

EFFECTS OF REGIONAL VS. ECOLOGICAL FACTORS ON PLANT SPECIES RICHNESS: AN INTERCONTINENTAL ANALYSIS

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Abstract. Conclusions from past studies on the roles that historical and regional factors and contemporary and ecological factors have played in regulating large-scale patterns of species richness have been controversial. Conflicting past results were likely affected by differences in the range of environments analyzed and the scales of observation. Eastern North America and eastern Asia are ideal regions for examining the relative effects of historical and regional factors and contemporary and ecological factors on large-scale patterns of plant species richness because these two regions are closely matched in terms of climate and because their floras originated from the same paleoflora but have experienced different histories of development since the late Paleogene when climate cooling caused their separation. We report on a comprehensive data set of 471 floras ranging from 10 km² to 4.7 × 10⁶ km² and spanning a wide range of climate and latitude (from 21° to 55° N) to examine whether the contribution of region relative to climate persists from small to large floras and increases from cooler to warmer climates. We found that eastern Asia is richer than eastern North America when sample area, maximum elevation, and climate are accounted for, that this difference diminishes toward higher latitudes, and that elevation plays a much stronger role in eastern Asia than in eastern North America. Our analysis reconciles contemporary/ecological and historical/regional explanations for species richness variation and helps explain why different conclusions have been reached by different authors working in the same geographical areas: the strength of the region effect itself varies with location and range of climatic conditions of the observations.

Key words: biodiversity; climate effect; eastern Asia; eastern North America; flowering plants; historical contingency; region effect; species richness.

INTRODUCTION

Global patterns of biodiversity can be regulated by both contemporary and ecological factors and historical and regional factors (Davis and Scholtz 2001, Willis and Whittaker 2002, Hawkins et al. 2003a, Qian and Ricklefs 2004b, Ricklefs 2004, 2006, Herzog and Kessler 2006). Contemporary and ecological factors include environmental variables such as temperature, precipitation, actual evapotranspiration, potential evapotranspiration, productivity, and habitat heterogeneity (Currie and Paquin 1987, Ricklefs et al. 1999, Hawkins et al. 2003a, Qian and Ricklefs 2004a). Historical and regional factors are those that acted during the past within regions and that might be unique to a region or may occur in multiple regions but with differential effects. Historical and regional factors and processes include continental drift, geologic uplift, glaciations, speciation, extinction, migration, origin of phylogenetic lineages, and evolution of physiological tolerance to stressful environments. Although many ecologists now accept

that both contemporary/ecological and historical/regional factors influence large-scale species richness patterns, the relative influences of these two broad types of factors are often difficult to assess. Differences in data type (range maps vs. on-the-ground inventories), the range of environmental conditions considered (tropical, temperate, boreal, etc.), and spatial scale (especially sample area) have led to quite different and often controversial conclusions. Thus some authors (e.g., Francis and Currie 1998, 2003) maintain that current global patterns of species diversity are determined by contemporary environmental factors, such as available energy, while others have argued that differences in biogeographic history are more important than contemporary environment (Latham and Ricklefs 1993, Ricklefs and Latham 1993).

Eastern Asia and eastern North America are ideal regions for examining the relative roles that contemporary/ecological and historical/regional factors have played in regulating large-scale patterns of plant species richness for several reasons. First, eastern Asia and eastern North America have a similar range of climatic conditions (Müller 1982) and similar forest vegetation in terms of generic composition and community structure (Wu 1980, Miyawaki et al. 1994). Second, paleontolog-

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ical evidence suggests that the floras of eastern Asia and eastern North America were derived from the same boreotropical flora of the Paleogene, which was continuously distributed across the northern continents including arctic areas (Wolfe 1975, Tiffney 1985). The two continental regions were separated when climates cooled in the Neogene, forcing temperate-climate plants southward. These two continental regions have a close floristic relationship: many Paleogene relicts are disjunctly distributed in the two regions (Gray 1846, Li 1952, Qian 2002*b*), reflecting historical and evolutionary links between their floras. Since the separation, each region has experienced a unique history in floristic development. For example, North America was influenced more by Pleistocene glaciations than eastern Asia (Pielou 1992), suggesting that more species went extinct in North America than in eastern Asia. In contrast, a greater degree of topographical heterogeneity in the southwestern part of eastern Asia, resulting primarily from the collision of the Indian subcontinent with the Asian continent, presumably provides more opportunities for allopatric speciation in this region (Qian and Ricklefs 2000).

In this paper, we analyze a comprehensive data set that allow us to compare angiosperm species richness among regions at a wide range of scales (10 km^2 to $1 \times 10^6 \text{ km}^2$) and across extensive variation in climatic conditions (warm temperate to boreal) and to differentiate the relative roles that contemporary climates and historical and regional factors have played in regulating species richness patterns. We address the following questions: Does eastern Asia have higher species richness than North America after accounting for variations in sample area and climate? What are the relative contributions of region (i.e., eastern Asia vs. eastern North America in this study) and contemporary climate to the variance in species richness? Do the relative contributions of region and climate on species richness themselves vary with latitude, or does region effect decrease toward northern latitudes and cooler climates because floras of northern latitudes have a more similar recent history than those in southern latitudes? Does elevation play a stronger role in influencing species richness in eastern Asia than in eastern North America (as suggested by Qian 2002*a*)? Though previous studies have compared plant species richness patterns in these two continental regions (e.g., Latham and Ricklefs 1993, Ricklefs et al. 2004), these studies focus on a relatively small group of species or a single scale or a small range of scales, and none of them have attempted to differentiate the relative roles of climate and region on species richness patterns. Our analysis helps explain why different conclusions can be reached by different authors working in the same geographical areas. As we will show, the region effect itself varies depending on the location and range of climatic conditions of the observations.

MATERIALS AND METHODS

In this study, we define eastern Asia (EAS) to include the eastern temperate-warm temperate portion of China extending from northeast to southwest, plus the southernmost part of the Russian Far East and Korea (Appendix A). We excluded the major islands of eastern Asia such as Japan, Taiwan, and Hainan to remove the effect of island endemism that is high in EAS and nearly absent in eastern North America (ENA). Eastern North America includes the eastern half of the United States (east of Minnesota, Iowa, Missouri, Arkansas, and Louisiana), and southeastern Canada, particularly southern Ontario, Quebec, and the Maritime Provinces (Appendix A). Most of eastern Asian and eastern North American disjunct genera of vascular plants are widely distributed within and restricted to these two continental regions (Li 1952, Hong 1993, Qian and Ricklefs 2004*a*). Most of the two regions are located in warm temperate climate zones (Müller 1982, Domrös and Peng 1988).

