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Species Distribution Patterns, Species-Area and Species-Temperature Relationships in Eastern Asian Plants

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1. Introduction

It is a fascinating issue for ecologists to develop a general theory or principle to interpret the mechanisms of global gradients and stabilization of biodiversity. This question has perplexed biogeographers and ecologists for about 100 years, and the diverse theories and hypotheses have been put forward to account for latitudinal gradients in biodiversity (Wright 1983; Rohde, 1992; Waide *et al.*, 1999; Colwell & Lees, 2000; Gaston, 2000; Allen *et al.* 2002; Hawkins *et al.*, 2003; Willig *et al.* 2003; Ricklefs, 2004; Evans & Gaston, 2005; Evans *et al.*, 2005; Mittelbach *et al.* 2007; Gillooly & Allen, 2007; Storch *et al.* 2007; Cardinale, *et al.*, 2009). Recent decade, the metabolic theory of biodiversity (MTB) is developed and attracting a lot of attentions of ecologists as a novel hypothesis based on metabolic theory of ecology (MTE) and the energetic-equivalence rule (West *et al.* 1997, 1999; Enquist *et al.* 1998; Allen *et al.* 2002, 2007; Brown *et al.* 2004; Deng *et al.* 2006, 2008). The MTB is recognized as a general principle that can quantify relationships between the dynamic processes of population and biodiversity patterns in ecosystem, and between species richness and environmental factors (see also Allen *et al.* 2003, 2006; Allen & Gillooly 2006; Gillooly & Allen 2007). The metabolic eco-evolutionary model of biodiversity, the most recent extension of the MTB, has been developed by Stegen *et al.*, (2009).

The MTB considered that species richness, S , in plots of fixed area, A , should be described by a form of equation as following $S = (J/A)(B_0/\overline{B_T})e^{-E/kT}$. In this expression, E is the activation energy of metabolism, -0.6 to -0.7 eV, k is Boltzmann's constant (8.62×10^{-5} eV K⁻¹, where K is degrees Kelvin), T is environmental temperature in degrees kelvin, $B_0 = b_0 M^{3/4}$, where b_0 is a normalization constant that varies by taxonomic group, M is individual body size, B_T is the total energy flux of a population per unit area, varying with taxonomic group and plot area A , and J/A is the total density of individual per unit area. Apparently, the species richness should vary as a function of abundance, body size and environmental temperature. So, when

abundance and size are both presumed constants across geographical space, the relationship between the natural logarithm of species richness ($\ln S$) and the inverse temperature ($1/kT$) will be re-expressed by a linear equation: $\ln S = -E(kT)^{-1} + C$. In this equation, the intercept term ($C = \ln[(B_0/\bar{B}_T)(J/A)]$) incorporates the effect of mean body size of the study taxon, area and total community abundance (Allen *et al.*, 2002; Gillooly & Allen, 2007).

The intense and continuous controversies for the MTB have been focusing on two primary predictions: 1) whether \ln -transformed species richness is linearly associated with an inverse rescaling of ambient temperature or not, and 2) if so, whether the slope of the relationship is encompassed in the theoretical value range of -0.6 to -0.7. The proponents argue that this theory accounts for diversity gradients over a range of spatial scales from mountain slopes to continental and global gradients, and for many groups of plants and ectothermic animals (Allen *et al.* 2002, 2003; Brown *et al.*, 2003, 2004; Gillooly & Allen, 2007). Kaspari *et al.*'s (2004) and Hunt *et al.*'s (2005) analyses using respectively ant communities and deep-sea communities datasets were also in favor of the Allen *et al.*'s (2002) predictions. Concomitantly, the disagreements for MTB emerged in some literature. Hawkins *et al.* (2007a) tested the predictions of this theory with 46 different data sets compiled from a variety of terrestrial plants, invertebrates, and ectothermic vertebrates, and found that the results were partly deviated from the predictions of the MTB (Allen *et al.* 2002; Brown *et al.* 2004). Accordingly, they considered that MTB was a poor predictor for the observed diversity gradients in most terrestrial system. Latimer (2007) subsequently reanalyzed some Hawkins *et al.*'s (2007a) data sets using a Bayesian approach and supported their conclusions. Algar *et al.* (2007) recently showed that the relationship between richness and temperature was actually curvilinear for several data sets in North America, and slopes varied systematically in geographical space, which were strongly consistent with Cassemiro *et al.* (2007) analyzing for New World amphibians. As a consequence, they claimed that Allen *et al.*'s (2002) model did not give an adequate fit to the data.

