ALTITUDINAL PATTERNS OF PLANT SPECIES RICHNESS IN THE HONGHE REGION OF CHINA

XIANG XU[1,2], HUAYONG ZHANG[1]*, DONGJIE ZHANG[1], WANG TIAN[1], HAI HUANG[1] AND ATHEN MA[2]

[1]*North China Electric Power University, Research Center for Engineering Ecology and Nonlinear Science, Beijing, 102206, China*
[2]*Queen Mary University of London, School of Electronic Engineering and Computer Science, London, E1 4NS, United Kingdom*
**Corresponding author's email: bjecology@gmail.com, Tel: +86-10-61773936, Fax: +86-10-61773936*

Abstract

Understanding the key mechanisms shaping the altitudinal patterns of biodiversity is critically important in ecology and biogeography. In this study, we examined the patterns of species richness of different plant groups characterized by different life forms and range sizes along the altitudinal gradient in the Honghe region of China, one of the global hotspots of biodiversity. The relative contributions of area, the mid-domain effect (MDE) and temperature in shaping these patterns were evaluated. Our results revealed that the altitudinal patterns of species richness of seed plants, trees, shrubs, herbaceous plants, narrow-range plants (range ≤ 600 m) and broad-range plants (range > 600 m) all exhibited bell-shaped distributions. The analyses showed that area accounted for the largest percentage of the variation in species richness for all plant groups, followed by mean annual temperature, which served as the measure of available ambient energy in our analyses. Although MDE determined the smallest percentage of the variation, it still explained ≥ 67.3% of the species richness for all plant groups except fornarrow-range plant species. The results of the variation partitioning analyses suggested that the majority of the variance in species richness was explained by the collinearity amongarea, MDE, and temperature. Moreover, different plant groups demonstrated different relationship sensitivities with the explanatory variables, which reflected the different physiological requirements of woody and herbaceous plants, and greater influence of geometric constraint on the placement of larger range sizes.

Key words: Species richness; Altitudinal pattern; Plant life form; Species–area relationship; Mid-domain effect.

Introduction

Geographical patterns of biodiversity and their underlying mechanisms are key research topics in ecology and biogeography (Colwell & Lees, 2000; Grytnes *et al.*, 2006; Khan *et al.*, 2014; Chan *et al.*, 2016). Broad-scale patterns of species richness are the most commonly studied topics (Rosenzweig, 1995; Zhang *et al.*, 2011; Khan *et al.*, 2013; Ullah *et al.*, 2015). In recent years, research on the altitudinal patterns of species richness has attracted considerable attention (Rahbek, 2005; Wang *et al.*, 2007; Guo *et al.*, 2013). Because temperature and the area available to plants vary with elevation, a distinct gradient in species richness can be seen (Acharya *et al.*, 2011; Karger *et al.*, 2011; Khan & Ahmad, 2015). Since mountains present a wide altitudinal range and complex topography, they provide large gradients in climate and other variables (Grytnes, 2003; Malhi *et al.*, 2010; Ghazal, 2015), harbor number of species, and include many of the world's protected areas (Gaston, 2000; Khan *et al.*, 2014). The altitudinal gradients in mountainous regions consequently offer an ideal natural environmental systemto explore the drivers determining species richness patterns (Körner, 2007; McCain, 2009; Khan *et al.*, 2012; Badshah *et al.*, 2016).

Species richness patterns of plants (Bhattarai & Vetaas, 2003; Wang *et al.*, 2007; Acharya *et al.*, 2011; Khan *et al.*, 2013), invertebrates (Beck & Chey, 2008), birds (McCain, 2009), and mammals (McCain, 2005) along altitudinal gradients have been investigated in many previous studies. These patterns differ depending on the taxa and altitudinal gradients in different mountain regions (Rahbek, 1995). Rahbek (2005) reviewed 204 studies conducted along altitudinal gradients and summarized three main forms of species richness patterns: (1) a monotonic decline with rising elevation, (2)

a plateau at low elevations, and (3) a bell-shaped distribution with peak species richness at middle elevations. The most common pattern observed was the bell-shaped curve, which was reported in approximately 50% of previous studies (Rahbek, 2005). Nevertheless, controversy still exists regarding which causal factors or hypotheses account for the altitudinal patterns in plant species richness (Colwell & Lees, 2000; Rahbek, 2005; Wang *et al.*, 2007).

The widely discussed species–area hypothesis predicts that the larger the area, the more species it will support (Rosenzweig, 1995; Sanders, 2002). Numerous studies have revealed that the area along altitudinal gradients accounts for a large percentage of the variation in species richness (Bachman *et al.*, 2004; Wang *et al.*, 2007). However, several authors have pointed out that area alone cannotaccount for all the variability in species richness and have therefore proposed other hypotheses (Rahbek, 1995; Wang *et al.*, 2007). The mid-domain effect (MDE) is another hypothesis used to explain the bell-shaped altitudinal pattern of species richness (Colwell & Hurtt, 1994; Colwell & Lees, 2000). The MDE results from the random placement of species ranges within a bounded geographical domain, which increases the overlap of species ranges toward the middle of the domain (Colwell & Hurtt, 1994; Colwell *et al.*, 2004). Thus, a bell-shaped relationship between species richness and elevation arises, regardless of ecological factors (Colwell *et al.*, 2004). However, debate still continues regarding whether or not to accept the MDE hypothesis to explain altitudinal patterns of species richness (Watkins *et al.*, 2006; Wang *et al.*, 2007; Trigas *et al.*, 2013). Besides these two important spatial hypotheses (the species–area and MDE hypotheses), the climate has been identified as one of the main drivers of the altitudinal gradient in species richness (O'Brien *et al.*,

1998; Bhattarai *et al.*, 2004; Acharya *et al.*, 2011). O'Brien*et al.* (1998) proposed aclimate based water-energy hypothesis to predict the large-scale (continental) distribution patterns of species richness for woody plants. Hawkins *et al.* (2003) extended this hypothesis to demonstrate species richness patterns along altitudinal gradients. However, other studies have tested this conjecture and found inconsistent support for the water-energy hypothesis along altitudinal gradients (Bhattarai& Vetaas, 2003; Hawkins *et al.*, 2003; Carpenter, 2005).

