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Full Length Research Paper

Effect of area and geometric constraints on altitudinal patterns of angiosperm plant richness in Mt. Taibai, the Qinling Mountains, China

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The altitudinal distribution patterns of angiosperms in Mt. Taibai, Qinling Mountains, China, were examined based on data of regional flora and Digital Elevation Model. Possible factors determining the distribution, such as geographical area effect and mid-domain effect (MDE) were assessed. The richness and density at species, genus, and family levels showed a hump-shaped pattern along the altitudinal gradient with peak at low-elevations. Similar patterns were identified for four life-forms (trees, lianas, shrubs and herbs), three biogeographical species groups (cosmopolitan, tropic and temperate), and two different range sizes (small- and large-ranged species). The endemic richness displayed a bimodal pattern with increasing altitude, but the proportion of endemism increased rapidly from low to high altitudes. The area of each altitudinal band was highly associated with the species richness, whereas the MDE could explain 87.0 and 50.3% of the richness variance for overall and endemic species, respectively. The collinearity between MDE and area could explain a large proportion (83.3%) of variance in species richness, implying the substitution between the two factors. Moreover, the explanatory power of MDE was stronger for large-ranged species than for small-ranged species. Our results confirmed that both MDE and area were all crucial factors to explain altitudinal richness patterns in Taibai Mountain, China.

Key words: Species richness, range sizes, mid-domain effect, area effect, altitudinal gradient.

INTRODUCTION

Regional variation in species richness is an old and highly emphasized topic in both ecology and biogeography (Stevens, 1992; Rosenzweig, 1995; Qian, 1998; Rahbek, 2005; Zhang and Zhang, 2011). Owing to the short geographical distances and large climatic differences, altitudinal gradients are ideal for researching large-scale patterns in diversity. There are two main patterns emerged for a variety of taxa and geographical areas: one is a decreasing trend in species richness with increasing altitude (Stevens, 1992; Vázquez and Givnish, 1998) and the other is a mid-altitude peak in richness (Lieberman et al., 1996; Rahbek, 1997; Fleishman et al., 1998). What drives the altitudinal patterns of species diversity? Several hypotheses have been proposed during the last decades, including measures of productivity (Rosenzweig, 1995), habitat heterogeneity (Gough et al., 2000), evolutionary history (Ricklefs et al., 1999), area (Rahbek, 1997), and geometric constraints (Colwell and Hurrt, 1994). In recent years, the relative role of area and geometric constraints in determining the richness patterns has been paid increasing attention (Sanders, 2002; Bachman et al., 2004; Kluge et al., 2006; Wang et al., 2007).

Geographical area hypothesis recognized that large areas often support more species than do smaller ones

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(Rosenzweig, 1995). Previous researches have indicated that the vertical projected area of each altitudinal band changes markedly with the shape or topography of mountains (Rosenzweig, 1995; Wang et al., 2007). Hence, a mid-altitude peak in species richness is understandable if the mid-altitude area is larger than both ends of the gradients. Even monotonic decline with increasing elevation in richness can be explained to a great extent by the large area in low altitude that usually supports more species (Rahbek, 1995). However, there was no relationship between species richness and altitude after the effects of area were eliminated (Lawton et al., 1987). Therefore, using the convenience of digital topographic map to evaluate the importance of area effect on species richness pattern is necessary in the further work.

Recently, some researches demonstrated that the geometric constraints such as sea level or the bottom of a valley and the top of a mountain may affect altitudinal diversity pattern (Colwell and Hurrt, 1994; Jetz and Rahbek, 2002). Colwell and Lees (2000) called this phenomenon the mid-domain effect (MDE), which suggested that a hump-shaped altitudinal richness pattern arises due to the increasing overlap of species ranges towards the centre of the domain, as the altitudinal ranges of species are limited by the spatial constraints in lower and higher elevations. Recent studies accumulate evidence of a potential role for MDE in explaining altitudinal gradients of species richness, particularly for large-ranged species and endemic species (Grytnes and Vetaas, 2002; McCain, 2005; Fu et al., 2006), while the MDE null model cannot be considered an exclusive reason for altitudinal distribution pattern of species (Hawkins and Diniz-Filho, 2002; Kerr et al., 2006). Many researches showed that species richness peaked at the lower half of the altitudinal gradient, which bias the mid-altitude predicted by MDE model (Bhattarai and Vetaas, 2006; Wang et al., 2007). Hence, MDE should be evaluated in combination with other factors (Colwell et al., 2004).

However, investigations of area and geometric constraints in determining the richness patterns have not yielded consistent results. Most studies suggested that area accounts for more variance of species richness than MDE in a variety of taxa (Rahbek, 1997; Kattan and Franco, 2004). The influence of MDE could be disappeared or inconsistent with mid-domain hypothesis after controlling the area effect (Kerr et al., 2006). More interestingly, MDE always exhibits collinearity with area, which might mask the possible relative importance of the excluded variables in regression analyses (Kluge et al., 2006). Therefore, it is still necessary to evaluate the importance of area and MDE on species richness patterns (Jetz and Rahbek, 2002; McCain, 2005; Mponela et al., 2010).

In this study, we delineated altitudinal patterns of angiosperm plants richness and endemic richness in Taibai Mountain, which lies in the middle part of the Qinling Mountains. Using well-documented local flora and graphical information, this study specifically aims to: (1) explore the altitudinal patterns of richness and density for angiosperm plants at three taxonomic levels (family, genus, and species), four life-forms (trees, lianas, shrubs and herbaceous), three biogeographical species types (tropic, temperate and cosmopolitan), and for endemic species in Taibai Mountain; (2) show how the area and MDE factors may explain the variation in species richness along the altitudinal gradients; and (3) compare the respective explanatory powers of area and MDE on the altitudinal patterns in this region.

METHODS

Study area

Mt. Taibai (107°45′E, 33°57′N, 3767 m a.s.l.) is located in the middle of the Qinling Mountains (104°30′E to 112°45′E and32°30′N to 34°45′N) of Shaanxi Province, China. Mt. Taibai is the highest mountain in the eastern mainland of China. This region approximately covers a total area of 3381 km^2 (Figure 1), spanning altitudinal gradient from 530 to 3767 m. Mean annual rainfall is 750 to 1100 mm, primarily falling in June through August, which are also the warmest months with mean monthly temperature of 13.9 and 12.1°C, and December and January are the coldest months with mean monthly temperature of -5.7 and -4.4°C. Taibai Mountain is one of the biodiversity hotspots in East Asia, encompassing at least 1893 vascular plants in 671 genera and 147 families, and accounting for 49.2, 62.9 and 78.6% of the totals in Qinling Mountains, respectively (Li et al., 1989; Ren et al., 2006).

