

LETTER

Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America

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Abstract

The diversity of a region reflects both local diversity and the turnover of species (beta diversity) between areas. The angiosperm flora of eastern Asia (EAS) is roughly twice as rich as that of eastern North America (ENA), in spite of similar area and climate. Using province/state-level angiosperm species floras, we calculated beta diversity as the slope of the relationship between the log of species similarity (S) and either geographic distance or difference in climate. Distance-based beta diversity was 2.6 times greater in the north–south direction in EAS than in ENA and 3.3 times greater in the east–west direction. When $\ln S$ was related to distance and climate difference in multiple regressions, both distance and climate PC1 were significant effects in the north–south direction, but only geographic distance had a significant, unique influence in the east–west direction. The general predominance of distance over environment in beta diversity suggests that history and geography have had a strong influence on the regional diversity of these temperate floras.

Keywords

Beta diversity, distance decay of similarity, geographic distance, region effect, Sørensen's index, species richness, species turnover.

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INTRODUCTION

A central goal of the study of biological diversity is to understand why some regions with similar environments have different numbers of species (Orians & Paine 1983; Latham & Ricklefs 1993a; Ricklefs & Schluter 1993; Huston 1994; Rosenzweig 1995; Qian & Ricklefs 2000; Ricklefs 2004). These differences can vary with spatial scale (Rahbek & Graves 2001; Whittaker *et al.* 2001) and they can have varied underlying causes.

The temperate floras of eastern Asia (EAS) and eastern North America (ENA) are closely matched in terms of latitude, climate, and vegetation (Li 1952), but the species richness of flowering plants is higher in EAS than in ENA at a 'mesoscale' (10^1 – 10^4 km²) (Ricklefs *et al.* 2004). At the regional scale, the southern, temperate part of EAS (7.3 million km²) harbours 1.4 times as many species of vascular plants than the southern part of North America (7.4 million km²) (Qian 2002a). Qian & Ricklefs (2000) suggested that the more complex topography of EAS, which might accelerate production of new species in allopatry, is in part responsible for higher local and regional species richness. In addition, the greater environmental

heterogeneity of EAS, which is related to its more complex topography and geography, might create higher regional diversity by increasing the turnover of species with respect to distance, often referred to as beta diversity (Whittaker 1960; Cody 1975, 1993; Wilson & Shmida 1984; Harrison *et al.* 1992; Rahbek 1997; Nekola & White 1999).

Beta diversity is a measure of the difference in species composition between two or more areas (Koleff *et al.* 2003). Ecologists have devised several ways to quantify beta diversity (Wilson & Shmida 1984; Magurran 1988; Koleff *et al.* 2003). Among the first of these was Whittaker's (1960, 1972) measure, $\beta_w = (\gamma/\alpha) - 1$, where γ (gamma) is the number of species in a region and α (alpha) is the average number of species occurring in n local areas within the region. β_w varies between 0 (all areas identical) and $N-1$ (all areas unique). Although β_w and several related indices of beta diversity have found wide application, they cannot be compared between regions unless they are normalized with respect to distance or environmental gradients (Vellend 2001). For this reason, it is useful to compare the slopes of the relationships between the similarity of species in different areas and the distances between those areas (Qian *et al.* 1998; Nekola & White 1999; Vellend 2001). Thus, here

we define beta diversity as the slope of the relationship between turnover of species (the natural logarithm of the Sørensen index of floristic similarity) and geographic distance or difference in climate.

In this study, we use the relationship between floristic similarity and distance to test the hypothesis that the higher species richness of EAS compared with ENA is associated not only with higher mesoscale species richness (Ricklefs *et al.* 2004) but also with higher beta diversity. We first compare the regional scale ($> 3 \times 10^6 \text{ km}^2$) species richness of angiosperms between EAS and ENA. We then analyse species turnover as a function of distance and climate differences for flowering plant (angiosperm) species between complete floras covering areas of $\approx 10^5 \text{ km}^2$ (i.e. provinces or states) in these two regions. We selected this spatial scale not only for convenience, but also because it integrates the effect of local environmental gradients due, for example, to topography, thereby allowing us to extract the effects of pervasive climate variation as the primary environmental axis. The comparison of species turnover with respect to distance and climate difference addresses the contribution of historical and geographic factors relative to that of the contemporary environment in establishing patterns of species richness (Latham & Ricklefs 1993a; Nekola & White 1999). Our results indicate that beta diversity is consistently higher in EAS than in ENA with respect to both latitudinal and longitudinal distance, and, in the latter case, independently of differences in climate variables.

