

Patterns of plant beta-diversity along elevational and latitudinal gradients in mountain forests of China

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Biodiversity patterns and their underlying mechanisms have long been focal topics of study for ecologists and biogeographers. However, compared with spatial variation in species richness (α - and γ -diversity), β -diversity, or the dissimilarity of species composition between two or more sites has until recently received limited attention. In this study, we explored the large-scale patterns of altitudinal turnover (β -diversity) of plants in montane forests of China, based on systematic inventories of 1153 plots from 46 mountains distributed over ~ 30 degrees of latitude (21.9 – 51.7°N) and ~ 4100 m of altitude (160 – 4250 m). The β -diversity of trees and shrubs declined significantly with increasing latitude. Along the altitudinal gradient, β -diversity of both trees and shrubs showed non-significant trends in most mountains. Differences in climate explained $\sim 30.0\%$ of the variation in tree β -diversity (27.7 , 36.5 , and 26.2% for the Jaccard's, β_j , Sorenson's, β_s , and Simpson's dissimilarity, β_{sim} , respectively), with mean annual temperature being most important, and $\leq 10.0\%$ of that in shrub β -diversity (10.0 , 8.2 , and 7.0% for β_j , β_s , and β_{sim} , respectively), with annual actual evapotranspiration and annual precipitation as the main predictors. However, climatic controls of β -diversity varied dramatically in different biogeographical regions. The β -diversity of trees exhibited stronger, whereas that of shrubs showed weaker, climatic patterns in temperate and arid than subtropical regions. These results suggest that mechanisms causing patterns of β -diversity may differ between latitudinal and altitudinal gradients, and among biogeographical regions; as a result, caution should be exercised in drawing close parallels between patterns and causes of β -diversity along latitudinal and altitudinal gradients and among regions.

Understanding biodiversity patterns and their underlying mechanisms is one of the central goals of macroecology and biogeography (Gaston 2000). Three basic sets of patterns have been recognized, α -diversity (or within-site diversity), β -diversity (or between-site diversity), and γ -diversity (or regional diversity) (Whittaker 1972). In recent decades, a great deal of attention has been paid to understanding patterns of species richness, at both local (α -diversity) and regional scales (γ -diversity), and the ecological and historical processes determining them (Gaston 2000, Hillebrand 2004, Wang et al. 2009, 2011). Indeed, there is general consensus about the nature of the patterns (including those with area, altitude, latitude, environmental energy and productivity), albeit a good deal less about the relative importance of the principal explanations that have been proposed (reviewed by Gaston 2000, Hillebrand 2004, Arita and Vázquez-Domínguez 2008). By comparison, broad-scale spatial variation in the composition of species assemblages between two or more sites, β -diversity, has been much less studied, both in terms of patterns and mechanisms (Koleff et al. 2003b, Gaston et al. 2007a, b, McKnight

et al. 2007, Buckley and Jetz 2008, Melo et al. 2009, Kraft et al. 2011, Tang et al. 2012, Wang et al. 2012).

Arguably, the most frequently reported pattern in β -diversity is a decline, i.e. an increase in the similarity in composition of local assemblages, with increasing latitude (Koleff et al. 2003b, Rodríguez and Arita 2004, Qian and Ricklefs 2007, Soininen et al. 2007, Kraft et al. 2011). However, other outcomes have also been documented (Gaston et al. 2007a, McKnight et al. 2007, Buckley and Jetz 2008, Melo et al. 2009), likely at least in part because of differences in the methods, including the measures of β -diversity, that have been used in different studies (Koleff et al. 2003a, Tuomisto 2010, Anderson et al. 2011).

Particular concerns in interpreting available studies of large scale spatial patterns in β -diversity are threefold. First, the great majority of such studies are based on space-filling species range maps (Gaston et al. 2007a, McKnight et al. 2007, Buckley and Jetz 2008, Wang et al. 2012, but see Kraft et al. 2011, Myers et al. 2012, Stegen et al. 2012, Tang et al. 2012), and have thus almost invariably been conducted at coarse spatial resolutions and document

patterns in which much of any underlying spatial heterogeneity in species composition has been smoothed out and the spatial autocorrelation increased (Hillebrand 2004, Hurlbert and White 2005).

Second, in the main, these studies mostly deal with animal taxa (Koleff et al. 2003b, McKnight et al. 2007, Buckley and Jetz 2008, Melo et al. 2009, Stegen et al. 2012), while studies on plants have been conducted only recently (Harrison et al. 2006, Qian 2009, Bin et al. 2010, Kraft et al. 2011, Myers et al. 2012, Tang et al. 2012, Wang et al. 2012). This paucity of plant-focused studies is somewhat ironic given that R. H. Whittaker, who first proposed the definition of β -diversity, was a plant ecologist (Whittaker 1972). As β -diversity for different taxonomic groups may respond to the same environmental gradient in rather different ways, patterns and determinants in this component of diversity are not necessarily congruent among different groups (Rodríguez and Arita 2004, McKnight et al. 2007, Melo et al. 2009, Chase 2010).

Third, large-scale spatial patterns in β -diversity have mostly concerned 'horizontal' (latitudinal and, sometimes, longitudinal) turnover in species composition. Here changes in environment and geography are particularly closely coupled, making it harder to partition their relative influence in shaping patterns of β -diversity (Koleff and Gaston 2001, Buckley and Jetz 2008). That said, more than forty years ago, Janzen (1967) predicted that, as species tend to be less climatically tolerant in more constant than more variable climates, the more constant climates of tropical mountains should increase the climatic barriers to organismal dispersal, leading to higher altitudinal turnover of species, relative to that in temperate mountains. However, to our knowledge, to date only very few studies have determined the empirical relationship between the altitudinal

turnover of species and latitude explicitly to test this prediction (Huey 1978, McCain 2009).