Of these species, 16 are gymnospermae, 110 are pteridophyta, and 1767 are angiospermae. In addition, species endemism is high, with 107 endemic species from 62 genera in 28 families (Ying, 1999). The vegetation in Taibai Mountain from low to high altitudes is approximately separated into warm temperate zone (< 1300 m) dominated by *Quercus variabilis* forest, temperate zone (1300 to 2600 m) dominated by a mixture of *Quercus aliena* var. *acuteserrata*, *Quercus mongolica* (only on the northern slope, 1650 to 2300 m), *Betula albo-sinensis* and *Betula utilis*, cool temperate zone (2600 to 3350 m) dominated by *Abies fargesii* and *Larix chinensis*, and subalpine zone (3350 to 3767 m) dominated by *Rhododendron capitatum* shrub.

Data sources

The data base utilized in the study consists of 1628 angiosperm plants, belonging to 597 genera and 126 families, covering the whole Taibai Mountain elevation gradient. The list of species, genera, and families and their ranges were derived from *Flora Tsinlingensis* (Instituto Botanico Boreali-Occidentali Academiae Sinicae Edita, 1974, 1976, 1981, 1983, 1985, http://www.cvh.org.cn/). The data on elevational ranges published in Comprehensive Survey of the Taibai Mountain Preserve (Li et al., 1989), Biodiversity, Conservation and Management of Mt. Taibai Nature Reserve (Ren et al., 2006), and Wild ornamental plants in Qingling Bashan Mountain area (Li and Ni, 2009). In addition, we divided the species into tropical, temperate, and cosmopolitan biogeographical groups according to The Areal-Types of Chinese Genera of Seed Plants (Wu, 1991) to compare their richness patterns. The maximum and minimum elevations for each species are recorded and endemic species are also noted in these references. The elevational range of each species was estimated as the difference between the minimum and maximum elevations

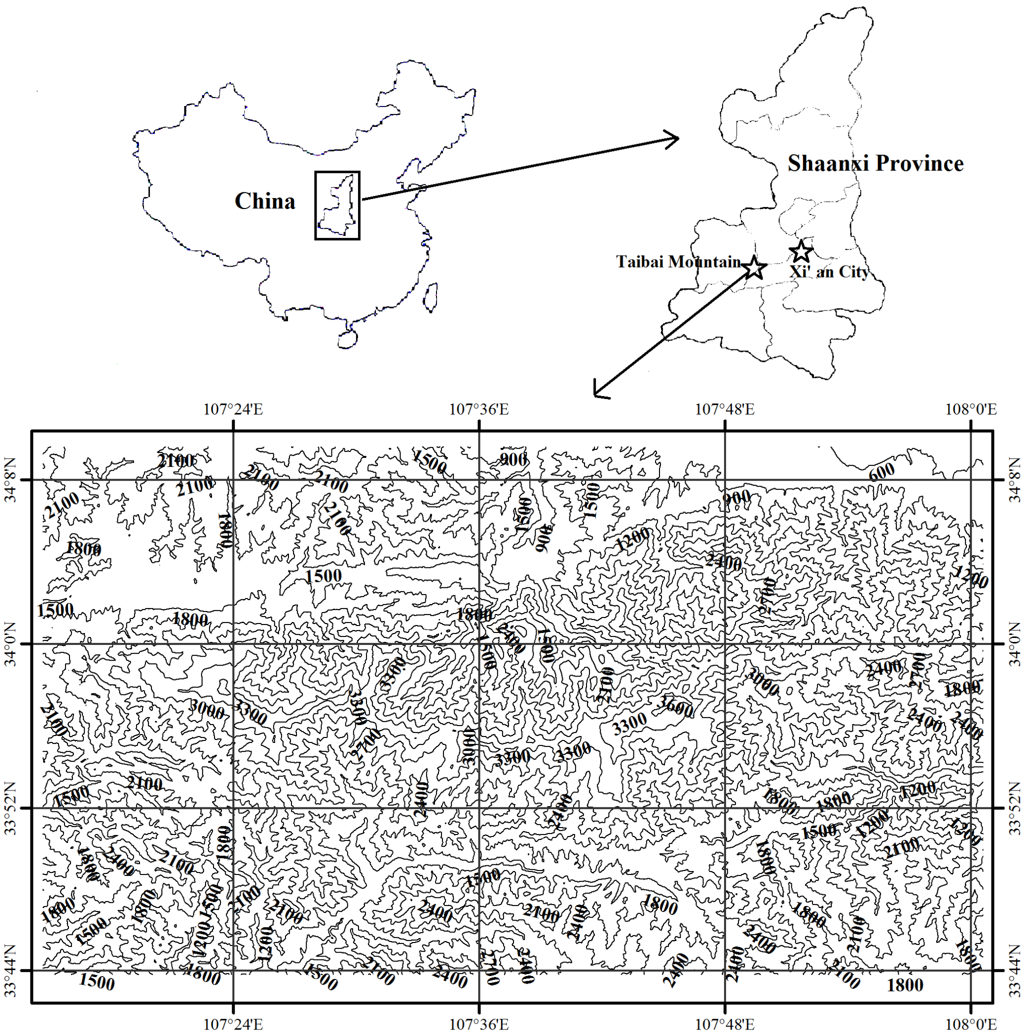

Figure 1. Topographic map of Mt. Taibai, in the Qinling Mountains, Central China.

recorded, and the elevational mid-point was calculated as the average of minimum and maximum elevations. The altitudinal gradient of richness was estimated by grouping species into 32 100-m elevational bands, assuming a continuous presence of species across their elevational ranges.

We used 1: 50000 scale digital topographic maps with 25 m contour intervals from the Shaanxi Bureau of Surveying and Mapping (SHASM) to calculate the area at each 100-m elevation band by calculating the number of 15 × 15 m grids in every elevational band. The area showed hump-shaped pattern across a broadly elevational range, and area extent at the middle mountain region (1400 to 2600 m) was nearly two or three times larger than all other regions (Figure 2). The relationship between available area and species richness was analyzed. We found that the exponential curve was the most suitable for species-area relationship in our study (regressing species accumulation curve using logarithmic model: $R^2 = 0.73$, $P < 0.0001$). Taking area into account, taxon density D is calculated as follows (Vetaas and Grytnes, 2002):

$$D = S/\log A$$

where A and S are area (km^2) and number of taxon in each altitudinal band, respectively.

