Species packing and the latitudinal gradient in local beta-diversity

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Abstract

The latitudinal gradient of declining species richness at higher latitudes is among the most fundamental patterns in ecology. However, whether changes in species composition across space (beta-diversity) contribute to this global gradient of species richness remains debated. Previous studies that failed to resolve the issue suffered from a well-known tendency for small samples in high gamma-diversity areas to inflate measures of beta-diversity. We provide here a rigorous test, comparing species-packing and local heterogeneity across a latitudinal gradient in tree species richness in Asia, using beta-diversity metrics that correct the gamma-diversity and sampling bias. Our data include 21 large forest plots across a wide environmental gradient in East Asia. We demonstrate that local beta-diversity increases with topographic heterogeneity, but after accounting for this and correcting the gamma-diversity bias, tropical forests still have higher beta-diversity than temperate, contributing to the latitudinal gradient of species richness. This supports the hypothesis of tighter species packing and larger niche space in tropical forests while demonstrating the importance of local processes in controlling beta-diversity.

Main Text

Beta-diversity is the spatial organization of local (alpha-) diversity at larger scales, and it is arguably more important to conservation than local diversity [1-3]. Conserving species richness, for example, must consider whether diversity is concentrated within sites or spread across

many sites [1]. Are observed gradients in species richness around the world caused by differences in beta-diversity [4-7]? For example, is the well-known latitudinal gradient in species richness associated with beta-diversity, in other words, do tropical communities have more habitat heterogeneity, larger niche space or narrower niches than temperate communities? These questions continue to be debated, with researchers reaching opposite conclusions [8-13]. Underlying the debate has been controversy about statistical biases in tools for measuring beta-diversity [12,14-16].

The bias arising in beta-diversity metrics is a dependence on sample size that interacts with overall species richness (gamma-diversity) [12,14-16]. It is easy to illustrate using simple measures of species overlap. Small samples never capture all local species, and it follows that two small samples will appear to differ by randomly capturing a different set of local species, causing an increase in species overlap with the fraction of species sampled [14,16]. As a result, high local species richness will artificially inflate beta-diversity [12]. This bias has led to metrics that correct for sample size [14,17,18] or tools based on comparisons with null models [12,15]. Crucial in the sample size bias is the dependence on gamma-diversity it engenders, since bigger samples are needed in richer communities [14,16,17]. Once correcting for sample size bias, gamma-diversity dependence should be removed, and it should be straightforward to compare beta-diversity across a gradient of species diversity in order to judge the importance of local species packing.

We carry out this comparison using the steep latitudinal gradient in tree species richness as documented in our census of 3 million trees at 21 sites spanning 50° of latitude in East Asia (Fig. 1 and Extended Data Table 1) [19,20]. In a simulation study [18], we tested several metrics of beta-diversity, including a null model approach plus sample size correction methods designed by Chao *et al*. [17]. We identified the corrected beta Shannon entropy and similar metrics as highly effective at removing dependence on gamma-diversity and sample size [18]. These

indices thus allow us to answer two fundamental questions about the source of local species richness: 1) Is there a latitudinal gradient in beta-diversity revealed by the corrected beta Shannon entropy? 2) Do local environmental heterogeneity, niche specialization (the ratio of the narrowness of available habitat of a plot to that of a species) and marginality (the distance between the species optimum relative to the mean habitat of a plot) contribute to the latitudinal patterns of local beta-diversity? By testing simultaneously the importance of local heterogeneity and latitude we can establish whether species-packing contributes to higher richness in tropical relative to temperate forests [21,22].

Gamma-diversity declined by more than forty-fold between tropical and temperate latitudes, from 818 species at Pasoh to 18 at Daxinganling (Extended Data Table 1). Local beta-diversity also declined with latitude, and this pattern was stronger at small scales (Fig. 2a). We found positive correlations between local topographic heterogeneity and beta-diversity (Fig. 2b). Further, beta-diversity was correlated with both latitude and topographic heterogeneity in multiple linear regression models, but the relative effect size varied as scale changed (Fig. 2c). Specifically, the effect of adjusted latitude decreased, whereas the effect of topographic heterogeneity increased at larger scales.

