gutianshan	29.250 N	118.119 E	Sub-tropical	1964	Oct.–Jan.	15.3	253
Changbaishan	42.383 N	128.083 E	Temperate	700	Oct.–May	2.8	17

Rainfall, mean annual rainfall (mm); dry season, months of dry season; Temp., minimum and maximum average daily temperature or average annual temperature when daily information was not available.

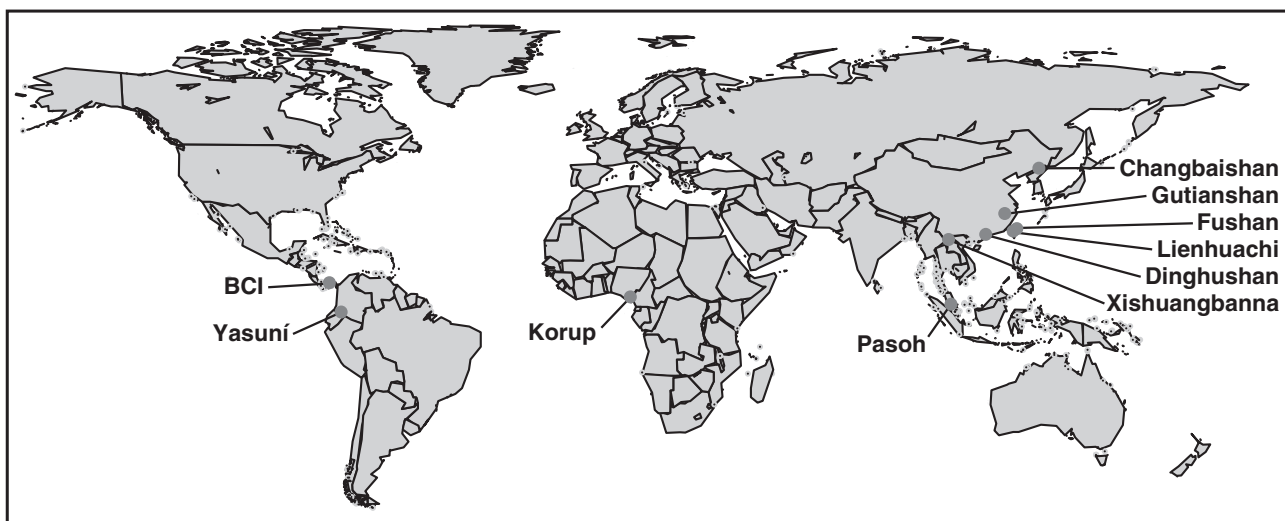


Figure 1 World map showing the locations of the 10 permanent forest plots studied in this paper. Details of the forests can be found in Tables 1 & 2.

plot (a proxy for environmental variation), and (3) the resolution (cell size) used in assessment of beta diversity.

MATERIALS AND METHODS

Stem-mapped forest plots

Over the past three decades, there has been an impressive international research effort coordinated by the Center for Tropical Forest Science (CTFS; <http://www.ctfs.si.edu/>) to assemble long-term, large-scale forest data from the tropics (Condit, 1995). The Chinese Forest Biodiversity Monitoring Network (<http://www.cfbiodiv.org/>) has recently extended the CTFS network by establishing large stem-mapping plots located along a latitudinal gradient from temperate to subtropical and tropical forests. We compare here 10 plots from the two networks, whose main features are summarized in Tables 1 & 2. The Yasuní, Barro Colorado Island, Korup, Pasoh and Xishuangbanna plots are

located within the tropics; the Dinghushan, Lienhuachi, Fushan and Gutianshan forests are considered subtropical, whereas the Changbaishan plot is located in the temperate region (Table 1, Fig. 1). These macro-climatic and geographic differences have an effect on the number of tree species that the forest plots support (Table 2). The 10 forest plots also differ markedly in the amount of internal topographical variation (see Fig. S1 in Supporting Information); the range of altitudes inside plots is very small in some cases (17 m in Changbaishan) and very high in others (237 m in Dinghushan).

Tree data

In all forest plots the census methodology was the same: all trees with diameter at breast height (d.b.h.) ≥ 1 cm were tagged, identified, measured and georeferenced. The years of census used in the present study are shown in Table 2, as well as the number of species and individuals counted. Although tree

Table 2 Size of the stem-mapping forest plots, year of tree census and overall statistics.

Forest plot	Size (m × m)	Year	No. of species	%rare	No. of individuals	Individuals/m ²
Yasuni	500×500	1995	1105	94	152,350	0.61
Pasoh	1000×500	1986	817	89	320,026	0.64
Korup	1000×500	1996	496	90	330,676	0.66
BCI	1000×500	1981–83	307	88	235,771	0.47
Xishuangbanna	400×500	2007	468	93	95,451	0.48
Dinghushan	400×500	2005	210	86	71,617	0.36
Lienhuachi	500×500	2008	145	75	203,313	0.81
Fushan	500×500	2003	109	72	166,589	0.67
Gutianshan	600×400	2005	159	77	140,676	0.59
Changbaishan	500×500	2004	52	75	38,902	0.16

Year, year(s) of the census used in the present study; No. of species, number of species in the whole plot; %rare, percentage of species occurring in fewer than 40% of the 20 m × 20 m plot cells; No. of individuals, number of individuals (stems of identified tree species) in the whole plot; individuals/m², number of individuals with d.b.h. ≥ 1 cm per m² (tree density). The data set version for the Yasuni plot is 2002.

diameters were available, we only used data on the species identity and the spatial location of trees within the plot for our analyses.