China, covering a huge territory from tropical to cool temperate and from hyper-humid to ultra-arid climates, and including nearly all of the major biome types in the world, provides an ideal area in which to investigate large scale biodiversity patterns (Tang et al. 2006, Wang et al. 2009, 2011, Fang et al. 2010). Here we exploit this opportunity, analyzing the patterns of β -diversity of woody plants in forests across China, based on 1153 plots systematically collected from nearly 50 mountains.

The objectives of this study are to answer the following questions: 1) are there latitudinal and altitudinal patterns of plant β -diversity in China's forests? 2) Are these patterns consistent in different biogeographic regions?

Material and methods

Study sites

Data on the composition of local species assemblages were collected from 46 mountains across China where vegetation is well protected, during 1997~2008 (Fig. 1). These mountains were located in three vegetation regions (Hou 2001), subtropical evergreen broadleaved forest region (subtropical region hereafter), temperate deciduous broad-leaved forest and cold temperate mixed forest region (temperate region), and temperate steppe and desert region (arid region). In each mountain, depending on the size of the mountain and how well it is protected, we selected one to several altitudinal transects spanning from the low to the high altitudes on different slopes to perform the plot survey (see Supplementary material Appendix 1, Table A1

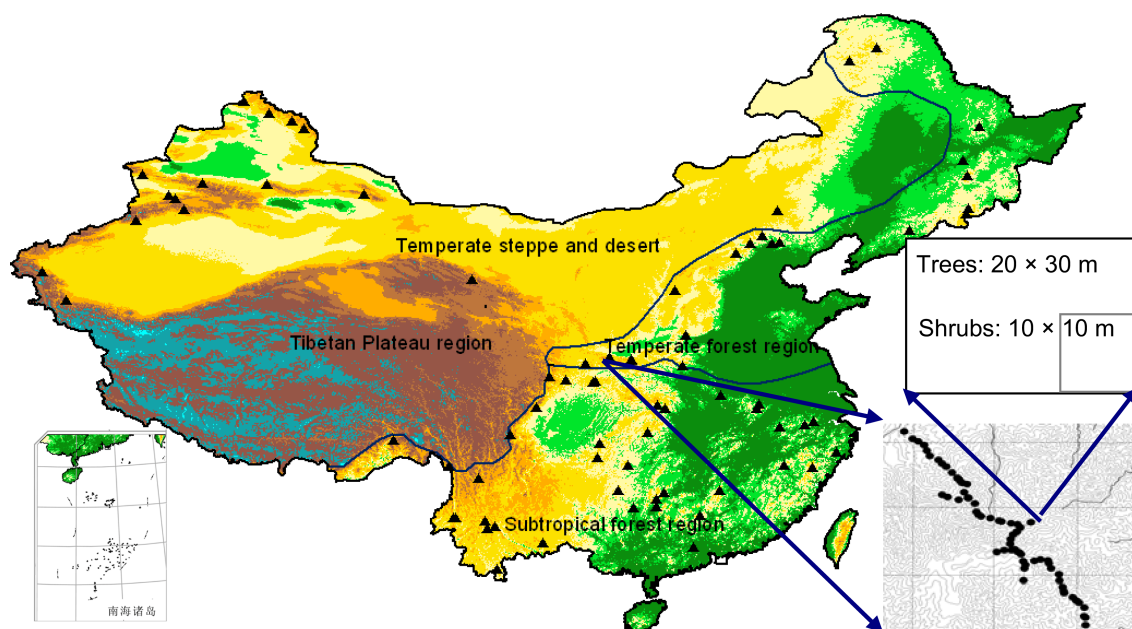


Figure 1. Location and plot setup for the investigation of β -diversity in China's mountains. The subsets illustrate location of plots in each mountain, using Mt Taibai as an example; in each mountain, one to several altitudinal transects spanning from the low to the high altitudes on different slopes were selected to perform the plot survey. In each plot, 20 × 30 m was investigated for trees, and 10 × 10 m was investigated for shrubs.

for the number of transects in each mountain). Along each transect, we placed plots at intervals of 50–100 m to represent the primary vegetation in different zones and excluded secondary vegetation types, apparently disturbed areas, rivers, and rocks when selecting the plots. Each plot comprised an area of 20 × 30 m used to characterize the tree layer, and one subplot of 10 × 10 m used to characterize the shrub layer. In tree layer, the diameter at breast height (DBH, breast height = 1.3 m) and height of all individuals with DBH ≥ 3 cm were measured, number of saplings with DBH < 3 cm were also recorded for each tree. In shrub layer, species name, abundance, average height and coverage of each woody plant species were recorded (Fang et al. 2010). In total, 1153 forest plots were surveyed from these mountains (Fig. 1, Supplementary material Appendix 1, Table A1).

Measurement of β - and γ -diversity

Here, we defined β -diversity in two ways: the decaying rate of similarity in species composition for all possible plot-pairs along the elevational gradient on the same mountain (rate of similarity decay) (Nekola and White 1999, Tuomisto 2010, Anderson et al. 2011), and the dissimilarity in species composition between pairs of the nearest neighbouring plots in the same mountain (dissimilarity of neighbouring plots) (Gaston et al. 2007b, Anderson et al. 2011).

