1 **Species packing and the latitudinal gradient in local beta-diversity**

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Abstract

56   The latitudinal gradient of declining species richness at higher latitudes is among the most

57   fundamental patterns in ecology. However, whether changes in species composition across

58   space (beta-diversity) contribute to this global gradient of species richness remains debated.

59   Previous studies that failed to resolve the issue suffered from a well-known tendency for

60   small samples in high gamma-diversity areas to inflate measures of beta-diversity. We

61   provide here a rigorous test, comparing species-packing and local heterogeneity across a

62   latitudinal gradient in tree species richness in Asia, using beta-diversity metrics that correct

63   the gamma-diversity and sampling bias. Our data include 21 large forest plots across a wide

64   environmental gradient in East Asia. We demonstrate that local beta-diversity increases with

65   topographic heterogeneity, but after accounting for this and correcting the gamma-diversity

66   bias, tropical forests still have higher beta-diversity than temperate, contributing to the

67   latitudinal gradient of species richness. This supports the hypothesis of tighter species packing

68   and larger niche space in tropical forests while demonstrating the importance of local

69   processes in controlling beta-diversity.

70

Main Text

72   Beta-diversity is the spatial organization of local (alpha-) diversity at larger scales, and it is

73   arguably more important to conservation than local diversity [1-3]. Conserving species richness,

74   for example, must consider whether diversity is concentrated within sites or spread across

75 many sites [1]. Are observed gradients in species richness around the world caused by

76 differences in beta-diversity [4-7]? For example, is the well-known latitudinal gradient in species

77 richness associated with beta-diversity, in other words, do tropical communities have more

78 habitat heterogeneity, larger niche space or narrower niches than temperate communities?

79 These questions continue to be debated, with researchers reaching opposite conclusions [8-13].

80 Underlying the debate has been controversy about statistical biases in tools for measuring

81 beta-diversity [12,14-16].

82 The bias arising in beta-diversity metrics is a dependence on sample size that interacts with

83 overall species richness (gamma-diversity) [12,14-16]. It is easy to illustrate using simple

84 measures of species overlap. Small samples never capture all local species, and it follows that

85 two small samples will appear to differ by randomly capturing a different set of local species,

86 causing an increase in species overlap with the fraction of species sampled [14,16]. As a result,

87 high local species richness will artificially inflate beta-diversity [12]. This bias has led to metrics

88 that correct for sample size [14,17,18] or tools based on comparisons with null models [12,15].

89 Crucial in the sample size bias is the dependence on gamma-diversity it engenders, since

90 bigger samples are needed in richer communities [14,16,17]. Once correcting for sample size bias,

91 gamma-diversity dependence should be removed, and it should be straightforward to compare

92 beta-diversity across a gradient of species diversity in order to judge the importance of local

93 species packing.

94 We carry out this comparison using the steep latitudinal gradient in tree species richness as

95 documented in our census of 3 million trees at 21 sites spanning 50° of latitude in East Asia

96 (Fig. 1 and Extended Data Table 1) [19,20]. In a simulation study [18], we tested several metrics of

97 beta-diversity, including a null model approach plus sample size correction methods designed

98 by Chao *et al*. [17]. We identified the corrected beta Shannon entropy and similar metrics as

99 highly effective at removing dependence on gamma-diversity and sample size [18]. These

4

100   indices thus allow us to answer two fundamental questions about the source of local species

101   richness: 1) Is there a latitudinal gradient in beta-diversity revealed by the corrected beta

102   Shannon entropy? 2) Do local environmental heterogeneity, niche specialization (the ratio of

103   the narrowness of available habitat of a plot to that of a species) and marginality (the distance

104   between the species optimum relative to the mean habitat of a plot) contribute to the

105   latitudinal patterns of local beta-diversity? By testing simultaneously the importance of local

106   heterogeneity and latitude we can establish whether species-packing contributes to higher

107   richness in tropical relative to temperate forests [21,22].

108

109   Gamma-diversity declined by more than forty-fold between tropical and temperate latitudes,

110   from 818 species at Pasoh to 18 at Daxinganling (Extended Data Table 1). Local beta-

111   diversity also declined with latitude, and this pattern was stronger at small scales (Fig. 2a).

112   We found positive correlations between local topographic heterogeneity and beta-diversity

113   (Fig. 2b). Further, beta-diversity was correlated with both latitude and topographic

114   heterogeneity in multiple linear regression models, but the relative effect size varied as scale

115   changed (Fig. 2c). Specifically, the effect of adjusted latitude decreased, whereas the effect of

116   topographic heterogeneity increased at larger scales.

117   Both community-level niche specialization (species-level niche specialization weighted by

118   relative species abundance) and niche marginality (species-level niche marginality weighted

119   by relative species abundance) decreased from tropical to temperate forests after controlling

120   local topographic heterogeneity, suggesting narrower niche width and larger niche space in

121   tropical forests (Figs. 3a-3d). Moreover, niche specialization and niche marginality were

122   positively correlated with each other across scales (Extended Data Figs. 2g-2i). Meanwhile,

123   they were both well predicted by local topographic heterogeneity across scales (Extended

124   Data Figs. 2a-2f). Furthermore, multiple linear regression models revealed that the effect sizes

125   of topographic heterogeneity were much larger than those of adjusted latitude across scales,

126   although their effect sizes were scale-dependent (Figs. 3b and 3d).

