

## The region effect on mesoscale plant species richness between eastern Asia and eastern North America

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The greater number of plant species in temperate eastern Asia compared to eastern North America has been ascribed to both local environment and regional characteristics, but the relative contributions of each have not been resolved. In this analysis, we related species richness of flowering plants in mesoscale floras ( $< 10^4$  km<sup>2</sup>) dominated by temperate forest vegetation to area, elevation, latitude, and several climate variables. When analyses were conducted separately within each region, area and, in eastern Asia, elevation, were the primary determinants of species richness. It appears that the number of species in mesic temperate floras within these regions is largely unrelated to the relatively narrow range of local climate factors associated with these floras. Analysis of covariance of the logarithm of species richness with the logarithm of area ( $b = 0.148$ ) and climate measurements as independent variables revealed a region effect, with species richness in eastern Asia exceeding that in eastern North America by 0.294 log<sub>10</sub> units, or a factor of 2.0. Similar regional differences in species richness were apparent in floras compiled from larger areas. Understanding differences in plant species richness between regions requires consideration of regional influences, whose effects should be tested in comparative analyses based on floristic surveys of ecologically characterized small areas.

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Broad-scale patterns in species richness have been related to variation in the capacity of environments to support coexisting species (local processes) as well as to variation between regions in the balance between proliferation and extinction of species (regional processes). The hypothesis that local processes, including competition and consumer-resource interactions, constrain local species richness has been supported by correlations between richness and climate or other environmental conditions (Wright 1983, Currie and Paquin 1987, Adams and Woodward 1989, Currie 1991, Huston 1993, O'Brien 1993, 1998, Francis and Currie 1998, 2003, O'Brien et al. 2000, Kleidon and Mooney 2000, Badgley and Fox 2000, Whittaker and Field 2000). Local processes are

responsible for assembly of local communities from the larger regional pool (Pärtel et al. 1996, Zobel 1997, Weiher et al. 1998). Differences in local species richness between regions with similar environments have been cited in support of the additional influence of regional factors, including aspects of geography, climate, and history that influence rates of species production and extinction (Orians and Paine 1983, Latham and Ricklefs 1993, Ricklefs and Latham 1993, Ricklefs et al. 1999, Qian and Ricklefs 2000). These hypotheses can be evaluated in a framework of analysis of covariance in which the statistical effect of region on local species richness is tested with environmental conditions included as covariates to account for differences within and

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between regions in local conditions. Specifically, region effects could be rejected if differences in species richness between regions paralleled differences in the local physical environment independently of regional differences in physiography and history.

The temperate floras of eastern Asia (EAS) and eastern North America (ENA) have figured prominently in an ongoing discussion concerning the relative contributions of local and regional factors (Latham and Ricklefs 1993, Francis and Currie 1998, 2003, Ricklefs et al. 1999, Qian and Ricklefs 2000, Whittaker and Field 2000). Much of this discussion has focused on analyses of the species richness of trees. In an early study, Currie and Paquin (1987) found that the number of tree species within  $2.5^\circ$  grid squares ( $2.5^\circ \times 5^\circ$  longitude north of  $50^\circ\text{N}$ ;  $0.5\text{--}1 \times 10^5 \text{ km}^2$ ) in North America was most strongly related to actual evapotranspiration (AET), a measure of habitat productivity (Rosenzweig 1968). Several other variables, including latitude, longitude, temperature, precipitation, insolation, elevation, and variation in these measures within latitude-longitude grid cells, made significant but less important contributions to variation in species richness. The relationship in North America also estimated tree species richness reasonably well in Europe (Currie and Pacquin 1987) and eastern Asia (Adams and Woodward 1989), lending support to the hypothesis that species richness is determined by local ecological conditions. These results have been supported by further analyses of species richness in trees (Currie 1991) and family richness in flowering plants (Francis and Currie 2003, but see Qian and Ricklefs 2004), as well as similar analyses of the diversity-climate correlation elsewhere (e.g., O'Brien 1998, O'Brien et al. 2000).