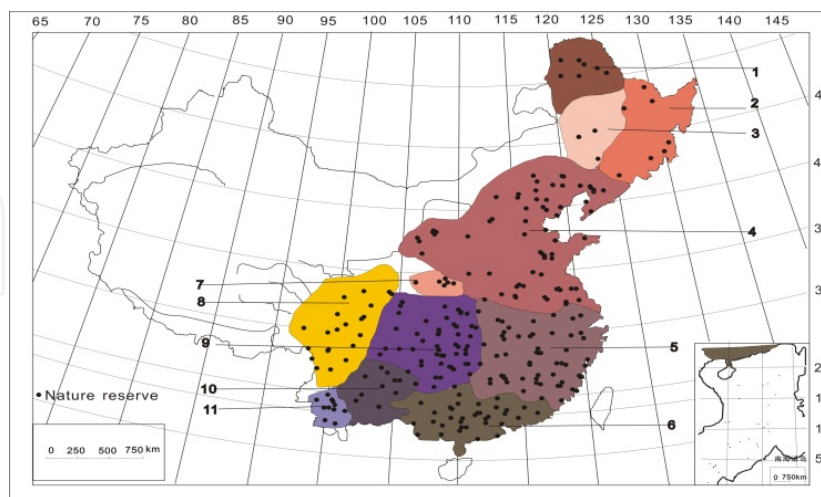


Figure 1. Location of the eleven floristic regions and 270 nature reserves of China used in this study. Floristic regions was marked with Arabic numerals as following (1, Daxinganling; 2, NE China; 3, NE China plain; 4, North China region; 5, East China; 6, Lingnan region China; 7, Tsinling Mountains; 8, The region of Hengduan Mountain; 9, Central China; 10, Dian-qian-gui region; 11, The region of Yunnan Plateau)(also see Zhang *et al.* 2011).

Sample type	Variable	N	Minimm	Maximum	Mean	SD	Skewness	Kurtosis
Floristic region	Species richness							
	Compositae	9	104	655	293.78	163.66	1.34	2.50
	Poaceae	9	86	597	254.44	155.37	1.29	2.52
	Rosaceae	9	49	406	197.33	122.44	0.45	-0.64
	Liliaceae	9	35	164	93.22	41.32	0.11	-0.32
	Labiatae	9	28	253	130.33	79.02	0.07	-1.10
	Angiosperm	11	1009	7891	4363.45	2513.16	-0.02	-1.47
	Gymnosperm	10	4	63	31.90	19.53	0.27	-0.73
	Seed plant	11	1019	7954	4392.45	2524.83	-0.03	-1.47
	Climatic variables							
	MAT (°C)	11	-2.80	20.88	12.34	7.48	-0.98	0.002
	Location and area							
	Mean latitude (°)	11	23	50	35.33	9.54	0.35	-1.49
	Mean longitude (°)	11	100	132	115.1	9.94	0.25	-0.44
	Area (km ²)	11	52000	960000	401660	273070	0.64	0.73
Nature reserve	Species richness							
	Compositae	71	11	324	78.66	44.51	2.55	12.34
	Poaceae	70	8	131	63.13	28.75	0.40	-0.16
	Rosaceae	71	2	185	54.93	33.76	1.27	2.24
	Liliaceae	49	1	85	31.7	19.52	1.08	0.93
	Labiatae	56	3	96	30.41	17.51	1.31	2.99
	Angiosperm	255	79	3893	1186.44	705.08	0.84	0.91
	Gymnosperm	234	1	110	14.21	12.33	3.32	19.32
	Pteridophyte	189	1	594	108.86	92.75	1.41	3.51
	Vascular plant	193	138	4543	1388.18	809.92	0.86	0.99
	Climatic variables							
	MAT (°C)	270	-2.8	29	13.93	5.71	-0.61	0.44
	Location and area							
	Mean latitude (°)	270	18.4	51.6	30.74	6.55	0.71	0.37
	Mean longitude (°)	270	95	130.6	111.88	7.04	0.12	-0.37
	Area (km ²)	270	0.64	6698	490.89	922.28	3.94	18.69

Table 1. Summary statistics of species richness in different plant groups, climate variables, and areas of 11 floristic regions and 270 nature reserve used in this paper.