127

128   Our results confirm that local beta-diversity increases from boreal toward tropical forests of

129   Asia after accounting for local topographic heterogeneity. Previous studies demonstrating this

130   pattern [3,5,21] have been questioned due to the bias of inflated beta-diversity at high gamma-

131   diversity regions [12,15]. We found that the gradient persisted, however, even after removing the

132   gamma-diversity bias and controlling for local topographic heterogeneity. This suggests that

133   local beta-diversity contributes to the latitudinal gradient in species richness.

134   Given higher species turnover with topography and greater niche specialization and

135   marginality at the same scales at lower latitude, there must be tighter species packing and

136   larger niche space in tropical relative to temperate forests [4,7,21,23,24]. This hypothesis has been

137   floated for decades, attributed to higher and more stable productivity in the tropics: a larger

138   niche space enables more species to persist at low abundance and allows species to specialize

139   on narrower subsets of the resources available [7,22-25]. Since topographic heterogeneity did not

140   vary with latitude (Extended Data Fig. 3), it appears that local topographic heterogeneity does

141   not contribute to the latitudinal gradient in local beta-diversity, in line with previous findings

142   of Ricklefs and He [26] and Chu et al. [27].

143   We also conclude that local beta-diversity is driven largely by local processes—specifically,

144   topographic heterogeneity and the niche differentiation it fosters (Figs. 2 and 3). This may

145   seem an unsurprising result, but the role of local ecological processes has been questioned

146   given the broad latitudinal gradient of gamma-diversity [4,12]. We suggest that the effect of local

147   processes has been obscured by gamma-diversity dependence in previous studies [15].

148   Moreover, our large samples over 55 degrees of latitude provide comparable measures of

149   niche differentiation, topographic heterogeneity, and beta-diversity, well beyond what was

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150 available in early studies [28,29]. Our results could be refined by considering the influence of

151 additional factors that contribute to local environmental heterogeneity and niche

152 differentiation, such as soil types and soil nutrients [30], because we expect these additional

153 local factors to contribute to beta-diversity. In addition, it is necessary to examine these

154 metrics of beta-diversity that incorporate gamma-diversity and sample size corrections in

155 other taxa and regions. Gamma-diversity dependence is also associated with other attributes

156 of ecosystem such as species abundance distribution [31] and should be examined in other

157 systems.

158 We found that a latitudinal gradient in local beta-diversity contributes to the broad latitudinal

159 pattern of species richness after separately controlling for gamma-diversity and local

160 topographic heterogeneity. The results suggest tighter species packing and larger niche space

161 in tropical forests [4,22,23], but also confirmed environmental heterogeneity as a determinant of

162 beta-diversity. Our findings may help resolve recent debates on the contribution of local beta-

163 diversity to latitudinal gradient of species richness.

164

165 **Materials and Methods**

166 **Forest dynamic plots** We used data from 21 forest dynamics plots that are part of the

167 ForestGEO and Chinese Forest Biodiversity Monitoring Networks [19,20] (Fig. 1a and Extended

168 Data Table 1). All stems with diameter at breast height (DBH) $\geq$ 1 cm were spatially mapped,

169 tagged, measured and identified to species [32]. The plots range from tropical rain forest at 2.98°

170 N latitude to boreal forest at 51.82° N latitude (Extended Data Table 1). Plots vary from sea

171 level to more than 1400 m elevation, and within-plot elevation range is as low as 17.7 m and

172 as high as 298.6 m (Extended Data Table 1 and Fig. 1b).

173

174   **Measurement of beta-diversity** To circumvent gamma-diversity dependence caused by

175   sample-size bias of beta-diversity metrics, we used a correction method designed for beta

176   Shannon entropy based on the relationship between cumulative diversity curve and sample

177   size [33]. The beta Shannon entropy measures the heterogeneity of pooled communities, and is

178   calculated as the effective number of compositionally distinct and equally abundant

179   communities [34,35]. As the beta Shannon entropy incorporates species abundance, it could

180   weight common or rare species more by changing the diversity order q [34]. Here we chose

181   diversity of order $q = 1$ for weighting all species by their abundance, without favoring either

182   common or rare species. Additionally, observed species diversity in a sample is known to be a

183   biased estimate of true species diversity, and is highly sensitive to the area surveyed, the

184   number of individuals counted, and the regional species pool size [36]. We thus used a sample-

185   size dependence correction method to produce accurate, low-bias estimates of the beta

186   Shannon entropy for comparing beta-diversity among regions [17,33]. In this approach, similar to

187   a species accumulation curve, the expected cumulative alpha- or gamma-diversity is

188   analytically depicted as a function of sample size, while sample completeness is estimated

189   from community structures of samples [17,33]. Beta-diversity can then be estimated from the

190   predicted alpha- and gamma-diversity under hypothetical complete sampling based on the

191   diversity-sample size curve. For a comparison, we also used a pairwise dissimilarity metric –

192   the Jaccard-Chao index (Extended Data Fig. 1), which corrects undersampling bias by

193   estimating the effect of undetected shared species [37]. Our simulations confirmed that β-

194   metrics that incorporate an undersampling correction method are more effective at removing

195   dependence on gamma-diversity and sample size, compared with other conventional beta-

196   diversity metrics [18].