Latham and Ricklefs (1993) analyzed tree species richness in smaller sampling areas ("mesoscale,"  $10^1\text{--}10^4 \text{ km}^2$ ) based on local studies or floras for small regions. They found an additional region effect, even when AET was accounted for statistically, indicating that tree species richness in eastern Asia exceeded that of North America. In the present study, we consider the species richness of all angiosperm (flowering) plants in a sample of complete floras from mesoscale areas of 10 to  $10^4 \text{ km}^2$  in eastern Asia and eastern North America. These floras each comprise  $<0.1\%$  of the total area of each region. Our analysis extends previous work in that complete floras are considered (contrasted with tree floras [Latham and Ricklefs 1993] or EAS-ENA disjunct genera [Qian and Ricklefs 2000]), and both survey area and physical environment are included in the analysis to control for the effects of these factors on species richness.

## Materials and methods

We define eastern Asia to include the eastern temperate and warm temperate portion of China extending from

northeast to southwest, and Korea. Arid regions of western China (Xizang [Tibet], Qinghai, Xinjiang, Gansu, Ningxia, and inner Mongolia provinces or autonomous regions) were excluded. We also excluded the major islands of eastern Asia, such as Japan, Taiwan, and Hainan, to remove the effect of island endemics on plant species richness. Eastern North America includes the eastern half of the United States (east of the western boundaries of Minnesota, Iowa, Missouri, Arkansas, and Louisiana). Most of the areas within the two regions are located in warm temperate climate zones (Müller 1982, Domrös and Peng 1988, Fig. 1) and are forested (Wu 1980, Barbour and Billings 1999).

To document floristic data, we searched literature sources including journal articles, floras, checklists, monographs, and atlases pertinent to the floras of eastern Asia and eastern North America. In total, we assembled 124 regional floras (39 in eastern Asia and 85 in eastern North America) having areas  $<10^4 \text{ km}^2$ . The areas of the selected floras ranged from  $10 \text{ km}^2$  to  $3981 \text{ km}^2$  in eastern Asia and from  $10 \text{ km}^2$  to  $9333 \text{ km}^2$  in eastern North America. Because we limited the size of floras to  $<10^4 \text{ km}^2$ , the characteristic dimension of each flora was  $<100 \text{ km}$ , or about 1 degree of latitude. Thus, these floras were smaller, by one to four orders of

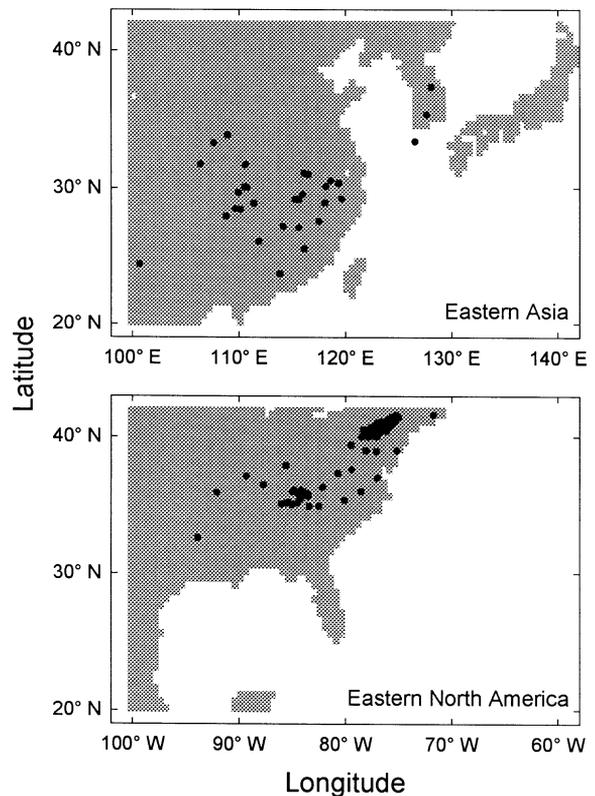


Fig. 1. Map showing the location of floras in eastern Asia and eastern North America.

magnitude, than the latitude-longitude blocks used by Currie (1991) and Francis and Currie (2003).