To document floristic data, we searched a large body of the literature including journal articles, floras, checklists, monographs, and atlases pertinent to the floras of the two continental regions. We only selected those floras whose species checklists were considered complete or nearly complete. Large floras (usually including two or more provinces in China or states in the United States) were generated from several continental and national plant databases such as Kartesz (1999) and Wu and Ding (1999). In total, 471 floras (247 for EAS and 224 for ENA) were assembled. These floras are located in a wide range of latitudes from 21° to 55° N (Appendix A). The vast majority of these floras were intensively surveyed by previous researchers. Because the comparison of how species richness increases with increasing sample area between the two continental regions is part of the objective of this study, the floras that we assembled cover a wide range of spatial scales (ranging from 10 km^2 to $4.3 \times 10^6 \text{ km}^2$ in EAS and 10 km^2 to $4.7 \times 10^6 \text{ km}^2$ in ENA). A comparable range of variations in sample area is used in previous studies with a similar research objective. For example, Latham and Ricklefs (1993), Fraser and Currie (1996), and Herzog and Kessler (2006) all aimed at examining contemporary and ecological vs. historical and regional effects on species richness patterns, and sample areas varied by six orders of magnitude in the first two studies and by five orders of magnitude in the other study. Because the assembled floras covered such a wide range of scales, some floras overlapped with others to some extent. Using overlapping sample sites is common in ecological studies, particularly in those examining the species–area relationships (e.g., Fridley et al. 2005, Stark et al. 2006).

For each flora, we recorded area and the number of species of indigenous angiosperms. We also recorded mean annual temperature (in degrees Celsius), mean coldest month (January) temperature (in degrees Celsius), difference between mean January temperature and mean July temperature (in degrees Celsius), annual

precipitation (in millimeters), summer (May through August) precipitation (in millimeters), actual evapotranspiration (in millimeters per year), potential evapotranspiration (in millimeters per year), and maximum elevation (in meters) for each flora. Climate data were extracted from the International Institute of Applied System Analysis (IIASA) climatic database (Leemans and Cramer 1991), and actual evapotranspiration and potential evapotranspiration were calculated following the approach developed by Cramer and Prentice (Cramer and Prentice 1988, Prentice et al. 1992, 1993).

Following previous authors (e.g., Latham and Ricklefs 1993, Fraser and Currie 1996, Francis and Currie 1998, Ricklefs et al. 1999), contemporary and ecological conditions were characterized by climatic variables and the effect of historical and regional processes on species richness patterns was determined by assessing the significance of a variable representing region in a statistic analysis. Climatic variables were recorded for the geographical midpoint of each flora. By using climate data from the midpoint of a flora, we assume that it represents the mean climate conditions of the flora. Using climate data from a single point to represent the mean climate condition of a meso-scale flora or fauna is common in large-scale species richness analyses (e.g., Currie and Paquin 1987, Francis and Currie 2003, Ricklefs et al. 2004). A large flora may include a wide range of climatic conditions. Therefore, we conducted an analysis to examine the correlation between the climate condition of a flora based on the midpoint of the flora with the climate condition of the flora documented based on five sites within the flora (one located at its center and the other four located in the cardinal directions approximately two-thirds of the distance from the center to the periphery of the flora area). We carried this out for all the climate variables in 43 large floras (18 for EAS, 25 for ENA). Because the two types of data are strongly correlated ($r = 0.96 \pm 0.05$, $P < 0.001$), we believe that the climate condition at the midpoint of a flora well represents the mean climate condition of the flora. Furthermore, because climate conditions of floras in both regions are characterized in the same way, there should be no systematic bias with regard to continent. Because of collinearity and redundancy between some climatic variables, we used mean annual temperature (MAT), summer precipitation (SRAIN), and actual evapotranspiration (AET) in the final analyses. Mean annual temperature is a measure of ambient energy (Rahbek and Graves 2001); SRAIN is the most important amount of annual precipitation to plant growth and can well account for plant species diversity in northern latitudes (O'Brien 1998, Field et al. 2005); and AET is a measure of energy–water balance closely associated with plant productivity (Rosenzweig 1968, Hawkins et al. 2003a). These variables are considered the most important climatic variables influencing broad-scale species richness patterns and thus were frequently used in previous studies examining

species diversity–contemporary environment relationships (e.g., Currie and Paquin 1987, O'Brien 1998, Qian 1998, Rahbek and Graves 2001, Francis and Currie 2003, Qian and Ricklefs 2004b, Ricklefs et al. 2004). In some analyses, we used mutually unrelated forms of the three climate variables derived from a principal component analysis (PCA) to remove collinearity among the three climate variables.

Elevation range (i.e., maximum minus minimum elevation) has been frequently used as a measure of habitat heterogeneity of a site (e.g., Currie 1991, Kerr and Packer 1997, Rahbek and Graves 2001). Because maximum elevation is strongly correlated with the diversity of habitat types (Ricklefs and Bermingham 2004), it has also been used as a measure of habitat heterogeneity of a site (e.g., Ricklefs and Bermingham 2004, Ricklefs et al. 2004, Davies et al. 2005). However, both elevation range and maximum elevation tend to underestimate the true habitat and topographic heterogeneity at broader spatial scales. Although elevation range was more often used than maximum elevation in previous studies, we didn't use elevation range in the present study because data on elevation range for many floras that we used are not available. However, we compared two regressions using 131 floras from EAS, one using $\log(\text{richness})$ regressed on $\log(\text{area})$, maximum elevation, MAT, SRAIN, and AET and the other using $\log(\text{richness})$ regressed on $\log(\text{area})$, elevation range, MAT, SRAIN, and AET. We found that the two regressions explained almost the same amount of the variance in $\log(\text{richness})$ (regression with maximum elevation, $R^2 = 0.79$, standard error of estimate [SEE] = 0.12, $F_{5,125} = 94$; regression with elevation range, $R^2 = 0.80$, SEE = 0.12, $F_{5,125} = 102$), suggesting that elevation range and maximum elevation can be used interchangeably.

We used SYSTAT version 7 (Wilkinson et al. 1992) for stepwise regressions, multiple regressions, and analysis of covariance (ANCOVA) and used PC-ORD version 4 (McCune and Mefford 1999) for PCA. We used ANCOVA to explore differences in species richness between EAS and ENA, with region as main effect and area, elevation, and the three climate variables as covariates. We also used multiple regression analyses to determine region (EAS vs. ENA) effect on species richness with area, elevation, the climatic variables, and region (as a dummy variable, 0 for EAS and 1 for ENA) as independent variables. We regressed $\log(\text{richness})$ on different combinations of the six independent variables to evaluate multiple independent variables based on information theory (Burnham and Anderson 2002). In each regression, we included both $\log(\text{area})$ and elevation, and at least two of the three climate variables. Akaike Information Criterion (AIC), which is considered as one of the most appropriate model selection criteria in many statistical and ecological publications (e.g., Sakamoto et al. 1986, Burnham and Anderson 2002, Triantis et al. 2003), was used to select the best-fit

TABLE 1. Analysis of covariance of log₁₀-transformed angiosperm species richness with region as main effect and log₁₀(area), elevation, and climate variables as covariates (model: *n* = 471, *R*² = 0.897).