197   **Local topographic heterogeneity, community-level niche differentiation** Local

198   topographic heterogeneity was quantified by the surface to planimetric area ratio [28]. Niche

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199   differentiation was described using attributes of specialization and marginality. Niche

200   specialization was defined as the ratio of the standard deviation of available habitat for a

201   community to that used by a species, and marginality was defined as the ecological distance

202   between a species optimum and the mean habitat within the plot [38,39]. Specialization and

203   marginality were calculated for each species with species composition data and six

204   topographic factors: mean elevation, convexity, slope, aspect, topographical wetness index

205   (TWI) and altitude above channel (ACH) - across spatial scales [40-42]. Aspect was computed as

206   sin(aspect) and cos(aspect), and other topographic variables were Box-Cox transformed

207   before being included into analysis [43]. We then calculated the mean community-level niche

208   specialization and marginality across all species occurring in at least ten subplots, weighting

209   by species abundance.

210   **Statistical analysis** To examine the significance of latitudinal gradients in explaining local

211   beta-diversity, niche specialization and niche marginality, we first modeled beta-diversity,

212   community-level niche specialization and niche marginality against topographic heterogeneity

213   and adjusted latitude (an upward shift of 100 m approximately equals to a poleward shift of

214   100 km) separately using simple linear regression models. Subsequently, to determine the

215   relative effect sizes of adjusted latitude and topography, we performed multiple linear

216   regression models with beta-diversity, niche specialization and marginality as response

217   variables respectively, and all variables were standardized by $(x-x')/SD(x)$ before being

218   included. To achieve normality of niche specialization (Extended Data Fig. 4a), the log- and

219   Box-Cox transformation [43] were employed (Extended Data Figs. 4b and 4c). Finally, the Box-

220   Cox transformed niche specialization were used in analyses, and for comparison, it was min-

221   max normalized into the range between [0, 1] using $((x-min(x))/(max(x)-min(x)))$. In total, we

222   conducted all the analyses across three spatial scales by dividing plots into quadrats of

223   different grain sizes (10 m × 10 m, 20 m × 20 m and 50 m × 50 m).

224   All statistical analyses were performed with R software, version 3.6.4 [44]. The corrected

225   Shannon entropy index was calculated using R package 'entropart' [45]. The topographic

226   variables were computed using 'RSAGA' package [46] and SAGA GIS [47]. Ecological niche

227   factor analysis (ENFA) was implemented to calculate niche metrics using R package

228   'adehabitatHS' [48].

229   **Data availability**

230   The data supporting Figure 1-3 have been deposited in the Dryad Digital Repository

231   (https://datadryad.org/stash/share/6bhhuxg5b3637cgOSzPVQzdyAPh9vy5hf29DCglp6hs).

232   Full census data are available upon reasonable request from the ForestGEO data portal,

233   http://ctfs.si.edu/datarequest/.

234   **Code availability**

235   The code used for data analysis have been deposited in the Dryad Digital Repository

236   (https://datadryad.org/stash/share/6bhhuxg5b3637cgOSzPVQzdyAPh9vy5hf29DCglp6hs).

