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BIODIVERSITY RESEARCH

Patterns of species richness for vascular plants in China's nature reserves

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ABSTRACT

Explaining the heterogeneous distribution of biodiversity across the Earth has long been a challenge to ecologists and biogeographers. Here, we document the patterns of plant species richness for different taxonomic groups in China's nature reserves, and discuss their possible explanations at national and regional scales, using vascular plant richness data coupled with information on climate and topographical variables. We found that water deficit, energy and elevation range (a surrogate of habitat heterogeneity) represent the primary explanations for variation in plant species richness of the nature reserves across China. There are consistent relationships between species richness and climate and habitat heterogeneity for different taxonomic vascular plant groups at the national scale. Habitat heterogeneity is strongly associated with plant richness in all regions, whereas climatic constraints to plant diversity vary regionally. In the regions where energy is abundant or water is scarce, plant richness patterns were determined by water and habitat heterogeneity, whereas in the region with low energy inputs, water interacting with energy, and habitat heterogeneity determined its species richness pattern. Our results also suggest that energy variables alone do not represent the primary predictor of plant richness.

Keywords

China, energy, habitat heterogeneity, nature reserves, plant richness, taxonomic groups, vegetation region, water.

INTRODUCTION

Explaining species richness patterns over broad geographical scales is a central issue of biogeography and macroecology (Gaston, 2000). Much effort has been put into identifying determinants constraining broadscale variability in species richness (e.g. Pianka, 1966; Whittaker, 1977; Wright, 1983; O'Brien, 1993; Davis & Scholtz, 2001; Francis & Currie, 2003; Rahbek, 2005). It is apparent that the factors influencing patterns of species richness vary with the geographical extent and sample resolution (grain) (Whittaker *et al.*, 2001; Willis & Whittaker, 2002). Therefore, only by multiple analyses for different locations and at various spatial scales can we derive general explanations of broadscale species richness patterns.

Previous studies on such a topic are mainly from North America (e.g. Richerson & Lum, 1980; Currie, 1991; Kerr & Packer, 1997; Hawkins & Porter, 2003). China's geographical extent and complex topography give it a broader range of climatic conditions, from tropical to subarctic/alpine, resulting in vegetation types that vary from rainforest to desert. This suggests that China should be an ideal location to explore patterns of species diversity at the regional level. Qian and Ricklefs (1999) compared the taxonomic richness of vascular plants in China and the USA using floristic data, suggesting the flora of China is more diverse than that of the USA due primarily to China's complex topography and because it is affected less by Quaternary glaciations. However, an effort to find the explanations for spatial variation in species diversity over the country, especially based on detailed climatic data from regional ground observations and topographical variables, is not yet available.

In this study, we used vascular plant richness data for the nature reserves in China, coupled with corresponding information on climate and topographical variables to explore plant richness patterns in China and their possible explanations.

METHODS

Data collection

We collected vascular plant richness data for 202 nature reserves across China, by reviewing published and unpublished literature (Liu, 1996; Wang, 2003; many others; for details see Appendix S1 in Supplementary Material). These nature reserves were located between 18°29′–51°37′ N in latitude and 80°17′–133°41′ E in