Both community-level niche specialization (species-level niche specialization weighted by relative species abundance) and niche marginality (species-level niche marginality weighted by relative species abundance) decreased from tropical to temperate forests after controlling local topographic heterogeneity, suggesting narrower niche width and larger niche space in tropical forests (Figs. 3a-3d). Moreover, niche specialization and niche marginality were positively correlated with each other across scales (Extended Data Figs. 2g-2i). Meanwhile, they were both well predicted by local topographic heterogeneity across scales (Extended Data Figs. 2a-2f). Furthermore, multiple linear regression models revealed that the effect sizes

of topographic heterogeneity were much larger than those of adjusted latitude across scales, although their effect sizes were scale-dependent (Figs. 3b and 3d).

Our results confirm that local beta-diversity increases from boreal toward tropical forests of Asia after accounting for local topographic heterogeneity. Previous studies demonstrating this pattern [3,5,21] have been questioned due to the bias of inflated beta-diversity at high gamma-diversity regions [12,15]. We found that the gradient persisted, however, even after removing the gamma-diversity bias and controlling for local topographic heterogeneity. This suggests that local beta-diversity contributes to the latitudinal gradient in species richness.

Given higher species turnover with topography and greater niche specialization and marginality at the same scales at lower latitude, there must be tighter species packing and larger niche space in tropical relative to temperate forests [4,7,21,23,24]. This hypothesis has been floated for decades, attributed to higher and more stable productivity in the tropics: a larger niche space enables more species to persist at low abundance and allows species to specialize on narrower subsets of the resources available [7,22-25]. Since topographic heterogeneity did not vary with latitude (Extended Data Fig. 3), it appears that local topographic heterogeneity does not contribute to the latitudinal gradient in local beta-diversity, in line with previous findings of Ricklefs and He [26] and Chu et al. [27].

We also conclude that local beta-diversity is driven largely by local processes—specifically, topographic heterogeneity and the niche differentiation it fosters (Figs. 2 and 3). This may seem an unsurprising result, but the role of local ecological processes has been questioned given the broad latitudinal gradient of gamma-diversity [4,12]. We suggest that the effect of local processes has been obscured by gamma-diversity dependence in previous studies [15].

Moreover, our large samples over 55 degrees of latitude provide comparable measures of niche differentiation, topographic heterogeneity, and beta-diversity, well beyond what was

available in early studies [28,29]. Our results could be refined by considering the influence of additional factors that contribute to local environmental heterogeneity and niche differentiation, such as soil types and soil nutrients [30], because we expect these additional local factors to contribute to beta-diversity. In addition, it is necessary to examine these metrics of beta-diversity that incorporate gamma-diversity and sample size corrections in other taxa and regions. Gamma-diversity dependence is also associated with other attributes of ecosystem such as species abundance distribution [31] and should be examined in other systems.

We found that a latitudinal gradient in local beta-diversity contributes to the broad latitudinal pattern of species richness after separately controlling for gamma-diversity and local topographic heterogeneity. The results suggest tighter species packing and larger niche space in tropical forests [4,22,23], but also confirmed environmental heterogeneity as a determinant of beta-diversity. Our findings may help resolve recent debates on the contribution of local beta-diversity to latitudinal gradient of species richness.

Materials and Methods

Forest dynamic plots We used data from 21 forest dynamics plots that are part of the ForestGEO and Chinese Forest Biodiversity Monitoring Networks [19,20] (Fig. 1a and Extended Data Table 1). All stems with diameter at breast height (DBH) ≥ 1 cm were spatially mapped, tagged, measured and identified to species [32]. The plots range from tropical rain forest at 2.98° N latitude to boreal forest at 51.82° N latitude (Extended Data Table 1). Plots vary from sea level to more than 1400 m elevation, and within-plot elevation range is as low as 17.7 m and as high as 298.6 m (Extended Data Table 1 and Fig. 1b).

Measurement of beta-diversity To circumvent gamma-diversity dependence caused by sample-size bias of beta-diversity metrics, we used a correction method designed for beta Shannon entropy based on the relationship between cumulative diversity curve and sample size [33]. The beta Shannon entropy measures the heterogeneity of pooled communities, and is calculated as the effective number of compositionally distinct and equally abundant communities [34,35]. As the beta Shannon entropy incorporates species abundance, it could weight common or rare species more by changing the diversity order q [34]. Here we chose diversity of order $q = 1$ for weighting all species by their abundance, without favoring either common or rare species. Additionally, observed species diversity in a sample is known to be a biased estimate of true species diversity, and is highly sensitive to the area surveyed, the number of individuals counted, and the regional species pool size [36]. We thus used a sample-size dependence correction method to produce accurate, low-bias estimates of the beta Shannon entropy for comparing beta-diversity among regions [17,33]. In this approach, similar to a species accumulation curve, the expected cumulative alpha- or gamma-diversity is analytically depicted as a function of sample size, while sample completeness is estimated from community structures of samples [17,33]. Beta-diversity can then be estimated from the predicted alpha- and gamma-diversity under hypothetical complete sampling based on the diversity-sample size curve. For a comparison, we also used a pairwise dissimilarity metric – the Jaccard-Chao index (Extended Data Fig. 1), which corrects undersampling bias by estimating the effect of undetected shared species [37]. Our simulations confirmed that β-metrics that incorporate an undersampling correction method are more effective at removing dependence on gamma-diversity and sample size, compared with other conventional beta-diversity metrics [18].