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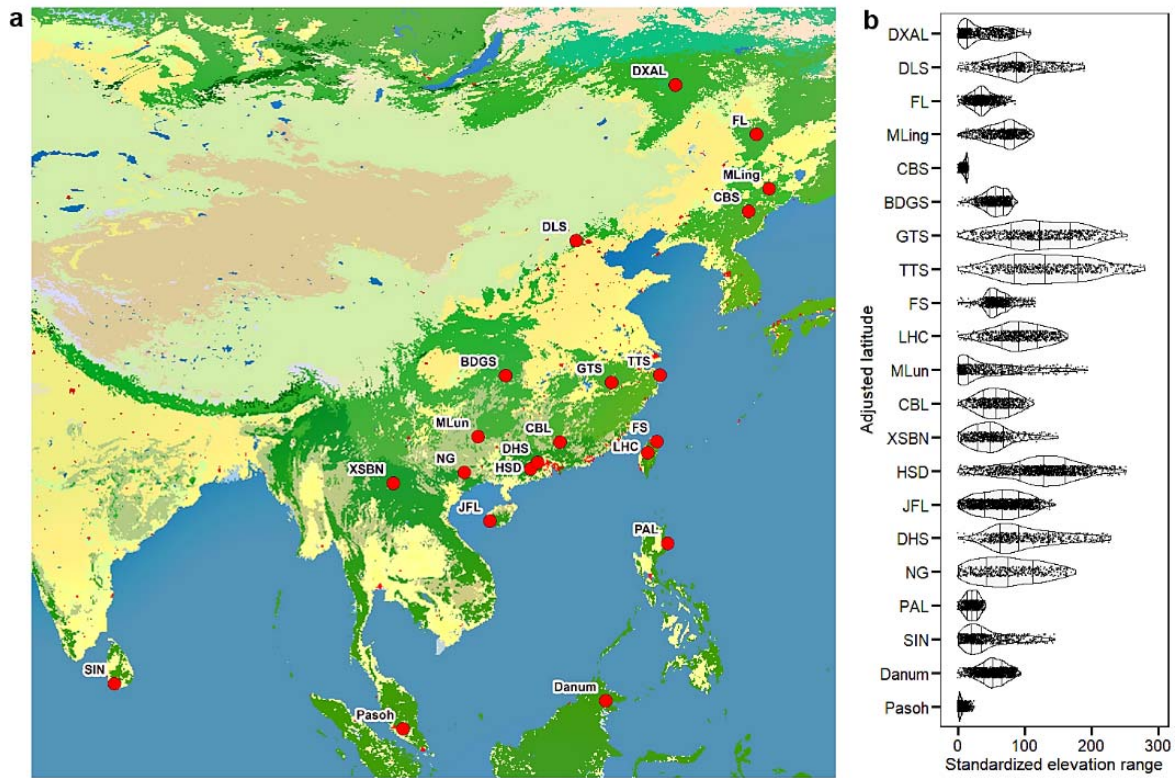
Figure 1 | The spatial distribution of forest dynamic plots (a, full plot names were listed in Extended Data Table 1) and the elevation range of each plot along latitude (b). Panel b shows the latitudinal pattern of elevation range, which was transformed by subtracting the minimum elevation of each plot. Latitude was adjusted with mean elevation (an upward shift of 100 m equal to a poleward shift of 100 km). The width of each violin plot reflects probability density distribution of mean elevation for 20 m × 20 m subplots in each forest dynamics plot.

