

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

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30 **ABSTRACT**

31 **Aims** With the aim of understanding why some forests of the world exhibit higher tree beta
32 diversity values than others, we asked: (a) What is the contribution of environmentally-related
33 variation versus pure spatial and local stochastic variation to tree beta diversity assessed at the
34 forest plot scale? (b) At what resolution are these beta diversity components more apparent?
35 (c) What determines the variation in tree beta diversity observed across regions/continents?

36 **Location** Worldwide.

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

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

51 **Main conclusions** Because different beta diversity components have different determinants,
52 comparisons of tree beta diversity across regions should quantify not only overall variation in
53 species composition but also its components. Global-scale patterns in tree beta diversity are

54 largely coupled with changes in gamma richness due to the relationship between the latter and
55 the variation generated by local stochastic assembly processes.

56

57 **Keywords** Beta diversity, community composition, latitudinal gradient, spatial variation,
58 stem-mapping forest plots, variation partitioning.

59

60 INTRODUCTION

61 The spatial distribution of species assemblages is often described using three components of
62 species diversity: alpha or local diversity, beta diversity, and gamma or regional diversity
63 (Whittaker, 1960). Alpha and gamma diversities describe the species composition observed
64 within sampling units, and are differentiated only by the scale (sampling unit size) at which
65 species inventories are conducted (Whittaker *et al.*, 2001; Jurasinsky, 2009). In contrast, the
66 beta diversity concept describes the variation in species composition observed when
67 comparing sampling units to one another. There are two main approaches to define beta-
68 diversity (Anderson *et al.*, 2011): *directional turnover* and *non-directional variation*. Studies
69 addressing beta diversity as directional turnover measure the change in community
70 composition from one sampling unit to another along a spatial, temporal or environmental
71 gradient (Nekola & White 1999; Morlon *et al.*, 2008). In contrast, the non-directional
72 variation approach to beta diversity does not define it in relation to any specific spatial or
73 environmental structure, but as the variation in community structure among a set of sampling
74 units within a given spatial extent (Koleff *et al.*, 2003; Legendre *et al.*, 2005; Anderson *et al.*,
75 2006). In both cases beta diversity plays a pivotal role in linking local and regional diversity
76 and it captures a fundamental facet of the spatial pattern of species assemblages.

77 Much macroecological research has focused on the description and analysis of the spatial
78 patterns of alpha/gamma species diversity (e.g., Rosenzweig, 1995; Gaston, 2000; Whittaker

79 *et al.*, 2001; Gotelli *et al.*, 2009). Only recently have efforts been made to describe and
80 compare the amount of beta diversity found in different areas (e.g., van Rensburg *et al.*, 2004;
81 Rodriguez & Arita, 2004; Harborne *et al.*, 2006; Gaston *et al.*, 2007; McKnight *et al.*, 2007;
82 Melo *et al.*, 2009) or measured at different scales (e.g., Normand *et al.* 2006). A limited
83 number of studies have so far specifically investigated the spatial variation of plant beta
84 diversity at large (regional to global) scales (Scheiner & Rey-Benayas, 1994; Condit *et al.*,
85 2002; Qian *et al.* 2005; Qian & Ricklefs 2007; Lenoir *et al.* 2010). Using angiosperm floras of
86 states/provinces (sampling units of $\sim 10^5 \text{ km}^2$), Qian *et al.* (2005) found larger rates of
87 similarity decay in eastern Asia compared to eastern North America, both along east-west and
88 north-south directions; and Qian & Ricklefs (2007) reported a latitudinal gradient in beta
89 diversity with lower latitudes exhibiting larger rates of decay compared to higher latitudes.
90 Similarly, Lenoir *et al.* (2010) analyzed vegetation plot records (sampling units of $< 0.1 \text{ ha}$)
91 and found both higher rates of similarity decay and higher values of non-directional variation
92 in the Alps (southern Europe) than in the Scandes (northern Europe).

93 Despite these recent efforts to describe and interpret spatial variation in plant beta diversity
94 at the global scale, little is known about the causes of this variation. In addition, the
95 determinants of beta diversity will depend on the scale (i.e. extent and grain) of study
96 (Whittaker *et al.* 2001). If we restrict our discussion to plant beta diversity assessed at the
97 local (forest plot) scale, several processes can contribute to creating compositional differences
98 among local communities, such as environmental filtering, biotic interactions and dispersal
99 limitation. Species composition of local communities will also depend on ecological and
100 evolutionary processes that operate at large spatial scales (regional/continental), such as
101 speciation, extinction or biogeographic dispersal (Whittaker *et al.*, 2001). Although these
102 latter processes are not the main focus of beta diversity assessments conducted at the local

103 scale, they need to be taken into account when comparing beta diversity values across regions
104 or continents (Kraft *et al.* 2011).

105 In this study we aim at understanding why some forests of the world exhibit higher tree
106 beta diversity values than others. We ask the following specific questions: (a) What is the
107 contribution of environmentally-related variation versus pure spatial and local stochastic
108 variation to tree beta diversity assessed at the scale of the forest plot? (b) At what resolution
109 (i.e. size of sampling units) are these components of tree beta diversity more apparent? (c)
110 How is tree species richness of the plot affecting its beta diversity? (d) What determines the
111 variation in tree beta diversity observed across regions/continents? To address these questions
112 we compare the tree beta diversity found *within* ten permanent stem-mapped forest plots that
113 comprise tropical, subtropical and temperate forests distributed worldwide (Table 1, Fig. 1).
114 We divide the surface of each forest plot into cells (i.e. quadrats) of equal sizes and calculate
115 the tree beta diversity of the plot as the non-directional variation in tree species composition
116 among cells. Because the ten forest plots are located in regions subjected to different
117 macroclimatic and biogeographical constraints, the plots are drastically different in number of
118 tree species (52 to 1105) and tree density (0.16 to 0.81 individuals/m²) (Table 2). Differences
119 in gamma species richness and the number of individuals per sampling unit may explain
120 differences in beta diversity (Kraft *et al.* 2011). We therefore compare the tree beta diversity
121 of each forest plot against the beta diversity expected under a null model that assumes random
122 allocation of individuals among plot cells. The difference between the observed and null
123 model beta diversities should provide evidence of the effect of ecological processes that
124 generate non-random spatial patterns in forest plots. To quantify the spatial variation created
125 by environmental filtering and other ecological processes, we use topographic and spatial
126 descriptors as explanatory variables to partition the total tree beta diversity of each forest plot
127 into four components: pure topographic (i.e. variation fitted by topographic descriptors but

128 not spatial ones), spatially-structured topographic (i.e. variation fitted by both spatial and
129 topographic descriptors), pure spatial (i.e. variation fitted by spatial descriptors but not
130 topographic ones) and unexplained (i.e. residual variation). In order to gain insights on the
131 determinants of tree beta diversity and its components, we study the relationship between beta
132 diversity values and three explanatory factors: (1) the tree species richness of the forest plot (a
133 proxy for drivers of diversity acting at spatial scales larger than the forest plot); (2) the
134 altitudinal range spanned in the forest plot (a proxy for environmental variation), and (3) the
135 resolution (cell size) used in beta diversity assessment.