MATERIALS AND METHODS

Assembly of the data

In this study, ENA is the area of the eastern, forested portion of the USA, including all states of the USA east of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas. This area encompasses $\approx 3.1 \times 10^6 \text{ km}^2$ and ranges from $24^\circ 30'$ to $47^\circ 28'$ N in latitude and from $66^\circ 57'$ to $97^\circ 12'$ W in longitude. Eastern Asia (EAS) is the area of the eastern, forested portion of China, including all provinces or autonomous regions east of Neimenggu (Inner Mongolia), Ningxia, Gansu, Qinghai, and Xizang (Tibet) except for Heilongjiang, the most north-eastern province, and Hainan and Taiwan Islands. This area encompasses $3.9 \times 10^6 \text{ km}^2$ and ranges from $20^\circ 29'$ to 46°N in latitude and from $96^\circ 54'$ to 131°E in longitude.

We compiled a plant database that included the presence or absence of angiosperm species in each province or autonomous region in EAS and in each state in ENA, with one exception: the floras of Connecticut, Massachusetts, New Hampshire, Rhode Island, and Vermont were considered as a single sample, often called the New England Flora,

to preserve approximate comparability among the flora areas ($1.58 \pm 0.91 \text{ SD} \times 10^5 \text{ km}^2$, which is equivalent to a circle with a diameter of $\approx 450 \text{ km}$). Because of these large areas, each flora samples a diversity of environments and differences between floras presumably reflect primarily regional trends in environmental conditions. Details concerning the compilation of the plant database can be found in Qian (2002a,b) and Qian *et al.* (2003).

It is well known that climate gradients differ between latitude and longitude. Climate changes faster with latitude than with longitude, and the principal changes in temperate EAS and ENA involve temperature and precipitation, respectively. Accordingly, we selected two directions (i.e. north–south and west–east) to simplify our analysis and discussion. This approach has been used in previous analyses by other authors (e.g. Harrison *et al.* 1992). Turnover of species, geographic distance, and climate difference were based on comparisons between pairs of provincial/state floras. To build similarity–distance relationships separately for the north–south (latitudinal) direction and the west–east (longitudinal) direction within each of the two regions, we selected 40 comparisons from 153 possible pairs between 18 floras within EAS (24 and 16 pairs in north–south and east–west directions, respectively) and 47 comparisons from 300 possible pairs between 25 floras within ENA (22 and 25 pairs, respectively). Our criterion for choosing pairs was to minimize differences in latitude (in the case of the east–west pairs) or longitude (in the case of the north–south pairs) between two floras. The subset included all pairs of floras that fit this criterion. Most of the selected floras were located in warm temperate climate zones in both regions (Müller 1982; Domrös & Peng 1988).

In the north–south direction, distances between the midpoints of a pair of floras varied from 411 to 1870 km in EAS and from 342 to 1893 km in ENA. In the east–west direction, they varied from 180 to 1656 km in EAS and from 219 to 1772 km in ENA. All the floras were located within the study area described above except for a single flora (Oklahoma), which was used in only one comparison to achieve a maximum east–west distance in southern ENA comparable with that in southern EAS.

For each flora, we recorded the latitude ($^\circ \text{N}$) of the geographic midpoint, area (km^2), and the number of species of indigenous angiosperms. We extracted climate variables for each flora from the International Institute of Applied System Analysis (IIASA) climatic database (Leemans & Cramer 1991). Climate data were assembled for the geographical midpoint of each flora area plus four additional points located in the cardinal directions approximately two-thirds of the distance from the centre to the periphery of the flora area. The climate variables were January temperature ($^\circ \text{C}$), July temperature ($^\circ \text{C}$), the difference between July and January temperature, May to August (summer) precipitation

(mm), and September to April (winter) precipitation (mm). In addition, we included two derived climate indices: the actual evapotranspiration (AET, mm), which is an index of actual water flux related to habitat productivity (Rosenzweig 1968), and the potential evapotranspiration (PET, mm), which is proportional to the drying power of the environment. AET and PET were calculated following the approach developed by Cramer and Prentice (Cramer & Prentice 1988; Prentice *et al.* 1992, 1993). We subjected the seven climate variables, each averaged over five points within the area of each flora, to a principal component analysis (PCA), based on the correlation matrix of the variables, to produce a smaller number of uncorrelated climate axes. Principal component (PC) axis scores were used as synthetic climate variables in further data analyses.

