

Temperature dependence, spatial scale, and tree species diversity in eastern Asia and North America

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The increase of biodiversity from poles to equator is one of the most pervasive features of nature. For 2 centuries since von Humboldt, Wallace, and Darwin, biogeographers and ecologists have investigated the environmental and historical factors that determine the latitudinal gradient of species diversity, but the underlying mechanisms remain poorly understood. The recently proposed metabolic theory of ecology (MTE) aims to explain ecological patterns and processes, including geographical patterns of species richness, in terms of the effects of temperature and body size on the metabolism of organisms. Here we use 2 comparable databases of tree distributions in eastern Asia and North America to investigate the roles of environmental temperature and spatial scale in shaping geographical patterns of species diversity. We find that number of species increases exponentially with environmental temperature as predicted by the MTE, and so does the rate of spatial turnover in species composition (slope of the species-area relationship). The magnitude of temperature dependence of species richness increases with spatial scale. Moreover, the relationship between species richness and temperature is much steeper in eastern Asia than in North America: in cold climates at high latitudes there are more tree species in North America, but the reverse is true in warmer climates at lower latitudes. These patterns provide evidence that the kinetics of ecological and evolutionary processes play a major role in the latitudinal pattern of biodiversity.

biodiversity | metabolic theory of ecology | species richness | kinetic energy | species-area relationship

The increase of species richness from poles to the equator is a pervasive feature of biodiversity and a central issue in biogeography and macroecology (1, 2). Among many ecological and historic mechanisms suggested to shape this pattern (1, 3–7), the recently proposed metabolic theory of ecology (MTE) (8–10) has generated widespread attention and controversy (11–18). The MTE seeks to explain ecological phenomena in terms of the metabolic processes of organisms, and in particular, in terms of the effects of body size and temperature on metabolic rate. Allen et al. (10, see also refs. 9, 14, and 19) extended the MTE to latitudinal and elevational diversity gradients, predicting that number of species increases exponentially with increasing environmental temperature. More quantitatively, they predicted that log-transformed number of species varies linearly with the reciprocal of absolute temperature ($1/kT$, where k is Boltzmann's constant, 8.62×10^{-5} eV K^{-1} ; and T is absolute temperature), and the slope of the relationship is between -0.70 and -0.60 (for the derivations of the theoretical predictions, see refs. 9 and 10). Preliminary empirical tests using the distributions of amphibians and trees along latitudinal gradients in North America and altitudinal gradients in Ecuador and Costa Rica appeared to support these predictions (10). Their treatment ignored the effects of spatial scale, which are known to affect species diversity (1, 16, 20, 21), and have recently received renewed attention (20, 21).

In this study, we use 2 extensive databases on tree distributions in eastern Asia (3,065 species) and North America (679 species)

to analyze the separate and interacting effects of environmental temperature and spatial scale on species diversity. To quantify effects of spatial scale on the temperature dependence of species diversity, we calculated tree species richness in grid-based nested quadrates at spatial resolutions ranging from 50×50 km to 400×400 km for both continents (see *Materials and Methods*).

Results and Discussion

Our analyses show strong effects of both temperature and spatial scale on tree species diversity. On both continents, species richness increases exponentially with increasing environmental temperature, but more rapidly at large than small spatial scales and more rapidly in eastern Asia than in North America. This is seen in Fig. 1, where so-called Arrhenius plots show consistent strong negative linear relationships between log-transformed species richness and the reciprocal temperature ($1/kT$) at all scales on both continents (Table S1; see ref. 22). These plots account for 43%–82% (R^2 values) of the variation in species richness. As quantified by the slopes of these relationships (E -values), the magnitude of temperature dependence of species richness increases consistently with increasing spatial scale, ranging from -0.93 to -1.02 in eastern Asia and from -0.52 to -0.67 in North America (Figs. 1 and 2). For reference, E -values can be expressed in terms of Q_{10} (defined as the rate of change with a $10^\circ C$ increase in temperature): $E \approx -0.50$ corresponds to $Q_{10} \approx 2.0$ and $E \approx -1.0$ to $Q_{10} \approx 4.1$; therefore, number of species increases ≈ 2 – 4 times for every $10^\circ C$ increase in mean annual environmental temperature. A large-scale plot-based dataset of 318 forest plots (23), each 600 m² in area, along a north-south latitudinal transect in eastern China, also reveals strong temperature dependence: slope = -0.81 , $R^2 = 0.65$ (Fig. 3; for other analyses in North America, see refs. 3 and 10). The explanatory power (R^2) of environmental temperature in shaping the diversity patterns also varies with spatial scale. As grid size increases from 50×50 km to 400×400 km, R^2 values increase modestly from 52% to 58% in eastern Asia, and much more steeply (from 43% to 82%) in North America (Fig. 2B).