136 Materials and Methods

137 Stem-mapped forest plots

138 Over the past three decades, there has been an impressive international research effort
139 coordinated by the Center for Tropical Forest Science (CTFS; <http://www.ctfs.si.edu/>) for
140 assembling long-term, large-scale forest data from the tropics (Condit, 1995). The Chinese
141 Forest Biodiversity Monitoring Network (<http://www.cfbiodiv.org/>) has recently extended the
142 CTFS network by establishing large stem-mapping plots located along a latitudinal gradient
143 from temperate to subtropical and tropical forests. We compare here ten plots from the two
144 networks, whose main features are summarized in Tables 1 and 2. The Yasuní, Barro
145 Colorado Island, Korup, Pasoh and Xishuangbanna plots are located within the tropics; the
146 Dinghushan, Lienhuachi, Fushan and Gutianshan forests are considered subtropical, whereas
147 the Changbaishan plot is located in the temperate region (Table 1, Fig. 1). These macro-
148 climatic and geographic differences have an effect on the number of tree species that the
149 forest plots support (Table 2). The ten forest plots also differ markedly in the amount of
150 internal topographical variation (see Fig. S1 in Supporting Information); the range of altitudes
151 inside plots is very small in some cases (17 m in Changbaishan) and very high in others (237
152 m in Dinghushan).

153 **Tree data**

154 In all forest plots the census methodology was the same: all trees with diameter at breast
 155 height (DBH) ≥ 1 cm were tagged, identified, measured, and georeferenced. The years of
 156 census used in the present study are shown in Table 2, as well as the number of species and
 157 individuals counted. Although tree diameters were available, we only used data on the species
 158 identity and the spatial location of trees within the plot for our analyses.

159 **Tree counts within plot cells**

160 We divided the surface of each forest plot into a grid of cells (i.e. quadrats). In order to assess
 161 the effect of sampling unit size on beta diversity, we considered five different cell sizes:
 162 10×10 m (0.01 ha), 20×20 m (0.04 ha), 25×25 m (0.0625 ha), 50×50 m (0.25 ha) and 100×100
 163 m (1 ha). The number of cells decreased as the cell size increased (see Appendix S2 and
 164 Table S3 in Supporting Information). Counting the number of living trees of each species in
 165 every cell in the grid we obtained, for each forest plot and cell size, an $n \times p$ (cells-by-species)
 166 data table $\mathbf{X} = [x_{ij}]$ where each x_{ij} element contained the number of live individuals of species j
 167 in cell i (Fig. 2, (1)).

168 **Hellinger transformation**

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

$$174 \quad y_{ij} = \sqrt{x_{ij} / \sum_{k=1}^p x_{ik}}, \quad (1)$$

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

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

181 Beta diversity measure

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

$$184 \quad BD_{\text{Total}} = \text{Var}(\mathbf{Y}) = SS(\mathbf{Y})/(n - 1) \quad (2)$$

185 where the total sum of squares, $SS(\mathbf{Y})$, is the sum, over all species and all grid cells, of the
 186 squared deviations from the species means. $\text{Var}(\mathbf{Y})$ has the advantage that it can also be
 187 interpreted in terms of the average dissimilarity between sampling units (Legendre *et al.*
 188 2005; Anderson *et al.* 2006). Since the Hellinger distance is bounded between 0 and $\sqrt{2}$,
 189 BD_{Total} is bounded between 0 (all cells have identical composition) and 1 (each cell contains a
 190 unique set of species). We calculated BD_{Total} for each forest plot at each cell size (Fig. 2, (3)).

191 Null model of total beta diversity

192 Following Kraft *et al.* (2011), we used a null model that randomizes the location of trees
 193 among cells of the forest plot, while keeping the number and abundance distribution of tree
 194 species and the number of individuals per cell constant. We ran 1,000 randomizations on the
 195 cell-by-species data table \mathbf{X} corresponding to each forest plot and cell size. As before, we
 196 applied the Hellinger transformation to each randomized data table \mathbf{X}' and calculated beta
 197 diversity as the total variance of the Hellinger-transformed table \mathbf{Y}' (eq. 2; Fig. 2, (4-6)). We
 198 then calculated the mean of the distribution of beta diversity values under the null model
 199 (BD_{Null}), as well as the difference between BD_{Total} and BD_{Null} (Fig. 2, (7)). This difference
 200 (BD_{Diff}) represents how much tree beta diversity varies with respect to the null model as a
 201 consequence of processes that create non-random spatial patterns.

202 **Environmental and spatial descriptors**

203 Topography is not a direct environmental variable, such as light or temperature, but a proxy
204 representing soil moisture and microclimate conditions. As topographic factors were the only
205 set of explanatory factors available for the ten stem-mapping forest plots, we used topography
206 as a proxy of the micro-environmental conditions prevailing within plot cells (Legendre *et al.*
207 2009). We calculated four topographic attributes for every grid cell – mean elevation,
208 convexity, slope and aspect – and constructed third-degree polynomials with them (details are
209 given in Appendix S2), obtaining a data table **E** for each forest plot and cell size (Fig. 2, (8)).

210 In order to assess the importance of spatial structuring in ecological communities, spatial
211 relationships must be explicitly introduced into statistical models. Moran eigenvector maps
212 (MEMs) are variables that describe spatial patterns at all scales that can be accommodated in
213 the sampling design (Dray *et al.*, 2006). We generated distance-based MEMs (Borcard &
214 Legendre, 2002) and obtained, for each cell size and forest plot, a data table **S** containing the
215 variables to be used as spatial predictors (Fig. 2, (9)) (details are given in Appendix S2).

216 **Variation partitioning**

217 Variation partitioning is an extension of partial canonical ordination techniques that models
218 the species composition of sampling units as a function of explanatory factors and then
219 partitions the total variation in community composition into several components (Borcard *et*
220 *al.*, 1992; Legendre *et al.* 2005). We conducted variation partitioning, using the Hellinger-
221 transformed species composition table **Y** as response matrix, and **E** and **S** tables as
222 explanatory matrices. This allowed dividing the total tree beta diversity of each forest plot
223 into four components: pure topographic ($BD_{[a]}$, variation fitted by topographic descriptors but
224 not spatial ones), spatially-structured topographic ($BD_{[b]}$, variation fitted by both spatial and
225 topographic descriptors), pure spatial ($BD_{[c]}$, variation fitted by spatial descriptors but not
226 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} :

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

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 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 .

239 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 sub-models of fixed factors and retained the model with lowest Akaike Information Criterion (AIC) value. BD_{Total} was also modeled but without model selection.

251 RESULTS

252 **Total tree beta diversity**

253 There were large differences in total tree beta diversity across forests (Fig. 3). As a result of
254 pooling information from smaller cells to larger cells, the total beta diversity steadily
255 decreased with the increase in cell size in all forests (Fig. 4, Table S3). Comparison of total
256 tree beta diversity values along the latitudinal gradient showed a clear decrease from the
257 tropical to the temperate forests ($r = -0.776$, p-value = 0.0083, $n = 10$) (Fig. S4.a in
258 Supporting Information).

259 **Beta diversity under the null model**

260 Beta diversity under the null model (i.e., calculated after permuting trees among plot cells),
261 BD_{Null} , was consistently lower than the observed total beta diversity (Fig. 4, Table S3). In
262 accordance with the results of Kraft *et al.* (2011), BD_{Null} decreased for increasing cell sizes
263 and along the latitudinal gradient ($r = -0.796$, p-value = 0.0058, $n = 10$) (Fig. S4.b). In
264 contrast, the difference between observed and expected beta diversity, BD_{Diff} , was often
265 highest for intermediate cell sizes (i.e., between 20×20 m and 50×50 m) (Table S3) and did
266 not show any significant relationship with latitude ($r = 0.278$, p-value = 0.4372, $n = 10$) (Fig.
267 S4.c).

