

CORRESPONDENCE



Large-scale patterns of tree species richness and the metabolic theory of ecology

ABSTRACT

The metabolic theory of ecology (MTE) endeavours to explain ecosystem structure and function in terms of the effects of temperature and body size on metabolic rate. In a recent paper (Wang *et al.*, 2009, *Proceedings of the National Academy of Sciences USA*, **106**, 13388), we tested the MTE predictions of species richness using tree distributions in eastern Asia and North America. Our results supported the linear relationship between log-transformed species richness and the inverse of absolute temperature predicted by the MTE, but the slope strongly depends on spatial scale. The results also indicate that there are more tree species in cold climate at high latitudes in North America than in eastern Asia, but the reverse is true in warm climate at low latitudes. Qian & Ricklefs (2011, *Global Ecology and Biogeography*, **20**, 362–365) recently questioned our data and some of the analyses. Here we reply to them, and provide further analyses to show that their critiques are primarily based on unsuitable data and subjective conjecture.

Keywords

Eastern Asia, metabolic theory of ecology, North America, temperature, tree species richness.

In a recent paper (Wang *et al.*, 2009) we tested the predictions of the metabolic theory of ecology (MTE) proposed by Brown and colleagues (Allen *et al.*, 2002; Brown *et al.*, 2004), using two databases of tree distributions in eastern Asia and North America. We

found that the MTE predicts well the linear relationship between the logarithm of species richness and the inverse of absolute temperature. However, the slope of the relationship increases with spatial scale. In addition, we found that tree species richness is higher in cold climates at high latitudes in North America than in eastern Asia, but the reverse is true in warmer climates at lower latitudes.

Qian & Ricklefs (2011) (Q&R hereafter) recently criticized our paper and questioned some of the conclusions. Their criticisms can be summarized as three points: (1) we did not cite relevant literature; (2) our data on tree species distributions are compromised because of low data quality and inconsistent data criteria, and therefore cannot be used to quantify and compare biogeographic patterns of tree species richness in eastern Asia and North America; and (3) the fundamental framework of the MTE is incorrect. Here we respond to their comments and criticisms. As the primary focus of Q&R's criticism is on our data quality, we put more emphasis on this issue in the response.

REFERENCE CITATIONS

Several publications have described the comparative biogeography and large-scale patterns of plant species richness in eastern Asia and North America (e.g. Li, 1952; Graham, 1972; Davidse, 1983; Tiffney, 1985; Wen, 1999; and references therein), but few attempt to identify the mechanisms of the patterns. In Wang *et al.* (2009), we cited the most relevant recent references. We did not cite those suggested by Q&R because they focused on the patterns of species richness whereas our paper focused on the mechanism underlying the patterns. Here we should note that of the four papers they suggested, three are written by Q&R themselves and one (Evans *et al.*, 2005) is about bird species diversity in Britain. Although we admire Q&R's contribution to the biogeography of plant diversity in Asia and North America, we restricted our citations to those which are directly relevant to the subject.

DATA QUALITY AND DATA COMPARABILITY

Taxonomic level

Q&R questioned the use of infra-specific taxa for China but not for North America. Comparability of taxonomic level is one of the most controversial issues in plant taxonomy and biogeography. Different specialists prefer different classifications, and this happens in both China and North America (e.g. *Fagus grandifolia* and *Fagus mexicana*; Williams-Linera *et al.*, 2000). Most ecologists and biogeographers generally respect and follow the current taxonomy.

In our analyses, we used infra-specific taxa (subspecies or variety) following *Flora of China* (<http://flora.huh.harvard.edu/china/index.html>). Nevertheless, the proportion of infra-species is very low in the flora of China: less than 10% of tree species. This is much lower than Q&R's estimation (23%), because they might have selected families with a higher proportion of infra-species. To further evaluate the potential influence of infra-species on the diversity pattern (Wang *et al.*, 2009), we merged infra-species and re-analysed the data. As shown in Tables 1 & 2, infra-species did not substantively change our findings presented in the original paper by Wang *et al.* (2009). The slopes of the relationships between species richness and temperature, and the species turnover (slopes of the species–area relationship) were very similar to those reported originally (for details, see Appendix S1 in Supporting Information).