Geometric constraints: The MDE

A MDE null model was used to estimate the effect of geometrical constraints on the altitudinal distribution of species (Sander, 2002; Colwell et al., 2004; Grytnes et al., 2006). We used Colwell's RangeModel software, version 5 (a Monte Carlo simulation tool for assessing geometric constraints on species richness) to generate a null distribution predicted by the MDE based on 5000 runs. Empirical species ranges were placed at random within the domain under the constraint that none exceeded domain limits. Owing to large-ranged species are more likely to be constrained by hard boundaries, whereas small-ranged species are more likely to show the effects of underlying environmental and historical drives (Colwell and Lees, 2000; Colwell et al., 2004), we were partitioning species into two halves with species of small and large elevational ranges for analysis (Jetz and Rahbek, 2002).

Data analysis

Spatial autocorrelation has an impact on the statistical tests especially on the gamma diversity studies, because some pairs of observations are not fully independent of each other (Dale, 2002;

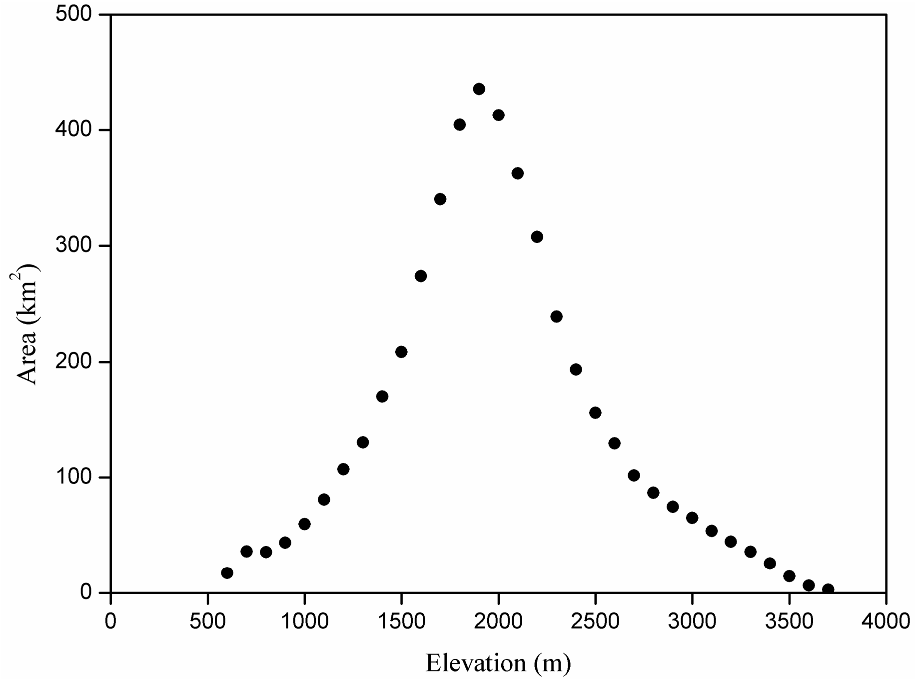

Figure 2. Altitudinal pattern of area in Taibai Mountain, showing a hump-shaped pattern with a peak of *c.* 435.6 km^2 at mid-elevation of 1900 m.

Tognelli and Kelt, 2004; Wang et al., 2007). We calculated the Moran's I for species richness and residuals, and found a significant positive spatial autocorrelation (Moran's I = 0.26). Thus, we used ordinary least squares model (OLS) and conditional autoregressive model (CAR) to explore the relationships between species richness and the log-transformed area, as well as the MDE model predicted richness. The relationships between the observed species density and the MDE predicted richness were also tested. The two models were performed in SAM 4.0 (http://www.ecoevol.ufg.br/sam). Since the response variables, species richness, or density, are discrete data and may have Poisson distribution errors, the logarithmic link function was used in the calibration of OLS and CAR models. The Akaike's information criteria (AIC) were used to compare the fit of the OLS and CAR models, and smaller AIC values indicated a better fit.

RESULTS

Patterns of taxonomic richness and density

There are 1628 angiosperm species, belonging to 597 genera and126 families in Taibai Mountain. More than half of the species are herbaceous (67.2%), with shrubs accounting for 16.6%, tree 13.4%, and liana 2.8%. The species-rich families are Asteraceae (49 genera, 186 species), Rosaceae (26 genera, 118 species), Poaceae (43 genera, 92 species), and Ranunculanceae (18 genera, 78 species). The species richness in Mt. Taibai at three taxonomic levels (species, genus and family) showed a left-skewed hump-shaped pattern with maximum near 1300 to 1400 m (Figure 3a). Although taxonomic richness might be adjusted by area, the patterns of taxonomic density remained the same as that of richness along elevation gradients (Figure 3b). Species partitioned into two groups (small- and large-ranged species, each group contains *c.* 814 species) exhibited distinct altitudinal centers (Figure 4). Small-ranged species had maximal richness at the lower (*c.* 1200 to 1300 m) and the upper (*c.* 2900 to 3000 m) ends of the gradients, respectively. In contrast, large-ranged species showed a mid-elevation peak in richness. There were higher correlation coefficients between large-ranged species richness and overall species richness (r = 0.94) than between small-ranged species and overall species richness (r = 0.65).

The best fit models, CARs, identified both area and MDE as strong predictors for overall and large-ranged species, whereas the explanatory power of MDE and area was low for small-ranged species (Table 1). The area explained 83.3% of the richness variance for all species, and MDE accounted for 87.0% of the variance, with a total explanation of 86.8% by both. For the small- and large-ranged species, the area explained 40.7 and 80.0% of the richness variance, respectively, while the MDE explained 31.8 and 86.1% (Table 1). As for the species density, MDE accounted for 67.4, 25.0 and 70.7% of the variance for all species, small- and large-ranged groups (Table 2). However, analysis of variance for CARs depicted that after controlling the area-effect in multivariable models, MDE only accounted for 3.5% of the variation in species richness, and 0.4 and 3.4% for