Rate of similarity decay, i.e. the slope of the relationship between the natural logarithm of similarity and spatial distance (or environmental divergence), was considered as a measure of spatial β -diversity (Nekola and White 1999). We first calculated the Jaccard's similarity (J , Jaccard 1912; see below for the definition) between all possible plot-pairs within the same mountain; we then regressed the natural logarithm of J ($\ln J$) on altitudinal divergence (δH) between the plot-pairs. The absolute value of the slope of the $\ln J$ – δH relationship was then used as a measure the β -diversity of the mountain (Nekola and White 1999).

Dissimilarity of neighbouring plots: the dissimilarity of species composition was calculated for neighbouring plots. We first calculated dissimilarity between the plots at the lowest and the second lowest altitudes; then the third and the fourth lowest plots and repeated this procedure up the altitudinal gradient, yielding a total of 563 neighbouring plot-pairs. The two most widely employed indices of β -diversity, Jaccard's index (β_j ; Jaccard 1912) and Sorenson's index (β_s ; Sorensen 1948) of dissimilarity, and a symmetric version of Simpson's index (β_{sim} ; Lennon et al. 2001), were used:

$$\begin{aligned}\beta_j &= 1 - c/(a + b + c) = (a + b)/(a + b + c) \\ \beta_s &= 1 - 2c/(a + b + 2c) = (a + b)/(a + b + 2c) \\ \beta_{sim} &= 1 - c/[\min(a, b) + c] = \min(a, b)/[\min(a, b) + c]\end{aligned}$$

where a and b are the numbers of species only occurring in the focal and neighbouring plots, respectively, and c is the number that occur in both. It has been suggested that both β_j and β_s are independent of α -diversity (Jost 2007), and β_{sim} controls for local gradients in species richness (Lennon et al. 2001).

γ -diversity: for each plot-pair, γ -diversity was defined as the number of species occurring in either plot of the neighbouring plot-pair.

Climate

Most of the plots are located in remote areas where climate data are not available. Because temperature and precipitation are highly correlated with latitude, longitude, and altitude in China (Fang and Yoda 1988, Tang and Fang 2006), we estimated mean monthly temperature (MMT) and mean monthly precipitation (MMP) for each plot based on an existing MMT and MMP data, i.e. WorldClim database (Hijmans et al. 2005; available at < www.worldclim.org/ >, resolution at 30 × 30 arc second), of its surrounding areas using the following procedures. First, we extracted the grid cells which were < 100 km away from the focal plot from the Worldclim database. Second, we extracted the longitude and latitude of the centroids of these grid cells and then used these co-ordinates to extract altitudes from the GTOPO30 digital elevation model (DEM) (available at < http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info >, resolution 30 × 30 arc second). Third, we developed linear models for each plot using MMT or MMP as independent variable and latitude, longitude, and altitude as predictors:

$$\text{MMT (MMP)} = a + b \times \text{longitude} + c \times \text{latitude} + d \times \text{altitude}$$

These models were then applied to estimate the MMT and MMP for each focal plot. Using estimated MMT and MMP of each plot we calculated mean annual temperature (MAT), mean temperature of the warmest (MTWM) and coldest month (MTCM), annual range of temperature (ART), annual precipitation (AP). We also calculated Thornthwaite water equivalent indices such as annual potential evapotranspiration (PET), annual actual evapotranspiration (AET), and moisture index (IM) (Thornthwaite and Hare 1955) and potential evapotranspiration ratio (PER, ratio of PET to AP, Holdridge 1967). For the detailed methods for calculating these variables, see Fang and Yoda (1988). For each β -diversity value, climate was represented by the average climate for the two respective neighbouring plots from which that value was derived.

Data analysis

To explore the influence of climate on β -diversity, we developed multiple linear models using the calculated β_j , β_s , and β_{sim} as dependent, and aforementioned climatic variables (MAT, MTWM, MTCM, PET, AP, AET, PER, IM) as predictors. We first examined all possible combinations of variables, with the number of variables increasing from one until the model selection stopped. Then the goodness-of-fit in relation to model complexity was evaluated by comparing values of the Akaike information criterion (AIC). For models with the same number of variables, the model with the smallest AIC was selected (and listed in Table 1). Model selection stopped when any added variable increased

Table 1. Relationships between β -diversity and climate variables in China's forests.

Region	β_j			β_s			β_{sim}		
	Factors	Cum. R^2 (%)	AIC	Factors	Cum. R^2 (%)	AIC	Factors	Cum. R^2 (%)	AIC
Trees									
Overall (563)	MAT	27.3	-1782.3	MAT	21.5	-1738.1	MAT	22.0	-1615.8
	PER	28.9	-1794.4	PET	22.9	-1748.3	PET	22.5	-1619.3
	PET	30.1	-1803.6	MTCM	26.2	-1772.8	MTCM	25.2	-1638.9
	MTCM	35.6	-1850.5	PER	27.0	-1778.3	PER	25.6	-1641.0
	MTWM	36.5	-1857.8	MTWM	27.7	-1782.7	MTWM	26.2	-1645.0
Subtropics (256)	MTWM	1.2	-896.6	NS			MTWM	1.8	-704.5
Temperate (225)	AET	20.8	-676.7	AET	17.8	-666.7	AET	15.4	-613.5
	AP	22.8	-681.5	AP	20.7	-672.7	AP	17.9	-619.2
Arid (82)	PET	15.7	-227.4	PET	14.6	-243.9	PET	10.2	-239.2
	PER	27.2	-237.5	PER	24.8	-255.1	PER	17.2	-245.5
							AET	24.2	-254.5
Shrub									
Overall (563)	AET	9.1	-2016.9	AP	6.6	-1726.0	AET	6.4	-1391.9
	AP	10.0	-2022.1	AET	7.6	-1731.6	AP	7.0	-1394.4
				ART	8.2	-1734.0			
Subtropics (256)	AP	6.3	-1059.5	MAT	7.6	-880.1	AET	7.1	-694.7
	PER	13.4	-1078.7	AP	12.8	-894.0	AP	10.6	-703.3
Temperate (225)	ART	2.5	-818.4	ART	3.0	-693.4	NS		
Arid (82)	NS			NS			NS		