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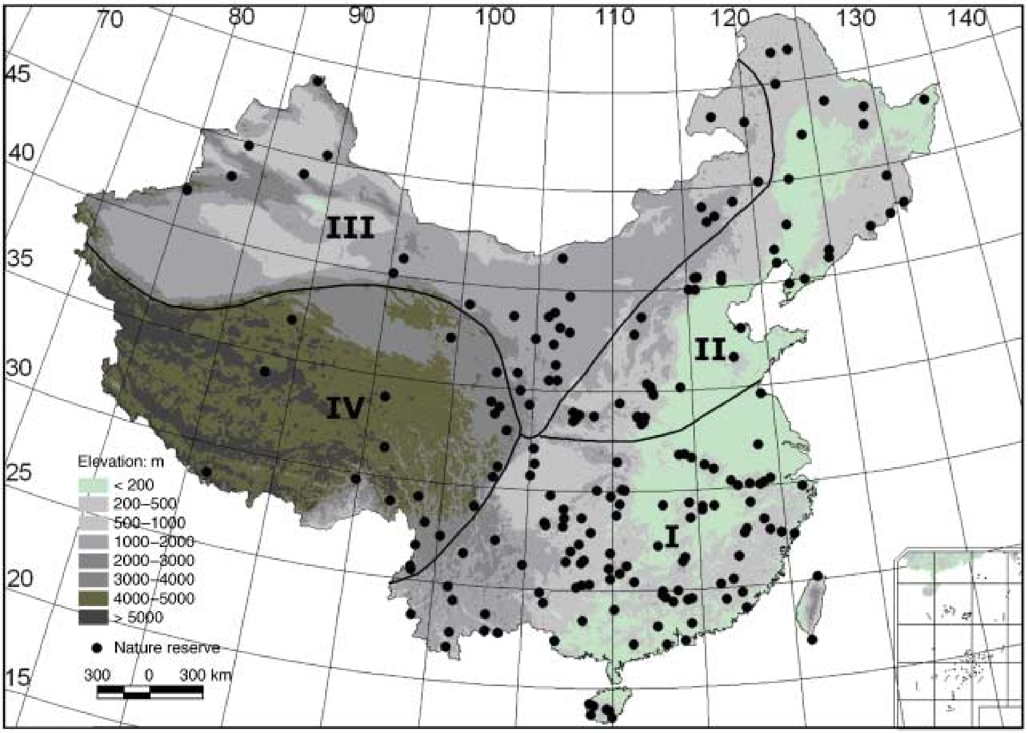

Figure 1 Location of the 202 nature reserves of China used in this study, and the extent of four vegetation regions: subtropical forest region (I: $N = 103$), temperate forest region (II: $N = 46$), temperate steppe and desert region (III: $N = 31$), and the Qinghai-Tibet Plateau region (IV: $N = 22$). The background map shows the topography of China, in an Albers equal-area conic projection.

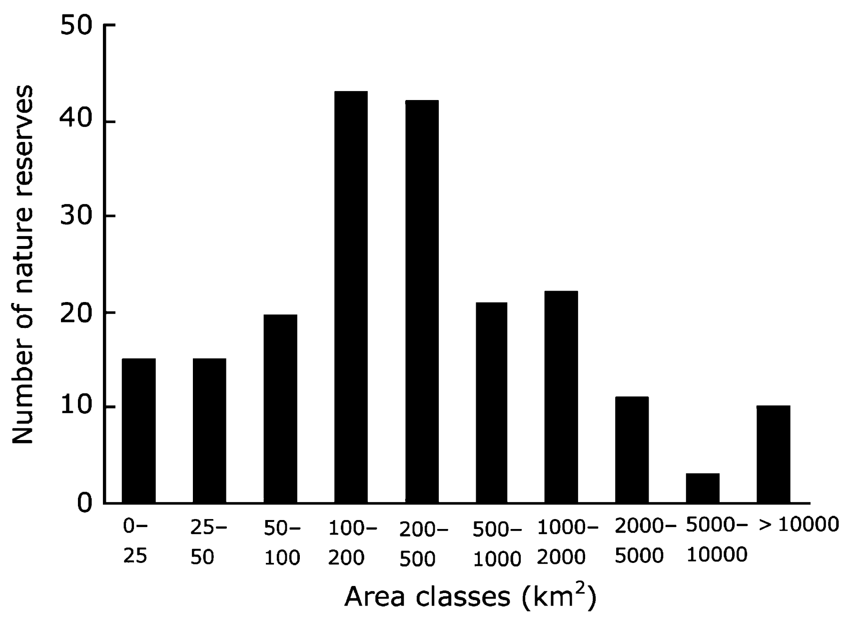

Figure 2 Area distribution of the 202 nature reserves of China used in this study.

longitude (Fig. 1) and covered a total area of 991,660 km^2 (10.3% of the country's total area). They were quite different in size. Figure 2 shows the size distribution of the 202 nature reserves in this study.

Vascular plant richness data collected included a number of pteridophyte, gymnosperm, and angiosperm species. We excluded alien species from data analysis to address the native species richness patterns. Other environmental variables such as reserve area, geographical range, minimum elevation, and maximum elevation were also documented. Elevation range (maximum elevation minus minimum elevation) was used as a measure of habitat heterogeneity.