Data analyses

To calculate the similarity between two floras, we used Sørensen's index, $S = c/\alpha$, where c is the number of species common to both floras and α the average number of species in each flora (Vellend 2001). Values of S range from 0 to 1. Sørensen's index, which is one of the most commonly used similarity indices, can be related to Whittaker's β_w by the expression $S = 1 - \beta_w$ when β_w is calculated for a single pair of floras. Sørensen's index is also related to Jaccard's index (J), another commonly used similarity index, by $S = 2J/(J + 1)$. In our dataset, S tends to decrease exponentially towards 0 with increasing distance, and so we transformed S to its natural logarithm ($\ln S$) to obtain a linear relationship (Nekola & White 1999). In this analysis, we defined beta diversity as the negative of the value of the slope relating the logarithm of Sørensen's similarity index to distance between pairs of floras. Hence, beta diversity is a measure of the exponential rate of increase in dissimilarity with distance.

We used linear regression and multiple linear regression to quantify the relationship between species turnover and geographic distance or difference in climate PC scores. We also used the distance \times region interaction in an analysis of covariance (ANCOVA) to test the hypothesis that the slopes of this relationship do not differ between regions. Because we used multiple pairwise comparisons between floras within each region, the values entered in the analyses were not strictly independent. Harrison *et al.* (1992, p. 153) suggest that statistical evaluation in such cases be based conservatively on $n-2$ degrees of freedom, where n is the number of floras used to construct pairwise comparisons. Here we take an intermediate course. We used only 40 of 153 (26%) of the EAS pairs and 47 of 300 (16%) of the ENA pairs in our analyses. Thus, a statistical criterion for significance of 0.01 rather than 0.05 is sufficient to account for the lack of independence in the pairwise comparisons.

Analyses were carried out using the general linear models (GLM) procedure of the Statistical Analysis System, version 8 (SAS Institute Inc. 1990; SAS Institute, Cary, NC, USA). We used PC-ORD version 4 (McCune & Mefford 1999) for PCA.

RESULTS

Species richness

The ENA region has 5920 species of angiosperms. To compare this value with species richness in an area of similar size with a comparable range of ecological conditions in EAS, we excluded the three southernmost provinces, Guangdong, Guangxi, and Yunnan, for which no comparable subtropical and tropical area exists in ENA. The resulting EAS area is slightly smaller than that of ENA (3.03×10^6 vs. 3.08×10^6 km²), but has 14 990 species of angiosperms. Thus, after we controlled for area, the species richness of angiosperms in EAS is 2.5 times higher than that in ENA. When we excluded an additional five provinces (Sichuan, Guizhou, Hunan, Jiangxi, and Fujian) located primarily south of 30°N, thereby reducing the area of EAS to 58% that of ENA, species richness of angiosperms in EAS was 8290, still 1.4 times higher than species richness in ENA. Thus, even using an overly conservative comparison with respect to area and range of climates, EAS harbours substantially more species of flowering plants than does ENA.

Species turnover in space

Sørensen's index of similarity (S) is higher in ENA than in EAS for a given distance separating two floras in both north–south and east–west directions (Fig. 1). The logarithm of S is negatively related to the geographic distance between floras in both north–south (Fig. 1a) and east–west (Fig. 1b) directions. We compared beta diversity, which is the negative value of the slope of $\ln S$ with respect to distance, in an analysis of covariance (ANCOVA) to determine whether the slopes of the relationship differed between regions. In the north–south direction, beta diversity was significantly higher in EAS than in ENA (interaction $F = 58.2$, d.f. = 1,42, $P < 0.0001$). Beta diversity calculated by linear regression in each region separately was -1.118 ± 0.085 per 1000 km ($R^2 = 0.888$) in EAS and -0.430 ± 0.035 ($R^2 = 0.876$) in ENA.