268 **Beta diversity partitioning**

269 Almost all beta diversity fitted by the topographic factors was also explained by the spatial
270 factors. That is, $BD_{[b]}$ accounted for most of $BD_{[a+b]}$, leaving a small fraction of spatially
271 unstructured environmental fit, $BD_{[a]}$ (Table S3). In general plots laid on flat terrains, such as
272 in Changbaishan or BCI (Fig. S1), obtained low values of beta diversity explained by
273 topography, $BD_{[a+b]}$, whereas plots set on mountain slopes or within hilly areas, such as in
274 Gutianshan or Dinghushan (Fig. S1), obtained higher $BD_{[a+b]}$ values. Differences across the
275 forest plots in the amount of beta diversity explained by topography did not appear to form a
276 latitudinal gradient ($r = 0.111$, p-value = 0.7602, $n = 10$) (Fig. S4.d). Except for Fushan, all

277 other forests had a maximum $BD_{[a+b]}$ value for intermediate cell sizes (i.e., between 20×20 m
278 and 50×50 m) (Fig. 4). We present a supplementary analysis of the contribution of single
279 topographic factors in Appendix S5 of Supporting Information. Pure spatial beta diversity,
280 $BD_{[c]}$, was generally large in the fine-scale analysis (10×10 m) and decreased with the
281 increase of cell size (Fig. 4, Table S3). $BD_{[c]}$ showed a non-significant negative relationship
282 with latitude ($r = -0.364$, p-value = 0.3013, $n = 10$) (Fig. S4.e). The unexplained component
283 of beta diversity, $BD_{[d]}$, was always the highest for small cells (10×10 m); it consistently
284 decreased with the increase of cell size (Fig. 4). Unlike the previous beta diversity
285 components, $BD_{[d]}$ showed a marked and statistically significant decrease along the latitudinal
286 gradient ($r = -0.771$, p-value = 0.0091, $n = 10$) (Fig. S4.f). Moreover, we observed a strong
287 linear correlation between $BD_{[d]}$ and BD_{Null} , the beta diversity expected under the null model
288 ($r = 0.986$; p-value <0.0001; $n = 40$).

289 **Meta-analysis of results**

290 BD_{Total} significantly decreased with increasing cell size, and significantly increased with the
291 increase of the number of species in the forest plot (Table 3). The effect of altitudinal range of
292 the plot on total beta diversity was positive and close to statistical significance. Among the
293 remaining regression models, the number of tree species in the forest plot was retained as a
294 positively related variable for $BD_{[d]}$, $BD_{[c+d]}$ and BD_{Null} . The size of the cells was retained in
295 all models except for $BD_{[a]}$. Intermediate cell sizes were related to higher beta diversity values
296 in models for $BD_{[b]}$, $BD_{[a+b]}$ and BD_{Diff} , whereas the relationship between the size of cells and
297 the response was negative for the remaining models. Finally, there was a significant positive
298 relationship between the altitudinal range of the plot and beta diversity for $BD_{[b]}$, $BD_{[a+b]}$ and
299 BD_{Diff} .

300 **DISCUSSION**

301 **Beta diversity components have different determinants**

302 In this study we demonstrated the usefulness of stem-mapped forest plot data to compare the
303 variation of tree beta diversity from one region to another. We investigated the structure of
304 non-directional beta diversity of tree species by dividing it into topographical ($BD_{[a+b]}$), pure
305 spatial ($BD_{[c]}$), and unexplained ($BD_{[d]}$) components (Legendre *et al.*, 2005; Legendre *et al.*
306 2009). We observed a positive significant relationship between the tree species richness and
307 $BD_{[d]}$, but we found no relationship between richness and $BD_{[a+b]}$ or $BD_{[c]}$. Moreover, the beta
308 diversity attributed to pure spatial and unexplained variation ($BD_{[c+d]}$) was more linearly
309 scale-dependent than that related to topography ($BD_{[a+b]}$). That different beta diversity
310 components exhibited different relationships with explanatory factors suggests that
311 comparisons of tree beta diversity should be done quantifying not only the total beta diversity
312 but also the different beta diversity components. For example, BCI and Gutianshan obtained
313 similar total beta diversity values (0.364 and 0.351 at 20×20 m cell size). However, this
314 similarity was only apparent. While BCI should have higher beta diversity than Gutianshan
315 because it had almost twice as many tree species (307 vs. 159), this difference is compensated
316 by a higher topography-related variation in the Gutianshan plot compared to BCI (253 m vs.
317 39 m in altitudinal range).

318 **Beta diversity components and ecological processes**

319 The answer to the question: *How is beta diversity generated* will ultimately depend on our
320 ability to relate the observed variation to the relative importance of ecological processes
321 potentially affecting it (Chave *et al.*, 2002). Variation partitioning is one of the most effective
322 approaches to quantify the effects of three specific processes causing variation in community
323 composition within landscapes, namely environmental control, limited dispersal and local
324 stochastic processes (Borcard *et al.*, 1992; Legendre *et al.*, 2005; Legendre *et al.*, 2009). The
325 rationale to interpret components of variation as the result of these three processes is as

326 follows. Local environmental conditions influence demographic rates and competitive
327 interactions between species; therefore they determine which species can survive in the local
328 community. If we assume that the environmental variables included are the appropriate proxy
329 for all important micro-environmental factors, the variation in forest species composition
330 fitted by environmental variables ($BD_{[a+b]}$) can be interpreted as the outcome of local
331 environmental control. On the other hand, dispersal limitation of plant propagules creates
332 spatially autocorrelated structures independent of environmental variation. The pure-spatial
333 beta diversity component ($BD_{[c]}$) will likely include this source of spatial variation provided
334 that the appropriate spatial descriptors are used. Finally, unexplained beta diversity ($BD_{[d]}$) is
335 often interpreted as the result of local stochastic processes arising from death and recruitment,
336 but it could include the effects of other non-spatial processes, such as gap disturbances.
337 Although these interpretations seem reasonable, recent discussions on the subject indicate that
338 caution is required when attributing beta diversity components to the outcome of these
339 processes. Most importantly, the effect of environmental control and dispersal processes may
340 be confounded by the fact that spatial patterns created by dispersal limitation often correlate
341 with the spatial arrangement of environment (Smith & Lundholm, 2010; Anderson *et al.*,
342 2010). As a result, part of the variation created by dispersal limitation may go to $BD_{[b]}$, and
343 hence the variation attributed to environmental control may be unduly inflated (Smith &
344 Lundholm, 2010). Moreover, $BD_{[c]}$ may include the signature of environmental factors that
345 have not been included in the analysis (Borcard & Legendre, 1994; Jones *et al.*, 2008;
346 Anderson *et al.* 2010; Legendre & Legendre, 2012).

347 While we acknowledge the above issues, we found two reasons supporting the
348 interpretation of $BD_{[a+b]}$ and $BD_{[c]}$ as the outcome of environmental control and dispersal
349 processes respectively. Firstly, we observed that $BD_{[a+b]}$ was larger at intermediate cell sizes
350 than at small cell sizes, whereas $BD_{[c]}$ consistently decreased when increasing the cell size.