Source	SS	df	<i>F</i>	<i>P</i>
Region	0.633	1	47.8	<1 × 10 ⁻⁹
log ₁₀ (area)	18.653	1	1409.6	<1 × 10 ⁻⁹
Elevation	2.718	1	205.4	<1 × 10 ⁻⁹
MAT	0.788	1	59.6	<1 × 10 ⁻⁹
AET	0.585	1	44.2	<1 × 10 ⁻⁹
SRAIN	0.532	1	40.2	<1 × 10 ⁻⁹
Error	6.140	464		

Note: Key to abbreviations: MAT, mean annual temperature; AET, actual evapotranspiration; SRAIN, summer precipitation.

model by comparing AIC values of different models using ΔAIC, which is the difference between AIC of each model and the minimum AIC found. The AIC is defined as -2 ln(*L*) + 2*p*, where *L* is the maximum likelihood of the model and *p* is the number of free parameters of the model. The model with the lowest AIC is considered to be the best (Burnham and Anderson 2002). A value higher than 10 indicates that a model is a poor fit relative to the best model (Olalla-Tárraga et al. 2006). We used a partial regression (Legendre and Legendre 1998) to partition the variance explained by climatic variables and that explained by region. In the partial regression, we obtained three coefficients of determination using three general linear models: one combining both climate and region, one including only climate, and the other including only region. By comparing the three coefficients of determination, unique effects of climate and region and the overlap between them can be determined (Legendre and Legendre 1998).

Due to spatial nonindependence among some samples, which occur in nearly all large-scale analyses of species richness patterns, the number of degrees of freedom in significance tests such as those with regression analyses will be overestimated. To remedy this problem, we compared probabilities of a model with probabilities calculated based on a very small number of samples used to parameterize the model (Zar 1984). This approach of reducing the number of degrees of freedom has been used in previous studies (e.g., Francis and Currie 2003, Hurlbert 2004) to account for the effect of nonindependence among sample sites in a statistical analysis. We found that all of the models parameterized in this study remained significant at *P* < 0.05 even if <5% of the floras included in each model were statistically independent. Even so, we present raw sample sizes, *F* ratios, and coefficients of determination for ANCOVAs and regression analyses should researchers wish to perform tests using their own criteria to determine the degree of freedom. In all the analyses, sample area and species richness were log₁₀-transformed to normalize residual distributions and to achieve

linearity (particularly between species richness and sample area).

RESULTS

The number of native angiosperm species in the study floras ranged from 256 to 23 660 in EAS and 407 to 8035 in ENA. When log(richness) was compared between the two continental regions in an analysis of covariance with region (EAS vs. ENA) as the main effect and log(area), elevation, MAT, SRAIN, and AET as covariates, region had an effect on species richness (Table 1). Log(richness) in EAS exceeded that in ENA by 3.5% (adjusted least squares mean of log(richness) ± SE: 3.315 ± 0.009 for EAS, 3.204 ± 0.010 for ENA). When log(richness) was regressed on different combinations of log(area), elevation, MAT, AET, SRAIN, and region, the best-fit model included all of these variables according to the AIC (Table 2). Because the difference in ΔAIC between the best and second best models is 37, much greater than 10, the best-fit model is clearly superior.

To determine how much of the variance in log(richness) can be accounted for uniquely by climate and uniquely by region after accounting for sample area and elevation, we first regressed log(richness) on log(area) and elevation (*n* = 471, *F*_{2,468} = 902, *R*² = 0.794) and then conducted a partial regression using the residuals of the abovementioned regression as the dependent variable. The partial regression partitioned the explained variance in the dependent variable into three portions: (a) variance explained uniquely by climatic variables (37.56%), (b) variance explained uniquely by region (2.53%), and (c) variance explained jointly by climatic variables and region (4.24%). Of the 40.09% of the variance to which unique effects could be attributed, region accounted for 5.77%.

To test whether region effect on species richness diminishes with increasing latitude, we compared the difference in residuals (resulting from the partial regression including all independent variables) of the floras <1 × 10⁴ km² located between 25° and 35° N (*n* = 109) between EAS and ENA with that of the floras <1 ×

TABLE 2. Multiple regression models for log₁₀(species richness) using 471 floras from eastern Asia and eastern North America.

Independent variables in model							AIC	ΔAIC	<i>R</i> ²
Area	Elev	MAT	AET	SRAIN	Region				
1	1	1	1	1	1	-2027	0	0.897	
1	1	1	1	0	1	-1990	37	0.888	
1	1	1	0	1	1	-1986	41	0.887	
1	1	1	1	1	0	-1983	44	0.886	
1	1	0	1	1	1	-1972	55	0.884	
1	1	1	1	0	0	-1902	125	0.864	

Notes: Models are ranked by Akaike Information Criterion (AIC) from best- to worst-fit model, and only the models with ΔAIC ≤ 125 are presented. Independent variables are: Area, log₁₀-transformed area; Elev, maximum elevation; MAT, mean annual temperature; AET, actual evapotranspiration; SRAIN, summer precipitation; and region, eastern Asia or eastern North America.

10^4 km² located between 35° and 45° N ($n = 101$) between the two continental regions. We didn't include larger floras in this analysis in order to avoid using the floras that occur in both latitudinal zones. The difference between the means of regression residuals for the two groups of the southern floras was larger than that for the two groups of northern floras by a factor of 2.4 (0.118 vs. 0.049). Because ENA has many fewer floras located south of 30° than EAS (Appendix A), which may bias the result of this analysis, we then conducted another analysis to compare the difference in residuals of the floras $<1 \times 10^4$ km² located in latitudes ranging from 30° to 35° N ($n = 48$) between EAS and ENA with that of the floras $<1 \times 10^4$ km² located in latitudes ranging from 35° to 45° N between the two continental regions. The difference (0.107) between the means of regression residuals for the two groups of the floras located between 30° and 35° N was larger than that for the two groups of northern floras by a factor of 2.2. In both analyses, region effect on species richness was stronger in southern latitudes than in northern latitudes.

To determine the relative strength of climate and region effects on species richness in the southern floras of EAS and ENA, we conducted a partial regression for the data set of the 109 southern floras to determine the amount of the variance explained uniquely by climate and uniquely by region using the residuals from the regression with log(area) and elevation being independent variables. Climate and region uniquely explained, respectively, 22.14% and 12.18% of the variance. The percentage of the unique effects explained by region is 35.49%, more than sixfold higher than the value we reported above for the data set of the 471 floras. Log(richness) in EAS exceeds that in ENA by 6.9% for the southern floras (adjusted least squares mean of log(species richness) \pm SE: 3.114 ± 0.016 for EAS, 2.912 ± 0.036 for ENA), a value which is approximately twice the value we reported above for the data set as a whole.

The following factors might influence the conclusions reported above: (a) the removal of the effect of elevation before the partial regressions were conducted to determine the relative importance of climate and region in influencing species richness, (b) incomparability in elevation between the two continental regions, (c) collinearity among the three climate variables used, (d) possible differences between EAS and ENA in the way in which climate variables map onto latitudes (i.e., latitudinal shifts of climate zones), and (e) a possible peninsula effect on species richness (Brown and Lomolino 1998) in ENA because nearly all of the area south of 30° N in ENA is in the Florida peninsula. Accordingly, we carried out a series of analyses to address these issues.