Local topographic heterogeneity, community-level niche differentiation Local topographic heterogeneity was quantified by the surface to planimetric area ratio [28]. Niche

differentiation was described using attributes of specialization and marginality. Niche specialization was defined as the ratio of the standard deviation of available habitat for a community to that used by a species, and marginality was defined as the ecological distance between a species optimum and the mean habitat within the plot [38,39]. Specialization and marginality were calculated for each species with species composition data and six topographic factors: mean elevation, convexity, slope, aspect, topographical wetness index (TWI) and altitude above channel (ACH) - across spatial scales [40-42]. Aspect was computed as sin(aspect) and cos(aspect), and other topographic variables were Box-Cox transformed before being included into analysis [43]. We then calculated the mean community-level niche specialization and marginality across all species occurring in at least ten subplots, weighting by species abundance.

Statistical analysis To examine the significance of latitudinal gradients in explaining local beta-diversity, niche specialization and niche marginality, we first modeled beta-diversity, community-level niche specialization and niche marginality against topographic heterogeneity and adjusted latitude (an upward shift of 100 m approximately equals to a poleward shift of 100 km) separately using simple linear regression models. Subsequently, to determine the relative effect sizes of adjusted latitude and topography, we performed multiple linear regression models with beta-diversity, niche specialization and marginality as response variables respectively, and all variables were standardized by $(x-x')/SD(x)$ before being included. To achieve normality of niche specialization (Extended Data Fig. 4a), the log- and Box-Cox transformation [43] were employed (Extended Data Figs. 4b and 4c). Finally, the Box-Cox transformed niche specialization were used in analyses, and for comparison, it was min-max normalized into the range between [0, 1] using $((x-min(x))/(max(x)-min(x))$. In total, we conducted all the analyses across three spatial scales by dividing plots into quadrats of different grain sizes (10 m × 10 m, 20 m × 20 m and 50 m × 50 m).

All statistical analyses were performed with R software, version 3.6.4 [44]. The corrected Shannon entropy index was calculated using R package 'entropart' [45]. The topographic variables were computed using 'RSAGA' package [46] and SAGA GIS [47]. Ecological niche factor analysis (ENFA) was implemented to calculate niche metrics using R package 'adehabitatHS' [48].

Data availability

The data supporting Figure 1-3 have been deposited in the Dryad Digital Repository (https://datadryad.org/stash/share/6bhhuxg5b3637cgOSzPVQzdyAPh9vy5hf29DCglp6hs). Full census data are available upon reasonable request from the ForestGEO data portal, http://ctfs.si.edu/datarequest/.

Code availability

The code used for data analysis have been deposited in the Dryad Digital Repository (https://datadryad.org/stash/share/6bhhuxg5b3637cgOSzPVQzdyAPh9vy5hf29DCglp6hs).