The relationship of $\ln S$ to distance in an east–west direction also had a steeper slope in EAS (-0.740 ± 0.098 per 1000 km, $R^2 = 0.803$) than in ENA (-0.244 ± 0.037 , $R^2 = 0.653$) ($F = 30.4$, d.f. = 1,37, $P < 0.0001$) (Fig. 1b). In an ANCOVA combining data from EAS and ENA in both directions, significant distance \times region ($F = 409.8$, d.f. = 1,83, $P < 0.0001$) and distance \times direction ($F = 60.7$,

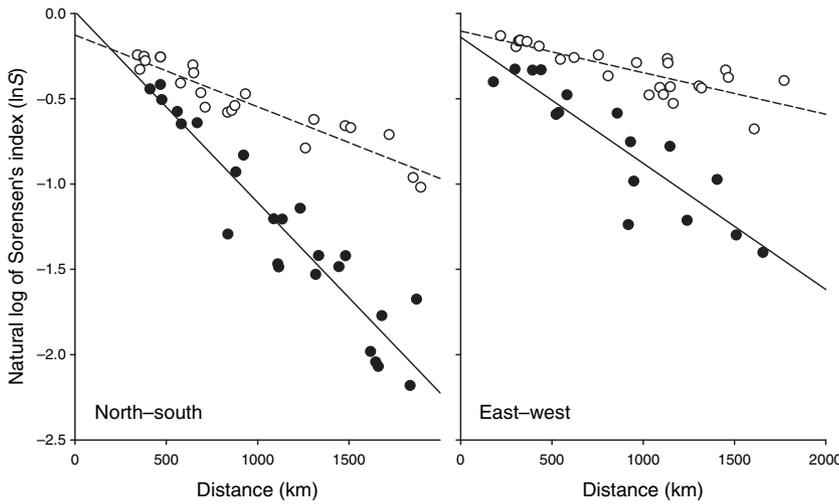


Figure 1 Relationship of the logarithm of Sørensen's index of floristic similarity ($\ln S$) to geographic distance in eastern Asia (filled circles) and eastern North America (open circles) along a north-south direction (left) and east-west direction (right). Correlation coefficients between $\ln S$ and distance were -0.94 in both regions in the north-south direction ($P < 0.001$) and -0.90 (EAS) and -0.81 (ENA) in the east-west direction ($P < 0.001$).

d.f. = 1,83, $P < 0.0001$) interactions confirmed that beta diversity was significantly higher in EAS than in ENA and in a north-south compared with an east-west direction.

The relationship of species turnover to climate

The first four axes produced by the PCA of the seven climate variables accounted for over 97% of the variance (Table 1). The first axis (PC1) had relatively even loadings for all the climate variables and represents increasing temperature, precipitation, AET, and PET, and decreasing annual temperature extremes. This axis closely parallels

latitude moving toward the equator. Of the next three axes, PC2 represents a contrast between summer temperature and summer precipitation, relatively cool and wet on one end and hot and dry on the other, and PC3 represents additional variation in winter precipitation unrelated to PC1; PC4, which accounted for only 4% of the total variance, was not strongly related to any of the climate variables. We did not evaluate these axes statistically and use them only as uncorrelated (statistically independent) climate variables.

Variation in the climate PC axes among floras was significantly greater in EAS than in ENA for the second and fourth PC axes, but not for the first and third (Table 2). Thus, one might expect differences in climate to result in higher beta diversity with respect to geographic distance in some directions in EAS if plant distributions responded to climate change in the same way in both regions. Accordingly, we calculated the differences between the scores on each of the first four PC axes to represent climate differences between floras as covariates in analyses of beta diversity.

Table 1 Results of a principal component analysis based on the correlation matrix between climate variables averaged over five points within the area of each flora ($n = 43$)

	PCA axis			
	1	2	3	4
Eigenvalue	4.645	1.188	0.687	0.299
Percentage of variance	66.4	17.0	9.8	4.3
Cumulative %	66.4	83.3	93.1	97.4
Eigenvectors				
January temperature	0.975	-0.060	0.053	-0.167
July temperature	0.678	0.619	0.327	0.148
January to July temperature difference	-0.855	0.409	0.111	0.289
Summer precipitation	0.493	-0.733	0.389	0.255
Winter precipitation	0.766	0.030	-0.599	0.195
Actual evapotranspiration	0.945	0.061	-0.103	0.190
Potential evapotranspiration	0.883	0.305	0.210	-0.164

Values in the body of the table represent the correlation coefficients of the original variables with each PCA axis. Boldface is used only to highlight the strongest contributions to each PC axis, not to indicate statistical significance.