Controlling for elevation effect before conducting the partial regressions might have reduced the climate signal left in the residuals resulting from the regression of log(species richness) on log(area) and elevation and hence increased the significance of region effect. To

address this issue, we repeated the partial regressions using the species richness residuals resulting from the regression of log(species richness) on only log(area) ($n = 471$) and considered elevation as an independent variable in subsequent partial regressions. Although elevation can be considered as a contemporary and ecological factor influencing species richness through increasing habitat heterogeneity, it can also be considered as a regional factor influencing species richness through promoting speciation and decreasing the rate of species extinction during glacial cycles. Here we assumed elevation to be a pure ecological variable in these partial regressions in order to examine the effect of elevation on the strength of the climate effect. Specifically, in these partial regressions, the set of ecological variables included four variables (i.e., MAT, SRAIN, AET, and elevation) and the other set included only one variable (i.e., region). The partial regression ($R^2 = 0.713$, SEE = 0.116, $F_{5,465} = 231$) determined that the variance uniquely explained by the set of the four ecological variables was 32.7% and that uniquely explained by region was 4.2%. Compared to the respective values (i.e., 37.56% vs. 2.53%) of the previous partial regression using the data set of the 471 floras, the relative importance of the ecological variables decreased and that of region increased. We conducted a similar analysis for the data set of the southern floras ($n = 109$). This partial regression ($R^2 = 0.627$, SEE = 0.105, $F_{5,103} = 35$) determined that the variance explained by the set of the four ecological variables alone was 8.2% and the variance explained by region alone was 11.8%. Compared to the respective values (i.e., 22.14% vs. 12.18%) of the previous partial regression using the same 109 floras, the relative importance of region in influencing species richness not only increased, but even exceeded that of the ecological variables. Furthermore, the trend of decreasing region effect from south to north remained the same when elevation was included as an independent ecological variable, together with the three climatic variables, in a multiple regression using the species richness residuals after removing the variation of sample area. For example, the difference between the means of regression residuals for the 109 southern floras was 0.137 and that for the 101 northern floras was 0.078. For the 48 southern floras located between 30° and 35° N, the difference was 0.132.

Maximum elevations are on average much higher in EAS than in ENA (Appendix B), and this is particularly true for large floras. Although elevation effect on species richness was statistically accounted for in all analyses reported above, the difference in elevation between the two continental regions (EAS > ENA) might to some extent result in the observed region effect on species richness with EAS having a higher level of species richness than ENA in similar climate. To examine whether this is the case, we conducted a comparison using floras of $<1 \times 10^4$ km² with comparable means of maximum elevations and mean annual temperatures

TABLE 3. Results of a principal components analysis (PCA) based on the correlation matrix between climate variables ($n = 471$).

Eigenvalue and eigenvector	PC1	PC2	PC3
Eigenvalue	2.341	0.419	0.240
Percentage of variance	78.04	13.95	8.01
Percentage of cumulative variance	78.04	91.99	100.00
Eigenvector			
MAT	-0.915	0.147	0.377
AET	-0.888	0.348	-0.299
SRAIN	-0.846	-0.525	-0.093

Notes: Values in the second part of the table represent the correlation coefficients of the original variables with each PCA axis. Boldface type is used only to highlight strongest ($|r| > 0.5$) contributions to each PCA axis. Key to abbreviations: MAT, mean annual temperature; AET, actual evapotranspiration; SRAIN, summer precipitation.

between EAS and ENA. Because using smaller floras would avoid overlapping of floras selected and thus increase the degree of spatial independence among floras analyzed, we only included smaller ($<1 \times 10^4 \text{ km}^2$) floras in this analysis. We took the following steps to select floras for this comparison. For the floras $<1 \times 10^4 \text{ km}^2$ in EAS, we excluded floras with maximum elevations higher than 1500 m and floras located south of 25° N . This exclusion resulted in a set of 32 floras. The means and standard deviations of the maximum elevations, mean annual temperatures, and sample areas of these floras were $1061.3 \pm 292.5 \text{ m}$, $13.1 \pm 4.4^\circ\text{C}$, and $443.5 \pm 849.8 \text{ km}^2$, respectively. For the floras $<1 \times 10^4 \text{ km}^2$ in ENA, we first excluded those floras whose maximum elevations were below 500 m and then selected a set of floras whose means of maximum elevations and mean annual temperature were comparable to those of selected floras for EAS. This selection resulted in a set of 31 floras for ENA. The means and standard deviations of the maximum elevations, mean annual temperatures, and sample areas of these floras were $1112.2 \pm 515.3 \text{ m}$, $13.2 \pm 1.9^\circ\text{C}$, and $2030.5 \pm 1659.2 \text{ km}^2$, respectively. Although the means of maximum elevations, mean annual temperatures, and sample areas were all smaller in the floras selected for EAS than in those selected for ENA, the species richness of the selected floras for EAS was much higher than that for ENA (1050.8 ± 271.4 vs. 867.5 ± 209.8). When $\log(\text{richness})$ was compared between the two regions in an analysis of covariance with region as main effect and $\log(\text{area})$, elevation, MAT, SRAIN, and AET as covariates using the data set of the 63 floras, region had a significant effect on species richness and elevation effect was not significant ($P = 0.184$; Appendix C). $\log(\text{richness})$ in EAS exceeded that in ENA by 4.7% (adjusted least squares mean of $\log(\text{richness}) \pm \text{SE}$: 3.033 ± 0.021 for EAS, 2.896 ± 0.021 for ENA), indicating a stronger region effect compared with the analysis of covariance using all the 417 floras as noted above. Because the F ratio for region was higher than those for the climatic variables by a factor of 1.7 to 7.5

(Appendix C), spatial nonindependence among some sample sites has the least influence on the significance of region effect, compared to all the climatic variables.

Collinearity among the climatic variables (Appendix D) may lead to biased parameter estimates when regression residuals are used as data in subsequent analyses (Freckleton 2002). To address this issue, we transformed the three climatic variables into three variables independent of each other through a principal components analysis. The first principal component (PC1) alone explains 78% of the variance in the three climatic variables (Table 3). We conducted an ANCOVA, which included the same variables as in the abovementioned ANCOVA using the 471 sample sites except that the three climatic variables were replaced by the three principal components. As in that ANCOVA, $\log(\text{richness})$ in EAS exceeds that in ENA by 3.5%, and region is a significant effect (Appendix E). Thus, our results are unaffected by collinearity among independent variables.

To test whether region effect on species richness varied with climate independently of latitude and was influenced by the peninsula effect, we used those floras in ENA that are $<1 \times 10^4 \text{ km}^2$ and are not located in Florida. Values of PC1 of these floras range from -2.5 to 2.8 . We then assembled a set of floras of $<1 \times 10^4 \text{ km}^2$ with a comparable range of PC1 values for EAS. As a result, a total number of 208 floras were assembled from EAS and ENA. We partitioned these floras into two groups: floras with $\text{PC1} \leq 0$ ($n = 100$) and floras with $\text{PC1} > 0$ ($n = 108$). We conducted three partial regressions: one including all the 208 floras, one including only floras with $\text{PC1} \leq 0$, and the other including only floras with $\text{PC1} > 0$. Variables included in each partial regression were the same as those reported above except that the three climatic variables were replaced with PC1 and PC2. The first principal component was significant, and PC2 was marginally significant according to a broken-stick test (Jackson 1993). In the partial regression including all the 208 floras, PC1, PC2, and region together explained 27.6% of the variance, of which 62% was uniquely explained by PC1 and PC2 and 2.2% was uniquely explained by region. In the partial regression including only floras with $\text{PC1} \leq 0$ (corresponding to warm climates), the three independent variables explained 34.5% of the variance, to which region contributed nearly as much as did the two principal components (11.0% contributed uniquely by PC1 plus PC2 and 9.9% uniquely by region, with 79.1% contributed jointly by region and the two PC variables). In the partial regression including only floras with $\text{PC1} > 0$ (i.e., cold climates), the three explanatory variables explained 21.9% of the variance, to which region contributed nearly no effect (0.5% contributed uniquely by region, 1.4% contributed jointly by region and the two PC variables, and 98.1% contributed uniquely by the two PC variables). The patterns revealed from this analysis are consistent with those reported

above, in which raw climatic data were used, floras were partitioned according to latitude, and peninsular Florida was included.