Climate data, assigned to each reserve based on its location, were used to analyse the relationship between climate and species richness. These data were compiled from a 1961–99 temperature/precipitation database of China at 0.1° × 0.1° resolution, generated from 680 climatic stations across the country (Fang *et al*., 2001; Piao *et al*., 2003). Climatic factors used in this study included mean annual temperature, annual precipitation, annual potential evapotranspiration (PET) and annual actual evapotranspiration (AET). PET and AET were estimated using Thornthwaite's method (Fang & Yoda, 1990). We also calculated water deficit as the difference between PET and AET (Stephenson, 1990).

According to vegetation zonation in the Vegetation Atlas of China (The Compilation Committee of Chinese Vegetation Atlas, 2001), we divided the 202 nature reserves into four vegetation regions (simplified as 'region' hereafter), the subtropical forest region, temperate forest region, temperate steppe and desert region, and the Qinghai-Tibet Plateau region to examine the patterns of vascular plant richness in different regions (Fig. 1).

Data analysis

We used SPSS version 10.0 for statistical analysis (Norusis, 2000). Descriptive statistics of plant richness and environmental variables were produced to interpret the information on the data distributions (Table 1). Correlation analyses between species richness and each independent environmental variable were carried out to interpret the relationships between them (Correlation matrix, see Appendix S2 in Supplementary Material). Stepwise regression analyses were performed to identify the factors explaining the variation in species richness for all of China and for different regions. Before performing the multiple regression models, all environmental variables were tested for nonlinear relationships with plant species richness using second-order polynomial models, and no significant nonlinearities were found. Therefore, we assumed that the relationships of plant richness to the environmental variables were linear. We $\log_{10}$-transformed plant species richness, reserve area, and elevation range to obtain an appropriate distribution for data according to the descriptive statistics, e.g. the skewness and kurtosis of these variables were more than 1 and 2.5, respectively (Table 1).

To explore whether vegetation region has an effect on plant species richness, we used a general linear model to perform analysis of covariance by using the vegetation region as a fixed factor; elevation range, mean annual temperature, water deficit, and reserve area as covariates; and plant species richness as a dependent variable.

RESULTS

National scale

Multiple regressions provided consistent primary predictors of species richness for different taxonomic vascular plant groups in the nature reserves across China: elevation range (a surrogate of habitat heterogeneity), water (water deficit) and energy (mean annual temperature or PET) together accounted for 66.4%, 53.7%, 54%, and 52.3% of the variation in pteridophytes, gymnosperms, angiosperms, and all vascular plants, respectively (Table 2). The relationships between species richness of these four plant groups and the three predictors, mean annual temperature, water deficit, and elevation range, are shown in Figs 3–5. In addition to the above-mentioned climatic variables and habitat heterogeneity, reserve area further increased the proportion of explained variation in angiosperms and all vascular plants by 1.8% and 1.7%, respectively.

Table 1 Summary statistics of species richness in different vascular plant groups, reserve areas, climatic variables, and habitat heterogeneity used in this study

Variable	*N*	Minimum	Maximum	Mean	SD	Skewness	Kurtosis
Species richness							
Pteridophyte	165	1	594	107.7	104.7	1.5	3.0
Gymnosperm	170	1	110	13.7	12.9	3.9	23.5
Angiosperm	175	79	5026	1150.4	868.0	1.3	3
All vascular plant	178	138	5547	1341	900.5	1.2	2.6
Location and area							
Mean latitude (°)	202	18.4	51.6	32.3	7.6	0.5	–0.5
Mean longitude (°)	202	80.3	133.7	110.4	9.3	–0.5	0.8
Reserve area (km^2)	202	0.7	318,000	4909	29,654	9	85
Climatic variables							
Annual precipitation (mm)	202	55.6	2295.1	1004	537.0	0.1	–1.1
Mean annual temperature (°C)	202	–4.2	24.9	12.4	6.5	–0.4	–0.6
Annual PET (mm)	202	387.9	1396.3	785.1	205.2	0.5	0.1
Annual AET (mm)	202	55.7	1213.5	687.3	274.7	–0.3	–0.6
Water deficit (mm)	202	0	581	98.1	143.0	1.7	2.0
Habitat heterogeneity							
Elevation range (m)	202	2.7	7408	1501.6	1248.4	2.0	5.5

Table 2 Determinants of species richness for the major groups of vascular plants in China's nature reserves at the national level as revealed by multiple stepwise regression analyses