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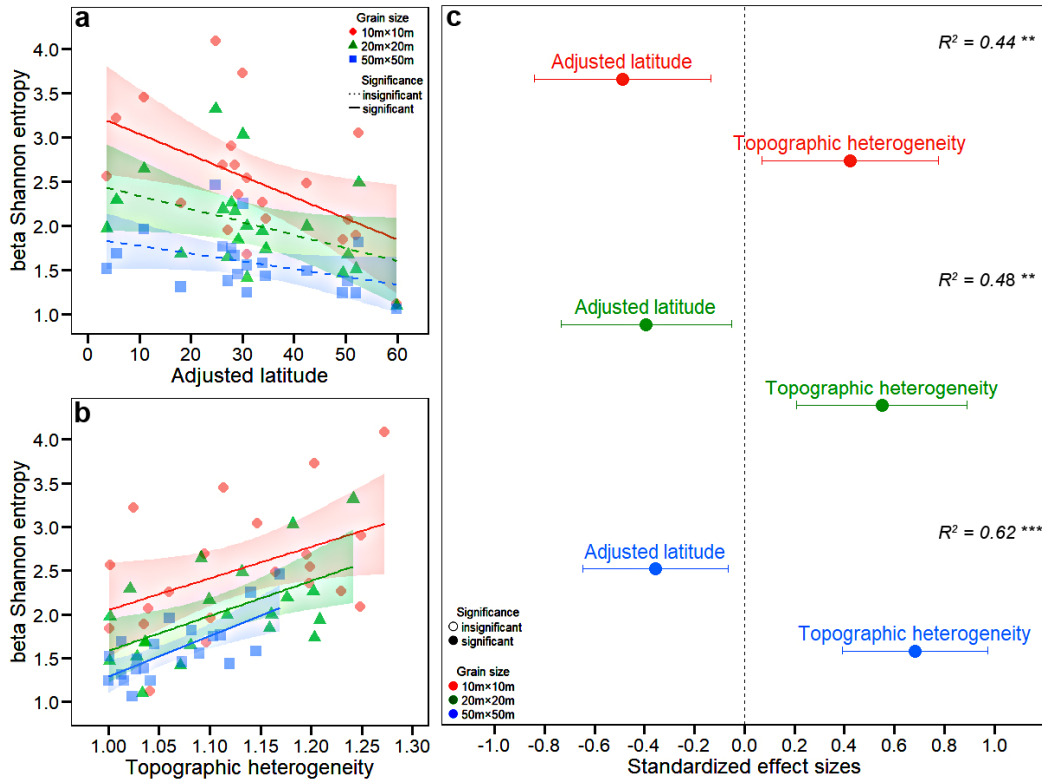
Figure 2 | The relationship of beta-diversity (corrected beta Shannon entropy) with adjusted latitude and local topographic heterogeneity across grain sizes. In each panel, different colours of points and lines represent grain sizes. In panel a and b, solid and dashed lines indicate significant and insignificant linear correlations (significance level, $\alpha = 0.05$), respectively. The shaded areas represent the 95% confidence interval of the predictions. The results of these linear regression models for beta-diversity across scales in panel a and b were listed in Extended Data Table 2. In panel c, points represent the standardized effect sizes of explanatory variables, and solid circles represent the standardized effect sizes of variables being significantly different from zero. The significance level of the total *R-square* are $\alpha < 0.001$, '***'; $\alpha < 0.01$, '**'; $\alpha < 0.05$ '*'.
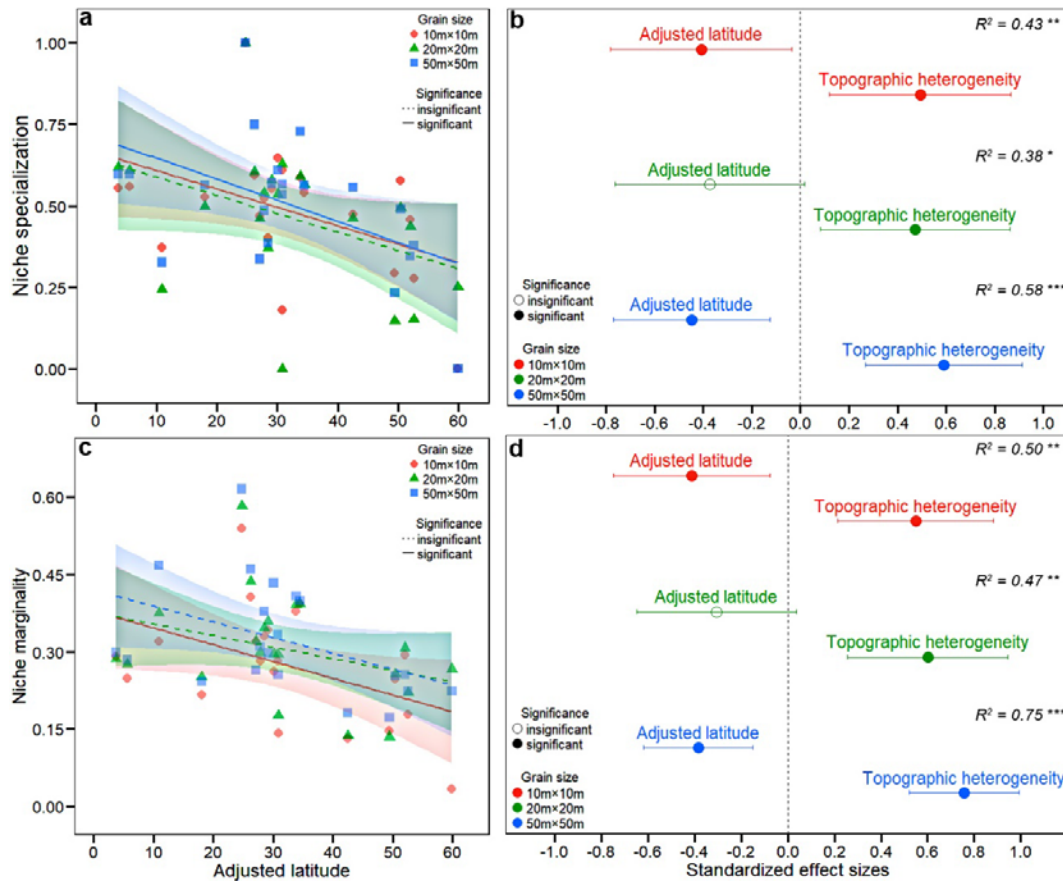
Figure 3 | The relationships of community-level niche specialization (a and b) and marginality (c and d) with adjusted latitude and local topographic heterogeneity across grain sizes. In each panel, different colours of points and lines represent grain sizes. In panel a and c, solid and dashed lines indicate significant and insignificant linear correlations (α = 0.05), respectively. The shaded areas represent the 95% confidence interval of the predictions. The results of these linear regression models for niche specialization and marginality in panel a and c were listed in Extended Data Table 3. In panel b and d, points represent the standardized effect sizes of explanatory variables, and solid and hollow circles represent the standardized effect sizes of variables being significantly and insignificantly different from zero. The significance level of the total *R-square* are $\alpha < 0.001$, '***'; $\alpha < 0.01$, '**'; $\alpha < 0.05$ '*'.

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405 **Author contributions**

406 KC, RC, XM, KM and JCS designed research, KC and XM compiled and analysed data; KC,

407 RC, XM, KM and JCS wrote drift with substantial input from LC, WX, DFRPB and MJB.

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408   Many authors contributed to data collection of forest censuses and all authors contributed to

409   revisions of the manuscript.