Empirical evaluations of how well observed richness patterns fit the central predictions of the MTB are now appearing in several literature (Allen *et al.*, 2002; Kaspari *et al.*, 2004; Hunt *et al.*, 2005; Algar *et al.*, 2007; Cassemiro *et al.*, 2007; Latimer, 2007; Hawkins *et al.*, 2007a, b; Sanders *et al.*, 2007). Although to date the observed patterns in biodiversity have been taxonomically and geographically limited (Ellison, 2007), the data sets for the detailed plant groups are relatively absent. Wang *et al.* (2009) showed that magnitude of temperature dependence (i.e. *E*) of tree species richness in both eastern Asia and North America increases with spatial scale at the large scale of 50×50km to 400×400km. Therefore, we conjectured that the species richness inherent dependence of spatial scale may influence on the successful tests for the predictions of the MTB (also see Zhang *et al.* 2011). However, it is unclear (i) how the species richness responds to temperature at the variant spatial scale, especially at the small scale level. (ii) what spatial scale range is appropriate to the MTB.

Here we aimed to evaluate how the relationship between species richness and temperature predicted by MTB varied with respect to sampling scales, as well as with respect to different plant taxonomic group using an extensive plant data sets including three divisions in vascular plant at two different sample scales including nature reserve grain and floristic grain.

2. Methods

We compiled species richness and other basic characteristics of 11 floristic regions and 270 natural reserves. All of the plant species richness data sets used in our analysis were collected from the previous reports involving eleven floristic regions and 270 nature reserves across the eastern China (Zhao & Fang, 2006, many others; for details see Zhang et al.2011). All species were compiled and classified into three groups (pteridophyte, gymnosperm, and angiosperm) at both floristic and reserve scales (the details see Zhang et al.2011). Here the alien species were excluded from our data analyses and only the native species retained. The areas of nature reserves and floristic regions were respectively range from 0.64 to 6689 and from 52000 to 960000 square kilometers (km²) between 18.4° N and 51.6° N latitude and between 95° E and 130.6° E longitude covering a total terrestrial area of 132,540 km² (See Fig1 and Table1). The temperature and the size distribution of the 270 nature reserves also were showed in Table 1.

The mean annual temperature (MAT), assigned to each nature reserve based on its location and used to analyze the relationship between temperature and species richness, was compiled from a 1971-2000 temperature database of China generated from 722 climate stations across China. Flora's MAT was an average value of all the covered climate stations within each floristic region. Other environmental variables such as geographical range and area were also documented.

Descriptive statistics of plant species richness and environmental variables were produced to interpret the information on the data distributions (Table1). The observed slopes of In-transformed richness versus $1/kT$ relationships and at the floristic and reserve grains across the taxonomic group (three divisions and five families of the angiosperms) were estimated by reduced major axis (RMA) regression (Brown *et al.*, 2004; Hawkins *et al.*, 2007). The species richness-area relationships were also analyzed to evaluate the effect of the region size on the species richness (See Fig 4 and 5).

3. Results

The natural logarithm of species richness was significantly linear with $(kT)^{-1}$ at the floristic grain. The 95% CI values of all slopes estimated by RMA did not exclude the second primary prediction of MTB, implying that no significant heterogeneity occurred in slopes among taxonomic groups (Fig2; Table2). However, at the nature reserve grain, only two of three large plant groups (angiosperm, Fig3-f and pteridophyte, Fig3-h) showed significantly linear relationship and met the first prediction of MTB, and gymnosperm were

not linear and rejected the entire MTB (Fig3-g; Table3). The slope values estimated by RMA regression for all taxonomic groups were significantly exclusive from the second prediction of MTB (Table2).

The species-area relationships for all taxonomic divisions at both the floristic and nature reserve special scales indicated that the area size of community have more impact on the species richness for subdivision (e.g. family) than for division (Fig. 4 and 5). Moreover, the observed slope values were close to or encompass (95% CI) the theoretical values predicted by MBT at the spatial scale range of 50- 6698 km², excluding the size of area class less than 50 km² (Fig. 6; Table 4).