Definition of trees

Q&R claimed that the height used to define trees was different in China and North America. This is not true. The distribution maps of North American trees were documented by Little (1971–1978), who defined a tree as a woody plant with an erect stem or trunk and 'a height at least 13 feet (4 meters)' (Little, 1979), which is similar to the definition in China (see Appendix S2 for details). Q&R further suggested that small changes in

Table 1 Comparison of the parameters (slope, $-E$, and intercept, C_0) in the linear relationship of the logarithm of species richness to the inverse of absolute temperature ($1/kT$) between the re-analysed and original data for China's tree species richness.

Grid size (km)	Original				Re-analysis			
	C_0		$-E$		C_0		$-E$	
	Estimation	SE	Estimation	SE	Estimation	SE	Estimation	SE
50 × 50	42.09	0.61	-0.93	0.01	43.78	0.63	-0.97	0.02
100 × 100	44.88	1.22	-0.99	0.03	46.33	1.26	-1.03	0.03
150 × 150	46.17	1.82	-1.02	0.04	47.30	1.86	-1.04	0.04
200 × 200	47.89	2.48	-1.05	0.06	48.84	2.55	-1.08	0.06
250 × 250	46.50	3.14	-1.01	0.08	48.66	3.24	-1.07	0.08
300 × 300	48.85	3.76	-1.07	0.09	49.53	3.86	-1.09	0.09
350 × 350	49.91	4.47	-1.09	0.11	51.23	4.47	-1.13	0.11
400 × 400	46.94	5.10	-1.02	0.12	49.24	5.29	-1.08	0.13

Table 2 Comparison of the slopes (z) of the species richness–area relationships (SAR) between the re-analysed and original data for China's tree species richness.

Temperature (°C)	Original		Re-analysis	
	z	SE	z	SE
-12	0.20	0.03	0.18	0.02
-4	0.24	0.02	0.22	0.02
0	0.26	0.02	0.24	0.01
4	0.28	0.02	0.26	0.01
12	0.31	0.01	0.30	0.01
20	0.35	0.02	0.33	0.01

the threshold for the minimum height of mature individuals would double or triple the number of tree species in North America. This may also not be true. Analyses of China's woody flora indicated that only 72 tree species (2.3% of the total = 72/3165) will be lost if the threshold of height for trees is changed from 4 m to 5 m.

Database of China's woody plants

The construction of the database on China's woody plants was started in 2003 (Fang *et al.*, 2011), and included two major steps, first the species checklist and then compiling the species distributions.

The checklist of China's woody species was based on the two most widely accepted, high-quality data sources, *Flora Reipublicae Popularis Sinicae* (Flora Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita, 1959–2004) and *Database of China's Seed Plants* (Wu & Ding, 1999), both of which have been widely used nation- and world-wide (e.g. in many previous studies of Q&R).

Exotic species were excluded from the checklist. To improve data quality, the checklist was further checked by several experienced taxonomists, and updated following the recently published *Flora of China*, in which the taxonomy reflects the current understanding of each taxonomic group. For the families that have not been completed (15 out of 170) in *Flora of China*, we used the *Catalogue of Life, China: 2008 Annual Checklist* (<http://www.sp2000.org>) to make a double check. The database finally contains 11,405 woody species, belonging to 1175 genera and 170 families.

Then we compiled the county-level distributions of each species using a consistent method from all available national, provincial and local floras, monographs of field surveys and peer-reviewed articles published before 2008, and herbarium specimen records (<http://www.cvh.ac.cn>). Because down-scaling from the provincial to county-level distributions can cause errors, we compiled only county-level distribution records, but excluded provincial or regional records. After a literature-review based compilation of the distribution data, we divided China into 20 regions and invited local experts in each region to examine and supplement the distribution records of the database. To further check the quality of the database, we compared our data with the distribution sites (survey-based occurrence sites) of 50 well-documented endemic species to China that have been compiled using independent and intensive surveys by the China Ministry of Forestry (2001), and found that our distribution ranges of these 50 species cover all the survey-based occurrence sites of each species. This suggests that the distribution maps in our database represent the real distribution ranges of woody species, and hence are comparable with those in North America. Q&R claimed that 'only few counties in the main-