Variables	Coefficient	P	Adjusted R^2
Log_{10} pteridophyte species richness			
Log_{10} elevation range	0.503	< 0.0001	0.295
Water deficit	–0.414	< 0.0001	0.559
Mean annual temperature	0.341	< 0.0001	0.664
Log_{10} gymnosperm species richness			
Log_{10} elevation range	0.542	< 0.0001	0.308
Water deficit	–0.429	< 0.0001	0.530
Mean annual temperature	0.109	0.057	0.537
Log_{10} angiosperm species richness			
Log_{10} elevation range	0.470	< 0.0001	0.248
Water deficit	–0.431	< 0.0001	0.463
Annual PET	0.358	< 0.0001	0.540
Log_{10} reserve area	0.172	0.0005	0.558
Log_{10} all vascular plants species richness			
Log_{10} elevation range	0.473	< 0.0001	0.258
Mean annual temperature	0.414	< 0.0001	0.446
Water deficit	–0.330	< 0.0001	0.523
Log_{10} reserve area	0.168	0.008	0.540

A general linear model using the region as a dummy variable indicated that vegetation region was a significant factor affecting plant species richness patterns, which, together with elevation range, mean annual temperature, water deficit, and reserve area, explained 56.3% of the total variation in all vascular plants species richness (Table 3).

Table 3 Analysis of effect of vegetation region on plant species richness using a general linear model, with vegetation region added as a dummy variable (see text for details). $F_{3,174} = 23.3$, $P < 0.0001$, adjusted $R^2 = 0.563$

Effect	P	F	Type III sums of squares
Log_{10} elevation range	< 0.0001	90.625	4.137
Mean annual temperature	< 0.0001	30.655	1.399
Water deficit	< 0.0001	27.603	1.260
Log_{10} reserve area	< 0.0001	14.479	0.661
Vegetation region	0.009	4.150	0.549

Regional scale

The species–area relationships for the four different regions indicated that reserve area positively affected the species richness of subtropical forests (Fig. 6a), negatively that of temperate forests (Fig. 6b), and was not related to species richness in the temperate steppe and desert, and the Qinghai-Tibet Plateau regions (Fig. 6c,d). This implies that the variation in area represents variations in other environmental factors, which vary inconsistently with the area (Martin, 1981; Palmer & White, 1994).

Simple bivariate relationships between plant richness and climatic variables varied with regions (Fig. 7a–e). Among the climatic variables we examined, species richness in the subtropical forest region was significantly correlated with only annual precipitation. Species richness in the temperate forest region significantly covaried with both energy and water-related variables. On the Qinghai-Tibet Plateau and in the temperate steppe and desert regions, species richness was significantly associated with

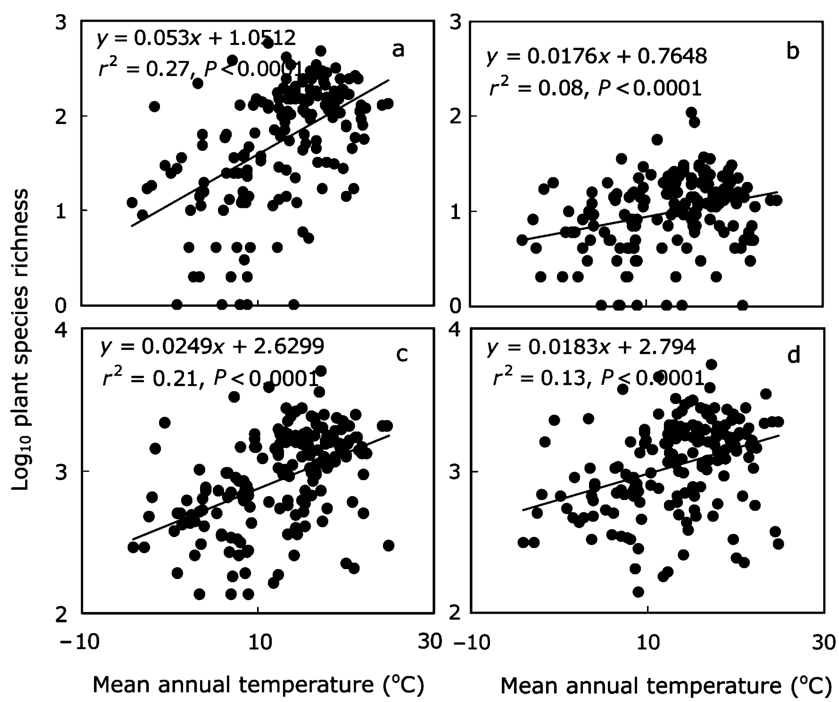

Figure 3 Relationships between plant species richness and mean annual temperature at the national scale. (a) pteridophytes (b) gymnosperms (c) angiosperms (d) all vascular plants.