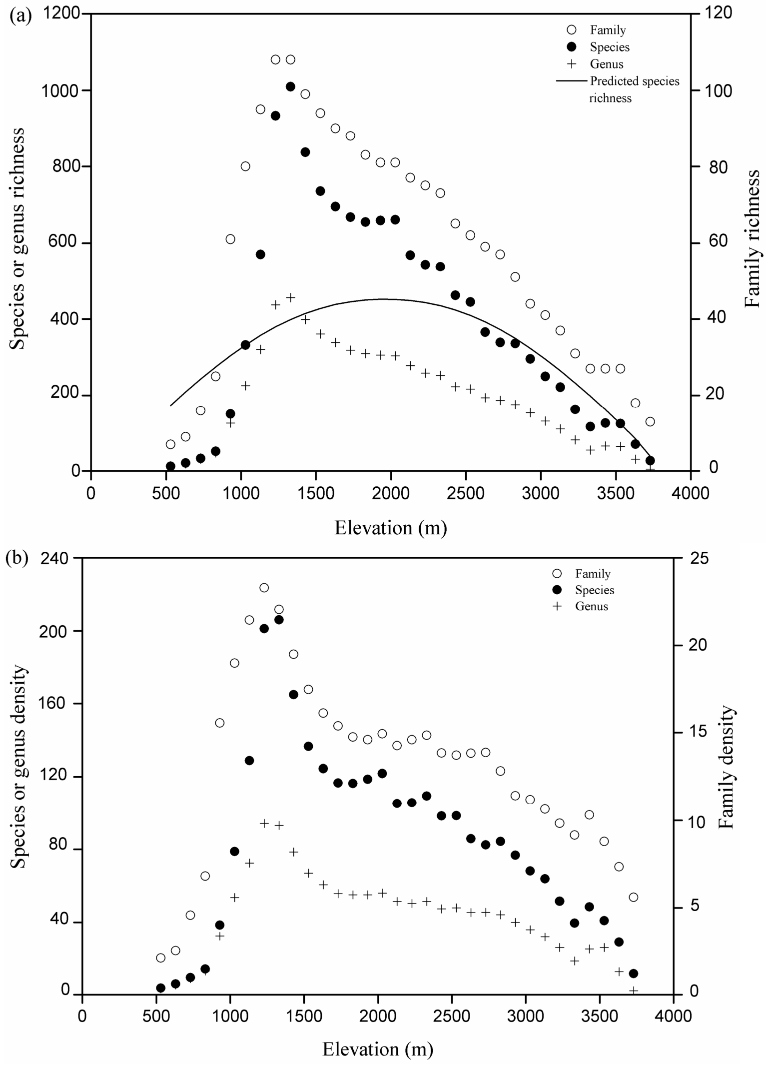

Figure 3. Altitudinal patterns of total species, genus and family richness (a) and their densities (b) in Taibai Mountain. The solid line represents predicted species richness using the RangeModel 5.

the small and large-ranged groups, respectively. Compared with this, area accounted for 0.2, 8.5 and 2.7% after MDE was controlled, respectively (Figure 5). In contrast, the collinear part between the two variables accounted for large proportions of variation in species richness (overlapping parts in Figure 5).

Species richness patterns of different life forms and biogeographic groups

The species richness of the different life-forms showed hump-shaped distributions along the altitudinal gradient, and had the similar altitude peak (1300 m a.s.l.) to overall species (Figure 6a). The CAR models also depicted that the patterns of four life-forms richness were correlated strongly with both area and MDE ($R^2 > 0.75$) (Table 1). For the species density, MDE accounted for 44.6, 48.1, 61.6 and 57.9% of the variance for trees, lianas, shrubs and herbaceous species, respectively (Table 2). The proportion of the four life-forms to overall species along the altitudinal gradient indicated three different patterns (Figure 6b). Herbaceous species had the largest proportion along the whole gradient, taking *c.* 60% of the overall species below 2000 m, and then its dominance sharply increased towards high elevations, reaching almost 93% above 3500 m. The proportion of lianas and trees was about 4 and 20%, respectively, at the low and middle elevations, but decreased at high elevations. While the proportion of shrubs was relatively stable, having a slightly decline above 2900 m. Different biogeographical species groups showed hump-shaped altitudinal patterns (Figure 7), with maxima at nearly the same altitudes (1200 to 1400 m a.s.l.) as that of overall