Numbers in the parentheses indicate the number of cases.

Abbreviations: AET = annual actual evapotranspiration, AP = annual precipitation, MAT = mean annual temperature, MTCM = mean temperature of the coldest month, MTWM = mean temperature of the warmest month, PER = potential evapotranspiration ratio, PET = potential evapotranspiration.

the AIC. We then applied the software SAM to test for spatial autocorrelation of the residuals of the model, with class size set as 'equal number of pairs' (Rangel et al. 2010). To compare the effects of climatic factors on β -diversity in different biogeographic regions, the multi-predictor model was also applied separately for each region.

To explore the latitudinal pattern of β -diversity, we first averaged all β_j , β_s , and β_{sim} of neighbouring plot-pairs within each mountain, and then plotted the average values against the latitude of the mountain. We also plotted the decay rates of species similarity (S) of all of the mountains against their latitudes.

To explore the altitudinal pattern of β -diversity, we selected mountains with altitudinal ranges ≥ 500 m, and containing ≥ 10 plots (five plot-pairs), and then characterized altitudinal patterns of β -diversity as decreasing, absent (no significant relationship), or increasing. These forms were determined by simple regression for β -diversity plotted against the average altitude of the plot-pair. A negative or positive relationship significantly at $p < 0.05$ represented a decreasing or increasing pattern, respectively, while non-significant relationship at $p < 0.05$ represented absent pattern.

We explored the relationship between β - and γ -diversity along both latitudinal and altitudinal gradients. Along the latitudinal gradient, we first averaged γ -diversity of neighbouring plot-pairs within each mountain, and then plotted the average β_j , β_s , and β_{sim} values against the log-transformed γ -diversity of the mountain. Along the altitudinal gradients, we characterized the relationship between β - and γ -diversity as positive, no significant, or negative for mountains with altitudinal ranges ≥ 500 m, and containing ≥ 10 plots (five plot-pairs). These forms were determined by simple

regression for β -diversity plotted against logarithm transformed γ -diversity of the plot-pair, with significance at $p < 0.05$.

All analyses except the spatial autocorrelation analyses were conducted in R 2.6 (R Development Core Team). The autocorrelation tests were conducted in SAM (Rangel et al. 2010).

Results

Latitudinal and altitudinal patterns of β -diversity across China's mountains

Overall, the average β -diversity between the neighbouring plot-pairs was 0.59 (SD = 0.27), 0.59 (SD = 0.25), and 0.53 (SD = 0.29) for β_j , β_s , and β_{sim} of trees, and 0.79 (SD = 0.20), 0.79 (SD = 0.18), and 0.59 (SD = 0.24) for β_j , β_s , and β_{sim} of shrubs, respectively. For each mountain, the average β -diversity varied between 0~0.87, 0~0.87, 0~0.76 for β_j , β_s , and β_{sim} of trees, and 0.50~1.0, 0.59~1.0, 0.30~1.0 for β_j , β_s , and β_{sim} of shrubs; the similarity decayed at slopes of 1.5~10, and 1.6~20 (per kilometer in altitudinal divergence), respectively (Supplementary material Appendix 1, Table A1).

The average β -diversity of each mountain declined significantly with increasing latitude for both trees ($R^2 = 0.59$, 0.62, and 0.63 for β_j , β_s , and β_{sim} , respectively, $p < 0.01$ for all) and shrubs ($R^2 = 0.20$, 0.24, and 0.25 for β_j , β_s , and β_{sim} , respectively, $p < 0.01$ for all) (Fig. 2A–C). Similarly, decaying rate of species composition similarity also declined as latitude increase, with $R^2 = 0.24$ ($p < 0.01$) and 0.21 ($p < 0.01$) for trees and shrubs, respectively (Fig. 2D).