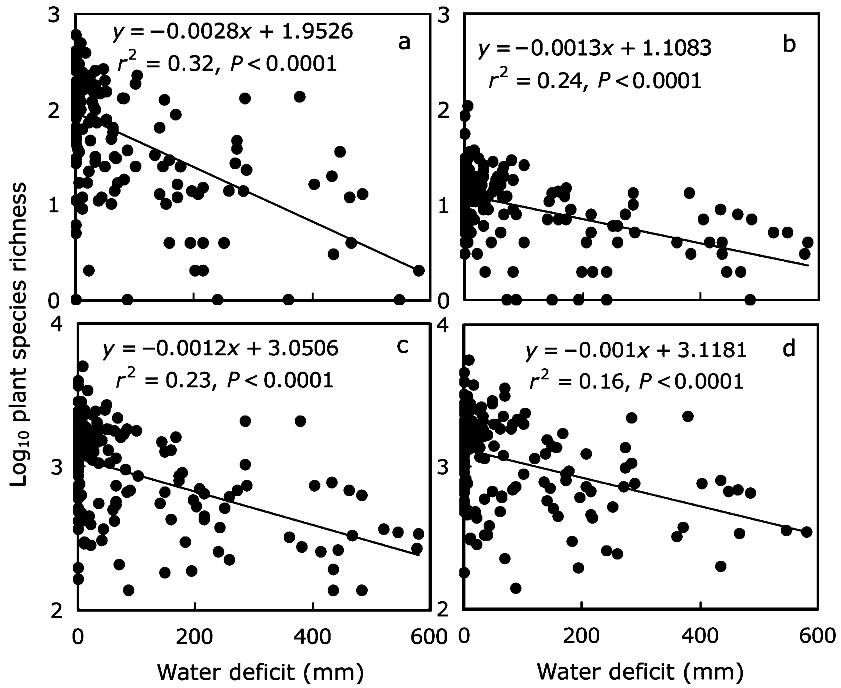

Figure 4 Relationships between plant species richness and water deficit at the national scale. (a) pteridophytes (b) gymnosperms (c) angiosperms (d) all vascular plants.

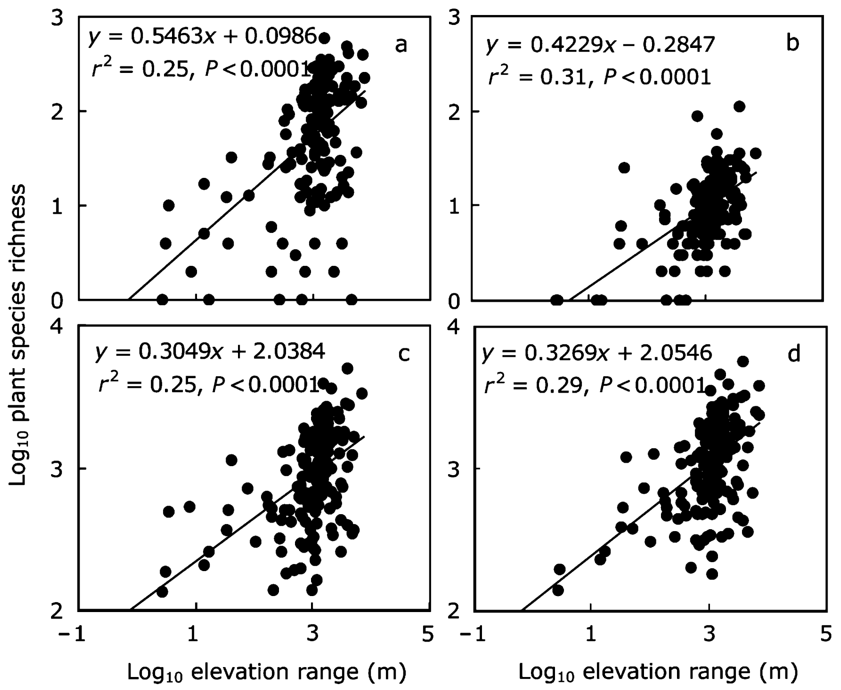

Figure 5 Relationships between plant species richness and elevation range at the national scale. (a) pteridophytes (b) gymnosperms (c) angiosperms (d) all vascular plants.

water-related variables (annual precipitation and water deficit) and with the integrated measure of both water and energy (annual AET). Consistent with the results at the national scale, elevation range was strongly and positively related to plant richness in all vegetation regions (Fig. 7f).