Tree counts within plot cells

We divided the surface of each forest plot into a grid of cells (i.e. quadrats). In order to assess the effect of sampling unit size on beta diversity, we considered five different cell sizes: 10 m × 10 m (0.01 ha), 20 m × 20 m (0.04 ha), 25 m × 25 m (0.0625 ha), 50 m × 50 m (0.25 ha) and 100 m × 100 m (1 ha). The number of cells decreased as the cell size increased (see Appendix S1 and Table S1 in Supporting Information). Counting the number of living trees of each species in every cell in the grid we obtained, for each forest plot and cell size, an $n \times p$ (cells-by-species) data table $\mathbf{X} = [x_{ij}]$ where each x_{ij} element contained the number of live individuals of species j in cell i (Fig. 2 (1)).

Hellinger transformation

We chose the Hellinger distance (Legendre & Gallagher, 2001) to measure the dissimilarity in the species composition between plot cells. Instead of directly calculating dissimilarity values between pairs of plot cells, however, we implicitly used the Hellinger distance by transforming each x_{ij} value using the Hellinger transformation (Legendre & Gallagher, 2001; Legendre & Legendre, 2012):

$$y_{ij} = \sqrt{x_{ij} / \sum_{k=1}^p x_{ik}} \quad (1)$$

For each forest plot and cell size, we applied the Hellinger transformation to the cell-by-species data table \mathbf{X} , obtaining a corresponding transformed cell-by-species data table $\mathbf{Y} = [y_{ij}]$ (Fig. 2 (2)). The Hellinger distance is implicitly used with this transformation because the Euclidean distance between

two transformed row vectors (cells) of species composition, \mathbf{y}_i and \mathbf{y}_h , is equal to the Hellinger distance between the original row vectors, \mathbf{x}_i and \mathbf{x}_h (Legendre & Gallagher, 2001).

Beta-diversity measure

Following Legendre *et al.* (2005), we used the total variance in the Hellinger-transformed data table \mathbf{Y} as the measure of tree beta diversity within a forest plot:

$$BD_{\text{Total}} = \text{Var}(\mathbf{Y}) = \text{SS}(\mathbf{Y}) / (n - 1) \quad (2)$$

where the total sum of squares, $\text{SS}(\mathbf{Y})$, is the sum, over all species and all grid cells, of the squared deviations from the species means. $\text{Var}(\mathbf{Y})$ has the advantage that it can also be interpreted in terms of the average dissimilarity between sampling units (Legendre *et al.*, 2005; Anderson *et al.*, 2006). Since the Hellinger distance is bounded between 0 and $\sqrt{2}$, BD_{Total} is bounded between 0 (all cells have identical composition) and 1 (each cell contains a unique set of species). We calculated BD_{Total} for each forest plot at each cell size (Fig. 2 (3)).

Null model of total beta diversity

Following Kraft *et al.* (2011), we used a null model that randomizes the location of trees among cells of the forest plot, while keeping the number and abundance distribution of tree species and the number of individuals per cell constant. We ran 1000 randomizations on the cell-by-species data table \mathbf{X} corresponding to each forest plot and cell size. As before, we applied the Hellinger transformation to each randomized data table \mathbf{X}' and calculated beta diversity as the total variance of the Hellinger-transformed table \mathbf{Y}' (eq. 2; Fig. 2 (4–6)). We then calculated the mean of the distribution of beta diversity values under the null model (BD_{Null}), as well as the difference between BD_{Total} and BD_{Null} (Fig. 2 (7)). This difference (BD_{Diff}) represents how much tree