Consequently, no universal agreement exists among ecologistsregarding the spatial constraint mechanisms that governthealtitudinal patterns of species richness (Zapata *et al.*, 2005; McCain, 2009; Lee *et al.*, 2013). Therefore, there is a need for further studies to identify the determining factors driving the altitudinal patterns of plant species richness. We chose theHonghe region of southern China, one of the global biodiversity hotspots (Myers *et al.*, 2000), as the site to conduct our analyses. TheHonghe region has a diverse topography, high levels of rain and heat, andtherefore a typical vertical sequence of tropical montane vegetation, which provides an ideal altitudinal gradient to explore the drivers governing the altitudinal patterns of plant species richness (Shui, 2003). Using well-documented flora records from the region, we initially identified the altitudinal patterns of species richness for seed plants, three groups characterized by different life forms (trees, shrubs, and herbs) and two groups having different range sizes (narrow-range: range ≤ 600 m; broad-range: range > 600 m). We chose 600 m as the cutoff to make the number of the narrow-range species comparable to that of thebroad-range species. Then, we examined the relative contributionsof thespecies–area, MDE, and climate hypothesesin these patterns for different plant groups. We also examined whether the strength of the relationship between species richness and each hypothesis was independent of plant life form and species range size.

Materials and Methods

Study area: The Honghe region (101°48'–104°17'E, 22°26'–24°45'N), or the Honghe Hani and Yi Nationalities Prefecture, lies in the southeast of Yunnan Province, China (Fig. 1a). The region has a mountainous topography with the elevation decreasing southeastward. The region covers a total area of 33,302 km^2, and most of the area is limestone. The highest elevation is 3057 m (Xilong Mountain) and the lowest is 17 m (Fig. 1b). The Tropic of Cancer crosses the region, so it has a tropical and subtropical monsoon climate, with the mean annual temperature ranging from 9.8°C to 25.1°C, and the mean annual precipitation from 876 mm to 1926 mm. Due to its abundant precipitation and heat, its complex topography and wide connection with the world flora, this region harbors a rich diversity of plant species (Myers *et al.*, 2000). Along the altitudinal gradient, the vegetation from lower to higher elevations isthe tropical rain forest,montane rain forest, monsoon evergreen broad-leaved forest, montane mossy evergreen broad-leaved forestandsummit mossy evergreen broad-leaved forest (Shui, 2003).

Data sources: We generated a species database based on the book Seed Plants of Honghe Region in SE Yunnan, China (Shui, 2003). This database includes the minimum and maximum elevationsfor each species, thelife form (tree, shrub, or herb), and whether this species is native or exotic. In this region, a total of 6021 plant species from 1511 genera and 229 families have been identified. Of these species, 5947 species (1488 genera and 225 families) are native and 74 species (60 genera and 43 families) are exotic. We derived land-use data from GlobeLand30 with a resolution of 30 m provided by the National Geomatics Center of China (DOI:10.11769/GlobeLand30.2010.db). We extracted elevation data from a digital elevation model with a resolution of 30 m (ASTER GDEM Version 2, DOI: 10.5067/ASTER/ASTGTM.002) and adopted climatic surface data from the WorldClim database with a resolution of 1 km (Hijmans *et al.*, 2005).
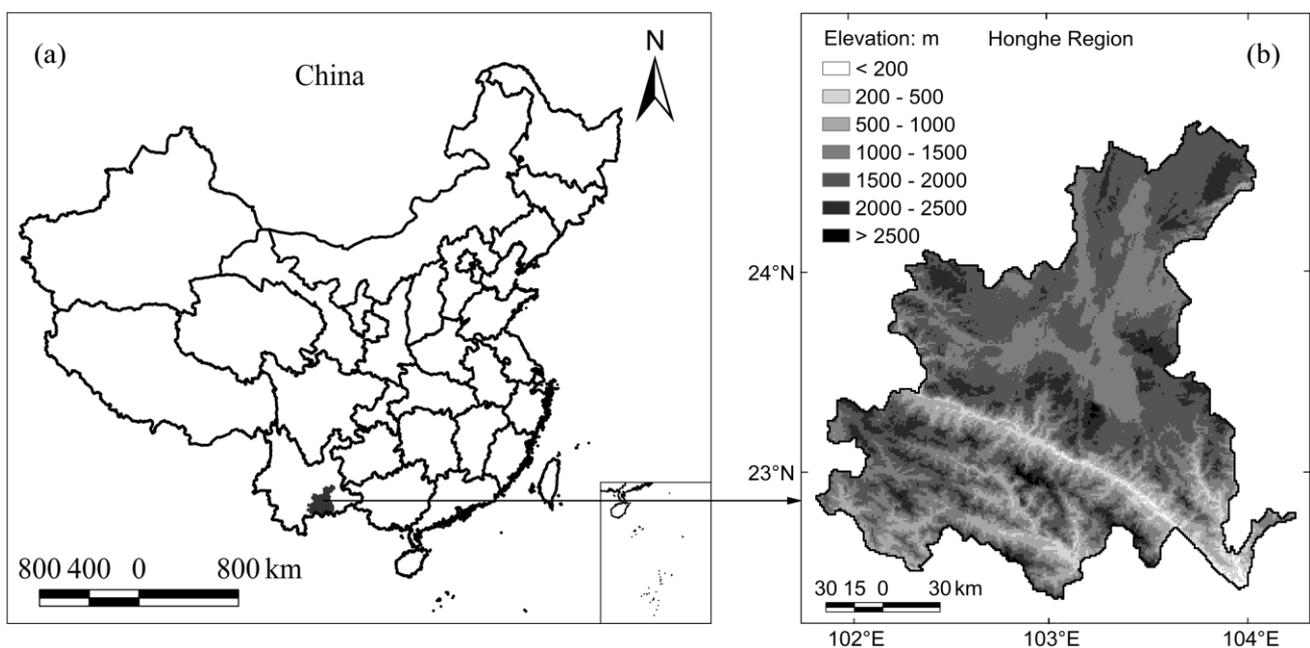
Fig. 1. The (a) location and (b) topographical distribution of the Honghe region in China.

Although precipitation influences energy flow, it indirectly shapes the altitudinal range of species and consequently the species richness patterns through its effect on thermodynamics (Chan *et al.*, 2016). Thus, we focused on the direct effect of temperature on thealtitudinal patterns of species richness in the further analyses. Moreover, previous studies have revealed inconsistent precipitation patterns along the altitudinal gradients, including monotonically increasing pattern (Lee *et al.*, 2013), monotonically decreasing pattern (Acharya *et al.*, 2011), bell-shaped pattern (Krömer*et al.*, 2013), and no clear pattern (Bhattarai *et al.*, 2004). However, all these studies have reported a consistently monotonically decreasing relationship between temperature and elevation (Bhattarai *et al.*, 2004; Acharya *et al.*, 2011; Krömer *et al.*, 2013; Lee *et al.*, 2013). The evaluation of the effect of complex precipitation patterns was not within the scope of this study, and we therefore excluded the precipitation variable from our analyses. We have only included mean annual temperature as the climatic predictor of the patterns of plant species richness.