351 Indeed, variogram studies have shown that autocorrelation in the Pasoh forest plot is largest at
352 small scales, although it can be detected up to 150 m (He *et al.*, 1996). Several other studies
353 have analyzed spatial distribution of species and shown that aggregation is a dominant pattern
354 (He *et al.*, 1997; Condit *et al.*, 2000; Li *et al.*, 2009). Secondly, the amount of $BD_{[a+b]}$
355 correlated with the altitudinal range of the forest plot, whereas $BD_{[c]}$ did not. That increased
356 topographical variation results in higher $BD_{[a+b]}$ supports the idea that this component
357 contains at least some variation derived from environmental control.

358 We envisage three ways in which our analyses could be further refined in order to avoid
359 misinterpretations and gain deeper insights. First, we are aware that soil types and soil
360 chemistry are the most important environmental factors missing in our analysis (John *et al.*,
361 2007; Jones *et al.*, 2008). Second, in order to separate the confounded effect of dispersal on
362 $BD_{[b]}$, we should compare its value against the value obtained under a null model where the
363 environment has the similar spatial structure but is unrelated to species composition. Third,
364 although large cell sizes should be avoided in survey designs because large cells may obscure
365 the effect of within-cell habitat heterogeneity, it is also true that broad-scale topographic
366 characteristics may be important locally. An interesting complementary analysis would be,
367 therefore, to conduct beta-diversity partitioning for small cell sizes while using topographic
368 explanatory variables computed for both small and large scales.

369 **Beta diversity under the null model and unexplained beta diversity**

370 Using a simple model where species were randomly distributed across space, Kraft *et al.*
371 (2011) recently showed that beta diversity values were largely determined by the size of the
372 species pool and the number of individuals in the sampling units. Among our results, we
373 found that the amount of unexplained beta diversity ($BD_{[d]}$) was strongly related to the beta
374 diversity expected under the model of Kraft *et al.* (2011) (BD_{Null}). Moreover, $BD_{[d]}$ varied
375 according to the same determinants as BD_{Null} . These findings are not completely surprising.

376 First, if species were randomly distributed over space, as in the model of Kraft *et al.* (2011),
377 the unexplained component ($BD_{[d]}$) would dominate the beta diversity decomposition with all
378 other components being non-significant. Second, although Kraft *et al.* (2011) presented their
379 null model as purely statistical, both their model and $BD_{[d]}$ can be interpreted as the outcome
380 of local stochastic processes. The limited area in a two-dimensional plot cell imposes a
381 limitation in the number of individuals that the cells can harbour (i.e., carrying capacity). In
382 addition, death and recruitment in the local community makes the composition of the cells to
383 be (randomly) different from each other (Alonso *et al.* 2006). This (stochastic) difference is
384 more apparent when using small cell sizes because the carrying capacity is then smaller. It is
385 also more apparent with higher numbers of species, because more species can be excluded by
386 local ecological drift. Regardless of the interpretation in terms of processes, we believe that
387 both BD_{Null} and $BD_{[d]}$ are useful to capture differences in local beta diversity that are due to
388 differences in the regional/continental species richness.

389 **Sources of variation of tree beta diversity**

390 It has long been recognized that the number of plant species per unit area decreases from the
391 tropics to the boreal zone, due to either historical or ecological mechanisms or both
392 (Rosenzweig, 1995; Gaston, 2000; Hawkins *et al.*, 2003). Previous studies have examined the
393 beta diversity-latitude relationship for vascular plants at continental scale and reported a
394 gradient of decreasing turnover rates from south to north (Qian & Ricklefs 2007; Lenoir *et al.*
395 2010). Our results with fine-grained data have confirmed that non-directional tree beta
396 diversity shows a strong decreasing gradient from the tropical to the temperate forests.
397 However, Kraft *et al.* (2011) recently questioned the interpretation of latitudinal (and
398 altitudinal) beta diversity patterns by demonstrating that the observed differences could be
399 simply due to differences in species richness and the number of individuals of sampling units.
400 Our results also show that differences in tree species richness and cell size alone can account

401 for most of the differences in tree beta diversity among forest plots. We found, however, that
402 the sampling unit size plays more than one role in this issue, because it not only affects the
403 signature of local stochastic variation ($BD_{[d]}$ or BD_{Null}) but also affects the signature of the
404 other processes creating spatial variation ($BD_{[a+b]}$ and $BD_{[c]}$).

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

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

425 diversity will be explained by different amounts of environmental variation of the areas being
426 compared.

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- 565
- 566 **Supplementary material**
- 567 Additional Supporting Information may be found in the online version of this article:
- 568 **Figure S1** Topography of the ten forest plots. Contour lines are drawn every 5 meters.
- 569 **Appendix S2** Supplementary Methods: Definition of the environmental and spatial
570 descriptors.

571 **Table S3** Beta diversity values for each forest plot and cell size.

572 **Figure S4** Relationship between beta diversity values (computed at 20×20 m) and latitude.

573 **Appendix S5** Supplementary analysis of the contribution of individual topographic factors to
574 tree beta diversity.

575

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580

581 **BIOSKETCH**

582 This study resulted from a collaborative international research initiative aiming at the
583 comparison of stem-mapped forests in terms of beta diversity. Author contributions: M.D.C.,
584 P.L. and F.H. designed the study. M.D.C. and P.L. analyzed the data. M.D.C., P.L. and F.H.
585 wrote the main portions of the paper. F.H., M.C., L-W.C., G.C., R.C., M.F., Z.H., C-F.H.,
586 S.H., D.K., K.M., X.M., M.N.S.N., A.R.K., H.R., S-H.S., I-F.S., D.T., R.V. and W.Y.
587 surveyed the Permanent Forest Plots and contributed to the interpretation of the results in the
588 paper.

589

589 **TABLES**

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

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

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

595

596

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

597 Year: year(s) of the census used in the present study; # spp: number of species in the whole
 598 plot; % rare: percentage of species occurring at in less than 40% of the 20×20 m plot cells; #
 599 ind: number of individuals (stems of identified tree species) in the whole plot; Ind/m²: number
 600 of individuals with DBH ≥ 1 cm per square meter (tree density). Data set version for the
 601 Yasuní plot is 2002.

Forest plot	Size (m×m)	Year	# spp	% rare	# ind	Ind/m ²
Yasuní	500×500	1995	1105	94%	152350	0.61
Pasoh	1000×500	1986	817	89%	320026	0.64
Korup	1000×500	1996	496	90%	330676	0.66
BCI	1000×500	1981-83	307	88%	235771	0.47
Xishuangbanna	400×500	2007	468	93%	95451	0.48
Dinghushan	400×500	2005	210	86%	71617	0.36
Lienhuachi	500×500	2008	145	75%	203313	0.81
Fushan	500×500	2003	109	72%	166589	0.67
Gutianshan	600×400	2005	159	77%	140676	0.59
Changbaishan	500×500	2004	52	75%	38902	0.16

602

603

603 **Table 3. Linear mixed effect models using beta diversity values as the response variables**604 (*n* = 40).

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

	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

613

614

614 **FIGURE LEGENDS**

615 **Fig. 1.** World map showing the locations of the 10 permanent forest plots studied in this
616 paper. Details of the forests can be found in Tables 1 and 2.

617 **Fig. 2.** Schematic representation of the beta diversity analyses conducted for each forest plot
618 and cell size. Numbers in parentheses indicate the analysis steps that are cited in the text.