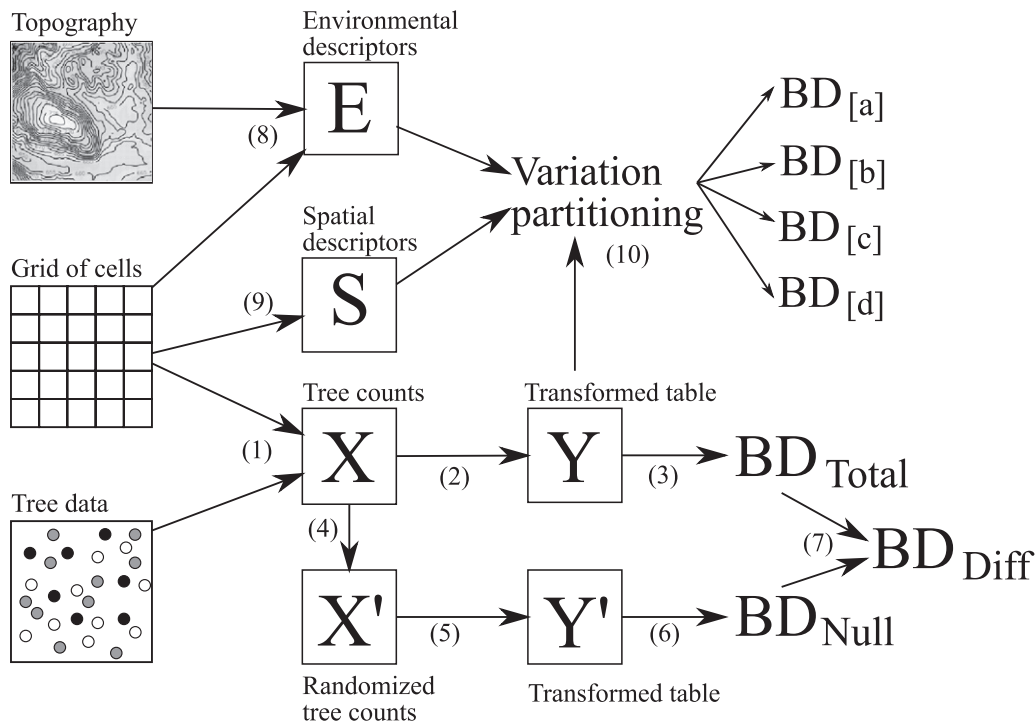


Figure 2 Schematic representation of the beta-diversity analyses conducted for each forest plot and cell size. Numbers in parentheses indicate the analysis steps that are cited in the text. BD_{Total} : total beta diversity; BD_{Null} : beta diversity under the null model; BD_{Diff} : difference between BD_{Total} and BD_{Null} . Beta-diversity components: pure topographic ($BD_{[a]}$, variation fitted by topographic descriptors but not spatial ones), spatially structured topographic ($BD_{[b]}$, variation fitted by both spatial and topographic descriptors), pure spatial ($BD_{[c]}$, variation fitted by spatial descriptors but not topographic ones) and unexplained ($BD_{[d]}$, residual variation).

beta diversity varies with respect to the null model as a consequence of processes that create non-random spatial patterns.

Environmental and spatial descriptors

Topography is not a direct environmental variable, such as light or temperature, but a proxy representing soil moisture and microclimatic conditions. As topographic factors were the only set of explanatory factors available for the 10 stem-mapping forest plots, we used topography as a proxy for the microenvironmental conditions prevailing within plot cells (Legendre *et al.*, 2009). We calculated four topographic attributes for every grid cell – mean elevation, convexity, slope and aspect – and constructed third-degree polynomials with them (details are given in Appendix S1), obtaining a data table E for each forest plot and cell size (Fig. 2 (8)). In order to assess the importance of spatial structuring in ecological communities, spatial relationships must be explicitly introduced into statistical models. Moran eigenvector maps (MEMs) are variables that describe spatial patterns at all scales that can be accommodated in the sampling design (Dray *et al.*, 2006). We generated distance-based MEMs (Borcard & Legendre, 2002) and obtained, for each cell size and forest plot, a data table S containing the variables to be used as spatial predictors (Fig. 2 (9)) (details are given in Appendix S1).

Variation partitioning

Variation partitioning is an extension of partial canonical ordination techniques that models the species composition of sam-

pling units as a function of explanatory factors and then partitions the total variation in community composition into several components (Borcard *et al.*, 1992; Legendre *et al.*, 2005). We conducted variation partitioning, using the Hellinger-transformed species composition table Y as response matrix, and tables E and S tables as explanatory matrices. This allowed us to divide the total tree beta diversity of each forest plot into four components: pure topographic ($BD_{[a]}$, variation fitted by topographic descriptors but not spatial ones), spatially structured topographic ($BD_{[b]}$, variation fitted by both spatial and topographic descriptors), pure spatial ($BD_{[c]}$, variation fitted by spatial descriptors but not topographic ones), and unexplained ($BD_{[d]}$, residual variation) (Fig. 2 (10)). Variation partitioning produces adjusted values of the coefficient of determination (R^2) that contain the relative contribution of each component to the overall variation. Applications of the method usually compare the adjusted R^2 values (Peres-Neto *et al.*, 2006). However, this approach does not allow the comparison of the amounts of variation accounted for by specific beta-diversity components with independence of the remaining components. In order to deal with independent quantities, we calculated the value of each beta-diversity component ω as the product of the corresponding adjusted R^2 value and BD_{Total} :

$$BD_{[\omega]} = BD_{Total} \times R_{Adj[\omega]}^2 \quad (3)$$

where $\omega \in \{a, b, c, d\}$. The beta-diversity component $BD_{[\omega]}$ can be interpreted as the amount (not the proportion) of variation in

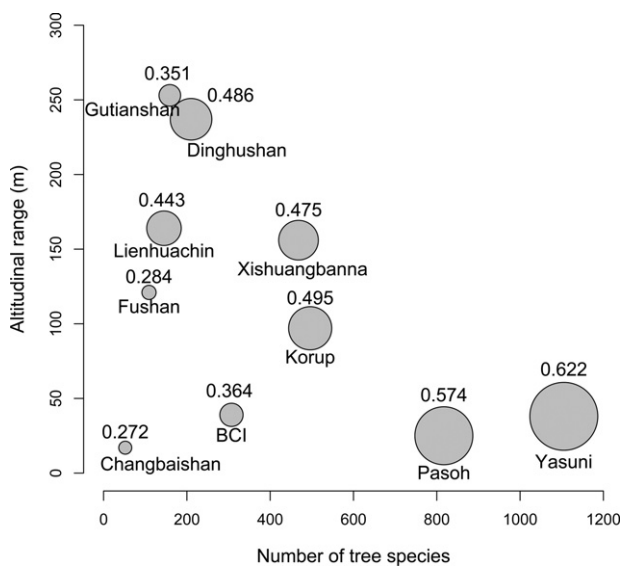


Figure 3 Total tree beta diversity (computed at 20 m × 20 m) in relation to species richness and the altitudinal range of forest plots. Sizes of circles are proportional to the square of the beta-diversity values indicated inside.