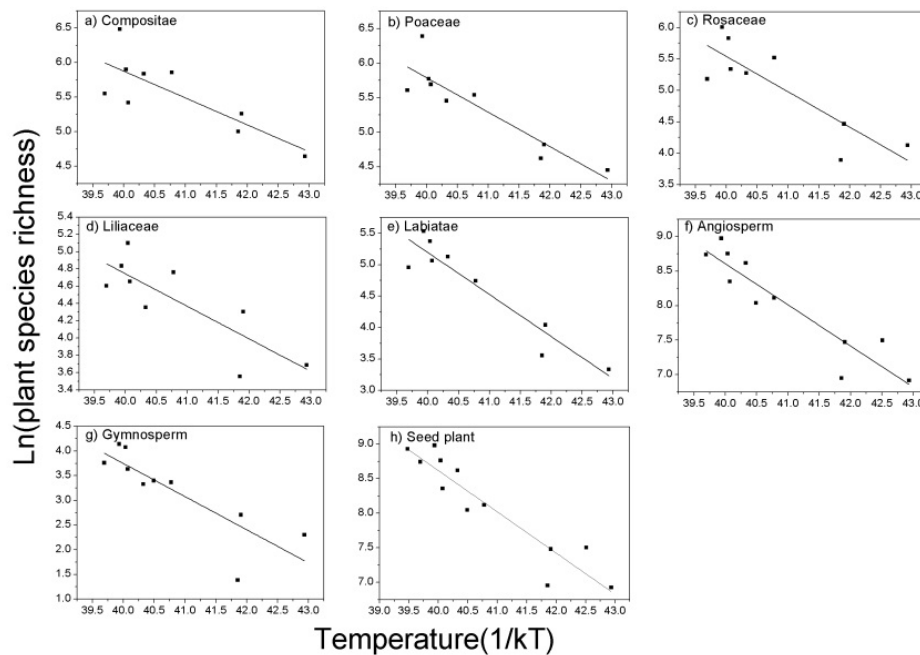


Figure 2. The relationship between natural logarithm of species richness ($\ln S$) and inverse temperature ($1/kT$) for seven groups in 11 floristic regions: two divisions (gymnosperm and angiosperm) and five families of angiosperm (Compositae, Poaceae, Rosaceae, Liliaceae and Labiatae).

Group	Figure	N	R ²	P	RMA slope(95%CI)
Compositae	2-a	9	0.64	0.009	-0.48(-0.74– -0.23)
Poaceae	2-b	9	0.82	<0.001	-0.55(-0.76– -0.34)
Rosaceae	2-c	9	0.73	0.003	-0.66(-0.97– -0.35)
Liliaceae	2-d	9	0.67	0.007	-0.46(-0.69– -0.22)
Labiatae	2-e	9	0.89	<0.001	-0.70(-0.92– -0.50)
Angiosperm	2-f	11	0.86	<0.001	-0.64(-0.83– -0.46)
Gymnosperm	2-g	10	0.71	0.002	-0.80(-1.15– -0.45)
Seed plant	2-h	11	0.89	<0.001	-0.64(-0.80– -0.48)

Table 2. Summary of regressions testing Model II (RMA) slopes of richness-temperature relationships for cases with linear relationship between inverse scaled temperature and \ln -transformed richness in 11 floristic regions.