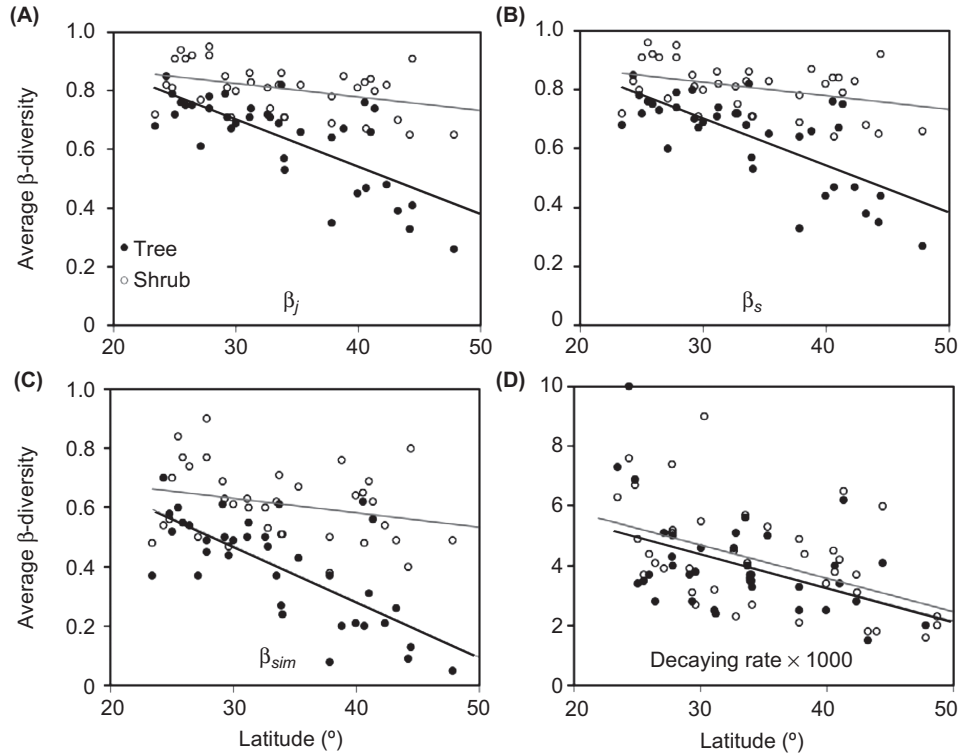


Figure 2. Latitudinal patterns of mean (A) β_j , (B) β_s , (C) β_{sim} , and (D) decaying rate of similarity across China's mountains. Solid dot and black line represent β -diversity of trees, and open dot and grey line represent that of shrubs.

β -diversity exhibited different altitudinal patterns across China's mountains. In total, forty mountains containing an altitudinal range of > 500 m and ≥ 10 plots have been surveyed. β_j of trees showed a decrease for 7 (17.5% of the total), no relationship for 31 (77.5%), increase for 2 (5.0%), the breakdowns were 6 (15.0%), 32 (80.0%), 2 (5.0%) for β_s and 7 (17.5%), 32 (80.0%), 1 (2.5%) for β_{sim} , respectively. For shrubs the corresponding numbers were 1 (2.5%), 36 (90.0%), 3 (7.5%) for β_j , 1 (2.5%), 36 (90.0%), 3 (7.5%) for β_s , and 2 (5.0%), 35 (87.5%), 3 (7.5%) for β_{sim} , respectively (Fig. 3).

Patterns of β -diversity in different regions

β -diversity exhibited different altitudinal patterns in different regions. For trees, β_j in the subtropical region decreased with altitude for one mountain (4.5% of the total), no relationship for 19 (86.4%), increase for 2 (9.1%). Corresponding values were 5 (33.3%), 10 (66.7%) and 0 (0%) in the temperate region, and 1 (33.3%), 2 (66.7%) and 0 (0%) in the arid region. The breakdowns for β_s were 1 (4.5%), 19 (86.4%), 2 (9.1%) in the subtropical region, 4 (26.7%), 11 (73.3%) and 0 (0%) in the temperate region, and 1 (33.3%), 2 (66.7%) and 0 (0%) in the arid region, respectively. For β_{sim} , the breakdowns were 4 (15.4%), 20 (76.9%), 2 (7.7%) in the subtropical region, 3 (20.0%), 12 (80.0%) and 0 (0%) in the temperate region, and 1 (33.3%), 2 (66.7%) and 0 (0%) in the arid region, respectively (Fig. 3).

For shrubs, β_j showed no relationship for all mountains in the subtropical region. It decreased, had no relationship,

and increased in 1 (6.7%), 12 (80.0%) and 2 (12.3%) mountains in the temperate region, and 0 (0.0%), 2 (66.7%) and 1 (33.3%) in the arid region. The breakdowns for β_s were 0 (0.0%), 22 (100.0%), 0 (0.0%) in the subtropical, 1 (6.7%), 12 (80.0%) and 2 (13.3%) in the temperate, and 0 (0.0%), 2 (66.7%) and 1 (33.3%) in the arid region, respectively. For β_{sim} , the breakdowns were 0 (0.0%), 22 (100.0%), 0 (0.0%) in the subtropical, 2 (13.3%), 11 (73.4%) and 2 (13.3%) in the temperate, and 0 (0.0%), 2 (66.7%) and 1 (33.3%) in the arid region, respectively (Fig. 3).

Relationship between β - and γ -diversity in China's mountains

Along the latitudinal gradient, the mountain based β -diversity and logarithm transformed γ -diversity were significantly correlated for both trees ($R^2 = 0.68, 0.63, 0.62$ for $\beta_j, \beta_s, \beta_{sim}$, respectively) and shrubs ($R^2 = 0.22, 0.12, 0.10$ for $\beta_j, \beta_s, \beta_{sim}$, respectively) (Fig. 4). Along the altitudinal gradient, the β - and γ -diversity relationship varied significantly among China's mountains. For trees, we observed positive relationship in 10 (25% of the total), no relationship for 29 (72.5%), negative for 1 (2.5%) mountains for β_j , the breakdowns were 8 (20.0%), 31 (77.5%), 1 (2.5%) for β_s and 10 (25%), 30 (75.0%), 0 (0%) for β_{sim} , respectively. For shrubs the corresponding numbers were 3 (7.5%), 35 (87.5%), 2 (5.0%) for β_j , 2 (5.0%), 38 (95.0%), 0 (0%) for β_s , and 2 (5.0%), 38 (95.0%), 0 (0%) for β_{sim} , respectively (Fig. 5). Such patterns persisted for different regions, with positive in several, no relationship in most