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411   **Competing interest**

412   The authors declare no competing financial interests.

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416   **Extended data**

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418   **Extended Data Table 1. | Basic information of 21 forest dynamic plots.**

Plot name	Area (ha)	Latitude (°N)	Longitude (°E)	Mean elevation (m)	Elevation range (m)	Gamma-diversity	Number of stems
Pasoh	50	2.98	102.31	80	24	818	335400
Danum Valley	50	5.1	117.69	54.1	101.12	642	234916
Sinharaja	25	6.4	80.4	499.5	151	239	250131
Palanan	16	17.04	122.38	111	55	415	66000
Jianfengling	60	18.73	108.9	932	150.4	290	439676
Xishuangbanna	20	21.6	101.57	765.1	159.87	467	95834
Nonggang	15	22.42	106.95	260	190	223	67870
Heishiding	50	22.7	111.99	568.8	263	236	264391
Dinghushan	20	23.17	112.52	339	240	195	71617
Lienhuachih	25	23.91	120.88	765.4	178	144	153268
Chebaling	20	24.72	114.22	488	131	222	86517
Fushan	25	24.76	121.56	675.3	133	110	114500
Mulun	25	25.13	108	547	208.8	254	144679
Gutianshan	24	29.25	118.12	580.6	268.6	159	140700
Badagongshan	25	29.77	110.09	1414	101	241	186556
Tiantongshan	20	29.81	121.79	447.25	298.63	152	115536
Donglingshan	20	40	115.43	1395	219.3	53	52136
Changbaishan	25	42.22	128.53	801.5	17.7	52	38902
Muling	25	43.95	130.07	719.5	123	57	63877
Fenglin	30	48.08	129.12	439	66	46	94920
Daxinganling	25	51.82	122.98	896.7	115.3	18	126532

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420   **Extended Data Table 2. | The results of simple linear regression models for beta-diversity across scales in Figure 2a and 2b.**

Explanatory variables	Grain size	Coefficients	Standard error	t-value	p-value	R-square
	10m × 10m	-0.024	0.01	-2.59	0.02	0.26
Adjusted	20m × 20m	-0.015	0.01	-2.01	0.06	0.18
latitude	50m × 50m	-0.0087	0.01	-1.86	0.08	0.15
	10m × 10m	3.62	1.65	2.19	0.04	0.20
Topographic	20m × 20m	4.00	1.33	3.02	0.007	0.32
heterogeneity	50m × 50m	4.63	1.08	4.28	<0.001	0.49

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423 **Extended Data Table 3. The results of simple regression models for niche specialization and marginality against adjusted latitude in**
424 **Figure 3a and 3c.**

| Response variables	Grain size	Coefficients	Standard error	t-value	p-value	R-square
	10m × 10m	-0.0057	0.0027	-2.10	0.049	0.19
Niche	20m × 20m	-0.0056	0.0030	-1.88	0.076	0.16
specialization	50m × 50m	-0.0065	0.0027	-2.38	0.028	0.23
	10m × 10m	-0.0033	0.0015	-2.15	0.044	0.20
Niche	20m × 20m	-0.0022	0.0014	-1.55	0.14	0.11
marginality	50m × 50m	-0.0031	0.0015	-2.04	0.013	0.055

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428 **Extended Data Table 4. | The results of the simple regression models for beta-diversity measured by the Jaccard-Chao index in**
429 **Extended Data Figure 1a and 1b.**

| Explanatory variables	Grain size	Coefficients	Standard error	t-value	p-value	R-square
	10m × 10m	-0.0025	0.001	-3.03	0.0068	0.33
Adjusted	20m × 20m	-0.0018	0.001	-2.49	0.022	0.25
latitude	50m × 50m	-0.00068	0.0003	-1.86	0.078	0.15
	10m × 10m	0.24	0.16	1.45	0.16	0.10
Topographic	20m × 20m	0.30	0.15	1.95	0.066	0.17
heterogeneity	50m × 50m	0.27	0.10	2.74	0.013	0.28

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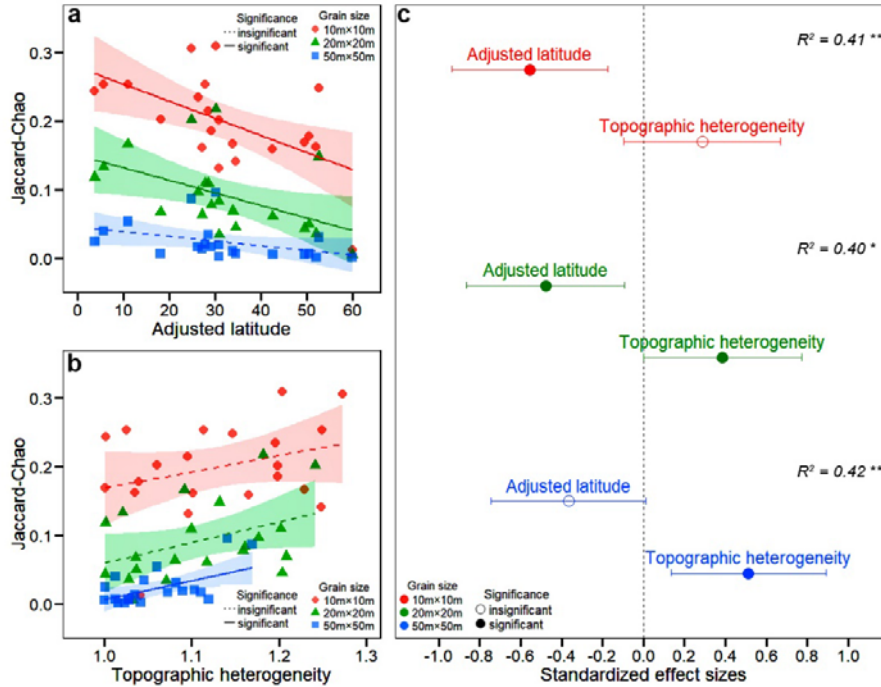
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435 **Extended Data Figure 1 | The linear relationship of beta-diversity (measured by the Jaccard-Chao index) with adjusted latitude (a) and**