species composition that is due to the ecological processes related to ω . Equivalently, it can also be interpreted as the increment (or decrement) in the average dissimilarity among plot cells that is due to the ecological processes related to ω .

Meta-analysis of the results

We determined whether the total number of tree species in the forest plot (i.e. tree species richness), the size of cells and/or the amount of topographic variability, as expressed by the altitudinal range spanned within plot boundaries, could explain the observed variation of beta-diversity values among forests. We regressed beta-diversity values on these three factors by means of linear mixed regression models (Zuur *et al.*, 2009). The number of species and the altitudinal range were used as fixed quantitative factors, whereas the cell size was included as a categorical factor and the forest plot identity was used as a random factor for the intercept. We first modelled the beta-diversity components as well as BD_{Null} and BD_{Diff} . For each response variable we compared the full model and all possible submodels of fixed factors and retained the model with lowest Akaike information criterion (AIC) value. BD_{Total} was also modelled but without model selection.

RESULTS

Total tree beta diversity

There were large differences in total tree beta diversity across forests (Fig. 3). As a result of pooling information from smaller cells to larger cells, the total beta diversity steadily decreased with the increase in cell size in all forests (Fig. 4, Table S1). Compari-

son of total tree beta-diversity values along the latitudinal gradient showed a clear decrease from the tropical to the temperate forests ($r = -0.776$, P -value = 0.0083, $n = 10$) (Fig. S2a in Supporting Information).

Beta diversity under the null model

Beta diversity under the null model (i.e. calculated after permuting trees among plot cells), BD_{Null} , was consistently lower than the observed total beta diversity (Fig. 4, Table S1). In accordance with the results of Kraft *et al.* (2011), BD_{Null} decreased for increasing cell sizes and along the latitudinal gradient ($r = -0.796$, P -value = 0.0058, $n = 10$) (Fig. S2b). In contrast, the difference between observed and expected beta diversity, BD_{Diff} , was often highest for intermediate cell sizes (i.e. between 20 m × 20 m and 50 m × 50 m) (Table S1) and did not show any significant relationship with latitude ($r = 0.278$, P -value = 0.4372, $n = 10$) (Fig. S2c).

Beta-diversity partitioning

Almost all beta diversity fitted by the topographic factors was also explained by the spatial factors. That is, $BD_{[b]}$ accounted for most of $BD_{[a+b]}$, leaving a small fraction of spatially unstructured environmental fit, $BD_{[a]}$ (Table S1). In general plots laid on flat terrains, such as in Changbaishan or BCI (Fig. S1), obtained low values of beta diversity explained by topography, $BD_{[a+b]}$, whereas plots set on mountain slopes or within hilly areas, such as in Gutianshan or Dinghushan (Fig. S1), obtained higher $BD_{[a+b]}$ values. Differences across the forest plots in the amount of beta diversity explained by topography did not appear to form a latitudinal gradient ($r = 0.111$, P -value = 0.7602, $n = 10$) (Fig. S2d). Except for Fushan, all other forests had a maximum $BD_{[a+b]}$ value for intermediate cell sizes (i.e. between 20 m × 20 m and 50 m × 50 m) (Fig. 4). We present a supplementary analysis of the contribution of single topographic factors in Appendix S2. Pure spatial beta diversity, $BD_{[c]}$, was generally large in the fine-scale analysis (10 m × 10 m) and decreased with the increase of cell size (Fig. 4, Table S1). $BD_{[c]}$ showed a non-significant negative relationship with latitude ($r = -0.364$, P -value = 0.3013, $n = 10$) (Fig. S2e). The unexplained component of beta diversity, $BD_{[d]}$, was always the highest for small cells (10 m × 10 m); it consistently decreased with the increase of cell size (Fig. 4). Unlike the previous beta-diversity components, $BD_{[d]}$ showed a marked and statistically significant decrease along the latitudinal gradient ($r = -0.771$, P -value = 0.0091, $n = 10$) (Fig. S2f). Moreover, we observed a strong linear correlation between $BD_{[d]}$ and BD_{Null} , the beta diversity expected under the null model ($r = 0.986$; P -value < 0.0001; $n = 40$).