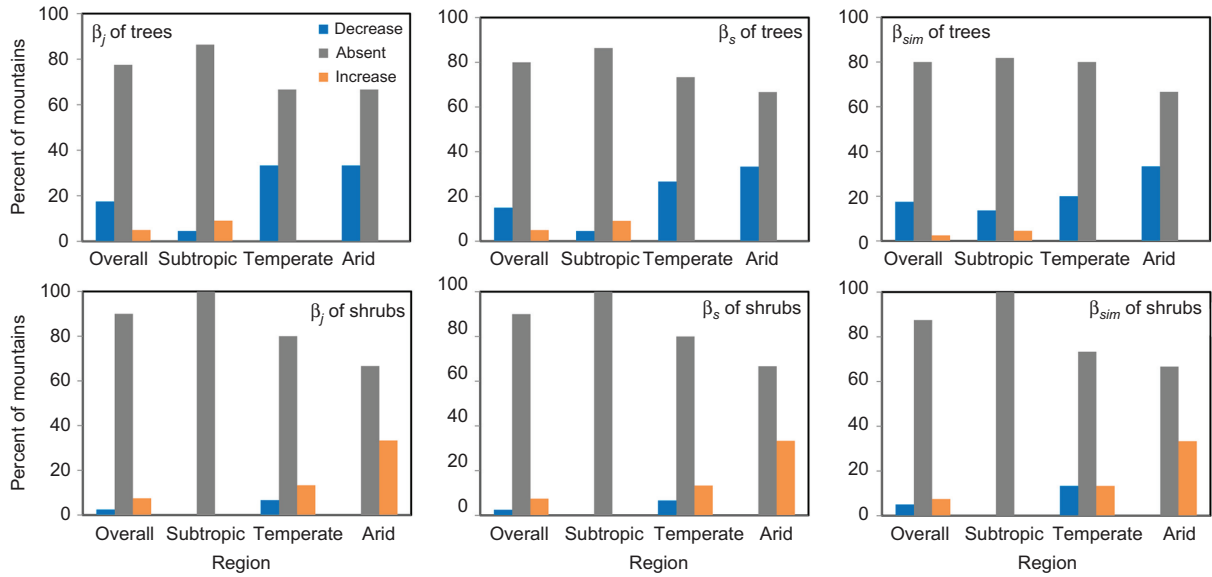


Figure 3. Altitudinal patterns of β -diversity for trees (above) and shrubs (bottom) in different regions across China. The colors represent different altitudinal patterns: cyan for decrease (slope < 0 , $p < 0.05$), grey for non-significant ($p > 0.05$), and orange for increase (slope > 0 , $p < 0.05$) of β -diversity as altitude increases.

and negative in few mountains for both shrubs and trees in all subtropical, temperate and arid regions (Fig. 5).

Relationship between β -diversity and climate in China's mountains

For trees, climate explained 36.5% of the total variance in β_j , with MAT as the primary correlate, which alone explained 27.3% of the variance. Climate explained 27.7% and 25.6% of the total variance in β_s and β_{sim} , both with MAT as most important (explained 21.5% and 22.0% for β_s and β_{sim} , respectively). For shrubs, climate explained 10.0%, 8.2%, and 7.0% of the total variance in β_j , β_s and β_{sim} , with AET (9.1%), AP (6.6%) and AET (6.4%) as most important, respectively (Table 1). The model residuals exhibited significant autocorrelation only in very few distance classes (Supplementary material Appendix 1, Fig. A1).

Climate correlates of the β -diversity patterns also varied amongst the different biogeographic regions. For trees, climate explained 1.2% (MTWM as most important),

0% (non-significant, NS), and 1.8% (MTWM) of the total variance in β_j , β_s , and β_{sim} in the subtropical region, and 22.8, 20.7 and 17.9% for β_j , β_s , and β_{sim} in the temperate region (all with AET as most important); 27.2, 24.8 and 24.2% for β_j , β_s , and β_{sim} in the arid region (all with PET as most important), respectively (Table 1). For shrubs, climate explained 13.4% (AP), 12.8% (MAT), 10.6% (AET) of the total variance in β_j , β_s , and β_{sim} in the subtropical region; 2.5% (ART), 3.0% (ART), 0% (NS) for β_j , β_s , and β_{sim} in the temperate region; no climatic factors were significantly associated with β_j , β_s , or β_{sim} in the arid region (Table 1).