Table 2 Climate variation among floras in eastern Asia (EAS) and eastern North America (ENA)

Region	Sample	Standard deviation of PC scores			
		PC1	PC2	PC3	PC4
EAS	18	2.36	1.39	0.49	0.79
ENA	25	2.06	0.59	0.62	0.30
<i>F</i> -ratio		1.32	5.55	1.60	6.93
<i>P</i> -value	d.f. = 18,25	0.26	< 0.0001	0.16	< 0.0001

Climate data are values averaged over five points within each of the flora areas reduced to scores on principal component axes.

The *F*-ratio is the square of the ratio of the larger to the smaller standard deviation.

Table 3 Simple correlations of the natural logarithm of Sørensen's similarity index with geographic distance and differences between floras in scores on PC1 to PC4

Direction	Region	Sample	Independent variables				
			Distance	PC1	PC2	PC3	PC4
North-south	EAS	24	-0.93***	-0.94***	-0.29	0.13	-0.05
	ENA	22	-0.93***	-0.94***	-0.67***	-0.67**	-0.40
East-west	EAS	16	-0.90***	-0.74**	-0.71**	-0.26	-0.23
	ENA	25	-0.83***	-0.56**	-0.56**	-0.19	0.07

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Because Sørensen's index was negatively related to differences in the synthetic climate variables, especially PC1 and PC2 (Table 3), as well as to distance, we wished to determine whether distance influenced species turnover independently of change in environmental conditions. As one would expect, environmental conditions, as well as species compositions, change over distance. For example, distance on PC axis 1 is positively related to north-south geographic distance between floras with a slope of 3.64 ± 0.45 per 1000 km in EAS and 2.88 ± 0.19 in ENA, and to east-west distance with a slope of 1.66 ± 0.46 in EAS and 0.71 ± 0.20 in ENA. Distance on PC axis 2 was significantly related to north-south geographic distance only in ENA (0.67 ± 0.14 , $P = 0.0002$), but to east-west distance in both EAS (2.07 ± 0.40 , $P = 0.0002$) and ENA (0.34 ± 0.09 , $P = 0.0008$). Thus, climate gradients defined by PC axis 2 tend to be steeper with respect to distance in EAS compared with ENA.

We used multiple regression to explore the relationship between Sørensen's index and differences in climate variables PC1 to PC4, with distance excluded from analyses. Only PC1 had a significant effect in the north-south direction (Fig. 2), and this was stronger in EAS than in ENA. The logarithm of S decreased significantly with distance on both PC1 and PC2 in the east-west direction,

with roughly equal contributions in EAS and a steeper relation with PC2 in ENA (Table 4). As in the case of geographic distance, beta diversity with respect to climate variable PC1 was higher in EAS than in ENA. Climate variables explained about the same amount of the variation in $\ln S$ as did distance in a north-south direction, but somewhat less in an east-west direction.

To separate the correlated effects of distance and environmental change, we conducted multiple regressions, in each region and each direction, in which $\ln S$ was related to distance and to differences in the scores of PC1 in the north-south direction and PC1 and PC2 in the east-west direction. In the north-south direction in EAS, both distance and difference on PC1 were significant effects, with roughly equal weights ($F = 28.2$ and 28.3 , respectively) in spite of their strong correlation. Together, the two variables explained 95.2% of the variation in $\ln S$. In ENA, distance and PC1, which together explained 89.9% of the variation, were so strongly intercorrelated that neither made a unique contribution to variation in $\ln S$. In the east-west direction, climate variables were so strongly correlated with distance in both regions that neither PC1 nor PC2 contributed significantly to $\ln S$ when distance was included in the multiple regression; the effect of distance was reduced by its correlation with the climate