Much of the remaining unexplained variation in the Arrhenius plots is due to water availability, which is well known to affect diversity, especially of plants, through some combination of productivity and drought stress. The residuals about the regression lines in Fig. 1 are positively correlated with annual precipitation (Fig. 4). This pattern holds at all scales on both continents, with precipitation accounting for an additional 4%–31% of the variation in richness. Therefore, temperature and rainfall together explain 63%–85% of the variation in tree species richness across these spatial scales and across both continents.

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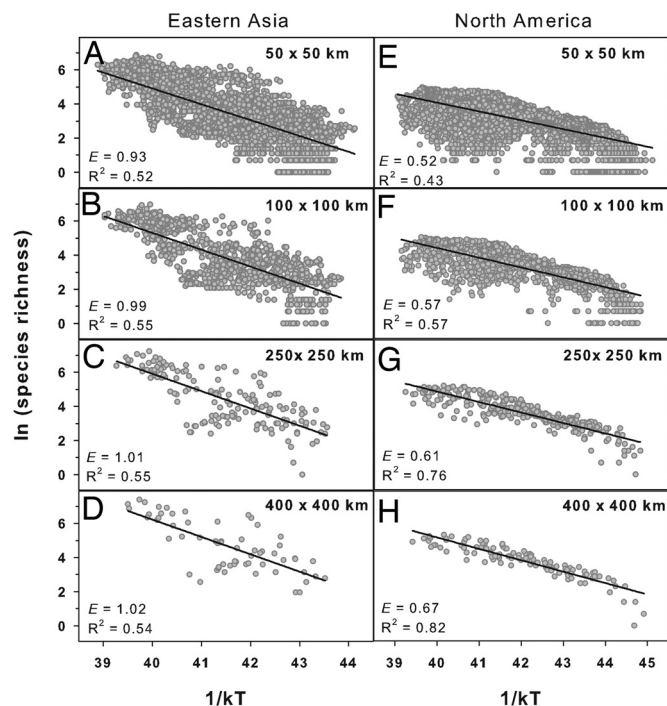


Fig. 1. Relationships between log-transformed species richness and reciprocal ambient temperature (1/kT) at different spatial scales in eastern Asia (A–D) and North America (E–H). Following the previous studies, these figures (log(S) ~ 1/kT) are usually termed as the Arrhenius plots, and $-E$ is the slope of the relationships, which represents the activation energy of metabolism (9). To save space, we show data for only 4 sample grids: 50 × 50 km (A and E), 100 × 100 km (B and F), 250 × 250 km (C and G), and 400 × 400 km (D and H).

The effect of precipitation was additionally evaluated by plotting log(species richness) vs. log(annual precipitation), fitting a regression line, and then plotting the residuals vs. 1/kT (SI Appendix and Figs. S1–S3). These additional analyses suggest that the log-transformed species richness is still a linear function of 1/kT at all spatial scales after controlling the effect of precipitation, confirming the pervasive exponential effects of ambient temperature on species richness. Water availability and water-energy interactions may affect the patterns of species richness and the E -values of the Arrhenius plots, but will not alter the fundamental exponential effects of temperature on geographic richness patterns or the scale dependence of the kinetic effects.

On both continents the effect of temperature on species richness increases with increasing spatial scale (grid size), suggesting that the species-area relationship, which describes changes in species richness with area, is temperature dependent. To quantify this, we used the species richness vs. temperature relationships for the spatially nested sample sites (some shown in Fig. 1, also in Table S1) to calculate species richness at each spatial scale at 6 different environmental temperatures, from -12°C to 20°C . Log-transformed species richness (S) was linearly and positively correlated with log-transformed sample area (A) at all temperatures (Fig. 5), so fitting a power-law model, $S = cA^z$, where z is the slope and c is the normalization constant or intercept (24). Further, the slopes (z -values) of these species-area relationships increased with increasing temperature, from 0.20 to 0.35 in eastern Asia and from 0.12 to 0.27 in North America (Fig. 5G; for the derivation of the temperature dependence of z , see SI Appendix). Therefore, number of species increases nonlinearly with sample area, by a factor of approximately 1.3–2.2 species for every factor of 10 increase in sample