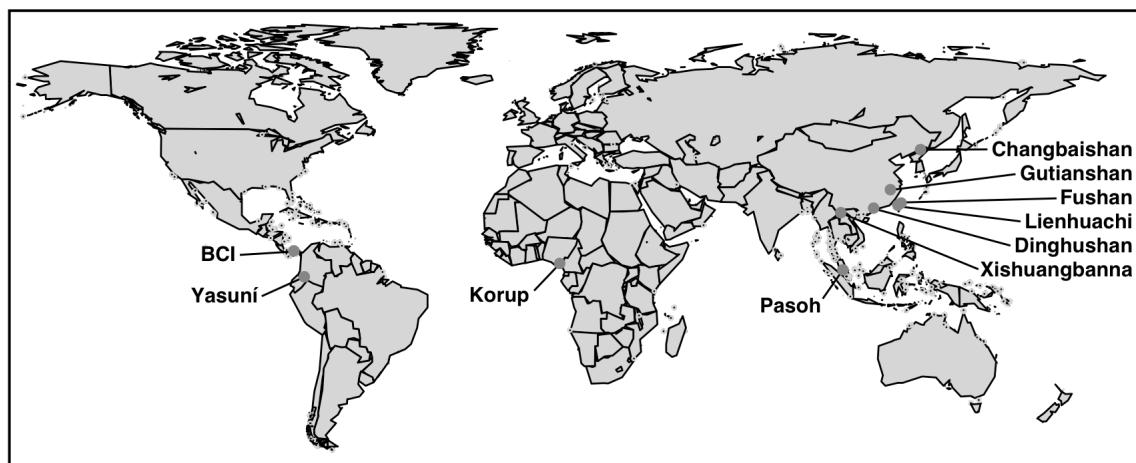
619 **Fig. 3.** Total tree beta diversity (computed at 20×20 m) in relation to species richness and the
620 altitudinal range of forest plots. Sizes of circles are proportional to the square of the beta
621 diversity values indicated inside.

622 **Fig. 4.** Beta diversity values plotted against scale (cell size) for the 10 forest plots (A-J).

623 BDTot: total beta diversity; BDNull: Beta diversity under the null model; BD[a+b]: Beta
624 diversity fitted by topography; BD[c]: pure-spatial beta diversity; BD[d]: unexplained beta
625 diversity. Panels A-E are tropical rain forests, while E-J are forest plots located along the
626 latitudinal gradient from south to north.

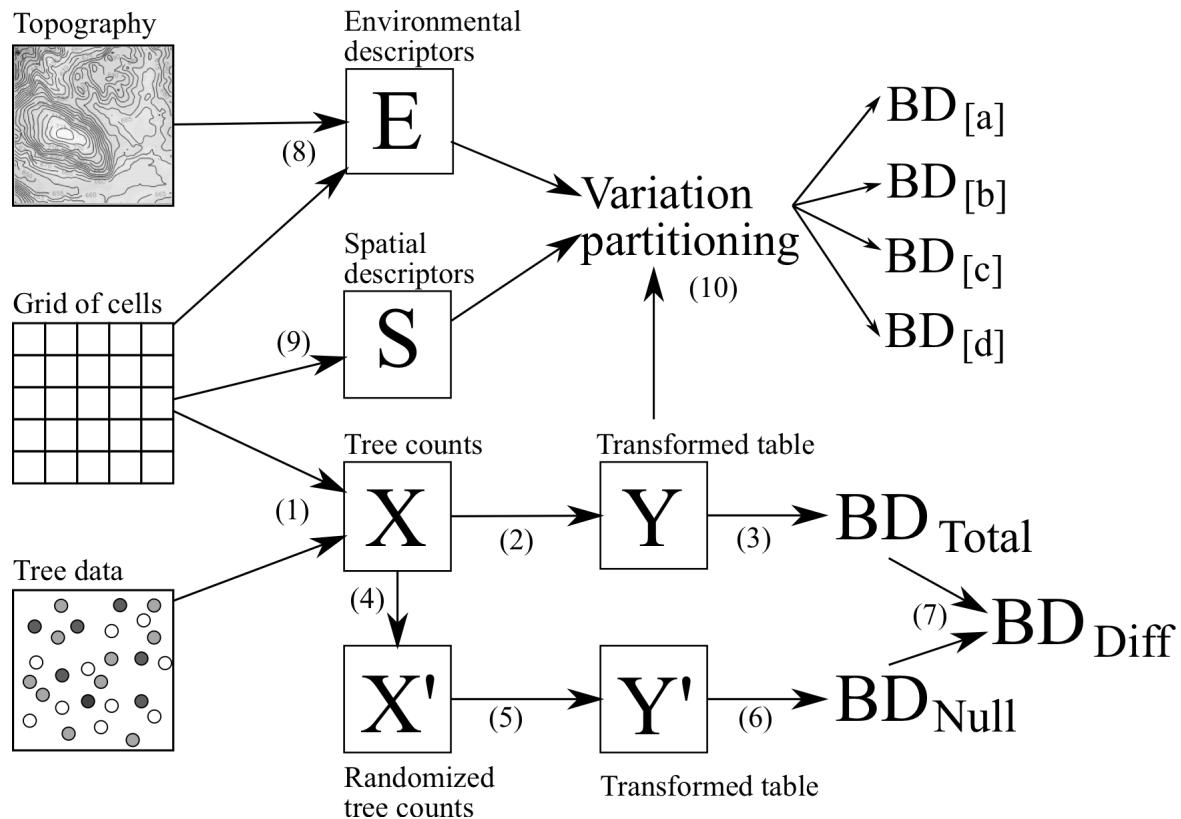
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627 **Fig. 1**



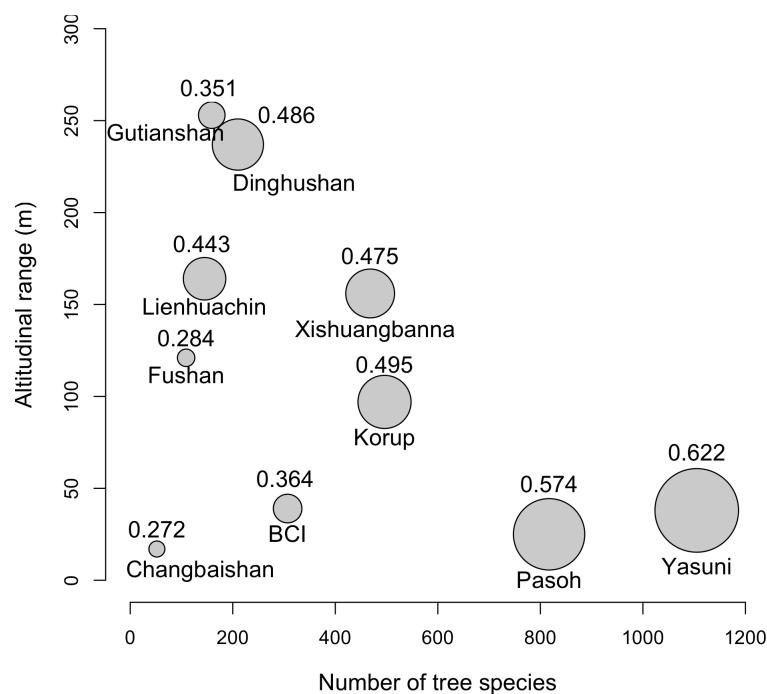
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629 **Fig. 2**