To determine the extent to which elevation plays a role in influencing species richness in EAS and ENA, we first regressed $\log(\text{richness})$ on $\log(\text{area})$ and the three climatic variables for each region and then expanded the two models by adding elevation as an independent variable. We determined elevation effect on species richness by comparing coefficients of determination and SEE between these two sets of models. The model without elevation explained 82.2% of the variance in $\log(\text{richness})$ for EAS ($n = 247$, $F_{4,242} = 279$, $\text{SEE} = 0.170$) and 90.3% of that for ENA ($n = 224$, $F_{4,219} = 507$, $\text{SEE} = 0.083$), and the SEE of the EAS model was much larger than that of the ENA model by a factor of 2. When elevation was added to the ENA model, the model ($n = 224$, $F_{5,218} = 443$, $\text{SEE} = 0.080$) explained only an additional 0.7% of the variance (90.3% vs. 91.0%), suggesting that elevation provides virtually no explanatory power in ENA. However, for EAS, the variance explained by the model with elevation ($n = 247$, $F_{5,241} = 434$, $\text{SEE} = 0.127$) increased by $\sim 8\%$ (82.2% vs. 90.0%), and variation in regression residuals was considerably narrowed. This indicates that elevation has played a more important role in regulating species richness patterns in EAS than in ENA.

Given these results, we sought to analyze the region effect on species richness in EAS and ENA by modeling richness as a continuous function of the combined effects of sample area, climate, and elevation. To this end, we used a general linear model to estimate parameters in the following equation for each region: $\log(\text{richness}) = a + b_1 \log(\text{area}) + b_2 \text{elevation} + b_3 \text{PC1} + \epsilon$. Because PC1 is highly correlated with all three climatic variables (Table 3), it is reasonable to consider PC1 as a surrogate for the three climatic variables. The parameterized model is $\log(\text{richness}) = 2.588 (\pm 0.041; 95\% \text{ CI}) + 0.1335 (\pm 0.0126) \log(\text{area}) + 0.00012 (\pm 0.00002) \text{elevation} - 0.091 (\pm 0.013) \text{PC1}$ for EAS ($n = 247$, $F_{3,243} = 605$, $R^2 = 0.88$, $\text{SEE} = 0.138$) and $\log(\text{richness}) = 2.276 (\pm 0.040) + 0.1994 (\pm 0.0106) \log(\text{area}) + 0.00004 (\pm 0.00002) \text{elevation} - 0.029 (\pm 0.007) \text{PC1}$ for ENA ($n = 224$, $F_{3,220} = 706$, $R^2 = 0.91$, $\text{SEE} = 0.081$). All coefficients in the models are significant at $P < 10^{-5}$, except for the coefficient of elevation for ENA, for which $P = 10^{-4}$. Although P values should be considered conservatively due to nonindependence of some floras, our focus was mainly on the predictive power of a model, which is indicated by the amount of the variance in $\log(\text{richness})$ explained (i.e., coefficients of determination, R^2). In general, these two models explained well the variation in species richness in both EAS and ENA, as demonstrated by the R^2 and SEE of each model as well as the relationships between observed and predicted species richness (Fig. 1D). Because these two models explained nearly the same amount of the variance as their

counterparts in which raw climatic variables were used (88% vs. 90% for EAS, 91% vs. 91% for ENA), we considered the models with PC1 to have approximately the same power to predict $\log(\text{richness})$ as the models with the three raw climatic variables. For ease of visualization, the four-dimensional relationships between species richness, area, PC1, and elevation were examined in a series of three-dimensional graphs (richness, area, and PC1), in each of which maximum elevation was set to a given level. Considering that in the data set of this study the mean of maximum elevations was 967 m for ENA and 2513 m for EAS (Appendix B), we predicted species richness for EAS and ENA at three selected elevations levels: 1000, 2000, and 3000 m. The relationships between richness, area, and PC1 for each of the three elevations are shown in Fig. 1.

The species richness response surface for ENA changed little at different elevation levels. Considering that the mean maximum elevation of the ENA floras examined in the study is 967 m (Appendix B) and that mountaintops around 1000 m widely spread from north (e.g., 1117 m in Maine) to south (e.g., 1323 m in Georgia), the response surface for 1000 m may be considered the one best representing the most general situation for the highest elevation in ENA. In contrast, the species richness response surface for EAS changed drastically from 1000 to 3000 m and, of the three elevation scenarios, the response surface of 3000 m may represent the most general situation for EAS, considering that the mean maximum elevation of the EAS floras examined is 2513 m and that many mountaintops exceed 2000 m in the eastern part of China and exceed 4000 m in southwestern China (Wu 1980). Comparing the ENA response surface in Fig. 1A with the EAS response surface in Fig. 1C, one would conclude that (1) species richness is higher in EAS than in ENA from smaller to larger areas, (2) the difference in richness between the two continental regions diminishes toward higher PC1 values and hence lower temperatures and higher latitudes, and (3) the difference in richness between the two continental regions increases toward larger areas.

We also conducted comparisons in species richness between EAS and ENA for different spatial scales. The primary objective of this analysis was to examine whether floras in EAS have a higher level of species richness than floras in ENA having the same or even larger values of sample areas and mean annual temperatures and whether there is a consistent pattern across spatial scales. We first excluded all floras in EAS that are located in latitudes south of 25°N in order to make the rest of EAS comparable to ENA in terms of latitude. We then divided the remaining floras of EAS and ENA into four spatial scale classes: $10\text{--}1 \times 10^4$ (including floras of $10\text{--}9999 \text{ km}^2$), 1×10^5 (including floras of $10\,000\text{--}99\,999 \text{ km}^2$), 1×10^6 (including floras of $100\,000\text{--}999\,999 \text{ km}^2$), and 1×10^7 (including floras of $1\,000\,000\text{--}9\,999\,999 \text{ km}^2$). Because our earlier analyses have already demonstrated that greater region effect