For each flora, we recorded the latitude ( $^{\circ}\text{N}$ ) of the geographic midpoint, area ( $\text{km}^2$ ), highest elevation (m), and the number of species of indigenous angiosperms. We also obtained several climate variables for the latitude-longitude half-degree grid point closest to the geographical midpoint of each flora using data in the International Institute of Applied System Analysis (IIASA) climatic database (Leemans and Cramer 1991). This database provides values for each 0.5 degrees of latitude and longitude interpolated from numerous climate stations worldwide. It has been widely used in ecological and biogeographic studies (e.g., Monserud et al. 1993, Tchebakova et al. 1993, Peng et al. 1995, Shao and Halpin 1995). The climate variables were January temperature ( $^{\circ}\text{C}$ ), July temperature ( $^{\circ}\text{C}$ ), May through August ("summer") precipitation (mm), and September through April ("winter") precipitation (mm). In addition, we included two derived climate indices: actual evapotranspiration (AET, mm) and potential evapotranspiration (PET, mm), which is proportional to the drying power of the environment, primarily a function of temperature. AET and PET were calculated following the approach developed by Cramer and Prentice (Cramer and Prentice 1988, Prentice et al. 1992, Prentice et al. 1993). Climate seasonality, which is correlated with species richness in studies covering a broader range of ecological conditions than ours (e.g., O'Brien 1993, 1998), is incorporated in this study by contrasting measures of precipitation and temperature at different seasons. Derived variables, such as the difference in temperature between January and July and the ratio of summer to winter precipitation, had no statistical effect beyond that of the original variables in our analyses and were not considered further.

Several floras were excluded because they were statistical outliers ( $> 3$  SD units [ $p < 0.001$ ] from the mean of the remaining floras) for one or more climate variables. Specifically, we excluded seven floras in eastern Asia with summer precipitation exceeding 1500 mm or  $< 200$  mm, winter precipitation  $< 200$  mm, or January temperature  $< -10^{\circ}\text{C}$ . We also excluded three floras in eastern North America with summer precipitation exceeding 600 mm. As a result of excluding these floras, the data conformed more closely to the normality assumptions of parametric statistics and the range of environmental conditions matched more closely between the regions. Number of species and area were  $\log_{10}$ -transformed to normalize the distributions of the data and to achieve a linear relationship between the two variables. Summer and winter precipitation were also  $\log_{10}$ -transformed to normalize their distributions. After trimming the dataset and transforming variables, none of the variables had skewness exceeding an absolute value of 1.3; all absolute values for kurtosis were  $< 2.0$

and most were  $< 1.0$ . The final data set included 32 floras in eastern Asia and 82 floras in eastern North America, for a total of 114 floras (Fig. 1).

Analyses of species richness of floras within regions included (i) simple correlations of species richness with each independent variable, (ii) stepwise regressions to identify independent variables making the strongest statistical contributions to variation in species richness within each region, and (iii) analysis of covariance to explore differences in species richness between eastern Asia and eastern North America, with continent as a main effect and the independent variables as covariates.

All statistical analyses were carried out using procedures in the Statistical Analysis System (SAS) version 6.12 software (Anon. 1990): correlations (Proc CORR); stepwise regressions (Proc STEPWISE with forward selection); analysis of covariance (ANCOVA, Proc GLM) testing differences between regions when species richness was related to the independent covariates area, latitude, elevation, and climate variables (Legendre and Legendre 1998). Details of these analyses are presented in the Results section.