land of China have been botanized', and therefore the national floras and databases 'contain little information about county-level distributions'. Then they claimed that low quality of species distributions plagued our database and biased our findings. However, their argument indicates that either they are unfamiliar with the current Chinese botanical literature or they chose to ignore the botanical surveys and data compilations conducted in the past several decades. For example, from 1956 to 1996 more than 34 'national teams' involving more than 20,000 scientists from about 850 academic institutions were organized to investigate the distributions of plants and animals in most counties of China (Sun, 2007). These national campaigns have produced more than 440 monographs, and enormous maps and peer-reviewed articles (Sun, 2007). Many provincial and local inventories have also been conducted since 1950 (see Appendix S3 for more details). The extensive publications based on these field surveys constructed the solid basis for our data compilation. The published floras in China contain extensive information on county-level distributions of plants. For example, *Flora Reipublicae Popularis Sinicae* and *Seed Plants of China* document more than 760,000 records of county-level distributions for vascular plants, in which about 290,000 records are for woody plants and about 81,000 for trees. Given these efforts, we are confident that the distribution maps in the database reflect the real ranges of most woody species in China, and the quality of the database did not bias our findings.

Forest plot data

In Wang *et al.* (2009), we reported higher tree species richness at high latitudes in North

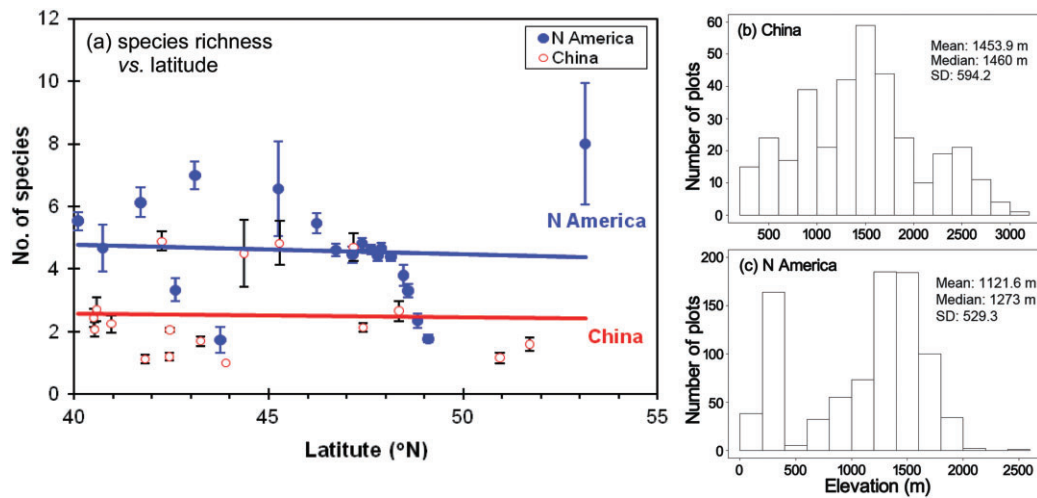


Figure 1 Changes in tree diversity in forest plots at higher latitudes in China and North America, together with altitudinal frequency distribution of plots. (a) Relationship between tree diversity and latitudes in China (red circles) and North America (blue solid circles); each point represents the average number of tree species for a site, and bars show their standard errors. The solid red and blue lines were fitted by linear regressions, indicating general trends of tree species richness versus latitude for China and North America, respectively. (b) Altitudinal frequency distribution for China's plots. (c) Altitudinal frequency distribution for North American plots. Plots are 400 m² in area and trees are larger than 10 cm diameter at breast height (d.b.h.).

America than in eastern Asia. This trend is further illustrated in Fig. 1(a) which shows the changes in plot-based tree species richness with latitude in China and North America. The plot data for China are based on systematic field studies conducted since the mid-1990s. All species occurring in the plots were recorded (Fang *et al.*, 2009). For comparison with the North American dataset in which only stems with diameter at breast height (d.b.h.) > 10 cm were reported, we counted the species richness of the individuals with d.b.h. > 10 cm. Q&R's claim that lower richness in north-east China 'may partly result from incomplete documentation of species' is not true. As showed below, their argument was primarily based on conjecture and incorrect analyses.

Elevation difference

Q&R argued that the plots in North America 'are primarily distributed at low elevations', which is based on 'guess' rather than analyses. Actually, the forest plots used in Wang *et al.* (2009) have similar average elevations in the two continents: 1121.6 m ($n = 972$, $SD = 529.3$, median = 1273 m) for North American plots, and 1453.9 m ($n = 398$; $SD = 594.2$, median = 1460 m) for those in China. Moreover, 65% of the plots in China, and 72% in North America were located at elevations of 800–2000 m (Fig. 1b,c). In contrast to

this, Q&R selected forest plots of eastern Asia that are located at elevations of 80–850 m to compare with our results for North America, hence leading to higher tree species richness in Asia than North America.