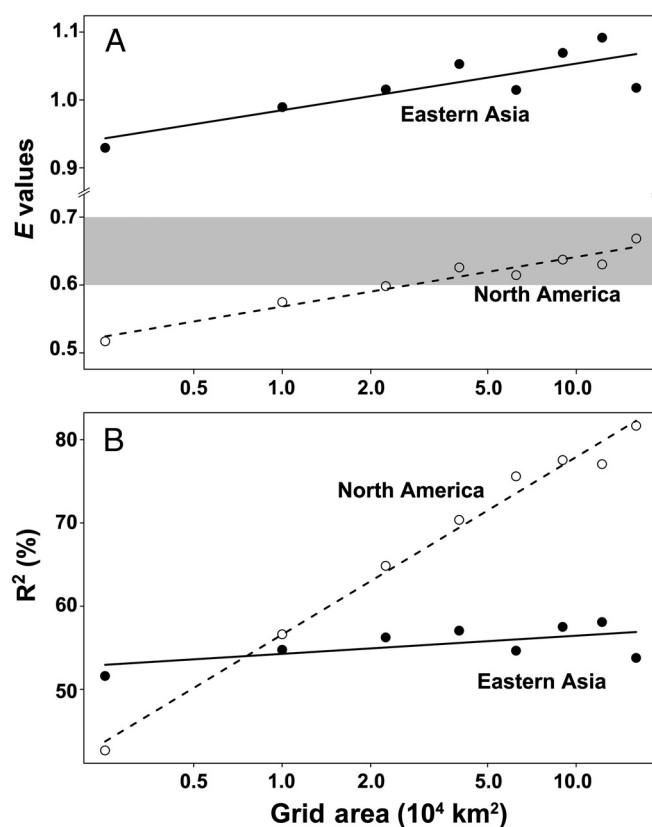


Fig. 2. Changes in slopes, E -values (A) and goodness of fit, R^2 values (B) of regression models for log-transformed species richness as a function of temperature (1/kT) with grid size for eastern Asia (points and solid line) and North America (circles and dashed line). The shaded region represents the slopes ($-0.7 \sim -0.6$) predicted by Allen et al. (10) and Brown et al. (9). Both slopes and R^2 values increase with spatial scales on the 2 continents. For details, see Table S1.

area. The slopes are within the range or somewhat higher than the z -values of 0.1–0.2 commonly observed for nonisolated sample sites on continents (1).

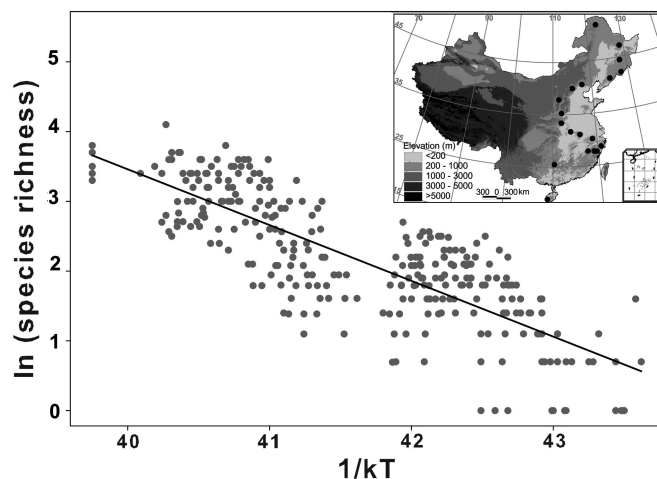


Fig. 3. Relationship between log-transformed tree species richness and temperature (1/kT) in forests of the mountainous regions in eastern Asia. The data, collected by the Department of Ecology of Peking University (23), come from 318 forest plots, each 600 m² in area, from 19 research sites across eastern China (inset map shows the site locations). This Arrhenius plot has a slope of -0.81 ($R^2 = 0.65$). For details of data collection, see ref. 23.