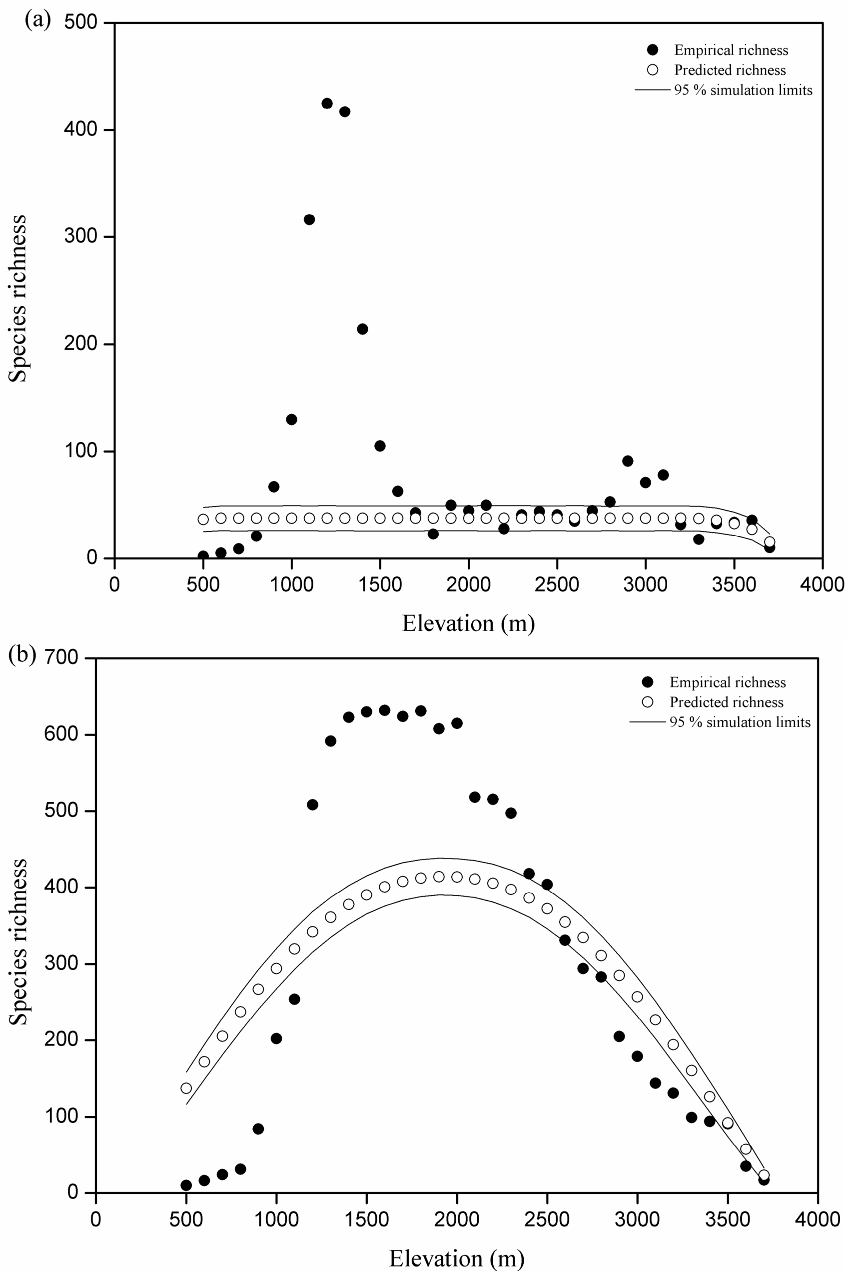

Figure 4. Empirical and predicted richness distributions for small-ranged species (a), and large-ranged species (b). Prediction was performed using RangeModel 5.

species and different life-forms species. And tropical group was more strongly correlated with MDE (R^2 = 0.82) than with area (R^2 = 0.77), while that of temperate group indicated a higher correlation to area (R^2 = 0.83) than to MDE (R^2 = 0.78).

Species richness pattern of endemic species

Both species richness and species density exhibited a bimodal relationship with altitude for the recorded 107 endemic species to Taibai Mountain, with two obviously peaks at the low and high elevations (Figure 8a). The CAR analysis indicated that the pattern of endemic species showed a stronger correlation to MDE (R^2 = 0.50) than area (R^2 = 0.42). The ratio of endemic species increased from low to high elevations, but above 3200 m a.s.l. there was a drop before it increased again (Figure 8b). Three distinct zones can be identified for the endemic species altitudinal pattern. The ratio of endemic component was small, only 1.2 to 3.5%, in the low altitudinal zone (< 1300 m), but increased sharply from

Table 1. Ordinary least squares (OLS) and conditional autoregressive (CAR) regressions for explained variables and species richness of overall species, small-ranged species and large-ranged species, and different life-forms in Taibai Mountain.

Species richness	**Variable**		**OLS models**			**CAR models**		
			Model 1	**Model 2**	**Model 3**	**Model 1**	**Model 2**	**Model 3**
All species	Ln (area)	t	1.23	-	8.05***	1.36	-	6.90***
	MDE	t	1.36	8.12***	-	1.41	7.05***	-
	AIC		201.4	200.5	200.81	177.5	174.3	182.7
	Model fit (R^2)		0.695	0.680	0.677	0.868	0.870	0.833
Small-ranged species	Ln (area)	t	1.38	-	1.91	0.95	-	1.28
	MDE	t	0.24	1.28	-	0.72	0.92	-
	AIC		199.1	198.5	196.6	189.6	191.2	186.6
	Model fit (R^2)		0.107	0.050	0.105	0.403	0.318	0.407
Large-ranged species	Ln (area)	t	1.79	-	9.75***	2.43	-	9.13***
	MDE	t	1.24	9.41	-	1.05	8.58***	-
	AIC		188.0	188.7	187.0	180.4	171.8	183.7
	Model fit (R^2)		0.766	0.741	0.754	0.834	0.861	0.800
Trees	Ln (area)	t	3.01	-	7.49***	2.58*	-	6.16***
	MDE	t	-0.91	6.14***	-	-0.49	5.16***	-
	AIC		325.8	332.0	324.1	288.8	298.4	284.7
	Model fit (R^2)		0.654	0.549	0.644	0.899	0.854	0.903
Lianas	Ln (area)	t	2.53*	-	6.65***	1.90	-	5.25***
	MDE	t	-0.88	5.71***	-	-0.35	4.66***	-
	AIC		231.0	234.8	229.3	200.6	201.8	196.4
	Model fit (R^2)		0.598	0.512	0.588	0.858	0.839	0.863
Shrubs	Ln (area)	t	1.82	-	8.78***	1.57	-	7.20***
	MDE	t	0.47	8.19***	-	0.70	6.95***	-
	AIC		328.9	329.7	326.5	288.9	285.4	292.2
	Model fit (R^2)		0.715	0.684	0.713	0.925	0.926	0.909
Herbaceous	Ln (area)	t	0.002	-	6.96***	0.285	-	6.23***
	MDE	t	1.92	7.63***	-	1.69	6.72***	-
	AIC		407.1	404.5	408.3	399.5	396.2	404.4
	Model fit (R^2)		0.652	0.652	0.61	0.754	0.758	0.689

Model 1 included all explained variables, model 2 only included the mid-domain effect (MDE), and model 3 only included area effect. We tested t-values for their significance (*P<0.05, **P<0.01, ***P<0.001). Model fit was assessed using the Akaike information criteria (AIC), smaller values indicate a better fit.

Table 2. Ordinary least squares (OLS) and conditional autoregressive (CAR) regressions for explained variables and species density of overall species, small-ranged species and large-ranged species, and different life-forms in Taibai Mountain.

Species density	**Variables**	**OLS models**			**CAR models**		
		t	**AIC**	**Model fit (R^2)**	**t**	**AIC**	**Model fit (R^2)**
All species	MDE	4.71**	162.6	0.417	3.87***	143.4	0.674
Small-ranged species	MDE	-0.12	151.4	<0.001	0.30	142.0	0.250
Large-ranged species	MDE	5.33***	151.7	0.478	4.58***	132.7	0.707
Trees	MDE	2.08*	245.1	0.123	1.54	233.5	0.446
Lianas	MDE	2.36*	145.2	0.152	1.79	132.6	0.481
Shrubs	MDE	3.66***	244.5	0.302	2.97**	228.3	0.616
Herbaceous	MDE	4.13***	311.3	0.355	3.50***	300.9	0.579

We tested t-values for their significance (*P<0.05, **P<0.01, ***P<0.001). Model fit was assessed using the Akaike information criteria (AIC), smaller values indicate a better fit.