Data analyses: To prevent the anthropogenic processes complicating the distribution of plant species richness, we restricted our study to elevation cells covered by forest, shrub, and grassland, using the ArcGIS 10.3 platform (ESRI, Redlands, CA, USA). After excluding 37.5% of the elevation cells, the study area was confined to 20,830 km^2. We then divided this area into 31 equal-elevation bands from 0 m to 3100 m with each band being 100 m wide. The area and mean annual temperature measured at equal-elevation bands exhibited bell-shaped and monotonic decreasing patterns, respectively (Fig. 2).
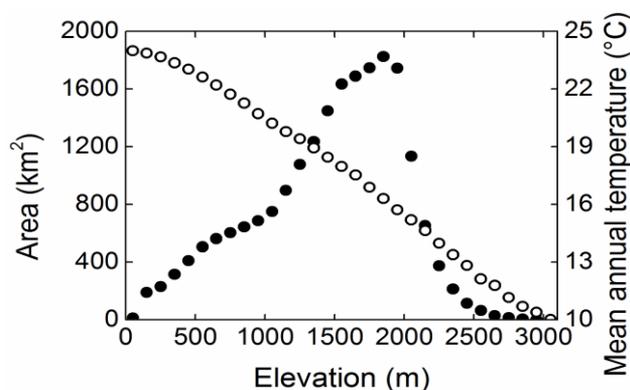
Fig. 2. Altitudinal distribution patterns of area (solid circles) and mean annual temperature (open circles) in the Honghe region.

We used only 5947 native species to delineate the species richness patterns. Of these, 4835 species have minimum and maximum elevation distribution records. We assumed that each of these species had a successive distribution range between its recorded minimum and maximum elevations, an assumption widely used in previous studies (e.g., Rahbek, 1997; Vetaas & Grytnes, 2002; Sanders, 2002). The remaining 1112 plant species (i.e., 18.7%) were found at only a single elevation. For each of these species, we subtracted and added 50 m from this single elevation record to obtain the minimum and maximum elevation limits (e.g., Watkins *et al.*, 2006; Bhattarai & Vetaas, 2006). We defined the range size of each species as the difference between its maximum and minimum elevation limits. To evaluate the effect of range size on the species richness patterns and their underlying determinants, we classified 5947 species into two plant groups: 2960 narrow-range species (range ≤ 600 m) and 2987 broad-range species (range > 600 m). Then, we counted the number of species present within eachaltitudinal band to give us observed species richness. Thus, these processes facilitated the determination of the observed species richness of different plant groups, i.e., seed plant species richness (SR), tree species richness (TSR), shrub species richness (SSR), herbaceous plant species richness (HSR), narrow-range species richness (NSR) and broad-range species richness (BSR).

We generated predicted species richness under the control of MDE by applying the RangeModel (Colwell, 2008). Following the MDE definition, only species range sizes that were fully contained in the one-dimensional domain were used in this analysis. We used the RangeModel to randomly place the empirical ranges of species within the geographical domain.For such simulation, the predicted species richness was calculated as the number of species present at each equal-elevation altitudinal band. These stochastic simulations were conducted 1000 times, and the mean predicted species richness was utilized as the measure of MDE. Similarly, the mean predicted species richness simulated by MDE was computed for each plant group (seed plant, tree, shrub, herbaceous plant, narrow-range species, and broad-range species).

To evaluate the effects of three explanatory variables (area, mean predicted species richness simulated by MDE and mean annual temperature) on observed species richness, we initially conducted bivariate analyses to determine the associations between observed species richness and each explanatory variable using ordinary least squares regression (OLS) models. The best-fit model for each explanatory variable was selected from its first- and second-order polynomials using the minimum Akaike information criterion (AIC). Then, we carried out multiple stepwise regression analyses for the selected forms of three explanatory variables. Because spatial autocorrelation may inflate type I error in parametric statistical analyses, we calculated the Moran's *I* for observed species richness and residuals from the stepwise regression model to evaluate the magnitude of spatial autocorrelation (Shen *et al.*, 2012). To tackle the collinearity among explanatory variables, we performed variation partitioning analyses to detect the relative effect of each variable (Legendre, 2008). Additionally, to determine if the strength of relationship between observed species richness and each explanatory variable was independent of plant life form and species range size, we performedz-teststo compare the difference between pairs of Pearson's correlation coefficients based on Fisher's transformation (Stein *et al.*, 2014). We performed all the statistical analyses using R version 3.1.1 (R Core Team, 2014).

Results

Altitudinal patterns of plant species richness: We compiled a total of 5947 native seed plant species along the altitudinal gradient in the Honghe region of China. Of these species, more than half were woody plant species (50.4%: 1745 tree species and 1250 shrub species),41.0% were herbaceous plant species (2436 herbaceous species), and the remaining plant species included 465 vine species and 51 bamboo species. The observed species richness for seed plants, trees, shrubs, herbaceous plants, plant species with range size ≤ 600 m and plant species with range size > 600 m all demonstrated the bell-shaped pattern along the altitudinal gradient (Fig. 3).The maximum species richness was identified at the altitudinal interval from 1200 m to 1500 m.
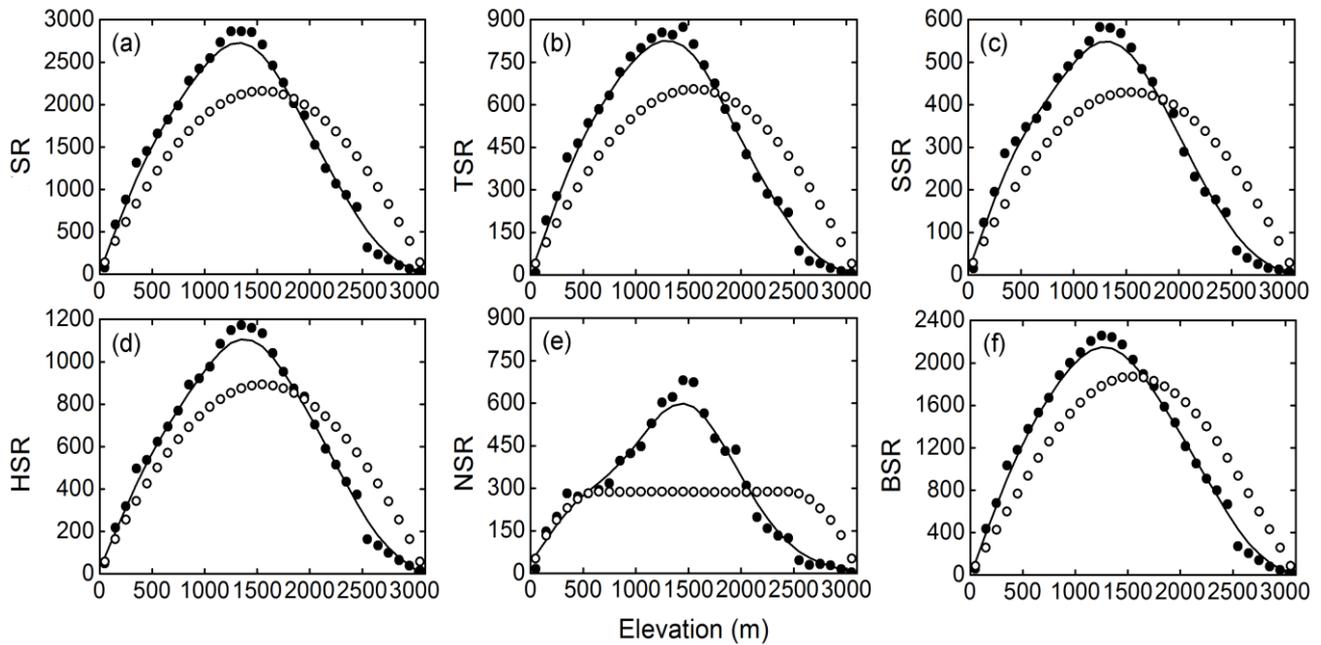
Fig. 3. Altitudinal distribution patterns of observed species richness for (a) seed plants (SR), (b) trees (TSR), (c) shrubs (SSR), (d) herbs (HSR), (e) narrow-range species (range ≤ 600 m, NSR), and (f) broad-range species (range > 600 m, BSR) (solid circles) in theHonghe region. The solid lines show the one-dimensional fitting curves generated using Friedman's smoother. The open circles indicate the simulated species richness estimated by the mid-domain effect.