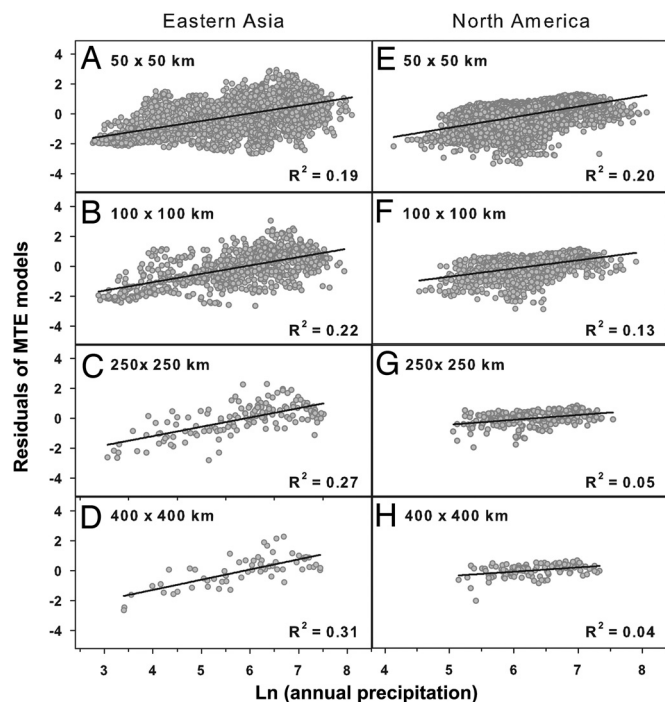


Fig. 4. Residuals of the Arrhenius plots (i.e., models of $\log(\text{species richness})$ vs. $1/kT$ shown in Fig. 1) as functions of log-transformed annual precipitation in eastern Asia (A–D) and North America (E–H). The R^2 in the figure represents the additional proportions of variance in species richness explained by annual precipitation after the effects of temperature are eliminated. To save space, we show plots at 4 spatial scales: 50×50 km (A and E), 100×100 km (B and F), 250×250 km (C and G), and 400×400 km (D and H).

Interestingly, the slopes of the species-area relationships at the same temperatures were consistently steeper in eastern Asia than in North America (Fig. 5G), revealing greater species turnover in eastern Asia. Moreover, the absolute diversity values differed between the 2 continents. Species richness was very similar at about 0°C ($1/kT = 42.5$; Fig. 5C), but in warmer climates it was higher in eastern Asia (Fig. 5D, E, and F), and in colder climates it was higher in North America (Fig. 5A and B). Plot-based data also support the finding of lower diversity in cold, high-latitude environments in eastern Asia compared with North America. As shown in Fig. 6, at latitudes greater than 42°N , plots of comparable area had higher species richness in North America than in eastern Asia. A recent comparison of regional floras between eastern Asia and North America confirms this finding, indicating that at high latitudes species diversity is similar in the 2 continents, but diversity of higher taxa (genera, families, and orders) is lower in eastern Asia than in North America (25). This finding challenges the conventional view that eastern Asia generally harbors more species than North America, regardless of environment and geographic region (e.g., 26, 27).

The fact that temperature and spatial scale had quantitatively different effects in eastern Asia and North America indicates that these are not the only processes shaping geographic patterns of tree species diversity on these continents. Eastern Asia has more than $4\times$ more tree species than North America ($\approx 3,100$ vs. ≈ 680). This is because species diversity increases more rapidly with both environmental temperature and spatial scale in eastern Asia, resulting in many more species in the warmer, lower-latitude regions of eastern Asia than North America. As suggested by previous authors (25–29), this difference is likely related to regional topography and historical factors. Eastern Asia is more mountainous than North America, especially