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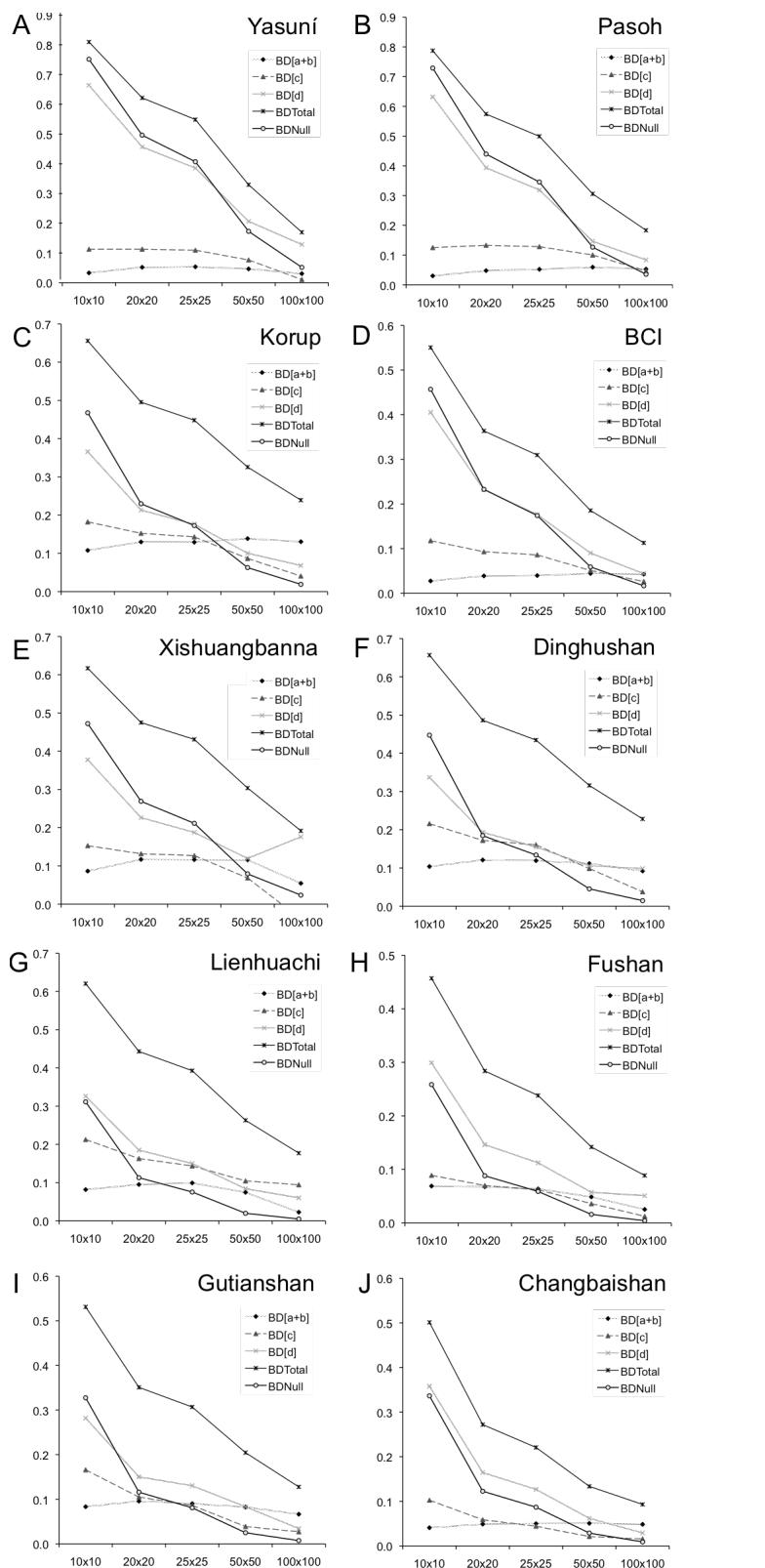
631 **Fig. 3**

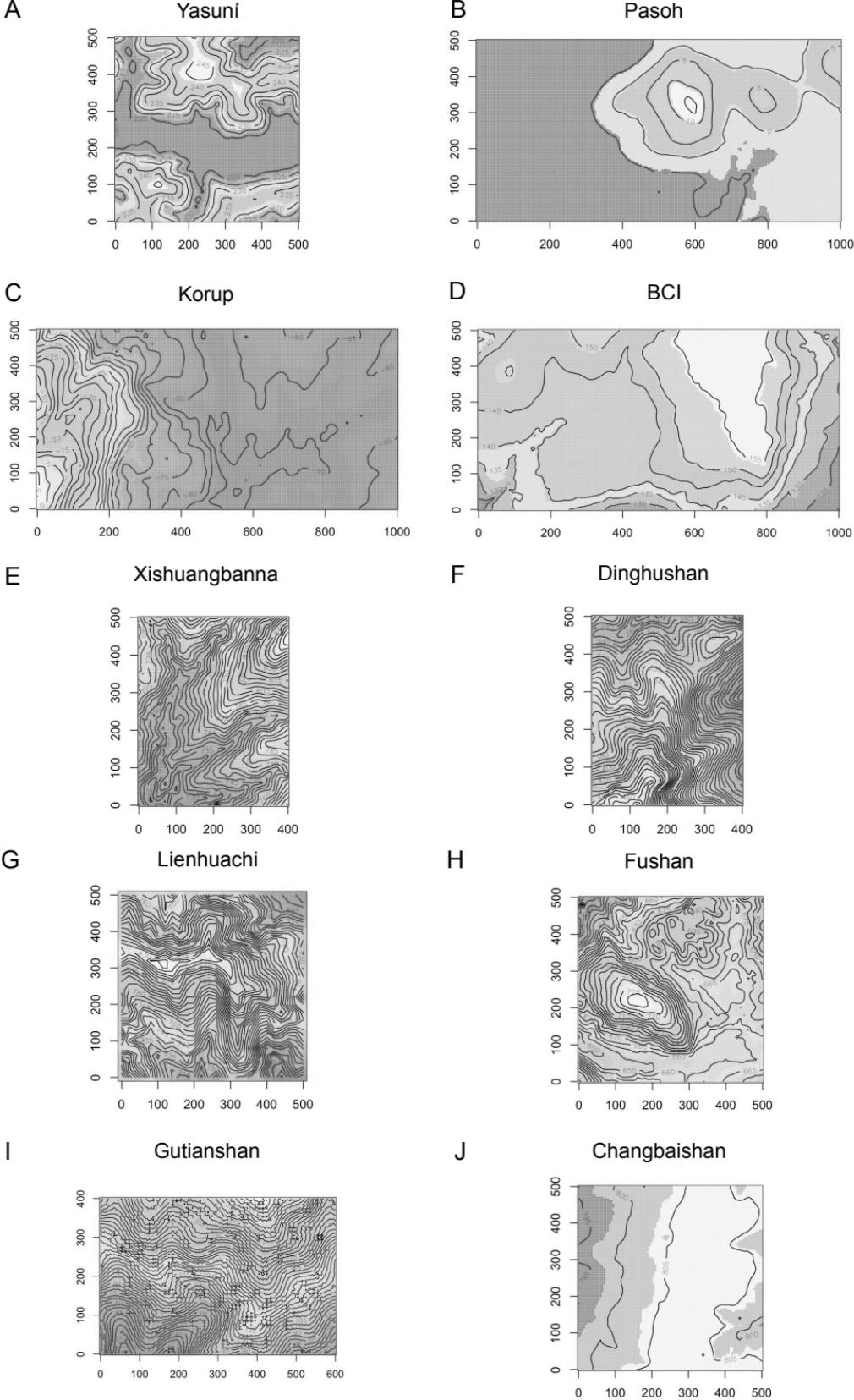


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633 Fig. 4





Appendix S2

Supplementary Methods: Definition of the environmental and spatial descriptors.