Meta-analysis of results

BD_{Total} significantly decreased with increasing cell size, and significantly increased with increase in the number of species in the forest plot (Table 3). The effect of altitudinal range of the plot on total beta diversity was positive and close to statistical

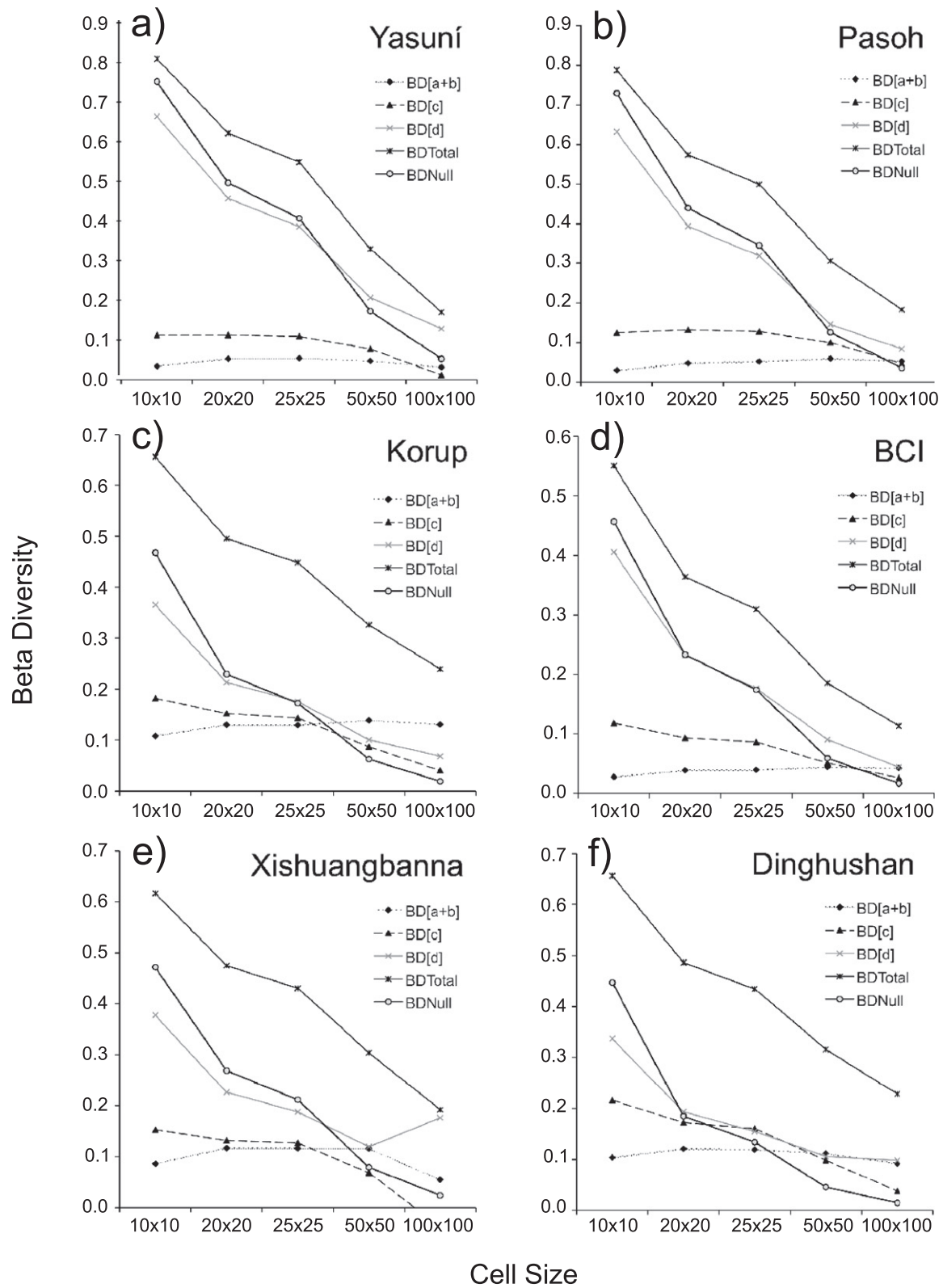


Figure 4 Beta-diversity values plotted against scale (cell size) for the 10 forest plots (a–j). BDTotal, total beta diversity; BDNul, Beta diversity under the null model; BD[a + b], beta diversity fitted by topography; BD[c], pure-spatial beta diversity; BD[d], unexplained beta diversity. Panels (a)–(e) are tropical rain forests. Panels (e)–(j) are forest plots located along the latitudinal gradient from south to north.