Discussion

Latitudinal patterns of plant β -diversity in China's mountains

In this study we document, for the first time, large-scale patterns of altitudinal turnover of plant species (β -diversity)

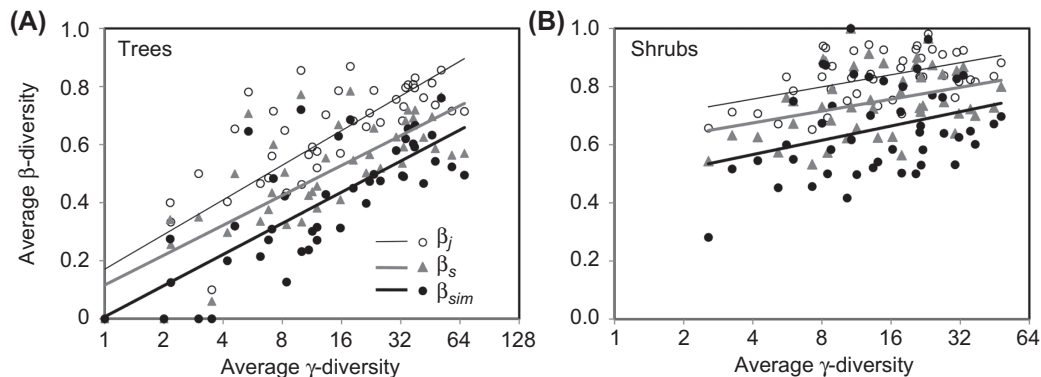


Figure 4. Relationship between mean β - and γ -diversity for (A) trees and (B) shrubs across China's mountains. Each point represents one mountain, open dot and thin black line represent β_j , grey triangle and grey bold line represent β_s , and solid dot and bold black line represent β_{sim} .

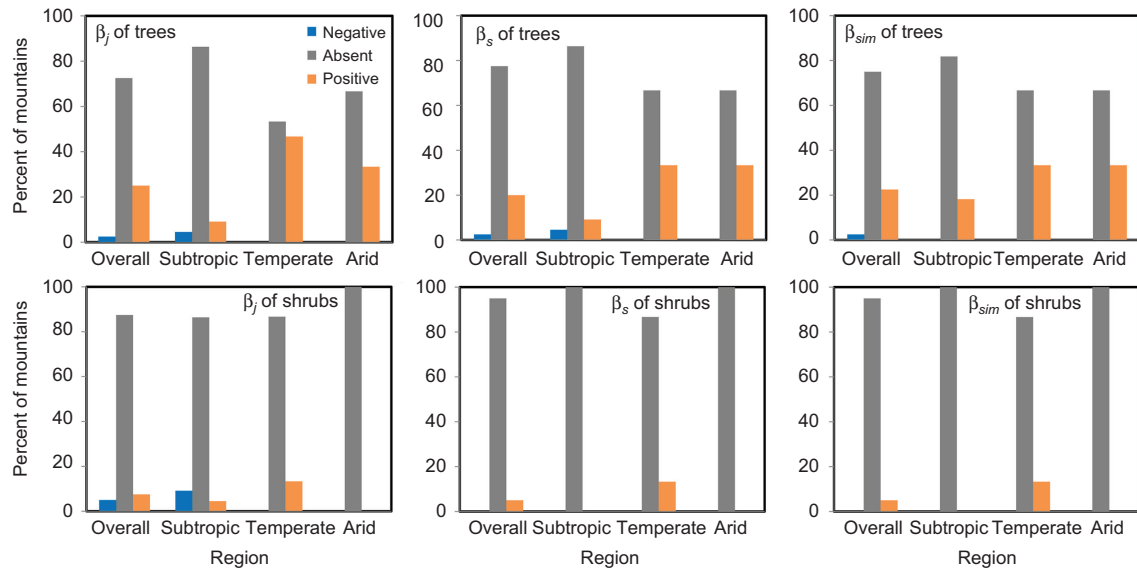


Figure 5. Percentage of different types of β - and γ -diversity relationship along altitudinal gradients for trees (above) and shrubs (bottom) in different regions across China. The colors represent different β - and γ -diversity relationships: cyan for negative (slope < 0 , $p < 0.05$), grey for non-significant ($p > 0.05$), and orange for positive (slope > 0 , $p < 0.05$) of β -diversity as γ -diversity increases.

based on large numbers of in situ plot surveys in an array of mountains. Consistent with Janzen's prediction, altitudinal turnover of species tended to be higher in the tropical than in the temperate mountains (Janzen 1967). In this sense, these results are similar to those derived from several previous studies on horizontal turnover of species based on species range maps of plants and animals (Koleff and Gaston 2001, Koleff et al. 2003b, McKnight et al. 2007, Buckley and Jetz 2008, Qian 2009), even though the methods are radically different. Perhaps most importantly, this suggests that broad latitudinal patterns in β -diversity are rather robust both to the kinds of data employed and to the spatial resolution of analysis.

Further evidence of a decline in β -diversity with increasing latitude can be deduced from studies of several other macroecological patterns. For example, species–area relationships have been found to be steeper, indicating greater turnover of species identities, at lower than higher latitudes (Drakare et al. 2006, Wang et al. 2009, Qiao et al. 2012a, b); latitudinal gradients of species richness have been found to be stronger at regional than local scales, indicating a higher level of species turnover where species richness is greater (i.e. low latitudes) (Hillebrand 2004); and the existence of unimodal relationships between species richness and productivity at local scales and positive relationships at regional scales, indicating a higher turnover rate of species identities in more productive landscapes (i.e. at lower latitudes) (Chase and Leibold 2002, Chalcraft et al. 2004). Together, these separate lines of evidence indicate higher species turnover in low than high latitudes. However, compared to the relatively large amount of variation in species richness that latitude explains both at local (α -diversity) and regional (γ -diversity) scales (Wang et al. 2009), latitude explains little variation in β -diversity across China's forests. This supports the argument that mechanisms determining large-scale patterns of β -diversity are likely to be more complicated than those for α - or γ -diversity

(Koleff et al. 2003b, Gaston et al. 2007b, Myers et al. 2012, Stegen et al. 2012).