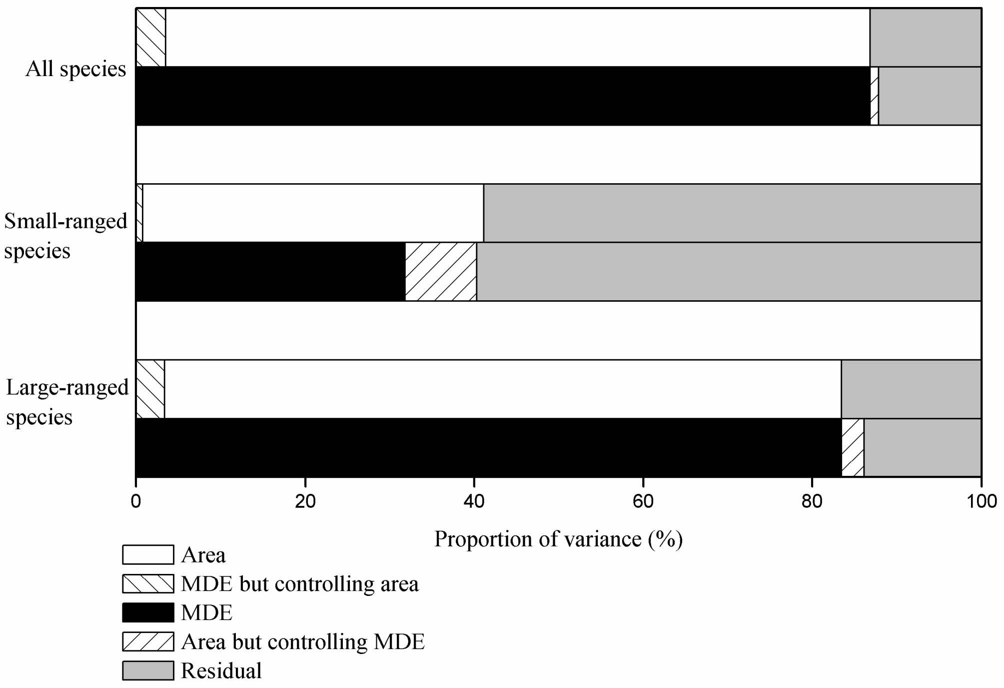

Figure 5. The proportions of variation in species richness explained by MDE (black bars), area (white bars) depending on CARs analysis. Overlapping parts display the collinearity between the two variables. Upward diagonal bars represent the proportions of variation in species richness explained by area after MDE was controlled; downward diagonal bars indicate the proportions explained by MDE after area was controlled; light grey bars represent the residual proportions of variation in species richness.

4.3 to 13.6% in the middle altitudinal zone (between 1300 and 3000 m, $R^2 = 0.97$, $P < 0.0001$), and in the high altitudinal zone (> 3000 m), it tended to decline, but fluctuated between 10.4 and 14.1%.

DISCUSSION

Understanding the distributions of plants and animals along altitudinal gradient and their underlying mechanisms would have profound implication to regional biodiversity conservation (Bhattarai and Vetaas, 2006; Chettri et al., 2010). Trees and bryophytes generally showed a monotonic decrease in species richness with increasing elevation (Stevens, 1992; Bhattarai and Vetaas, 2003), although the unimodal patterns between species richness and elevation have been observed in particular habitats (Bhattarai and Vetaas, 2006; Grytnes and Beaman, 2006). However, growing evidence suggested that mid-elevation peaks in species richness for a wide variety of taxa are perhaps more general (Rahbek, 1995, 2005). Corresponding with some studies (Kessler, 2002; Wang et al., 2007), our results showed that species richness increased with elevation at lower altitudes, and then declined towards high altitudes at family, genus and species levels. Similar patterns were also identified for the four life-forms (trees, lianas, shrubs and herbs), and three biogeographical species groups (cosmopolitan, tropic and temperate).

The different patterns and processes for overall species and endemism across altitudinal gradient were observed for both plants (Whittaker et al., 2001; Kessler, 2002; Vetaas and Grytnes, 2002) and animals (Fu et al., 2006). In Mt. Taibai, the endemic richness showed a bimodal pattern, different from the unimodal pattern for overall species. The mismatch of the distribution patterns of endemic species and overall species might be associated with alternative response of different species groups to factors controlling distribution limits, including timber line which situates at *c.* 3300 m a.s.l., and glacial limits that penetrated down to 2800 to 3000 m a.s.l. in the Late Glacial Period (Colwell and Lee, 2000; Vetaas and Grytnes, 2002). The proportion of endemic species increased with elevation, reaching a maximum between 3000 and 3300 m. The proportional increase was due mainly to a sharp decrease in overall species richness. This could be observed from the coincidence of the maximum number of endemic species (Figure 8a) with a sudden drop in species richness (Figure 3a) between 1500 and 3000 m.

What determines the unimodal patterns of richness and the location of the peak is not fully understood. The