Incorrect data analyses

Q&R stated that 52 canopy tree species were found in a 25-ha plot located in Changbai Mountains in north-east China. However, our re-analysis of this plot indicated that only 20 species were trees having stems of d.b.h. > 10 cm, and the other species include 22 shrubs, 8 tree seedlings with stems of d.b.h. < 10 cm and 2 lianas (for species checklist, see Hao *et al.*, 2008; Wang *et al.*, 2010). Q&R used another dataset (Zhang *et al.*, 2007) containing 99 forest plots in northernmost China, and again included the species richness of individuals with d.b.h. < 10 cm, which will significantly increase the species richness. Therefore, their results were not comparable with ours. Q&R also used forest plots in Far East Russia in their analyses. However, a 'narrow' species concept is generally used in Russia, which is not comparable with that used in China and North America and can increase the number of tree species (Krestov & Nakamura, 2002; Krestov *et al.*, 2006).

In addition, Q&R argued that the higher tree species richness in North America than eastern Asia at high latitudes was because of higher temperature in the former than the later. This statement matches our findings that temperature determines the richness patterns (Wang *et al.*, 2009).

THE MTE AS AN EXPLANATION OF LARGE-SCALE PATTERNS OF SPECIES RICHNESS

The MTE explains large-scale latitudinal and elevational patterns of biodiversity using the principles of biochemical kinetics and the scaling of biological metabolism (Allen *et al.*, 2002; Brown *et al.*, 2004). Although it has been debated widely, the MTE has been viewed as 'a new window through which we can ponder nature' (Tilman *et al.*, 2004) because its approaches differ from those based on statistical models. Q&R made some criticisms concerning MTE, but their points have been discussed in several previous debates (see Allen *et al.*, 2002; Brown *et al.*, 2004; Algar *et al.*, 2007; Hawkins *et al.*, 2007a,b; Gillooly & Allen, 2007; McCain & Sanders, 2010). We address some of these issues here.

1. In assessing the kinetic effects of temperature predicted by the MTE, as we have done in Wang *et al.* (2009), other environmental conditions, such as precipitation,

need to be held constant. However, naturally precipitation often co-varies with temperature, and this will cause significant residual variations in the species richness–temperature relationship.

2. The power relationship between individual density (N) and body size (M) predicted by MTE, i.e. $N \propto M^{-3/4}$, is observed in equilibrium ecosystems, where the individuals occupy the available space and compete for resources (Enquist & Niklas, 2001). This relationship is not expected to hold in non-equilibrium conditions, such as secondary succession following disturbance. The plots in China used in Wang *et al.* (2009) were sampled in natural forests subjected to minimal disturbance, and hence suitable for evaluating MTE.

3. MTE addresses the kinetic effect of environmental temperature on ectothermic animals and plants, but never closes ‘the door to alternative hypotheses’ (see Allen *et al.*, 2002; Brown *et al.*, 2004; Wang *et al.*, 2009). Allen *et al.* (2002) clearly stated that the MTE doesn’t imply ‘that temperature is the only variable that affects biodiversity’. Indeed, we have found residual variation in the relationship between species richness and temperature that might reflect the potential importance of precipitation (Wang *et al.*, 2009).

4. We recognize that neither Wang *et al.* (2009) nor MTE as currently conceived offer a complete explanation of the mechanistic processes underlying the latitudinal gradient of biodiversity. But Wang *et al.* (2009) demonstrate quantitative patterns of tree species richness in eastern Asia and North America that are consistent with a major direct effect of temperature on biochemical kinetics, biological metabolism, ecological interactions and evolutionary processes.

5. We take this opportunity to correct a descriptive error in Wang *et al.* (2009). As is readily apparent in their Fig. 5, the relationship between inverse temperature and beta diversity as measured by the slope (z -value) of the species–area relationship is *linear* not *exponential* as incorrectly stated in their abstract. This effect of temperature on spatial turnover in species composition is an important feature that will need to be explained before we can claim to understand the latitudinal

gradient and other geographic patterns of biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Main results obtained from re-analysed data by merging all infra-species.

Appendix S2 Definition of trees.

Appendix S3 A brief introduction to botanical surveys in China.

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Editor: Richard Field

doi: 10.1111/j.1466-8238.2010.00688.x