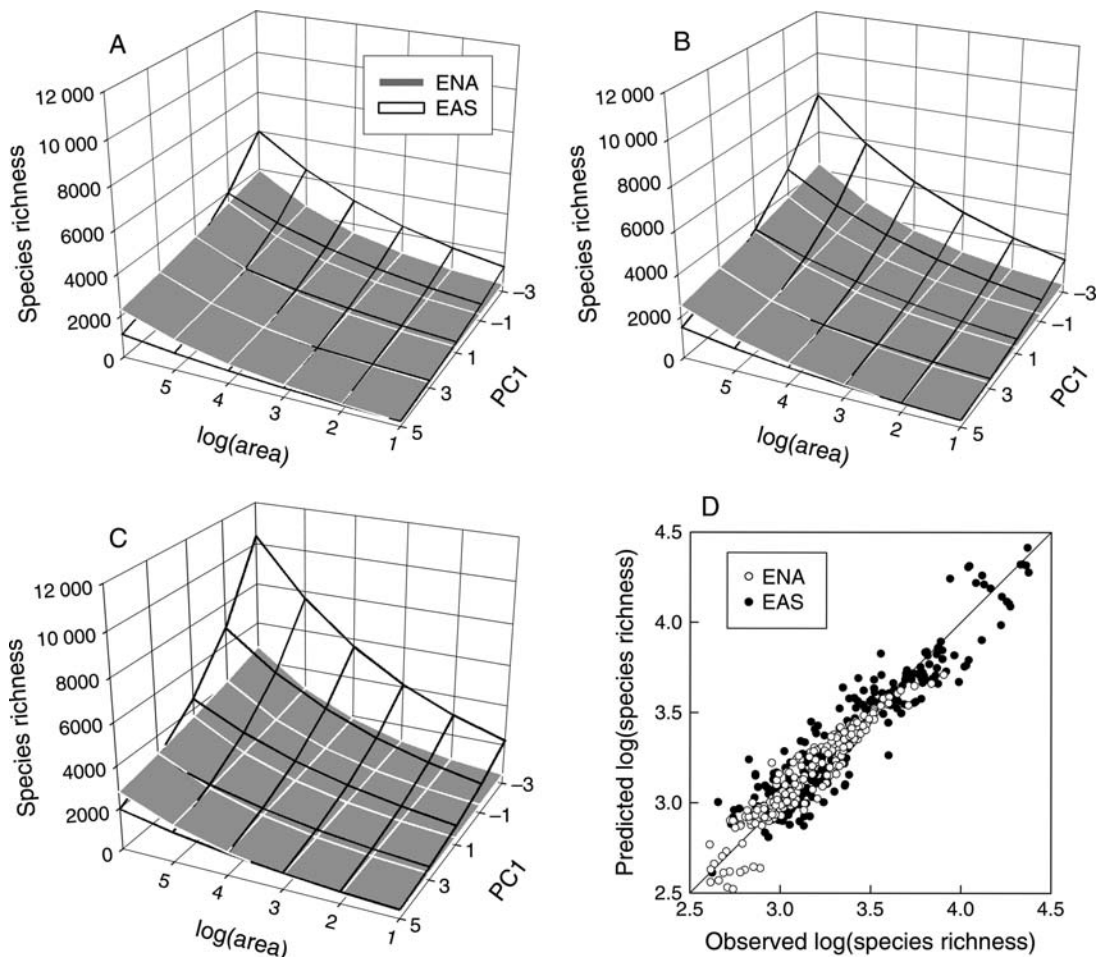


FIG. 1. (A–C) Comparison of predicted species richness in floras of different area sizes and with different climate conditions represented by principal component axis 1 (PC1) between eastern Asia (EAS) and eastern North America (ENA) for three selected maximum elevations: (A) 1000 m, (B) 2000 m, and (C) 3000 m. [Models: $\log(\text{species number}) = 2.588 + 0.1335 \times \log(\text{area}) + 0.00012 \times \text{elevation} - 0.091 \times \text{PC1}$ for EAS; $\log(\text{species number}) = 2.276 + 0.1994 \times \log(\text{area}) + 0.00004 \times \text{elevation} - 0.029 \times \text{PC1}$ for ENA; see *Results* for details about the models.] (D) Comparison of observed $\log(\text{species richness})$ to $\log(\text{species richness})$ predicted by the above-mentioned models.

occurs in more southern latitudes, we excluded floras of scale $10\text{--}1 \times 10^4$ located north of 35°N in both EAS and ENA (we didn't do this exclusion for larger-scale classes because floras in these classes often occupy latitudes both south and north of 35°N). Because it is not possible to assemble a set of floras for which the means of sample areas and temperatures are exactly the same in the two continental regions for each of the four scale classes, we purposely excluded some larger floras with higher temperatures in EAS in order to make the mean area and temperature of EAS comparable with or smaller than those of ENA.

As shown in Table 4, for each scale class, the means of sample areas and temperatures in the floras of ENA exceed those of EAS, but the mean of species richness in the former is much lower than that in the latter. For example, the mean area of the floras for EAS in class $10\text{--}1 \times 10^4$ is only $\sim 21\%$ of that for ENA, but the mean

species richness for the former is higher than the latter by a factor of 1.2, despite the mean of temperatures in the former being much lower than the latter (13.4°C vs. 20.3°C). At the largest scale, the mean sample area of the floras of EAS is only 55.7% of that of ENA and the mean temperature of the former is lower than that of the latter by 2.5°C , but the species richness of EAS is higher than that of ENA by a factor of 1.27 (Table 4). Furthermore, Table 4 demonstrates that the same latitudes have a lower temperature in EAS than in ENA, suggesting that equivalent climatic zones are located in more northern latitudes in ENA than in EAS. Because contrasts in sample area, temperature, and species richness between the two continental regions are so striking in these comparisons, it is reasonable to conclude that species richness is higher in EAS than in ENA across all spatial scales examined.

TABLE 4. Comparison of the means of midpoint latitudes, sample areas, temperatures, and numbers of angiosperm species in 203 selected floras between eastern Asia (EAS) and eastern North America (ENA) according to five spatial scales.

Scale (km ²)	Continent	<i>n</i>	Latitude (°)	Area size (km ²)	Temperature (°C)	No. species
10–1 × 10 ⁴	EAS	67	29.2	644	13.4	1283
	ENA	29	30.0	3073	20.3	1036
1 × 10 ⁵	EAS	5	31.8	28 185	9.8	2023
	ENA	24	38.9	34 519	14.5	1691
1 × 10 ⁶	EAS	28	34.5	353 517	10.8	3194
	ENA	37	38.2	390 258	14.8	3017
1 × 10 ⁷	EAS	6	35.7	1 224 636	11.0	6761
	ENA	7	37.6	2 196 708	13.5	5340

DISCUSSION

This study is the first examination of the relative importance of historical and regional factors vs. contemporary and ecological factors in influencing large-scale angiosperm species richness patterns using a large set of survey-based floristic data (including 471 localities) and covering a wide range of environmental factors and scales. Most previous studies have estimated species richness using maps of species distributions, because large-scale survey-based species richness data are rarely available (Hurlbert and White 2005). However, range map-based species richness can substantially overestimate true species richness in an area. Most species only occur in a small proportion of the areas within their distribution ranges; therefore, the mapped range of a species may include large areas from which the species is absent (Hawkins and Porter 2003, Rodrigues et al. 2004). For example, Rodrigues et al. (2004) reported that 15% of occurrences resulting from species range maps in their study were errors. Based on their study on bird species richness across North America, Hurlbert and White (2005) demonstrated that bird species were detected only on 60% of the surveys within their range even in the case that all survey records of a 10-year period were considered. Thus, on average, ~40% of bird species occurrences derived from range maps for a given locality are false species occurrences. Such false species occurrences can substantially obscure species richness–environment relationships. Hurlbert and White (2005) demonstrated that the relative importance of predictive variables included in a regression analysis varied not only in magnitude but also in direction because of the false positive effect. Compared to range map-derived data, species richness data derived from complete species lists based on intensive surveys are more accurate. Survey-based species richness may underestimate true species richness because rare species may be missed during surveys, but using species richness data resulting from intensive surveys with the aim of providing complete species lists of focal localities minimizes the underestimation of species richness.