Stepwise regressions accounted for 48.1%, 67.7%, 75.5%, and 60.2% of the variation in species richness for subtropical forest, temperate forest, temperate steppe and desert, and Qinghai-Tibet Plateau regions, respectively (see Table 4 for significant predictors of species richness in the four regions studied).

DISCUSSION

Many hypotheses have been proposed to explain the heterogeneous distribution of biodiversity across the earth (Pianka, 1966; Rosenzweig, 1995), and these encompass primarily two groups. One group of the hypotheses proposes that climatic variables, such as climatic seasonality, energy and water availability, or integrated measure of energy and water (AET, NPP), are the primary predictors of broadscale species richness pattern (Klopfer, 1959; Wright, 1983; Hawkins *et al.*, 2003). The second group suggests

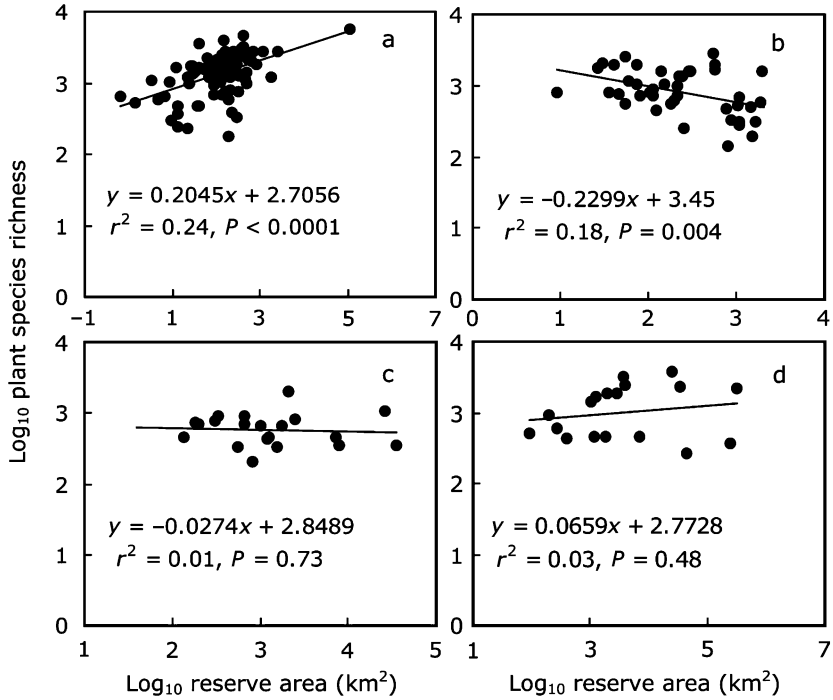

Figure 6 Species richness–area relationships for four vegetation regions. (a) subtropical forest region (b) temperate forest region (c) temperate steppe and desert region (d) the Qinghai-Tibet Plateau region.

that the variation in species richness is affected by several other factors but not by climatic variables, for example, habitat heterogeneity (O'Brien *et al*., 2000; Rahbek & Graves, 2001), or historical / regional differences based on different speciation or extinction rates, coupled with unique events in Earth's history (Ricklefs, 1987; McGlone, 1996; Ricklefs *et al*., 2004). Our results suggested that the spatial variation in species richness of vascular plants in China's nature reserves resulted primarily from the integrated influences of climate and topography, resembling the explanation for global tree species richness proposed by Whittaker and Field (2000).