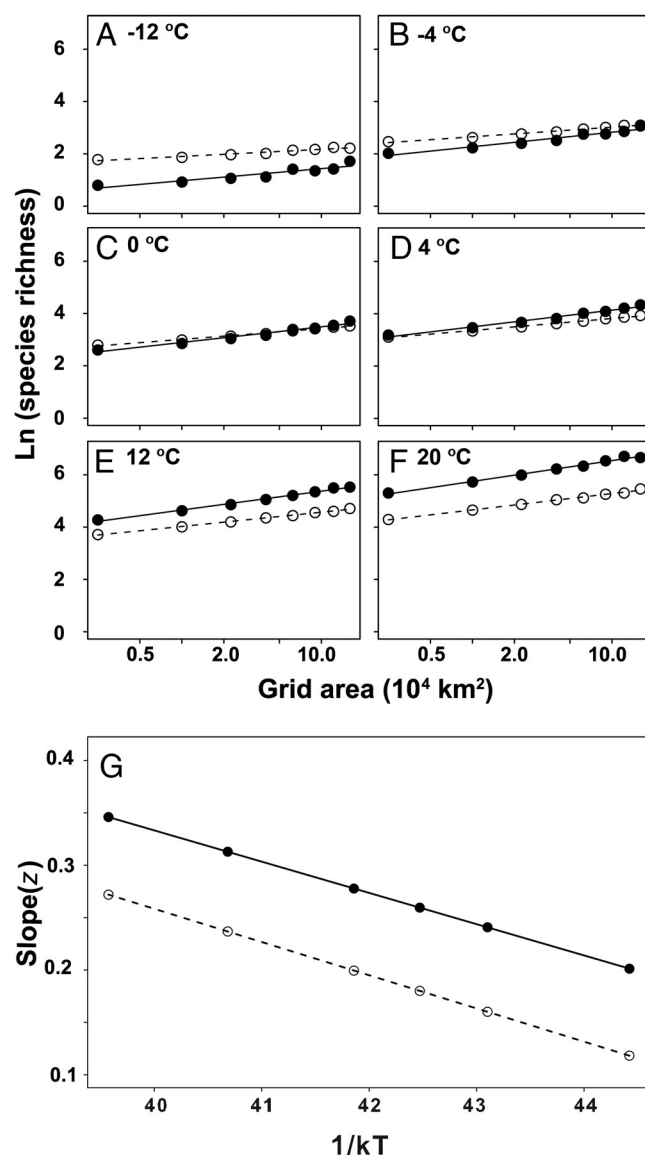


Fig. 5. Relationships between species richness, area, and temperature along a gradient of increasing average annual environmental temperature in eastern Asia and North America. (A–F) Species-area relationships, plotting average species richness as a function of sample area on logarithmic axes, for sample sites with different temperatures in eastern Asia (points and solid line) and North America (circles and dashed line); to save space, we show relationships for only 6 temperatures: -12°C , -4°C , 0°C , 4°C , 12°C , and 20°C . (G) Relationship between the slopes of species-area relationships (as shown in A–F) and environmental temperature in eastern Asia (points and solid line) and North America (circles and dashed line). For the derivation of the temperature dependence of z , see SI Appendix.

toward the south. The greater physiographic heterogeneity in eastern Asia provides more habitats harboring specialized species with restricted geographic ranges and consequently offers more opportunities for allopatric speciation (25, 29). Moreover, the geological and climatic history of eastern Asia may have allowed the tropical zones to serve both as a center of speciation and as a refuge during periods of global cooling (28, 29). By contrast, in eastern North America the Gulf of Mexico may have acted as a barrier to the tropics, somewhat similar to the hypothesized role of the Alps and Pyrenees Mountains in western Europe, where tree species diversity is even lower than in North America.

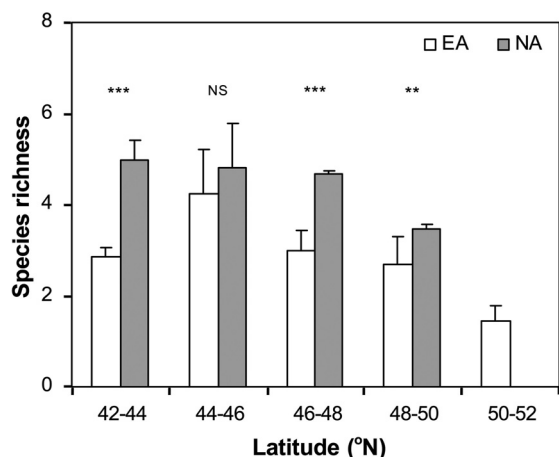


Fig. 6. Comparisons of species richness at high latitudes (>42°N) in eastern Asia (white bars) and North America (dark bars) using data of 1,370 forest plots in the 2 continents (398 plots for eastern Asia, see ref. 23; and 972 plots for North America, see <http://www.vegbank.org/>). Species richness of canopy trees (DBH > 10 cm) is compared using a *t* test in every latitudinal band of 2° (i.e., 42–44°N, 44–46°N, 46–48°N, and 48–50°N) from 42°N to 50°N. The result indicates that North America has significantly more tree species than eastern Asia at high latitudes. ****P* < 0.01; ***P* < 0.001; N.S., *P* > 0.05.