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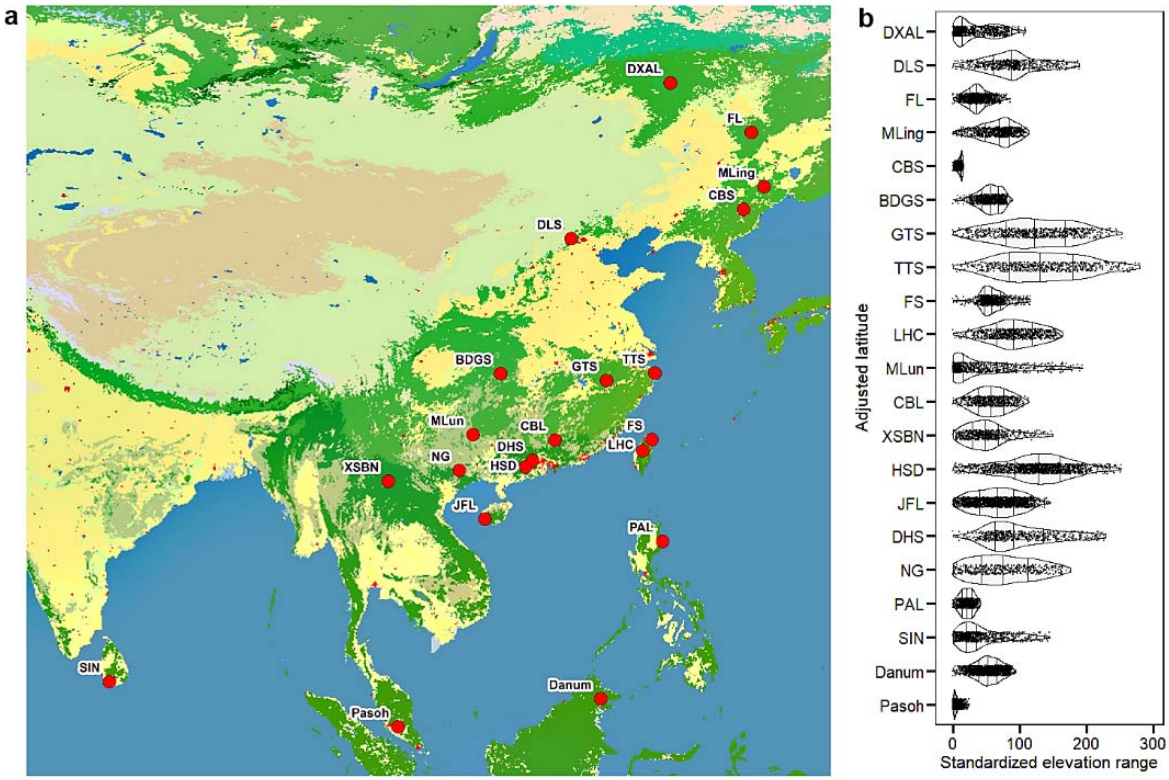


Figure 1 | The spatial distribution of forest dynamic plots (a, full plot names were listed in Extended Data Table 1) and the elevation range of each plot along latitude (b). Panel b shows the latitudinal pattern of elevation range, which was transformed by subtracting the minimum elevation of each plot. 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.