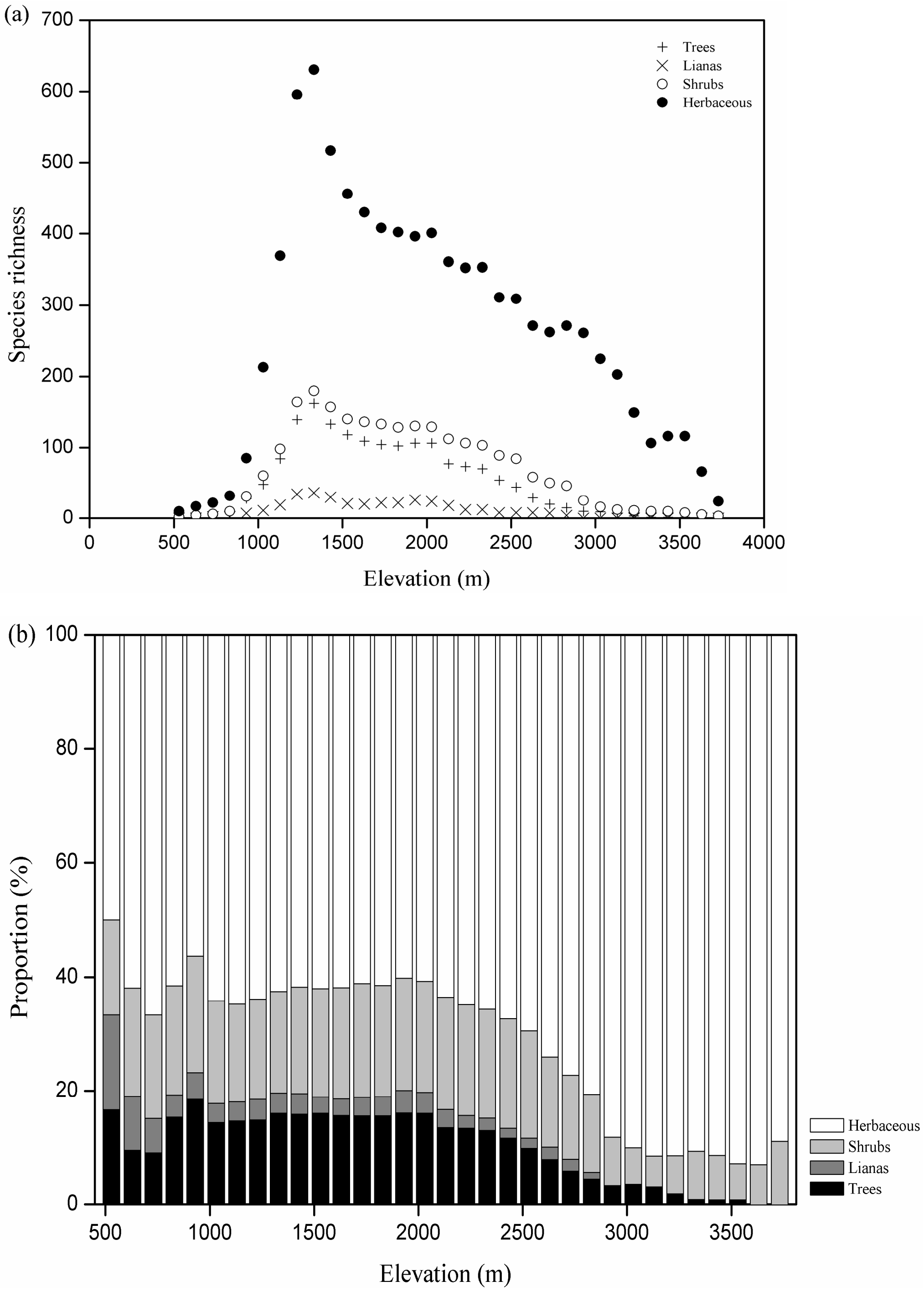

Figure 6. (a) Richness patterns of species belonging to different life-forms along the altitudinal gradient. (b) The proportion of each life-form (tree, liana, shrub and herbaceous) to total richness in each altitudinal band.

methodological approach of interpolation may be a potential factor for creating a unimodal pattern (Vetaas and Grytnes, 2002; Bhattarai and Vetaas, 2006; Wang et al., 2007). Interpolating species presence between lower and upper elevational limits to estimate species richness may create an artificially steep decrease in species richness toward the both ends of the gradient (Grytnes and Vetaas, 2002), and likely result in a pseudo-unimodal pattern. The reason is that richness toward the boundaries consists only of observed species, whereas at

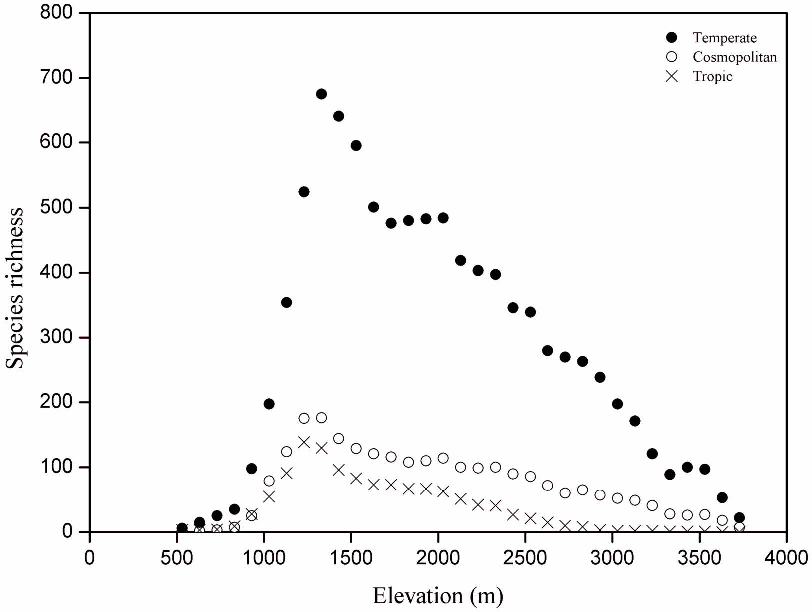

Figure 7. Altitudinal richness patterns of different biogeographical species groups (cosmopolitan, tropic and temperate).

other altitudes, richness consists of observed species plus the species added by interpolation (Grytnes and Vetaas, 2002; Moreno et al., 2008). Thus, Grytnes and Vetaas (2002) recommended using small-ranged species to evaluate the species-altitudinal patterns (Wang et al., 2007). In our study, we investigated the richness patterns of species with range sizes of 100 m and < 200 m without interpolation, and found that the species richness still showed unimodal patterns, with the same peak at 1300 m a.s.l., respectively, implying that interpolating artifacts were not operating. The unimodal richness pattern of angiosperm species observed in this region is reliable, although how to further eliminate such methodological artifacts will be a challenge in the further studies.

Generally, area may be a crucial factor determining altitudinal diversity patterns because species richness increases as a function of area (Rosenzweig, 1995; Rahbek, 1997; Bachman et al., 2004). The effect of area in determining regional species richness in elevational ranges has been supported by different taxa (Bachman et al., 2004; Kluge et al., 2006). In Mt. Taibai, the area showed a unimodal distribution along an elevational gradient (Figure 2). This distribution nearly corresponded to the elevational change in species richness has encouraged the belief that the area may be a cause for the pattern of species richness. The results from the CAR indicated that the area explained 83.3% of the variance in species richness. However, when the influence of area was eliminated using species density (that is the number of richness per log-transformed area, Vetaas and Grytnes, 2002), the patterns of species, generic and familial density, as well as endemic species density still displayed hump-shaped trend. Thus, area as a single predictor might have a limited role in explaining the altitudinal richness patterns of angiosperm species in Taibai Mountain.