The role of explanatory variables: The relationships between area, temperature and observed species richness were quadratic shaped (Figs. 4, 6), while the simulated species richness estimated by MDE had a positive linear relationship with observed species richness (Fig. 5). The area of altitudinal bands accounted for the largest proportion (86.2–92.0%) of the variance in observed species richness for all plant groups (Table 1). Mean annual temperature was responsible for 77.2–87.7% of the variance, i.e., the second largest percentage. AlthoughMDE explained the smallest percentage of the variation in observed species richness compared with area and temperature, MDE still determined 67.3–80.8% of the variance in observed species richness for all plant groups except for narrow-range species. MDE only accounted for 32.9% of the variation in NSR. The results of the Pearson's correlation coefficient tests based on Fisher's transformation showed that the observed species richness for trees and shrubs exhibited similarly strong relationships with each explanatory variable (Area: $z = 1.46$, P = 0.144; MDE: $z = 0.61$, P = 0.542; Temperature: $z = 0.28$, P = 0.780). However, the strength of the relationships between observed species richness and each explanatory variable differed between trees and herbs (Area: $z = 6.90$, p<0.01; MDE: $z = 9.82$, p<0.01; Temperature: $z = 4.29$, p<0.01), shrubs and herbs (Area: $z = 4.66$, p<0.01; MDE: $z = 8.21$, p<0.01; Temperature: $z = 3.56$, p<0.01), narrow-range species and broad-range species (Area: $z = 10.76$, p<0.01; MDE: $z = 24.17$, p<0.01; Temperature: $z = 2.58$, p< 0.01). Each variable accounted for more variance in the observed species richness of herbaceous plants than woody plants. Each variable explained more variance in the observed species richness of broad-range than narrow-range species.

The multiple stepwise regression model selected MDE and temperature as the best predictors of observed species richness of all plant groups except for NSR (Table 2). For NSR, only area was identified in the stepwise regression analysis. Comparing Moran's I of observed species richness with that of the residuals from the stepwise regression models indicated that the spatial autocorrelation in observed species richness was constrained by the stepwise regression models (Fig. 7). This suggested that the effects of the explanatory variables on observed species richness obtained using the OLS models were reliable to some extent. The results of the variation partitioning analyses suggested the presence of a strong collinearity (32.3–77.8%) between area, MDE,and temperature (Fig. 8). The pure effect of each factor was limited to a relatively small percentage (≤ 8.3%) for all plant groups. For narrow-range species, temperature alone appeared to have no effect on species richness. However, for broad-range species, temperature itself explained 8.3% of the variation in species richness, which was the largest proportion across the plant groups. Area contributed 8.1%to the variation in narrow-range species richness, while this factor only accounted for 0.1% of the variation in broad-range species richness.