436 **local topographic heterogeneity (b) across grain sizes.** In each panel, different colours of points and lines represent grain sizes. In panel a and

437 b, solid and dashed lines indicate significant and insignificant linear correlations (significance level, α = 0.05), respectively. The shaded areas

438 represent the 95% confidence interval of the predictions. In panel c, points represent the standardized effect sizes of explanatory variables, and

439 solid and hollow circles represent variables with values significantly and insignificantly different from zero, respectively. The output of these linear

440 regression models in panel a and b were listed in Extended Data Table 4. The total *R-square* and significance level (α < 0.001, '***'; α < 0.01, '**';

441 α < 0.05 '*') were annotated at the top-right corner for each multiple linear model in panel c.

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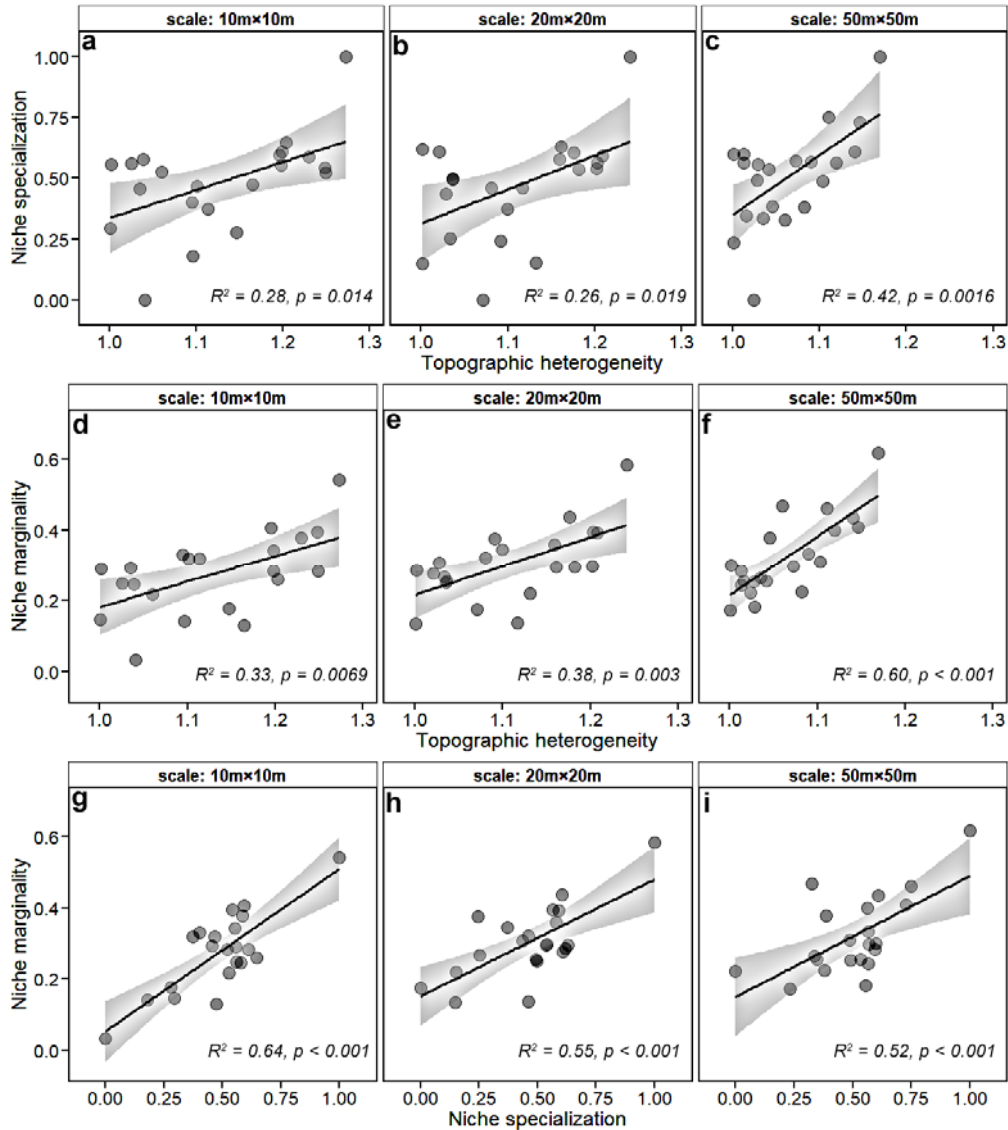
Extended Data Figure 2 | The linear relationships between topographic heterogeneity, community-level niche specialization and niche marginality across grain sizes (a, d and g: 10 m × 10 m; b, e and h: 20 m × 20 m; c, f and i: 50 m × 50 m). The niche specialization was transformed into normality using a Box-Cox transformation, and then was rescaled to the range in [0, 1] with the min-max normalization. Topographic heterogeneity was quantified as surface: Planimetric area ratio. The *R-square* and *p-value* were shown in each panel for simple linear regression models.
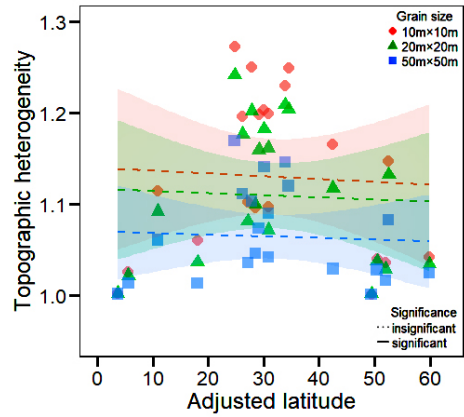
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Extended Data Figure 3 | **The linear relationship between topographic heterogeneity (quantified by the surface to planimetric area ratio)**