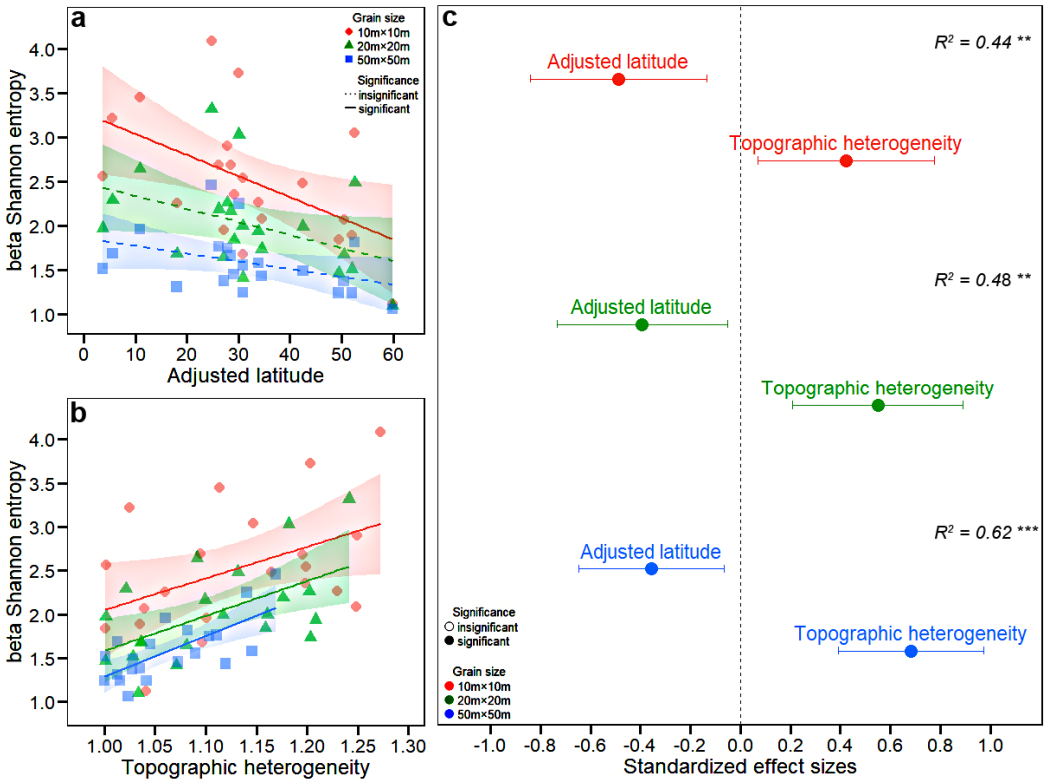


Figure 2 | The relationship of beta-diversity (corrected beta Shannon entropy) with adjusted latitude and local topographic heterogeneity across grain sizes. In each panel, different colours of points and lines represent grain sizes. In panel a and b, solid and dashed lines indicate significant and insignificant linear correlations (significance level, α = 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 α < 0.001, '***'; α < 0.01, '**'; α < 0.05 '*'.

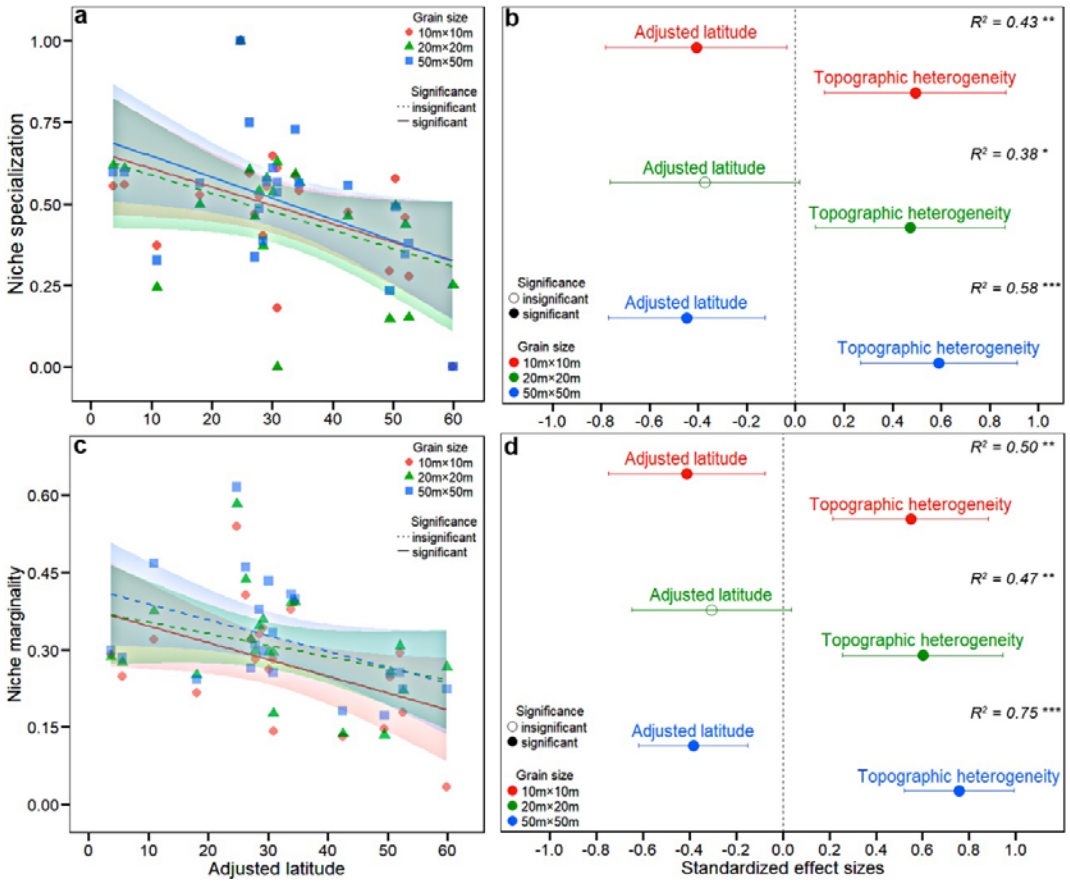


Figure 3 | The relationships of community-level niche specialization (a and b) and marginality (c and d) with adjusted latitude and local topographic heterogeneity across grain sizes. In each panel, different colours of points and lines represent grain sizes. In panel a and c, solid and dashed lines 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 $\alpha < 0.001$, '***'; $\alpha < 0.01$, '**'; $\alpha < 0.05$ '*'.