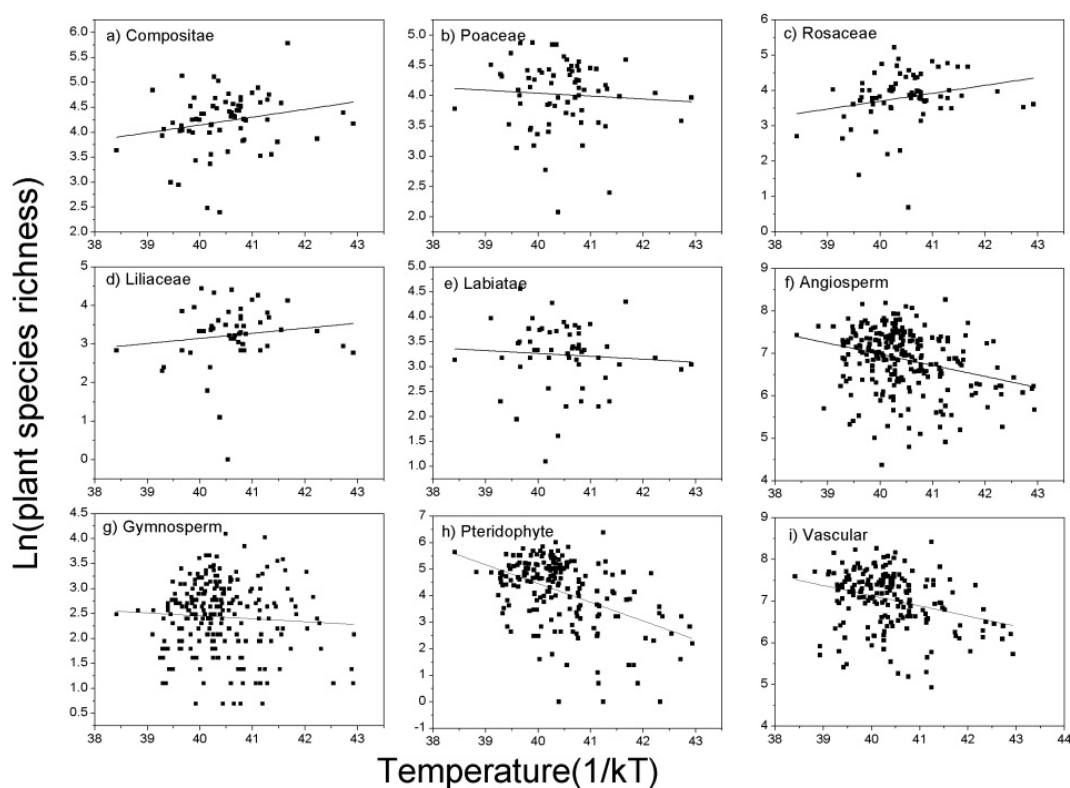


Figure 3. The relationship between natural logarithm of species richness ($\ln S$) and inverse temperature ($1/kT$) for eight plant groups in 270 nature reserve: three divisions (Pteridophyte, Gymnosperm and Angiosperm) and five families of angiosperm (Compositae, Poaceae, Rosaceae, Liliaceae and Labiatae).

Group	Figure	N	R ²	P	RMA slope(95%CI)
Compositae	3-a	71	0.05	0.08	0.73(0.56– 0.91)
Poaceae	3-b	70	0.00	0.58	-0.71(-0.89– -0.54)
Rosaceae	3-c	71	0.05	0.05	0.96(0.73– 1.18)
Liliaceae	3-d	49	0.02	0.36	0.81(0.58– 1.05)
Labiatae	3-e	56	0.01	0.60	-0.81(-1.03– -0.59)
Angiosperm	3-f	255	0.05	0.09	-0.90(-1.01– -0.79)
Gymnosperm	3-g	234	0.00	0.326	-0.91(-1.03– -0.79)
Pteridophyte	3-h	189	0.21	<0.001	-1.55(-1.75– -1.35)
Vascular plant	3-i	193	0.09	<0.001	-0.82(-0.93– -0.71)

Table 3. Summary of regressions testing Model II (RMA) slopes of richness-temperature relationships for cases with linear relationship between inverse rescaled temperature and \ln -transformed richness in nature reserve.