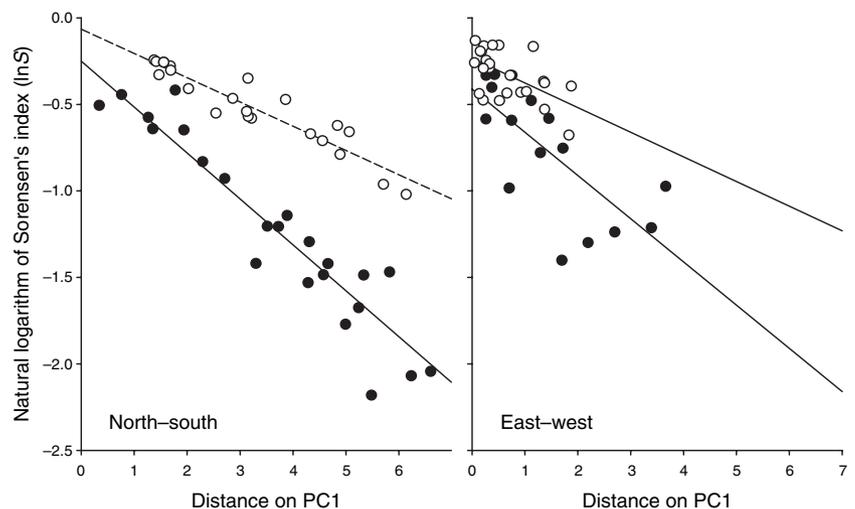


Figure 2 Relationship of the logarithm of Sørensen's index of floristic similarity ($\ln S$) to difference in scores on climate PC1 axis in eastern Asia (filled circles) and eastern North America (open circles) along a north-south direction (left) and east-west direction (right).

Region	Direction		Slope	SE	d.f.	F-value	P-value	R ²
EAS	North–south	PC1	–0.266	0.020	1,22	175.16	< 0.0001	0.888
EAS	East–west	PC1	–0.160	0.063	1,13	6.48	0.024	0.692
		PC2	–0.155	0.059	1,13	6.96	0.021	
ENA	North–south	PC1	–0.140	0.011	1,20	152.56	< 0.0001	0.884
ENA	East–west	PC1	–0.111	0.040	1,22	7.55	0.012	0.481
		PC2	–0.228	0.089	1,22	6.50	0.018	

Table 4 Regression statistics for the relationship between the logarithm of Sørensen's index and the difference in values of PC1 and PC2 (significant only in the east–west direction)

variables but nonetheless remained significant ($F = 9.11$, d.f. = 1,12, $P = 0.01$ in EAS; $F = 12.19$, d.f. = 1,21, $P = 0.002$ in ENA). This suggests that distance, rather than climate change, is the primary driver of beta diversity in the east–west direction.

DISCUSSION

We found that for a given geographic and climate distance, floras covering areas on the order of 10^5 km² are more dissimilar with respect to species composition in EAS than in ENA. This discrepancy occurs in both north–south and east–west directions and it is largely independent of differences in climate with increasing geographic distance in an east–west direction. Indeed, species turnover consistently is more strongly related to geographic distance than to change in climate conditions.

In many studies, beta diversity decreases at coarser scales, as habitat heterogeneity is increasingly included within sample areas rather than partitioned between them (e.g. Lennon *et al.* 2001). In this study, beta diversity in EAS was measured at a grain size somewhat larger than in ENA: the areas of the floras in EAS were an average of 1.66 times larger than those in ENA. However, it is unlikely that this difference would have affected the primary conclusion of this analysis, namely that beta diversity is higher in EAS than in ENA, because larger flora area presumably would reduce the turnover of species between floras (Vellend 2001). Thus, we expect that our conclusion would be enhanced, rather than weakened, if sample areas for the EAS floras were the same as for the ENA floras.

Although floristic similarity was more closely related to geographic distance than to climate difference in this analysis, our measures of environment, based solely on temperature and precipitation, were limited. We lacked data on soils, whose variation can have a strong effect on plant diversity and species composition (e.g. Huston 1993). In addition, we used climate data averaged over only five points to represent the conditions within a flora area. The use of averaged values disregards environmental heterogeneity within areas. However, these limitations would not likely create a bias in one vs. the other of the two continental regions of this study.

High beta diversity undoubtedly accounts in part for the higher regional diversity in EAS compared with ENA. Species turnover occurs more rapidly with respect to both climate and distance in EAS. Combined with the somewhat greater range in climate in EAS, it is not surprising that overall species diversity in EAS is substantially higher on the scale of 10^6 km². The basic character of beta diversity differs between north–south and east–west directions, as found for many types of organisms in Great Britain (Harrison *et al.* 1992). Because of the strong correlation between geographic distance and the PC1 climate difference in a north–south direction, the different effects of distance and climate are difficult to sort out. Multiple regressions showed that small components of variation in both geographic distance and climate variable PC1 were uniquely related to variation in floristic similarity in a north–south direction, although most of the variation in floristic similarity could not be partitioned between the two. Climate made no unique contribution to beta diversity in an east–west direction in either continent. Thus, climate variation statistically contributes little to variation in the Sørensen's index apart from its correlation with geographic distance in either direction.