Recently, the MDE based on geometric constraints have been increasingly considered as the null hypothesis against which to test spatial patterns of richness, especially for hump-shaped altitudinal patterns (Jetz and Rahbek, 2002; Fu et al., 2006; Brehm et al., 2007). The angiosperm plant datasets in Taibai Mountain depicted that MDE accounted for a large proportion of the variation in the total species and endemic species richness along the altitudinal gradients. However, if the MDE was the main explanation, one would expect a peak in species richness at *c.* 2100 m a.s.l. (midpoint between 530 to 3760 m a.s.l.). But the observed ones were left skewed with their richness peaks at lower elevations (*c.* 1300 m a.s.l.). Such a deviation has also been observed in previous studies (Wang et al., 2007), and suggested the impacts of area. However, when the area effect was eliminated using species density as dependent variable, percentage of variance explained by MDE tended to decrease for all species, small-ranged species, large-ranged species and different life-forms species (Table 2). Moreover, the area's near-mid-peak distribution in Mt. Taibai also could not explain the richness skew. There must be some other factors such as topographic heterogeneity and even soil pH, affecting the richness pattern besides area and the MDE. But the coordination of area and the MDE might be confirmed by collinearity analysis, which showed the two factors accounted to large proportions of variation in species richness

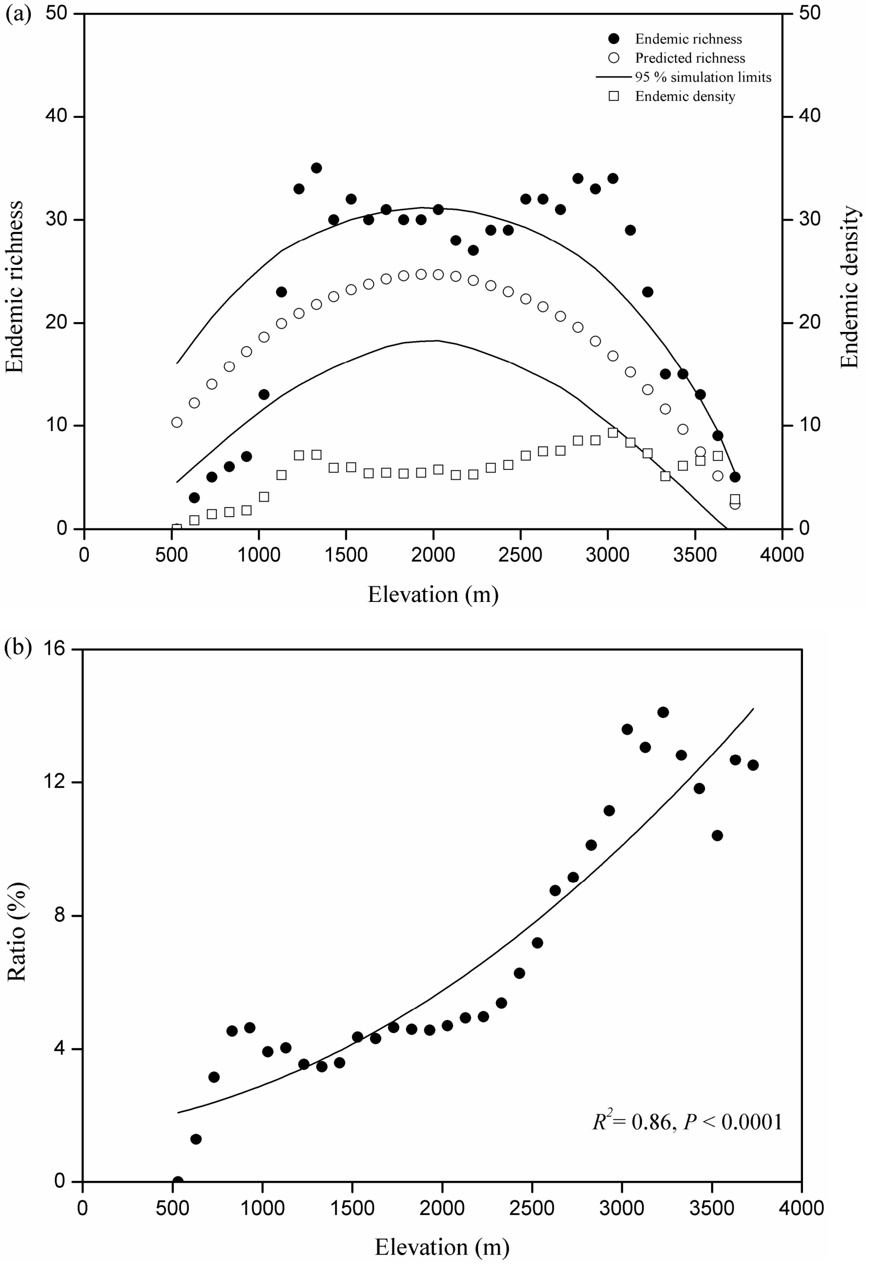

Figure 8. Altitudinal patterns of endemic species richness and its density a, and ratio of endemic species to overall species richness (b) in Taibai Mountain.

(overlapping parts in Figure 5). These results indicated that the species richness patterns could not be completely ascribed to only one variable or the other (Kluge et al., 2006; Wang et al., 2007).

Additionally, different range-size groups (that is small- and large-ranged species) often have different richness patterns, and the large-ranged component contributes more to a species richness pattern than do small-ranged species (Jetz and Rahbek, 2002; Kreft et al., 2006; Kluge et al., 2006). These features were supported by this study. Moreover, we found that the explanatory power of MDE was stronger for large-ranged species than for small-ranged species. Climate effects may be an underlying factor to explain the altitudinal biodiversity patterns as many previous studies suggested (Bhattarai and Vetaas, 2003; Watkins et al., 2006), although we did not analyze its role quantitatively. It is widely recognized that optimal environmental conditions (maximum humidity, optimum temperature-precipitation conditions) in middle of the gradients lead to higher species richness (Hawkins and Diniz-Filho, 2004). In Taibai Mountain, highest rainfall occurs between 1300 and 2600 m, but the number of rainy days is highest at 2600 m.

Moreover, above 2600 m a.s.l. higher relative humidity and frequent fog and cloudy days will increase with elevation (Li et al., 1989; Tang and Fang, 2006) and available energy will gradually be reduced at higher elevations (Tang and Fang, 2006). Thus, it could be expected that maximum species richness should fall between 1300 and 2600 m a.s.l., because this section may provide the best combinations of water and heat for plant growth, and consequently allow a higher resource use rate and maintenance of more species (McCain, 2007; Wang et al., 2007). Our results supported this estimated to some extent, although the richness showed unimodal pattern with peak at low-elevation (*c.* 1300 m) rather than a symmetric distribution with peak at mid-elevation (*c.* 2100 m) as predicted by the optimum climatic model. Therefore, the species richness altitudinal patterns can not be ascribed to one single factor but to several factors, such as geometric constraints, available area, and climate. To investigate the environmental conditions, in particular topography, habitat heterogeneity, soil moisture and soil pH, to disentangle the drives of altitudinal patterns of diversity, especially small-ranged species diversity in different mountains remains a challenge for further work.

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