We found that water alone or its combination with energy variables is the measure of climatic factors constraining plant richness, which is consistent with the results of many previous studies (Hawkins *et al*., 2003 and references therein). Francis and Currie (2003) suggested that a globally consistent relationship exists between angiosperm family richness and climate characterized by water deficit and PET (temperature). Our results at the national scale support this prediction. Because China includes all the major ecosystem types of the Earth, covering a broad range of climatic variation, from tropical to subarctic/alpine and from rain forest to desert, and across a great altitudinal range, from below sea level to the Qinghai-Tibet Plateau, the findings of this study at the national scale are likely to be representative of the global relationship between plant richness and climate. More significantly, our results have extended the consistent relationship between climate and angiosperm richness to all major taxonomic groups of vascular plants (Figs 3–5 and Table 2). In contrast, there were differences in the plant richness–climate relationships between different regions (Fig. 7a–e and Table 4). In the subtropical forest region, where energy is abundant, water availability becomes the primary predictor of plant richness. Water is scarce in the temperate steppe and desert region, and thus it also represents the primary limiting factor. The Qinghai-Tibet Plateau region spans various vegetation types, including tropical seasonal rainforest, subtropical evergreen broadleaved forest, high-cold shrub, high-cold steppe, and high-cold desert vegetation from east to west as a result of Himalayan uplift events in the Cenozoic era (The Compilation Committee of Chinese Vegetation Atlas, 2001); therefore, the climatic constraint to plant richness in this region should be water availability. Energy, coupled with water availability, determined the plant richness pattern in the temperate forest region, where the energy supply is lower and thus more likely to be a constraint. We found that energy variables alone never represent the primary predictor of plant richness patterns, as also observed in a meta-analysis of broadscale geographical patterns of species richness by Hawkins *et al*. (2003).

Elevation range, a surrogate of habitat heterogeneity, was found to represent a strong predictor of diversity for a wide range of taxa, including plants in California (Richerson & Lum, 1980), trees in South Africa (O'Brien *et al*., 2000), birds in South America (Rahbek & Graves, 2001), and mammals in North America (Kerr & Pack, 1997). Consistent with these documented patterns, our study suggests that elevation range is strongly associated with species richness in all groups of vascular plants across China. This association was consistent at the national and regional scales.

Our results showed that vegetation region, a proxy for historical/ regional processes, was of only marginal importance in predicting the plant richness (the addition of the vegetation region only improved the predictive model R^2 by 2.3%). Given we did not have direct information on historical factors, such as glaciations and dispersal, more refined studies are required