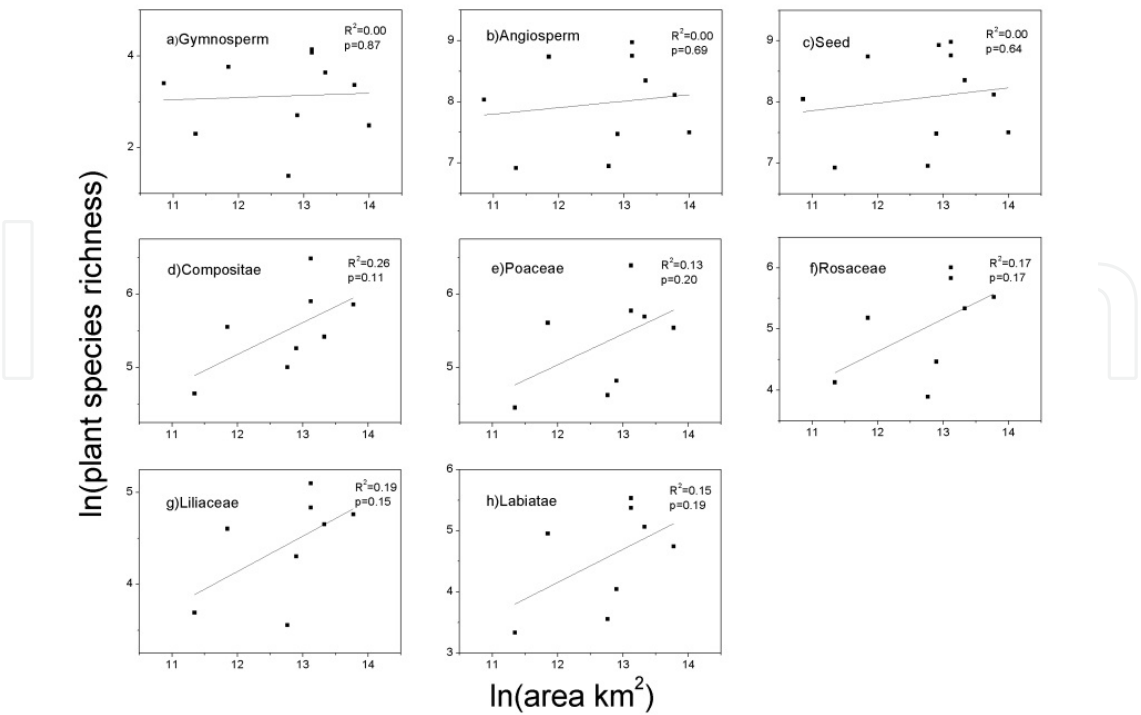


Figure 4. Species richness-area relationships for the seven plant groups in floristic regions: two divisions (gymnosperm and angiosperm) and five families of angiosperm (Compositae, Poaceae, Rosaceae, Liliaceae and Labiatae).

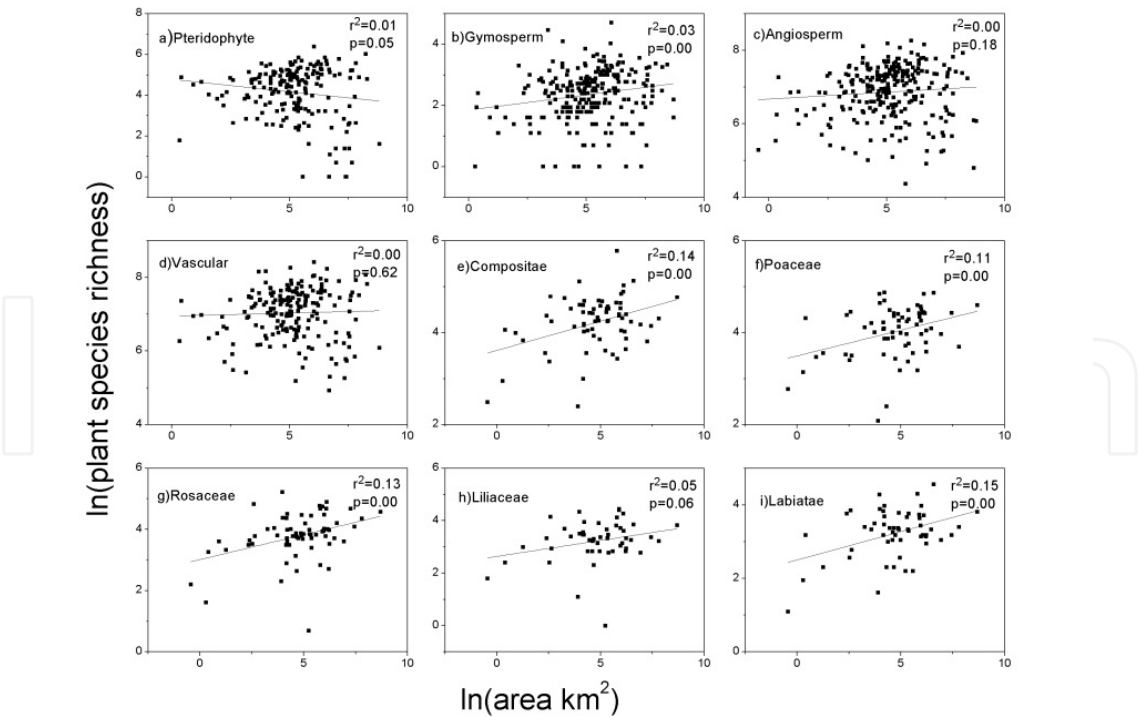


Figure 5. Species richness-area relationships for the eight plant groups in 270 nature reserves: three divisions (Pteridophyte, Gymnosperm and Angiosperm) and five families of angiosperm (Compositae, Poaceae, Rosaceae, Liliaceae and Labiatae).