Floras examined in this study range from 10 km² to 4.7 × 10⁶ km². This range of spatial scales includes nearly all spatial scales used in previous studies on large-scale species richness–climate relationships (e.g., latitude-longitude quadrats ranging from 1° to 10° used in

Currie [1991], Anderson and Marcus [1993], Rahbek and Graves [2001], Francis and Currie [2003], and Hawkins et al. [2003a]; sample sites of 10–1 × 10⁴ km² used in Lyons and Willig [1999], Ricklefs et al. [2004], and Hawkins et al. [2005]). We demonstrated that eastern Asia is more diverse in angiosperm species than eastern North America in floras ranging from 10 km² to ~4.5 × 10⁶ km², that the region effect is stronger in the south than in the north, suggesting that species richness converges toward cooler environments and more northern latitudes, and that elevation plays a stronger role in eastern Asia than in eastern North America. Species richness at a continental scale (1.97 × 10⁷ km²) has previously been shown to be higher in eastern Asia than in North America by a factor of 1.5 (Qian 2002a). Taken together, the diversity anomaly between eastern Asia and North America occurs at all spatial scales >10 km².

Some of the floras examined in this study are spatially nonindependent. Nonindependence of sample sites may inflate the Type I error in a statistical test because the number of degrees of freedom may be overestimated (Diniz-Filho et al. 2003, Hurlbert 2004). This is an issue associated with most, if not all, studies examining large-scale species richness patterns, although most previous studies on large-scale species richness patterns did not take this issue into account. According to several studies (e.g., Diniz-Filho et al. 2003, Hurlbert 2004), spatial autocorrelation of residuals of species richness in a regression decreases to a nonsignificant level after adding several environmental variables.

It is unlikely that the significant effect of region on species richness observed in this study would have primarily resulted from the effect of nonindependence of some sample sites for several reasons. First, following previous studies (e.g., Francis and Currie 2003, Hurlbert 2004), we accounted for the effect of nonindependence among sample sites by reducing the number of degrees of freedom to a very low level (equivalent to 5% of sample size). Second, if the region effect observed in this study were an artifact due to the effect of nonindependence of sample sites, the significant effects of AET and summer rainfall on species richness must also have resulted from the effect of nonindependence of sample sites because *F* ratios for these two variables are smaller than the *F* ratio for region as shown in Table 1. Because many previous studies (Currie and Paquin 1987, Currie

1991, Hawkins et al. 2003b) have demonstrated that AET and rainfall are strongly correlated with species richness in many regions on the earth, including eastern Asia and eastern North America, it is unlikely that AET and rainfall would have no influence on plant species richness in the two continental regions examined in this study. Third, some comparisons that showed a higher level of species richness in eastern Asia than in eastern North America in this study did not involve any statistical test and thus are irrelevant to the issue of inflating the Type I error due to nonindependence of sample sites. As shown in this study, plant species richness is higher in eastern Asia than in eastern North America in all four spatial scale classes despite the fact that the sites of eastern North America have on average a larger sample area and a higher temperature than those of eastern Asia (Table 4). Thus, our main conclusion that species richness between areas of similar environment can differ substantially between regions (i.e., region effect) is robust to the issue of nonindependence of sample sites.

This study and the study of Qian (2002a) demonstrate that region effect on plant species richness diminishes poleward, suggesting that region effect may be small or even undetectable if more sample sites from northern latitudes are included in an analysis. When floras sampled from a wide range of an environmental gradient are pooled, climatic variables may explain more variance in species richness than region, leading to the result that the effect of regional and historical processes on continental diversity patterns can be masked by contemporary climatic variables (Whittaker and Field 2000, Hawkins et al. 2003a). For example, in our analysis, the importance of the region effect was sixfold higher in southern (warmer) environments than for the data set as a whole. Thus, there is a danger that the climate effect can mask the region effect when more northern latitudes are included in an analysis and no effort is made to model the relationship of the region effect to latitude. We suspect that some of the controversy over climate effect vs. region effect in temperate forests has occurred because of the failure to address this phenomenon.

Even when there are strong correlations between species richness and climate, interpretation is not straightforward (Hawkins et al. 2003a, Ricklefs 2004). A climatic variable can influence richness in opposite directions. For example, Schall and Pianka (1978) found that temperature is positively correlated with richness of birds and mammals in the United States but negatively correlated in Australia. Furthermore, correlation between richness and climate can have contemporary and ecological as well as historical and regional causes (Farrell et al. 1992, Latham and Ricklefs 1993, Qian and Ricklefs 2004b), as we will discuss in more depth below. What is clear from the present study is that different regions of similar contemporary environment can have

different levels of species richness, as opposed to the prediction of a hypothesis based on local determinism.

The present study showed that the effect of region on species richness can exceed that of climatic variables on species richness in southern and warm latitudes and that the region effect diminishes northward. Approximately 35% of the total variance in species richness that is accounted for independently by either climate or region is explained by region alone when floras located between 25° and 35° N latitude are compared, and the region effect on species richness diminishes toward higher latitudes. We believe this is an important finding and a major caution to anyone looking for or against region effect because the strength of the effect itself varies. Adams and Woodward (1989) examined the global predictive power of the relationship between large-scale tree species richness and contemporary environmental variables. Their study shows that eastern Asia tends to have a higher tree species richness than Europe at higher productivity levels (e.g., $>1 \times 10^4 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), and tends to have a higher tree species richness than eastern North America at all productivity levels. Differences in tree species richness between eastern Asia and either Europe or eastern North America increase toward higher productivity levels, corresponding to warmer and lower latitudes. In other words, their study demonstrates that the relationships between productivity and species richness differ between continents (with eastern Asia having the steepest slope) and that region effect on species richness increases with productivity. Their findings are consistent with those of the present study.

A lower region effect on species richness in northern latitudes may have resulted from the fact that the northern parts of the two continents share more common regional and historical processes that regulate contemporary species diversity patterns in northern latitudes. The northernmost parts of Asia and North America were connected by the Bering Land Bridge between Alaska and eastern Siberia during the mid-Cretaceous (1×10^8 years ago) (Sanmartín et al. 2001) and throughout most of the Paleogene and Neogene (McKenna 1983). During Pleistocene glaciations, terrestrial connections between Asia and North America were reestablished (Sanmartín et al. 2001). Thus, the paleo-floras of the northern parts of Asia and North America were interconnected for a long period of time in the past and thus shared the same recent history of floristic development. The fact that areas of similar environment in northern (particularly boreal and arctic) latitudes have similar levels of angiosperm species richness may reflect the common evolutionary processes of plant tolerance to stressful environments (frost tolerance in this case). Angiosperms originated in warm and wet climate (Tiffney 1985). Most of the land surface of the earth, including the current arctic region, was under tropical or subtropical climate conditions throughout much of the Paleogene and Neogene (Behrensmeyer et al. 1992). When climate cooled in the Paleogene and

Neogene, tropical-warm temperate plants were forced to move toward the equator, because the climatic tolerances of many angiosperm taxa could not be altered (Tiffney 1985). It is the process of climate cooling that resulted in the origin and evolution of frost tolerance of angiosperms (Latham and Ricklefs 1993). Thus, the evolution of frost tolerance can be considered a climate-driven process. Different taxa have crossed the major evolutionary barrier of frost tolerance at different degrees, and fewer taxa could tolerate colder climate, which has, to some extent, resulted in the diversity–temperature relationship as well as the well-known latitude–diversity gradient (Pianka 1966). The fact that many, if not most, species distributed in boreal and arctic latitudes belong to the same genera, many of which in turn belong to the same families, suggests that crossing the barrier of frost tolerance is a clade-specific evolutionary process. Because the degree of frost tolerance varies among taxa and because a higher proportion of taxa common to eastern Asia and eastern North America would be found at higher latitudes, one would expect that local and regional species richness would converge and beta diversity would decrease toward higher latitudes.