Discussion

Plant species richness and an interpolation effect: The altitudinal gradient in species richness and its underlying mechanisms have received considerable attention over the last two decades (Rahbek, 1995; McCain, 2009; Khan & Ahmad, 2015). Our study revealed the altitudinal patterns of species richness not only for plant groups characterized by different life forms,but also for plant groups occupying different range sizes (Fig. 2). They all exhibitedbell-shaped curves, which are consistent with current biodiversity research (Colwell & Lees, 2000; Rahbek, 2005; Wang *et al.*, 2007).
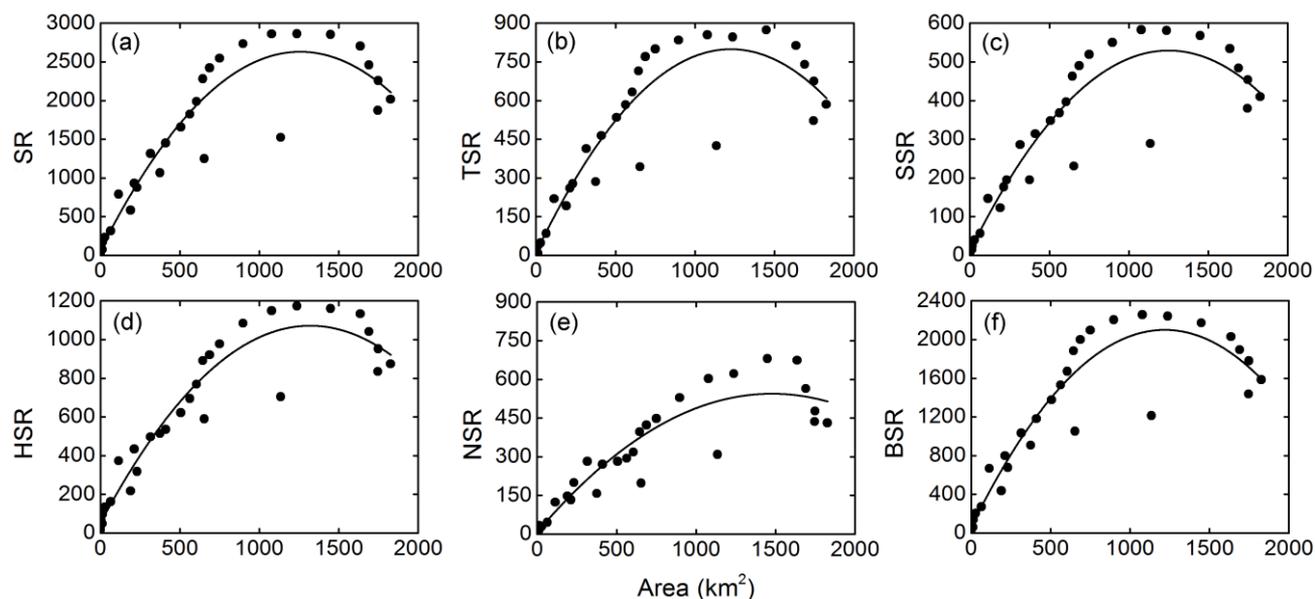
Fig. 4. Scatter plots of the relationships between area and observed species richness for (a) seed plants (SR), (b) trees (TSR), (c) shrubs (SSR), (d) herbs (HSR), (e) narrow-range species (range ≤ 600 m, NSR), and (f) broad-range species (range > 600 m, BSR) (solid circles) along the altitudinal gradient in the Honghe region. The solid lines show the second-order polynomial fitting curves generated using the ordinary least squares regression model.
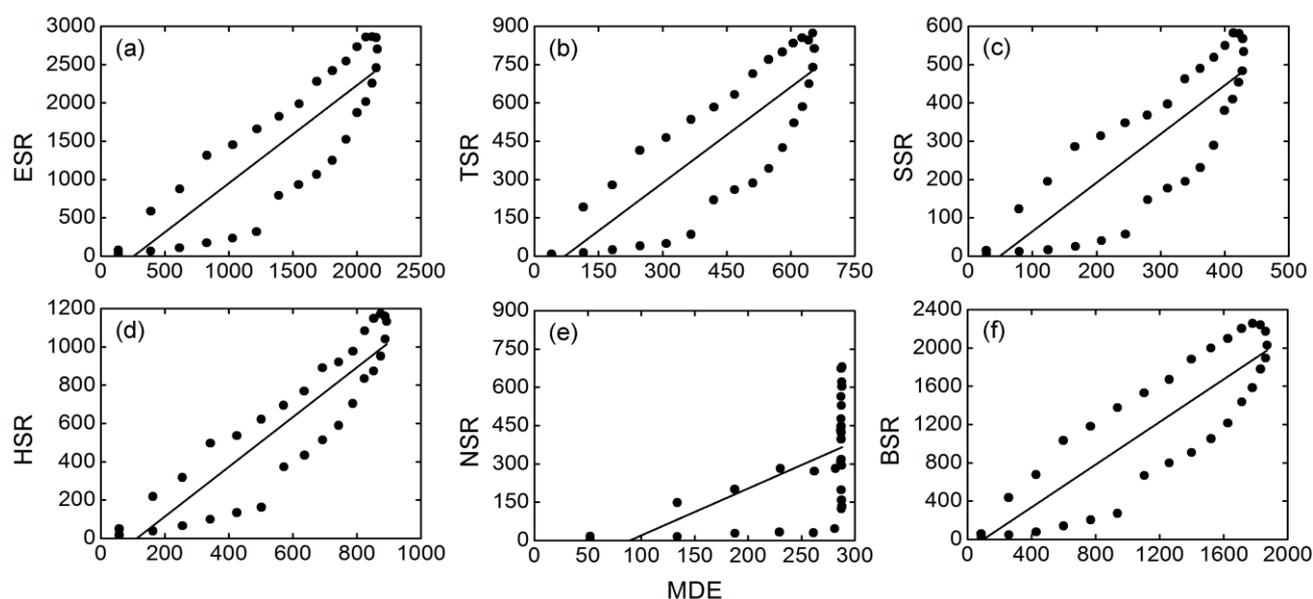
Fig. 5. Scatter plots of the relationships between observed species richness and simulated species richness predicted by the mid-domain effect (MDE) for (a) seed plants (SR), (b) trees (TSR), (c) shrubs (SSR), (d) herbs (HSR), (e) narrow-range species (range ≤ 600 m, NSR), and (f) broad-range species (range > 600 m, BSR) (solid circles) along the altitudinal gradient in the Honghe region. The solid lines show the first-order polynomial fitting curves generated using the ordinary least squares regression model.

Table 1. The bivariate relationships between observed species richness and the predictors included in the ordinary least squares regression models. The models were selected from the first- and second-order polynomials and based on their minimum Akaike information criterion (AIC), and all terms included were significant at $p<0.001$. Bold symbols indicated negative relationships.

	SR		TSR		SSR		HSR		NSR		BSR	
	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC
Area² + Area	89.2	451	86.6	385	87.8	356	92.0	384	86.2	364	89.1	436
MDE	72.8	478	67.3	411	68.5	384	80.8	410	32.9	412	73.4	463
MAT² + MAT	83.7	463	81.2	395	82.4	367	87.7	397	77.2	380	83.8	448