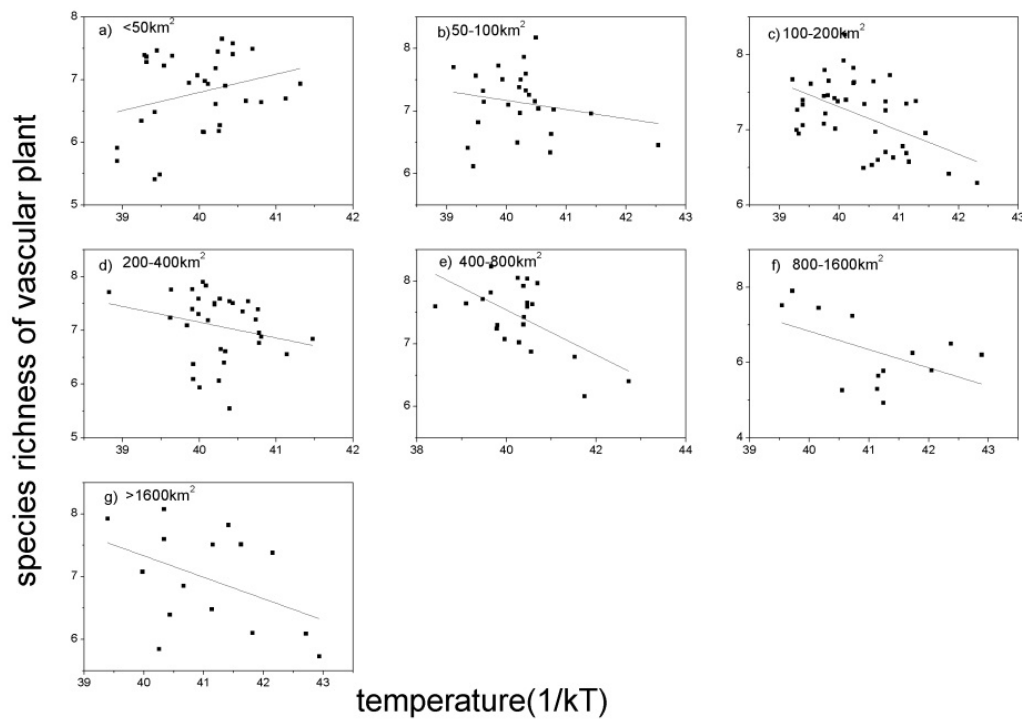


Figure 6. Temperature–richness relationships for the vascular plant group along an area classes. Note that the classification of area is following: a)<50, b)50-100, c)100-200, d)200-400, e)400-800, f)800-1600, g)>1600.

Area classes(km ²)	Figure	N	R ²	P	RMA slope(95%CI)
<50	7-a	32	0.08	0.12	1.04(0.67-1.42)
50-100	7-b	25	0.04	0.32	-0.72(-1.02– -0.41)
100-200	7-c	44	0.25	<0.001	-0.63(-0.80– -0.46)
200-400	7-d	33	0.06	0.19	-1.24(-1.69– -0.80)
400-800	7-e	22	0.36	0.003	-0.60(-0.82– -0.37)
800-1600	7-f	12	0.25	0.08	-0.96(-1.55– -0.38)
>1600	7-g	16	0.18	0.10	-0.84(-1.27– -0.40)

Table 4. Summary of regressions testing Model II (RMA) slopes of richness-temperature relationships for vascular plant group with linear relationship between inverse rescaled temperature and ln-transformed richness along an area classes.