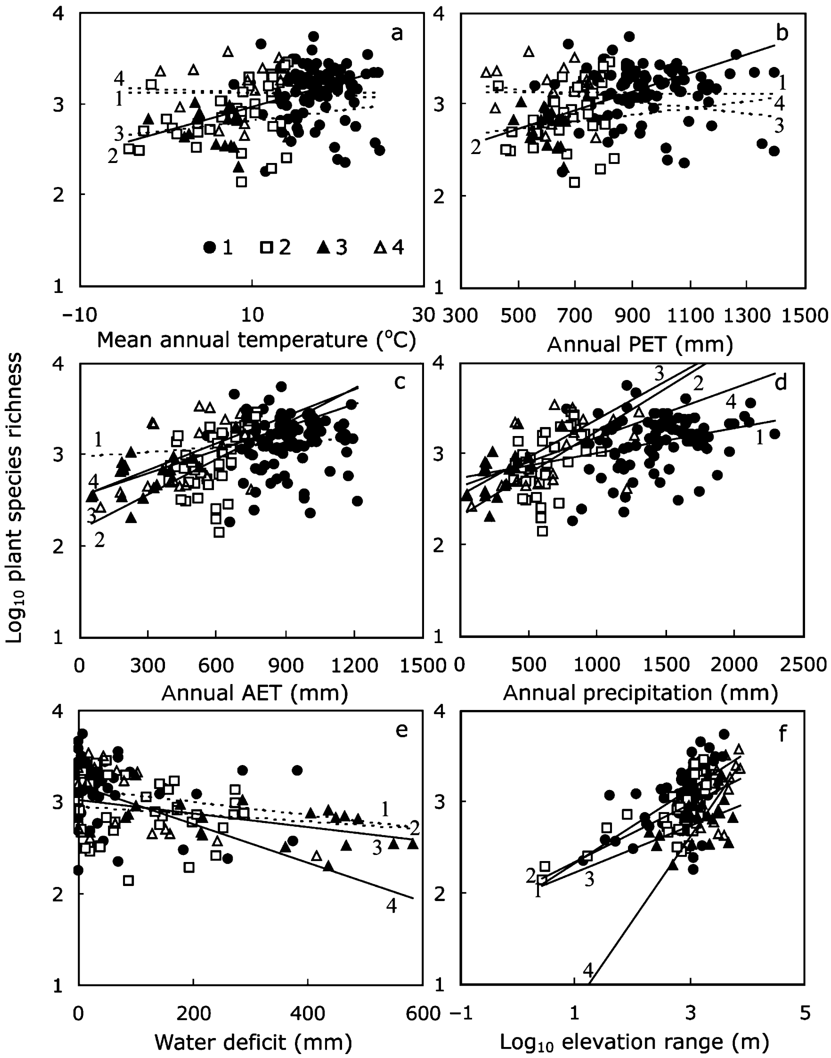

Figure 7 Relationships between plant species richness and climatic variables and elevation range in four vegetation regions. (1) subtropical forest region (2) temperate forest region (3) temperate steppe and desert region (4) the Qinghai-Tibet Plateau region. Dashed lines indicate the correlations are not statistically significant. Solid lines are statistically significant. (a) mean annual temperature (a2: $r^2 = 0.18$, $P = 0.005$); (b) annual PET (b2: $r^2 = 0.11$, $P = 0.032$); (c) annual AET (c2: $r^2 = 0.19$, $P = 0.004$; c3: $r^2 = 0.36$, $P = 0.006$; c4: $r^2 = 0.26$, $P = 0.022$); (d) annual precipitation (d1: $r^2 = 0.08$, $P = 0.004$; d2: $r^2 = 0.26$, $P = 0.001$; d3: $r^2 = 0.39$, $P = 0.005$; d4: $r^2 = 0.27$, $P = 0.019$); (e) water deficit (e3: $r^2 = 0.29$, $P = 0.017$; e4: $r^2 = 0.35$, $P = 0.006$); and (f) elevation range (f1: $r^2 = 0.36$, $P < 0.0001$; f2: $r^2 = 0.48$, $P < 0.0001$; f3: $r^2 = 0.23$, $P = 0.036$; f4: $r^2 = 0.38$, $P = 0.018$).

Table 4 Determinants of species richness for all vascular plants in the different vegetation regions as revealed by stepwise multiple regressions

Variables	Coefficient	P	Adjusted R^2
Subtropical forest vegetation region			
Log_{10} elevation range	0.443	< 0.0001	0.351
Log_{10} reserve area	0.332	< 0.0001	0.430
Annual precipitation	0.238	0.002	0.481
Temperate forest vegetation region			
Log_{10} elevation range	0.617	< 0.0001	0.465
Mean annual temperature	0.335	0.001	0.625
Annual precipitation	0.259	0.010	0.677
Temperate steppe and desert vegetation region			
Annual precipitation	0.758	< 0.0001	0.350
Log_{10} elevation range	0.644	< 0.0001	0.755
Qinghai-Tibet Plateau vegetation region			
Log_{10} elevation range	0.532	0.004	0.394
Water deficit	–0.484	0.008	0.602

to explore the historical/regional influence on China's plant richness.

Since the reserve area was not held constant, its effect on species richness could be examined. We found that the reserve area is a predictor of angiosperm and all vascular plant species richness at the national scale, but improved only a little (*c.* 2%) to the variation already explained by climate and habitat heterogeneity. This finding indicates that the range of climatic variation and topography across China is sufficient to mask the area effect. It is undoubted that the area and other environmental variables affect the species richness pattern; the strength of the contribution depends on the range of their variability. For example, in the subtropical forest region, the reserve area represents a strong predictor of species richness where other environmental conditions are relatively homogeneous, consistent with the finding of a study on plant species richness of the nature reserves in the Czech Republic (Pyšek *et al.*, 2002).

In conclusion, our results suggested that water, energy, and habitat heterogeneity represent the primary explanations for the variation in species richness of the nature reserves across China.

More significantly, there are consistent relationships between species richness and climate and habitat heterogeneity for different taxonomic groups. Habitat heterogeneity, measured by elevation range, was strongly associated with plant richness both at the national and at the regional scales. Climatic constraints to plant diversity varied with the vegetation regions.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/ddi

Appendix S1 Original information on species richness for the major groups of vascular plants and other basic characteristics for the 202 nature reserves.

Appendix S2 Correlation matrix of species richness for the major groups of vascular plant and environmental variables.