Acknowledgements We thank Dingliang Xing, Tak Fung and Fangliang He for comments on earlier draft. The data analyses reported in this study were financially supported by Strategic Priority Research Program of the Chinese Academy of Sciences (XDB310300) and National Natural Science Foundation of China (NSFC 31770478). Data collection was funded by many organizations, principally, NSFC 31470490, 31470487, 41475123, 31570426, 31570432, 31570486, 31622014, 31660130, 31670441, 31670628, 31700356, 31760141, and 31870404, the Southeast Asia Rain Forest Research Programme (SEARRP), National Key Basic Research Program of China (Grant No. 2014CB954100), SEARRP partners especially Yayasan Sabah, HSBC Malaysia, financial project of Heilongjiang Provience (XKLY2018ZR01), National Key R&D Program of China (2016YFC1201102 and 2016YFC0502405), the Central Public-interest Scientific Institution Basal Research Fund (CAFYBB2017ZE001), Taiwan Forestry Research Institute grant under the project 97 AS-7.1.1.F1-G1 and the Forestry Bureau of Taiwan (No. tfbm960226), CTFS Forest GEO for funding for Sinharaja forest plot, the Taiwan Forestry Bureau, the Taiwan Forestry Research Institute and the Ministry of Science and Technology of Taiwan for funding the census of Fushan forest plot. We thank Alex Karolus for leading the census in Danum Valley forest plot, and we are grateful to Mike Bernados and Bill McDonald for species identifications, to Fangliang He, Stuart Davies and Shameema Esufali for advice and training, to Qianjiangyuan National Park, Fushan Research Center and Sri Lankan Forest Department for logistical support and the hundreds of field-workers who measured and mapped the trees analyzed in this study.

Author contributions

KC, RC, XM, KM and JCS designed research, KC and XM compiled and analysed data; KC, RC, XM, KM and JCS wrote drift with substantial input from LC, WX, DFRPB and MJB.

Many authors contributed to data collection of forest censuses and all authors contributed to revisions of the manuscript.

Competing interest

The authors declare no competing financial interests.

Extended data

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

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

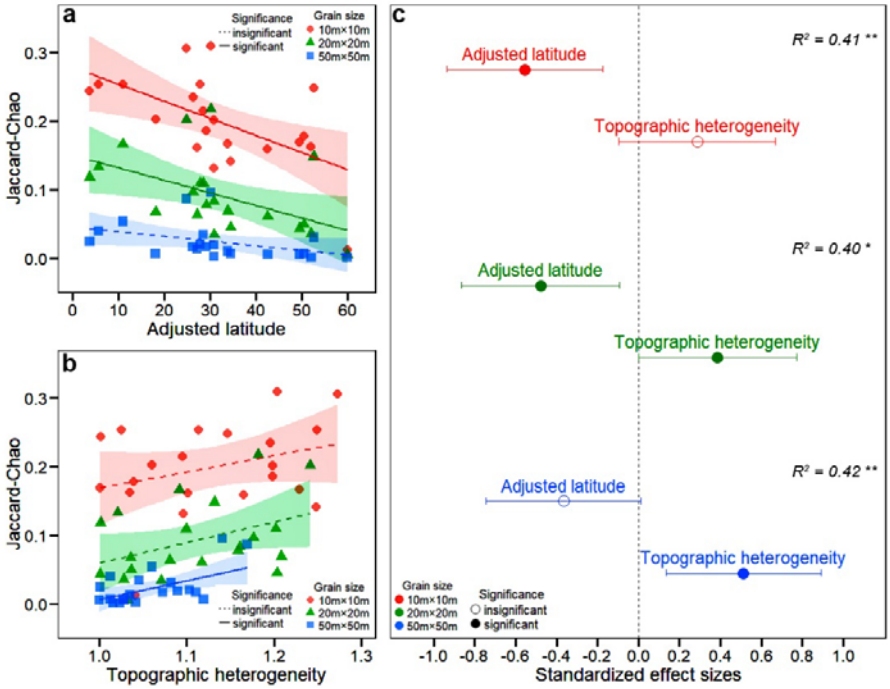
Explanatory variables	Grain size	Coefficients	Standard error	t-value	p-value	R-square
Adjusted latitude	10m × 10m	-0.024	0.01	-2.59	0.02	0.26
	20m × 20m	-0.015	0.01	-2.01	0.06	0.18
	50m × 50m	-0.0087	0.01	-1.86	0.08	0.15
Topographic heterogeneity	10m × 10m	3.62	1.65	2.19	0.04	0.20
	20m × 20m	4.00	1.33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