Abbreviations: SR, seed plant species richness; TSR, tree species richness; SSR, shrub species richness; HSR, herb species richness; NSR, narrow-range species richness; BSR, broad-range species richness; MDE, simulated species richness estimated by the mid-domain effect; MAT, mean annual temperature (°C); R^2, adjusted coefficient of determination (%).
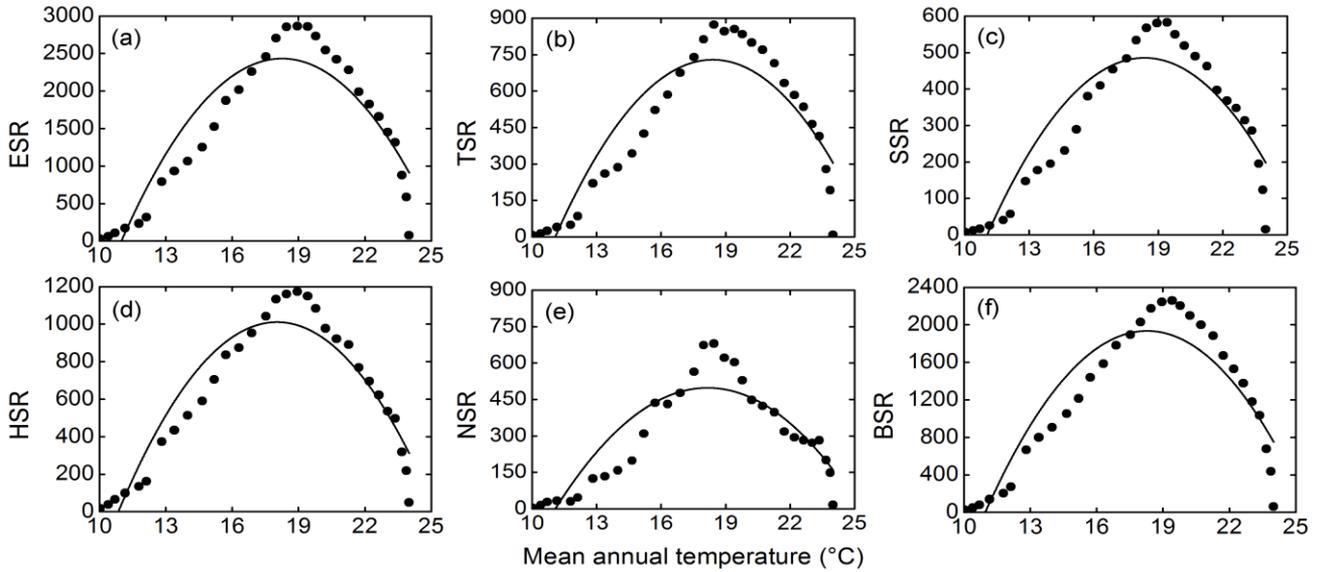
Fig. 6. Scatter plots of the relationships between mean annual temperature and observed species richness for (a) seed plants (SR), (b) trees (TSR), (c) shrubs (SSR), (d) herbs (HSR), (e) narrow-range species (range ≤ 600 m, NSR), and (f) broad-range species (range > 600 m, BSR) (solid circles) along the altitudinal gradient in the Honghe region. The solid lines show the second-order polynomial fitting curves generated using the ordinary least squares regression model.
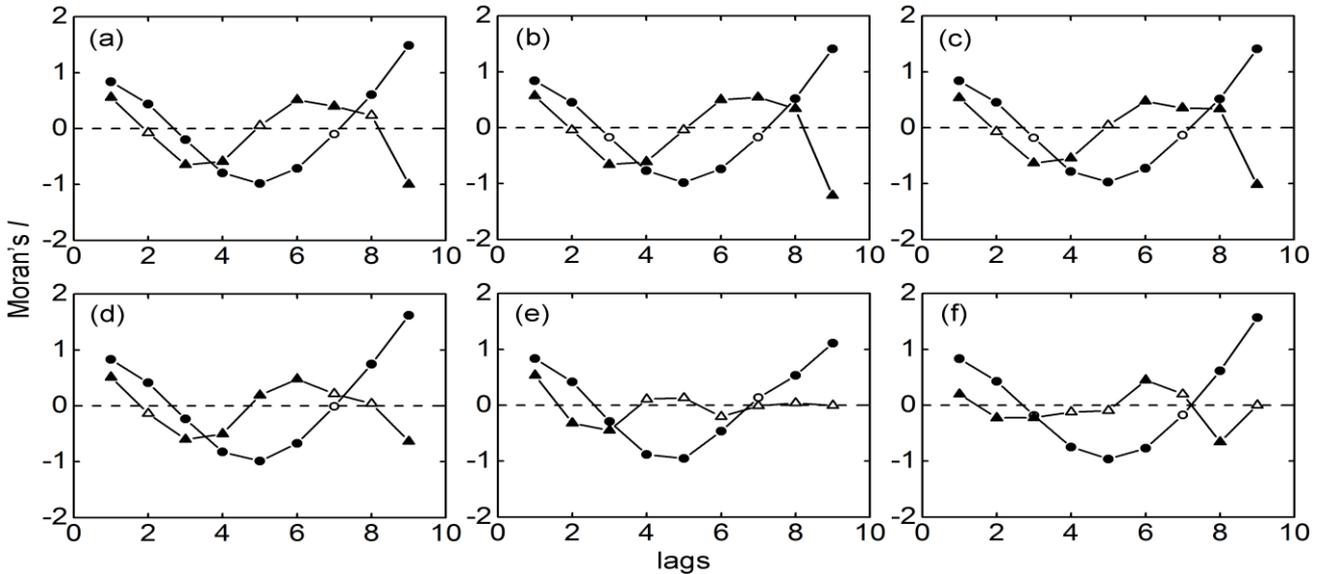
Fig. 7. Spatial correlograms for species richness (circles) and the residuals (upper triangles) of ordinary least squares regression models for (a) seed plants, (b) trees, (c) shrubs, (d) herbs, (e) narrow-range species (range ≤ 600 m), and (f) broad-range species (range > 600 m). The solid symbols indicate significant results ($P < 0.05$) after 1000 permutations, and open symbols denote non-significant results.