## Results

### Descriptive statistics

Variables are compared between regions in Table 1. Average angiosperm species richness in floras in eastern Asia exceeded that in eastern North America by 0.20  $\log_{10}$  units, or a factor of 1.58. On average, floras were obtained from larger areas in eastern North America than in eastern Asia (3.09 vs 2.26, a difference of 0.83  $\log_{10}$  units, or a factor of 6.8) (Fig. 2). In addition, maximum elevations were higher in eastern Asia ( $1742 \pm 636$  m) than in eastern North America ( $783 \pm 459$  m). The Asian sites were distributed over a wider and, on average, more southerly latitudinal range, owing to the extension of temperate vegetation far to the south at higher elevations in China. Thus, the most southerly Asian sites were 8.9 degrees further south ( $23.7^{\circ}\text{N}$ ) than the most southerly North American sites ( $32.6^{\circ}\text{N}$ ). Differences in climate between the two regions derive in part from the monsoon weather system of eastern Asia, which results in higher summer (May–Aug) precipitation (714 vs 383 mm) but similar winter (Sep–Apr) precipitation (635 vs 660 mm) in eastern Asia. The ranges of PET and AET were similar in the two regions. Our samples did not include semiarid, typically non-forested areas.

### Relationship of species richness to environmental variables within regions

When variables were tested individually, only area was strongly correlated with species richness in eastern North

Table 1. Descriptive statistics for angiosperm species richness and site characteristics for floras in temperate eastern Asia and temperate eastern North America.

Variable	Eastern Asia (n = 32)					Eastern North America (n = 82)					ANOVA	
	Mean	SD	Min	Max		Mean	SD	Min	Max	F <sub>1,112</sub>	p	R <sup>2</sup>
Angiosperm species richness (log <sub>10</sub> )	3.11	0.13	2.74	3.41		2.91	0.13	2.61	3.21	52.6	< 0.0001	0.320
Latitude (°N)	29.72	2.94	23.68	37.33		38.84	2.44	32.58	41.60	286.0	< 0.0001	0.719
Elevation (m)	1742	636	964	3306		783	459	27	2025	80.2	< 0.0001	0.417
Area (log <sub>10</sub> km <sup>2</sup> )	2.26	0.65	1	3.60		3.09	0.67	1	3.97	35.1	< 0.0001	0.239
January temperature (°C)	2.75	4.13	-7.5	12.3		0.64	3.06	-4.4	8.0	8.9	0.0036	0.073
July temperature (°C)	24.18	3.42	17.0	31.6		23.62	1.68	19.9	28.6	1.34	0.25	0.012
Precipitation in May–August (mm)	714.3	182.6	330	1087		383.3	33.1	327	499	310.7	< 0.0001	0.735
Precipitation in September–April (mm)	634.7	168.7	312	926		660.1	93.2	567	929	3.06	0.083	0.027
Annual actual evapotranspiration (mm)	908.9	105.3	642	1094		880.0	71.3	773	1044	2.86	0.094	0.025
Annual potential evapotranspiration (mm)	925.2	97.4	723	1107		930.4	93.4	784	1153	0.07	0.79	0.001

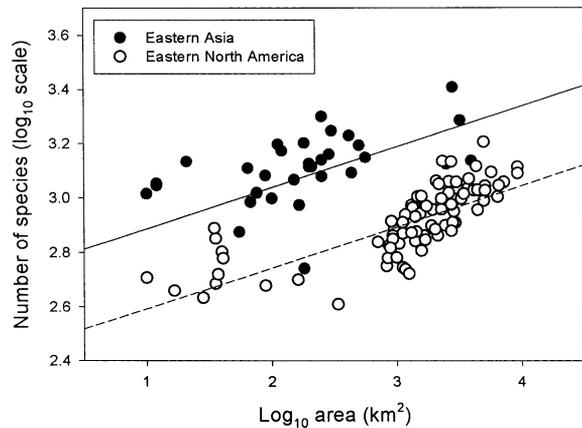


Fig. 2. The relationship between the logarithm of angiosperm species richness (vertical axis) in floras in eastern Asia (solid symbols) and eastern North America (open symbols) and the logarithm of flora area. Regression lines are from the analysis of covariance in Table 3.