The dominance of distance over climate in floristic turnover might arise because climate change during glacial cycles shifted plant distributions in a primarily north–south direction. Although this tended to homogenize floras along this axis, lags in migration of species with respect to shifting climate spaces would have decoupled distribution and climate to some extent, leaving behind the signature of distance *per se*. Parallel movements of plant populations in a north–south direction in both EAS and ENA also might have maintained differences between floras along an east–west gradient, in spite of similarities in climate along this axis.

Greater beta diversity in a north–south direction in EAS compared with North America probably reflects the greater climatic, and perhaps other environmental, heterogeneity of EAS (see, for example, Qian & Ricklefs 2000), the relatively smaller impact of climate change during glacial periods, and the broad connection of temperate EAS with tropical regions to the south. The north–south climate gradient probably is not a factor, however, because

climate variation does not differ substantially on PC1 between the regions (Table 2) whereas beta diversity with respect to PC1, as well as geographic distance, is much greater in EAS. The connection between tropical and temperate floras has resulted in the presence of many tropical lineages in temperate EAS (Latham & Ricklefs 1993b), and possibly has fostered more rapid turnover of species from south to north as tropical lineages drop out. In addition, a high rate of species production in the mountainous region of south-western China, which is one of the world's 25 biodiversity hotspots (Myers *et al.* 2000), has further contributed to the diversity of EAS along a primarily south-to-north axis. The Tertiary collision of the Indian plate with the Eurasian landmass resulted in the Himalayan–Tibetan uplift, creating many rugged mountain ranges in the southern part of EAS (particularly south-western China) harbouring a wide variety of habitats that have persisted for long periods. Multiple lines of evidence show that this mountainous area is a centre of speciation for flowering plants. Because newly evolved species have extended their ranges to the north at different rates and over different periods, these species might contribute to the differentiation of floras towards the north.

Greater beta diversity in an east–west direction in EAS compared with ENA would seem to reflect the greater physiographic heterogeneity of the region rather than a longitudinal gradient in climate. Particularly in the south of China, major mountain ranges extend in a north–south direction as a result of the collision of the Indian plate with the Eurasian landmass, not only providing corridors for the north–south movement of plants during the Pleistocene, but also blocking dispersal of plant populations to the east and west, potentially leading to differentiation of the flora in an east–west direction. Furthermore, to the extent that the development of beta diversity reflects reduction of geographic distribution due to specialization or declining competitive ability, rapid shifting of climates during glacial cycles would tend to cause these species to go extinct, leaving more widespread species and tending to reduce turnover of species with distance. This factor is likely to have been more important in ENA than in EAS.

The difference in beta diversity between EAS and ENA is strong in both directions, but more marked along an east–west axis, reflecting the extreme heterogeneity of the region with a predominately north–south orientation. Physiographic heterogeneity contributes to regional diversity at both large and small scales. At small distances, it may provide the habitat heterogeneity that allows the coexistence of more species within a small area. At larger distances, physiographic heterogeneity may accelerate species formation through creating barriers to dispersal and gene flow. Clearly, understanding regional species diversity requires analyses at all scales and particularly of the way in which beta diversity,

or species turnover, connects patterns of diversity at different scales.

Beta diversity may be caused both by environmental factors acting in the present (the niche-difference model of Nekola & White 1999) and by spatial factors and historical events (the model of temporal and spatial constraint of Nekola & White 1999). While both are clearly important, the consistent predominance of distance over climate and the greater beta diversity in EAS compared with ENA for comparable differences in climate variables suggest that present species richness cannot be understood entirely from current environmental patterns alone. Because the distribution of other groups is often correlated with the distribution of plants, the result from this study has implications for understanding biological diversity more broadly. Further, whereas conserving alpha diversity can be accomplished in single nature reserves, regional beta diversity (as represented by the distance decay of similarity) suggests the need for spatial networks of reserves, with the rate of distance decay determining the number and spacing of those reserves (Nekola & White 2002).

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