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

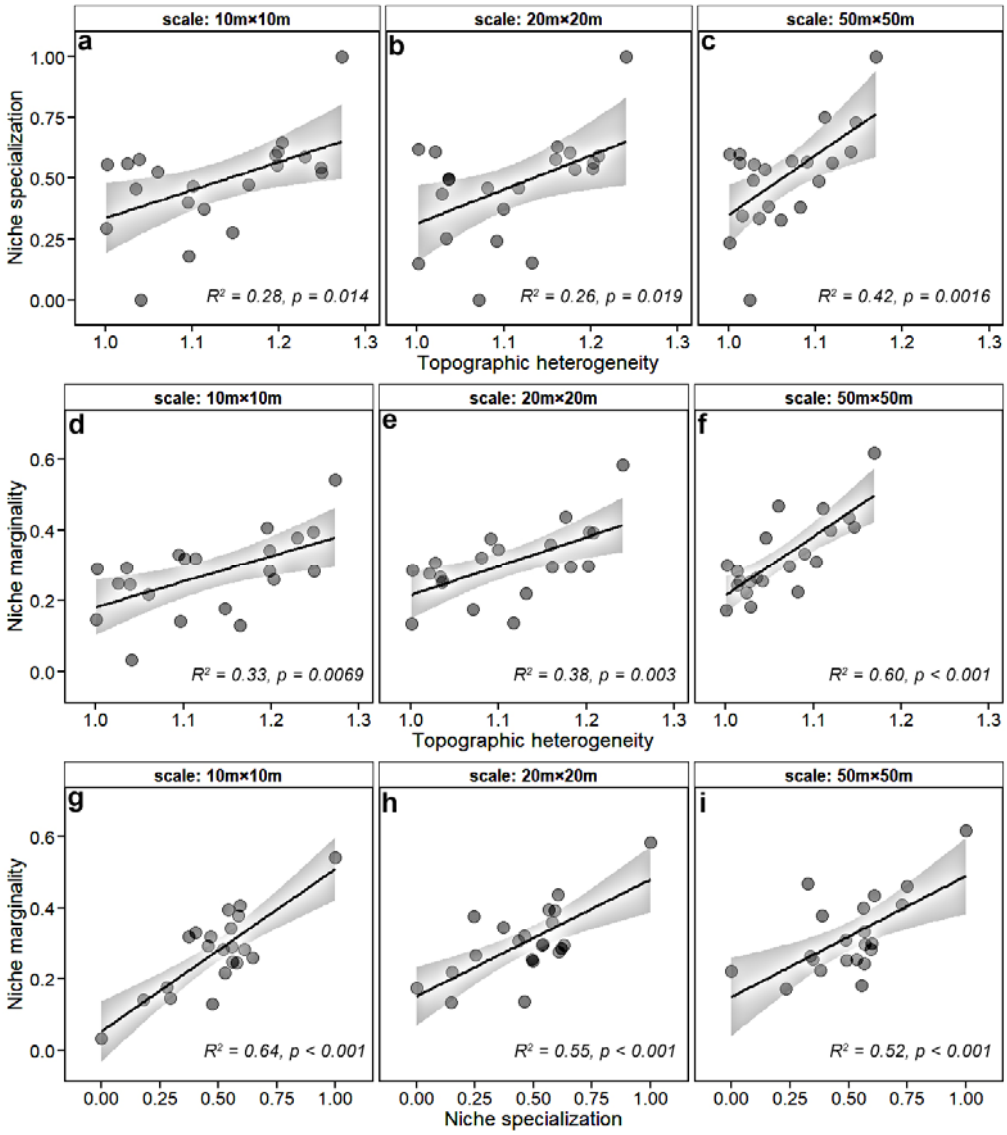
Response variables	Grain size	Coefficients	Standard error	t-value	p-value	R-square
	10m × 10m	-0.0057	0.0027	-2.10	0.049	0.19
Niche	20m × 20m	-0.0056	0.0030	-1.88	0.076	0.16
specialization	50m × 50m	-0.0065	0.0027	-2.38	0.028	0.23
	10m × 10m	-0.0033	0.0015	-2.15	0.044	0.20
Niche	20m × 20m	-0.0022	0.0014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