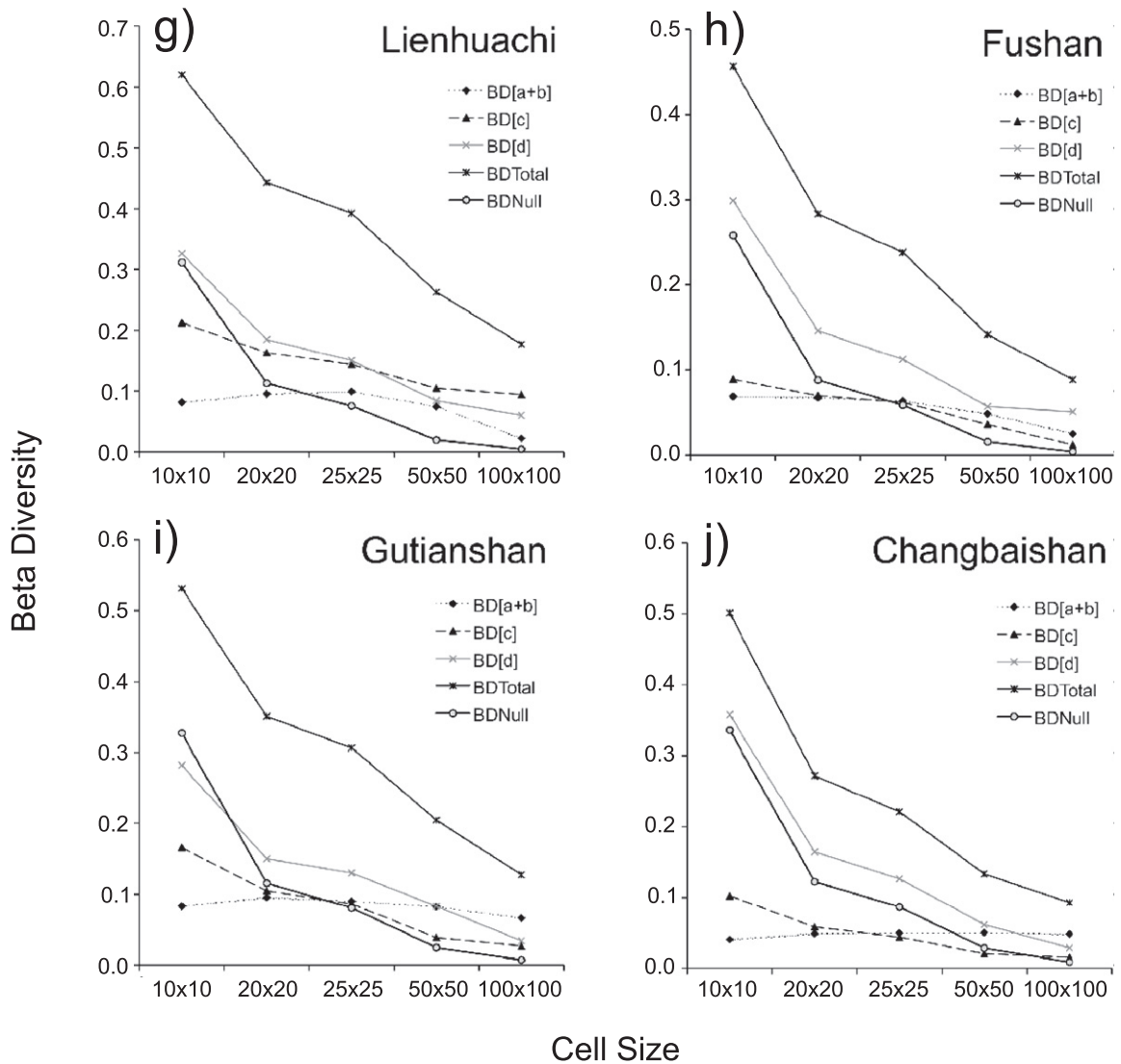


Figure 4 Continued

significance. Among the remaining regression models, the number of tree species in the forest plot was retained as a positively related variable for $BD_{[d]}$, $BD_{[c+d]}$ and BD_{Null} . The size of the cells was retained in all models except for $BD_{[a]}$. Intermediate cell sizes were related to higher beta-diversity values in models for $BD_{[b]}$, $BD_{[a+b]}$ and BD_{Diff} , whereas the relationship between the size of cells and the response was negative for the remaining models. Finally, there was a significant positive relationship between the altitudinal range of the plot and beta diversity for $BD_{[b]}$, $BD_{[a+b]}$ and BD_{Diff} .

DISCUSSION

Beta-diversity components have different determinants

In this study we demonstrated the usefulness of stem-mapped forest plot data to compare the variation of tree beta diversity

from one region to another. We investigated the structure of non-directional beta diversity of tree species by dividing it into topographical ($BD_{[a+b]}$), pure spatial ($BD_{[c]}$) and unexplained ($BD_{[d]}$) components (Legendre *et al.*, 2005, 2009). We observed a positive significant relationship between the tree species richness and $BD_{[d]}$, but we found no relationship between richness and $BD_{[a+b]}$ or $BD_{[c]}$. Moreover, the beta diversity attributed to pure spatial and unexplained variation ($BD_{[c+d]}$) was more linearly scale-dependent than that related to topography ($BD_{[a+b]}$). That different beta-diversity components exhibited different relationships to explanatory factors suggests that comparisons of tree beta diversity should be done by quantifying not only the total beta diversity but also the different beta-diversity components. For example, BCI and Gutianshan obtained similar total beta-diversity values (0.364 and 0.351 at 20 m × 20 m cell size). However, this similarity was only apparent. While BCI should have higher beta diversity than Gutianshan because it had almost twice as many tree species (307 vs. 159), this difference is

Table 3 Linear mixed effect models using beta-diversity values as the response variables ($n = 40$).