Previous studies have frequently applied the interpolation method of species presences between the extreme distribution elevations (e.g., Sanders, 2002; Wang *et al.*, 2007). However, this interpolation method may result in the identification of a bell-shaped relationship between elevation and species richness (Wang *et al.*, 2007). Grytnes & Vetaas (2002) investigated the species richness pattern of plants along the latitudinal gradient in the Nepalese Himalayas and demonstrated that the interpolation method itself may generate a bell-shaped pattern in species richness. Species richness reached its peak in the middle of the gradient and declined as it approached the gradient extremes. The reason for this decline was likely that only observed species contributed to species richness approaching the gradient extremes, while both observed and interpolated species contributed to the species richness at other positions along the gradient (Grytnes & Vetaas, 2002). Therefore, Vetaas & Grytnes (2002) suggested checking species richness patterns for species that occurred at only one 100-m interval. According to this suggestion, we examined the species richness pattern for a plant subset (i.e., 1112 species present at only a single elevation) without interpolation. In our study, the relationship between elevation and species richness demonstrated a parabolic shape, and changes in elevation explained 56.7% of the variation in species richness (Fig. 9). This implies that the contribution of the interpolation approach to the peak species richness in the middle of the gradient does not play an essential role in this study. Wang *et al.* (2007) also came to a similar conclusion in the Gaoligong Mountains when investigating species richness patterns for plant species with range sizes of ≤ 100 m and ≤ 200 m without interpolation.
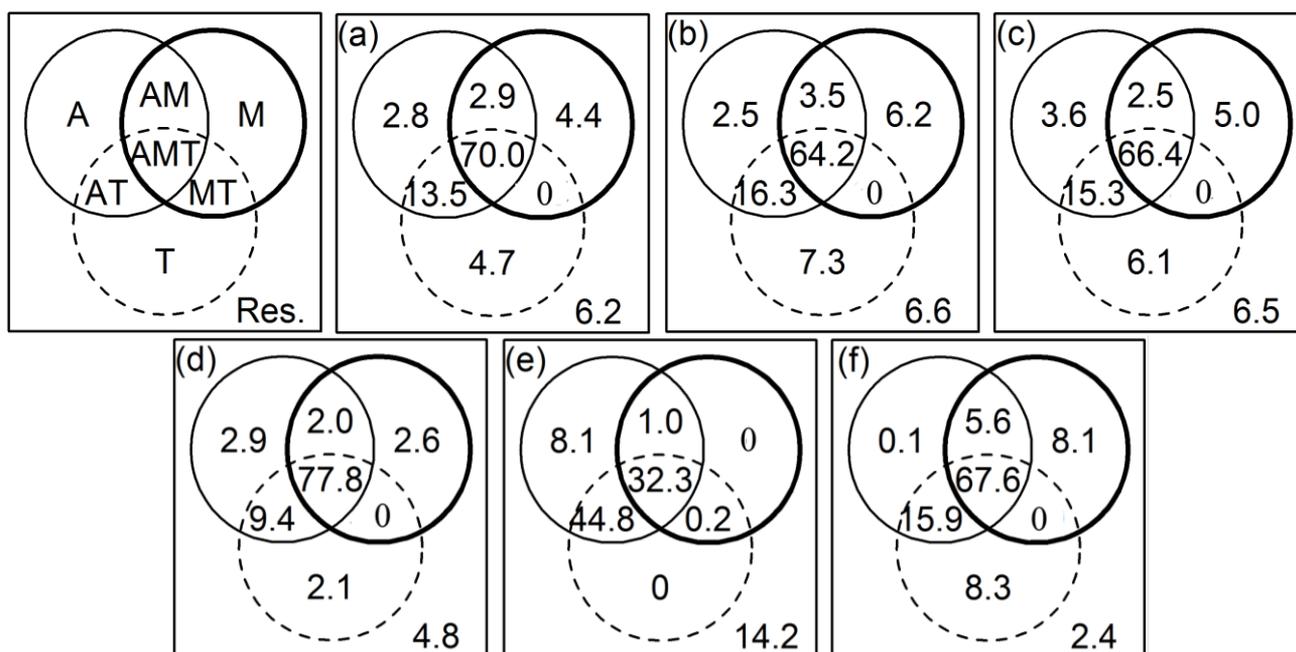
Fig. 8. Diagrams describing the variation partitioning of the ordinary least squares regression (OLS) models constructed to explain observed species richness for (a) seed plants, (b) trees, (c) shrubs, (d) herbs, (e) narrow-range species (range ≤ 600 m), and (f) broad-range species (range > 600 m). The variation in observed species richness is explained by the following three variables: area (A), mid-domain effect (M) and mean annual temperature (T). Res. isthe residual of the OLS model, i.e.,the unexplained proportion of the variation in observed species richness. The values indicate the adjusted coefficients of determination (%).
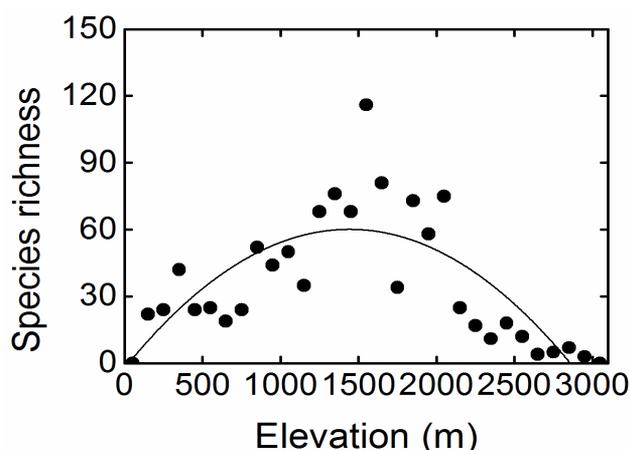
Fig. 9. The altitudinal pattern of species richness for a plant species set (species with only a single elevation record). The solid line represents the second-order polynomial fit.

Table 2. Summary of the relationships between observed species richness and the predictors included in the ordinary least squares multiple stepwise regression models. The models were selected based on their minimum Akaike information criterion (AIC), and only terms significant at $p<0.001$ were included.

	R^2	AIC	Multiple regression model
SR	89.3	450	$1.3SM + 2.5MAT^2 - 1188.5$
TSR	87.6	382	$1.3TSM + 8.6 \times 10^{-1}MAT^2 - 383.1$
SSR	88.0	355	$1.3SSM + 5.6 \times 10^{-1}MAT^2 - 252.5$
HSR	91.9	384	$1.3HSM + 8.2 \times 10^{-1}MAT^2 - 427.6$
NSR	86.2	364	$-2.5 \times 10^{-4}Area^2 + 7.3 \times 10^{-1}Area + 7.9$
BSR	97.5	391	$3.7BSM + 93.9MAT^2 - 3180.2MAT + 21838.5$

Abbreviations: SM, simulated seed plant species richness by the mid-domain effect (MDE); TSM, simulated tree species richness by MDE; SSM, simulated shrub species richness by MDE; HSM, simulated herb species richness by MDE; BSM, simulated broad-range species richness by MDE; other abbreviations are the same as seen in Table 1

Species–area hypothesis: Several factors have been identified to contribute to explaining the observed bell-shaped relationship between species richness and elevation. The species–area hypothesis, proposed by plant ecologists early in the last century, is one of the crucial factors that may governthese patterns (Rahbek, 1997). Earlier studies indicated that the increase in area size boosted species richness (Sanders, 2002). The area at each altitudinal band ascended steeply with the increase inelevation and then descended above the elevation of 1750−1850 m (Fig. 2). The total area in the seven largest altitudinal bands (from 1300 m to 1900 m) was 11,330 km² or approximately 54.4% of the entire study area. This finding was consistent with the trend in observed species richness along the altitudinal gradient (Fig. 3). The OLS models showed that area determined the largest proportion of the variation in observed species richness (Table 1). Although area was not selected as a significant predictor ofthe observed species richness for any plant groups except for NSR in the stepwise regression analyses (Table 2), results of the variation partitioning analyses revealed the presence of the strong collinearity between area and the other two explanatory variables (Fig. 8). This suggests that the effect of area may be masked by the effects of MDE and temperature. Thus, we can conclude that area is one of the main reasons for the bell-shaped relationship between species richness and elevation for plants in the Honghe region of China.

The following three main mechanisms may explain the species–area hypothesis (Rosenzweig, 1995): passive sampling, colonization-extinction dynamics, and habitat heterogeneity. The passive sampling explanation indicates that sampling more individuals may correspond to the identification of more species (Connor & McCoy, 2001).

The dynamics explanation contends that a dynamic equilibrium between colonization and extinction results in species richness (Rosenzweig, 1995). The habitat heterogeneity explanation suggests that area may serve as an effective surrogate variable to measure habitat heterogeneity. The largerarea maintains more diverse habitats, which can support more species (Bachman *et al.*, 2004). The evaluation of the relative contributions of the three mechanisms to the species–area hypothesis remains a challenge for ecologists (Holt *et al.*, 1999).