Environmental descriptors

As topographic factors were the only set of explanatory factors available for the ten stem-mapping forest plots, we used the topography of the forest plot as a proxy of the micro-environmental conditions prevailing within plot cells. For each forest plot and cell size we calculated four topographic attributes – mean elevation, convexity, slope and aspect. Following Valencia *et al.* (2004), the mean elevation of a cell was defined as the mean of the elevation values of its four corners. Convexity was the mean elevation of the target cell minus the mean elevation of the eight surrounding cells; for the edge cells, convexity was the elevation of the centre point minus the mean of the four corners. Slope was the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three of its corners. Aspect (in degrees from North) was calculated using the formula:

$$\text{Aspect} = 180 - \arctan(fy/fx) \cdot (180/\Pi) + 90 \cdot (fx/|fx|) \quad (\text{S1.1})$$

where fx and fy are the changes in elevation from east to west and from north to south, respectively. Aspect was then decomposed into two fractions: east-west orientation (the sine of aspect) and north-south orientation (the cosine of aspect). Table S2 below reports the means and standard deviations of the topographic factors across cells for each forest and cell size. In order to increase the predictive ability of topographic factors and allow them to model nonlinear relationships with the abundance of trees, mean elevation, convexity, and slope were used to construct third-degree polynomial equations for a total of nine monomials, as in Legendre *et al.* (2009). With these calculations we obtained, for each forest plot and cell size, a data table **E** that described the micro-environmental conditions on each cell by means of eleven (nine monomials plus two aspect) topographic variables.

Spatial descriptors

Moran eigenvector maps (MEMs) are variables obtained using a spectral decomposition of the spatial relationships among sampling units (Dray *et al.*, 2006; Legendre & Legendre, 2012). The method consists of diagonalizing a spatial weighting matrix, then extracting the eigenvectors that maximize the Moran's index of autocorrelation (see details in Dray *et al.* 2006). The resulting eigenvectors describe spatial patterns at all scales that can be accommodated in the sampling design. These eigenvectors can then be incorporated into statistical models, such as multiple regression or canonical analysis, in order to identify the amount and kind of spatial patterns that the response variables show. In our case, we generated distance-based MEMs, formerly called PCNMs (Borcard & Legendre, 2002), because we used the spatial distance relationships among plot cells to create the spatial weighting matrix. We used a truncation distance that retained the horizontal, vertical, and diagonal links among neighbouring cells. We kept all eigenvectors associated with Moran's I coefficients larger than the expected value of I , in order to model positive autocorrelation patterns (Dray *et al.*, 2006). Summarizing, we created for each cell size and each forest plot a data table \mathbf{S} containing the eigenvectors to be used as spatial predictors.

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Table S2 Summary statistics of the topography variables calculated for the ten forest plots. For each topographic factor, we report the mean and standard deviation of values measured at the different cell sizes. #Cells: Number of grid cells.

	Cell size	#Cells	Elev. (m)		Convexity		Slope (°)		EW aspect		NS aspect	
			Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Yasuni	10×10	5,000	228	8.3	0.008	1.94	12.1	7.14	-0.03	0.76	-0.02	0.64
	20×20	1,250	228	8.1	-0.044	2.78	12.5	7.11	-0.04	0.77	-0.01	0.64
	25×25	800	228	7.9	0.000	1.71	11.2	6.09	-0.04	0.77	-0.03	0.63
	50×50	200	228	6.9	-0.153	2.94	9.4	4.09	-0.03	0.79	-0.02	0.62
	100×100	50	229	5.4	0.208	3.94	7.4	2.21	-0.19	0.83	-0.08	0.55
Pasoh	10×10	5,000	-3	4.7	-0.001	0.36	2.8	2.45	-0.23	0.66	-0.01	0.72
	20×20	1,250	-3	4.7	0.007	0.56	2.9	2.41	-0.24	0.66	-0.01	0.72
	25×25	800	-3	4.7	0.111	1.27	2.7	2.39	-0.26	0.66	-0.01	0.71
	50×50	200	-3	4.5	-0.557	2.05	2.5	2.25	-0.31	0.62	-0.04	0.72
	100×100	50	-3	4.2	-1.295	3.17	2.3	2.03	-0.39	0.64	-0.05	0.68
Korup	10×10	5,000	79	24.3	0.020	1.16	8.3	7.41	-0.07	0.64	-0.21	0.74
	20×20	1,250	79	24.2	0.000	1.59	8.5	7.36	-0.06	0.63	0.21	0.74
	25×25	800	79	24.2	0.642	4.09	7.8	6.92	-0.07	0.64	0.23	0.73
	50×50	200	79	23.9	6.066	12.84	7.2	6.46	-0.08	0.63	0.24	0.73
	100×100	50	79	23.6	23.488	26.27	6.3	5.55	-0.06	0.61	0.33	0.73
BCI	10×10	5,000	144	8.0	0.006	0.63	5.2	4.13	-0.03	0.72	-0.37	0.58
	20×20	1,250	144	7.9	0.078	0.76	5.0	3.70	-0.03	0.71	-0.39	0.58
	25×25	800	144	7.9	0.737	4.43	4.9	3.52	-0.03	0.72	-0.39	0.57
	50×50	200	144	7.7	-0.443	4.77	4.7	3.09	-0.02	0.72	-0.40	0.56
	100×100	50	144	7.4	-2.859	7.77	4.4	2.76	-0.05	0.74	-0.40	0.55
Xishuangbanna	10×10	2,000	765	31.1	0.195	4.09	28.6	7.66	-0.22	0.65	-0.21	0.69
	20×20	500	765	30.8	0.328	5.77	27.1	6.51	-0.25	0.64	-0.22	0.69
	25×25	320	765	30.6	0.247	3.83	25.9	6.74	-0.27	0.62	-0.25	0.70
	50×50	80	765	29.3	0.608	7.31	22.5	7.12	-0.35	0.58	-0.29	0.68
	100×100	20	767	25.9	1.647	10.80	17.5	4.41	-0.35	0.46	-0.38	0.75
Dinghushan	10×10	2,000	339	51.0	0.240	3.98	32.3	8.49	0.40	0.58	0.23	0.67
	20×20	500	339	50.8	0.172	5.61	32.6	7.96	0.40	0.58	0.23	0.67
	25×25	320	339	50.6	4.977	12.14	31.3	7.73	0.42	0.58	0.24	0.66
	50×50	80	339	49.6	36.767	55.35	29.4	7.04	0.45	0.59	0.26	0.63
	100×100	20	339	48.0	70.396	56.38	25.6	7.55	0.58	0.44	0.40	0.59
Lienhvachi	10×10	2,500	764	35.8	-0.123	4.16	31.9	8.75	0.13	0.74	0.10	0.66
	20×20	625	764	35.9	-0.257	7.54	33.4	8.69	0.14	0.73	-0.11	0.66
	25×25	400	765	35.2	-0.151	4.06	28.6	7.80	0.14	0.73	-0.12	0.65
	50×50	100	765	33.6	-0.665	9.04	27.2	6.98	0.10	0.74	-0.15	0.66
	100×100	25	766	30.7	-4.258	19.17	23.9	4.64	0.08	0.72	-0.21	0.68
Fushan	10×10	2,500	675	20.2	0.057	3.36	21.9	11.5	0.019	0.73	-0.100	0.67
	20×20	625	675	19.7	-0.012	4.83	21.2	10.7	0.021	0.74	-0.108	0.66
	25×25	400	675	19.6	0.004	3.14	20.0	10.3	0.020	0.74	-0.126	0.66
	50×50	100	676	18.3	-0.226	6.54	18.6	9.19	0.029	0.76	-0.150	0.64
	100×100	25	676	15.5	-1.857	11.81	15.9	8.35	0.035	0.75	-0.114	0.69
Gutian-shan	10×10	2,400	135	56.1	0.007	4.17	37.0	8.89	0.00	0.63	-0.71	0.31
	20×20	600	134	56.5	0.237	6.40	37.5	6.59	-0.01	0.69	-0.57	0.45
	25×25	384	135	55.5	-0.017	4.04	30.2	6.78	-0.01	0.63	-0.71	0.32
	50×50	96	135	55.2	0.508	5.95	30.1	5.98	-0.01	0.59	-0.76	0.27
	100×100	24	134	54.5	-1.081	14.17	27.6	5.97	-0.01	0.55	-0.83	0.17
Changbai-shan	10×10	2,500	803	3.5	0.007	0.40	3.0	2.14	0.16	0.55	-0.35	0.74
	20×20	625	803	3.5	0.016	0.42	3.1	2.38	0.17	0.55	-0.35	0.74
	25×25	400	803	3.5	0.101	0.86	2.6	1.38	0.18	0.54	-0.37	0.74
	50×50	100	803	3.5	-0.258	1.62	2.4	1.02	0.18	0.50	-0.38	0.76
	100×100	25	803	3.3	-1.462	2.94	2.1	0.79	0.17	0.47	-0.36	0.81