America (log-transformed variables,  $r = 0.75$ ,  $p < 0.0001$ ). Species richness was positively related to elevation ( $r = 0.30$ ,  $p < 0.05$ ) and negatively related ( $p < 0.05$ ) to summer temperature ( $r = -0.18$ ), summer precipitation ( $-0.32$ ), and annual evapotranspiration ( $-0.25$ ). In eastern Asia, area ( $r = 0.49$ ) and elevation ( $r = 0.56$ ) were significantly correlated with species richness. No climate variables had significant simple correlations with species richness in Asia.

Stepwise multiple regressions incorporate correlations among the independent variables in their influence on species richness. Stepwise regressions accounted for 56% of the variation in species richness in eastern Asia and 65% in eastern North America. The analyses provided support for the association of species richness with elevation and January temperature in eastern Asia, and with area, January temperature, and summer precipitation (weak and negative) in eastern North America (Table 2).

### The region effect on species richness

To assess the effect of region on species richness, we included region as a main effect in an analysis of covariance. Because of its strong correlation with climate variables, latitude was excluded from the analysis. Flora area and January temperature were the only variables making significant unique contributions to species richness (Table 3). When the analysis was restricted to these covariates, the logarithmic slope of species richness with respect to area was  $0.148 \pm 0.013$ , and species richness increased by 2.4% for each 1°C increase in January temperature. Region had a strong effect on species richness, with values in eastern Asia exceeding those in eastern North America by a factor of almost 2.0 (Table 3 and Fig. 2).

Table 2. Analysis of variance of the log-transformed species richness of flowering plants with respect to area, latitude, elevation, and climate variables. Models were reduced by stepwise regression to exclude non-significant variables.

Model	Eastern Asia (n = 32)				Eastern North America (n = 82)			
	F <sub>2,29</sub> = 18.6, p < 0.0001, R <sup>2</sup> = 0.562				F <sub>3,78</sub> = 47.8, p < 0.0001, R <sup>2</sup> = 0.648			
	F	p	Estimate	SE	F	p	Estimate	SE
Log <sub>10</sub> area								
Elevation (km)	31.1	0.0001	0.142	0.025	120.5	0.0001	0.164	0.015
January temperature (°C)	16.2	0.0004	0.0157	0.0039	18.9	0.0001	0.014	0.003
Summer precipitation (mm)					4.5	0.0378	-0.575	0.272

Note: Estimated slope for elevation in meters was multiplied by 1000.

To examine the possibility that region effects may differ among floras having different area, we also analyzed data for seven floras in eastern Asia and 34 floras in eastern North America having areas between 10<sup>4</sup> and 10<sup>5</sup> km<sup>2</sup>, that is, similar to the areas considered by Currie and his colleagues (0.5–1.0 × 10<sup>5</sup> km<sup>2</sup>). Species richness in these areas in eastern Asia exceeded that in eastern North America by 0.30 log<sub>10</sub> units, or a factor of 2.0. When these floras were subjected to an analysis of covariance, the effect of region was significant (F<sub>1,37</sub> = 23.9, p < 0.0001), with species richness in eastern Asia exceeding that in eastern North America by 0.245 ± 0.050, a factor of 1.76. The logarithmic regression of species richness on area had a slope of 0.174 ± 0.056.

Among floras having areas between 10<sup>5</sup> and 10<sup>6</sup> km<sup>2</sup> (EAS n = 50, ENA n = 70), the slope of the species-area relationship increased to 0.299 ± 0.028. The more than two-fold excess of species richness in these large floras in eastern Asia was reduced when area, elevation, and January temperature were included as covariates, to a difference of 0.119 ± 0.019 log<sub>10</sub> units, or a factor of 1.32 (F<sub>1,115</sub> = 40.2, p < 0.0001).

## Discussion

Our analyses indicated that the roughly six-fold range of variation in angiosperm species richness in forested areas

of both eastern Asia and eastern North America is, in part, related to climate variables, with winter (January) temperature having the greatest effect, and that species richness in eastern Asia exceeds that in eastern North America by a factor of almost two when the influences of area and climate are taken into account. These results for mesoscale (< 10<sup>4</sup> km<sup>2</sup>) floras extend the conclusions of Currie and Paquin (1987), Currie (1991), Whittaker and Field (2000), and Francis and Currie (2003) that climate exerts a dominating influence on species richness on a global scale. Our analyses do not reject the existence of a region effect on species richness that is independent of differences between regions in local climate conditions.