4. Discussion

Hawkins' *et al.* (2007a) suggested that the relationship of logarithm transformed species richness and inverse temperature was nonlinear through analyzing the datasets of Chinese angiosperm taken from nature reserves with a range of area from 100 km² to 247 km². Here we similarly failed to observe significantly linear relationships between them at the nature reserve grain with the regions ranging from 0.64 km² to 6689 km², excepting for two large groups (angiosperm and pteridophyte). Moreover, almost all slope values were exclusive from the predictive range of MTB (Table 2) as the pattern of tree species distribution in

eastern Asia (Wang *et al.*, 2009). However, when we analyzed these data sets at the floristic regions ranging from 52000 km² to 960000 km², not only this linear relationship was observed, but also the slopes is highly in agreement with the theoretical values of MTB (Allen *et al.* 2002; Brown *et al.* 2004). Therefore, the plant species richness patterns predicted by MTB apparently depended on the grain size (Ellison, 2007). This scenario may be due to the fact that the number of species at the large scale overwhelmed the number of species at the relative small sample scale (e.g. nature reserve). However our analysis of species richness-area relationships showed no significant relations at floristic grain (Fig 4). The adjacent nature reserves frequently have the similar annual temperature, but the other environmental factors (i.e. water, elevation and nutrition) may exhibit a lot of variations between them that can also strongly influence the local plant species richness (Storch *et al.*, 2007). The large-scale (floristic region) patterns are not simply explicable in terms of knowledge of small-scale (nature reserve) processes (Storch and Gaston, 2004). On the contrary, despite the habitat heterogeneity including annual temperature is large between plant flora, it is usually overwhelmed within plant flora because of the enormous sample scale (Field *et al.*, 2009).

For the purpose of evaluating the MBT's robustness, Hawkins *et al.* (2007a) show the relationship between the inverse of temperature and the natural log of richness in terrestrial ectotherms (including amphibians, reptiles), invertebrates, mammals and plant around the world. However, in their plant data sets, detailed taxonomic unit (e.g. pteridophyte, gymnosperm and family unit) were not contained. In their 46 data sets, 14 had no significant relationship; 9 of the remaining 32 were linear, meeting the first prediction of the MBT, but the slope values against its second prediction. So, they contended that it was important to use appropriate taxonomic ranges for accepting or refusing the prediction of MBT (see also, Ellison, 2007).

Our results clearly showed that the significant taxonomic dependence in the nature reserve data sets. Pteridophyte unit which potentially supported the first prediction of MTB dominantly differs from the other groups in particular. Pteridophytes have a reproductive strategy based on the high dispersibility of spores, and have a strong moisture dependence of the sexual reproduction (Pausas & Sáez, 2000; Lehmann, *et al.*, 2002; Castán & Vetaas, 2005). Thus, the life history and growth cycle for pteridophytes are probably more directly and tightly linked to abiotic factors than many other groups of plants because of the lack of co-evolved relationships with animal vectors (Barrington, 1993; Lwanga *et al.*, 1998; Pausas & Sáez, 2000; Castán & Vetaas, 2005). So our results possibly support the perspective that the ability of MBT to predict richness patterns will also depend on dispersal ability (Latimer, 2007).

The plant species were not subdivided into division group to test the slopes converge around the predicted value -0.65 by MTB (Allen *et al.* 2002; Brown *et al.* 2004). Whereas the significant heterogeneity of slopes were observed at both floristic region and reserve scale among the different taxonomic groups as the most recently reported by Hawkins *et al.* (2007a,b) and Wang *et al.* (2009), indicating that the plant groups may hold variable

activation energies rather than an invariant value. Our more recently research showed that validity of the MTB lies on if the area size of the community has no significant effect on species richness (Zhang et al. 2011). Therefore we believe that the slope value for each taxonomic group should be co-influenced by the restriction of distribution range, the area size of sampling community and other abiotic factors, as well as the inherent activation energy differences.

5. Conclusion

Our results suggested that the relationship predicted by MTB between the plant richness and temperature can be tested at the larger regional scale (e.g. floristic region) well. However, at the small scale (e.g. nature reserve), the predicted relationships were easily influenced by the many other factors such as area size of community, taxonomic divisions, seed dispersal and so on. Allen *et al.* (2003) claimed that the theory of biodiversity proposed by themselves is not complete and comprehensive. Here we consider that the theory must integrate the fundamental influences of multifactor involving temperature, area size, water, elevation and nutrition on the species richness patterns in small scale regions where the disturbance of environmental factors easily result in change of the species diversity. At the same time, we should also seek the more biological interpretation for the noticeable differences among taxonomic groups in the future.

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