Mid-domain effect: The MDE hypothesis, which evaluates the effect of geometric constraints on species richness, is another potential driver of the bell-shaped relationship between elevation and species richness (Colwell & Hurtt, 1994; Colwell *et al.*, 2004). Watkins *et al.* (2006) studied the altitudinal pattern of fern species richness in Costa Rica and found that MDE was a contributor to the observed pattern. Similarly, our results suggest that the predicted species richness generated by MDE along the latitudinal gradient exhibitedbell-shaped patterns for all plant groups (Fig. 2) and significantly affected observed species richness patterns (Table 1, Fig. 5). However, McCain (2005) tested the predictions generated by MDE using 56 data sets on altitudinal distributions of small mammals and found that MDE only explained a small proportion (29.5%) of the variation in species richness. In contrast, in our study, MDE accounted for more than 67.3% of the variation in species richness for all plant groups, except for NSR (Table 1). For NSR, MDE only accounted for 32.9% of the variation. Furthermore, in the stepwise regression models, MDE was not identified as a determinant of NSR, whileMDE was included within the determinants of BSR (Table 2). The results of the Pearson's correlation coefficient z-tests based on Fisher's transformation also indicated that the explanatory power of MDE for NSR and BSR was significantly different. This finding implies that MDE is more important for widespread species than for restricted species. This is consistent with the conclusion derived by Colwell *et al.* (2004). The reason for this finding may be that restricted species are relatively free to occur (or not occur) at arbitrary positions along a gradient, while widespread species have to cluster toward the middle of this gradient (Colwell *et al.*, 2004).

In a recent study, Lee *et al.* (2013) reported the species richness patternsof plants along the Baekdudaegan altitudinal gradientlocated in South Korea. He found that MDE was more important for predicting woody plant species richness than herbaceous plant species richness (Lee *et al.*, 2013). Herbaceous plants had more singletons and doubletons (defined as a species only occurring in one or two samples, respectively) than woody plants in their study (Lee *et al.*, 2013). Therefore, they suggested that these singletons and doubletons may result in the identification of a larger deviation between observed species richness and predictions based on MDE for herbaceous plants than for woody plants (Lee *et al.*, 2013). Similarly, in our study, herbaceous plants had more singletons than woody plants (Fig. 10; 21.6% and 16.5% for herbaceous and woody plants, respectively). However, the effect of MDE was stronger for the altitudinal

biodiversity patterns of herbaceous plants thanwoody plants (i.e., trees and shrubs) in our study. In addition, we found that herbaceous plants had more species with a wide range size than woody plants (12.8% of herbaceous plant species and 9.6% of woody plant species had a range size larger than half of the altitudinal gradient, i.e., 1550 m). Therefore, our study infers that the smaller deviation between herbaceous plant species richness and MDE was due to a larger proportion of species with a wide range size, which confirmed the findings reported by Colwell *et al.* (2004).

Energy hypothesis: The species–energy relationship states that the amount of energy entering into an ecosystem limits species richness, and it isclassified into two hypotheses: the ambient-energy hypothesis and the productivity hypothesis (Wright, 1983). Higher temperatures promote higher biological activity, faster population growth and, therefore, increase species richness, supporting the ambient-energy hypothesis (Hawkins *et al.*, 2003). Our results revealed that plant species richness had aclose relationship with the quadratic distribution of mean annual temperature, which supports the ambient-energy hypothesis and the energy portion of the climate based water-energy hypothesis. In agreement with the findings of several other studies evaluating biodiversity patterns along altitudinal gradients, temperature may cause lethal frost at high elevations and enhance evapotranspiration at lower elevations (Hawkins *et al.*, 2003; Carpenter, 2005). In our study, the strength of the responses of the species richness for woody plants and herbaceous plants to the ambient temperature differed. This suggests that there are different physiological requirements of organisms characterized by different life forms. Wang *et al.* (2009) and Lee *et al.* (2013) have also obtained the same conclusion based on their research.

In conclusion, the species richness of seed plants, plant groups characterized by different life forms (i.e., trees, shrubs and herbaceous plants), and plant groups with different range sizes (i.e., narrow-range and broad-range species) all exhibitedbell-shaped patterns along the altitudinal gradient in the Honghe region, China. Area, MDE and temperature all significantly influenced the observed species richness patterns. However, the pure effect of each determinant variable accounted for a relatively limited proportion of the variation in species richness. The majority of the variance in species richness was explained by the collinearity between area, MDE,and temperature. The responses of species richness to the determinant variables were not independent of the species' life forms and range sizes. Plants characterized by different life forms (woody and herbaceous plants) represent different physiological demands, environmental tolerances and, thus, showed different strengths of the correlations between climate and species richness. Thegeometric constraint exhibited a greater influence on the placement of larger range sizes, while smaller range sizes were relatively free to present at any location in the one-dimensional domain.
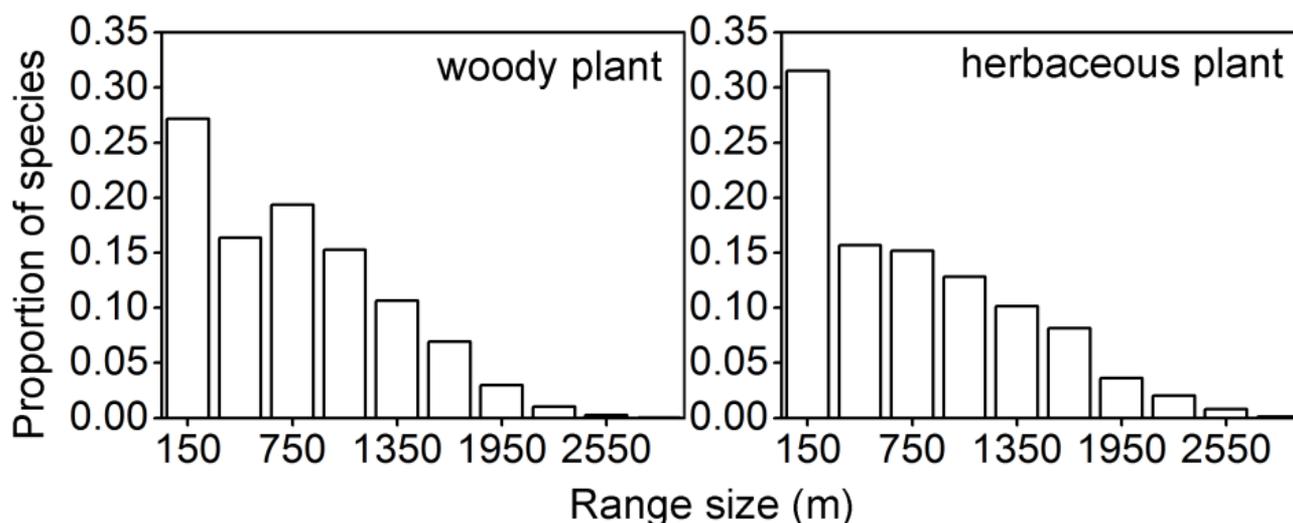
Fig. 10. Frequency distributions of species range sizes for different life forms.

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