	Intercept	20 × 20	25 × 25	50 × 50	Species richness	Altitudinal range	Forest	Residual
BD _[a]	0.000 (1.0000)	–	–	–	–	–	0.086	0.997
BD _[b]	–0.152 (0.5749)	0.378 (0.0190)	0.352 (0.0278)	–0.121 (0.4311)	–	0.594 (0.0481)	0.777	0.339
BD _[c]	0.783 (0.0055)	–0.609 (0.0003)	–0.825 (< 0.0001)	–1.698 (< 0.0001)	–	–	0.750	0.330
BD _[d]	1.172 (< 0.0001)	–1.161 (< 0.0001)	–1.466 (< 0.0001)	–2.060 (< 0.0001)	0.585 (< 0.0001)	–	0.115	0.281
BD _[a+b]	–0.234 (0.3618)	0.480 (0.0043)	0.477 (0.0045)	–0.020 (0.8999)	–	0.638 (0.0276)	0.721	0.344
BD _[b+c]	0.449 (0.0888)	–0.228 (0.1056)	–0.383 (0.0089)	–1.186 (< 0.0001)	–	0.508 (0.0705)	0.745	0.304
BD _[c+d]	1.183 (< 0.0001)	–1.065 (< 0.0001)	–1.358 (< 0.0001)	–2.307 (< 0.0001)	0.483 (0.0001)	–	0.189	0.220
BD _[a+b+c]	0.427 (0.0996)	–0.196 (0.1829)	–0.345 (0.0235)	–1.166 (< 0.0001)	–	0.526 (0.0576)	0.723	0.321
BD _{Null}	1.189 (< 0.0001)	–1.198 (< 0.0001)	–1.486 (< 0.0001)	–2.073 (< 0.0001)	0.587 (< 0.0001)	–	0.071	0.271
BD _{Diff}	–0.176 (0.4503)	0.581 (0.0025)	0.583 (0.0024)	–0.461 (0.0135)	–	0.600 (0.0195)	0.612	0.390
BD _{Total}	1.144 (< 0.0001)	–0.985 (< 0.0001)	–1.279 (< 0.0001)	–2.313 (< 0.0001)	0.528 (0.0008)	0.181 (0.0949)	0.241	0.202

The cell size of analysis is a fixed categorical factor, whereas the number of species and the altitudinal range of the forest plot are quantitative explanatory variables and the plot identity is modelled as a random factor for the intercept of the model. Beta-diversity values coming from analyses at 100 m × 100 m cell size were excluded from this meta-analysis because the small number of cells prevented an accurate estimation of beta diversity at that scale. Model parameter estimates (along with P -values in parentheses) are given for each response variable. All variables were standardized to facilitate the comparison of parameter estimates across models.

compensated by a higher topography-related variation in the Gutianshan plot compared to BCI (253 m vs. 39 m in altitudinal range).

Beta-diversity components and ecological processes

The answer to the question ‘How is beta diversity generated?’ will ultimately depend on our ability to relate the observed variation to the relative importance of ecological processes potentially affecting it (Chave *et al.*, 2002). Variation partitioning is one of the most effective approaches to quantify the effects of three specific processes causing variation in community composition within landscapes, namely environmental control, limited dispersal and local stochastic processes (Borcard *et al.*, 1992; Legendre *et al.*, 2005, 2009). The rationale to interpret components of variation as the result of these three processes is as follows. Local environmental conditions influence demographic rates and competitive interactions between species; therefore they determine which species can survive in the local community. If we assume that the environmental variables included are the appropriate proxy for all important microenvironmental factors, the variation in forest species composition fitted by environmental variables (BD_[a+b]) can be interpreted as the outcome of local environmental control. On the other hand, dispersal limitation of plant propagules creates spatially autocorrelated structures independent of environmental variation. The pure-spatial beta-diversity component (BD_[c]) is likely to include this source of spatial variation provided that the appropriate spatial descriptors are used. Finally, unexplained beta diversity (BD_[d]) is often interpreted as the result of local stochastic processes arising from death and recruitment, but it could include the effects of other non-spatial processes, such as gap disturbances. Although these interpretations seem reasonable, recent discussions on the subject indicate that caution is required when

attributing beta-diversity components to the outcome of these processes. Most importantly, the effect of environmental control and dispersal processes may be confounded by the fact that spatial patterns created by dispersal limitation often correlate with the spatial arrangement of environment (Anderson *et al.*, 2011; Smith & Lundholm, 2010). As a result, part of the variation created by dispersal limitation may go to BD_[b], and hence the variation attributed to environmental control may be unduly inflated (Smith & Lundholm, 2010). Moreover, BD_[c] may include the signature of environmental factors that have not been included in the analysis (Borcard & Legendre, 1994; Jones *et al.*, 2008; Anderson *et al.* 2011; Legendre & Legendre, 2012).

While we acknowledge the above issues, we found two reasons to support the interpretation of BD_[a+b] and BD_[c] as the outcome of environmental control and dispersal processes, respectively. Firstly, we observed that BD_[a+b] was larger at intermediate cell sizes that at small cell sizes, whereas BD_[c] consistently decreased when the cell size was increased. Indeed, variogram studies have shown that autocorrelation in the Pasoh forest plot is largest at small scales, although it can be detected up to 150 m (He *et al.*, 1996). Several other studies have analysed spatial distribution of species and shown that aggregation is a dominant pattern (He *et al.*, 1997; Condit *et al.*, 2000; Li *et al.*, 2009). Secondly, the amount of BD_[a+b] correlated with the altitudinal range of the forest plot, whereas BD_[c] did not. That increased topographical variation results in higher BD_[a+b] supports the idea that this component contains at least some variation derived from environmental control.