Our findings have important implications for the MTE. On the one hand, species richness is strongly temperature dependent, as seen in the Arrhenius plots. Over the geography of both eastern Asia and North America, tree species richness increases exponentially with increasing environmental temperature. On the other hand, the slopes of the Arrhenius plots were much more variable than predicted by the simple model of Allen et al. (10) and Brown et al. (9). Indeed, the systematic variation in the slopes (*E*-values) across spatial scales and on the different continents do not support the prediction that there is a single canonical value of *E* of approximately -0.7 , corresponding to an average activation energy of ≈ 0.7 eV for the biochemical reactions of aerobic respiration and overall metabolic rate. Because the model of Allen et al. (10) predicted such a canonical value based on assumptions about the form of the species abundance distribution and the scaling of total community abundance with temperature, our findings suggest that these assumptions and the resulting model may be incorrect. Both local species richness (alpha diversity) and spatial turnover in species composition (beta diversity) increase exponentially with environmental temperature.

Our findings and qualitatively similar findings from other studies (10, 30) document a pervasive influence of environmental temperature that underlies latitudinal, elevational, and other gradients of species diversity. There are at least 2 distinct mechanisms by which increasing temperature can generate and maintain higher species diversity (31). First, in terrestrial environments, higher environmental temperatures are often associated with higher rates of primary production, which can support more species because “a larger pie can be divided into more pieces” (31, 32). The relationship between species richness and precipitation is consistent with this mechanism, because lower water availability has been hypothesized to lead to reduced species diversity by decreasing productivity and increasing drought stress (1, 3, 33). Second, higher temperatures are associated with higher rates of metabolism, ecological interactions, and evolutionary processes, and these kinetics can generate and maintain higher diversity because “the Red Queen runs faster when she is hot” (9, 31). Much more theoretical and empirical work will be required to understand the separate and interacting effects of these 2 mechanisms. However, it appears

that the effect of productivity is usually modest and sublinear, as seen in the relatively constant values of Fisher’s α (1, 5) and in the consistent slopes ($z \approx 0.25$) of species-area for islands (e.g., 1, 34–36). By contrast, the kinetic effect is strong and exponential, as seen in effects of temperature on rates of metabolism (8), population growth (37), molecular evolution (38), and speciation (18, 39). Our findings documenting effects of both temperature (Fig. 1) and precipitation (Fig. 4) suggest that both mechanisms are operating, but the strong exponential temperature dependence is evidence that the kinetics of ecological and evolutionary processes play a major role.

In summary, our findings reveal the scale dependence of the temperature effects on biodiversity, putting together 2 relationships that have often been considered separately (19, 20). These relationships have more general implications. The effect of temperature on species-area relationships implies that metabolic rate affects the rates of ecological interactions over all spatial scales from local communities, to landscapes, to global geography. We speculate that these kinetic effects also operate over all temporal scales from the seconds to years of ecological processes, and millennia of evolutionary dynamics.

Materials and Methods

Data on Species Distribution and Environmental Temperature. We evaluated the separate and interacting effects of environmental temperature and spatial scale on species diversity using 2 extensive databases on tree distributions in eastern Asia and North America. Both continents have similar latitudes, comparable climatic gradients, and many of the same families and genera of trees (25–29), so they are ideal for such a comparative study. The databases used are the Database of China’s Woody Plants (for details, see <http://www.ecology.pku.edu.cn/plants/woody/index.asp>) for China and the *Atlas of North American Trees* (<http://esp.cr.usgs.gov/data/atlas/little/>) for North America. The former is the most comprehensive database for species distributions in China, documenting distributions of all 13,570 native woody plants, which were compiled based on all published country-level floras, including *China’s Flora* (125 volumes, a result of more than 450 well-qualified Chinese taxonomists over the past 50 years) (40) and *Higher Plants of China* (10 volumes) (41), all provincial floras (more than 120 volumes), and a great number of published local floras. To improve precision of the database, 26 experts (botanists, ecologists, and taxonomists) from different regions were invited to check the distribution for each species in each region. Therefore, the distribution ranges of woody species in China are accurate and credible. In the database, woody plants were categorized into 3 life forms: trees (3,065 species), shrubs (9,686 species), and woody lianas (819 species). In this study we used only the data for trees so that it would be comparable to the data for North America. The latter dataset maps the distribution of 679 North American trees, digitized from the maps of Critchfield and Little (42) and Little (43–46), which was widely accepted and used in previous studies about geographical patterns in tree species richness (3, 10, 13, 15). All of the distribution maps were compiled with equal area projection (Albers cubic equal area projection) in ArcGIS 9.2 (ESRI, Inc.).