The analyses of Currie and Paquin (1987), Currie (1991), and Francis and Currie (2003) applied to larger sampling areas and extended over the whole of North America, including areas with scant precipitation in the western part of the continent. The lower limit of AET in those studies was about 100 mm – too little to support forested habitats – compared to 642 mm in eastern Asia and over 773 mm in eastern North America in this study. The extended range of climate variation including areas with low plant species richness undoubtedly increased the statistical correlation between species richness and climate, reducing the relative importance of the region effect. It also appears that the difference in species richness between regions diminishes at larger

Table 3. Analyses of covariance of the common logarithm of species richness with region as an effect.

Effect	F	p	Type III SS <sup>a</sup>	b <sup>b</sup>	SE <sub>b</sub>
All covariates included: F <sub>9,104</sub> = 27.3, p < 0.0001, R <sup>2</sup> = 0.702, SS = 2.729					
Log <sub>10</sub> area	75.9	< 0.0001	0.592	0.131 <sup>c</sup>	0.015
January temperature	8.1	0.0055	0.063	0.017 <sup>d</sup>	0.006
Region	19.8	< 0.0001	0.154	0.274 <sup>e</sup>	0.062
Remaining variables	< 2.2	> 0.05	1.108		
Error			0.812		
Only significant covariates included: F <sub>3,110</sub> = 77.6, p < 0.0001, R <sup>2</sup> = 0.679, SS = 2.729					
Log <sub>10</sub> area	122.9	< 0.0001	0.979	0.148 <sup>c</sup>	0.013
January temperature	15.4	0.0002	0.122	0.010 <sup>d</sup>	0.003
Region	189.1	< 0.0001	1.505	0.294 <sup>e</sup>	0.021
Error			0.876		

<sup>a</sup>SS = sums of squares. <sup>b</sup>Slope of the regression equation, followed by the standard error of the slope. <sup>c</sup>Logarithmic regression slope.

<sup>d</sup>Units are log<sub>10</sub> units per °C. <sup>e</sup>Log<sub>10</sub> units by which eastern Asia exceeds eastern North America.

(> 10<sup>5</sup> km<sup>2</sup>) sampling areas. Without a better understanding of how species richness is related to environmental heterogeneity, and how the scale of environmental heterogeneity differs between the regions, it is difficult to interpret differences between the results for larger and smaller areas.

### The effect of region on species richness

The angiosperm flora of the southern part of North America north of Mexico (an area including almost the entire contiguous USA with 7.4 million km<sup>2</sup>) has about 14 240 native species of angiosperms while an area of the same size and latitude range in eastern Asia has about 20 000 native species of angiosperms, a factorial difference of about 1.4 (Qian 2002). The continental-scale difference in species richness between eastern Asia and North America is greater in older groups of plants with strong tropical affinities, and it is reduced or even reversed in more recent groups with temperate centers of species richness (Qian and Ricklefs 1999). Moreover, the difference in species richness is more pronounced in taxa restricted to primarily forested habitats in eastern North America, while some taxa distributed in the physiographically more heterogeneous west are more diverse than their Asian relatives (Qian and Ricklefs 2000).

In this study, we found that the average species richness of angiosperms in floras ranging from 10<sup>1</sup> to nearly 10<sup>4</sup> km<sup>2</sup> in area is greater in temperate eastern Asia than in temperate eastern North America. This region effect appears to be maintained, albeit less strongly, in larger floras closer to the size of the latitude-longitude blocks in the analyses by Currie and his collaborators (0.5–1.0 × 10<sup>5</sup> km<sup>2</sup>), although climate covariates for a single point might represent climate data less well within the larger areas. Data for smaller areas in eastern Asia are largely lacking. Latham and Ricklefs (1993) found that tree species richness on ca 1-ha plots (10<sup>-2</sup> km<sup>2</sup>) was higher in Japan than in eastern North America, but such comparisons are not yet available more broadly.