Table S3: Beta diversity values for each forest plot and cell size. #Cells: Number of grid cells; BD_{Total}: Total observed beta diversity; BD_{Null}: Mean of the distribution of beta diversity values under the null model; BD_{Diff}: Difference between BD_{Total} and BD_{Null}; BD_[a] to BD_[d]: Beta diversity components obtained from variation partitioning.

	Cell size	#Cells	BD _{Total}	BD _{Null}	BD _{Diff}	BD _[a]	BD _[b]	BD _[c]	BD _[d]
Yasuni	10×10	5,000	0.8095	0.7514	0.0581	0.000	0.033	0.113	0.664
	20×20	1,250	0.6216	0.4962	0.1254	0.003	0.049	0.113	0.457
	25×25	800	0.5486	0.4070	0.1417	0.007	0.047	0.109	0.386
	50×50	200	0.3295	0.1728	0.1567	0.007	0.039	0.077	0.206
	100×100	50	0.1697	0.0517	0.1180	-0.002	0.032	0.011	0.129
Pasoh	10×10	5,000	0.7873	0.7290	0.0583	0.000	0.030	0.125	0.632
	20×20	1,250	0.5742	0.4399	0.1344	0.001	0.047	0.133	0.394
	25×25	800	0.4993	0.3456	0.1537	0.002	0.050	0.128	0.319
	50×50	200	0.3058	0.1266	0.1792	0.001	0.058	0.100	0.146
	100×100	50	0.1833	0.0353	0.1480	0.010	0.043	0.047	0.084
Korup	10×10	5,000	0.6558	0.4676	0.1881	0.001	0.107	0.182	0.366
	20×20	1,250	0.4954	0.2297	0.2657	0.002	0.128	0.152	0.213
	25×25	800	0.4482	0.1728	0.2754	0.003	0.126	0.143	0.176
	50×50	200	0.3256	0.0627	0.2629	0.009	0.129	0.087	0.100
	100×100	50	0.2392	0.0189	0.2203	0.005	0.126	0.040	0.068
BCI	10×10	5,000	0.5505	0.4569	0.0936	0.000	0.027	0.118	0.405
	20×20	1,250	0.3636	0.2328	0.1308	0.001	0.038	0.093	0.232
	25×25	800	0.3096	0.1741	0.1355	0.001	0.039	0.086	0.176
	50×50	200	0.1853	0.0591	0.1263	0.003	0.041	0.051	0.090
	100×100	50	0.1129	0.0167	0.0962	0.009	0.033	0.026	0.044
Xishuang- banna	10×10	2,000	0.6169	0.4721	0.1448	0.001	0.085	0.153	0.378
	20×20	500	0.4749	0.2690	0.2059	0.004	0.113	0.132	0.226
	25×25	320	0.4308	0.2113	0.2195	0.007	0.110	0.127	0.187
	50×50	80	0.3037	0.0792	0.2245	0.020	0.095	0.068	0.119
	100×100	20	0.1917	0.0236	0.1681	-0.056	0.111	-0.039	0.176
Dinghushan	10×10	2,000	0.6567	0.4474	0.2093	0.001	0.102	0.216	0.337
	20×20	500	0.4864	0.1846	0.3018	0.003	0.118	0.172	0.193
	25×25	320	0.4346	0.1339	0.3007	0.004	0.115	0.160	0.155
	50×50	80	0.3159	0.0455	0.2705	0.014	0.097	0.098	0.106
	100×100	20	0.2283	0.0146	0.2137	-0.011	0.103	0.038	0.098
Lienhuachi	10×10	2,500	0.6205	0.3113	0.3092	0.000	0.081	0.213	0.326
	20×20	625	0.4431	0.1129	0.3303	0.006	0.089	0.163	0.185
	25×25	400	0.3928	0.0755	0.3173	0.006	0.093	0.144	0.150
	50×50	100	0.2631	0.0199	0.2432	0.014	0.060	0.104	0.084
	100×100	25	0.1772	0.0049	0.1723	0.020	0.003	0.094	0.060
Fushan	10×10	2,500	0.4570	0.2585	0.1985	0.001	0.068	0.089	0.299
	20×20	625	0.2838	0.0881	0.1958	0.005	0.064	0.070	0.146
	25×25	400	0.2381	0.0588	0.1793	0.004	0.060	0.062	0.112
	50×50	100	0.1419	0.0160	0.1259	0.009	0.040	0.036	0.057
	100×100	25	0.0887	0.0042	0.0844	0.008	0.017	0.012	0.051
Gutian- shan	10×10	2,400	0.5311	0.3274	0.2037	0.001	0.082	0.166	0.282
	20×20	600	0.3508	0.1159	0.2349	0.006	0.090	0.105	0.150
	25×25	384	0.3067	0.0808	0.2260	0.004	0.086	0.086	0.130
	50×50	96	0.2045	0.0249	0.1795	0.016	0.066	0.039	0.083
	100×100	24	0.1277	0.0073	0.1203	0.041	0.026	0.027	0.034
Changbai- shan	10×10	2,500	0.5012	0.3364	0.1648	0.001	0.040	0.103	0.358
	20×20	625	0.2720	0.1226	0.1493	0.002	0.047	0.059	0.164
	25×25	400	0.2208	0.0868	0.1340	0.002	0.048	0.044	0.127
	50×50	100	0.1336	0.0288	0.1047	-0.001	0.052	0.021	0.062
	100×100	25	0.0930	0.0090	0.0840	0.013	0.036	0.016	0.029