The present study revealed that elevation plays a larger role in regulating species richness patterns in eastern Asia than in eastern North America. For example, a model with elevation as an independent variable explained 8% more variance in species richness in eastern Asia but explained only 1% more variance in species richness in eastern North America compared to a model without elevation. Elevation could have influenced species richness patterns through both contemporary/ecological and historical/regional processes. Elevated montane areas would be expected to provide more types of habitats as well as more opportunities for speciation. Areas of high relief also have strong elevational zonation of habitats, which is the case in southwestern China, and are therefore expected to support more species than areas of low relief such as in much of eastern North America. However, comparing the results from the two sets of partial regressions suggests that the effect of elevation on species richness patterns is more likely through historical processes than through ecological processes. Higher rates of compositional turnover along geographical gradients in eastern Asia than in eastern North America (Qian et al. 2005) also suggest that the greater species richness in eastern Asia is not because eastern Asian topography provides more habitats, but because the high, rugged mountain areas in southwestern China have likely provided more opportunities for speciation than areas in eastern North America, as discussed above.

Some authors (e.g., Francis and Currie 1998, 2003) have used diversity–climate correlations to support the idea that species richness is directly determined by factors in the physical environment that determine the number of species coexisting locally, an idea termed the

local determinism hypothesis (Ricklefs 2004, 2005a, b, 2006). However, as Ricklefs (2006:S6) pointed out, “such correlations might also be predicted by evolutionary theories of species richness patterns, where diversity reflects either environmental history combined with evolutionary inertia, or the influence of environment on net species proliferation.” Therefore, climatic variables may influence both regional/historical processes and local/ecological processes, both of which influence species richness (Ricklefs et al. 1999). Many contemporary environmental variables that are correlated with species richness and have been used to support the idea of local determinism can also influence species richness patterns through regional and historical processes. For example, correlations of species richness with topographic relief, temperature, and water have been considered as evidence supporting the effect of contemporary and ecological factors on species richness patterns, but they can also influence species richness patterns through historical and regional processes. High topographic relief could have promoted the rate of speciation and reduced the rate of extinction, and the relationships of species richness with temperature and water could have, to some extent, resulted from the evolutionary processes of individual species and higher taxa involved in crossing barriers of stressful environments. For example, plant species must cross, to some degree, the barriers of frost tolerance, drought tolerance, and salt tolerance to become distributed in boreal, desert, and mangrove environments, respectively. Thus, it is superficial to consider the relationships between species richness and contemporary environmental variables completely as the outcome of ecological effect on species richness. Furthermore, because most of the land surface of the earth, including the current arctic region, was under tropical or subtropical climate conditions throughout much of the Paleogene (Behrensmeyer et al. 1992), it is possible that a greater diversity in an area with higher temperature may reflect historical and/or evolutionary processes (Lidgard and Crane 1990, Ricklefs 2004). This is particularly true of angiosperms, which are thought to have originated in tropical climate (Takhtajan 1969, Raven and Axelrod 1974, Wu 1980, Lidgard and Crane 1990), with tolerance of frost posing a major barrier to invasion of areas with low temperatures (Sakai and Larcher 1987, Qian and Ricklefs 2004b). Differences in frost tolerance among plants could, by themselves, create the diversity–climate gradient that is found in modern floras. This idea is supported by the evidence that plant genera in a more northerly latitudinal zone are largely a subset of plant genera in the latitudinal zone south of it in eastern Asia (Qian et al. 2003). For example, ~79% of the genera present in latitudes north of 60° N also occurred in latitudes south of 30° N (Qian et al. 2003). Thus, a species richness–climate relationship in angiosperms may, to some extent, reflect evolutionary and historical processes.

Both contemporary/ecological and historical/regional mechanisms have played a role in regulating current species richness patterns but their relative importance depends on space and time scales (e.g., Willis and Whittaker 2002, Hawkins et al. 2003a, Ricklefs et al. 2004). Regional and historical processes such as speciation, extinction, and glaciations may have little explanatory power at small spatial and temporal scales but they play increasing roles at larger scales of space and time (e.g., McGlone 1996, Whittaker et al. 2001, Hawkins et al. 2003b, Qian and Ricklefs 2004b). Historical/regional and contemporary/ecological mechanisms influencing diversity interact on a continuum of space and time (Ricklefs 2004). Differences in species richness between areas of similar environment, as shown in this and other studies (e.g., Orians and Paine 1983, Ricklefs and Latham 1993, Westoby 1993, Ricklefs et al. 2004), suggest that the idea that patterns of species richness result only from regulation of contemporary environments should be abandoned. Ecologists should recognize that correlations do not mean mechanism (Ricklefs 2004) and that finding that a variable describing modern conditions explains more variance than a historical and regional variable does not imply that the former is important whereas the latter is not, or vice versa (McGlone 1996). Moreover, ecologists should not consider historical/regional and contemporary/ecological hypotheses as competing hypotheses (Ricklefs et al. 1999, Whittaker and Field 2000, Whittaker et al. 2001, Hawkins et al. 2003a, Qian and Ricklefs 2004b, Ricklefs 2004) and should not interpret diversity–environment relationships exclusively as a result of contemporary and ecological processes because historical and regional processes can also result in these relationships (Ricklefs 2005a). This is particularly the case when the effect of an ecological process parallels the effect of an historical process (e.g., parallel effects of temperature vs. frost tolerance on species richness). The correlations between species richness and climatic variables (e.g., temperature, precipitation, and synthetic variables derived from the two such as actual evapotranspiration) may to some extent reflect the history of ecological diversification of angiosperm species from their wet tropical birthplace (Ricklefs 2005a).

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APPENDIX A

A map showing the location of the midpoints of the eastern Asian and eastern North American floras used in this study (*Ecological Archives* E088-088-A1).

APPENDIX B

Descriptive statistics for sample area, maximum elevation, mean annual temperature, summer precipitation, and actual evapotranspiration for floras used in this study (*Ecological Archives* E088-088-A2).

APPENDIX C

Analysis of covariance of \log_{10} -transformed angiosperm species richness with region as main effect and $\log_{10}(\text{area})$, maximum elevation, and climate variables as covariates, using 63 floras of 10^4 km^2 with the means of elevations and temperatures being comparable between EAS and ENA (*Ecological Archives* E088-088-A3).

APPENDIX D

Pearson correlation coefficients between environmental variables (*Ecological Archives* E088-088-A4).

APPENDIX E

Analysis of covariance of \log_{10} -transformed angiosperm species richness with region as main effect and $\log_{10}(\text{area})$, elevation, and the principal components of climate variables as covariates (*Ecological Archives* E088-088-A5).