Lacking information on environmental heterogeneity within flora areas, we cannot comment on the contribution of heterogeneity to the difference in species richness between eastern Asia and eastern North America. Maximum elevations are greater in eastern Asia, which suggests greater topographic heterogeneity. However, when maximum elevation was included in an analysis of covariance among mesoscale floras, the difference in species richness between the two regions persisted. If the regions did not differ in environmental heterogeneity, the greater species richness of small floras in eastern Asia would result from greater plant species richness within habitats at a local scale. This is supported by tree species

richness in small plots in Japan, as mentioned above, but data for the richer floras of temperate China are lacking.

This study has addressed the relative contributions of local conditions and region effects to local species richness of angiosperm plants. Differences in environment between the regions, including a greater range of elevations within floras and a monsoon pattern of precipitation in eastern Asia, and the lack of floristic data from small, ecologically defined areas, has made this task difficult. We have no doubts that our analysis will be modified as sampling improves and more data become available, but we believe that the difference in species richness between eastern Asia and eastern North America found in this study will remain. Whether the region effect reflects unmeasured environmental differences between eastern Asia and eastern North America cannot be resolved at this point. Ecological conditions within mesoscale areas can be characterized only crudely at present. For example, data are lacking on soils, whose variation can have a strong effect on plant diversity (e.g. Huston 1993). The environmental variables used in most studies, including ours, are average or representative conditions within the area of each flora and do not reflect the heterogeneity of these variables. Nor do most studies include information about the distribution of species within flora areas that would show how mesoscale species richness is constituted from local species richness within habitats and turnover of species between habitats within floras. A complete resolution of patterns of species richness between eastern Asia and eastern North America will require planned comparisons among carefully matched, environmentally characterized plots of 1–10 ha, nested within larger sample areas, to assess both local species richness and turnover of species along the same ecological gradients of conditions.

Finally, the role of history and physiographic heterogeneity within regions in generating and maintaining the regional species pool must be taken into account (Qian and Ricklefs 2000). The difference in species richness in local floras between eastern Asia and eastern North America might have resulted from some combination of regional factors, including a higher rate of invasion of plant lineages in Asia from more tropical regions to the south, a higher rate of production of new species within temperate forest regions of eastern Asia (Qian and Ricklefs 2000), and less extinction in eastern Asia due to late Tertiary climate cooling and glaciation. Addressing these issues will require new data.

Many elements of the temperate flora of eastern Asia have close relatives in the tropics (Latham and Ricklefs 1993), where angiosperm plants are thought by many authors (e.g., Takhtajan 1969, Wu 1980, Lidgard and Crane 1990) to have originated and diversified. The invasion of comparatively harsh temperate environments, particularly the requirements of frost tolerance and a long dormancy period, may depend upon physio-

logical adaptation that slows the invasion of temperate regions by tropical lineages (Farrell et al. 1992, Latham and Ricklefs 1993). If this were the case, transitions between tropical and temperate latitudes might have occurred more frequently in eastern Asia than in eastern North America, where there is no direct connection between tropical and temperate floras and where temperate floras harbor fewer lineages with close affinities to the tropics (Latham and Ricklefs 1993). The latitudinal range of temperate habitats in eastern Asia also exceeds that in eastern North America, primarily because mesic temperate regions in North America are bounded by the Gulf of Mexico to the south. North America also lacks high mountains in southern latitudes comparable to the Himalayas and other ranges of southern China. The mountains of southern China are an area of extremely high plant species richness (Barthlott et al. 1996). Furthermore, cooling climates of the late Tertiary and glacial climates of the Pleistocene may have had less influence on the floras of eastern Asia, in spite of the fact that tundra environments moved southward to 43–44° N (northeastern China) during glacial maxima. Until comparative studies include hypotheses incorporating regional as well as local influences on species richness, it is unlikely that such studies will be able to unravel the relationships between species richness, environment, and history.

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