and adjusted latitude across grain sizes (10 m × 10 m, 20 m × 20 m and 50 m × 50 m). Dashed lines indicate insignificant linear correlations

(significance level, $\alpha = 0.05$), and different colours of points and lines represent grain sizes.

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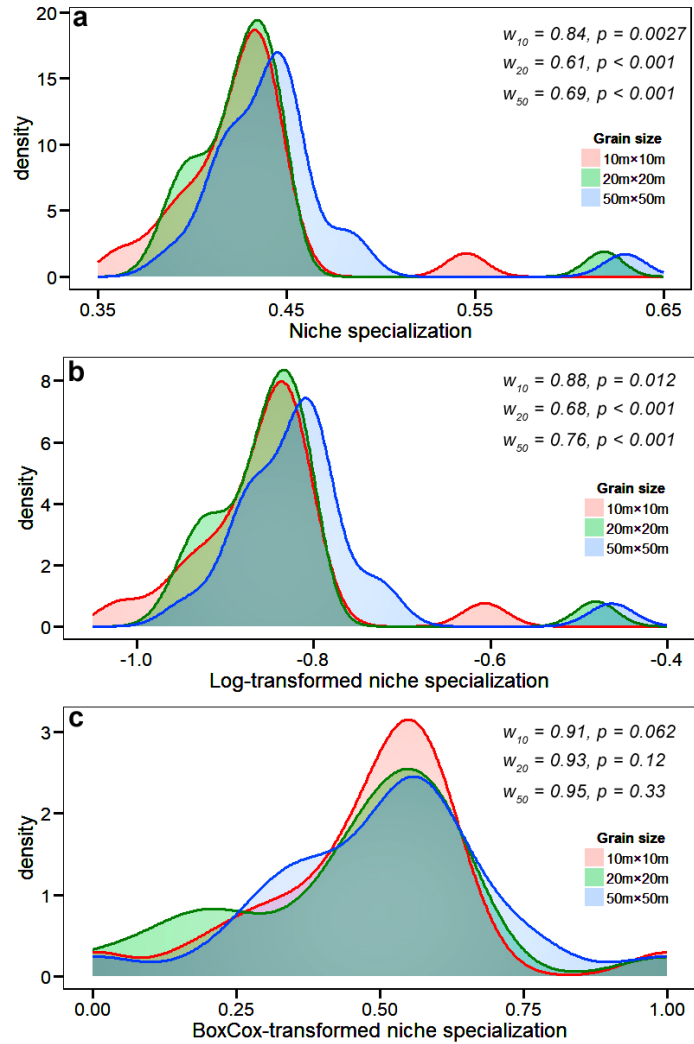
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470 **Extended Data Figure 4 | The Shapiro-Wilk test of normality for the observed (a), log-transformed (b), and Box-Cox transformed (c)**

471 **niche specialization.** In each panel, the kernel density curves with different colours showed the probability distribution of niche specialization

472 across grain sizes. The value of the Shapiro-Wilk statistic (w) and p-value across grain sizes were annotated at the top-right corner in each panel.

473 W10, W20 and W50 were values of the Shapiro-Wilk statistic at scales of 10 m × 10 m, 20 m × 20 m and 50 m × 50 m.

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