The reasons for the decline in β -diversity with increasing latitude are manifold, among which latitudinal gradients in climatic tolerance and sampling effects of the species pool are mostly reported. One widely accepted patterns in ecology is that species may be more climatically tolerant, and disperse farther in more variable and harsher climates (i.e. high latitudes) than in more stable and generally favorable climates (i.e. low latitudes); therefore allopatric speciation may be faster in tropical mountains (climatically more stable) than in their temperate counterparts (more variable) (Janzen 1967, Armesto et al. 1986, Ghalambor et al. 2006, Kozak and Wiens 2007, Jocque et al. 2010). The lower climatic tolerance, shorter dispersal, and faster allopatric speciation may further lead to narrower niche breadths and smaller range sizes in tropical than in temperate mountains (Huey 1978, Vázquez and Stevens 2004, Morin and Chuine 2006, Köckemann et al. 2009, McCain 2009, Morin and Lechowicz 2012), which decreases the likelihood of co-occurrence of different species and increases the turnover of species (β -diversity).

The sampling effect hypothesis claims that the decreasing β -diversity results from decreasing γ -diversity (species pool) as latitude increases (Kraft et al. 2011). It arises when the individuals in local communities are randomly recruited from the larger regional species pools. In species-rich (high γ -diversity) regions, it is likely that some species will only be found in one location due to their limited individuals, whereas in species poor (low γ -diversity) regions, most species will be found in both locations and plots can only differ by a limited amount of species; β - and γ -diversity might therefore be significantly correlated only because of the sampling effect (Kraft et al. 2011). Similar sampling effects of γ -diversity have been reported in other recent studies as well (Myers et al. 2012, Stegen et al. 2012). In this study, β - and γ -diversity were positively correlated along the latitudinal

gradients for both trees and shrubs (Fig. 4), but exhibited no significant relationship in most mountains along altitudinal gradients (Fig. 5). These results indicated that, although the sampling effect hypothesis maybe applicable along the latitudinal gradient of β -diversity, it is not applicable to the altitudinal pattern of β -diversity, at least in this system (but see Kraft et al. 2011). However, because of the commonly observed co-variation between latitude and β -diversity, together with the argument that mechanisms of community assembly may shift between tropical and temperate forests (Freestone and Osman 2011, Myers et al. 2012), further analysis is needed to distinguish the effects of climatic tolerance of species and sampling effects of γ -diversity in controlling latitudinal and altitudinal gradients of β -diversity in China and elsewhere.

Altitudinal patterns of plant β -diversity in China's mountains

Altitudinal transects have commonly been championed as useful models of larger scale ecological patterns, because they compress marked changes in climate into relatively small distances (Körner 2004). Interestingly, in the present study, whilst β -diversity of trees and shrubs similarly declined with latitude, this was not the case with altitude. Rather, they frequently showed different patterns of altitudinal change in β -diversity among different mountains; in most mountains the β -diversity showed no significant trend with increasing altitude (Fig. 3). This suggests that caution should be exercised in drawing close parallels between patterns of β -diversity along latitudinal and altitudinal gradients.

Twenty years ago, Stevens (1992) extended Janzen's hypotheses to explain the altitudinal patterns of species richness, with the assumption that climate is more temporal variable at the high than the low altitudes; one can, therefore, deduce that β -diversity declines with increasing altitude (Stevens 1992). In the present study, we failed to detect either a general decline in β -diversity, or an increase of species occurrence ($R^2 < 0.01$, $p = 0.3$ for trees, $R^2 < 0.01$, $p = 0.1$ for shrubs), with increasing altitude. Furthermore, the assumption that climate variability increases with altitude is not applicable in China's mountains. By using in situ measurement of climate along the southern and northern slopes of Mt Taibai, China, we found that annual range of temperature declined significantly as altitude increases, and diurnal range of temperature didn't show significant trend (Tang and Fang 2006). In the present study, the estimated annual range of temperature declined along altitude in nearly all the mountains across China. These results imply that, extension of Janzen's hypothesis to altitude gradient (Stevens 1992) is not applicable for β -diversity in China's mountains.

In conclusion, consistent with the horizontal turnover of species, the altitudinal turnover of plant species (β -diversity) in China's mountain forests declines as latitude increases. However, β -diversity of both trees and shrubs showed non-significant trends along altitudinal gradients in most mountains. Differences in climate explained $\sim 30.0\%$ of the variation in tree β -diversity and $\leq 10.0\%$ of that in shrub β -diversity. However, altitudinal patterns and climatic controls

of β -diversity varied dramatically in different biogeographical regions. The β -diversity of trees exhibited stronger, whereas that of shrubs showed weaker, climatic patterns in temperate and arid than subtropical regions. These results suggested that mechanisms causing patterns of β -diversity may differ along latitudinal and altitudinal gradients, and among biogeographical regions. Taken together, these results suggest that caution should be exercised in drawing close parallels between patterns of β -diversity along latitudinal and altitudinal gradients.

Acknowledgements – This work was largely completed when ZYT worked as a visiting researcher in KJG's laboratory. KJG holds a Royal Society-Wolfson Research Merit Award. We are grateful to A. P. Chen, Z. L. Liu, S. Q. Zhao, B. Zhu and many others from the Terrestrial Ecosystem Ecology Group, Peking Univ., local experts and other people, and the nature reserves for their help during the investigation, to S. P. Wang for helpful discussion, to N. J. Sanders for insightful comments on early versions of this manuscript. This work was partly supported by NSFC (no. 31021001, 31170499 and 40638039).

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