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

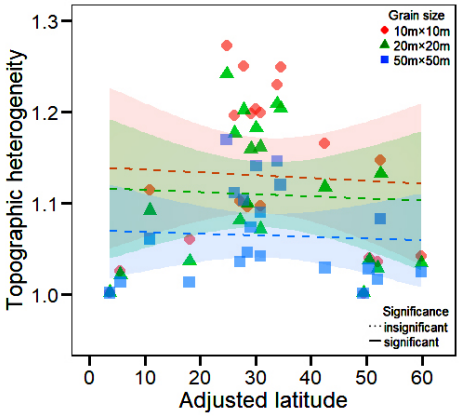
Explanatory variables	Grain size	Coefficients	Standard error	t-value	p-value	R-square
	10m × 10m	-0.0025	0.001	-3.03	0.0068	0.33
Adjusted	20m × 20m	-0.0018	0.001	-2.49	0.022	0.25
latitude	50m × 50m	-0.00068	0.0003	-1.86	0.078	0.15
	10m × 10m	0.24	0.16	1.45	0.16	0.10
Topographic	20m × 20m	0.30	0.15	1.95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



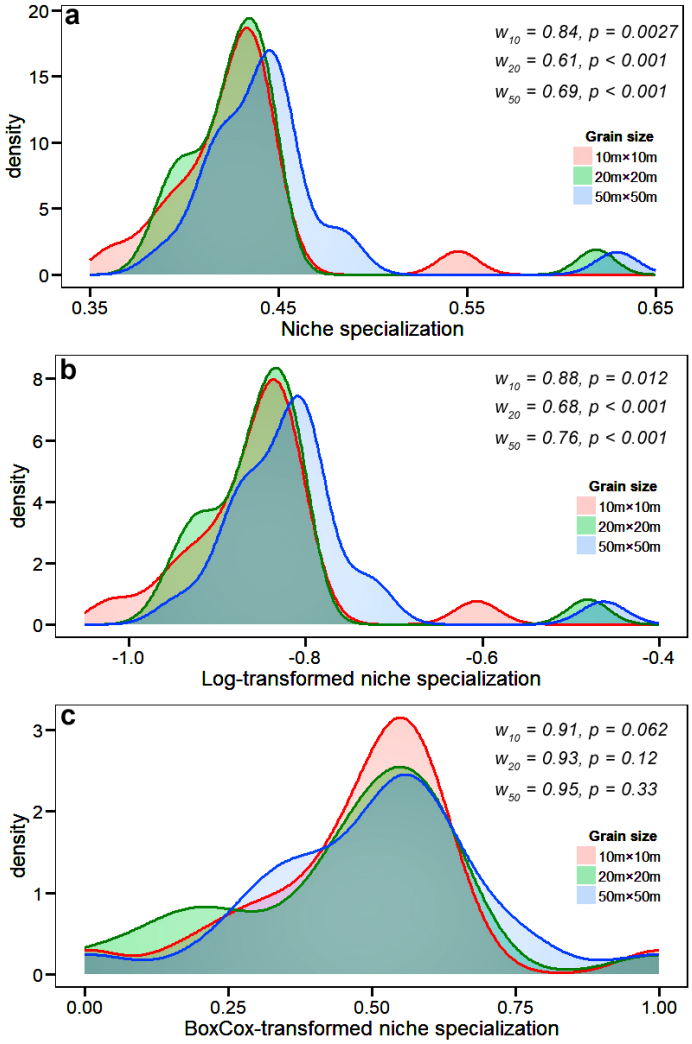
Extended Data Figure 1 | The linear relationship of beta-diversity (measured by the Jaccard-Chao index) with adjusted latitude (a) and local topographic heterogeneity (b) across grain sizes. In each panel, different colours of points and lines represent grain sizes. In panel a and b, solid and dashed lines indicate significant and insignificant linear correlations (significance level, α = 0.05), respectively. The shaded areas represent the 95% confidence interval of the predictions. In panel c, points represent the standardized effect sizes of explanatory variables, and solid and hollow circles represent variables with values significantly and insignificantly different from zero, respectively. The output of these linear 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, '**'; α < 0.05 '*') were annotated at the top-right corner for each multiple linear model in panel c.



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.



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, α = 0.05), and different colours of points and lines represent grain sizes.



Extended Data Figure 4 | The Shapiro-Wilk test of normality for the observed (a), log-transformed (b), and Box-Cox transformed (c) niche specialization. In each panel, the kernel density curves with different colours showed the probability distribution of niche specialization 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. 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.