We envisage three ways in which our analyses could be further refined in order to avoid misinterpretations and gain deeper insights. First, we are aware that soil type and soil chemistry are the most important environmental factors missing in our analysis (John *et al.*, 2007; Jones *et al.*, 2008). Second, in order to separate the confounded effect of dispersal on BD_[b], we should

compare its value against the value obtained under a null model where the environment has a similar spatial structure but is unrelated to species composition. Third, although large cell sizes should be avoided in survey designs because large cells may obscure the effect of within-cell habitat heterogeneity, it is also true that broad-scale topographic characteristics may be important locally. An interesting complementary analysis would therefore be to conduct beta-diversity partitioning for small cell sizes while using topographic explanatory variables computed for both small and large scales.

Beta diversity under the null model and unexplained beta diversity

Using a simple model where species were randomly distributed across space, Kraft *et al.* (2011) recently showed that beta-diversity values were largely determined by the size of the species pool and the number of individuals in the sampling units. Among our results, we found that the amount of unexplained beta diversity ($BD_{[d]}$) was strongly related to the beta diversity expected under the model of Kraft *et al.* (2011) (BD_{Null}). Moreover, $BD_{[d]}$ varied according to the same determinants as BD_{Null} . These findings are not completely surprising. First, if species were randomly distributed over space, as in the model of Kraft *et al.* (2011), the unexplained component ($BD_{[d]}$) would dominate the beta-diversity decomposition with all other components being non-significant. Second, although Kraft *et al.* (2011) presented their null model as purely statistical, both their model and $BD_{[d]}$ can be interpreted as the outcome of local stochastic processes. The limited area in a two-dimensional plot cell imposes a limitation in the number of individuals that the cells can harbour (i.e. the carrying capacity). In addition, death and recruitment in the local community makes the composition of the cells (randomly) different from each other (Alonso *et al.*, 2006). This (stochastic) difference is more apparent when using small cell sizes because the carrying capacity is then smaller. It is also more apparent with higher numbers of species, because more species can be excluded by local ecological drift. Regardless of the interpretation in terms of processes, we believe that both BD_{Null} and $BD_{[d]}$ are useful for capturing differences in local beta diversity that are due to differences in the regional/continental species richness.

Sources of variation of tree beta diversity

It has long been recognized that the number of plant species per unit area decreases from the tropics to the boreal zone, due to historical or ecological mechanisms or both (Rosenzweig, 1995; Gaston, 2000; Hawkins *et al.*, 2003). Previous studies have examined the beta-diversity–latitude relationship for vascular plants at continental scale and reported a gradient of decreasing turnover rates from south to north (Qian & Ricklefs, 2007; Lenoir *et al.*, 2010). Our results with fine-grained data have confirmed that non-directional tree beta diversity shows a strong decreasing gradient from tropical to the temperate forests. However, Kraft *et al.* (2011) recently questioned the interpretation of lati-

tudinal (and altitudinal) beta-diversity patterns by demonstrating that the observed differences could simply be due to differences in species richness and the number of individuals of sampling units. Our results also show that differences in tree species richness and cell size alone can account for most of the differences in tree beta diversity among forest plots. We found, however, that the size of the sampling unit plays more than one role in this issue, because it not only affects the signature of local stochastic variation ($BD_{[d]}$ or BD_{Null}) but also affects the signature of the other processes creating spatial variation ($BD_{[a+b]}$ and $BD_{[c]}$).

Measures of water–energy (evapotranspiration, productivity, etc.) are commonly considered to be good predictors of species richness at the global scale, both for plants and other taxa (Hawkins *et al.*, 2003). When comparing forests with similar internal environmental variation and using the same sampling unit size, one expects that macroclimatic differences affecting gamma richness will be the primary cause of the corresponding differences in tree beta diversity (Lenoir *et al.*, 2010). As an example, one can compare the results for BCI (tropical) with those for Changbaishan (temperate), both lacking strong variations in topography. Moreover, if the explanation about the limited carrying capacity holds, climatic differences could also modulate beta diversity by changing the tree density of forests. Since tree density is related to tree size, and older trees are bigger than younger ones, the age structure of forest stands could also affect the number of individuals within cells and hence influence beta-diversity assessments. Future studies should address whether these additional effects occur.

Notwithstanding the importance of climate, we have shown here that local environmental variation also plays a role in tree beta diversity. We found that total tree beta diversity was always higher than dictated by the null model. Moreover, this difference (BD_{Diff}) was not linearly scale dependent and it was positively correlated with the amount of topographic variation (i.e. altitudinal range) of the forest plot (McKnight *et al.*, 2007; Melo *et al.*, 2009). Hence, once the effects of gamma species richness and sampling unit size are taken into account, our prediction is that a significant portion of the observed differences in beta diversity will be explained by different amounts of environmental variation of the areas being compared.

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SUPPORTING INFORMATION

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

- Appendix S1** Supplementary methods: definition of the environmental and spatial descriptors.
- Appendix S2** Supplementary analysis of the contribution of individual topographic factors to tree beta diversity.
- Figure S1** Topography of the ten forest plots.
- Figure S2** Relationship between beta-diversity values and latitude.
- Table S1** Beta-diversity values for each forest plot and cell size.

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