Mean annual temperature (in degrees Celsius) and precipitation (in millimeters) for each grid was obtained from the world climate database with a resolution of 1×1 km (<http://www.worldclim.org/>).

Plot-Based Species Richness Data. To further explore the kinetic effects of environmental temperature on species diversity, and to compare the species richness at higher latitudes of the 2 continents, plot-based data were also used in our analyses. First, a dataset on species richness of 318 forest plots in the eastern part of China was used to examine the relationships between log-transformed tree species richness and reciprocal temperature ($1/kT$) in forests of the mountainous regions (Fig. 3), as forests are continuously distributed across eastern China from tropical rain forests in the south to boreal forests in the north. These plot-based data were extracted from a larger database, which was constructed by Peking University’s Survey Plan for Plant Species Diversity of China’s Mountains (PKU-PSD) and contains 1,302 forest plots collected across major mountains in China by the Department of Ecology of Peking University from 1997 to 2008 (23). The sampling size for each plot was 600 m^2 ($20 \times 30 \text{ m}$). In the database, the locations and physiographic attributes (i.e., the latitude, longitude, elevation, aspect, and slope) were documented for each plot in situ. In each plot, all trees, shrubs, and herb species were recorded, and the diameter at breast height (DBH) was measured for all trees

with DBH >3 cm. The mean annual temperature for each plot was estimated by linear regressions, using latitude, longitude, and elevation for each plot as predictors (for details, see ref. 23).

Second, to compare the plot-based species richness of trees at high latitudes in eastern Asia and North America (Fig. 6), we obtained 972 forest plots (400 m² for each in size) located at latitudes >42°N from the VegBank website (<http://www.vegbank.org/>) for North America, and extracted 398 forest plots with the similar latitudes from the PKU-PSD database in China. Considering that the plots of North America are 400 m² for each in size, and only trees with DBH >10 cm were measured in these plots, we truncated the plots in China to an area of 400 m² (originally 600 m²) for each according to the subplot (10 × 10 m for each) records, and only accounted the trees with DBH >10 cm (originally, trees with DBH >3 cm were measured). The comparisons were conducted between the 2 continents in each 2° latitudinal bands (i.e., 42–44°N, 44–46°N, 46–48°N, and 48–50°N) from 42°N to 50°N using a *t* test.

Effects of Spatial Scale. To quantify effect of spatial scale on relationships between species diversity and temperature, tree species richness was calculated for equal-area grids at 8 spatial resolutions ranging from 50 × 50 km, to 100 × 100 km, to 400 × 400 km for both continents. Because data quality limitations, only regions north of Mexico (i.e., United States and Canada) were included in the analysis for North America. For both continents, grids on islands, and along coasts/country borders where the land area was less than half of grid area, were excluded from the analysis to eliminate the area effect on species richness (1).

Models and Statistical Analysis. For each spatial scale, we performed ordinary least square (OLS) regressions (13, 15) to analyze the relationships between log-transformed species richness and reciprocal temperature (1/kT) using the following model:

$$\text{Log}(S) = C_0 \cdot E \cdot (1/kT), \quad [1]$$

where *S* is the number of tree species, *C*₀ is a normalization constant equivalent to the intercept, *T* is the absolute temperature (Kelvin), *k* is Boltzmann's constant (8.62×10^{-5} eV K⁻¹), and *E* is the slope (*E* has been related to the activation energy for metabolism).

Data of species richness usually have strong spatial autocorrelation, especially at small scales, which can inflate type I errors in statistical tests (13, 47). Therefore, in this paper we used the coefficient of determination, *R*², as a robust measure of goodness of fit rather than trying to estimate confidence intervals and *P* values.

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